A STUDY OF AQUATIC PLANT-SNAIL ASSOCIATIONS

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by

Eva Pip

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BY

EVA PIP

A dissertation submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

This thesis is dedicated to all those,
who in the course of their research on living creatures,
have deliberately avoided inflicting senseless cruelty
or the wasteful taking of the lives of their subjects
if other perhaps more roundabout and time-consuming methods
of gaining comparable information could be found.
Let us speak out against the atrocities
that all too often are committed in the name of research
by heartless people.

Countless are the things thou hast made, O Lord.
Thou hast made all by thy wisdom;
And the earth is full of the fruits of thy creation.

Psalms, 104:24

Seven sandhill cranes

Seven sandhill cranes,
Suspended in a broad expanse of pallid sky,
Were flying southwards, fleeing from the autumn rains
And growing winds that bent the yellow grass. Their cry
In sudden sorrow burst upon the marsh; the strains
Were harsh and strangely moving, fading to a sigh
And softly dying, disappearing, now
Horizon-bound with seven sandhill cranes.

Seven sandhill cranes
Had come and swiftly vanished in the sky's embrace,
Their calls unanswered from the stillness of the plains
That lay stretched out below, where all prepared to face
The coming winter: some to starve among the canes
Of rustling reed and cattail, some without a trace
To fall as prey, and some to greet again
The beating wings of seven sandhill cranes.

Eva Pip I/77

ABSTRACT

In the first portion of this study, a small number of aquatic plant-snail associations were examined quantitatively with time. During the 1972 season, three sites in the Delta Marsh on the southern shore of Lake Manitoba were sampled periodically by Ekman dredge. The results showed that many species of molluscs tended to occur significantly more frequently in vegetated than in bare areas and that some tended to occur in stands of particular macrophytes at certain times of the season. The two major associations consisted of Physa gyrina and Potamogeton pectinatus, and Lymnaea stagnalis and P. richardsonii.

During the 1973 season the submerged communities at four sites, including one outside the Delta Marsh, were sampled quantitatively with a modified macrophyte sampler. The results showed that the two major associations were real in terms of snail numbers and biomass per unit plant dry weight and surface area. The mean numbers of snails per plant unit showed peaks which occurred during periods of active growth of the host plants and at these times differential distributions were generally most pronounced. The peaks consisted largely of newly hatched young and times of reproduction and hatching appeared to be synchronized with the growth of the preferred host plants. The two associations were mutually independent but the amount of grazing sustained by the plants at different times appeared to be related to the total numbers of gastropods present on the plants.

During the 1974 season sampling was repeated at two of the

four sites, with similar results despite altered environmental conditions. The timing of the associations could not be correlated with any of the monitored environmental parameters.

Plant material was examined for total soluble carbohydrate, total titratable acids, total extractable protein and carotenes, but only total soluble carbohydrates appeared to be related to the timing of the association peaks, at least for P. gyrina. During a large part of the season, P. pectinatus contained greater concentrations of fructose and glucose than did P. richardsonii, which contained greater proportions of sucrose. This suggested a possible mechanism for inception of differential snail distributions, since aquatic pulmonates are capable of distinguishing between different sugars. Reproduction in the snails followed high sugar levels in the host plants, suggesting that regulation by plants of the population dynamics of their grazers may operate through a complex physiological mechanism. The young hatch when sugar levels in the plants are again high and their survival is enhanced. Differential distributions of snails mediated by specific attractants have the advantage of reducing interspecific competition for food and space.

In the second part of this study, a survey of submerged plants and gastropods was carried out at 305 sites in southern Manitoba and its peripheral regions. Several new records for plants in Manitoba were established. Chi-square analysis showed that characteristic plant communities and snail communities tended to occur in the region. At least 161 significant positive and 31 negative tendencies for plant and gastropod species to occur jointly were found, some of which could not be explained on the basis of net similarities or dissimilarities

in preferences for the monitored environmental variables. This suggested that the potential for different plant-snail associations was quite great, especially since many species showed multiple significant tendencies for joint occurrence. Such plasticity regarding possible alternate food sources may be important in the survival of gastropods. However the particular combination of associations operative within a given site is probably dependent upon a complex array of poorly understood factors.

TABLE OF CONTENTS

PAGE

ABSTRACT..... v

LIST OF TABLES..... xv

LIST OF FIGURES..... xxi

ACKNOWLEDGEMENTS..... xxx

INTRODUCTION..... 1

PART I: A quantitative study of the dynamics of two aquatic plant-snail associations

SECTION I: Season I(1972)

INTRODUCTION..... 7

I. OBJECTIVES..... 7

II. LITERATURE REVIEW..... 8

III. DESCRIPTION OF THE STUDY AREAS..... 11

A. Site 1..... 13

B. Site 5..... 14

C. Site 6..... 15

MATERIALS AND METHODS..... 17

I. ENVIRONMENTAL MEASUREMENTS..... 17

A. Water chemistry..... 17

B. Light and temperature measurements..... 20

II. BIOTIC SAMPLING..... 20

A. Bottom sampling..... 20

B. Live counts..... 24

TABLE OF CONTENTS (continued)

PAGE

RESULTS..... 26

I. ENVIRONMENTAL MEASUREMENTS..... 26

A. Water chemistry..... 26

B. Light and temperature..... 32

II. BIOTIC SAMPLING..... 36

A. Site 1..... 36

a. Vegetation..... 36

b. Density of live and dead molluscs..... 38

c. Live counts..... 61

d. Size distribution patterns of gastropods 65

B. Site 5..... 72

a. Vegetation..... 72

b. Density of live and dead molluscs..... 72

c. Size distribution patterns of gastropods 84

C. Site 6..... 91

a. Vegetation..... 91

b. Density of live and dead molluscs..... 92

DISCUSSION..... 98

SECTION II: Seasons II and III (1973-4)

INTRODUCTION..... 108

I. OBJECTIVES..... 108

II. DESCRIPTION OF THE STUDY AREAS..... 111

A. Sites 1 and 2..... 111

B. Site 3..... 115

C. Site 4..... 117

TABLE OF CONTENTS (continued)

PAGE

MATERIALS AND METHODS..... 119

I. ENVIRONMENTAL MEASUREMENTS..... 119

A. Water chemistry..... 119

B. Light and temperature measurements..... 121

II. BIOTIC SAMPLING..... 121

A. Field apparatus and procedures..... 121

a. Modified macrophyte sampler..... 121

b. Sampling procedure..... 123

B. Vegetation..... 124

a. Shoot length..... 124

b. Surface area..... 124

c. Lesion index..... 130

d. Dry weight..... 133

C. Gastropods..... 133

a. Numbers and size class distributions... 133

b. Biomass..... 133

RESULTS..... 138

I. ENVIRONMENTAL MEASUREMENTS..... 138

A. Water chemistry..... 138

a. Season II (1973)..... 138

b. Season III (1974)..... 146

B. Light and temperature..... 150

a. Season II (1973)..... 150

b. Season III (1974)..... 153

TABLE OF CONTENTS (continued)

PAGE

II. BIOTIC SAMPLING..... 156

A. Season II (1973)..... 156

a. Vegetation..... 156

i. Mean shoot length..... 156

ii. Mean dry weight per quadrat sample 158

iii. Surface area per quadrat sample.. 162

b. Gastropods..... 164

i. Mean density per quadrat sample.. 164

ii. Mean numbers of individuals per unit plant dry weight..... 174

iii. Total grazer population and lesion index..... 187

iv. Mean numbers of individuals per unit plant surface area..... 192

v. Snail biomass..... 198

vi. Size class distributions..... 206

B. Season III (1974)..... 222

a. Vegetation..... 222

i. Mean shoot length..... 222

ii. Mean dry weight per quadrat sample 222

iii. Surface area per quadrat sample.. 225

b. Gastropods..... 227

i. Mean density per quadrat sample.. 227

ii. Mean numbers of individuals per unit plant dry weight..... 232

iii. Composition of the total gastropod population..... 238

TABLE OF CONTENTS (continued)

PAGE

iv. Mean numbers of individuals per unit plant surface area..... 242

v. Snail biomass..... 245

vi. Size class distributions..... 248

DISCUSSION..... 257

SECTION III: The biochemical status of the plants

INTRODUCTION..... 272

MATERIALS AND METHODS..... 273

I. SEASON I (1972)..... 273

A. Total soluble carbohydrate..... 273

B. Total titratable acids..... 274

C. Total protein..... 275

D. Carotenoids..... 276

II. Seasons II and III (1973-4)..... 276

RESULTS..... 279

I. SEASON I (1972)..... 279

II. SEASONS II and III (1973-4)..... 282

DISCUSSION..... 296

INTEGRATION OF SECTIONS I, II AND III..... 306

PART II: A survey of submerged plant-snail communities and associations

INTRODUCTION..... 310

I. OBJECTIVES..... 310

II. LITERATURE REVIEW..... 311

A. Aquatic macrophyte associations..... 311

TABLE OF CONTENTS (continued)

PAGE

B. Aquatic gastropod associations..... 313

C. Plant-snail associations..... 314

D. Analysis of association..... 314

III. STUDY AREA AND SITE SELECTION..... 315

MATERIALS AND METHODS..... 319

I. BIOTIC SAMPLING..... 319

II. ENVIRONMENTAL MEASUREMENTS..... 319

RESULTS..... 321

I. MACROPHYTES..... 321

A. Systematics..... 321

B. Ecology..... 326

C. Plant associations..... 338

II. GASTROPODS..... 362

A. Systematics..... 362

B. Ecology..... 365

C. Gastropod associations..... 376

III. PLANT-SNAIL ASSOCIATIONS..... 388

DISCUSSION..... 411

INTEGRATION OF PARTS I AND II..... 428

SUMMARY..... 432

LITERATURE CITED..... 440

APPENDIX I..... 455

APPENDIX II..... 461

APPENDIX III..... 479

TABLE OF CONTENTS (continued)

PAGE

APPENDIX IV..... 491

APPENDIX V..... 497

LIST OF TABLES

TABLE — PAGE

I. Dates of sampling times during the 1972 season..... 18

II. Heterogeneity of plant samples at site 1 during the 1972 season..... 39

III. Mean numbers of dead shells of Planorbula armigera, Armiger crista, Valvata tricarinata, Amnicola spp., Pisidium sp., Helisoma anceps and Aplexa hypnorum per subsample in the 5 habitat types at site 1 during the 1972 season..... 49

IV. Mean relative density per unit bottom area for dead and live molluscs at site 1 expressed as a percent of the total numbers of molluscs of all species present in each habitat type at each sampling time during the 1972 season..... 52

V. Results of unpaired t-tests for the significance of the difference of mean densities per unit bottom area of dead and live molluscs between samples from nonvegetated areas and those from each vegetated habitat type at site 1 during the 1972 season..... 57

VI. Results of t-tests for the significance of the difference between sample proportions for live snails observed on different macrophytes at site 1 during the 1972 season..... 62

VII. Mean axial length of shells of dead and live individuals of Stagnicola palustris and Fossaria modicella present in bottom samples from the 5 habitat types at site 1 during the 1972 season..... 69

VIII. Mean maximum diameter of shells of dead and live individuals of Helisoma trivolvis and Gyraulus parvus present in bottom samples from the 5 habitat types at site 1 during the 1972 season..... 71

IX. Mean relative density per unit bottom area for dead and live molluscs at site 5 expressed as a percent of the total numbers of molluscs of all species present in vegetated and nonvegetated habitats at each sampling time during the 1972 season..... 80

LIST OF TABLES (continued)

TABLE PAGE

X. Results of unpaired t-tests for the significance of the difference of mean densities per unit bottom area of dead and live molluscs between vegetated and nonvegetated habitats at sites 5 and 6 during the 1972 season..... 83

XI. Mean axial length or mean diameter of shells of dead and live individuals of F. modicella, S. palustris, H. trivolvis and G. parvus present in vegetated and nonvegetated samples at site 5 during the 1972 season.. 88

XII. Mean diameter of shells of dead P. exacuous and A. crista present in vegetated and nonvegetated samples at site 5 during the 1972 season..... 89

XIII. Mean numbers of dead and live shells per sample in vegetated and nonvegetated habitats at site 6 during the 1972 season..... 93

XIV. Mean relative density per unit bottom area for dead and live molluscs at site 6 expressed as a percent of the total numbers of molluscs of all species present in vegetated and nonvegetated habitats at each sampling time during the 1972 season..... 96

XV. Dates of sampling times during the 1973 and 1974 seasons..... 120

XVI. Results of the analysis of the total precipitation and fallout occurring during the two-week period from times 3 to 4, 1973, at sites 1, 3 and 4..... 145

XVII. Mean dry weight of seeds and mature reproductive parts per quadrat sample of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season..... 161

XVIII. Mean numbers of F. modicella and S. palustris per sample quadrat in P. pectinatus and P. richardsonii stands at sites 1-4 during the 1973 season..... 169

XIX. Mean numbers of H. trivolvis per sample quadrat in P. pectinatus and P. richardsonii stands at sites 1-3 during the 1973 season..... 172

XX. Mean total numbers of gastropods per gram dry host plant weight at sites 1-4 during the 1973 season..... 188

LIST OF TABLES (continued)

TABLE PAGE

XXI. Values for lesion index at sites 1, 2 and 4 during the 1973 season..... 189

XXII. Mean numbers of each gastropod species per unit dry plant weight expressed as a percent of all species present at sites 1-4 during the 1973 season..... 191

XXIII. Mean numbers per 100 cm^2 of plant surface area of F. modicella and S. palustris (combined), and H. trivolvis in P. pectinatus and P. richardsonii stands at sites 1-4 during the 1973 season..... 197

XXIV. Mean dry weight of seeds and mature reproductive parts per quadrat sample of P. pectinatus and P. richardsonii at sites 1 and 2 during the 1974 season..... 226

XXV. Mean combined numbers of F. modicella and S. palustris per quadrat sample in the two types of stands at sites 1 and 2 during the 1974 season, and the mean numbers of S. palustris expressed as a fraction of the total numbers of S. palustris and F. modicella per quadrat sample..... 229

XXVI. Mean numbers of H. trivolvis and P. exacuous per quadrat sample in the two types of stands at sites 1 and 2 during the 1974 season..... 231

XXVII. Mean total numbers of gastropods per gram dry host plant weight at sites 1 and 2 during the 1974 season... 239

XXVIII. Mean numbers of each gastropod species per unit plant weight expressed as a percent of all species present at sites 1 and 2 during the 1974 season..... 241

XXIX. Mean numbers per 100 cm^2 of plant surface area of F. modicella and S. palustris (combined), H. trivolvis and P. exacuous in the two types of stands at sites 1 and 2 during the 1974 season..... 244

XXX. Mean total soluble carbohydrate and mean total soluble protein content of tissues of M. exalbescens at site 5 and P. pectinatus at site 6 during the 1972 season..... 281

XXXI. Fructose, glucose and sucrose content of P. pectinatus and P. richardsonii tissues at sites 1-4 during the 1973 season..... 288

LIST OF TABLES (continued)

TABLE PAGE

XXXII. Fructose, glucose and sucrose content of Potamogeton pectinatus and P. richardsonii tissues at sites 1 and 2 during the 1974 season..... 290

XXXIII. Sucrose to combined fructose and glucose ratios in Potamogeton pectinatus and P. richardsonii tissue at sites 1-4 during the 1973 season..... 291

XXXIV. Sucrose to combined fructose and glucose ratios in Potamogeton pectinatus and P. richardsonii tissue at sites 1 and 2 during the 1974 season..... 294

XXXV. Percent relative frequency within the study area of macrophytes at least partially submerged at the time of sampling..... 322

XXXVI. Significance of the distribution of macrophytes with respect to 8 water chemistry parameters..... 335

XXXVII. Net similarities in the significant parameter preferences for each possible macrophyte species or species group pair..... 342

XXXVIII. Results of Chi-square tests for the significance of the discrepancy between theoretical frequencies and the observed frequencies for the members of each possible pair of macrophytes to occur together or apart..... 346

XXXIX. Significant positive and negative macrophyte associations ranked in descending order of significance according to decreasing Chi-square values..... 349

XL. Total numbers of significant positive and negative associations observed for each macrophyte species or species group, and the numbers of these associations that did not coincide with net similarities or dissimilarities respectively in significant preferences for the monitored environmental parameters..... 351

XLI. Macrophyte association similarity indices for possible species or species group pairs..... 355

XLII. Percent relative frequency of gastropods within the study area..... 363

XLIII. Significance of the distribution of gastropods with respect to 8 water chemistry parameters..... 370

LIST OF TABLES (continued)

TABLE PAGE

XLIV. Net similarities in the significant parameter preferences of each possible gastropod species pair.... 374

XLV. Results of Chi-square tests for the significance of the discrepancy between theoretical frequencies and the observed frequencies for the members of each possible pair of gastropods to occur together or apart..... 377

XLVI. Significant positive and negative gastropod associations ranked in descending order of significance according to decreasing Chi-square values..... 378

XLVII. Total numbers of significant positive and negative associations observed for each gastropod species and the numbers of these associations that did not coincide with net similarities or dissimilarities respectively in significant preferences for the monitored environmental parameters..... 380

XLVIII. Gastropod association similarity indices for possible species pairs..... 382

XLIX. Results of Chi-square tests for the significance of the discrepancy between theoretical frequencies and the observed frequencies for the members of each plant-snail pair to occur together or apart..... 389

L. Significant positive and negative gastropod-plant associations ranked in descending order of significance according to decreasing Chi-square values..... 391

LI. Total numbers of significant positive and negative gastropod associations observed for each macrophyte species or species group and the numbers of these associations that did not coincide with net similarities or dissimilarities respectively in significant preferences for the monitored environmental parameters. 395

LII. Total numbers of significant positive and negative macrophyte associations observed for each gastropod species and the numbers of these associations that did not coincide with net similarities or dissimilarities respectively in significant preferences for the monitored environmental parameters..... 398

LIII. Gastropod association similarity indices for possible macrophyte species or species group pairs..... 400

LIST OF TABLES (continued)

TABLE PAGE

LIV. Macrophyte association similarity indices for possible gastropod species pairs..... 406

APPENDIX I-1. Fixed p values, mean calculated r values and the variance of r for examples 1 and 2..... 457

I-2. Numbers of individuals present in each size class grouping at successive time intervals..... 459

LIST OF FIGURES

FIGURE		PAGE
1.	Location of sites 1, 2, 3, 5 and 6 in the Delta Marsh on the southern shore of Lake Manitoba.....	12
2.	Estimation of submerged plant cover at site 5 using a calibrated 0.5 m rule.....	23
3.	Values for pH, total filtrable residue, total alkalinity and chloride of surface water at sites 1, 5 and 6 during the 1972 season.....	27
4.	Values for sulphate, combined nitrate and nitrite, molybdenum-blue phosphorus and dissolved oxygen of surface water at sites 1, 5 and 6 during the 1972 season	29
5.	Values for calcium activity of surface water at sites 1, 5 and 6 during the 1972 season.....	31
6.	Values for light intensity and temperature at sites 1, 5 and 6 at 0.25 m depth intervals during the 1972 season	33
7.	Mean shoot length of Potamogeton pectinatus, P. richardsonii, Myriophyllum exalbescens and Ceratophyllum demersum at site 1 during the 1972 season.....	37
8.	Mean densities of dead and live individuals of Lymnaea stagnalis in subsamples from the 5 habitat types at site 1 during the 1972 season.....	41
9.	Mean densities of dead and live individuals of Stagnicola palustris in subsamples from the 5 habitat types at site 1 during the 1972 season.....	43
10.	Mean densities of dead and live individuals of Fossaria modicella in subsamples from the 5 habitat types at site 1 during the 1972 season.....	44
11.	Mean densities of dead and live individuals of Physa gyrina in subsamples from the 5 habitat types at site 1 during the 1972 season.....	46
12.	Mean densities of dead and live individuals of Gyraulus parvus in subsamples from the 5 habitat types at site 1 during the 1972 season.....	47
13.	Mean densities of dead and live individuals of Helisoma trivolvis and Promenetus exacuous in subsamples from the 5 habitat types at site 1 during the 1972 season.....	48

LIST OF FIGURES (continued)

FIGURE		PAGE
14.	Proportions of the total numbers of gastropods of all species comprised by P. gyrina and L. stagnalis that were observed on shoots of P. pectinatus and P. richardsonii at site 1 during the 1972 season.....	64
15.	Mean axial length of dead and live individuals of L. stagnalis in subsamples from the 5 habitat types at site 1 during the 1972 season.....	66
16.	Mean axial length of dead and live individuals of P. gyrina in subsamples from the 5 habitat types at site 1 during the 1972 season.....	68
17.	Mean shoot length of M. exalbescens at site 5 and P. pectinatus at site 6 during the 1972 season.....	73
18.	Mean densities of dead and live individuals of S. palustris, F. modicella and P. gyrina in subsamples from vegetated and nonvegetated areas at site 5 during the 1972 season.....	74
19.	Mean densities of dead and live individuals of G. parvus and H. trivolvis in subsamples from vegetated and nonvegetated areas at site 5 during the 1972 season.....	77
20.	Mean densities of dead and live individuals of Promenetus exacuous, Armiger crista, Valvata tricarinata and Amnicola limosa in subsamples from vegetated and nonvegetated areas at site 5 during the 1972 season.....	79
21.	Mean axial length of dead and live individuals of P. gyrina in subsamples from vegetated and nonvegetated areas at site 5 during the 1972 season.....	85
22.	Size class frequency-time surface for live P. gyrina populations from vegetated subsamples at site 5 during the 1972 season.....	86
23.	Position of P. pectinatus and P. richardsonii dominated stands within site 1 during the 1972-3 seasons.....	112
24.	Position of P. pectinatus and P. richardsonii dominated stands within site 2 during the 1973 season.....	113
25.	Position of P. pectinatus and P. richardsonii dominated stands within site 4 and site 3 during the 1973 season..	116

LIST OF FIGURES (continued)

FIGURE		PAGE
26.	Side and bottom views of modified macrophyte sampler....	122
27.	Regression of plant surface area on weight of surface film of Teepol 610 in P. pectinatus and P. richardsonii.	127
28.	Scatter diagram illustrating the relationship between shoot dry weight and surface area in P. pectinatus.....	128
29.	Scatter diagram illustrating the relationship between shoot dry weight and surface area in P. richardsonii....	129
30.	Lesions in leaves of P. richardsonii produced by pulmonates.....	131
31.	Regression of log live weight on log axial length in P. gyrina.....	134
32.	Regression of log live weight on log axial length in L. stagnalis.....	135
33.	Values for pH and total filtrable residue of surface water at sites 1-4 during the 1973 season.....	139
34.	Values for total alkalinity and chloride of surface water at sites 1-4 during the 1973 season.....	140
35.	Values for molybdenum-blue phosphorus and sulphate of surface water at sites 1-4 during the 1973 season.....	142
36.	Values for combined nitrate and nitrite, and calcium activity of surface water at sites 1-4 during the 1973 season.....	143
37.	Values for pH, total filtrable residue, total alkalinity and chloride of surface water at sites 1 and 2 during the 1974 season.....	147
38.	Values for molybdenum-blue phosphorus, sulphate and combined nitrate and nitrite of surface water at sites 1 and 2 during the 1974 season.....	149
39.	Values for light intensity and temperature at sites 1-4 at 0.25 m depth intervals during the 1973 season.....	151
40.	Values for light intensity and temperature at sites 1 and 2 at 0.25 m depth intervals during the 1974 season..	154

LIST OF FIGURES (continued)

FIGURE		PAGE
41.	Mean shoot length of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.....	157
42.	Mean dry weight of shoots (excluding reproductive parts) per quadrat sample of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.....	159
43.	Mean surface area of shoots (excluding reproductive parts) per quadrat sample of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.....	163
44.	Mean numbers of P. gyrina per quadrat sample from stands of P. pectinatus and P. richardsonii at sites 1, 2 and 4 during the 1973 season.....	165
45.	Mean numbers of P. gyrina per quadrat sample from stands of P. pectinatus at site 3 during the 1973 season.....	166
46.	Mean numbers of L. stagnalis per quadrat sample from stands of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.....	167
47.	Mean numbers of P. gyrina per gram dry P. pectinatus and P. richardsonii at sites 1, 2 and 4 during the 1973 season.....	175
48.	Mean numbers of P. gyrina per gram dry P. pectinatus at site 3 during the 1973 season.....	177
49.	Mean numbers of L. stagnalis per gram dry P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.	178
50.	Mean numbers of F. modicella per gram dry P. pectinatus and P. richardsonii at sites 1, 2 and 4 during the 1973 season.....	180
51.	Mean numbers of F. modicella per gram dry P. pectinatus at site 3 during the 1973 season.....	182
52.	Mean numbers of S. palustris per gram dry P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.	183
53.	Mean numbers of H. trivolvis per gram dry P. pectinatus and P. richardsonii at sites 1 and 2 during the 1973 season.....	185

LIST OF FIGURES (continued)

FIGURE		PAGE
54.	Mean numbers of P. gyrina per 100 cm^2 surface area of P. pectinatus and P. richardsonii at sites 1, 2 and 4 during the 1973 season.....	193
55.	Mean numbers of P. gyrina per 100 cm^2 surface area of P. pectinatus at site 3 during the 1973 season.....	195
56.	Mean numbers of L. stagnalis per 100 cm^2 surface area of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.....	196
57.	Mean total live weight of P. gyrina per quadrat sample in stands of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.....	199
58.	Mean live weight of P. gyrina per gram dry weight of P. pectinatus and P. richardsonii at sites 1, 2 and 4 during the 1973 season.....	200
59.	Mean live weight of P. gyrina per gram dry weight of P. pectinatus at site 3 during the 1973 season.....	202
60.	Mean live weight of P. gyrina per 100 cm^2 surface area of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.....	203
61.	Mean total live weight of L. stagnalis per quadrat sample in stands of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.....	204
62.	Mean live weight of L. stagnalis per gram dry weight of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.....	205
63.	Mean live weight of L. stagnalis per 100 cm^2 surface area of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.....	207
64.	Mean axial length of P. gyrina in stands of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.	208
65.	Size class distribution of P. gyrina in stands of P. pectinatus and P. richardsonii at site 1 during the 1973 season.....	209
66.	Size class distribution of P. gyrina in stands of P. pectinatus and P. richardsonii at site 2 during the 1973 season.....	211

LIST OF FIGURES (continued)

FIGURE		PAGE
80.	Mean numbers of P. gyrina and L. stagnalis per 100 cm^2 surface area of P. pectinatus and P. richardsonii at sites 1 and 2 during the 1974 season.....	243
81.	Mean total live weight of P. gyrina and L. stagnalis per quadrat sample in stands of P. pectinatus and P. richardsonii at sites 1 and 2 during the 1974 season....	246
82.	Mean live weight of P. gyrina and L. stagnalis per gram dry weight of P. pectinatus and P. richardsonii at sites 1 and 2 during the 1974 season.....	247
83.	Mean live weight of P. gyrina and L. stagnalis per 100 cm^2 surface area of P. pectinatus and P. richardsonii at sites 1 and 2 during the 1974 season.....	249
84.	Mean axial length of P. gyrina and L. stagnalis in stands of P. pectinatus and P. richardsonii at sites 1 and 2 during the 1974 season.....	250
85.	Size class distribution of P. gyrina in stands of P. pectinatus and P. richardsonii at site 1 during the 1974 season.....	251
86.	Size class distribution of P. gyrina in stands of P. pectinatus and P. richardsonii at site 2 during the 1974 season.....	253
87.	Size class distribution of L. stagnalis in stands of P. pectinatus and P. richardsonii at site 1 during the 1974 season.....	254
88.	Size class distribution of L. stagnalis in stands of P. pectinatus and P. richardsonii at site 2 during the 1974 season.....	256
89.	Total soluble carbohydrate, total titratable organic acids, total extractable protein and carotene content of P. pectinatus and P. richardsonii tissues at site 1 during the 1972 season.....	280
90.	Total soluble carbohydrate content of tissues of P. pectinatus and P. richardsonii at sites 1-4 during the 1973 season.....	283
91.	Total soluble carbohydrate content of tissues of P. pectinatus and P. richardsonii at sites 1 and 2 during the 1974 season.....	286

LIST OF FIGURES (continued)

FIGURE PAGE

92. Distribution of the sites within the study region..... 317

93. Mean values for pH at sites where each macrophyte species or species group was present and where it appeared to be absent 327

94. Mean values for total filtrable residue at sites where each macrophyte species or species group was present and where it appeared to be absent..... 328

95. Mean values for total alkalinity at sites where each macrophyte species or species group was present and where it appeared to be absent..... 329

96. Mean values for chloride at sites where each macrophyte species or species group was present and where it appeared to be absent..... 330

97. Mean values for sulphate at sites where each macrophyte species or species group was present and where it appeared to be absent..... 331

98. Mean values for estimated total nitrate and nitrite at sites where each macrophyte species or species group was present and where it appeared to be absent..... 332

99. Mean values for organic indices at sites where each macrophyte species or species group was present and where it appeared to be absent..... 333

100. Mean values for molybdenum-blue phosphorus at sites where each macrophyte species or species group was present and where it appeared to be absent..... 334

101. An abstract representation of the interrelations between macrophyte species for which the association similarity index exceeded a value of 0.70..... 359

102. Mean values for pH and total filtrable residue at sites where each gastropod species was present and where it appeared to be absent..... 366

103. Mean values for total alkalinity and chloride at sites where each gastropod species was present and where it appeared to be absent..... 367

104. Mean values for sulphate and estimated total nitrate and nitrite at sites where each gastropod species was present and where it appeared to be absent..... 368

LIST OF FIGURES (continued)

FIGURE PAGE

105. Mean values for organic indices and molybdenum-blue phosphorus at sites where each gastropod species was present and where it appeared to be absent..... 369

106. An abstract representation of the interrelations between gastropod species for which the association similarity index exceeded a value of 0.60..... 384

107. An abstract representation of the interrelations between macrophyte species for which the association similarity index for significant gastropod associations exceeded a value of 0.70..... 404

108. An abstract representation of the interrelations between gastropod species for which the association similarity index for significant macrophyte associations exceeded a value of 0.60..... 409

APPENDIX I-1. Relationship between p and r values for Examples 1 and 2..... 458

I-2. Variance of r plotted against the respective values of p for Examples 1 and 2..... 458

I-3. Real and predicted values for total number of individuals of Physa gyrina..... 460

IV-1. Achenes of Potamogeton amplifolius, P. epihydrus, P. filiformis, P. friesii and P. foliosus..... 494

IV-2. Achenes of Potamogeton natans, P. gramineus, P. obtusifolius and P. pectinatus..... 495

IV-3. Achenes of Potamogeton praelongus, P. pusillus, P. spirillus, P. richardsonii and P. zosteriformis. 496

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Introduction

Submerged plant communities are among the most conspicuous features of aquatic ecosystems. To the casual observer, extensive submerged plant stands are striking in their apparent homogeneity and in the diversity of the organisms they support. Because submerged communities are dependent upon a variety of elusive physical factors, many of which are unknown to their terrestrial counterparts, their stability presents a problem of unique complexity. Their rapid and often profuse growth fluctuates unpredictably from year to year, while accompanied by erratic changes in species composition, productivity and distribution, and reflects the sensitivity and precariousness of the relationships of submerged communities with the physicochemical environment and other biotic components therein.

Submerged macrophyte communities are important but usually little-studied components of aquatic ecosystems. Their distribution is influenced to a large extent by light, substrate composition and water quality and movement (e.g. Spence, 1967, 1972). In turn, they modify these factors by intercepting light and enriching the substrate with organic materials. They modify water quality through the uptake and release of nutrients and, through the fundamental processes of photosynthesis, they alter the balance of dissolved gases, and concomitantly the pH of the medium, which in turn regulate many other physicochemical processes within the limnosphere. Submerged plant stands provide pockets of resistance where currents are encouraged to drop their sediment loads, reducing turbidity and enhancing nutrient accumulation in the immediate areas of the stands.

Submerged macrophyte stands are perhaps most remarkable in the uniqueness of the assemblages of other organisms that coexist in association with them. The vascular plants and bryophytes that comprise submerged stands provide a base for a large variety of micro- and macro-organisms that complete all or part of their life cycles in the ephemeral shelter of seasonal generations of plant shoots. The plants greatly influence the organisms in the medium around them, assailing them constantly with a chaos of metabolites. These organisms may be divided on various levels into characteristic, often overlapping communities, each of which is ultimately dependent upon the macrophytes for its existence.

Of the communities found within submerged macrophyte stands, the most specialized are the biocoenoses of the Aufwuchs. This term defines the complex collection of organisms that are attached to, but do not penetrate into, the substrate, as well as any free-living forms associated with the sessile forms (Ruttner, 1953). The term periphyton, in contrast, defines only the sessile forms. The Aufwuchs communities of macrophytes occupy singularly specialized ecological positions because:

1. Although they are influenced by the external medium, they exist in direct interface with living plant tissue and are therefore highly likely to be influenced by its metabolites, and
2. They exist on an impermanent substratum which itself undergoes growth and senescence, requiring of the Aufwuchs,

rapid growth and transitory successional stages that never culminate in stability.

The organisms which normally comprise the Aufwuchs are bacteria, nonparasitic fungi, diatoms, green and bluegreen algae, protozoans, sponges, bryozoans, nematodes, arthropods and molluscs, and successful coexistence of such diverse forms in close association must, of necessity, entail varying types and degrees of ordered interaction with each other and the living substrate.

Study of such interactions on an integrated scale is difficult because of the diversity of organisms and the complexity of influencing factors, while isolation of individual minority species is often not practical nor realistic in view of the intricacy of the system within which such species normally function. On the other hand, majority species exert collective effects on the system which are more easily observed, although the complexity of the system nevertheless cannot be discounted. In terms of biomass, the most prominent heterotrophs of the Aufwuchs of macrophyte communities are the macroinvertebrates, of which aquatic molluscs are especially important because of their large size, mobility and complex behavior. Their central position in aquatic food chains provides a continuity with organisms outside the Aufwuchs, such as fish, amphibians, waterfowl and mammals (e.g. Chura, 1961; Dirschl, 1969; Bartonek and Hickey, 1969; Eddy, 1976) which comprise yet other levels of community organization that depend both directly and indirectly upon the macrophytes. Thus, knowledge of the biology of molluscs is important in wildlife management and in physiological and medical disciplines where molluscs are used in studies of pathological

processes and where they serve as natural vectors of trematodes that infect a large variety of animals including man (e.g. MacInnis et al, 1974). An improved understanding of plant-snail associations would provide insight into the mechanisms operative within, and structure of, some of the most basic components of aquatic communities, both present and past (e.g. Harris and Pip, 1972).

The present study was carried out with two fundamental objectives:

1. To conduct a quantitative study of plant-snail interactions at a small number of selected sites in order to observe their flux with time, i.e. in space-limited, time-unlimited observation.
2. Conversely, to conduct a qualitative study of plant-snail association potentials at many sites at a single point in time, i.e. in space-unlimited, time-limited observation.

Accordingly the present work has been divided into two parts, each dealing with one of these basic objectives.

PART I

A QUANTITATIVE STUDY OF THE DYNAMICS OF TWO AQUATIC PLANT-SNAIL ASSOCIATIONS

SECTION I:

Season I (1972)

Introduction

I. Objectives

Because molluscs comprise a significant component of the Aufwuchs of macrophytes, their presence implies, or rather necessitates, some interaction with the host plants. An approach to the problem of plant-snail interactions must begin with a clarification of the degree of passivity or randomness such a system possesses, i.e.:

1. Can the distributions of molluscs in various macrophyte stands and in other available habitats within the same water body be explained on the basis of chance alone?
2. If not due to chance alone, can they be explained on the basis of selection for physical factors?
3. If not due to physical factors alone, are they possibly due to active biotic interaction with the macrophytes?

The initial aim of the first season's work was to address the study to the first two questions, i.e. to determine whether significant differential distributions of molluscs existed in space and time within the same water body with respect to:

1. areas occupied by submerged vegetation as opposed to bare areas,
2. areas occupied by different macrophyte stands, and
3. areas showing differences in selected physical parameters.

The problem was approached in three ways:

1. Using bottom sampling, densities and size class distribution patterns of live molluscs were compared: a) among samples from bare areas and those containing various macrophytes, and

b) with temporal fluctuations in temperature and water chemistry.

2. Using bottom sampling, densities and size class distribution patterns of dead shells were compared among samples from bare areas and those containing various macrophytes.
3. Direct observations of live snails were made on various macrophytes independently of the bottom sampling.

II. Literature review

F.C. Baker (1911, 1928) was one of the first workers to recognize, on a qualitative basis, the importance of aquatic macrophytes in the ecology of various gastropods, but Krecker (1939) was the first to suggest that density differences of gastropods may be due to the plants with which they are associated, and the first to attempt to relate quantitatively the submerged macrophytes and macroinvertebrates. He collected individual plant shoots by hand from a site in western Lake Erie and counted the numbers of animals that remained on the plants. Comparisons were based on the numbers of animals per unit of linear stem length. Since the different macrophyte species showed varying degrees of branching, and leaf size, number and dissection, and since the amounts of faunal loss were unknown, the results were not truly quantitative.

Rosine (1955) found that the variety and abundance of the aquatic flora in Muskee Lake, Colorado were correlated with those of the associated fauna, and that seasonal variations occurred in the distributions of animals over given areas of plant surfaces. Samples were obtained by lowering a dip net over an individual plant shoot to minimize escape of the macrofauna and breaking off the stem near

the substrate level. Results were expressed in terms of the numbers of animals per unit host plant surface area.

Petr (1968) found that quantitative changes in the biomass of animals, based on numbers per unit host plant dry weight, in Volta Lake, Ghana were closely related to the season and that some molluscs appeared to show preferences for certain types of plants. In this study, floating vegetation was sampled by inserting a bucket into the water underneath the plants and lifting them out together with the bucket; submerged macrophytes were sampled by setting a wire frame on the bottom and collecting the enclosed shoots by hand. However both methods involved unknown amounts of loss of animals from the plants.

In 1970, DeCosker and Persoone found that seasonal density differences in gastropods existed in a Belgian swamp community and that the snails appeared to show preferences for some macrophytes at certain times of the season. Sampling was carried out by hand-collecting individual plant shoots and packing them into liter jars; the plants enclosed in this volume provided the basis for comparison of the numbers of gastropods that remained attached to the plants after collection. However these results were not truly quantitative because the degree of packing varied with the species and the method of collection was attended by unknown amounts of loss of snails from the plants. Bownik (1970) attempted a plant-snail association study in Mikolajskie Lake, Poland, with inconclusive results. Korinkova (1971) attempted to relate the plant-snail components of a Rumanian pond community, but the sampling apparatus was not described. In southern Manitoba, a number of sites were studied using bottom sampling (Pip and Paulishyn, 1971) but snail density could not be related quantitatively

to the macrophytes because the benthos could not be separated from the snails originally present on the plants, and because sampling involved unknown amounts of loss.

Calow (1973) conducted a semiquantitative study of several communities within a single water body in Yorkshire. This work suggested that some distributional differences of molluscs existed with respect to the different plant stands examined, but these could not be quantified beyond a comparison based on relative abundance nor could they be related quantitatively to the host vegetation. Bishop and Bishop (1973) conducted a study of the animals associated with marine macrophytic algae; sampling was carried out by placing large plastic bags over individual plants and severing the stems (cf. Rosine, 1955). These workers found that distributional differences of marine gastropods appeared to be related to the host species. Orth (1973) sampled eelgrass (Zostera marina L.) communities in Chesapeake Bay using a coring device and found that the density of macroinvertebrates in stands of this vascular plant was higher than that observed in any other benthic habitat.

Voigts (1975) related the marsh plants of four aquatic prairie communities in Iowa to abundance of invertebrates by estimating the plant cover in a series of randomly placed quadrats along a permanent transect, and sampling the invertebrates by dip net along the transect. This semiquantitative approach showed that little seasonal change in snail density occurred except in areas of dense submerged and free-floating vegetation, where snail numbers increased greatly as vegetation cover increased.

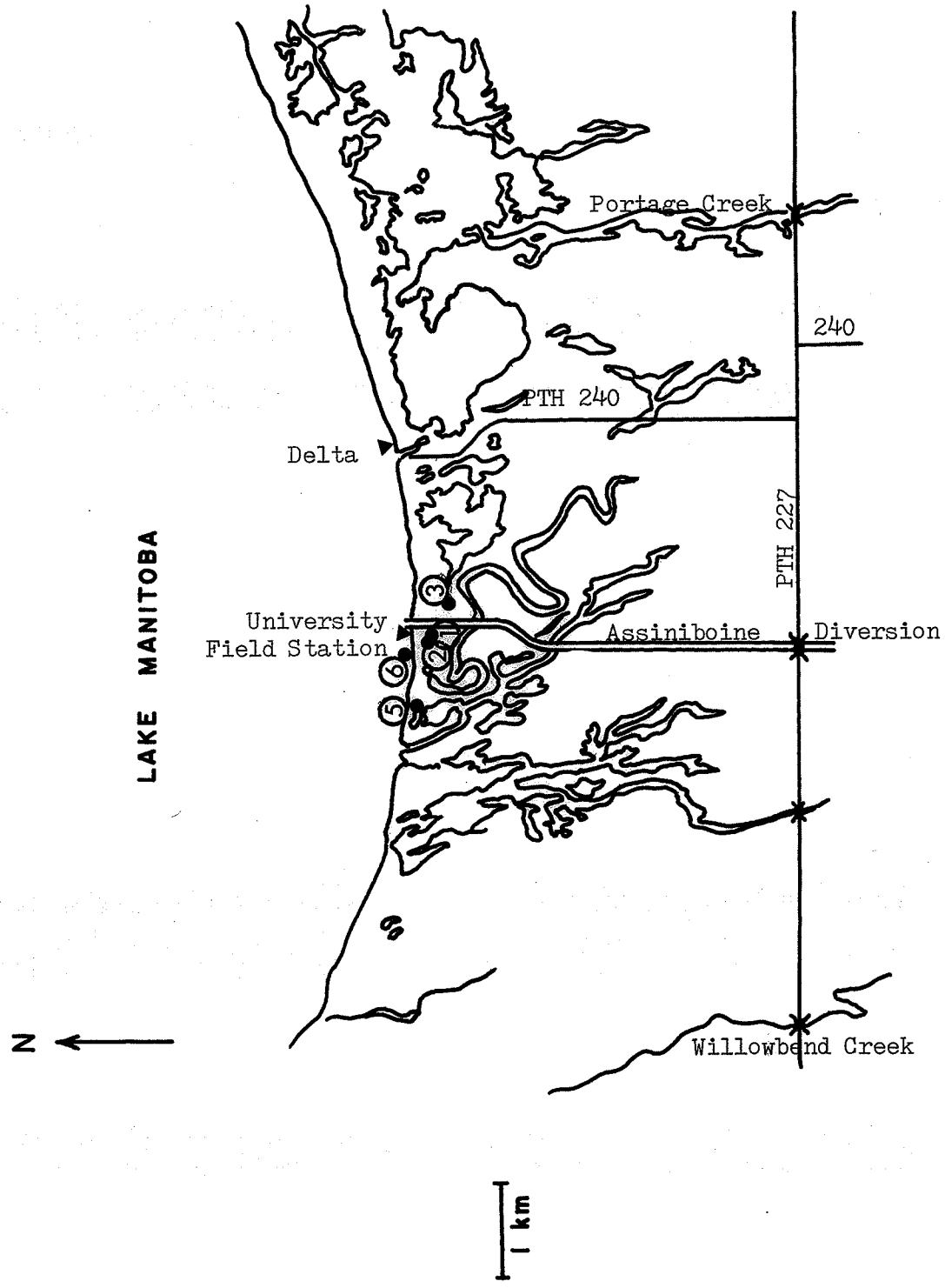
Verhoeven (1975) conducted qualitative observations of the

macrofauna associated with submerged macrophyte communities in the Camargue, France, by collecting by hand and dip net, and found that some species of molluscs appeared to be associated with the macrophytes. Lévêque (1975) hand-collected macrophytes from several sites in Lake Chad, Ivory Coast, and found that variations in snail abundance, based on numbers per unit plant dry weight, could not be correlated with the main ecological (physical) factors of the lake. LaCoursière et al (1975) hand-collected plant shoots in Quebec and counted the numbers of snails that persisted on the shoots; they found no affinities for vegetation among prosobranch molluscs, while pulmonates tended to occur largely on emergent plants. Sankurathri and Holmes (1976) hand-collected submerged macrophyte shoots in Lake Wabamun, Alberta; these workers found that the temporal distributions of snails appeared to be related to growth of the host macrophytes.

III. Description of the study areas

During the 1972 season, three study sites were selected on the southern shore of Lake Manitoba in the Delta Marsh (50°11'N, 98°23'W) (Fig. 1) which covers an area of approximately 15,000 hectares and serves as the main discharge area for the region bounded on the south by the Assiniboine River and on the north by Lake Manitoba (Meyboom, 1962). The underlying deposits of the marsh are composed of glacial till (Ehrlich et al, 1957) covered with a layer of partially decomposed organic materials of varying thickness. The physiography and vegetation of the marsh have been dealt with in detail by Walker (1965), and Phillips (1976) has described the climate of the region.

Figure 1. Location of sites 1, 2, 3, 5 and 6 in the Delta Marsh on the southern shore of Lake Manitoba. Site 4 was located outside of the Delta Marsh.


Portage Creek
240
PTH 240
Delta
PTH 227
LAKE MANITOBA
University
Field Station
Assiniboine
Diversion
N
Willowbend Creek
1 km

The sites selected had the following features:

1. Submerged macrophyte stands were well established, permanently submerged, and subject to little direct human interference.
2. The sites represented different basin origins and structures, as well as different degrees of exposure.
3. The sites were accessible in all types of weather.

A. Site 1

Site 1 (Fig. 23, p.112) consisted of an L-shaped roadside ditch with an approximate surface area of 1400 m^2, located immediately southeast of the University Field Station buildings. It originated as an artificial excavation for road drainage and was a closed system except during periods of high water when it connected with an adjacent ditch by means of a screened culvert underneath the road at the western end of the ditch. Maximum water depth during midsummer was approximately 1 m. The bottom consisted of a fine organic silt with a clay base containing a small proportion of sand. The site was well sheltered from wind, resulting in pronounced vertical thermal gradients throughout much of the growing season.

The northern arm of the ditch was occupied by dense stands of Potamogeton pectinatus L., interspersed with Ceratophyllum demersum L. The western arm was occupied by mosaic stands of Potamogeton richardsonii (Benn.) Rydb. and Myriophyllum exalbescens Fern. An interaction zone was present between the two types of stands at the bend of the ditch and consisted of a largely bare area colonized passim by isolated individuals of all four species. The sparse floating vegetation consisted of Lemna trisulca L. which was limited to the

zone of emergent vegetation. The latter zone was composed of communities dominated by Typha latifolia L., Phragmites communis Trin. and Carex atherodes Spreng.

The molluscan fauna at site 1 was diverse and reflected a well established community. Sponges (Spongillidae) were seasonally common on submerged objects and on decaying vegetation. Oligochaetes occurred infrequently in the bottom sediments, while leeches (Hirudinea), including the snailivorous Helobdella stagnalis L., were excessively abundant. Crustaceans and insects were also abundant: chironomid, odonatan and dipteran larvae were present during most of the growing season and trichopteran larval cases were frequently found attached to the plants. Small fishes, particularly sticklebacks, were abundant within the submerged macrophyte stands. Various developmental stages of leopard frogs (Rana pipiens Schreber) were also abundant and the ditch was used frequently by waterfowl and muskrats (Ondatra zibethica L.). Trematode cercariae were seasonally very abundant.

B. Site 5[1]

Site 5 consisted of a 900 m^2 area (30 x 30 m) at the northeastern end of Crescent Pond, which was located 1.6 km west of the University Field Station buildings (Fig. 1). Crescent Pond was a remnant of a natural marsh drainage channel which no longer had surface connections with either the lake or the present surface drainage system; its maximum total surface area was approximately 8.6 hectares. The bottom sediments consisted of a fine silt overlain by a thick layer

[1] Sites 2, 3 and 4 appear in Section II.

of partially decomposed organic matter. The site was well exposed to wind, and vertical thermal gradients existed only during periods of calm weather. Maximum seasonal depth within the sampling area was 0.75 m.

Crescent Pond exhibited dramatic fluctuations in the composition of the submerged macrophyte stands from year to year. During the 1972 season it was occupied by homogeneous stands of Myriophyllum exalbescens, bordered passim by clumps of Potamogeton pectinatus in shallower areas; however the latter was rare within the sampling area. The dense emergent communities that completely encircled Crescent Pond were dominated by Typha latifolia, Phragmites communis and Scirpus acutus Muhl.

The molluscan fauna at site 5 was slightly less diverse than that at site 1, but far more abundant. Other invertebrate groups were less abundant than at site 1. Frogs were less common and fishes were not observed at all. The site was used extensively by waterfowl.

C. Site 6

Site 6 consisted of a 10,000 m^2 (100 x 100 m) area of the southern lakeshore of Lake Manitoba, located northwest of the University Field Station buildings (Fig. 1). The site was exposed to strong wind and wave action; maximum seasonal depth of the sampling area was 1 m. The bottom sediments were composed of a layer of sand of uneven thickness overlying a clay base.

The sampling area contained discrete stands of Potamogeton pectinatus which occurred in clay pockets within a largely bare area of sand. A Chara sp. occurred sporadically in the area, while Potamogeton

richardsonii and Myriophyllum exalbescens were extremely rare.

The molluscan fauna at site 6 was highly diversified but sparsely distributed. Conchostracans and other crustaceans were common. The area was characterized by a diverse fish fauna and received moderate use by waterfowl.

Materials and methods

During the May to August, 1972 season, sites 1, 5 and 6 were each visited at approximately two week intervals. The dates on which each site was sampled are given in Table I. The sequence in which the sites were visited during any sampling period was determined by weather conditions.

I. Environmental measurements

A. Water chemistry

A surface water sample was collected at each site in the early afternoon and was frozen within one hour of collection. The sample was thawed 1-2 days later and was analyzed according to methods recommended by the American Public Health Association (1971).

Total filtrable residue was determined by filtering a known volume (100 ml) of the sample through a single layer of Whatman No. 1 filter paper under suction, and evaporating the filtrate at 105 C. Total alkalinity was estimated by titration with 0.02N H_2SO_4 to the second endpoint of phenolphthalein at pH 4.2, using a pH meter. Accuracy fell within $\pm$ 2 mg/l $CaCO_3$. Chloride was determined by titration of a 100:1 v/v mixture of sample water and K_2CrO_4 solution (50 g K_2CrO_4/liter aq. with 0.0141N $AgNO_3$ added until precipitate forms, let stand 12 hours then filter under suction) with 0.0141N $AgNO_3$ to a pinkish endpoint. Accuracy of this method ranged from $\pm$ 1-4 mg/l; the larger errors resulted from observer discrepancies due to the subjective nature of assessing degree of pinkness, especially in saline samples.

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TABLE I. Dates of sampling times for sites 1, 5 and 6 during the 1972 season.

Sampling time	site 1	site 5	site 6
1	May 17	May 18	May 19
2	May 29	May 31	May 30
3	June 13	June 14	June 12
4	June 28	June 26	June 27
5	July 12	July 11	July 10
6	July 24	July 25	July 26
7	August 9	August 8	August 10
8	August 21	August 22	August 23

Sulphate was estimated using a turbidimetric method: a 20:1 v/v proportion of sample water and a conditioning reagent (50 ml glycerol, 30 ml conc. HCl, 300 ml dist. H_2O, 100 ml 95% ethanol, 75 g NaCl) was swirled for 60 seconds with excess $BaCl_2$. Optical density was determined at 420 nm in a 1 cm light path in a spectrophotometer at 30 second intervals during the subsequent 4 minutes. The maximum value observed during this time was used to compute the concentration from a calibration curve. The blank consisted only of the water sample and conditioning reagent. This method was found to be accurate to within 1 mg/l.

Estimates of total nitrate and nitrite were made by measuring the optical density of a 50:1 v/v mixture of sample water and 1N HCl at 220 and 275 nm in a spectrophotometer. Distilled water was used in place of the unknown for the blank. Twice the reading at 275 nm was subtracted from the reading at 220 nm and the difference was used to calculate the total estimated concentration from a calibration curve. The reading at 275 nm reflected in large part the amount of interference from organic matter. The accuracy of this method was not known, although it provided readings consistent above the 95% confidence level.

Phosphate was estimated using a molybdenum-blue reaction: a 5 ml sample of water was placed in a 10 ml volumetric flask; to it were added 2 ml Na acetate: acetic acid buffer (0.025N : 0.1N at pH 4.0), 0.5 ml ammonium molybdate (5% aq.) solution and 1 ml 1% ascorbic acid. The mixture was made to volume with distilled water and the optical density was measured after 5 minutes at 650 nm in a spectrophotometer. Distilled water was used in place of the unknown

for the blank. Concentrations were calculated from a calibration curve.

Calcium activity was determined directly by using a calibrated Orion Ionalyzer model 407 with calcium ion electrode model 92-20. Measurements of surface pH were made in the field with a pH meter. Dissolved oxygen concentrations were determined at midday just below the surface, using a YSI Oxygen Meter model 51, by means of the simultaneous calibration method.

B. Light and temperature measurements

Light and temperature measurements were made at midday using a calibrated Griffin environmental comparator (S51-712), a field light probe (S51-718/074) and a thermistor probe (S51-718/082). The field light probe contained a cadmium sulphide light cell which was relatively more sensitive to longer wavelengths. Readings of light intensity and temperature were made at 0.25 m depth intervals.

II. Biotic sampling

A. Bottom sampling

Bottom sampling at the three sites was carried out from a small boat, using a 15 x 15 x 15 cm Ekman dredge with dulled jaws to minimize cutting of the plant shoots. Sampling points were located by tossing the dredge into the water at scattered points throughout each site. The dredge yielded sediment samples from sites 1 and 5 which were approximately 7.5 cm deep, while samples from site 6 were shallower because of the predominantly sandy substrate. The samples contained the rooted shoots encompassed by the area of the dredge,

the snails present in or on the substrate and a proportion of the snails attached to the plants.

After allowing excess water to drain, samples from sites 1 and 5 were subsampled in order to reduce their size, using a coring device. Subsamples consisted of the bottom substrate enclosed within a cross-sectional area of 78.5 cm^2 and a volume of 590 ml, i.e. 34.9% of the original sample cross-sectional area and volume, respectively. Any macrophyte shoot, all or part of which was included in the subsample, was treated as part of the subsample. This subsample size, determined from an area-species curve, was still large enough to contain the macrophyte and mollusc species present in the original sample. Ekman samples from site 6 were not subsampled because of the small numbers of molluscs that were present.

The samples or subsamples were filtered in the field through 1 mm mesh sieves to reduce their volume, sealed in plastic bags and stored at 4 C until processing. The latter, completed prior to the next sampling time, consisted of filtering the samples under a jet of water through 1 mm mesh sieves and sorting the material by hand. Molluscs below 1 mm in size were excluded because they were in embryonic stages and were not readily identifiable (Pip and Paulishyn, 1971). The plants present in the samples were air-dried and weighed, and the length was measured for at least 10 shoots of each species, if present, prior to drying. Measurements were taken from substrate level which was judged from the position of greening on the stem. For unbroken live and dead shells, axial length, or diameter in the case of planorbids, was measured to the nearest 0.5 mm using Vernier

calipers. The presence of land shells in the samples was recorded to provide an index for assessing passive redistribution of dead shells. Live snails were returned to the field.

Twenty Ekman samples were taken during each sampling time at site 1. At site 5, 20 samples were collected on each sampling day until time 5, after which only 15 were taken because of the greatly increasing numbers of snails. At site 6, 25 samples were collected on each sampling day.

The efficiency of Ekman sampling was tested with respect to both the vegetation and the molluscs as outlined below.

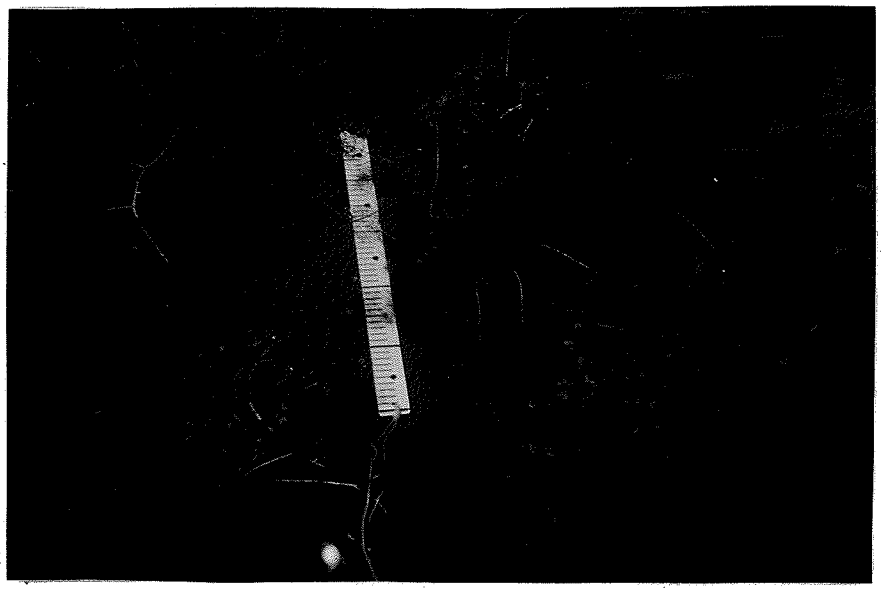
a. Vegetation

Cover was estimated for submerged macrophytes during July at site 5, since this was the only site where the water was clear enough to provide a good view of the bottom for all samples. Cover estimates were made using a modification of a line-intercept procedure. A reflecting rule, 0.5 m long and calibrated in 1 cm units, was tossed into the water and the number of units covered by vegetation was noted (Fig. 2). The rule was removed and an Ekman sample was collected at the same point. The substrate samples were subsampled and treated as described above. A regression analysis of plant weight on cover showed significant ($p < .001$, $n=21$) positive correlation of these two variables, suggesting that the subsampling procedure reflected macrophyte abundance at an acceptable level of constancy.

b. Molluscs

Although there was little loss of molluscs present in the substrate due to enclosure within the dredge, a variable amount of

Figure 2. Estimation of submerged plant cover at site 5 using a calibrated 0.5 m rule.



loss of live snails was expected from the unenclosed portions of the plant shoots. Previous workers, although not sampling by Ekman dredge, assumed that little loss of snails attached to plants occurs when the latter are removed from the water (e.g. Krecker, 1939; Petr, 1968; DeCosker and Persoone, 1970; Lévêque, 1975, LaCoursière et al, 1975). To examine the efficiency of sampling live snails by Ekman dredge, several 50 x 50 cm quadrats were set up in thick vegetation in areas of site 1 where the water was shallow enough to allow for clear visibility of the bottom. All live snails present on the bottom and on the plant shoots rooted within the quadrat were counted; then two 15 x 15 cm Ekman grabs were taken from each quadrat. The material was treated as a normal sample except that subsamples were not taken because only live snails were considered. The expected, non-integer values correlated well ($p < .01$, $n=18$) with the observed integer values for snails recovered from the Ekman grabs. The values were slightly, but not significantly smaller than the expected values, suggesting that relatively little loss occurred.

B. Live counts

When the submerged vegetation began to reach the surface in the beginning of June (time 3), live counts of snails present on different macrophyte species were started at site 1, since this was the only site where several plant species occurred in large numbers, where snails were found on the plants in all types of weather and where lack of turbulence facilitated observation. Visible snails present on different macrophytes were counted from a small boat

during midmorning along several transects which ran parallel to the margins of the ditch. Results were expressed as proportions of various gastropod species present on the different macrophytes.

Results

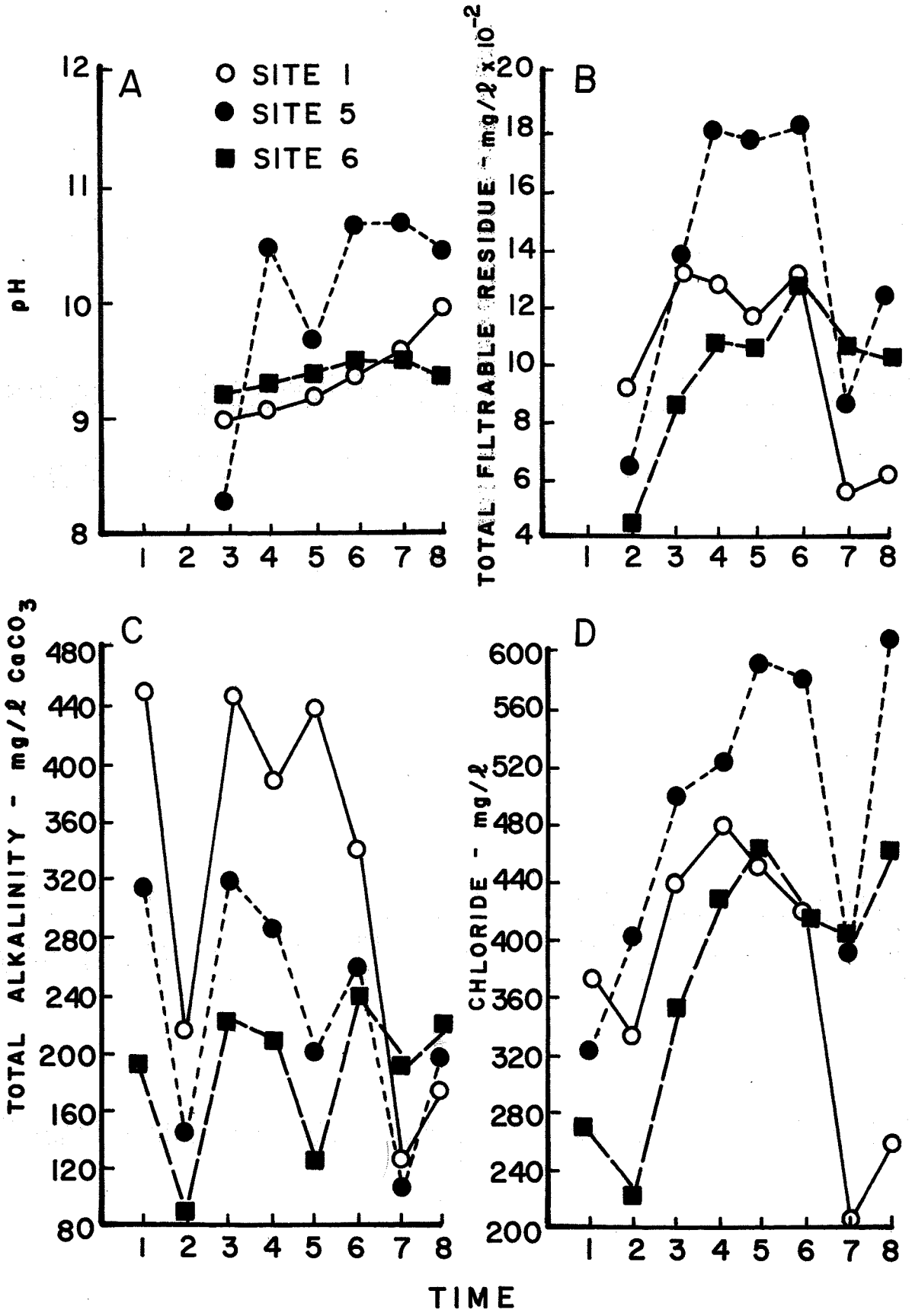
I. Environmental measurements

A. Water chemistry

Values for pH of surface water at site 1 (Fig. 3A) showed a steady upward trend which persisted throughout the season. At site 5, a sharp increase was observed after sampling time 3, followed by a decrease at time 5 and again by another increase at time 6, after which the pH remained at a very high level until the end of the sampling season. At site 6 the surface pH fluctuated very little during the season, rising a net total of 0.3 pH units from time 3 to 6, then remaining level and decreasing slightly by time 8.

Since, in natural waters, pH is largely determined by bicarbonate-free carbon dioxide concentrations, it reflects, aside from atmospheric diffusion, the net rate of carbon fixation within the system (Ruttner, 1953). The rise in pH at sites 1 and 5 was probably largely biogenic, resulting from photosynthesis by increasingly dense macrophyte and phytoplankton communities within a closed system. The pH at site 5 did not rise beyond a value of 10.7 after time 6; according to Ruttner (1953), pH values higher than 11 cannot be reached under normal conditions because calcium carbonate precipitates before the hydroxide concentration, which results from decomposition of bicarbonate, reaches a higher level, and also because photosynthesis may be inhibited by high pH. At site 6, macrophyte communities had proportionately little influence on pH in relation to the volume of

Figure 3. Values for pH (A), total filtrable residue (mg/l x 10^{-2}) (B), total alkalinity (mg/l $CaCO_3$) (C) and chloride (mg/l) (D) of surface water at sites 1, 5 and 6 during the 1972 season.


A
SITE 1
SITE 5
SITE 6
pH
12
11
10
9
8
B
TOTAL FILTRABLE RESIDUE - mg/ℓ x 10⁻²
20
18
16
14
12
10
8
6
4
C
TOTAL ALKALINITY - mg/ℓ CaCO3
480
440
400
360
320
280
240
200
160
120
80
D
CHLORIDE - mg/ℓ
600
560
520
480
440
400
360
320
280
240
200
1 2 3 4 5 6 7 8
TIME

water and the slight rise in pH at this site was probably largely due to physical factors such as dropping water level.

Total filtrable residue (Fig. 3B) showed considerable variation during the season at all three sites. In general, an increase from an initially low level occurred after time 2, a moderate decrease was observed at time 5, followed by an increase at time 6 and a decrease at time 7. The highest values were observed at site 5, approaching 2 g/l during midseason.

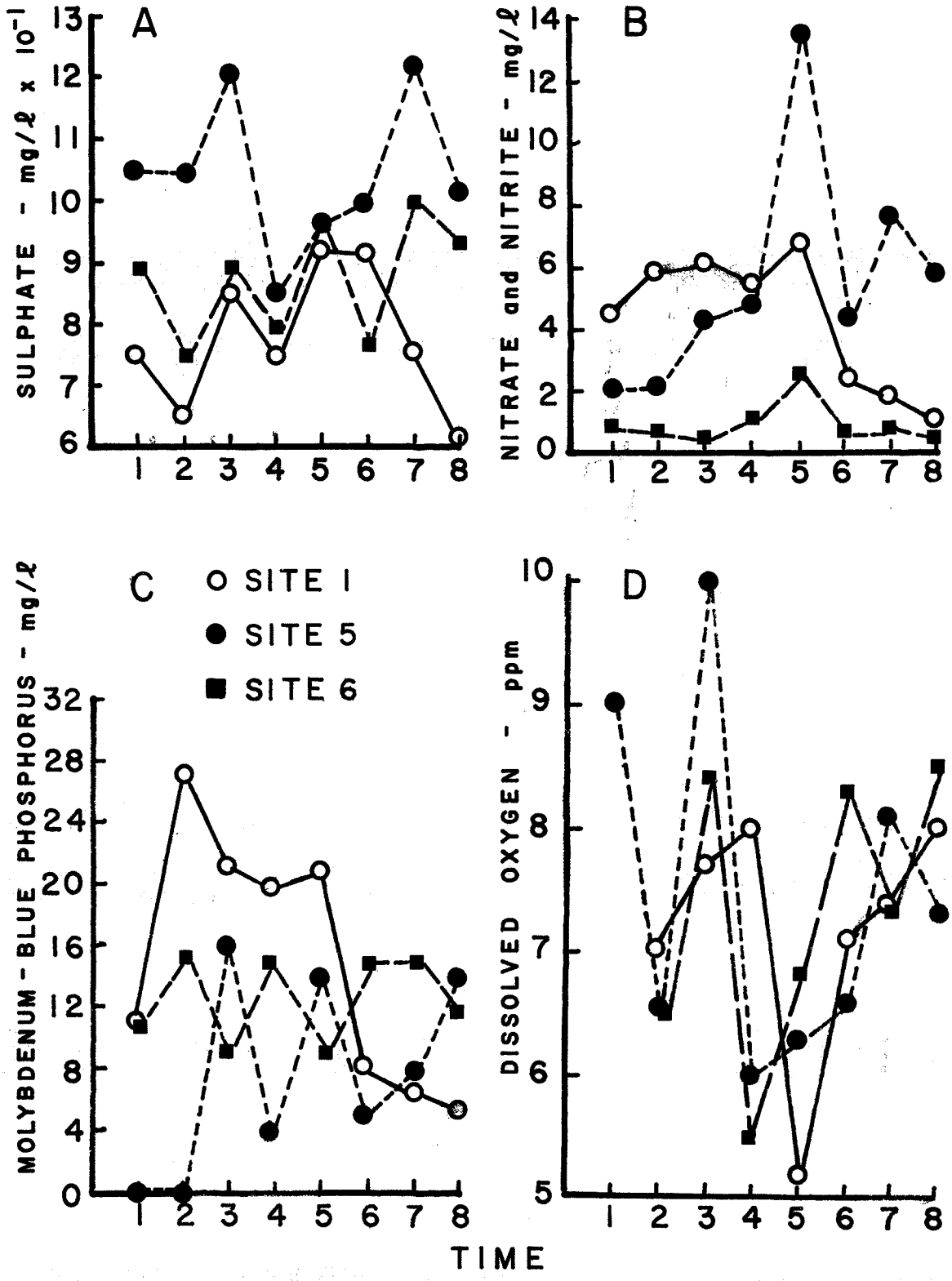
The seasonal patterns for total alkalinity (Fig. 3C) were essentially similar at the three sites. A sharp decrease occurred after time 1 from an initially high level, followed by an equally sharp increase to a peak at time 3; another decrease occurred at time 4 at site 1 and at time 5 at sites 5 and 6. All sites showed a drop at time 7, followed by a slight rise at time 8.

With respect to chloride (Fig. 3D), sites 5 and 6 showed parallel patterns with a maximum at time 5, but at site 1 a maximum occurred at time 4. Chloride values were minimal at time 7 at all sites, and increased again at time 8.

A maximum value for sulphate concentration (Fig. 4A) occurred at time 3 at all sites, followed by a decrease at time 4 and an increase at time 5. After time 5 sulphate values continued to rise at site 5, but decreased at site 6, while at site 1 they remained level until time 6 and then decreased. A second peak occurred at time 7 at sites 5 and 6.

Estimated values for total nitrate and nitrite (Fig. 4B) showed similar patterns at all sites; a peak occurred at time 5 and

Figure 4. Values for sulphate (mg/l x 10^{-1}) (A), combined nitrate and nitrite (mg/l)(B), molybdenum-blue phosphorus (mg/l) (C) and dissolved oxygen (ppm)(D) of surface water at sites 1, 5 and 6 during the 1972 season.


A
SULPHATE - mg/ℓ x 10^{-1}
B
NITRATE and NITRITE - mg/ℓ
C
SITE 1
SITE 5
SITE 6
MOLYBDENUM - BLUE PHOSPHORUS - mg/ℓ
D
DISSOLVED OXYGEN - ppm
TIME

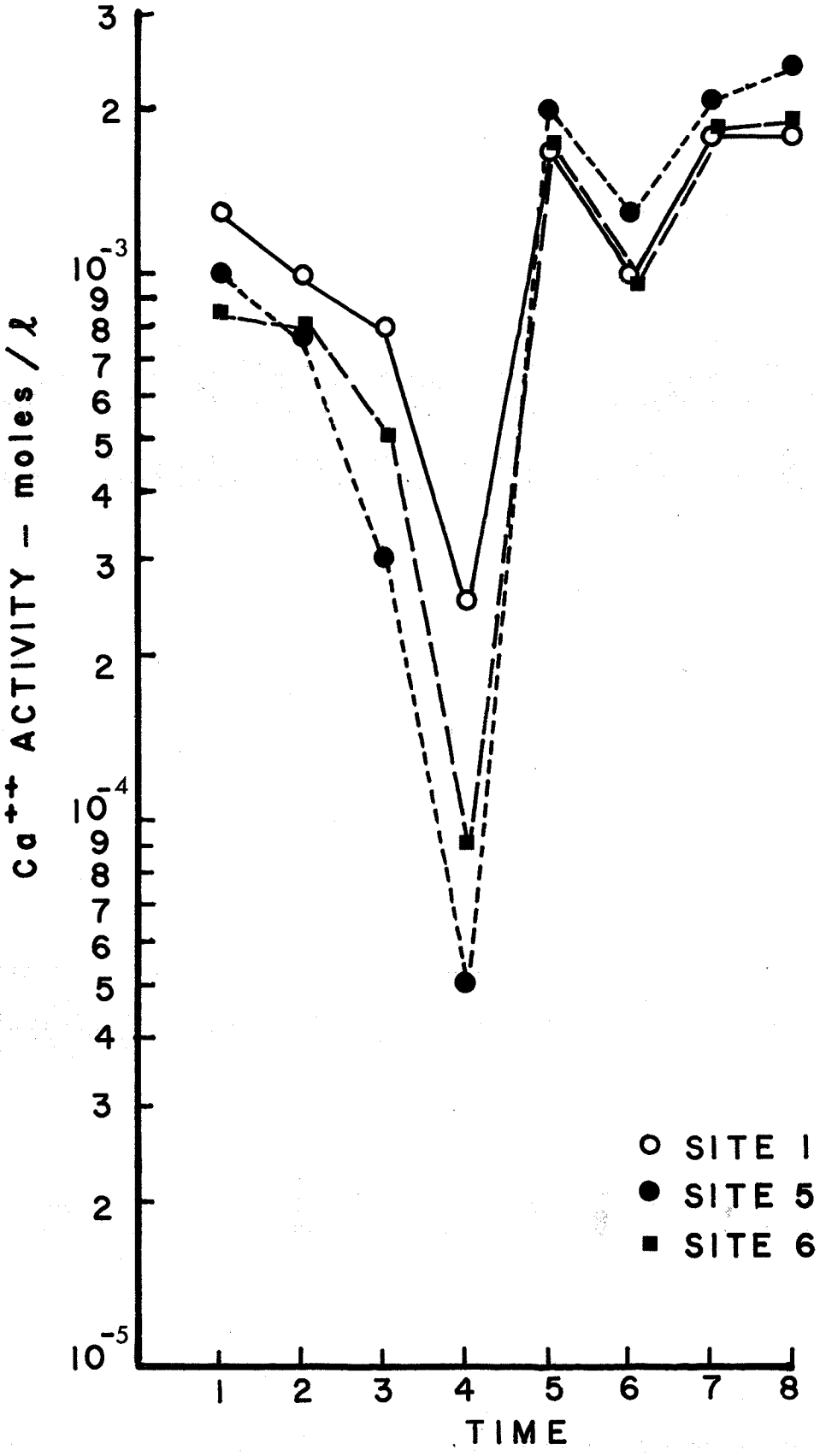
was most pronounced at site 5. The greatest dissimilarity between sites was observed for molybdenum-blue phosphorus (Fig. 4C); the values at sites 5 and 6 were inversely related.

Dissolved oxygen content of surface water (Fig. 4D) was highly variable at all sites throughout the season: this was to be expected since this factor was dependent upon both biotic and physical conditions. Values at the three sites were generally close to saturation; during midseason temperatures were high and solubility was reduced. The values reflected to a large extent the photosynthetic activity of the primary producers which itself was dependent upon incident light intensity and quality, turbidity of the water, temperature and numbers and metabolic state of the primary producers. On sunny days during midseason, the rate of oxygen evolution by submerged macrophytes exceeded its solubility, resulting in supersaturation in the areas of the stands and active escape of oxygen to the surface.

The patterns for calcium activity (Fig. 5) were similar at all sites, where a midseason minimum was observed at time 4. The greatest amplitude in the fluctuations occurred at site 5, where nearly a 100-fold increase was observed from time 4 to 5.

Generally, site 1 was the least similar of the three sites with respect to the seasonal patterns of the monitored parameters. Site 5 showed the most extreme conditions, both in terms of the amplitude of fluctuations and in terms of the highest values for pH, total filtrable residue, chloride and sulphate. The most moderate conditions were seen at site 6, which was characterized by the lowest concentrations and smallest fluctuations of solutes.

Figure 5. Values for calcium activity (moles/l) of surface water at sites 1, 5 and 6 during the 1972 season.


3
2
10-3
9
8
7
6
5
4
3
2
10-4
9
8
7
6
5
4
3
2
10-5
Ca++ ACTIVITY – moles / ℓ
1
2
3
4
5
6
7
8
TIME
SITE 1
SITE 5
SITE 6

B. Light and temperature

At site 1 at time 1 (Fig. 6A) the water still showed some residual turbidity from spring runoff and circulation but by time 2 the water had increased in clarity, which remained high until after time 3. Light intensity at the 0.75 m level dropped after time 2 as the submerged vegetation began to grow towards the surface. A drop in light intensity was observed at all levels at time 4 because the macrophytes had reached the surface and had begun to branch; water clarity was also reduced by increasing phytoplankton populations and suspended debris. The decrease at time 5 was exaggerated because of cloudy atmospheric conditions. Values at times 6 and 7 showed relatively low light penetration below the surface because of heavy vegetation cover, visibly higher phytoplankton density and decaying debris.

At site 5 (Fig. 6B) light penetration below the surface was low at time 1, but increased by time 2. Readings could not be obtained at time 3 because of a severe storm, the effects of which were still reflected in the decreased values at time 4 as circulation continued and particles of flocculent organic matter remained suspended. The water cleared again by time 5, but not to the extent observed at time 2 because of obstruction by submerged vegetation. The decrease at time 6 was again due to a storm, which was of lesser intensity than that at time 3 and the water cleared by time 7. Storms had profound effects on light attenuation at this site because of its exposure, large surface area in relation to volume and easily suspended sediment.

Figure 6. Values for light intensity (ft-candles x 10^{-3})(1 ft-c = 10.763 lm/m^2) at sites 1 (A), 5 (B) and 6 (C), and values for temperature (°C) at sites 1 (D), 5 (E) and 6 (F) at depths just below the surface (1), at 0.25 m (2), at 0.50 m (3) and at 0.75 m (4) during the 1972 season.

weather, some stratification was apparent and heating continued, but stratification was destroyed by a storm at time 3. A thermal gradient was evident at time 4, after which temperatures dropped and homothermic conditions persisted for the remainder of the sampling season. Because the sampling area was located in the epilimnion, temperature gradients were observed only during periods of exceptional calm.

II. Biotic sampling

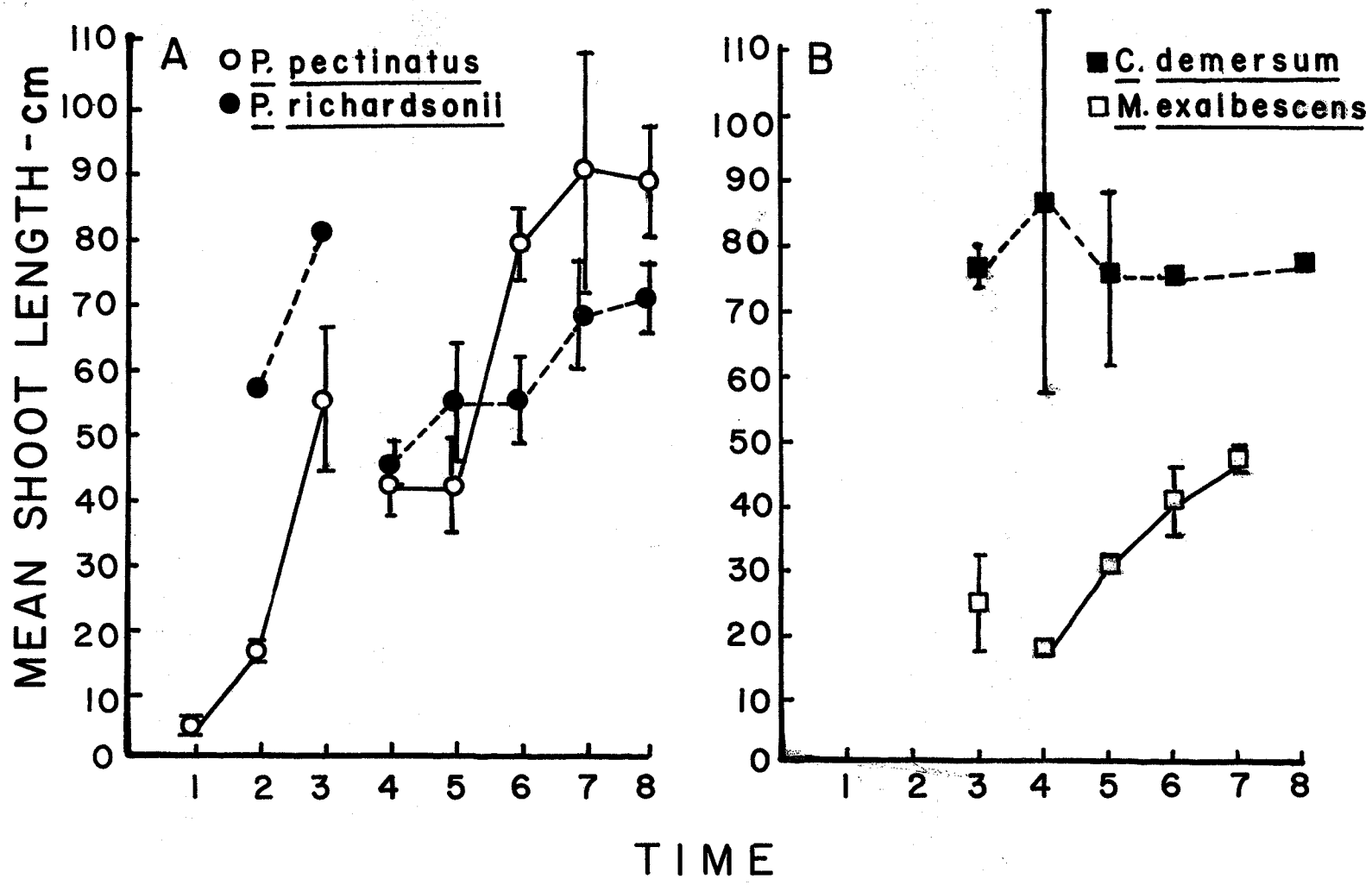
A. Site 1

a. Vegetation

At site 1, the first order shoots of Potamogeton pectinatus and P. richardsonii (Fig. 7A) began to reach the surface and the first inflorescences appeared at time 3. The mean shoot length decreased at time 4 as second order shoots began to contribute to the mean values, and a similar drop was observed at this time for Myriophyllum exalbescens (Fig. 7B). Ceratophyllum demersum (Fig. 7B) showed little net increase in length, growth occurring in large part through branching. Measurements for the latter species represented maximum branch end-to-end length because of the absence of roots in this macrophyte.

The mean dry weight of individual P. pectinatus shoots increased from 0.12 g at time 2 to 0.60 g at time 8; the greatest rate of increase occurred from time 5 to 6 when mean dry weight doubled due to increase in shoot length and branching. The mean dry weight of P. richardsonii shoots increased from 1.0 g at time 2 to 1.6 g at time 3; a slight decrease in weight occurred after time 3 as the lower leaves began to deteriorate. At time 4 dry weight began to increase and culminated in a maximum value of 1.59 g at time 6, after which mean dry weight decreased, despite continued increase of stem length, as the lower leaves disappeared. The mean dry weight of M. exalbescens shoots increased from 0.14 to 0.39 g during the season while the maximum mean dry weight attained by C. demersum was 0.71 g. The latter species was rare in the samples until after time 3.

Figure 7. Mean shoot length (cm) of Potamogeton pectinatus and P. richardsonii (A) and of Myriophyllum exalbescens and Ceratophyllum demersum (B) at site 1 during the 1972 season. Disjunctions in the curves are due to different shoot generations. Vertical bars represent standard errors.


A
P. pectinatus
P. richardsonii
B
C. demersum
M. exalbescens
MEAN SHOOT LENGTH - cm
TIME
0
10
20
30
40
50
60
70
80
90
100
110
1
2
3
4
5
6
7
8

Due to the nonselective method of locating sampling points, many samples were heterogeneous, containing more than one species of plant. Degrees of sample heterogeneity are given in Table II where values (Q) represent the total weight of species x expressed as a percent of the total weight of all species in the samples that contain species s, the species under consideration. This relationship can be expressed as follows:

$$Q_x\,(\%) = \frac{\sum_{x=1}^{k} w_x}{\sum_{z=1}^{n} \sum_{y=1}^{m} w_{yz}} \cdot 100 \quad \ldots\ldots\ldots (1),$$

where w_x represents the weights of species x in individual samples containing species s, w_y represents the individual sample weights of each species present in individual samples containing species s, and w_z represents the total weight of each species in all samples containing species s. Where x=s, the value Q_s may be interpreted as an index of homogeneity for samples of species s.

From Table II it was apparent that the totality of species s samples often contained only a minor proportion of species s by weight. Of all samples collected, 15-20% contained no vegetation.

b. Density of live and dead molluscs

The bottom samples were divided into five habitat types based on whether or not they contained vegetation and on the type of vegetation, if present. Since many samples were heterogeneous with respect to vegetation (Table II), these were classified redundantly into each of the categories of vegetation they contained;

TABLE II. Heterogeneity of plant samples. Values represent weight of species x expressed as a percent of the total weight of all species in the samples containing the species under consideration, species s. Read horizontally to obtain the percentages that species s samples contained of the following species x: P= Potamogeton pectinatus, R= P. richardsonii, M= Myriophyllum exalbescens, C= Ceratophyllum demersum. Values in parentheses indicate percent homogeneity of species s samples, since x=s.

	Time	1				2			
Species s	Sp. x	P	R	M	C	P	R	M	C
P. pectinatus		-	-	-	-	(58.3)	39.3	2.3	0.1
P. richardsonii		-	-	-	-	7.9	(89.2)	2.9	0
M. exalbescens		-	-	-	-	13.8	77.1	(9.1)	0
C. demersum		-	-	-	-	98.1	0	0	(1.9)

	Time	3				4			
Species s	Sp. x	P	R	M	C	P	R	M	C
P. pectinatus		(26.1)	72.1	1.7	0.1	(38.8)	3.4	0.7	57.1
P. richardsonii		3.8	(93.8)	2.3	0.1	18.0	(80.9)	0.7	0.4
M. exalbescens		1.8	91.3	(6.8)	0.1	0.7	39.8	(59.5)	0
C. demersum		4.6	84.4	10.5	(0.5)	18.7	1.1	0	(80.2)

	Time	5				6			
Species s	Sp. x	P	R	M	C	P	R	M	C
P. pectinatus		(36.0)	34.1	5.6	24.3	(71.3)	0.6	12.8	15.3
P. richardsonii		1.6	(82.1)	15.3	1.0	23.3	(70.5)	2.0	4.2
M. exalbescens		1.7	66.4	(31.9)	0	3.4	46.2	(48.2)	2.2
C. demersum		23.7	42.4	0	(33.9)	68.4	0.7	11.3	(19.6)

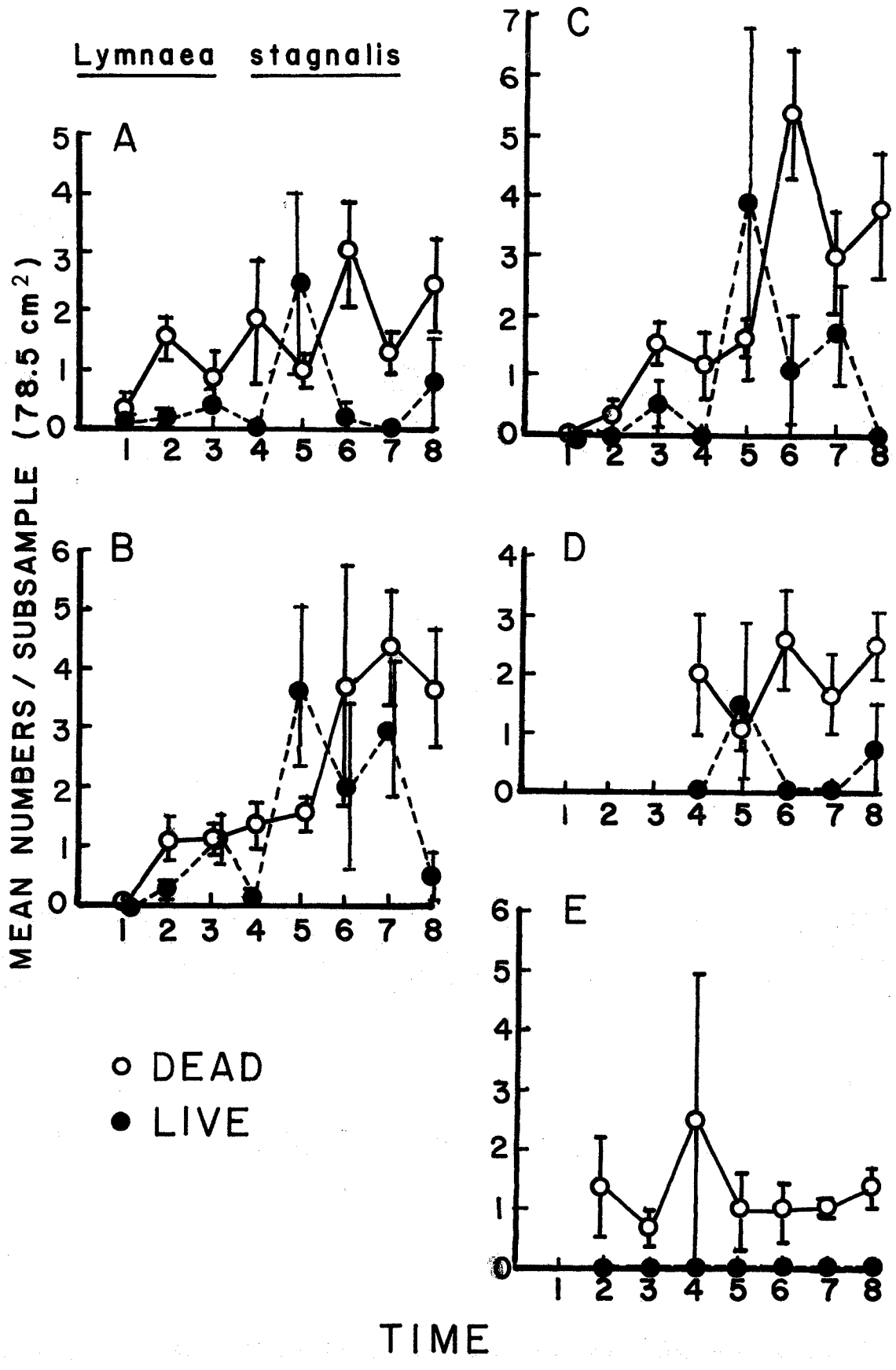
	Time	7				8			
Species s	Sp. x	P	R	M	C	P	R	M	C
P. pectinatus		(67.3)	11.1	8.8	12.8	(76.8)	0	3.1	20.1
P. richardsonii		0.2	(95.6)	4.2	0	0	(86.7)	10.0	3.3
M. exalbescens		1.7	77.7	(20.5)	0.1	21.4	10.5	(43.0)	25.1
C. demersum		62.2	0	0.9	(36.9)	58.5	4.5	17.2	(19.8)

thus samples containing more than one macrophyte species were counted with each of the habitat types represented by the macrophytes present. This approach was based on the hypothesis that differences in snail distribution could be correlated with distributions of macrophytes. Once distribution patterns were known, the information could be weighted to offset the masking that was expected as a result of high sample heterogeneity. The alternative approach, of assigning proportional values to snail densities according to plant weight, was discarded because it would require the assumption that densities of all snails were proportional to the weights of all plants, and therefore equal, and would conceal extant tendencies for association; furthermore this method would cause difficulties in apportioning size class data.

The purpose of studying dead populations was to observe their net rates and directions of flux, from which could be deduced the nature of their most recent increments and hence the nature of the living populations from which the dead were drawn. Such data was complementary to that obtained directly for the live populations and was necessary because the latter were in large part too small to provide conclusive results with the type of sampling employed.

The mean densities of live Lymnaea stagnalis L. per subsample (78.5 cm^2 bottom area) (Fig. 8) showed maximal values in all vegetation types at time 5. This peak was followed by an increase in dead shell density at time 6 in all vegetated samples; in Potamogeton richardsonii samples dead shell density continued to increase until time 7 as the larger live population in this habitat

Figure 8. Mean densities of dead and live individuals of *Lymnaea stagnalis* per subsample (78.5 cm^2 bottom area) in samples containing *Potamogeton pectinatus* (A), *P. richardsonii* (B), *Myriophyllum exalbescens* (C), *Ceratophyllum demersum* (D) and samples from nonvegetated areas (E) at site 1 during the 1972 season. Vertical bars represent standard errors.


Lymnaea stagnalis
A
B
C
D
E
MEAN NUMBERS / SUBSAMPLE (78.5 cm²)
o DEAD
● LIVE
TIME

continued to contribute proportionately more dead individuals. Secondary peaks of smaller amplitude occurred at time 7 in P. richardsonii and Myriophyllum exalbescens samples and at time 8 in samples containing P. pectinatus and Ceratophyllum demersum. No live individuals were observed in samples containing no vegetation. The half life of dead shells of L. stagnalis appeared to be less than 4 weeks at this site.

The mean densities of dead individuals of Stagnicola palustris Müller (Fig. 9) showed a peak at time 3 in all habitats except for those of C. demersum which was not present in more than one sample until time 4. In samples containing P. richardsonii and M. exalbescens a subsequent peak occurred at time 5 while in P. pectinatus, C. demersum and nonvegetated samples it occurred at time 6. The small numbers of live individuals that were observed showed peaks at times 2 and 6 in vegetated samples while none occurred in nonvegetated samples until time 7.

The density distribution patterns of dead shells of Fossaria modicella Say (Fig. 10) were similar for P. richardsonii, M. exalbescens and nonvegetated samples in that maxima occurred at time 6. Samples containing P. pectinatus and C. demersum showed parallel patterns during the second half of the season with maxima at time 7. Peaks in live snail density occurred at times 2 and 6 in P. richardsonii and M. exalbescens samples while in P. pectinatus samples the greatest density was observed at time 2. The pattern for C. demersum samples appeared unrelated to those of the other habitats. No live individuals were observed in nonvegetated samples.

Figure 9. Mean densities of dead and live individuals of Stagnicola palustris per subsample (78.5 cm^2 bottom area) in samples containing Potamogeton pectinatus (A), P. richardsonii (B), Myriophyllum exalbescens (C), Ceratophyllum demersum (D) and samples from nonvegetated areas (E) at site 1 during the 1972 season. Vertical bars represent standard errors.

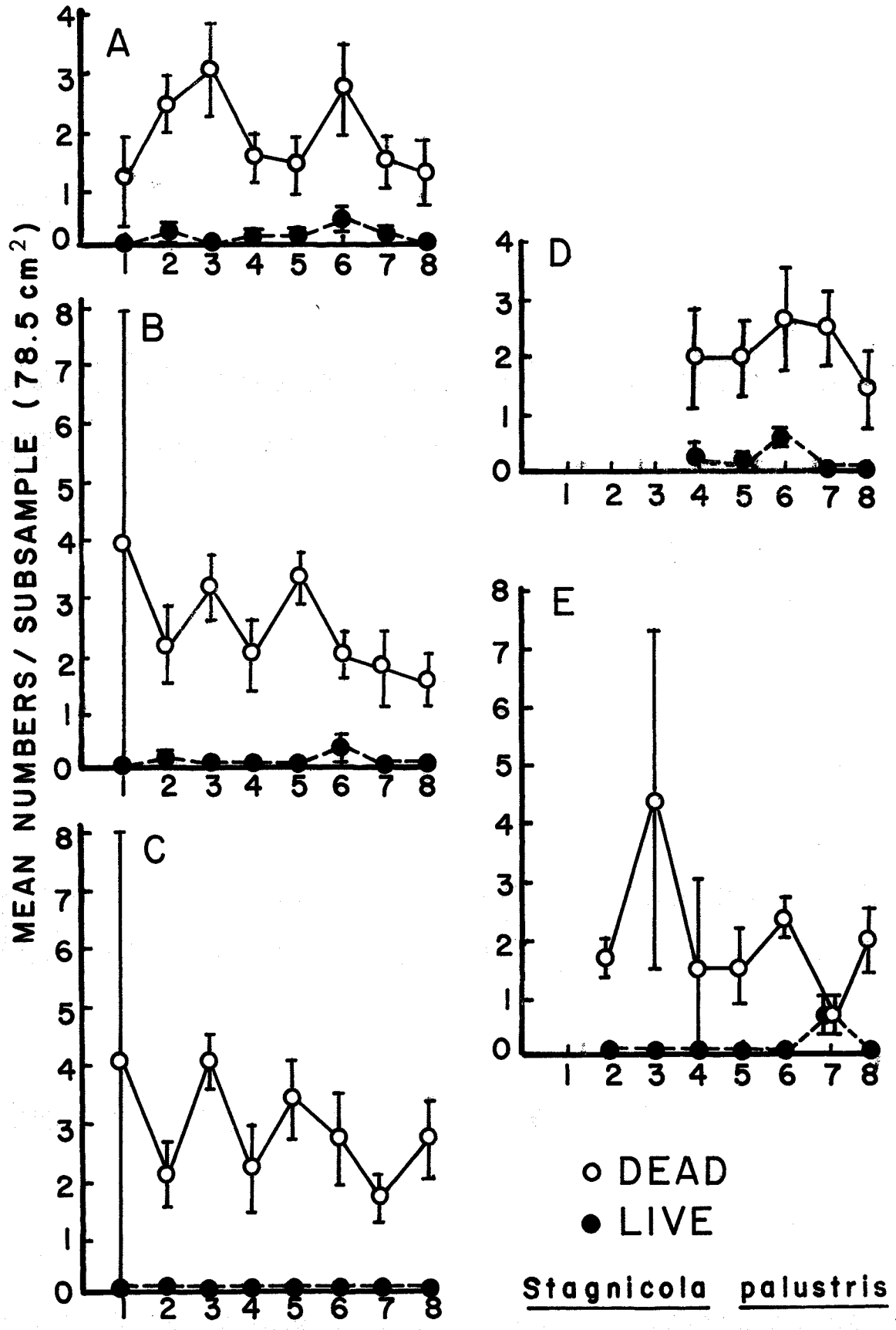

A
B
C
D
E
MEAN NUMBERS / SUBSAMPLE (78.5 cm²)
o DEAD
● LIVE
Stagnicola palustris

Figure 10. Mean densities of dead and live individuals of Fossaria modicella per subsample (78.5 cm^2 bottom area) in samples containing Potamogeton pectinatus (A), P. richardsonii (B), Myriophyllum exalbescens (C), Ceratophyllum demersum (D) and samples from nonvegetated areas (E) at site 1 during the 1972 season. Vertical bars represent standard errors.

The mean densities of live and dead individuals of Physa gyrina Say (Fig. 11) in both P. pectinatus and C. demersum samples showed a maximum at time 4; another peak for dead shells occurred at time 6 in all habitat types. No live individuals occurred in nonvegetated samples.

Density distributions for dead shells of Gyraulus parvus Say (Fig. 12) were similar for P. richardsonii and M. exalbescens samples in that maxima were observed at times 3, 6 and 8. In P. pectinatus samples, although a peak occurred at time 3, the subsequent pattern was out of phase with the former two habitat types. A maximum for live individuals was observed at time 2 in all vegetated habitats except that of C. demersum.

Mean densities of dead shells of Helisoma trivolvis Say (Fig. 13) showed a peak at time 6 in all vegetated habitats while in nonvegetated samples a maximum occurred at time 3. A peak in live individuals occurred at time 2 in P. richardsonii and M. exalbescens samples and at time 6 in all vegetated samples except those containing P. richardsonii where the secondary peak occurred at time 7. No live individuals were observed in nonvegetated samples.

Dead shells of Promenetus exacuous Say (Fig. 13) showed relatively high values at times 4 and 6 in all habitats except that of M. exalbescens which showed a peak at times 4 and 5. Live individuals were rare and were observed only at time 3 in P. pectinatus samples.

Planorbula armigera Say (Table III) showed similar density patterns in P. pectinatus and C. demersum samples while distributions in the remaining samples appeared unrelated. Live individuals were not observed. A pattern similar to that of the preceding species was

Figure 11. Mean densities of dead and live individuals of Physa gyrina per subsample (78.5 cm^2 bottom area) in samples containing Potamogeton pectinatus (A), P. richardsonii (B), Myriophyllum exalbescens (C), Ceratophyllum demersum (D) and samples from nonvegetated areas (E) at site 1 during the 1972 season. Vertical bars represent standard errors.

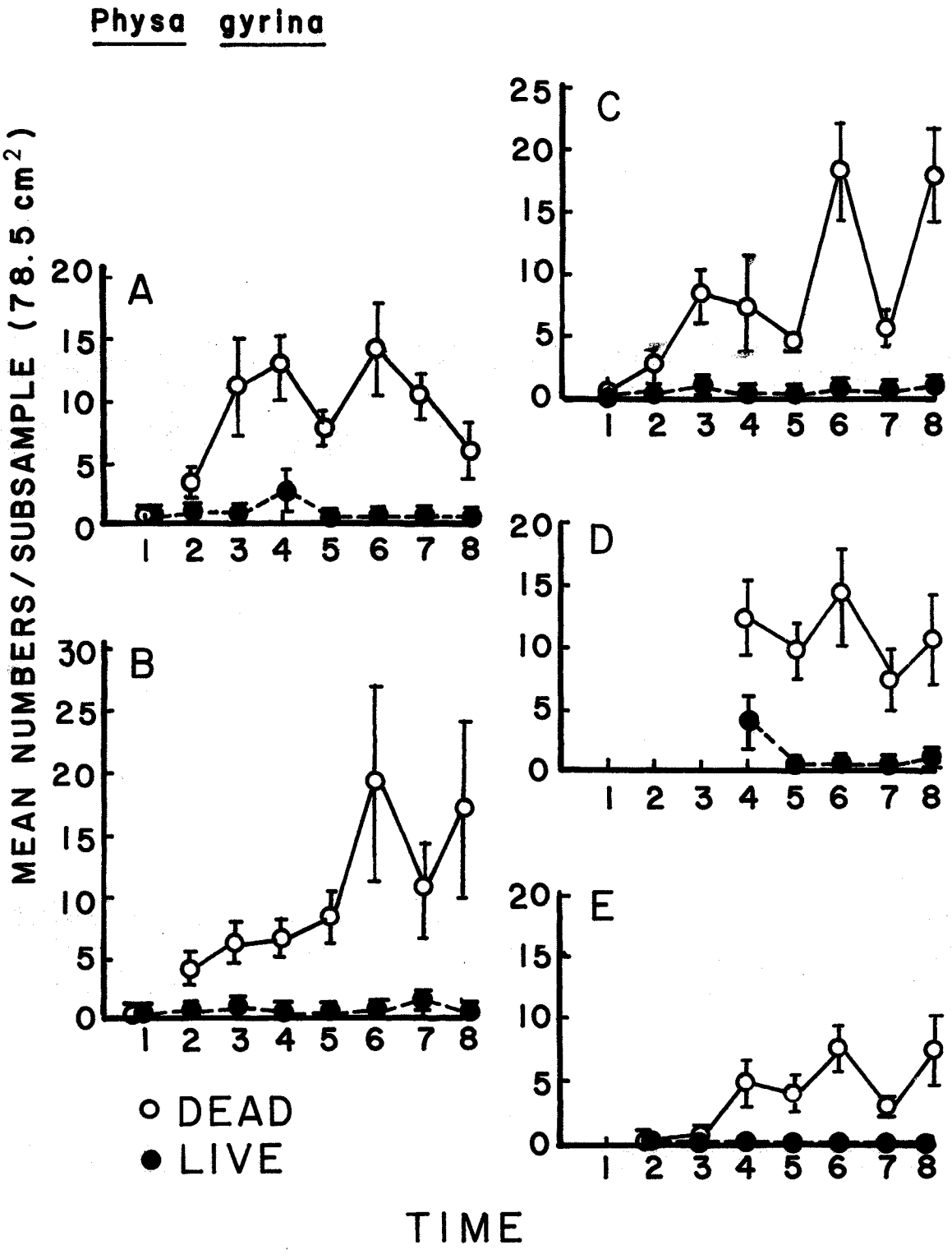

Physa gyrina
MEAN NUMBERS/SUBSAMPLE (78.5 cm²)
A
B
C
D
E
DEAD
LIVE
TIME

Figure 12. Mean densities of dead and live individuals of Gyraulus parvus per subsample (78.5 cm^2 bottom area) in samples containing Potamogeton pectinatus (A), P. richardsonii (B), Myriophyllum exalbescens (C), Ceratophyllum demersum (D) and samples from nonvegetated areas (E) at site 1 during the 1972 season. Vertical bars represent standard errors.

Gyraulus parvus

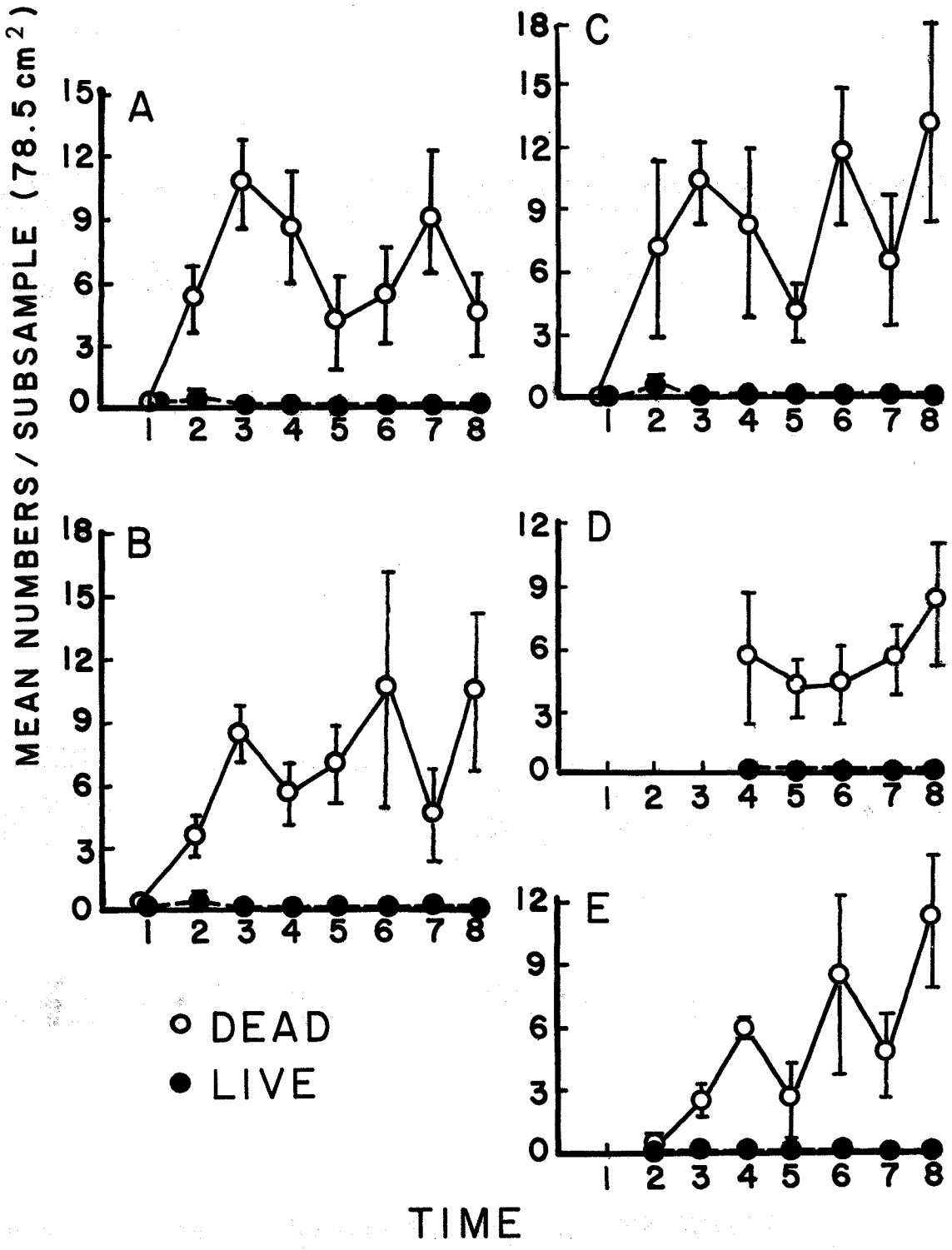


Figure 13. Mean densities of dead and live individuals of Helisoma trivolvis and Promenetus exacuous respectively per subsample (78.5 cm^2 bottom area) in samples containing Potamogeton pectinatus (A and F), P. richardsonii (B and G), Myriophyllum exalbescens (C and H), Ceratophyllum demersum (D and I) and samples from nonvegetated areas (E and J) at site 1 during the 1972 season. Vertical bars represent standard errors.

TABLE III. Mean numbers of dead shells per subsample (78.5 cm^2 bottom area) in the 5 habitat types. Values in parentheses are standard errors.

A. *POTAMOGETON PECTINATUS* SAMPLES

Species	Time	1	2	3	4	5	6	7	8
Planorbula armigera		0	0.18(0.12)	0.13(0.11)	0	0.38(0.18)	0.18(0.12)	0.11(0.11)	0.14(0.14)
Armiger crista		0	0	0.13(0.11)	0	0	0.27(0.19)	0	0
Valvata tricarinata		0	0.18(0.12)	0	1.00(0.52)	0	0.27(0.19)	0.89(0.51)	0
Amnicola spp.		0	0	0	0.17(0.17)	0	0.22(0.22)	0	0
Pisidium sp.		0	0	0	0.34(0.33)	0	0	0	0
Helisoma anceps		0	0	0	0	0	0.09(0.09)	0	0
Aplexa hypnorum		0	0	0	0	0	0.09(0.09)	0	0

B. *POTAMOGETON RICHARDSONII* SAMPLES

Species	Time	1	2	3	4	5	6	7	8
Planorbula armigera		0	0	0	0	0.33(0.24)	0	0.20(0.20)	0
Armiger crista		0	0	0	0	0	0	0	0
Valvata tricarinata		0	0.62(0.18)	0.25(0.16)	0.33(0.33)	0.22(0.22)	0.25(0.25)	0.20(0.20)	0.14(0.14)
Amnicola spp.		0	0.13(0.11)	0.25(0.16)	0.22(0.15)	0.11(0.11)	0.60(0.44)	0	0
Pisidium sp.		0	0	0	0.22(0.15)	0	0	0.40(0.24)	0
Helisoma anceps		0	0	0	0	0	0	0	0
Aplexa hypnorum		0	0	0	0	0	0	0	0

C. *MYRIOPHYLLUM EXALBESCENS* SAMPLES

Species	Time	1	2	3	4	5	6	7	8
Planorbula armigera		0	0.33(0.33)	0	0.17(0.17)	0	0.17(0.17)	0.13(0.12)	0
Armiger crista		0	0	0.20(0.20)	0.20(0.20)	0	0	0	0
Valvata tricarinata		0	0.33(0.33)	0.20(0.20)	0.50(0.50)	0	0.17(0.17)	0.63(0.50)	0
Amnicola spp.		0	0	0.33(0.33)	0.14(0.11)	0	0.50(0.19)	0	0
Pisidium sp.		0	0	0	0	0	0	0.25(0.16)	0
Helisoma anceps		0	0	0	0	0	0	0	0
Aplexa hypnorum		0	0	0	0	0	0.17(0.17)	0	0

(continued)

TABLE III. (continued)

D. CERATOPHYLLUM DEMERSUM SAMPLES

Species	Time	1	2	3	4	5	6	7	8
Planorbula armigera		-	-	-	0	0.33(0.21)	0.22(0.15)	0	0
Armiger crista		-	-	-	0	0	0.33(0.24)	0	0
Valvata tricarinata		-	-	-	1.50(0.65)	0.67(0.67)	0.11(0.11)	1.00(1.00)	0
Amnicola spp.		-	-	-	0.25(0.25)	0.17(0.17)	0	0	0
Pisidium sp.		-	-	-	0	0	0	0	0
Helisoma anceps		-	-	-	0	0	0.11(0.11)	0	0
Aplexa hypnorum		-	-	-	0	0	0	0	0

E. SAMPLES FROM BARE AREAS

Species	Time	1	2	3	4	5	6	7	8
Planorbula armigera		-	0	0	0.50(0.50)	0	0.33(0.33)	0	0
Armiger crista		-	0	0	0	0	0	0	0
Valvata tricarinata		-	0	0	0	0	0	0	0
Amnicola spp.		-	0	0	0.50(0.50)	0	0	0	0
Pisidium sp.		-	0	0	0	0	0	0	0
Helisoma anceps		-	0	0	0	0	0	0	0
Aplexa hypnorum		-	0	0	0	0	0	0	0

observed for Armiger crista L. (Table III) but again live individuals were not observed. For Valvata tricarinata Say, and Amnicola limosa Say and A. lacustris F.C. Baker (Table III), P. pectinatus and C. demersum samples were mutually similar as were those of P. richardsonii and M. exalbescens. A Pisidium sp. occurred sporadically. Dead shells of Helisoma anceps Menke and Aplexa hypnorum L. were observed only once, at time 6, and were probably the result of accidental introduction from the lake.

The similarity between samples containing P. pectinatus and C. demersum, and between those containing P. richardsonii and M. exalbescens was due in part to the spatial distribution of these plants in the ditch, resulting in a greater degree of sample overlap between the members of each pair.

The mean relative density of dead shells in the 5 habitat types (Table IVA) showed that the species occurred in a similar order of frequency in all vegetated habitats. Fossaria modicella was the commonest species observed in the dead shell fauna and seasonal variation of its relative density depended largely upon the fluctuations of other species numbers. The next most frequent species, Physa gyrina, showed frequency differences between different habitat types, comprising larger proportions of the total shell fauna in P. pectinatus and C. demersum samples, with maxima at times 5 and 6. The latter were responsible for corresponding minima observed at these times for F. modicella. Gyraulus parvus, the third most frequent species, showed maxima in all habitats at times 2 and 3, with a secondary maximum towards the end of the season. Stagnicola palustris

TABLE IV. Mean relative density per unit bottom area for dead (A) and live (B) molluscs at site 1 expressed as a percent of the total numbers of molluscs of all species present in each habitat type at each sampling time. Species numbers represent the following taxa:

1. Lymnaea stagnalis
2. Stagnicola palustris
3. Fossaria modicella
4. Physa gyrina
5. Aplexa hypnorum
6. Helisoma trivolvis
7. H. anceps
8. Gyraulus parvus
9. Planorbula armigera
10. Promenetus exacuous
11. Armiger crista
12. Amnicola limosa and A. (=Probythinella) lacustris
13. Valvata tricarinata
14. Pisidium sp.

TABLE IV.

A. DEAD

	POTAMOGETON PECTINATUS SAMPLES								POTAMOGETON RICHARDSONII SAMPLES							
Species Time	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	7.7	6.7	2.0	3.9	4.4	7.2	3.4	8.9	0	5.3	2.9	3.6	3.9	5.3	11.1	6.9
2	23.0	10.5	6.9	3.3	6.1	6.6	3.7	4.4	54.5	10.0	8.0	5.4	7.8	2.9	4.5	2.9
3	38.5	41.4	38.8	38.3	28.9	28.8	37.1	44.4	31.8	43.7	48.1	52.3	47.1	44.2	40.9	36.6
4	16.7	14.4	25.6	28.2	35.0	34.7	27.1	22.7	13.6	19.5	15.9	18.5	19.3	27.5	26.8	32.1
5	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0
6	2.6	1.5	1.4	2.2	3.9	4.4	1.4	2.2	0	0.6	2.5	1.2	2.6	2.1	2.0	0.8
7	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0
8	11,5	23.0	24.7	19.1	19.4	12.9	23.8	16.0	0	16.5	21.0	14.9	16.9	15.3	12.1	19.8
9	0	0.8	0.3	0	1.7	0.4	0.3	0.5	0	0	0	0	0.8	0	0.5	0
10	0	0.8	0	1.7	0.6	2.6	0.8	0.9	0	0.7	0.3	2.0	0.8	1.4	0.5	0.5
11	0	0	0.3	0	0	0.7	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0.4	0	0.5	0	0	0	0.7	0.6	0.6	0.3	0.9	0	0
13	0	0.8	0	2.2	0	0.7	2.3	0	0	2.9	0.6	0.9	0.5	0.4	0.5	0.3
14	0	0	0	0.7	0	0	0	0	0	0	0	0.6	0	0	1.0	0

B. LIVE	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	33.3	15.4	59.4	0	79.6	15.8	0	63.8	0	18.7	56.2	50.0	73.0	42.1	62.5	57.0
2	0	15.4	0	4.9	4.1	26.3	20.0	0	0	8.4	0	0	0	5.3	0	0
3	0	38.5	0	9.4	12.1	15.8	40.0	0	0	32.3	0	25.0	22.0	31.6	4.2	14.0
4	66.7	23.1	20.3	80.9	4.2	15.8	40.0	36.2	0	16.1	43.8	25.0	5.0	15.8	33.3	29.0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	4.8	0	26.3	0	0	0	16.1	0	0	0	5.2	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	7.6	0	0	0	0	0	0	0	8.4	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	20.3	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(continued)

TABLE IV. (continued)

A. DEAD

	MYRIOPHYLLUM EXALBESCENS SAMPLES								CERATOPHYLLUM DEMERSUM SAMPLES							
Species Time	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	0	1.3	3.0	2.6	5.1	8.0	8.4	6.3	-	-	-	4.9	3.3	6.4	4.8	6.6
2	54.5	7.7	7.6	4.8	10.2	3.9	4.6	4.4	-	-	-	4.9	6.6	6.7	7.6	3.9
3	31.8	47.5	50.6	50.5	49.0	39.8	48.4	35.2	-	-	-	38.9	36.5	31.8	46.1	36.5
4	13.6	11.5	16.4	17.1	14.3	27.0	16.1	30.2	-	-	-	30.2	32.6	35.6	21.1	28.9
5	0	0	0	0	0	0.2	0	0	-	-	-	0	0	0	0	0
6	0	1.3	1.5	2.6	5.1	2.4	0.7	1.6	-	-	-	1.9	3.9	4.2	1.5	2.0
7	0	0	0	0	0	0	0	0	-	-	-	0	0	0.3	0	0
8	0	28.2	19.4	18.2	13.3	16.7	18.6	22.0	-	-	-	14.2	13.3	10.6	15.9	21.4
9	0	1.3	0	0.4	0	0.2	0.4	0.3	-	-	-	0	1.1	0.6	0	0
10	0	0	0	1.9	3.0	0.8	0.4	0	-	-	-	0.6	0	2.8	0	0.7
11	0	0	0.4	0.4	0	0	0	0	-	-	-	0	0	0.8	0	0
12	0	0	0.6	0.3	0	0.8	0	0	-	-	-	0.6	0.6	0	0	0
13	0	1.2	0.4	1.1	0	0.2	1.8	0	-	-	-	3.7	2.1	0.2	3.0	0
14	0	0	0	0	0	0	0.6	0	-	-	-	0	0	0	0	0

B. LIVE	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	0	0	33.3	0	80.0	41.2	60.8	0	-	-	-	0	59.8	0	0	42.9
2	0	0	0	0	0	0	0	0	-	-	-	5.3	6.8	31.5	0	0
3	0	42.9	0	0	13.4	35.2	4.5	0	-	-	-	5.3	26.7	18.5	50.0	0
4	0	14.2	66.7	100.0	6.6	17.6	34.7	100.0	-	-	-	84.2	6.7	18.5	50.0	0
5	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0
6	0	28.8	0	0	0	6.0	0	0	-	-	-	5.2	0	31.5	0	57.1
7	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0
8	0	14.1	0	0	0	0	0	0	-	-	-	0	0	0	0	0
9	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0
10	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0
11	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0
12	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0
13	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0
14	0	0	0	0	0	0	0	0	-	-	-	0	0	0	0	0

(continued)

TABLE IV. (continued)

A. DEAD

SAMPLES FROM BARE AREAS

Species	Time	1	2	3	4	5	6	7	8
1		-	11.7	2.9	9.6	4.0	2.2	5.8	3.4
2		-	14.7	18.8	5.8	6.0	5.2	3.9	5.0
3		-	58.8	58.0	32.7	62.0	55.2	46.1	44.6
4		-	8.8	5.8	19.2	16.0	17.2	15.4	18.5
5		-	0	0	0	0	0	0	0
6		-	0	4.3	1.9	0	0.7	1.9	0.8
7		-	0	0	0	0	0	0	0
8		-	5.9	10.1	23.1	11.0	18.7	26.9	27.7
9		-	0	0	1.9	0	0.7	0	0
10		-	0	0	3.8	1.0	0	0	0
11		-	0	0	0	0	0	0	0
12		-	0	0	1.9	0	0	0	0
13		-	0	0	0	0	0	0	0
14		-	0	0	0	0	0	0	0

B. LIVE

	1	2	3	4	5	6	7	8
1	-	0	0	0	0	0	0	0
2	-	0	0	0	0	0	100.0	0
3	-	0	0	0	0	0	0	0
4	-	0	0	0	0	0	0	0
5	-	0	0	0	0	0	0	0
6	-	0	0	0	0	0	0	0
7	-	0	0	0	0	0	0	0
8	-	0	0	0	0	0	0	0
9	-	0	0	0	0	0	0	0
10	-	0	0	0	0	0	0	0
11	-	0	0	0	0	0	0	0
12	-	0	0	0	0	0	0	0
13	-	0	0	0	0	0	0	0
14	-	0	0	0	0	0	0	0

was consistently fourth in order of frequency, showing an initially high value followed by a steep decrease at time 2. For Lymnaea stagnalis, higher values of relative density were observed in samples containing P. richardsonii and M. exalbescens with maxima occurring towards the end of the season. The species comprising the remainder were each of minor (< 5%) importance and generally occurred in the following order: Helisoma trivolvis, Promenetus exacuous, Planorbula armigera, Valvata tricarinata, Amnicola spp., Armiger crista, Pisidium sp., Helisoma anceps and Aplexa hypnorum. This order of frequency was observed in nonvegetated samples as well, except that Gyraulus parvus was slightly more frequent than Physa gyrina and some of the minor species were not observed.

The mean relative density of live snails (Table IVB) showed a different order of frequency from that seen for dead shells. Here Physa gyrina and Lymnaea stagnalis comprised the majority of the fauna. A maximum relative frequency was observed at time 4 for Physa gyrina in all vegetation types except that of P. richardsonii where a maximum was observed at time 3. The high values at times 4 and 8 in M. exalbescens samples were due to the absence of other species. The peaks at time 4 were accompanied by minima in the relative density of Lymnaea stagnalis. The latter species showed maxima at time 5 in all vegetation types, resulting in concurrent minima for Physa gyrina. The frequency of Lymnaea stagnalis appeared to be most consistent in samples containing P. richardsonii. Fossaria modicella and Stagnicola palustris were the next most frequent species, the latter showing a maximum at time 6 in P. pectinatus and C. demersum samples. A maximum for Helisoma trivolvis occurred at time 6, with a higher relative

density seen in P. pectinatus and C. demersum samples. Gyraulus parvus and Promenetus exacuous occurred sporadically. In nonvegetated samples, only one live individual of Stagnicola palustris was observed, resulting in 100% relative density for this species at time 7.

The frequencies of dead and live molluscs did not coincide largely due to different rates of disintegration of shell material among different species, although it was assumed that, within a single site, disintegration rates for a given species were the same in all habitat types. Fossaria modicella persisted longer than the more fragile Physa gyrina, resulting in its greater frequency among dead material. Of the majority species, Gyraulus parvus remained intact for the longest time, giving rise to the greatest disparity between densities of live and dead shells.

In order to ascertain whether apparent distributional differences could be explained on the basis of chance variation among samples, unpaired t-tests were conducted to examine the significance of the difference between means for samples from nonvegetated areas and those from each of the vegetated habitat types. Expected values for t were obtained from tables given by Fisher and Yates (1957). The results for dead shells (Table VA) showed that towards the end of the season, Lymnaea stagnalis occurred significantly more frequently in P. richardsonii and M. exalbescens samples than in nonvegetated areas. Physa gyrina occurred significantly more frequently, although often irregularly, in all vegetated habitats than in samples from bare areas. Fossaria modicella showed a significant tendency to accumulate in all vegetated habitats at time 4. Helisoma trivolvis, Gyraulus parvus, Stagnicola palustris, Amnicola spp. and Planorbula armigera also

TABLE V. Results of unpaired t-tests for the significance of the difference of mean densities per unit bottom area of dead (A) and live (B) molluscs between samples from nonvegetated areas and those from each vegetated habitat type at site 1. Symbols indicate: + = significantly ($p < .05$) greater values in vegetated than in nonvegetated samples, 0 = no significant difference. Values in parentheses denote tests for which graveyard indices were significantly ($p < .05$) high. Species numbers represent the following taxa:

1. Lymnaea stagnalis
2. Stagnicola palustris
3. Fossaria modicella
4. Physa gyrina
5. Aplexa hypnorum
6. Helisoma trivolvis
7. H. anceps
8. Gyraulus parvus
9. Planorbula armigera
10. Promenetus exacuous
11. Armiger crista
12. Amnicola limosa and A. (=Probythinella) lacustris
13. Valvata tricarinata
14. Pisidium sp.

TABLE V.

SAMPLES CONTAINING

A. DEAD		P. PECTINATUS								P. RICHARDSONII								M. EXALBESCENS								C. DEMERSUM							
Species	Time	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1		0	0	0	0	0	0	0	0	0	0	0	0	0	+	+		0	0	0	0	+	(+)	+		0	0	0	0	0	0		
2		0	0	0	0	0	0	0	0	0	0	0	+	0	0	0		0	0	0	0	0	0	0		0	0	0	+	0			
3		0	0	+	0	0	0	0		0	0	+	0	0	0	0		0	+	+	0	0	(+)	0		+	0	0	0	0			
4		(+)	+	+	+	0	+	0		+	+	0	+	0	+	0		0	+	0	0	+	0	+		0	+	0	0	0			
5		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
6		(+)	0	0	+	+	0	0		0	0	0	+	0	0	0		0	0	0	0	0	0	0		0	+	+	0	0			
7		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
8		(+)	+	0	0	0	0	0		+	+	0	0	0	0	0		0	+	0	0	0	0	0		0	0	0	0	0			
9		0	0	0	+	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
10		0	0	0	0	+	+	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
11		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
12		0	0	0	0	+	0	0		0	0	0	0	0	0	0		0	0	0	0	0	(+)	0		0	0	+	0	0			
13		0	0	+	0	0	0	0		+	0	0	0	0	0	0		0	0	0	0	0	0	0		+	0	0	0	0			
14		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
B. LIVE		1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1		0	0	0	0	0	0	0		0	+	0	+	0	+	0		0	0	0	0	0	+	0		0	0	0	0	0			
2		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
3		+	0	0	0	0	0	0		+	0	0	+	0	0	0		+	0	0	0	0	0	0		0	0	0	0	0			
4		+	0	0	0	0	0	+		0	+	0	0	0	0	0		0	+	0	0	0	0	+		0	0	0	0	+			
5		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
6		0	0	0	0	+	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	+	0	0			
7		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
8		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
9		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
10		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
11		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
12		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
13		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			
14		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0			

showed some affinities for vegetation.

Because accumulation of dead shells is passive to a variable extent in that winds and currents may redistribute dead shells, creating a graveyard effect, unpaired t-tests were used to test the significance of the difference of the mean numbers of land shells occurring in the samples from nonvegetated areas and those from each of the vegetated habitat types. Because presence of land shells in bottom sediments is the result of passive distribution, they served as ideal markers from which the degree of graveyard effect could be extrapolated, assuming that physical forces acted equally to distribute both land and aquatic shells. Land shells found in the samples belonged to the following taxa: Oxyloma retusa Lea, Nesovitrea electrina Gould, Zonitoides arboreus Say, Discus cronkhitei Newcomb, Vallonia spp., Vertigo spp. and Cionella lubrica Muller. These shells originated from the nonsubmerged lands immediately surrounding the ditch. The symbols in parentheses in Table V indicate significant tests which must be considered questionable on the basis of significantly ($p < .05$) high graveyard indices.

Unpaired t-tests for live snails in the samples (TABLE VB) showed general agreement with the results for dead shells, although some of the less frequent species failed to show significant tests because of their low numbers. Lymnaea stagnalis showed strong affinity for samples containing P. richardsonii, and secondarily for samples containing M. exalbescens. Physa gyrina showed some degree of seasonal affinity for all vegetation types, particularly for samples containing P. pectinatus and M. exalbescens. Fossaria modicella showed a tendency to occur in all vegetation types except samples

containing C. demersum. Helisoma trivolvis showed some affinity for samples containing P. pectinatus and C. demersum at time 6.

Up to this point, sample heterogeneity with respect to vegetation has been ignored. By examining the results of Table V in the light of Table II, several trends emerged:

1. Lymnaea stagnalis was significantly more frequent in P. richardsonii samples at times 3, 5 and 7; at these times these samples were indeed composed of a majority by weight of P. richardsonii. The significant affinity for M. exalbescens samples at time 7 may have been an affinity for the P. richardsonii present in these samples, since at this time these were composed of 77.7% by weight of P. richardsonii.
2. Physa gyrina was significantly more frequent in P. pectinatus samples at times 2 and 8; at these times P. pectinatus composed the majority by weight of these samples. The affinity for C. demersum samples at time 8 may have been an affinity for P. pectinatus which composed 58.5% of the vegetation by weight in these samples at time 8. Physa gyrina was significantly more frequent at time 3 in P. richardsonii samples; at this time P. richardsonii was the major species present in these samples, suggesting that affinity for this plant was also real. Significant affinity was also detected for M. exalbescens samples at time 3, when these samples contained P. richardsonii in the majority. At time 8, an affinity for M. exalbescens samples suggested that this plant was also important, since it composed the majority of the vegetation present in these samples at time 8.

3. Fossaria modicella was significantly more frequent in P. pectinatus samples at time 2, when these samples contained 58.3% by weight of this plant. Significant affinity for P. richardsonii samples at times 2 and 5 occurred when this species comprised 89.2% and 82.1% of these samples, respectively, suggesting that F. modicella tended to occur with this plant as well. An affinity for M. exalbescens samples at time 2 may have been an affinity for the P. richardsonii in these samples since the latter plant comprised 77.1% of these samples.
4. Helisoma trivolvis was significantly more frequent in P. pectinatus and C. demersum samples at time 6. At this time the former samples contained 71.3% and the latter 68.4% by weight of P. pectinatus.

These results did not discount the possibility that concurrent affinities existed as well for species present in the minority in the samples, but these could not be detected. The results were tested further by conducting unpaired t-tests internally among samples from the vegetated habitats in order to determine whether differential distributions could still be demonstrated among different vegetation types. These tests showed that Lymnaea stagnalis tended to occur significantly more frequently in samples containing P. richardsonii than in those containing P. pectinatus, particularly towards the end of the season. Physa gyrina tended to occur significantly more frequently in samples containing P. pectinatus than in those containing P. richardsonii during the population peak of this gastropod at time 4. The significant affinity of Physa gyrina for P. richardsonii samples that had been observed when compared with nonvegetated samples, became insignificant when compared with P. pectinatus samples. The distributions of

Fossaria modicella and Helisoma trivolvis agreed with the results outlined above for these species, although the affinities were less defined.

c. Live counts

When the plants began to reach the surface by time 3, live counts of snails present on different macrophytes were started. Results were examined using t-tests for the significance of the differences between sample proportions x_1/y_1 and x_2/y_2 where x represented the numbers of species a, the species under consideration, and y represented the total numbers of individuals of all species observed on the macrophyte species in question, i.e.,

$$\frac{x}{y} = \frac{N_a}{\sum_{k=1}^{n} N_k} \qquad \ldots\ldots\ldots (2).$$

The results (Table VI) showed that Physa gyrina tended to occur in significantly ($p < .05$) greater proportions on P. pectinatus as opposed to P. richardsonii during times 3, 4 and 6. Few individuals were observed on the plants at times 7 and 8, and at these times the distributions of this snail on these two macrophytes were not significantly different, agreeing in general with the results of the bottom sampling. At time 4 an occurrence of secondary importance on M. exalbescens was not significant when compared with P. pectinatus. Association with M. exalbescens was again evident at time 6, when breakdown of the association with P. pectinatus had commenced.

Lymnaea stagnalis was present in significantly greater

TABLE VI. Results of t-tests for the significance of the difference between sample proportions for live snails observed on different macrophytes at site 1. In the row and column headings, P = Potamogeton pectinatus, R = P. richardsonii, M = Myriophyllum exalbescens, C = Ceratophyllum demersum. Within the tables the letters indicate significantly ($p < .05$) higher proportions of snails on the macrophyte designated by the respective letter within each test pair; 0 indicates no significant difference and - indicates no observations of the particular snail species on either member of the plant test pair.

TIME	Lymnaea stagnalis	Stagnicola palustris	Fossaria modicella	Physa gyrina	Helisoma trivolvis
3	P: R - P R: - R M: -	P: R - 0 R: - R M: -	P: 0 - 0 R: - C M: -	P: P - C R: - C M: -	P: 0 - 0 R: - 0 M: -
4	P: R 0 - R: R - M: -	P: 0 0 - R: 0 - M: -	P: P 0 - R: M - M: -	P: P 0 - R: M - M: -	P: 0 0 - R: 0 - M: -
5	P: R 0 - R: 0 - M: -	P: 0 0 - R: 0 - M: -	P: 0 0 - R: 0 - M: -	P: 0 0 - R: 0 - M: -	P: 0 0 - R: 0 - M: -
6	P: R 0 0 R: R R M: 0	P: P 0 0 R: 0 C M: 0	P: 0 0 0 R: 0 C M: 0	P: P M P R: M 0 M: M	P: 0 - - R: 0 0 M: -
7	P: R M 0 R: 0 R M: M	P: P P 0 R: 0 C M: 0	P: - - 0 R: - 0 M: 0	P: 0 0 0 R: 0 0 M: 0	P: 0 0 0 R: - 0 M: 0
8	P: 0 0 - R: 0 - M: -	P: - - - R: - - M: -	P: - - - R: - - M: -	P: 0 - - R: 0 - M: -	P: - - - R: - - M: -

proportions on P. richardsonii than on P. pectinatus during times 3-7, agreeing with the results of the bottom sampling. A secondary occurrence on M. exalbescens at time 7 was not significant when compared with P. richardsonii.

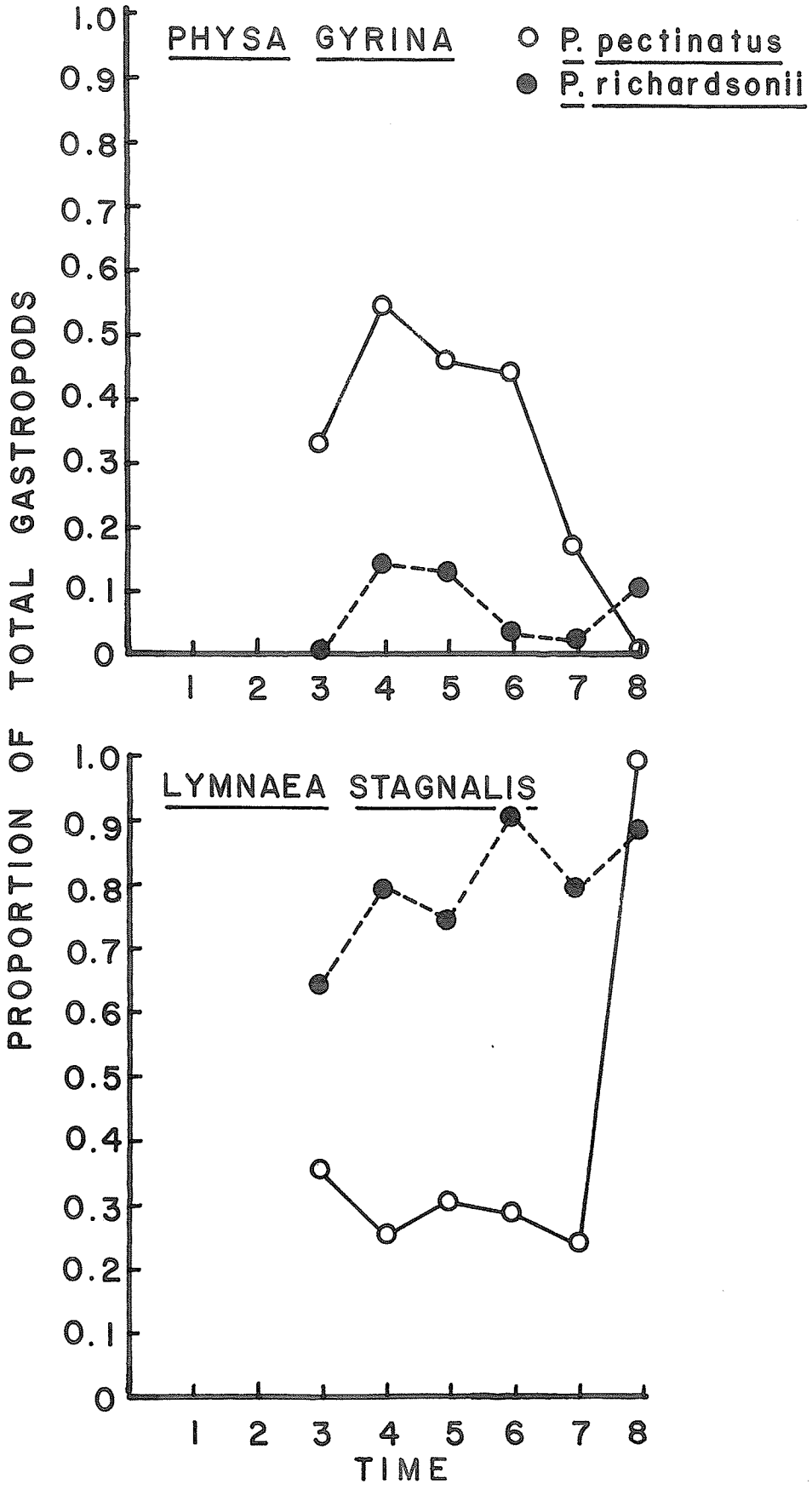
Physa gyrina and Lymnaea stagnalis together comprised the majority of the gastropods observed on the plants. The difference between the proportions of these snails in relation to the total gastropod fauna on P. pectinatus and P. richardsonii declined towards the end of the season (Fig. 14) as the host plants began to decay.

Fossaria modicella showed less pronounced affinities for particular macrophytes; a significantly greater proportion of this snail was present on P. pectinatus than on P. richardsonii at time 4, and a greater proportion was present on M. exalbescens than on P. richardsonii at this time, similar to the distribution of Physa gyrina. Stagnicola palustris showed an affinity for P. richardsonii at time 3, followed by a tendency to occur on P. pectinatus at times 6 and 7. Helisoma trivolvis showed no significant affinities, largely because of the small numbers observed.

The combined results from the bottom sampling and the live counts suggested the following common factors:

1. Lymnaea stagnalis was strongly associated with P. richardsonii during a large part of the growing season.
2. Physa gyrina was significantly associated with P. pectinatus during a restricted period when density was maximal; this period was preceded and succeeded by periods of reduced spatial differentiation.
3. Fossaria modicella, Stagnicola palustris and Helisoma trivolvis

Figure 14. Proportions of the total numbers of gastropods of all species comprised by Physa gyrina (upper) and Lymnaea stagnalis (lower) that were observed on shoots of Potamogeton pectinatus and P. richardsonii respectively at site 1 during the 1972 season.


PHYSA GYRINA
P. pectinatus
P. richardsonii
LYMNAEA STAGNALIS
PROPORTION OF TOTAL GASTROPODS
TIME
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1 2 3 4 5 6 7 8

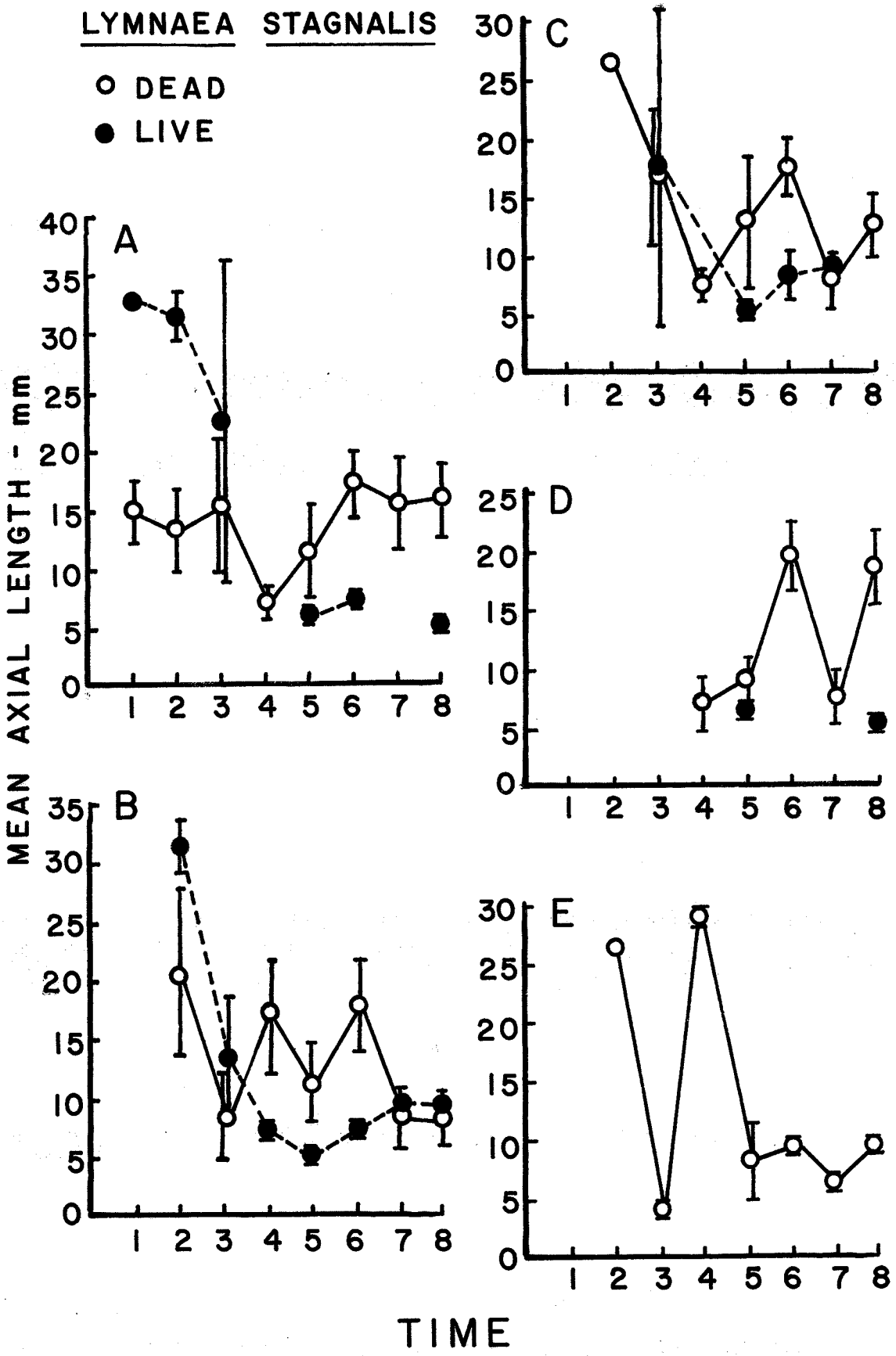
showed less pronounced affinities for specific macrophytes, and these appeared to be quite localized in time.

d. Size distribution patterns of gastropods

In order to examine the behavior of the respective populations more closely, the net flux of size distribution patterns was studied for both the live and dead gastropod populations.

Size distribution patterns for Lymnaea stagnalis (Fig. 15) showed that, in samples containing P. pectinatus, M. exalbsecens and C. demersum, a minimum value for mean axial length of dead shells occurred at time 4, while in P. richardsonii samples the first minimum was observed at time 3. These results, together with the sharp decrease observed for the live population after time 2 in the latter samples, suggested that hatching of the young was proportionally greater and began earlier in P. richardsonii stands. Crossover of mean length between live and dead populations was seen after time 3, indicating mortality of adults after reproduction, which resulted in a population composed largely of young. Secondary periods of hatching were evident from the decreased values observed for both live and dead shells at time 5 in P. richardsonii samples and at time 7 in all habitat types. Large standard errors for the live population were due to its variability and the small numbers of individuals that were collected. Size distributions of dead shells in nonvegetated samples most reflected those of P. richardsonii samples, suggesting that the latter pattern was numerically predominant, although the amplitudes of the fluctuations differed because of the smaller numbers of individuals that were present in the nonvegetated samples.

Figure 15. Mean axial length of dead and live individuals of Lymnaea stagnalis in subsamples containing Potamogeton pectinatus (A), P. richardsonii (B), Myriophyllum exalbescens (C), Ceratophyllum demersum (D) and those containing no vegetation (E) at site 1 during the 1972 season. Vertical bars represent standard errors.


LYMNAEA STAGNALIS
DEAD
LIVE
A
B
C
D
E
MEAN AXIAL LENGTH - mm
TIME

For Physa gyrina (Fig. 16), hatching of the first young in samples containing P. pectinatus appeared to have taken place after time 1, while in P. richardsonii and M. exalbescens samples hatching was not evident until after time 2. Mean axial length of both live and dead populations decreased in all vegetated samples until time 4, after which values for live individuals in P. pectinatus and C. demersum samples continued to decrease, while accompanied by an increase in mean length for dead shells in all samples, reflecting adult mortality. The large decrease at time 8 in P. pectinatus and C. demersum samples suggested a second period of reproduction. The patterns for the latter two habitat types were similar to a large extent because of sample overlap.

For Stagnicola palustris (Table VIIA), an initial decrease in mean axial length of dead shells was observed after time 1 in the three vegetated habitats for which values were available, and indicated the beginning of hatching. After time 2, mean length of dead shells in P. pectinatus and P. richardsonii samples was relatively stable until time 3, while in M. exalbescens and nonvegetated samples it had begun to increase. This reflected mortality of overwintered adults and was especially pronounced after time 4. A reduced second period of reproduction in the second half of the season was suggested by the moderate decrease in mean length observed at time 7 in all habitat types. Few live individuals of this species were collected.

Fossaria modicella (Table VIIB) showed a decrease in mean length in vegetated habitats after time 1, indicating the beginning of production of young which continued until midseason. Crossover of mean length between live and dead populations occurred between

Figure 16. Mean axial length of dead and live individuals of Physa gyrina in subsamples containing Potamogeton pectinatus (A), P. richardsonii (B), Myriophyllum exalbescens (C), Ceratophyllum demersum (D) and those containing no vegetation (E) at site 1 during the 1972 season. Vertical bars represent standard errors.

TABLE VII. Mean axial length of shells of dead and live individuals of Stagnicola palustris (A) and Fossaria modicella (B) present in bottom samples from the 5 habitat types. Values are in mm; values in parentheses represent standard errors.

A. Stagnicola palustris

DEAD

Time	P. pectinatus	P. richardsonii	M. exalbescens	C. demersum	nonvegetated
1	16.8 (0.9)	16.4 (0.9)	16.4 (0.9)	-	-
2	13.6 (1.0)	14.7 (1.1)	11.3 (1.0)	-	14.0 (2.8)
3	13.7 (1.3)	14.8 (1.3)	15.6 (1.4)	-	15.7 (2.1)
4	17.1 (1.6)	16.0 (1.2)	19.9 (1.7)	15.2 (1.7)	20.3 (4.4)
5	17.9 (1.2)	15.4 (1.0)	15.2 (1.2)	17.9 (1.8)	10.1 (1.2)
6	16.4 (1.1)	16.5 (1.9)	18.1 (1.2)	15.5 (0.9)	12.8 (0.9)
7	16.2 (1.2)	15.2 (1.4)	15.8 (1.5)	15.3 (1.5)	12.0 (2.0)
8	16.6 (2.0)	17.7 (1.6)	17.4 (1.3)	17.7 (1.7)	12.2 (2.5)

LIVE

1	-	-	-	-	-
2	13.0 (3.0)	20.0 (x)	-	-	-
3	10.0 (x)	20.5 (x)	-	-	-
4	-	-	-	-	-
5	-	-	-	10.0 (x)	-
6	13.8 (1.1)	-	-	13.8 (1.1)	-
7	-	-	-	-	-
8	-	-	-	-	-

B. Fossaria modicella

DEAD

Time	P. pectinatus	P. richardsonii	M. exalbescens	C. demersum	nonvegetated
1	6.7 (0.4)	7.1 (0.9)	7.1 (0.9)	-	-
2	5.0 (0.2)	5.0 (0.3)	4.9 (0.3)	-	4.7 (0.5)
3	3.9 (0.2)	3.6 (0.1)	3.5 (0.2)	-	4.5 (0.4)
4	3.8 (0.2)	4.4 (0.2)	4.3 (0.3)	3.7 (0.3)	6.5 (1.0)
5	3.3 (0.3)	4.5 (0.2)	3.3 (0.4)	4.5 (0.4)	4.6 (0.4)
6	4.3 (0.2)	3.5 (0.3)	4.1 (0.2)	4.3 (0.2)	5.1 (0.3)
7	4.8 (0.2)	3.8 (0.2)	4.0 (0.2)	5.4 (0.4)	5.3 (0.9)
8	5.0 (0.4)	5.1 (0.3)	4.5 (0.3)	5.2 (0.4)	6.6 (0.9)

LIVE

1	-	-	-	-	-
2	6.3 (1.0)	5.4 (0.9)	7.2 (0.7)	-	-
3	-	-	-	-	-
4	7.5 (0)	7.5 (0)	-	7.5 (0)	-
5	4.3 (2.8)	1.9 (0.2)	1.5 (0)	6.8 (3.3)	-
6	2.5 (x)	2.7 (0.4)	2.7 (0.4)	2.5 (x)	-
7	3.0 (x)	2.5 (x)	2.5 (x)	-	-
8	-	2.0 (x)	-	-	-

times 4 and 6 in all vegetated habitats, indicating that the bulk of adult postreproductive mortality occurred during this period.

Initial reproduction of Helisoma trivolvis (Table VIIIA) was evident after time 2, while adult mortality occurred largely during times 4 to 5. After time 5 a second period of hatching was observed whose effects persisted in the dead shell population until time 7 in P. pectinatus and C. demersum samples. Few intact live individuals of this species were collected.

Gyraulus parvus (Table VIIIB) was included because it comprised a large portion of the total dead shell population. For this species, the effects of the appearance of the young of the year were evident in the dead shell population after time 2. Mean shell diameter reached a maximum during midseason; this was followed by another decrease which indicated a second period of reproduction. Due to the small size of this species, net changes were less pronounced and many young were lost during processing of the samples since all material less than 2 mm in size was discarded.

TABLE VIII. Mean maximum diameter (mm) of shells of dead and live individuals of Helisoma trivolvis (A) and Gyraulus parvus (B) present in bottom samples from the 5 habitat types. Values in parentheses represent standard errors.

A. Helisoma trivolvis

DEAD

Time	P. pectinatus	P. richardsonii	M. exalbescens	C. demersum	nonvegetated
1	-	-	-	-	-
2	6.5 (1.8)	4.5 (x)	11.5 (x)	-	-
3	6.9 (1.0)	5.8 (1.3)	4.0 (2.5)	-	7.2 (0.8)
4	2.9 (0.5)	2.0 (0.6)	8.8 (5.3)	3.8 (1.2)	-
5	9.5 (3.4)	6.2 (2.9)	10.8 (7.9)	13.0 (4.8)	-
6	6.8 (1.3)	1.8 (0.3)	6.9 (1.1)	6.4 (2.2)	5.0 (x)
7	2.0 (0)	12.5 (6.2)	23.3 (0.3)	2.0 (x)	4.5 (x)

LIVE

1	-	-	-	-	-
2	-	22.5 (1.5)	22.5 (1.5)	-	-
3	-	-	-	-	-
4	-	-	-	-	-
5	-	-	-	-	-
6	16.6 (1.5)	13.5 (x)	20.5 (x)	16.6 (1.5)	-
7	-	-	-	-	-
8	-	-	-	-	-

B. Gyraulus parvus

DEAD

Time	P. pectinatus	P. richardsonii	M. exalbescens	C. demersum	nonvegetated
1	2.2 (0.2)	-	-	-	-
2	2.2 (0.1)	2.6 (0.1)	2.3 (0.1)	-	3.3 (0.3)
3	2.2 (0.1)	2.1 (0.1)	2.1 (0.1)	-	2.5 (0.5)
4	2.0 (0.1)	1.9 (0.1)	2.2 (0.1)	2.0 (0.1)	2.1 (0.2)
5	1.8 (0.1)	2.0 (0.1)	2.4 (0.3)	1.9 (0.1)	2.4 (0.3)
6	2.0 (0.1)	2.1 (0.1)	2.0 (0.1)	2.0 (0.1)	2.3 (0.2)
7	2.0 (0.1)	2.0 (0.1)	2.1 (0.1)	2.1 (0.2)	1.6 (0.1)
8	2.5 (0.5)	2.0 (0.2)	3.0 (x)	2.5 (0.5)	1.5 (0)

LIVE

1	-	-	-	-	-
2	2.0 (x)	3.0 (x)	3.0 (x)	-	-
3	-	-	-	-	-
4	-	-	-	-	-
5	-	-	-	-	-
6	-	-	-	-	-
7	-	-	-	-	-
8	-	-	-	-	-

B. Site 5

a. Vegetation

The first order shoots of Myriophyllum exalbescens at site 5 (Fig. 17A) had reached the surface and the first inflorescences had appeared by time 4. Second and subsequent order shoots were progressively shorter because of falling water levels; increasing standard errors reflected the increasing variability of shoot lengths as samples included shoots of different orders. The growth pattern at this site was not correlated with that of M. exalbescens at site 1 (Fig. 7B).

The mean dry weight of individual shoots of M. exalbescens increased from an initial mean value of 0.07 g at time 1 to a maximum of 0.70 g at time 7; at time 8 this value was only 0.49 g due to deterioration of older shoots, incomplete maturity of younger shoots and possibly grazing. The maximum mean dry weight of this macrophyte was approximately twice that observed at site 1. Of the total bottom samples collected, 13-20% contained no vegetation.

b. Density of live and dead molluscs

Because Lymnaea stagnalis was represented by only one dead individual collected during the entire season, this species was not believed to be a normal component of the fauna at this site. Stagnicola palustris (Fig. 18A-B) was present in moderate numbers and live and dead populations, respectively, in both vegetated and nonvegetated samples showed similar density patterns. These in turn were similar to the pattern observed for dead shells in M. exalbescens samples at site 1 (Fig. 9C) in that peaks occurred at times 3 and 5, although

Figure 17. Mean shoot length (cm) of Myriophyllum exalbescens at site 5 (A) and Potamogeton pectinatus at site 6 (B) during the 1972 season. Disjunctions in the curves are due to different shoot generations. Vertical bars represent standard errors.

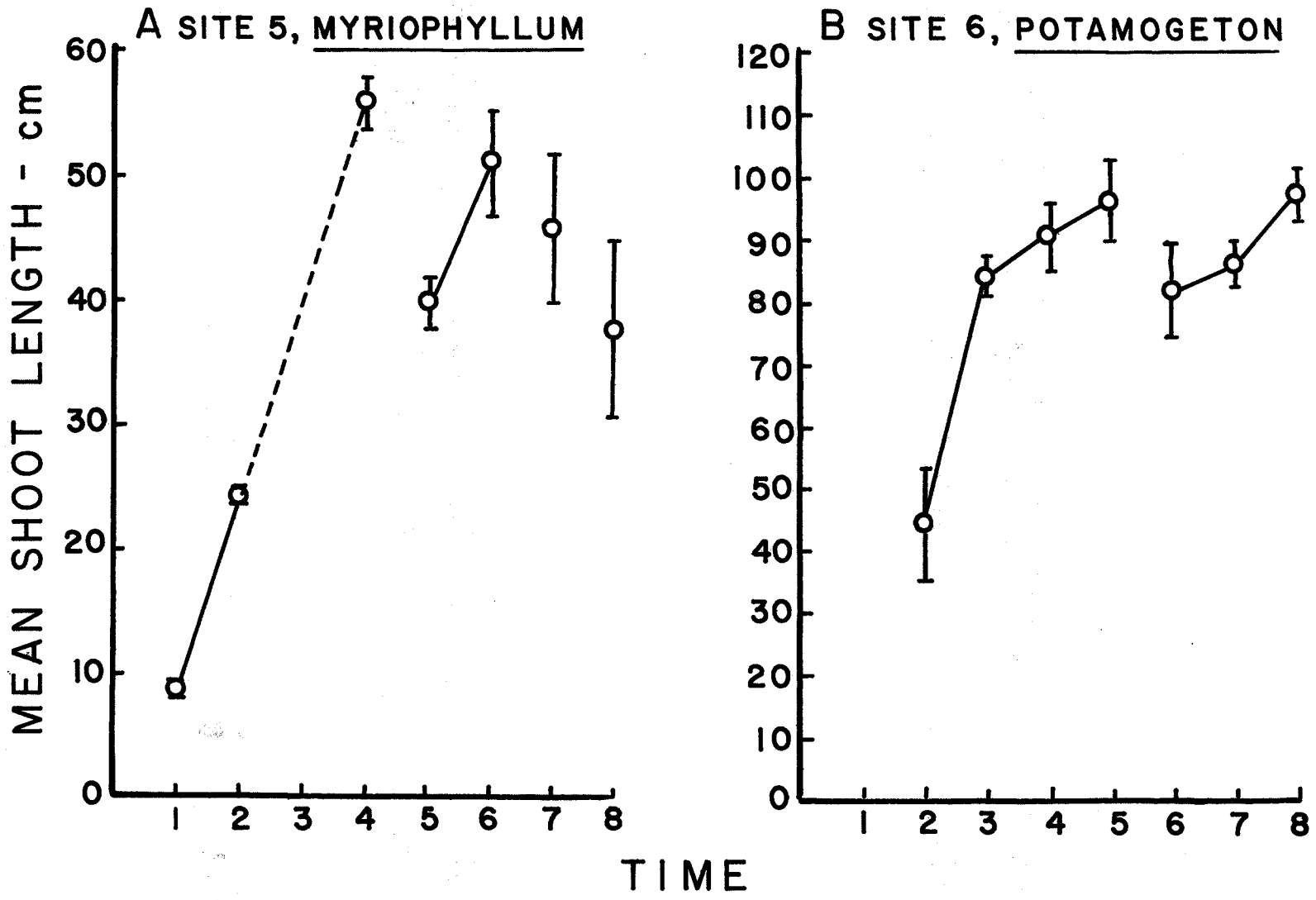

A SITE 5, MYRIOPHYLLUM
B SITE 6, POTAMOGETON
MEAN SHOOT LENGTH - cm
TIME
0
10
20
30
40
50
60
70
80
90
100
110
120
1
2
3
4
5
6
7
8

Figure 18. Mean densities of dead and live individuals of Stagnicola palustris (A and B), Fossaria modicella (C and D) and Physa gyrina (E and F) in vegetated and nonvegetated subsamples (78.5 cm^2 bottom area) respectively at site 5 during the 1972 season. Vertical bars represent standard errors.

the former peak at site 5 was questionable because of the large standard error. In general, density of dead S. palustris at site 1 was more than twice that at site 5. However densities of live individuals were comparable in magnitude at the two sites; therefore dead shells of this species persisted twice as long at site 1.

Mean density of dead individuals of Fossaria modicella (Fig. 18C-D) showed maxima at times 3 and 7 in vegetated samples, while live individuals showed a peak at time 7 and occurred in greater numbers in vegetated areas. For M. exalbescens samples at site 1 (Fig. 10C), the first peak for dead shell densities also occurred at time 3 but the second peak occurred at time 6. Density peaks for live individuals at site 1 occurred earlier than at site 5, i.e. at times 2 and 6. Densities of both live and dead individuals of F. modicella at Site 5 were approximately one-third of those observed in M. exalbescens samples at site 1, suggesting that rates of disintegration of dead shells of this species were similar at both sites.

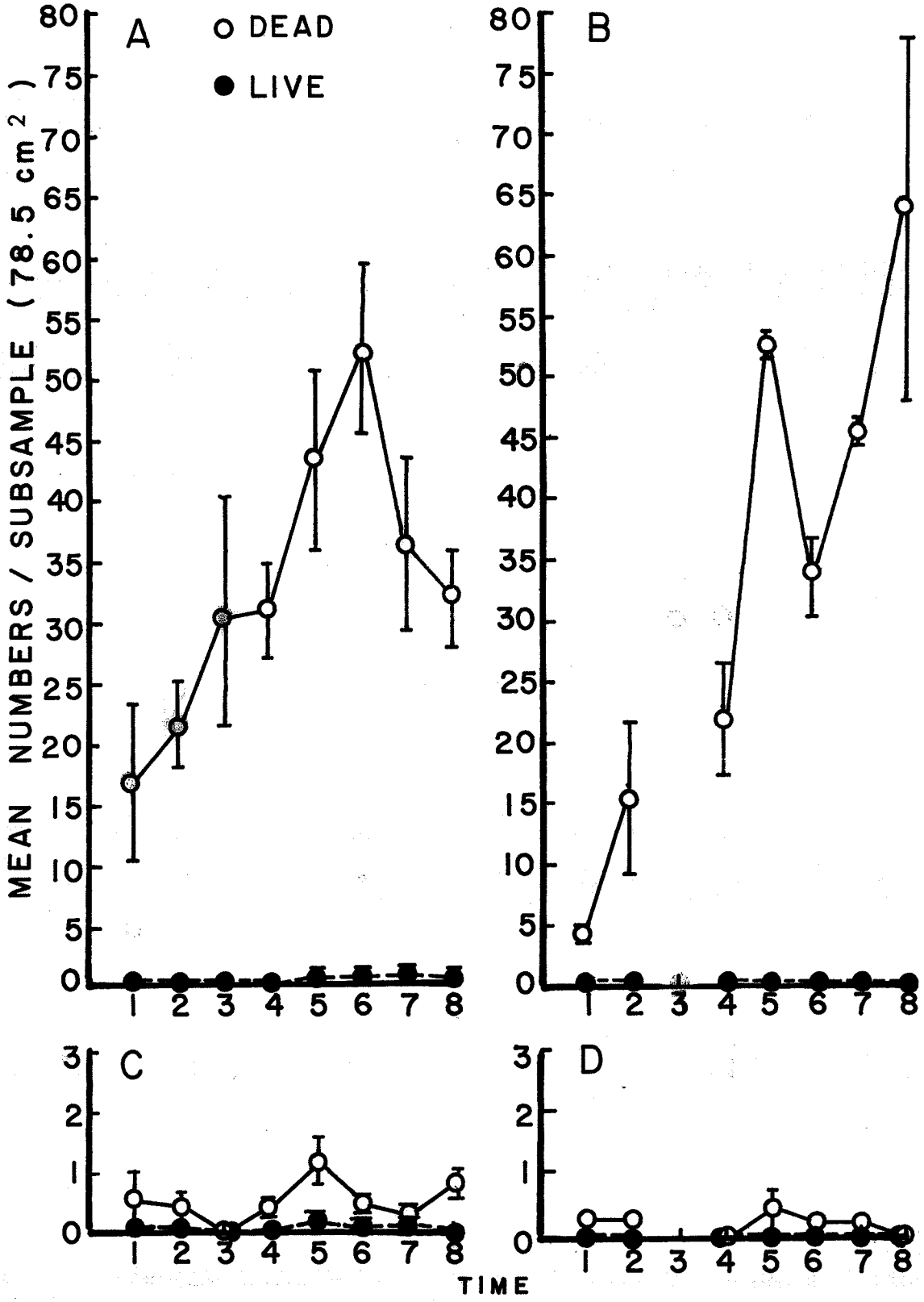
Mean density of dead shells of Physa gyrina (Fig. 18E-F) showed increasing values until a maximum at time 7. Greater numbers of shells accumulated in vegetated areas. Live individuals showed an initial peak at time 3 in vegetated samples which was followed by a slight decline at time 4. During times 5 to 7, the population underwent a period of geometric growth where the density doubled every two weeks. A decrease was observed after time 7. The density pattern of dead shells with time at site 5 bore little resemblance to that seen in M. exalbescens samples at site 1 (Fig. 11C), although live individuals at both sites showed a peak at time 3 and a late-season increase at

time 7. The density of dead shells at site 5 was approximately twice that of M. exalbescens samples at site 1 while density of live individuals at site 5 was 6-24 times as great, suggesting that shells of Physa disappeared 3-12 times more quickly at site 5. Shells of this species had the shortest half-life of all gastropod shells present in the sediments at this site.

Mean density of dead shells of Gyraulus parvus (Fig. 19A-B) showed a peak at time 6 in vegetated areas and at times 5 and 8 in nonvegetated samples. The reduced rate of increase between times 3 and 4 corresponded to the peak at time 3 in M. exalbescens samples at site 1 (Fig. 12C); subsequent peaks were observed at time 6 at both sites. At site 1 a peak in live population density was observed at time 2 while at site 5 it occurred during the latter half of the season. Density of dead shells at site 5 was 3-5 times as great as that at site 1 while density of live individuals was similar at both sites, suggesting that dead shells of this species persisted longer at site 5. A proportion of the dead shells of this species present in the samples did not originate during the current season on account of the longevity of this species in the sediments.

For Helisoma trivolvis (Fig. 19C-D), a peak in both live and dead shell densities was observed at time 5. At site 1, maximum dead shell density in M. exalbescens samples occurred at times 5 and 6, while maximum density of live snails was observed at times 2 and 6. The magnitude of density values for both live and dead shells was similar at both sites, suggesting that deterioration of dead shells proceeded at approximately equal rates at the two sites.

Figure 19. Mean densities of dead and live individuals of Gyraulus parvus (A and B) and Helisoma trivolvis (C and D) in vegetated and nonvegetated subsamples (78.5 cm^2 bottom area) respectively at site 5 during the 1972 season. Vertical bars represent standard errors.


A
B
C
D
O DEAD
● LIVE
MEAN NUMBERS / SUBSAMPLE (78.5 cm²)
TIME
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
1
2
3
4
5
6
7
8

Density of dead shells of Promenetus exacuous (Fig. 20A-B) showed a small peak at time 2 and a major peak at time 5. Nonvegetated samples showed consistently higher densities than vegetated samples. At site 1, this species also showed a peak at time 5 in M. exalbescens samples (Fig. 13H). Dead shells were up to 15 times more frequent at site 5 but no live individuals were collected.

Armiger crista (Fig. 20C-D) showed a density distribution pattern that was similar to that of P. exacuous; densities of this species were higher in nonvegetated samples. Dead shells were up to 45 times more frequent at site 5 than at site 1 but no live individuals were collected. Planorbula armigera was observed only at time 2 in nonvegetated samples and no live individuals were observed.

Dead shells of Valvata tricarinata (Fig. 20E-F) showed similar values for density at both sites 1 and 5 although timing of the peaks did not coincide. Live individuals showed peak densities at times 4 and 6 in vegetated samples at site 5.

A peak occurred at time 5 for densities of dead shells of Amnicola limosa (Fig. 20G-H) which was preceded by a peak at time 4 for live individuals in nonvegetated samples. This distribution was not correlated with that observed at site 1 (Table IIIC). A Pisidium sp. occurred sporadically but was very rare.

The mean relative densities of dead shells in the sediment samples (Table IXA) showed that Gyraulus parvus occurred in the greatest numbers in both vegetated and nonvegetated areas. Physa gyrina was the next most frequent species and showed higher relative densities in vegetated samples, with a peak at time 7. Beyond this

Figure 20. Mean densities of dead and live individuals of Promenetus exacuous (A and B), Armiger crista (C and D), Valvata tricarinata (E and F) and Amnicola limosa (G and H) in vegetated and nonvegetated subsamples (78.5 cm^2 bottom area) respectively at site 5 during the 1972 season. Vertical bars represent standard errors.

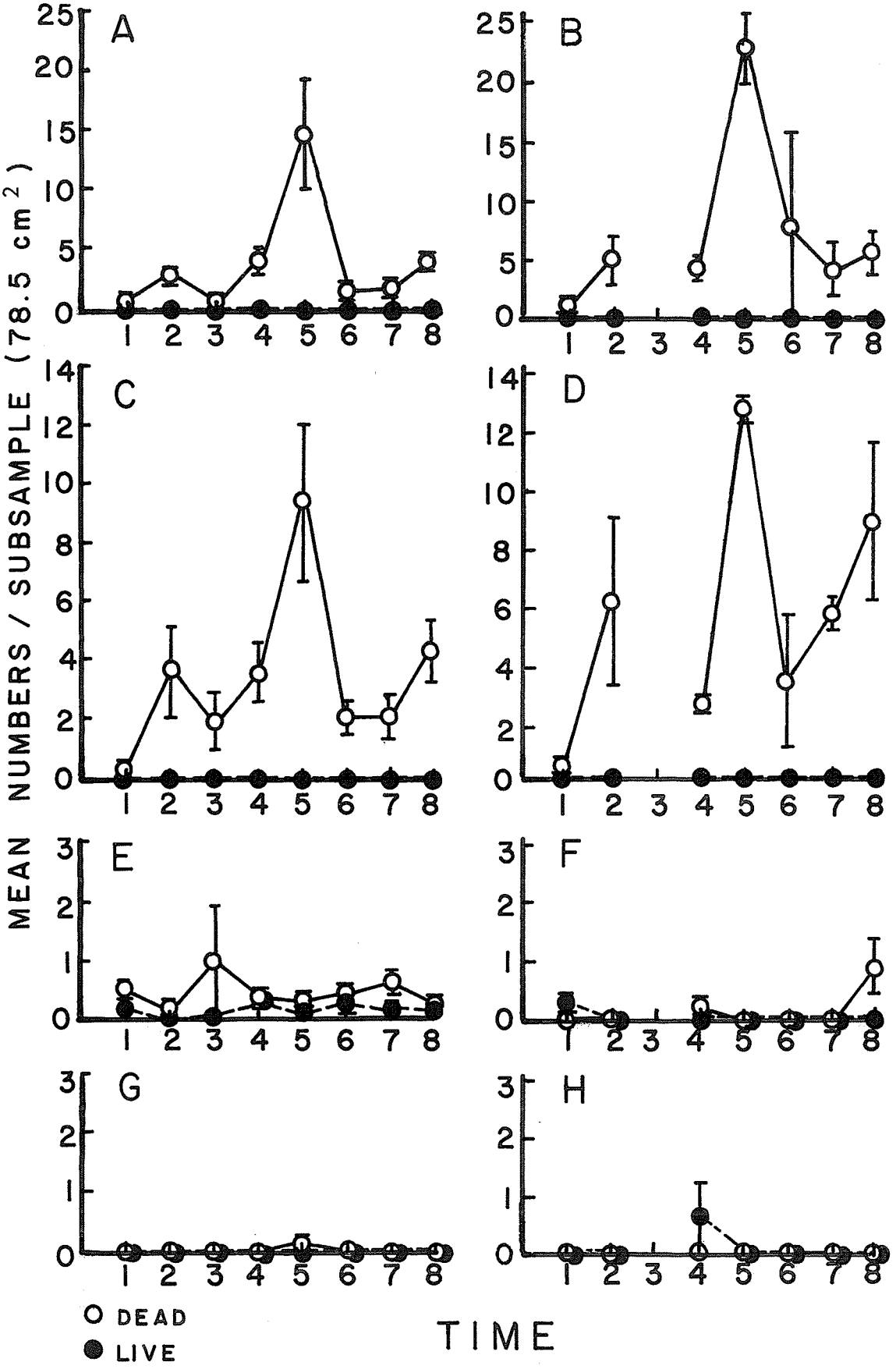

A
B
C
D
E
F
G
H
MEAN NUMBERS / SUBSAMPLE (78.5 cm²)
TIME
O DEAD
● LIVE

TABLE IX. Mean relative density per unit bottom area for dead (A) and live (B) molluscs at site 5 expressed as a percent of the total numbers of all species present in vegetated and nonvegetated samples, respectively. Species numbers represent the following taxa:

1. Lymnaea stagnalis
2. Stagnicola palustris
3. Fossaria modicella
4. Physa gyrina
5. Helisoma trivolvis
6. Gyraulus parvus
7. Planorbula armigera
8. Promenetus exacuous
9. Armiger crista
10. Amnicola limosa
11. Valvata tricarinata
12. Pisidium sp.

TABLE IX.

A. DEAD

	MYRIOPHYLLUM EXALBESCENS SAMPLES								SAMPLES FROM BARE AREAS							
Species Time	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	0	0	0	0	0	0	0	0.1	0	0	-	0	0	0	0	0
2	0.9	1.5	2.6	0.9	1.4	0.4	0.6	0.3	3.3	1.0	-	2.1	1.3	0.4	0.4	0
3	10.6	6.6	12.9	6.6	6.8	7.0	9.4	6.4	6.7	5.0	-	7.5	3.1	5.4	6.2	4.4
4	37.9	23.8	25.9	26.6	23.3	39.5	48.2	39.9	19.9	11.4	-	29.4	16.4	32.7	28.6	20.9
5	1.3	1.0	0	0.6	1.1	0.4	0.3	1.0	3.3	1.0	-	0	0.4	0.4	0.4	0
6	44.5	50.6	52.6	51.1	42.5	48.5	36.5	40.2	46.9	46.0	-	45.9	47.1	45.1	52.9	59.8
7	0	0	0	0	0	0	0	0	0	3.0	-	0	0	0	0	0
8	2.6	7.0	0.9	7.4	15.2	1.8	2.1	6.1	10.0	14.9	-	8.9	20.5	10.8	5.0	5.7
9	0.9	9.1	3.4	6.1	9.4	1.9	2.2	5.6	10.0	17.7	-	5.5	11.2	4.6	6.5	8.2
10	0	0	0	0	0.1	0	0	0	0	0	-	0	0	0	0	0
11	1.3	0.4	1.7	0.7	0.2	0.5	0.7	0.3	0	0	-	0.7	0	0	0	1.0
12	0	0	0	0	0	0	0	0.1	0	0	-	0	0	0	0	0
B. LIVE	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0
2	0	0	0	0	2.0	1.8	2.5	0	0	0	-	0	0	0	40.1	0
3	0	0	0	19.8	29.5	16.8	11.2	4.1	0	0	-	0	0	100.0	19.8	0
4	0	0	100.0	76.0	62.1	77.2	83.7	94.7	50.0	0	-	33.3	100.0	0	40.1	100.0
5	0	0	0	0	2.0	0.6	0.2	0	0	0	-	0	0	0	0	0
6	0	0	0	0	2.9	1.8	1.9	0.4	0	0	-	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	-	66.7	0	0	0	0
11	0	0	0	4.2	1.5	1.8	0.5	0.8	50.0	100.0	-	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0

point the order in which subsequent species occurred differed between vegetated and nonvegetated samples.

In vegetated samples, Fossaria modicella was the third most frequent species, followed consecutively by Promenetus exacuous, Armiger crista, Stagnicola palustris, Helisoma trivolvis, Valvata tricarinata, Amnicola limosa and Pisidium sp. In nonvegetated samples, the third most frequent species was Promenetus exacuous, followed by Armiger crista, Fossaria modicella, Stagnicola palustris, Helisoma trivolvis, Planorbula armigera and Valvata tricarinata. Amnicola limosa and Pisidium sp. were not observed in the latter samples, while Planorbula armigera was not present in the former.

Among live molluscs (Table IXB), Physa gyrina was the most frequent species in all samples, followed by Fossaria modicella and Valvata tricarinata. In vegetated samples, the remainder of the live fauna was made up of Gyraulus parvus, Stagnicola palustris and Helisoma trivolvis. In nonvegetated samples the only other live individuals present were those of Amnicola limosa and Stagnicola palustris. The 100% values for relative density for some species in the nonvegetated samples were due to the occurrence therein of single live individuals of only that species.

The order of frequency in which species occurred was not the same for live and dead molluscs because of the varying rates at which shells of different species were destroyed in the sediments. As at site 1, the small planorbids such as Gyraulus parvus and Armiger crista appeared to persist for the longest period of time.

In order to determine whether any significant distributional differences existed between vegetated and nonvegetated samples,

unpaired t-tests were conducted to examine the significance of the difference between the two types of sample means. Among the dead shell fauna (Table XA), Fossaria modicella, Physa gyrina, Helisoma trivolvis and Valvata tricarinata showed significant ($p < .05$) positive tendencies to occur in samples containing vegetation; Gyraulus parvus showed a positive tendency at times 2 and 6 but a negative tendency at time 8. Stagnicola palustris, Planorbula armigera and Armiger crista each showed a significant negative tendency to accumulate in vegetated areas at a single point in time.

Land shells present in the sediment samples from site 5 belonged to the taxa Oxyloma retusa Lea and Vertigo spp. Graveyard indices (see p. 58) were estimated for the land shells using unpaired t-tests to test the significance of the difference between the mean numbers present in vegetated and nonvegetated samples. The symbols in parentheses in Table X indicate significant tests which must be considered questionable on the basis of significantly ($p < .05$) high graveyard indices.

Unpaired t-tests conducted for live snails (Table XB) showed that Physa gyrina and Fossaria modicella were significantly associated with vegetated areas during much of the growing season. Valvata tricarinata showed a positive tendency to occur in vegetated areas at times 4 and 6 while Stagnicola palustris and Gyraulus parvus both showed a positive tendency at time 6. These results agreed with those from site 1, where both live and dead Physa gyrina and Fossaria modicella showed a greater tendency to occur in samples containing M. exaltbescens than did any other mollusc species except Lymnaea stagnalis (Table V) although these samples were composed largely of

TABLE X. Results of unpaired t-tests for the significance of the difference of mean densities per unit bottom area of dead (A) and live (B) molluscs between vegetated and nonvegetated habitats at sites 5 and 6 during 1972. Symbols indicate: + = significantly ($p < .05$) greater values in vegetated than in nonvegetated samples, 0 = no significant difference, - = significantly ($p < .05$) greater values in nonvegetated than in vegetated samples. Values in parentheses denote tests for which graveyard indices were significantly ($p < .05$) high. Species numbers represent the following taxa:

Site 5

1. Lymnaea stagnalis
2. Stagnicola palustris
3. Fossaria modicella
4. Physa gyrina
5. Helisoma trivolvis
6. Gyraulus parvus
7. Planorbula armigera
8. Promenetus exacuous
9. Armiger crista
10. Amnicola limosa
11. Valvata tricarinata
12. Pisidium sp.

Site 6

1. Lymnaea stagnalis
2. Stagnicola palustris
3. Fossaria modicella
4. Physa gyrina
5. Ferrissia rivularis
6. Gyraulus parvus
7. Planorbula armigera
8. Promenetus exacuous
9. Armiger crista
10. Amnicola limosa and A. (=Probythinella) lacustris
11. Valvata tricarinata
12. Pisidium casertanum

TABLE X.

A. DEAD

Species	Time	SITE 5								SITE 6							
		1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2		0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0
3		0	0	0	0	+	+	0	0	0	0	+	0	0	+	0	0
4		0	+	0	0	0	+	+	0	0	0	0	0	0	0	0	0
5		0	0	+	0	0	0	+	0	0	0	0	0	0	0	0	0
6		0	+	0	0	+	0	-	0	(+)	+	0	0	+	+	+	0
7		0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8		0	0	0	0	0	0	0	0	0	0	+	0	+	0	0	0
9		0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0
10		0	0	0	0	0	0	0	0	0	+	+	+	+	0	+	0
11		0	0	0	(+)	+	+	0	0	0	0	0	0	+	+	0	0
12		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

B. LIVE

Species	Time	SITE 5								SITE 6							
		1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2		0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0
3		0	0	+	+	+	+	+	0	0	0	0	0	0	0	0	0
4		0	0	+	+	+	+	+	0	0	0	0	0	0	0	0	0
5		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6		0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0
7		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10		0	0	0	0	0	0	0	0	0	0	0	0	+	+	+	0
11		0	0	+	0	+	0	0	0	0	0	0	0	0	0	0	0
12		0	0	0	0	0	0	0	0	+	+	0	+	0	+	+	0

Potamogeton richardsonii.

Essentially the following features were seen at site 5:

1. Lymnaea stagnalis was absent.
2. Physa gyrina and Fossaria modicella showed significantly high tendencies to occur in samples containing M. exalbescens as opposed to those from bare areas. These tendencies persisted during a large part of the growing season.
3. Valvata tricarinata, Gyraulus parvus and Stagnicola palustris showed less pronounced but still significant tendencies to occur in samples containing M. exalbescens but these were more restricted in time.

c. Size distribution patterns of gastropods

The mean axial length of dead shells of Physa gyrina (Fig. 21) decreased in both vegetated and nonvegetated habitats after time 1 and again after time 3 due to influx of young into the population. Live snails in vegetated areas showed a midseason maximum at time 4; subsequent decrease of mean axial length was due to increasing numbers of young as well as to mortality of adults. The structure of the live population in vegetated areas, represented by the frequency-time surface in Fig. 22, showed a progressive reduction of adults toward the end of the season; the sharp peaks at times 6 and 7 indicated that the bulk of the population was then made up of the young of the year. The peak evident at time 7 had advanced to the next higher size classes by time 8, but its base was broader because of the continued influx of young and its amplitude was diminished because of mortality. Similarly the peak at time 6 had recruited upwards to comprise much

Figure 21. Mean axial length of dead and live individuals of Physa gyrina in vegetated (A) and nonvegetated (B) subsamples at site 5 during the 1972 season. Vertical bars represent standard errors.

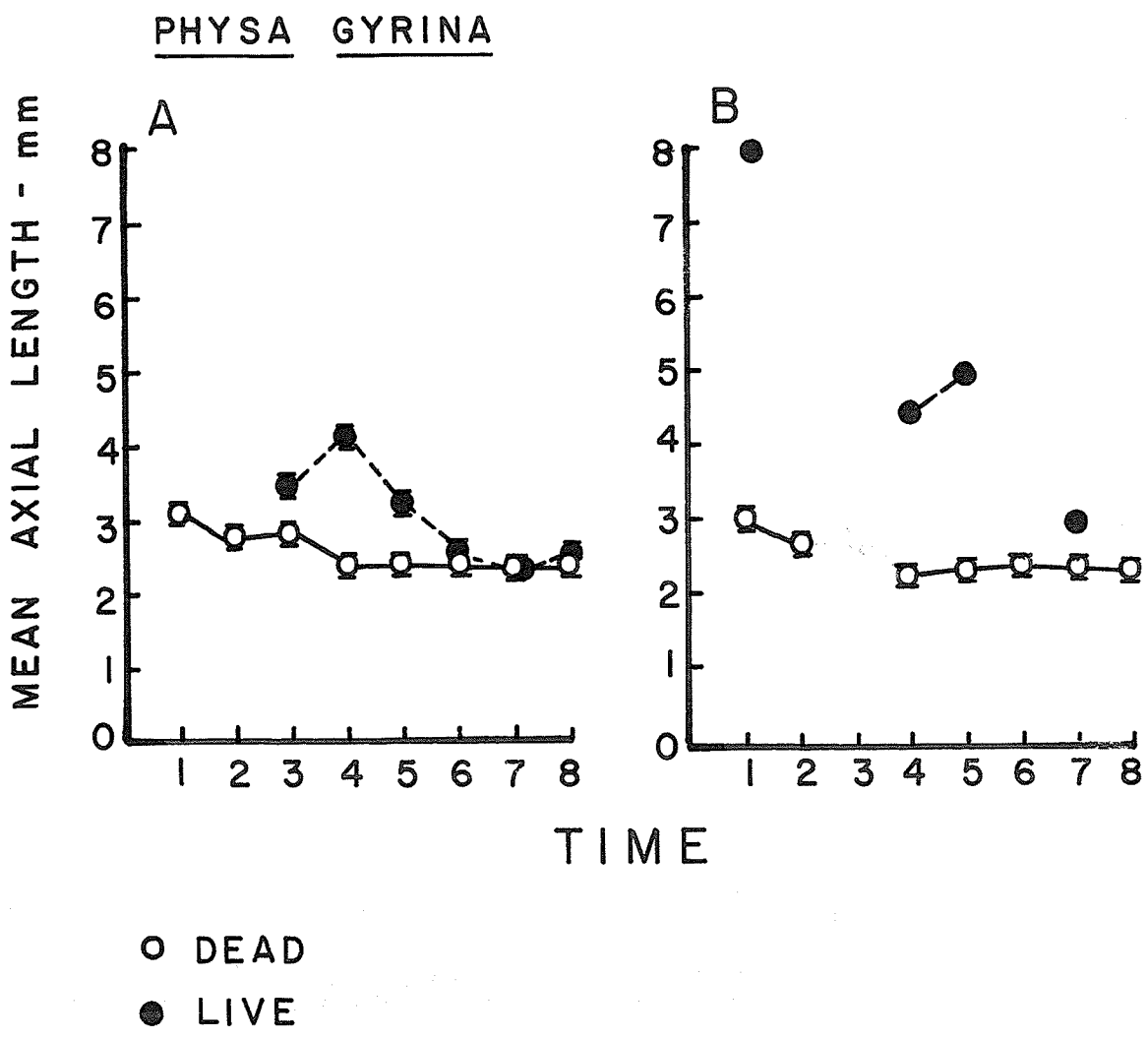

PHYSA GYRINA
A
B
MEAN AXIAL LENGTH - mm
0
1
2
3
4
5
6
7
8
TIME
O DEAD
● LIVE

Figure 22. Frequency-time surface for live Physa gyrina populations from vegetated subsamples at site 5 during the 1972 season. Size classes were constructed at 0.5 mm intervals.

of the outward flank of the peak at time 7. Since population growth during times 5-7 followed a geometric progression, essentially the population was expanding without limitations until time 8, when perhaps declining temperature, photoperiod and decreasing food supply as well as crowding caused reproduction to decline.

For Fossaria modicella (Table XIA), mean axial length of dead shells in vegetated areas showed two periods of decline, after times 3 and 6, indicating addition of young to the population. As with Physa, mean axial length of the live population was greater than that of the dead population because the latter contained cumulative numbers of young which predominated in the sediments on account of high fecundity and high mortality.

Dead shells of Stagnicola palustris (Table XIB) showed minima in mean axial length at times 2, 4 and 7, indicating appearance of young. Helisoma trivolvis (Table XIC) showed a relatively high mortality of young, since the latter predominated in the dead shell fauna at times 2 and 6. Live individuals of both of these species were collected only during the second half of the season.

Gyraulus parvus (Table XID) showed an initial decrease in mean diameter of dead shells after time 1, with subsequent continued decrease to a minimum at time 5, reflecting the influx of young. Promenetus exacuous (Table XIIA) showed evidence of hatching after times 2 and 6 but no live individuals were collected. The mean shell diameter of Armiger crista (Table XIIB) appeared to remain relatively constant throughout the season, but this was not believed to reflect the entire population. The young of the latter three species were not

TABLE XI. Mean axial length or mean diameter (mm) of shells of dead and live individuals of Fossaria modicella (A), Stagnicola palustris (B), Helisoma trivolvis (C) and Gyraulus parvus (D) present in vegetated and nonvegetated samples, respectively, from site 5. Values in parentheses represent standard errors.

A. Fossaria modicella

Time	DEAD M. exalbescens	DEAD nonvegetated
1	3.7 (0.3)	8.0 (x)
2	3.3 (0.3)	3.3 (0.5)
3	2.8 (0.4)	-
4	2.7 (0.2)	4.1 (1.0)
5	2.9 (0.3)	1.9 (0.3)
6	3.4 (0.2)	2.4 (0.3)
7	3.1 (0.2)	3.9 (0.9)
8	3.4 (0.3)	3.4 (1.3)
	LIVE	
1	-	-
2	-	-
3	-	-
4	4.6 (0.4)	-
5	4.6 (0.4)	-
6	5.1 (0.5)	-
7	4.9 (0.4)	9.5 (x)
8	5.1 (1.0)	-

B. Stagnicola palustris

	DEAD M. exalbescens	DEAD nonvegetated
1	16.5 (1.5)	-
2	11.6 (1.1)	15.8 (0.8)
3	16.0 (2.8)	-
4	11.8 (0.9)	16.5 (x)
5	13.2 (1.7)	8.0 (x)
6	18.9 (3.7)	18.0 (x)
7	13.1 (0.9)	-
8	-	-
	LIVE	
1	-	-
2	-	-
3	-	-
4	-	-
5	11.5 (0.5)	-
6	13.0 (x)	-
7	11.4 (1.1)	13.0 (2.0)
8	-	-

C. Helisoma trivolvis

Time	DEAD M. exalbescens	DEAD nonvegetated
1	-	-
2	2.0 (0)	2.5 (x)
3	-	-
4	2.7 (0.2)	-
5	3.7 (0.7)	-
6	2.0 (0)	-
7	5.8 (2.9)	-
8	5.0 (1.4)	-
	LIVE	
1	-	-
2	-	-
3	-	-
4	-	-
5	9.0 (x)	-
6	10.0 (x)	-
7	13.0 (x)	-
8	-	-

D. Gyraulus parvus

	DEAD M. exalbescens	DEAD nonvegetated
1	2.7 (0.1)	3.7 (x)
2	2.3 (0.1)	2.4 (0.1)
3	2.2 (0.1)	-
4	2.0 (0)	2.0 (0.1)
5	2.0 (0)	2.0 (0)
6	2.1 (0)	1.8 (0.1)
7	2.1 (0.1)	2.3 (0.2)
8	-	-
	LIVE	
1	-	-
2	-	-
3	-	-
4	2.0 (x)	-
5	2.4 (0.3)	-
6	2.5 (0.3)	-
7	2.0 (0.2)	-
8	-	-

TABLE XII. Mean diameter of shells of dead Promenetus exacuous (A) and Armiger crista (B) present in vegetated and nonvegetated samples, respectively, from site 5. Values are in mm; values in parentheses represent standard errors.

A. Promenetus exacuous DEAD			B. Armiger crista DEAD	
Time	M. exalbescens	nonvegetated	M. exalbescens	nonvegetated
1	2.1 (0.2)	2.3 (0.8)	1.8 (0.1)	1.5 (0)
2	3.0 (0.2)	2.9 (0.3)	1.9 (0.1)	1.8 (0.1)
3	2.0 (x)	-	1.6 (0.1)	-
4	2.3 (0.1)	2.6 (0.2)	1.7 (0.1)	2.0 (0.1)
5	2.2 (0.1)	2.4 (0.2)	1.7 (0)	1.6 (0.1)
6	2.5 (0.3)	2.6 (0.3)	1.7 (0.1)	1.8 (0.1)
7	2.1 (0.3)	3.0 (0.3)	1.7 (0.1)	1.8 (0.1)
8	2.0 (0.1)	2.4 (0.2)	1.8 (0)	1.8 (0.1)

represented to their true extent in the samples since in these species the newly hatched individuals were less than 1 mm in diameter and consequently most of the young were lost during processing of the sediment samples.

C. Site 6

a. Vegetation

The first order shoots of Potamogeton pectinatus at site 6 (Fig. 17B) had reached the surface and the first inflorescences had appeared by time 3, as at site 1, although the distance required to reach the surface was greater at site 6. The decrease in mean shoot length at time 6 was due to the appearance of second order shoots at the water surface.

The mean dry weight of individual shoots increased from a mean value of 0.13 g at time 2 to 0.94 g at time 5. By time 6 the first order shoots had increased to a mean value of 1.42 g while the second order shoots had a mean value of 0.52 g. At time 7, the mean dry weight of combined first and second order shoots, which were by now indistinguishable, was 1.16 g. This value dropped to 0.89 g at time 8 as general deterioration of the leaves became evident. The maximum mean value for shoot dry weight at site 6 was approximately $2\frac{1}{2}$ times that observed at site 1; at site 6 the plant stems were more robust and less branched than at site 1 because of the severe wave action characteristic of site 6.

Macrophyte stands occurred only in areas where the substrate consisted of clay that was sufficiently near the surface of the bottom sediments that it could be penetrated by the rhizomes. Apparently the unstable nature of purely sandy substrates discouraged the establishment of submerged macrophytes at this site. Of the total bottom samples collected on each sampling day, 24-48% contained no vegetation.

b. Density of live and dead molluscs

Despite the great diversity of species present at site 6, the densities of molluscs were very low and during the sampling season live individuals of only three species were collected.

In both the live and dead populations, the amnicolids Amnicola limosa and A. (=Probythinella) lacustris (Table XIII) showed the highest densities per unit bottom area. Maxima were observed for dead shells of these species at times 2 and 7 while live individuals showed the greatest densities at times 3 and 7. These peaks did not coincide with those observed at either sites 1 or 5.

Dead shells of Gyraulus parvus (Table XIIIA) showed peak densities in vegetated samples at times 2, 4 and 6 but live individuals (Table XIIIB) were observed only at time 3 in vegetated samples. Live individuals of Pisidium casertanum Poli, a bivalve mollusc, showed maximum densities at times 2 and 7, and like live individuals of the other species, occurred predominantly within areas occupied by submerged macrophyte stands.

All other species were represented in the samples only by dead shells. Lymnaea stagnalis, Stagnicola palustris and Planorbula armigera (Table XIII) were each collected only during one sampling period. Fossaria modicella showed maximum mean densities at times 4 and 7 in vegetated samples. Dead shells of Physa gyrina and Armiger crista were collected at times 3, 5 and 7 in vegetated samples. Promenetus exacuous showed peak densities at times 4 and 6 in vegetated samples, while Valvata tricarinata showed peak densities at times 2 and 7. Ferrissia rivularis Say showed a major peak at time 7

TABLE XIII. Mean numbers of dead (A) and live (B) shells per sample (225 cm^2 bottom area) in vegetated and nonvegetated samples, respectively, from site 6. Values in parentheses are standard errors.

A. DEAD

POTAMOGETON PECTINATUS SAMPLES

Species	Time	1	2	3	4	5	6	7	8
Lymnaea stagnalis		0	0	0	0	0	0.06(0.06)	0	0
Stagnicola palustris		0	0	0	0	0.06(0.06)	0	0	0
Fossaria modicella		0	0	0.11(0.08)	0.24(0.11)	0.06(0.06)	0.12(0.09)	0.25(0.14)	0.13(0.13)
Physa gyrina		0	0	0.06(0.06)	0	0.06(0.06)	0	0.06(0.06)	0
Gyraulus parvus		0	0.77(0.32)	0.50(0.19)	1.12(0.31)	0.76(0.29)	0.94(0.21)	0.63(0.20)	0.75(0.21)
Planorbula armigera		0	0	0	0	0	0	0.06(0.06)	0
Promenetus exacuous		0	0	0.11(0.08)	0.24(0.11)	0.06(0.06)	0.19(0.10)	0.06(0.06)	0
Armiger crista		0	0	0.06(0.06)	0	0.06(0.06)	0	0.06(0.06)	0
Ferrissia rivularis		0	0	0	0.06(0.06)	0.06(0.06)	0.06(0.06)	0.25(0.14)	0.13(0.13)
Amnicola spp.		0	3.31(2.65)	1.59(0.72)	2.06(0.60)	2.06(0.75)	3.56(1.18)	4.56(2.04)	2.25(1.13)
Valvata tricarinata		0	2.23(1.76)	0.94(0.36)	0.59(0.26)	0.88(0.44)	0.69(0.25)	2.88(1.09)	0.81(0.32)
Pisidium casertanum		0	0	0	0	0	0	0	0

SAMPLES FROM BARE AREAS

Species	Time	1	2	3	4	5	6	7	8
Lymnaea stagnalis		0	0	0	0	0	0	0	0
Stagnicola palustris		0	0	0	0	0	0	0	0
Fossaria modicella		0.67(0.67)	0	0	0	0.13(0.13)	0	0	0
Physa gyrina		0	0	0	0	0	0	0	0
Gyraulus parvus		1.33(1.33)	0.15(0.10)	0	0.57(0.37)	0.57(0.43)	0.25(0.25)	0.11(0.11)	0
Planorbula armigera		0	0	0	0	0	0	0	0
Promenetus exacuous		0	0	0	0	0	0	0	0
Armiger crista		0	0	0	0	0	0	0	0
Ferrissia rivularis		0	0	0	0	0	0	0	0
Amnicola spp.		3.67(3.67)	0.50(0.50)	0.34(0.34)	0.14(0.14)	0.50(0.19)	0.25(0.16)	0.89(0.77)	0.22(0.15)
Valvata tricarinata		1.00(1.00)	0.67(0.67)	0	0.57(0.37)	0.13(0.13)	0.13(0.12)	0	0.22(0.22)
Pisidium casertanum		0	0	0	0	0	0	0	0

(continued)

TABLE XIII. (continued)

B. LIVE

POTAMOGETON PECTINATUS SAMPLES

Species	Time 1	2	3	4	5	6	7	8
Lymnaea stagnalis	0	0	0	0	0	0	0	0
Stagnicola palustris	0	0	0	0	0	0	0	0
Fossaria modicella	0	0	0	0	0	0	0	0
Physa gyrina	0	0	0	0	0	0	0	0
Gyraulus parvus	0	0	0.11(0.08)	0	0	0	0	0
Planorbula armigera	0	0	0	0	0	0	0	0
Promenetus exacuous	0	0	0	0	0	0	0	0
Armiger crista	0	0	0	0	0	0	0	0
Ferrissia rivularis	0	0	0	0	0	0	0	0
Amnicola spp.	0	0	0.85(0.82)	0.19(0.14)	0.06(0.06)	0.25(0.14)	3.50(0.94)	0.38(0.15)
Valvata tricarinata	0	0	0	0	0	0	0	0
Pisidium casertanum	0	0.77(0.34)	0.29(0.14)	0.24(0.18)	0.18(0.09)	0.38(0.26)	3.88(0.84)	0.50(0.16)

SAMPLES FROM BARE AREAS

Species	Time 1	2	3	4	5	6	7	8
Lymnaea stagnalis	0	0	0	0	0	0	0	0
Stagnicola palustris	0	0	0	0	0	0	0	0
Fossaria modicella	0	0	0	0	0	0	0	0
Physa gyrina	0	0	0	0	0	0	0	0
Gyraulus parvus	0	0	0	0	0	0	0	0
Planorbula armigera	0	0	0	0	0	0	0	0
Promenetus exacuous	0	0	0	0	0	0	0	0
Armiger crista	0	0	0	0	0	0	0	0
Ferrissia rivularis	0	0	0	0	0	0	0	0
Amnicola spp.	0	0	0.17(0.17)	0	0	0	0	0
Valvata tricarinata	0	0	0	0	0	0	0	0
Pisidium casertanum	0	0	0	0.14(0.14)	0	0	0	0

and occurred only in vegetated samples.

The greatest percentage of the dead shell fauna (Table XIVA) consisted of the amnicolids Amnicola limosa and A. (=Probythinella) lacustris; the mean relative densities of these species showed great variation in nonvegetated samples because of the comparatively small numbers present. Valvata tricarinata showed the next highest relative density in both vegetated and nonvegetated samples, followed by Gyraulus parvus, Promenetus exacuous, Fossaria modicella, Ferrissia rivularis, Physa gyrina, Armiger crista, Stagnicola palustris, Lymnaea stagnalis and Planorbula armigera. Other species present at site 6 but too rare to be collected in the sediment samples were: Helisoma trivolvis, H. anceps, Aplexa hypnorum, and Fossaria decampi Streng, and Stagnicola catascopium Say. The bivalves Anodonta grandis grandis Say and Lampsilis radiata siliquoidea Barnes generally occurred in deeper water outside the northern boundary of the sampling ground.

Little accumulation of dead shells occurred at site 6 because the shells were soon broken up by the heavy wave action; this was particularly true for the larger species.

Live populations (Table XIVB) were numerically dominated by Pisidium casertanum; the two species of Amnicola and Gyraulus parvus comprised the remainder of the live populations that were collected in the bottom samples. In nonvegetated samples, the 100% values for relative density were due to the occurrence of single live individuals of only that species in the samples.

Unpaired t-tests were conducted to examine the significance of the difference of sample means from vegetated and nonvegetated

TABLE XIV. Mean relative density per unit bottom area for dead (A) and live (B) molluscs at site 6 expressed as a percent of the total numbers of molluscs of all species present in vegetated and nonvegetated habitats, respectively. Species numbers represent the following taxa:

1. Lymnaea stagnalis
2. Stagnicola palustris
3. Fossaria modicella
4. Physa gyrina
5. Gyraulus parvus
6. Planorbula armigera
7. Promenetus exacuous
8. Armiger crista
9. Ferrissia rivularis
10. Amnicola limosa and A. (=Probythinella) lacustris
11. Valvata tricarinata
12. Pisidium casertanum

TABLE XIV.

A. DEAD

	POTAMOGETON PECTINATUS SAMPLES								SAMPLES FROM BARE AREAS							
Species Time	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	1.5	0	0	0	0	0	0	0	0	0	0	0
3	0	0	3.3	5.6	1.5	2.1	2.8	3.2	10.0	0	0	0	9.8	0	0	0
4	0	0	1.8	0	1.5	0	0.7	0	0	0	0	0	0	0	0	0
5	0	12.2	14.8	26.0	18.7	16.7	7.2	18.4	20.0	11.4	0	44.5	42.9	39.7	11.0	0
6	0	0	0	0	0	0	0.7	0	0	0	0	0	0	0	0	0
7	0	0	3.3	5.6	1.5	3.4	0.7	0	0	0	0	0	0	0	0	0
8	0	0	1.8	0	1.5	0	0.7	0	0	0	0	0	0	0	0	0
9	0	0	0	1.4	1.5	1.1	2.8	3.2	0	0	0	0	0	0	0	0
10	0	52.5	47.2	47.8	50.7	63.3	51.8	55.3	55.0	37.9	100.0	11.0	37.6	39.7	89.0	50.0
11	0	35.3	27.8	13.6	21.6	12.3	32.6	19.9	15.0	50.7	0	44.5	9.7	20.6	0	50.0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

B. LIVE	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	8.8	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	68.0	44.2	25.0	39.7	47.4	43.2	0	0	100.0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	100.0	23.2	55.8	75.0	60.3	52.6	56.8	0	0	0	100.0	0	0	0	0

areas. The results for dead shells (Table XA) showed that Amnicola limosa, A. (=Probythinella) lacustris, Gyraulus parvus, Fossaria modicella, Promenetus exacuous and Valvata tricarinata tended to accumulate significantly ($p < .05$) more frequently in vegetated areas than in nonvegetated areas.

Land shells present in the sediment samples from site 6 belonged to the following taxa: Succinea avara Say, Vallonia spp., Discus cronkhitei Newcomb, Nesovitrea electrina Gould, Vertigo spp. and Euconulus fulvus Müller. Graveyard indices were assessed by testing the significance of the difference between sample means for land shells from vegetated and nonvegetated areas by means of unpaired t-tests (p. 58). A significantly ($p < .05$) high graveyard index was found only at time 2; accordingly the significant test for Gyraulus parvus at this time must be regarded as questionable.

Among live populations (Table XB), Pisidium casertanum showed a significantly ($p < .05$) high tendency to occur in vegetated samples during much of the season except for times 4 and 6, while Amnicola limosa and A. (=Probythinella) lacustris showed significant tendencies to occur in vegetated samples during the latter part of the season.

Essentially, for site 6:

1. Densities of molluscs were very low.
2. Pisidium casertanum and the amnicolids Amnicola limosa and A. (=Probythinella) lacustris showed significant tendencies to occur in samples containing P. pectinatus as opposed to those from nonvegetated areas.

Discussion

The distributions of several species of molluscs at sites 1, 5 and 6 with respect to vegetated and nonvegetated habitats, and with respect to different types of vegetation, could not be explained by chance alone. Live snails generally showed significant tendencies to occur in vegetated habitats, and at site 1, often showed affinities for specific vegetation types. The times of maximum mean density in samples containing the "preferred" species of plant were correlated with hatching of the young. The species of plant with which some snails tended to associate was not necessarily constant or unique in time. The results for the live populations were supported by data for dead shell accumulation in the various types of habitats and distributional differences could be attributed to passive redistribution only some of the time.

The snail species for which significant affinities for vegetated habitats were detected were largely majority species. The possibility that many minority species also showed affinities for vegetated habitats could not be excluded, since the small numbers of such species that were collected with the method of sampling may have precluded the demonstration of significant distributional differences.

At site 1, the major associations that were detected showed a polarity of distribution that coincided with the distributions of the respective macrophytes. Lymnaea stagnalis was strongly associated with Potamogeton richardsonii during much of the growing season. Snail density peaks in samples containing this plant occurred at times 3, 5

and 7 and were composed of significant proportions of young which hatched in large part just prior to these times, with the main peak occurring at time 5. Hatching in P. richardsonii stands appeared to commence earlier and was of greater magnitude than in other vegetated habitats at this site. These results suggested that P. richardsonii stands contained some factor that was favorable or perhaps attractive to L. stagnalis.

The other numerically predominant species at site 1, Physa gyrina, was significantly associated with Potamogeton pectinatus at the beginning of the season, but by time 3 also showed affinity for P. richardsonii. Numbers of snails per unit bottom area continued to be greater in P. pectinatus than in P. richardsonii stands until time 6; after time 6 no differential affinities could be demonstrated until time 8, when significantly greater numbers were again present in samples containing P. pectinatus. Physa gyrina also showed a significant affinity for Myriophyllum exalbescens at time 8. The first hatching of the young of P. gyrina occurred after time 1 in P. pectinatus stands, and this appeared to precede hatching of this snail in other vegetation types. Major reproduction occurred at times 4 and 8.

Fossaria modicella, the third most frequent species in the live populations at site 1, showed some similarities to the distribution of P. gyrina in that it was associated with P. pectinatus early in the season but also showed affinity for P. richardsonii. Reproduction in this species commenced after time 1 and continued until midseason in stands of both Potamogeton species.

Stagnicola palustris, on the other hand, was associated with

P. richardsonii until time 3 in terms of numbers per unit bottom area, but by time 6 it was associated with P. pectinatus, as seen from the results of the live counts. Reproduction of this snail appeared to take place in both types of Potamogeton stands. The results of the bottom sampling showed that live individuals of Helisoma trivolvis were significantly associated with P. pectinatus at time 6, which was also the time of major reproduction in this species.

Snail associations with Myriophyllum exalbescens and Ceratophyllum demersum were weak during the first half of the season; this may have been an effect of masking by the more dominant Potamogeton species in the samples, or it may have been due to a real absence of snails beyond the numbers expected due to chance from these samples during the first part of the season. DeCosker and Persoone (1970), working near Ghent, Belgium, also found that C. demersum appeared to be preferred by gastropods later in the growing season. According to Lawalree (1955), young Ceratophyllum and Myriophyllum shoots produce the inhibitor, myriophyllin, which protects young plants from grazing by discouraging aquatic gastropods.

With respect to seasonal numerical relationships between major species, DeCosker and Persoone (1970) found that densities of Lymnaea stagnalis in vegetated habitats were inversely correlated with those of other, smaller species. To some extent this was true at site 1, particularly for relative densities of L. stagnalis and P. gyrina during midseason (see Table IVB). At site 1 this could be explained by non-simultaneous reproduction of these two species.

At site 5, where the vegetation consisted almost entirely

of Myriophyllum exalbescens, major positive associations with this plant were observed for Physa gyrina and Fossaria modicella after time 3. Prior to time 3 all of the shoots were young and perhaps contained high levels of snail repellant. These two gastropod species were also predominant at site 1 in samples containing M. exalbescens. Hatching of Physa in M. exalbescens stands at both sites 1 and 5 did not occur until after time 2 even though it commenced earlier in P. pectinatus stands at site 1, suggesting that M. exalbescens may not have been as favorable a habitat early during the growing season.

The unrestricted growth of the Physa population at site 5 during the second half of the season in M. exalbescens stands rendered this plant-snail association particularly striking. Krecker (1939) and Mackie and Qadri (1971) have also noted the presence of Physa on Myriophyllum. The reasons why the spectacular expansion of the population occurred at site 5 whereas at site 1 it remained in check may have been due to a combination of factors. The absence from site 5 of Lymnaea stagnalis, an important competitor for food at site 1 because of its large size and numbers, may have contributed to the continued population increase of Physa as the mean dry weight of the host plants continued to increase. Both snail density and mean shoot weight decreased sharply at time 8. Fossaria modicella, the second most frequent species among the live populations at site 5, was not an important competitor in this regard because, although its size was similar to that of Physa, its density per unit bottom area was significantly smaller. Another factor may have been the lesser degree of predation at site 5. Leopard frogs, which account for some predation on snails in the Delta Marsh (Eddy, 1976) and

snailivorous leeches were less abundant and feeding by waterfowl was spread over a much larger surface area than at site 1; also fish were not seen at site 5. Yet another factor may have been an intrinsic characteristic of the population: since the reproduction during the second half of the season was due to the young of the year that had hatched during the first part of the season, there remaining no adults during the second half of the season, the young of the year at this site were reproducing when their size, and age, was smaller than the size of the young of the year that were reproducing at site 1 (compare Figs. 16 and 21). This, combined with the fact that surface temperatures remained high at site 5 until the end of the season (Fig. 6), may have contributed to larger amounts of egg-laying since temperature is known to influence growth rate (Imhof, 1973). Higher temperatures may also have shortened the time required for embryonic development (DeWitt, 1954).

At site 6, where pure stands of Potamogeton pectinatus were present, major positive associations were detected only for the two Amnicola species and Pisidium casertanum. However these species were unlikely to feed directly upon living plant tissue to any significant extent. Pisidium casertanum, a bivalve, is a truly benthic organism and relies upon filter-feeding. Its significant tendency to occur in macrophyte stands was probably due to the more sheltered conditions prevalent therein in terms of reduced turbulence and turbidity and enhanced substrate stability. The consistency of the substrate, which was different in vegetated and nonvegetated areas, as well as possibly differences in the numbers and types of filterable organisms

between the two types of habitats may also have been contributing factors which influenced the distribution of this species.

The amnicolids, Amnicola limosa and A. (=Probythinella) lacustris, were unlikely to feed significantly upon living plant tissue because of their small size and the weak radula characteristic of these prosobranch gastropods. Monakov (1972) reported that prosobranchs ingest sand grains, silt, diatoms, unicellular green algae and bacteria although some evidence was found that higher plant tissues are eaten as well. The amnicolids at site 6 were observed to be present directly upon the macrophytes but may have been feeding largely upon periphyton.

Although many species of pulmonates were present at site 6, their densities were very low and live individuals were neither collected in the bottom samples nor observed upon the macrophytes. This may have been due in part to the turbulence at this site which made it difficult for large snails to stay on the plants. At site 5 snails were observed to disappear from the upper portions of the plants during periods of turbulence. These observations support those of Szczepánska (1958 in Bownik, 1970) who found that wave action can completely eliminate the molluscs from the plants.

In general, the results gained from study of dead shell accumulations augmented the data obtained for live populations insofar as sequential sampling was employed. However it was discovered that shells of different species disintegrate at different rates at the same and at different sites and therefore must not be used in stratigraphic studies to extrapolate the structures of past aquatic communities since the composition of dead assemblages is not

proportional to that of the living populations from which they have been drawn.

The plant-snail associations that were demonstrated at the three sites were examined with respect to the monitored environmental parameters. Since density peaks consisted of a large proportion of young as well as some adults, it was possible that certain factors could be correlated temporally with the distribution of adults and with reproduction. However correlation coefficients for snail density and each of the monitored parameters for water chemistry failed to show any significant correlations. These results were thus the same as those of Lévèque (1975), who studied Ceratophyllum demersum communities in Lake Chad, Ivory Coast, and also could not correlate snail densities with any of the principal ecological parameters of the lake.

According to DeWitt (1954, 1955, 1967), temperature, and possibly to a lesser extent, photoperiod, influence egg-laying in Physa and Lymnaea. He found that, in Michigan populations of Physa gyrina, oviposition commenced at a water temperature above 10 C. These results were supported by those of Sankurathri and Holmes (1976) who studied a population in Lake Wabamun, Alberta. However at sites 1 and 5, the earliest hatching of P. gyrina was not observed until after time 1, when water temperatures were already high (Fig. 6). Allowing more than a week for embryonic development at 20 C (DeWitt, 1954), which was close to the mean temperatures at both sites at time 1, temperatures were nonetheless well above 10 C during the first oviposition, at or slightly prior to time 1. Furthermore, at site 1,

hatching in Potamogeton pectinatus stands slightly preceded that observed in other types of stands; if temperature differences did exist between the different types of stands, these were not detected. This suggests that other factors in addition to temperature may have influenced reproduction. Photoperiod was obviously the same in all habitats.

Essentially, the results of the 1972 season suggested that:

1. Many species of molluscs occurred significantly more frequently in vegetated than in nonvegetated habitats.
2. At site 1, majority species of molluscs often occurred significantly more frequently in certain types of vegetation than in other available vegetated habitats.
3. The plant-snail associations, in terms of snail density per unit bottom area in the stands, were time-dependent and were related to reproduction.
4. The differential snail distributions could often not be explained on the basis of chance nor could they be correlated with any of the monitored environmental parameters, but appeared to be correlated with the distributions of (specific) macrophytes.
5. The specific associations appeared to show some flexibility from site to site, depending upon the types of macrophytes that were present.

On the basis of these observations, the following plant-grazer models were postulated, assuming that grazing of the plants by snails did indeed occur:

1. At site 1, the basic model consisted of the macrophytes Potamogeton pectinatus and P. richardsonii, and the pulmonates

Physa gyrina and Lymnaea stagnalis. Fossaria modicella, Stagnicola palustris and Helisoma trivolvis formed smaller subsidiary associations with the two macrophytes.

2. At site 5, the basic model consisted of Myriophyllum exalbescens and the pulmonates Physa gyrina and Fossaria modicella. This model coexisted with model 1 at site 1 on a reduced scale.
3. At site 6, the basic model consisted of Potamogeton pectinatus and the prosobranch Amnicola species. This model was not believed to represent a true plant-grazer model, although there was some evidence for the existence of this model on a minor scale at site 1.

The first model was the most complex since it involved the simultaneous interaction of several species of plants and snails on a similar scale; differential association patterns within such a system would represent a high order of adaptation. The second and third models represented a single-macrophyte system, and therefore a lower order of adaptation because any tendencies to occur in vegetation involved obligatory interspecific competition among the snails. Models 1 and 2 were examined in greater depth during the subsequent seasons, while model 3 was set aside for the balance of Part I.

SECTION II

Seasons II and III (1973-4)

Introduction

I. Objectives

In order to examine the plant-snail communities more closely, sampling by Ekman dredge was no longer suitable since, with this method, the benthos was not separable from the snails that had been originally present on the plants, and, since the quadrat size was too small to allow for quantitative sampling of the latter, the snails could not be related quantitatively to the plants. Although sampling by Ekman dredge probably entailed little loss of snails from the plants, agreeing with the contentions of DeCosker and Persoone (1970) that snails are not easily removed from the plants, Mackie and Qadri (1971) found that the Ekman dredge operated with varying degrees of efficiency in recovering snails from different types of macrophyte stands. Therefore, before the problem could be pursued further, a revised method of sampling was necessary that would:

1. sample both macrophytes and associated macrofauna quantitatively with a minimum of disturbance to the communities being sampled, and
2. exclude benthos.

Such a sampler was not commercially available and previous workers (pp. 8-11) had little success in overcoming these difficulties. The sampler proposed by Gerking (1957), although it excluded the benthos, had the disadvantages that:

1. because of its manual operation, it could only be used in shallow water and could not be operated from a boat, resulting

in trampling and disturbance to portions of the community that were not included in the sample,

2. in dense stands, the vegetation was not cut completely because insufficient shearing force was generated by hand,
3. the vegetation was sheared above substrate level, excluding lower portions of the shoots and young plants from the sample, and
4. the time which elapsed between positioning of the sampler and insertion of the bottom screen allowed disturbed fauna within the sampler to settle to the bottom and be excluded from the sample.

In 1971, Mackie and Qadri proposed an apparatus for the quantitative sampling of aquatic phytomacrofauna. This sampler had the advantages that it could be operated at any depth from a boat, it excluded the benthos, and its operation was fast and efficient. However the size of the sampled quadrat was too small to allow for quantitative sampling of macrophytes, the sampling error due to edge effect (Kershaw, 1964) was large, and the quadrat size was fixed. The design was altered and a modified macrophyte sampler (Pip and Stewart, 1976) was constructed that would sample both the macrophytes and associated phytomacrofauna with a minimum of error.

The primary objectives of the 1973-4 seasons' work were:

1. To examine quantitatively the validity and nature of the plant-snail model proposed for site 1 on the basis of the results of the 1972 season, which consisted of the macrophytes Potamogeton pectinatus and P. richardsonii and the pulmonates

Physa gyrina and Lymnaea stagnalis, and on a subsidiary scale, of Fossaria modicella, Stagnicola palustris and Helisoma trivolvis. If this model were true, then:

a. these five gastropods would be expected to occur largely on the plant shoots while the remainder of the molluscs would occur in the benthos, and

b. the differential temporal and spatial distribution patterns suggested by the model could be demonstrated quantitatively in terms of host plant units.

2. To determine whether this model was true in other sites.

3. To examine quantitatively an example of the second model, i.e. a single-macrophyte system.

These objectives were approached in the following ways:

1. Densities of all molluscs present on the plants in the respective Potamogeton stands at different sites were examined with time in relation to: a) unit bottom area, b) unit dry plant weight and c) unit plant surface area.

2. Biomass of the two major gastropods in model 1 was examined with time in the respective Potamogeton stands at different sites in relation to: a) unit bottom area, b) unit dry plant weight and c) unit plant surface area.

3. The population dynamics of the the major gastropods in model 1 were examined with respect to the phenological cycles of the host plants.

4. The grazing damage sustained by the plants at different times was estimated.

5. Environmental parameters continued to be monitored.

II. Description of the study areas

The sites selected during the 1973 season, apart from site 1, had the following features:

1. The sites contained one or both of Potamogeton pectinatus and/or P. richardsonii, and a molluscan fauna that included, but consisted of more than, the two major species stipulated by model 1.
2. The sites were relatively protected from wind and turbulence. Results from the 1972 season had suggested that wave action drives larger snails from the plants.
3. The sites were accessible in all types of weather.
4. The sites were subject to little direct human interference. Such sites were established for several years, and the surrounding vegetation was undisturbed and continuous. The remains of plant and animal material from the previous season represented the same types of communities as those of the current season.

During the 1973 season, four sites were studied; of these, sites 1, 2 and 4 contained both Potamogeton species and were thus suitable for testing model 1, while site 3 contained only P. pectinatus and was suitable for observing a single-macrophyte system. During the 1974 season, only sites 1 and 2 were studied.

A. Sites 1 and 2

Site 1 (Fig. 23) had been studied in 1972 and has been described on p. 13.

Site 2 (Fig. 24) consisted of an L-shaped drainage ditch that

Figure 23. Position of Potamogeton pectinatus and P. richardsonii dominated stands within site 1 during the 1972-3 seasons.

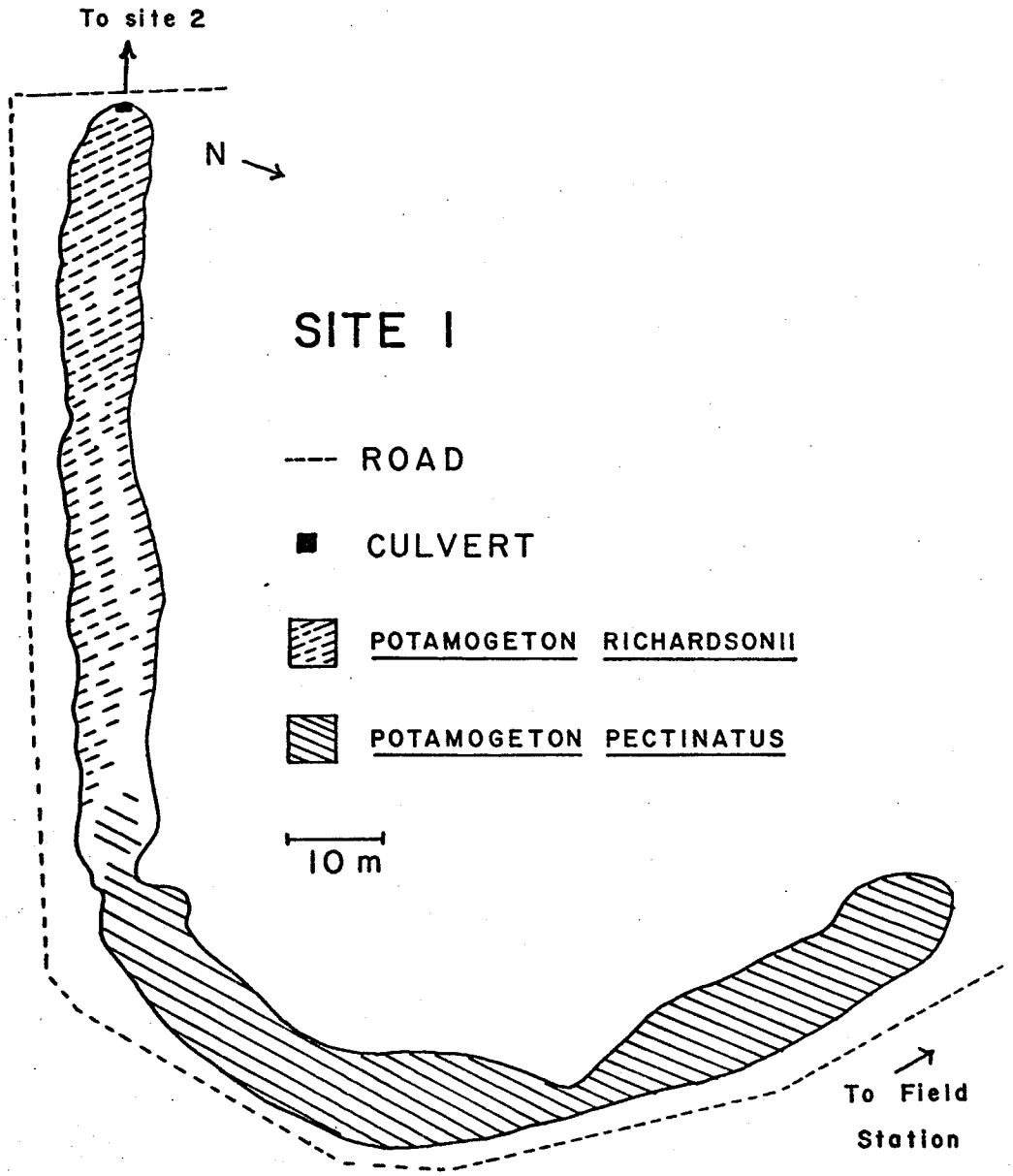
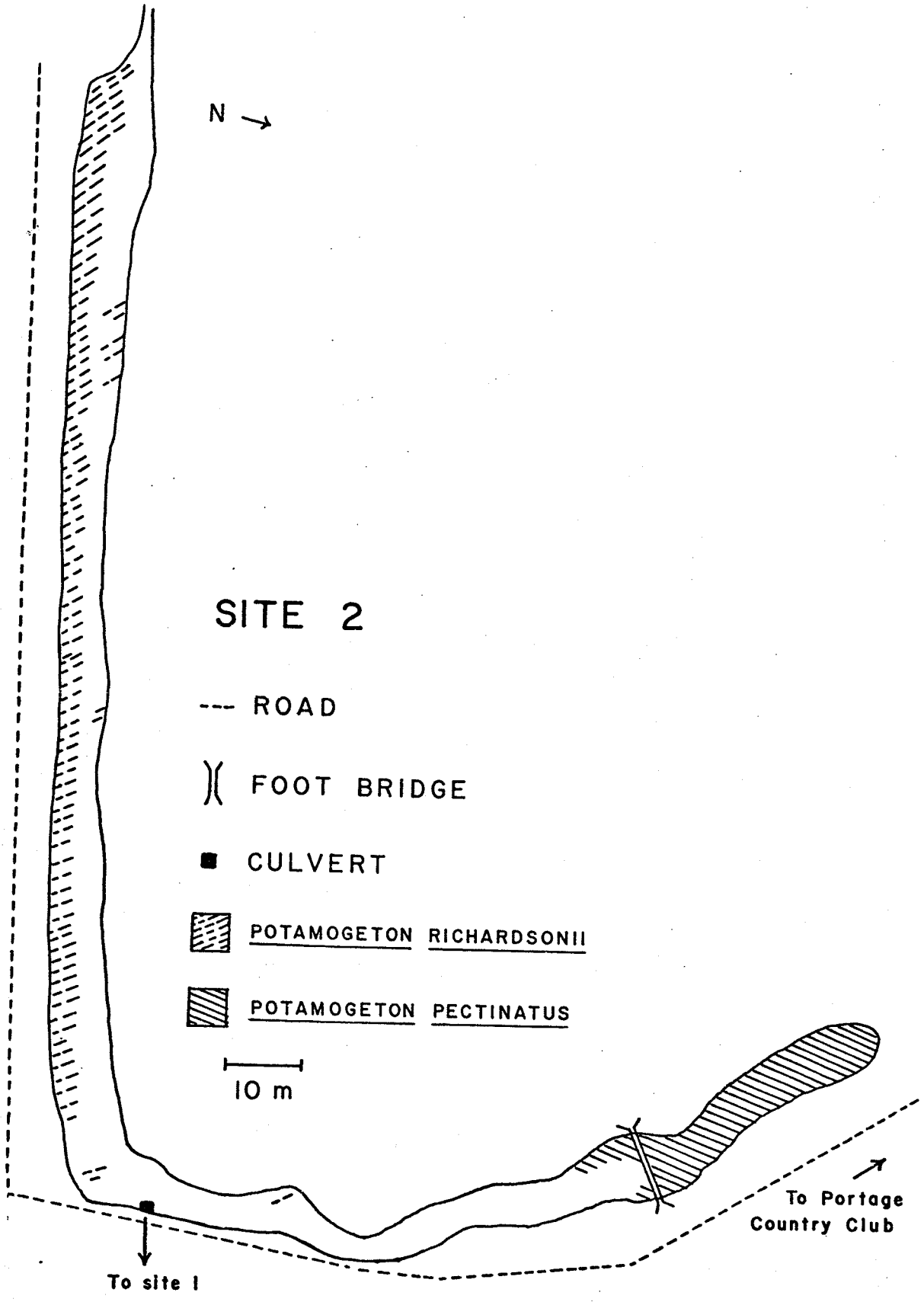

To site 2
N
SITE I
ROAD
CULVERT
POTAMOGETON RICHARDSONII
POTAMOGETON PECTINATUS
10 m
To Field Station

Figure 24. Position of Potamogeton pectinatus and P. richardsonii dominated stands within site 2 during the 1973 season.


N
SITE 2
--- ROAD
FOOT BRIDGE
CULVERT
POTAMOGETON RICHARDSONII
POTAMOGETON PECTINATUS
10 m
To Portage Country Club
To site 1

was similar in aspect and origin to site 1. It was located adjacent to site 1 but was not connected to it during the 1973 season. Site 2 contained a small passage at its western end to a shallow marsh bay which was ultimately connected to the Blind Channel. The site was well-protected from wind and the maximum seasonal depth was 0.75 m. The bottom consisted of a fine organic silt with a clay base and varying proportions of sand and gravel.

The northernmost portion of the northern arm contained an undisturbed pocket of Potamogeton pectinatus interspersed with Ceratophyllum demersum; the western arm contained mosaic stands of P. richardsonii and Myriophyllum exalbescens. The intervening bare area between the two types of stands was disturbed by boat traffic since the site provided indirect access to the Blind Channel. Lemna minor L. occurred sporadically among the emergent vegetation in the northern arm. The margins of the ditch were occupied by stands dominated by Phragmites communis, Typha latifolia and Carex atherodes. The species composition of the molluscan fauna at site 2 was identical to that of site 1.

During the 1974 season, the character of sites 1 and 2 changed abruptly as the result of severe flooding in the Delta Marsh during the spring. During April, surface connections between sites 1 and 2 and the surrounding marsh allowed for the unrestricted migration of fauna. At this time carp gained access to both sites and persisted throughout the 1974 season. During May and June, sites 1 and 2 were still connected by means of a culvert and during this period muskrats frequented both sites. Water levels remained high until the end of the season.

The increased influx of silt into the sites and related factors associated with the flooding had a pronounced effect on the submerged communities. Myriophyllum exalbescens disappeared completely from both sites during the 1974 season, even though at the beginning of May it appeared to be germinating normally from perennating buds. The P. pectinatus stands were very sparse and grew poorly, especially at site 1, although P. richardsonii appeared to be less affected. Ceratophyllum demersum, which had previously been present only in the P. pectinatus stands, spread completely throughout both sites. At site 2, the discontinuation of motor-propelled boats allowed the P. pectinatus stands to advance farther south along the ditch, making contact with the P. richardsonii zone.

A phenomenon with particularly far-reaching effects on the submerged communities was the explosion of Lemna trisulca and L. minor at both sites. By the end of July the water surface was entirely covered with dense mats of these plants.

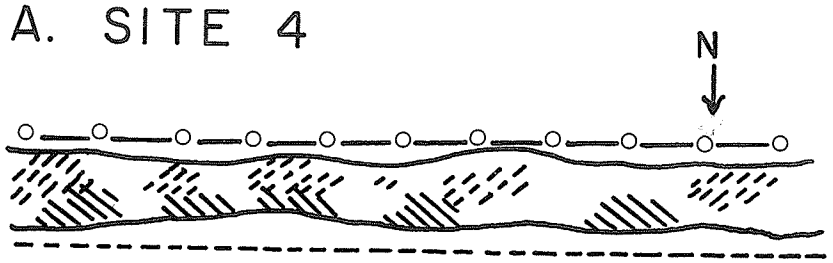
During the 1974 season, both Physa gyrina and Lymnaea stagnalis populations declined at both sites, while other gastropods, notably Stagnicola palustris, increased in importance.

B. Site 3

Site 3 consisted of the northernmost 50 m portion of a drainage ditch located in the east Delta Marsh at the entrance to the Inkster property, with access via the east dyke road (Fig. 1). The ditch was directly connected to the Blind Channel, but was completely undisturbed and well-protected from wind. The bottom sediments consisted largely of clay and incompletely decomposed organic matter.

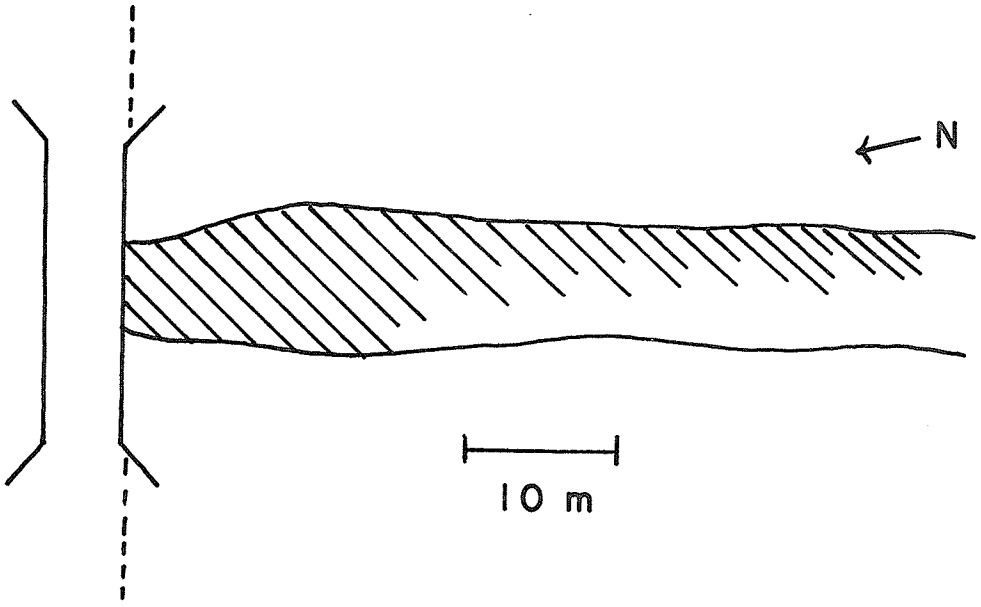
Figure 25. Position of Potamogeton pectinatus and P. richardsonii dominated stands within site 4 (A) and site 3 (B) during the 1973 season.

A. SITE 4



10 m

B. SITE 3



10 m

ROAD

FENCE

BRIDGE

POTAMOGETON RICHARDSONII

POTAMOGETON PECTINATUS

Although the site was spanned by a bridge (Fig. 25B), traffic was very light. The maximum seasonal depth was 0.5 m, but this site was subject to sharp fluctuations in water level, particularly towards the end of the season.

The submerged vegetation consisted of a dense stand of Potamogeton pectinatus at the northern end. The remainder of the ditch was occupied by scattered clumps of Myriophyllum exalbescens. Filamentous algae were common. The emergent vegetation was dominated by Carex spp., Phragmites communis and Sparganium sp. The invertebrate fauna at site 3 was similar to that at sites 1 and 2. Fishes were not observed but the site was extensively used by waterfowl and small mammals.

C. Site 4

Site 4 was located in the Big Grass Marsh west of Langruth. The Big Grass Marsh covers an area of approximately 18,600 hectares west of Lake Manitoba. The underlying deposits are composed largely of poorly sorted calcareous till containing a small proportion of granitic materials.

Site 4 was composed of a portion of a linear drainage ditch with an east-west orientation that was continuous for several kilometers along the southern side of Provincial Trunk Highway No. 265. A 50 m section of the ditch located 12.5 km west of Langruth was used for study (Fig. 25A). The bottom sediments consisted of coarse sand, gravel and scattered rock covered by a layer of calcium carbonate and organic debris. Maximum water depth at site 4 ranged from 1.0 m during the early part of the season to 0.25 m by August. The site

was relatively exposed to the prevailing winds.

The submerged vegetation was dense and diverse, and consisted of Potamogeton pectinatus, P. richardsonii, P. vaginatus Turcz., P. natans L., Myriophyllum exalbescens, Utricularia vulgaris L. and a Chara sp. The Potamogeton species occurred in fairly discrete, although scattered stands; P. pectinatus and P. vaginatus were common along the shallower margins of the ditch, while P. richardsonii and P. natans tended to occur in the deeper central portions. Emergent vegetation was composed of Hippuris vulgaris L., Sagittaria sp., Alisma triviale Pursh, Mentha arvensis L., Carex spp., Phragmites communis, Typha latifolia and Scirpus acutus Muhl.

The molluscan fauna was similar to that of sites 1-3. Small crustaceans and insects were common. The sampling grounds contained a family of crayfish (Cambarinae) while nematomorphans were found entwined about the plant shoots fairly commonly. The site was used by waterfowl.

Materials and methods

In 1973 sites 1-4 were sampled at two-week intervals from May to August while in 1974 sites 1-2 were sampled with the same frequency and for the same period. Sites 1 and 2, and sites 3 and 4, respectively, were sampled on the same days. The dates for sampling times during the 1973-4 seasons are given in Table XV.

I. Environmental measurements

A. Water chemistry

A surface water sample was collected at each site in the early afternoon, placed immediately in iced, lightproof containers and frozen within 5 hours of collection. The samples were thawed 1-3 days later and analyzed according to methods recommended by the American Public Health Association (1971) which have been described on p. 17 . Measurements of surface pH were made with a pH meter. Calcium activity was determined during 1973 by using a calibrated Orion Ionalyzer model 407 with calcium electrode model 92-20.

Because the sites were located close to unpaved roads and were subject to fallout from dust, the influx of solutes from atmospheric sources, in the form of dust or dissolved in rainwater, was estimated by placing glass jars that were 16.5 cm deep and had an opening of 38.5 cm^2 near the edge of the water at sites 1, 3 and 4 at time 3, chosen randomly, during 1973. The jars were retrieved at time 4 and their contents were treated as normal water samples.

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TABLE XV. Dates of sampling times for sites 1-4 during 1973 (A) and for sites 1-2 during 1974 (B).

A. 1973

Sampling time	sites 1-2	sites 3-4
1a	May 11	-
1	May 16	-
2	May 30	May 28
3	June 13	June 11
4	June 27	June 25
5	July 11	July 9
6	July 25	July 23
7	August 8	August 7
8	August 22	August 20

B. 1974

Sampling time	sites 1-2
1	May 13
2	May 27
3	June 10
4	June 26
5	July 8
6	July 22
7	August 6
8	August 19

B. Light and temperature measurements

Light measurements were made at 0.25 m depth intervals with a Griffin environmental comparator (p. 20). Temperature measurements were made at 0.25 m depth intervals with a thermometer.

II. Biotic sampling

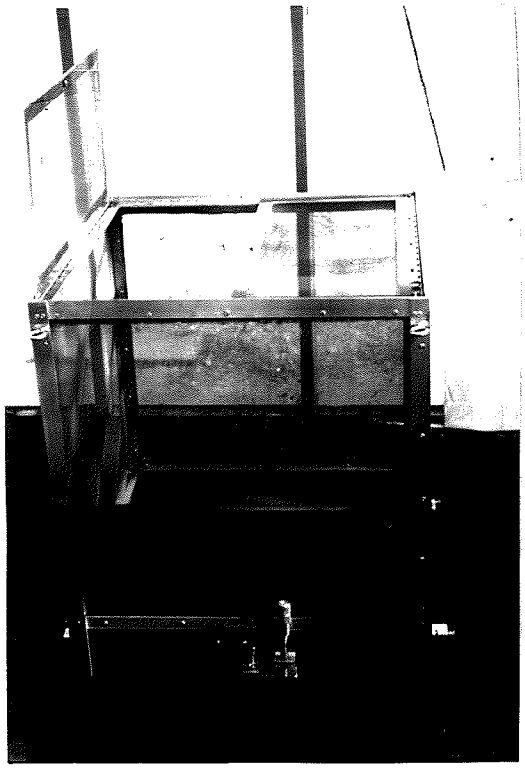
A. Field apparatus and procedures

a. Modified macrophyte sampler

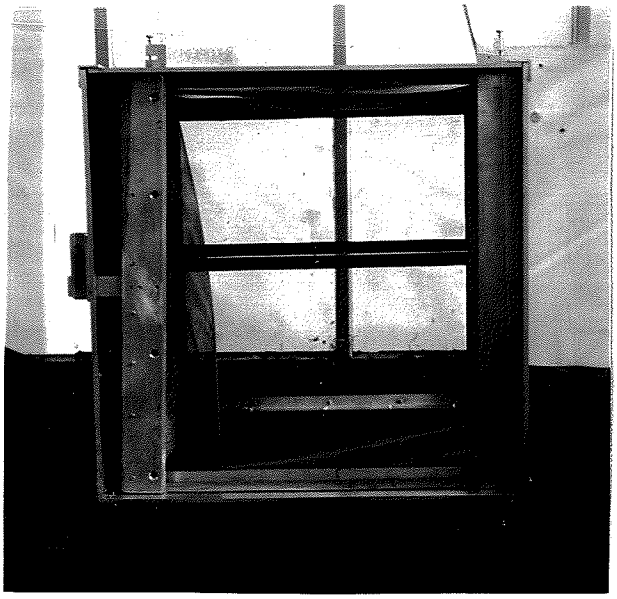
The modified macrophyte sampler (Fig. 26) consisted of a heavy guage (6 mm) aluminum frame with inside dimensions of 50 x 50 x 58 cm. One stationary and one movable blade, each 3 cm wide, were set in runner slits 3 cm above the base of the frame. When the sampler was in position, the 3 cm of clearance between the base and the blades sank into the substrate, placing the blades at substrate level and anchoring the sampler during operation. The method of operation was essentially the same as that proposed by Mackie and Qadri (1971). A 0.85 kg messenger released the trigger mechanism, and if the safety pin was not engaged, the movable blade was pulled rapidly towards the stationary blade by a series of heavy-duty rubber bands attached to the protruding ends of the blades, shearing the enclosed vegetation at substrate level. A folding vinyl screen with 1 mm mesh was attached to the movable blade; this closed the bottom opening and prevented escape of the contents. Vinyl screening with a 1 mm mesh covered all sides and the top hinged doors of the sampler.

The size of the enclosed quadrat could be reduced from the maximum dimensions of 37.5 x 50 cm by inserting blades of varying

Figure 26. Side (A) and bottom (B) views of the modified macrophyte sampler.



A



B

width in front of the stationary blade. The quadrat size used in this study had dimensions of 30.5 x 50 cm (1525 cm^2). This quadrat size was large enough to minimize both the effects of possible heterogeneous faunal distributions within a clump and the effects of edge and contagion within a plant stand, but was small enough that the quadrat size did not exceed mean clump size (Kershaw, 1973) of the two Potamogeton species at sites 1 and 2.

The efficiency of the sampler with respect to the two Potamogeton species was estimated by comparing the numbers of shoots enclosed by the sampler before sampling with the numbers recovered from the sampler after sampling and was found to vary from 80 to 100%, depending on bottom contours and presence of extraneous materials. The samples comprised the contents of the water column that exceeded 1 mm in size and included free-swimming invertebrates and fish.

b. Sampling procedure

Sampling was conducted at all times from a small boat. Sampling points were selected randomly within areas occupied by homogeneous plant stands; such stands were defined by the absence of other species when examined visually.

Five samples were taken in each of the two types of Potamogeton stands at each site, except site 3 which contained only one type of Potamogeton stand, on each sampling day. This number of samples was determined from an examination of the sampling distribution of the mean (Spiegel, 1961) for plant dry weight from the sites.

During the 1974 season, selection of sampling points after time 6 was completely random because the dense surface mats of Lemna at sites 1 and 2 precluded any visual assessment of stand homogeneity.

However, except for the Lemna, heterogeneity of the samples was minimal since Myriophyllum exalbescens was absent from these sites during 1974.

The samples were sealed in plastic bags, refrigerated at 3 C. and processed within 10 days. Initial processing consisted of washing the samples under a jet of water through a nest of sieves, the smallest mesh being 1 mm. The residue was sorted by hand into plant and animal components.

B. Vegetation

a. Shoot length

During each sampling period, a total of at least 10 randomly chosen shoots of each of the two Potamogeton species from each site was set aside from the samples for measurement of length, surface area and individual dry weight. Shoot length was determined by measuring from the severed proximal end, assumed to represent substrate level, to the distal terminus of the longest branch or inflorescence.

b. Surface area

The surface areas of the shoots that had been set aside in section a above were determined using the procedure described by Harrod and Hall (1962). The inflorescences were removed because the weight-area relationships for these parts differed from those of the submerged vegetative portions, and being emergent, they were not subject to the same degree of grazing by aquatic organisms.

i. Weight of surface film

Each shoot was briefly immersed in acetone to remove the periphyton (Harrod and Hall, 1962), the acetone was allowed to dry and the shoot was weighed. Immediately after weighing, the shoot was immersed in Teepol 610 (Shell Oil Co., distributed by BDH Chemicals), removed and shaken for 20 sec at the rate of 4 times per sec to remove excess solution and to allow an even film to spread over the plant surfaces. The shoot was then weighed. This procedure was repeated 5 times for each shoot. The initial weight of the tissue was subtracted from the mean value for the 5 readings to obtain the mean weight of the surface film.

ii. Weight of surface film vs. surface area

After determination of the weight of the surface film, shoots used for the calibration curve were thoroughly washed to remove the Teepol detergent. The plants were cut into small parallelograms and triangles, each having a surface area of 0.4-2.0 cm^2. The dimensions of each section were measured and the combined area of the upper and lower surfaces was calculated using the relationships,

$$A = 2\ lw \quad \ldots\ldots\ldots (3)$$

for parallelograms and

$$A = lw \quad \ldots\ldots\ldots (4)$$

for triangles. The surface area of the stem was estimated by treating it as a cylinder with area

$$A = \pi\, dh \quad \ldots\ldots\ldots (5).$$

The areas thus obtained were summed.

The relationship between surface area and weight of surface film (Fig. 27) was shown by both species of Potamogeton at a high degree of correlation between the two variables ($p < .005$, $n=17$) and could be expressed as:

$$A = \frac{F - 0.0023}{0.0071} \quad \ldots\ldots\ldots (6),$$

where F represents the weight of the surface film (g) and A is the surface area (cm^2).

iii. Surface area vs. dry weight

Although the procedure for estimating surface area from the weight of the surface film was accurate, its application to whole samples was impractical because of their large size and the amount of time required. In an attempt to overcome this difficulty, the relationships between surface area and dry weight were examined.

Scatter diagrams for the regression of dry weight on surface area in P. pectinatus (Fig. 28) and P. richardsonii (Fig. 29) were constructed using values for shoots collected throughout the 1973 season at all study sites. For P. pectinatus, ($p < .001$, $n=79$), this relationship could be expressed as:

$$A = (W/0.0014) - 15.2143 \quad \ldots\ldots\ldots (7),$$

while for P. richardsonii, ($p < .001$, $n=57$), it could be expressed as:

$$A = (W/0.0017) + 27.4706 \quad \ldots\ldots\ldots (8),$$

where A = surface area (cm^2) and W = dry weight (g). There were no significant differences in weight-area relationships between shoots originating from different sites nor was there any significant deviation throughout the season within a single site.

Figure 27. Regression of plant surface area (cm^2) on weight of surface film (g) of Teepol 610 in Potamogeton pectinatus and P. richardsonii. This relationship can be approximated by equation 6:

$$A = \frac{F - 0.0023}{0.0071}$$

where A = surface area (cm^2) and F = weight of surface film (g).

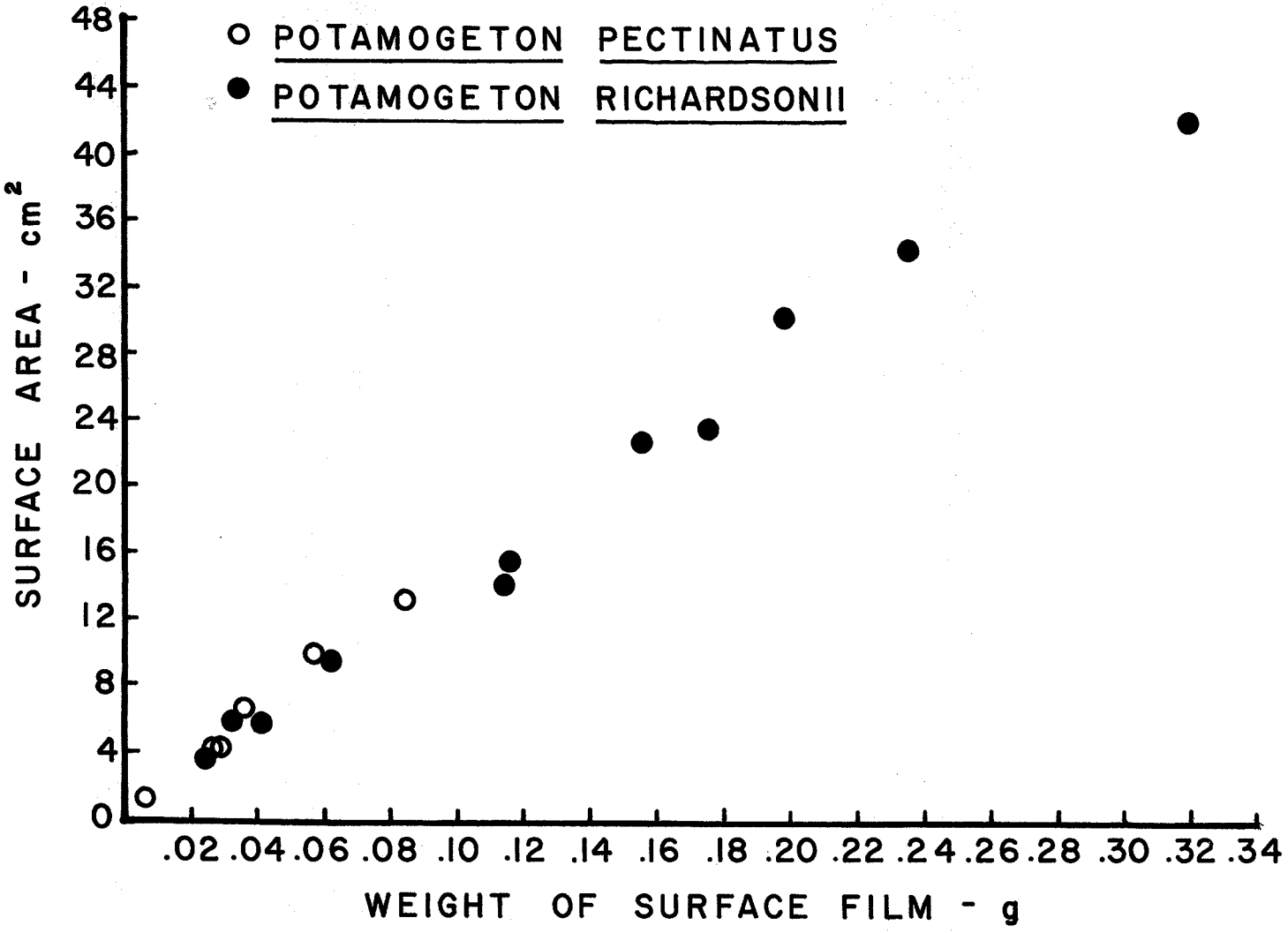

POTAMOGETON PECTINATUS
POTAMOGETON RICHARDSONII
SURFACE AREA - cm²
0
4
8
12
16
20
24
28
32
36
40
44
48
.02 .04 .06 .08 .10 .12 .14 .16 .18 .20 .22 .24 .26 .28 .30 .32 .34
WEIGHT OF SURFACE FILM - g

Fig. 28. Scatter diagram illustrating the relationship between shoot dry weight (g) and surface area (cm^2) in Potamogeton pectinatus from sites 1, 2 and 3. This relationship can be approximated by equation 7:

$$A = (W/0.0014) - 15.2143$$

where A = surface area (cm^2) and W = dry weight (g).

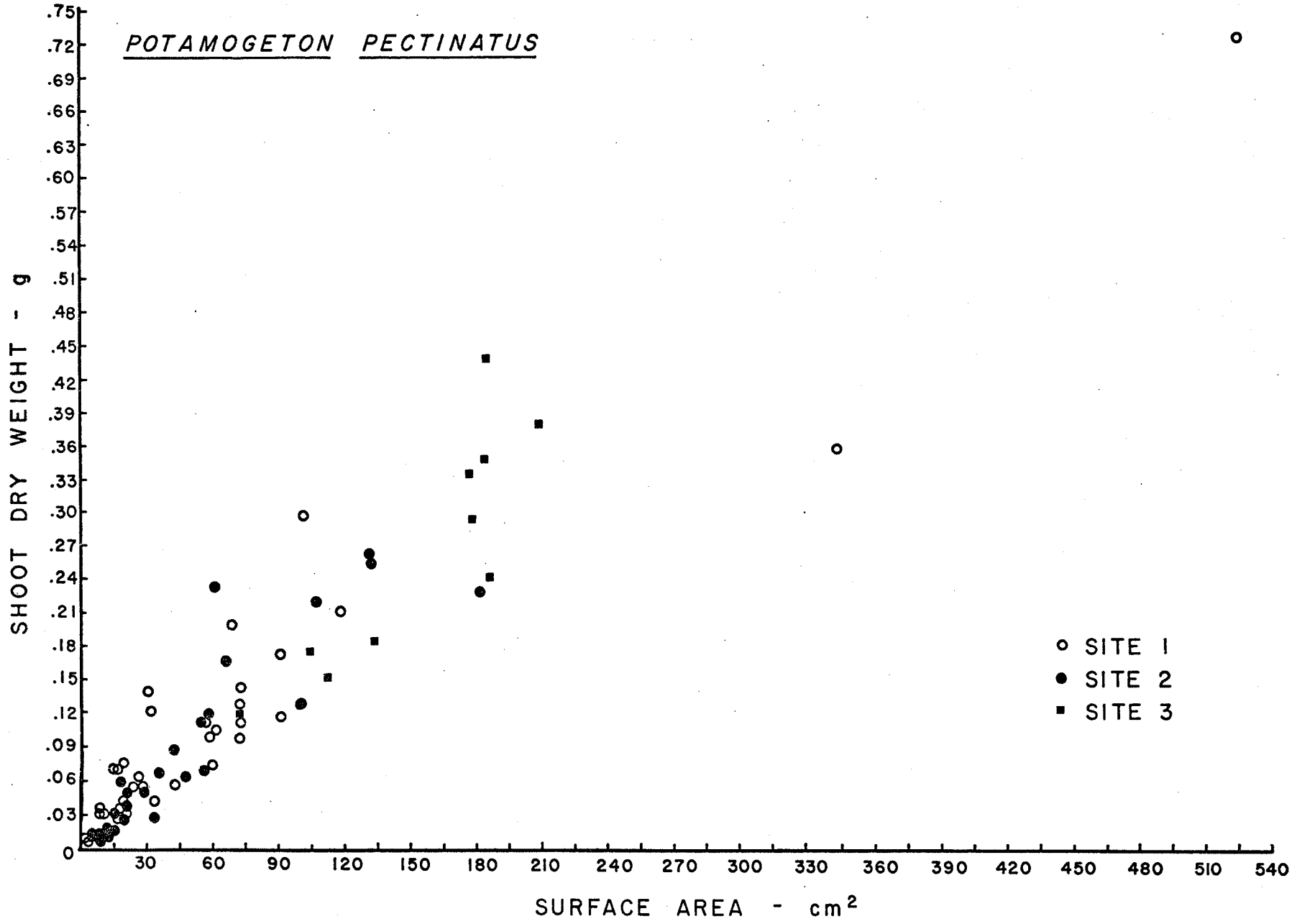
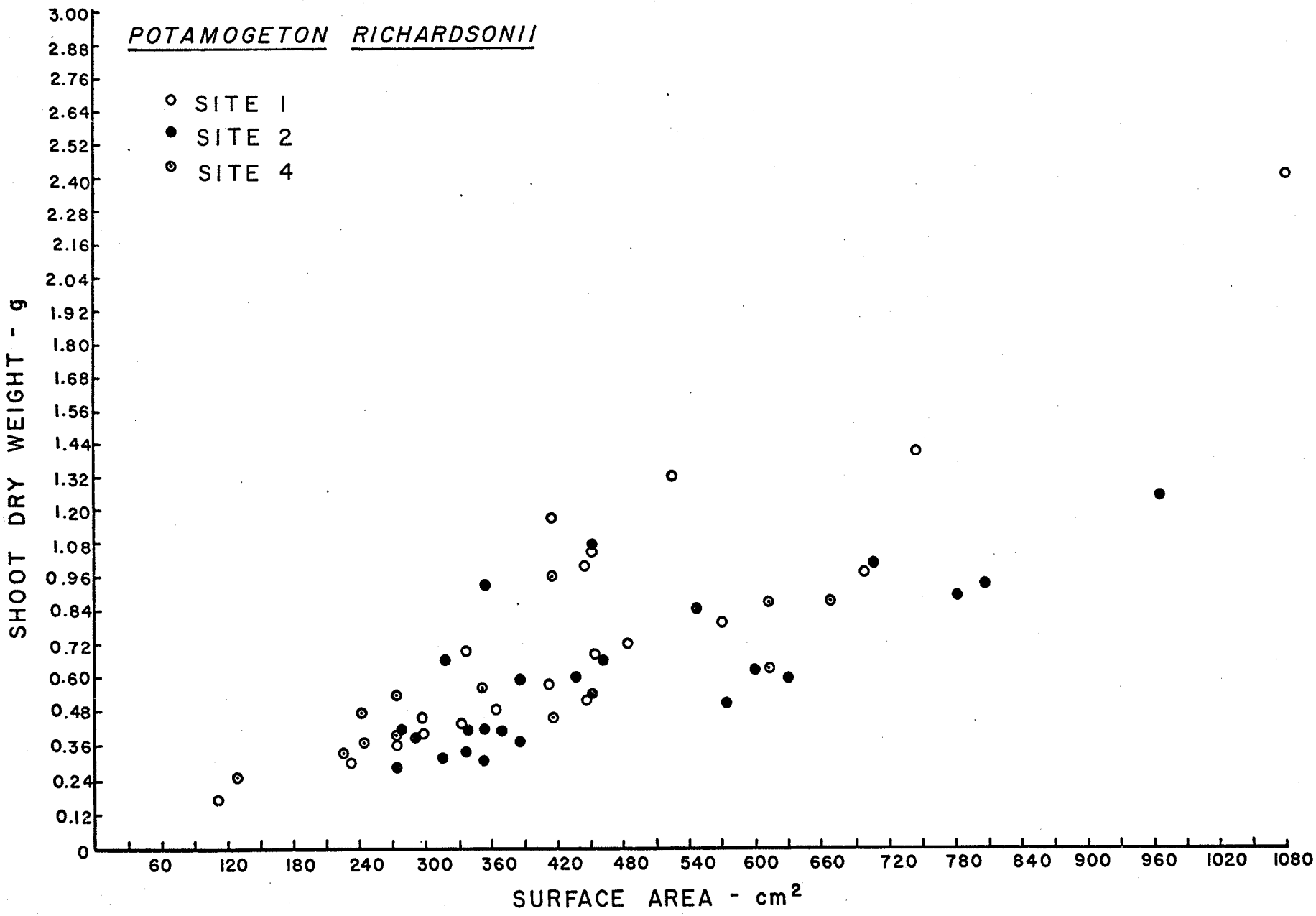

POTAMOGETON PECTINATUS
SHOOT DRY WEIGHT - g
.75
.72
.69
.66
.63
.60
.57
.54
.51
.48
.45
.42
.39
.36
.33
.30
.27
.24
.21
.18
.15
.12
.09
.06
.03
0
30
60
90
120
150
180
210
240
270
300
330
360
390
420
450
480
510
540
SURFACE AREA - cm²
SITE 1
SITE 2
SITE 3

Figure 29. Scatter diagram illustrating the relationship between shoot dry weight (g) and surface area (cm^2) in Potamogeton richardsonii from sites 1, 2 and 4. This relationship can be approximated by equation 8:

$$A = (W/0.0017) + 27.4706$$

where A = surface area (cm^2) and W = dry weight (g).


POTAMOGETON RICHARDSONII
SITE 1
SITE 2
SITE 4
SHOOT DRY WEIGHT - g
3.00
2.88
2.76
2.64
2.52
2.40
2.28
2.16
2.04
1.92
1.80
1.68
1.56
1.44
1.32
1.20
1.08
0.96
0.84
0.72
0.60
0.48
0.36
0.24
0.12
0
60
120
180
240
300
360
420
480
540
600
660
720
780
840
900
960
1020
1080
SURFACE AREA - cm2

Using equations 7 and 8, the total surface area of the macrophytes in each quadrat sample was estimated from their total dry weight.

c. Lesion index

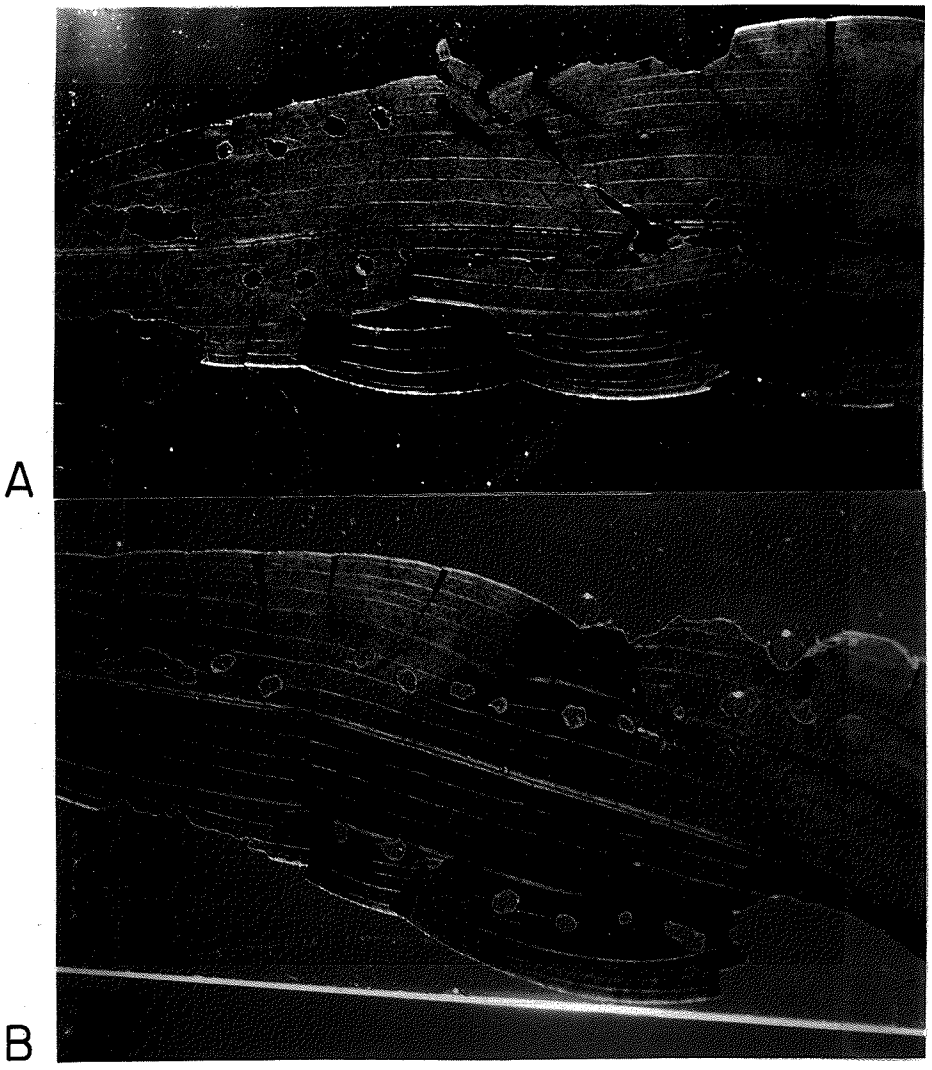
The vegetation remaining in the samples after selection of the shoots for sections a and b above was used for estimating lesion index. One hundred randomly selected discs 1 cm in diameter were punched from the leaves of P. richardsonii with a cork borer. For P. pectinatus, where flat leaf blades were present, 100 blade sections about 1.5 cm long were cut randomly from the plants. An equal number (20) of sections was taken from each quadrat sample. The sections were blotted to remove excess water and frozen in airtight containers. Freezing had no effect on lesion morphology.

On thawing, the leaf sections were examined under transmitted light under a dissecting microscope for the presence of characteristic lesions (Fig. 30) which were compared with those made by snails in the laboratory. Such lesions had well-defined, although jagged edges, the pigmentation along the margins was not altered and they often occurred in series which ran parallel to the leaf axis, although the lesions themselves could have any orientation. Perforation was either complete or incomplete, depending on the size of the grazer and the grazing intensity.

In P. richardsonii, grazer-induced lesions could further be distinguished from other types of lesions by the following characteristics:

1. Grazer-induced lesions were not characterized by mottling of the margins with red pigments.

Figure 30. Lesions made by snails in Potamogeton richardsonii leaves.


A
B
1 cm

2. Grazer-induced lesions had curved, irregular margins which did not follow the pattern of venation in the leaf, although they often occurred between major veins. Mechanical tears of the leaf, as a rule, had margins that were always parallel to the leaf venation.
3. Grazer-induced lesions were often, but not always, enclosed on all sides by undamaged lamina, and when perforated, had a characteristic "shot" appearance.

In P. pectinatus, grazer-induced lesions were harder to recognize on account of the filiform morphology of the leaves but could nonetheless be differentiated by the following features:

1. Mechanically induced lesions caused by creasing of the leaf were, as a rule, linear and extended across the width of the entire leaf.
2. Lesions caused by fungal infection were circular and small; during the early stages of development they were light green in color, developing later into necrotic reddish-orange or black spots. These lesions never perforated the leaf and were often grouped in large numbers along a single blade.
3. Grazer-induced lesions were irregularly shaped and were often perforated.

A lesion index was estimated by scoring the leaf sections according to presence or absence of grazer-induced lesions, and expressing the number of leaf sections exhibiting lesions as a percentage of the total number of sections examined.

d. Dry weight

All macrophytes were washed under a jet of water to remove as much as possible of attached sponges, insect larval cases, lime incrustations and epiphytic algae. Dry weight of plant material was determined after drying to constant weight at 105 C. Reproductive structures were treated separately from the vegetative portions.

C. Gastropods

a. Numbers and size class frequencies

The numbers of all gastropods present in the quadrat samples were recorded. The axial lengths of all intact individuals of Physa gyrina and Lymnaea stagnalis were measured to the nearest 0.5 mm using Vernier calipers.

b. Biomass

Because of the large size of the samples, it was not practical to clean, blot and weigh all snails directly. Instead, individuals of P. gyrina and L. stagnalis chosen randomly from the quadrat samples were cleaned, blotted to remove excess water and weighed. From these values, relationships were constructed between axial length and live weight (e.g. Stiven and Walton, 1967; Daniels and Armitage, 1969; Burky, 1971; Boerger, 1975b; Herrmann and Harman, 1975).

Scatter diagrams for log live weight versus log axial length are given for P. gyrina in Fig. 31 and for L. stagnalis in Fig. 32. These relationships could be approximated by the general equation,

$$\log y_i = k \log x_i + Q \quad \ldots\ldots\ldots (9),$$

Figure 31. Regression of log live weight (g) on log axial length (mm) in Physa gyrina from sites 1, 2, 3 and 4. This relationship can be approximated by equation 10:

$$\log y_i = 2.72 \log x_i - 3.63$$

where y_i = individual live weight (g) and x_i = axial length (mm).

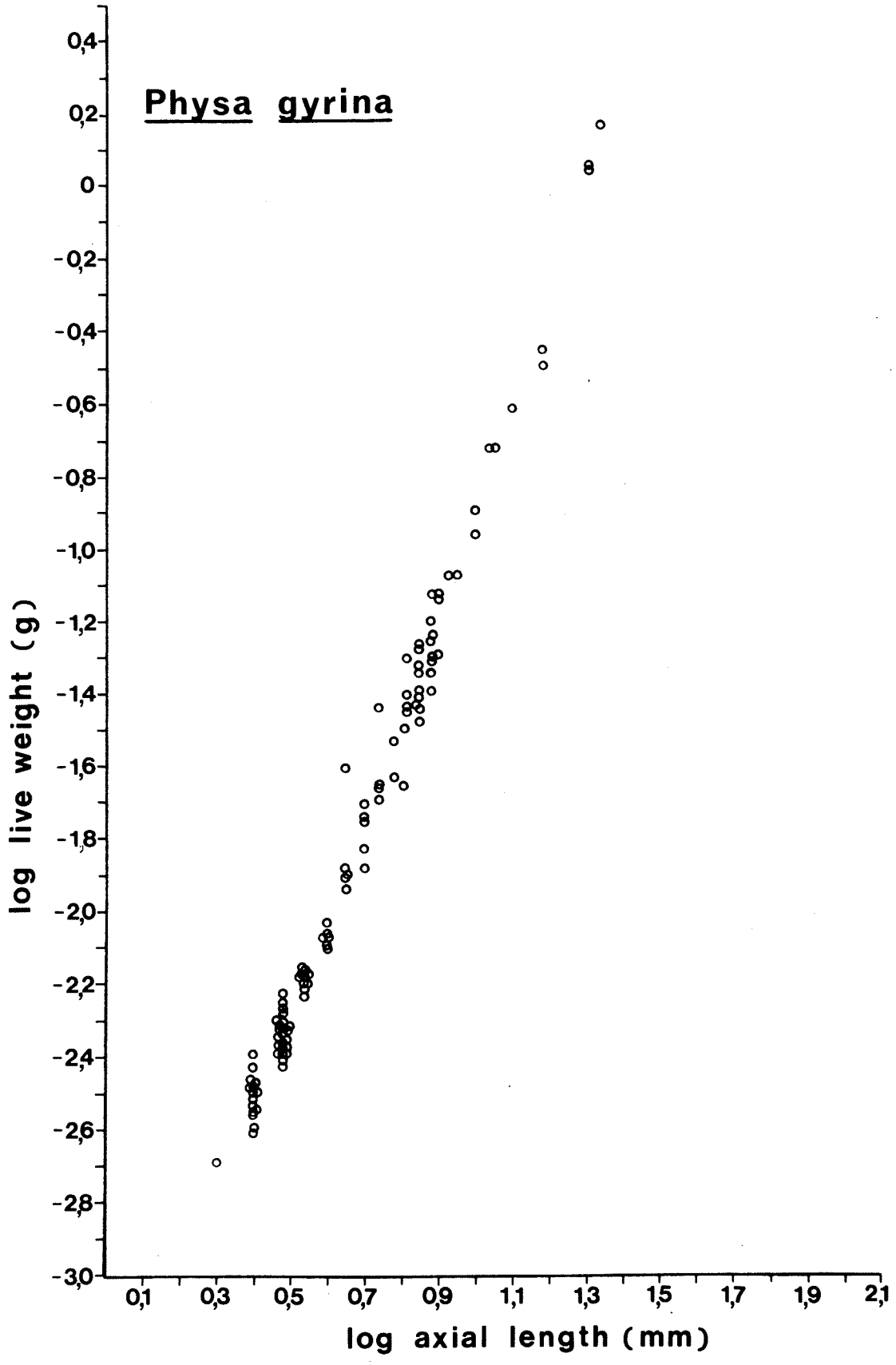
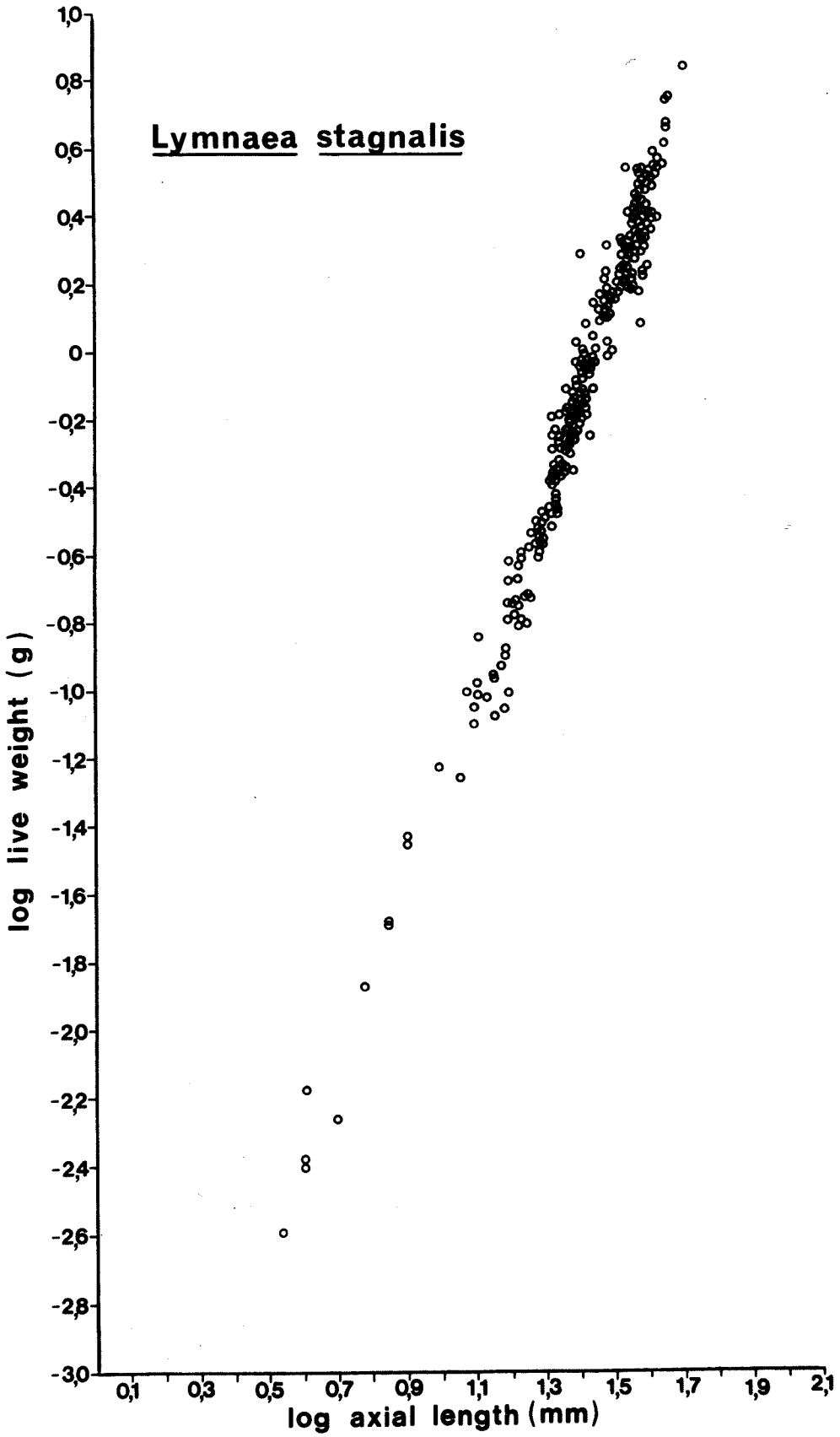

Physa gyrina
0,4
0,2
0
-0,2
-0,4
-0,6
-0,8
-1,0
-1,2
-1,4
-1,6
-1,8
-2,0
-2,2
-2,4
-2,6
-2,8
-3,0
log live weight (g)
0,1
0,3
0,5
0,7
0,9
1,1
1,3
1,5
1,7
1,9
2,1
log axial length (mm)

Figure 32. Regression of log live weight (g) on log axial length (mm) in Lymnaea stagnalis from sites 1, 2, 3 and 4. This relationship can be approximated by equation 11:

$$\log y_i = 2.94 \log x_i - 4.29$$

where y_i = individual live weight (g) and x_i = axial length (mm).


Lymnaea stagnalis
log live weight (g)
1,0
0,8
0,6
0,4
0,2
0
-0,2
-0,4
-0,6
-0,8
-1,0
-1,2
-1,4
-1,6
-1,8
-2,0
-2,2
-2,4
-2,6
-2,8
-3,0
0,1
0,3
0,5
0,7
0,9
1,1
1,3
1,5
1,7
1,9
2,1
log axial length (mm)

where y_i = individual live weight (g), x_i = axial length (mm) and k and Q are constants (Pip and Stewart, 1976). For P. gyrina from the combined sites, this relationship was, at $p < .001$, n=119;

$$\log y_i = 2.72 \log x_i - 3.63 \quad \ldots\ldots (10),$$

and for L. stagnalis, at $p < .001$, n=221, it was:

$$\log y_i = 2.94 \log x_i - 4.29 \quad \ldots\ldots (11).$$

No differences in weight-length relationships were found between individuals grouped according to different sites.

The snails present in each quadrat sample were grouped into size classes at 0.5 mm intervals. Rewriting equation 9 in exponential form, the mean live weight of an individual in each size class (y_i) was calculated:

$$y_i = 10^{Q x_i^k} \quad \ldots\ldots\ldots\ldots (12).$$

This value was multiplied by the number of individuals present in each size class (n_c) to give the total live weight of the size class (y_c):

$$y_c = n_c y_i = n_c (10^{Q x_i^k}) \quad \ldots\ldots\ldots (13).$$

The estimated weights of all size classes were summed to give an estimate of the total live weight of each species in the sample (Y):

$$Y = \Sigma y_c = \Sigma n_c (10^{Q x_i^k}) \quad \ldots\ldots\ldots (14).$$

Since in L. stagnalis the variability in live weight increases in the larger size classes, the comparatively few individuals of this species

that exceeded 25 mm in axial length were all weighed to increase the accuracy of the total estimate. Where damaged individuals occurred for which the axial length could not be determined, the live weight for these was estimated from the mean axial length for the subpopulation at the particular site, habitat and time. Snails were returned to the field after measurement.

Results

I. Environmental measurements

A. Water chemistry

a. Season II (1973)

At sites 1 and 2 (Fig. 33A), initial pH values for surface water were similar, but after time 1 they diverged progressively until the greatest difference between the two sites was observed at time 5. Convergence occurred after time 5 but the values at site 1 remained consistently higher throughout the season, possibly because of the smaller volume and denser submerged vegetation at this site.

The pH values for sites 3 and 4 (Fig. 33B), although higher at site 3, showed similar fluctuation patterns, with minima at time 4, followed by a sharp rise at time 5. Another peak was observed at time 7 at site 4.

Values for total filtrable residue at sites 1 and 2 (Fig. 33C) followed similar patterns; values were slightly higher at site 1 during the second half of the season, but by time 8 values at site 1 decreased sharply while those at site 2 showed a moderate increase. Values at site 1 during the 1973 season were higher than those observed during 1972 (Fig. 3B).

The patterns for total filtrable residue at sites 3 and 4 (Fig. 33D) showed similar timing of fluctuations, with minima observed at both sites at time 5. Values at site 4 were very high at the beginning of the season, exceeding 3 g/l at time 3.

Values for total alkalinity at sites 1 and 2 (Fig. 34A) were

Figure 33. Values for pH (A and B) and total filtrable residue ($mg/l \times 10^{-2}$) (C and D) of surface water at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season.

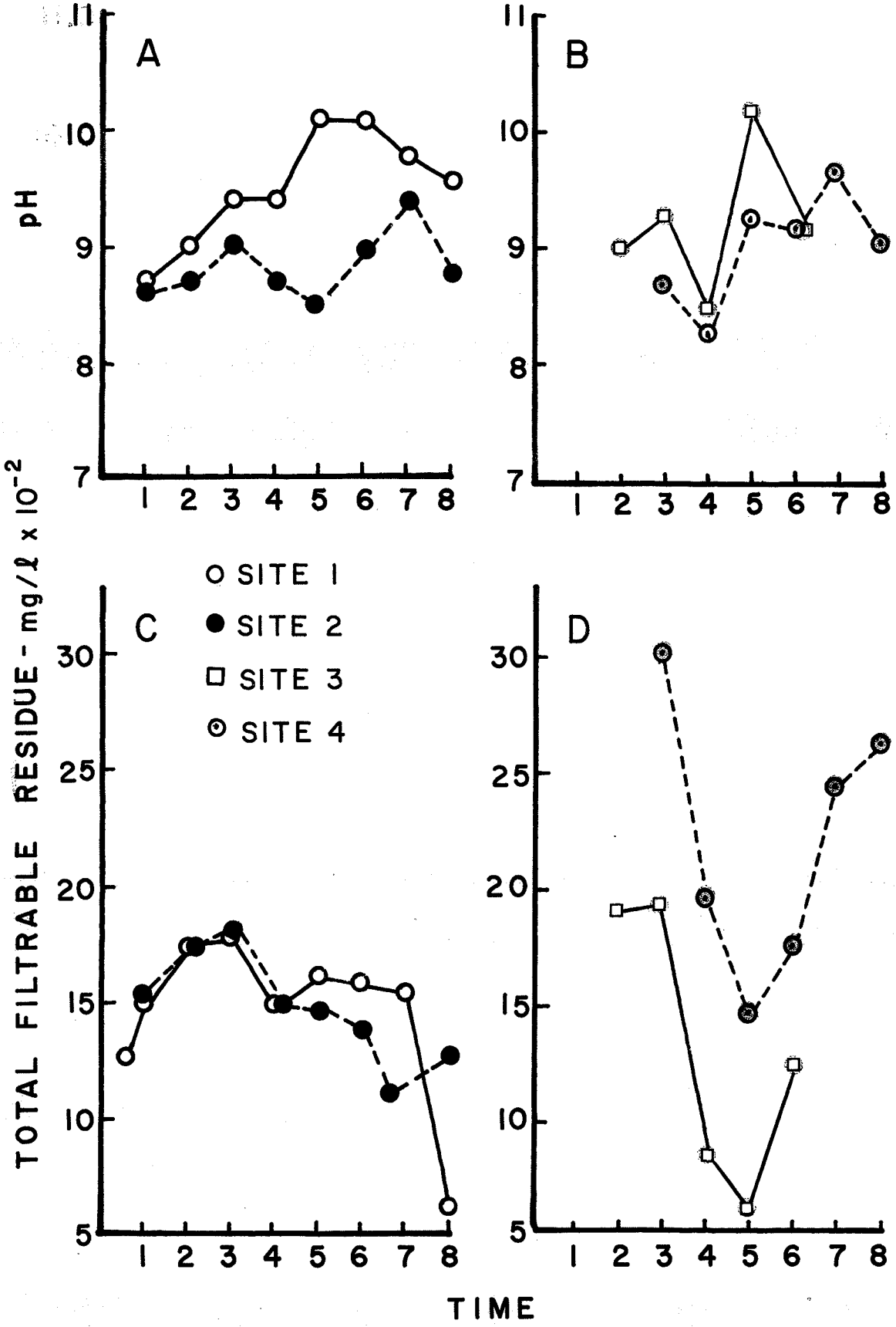
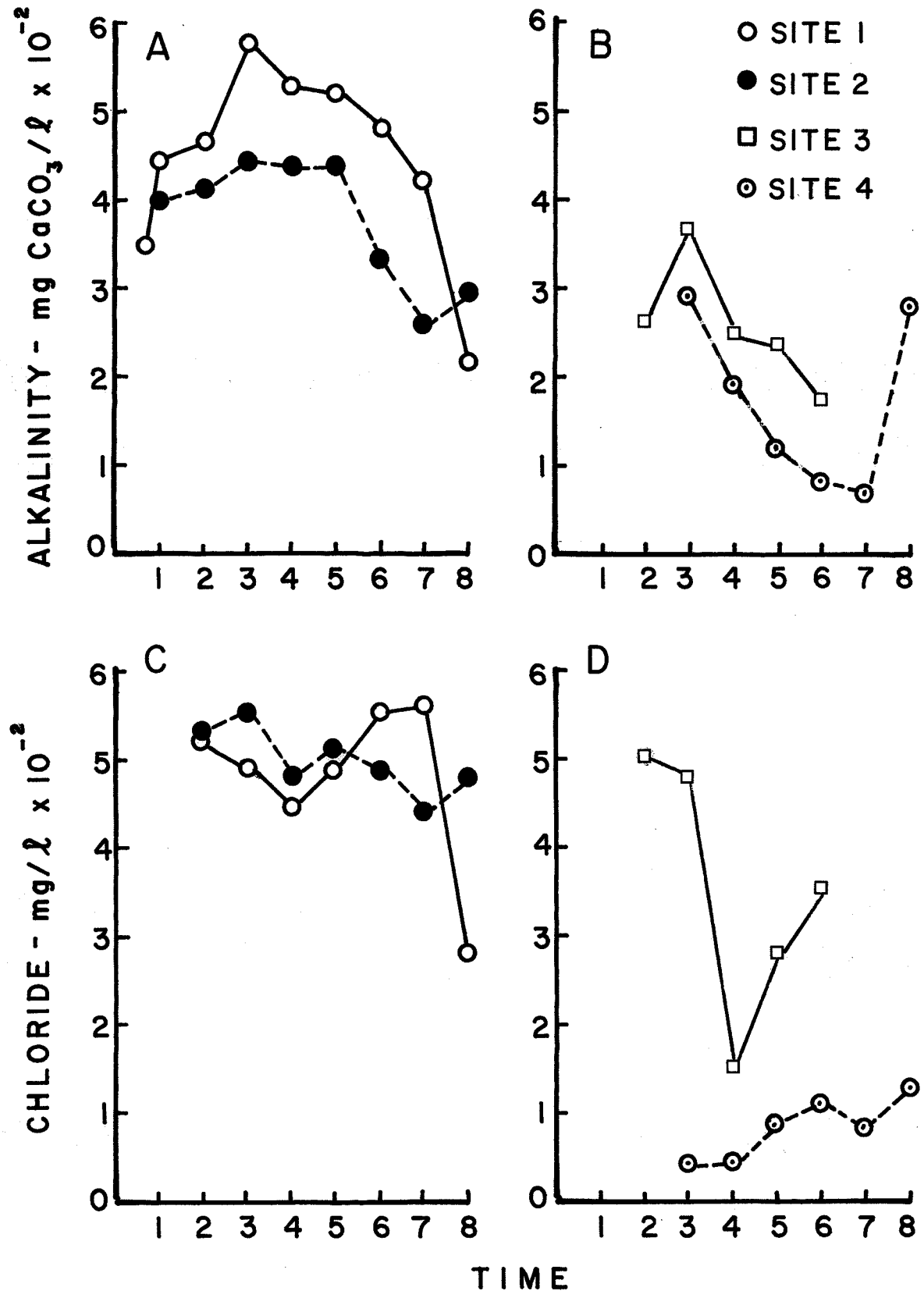

A
B
C
D
pH
TOTAL FILTRABLE RESIDUE - mg/l x 10⁻²
TIME
SITE 1
SITE 2
SITE 3
SITE 4
11
10
9
8
7
30
25
20
15
10
5
1 2 3 4 5 6 7 8

Figure 34. Values for total alkalinity (mg/l $CaCO_3$ x 10^{-2}) (A and B) and chloride (mg/l x 10^{-2}) (C and D) of surface water at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season.


A
B
C
D
SITE 1
SITE 2
SITE 3
SITE 4
ALKALINITY - mg $CaCO_3/\ell \times 10^{-2}$
CHLORIDE - mg/$\ell \times 10^{-2}$
TIME
0
1
2
3
4
5
6
7
8

highest during times 3-5, those at site 1 being consistently higher than those at site 2, except for time 8. The values for sites 3 and 4 (Fig. 34B) were lower than those at sites 1 and 2, with a high value at time 3 followed by a general decline. An abrupt increase was observed at site 4 after time 7.

Chloride values at sites 1 and 2 (Fig. 34C) followed a pattern that was similar to that of total filtrable residue; values during the first part of the season were slightly higher at site 2, but after time 5 values were higher at site 1. As with total filtrable residue, a sharp decline occurred at site 1 after time 7 while a moderate increase was observed at site 2. The values at sites 3 and 4 (Fig. 34D) were generally lower and large fluctuations were apparent at site 3.

Values for molybdenum-blue phosphorus at sites 1 and 2 (Fig. 35A) were out of phase by one sampling period, a peak occurring at time 3 at site 1 and at time 4 at site 2. Values for sites 3 and 4 (Fig. 35B) appeared to fluctuate in synchrony.

The patterns for sulphate (Fig. 35C and D) showed little correlation between sites 1 and 2 and sites 3 and 4. A minimum was observed at time 5 at sites 2 and 3 and at time 7 at sites 2 and 4. A peak occurred at time 6 at sites 2 and 4. Site 1 showed the smallest amplitude of the fluctuations of this parameter.

Combined nitrate and nitrite estimates were consistently higher at site 1 than at site 2 (Fig. 36A) but the timing of the fluctuations was poorly correlated. Sites 3 and 4 (Fig. 36B) showed patterns that were similar during times 3-6.

Calcium activity at both sites 1 and 2 (Fig. 36C) showed a general increase from an initially low value until a peak at times

Figure 35. Values for molybdenum-blue phosphorus (mg/l) (A and B) and sulphate (mg/l x 10^{-1}) (C and D) of surface water at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season.

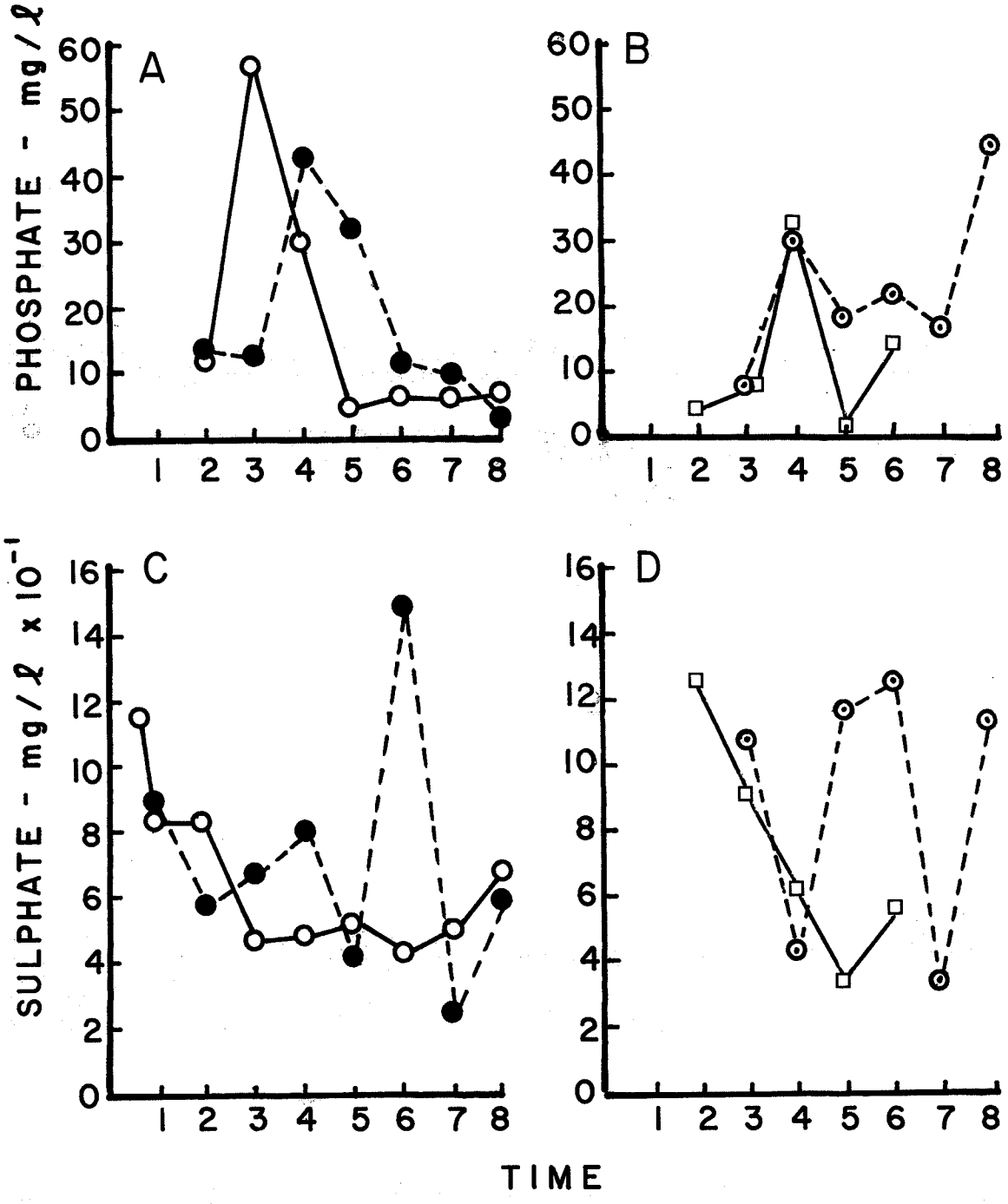
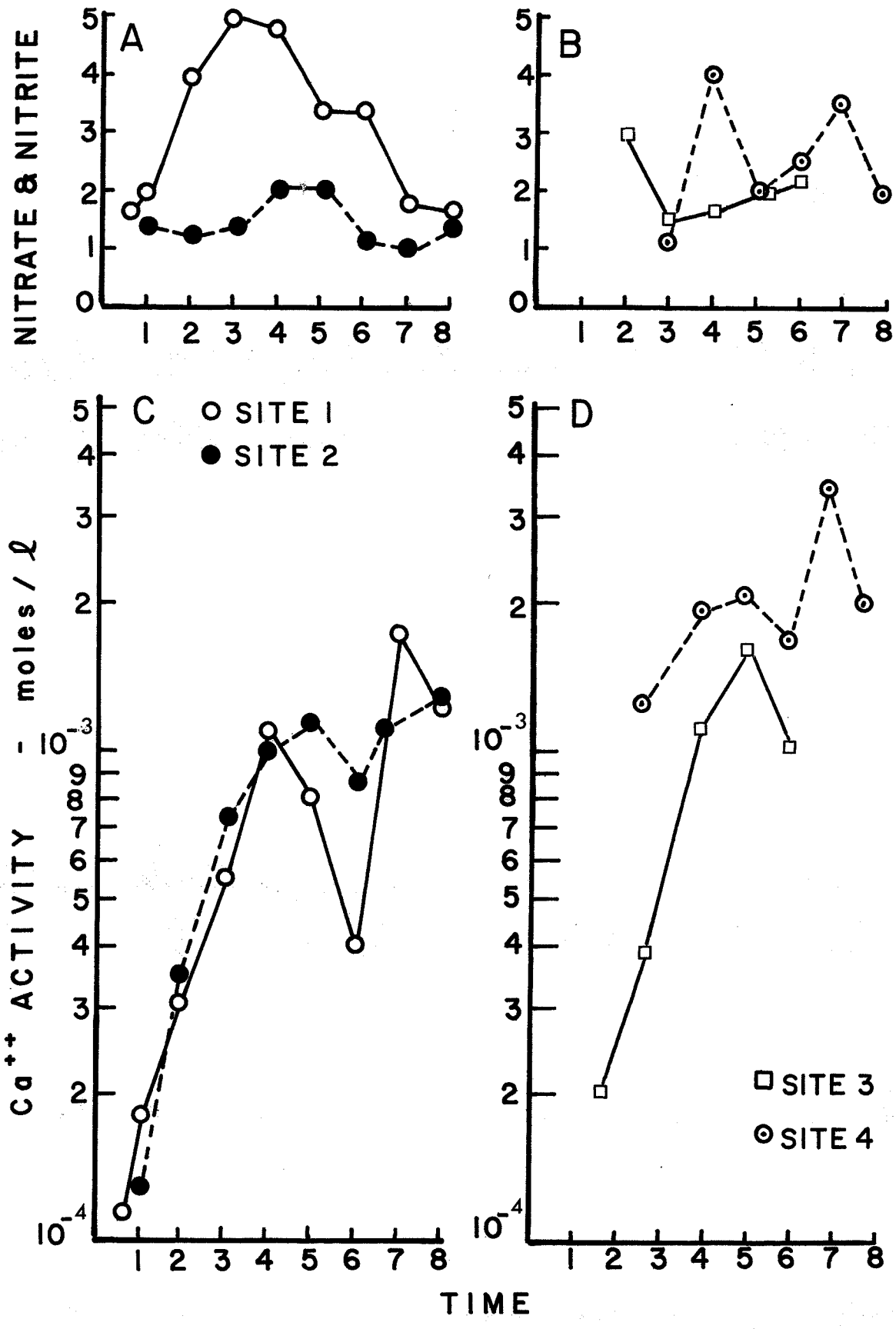

A
B
C
D
PHOSPHATE - mg / ℓ
SULPHATE - mg / ℓ x 10⁻¹
TIME
SITE 1
SITE 2
SITE 3
SITE 4

Figure 36. Values for combined nitrate and nitrite (mg/l) (A and B) and calcium activity (moles/l) (C and D) of surface water at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season.


A
B
C
D
NITRATE & NITRITE
Ca++ ACTIVITY - moles / ℓ
SITE 1
SITE 2
SITE 3
SITE 4
TIME

4 and 5 respectively. Minima were observed at both sites at time 6. The patterns for sites 3 and 4 (Fig. 36D) were similar and also showed decreases at time 6. The high values observed at site 4 for calcium activity reflected the calcareous nature of the parent material. At this site the stems and upper surfaces of the leaves of submerged macrophytes were heavily encrusted with calcium carbonate which resulted from decomposition of bicarbonate at these surfaces.

In general, sites 1 and 2 were similar with respect to water chemistry; site 1 showed higher values for pH, total alkalinity and combined nitrate and nitrite while site 2 was characterized by large fluctuations of sulphate. Although site 3 was also located in the Delta Marsh, it showed greater similarity to site 4, which was situated in a separate hydrological system, than to sites 1 and 2, with respect to levels and fluctuations of pH, total filtrable residue, total alkalinity, molybdenum-blue phosphorus, calcium activity and combined nitrate and nitrite. Site 4 represented the most extreme conditions in that it showed the highest values for total filtrable residue and calcium activity but the lowest values for total alkalinity and chloride.

i. Chemical fallout

The proximity of unpaved roads at all of the sites caused some concern since the contributed solutes, in the form of dust carried by wind or deposited with precipitation, may have been of sufficient magnitude to affect water quality at the sites. In an effort to assess the magnitude of such fallout, the precipitation accumulated at water level during the two week period from time 3 to 4 was examined, yielding the results in Table XVI. These values represented

TABLE XVI. Results of the analysis of the total precipitation and fallout occurring during the two-week period from times 3 to 4, 1973, at sites 1, 3 and 4.

	site 1	site 3	site 4
Total sample volume, ml	250	195	147
pH	9.4	8.5	8.1
Total filtrable residue, mg/l	596	137	0
Total alkalinity, mg $CaCO_3$/l	130	14.4	15.0
Chloride, mg/l	156	73	0
Molybdenum-blue phosphorus, mg/l	4.0	6.5	0
Sulphate, mg/l	47	12	0
Nitrate and nitrite, mg/l	0.8	9.0	0.4
Calcium activity, moles/l	2.7×10^{-4}	0	0

the influx of solutes from atmospheric sources only and did not include the contributions from surface runoff.

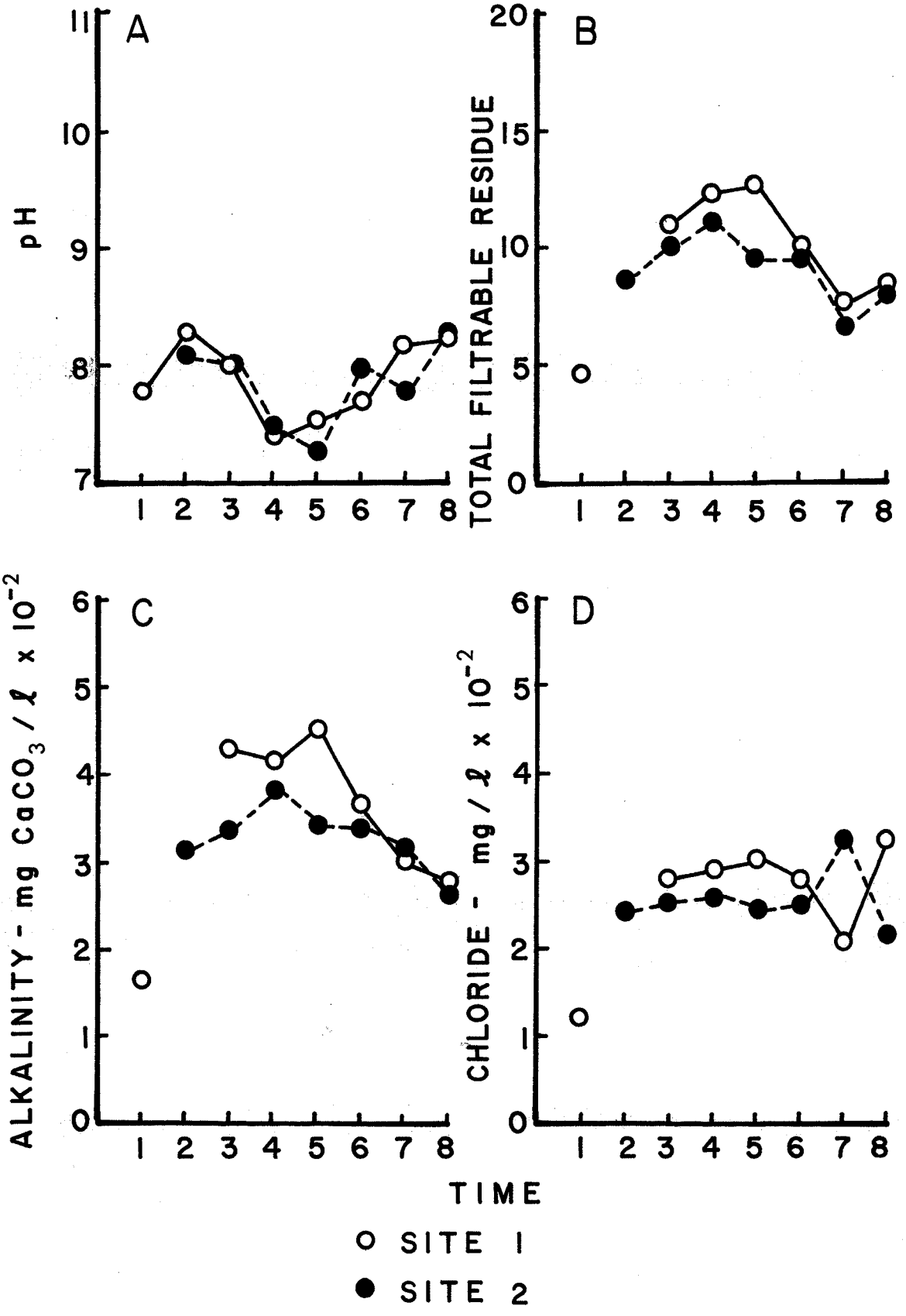
The greatest influx of solutes from atmospheric sources occurred at site 1, and presumably, at the adjacent site 2. Here, all of the monitored variables showed surprisingly high values, suggesting that use of the adjacent roads had a significant effect on the water quality at these sites. The values at site 3 showed comparatively smaller values for total filtrable residue, total alkalinity, chloride, sulphate and calcium activity but greater values for molybdenum-blue phosphorus and combined nitrate and nitrite. The generally reduced values perhaps reflected the limited amount of traffic using the road; the increased values for phosphorus and nitrogen may have reflected the proximity of commercial farming operations. Site 4, adjacent to a gravelled provincial trunk highway, showed the least contribution due to fallout of all of the sites. Measurable levels were recorded for total alkalinity and combined nitrate and nitrite. Thus, paradoxically, the most exposed site with respect to public access was also the least affected in terms of water quality by human activity.

b. Season III (1974)

Values for surface pH at sites 1 and 2 (Fig. 37A) were significantly lower than those of the 1973 season and reached a minimum during times 4 and 5. These low values were probably a consequence of the spring flooding which diluted the water and retarded the growth of submerged macrophytes.

Values for total filtrable residue (Fig. 37B) showed maxima at both sites during midseason. The values at site 1 were

Figure 37. Values for pH (A), total filtrable residue (mg/l x 10^{-2}) (B), total alkalinity (mg $CaCO_3$/l x 10^{-2}) (C) and chloride (mg/l x 10^{-2}) (D) of surface water at sites 1 and 2 during the 1974 season.


A
B
C
D
pH
TOTAL FILTRABLE RESIDUE
ALKALINITY - mg $CaCO_3$ / ℓ x 10^{-2}
CHLORIDE - mg / ℓ x 10^{-2}
TIME
SITE 1
SITE 2

slightly higher than those at site 2, but were still significantly lower than the values of the 1973 season, although they were similar to the 1972 levels at site 1.

Values for total alkalinity (Fig. 37C) were higher at site 1 than at site 2 during much of the growing season. Like those of total filtrable residue, these values were lower than those of 1973, but similar to those of 1972.

Values for chloride (Fig. 37D) were similar at both sites but were almost half of the concentrations observed during both 1973 and 1972.

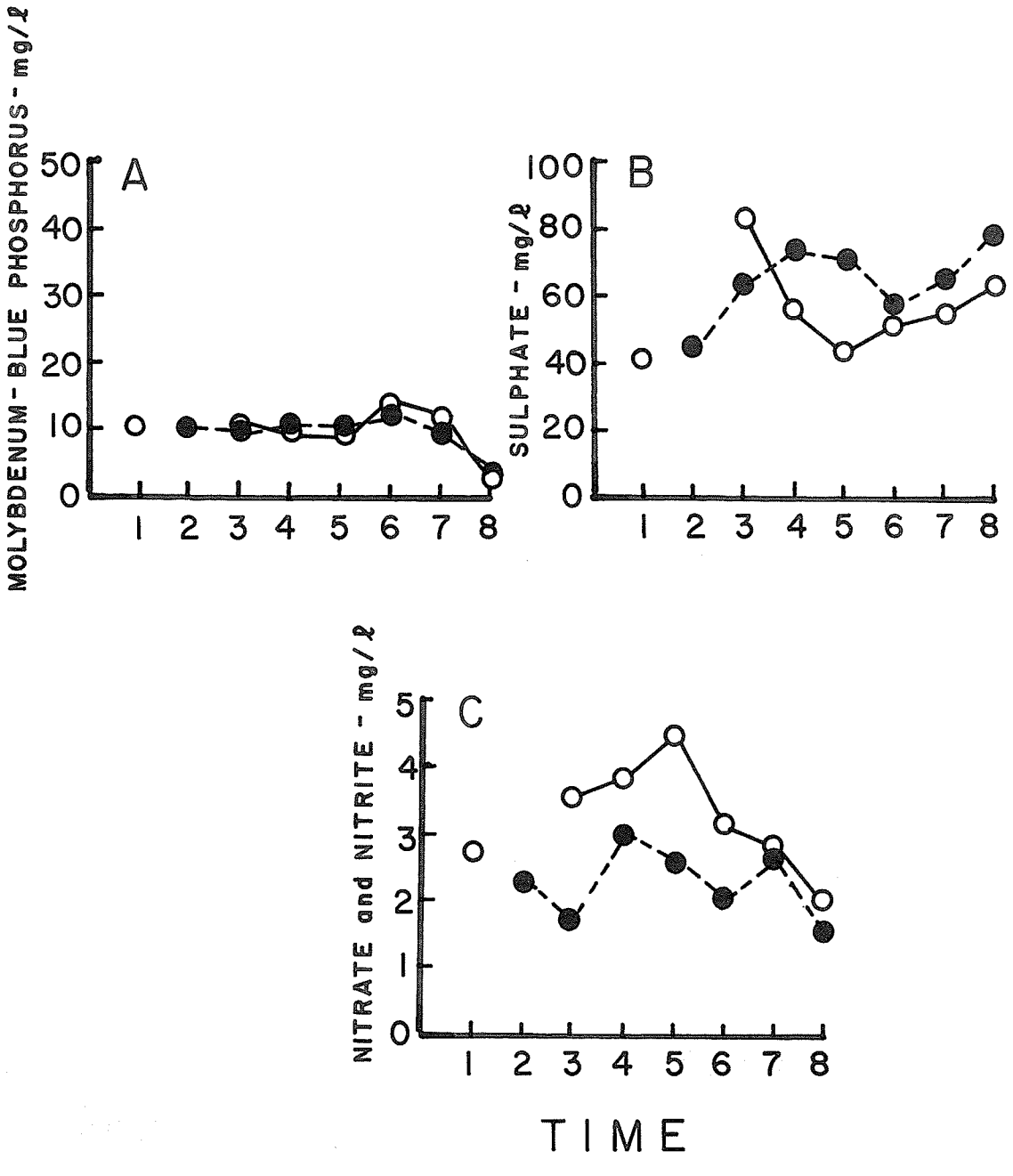
Values for molybdenum-blue phosphorus (Fig. 38A) were very similar at both sites and no lag between the two sites was observed such as had been seen during 1973. The values were lower than those observed during both the 1973 and 1972 seasons.

Sulphate levels (Fig. 38B) fluctuated relatively little during the 1974 season but were not reduced significantly from those of the previous two seasons, aside from the peaks at site 2 in 1973 (Fig. 35C).

Combined nitrate and nitrite values (Fig. 38C) were higher at site 1 than at site 2, as they had been during 1973. The magnitude of the values was similar to those of 1973 but were slightly lower than those observed at site 1 in 1972.

In general, the water quality during the 1974 season reflected the effects of the spring flooding in the decreased values, as compared with the previous season, for pH, total filtrable residue, total alkalinity and molybdenum-blue phosphorus. However the 1972 season, during which no flooding occurred, was also characterized by lower values at site 1, as compared with the 1973 season, for total

Figure 38. Values for molybdenum-blue phosphorus (mg/l) (A), sulphate (mg/l)(B) and combined nitrate and nitrite (mg/l)(C) of surface water at sites 1 and 2 during the 1974 season.


MOLYBDENUM - BLUE PHOSPHORUS - mg/ℓ
A
50
40
30
20
10
0
1 2 3 4 5 6 7 8
SULPHATE - mg/ℓ
B
100
80
60
40
20
0
1 2 3 4 5 6 7 8
NITRATE and NITRITE - mg/ℓ
C
5
4
3
2
1
0
1 2 3 4 5 6 7 8
TIME
SITE 1
SITE 2

filtrable residue and total alkalinity. The parameters most affected by flooding at site 1 appeared to be pH, chloride and molybdenum-blue phosphorus.

B. Light and temperature

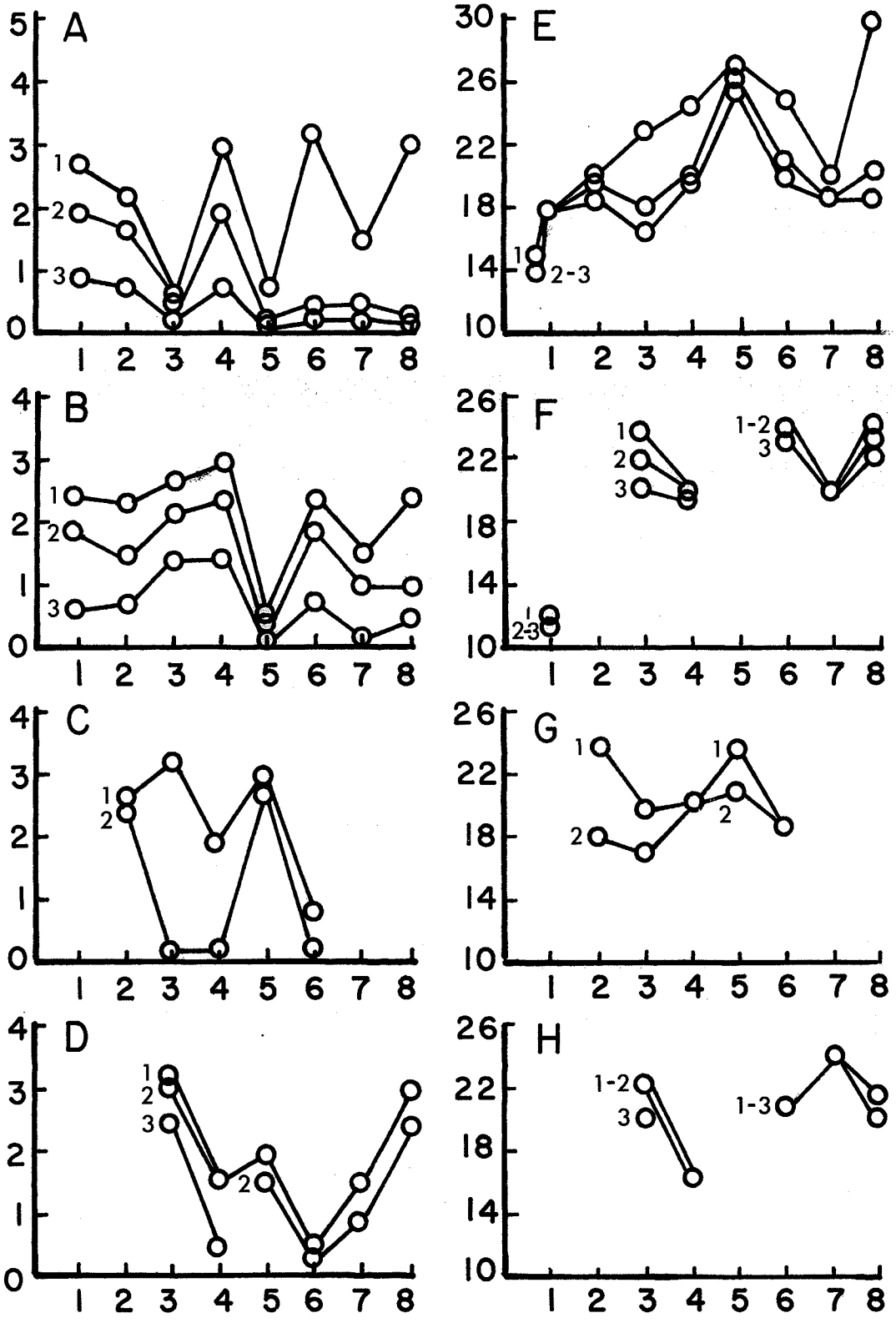
a. Season II (1973)

At site 1 (Fig. 39A), light penetration was decreased at time 1 largely on account of residual suspended particles and coloration persisting from spring runoff and circulation; water clarity continued to decrease until a minimum at time 3. By time 4 the water had cleared but light intensity at deeper strata was reduced because the submerged vegetation had begun to reach the surface. The decreased values observed at times 5 and 7 were exaggerated due to heavy cloud and rain at the time of measurement. The extreme attenuation observed from times 6 to 8 was due to obstruction by dense submerged vegetation.

At site 2 (Fig. 39B), light penetration at time 1 was similar to that at site 1; however after time 1 light penetration continued to increase until a maximum at time 4. The minima at times 5 and 7 were exaggerated due to cloudy atmospheric conditions. Degree of light attenuation at times 6 to 8 was not as pronounced as at site 1 because the submerged vegetation at site 2 was not as dense.

At site 3 (Fig. 39C), light penetration was high at time 2, but dropped sharply by time 3 as the submerged vegetation reached the surface and filamentous algae continued to proliferate. By time 5 light penetration showed an increase; the sharp decline at time 6 was due to dense branching of the macrophytes combined with falling water

Figure 39. Values for light intensity (ft-candles x 10^{-3}) (1 ft-c = 10.763 lm/m^2) at sites 1 (A), 2 (B), 3 (C) and 4 (D), and values for temperature (^{o}C) at sites 1 (E), 2 (F), 3 (G) and 4 (H) at depths just below the surface (1), at 0.25 m (2) and at 0.50 m (3) during the 1973 season.


A
B
C
D
E
F
G
H
1
2
3
1-2
2-3
1-3
TIME

levels, and was exaggerated by cloudy atmospheric conditions.

At site 4 (Fig. 39D), the water showed a high degree of transparency at time 3; the decreased values at times 4, 6 and 7 were due to heavy cloud overcast at the time of measurement. The relatively low values at time 5 were a reflection of the turbidity due to runoff and turbulence that resulted from storms preceding time 5; the bottom at this site was covered by a flocculent layer of carbonates and organic debris whose particles were easily suspended. By time 8 water clarity had improved but was not as pronounced as it had been at time 3. Of the four sites, light penetration with depth was generally greatest at site 4.

The temperature regimes at site 1 (Fig. 39E) showed a period of rapid warming prior to time 1, followed by a state of homothermy at time 1. As warming continued, vertical thermal gradients developed by time 2 and became highly pronounced by time 3. Temperatures continued to rise and all strata reached a maximum at time 5. After time 5 temperatures began to decrease until a minimum was reached at time 7. A period of warming after time 7 heated the surface layers and resulted in the extreme stratification observed at time 8. Thus, after time 1, thermal gradients persisted throughout the season and were not interrupted by a period of homothermy during midseason such as had been observed during 1972 (Fig. 6D).

At site 2 (Fig. 39F), temperatures at time 1 were significantly lower than those at site 1. Thermal stratification was apparent by time 3, but was less pronounced than at site 1. Temperatures decreased after time 3. A decrease accompanied by homothermy was observed at time 7; this was followed by increased temperatures but the different

strata were heated much more uniformly than at site 1. The reduced intensity of thermal stratification at site 2, compared with site 1, was due to its larger surface area and lesser depth, facilitating mixing and heat exchange between various strata; the use of motor-propelled boats at this site may also have disturbed the stratification.

At site 3 (Fig. 39G), temperatures were already high and thermal gradients were pronounced by time 2. Temperatures decreased after time 2 and a state of homothermy ensued at time 4. The midseason peak occurred at time 5, accompanied by stratification, after which temperatures decreased and stratification broke down, resulting in homothermy at time 6.

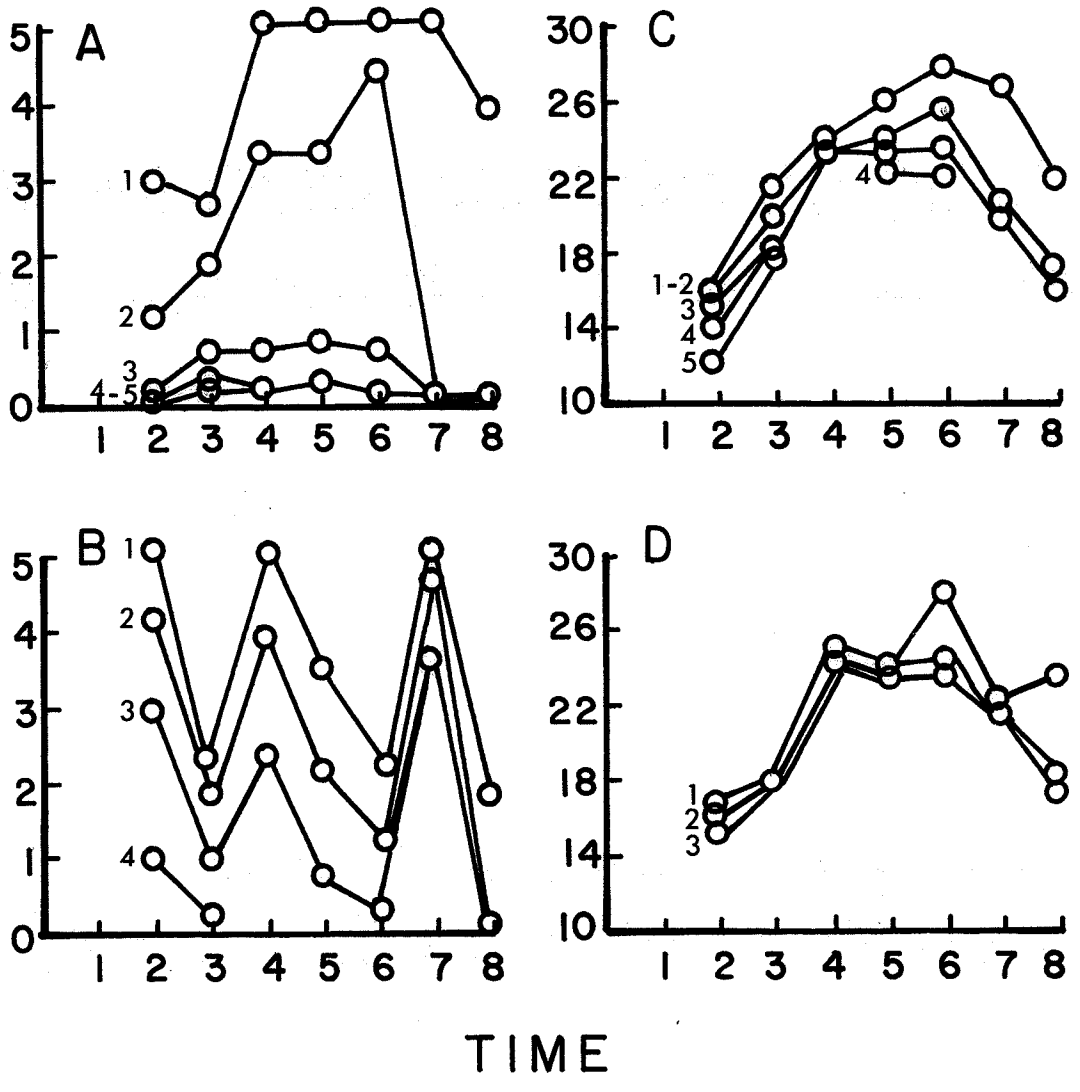
At site 4 (Fig. 39H), thermal gradients were not pronounced due to the relatively exposed aspect of this site. Weak stratification was observed at times 3 and 8; however thermal gradients were usually evident only below the 0.5 m level. A homothermic maximum occurred at time 7, compared to the minimum observed at this time at sites 1 and 2.

The highest temperatures were attained at site 1 while both sites 1 and 3 showed the most pronounced vertical thermal gradients.

b. Season III (1974)

Light attenuation patterns at site 1 (Fig. 40A) were exaggerated at time 2 due to overcast atmospheric conditions. Although light intensity decreased just below the surface at time 3 due to growth of Lemna, light intensity at deeper strata increased due to increasing water transparency. The marked attenuation observed at times 4-8 was due largely to obstruction by a dense surface mat of Lemna.

Figure 40. Values for light intensity (ft-candles x 10^{-3}) (1 ft-c = 10.763 lm/m^2) at sites 1 (A) and 2 (B), and values for temperature (^{o}C) at sites 1 (C) and 2 (D) at depths just below the surface (1), at 0.25 m (2), at 0.50 m (3), at 0.75 m (4) and at 1.00 m (5) during the 1974 season.


A
B
C
D
1
2
3
4
4-5
1-2
TIME

At site 2 (Fig. 40B), the pattern of light attenuation at time 2 suggested that the water was fairly clear. Light penetration was reduced at time 3 due to growth of Lemna, but increased by time 4, paralleling the increase observed at site 1. Decreased light intensity at times 5, 6 and 8 was due to heavy growth of Lemna. At time 7, high light intensities reflected the high degree of water transparency resulting from the absence of significant phytoplankton populations; the readings at this time were taken at a break in the surface mat.

Temperature patterns at site 1 (Fig. 40C) showed some gradients at times 2 and 3 but these were reduced to a state of near homothermy at time 4. Stratification developed again at time 5, temperatures reached maximum values at time 6 and stratification was most marked at times 7 and 8, although temperatures had begun to decline.

At site 2 (Fig. 40D), some stratification was evident at time 2; this was followed by a state of homothermy at time 3. Subsequent development of stratification was generally weak; maximum temperatures were observed at time 6 and stratification was well-developed only at times 6 and 8. Thus, stratification was less pronounced at site 2 than at site 1, as had been the case during the 1973 season, largely on account of the physical conformation of the water basin.

II. Biotic sampling

A. Season II (1973)

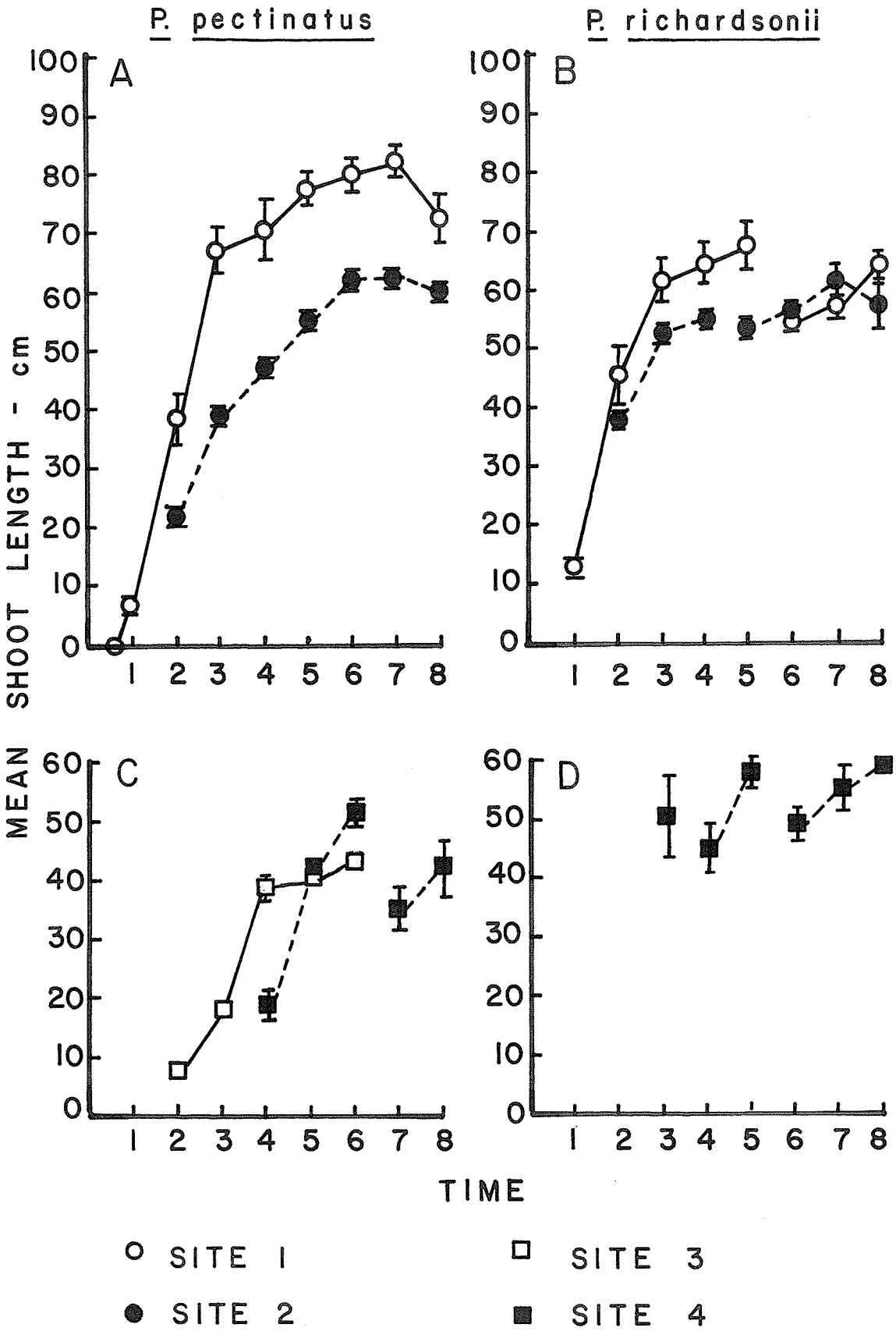
a. Vegetation

i. Mean shoot length

The growth of Potamogeton pectinatus in terms of mean shoot length at sites 1 and 2 (Fig. 41A) was greater at site 1 than at site 2 because of the shallower depth of the latter site. The period between times 1 and 2 was marked by intensive growth towards the surface; when the surface had been reached at time 3, the first inflorescences appeared. The rate of net increase in length decreased after time 3 and second order shoots were produced. Since the first order shoots had deteriorated by time 8, the measurements at this time were based on secondary shoots, accounting for the slight decrease in mean stem length observed after time 7. This pattern of growth was similar to that observed at site 1 during 1972 (Fig. 7A) although the mean shoot lengths during the second half of the 1972 season were greater than those during 1973 because of higher water levels.

The mean shoot lengths of P. pectinatus at sites 3 and 4 (Fig. 41C) were not as great as those at sites 1 and 2 because at both of the former sites this macrophyte occurred in shallower water. Although increase in stem length appeared to be out of phase at sites 3 and 4, flowering began at both sites at time 4, when most of the shoots at site 3 and the shoots in shallower water at site 4 had reached the surface. The continued increase in mean stem length at site 4 after time 4 was due to growth of plants from deeper areas.

Figure 41. Mean shoot length (cm) of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Disjunctions in the curves are due to different shoot generations. Vertical bars represent standard errors.


P. pectinatus
P. richardsonii
A
B
C
D
MEAN SHOOT LENGTH - cm
TIME
SITE 1
SITE 2
SITE 3
SITE 4

The mean shoot lengths of Potamogeton richardsonii at sites 1 and 2 (Fig. 41B) showed similar patterns; the disjunctions during midseason were due to shoots of different orders. The value at time 1 represented linear shoots that already had approximately 11 leaves; by time 2, 22-23 leaves were present and branching and flowering had commenced by time 3, when some of the shoots had reached the surface. Flowering and achene production by different order shoots continued until the end of the season although by time 8 senescence was generally evident.

Increase in stem length of P. richardsonii shoots at site 4 (Fig. 41D) was more rapid than that of P. pectinatus at this site, since by time 3 shoots of the former species were more than twice as long as shoots of the latter. In P. richardsonii, the first shoots had already reached the surface, branched and produced inflorescence buds by time 3. The appearance of second and third order shoots followed after the first order shoots had begun to flower.

ii. Mean dry weight per quadrat sample

The mean values for dry weight of P. pectinatus per quadrat sample (1525 cm^2) at sites 1 and 2 (Fig. 42A) suggested that growth at the two sites was synchronous. The larger values observed at site 2 during the second half of the season were due to increased branching of the plants at that site. Even though the rate of stem length increase decreased after time 3, the bulk of growth, in terms of dry weight, occurred only after the plants had reached the surface at time 3.

The mean dry weight of P. pectinatus per quadrat sample at site 3 (Fig. 42C) appeared to show development that was later than that at sites 1 and 2. A small increase in mean dry weight was observed at

Figure 42. Mean dry weight (g) of shoots (excluding reproductive parts) per quadrat sample (1525 cm^2 bottom area) of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors.

time 3, but growth did not accelerate until after time 4. Growth of P. pectinatus at site 4 (Fig. 42C) was reduced, compared with that at sites 1-3, and was less synchronized within the site since shoots in shallower water reached the surface slightly sooner than those from deeper areas. The first increase in growth occurred after the first inflorescences had appeared at time 4.

The mean values for dry weight of P. richardsonii per quadrat sample at sites 1 and 2 (Fig. 42B) showed a two-week lag in development between the two sites which first became evident after time 2. Maximum dry weight per unit area was observed at time 5 at site 1 and at time 6 at site 2. The maxima were followed by steep decreases as the shoots deteriorated.

The growth of P. richardsonii at site 4 (Fig. 42D) in terms of mean dry weight per quadrat sample was of far smaller magnitude than that at sites 1 and 2, and showed two maxima, at times 5 and 7.

The mean dry weight of seeds and mature reproductive parts of P. pectinatus per quadrat sample (Table XVII) was greater at site 1 than at site 2, despite the greater mean dry weight of above-ground vegetative parts of this plant at site 2. At site 1, the mean ratio of reproductive to vegetative dry weight rose from a value of 0.003 at time 4 to a maximum of 0.164 at time 7 and declined to 0.127 at time 8. At site 2, the value for this ratio increased from 0.015 at time 5 to 0.052 at time 7 and declined to 0.041 at time 8. This suggested that the relative energy channelled into reproduction at site 2 was less than one-third of that at site 1.

At site 3, mature reproductive parts of P. pectinatus were present only at time 6; these represented a reproductive to vegetative

TABLE XVII. Mean dry weight (g) of seeds and mature reproductive parts per quadrat sample (1525 cm^2) of Potamogeton pectinatus and P. richardsonii at sites 1-4 during the 1973 season. Values in parentheses indicate standard errors.

	site 1		site 2	
Time	P. pectinatus	P. richardsonii	P. pectinatus	P. richardsonii
1	0	0	-	0
2	0	0	0	0
3	0	0	0	0
4	0.08 (0.07)	0	0	0.59 (0.23)
5	1.64 (0.48)	12.41 (1.76)	0.34 (0.15)	2.00 (0.70)
6	4.03 (1.25)	2.82 (1.00)	1.97 (0.61)	3.75 (0.58)
7	4.55 (1.23)	0.68 (0.13)	1.89 (0.64)	1.15 (0.25)
8	2.24 (0.48)	0.48 (0.17)	1.00 (0.32)	0.37 (0.18)

	site 3	site 4	
Time	P. pectinatus	P. pectinatus	P. richardsonii
1	-	-	-
2	0	-	-
3	0	0	0
4	0	0	0.03 (0.03)
5	0	0	0.31 (0.15)
6	0.13 (0.04)	0.12 (0.05)	0.59 (0.41)
7	-	0.06 (0.03)	0.26 (0.21)
8	-	0.44 (0.24)	0.26 (0.20)

dry weight ratio of only 0.009. Apparently sexual reproduction was rare at this site. At site 4, the maximum dry weight of reproductive parts of P. pectinatus per quadrat sample was observed at time 8; this represented a maximum reproductive to vegetative dry weight ratio of 0.063.

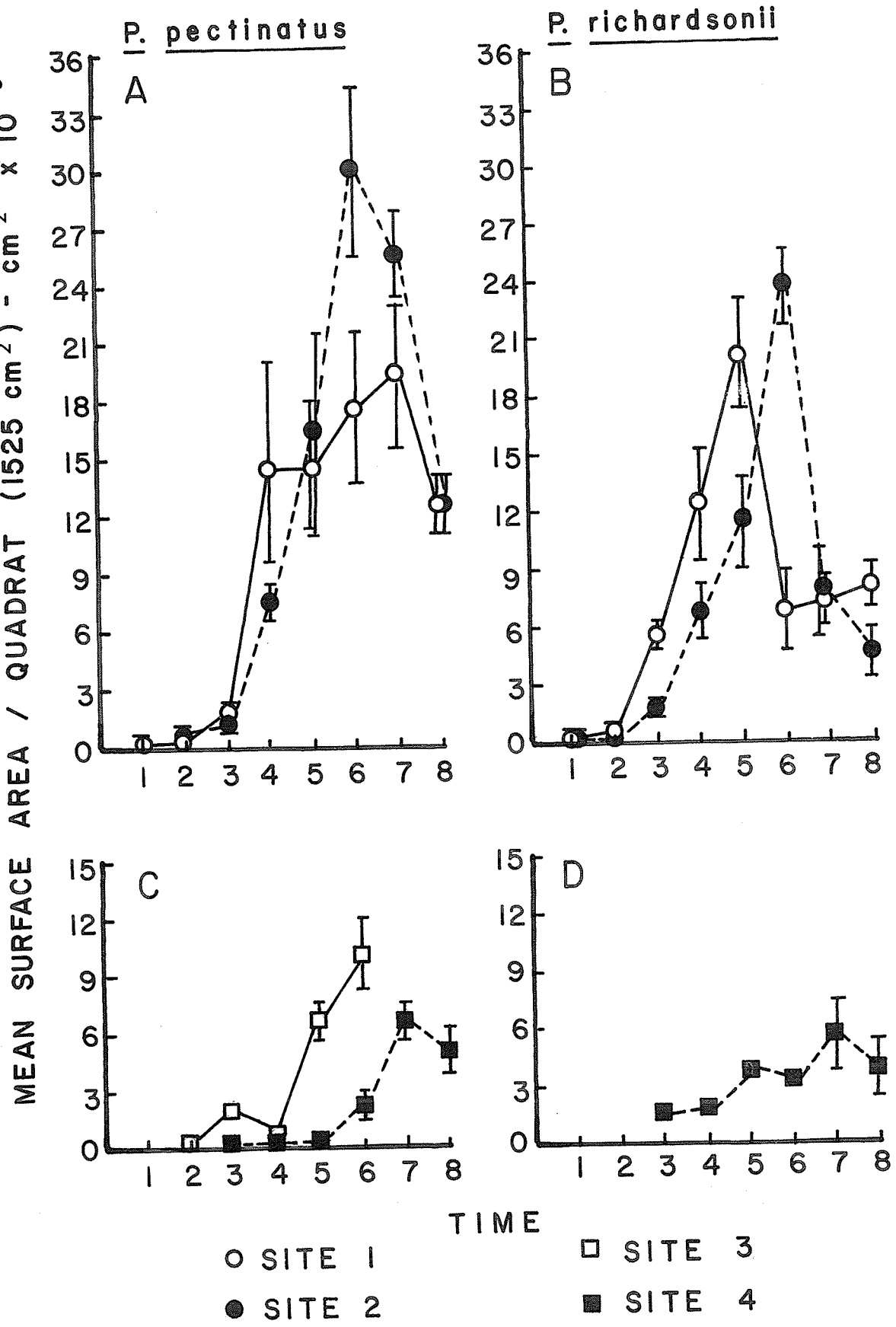
As had been the case with P. pectinatus, the mean dry weight of reproductive parts of P. richardsonii was also significantly greater per unit bottom area at site 1 than at site 2. A well-defined maximum occurred at time 5 at site 1 while at site 2, the maximum occurred at time 6 but was less than one-third the magnitude of the maximum at site 1. The reproductive to vegetative dry weight ratio at site 1 declined from a maximum of 0.364 at time 5 to a value of 0.035 at time 8. At site 2, this ratio declined from a value of 0.102 at time 6 to 0.044 at time 8.

At site 4, maximum dry weight of reproductive parts per quadrat sample was observed for P. richardsonii at time 6; this represented a maximum reproductive to vegetative dry weight ratio of 0.113.

iii. Surface area per quadrat sample

The mean values for surface area of above-ground parts of P. pectinatus and P. richardsonii per quadrat sample, excluding reproductive parts, followed patterns at the four sites (Fig. 43A-D) that paralleled those of dry weight. However the proportions of surface area to dry weight were different for the two species, resulting in accentuation of the fluctuations in P. richardsonii relative to those of P. pectinatus.

Figure 43. Mean surface area ($cm^2 \times 10^{-3}$) of shoots (excluding reproductive parts) per quadrat sample (1525 cm^2 bottom area) of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors.


P. pectinatus
P. richardsonii
A
B
C
D
MEAN SURFACE AREA / QUADRAT (1525 cm^2) - cm^2 x 10^{-3}
TIME
SITE 1
SITE 2
SITE 3
SITE 4

b. Gastropods

i. Mean density per quadrat sample

The mean numbers of Physa gyrina per quadrat sample (1525 cm^2) in stands of Potamogeton pectinatus (Fig. 44A) showed synchronous patterns at sites 1 and 2, with maximum density observed at time 5. The maximum density at site 2 was approximately one-third of that at site 1. The density patterns in stands of P. richardsonii (Fig. 44B) were synchronous and of the same magnitude at both sites, with a maximum observed at times 4 and 5.

At site 1, density per unit bottom area was greater in P. pectinatus than in P. richardsonii stands throughout the season. Paired t-tests showed this difference to be significant ($p < .001$-$.05$, n=10) during times 5-8. At site 2, density per unit bottom area was greater in P. richardsonii than in P. pectinatus stands; this difference was significant ($p < .02$-$.05$, n=10) at times 4, 5 and 8.

At site 4 (Fig. 44C and D), densities of P. gyrina were slightly, but not significantly higher in P. richardsonii than in P. pectinatus stands except during the major density peak at time 8, when the reverse was true. A minor density peak was also observed at time 5 in P. pectinatus stands, and at times 4-5 in P. richardsonii stands.

At site 3 (Fig. 45), densities of P. gyrina reached extremely high levels in the P. pectinatus stands, with a maximum occurring at time 4.

The density patterns for Lymnaea stagnalis in terms of mean numbers per quadrat sample at sites 1 and 2 were synchronous in stands of P. pectinatus (Fig. 46A) with the highest values observed at time 6. Densities at site 2 were approximately half of those at site 1 in these

Figure 44. Mean numbers of Physa gyrina per quadrat sample (1525 cm^2 bottom area) from stands of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and site 4 respectively during the 1973 season. Vertical bars represent standard errors.

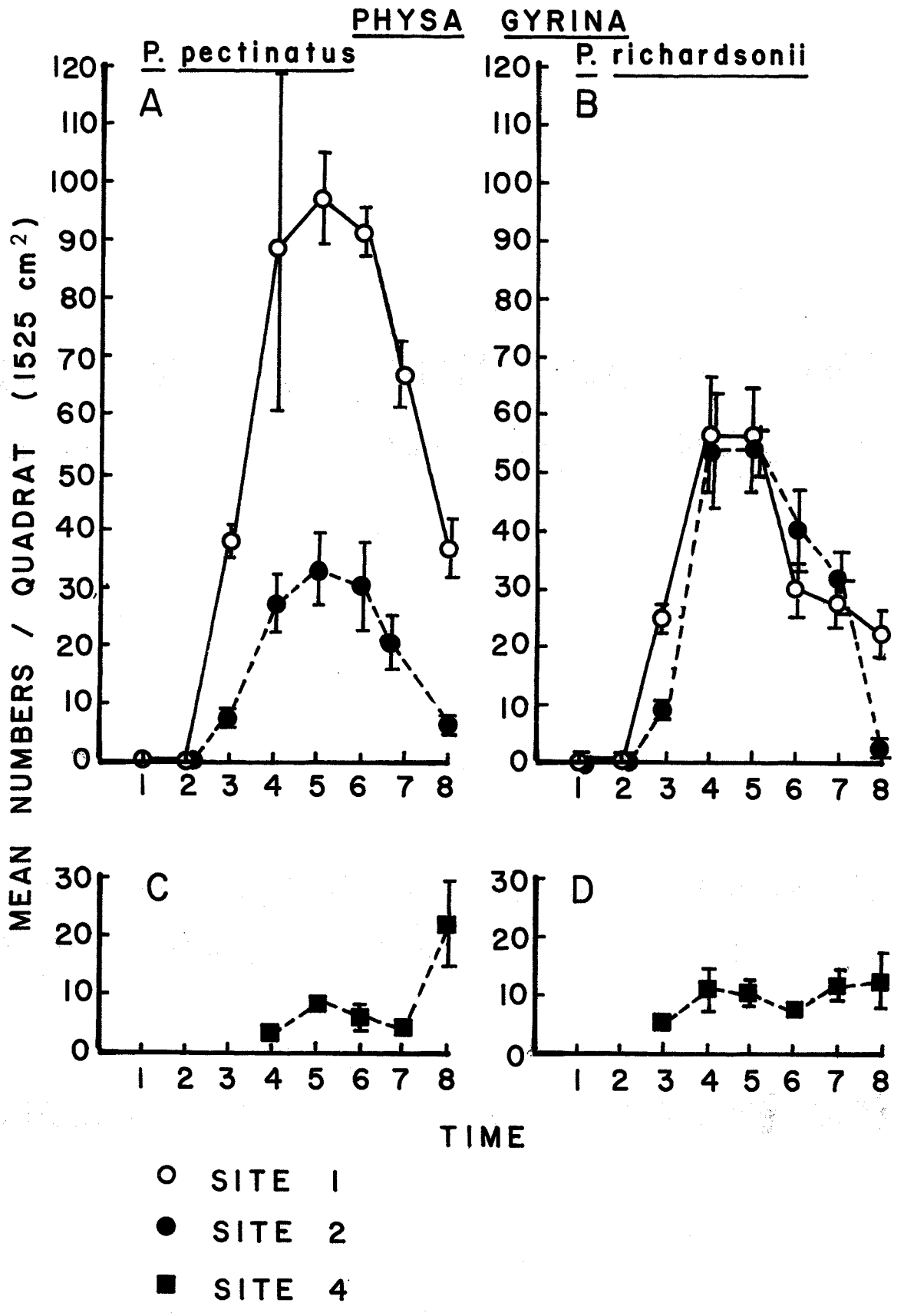

PHYSA
GYRINA
P. pectinatus
P. richardsonii
A
B
C
D
MEAN NUMBERS / QUADRAT (1525 cm²)
TIME
SITE 1
SITE 2
SITE 4

Figure 45. Mean numbers of Physa gyrina per quadrat sample (1525 cm^2 bottom area) from stands of Potamogeton pectinatus at site 3 during the 1973 season. Vertical bars represent standard errors.

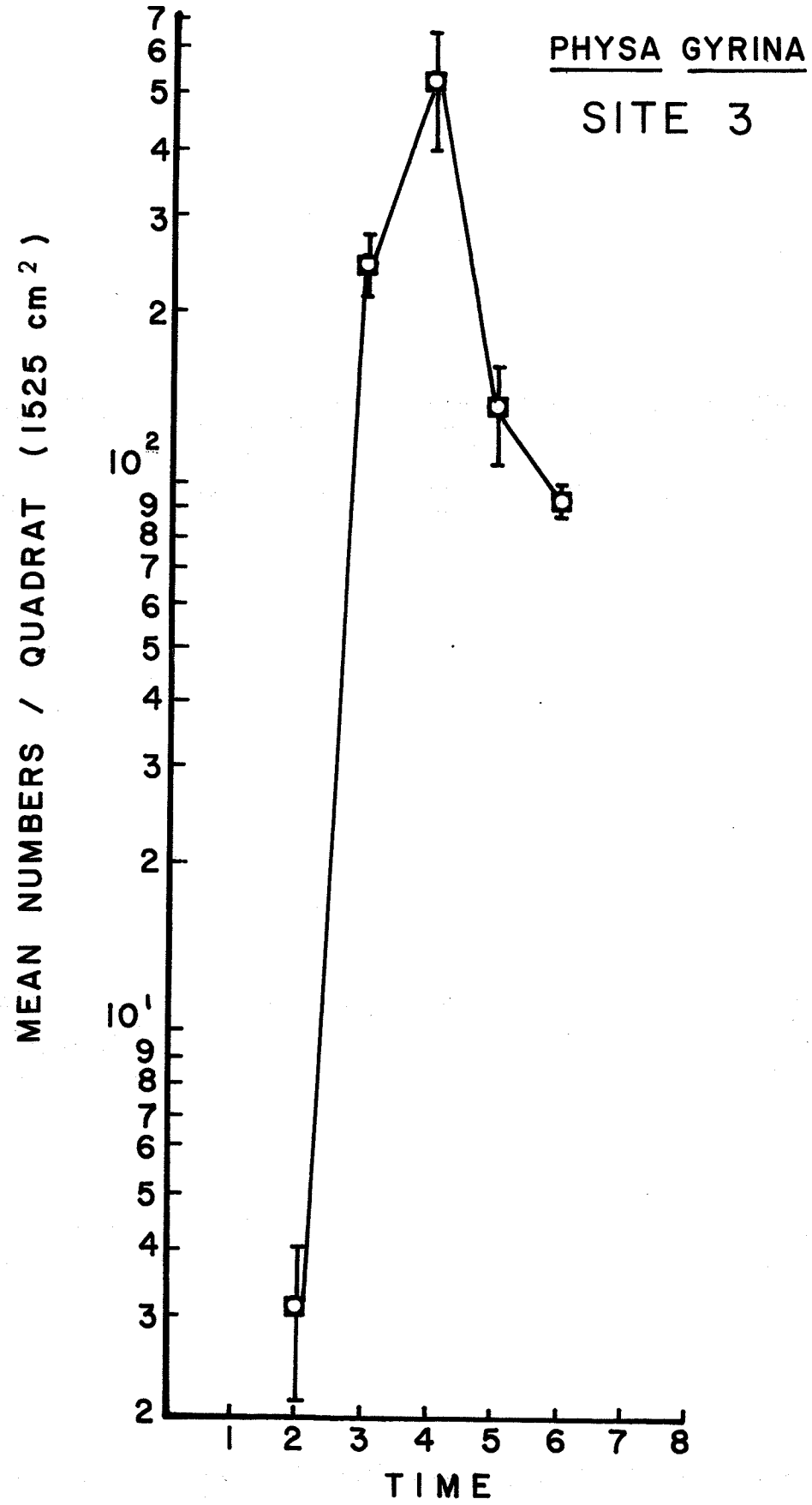
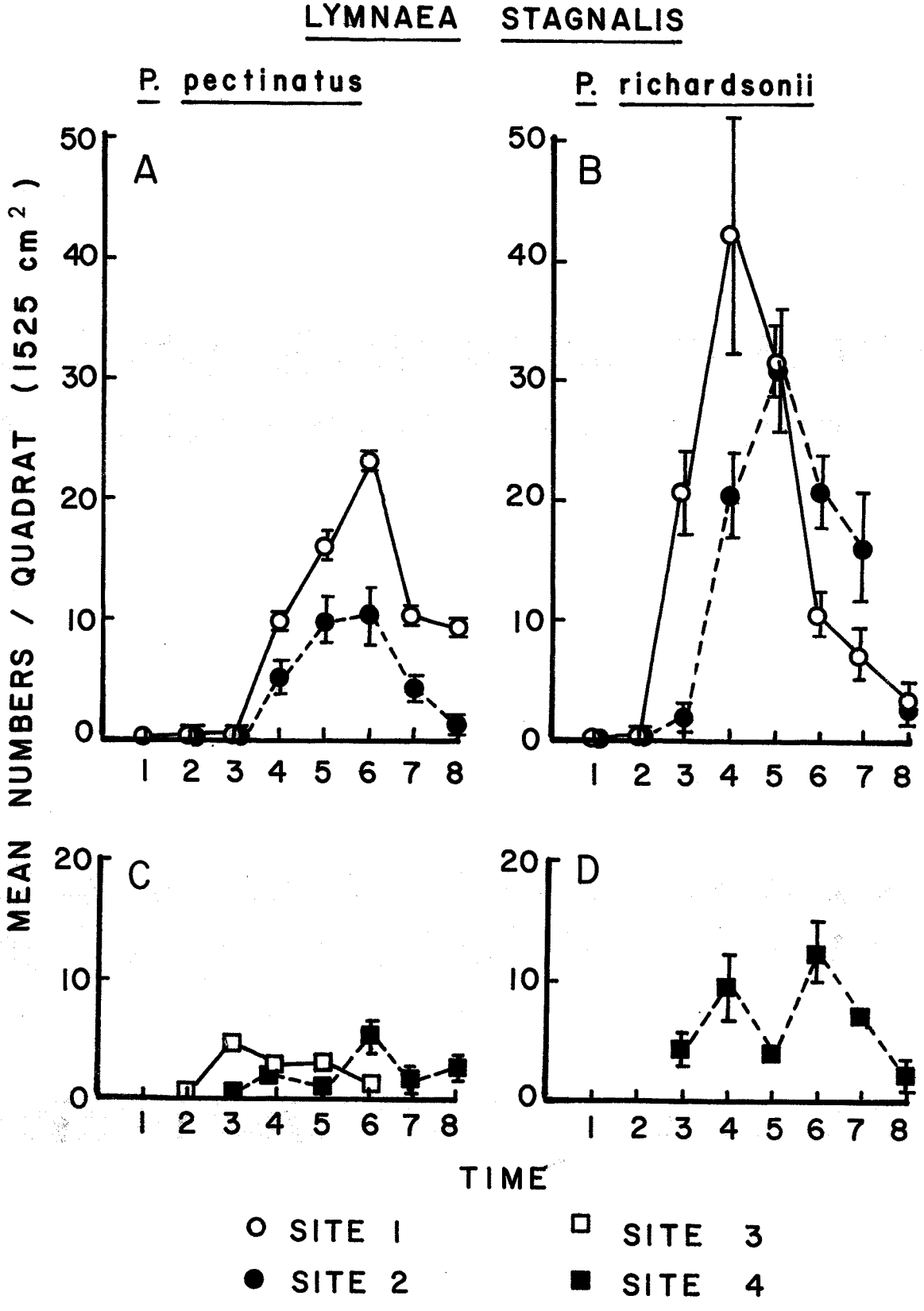

PHYSA GYRINA
SITE 3
MEAN NUMBERS / QUADRAT (1525 cm²)
TIME
7
6
5
4
3
2
10²
9
8
7
6
5
4
3
2
10¹
9
8
7
6
5
4
3
2
1 2 3 4 5 6 7 8

Figure 46. Mean numbers of Lymnaea stagnalis per quadrat sample (1525 cm^2 bottom area) from stands of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors.


LYMNAEA STAGNALIS
P. pectinatus
P. richardsonii
A
B
C
D
MEAN NUMBERS / QUADRAT (1525 cm²)
TIME
SITE 1
SITE 2
SITE 3
SITE 4

stands for most of the season. The density patterns in P. richardsonii stands (Fig. 46B) showed a two-week lag between the two sites; divergence began after time 2 because of failure to reproduce at site 2 in these stands, resulting in a density peak at time 4 at site 1 and at time 5 at site 2.

At site 1, significantly ($p < .001$-$.05$, n=10) greater densities of L. stagnalis were observed in P. richardsonii than in P. pectinatus stands during times 3-5. At time 6, significantly ($p < .01$, n=10) greater densities were observed in P. pectinatus stands, while differences between the two types of stands at times 7 and 8 were not significant. At site 2, significantly ($p < .01$-$.05$, n=10) greater densities of L. stagnalis were observed in P. richardsonii than in P. pectinatus stands during times 3-7. Differences between the two types of stands at time 8 were not significant.

At site 4 (Fig. 46C and D), densities of L. stagnalis were significantly ($p < .01$-$.05$, n=10) greater in P. richardsonii than in P. pectinatus stands during times 4-7. Density peaks occurred in both types of stands at times 4 and 6.

At site 3 (Fig. 46C), density levels of L. stagnalis were comparable to those observed in P. pectinatus stands at site 4, although a peak was observed at time 3.

The only other gastropods that were present in the samples from sites 1-4 were Fossaria modicella, Stagnicola palustris and Helisoma trivolvis, although the latter species was absent from site 4.

The mean numbers of Fossaria modicella per quadrat sample (Table XVIIIA) at site 1 were significantly ($p < .001$-$.005$, n=10) greater in P. pectinatus than in P. richardsonii stands during times

TABLE XVIII. Mean numbers of *Fossaria modicella* (A) and *Stagnicola palustris* (B) per sample quadrat (1525 cm^2) in *Potamogeton pectinatus* and *P. richardsonii* stands, respectively, at sites 1-4. Values in parentheses represent standard errors.

A. *Fossaria modicella*

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	0	0	-	0
2	0	0	0	0
3	1.4 (1.0)	0	0.2 (0.2)	0
4	31.6 (11.1)	28.0 (8.5)	3.8 (0.8)	7.8 (1.0)
5	60.2 (11.2)	13.2 (1.2)	3.6 (0.7)	11.8 (7.9)
6	72.0 (18.2)	0.6 (0.4)	1.4 (0.7)	0.6 (0.4)
7	34.2 (3.4)	0.2 (0.2)	0.4 (0.2)	0.2 (0.2)
8	0.4 (0.4)	0	20.8 (6.9)	0

	site 3	site 4	
Time	*P. pectinatus*	*P. pectinatus*	*P. richardsonii*
1	-	-	-
2	0	-	-
3	138.5 (9.4)	0	0
4	209.5 (84.0)	23.4 (10.9)	13.8 (1.7)
5	219.5 (75.4)	4.2 (0.7)	8.4 (2.1)
6	92.0 (34.6)	3.6 (0.7)	3.4 (0.7)
7	-	1.6 (0.8)	1.0 (0.6)
8	-	3.0 (0.8)	1.2 (0.5)

B. *Stagnicola palustris*

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	0	0	-	0
2	0	0.2 (0.2)	0.2 (0.2)	0
3	0.8 (0.5)	0	0	0
4	0	0.6 (0.6)	0.2 (0.2)	0.4 (0.4)
5	0.4 (0.2)	3.4 (0.7)	3.4 (0.7)	3.2 (1.8)
6	0.4 (0.2)	11.6 (2.1)	3.4 (1.2)	6.0 (2.1)
7	3.4 (1.6)	16.4 (2.5)	7.6 (1.3)	8.0 (1.0)
8	1.6 (0.7)	1.2 (0.6)	5.2 (3.5)	13.0 (3.1)

	site 3	site 4	
Time	*P. pectinatus*	*P. pectinatus*	*P. richardsonii*
1	-	-	-
2	0.7 (0.2)	-	-
3	0.5 (0.5)	1.5 (1.0)	2.0 (0.9)
4	4.3 (2.1)	0.6 (0.6)	1.0 (0.3)
5	1.5 (0.9)	0.6 (0.4)	0.8 (0.5)
6	0.5 (0.5)	0.6 (0.2)	2.2 (1.1)
7	-	1.4 (0.7)	0.8 (0.2)
8	-	1.0 (1.0)	0.8 (0.4)

5-7. At site 2, mean density was significantly ($p < .01$, n=10) greater in P. pectinatus stands at time 8, and significantly ($p < .01$, n=10) greater in P. richardsonii stands at time 4. A similar dualism of preference had been seen for this species at site 1 during 1972.

At site 1, a density peak occurred in P. pectinatus stands at time 6 while at site 2 it occurred abruptly at time 8. In P. richardsonii stands, the maximum occurred at time 4 at site 1 and at time 5 at site 2, and thus showed a two-week lag.

At site 4, densities of F. modicella were greater, but not significantly so, in P. pectinatus stands at times 4, 6, 7 and 8, and greater in P. richardsonii stands at time 5. Maximum densities were observed at time 4 in both types of stands.

At site 3, densities of F. modicella in the P. pectinatus stands reached very high levels and the maximum was observed at time 5.

The mean numbers of Stagnicola palustris per quadrat sample (Table XVIIIB) at site 1 were significantly ($p < .005$-$.001$, n=10) greater in P. richardsonii than in P. pectinatus stands during times 5-7. At site 2, mean densities were greater, but not significantly so, in P. richardsonii stands at times 4, 6, 7 and 8. Density peaks occurred in P. pectinatus stands at time 7 at both sites; in P. richardsonii stands the peaks were out of phase, occurring at time 7 at site 1 and at time 8 at site 2.

At site 4, densities of S. palustris were slightly but not significantly greater in P. richardsonii stands during times 3-6. Maxima occurred at times 3 and 7 in P. pectinatus stands and at times 3 and 6 in P. richardsonii stands.

At site 3, values for mean density were comparable to those observed in P. pectinatus stands at the other sites and showed a maximum at time 4.

The mean numbers of Helisoma trivolvis per quadrat sample (Table XIX) at site 1 were significantly ($p < .02$-$.001$, $n=10$) greater in P. pectinatus than in P. richardsonii stands during times 5-8. At site 2, mean density was significantly ($p < .01$-$.001$, $n=10$) greater in P. pectinatus than in P. richardsonii stands at times 7 and 8. Although values were greater in P. richardsonii stands at site 2 during times 3-6, the difference was not significant because of the large variance of these values. Maximum density in P. pectinatus stands occurred at times 5-6 at site 1 and at times 5 and 7 at site 2.

At site 3, H. trivolvis was rare and was observed in the samples only at time 6.

Thus, the mean density values suggested the following features:

1. At site 1, Physa gyrina (major species) and Fossaria modicella and Helisoma trivolvis (minor species) occurred significantly more frequently in P. pectinatus than in P. richardsonii stands during part of the season. Lymnaea stagnalis (major species) and Stagnicola palustris (minor species) occurred significantly more frequently in P. richardsonii stands for part of the season. These findings agreed with model 1.
2. At site 2, although temporal distributions of the snails were similar to those at site 1, P. richardsonii stands appeared to show relatively higher gastropod densities, compared with P. pectinatus, than at site 1. This was apparent for all 5 gastropods and suggested that the P. pectinatus stands at site 2 were

TABLE XIX. Mean numbers of *Helisoma trivolvis* per sample quadrat (1525 cm^2) in *Potamogeton pectinatus* and *P. richardsonii* stands, respectively, at sites 1-3. Values in parentheses represent standard errors.

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	0	0	-	0
2	0	0	0	0
3	0.4 (0.4)	0	0	0.2 (0.2)
4	3.0 (2.0)	1.0 (0.6)	0.4 (0.2)	4.4 (3.2)
5	4.6 (0.7)	1.4 (0.5)	2.0 (0.3)	4.0 (1.5)
6	4.6 (0.7)	1.2 (0.4)	1.0 (0.3)	2.2 (0.6)
7	3.2 (0.6)	0.8 (0.2)	5.4 (1.2)	0.4 (0.2)
8	1.2 (0.5)	0	4.0 (1.1)	0.6 (0.2)

	site 3
Time	*P. pectinatus*
1	-
2	0
3	0
4	0
5	0
6	0.3 (0.3)
7	-
8	-

comparatively less favorable than those at site 1 since mean densities in the P. richardsonii stands were similar at both sites, unlike those in the P. pectinatus stands.

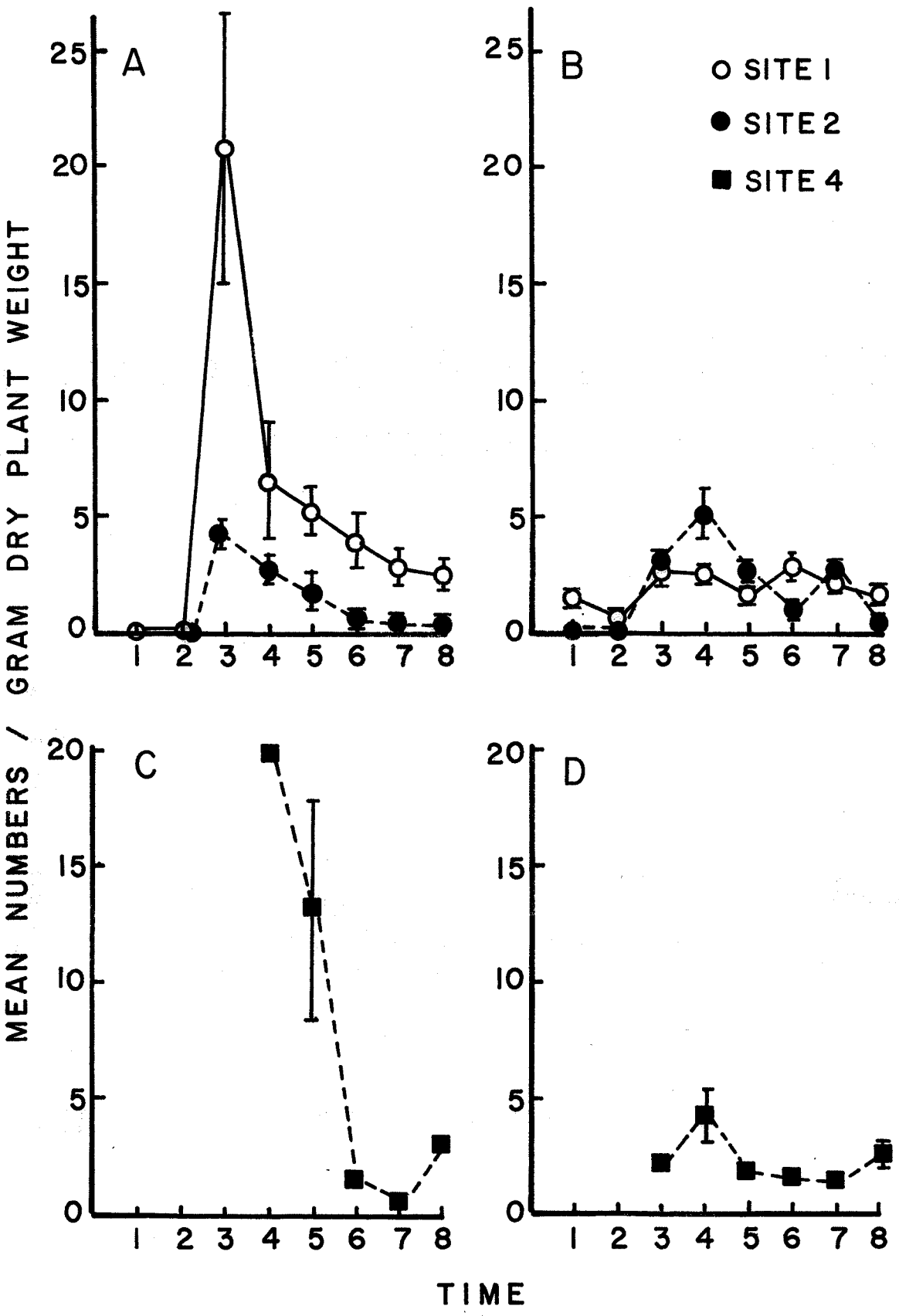
3. A lag between sites 1 and 2 appeared to exist for density patterns in the P. richardsonii stands. Subpopulations of L. stagnalis in the latter stands were out of phase at the two sites, as were, to a lesser extent, those of the lymnaeids F. modicella and S. palustris. The nonlymnaeids Physa gyrina and H. trivolvis did not show this lag. Growth of the P. richardsonii itself was out of phase.
4. At site 4, the above affinities were still present, but, as at site 2, P. richardsonii stands appeared to show relatively higher gastropod densities relative to P. pectinatus than at site 1. The density peaks of L. stagnalis and F. modicella in the P. richardsonii stands coincided with those observed at site 1 while those of S. palustris did not.
5. Site 3 represented a special case that was characterized by extremely high densities of the major species P. gyrina and F. modicella, and by normal densities, relative to the other sites, of the minor species L. stagnalis and S. palustris. Helisoma trivolvis was rare. The population dynamics of the gastropods at site 3 were similar to those observed at site 5 during the 1972 season.
6. Other molluscs present at the sites did not occur in the macrophyte samples, suggesting that these were benthic, and that supposition 1a (p. 110) of the basic model was correct.

ii. Mean numbers of individuals per unit plant dry weight

Although density differences suggested some affinities for the respective plants, they may also have reflected differences in the amount of plant substrate available per unit bottom area in the various stands. Thus, denser stands may have provided more food and surface area than sparse stands of the same species, or, stands of different macrophyte species may have provided more substrate per unit bottom area than those of other species present at the same site. Because affinities had been shown for two respective macrophyte species, the possibility was examined that one of the association types may have been due to differences in the amount of available substrate, i.e. plant dry weight and/or surface area.

The mean numbers of Physa gyrina per gram dry weight of the above-ground vegetative parts of P. pectinatus (Fig. 47A) showed fluctuation patterns at sites 1 and 2 that were significantly ($p < .001$, $n=7$) correlated (syntonic), with a well-defined peak at time 3. The magnitude of the peak at site 2 was approximately one-fifth of that at site 1. The patterns in P. richardsonii stands (Fig. 47B) were not significantly correlated with respect to simultaneity and the values were slightly larger at site 2 at times 3, 4, 5 and 7. Paired t-tests showed that at site 1, time 3, significantly ($p < .02$, $n=10$) greater numbers of snails were present per unit dry weight of P. pectinatus than of P. richardsonii. At site 2, time 3, there were also more snails present per unit dry weight of P. pectinatus although the difference between the two types of stands was reduced, perhaps because the stands of P. pectinatus at this site were smaller and

Figure 47. Mean numbers of Physa gyrina per gram dry weight of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and site 4 respectively during the 1973 season. Vertical bars represent standard errors.


A
B
C
D
SITE 1
SITE 2
SITE 4
MEAN NUMBERS / GRAM DRY PLANT WEIGHT
TIME
0
5
10
15
20
25
1
2
3
4
5
6
7
8

movement of small fauna between the different stands was restricted by an intervening area disturbed by boat traffic.

At site 4 (Fig. 47C and D), significantly ($p < .025$, $n=10$) greater numbers of P. gyrina were present per unit dry weight of P. pectinatus than of P. richardsonii at times 4 and 5. The greatest numbers were observed at time 4 in both types of stands.

At site 3 (Fig. 48), an extremely sharp peak composed largely of newly hatched young was observed at time 4. During the interval between times 3 and 4, a greater than ten-fold increase in population relative to host plant dry weight was observed; this was followed by a steep decrease at time 5.

The mean numbers of Lymnaea stagnalis per gram dry weight of P. pectinatus (Fig. 49A) were significantly correlated ($p < .01$, $n=10$) (syntonic) at sites 1 and 2, with the greatest numbers observed at time 2. The large values for means and standard errors in these stands during the early part of the season were due to chance occurrence of a few snails in some samples at a time when the host plant mass was very small. The fluctuation patterns in P. richardsonii stands (Fig. 49B) at sites 1 and 2 were out of phase by two weeks. This lag period was significantly ($p < .01$, $n=6$) consistent during times 2-8. Paired t-tests showed a significant tendency for L. stagnalis to occur in stands of P. richardsonii as opposed to those of P. pectinatus. At site 1, a maximum in P. richardsonii stands occurred at time 3 ($p < .01$, $n=10$) while at site 2 the maximum occurred two weeks later at time 4 ($p < .05$, $n=10$). The rise at time 7 in P. richardsonii stands at site 2 was partly due to a decrease in host plant dry weight that was not accompanied by a simultaneous decrease in snail numbers. Such an

Figure 48. Mean numbers of Physa gyrina per gram dry weight of Potamogeton pectinatus at site 3 during the 1973 season. Vertical bars represent standard errors.

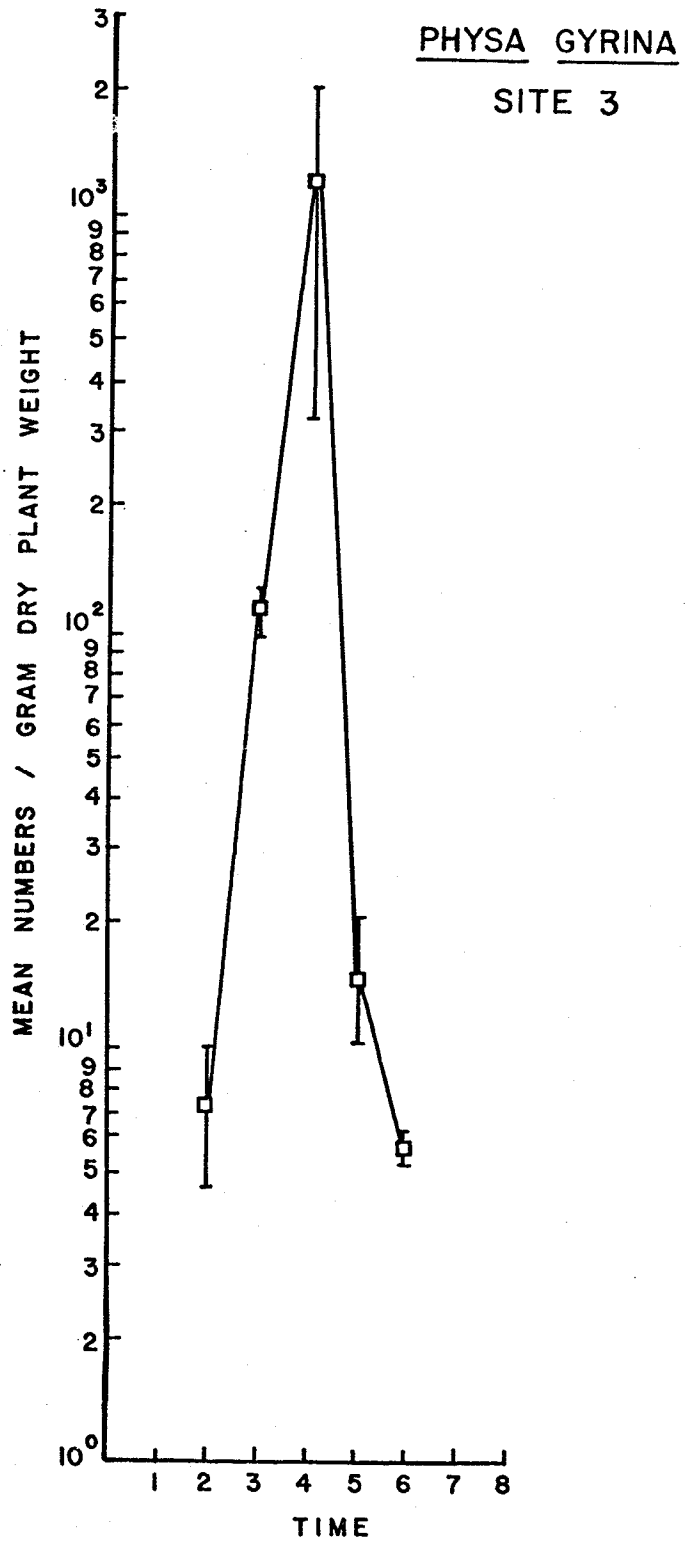
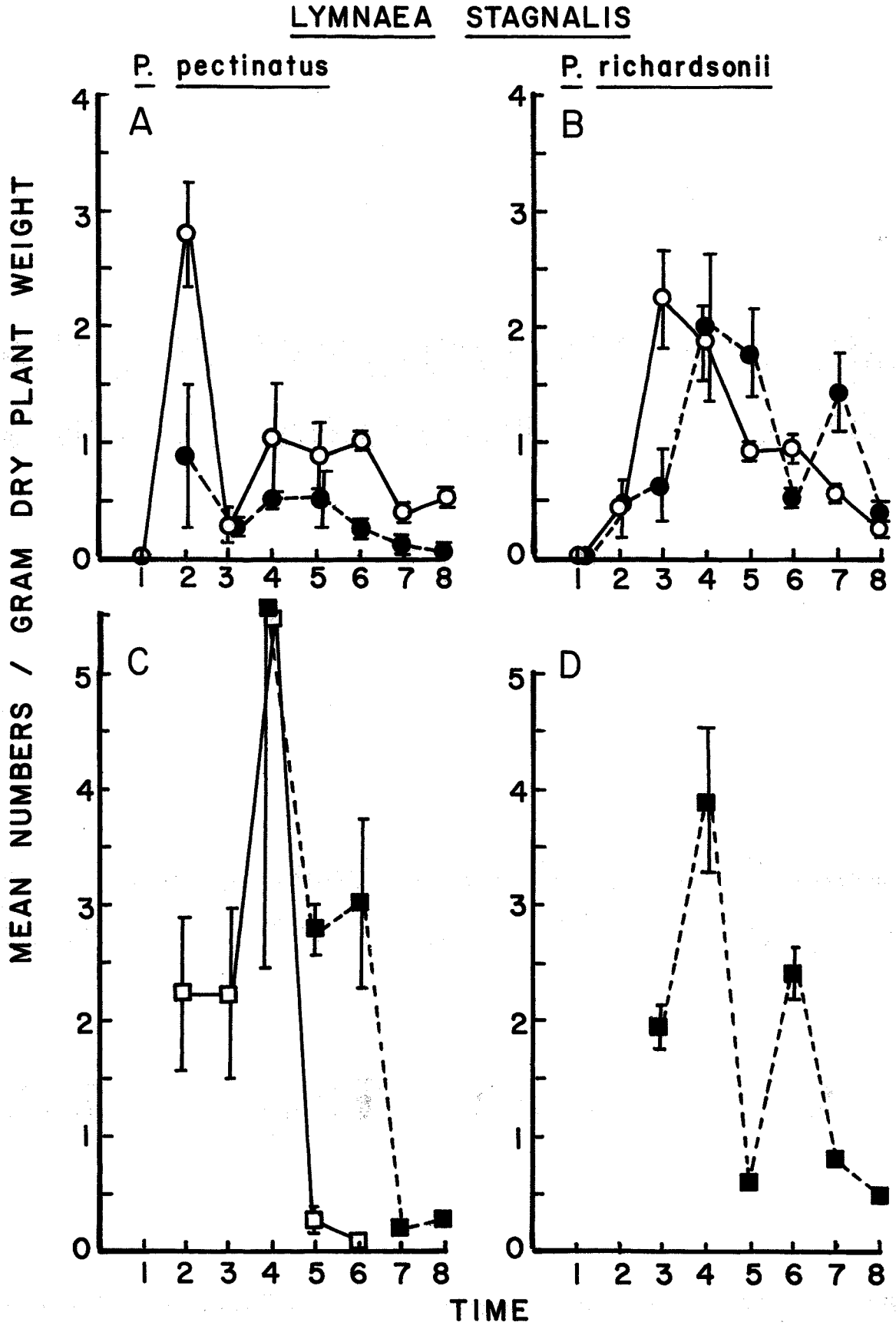

PHYSA GYRINA
SITE 3
MEAN NUMBERS / GRAM DRY PLANT WEIGHT
TIME
1 2 3 4 5 6 7 8

Figure 49. Mean numbers of Lymnaea stagnalis per gram dry weight of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors. ○ = site 1, ● = site 2, □ = site 3, ■ = site 4.


LYMNAEA STAGNALIS
P. pectinatus
P. richardsonii
A
B
C
D
MEAN NUMBERS / GRAM DRY PLANT WEIGHT
TIME
0
1
2
3
4
5
6
7
8

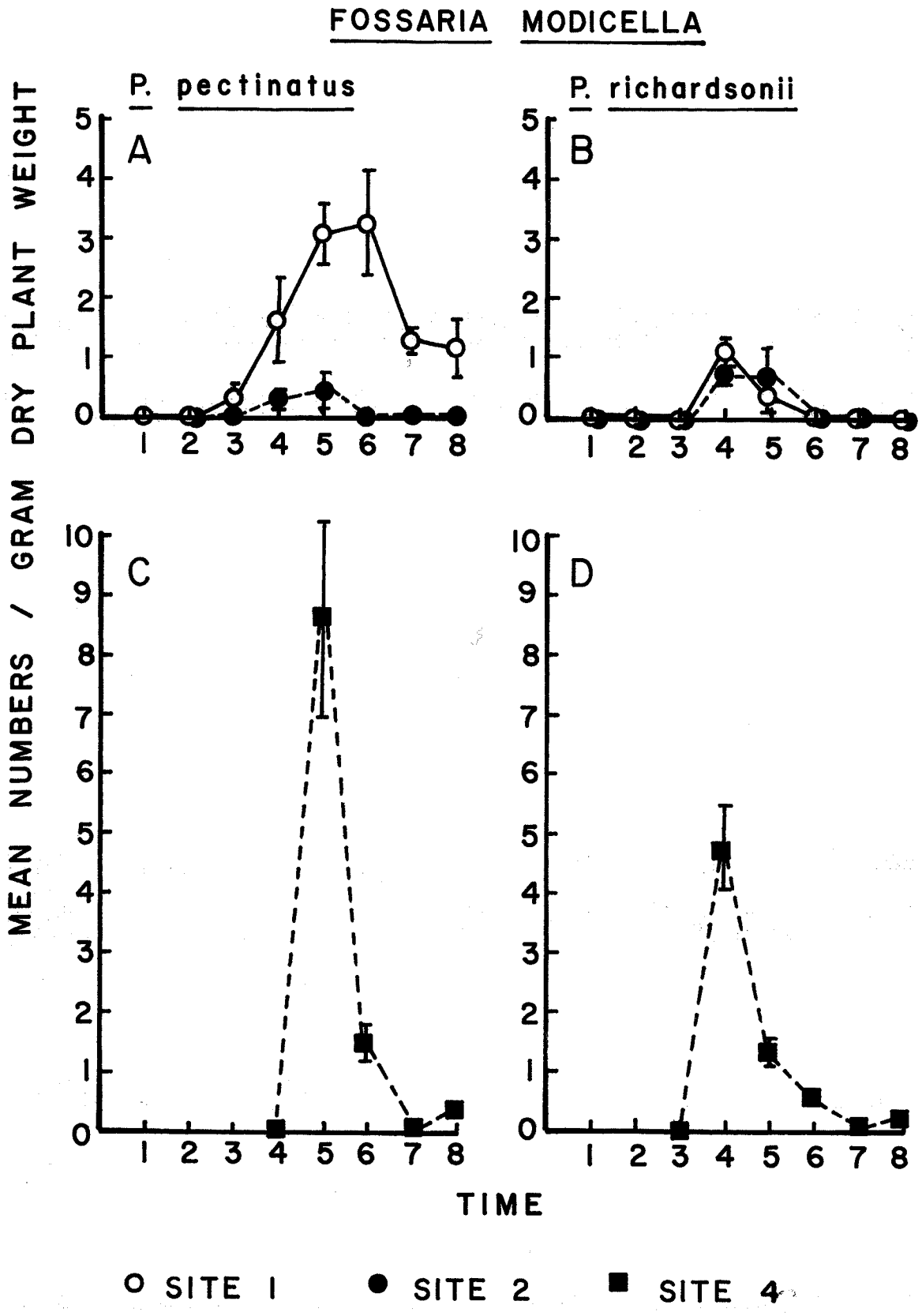
increase had also been seen for P. gyrina in P. richardsonii stands at this time (Fig. 47B).

At site 4 (Fig. 49C and D), L. stagnalis was present in significantly ($p < .001$, n=10) greater numbers per unit dry weight of P. pectinatus than of P. richardsonii at times 4 and 5; however at time 6 this difference was no longer significant, and by time 7, significantly ($p < .01$, n=10) greater numbers were observed per unit dry weight of P. richardsonii than of P. pectinatus. Two peaks, at times 4 and 6, were observed for snails present in P. richardsonii stands.

At site 3 (Fig. 49C), L. stagnalis was present in numbers that were similar, on a host plant dry weight basis, to those present in P. pectinatus stands at site 4. A peak was observed at time 4.

Of the minor species, Fossaria modicella (Fig. 50A and B) occurred in significantly ($p < .001$-$.01$, n=10) greater numbers per unit dry weight of P. pectinatus than of P. richardsonii at site 1 during times 5-8. At site 2, F. modicella was slightly, but not significantly more frequent in P. richardsonii stands at times 4 and 5. In P. pectinatus stands at site 1, a diffuse peak was observed at times 5 and 6, while at site 2 it was largely centred at time 5 and was of considerably smaller magnitude than that at site 1. In P. richardsonii stands, the converse occurred: peaks were observed at time 4 at both sites but the peak at site 2 extended to time 5. The distribution of F. modicella with respect to the two stands at both sites was similar to the distribution of P. gyrina in that consistent association with P. pectinatus was observed for both species at site 1, whereas at site 2, values for P. pectinatus stands were higher only

Figure 50. Mean numbers of Fossaria modicella per gram dry weight of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and site 4 respectively during the 1973 season. Vertical bars represent standard errors.


FOSSARIA MODICELLA
P. pectinatus
P. richardsonii
A
B
C
D
MEAN NUMBERS / GRAM DRY PLANT WEIGHT
TIME
O SITE 1
● SITE 2
■ SITE 4

at time 3.

At site 4 (Fig. 50C and D), F. modicella was present in significantly ($p < .001$-$.025$, n=10) greater numbers per unit dry weight of P. pectinatus than of P. richardsonii at times 5 and 6. The peak occurred at time 5 in P. pectinatus stands while in P. richardsonii stands it occurred two weeks earlier, at time 4, and was thus similar to the timing observed for the subpopulations of this species present in the two types of stands at site 1.

At site 3 (Fig. 51), F. modicella was present in very high numbers per unit dry weight of P. pectinatus during times 3-5, and the peak, composed largely of young, was observed at time 4.

Stagnicola palustris (Fig. 52A and B) at site 1 occurred in significantly ($p < .01$-$.001$, n=10) greater numbers per unit dry weight of P. richardsonii than of P. pectinatus during times 6-8. At site 2, S. palustris occurred in greater, but not significantly so, numbers in P. richardsonii stands during times 6-8. Maxima in stands of P. richardsonii occurred at time 7 at both sites while the distribution in P. pectinatus stands showed little definition with time.

At site 4 (Fig. 52C and D), a greater number of individuals occurred in P. pectinatus than in P. richardsonii stands at times 4 and 5 while at time 6 the reverse was true, although this difference was not significant. Peaks were observed at times 3 and 6 in P. richardsonii stands while in P. pectinatus stands a maximum occurred at time 4.

At site 3 (Fig. 52C), numbers of S. palustris per unit dry weight of P. pectinatus attained a maximum at time 4.

Figure 51. Mean numbers of Fossaria modicella per gram dry weight of Potamogeton pectinatus at site 3 during the 1973 season. Vertical bars represent standard errors.

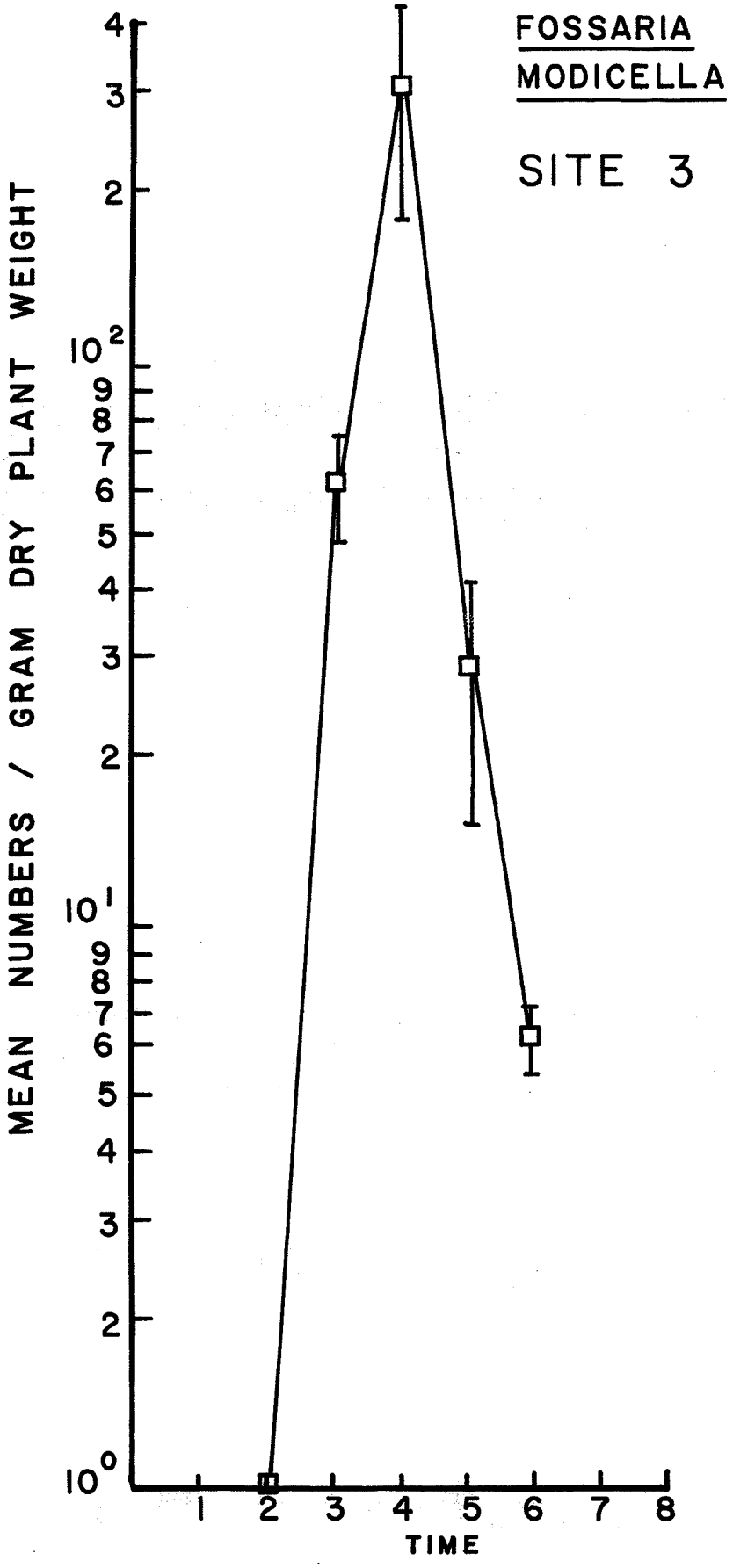
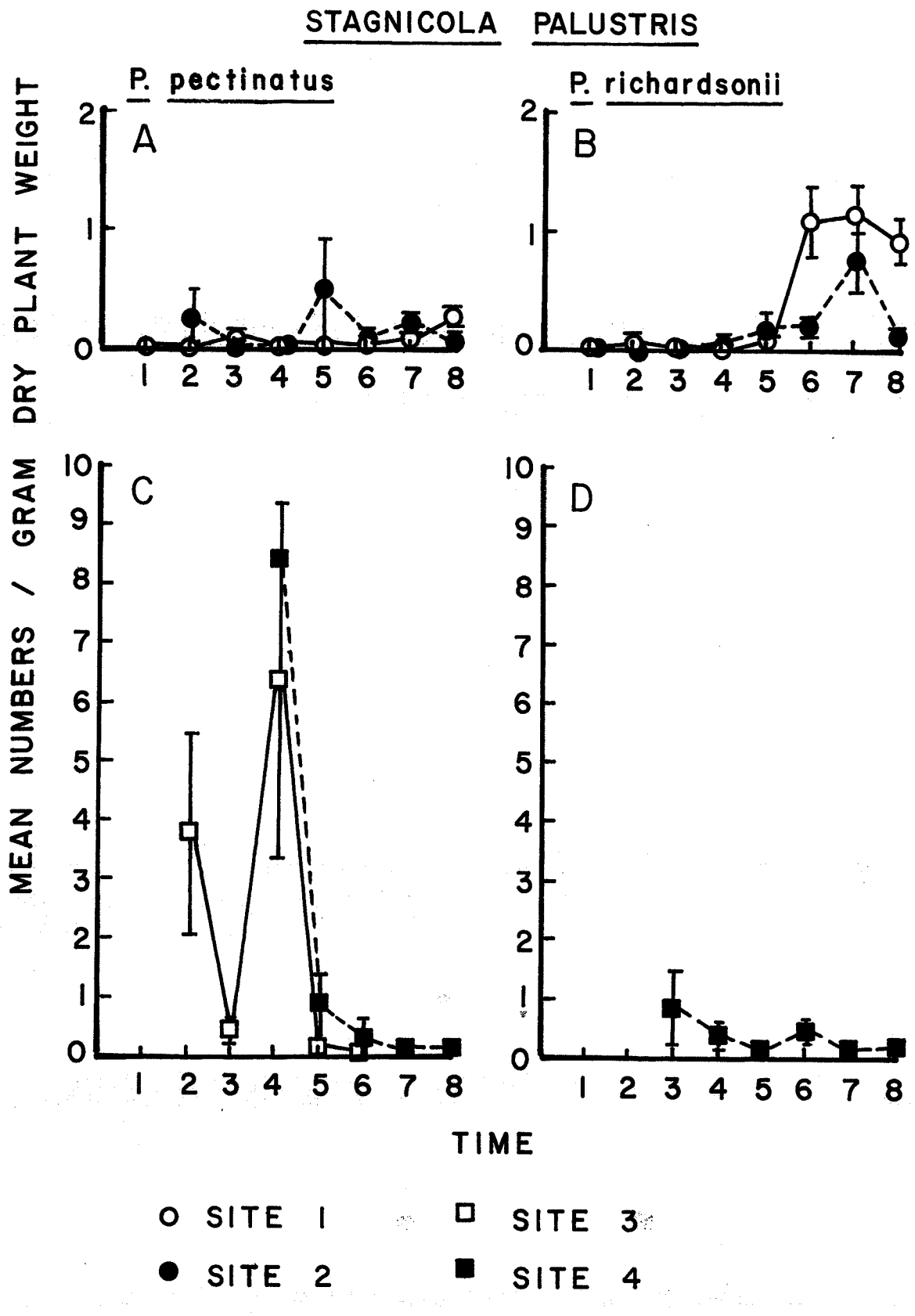

FOSSARIA
MODICELLA
SITE 3
MEAN NUMBERS / GRAM DRY PLANT WEIGHT
4
3
2
10²
9
8
7
6
5
4
3
2
10¹
9
8
7
6
5
4
3
2
10⁰
1
2
3
4
5
6
7
8
TIME

Figure 52. Mean numbers of Stagnicola palustris per gram dry weight of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors.


STAGNICOLA PALUSTRIS
P. pectinatus
P. richardsonii
A
B
C
D
MEAN NUMBERS / GRAM DRY PLANT WEIGHT
TIME
SITE 1
SITE 2
SITE 3
SITE 4

Helisoma trivolvis (Fig. 53A and B) occurred in significantly ($p < .025$-$.001$, $n=10$) greater numbers per unit dry weight of P. pectinatus than of P. richardsonii at site 1 at times 5 and 8. At site 2, H. trivolvis occurred in significantly ($p < .025$-$.01$, $n=10$) greater numbers per unit dry weight of P. pectinatus than of P. richardsonii at times 7 and 8. Peaks in P. pectinatus stands occurred at time 5 at both sites while in P. richardsonii stands the distributions did not appear to be correlated. In the former stands at site 1, other maxima also occurred at times 6 and 8, while at site 2 another peak occurred at time 7.

Helisoma trivolvis was not present at site 4. At site 3 it was collected only at time 6, when a mean number of 0.02 individuals per gram dry P. pectinatus was observed.

In summary, the numbers per unit plant dry weight showed the following features:

1. Physa gyrina was associated with P. pectinatus at least during the period when snail numbers were highest in relation to dry weight of the preferred plant. Peak numbers per unit dry weight of P. pectinatus occurred at time 3 at sites 1 and 2, where the growth of this macrophyte was also synchronous. Peaks occurred at time 4 at sites 3 and 4 where growth of P. pectinatus lagged behind that at sites 1 and 2.
2. Lymnaea stagnalis was associated with P.richardsonii during a large part of the growing season. Peak numbers per unit dry weight of P. richardsonii occurred at time 3 at site 1 and at time 4 at site 2, coinciding with the lag period observed for growth of this plant at the two sites. Peaks occurred at

Figure 53. Mean numbers of Helisoma trivolvis per gram dry weight of Potamogeton pectinatus (A) and P. richardsonii (B) at sites 1 and 2 during the 1973 season. Vertical bars represent standard errors.

times 4 and 6 at site 4, and appeared to be related to the two peaks observed for the growth of P. richardsonii in terms of dry weight per unit bottom area at this site.

3. The peaks in numbers of P. gyrina and L. stagnalis per unit dry weight of the respectively associated plants coincided with the early stages of a steep increase in the dry weight of these plants.

4. Fossaria modicella was associated with P. pectinatus for at least part of the growing season. Peak numbers per unit dry weight of this plant occurred at time 5 at sites 1, 2 and 4 while at site 3 the maximum occurred at time 4. In P. richardsonii stands maxima were observed at time 4 at sites 1, 2 and 4. These peaks did not coincide with the timing of growth of the host plants.

5. Stagnicola palustris was associated with P. richardsonii during the second half of the season. Maxima were observed in these stands at time 7 at sites 1 and 2, and at times 3 and 6 at site 4. These peaks were not correlated with growth of the host plants.

6. Helisoma trivolvis was associated with P. pectinatus during the second half of the season. A maximum was observed in these stands at time 5 at both sites 1 and 2, and at time 6 at site 3. Some correlation of these peaks could be demonstrated with respect to growth of the plants. However, a) the difference between the two types of stands was not significant during the peaks, and b) the peaks did not coincide with a period of increasing growth of the plants.

At sites 2 and 4, the P. richardsonii stands continued to show higher numbers of snails in terms of plant dry weight relative to those of P. pectinatus than did the P. richardsonii stands at site 1, suggesting that the factor(s) affecting snail distributions were less effective in the P. pectinatus stands at sites 2 and 4 than at site 1. This may have been possibly due to disturbance by boat traffic at site 2 and the mixed nature of the stands at site 4, which may have reduced the intensity of the difference of the active factor(s) between the two types of stands. The two-week lag periods observed for the density patterns of F. modicella and S. palustris in the P. richardsonii stands at sites 1 and 2 in terms of numbers per unit bottom area turned out to be spurious when examined in relation to plant dry weight.

iii. Total grazer population and lesion index

At sites 1 and 2, maximum mean total numbers of snails per unit dry weight of P. pectinatus (Table XX) were observed at time 3. This maximum was followed at time 4 by an increase in the lesion index (Table XXI) at site 1 for P. pectinatus. Lesion index at this site decreased by time 5, reflecting the abrupt decrease in total snail numbers per unit plant dry weight at time 4. At site 2, the decrease in snail numbers at time 4 was relatively less sharp and lesion index at this site continued to increase until time 5, perhaps reflecting the increasing sizes of the snails which may have compensated for the slightly reduced numbers. Estimation of lesion index towards the end of the season involved increasing error because of extensive fungal infections. At site 4, the maximum numbers of snails per unit dry plant weight in the P. pectinatus stands occurred at time 5, but the lesion index could not be estimated for plants from this site because

TABLE XX. Mean total numbers of gastropods per gram dry host plant weight at sites 1-4 during the 1973 season.

	site 1		site 2	
Time	P. pectinatus	P. richardsonii	P. pectinatus	P. richardsonii
1	0	1.5	-	0
2	2.9	1.2	1.2	0.5
3	21.7	5.0	4.8	3.7
4	9.3	5.8	3.7	8.2
5	9.6	3.3	3.7	6.0
6	8.5	5.2	1.2	1.9
7	4.6	4.2	1.0	5.2
8	4.6	3.0	0.5	1.0

	site 3	site 4	
Time	P. pectinatus	P. pectinatus	P. richardsonii
1	-	-	-
2	13.4	-	-
3	179.2	-	5.0
4	1522.3	33.7	13.4
5	45.6	25.6	3.9
6	12.3	6.5	5.1
7	-	1.1	2.6
8	-	4.0	3.3

the leaves were too narrow to allow for accurate scoring.

In P. richardsonii stands, maximum total numbers of snails per unit plant dry weight were observed at time 4 at both sites 1 and 2. This maximum was followed by a maximum in the lesion index at time 5 at both sites. At site 4, maximum numbers of snails in P. richardsonii stands were observed at time 4 but lesion index did not show an increase until time 6, perhaps because heavy calcareous deposits on the upper leaf surfaces at this site may have interfered with grazing by young snails which composed the bulk of the snail density maxima.

In general, lesion index reflected grazing changes only within each particular site; comparisons between sites could not be made since grazing intensity at different sites depended on other factors such as the relative sizes of the different plant stands, degree of exposure to physical disturbance, and, in P. pectinatus stands, the proportions of the plants that were suitable for sampling for lesion index estimation. The latter factor was compounded by the possibility that the proportion of the gastropod population that grazed upon the proportion of plants that was suitable for sampling may not have been constant at different sites or different times within the same site,

The numbers of each species present per gram dry plant weight, expressed as a percent of the total numbers of snails of all species (Table XXII), showed that the dominant species in P. pectinatus stands at all sites was P. gyrina. This species was also the most frequent in P. richardsonii stands, but here its importance was reduced while that of L. stagnalis was increased. Fossaria modicella

TABLE XXII. Mean numbers of each gastropod species per unit dry plant weight expressed as a percent of all species present at sites 1-4 during the 1973 season. Species numbers represent the following taxa:

1. Physa gyrina
2. Lymnaea stagnalis
3. Fossaria modicella
4. Stagnicola palustris
5. Helisoma trivolvis

TABLE XXII.

SITE 1

		POTAMOGETON PECTINATUS SAMPLES								POTAMOGETON RICHARDSONII SAMPLES							
Species	Time	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1		0	0	95.8	69.8	54.8	46.4	57.1	49.2	100.0	55.0	54.3	45.4	53.4	56.5	53.1	57.6
2		0	100.0	1.6	11.4	9.4	11.9	9.3	12.0	0	39.2	45.7	32.6	29.1	18.7	13.7	9.6
3		0	0	1.6	17.7	33.0	38.9	28.4	27.8	0	0	0	20.6	12.9	0.8	0.5	0
4		0	0	0.5	0	0.3	0.2	2.6	5.9	0	5.8	0	0.5	3.4	21.7	31.0	31.1
5		0	0	0.5	1.1	2.5	2.6	2.6	5.1	0	0	0	0.9	1.2	2.3	1.7	1.7

SITE 2

Species	Time	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1		-	0	90.8	73.8	50.4	64.3	53.1	59.6	0	0	81.0	61.2	50.8	55.4	55.5	42.6
2		-	78.0	7.1	14.1	14.5	24.3	12.1	13.5	0	100.0	18.0	24.9	30.6	28.0	28.6	42.6
3		-	0	2.1	10.5	13.7	2.6	0.4	3.8	0	0	1.0	9.5	12.1	1.0	0.2	0
4		-	22.0	0	0.5	14.2	7.0	20.5	13.5	0	0	0	0.4	3.2	11.9	15.1	14.9
5		-	0	0	1.1	7.2	1.8	13.9	9.6	0	0	0	4.0	3.3	3.7	0.6	0

SITE 3

Species	Time	1	2	3	4	5	6	7	8
1		-	54.7	63.1	79.0	34.3	46.6	-	-
2		-	16.8	1.2	0.4	0.6	0.8	-	-
3		-	0	35.4	20.2	64.7	52.0	-	-
4		-	28.5	0.3	0.4	0.4	0.4	-	-
5		-	0	0	0	0	0.2	-	-

SITE 4

Species	Time	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1		-	-	-	58.3	51.4	24.5	56.3	79.2	-	-	43.7	31.8	45.0	31.1	58.2	75.7
2		-	-	-	16.7	11.0	46.8	17.9	7.5	-	-	39.4	29.3	15.9	47.3	32.2	15.3
3		-	-	-	0	34.1	23.7	12.5	10.3	-	-	0	36.0	35.5	12.7	5.0	5.7
4		-	-	-	25.0	3.5	5.0	13.3	3.0	-	-	16.9	2.9	3.6	8.9	4.6	3.3
5		-	-	-	0	0	0	0	0	-	-	0	0	0	0	0	0

composed a greater percentage of the snails in P. pectinatus than in P. richardsonii stands, although it was least important at site 2. Stagnicola palustris and H. trivolvis were largely minor components of the total fauna that was present on the plant shoots.

Physa gyrina and L. stagnalis together comprised the bulk of the molluscan fauna present on the plants throughout the season at all sites. In P. pectinatus stands, the combined percentage of these two species ranged from 58.3-100% at site 1, 64.9-97.9% at site 2, 34.9-79.4% at site 3 and 62.4-86.7% at site 4. In P. richardsonii stands, these values ranged from 66.8-100% at site 1, 81.4-100% at site 2 and 60.9-91.0% at site 4. Thus the lesion index was probably largely attributable to these species. Because of the relatively small numbers of non-dominant snails, their input into the total grazing sustained by the plants at these sites was probably minor, particularly during times of peak numbers of the dominant species.

iv. Mean numbers of individuals per unit plant surface area

In general, the patterns for numbers of individuals per unit plant surface area were similar to those expressed in terms of plant dry weight, although the P. richardsonii associations appeared slightly more pronounced relative to those of P. pectinatus.

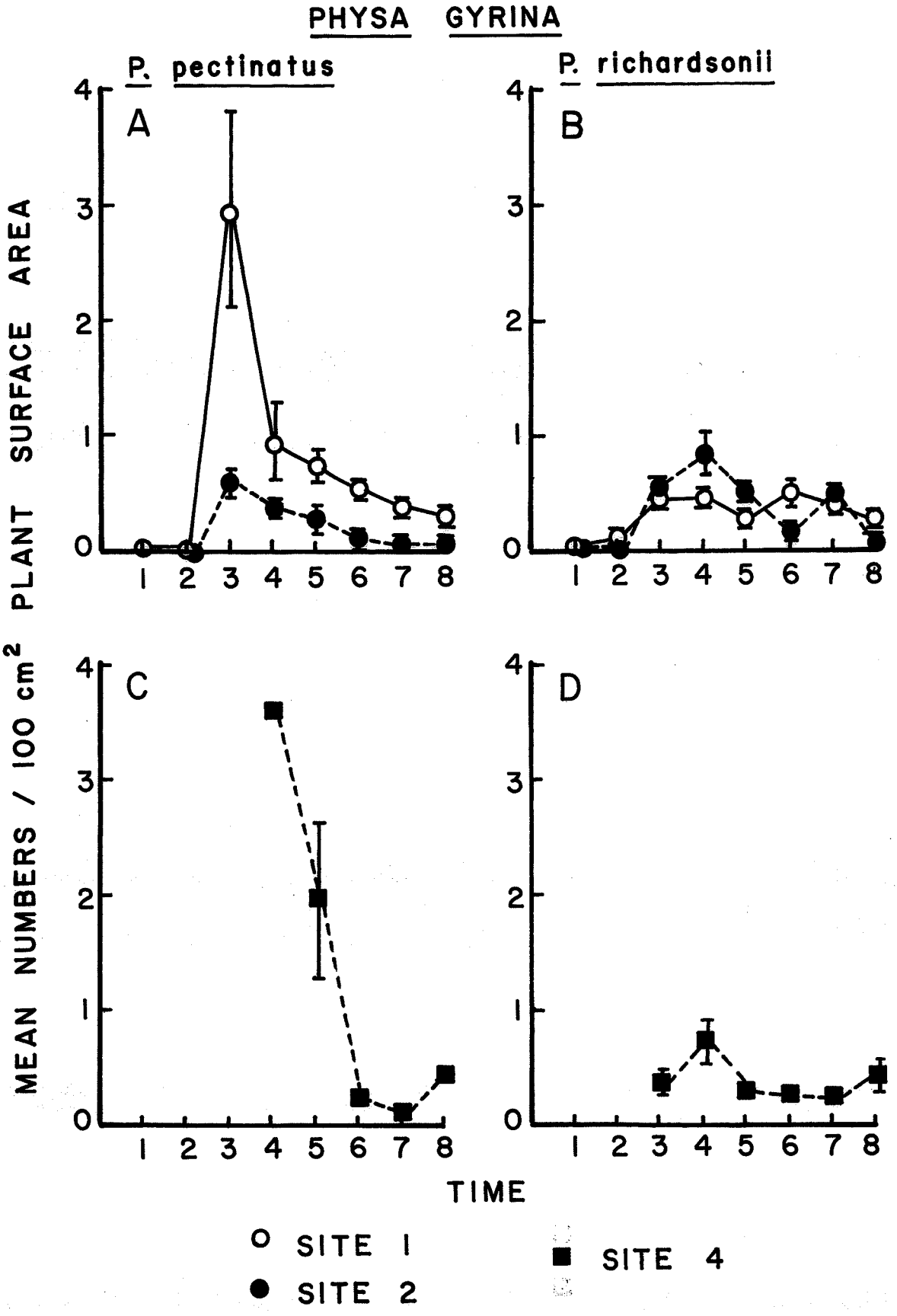
The mean numbers of P. gyrina per 100 cm^2 of plant surface area (Fig. 54A and B) at site 1 were significantly ($p < .01$-$.02$, $n=10$) greater in P. pectinatus than in P. richardsonii stands at times 3 and 5. At site 2, P. gyrina was present in slightly, but not significantly greater numbers in P. pectinatus stands at time 3; at times 4 and 7 it was present significantly ($p < .01$-$.05$, $n=10$) more frequently in P. richardsonii stands.

TABLE XXI. Values for lesion index at sites 1, 2 and 4 during the 1973 season, representing the numbers of leaf sections with grazer-induced lesions as a fraction of the total number of sections examined.

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	-	-	-	-
2	0.07	0.26	0.18	0.43
3	0.24	0.29	0.21	0.31
4	0.40	0.33	0.30	0.24
5	0.26	0.44	0.39	0.38
6	-	0.32	-	0.18
7	0.14	0.25	-	0.25
8	-	0.25	-	-

	site 4	
Time	*P. pectinatus*	*P. richardsonii*
1	-	-
2	-	-
3	-	0.27
4	-	0.34
5	-	0.30
6	-	0.38
7	-	0.40
8	-	-

Figure 54. Mean numbers of Physa gyrina per 100 cm^2 surface area of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and site 4 respectively during the 1973 season. Vertical bars represent standard errors.


PHYSA GYRINA
P. pectinatus
P. richardsonii
A
B
C
D
MEAN NUMBERS / 100 cm² PLANT SURFACE AREA
TIME
SITE 1
SITE 2
SITE 4

At site 4 (Fig. 54C and D), P. gyrina was present in significantly ($p < .05$, n=10) greater numbers in P. pectinatus than in P. richardsonii stands at times 4 and 5.

At site 3 (Fig. 55), the maximum numbers of P. gyrina per unit surface area of P. pectinatus were observed at time 4.

Lymnaea stagnalis (Fig. 56A and B) at site 1 was significantly ($p < .01$, n=10) more frequently associated with P. richardsonii in terms of surface area than with P. pectinatus during the maximum in the former stands at time 3. At site 2, L. stagnalis was significantly ($p < .01$-$.05$, n=10) more frequently associated with P. richardsonii during the maximum at time 4 in these stands, and during times 6-8.

At site 4 (Fig. 56C and D), L. stagnalis was significantly ($p < .001$, n=10) more frequently associated with P. pectinatus at times 4-5 and with P. richardsonii ($p < .01$, n=10) at time 7.

At site 3 (Fig. 56C), maxima were observed at times 2 and 4.

The results for the minor species F. modicella, S. palustris and H. trivolvis (Table XXIII) generally showed affinities similar to those ascribed on the basis of plant weight. Paired t-tests showed that at site 1, F. modicella was present significantly ($p < .001$-$.05$, n=10) more frequently in P. pectinatus stands at times 3 and 5 while at site 2 it was present slightly more frequently in P. richardsonii stands at time 4. At site 4, it was present significantly ($p < .01$, n=10) more frequently in P. pectinatus stands at time 5.

Stagnicola palustris occurred more frequently in P. richardsonii stands during the second half of the season at sites 1 and 2. The numbers of H. trivolvis in terms of plant surface area were too small to show significant trends.

Figure 55. Mean numbers of Physa gyrina per 100 cm^2 surface area of Potamogeton pectinatus at site 3 during the 1973 season. Vertical bars represent standard errors.

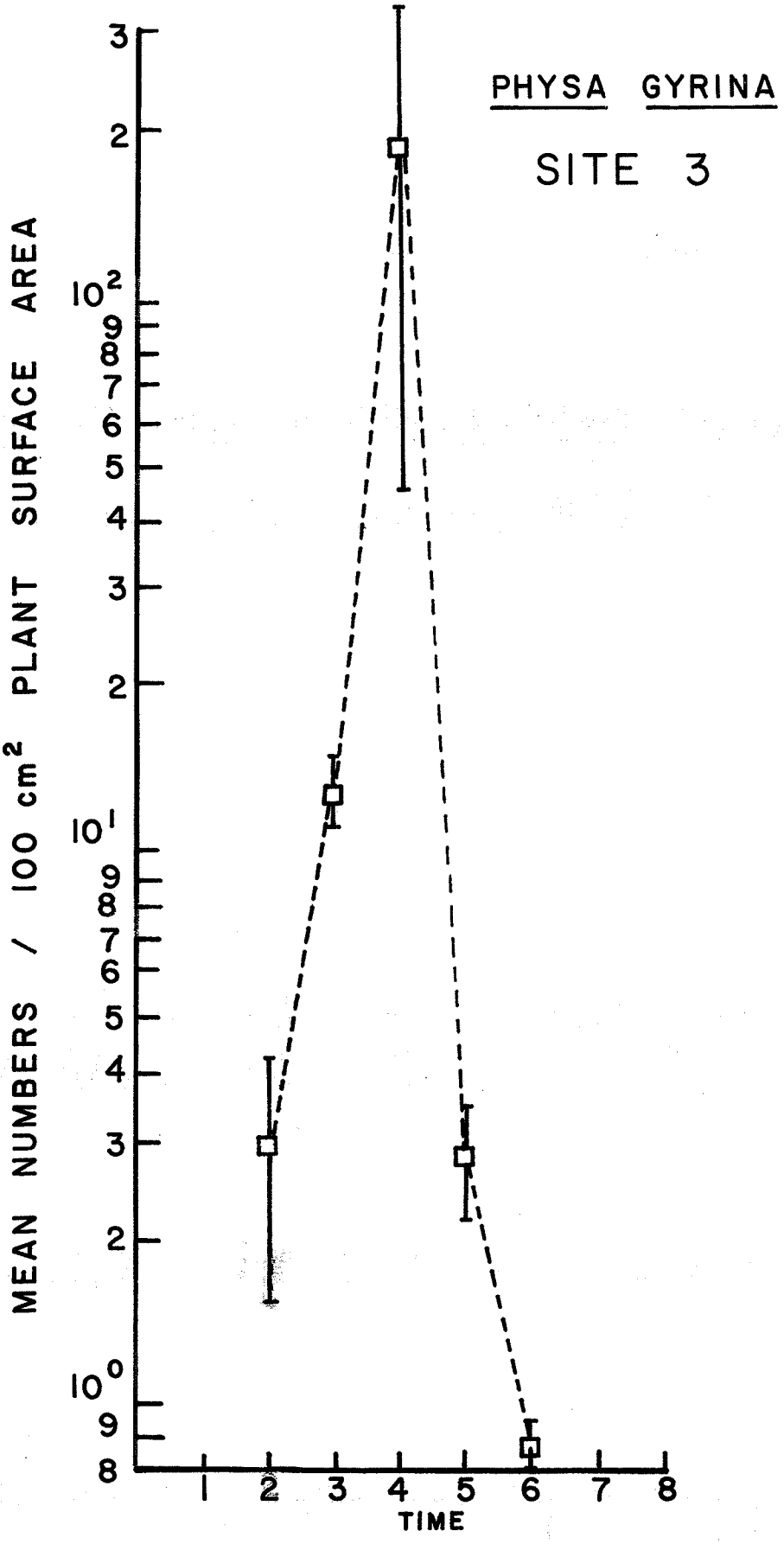

PHYSA GYRINA
SITE 3
MEAN NUMBERS / 100 cm² PLANT SURFACE AREA
TIME
3
2
10²
9
8
7
6
5
4
3
2
10¹
9
8
7
6
5
4
3
2
10⁰
9
8
1
2
3
4
5
6
7
8

Figure 56. Mean numbers of Lymnaea stagnalis per 100 cm^2 surface area of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors.

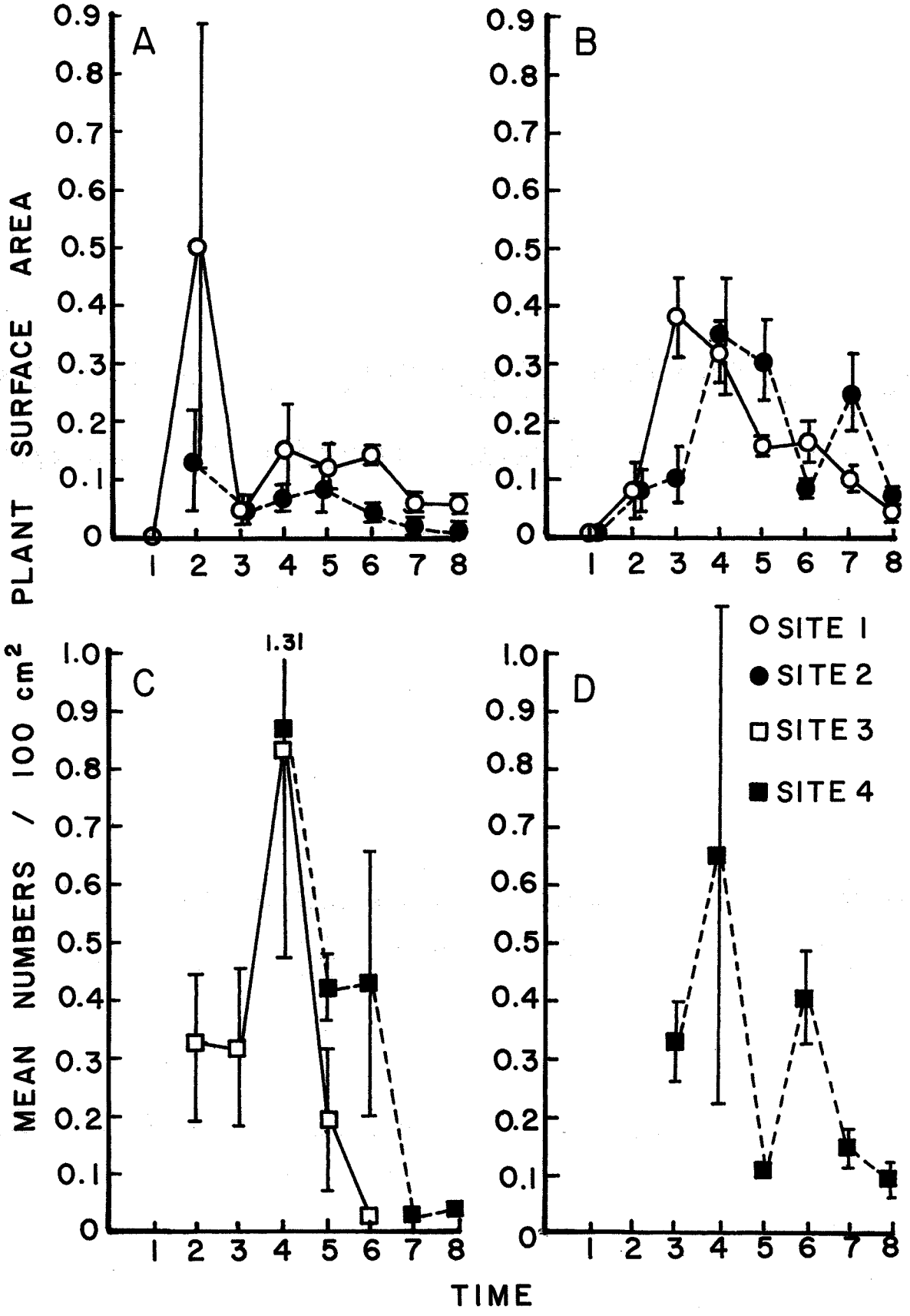

A
B
C
D
1.31
PLANT SURFACE AREA
MEAN NUMBERS / 100 cm²
TIME
SITE 1
SITE 2
SITE 3
SITE 4

TABLE XXIII. Mean numbers per 100 cm^2 of plant surface area of *Fossaria modicella* and *Stagnicola palustris* (combined)(A) and *Helisoma trivolvis* (B) in the respective stands at sites 1-4. Values in parentheses represent standard errors.

A. *Fossaria modicella* and *Stagnicola palustris* (combined)

Time	site 1		site 2	
	P. pectinatus	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	0	0	-	0
2	0	0.01 (0.01)	0	0
3	0.11 (0.04)	0	0.01 (0.01)	0.01 (0)
4	0.39 (0.18)	0.21 (0.03)	0.06 (0.01)	0.14 (0.03)
5	0.45 (0.07)	0.09 (0.02)	0.14 (0.10)	0.15 (0.10)
6	0.47 (0.15)	0.20 (0.04)	0.02 (0)	0.04 (0)
7	0.20 (0.03)	0.23 (0.03)	0.03 (0)	0.13 (0.05)
8	0.22 (0.04)	0.16 (0.03)	0.02 (0)	0.03 (0.01)

Time	site 3	site 4	
	P. pectinatus	*P. pectinatus*	*P. richardsonii*
1	-	-	-
2	0.62 (0.27)	-	-
3	7.15 (0.80)	-	0.15 (0.06)
4	46.68 (19.66)	-	0.87 (0.14)
5	4.04 (2.06)	1.42 (0.24)	0.27 (0.06)
6	0.91 (0.12)	0.26 (0.07)	0.19 (0.05)
7	-	0.04 (0.01)	0.04 (0.02)
8	-	0.07 (0.03)	0.07 (0.03)

B. *Helisoma trivolvis*

Time	site 1		site 2	
	P. pectinatus	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	0	0	-	0
2	0	0	0	0
3	0.02 (0.02)	0	0	0
4	0.02 (0)	0.01 (0)	0.01 (0)	0.06 (0.04)
5	0.04 (0)	0	0.04 (0.02)	0.03 (0.01)
6	0.03 (0.01)	0.02 (0)	0	0.01 (0)
7	0.02 (0)	0.01 (0)	0.02 (0)	0.01 (0)
8	0.03 (0)	0.01 (0)	0.01 (0)	0

Time	site 3
	P. pectinatus
1	-
2	0
3	0
4	0
5	0
6	0.003 (0)
7	-
8	-

v. Snail biomass

The mean live weight of P. gyrina per quadrat sample (1525 cm^2) (Fig. 57A and B) at site 1 was greater in P. pectinatus than in P. richardsonii stands at times 3 and 4, but during times 5-7 differences between the two types of stands declined and at time 8 greater live weights were observed in P. richardsonii stands. At site 2, greater live weights were observed in P. pectinatus stands at times 5 and 8. A peak was observed in P. richardsonii stands at time 7. The patterns were synchronous at both sites in the latter stands and approximately so in the P. pectinatus stands.

At site 4 (Fig. 57C and D), greater live weights were observed for P. gyrina at times 3 and 8 in P. pectinatus stands but this difference was not significant.

At site 3 (Fig. 57C), P. gyrina showed maximum live weight per unit bottom area at time 4 in the P. pectinatus stands.

An examination of the values for live weight of P. gyrina in relation to plant dry weight (Fig. 58A and B) showed that a time-dependent relationship existed between snail and plant mass. At site 1, time 3, the mean live weight per unit plant dry weight was significantly ($p < .02$, $n=10$) higher in P. pectinatus than in P. richardsonii stands and this difference was still significant at time 4. After time 5, a significant ($p < .01$, $n=10$) shift of biomass occurred towards the P. richardsonii stands. At site 2, time 3, biomass of P. gyrina was significantly ($p < .05$, $n=10$) greater in P. pectinatus stands. As at site 1, the biomass of Physa predominated significantly ($p < .001$-$.05$, $n=10$) in the P. richardsonii stands after time 5, and was due to the presence of larger individuals during the latter part of the season

Figure 57. Mean total live weight (g) of Physa gyrina per quadrat sample (1525 cm^2 bottom area) in stands of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors.

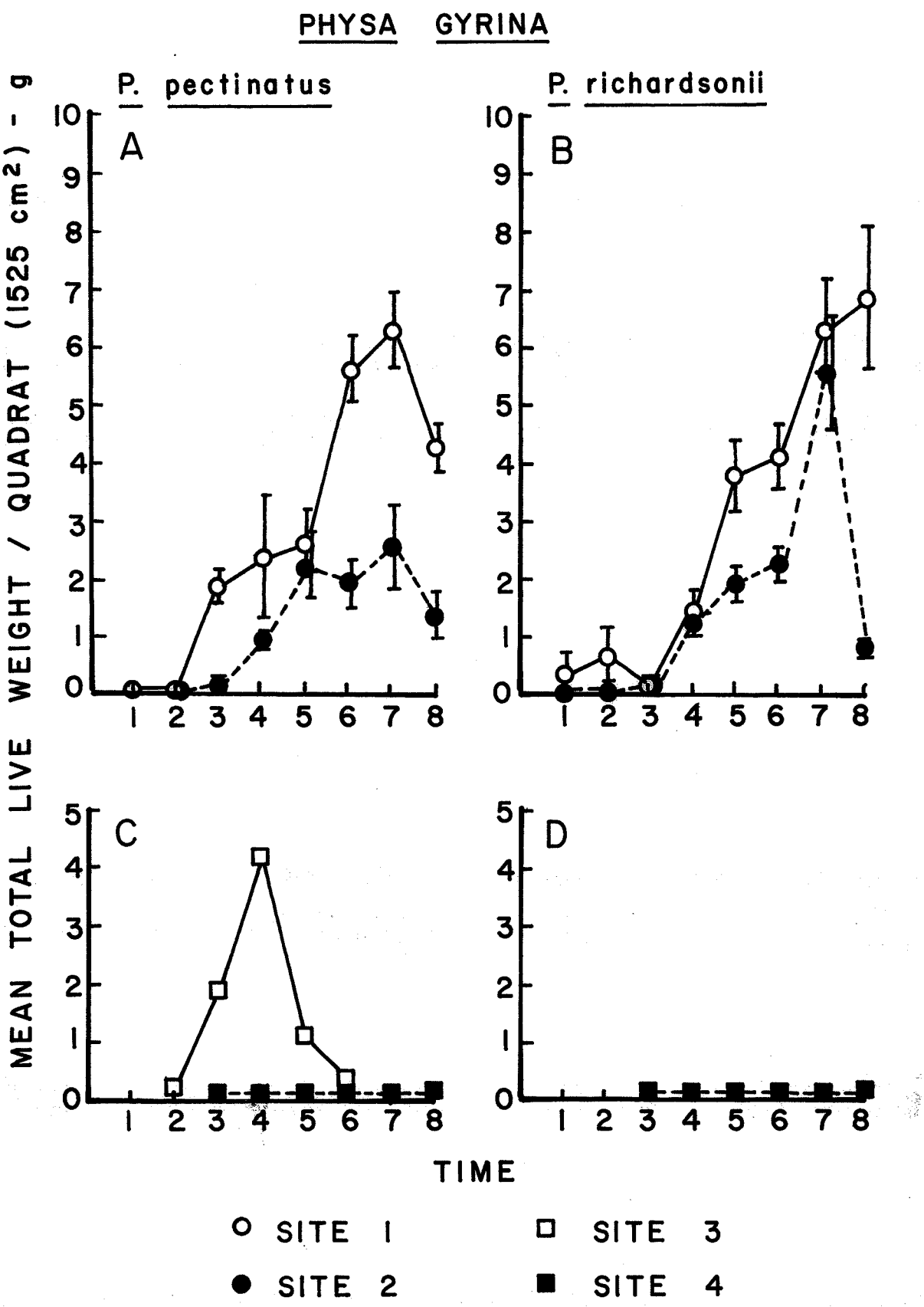
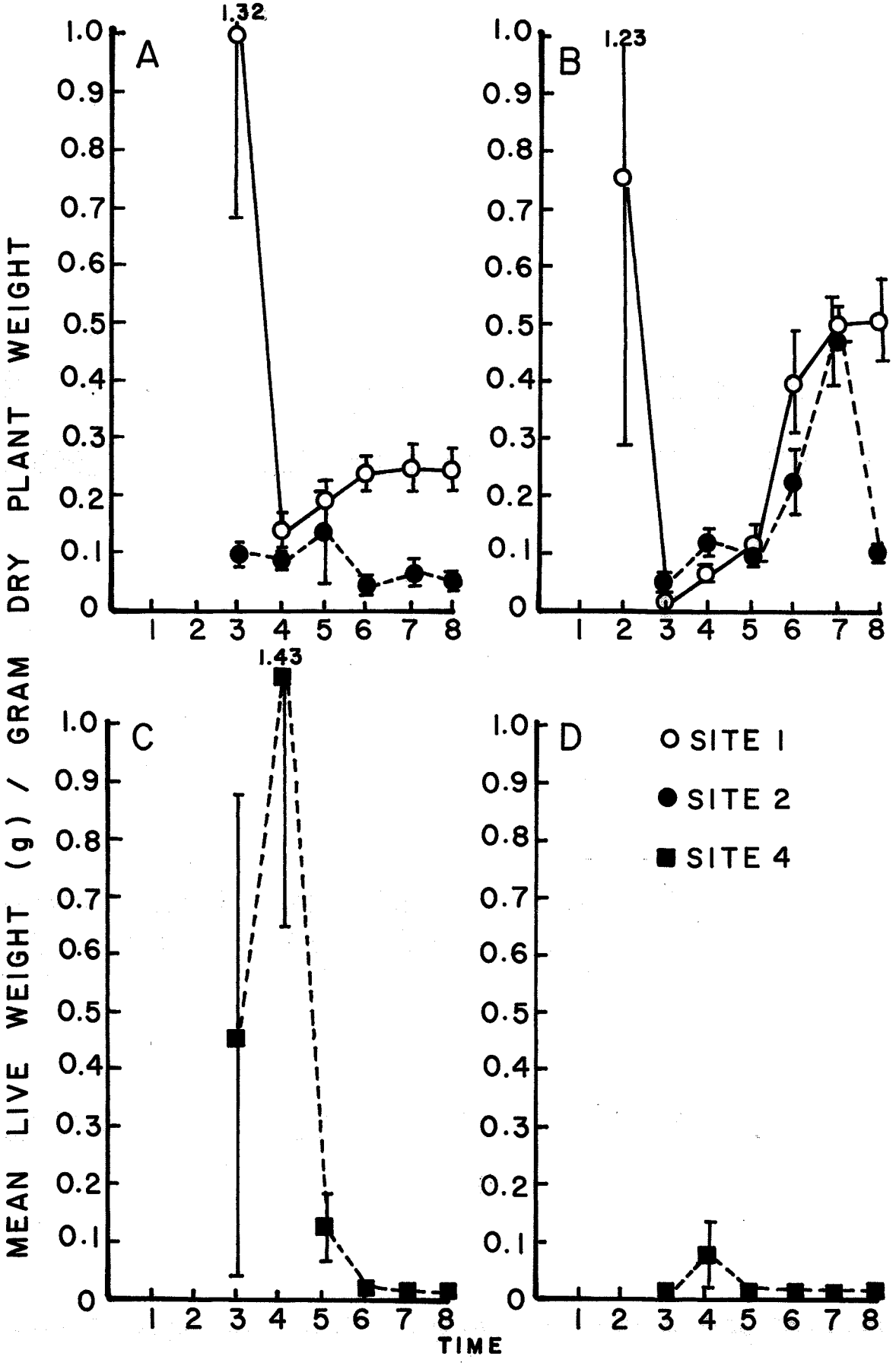

PHYSA GYRINA
P. pectinatus
P. richardsonii
A
B
C
D
MEAN TOTAL LIVE WEIGHT / QUADRAT (1525 cm²) - g
TIME
SITE 1
SITE 2
SITE 3
SITE 4

Figure 58. Mean live weight (g) of Physa gyrina per gram dry weight of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and site 4 respectively during the 1973 season. Vertical bars represent standard errors.


A
B
C
D
1.32
1.23
1.43
MEAN LIVE WEIGHT (g) / GRAM DRY PLANT WEIGHT
TIME
SITE 1
SITE 2
SITE 4
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1 2 3 4 5 6 7 8

in these stands.

At site 4 (Fig. 58C and D), significantly ($p < .05$, n=10) greater values for biomass of P. gyrina were observed in P. pectinatus stands at time 4; at time 5 biomass was still greater in these stands but the difference was no longer significant.

At site 3 (Fig. 59), maximum biomass of Physa per unit dry weight of P. pectinatus was observed at time 4.

The mean live weight of P. gyrina per unit plant surface area of the two macrophytes (Fig. 60) showed patterns similar to those expressed in terms of plant dry weight.

The mean live weight of L. stagnalis per unit bottom area (Fig. 61A and B) at site 1 was greater in P. richardsonii than in P. pectinatus stands during times 3-7. At site 2, higher values were observed in P. richardsonii stands at times 3-4 and 6-8.

At site 4 (Fig. 61Cand D), greater values were observed in P. richardsonii stands at times 3 and 6-8.

At site 3 (Fig. 61C), maximum live weight per unit bottom area was observed at time 3.

The mean live weight of L. stagnalis per unit plant dry weight (Fig. 62A and B) at site 1 was significantly ($p < .001$-$.02$, n=10) greater in P. richardsonii than in P. pectinatus stands during times 4-7. At site 2, biomass was significantly ($p < .02$, n=10) greater in P. richardsonii stands at times 4 and 7. The two-week lag between P. richardsonii stands at sites 1 and 2 was evident during the first half of the season.

At site 4 (Fig. 62C and D), biomass was greater in P. richardsonii stands at times 4 and 6 but this difference was not

Figure 59. Mean live weight (g) of Physa gyrina per gram dry weight of Potamogeton pectinatus at site 3 during the 1973 season. Vertical bars represent standard errors.

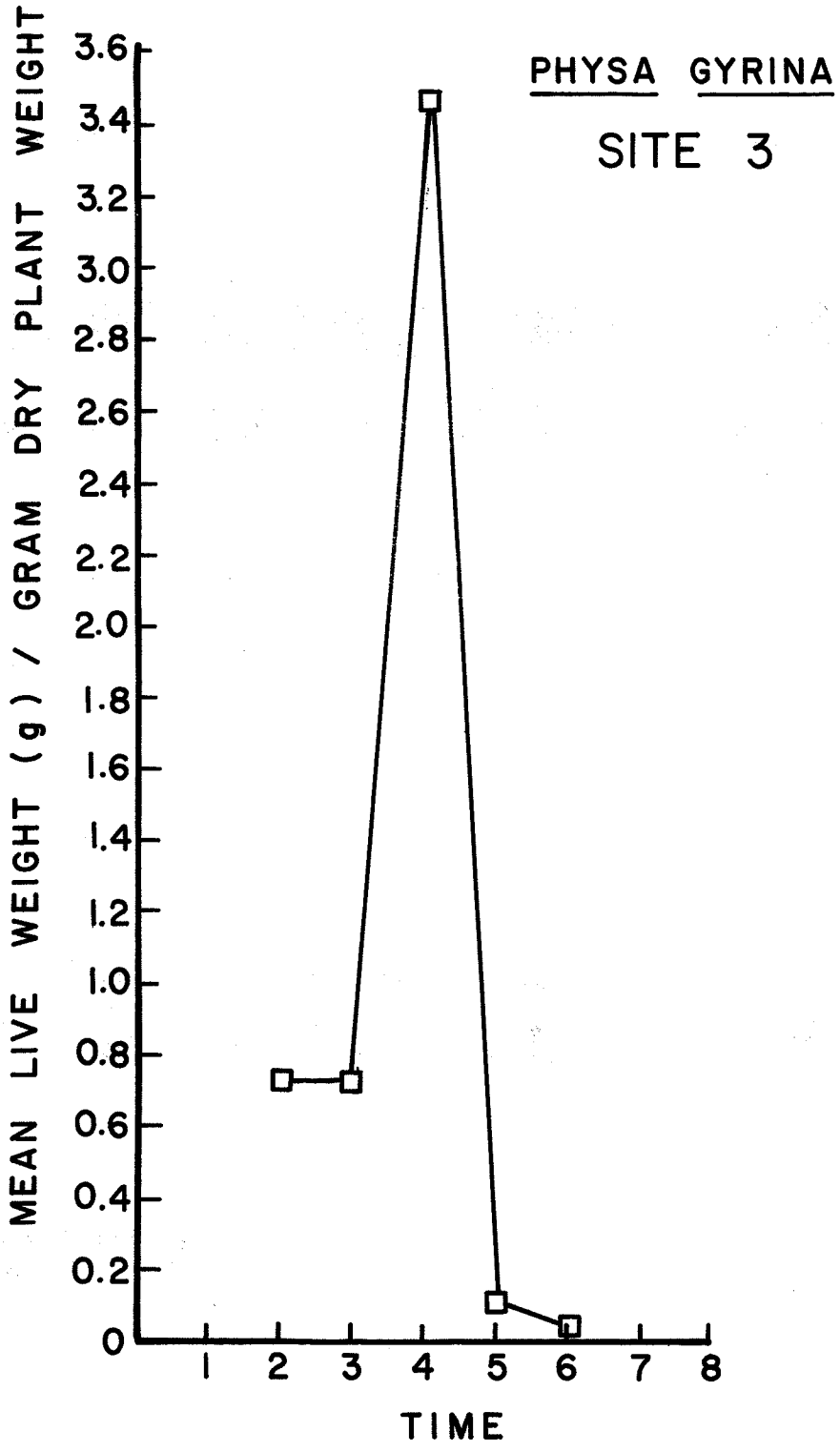

PHYSA GYRINA
SITE 3
MEAN LIVE WEIGHT (g) / GRAM DRY PLANT WEIGHT
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
1
2
3
4
5
6
7
8
TIME

Figure 60. Mean live weight (g) of Physa gyrina per 100 cm^2 surface area of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors.

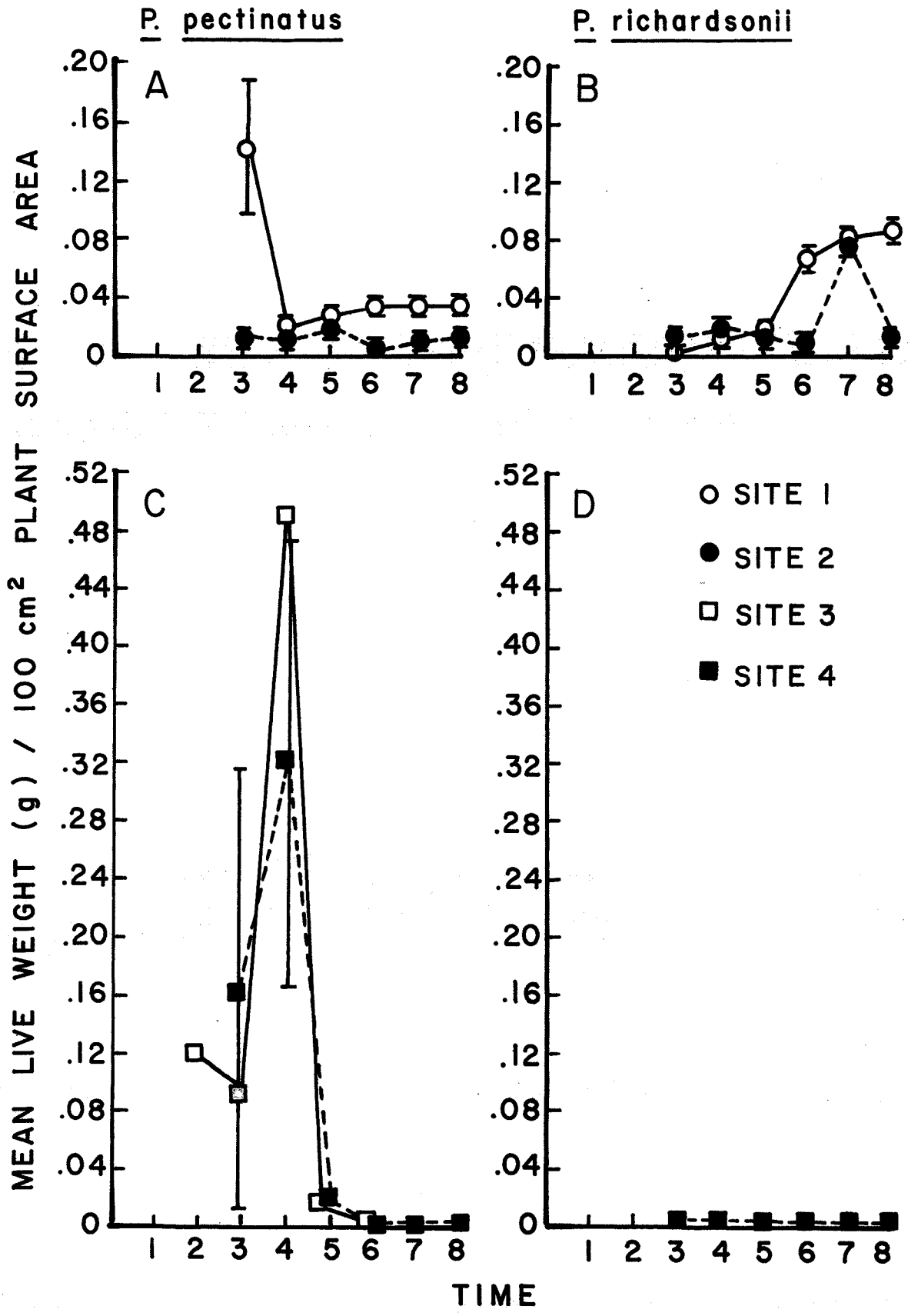

P. pectinatus
P. richardsonii
A
B
C
D
.20
.16
.12
.08
.04
0
.52
.48
.44
.40
.36
.32
.28
.24
.20
.16
.12
.08
.04
0
1 2 3 4 5 6 7 8
MEAN LIVE WEIGHT (g) / 100 cm² PLANT SURFACE AREA
TIME
SITE 1
SITE 2
SITE 3
SITE 4

Figure 61. Mean total live weight (g) of Lymnaea stagnalis per quadrat sample (1525 cm^2 bottom area) in stands of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors.

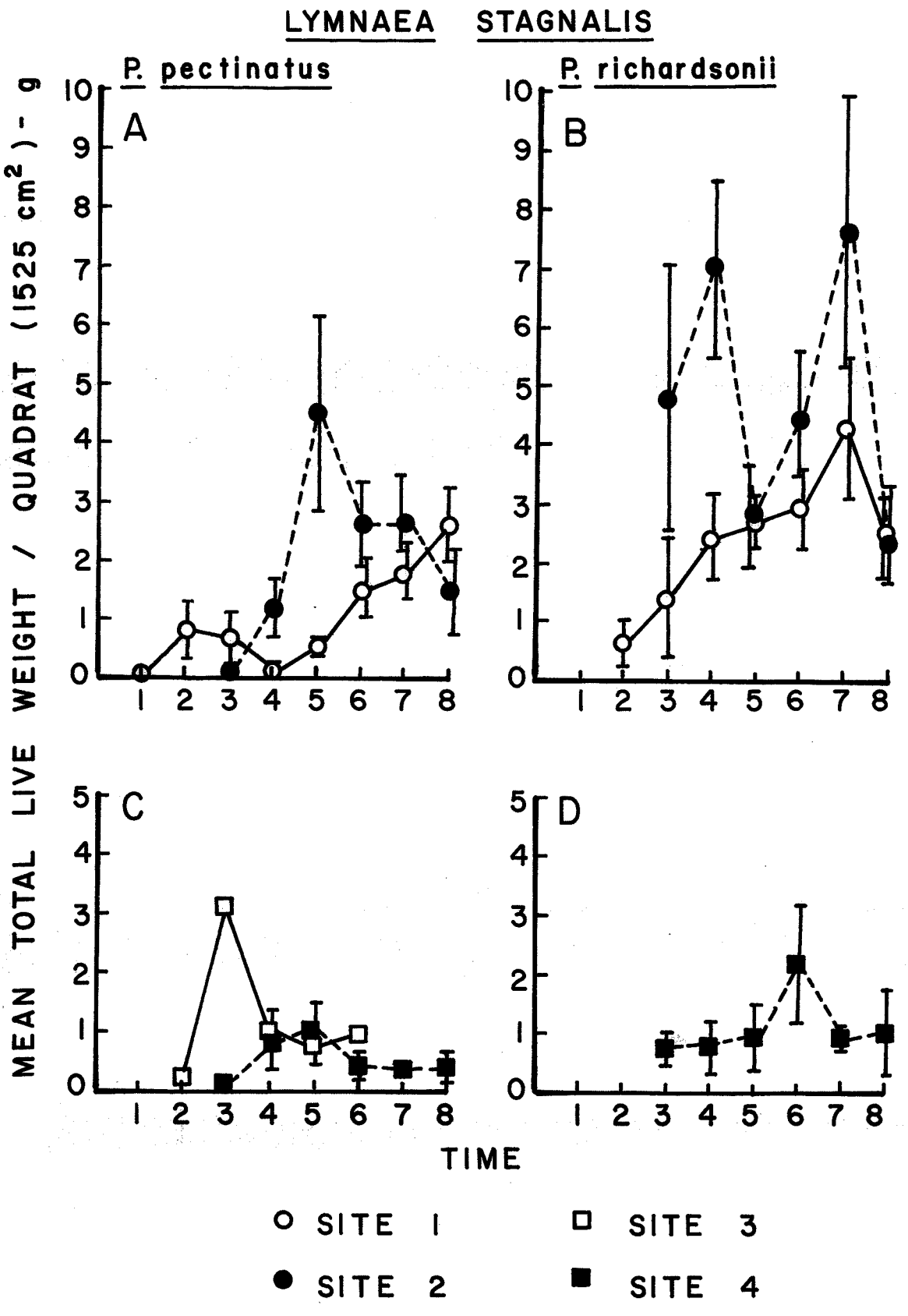
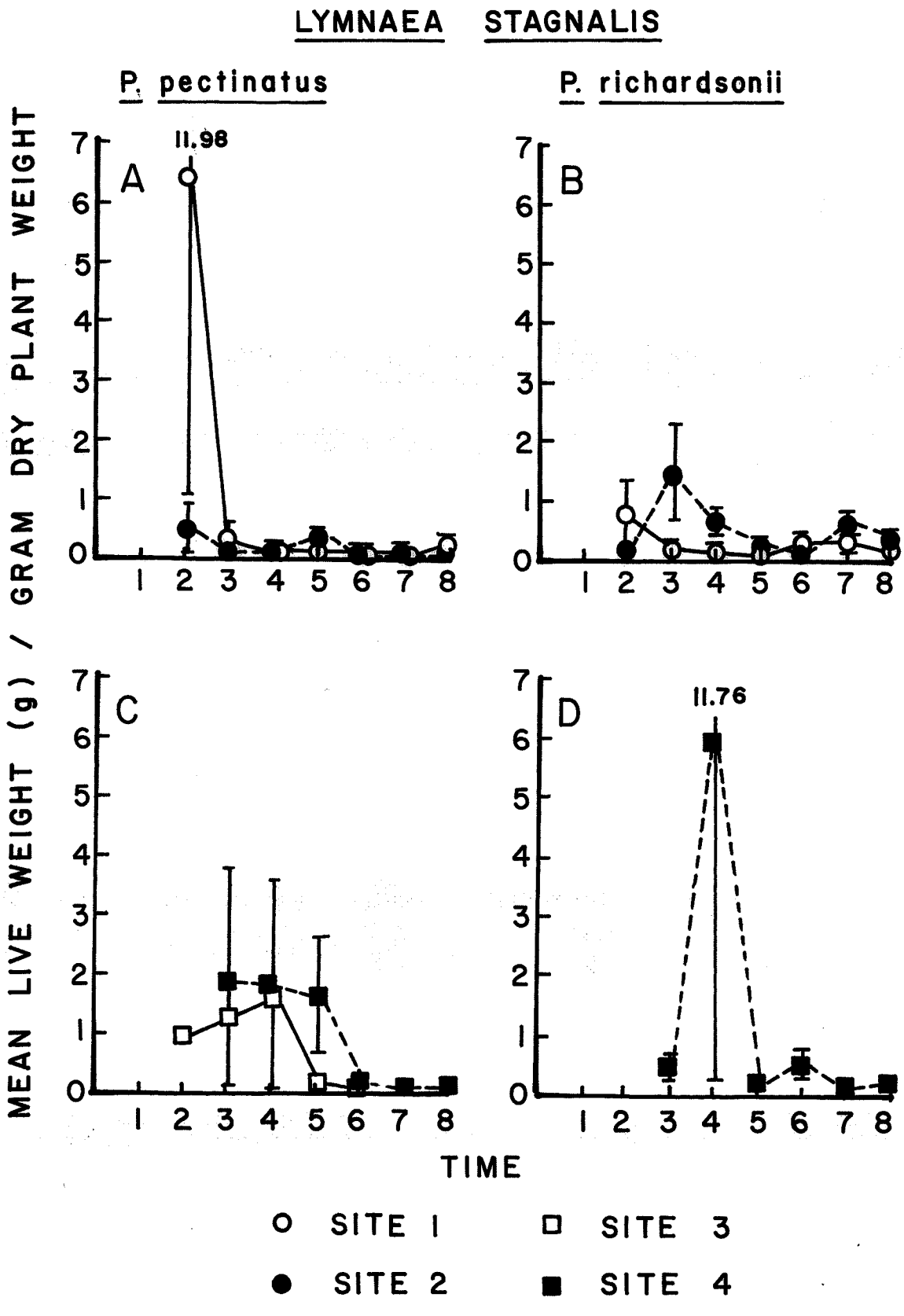

LYMNAEA STAGNALIS
P. pectinatus
P. richardsonii
A
B
C
D
MEAN TOTAL LIVE WEIGHT / QUADRAT (1525 cm²) - g
TIME
SITE 1
SITE 2
SITE 3
SITE 4

Figure 62. Mean live weight (g) of Lymnaea stagnalis per gram dry weight of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors.


LYMNAEA STAGNALIS
P. pectinatus
P. richardsonii
A
B
C
D
11.98
11.76
MEAN LIVE WEIGHT (g) / GRAM DRY PLANT WEIGHT
TIME
SITE 1
SITE 2
SITE 3
SITE 4

significant because of the large variance among the samples.

At site 3 (Fig. 62C), maximum biomass of L. stagnalis per unit dry weight of P. pectinatus was observed at time 4.

The mean live weight of L. stagnalis per unit plant surface area (Fig. 63) continued to show the tendencies that were significant in terms of plant dry weight.

vi. Size class distributions

At site 1, P. gyrina (Fig. 64A and B) showed initially high mean axial lengths that represented the overwintered adults. The axial length decreased by time 3 in both types of stands, indicating the appearance of young. However, at this time the values in the P. pectinatus stands were slightly higher than those in the P. richardsonii stands because hatching of the young in the former stands had already occurred before time 3 (Fig. 65A), and by time 3 these individuals had advanced to several higher size classes, accounting for the higher mean axial length. Hatching began later in the P. richardsonii stands (Fig. 65B), i.e. approximately at time 3, since at that time most of the individuals were still in the lower size classes. Although more young hatched per unit bottom area in the P. pectinatus stands, the growth rate of the snails was more rapid in the latter part of the season in the P. richardsonii stands, accounting for the greater snail biomass observed in these stands after time 5 (Fig. 58A and B).

At site 2, again mean axial length (Fig. 64A and B) was greater in the P. pectinatus than in the P. richardsonii stands during the first part of the season. Reversal between the two types of stands in terms of mean axial length occurred later than at site 1 because a relatively greater proportion of adults persisted in the P. pectinatus

Figure 63. Mean live weight (g) of Lymnaea stagnalis per 100 cm^2 surface area of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors.

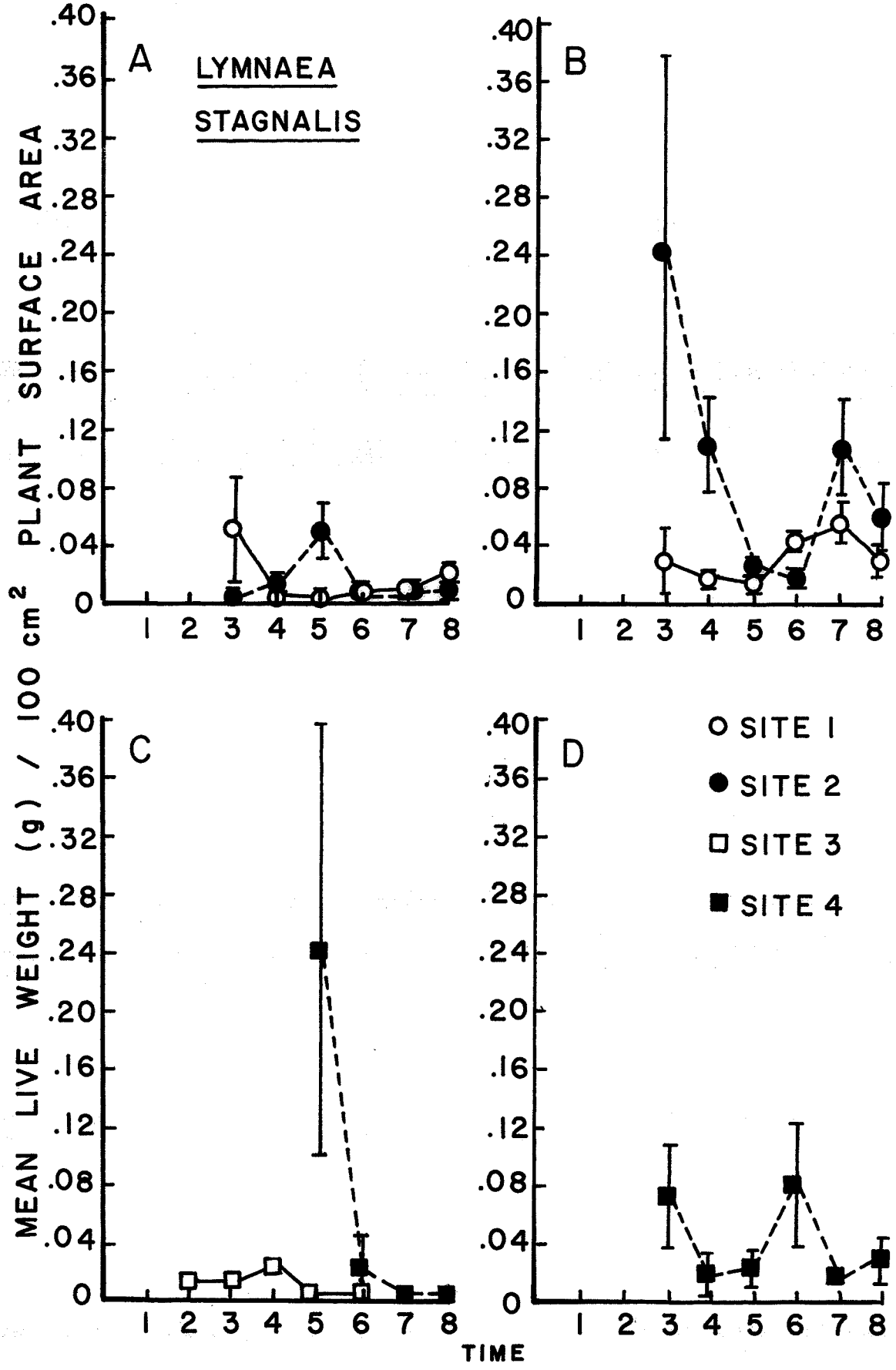

A
LYMNAEA
STAGNALIS
B
C
D
SITE 1
SITE 2
SITE 3
SITE 4
MEAN LIVE WEIGHT (g) / 100 cm² PLANT SURFACE AREA
TIME
.40
.36
.32
.28
.24
.20
.16
.12
.08
.04
0
1 2 3 4 5 6 7 8

Figure 64. Mean axial length (mm) of Physa gyrina in stands of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors.

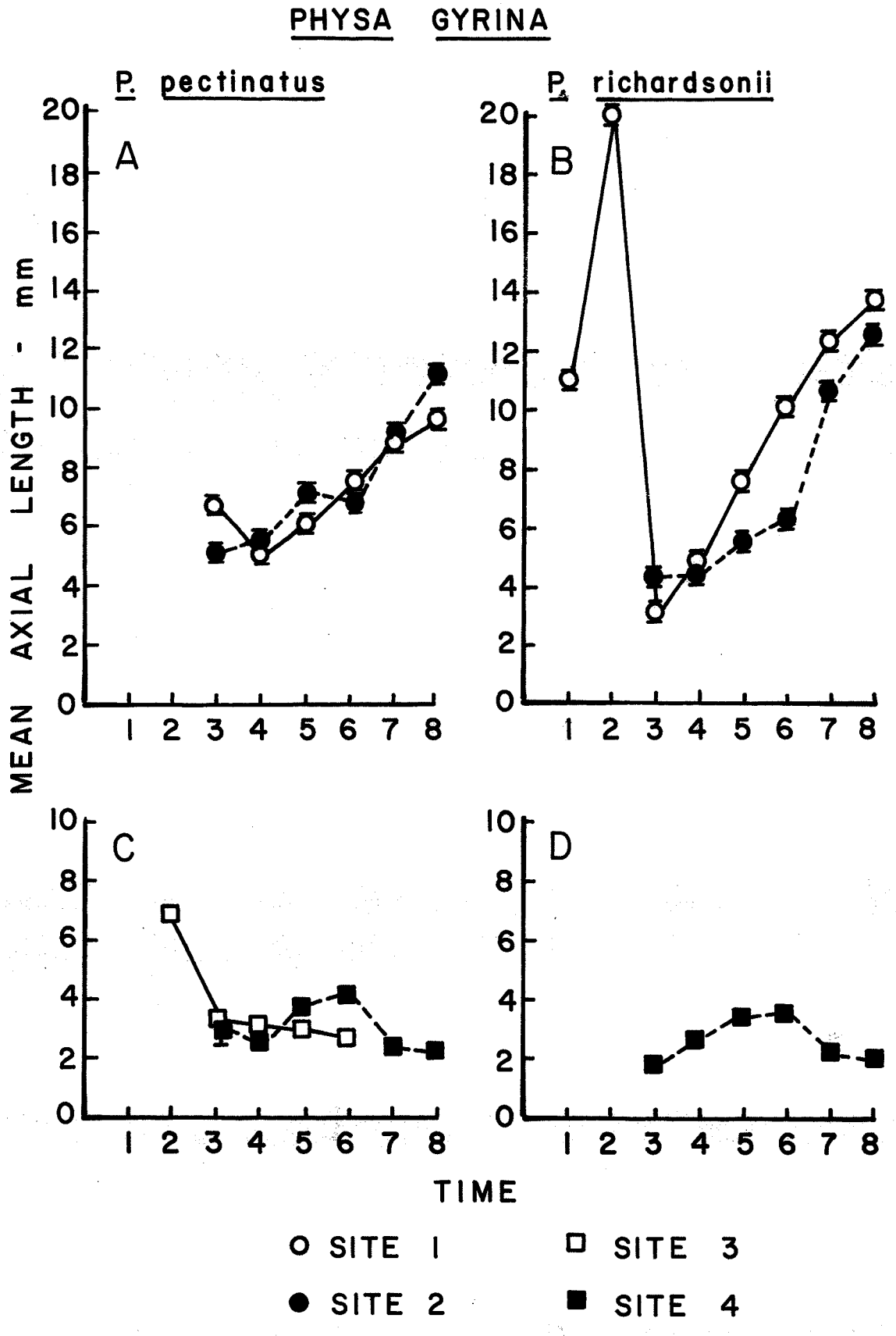
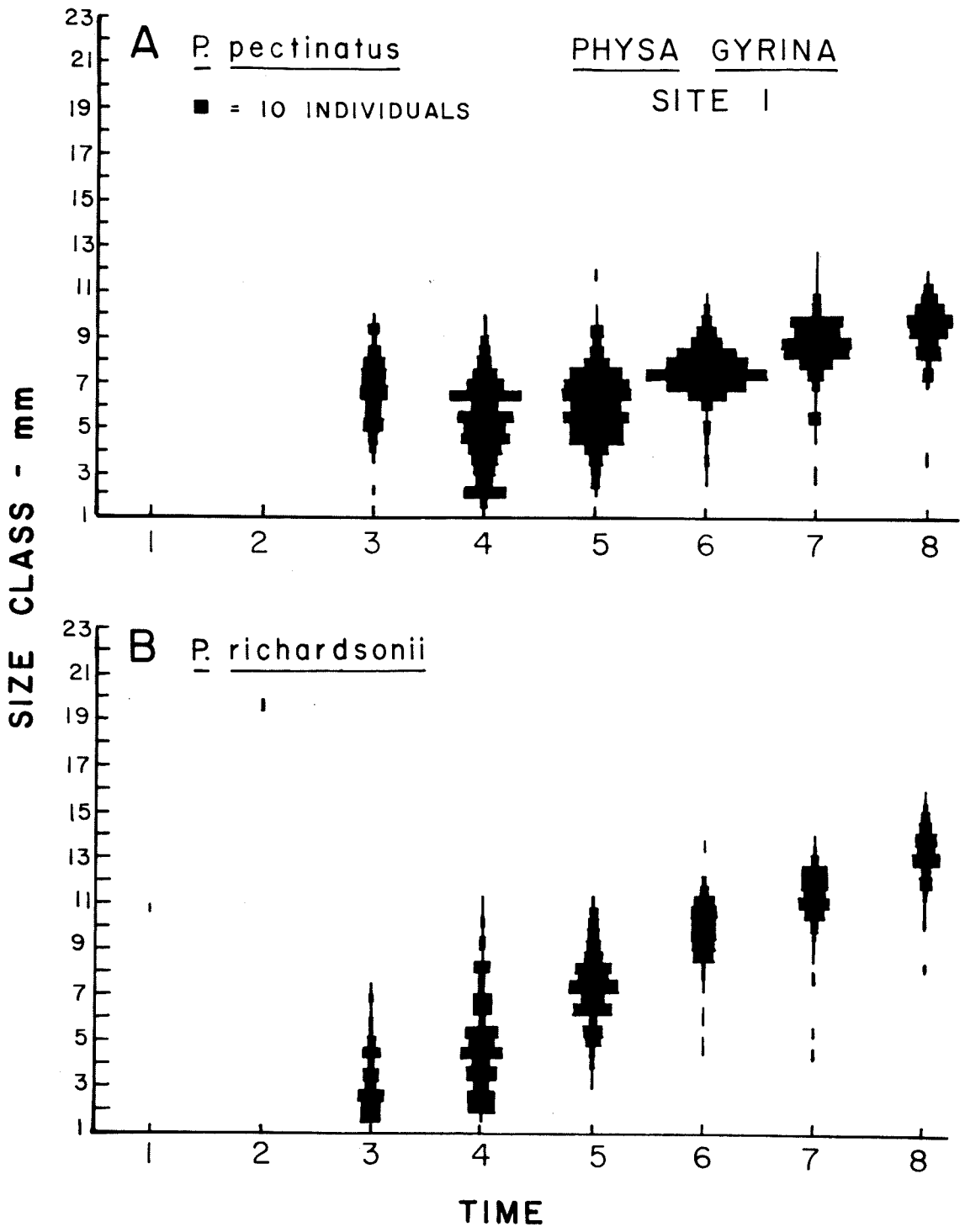

PHYSA GYRINA
P. pectinatus
P. richardsonii
A
B
C
D
MEAN AXIAL LENGTH - mm
TIME
SITE 1
SITE 2
SITE 3
SITE 4

Figure 65. Size class distribution of Physa gyrina in stands of Potamogeton pectinatus (A) and P. richardsonii (B) at site 1 during the 1973 season. Values represent the total numbers of individuals recorded in five sample quadrats (7625 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.


A P. pectinatus
■ = 10 INDIVIDUALS
PHYSA GYRINA
SITE I
B P. richardsonii
SIZE CLASS - mm
TIME
1
3
5
7
9
11
13
15
17
19
21
23
2
4
6
8

stands at site 2 (Fig. 66). Hatching again occurred slightly earlier in the P. pectinatus than the P. richardsonii stands, but, as at site 1, growth of the snails occurred at a faster rate in the P. richardsonii stands. The greater numbers subsequently present in the P. richardsonii stands reflected the approximately equal densities of this snail observed in these stands at the two sites.

At sites 1 and 2, the few adults present in the spring died out almost completely after reproducing early in the season. Reproduction later in the season may have been due to some young of the year that had reached reproductive maturity while conditions were still suitable for mating. This finding is consistent with those of DeWitt (1955) and Sankurathri and Holmes (1976). However reproduction soon declined and ceased at these sites, perhaps because of generally declining temperatures (except at time 8) or diminishing food quality or supply. The behavior of the population at site 1 with time has been described in detail in terms of a matrix model by Pip and Stewart (1975) (Appendix I).

At site 4, values for mean axial length of P. gyrina (Fig. 64C and D) were higher in the P. pectinatus than in the P. richardsonii stands during the first part of the season because greater proportions of adults persisted in these stands, and therefore the shift to P. richardsonii stands that had been observed at sites 1 and 2 during the second half of the season was not observed at site 4. Some hatching (Fig. 67A and B) was evident by time 3, and it appeared to have commenced slightly earlier in the P. pectinatus stands, although at times 3 and 4 it was of greater magnitude in the P. richardsonii stands in terms of unit bottom area because of the larger

Figure 66. Size class distribution of Physa gyrina in stands of Potamogeton pectinatus (A) and P. richardsonii (B) at site 2 during the 1973 season. Values represent the total numbers of individuals recorded in five sample quadrats (7625 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.

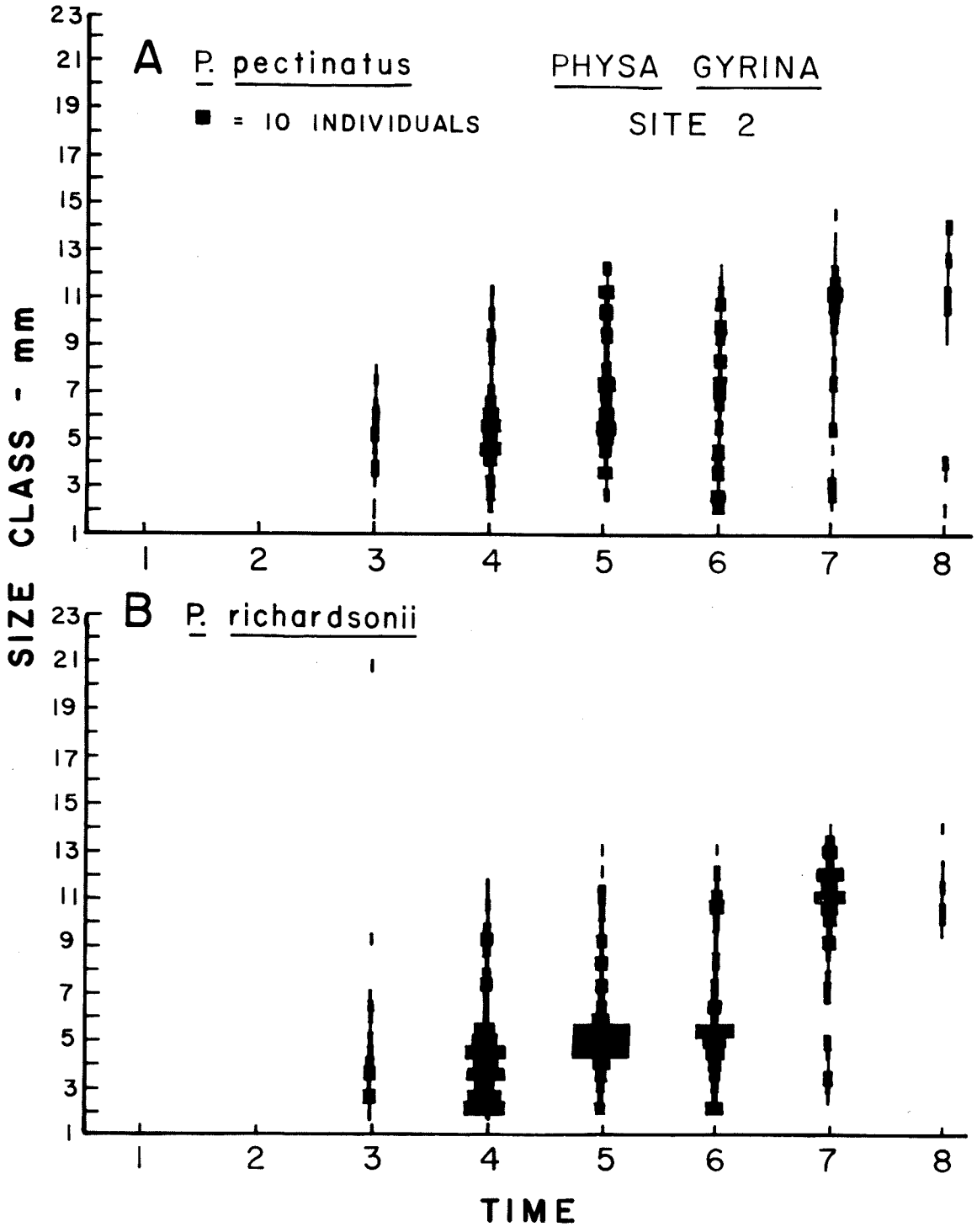
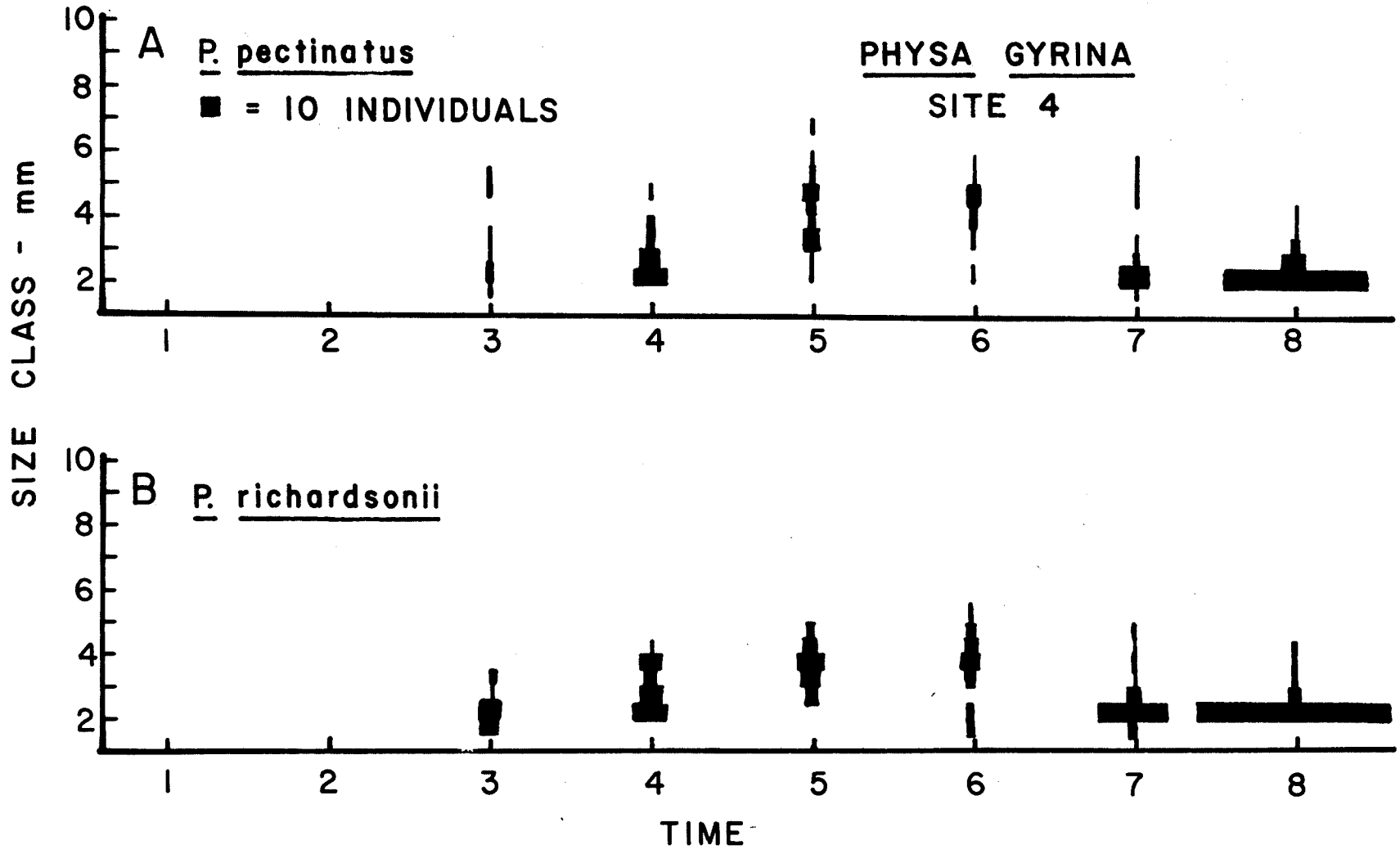

A P. pectinatus
PHYSA GYRINA
■ = 10 INDIVIDUALS
SITE 2
B P. richardsonii
SIZE CLASS - mm
TIME
1
3
5
7
9
11
13
15
17
19
21
23
2
4
6
8

Figure 67. Size class distribution of Physa gyrina in stands of Potamogeton pectinatus (A) and P. richardsonii (B) at site 4 during the 1973 season. Values represent the total numbers of individuals recorded in five sample quadrats (7625 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.


A
P. pectinatus
■ = 10 INDIVIDUALS
PHYSA GYRINA
SITE 4
B
P. richardsonii
SIZE CLASS - mm
TIME
10
8
6
4
2
1
2
3
4
5
6
7
8

plant mass in the latter stands. After time 6, hatching was of greater magnitude in the P. pectinatus stands, and a large cohort hatched at time 8. Because the population was composed entirely of young during the second half of the season, this peak was due to reproduction by the young of the year that had hatched earlier during the season. Reproduction on such a large scale so late in the season may have been partly influenced by the rise in temperature at this site after time 6 (Fig. 39H).

At site 3 (Fig. 64C), mean axial length of Physa showed a sharp decrease due to hatching of young (Fig. 68) which commenced before time 3 at this site. A very large number of young appeared before time 4 but reproduction declined at times 5 and 6. The mean axial length continued to decrease throughout the season as young continued to hatch and the adults disappeared. The population dynamics at this site were similar to those observed at site 5 during 1972.

The mean axial length of L. stagnalis (Fig. 69A and B) at site 1 decreased at time 3 in P. richardsonii and at time 4 in P. pectinatus stands since hatching started slightly before time 3 in the former stands while in the latter stands it was limited and the young were not present in these samples until time 4 (Fig. 70A and B). The overwintered adults were present during the first half of the season but became less common as the juveniles continued to increase in size. Growth during the second half of the season occurred at a faster rate in the P. richardsonii stands.

At site 2, mean axial length (Fig. 69A and B) decreased in the P. richardsonii stands two weeks later than at site 1. The reduced value at time 3 in the P. pectinatus stands was due to the absence of

Figure 68. Size class distribution of Physa gyrina in stands of Potamogeton pectinatus at site 3 during the 1973 season. Values represent the total numbers of individuals recorded in four sample quadrats (6100 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.

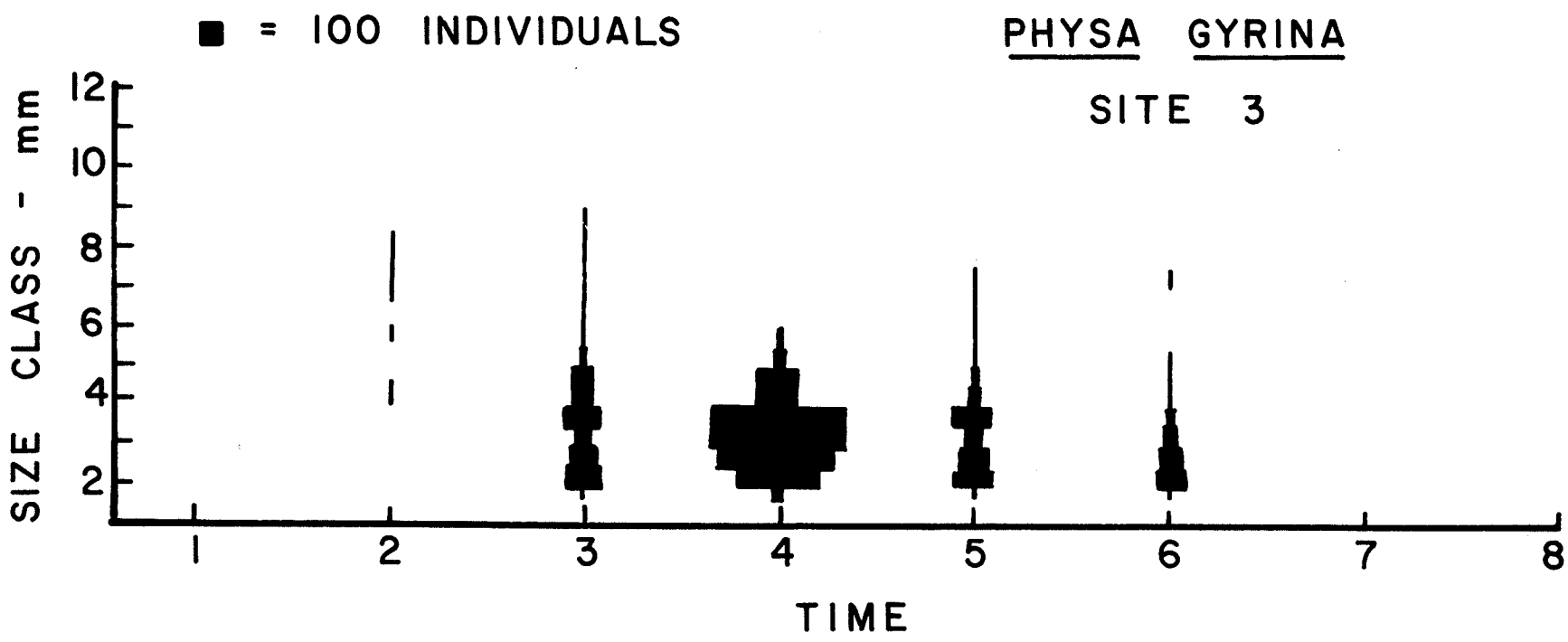

■ = 100 INDIVIDUALS
PHYSA GYRINA
SITE 3
SIZE CLASS - mm
12
10
8
6
4
2
1
2
3
4
5
6
7
8
TIME

Figure 69. Mean axial length (mm) of Lymnaea stagnalis in stands of Potamogeton pectinatus (A and C) and P. richardsonii (B and D) at sites 1 and 2 and sites 3 and 4 respectively during the 1973 season. Vertical bars represent standard errors. ○ = site 1, ● = site 2, □ = site 3, ■ = site 4.

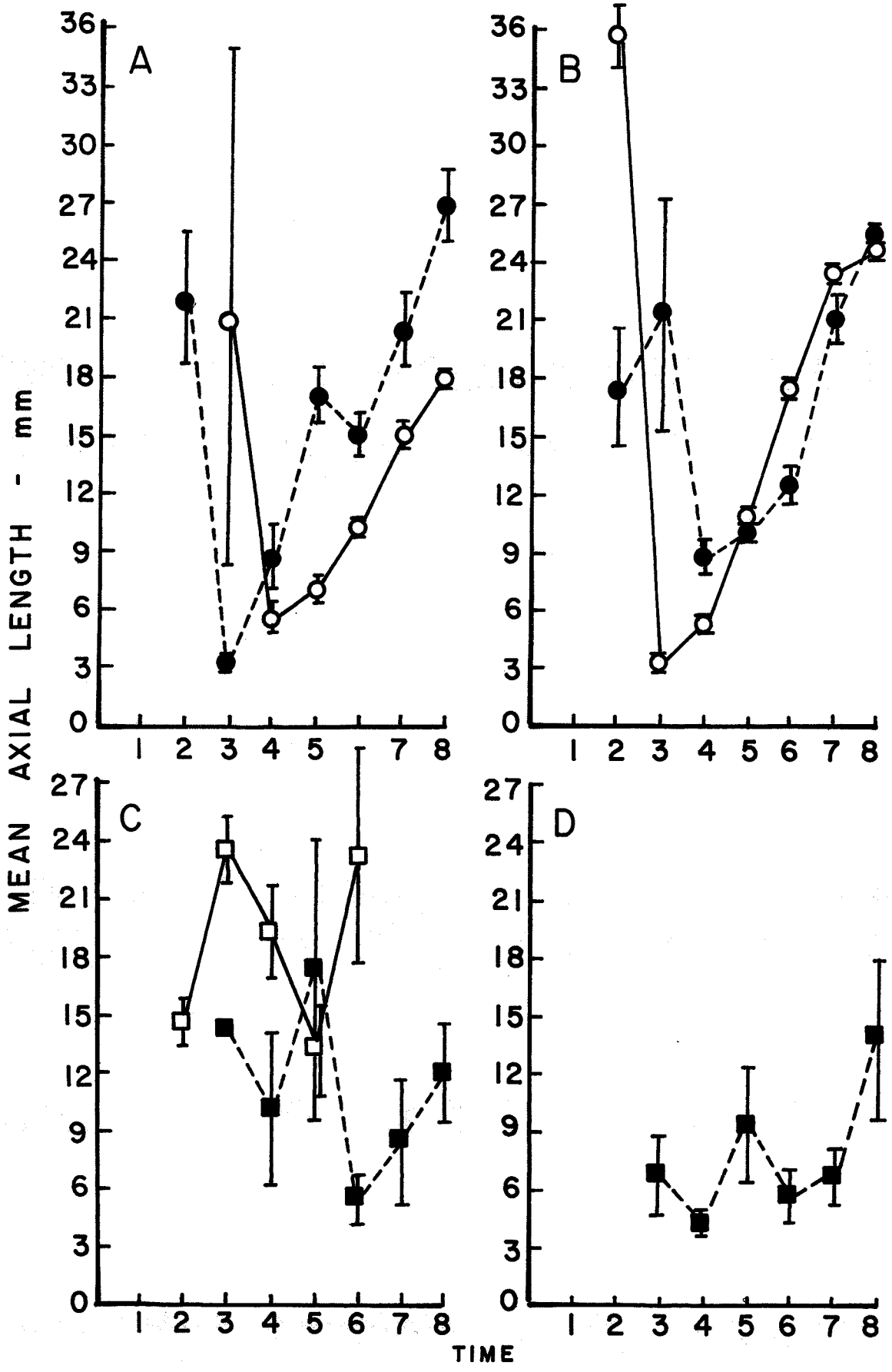
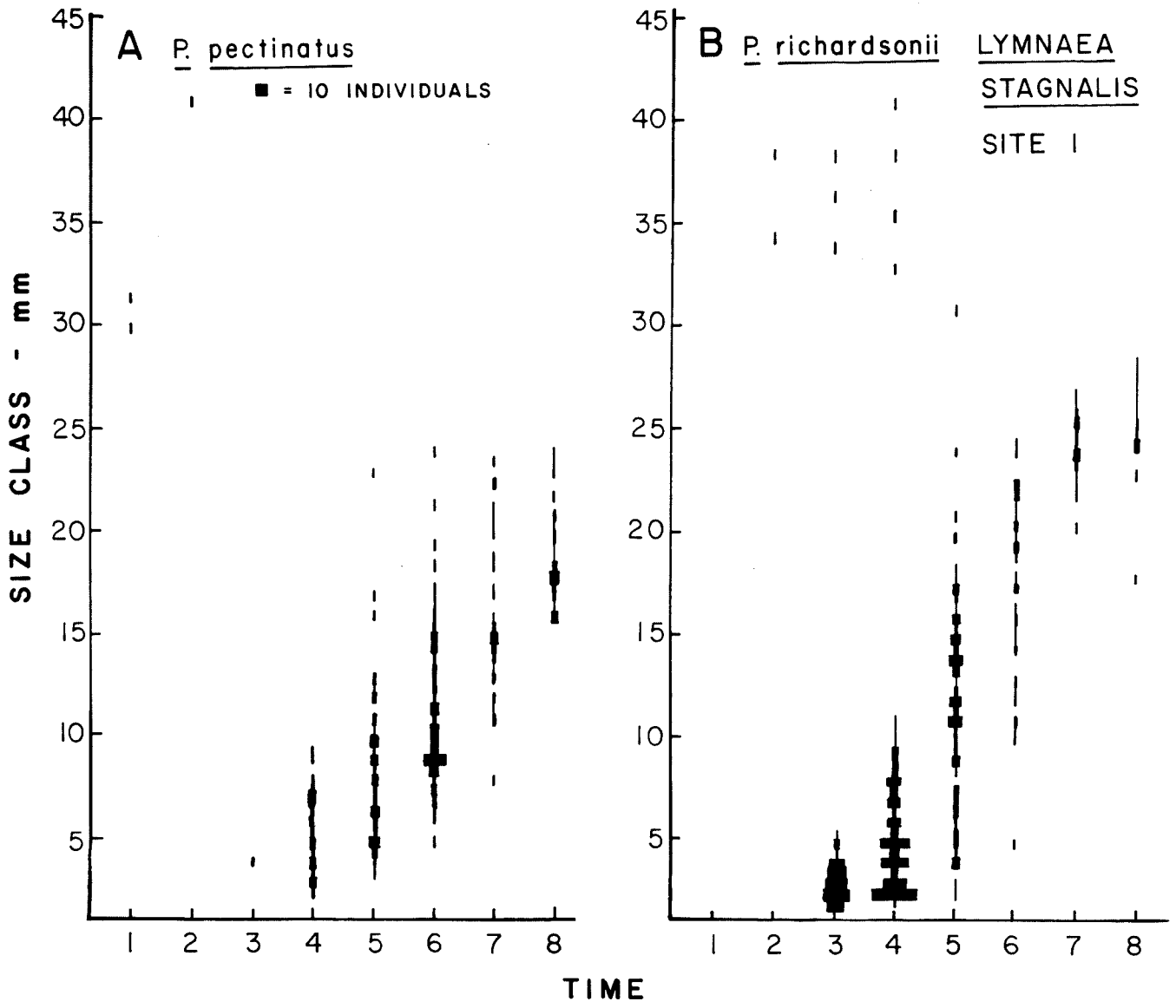

A
B
C
D
MEAN AXIAL LENGTH - mm
TIME
0
3
6
9
12
15
18
21
24
27
30
33
36
1
2
3
4
5
6
7
8

Figure 70. Size class distribution of Lymnaea stagnalis in stands of Potamogeton pectinatus (A) and P. richardsonii (B) at site 1 during the 1973 season. Values represent the total numbers of individuals recorded in five sample quadrats (7625 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.


A P. pectinatus
■ = 10 INDIVIDUALS
B P. richardsonii LYMNAEA STAGNALIS
SITE 1
SIZE CLASS - mm
TIME
45
40
35
30
25
20
15
10
5
1 2 3 4 5 6 7 8

adults from these samples. Adults were present in P. pectinatus samples from site 1 and accounted for the large standard error of the value at time 3. At site 2, time 3 (Fig. 71A and B), insignificant numbers of newly hatched individuals were present in the P. richardsonii stands and the bulk of the young did not appear until time 4. Smaller numbers of young were observed in P. pectinatus stands. Again, the numbers of adults gradually decreased towards the end of the season but did not disappear completely. It appears that individuals of both P. gyrina and L. stagnalis may survive beyond the second summer, although most of the population does not. Differences between growth rates in the two types of stands during the second half of the season at site 2 were not significant.

Egg cases of L. stagnalis were frequently observed attached to the stems and leaves of P. richardsonii during the sampling periods preceding hatching at sites 1 and 2. Adults collected at time 2 at site 1 laid eggs in the laboratory, where embryonic development at 20 C. required approximately 14 days.

At site 4 (Fig. 69C and D), axial lengths of the subpopulations in both types of stands showed decreases at times 4 and 6. Hatching of L. stagnalis began before time 3 in the P. richardsonii stands (Fig. 72); young were not present in P. pectinatus stands until time 4. Hatching in the P. richardsonii stands continued until time 4 and was followed by another period of hatching which began at time 6. Fewer young were observed in P. pectinatus stands in terms of unit bottom area.

At site 3 (Fig. 69C), minimum axial length for L. stagnalis was observed at time 5 but no sharp decrease occurred that could define

Figure 71. Size class distribution of Lymnaea stagnalis in stands of Potamogeton pectinatus (A) and P. richardsonii (B) at site 2 during the 1973 season. Values represent the total numbers of individuals recorded in five sample quadrats (7625 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.

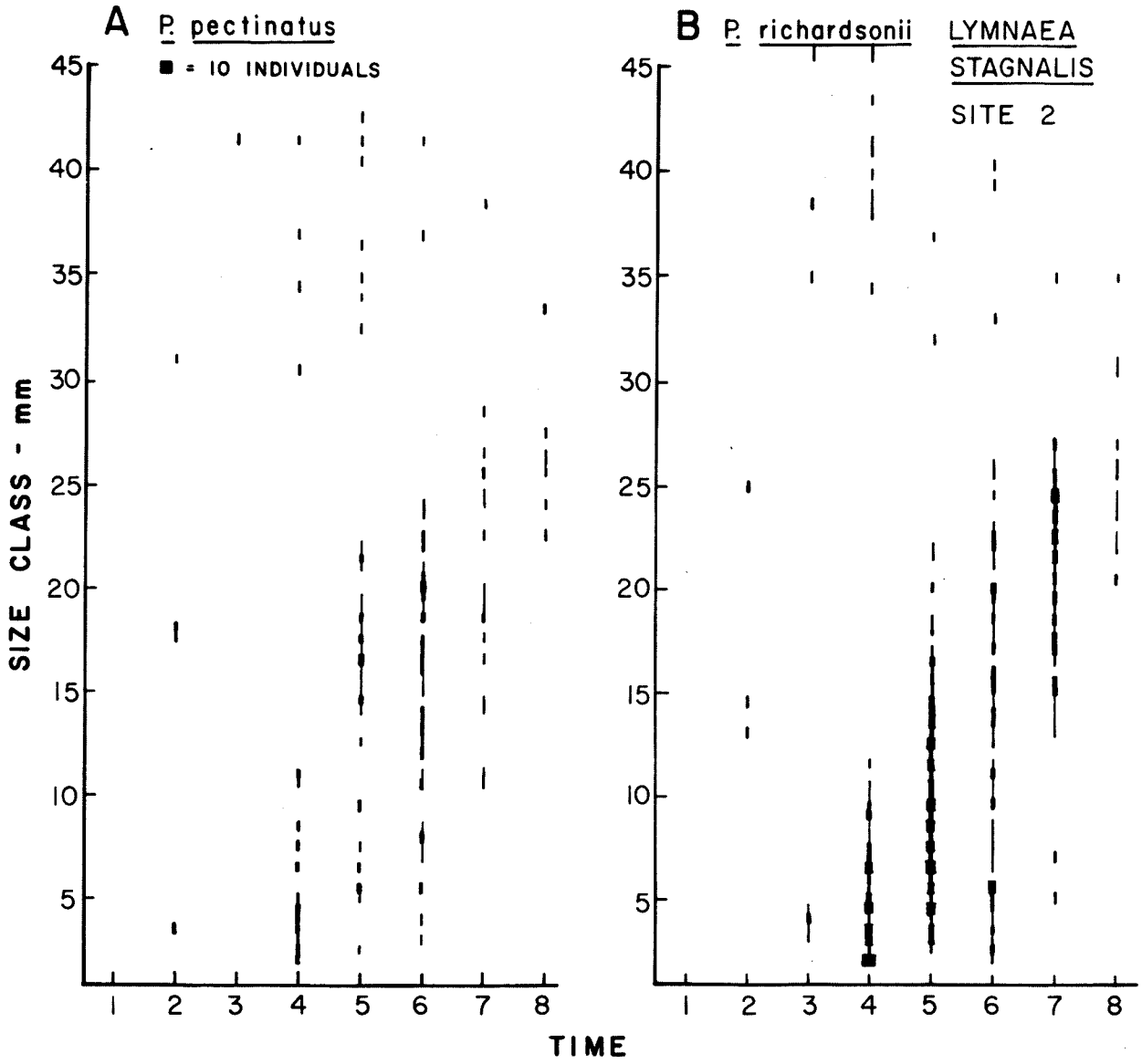

A
P. pectinatus
■ = 10 INDIVIDUALS
B
P. richardsonii
LYMNAEA STAGNALIS
SITE 2
SIZE CLASS - mm
45
40
35
30
25
20
15
10
5
1
2
3
4
5
6
7
8
TIME

Figure 72. Size class distribution of Lymnaea stagnalis in stands of Potamogeton pectinatus (A) and P. richardsonii (B) at site 4 during the 1973 season. Values represent the total numbers of individuals recorded in five sample quadrats (7625 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.

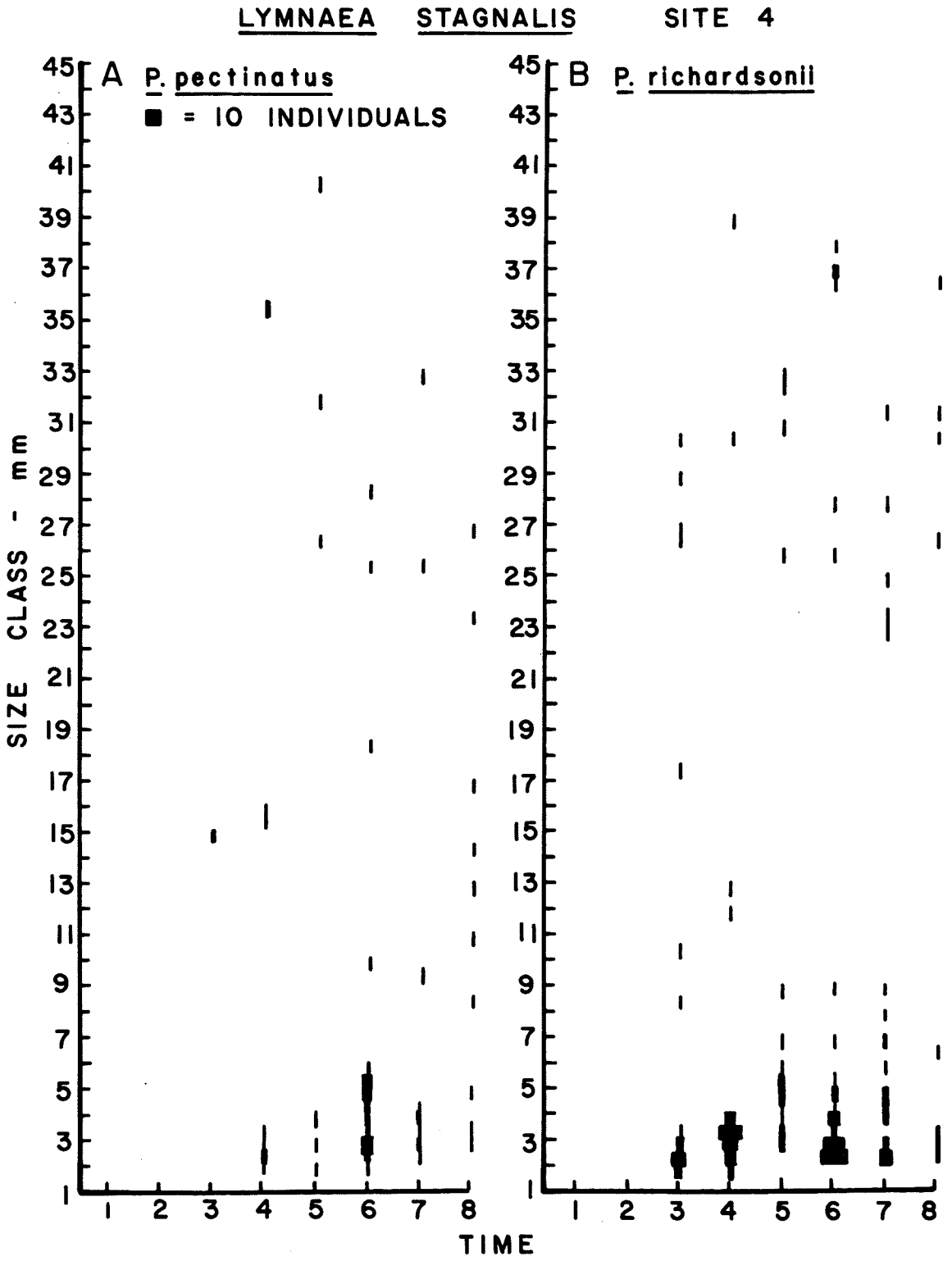
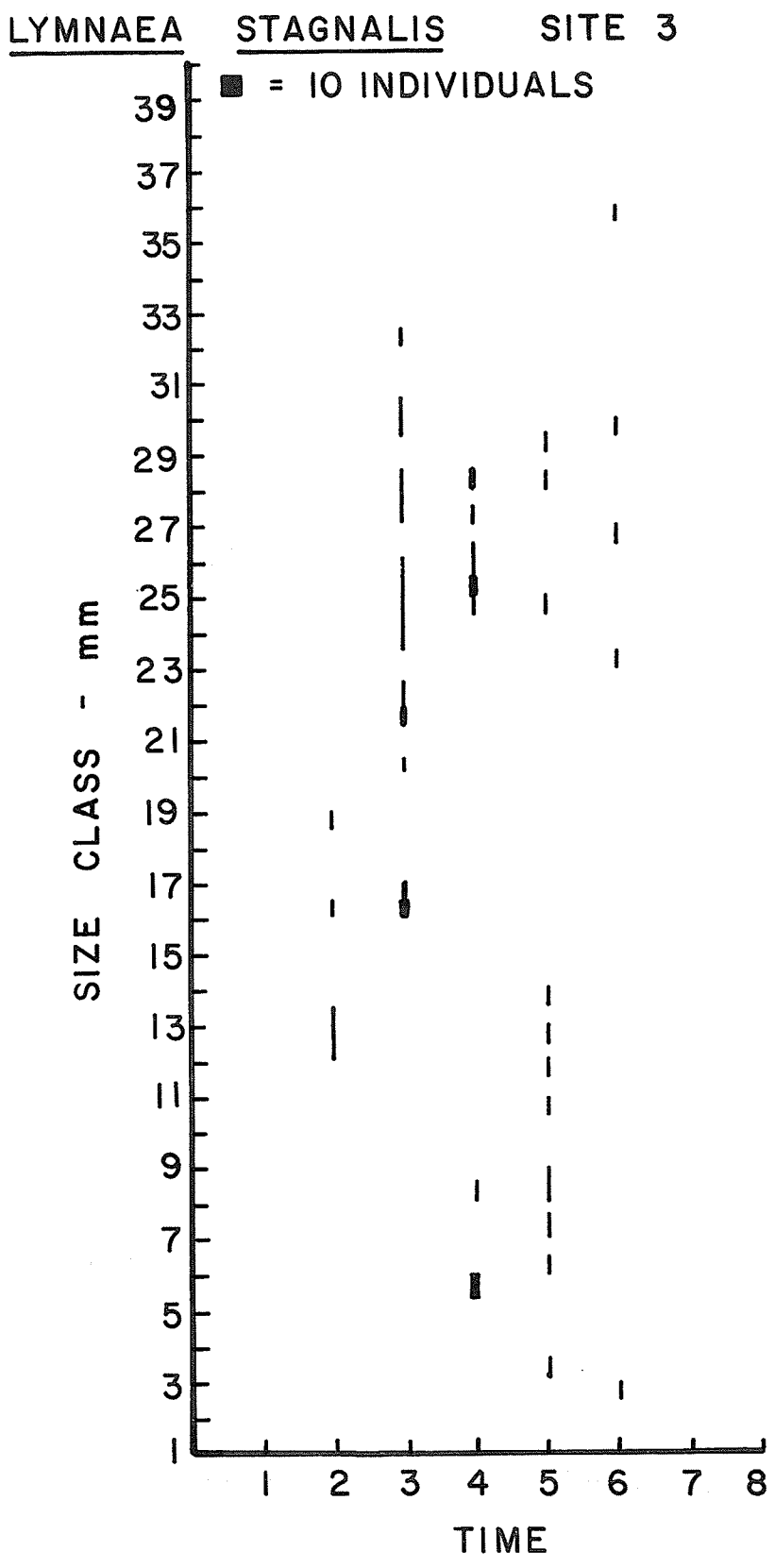

LYMNAEA STAGNALIS SITE 4
A P. pectinatus
■ = 10 INDIVIDUALS
B P. richardsonii
SIZE CLASS - mm
TIME
45
43
41
39
37
35
33
31
29
27
25
23
21
19
17
15
13
11
9
7
5
3
1
1 2 3 4 5 6 7 8

Figure 73. Size class distribution of Lymnaea stagnalis in stands of Potamogeton pectinatus at site 3 during the 1973 season. Values represent the total numbers of individuals recorded in four sample quadrats (6100 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.


LYMNAEA STAGNALIS SITE 3
■ = 10 INDIVIDUALS
SIZE CLASS - mm
39
37
35
33
31
29
27
25
23
21
19
17
15
13
11
9
7
5
3
1
1 2 3 4 5 6 7 8
TIME

a period of coordinated hatching. The first young began to hatch before time 4 (Fig. 73) and hatching continued at times 5 and 6.

Essentially, the size class distribution data suggested the following features:

1. The subpopulations of the gastropods present in each of the two types of plant stands within the same site behaved as recognizably distinct units.
2. Hatching of young often started earlier in stands of the preferred macrophyte than in those of the alternate stand and was generally of greater magnitude.
3. Periods of hatching appeared to coincide with the early stages of increased growth of the preferred macrophytes.
4. Growth rates of both gastropods were often higher during the second half of the season in P. richardsonii stands.

B. Season III (1974)

a. Vegetation

i. Mean shoot length

The growth of Potamogeton pectinatus in terms of mean shoot length was synchronous at both sites 1 and 2 (Fig. 74A), but, as in 1973, the mean shoot length was smaller at site 2 than at site 1 because of the shallower water depth at site 2. The shoots began to reach the surface at both sites after time 4 and the first inflorescences appeared after time 5 but these were very rare, perhaps because of disturbances related to the heavy spring flooding.

The mean shoot lengths of P. richardsonii at the two sites (Fig. 74B) showed smaller growth increments at site 2 after time 2 than at site 1, but mean stem lengths were again similar at both sites at time 4. Inflorescence buds were not evident until time 4 and flowering commenced approximately at time 5. The phenological cycles of both macrophytes were significantly delayed when compared with those of the 1973 season.

ii. Mean dry weight per quadrat sample

The mean dry weight of P. pectinatus per quadrat sample (1525 cm^2) at sites 1 and 2 (Fig. 75A) indicated that growth of this plant was approximately synchronous at the two sites. As in 1973, plants from site 2 showed greater values for mean dry weight than those from site 1 during the latter part of the season because of increased branching. The mean dry weight per unit bottom area at both sites was approximately one-third of that observed during corresponding stages of the growth curve at these sites in 1973.

The mean values for dry weight of P. richardsonii per quadrat

Figure 74. Mean shoot length (cm) of Potamogeton pectinatus (A) and P. richardsonii (B) at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.

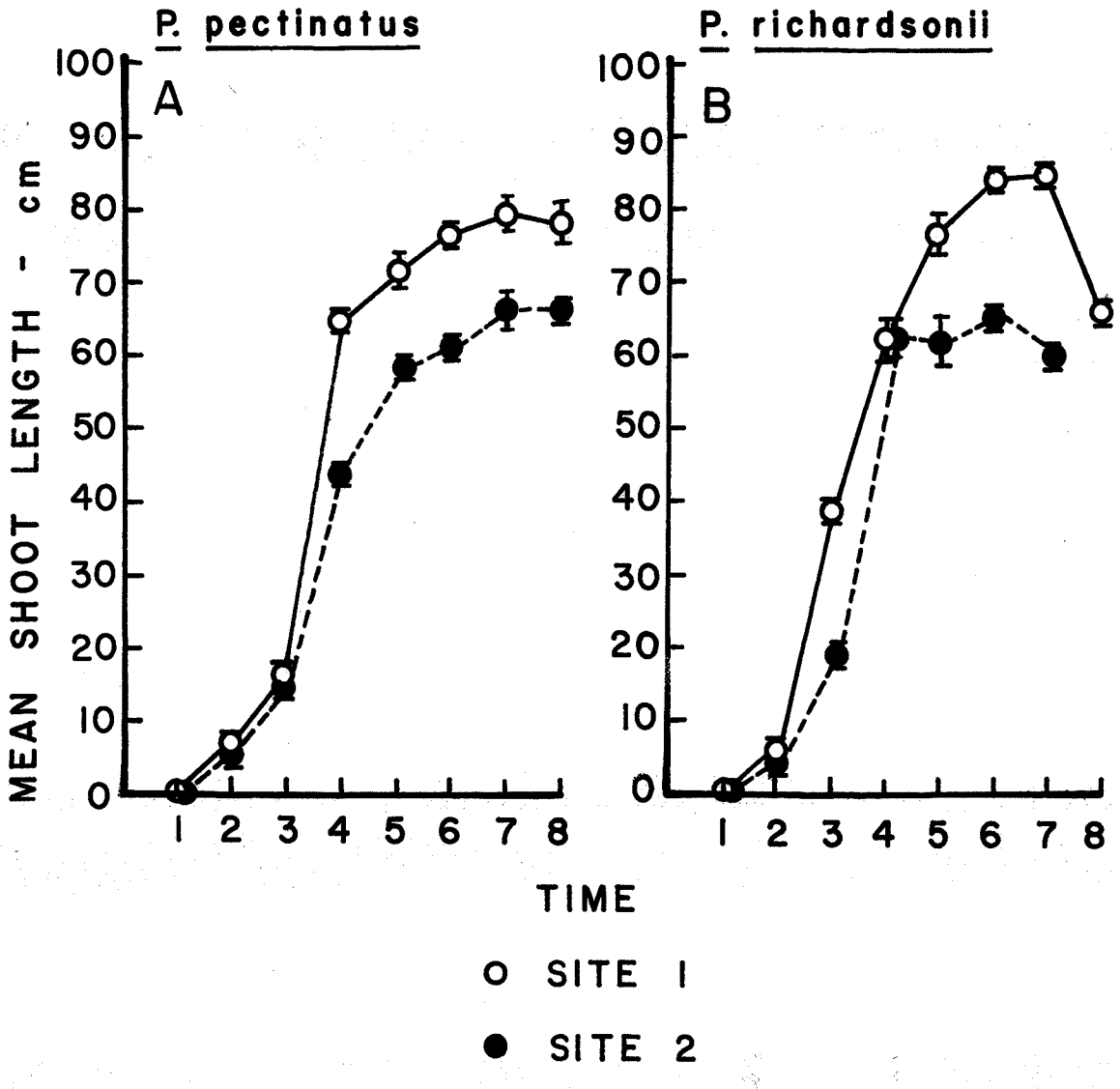
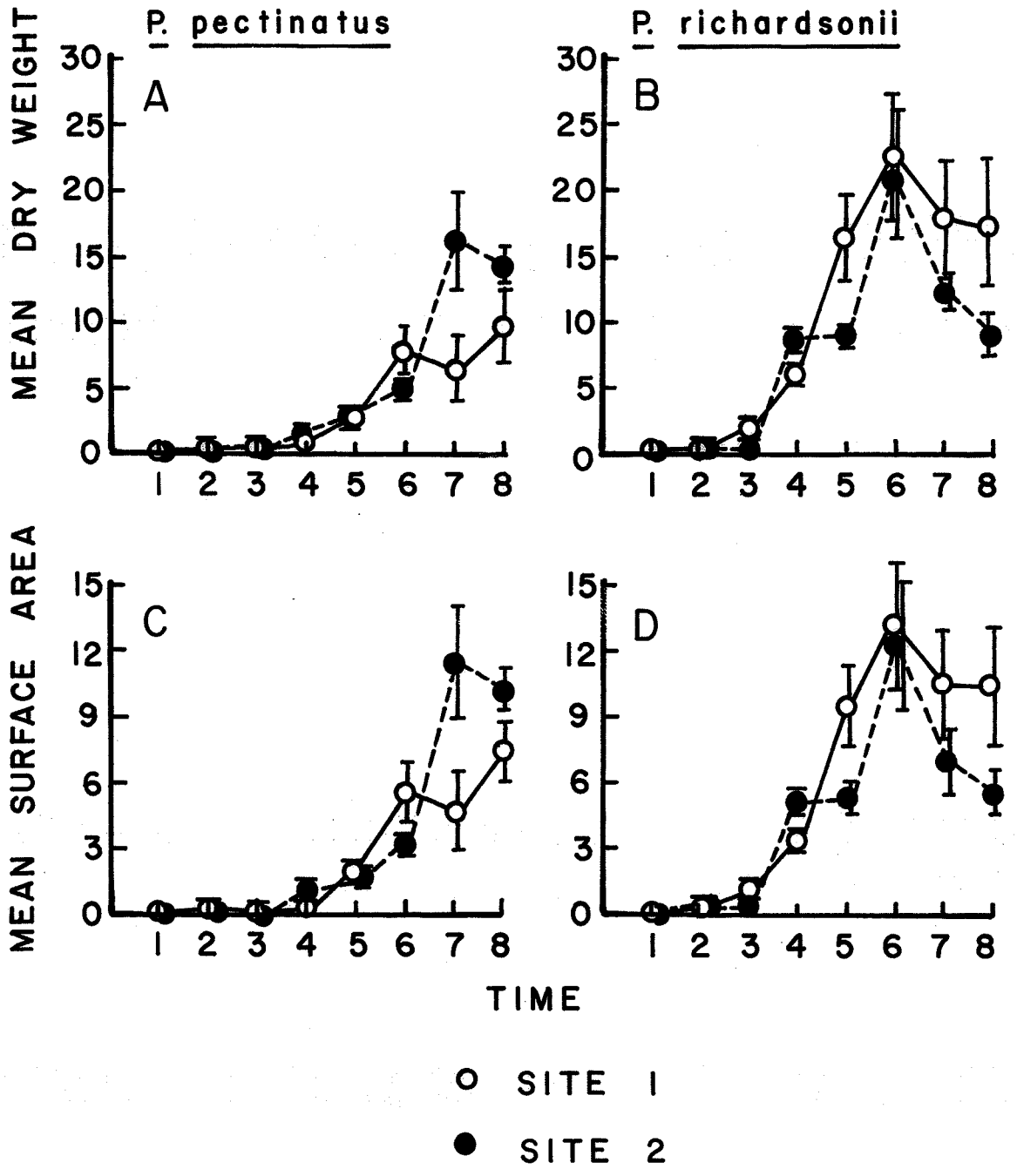

P. pectinatus
A
P. richardsonii
B
MEAN SHOOT LENGTH - cm
0
10
20
30
40
50
60
70
80
90
100
1 2 3 4 5 6 7 8
TIME
SITE 1
SITE 2

Figure 75. Mean dry weight (g) (A and B) and mean surface area (cm^2) (C and D) of Potamogeton pectinatus and P. richardsonii shoots respectively (excluding reproductive parts) per quadrat sample (1525 cm^2 bottom area) at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.


P. pectinatus
P. richardsonii
A
B
C
D
MEAN DRY WEIGHT
MEAN SURFACE AREA
TIME
SITE 1
SITE 2

sample (Fig. 75B) suggested that growth was synchronous at both sites until time 4 when a lag between the two sites became apparent. After time 4, mean dry weight at site 1 continued to increase rapidly while at site 2 a temporary halt in growth was observed until time 5, when branching occurred. Maxima for mean dry weight were observed at both sites at time 6 and were followed by accelerated deterioration as Lemna proliferated at both sites and obscured the water surface.

No mature reproductive parts of P. pectinatus (Table XXIV) were observed at site 1 while at site 2 these were recorded only at times 7 and 8 and represented a mean ratio of reproductive to above-ground vegetative parts of only 0.002-0.008. Thus, less than one-sixth of the maximum net energy channelled into sexual reproduction during 1973 was used for this purpose during 1974 at site 2 while at site 1, sexual reproduction apparently did not occur.

As in 1973, the mean dry weight of reproductive parts of P. richardsonii per unit bottom area was greater at site 1 than at site 2. The ratio of reproductive to vegetative parts by weight at site 1 achieved a maximum value of 0.166 at time 7, i.e. less than half of the maximum value observed at this site during 1973. At site 2, this ratio achieved a maximum value of 0.043 at time 6, which again was less than half of the maximum value seen at this site during 1973.

iii. Surface area per quadrat sample

The mean values for surface area of the above-ground vegetative parts of P. pectinatus and P. richardsonii per quadrat sample (Fig. 75C and D) followed patterns similar to those of dry weight, although the surface area of P. richardsonii was smaller in proportion to dry weight relative to that of P. pectinatus.

TABLE XXIV. Mean dry weight (g) of seeds and mature reproductive parts per quadrat sample (1525 cm^2) of Potamogeton pectinatus and P. richardsonii at sites 1 and 2 during the 1974 season. Values in parentheses indicate standard errors.

	site 1		site 2	
Time	P. pectinatus	P. richardsonii	P. pectinatus	P. richardsonii
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0	0	0
5	0	0	0	0.02 (0.02)
6	0	1.61 (0.37)	0	0.89 (0.21)
7	0	2.98 (1.02)	0.03 (0.01)	0.22 (0.10)
8	0	1.76 (1.27)	0.11 (0.04)	0.22 (0.08)

b. Gastropods

i. Mean density per quadrat sample

The density patterns for Physa gyrina in terms of the mean numbers per quadrat sample (1525 cm^2) at sites 1 and 2 (Fig. 76A) were synchronous in the P. pectinatus stands, with a maximum at time 6 at both sites. In P. richardsonii stands (Fig. 76B), maxima occurred at time 6 at both sites although at site 1 high values were observed at time 5 as well. At site 1, greater densities of P. gyrina were observed in P. richardsonii stands during most of the season, perhaps because of the greatly reduced P. pectinatus stands, while at site 2 densities in both types of stands were approximately equal.

The mean numbers of Lymnaea stagnalis per quadrat sample (Fig. 76C and D) were greater in P. richardsonii than in P. pectinatus stands during times 3-7. The density patterns in the P. richardsonii stands from the two sites were out of phase by two weeks and the greatest divergence between the sites occurred after time 4. The density patterns in the P. pectinatus stands, although of reduced magnitude, were also out of phase at the two sites, resulting in synchronous density patterns for the two types of stands within each site.

The density values for other gastropods during the 1974 season were characterized by the steady increase in importance of Stagnicola palustris relative to that of Fossaria modicella (Table XXVB), and by time 6 the latter species had all but disappeared. A large peak (Table XXVA) in the combined values of mean numbers of these two species per quadrat sample was observed at time 6 in all stands at both sites and consisted largely of S. palustris.

Figure 76. Mean numbers of Physa gyrina (A and B) and Lymnaea stagnalis (C and D) per quadrat sample (1525 cm^2 bottom area) from stands of Potamogeton pectinatus and P. richardsonii respectively at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.

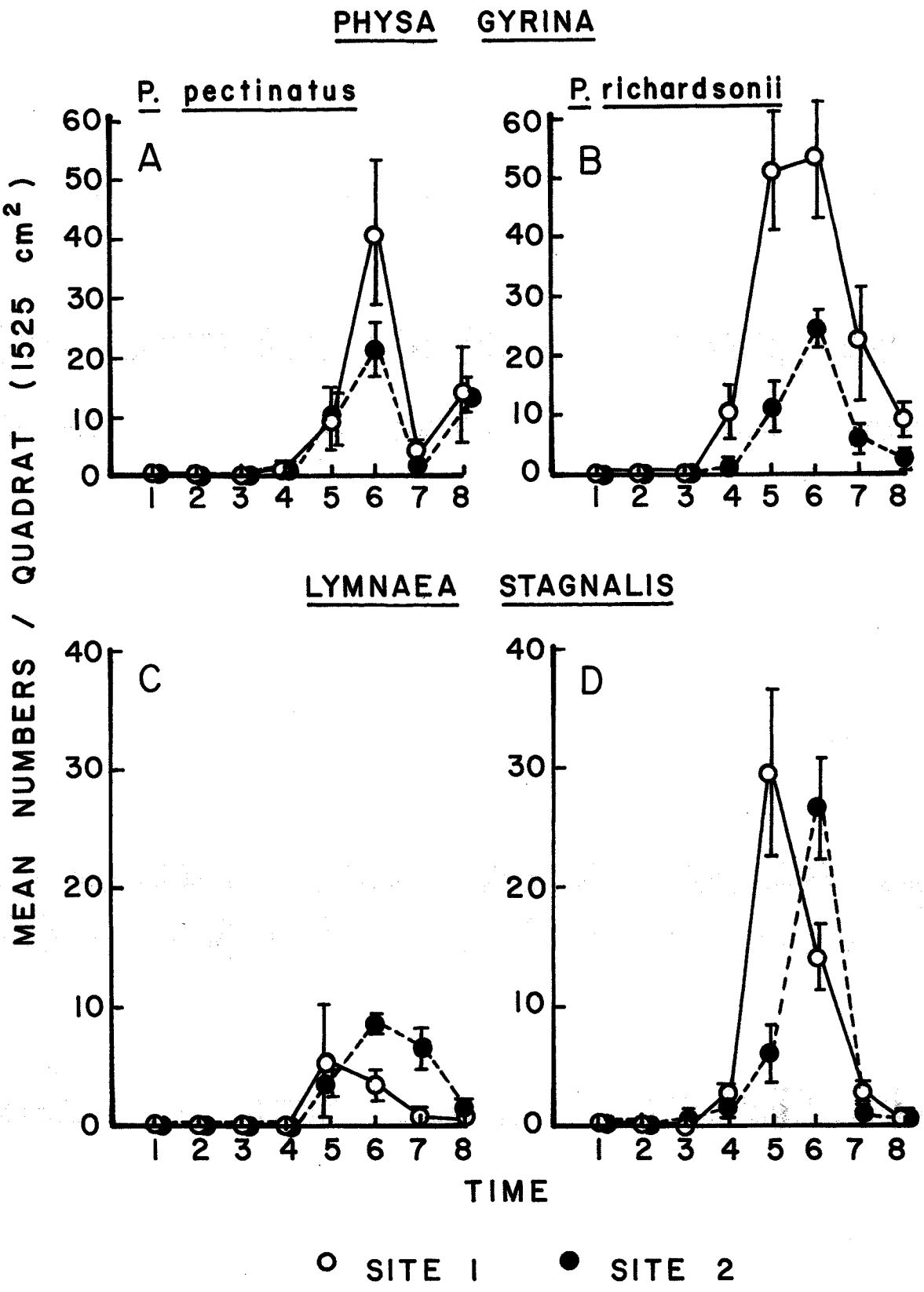

PHYSA GYRINA
P. pectinatus
P. richardsonii
A
B
LYMNAEA STAGNALIS
C
D
MEAN NUMBERS / QUADRAT (1525 cm²)
TIME
SITE 1
SITE 2

TABLE XXV.

A. Mean combined numbers of *Fossaria modicella* and *Stagnicola palustris* per quadrat sample (1525 cm^2) in the two types of stands at sites 1 and 2 during 1974. Values in parentheses represent standard errors.

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0.60 (0.40)	6.40 (1.36)	0.20 (0.20)	0.60 (0.24)
5	18.60 (11.93)	48.20 (9.70)	31.20 (8.60)	14.40 (3.93)
6	92.00 (8.02)	55.80 (14.85)	62.20 (12.30)	31.40 (4.70)
7	16.40 (2.54)	6.20 (1.02)	23.80 (4.37)	0.60 (0.24)
8	3.60 (1.36)	0.40 (0.24)	3.80 (1.39)	0

B. Mean numbers of *Stagnicola palustris* expressed as a fraction of the above total numbers of *S. palustris* and *F. modicella* per quadrat sample from the two types of stands at sites 1 and 2.

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	(0)	(0)	(0)	(0)
2	(0)	(0)	(0)	(0)
3	(0)	(0)	(0)	(0)
4	1.00	0.16	(0)	0.33
5	0.62	0.54	0.67	0.47
6	0.78	0.93	0.97	0.94
7	0.95	1.00	0.99	1.00
8	0.94	1.00	1.00	(0)

At site 1, time 4, paired t-tests showed that S. palustris was present in significantly ($p < .01$, $n=10$) greater densities in P. richardsonii than in P. pectinatus stands while at times 7 and 8 these values were significantly ($p < .02$-$.05$, $n=10$) greater in P. pectinatus stands. At site 2, S. palustris was present in significantly ($p < .001$-$.05$, $n=10$) greater densities in P. pectinatus stands during times 6-8. No significant tendencies could be detected for F. modicella because of the small numbers of this gastropod observed during the 1974 season.

The density patterns of Helisoma trivolvis per quadrat sample (Table XXVIA) showed maxima at time 5 in the P. richardsonii stands at both sites followed by peaks at time 6 in both P. pectinatus stands. At site 1, time 5, H. trivolvis was present in significantly ($p < .05$, $n=10$) greater densities in P. richardsonii than in P. pectinatus stands. At site 2, densities of this snail were significantly ($p < .01$, $n=10$) greater in P. richardsonii stands at times 5 and 6.

The 1974 season was characterized by the appearance of a sixth gastropod species on the plant shoots, Promenetus exacuous (Table XXVIB), which was present only in P. richardsonii stands at both sites. Densities in these stands were significantly ($p < .05$, $n=10$) greater at site 1 during times 4-6 and at site 2 at time 5. During the 1973 season, although P. exacuous occurred at both sites, it occupied benthic habitats and was never encountered on the plant shoots.

Essentially, the density patterns for the 1974 season suggested the following features:

TABLE XXVI. Mean numbers of Helisoma trivolvis (A) and Promenetus exacuous (B) per quadrat sample (1525 cm^2) from the two types of stands at sites 1 and 2 during 1974. Values in parentheses represent standard errors.

A. Helisoma trivolvis

	site 1		site 2	
Time	P. pectinatus	P. richardsonii	P. pectinatus	P. richardsonii
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0.60 (0.40)	0	0.40 (0.40)
5	0.60 (0.60)	3.60 (1.03)	0.20 (0.20)	10.20 (2.56)
6	1.40 (0.51)	2.00 (0.55)	1.80 (0.58)	9.80 (1.77)
7	0.20 (0.20)	1.00 (0.55)	0.80 (0.37)	0.60 (0.40)
8	0.60 (0.40)	0.20 (0.20)	0.20 (0.20)	0.20 (0.20)

B. Promenetus exacuous

	site 1		site 2	
Time	P. pectinatus	P. richardsonii	P. pectinatus	P. richardsonii
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0.60 (0.24)	0	0.20 (0.20)
5	0	1.20 (0.58)	0	1.60 (0.60)
6	0	2.20 (1.07)	0	1.40 (0.98)
7	0	0.20 (0.20)	0	0
8	0	0.20 (0.20)	0	0

1. Density patterns for P. gyrina were synchronous in P. pectinatus stands at both sites.
2. A two-week lag period was observed between the density patterns of L. stagnalis in the P. richardsonii stands at the two sites; the reduced patterns in the P. pectinatus stands were also out of phase.
3. Stagnicola palustris increased sharply in importance and the affinities for macrophytes of both this species and H. trivolvis were the reverse of those observed during the previous two seasons.
4. Promenetus exacuous appeared on the P. richardsonii shoots.

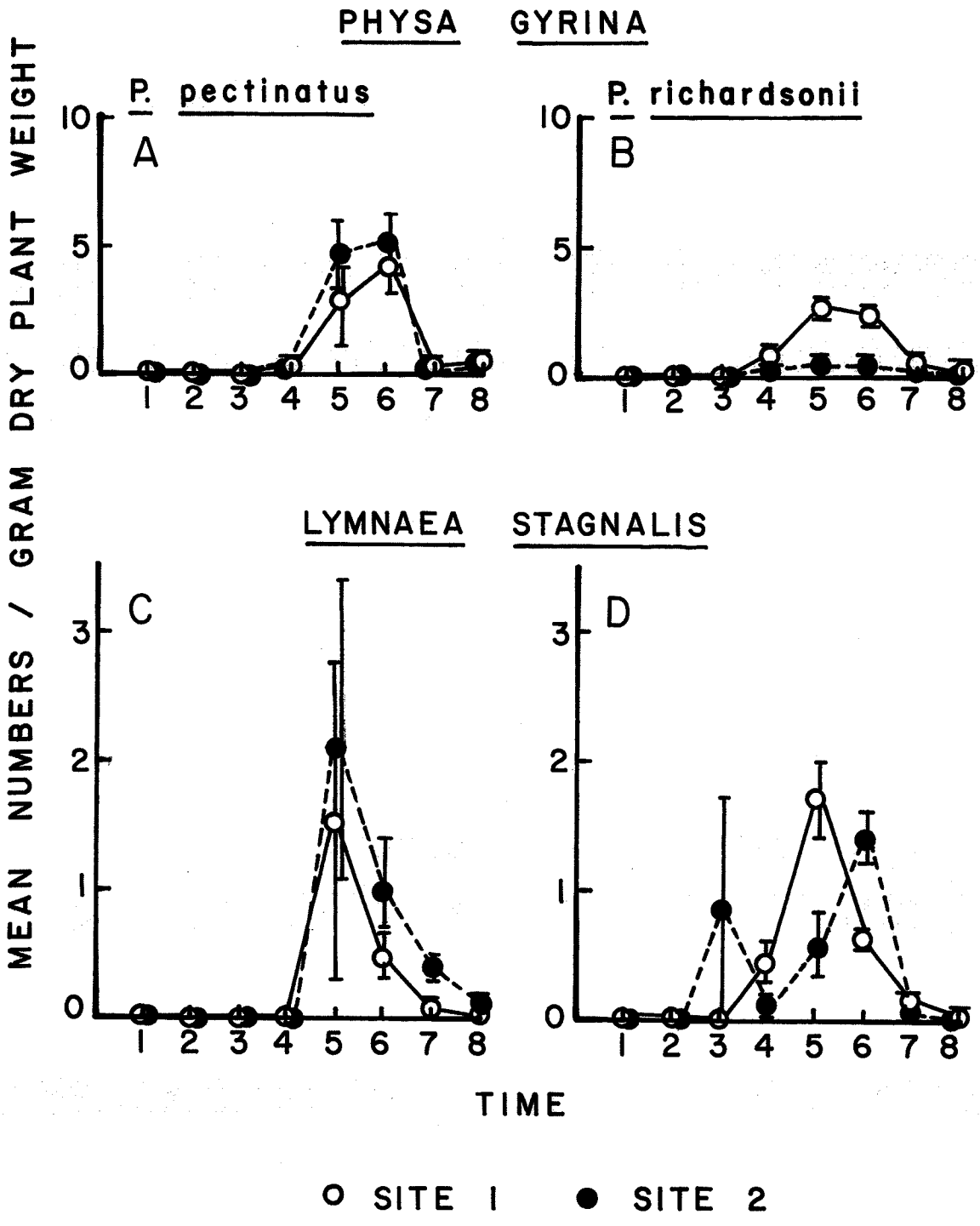
ii. Mean numbers of individuals per unit plant dry weight

The mean numbers of P. gyrina per unit dry weight of the above-ground vegetative parts of P. pectinatus (Fig. 77A) at sites 1 and 2 rose sharply after time 4 and the values continued to increase until a maximum at time 6. The patterns were significantly ($p < .001$, $n=8$) correlated in time (syntonic) at both sites. In the P. richardsonii stands (Fig. 77B), the patterns were slightly, but not significantly out of phase: divergence between the sites commenced after time 3.

At site 1, significantly ($p < .05$, $n=10$) greater numbers per unit plant dry weight were observed in P. pectinatus stands at times 4 and 6. At site 2, significantly ($p < .01$-$.05$, $n=10$) greater numbers were observed in P. pectinatus stands at times 5, 6 and 8.

The patterns for mean numbers of L. stagnalis per unit dry weight of P. richardsonii (Fig. 77D) were out of phase by two weeks; this lag period was significantly ($p < .01$, $n=4$) consistent during times 3-7. The maximum occurred at time 5 at site 1 and at time 6 at

Figure 77. Mean numbers of Physa gyrina (A and B) and Lymnaea stagnalis (C and D) per gram dry weight of Potamogeton pectinatus and P. richardsonii respectively at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.


PHYSA GYRINA
P. pectinatus
A
P. richardsonii
B
LYMNAEA STAGNALIS
C
D
MEAN NUMBERS / GRAM DRY PLANT WEIGHT
TIME
SITE 1
SITE 2

site 2. The peak at time 3 at site 2 was due to the chance occurrence, reflected by the large standard error, of a few individuals in the samples when plant mass was very small. The patterns for snails in P. pectinatus samples (Fig. 77C) were synchronous and significantly ($p < .001$, n=8) correlated (syntonic) at both sites, with a maximum at time 5.

Lymnaea stagnalis was present significantly ($p < .02$, n=10) more frequently in P. richardsonii than in P. pectinatus stands at time 4 at site 1, while at site 2 it was present significantly ($p < .02$, n=10) more frequently in P. richardsonii stands at times 4 and 7.

The combined values of F. modicella and S. palustris (Fig. 78) showed maxima in P. pectinatus stands at time 5 at site 2 and at time 6 at site 1; these consisted largely of S. palustris (Table XXVB). Values in P. richardsonii stands were much reduced. At site 1, S. palustris was significantly ($p < .001$, n=10) associated with P. pectinatus at time 6, while at site 2 it was significantly ($p < .01$-$.05$, n=10) associated with P. pectinatus during times 5-8. Fossaria modicella showed no significant affinities because of its small numbers.

The mean numbers of H. trivolvis (Fig. 79A and B) per unit dry P. pectinatus reached a maximum value at time 6 at both sites, while in P. richardsonii stands the maximum occurred at time 5 at both sites. Although at site 1 values were slightly greater in P. richardsonii stands at time 5 and greater in P. pectinatus stands at time 6, these differences were not significant. At site 2, values were significantly ($p < .05$, n=10) greater in P. richardsonii stands at time 5.

The mean numbers of P. exacuous (Fig. 79C and D) per unit dry P. richardsonii were generally small but maximum values were

Figure 78. Mean combined numbers of Stagnicola palustris and Fossaria modicella per gram dry weight of Potamogeton pectinatus (A) and P. richardsonii (B) at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.

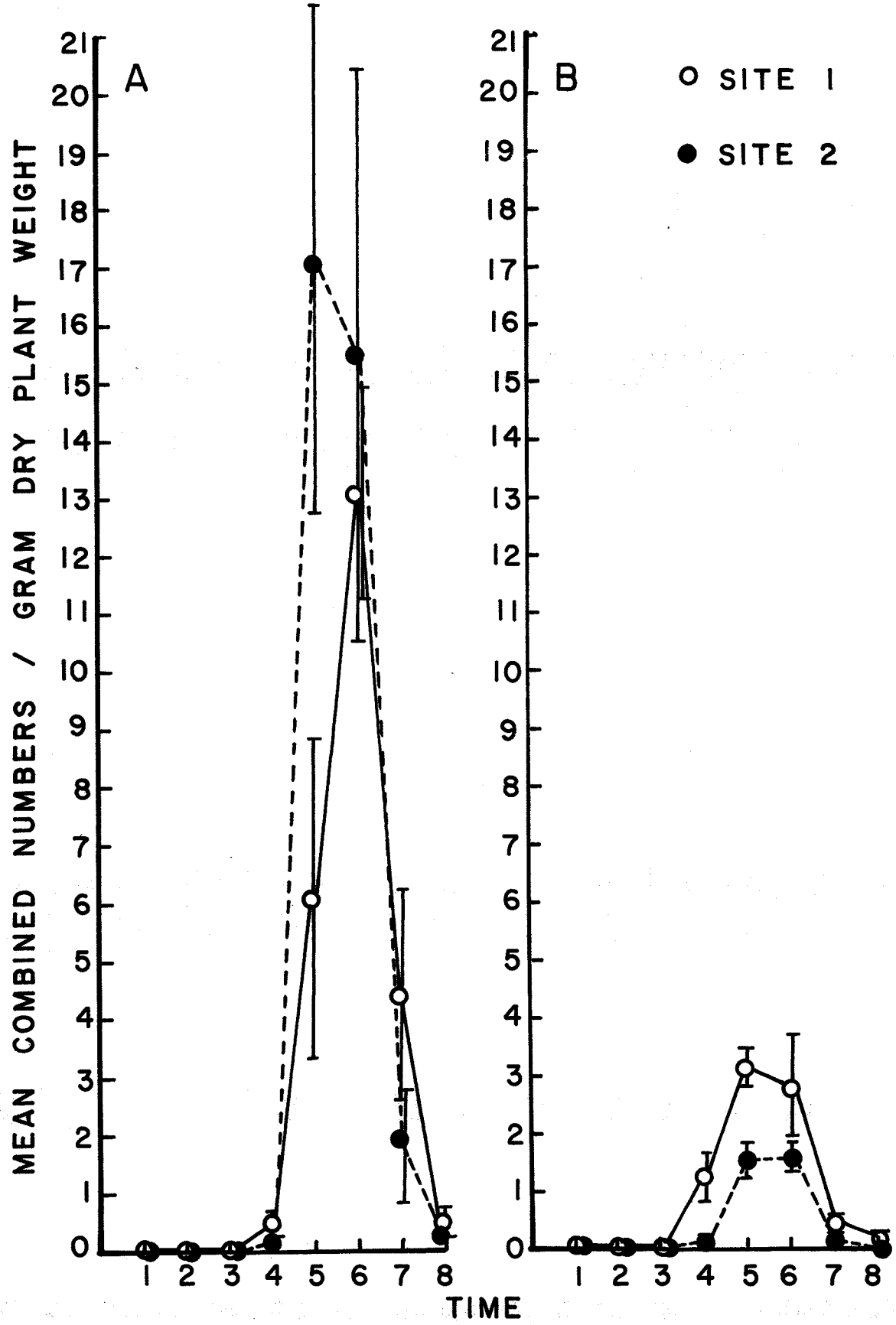
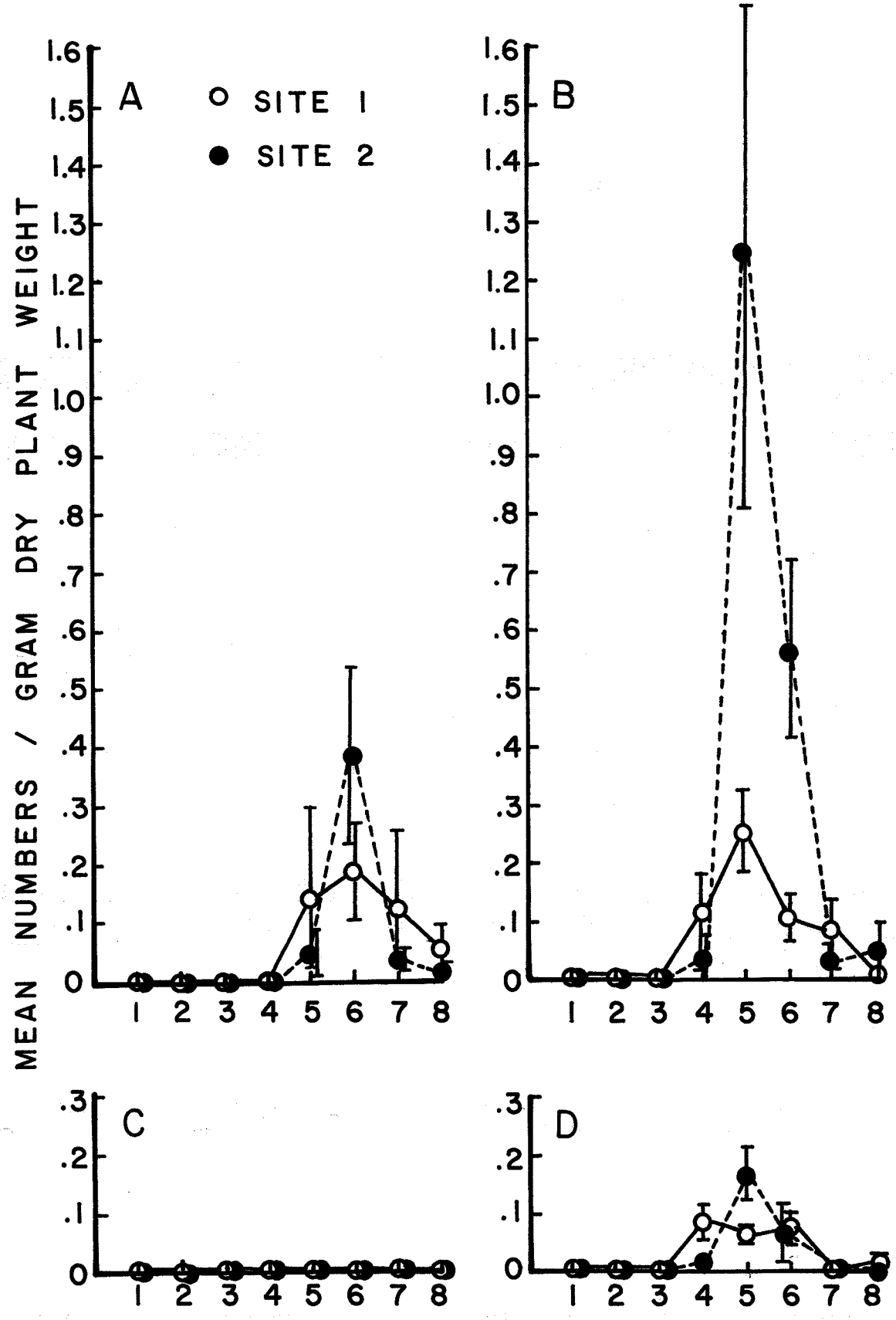

A
B
SITE 1
SITE 2
MEAN COMBINED NUMBERS / GRAM DRY PLANT WEIGHT
TIME
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21

Figure 79. Mean numbers of Helisoma trivolvis (A and B) and Promenetus exacuous (C and D) per gram dry weight of Potamogeton pectinatus and P. richardsonii respectively at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.


A
SITE 1
SITE 2
B
C
D
MEAN NUMBERS / GRAM DRY PLANT WEIGHT
1.6
1.5
1.4
1.3
1.2
1.1
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
1 2 3 4 5 6 7 8

observed during midseason. At site 1, values were significantly ($p<.05$, n=10) greater in P. richardsonii stands at times 4 and 6 while at site 2 they were significantly ($p<.02$, n=10) greater in P. richardsonii stands at time 5. None occurred in P. pectinatus stands.

In summary, the numbers per unit dry plant weight showed the following features:

1. Physa gyrina was associated with P. pectinatus with the association peak occurring at times 5 and 6 at both sites. During both 1973 and 1974, the numbers of P. gyrina per unit dry plant weight were syntonic in the two P. pectinatus stands, but incompletely correlated in the P. richardsonii stands. The behavior of the two subpopulations at each site appeared to be related in time to the growth of the host plants.
2. Lymnaea stagnalis was associated with P. richardsonii; association peaks in stands of this plant occurred at times 5 and 6, respectively, at sites 1 and 2. The two-week lag period between the sites was maintained during both the 1973 and 1974 seasons and appeared to coincide with the lag period observed for the growth of P. richardsonii at these sites. Patterns in P. pectinatus stands were syntonic at the two sites during both the 1973 and 1974 seasons, and also appeared to be related in time to the growth of these plants.
3. Stagnicola palustris was associated with P. pectinatus during the second half of the season, while H. trivolvis tended to associate with P. richardsonii during midseason. These affinities were the reverse of those observed during the 1973 season, and did not

appear to be related in time to growth of the host plants.

4. Promenetus exacuous was associated with P. richardsonii during midseason but again this association did not appear to be related to growth of the host plants.

Thus the two major plant-snail associations suggested in model 1 remained constant despite the dramatic alteration of environmental conditions that had resulted from the spring flood. This suggested that the population dynamics of the members of each plant-snail association system were either: a) both regulated by the same external factor, or b) largely independent of external factors, aside from limiting conditions. The association peaks commenced during the early stages of increases in the growth rate of the respective host plants. The climactic point of the association, i.e. the point on the growth curve of the host plant where snail numbers per unit dry weight were maximal, was located relatively earlier on the growth curve of P. pectinatus than of P. richardsonii, suggesting that the specific regulatory agent was different for the two associations.

The results obtained for S. palustris and H. trivolvis confirmed the suspicions of the previous season's work that, although these species showed differential distributions, these patterns were not correlated with growth of the host plants. Promenetus exacuous could also be included in the latter category.

iii. Composition of the total gastropod population

The mean total numbers of snails per unit dry plant weight (Table XXVII) in P. pectinatus stands at site 1 were maximal at time 6 while at site 2 the maximum in these stands occurred at time 5, with only a slightly lower value at time 6. In P. richardsonii stands, the

TABLE XXVII. Mean total numbers of gastropods per gram dry host plant weight at sites 1 and 2 during the 1974 season.

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0.9
4	0.5	3.6	0.2	0.4
5	11.1	8.4	23.8	4.6
6	18.6	6.1	23.0	5.0
7	5.5	1.8	2.5	0.6
8	1.7	0.6	1.4	0.5

maximum at site 1 was observed at time 5 while at site 2 it occurred at time 6.

The mean percentage species composition of these grazer communities (Table XXVIII) differed in several major respects from that of the 1973 season. Whereas the P. pectinatus stands at sites 1 and 2 during the 1973 season were numerically dominated by P. gyrina and F. modicella, during the 1974 season these stands were dominated by S. palustris and to a lesser extent by P. gyrina. Stagnicola palustris composed the majority of the grazer population in these stands until a decrease at time 8 at both sites, which resulted in an apparent increase in the relative frequency of P. gyrina. The relative frequency of F. modicella was slightly greater in P. pectinatus than in P. richardsonii stands but in both habitats it decreased steadily throughout the season as the frequency of S. palustris increased. The relative frequency of P. gyrina was higher in P. richardsonii than in P. pectinatus stands because of the greatly reduced importance of S. palustris in the former stands. The relative frequencies of L. stagnalis and H. trivolvis were also greater in P. richardsonii stands.

Despite the increased numbers of S. palustris observed during the 1974 season, the combined numbers of P. gyrina and L. stagnalis still formed a significant proportion of the total grazer population at both sites, particularly in P. richardsonii stands. In P. pectinatus stands, the combined mean percentage of these two species ranged from 18.2-69.7% at site 1 and from 22.7-77.7% at site 2. In P. richardsonii stands, these values ranged from 51.8-93.6% at site 1 and from 37.1-100% at site 2.

TABLE XXVIII. Mean numbers of each gastropod species per unit dry plant weight expressed as a percent of all species present at sites 1 and 2 during the 1974 season. Species numbers represent the following taxa: 1. Physa gyrina, 2. Lymnaea stagnalis, 3. Fossaria modicella, 4. Stagnicola palustris, 5. Helisoma trivolvis, 6. Promenetus exacuous.

SITE 1

		POTAMOGETON PECTINATUS SAMPLES								POTAMOGETON RICHARDSONII SAMPLES							
Species	Time	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1		0	0	0	25.9	30.1	26.2	16.0	68.5	0	0	0	46.6	39.2	41.0	64.6	90.4
2		0	0	0	0	13.8	2.6	2.2	1.2	0	0	0	12.9	20.5	10.8	9.4	3.2
3		0	0	0	0	20.8	15.4	4.0	1.6	0	0	0	29.1	16.7	3.2	0	0
4		0	0	0	74.1	33.9	54.8	75.5	25.2	0	0	0	5.5	19.7	41.9	20.4	3.2
5		0	0	0	0	1.4	1.0	2.3	3.5	0	0	0	0	1.4	1.0	2.3	3.5
6		0	0	0	0	0	0	0	0	0	0	0	2.5	0.8	1.3	0.6	1.6

SITE 2

		POTAMOGETON PECTINATUS SAMPLES								POTAMOGETON RICHARDSONII SAMPLES							
Species	Time	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
1		0	0	0	50.0	18.8	22.3	5.6	69.6	0	0	0	30.0	24.1	26.3	71.8	73.3
2		0	0	0	0	9.4	8.7	17.1	8.1	0	0	100.0	35.0	13.0	28.8	14.1	15.6
3		0	0	0	50.0	23.6	2.0	0.8	0	0	0	0	13.4	17.1	1.9	0	0
4		0	0	0	0	48.0	65.3	74.9	20.7	0	0	0	6.6	15.1	30.1	7.8	0
5		0	0	0	0	0.2	1.7	1.6	1.5	0	0	0	10.0	27.0	11.5	6.3	11.1
6		0	0	0	0	0	0	0	0	0	0	0	5.0	3.7	1.4	0	0

iv. Mean numbers of individuals per unit plant surface area

At site 1, P. gyrina occurred in greater numbers per unit plant surface area (Fig. 80A and B) in P. richardsonii than in P. pectinatus stands at time 4 but by time 6 the reverse was true. At site 2, the differences in snail numbers in the two types of stands were more defined than at site 1; significantly ($p < .01$-$.05$, n=10) greater numbers were observed in P. pectinatus stands at times 5, 6 and 8.

The mean numbers of L. stagnalis per unit surface area at site 1 (Fig. 80C and D) were significantly ($p < .01$, n=10) greater in P. richardsonii stands at time 4 while at site 2, significantly ($p < .02$, n=10) greater numbers were observed in P. richardsonii stands at time 4, but by time 7 significantly ($p < .01$, n=10) greater numbers were present in P. pectinatus stands.

The mean combined numbers of F. modicella and S. palustris (Table XXIXA) were higher in P. pectinatus stands during most of the season, with maxima observed at times 5 and 6 in both types of stands at both sites. For S. palustris, the difference between the two types of stands at site 1 was significant ($p < .001$, n=10) at time 6 while at site 2 it was significant ($p < .01$-$.05$, n=10) during times 5-8.

The values for H. trivolvis (Table XXIXB) were generally low; at site 2, time 5, significantly ($p < .05$, n=10) greater numbers were present in P. richardsonii stands while at site 1 the values were too small to show any significant affinities, as were the values for P. exacuous at both sites.

Figure 80. Mean numbers of Physa gyrina (A and B) and Lymnaea stagnalis (C and D) per 100 cm^2 surface area of Potamogeton pectinatus and P. richardsonii respectively at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.

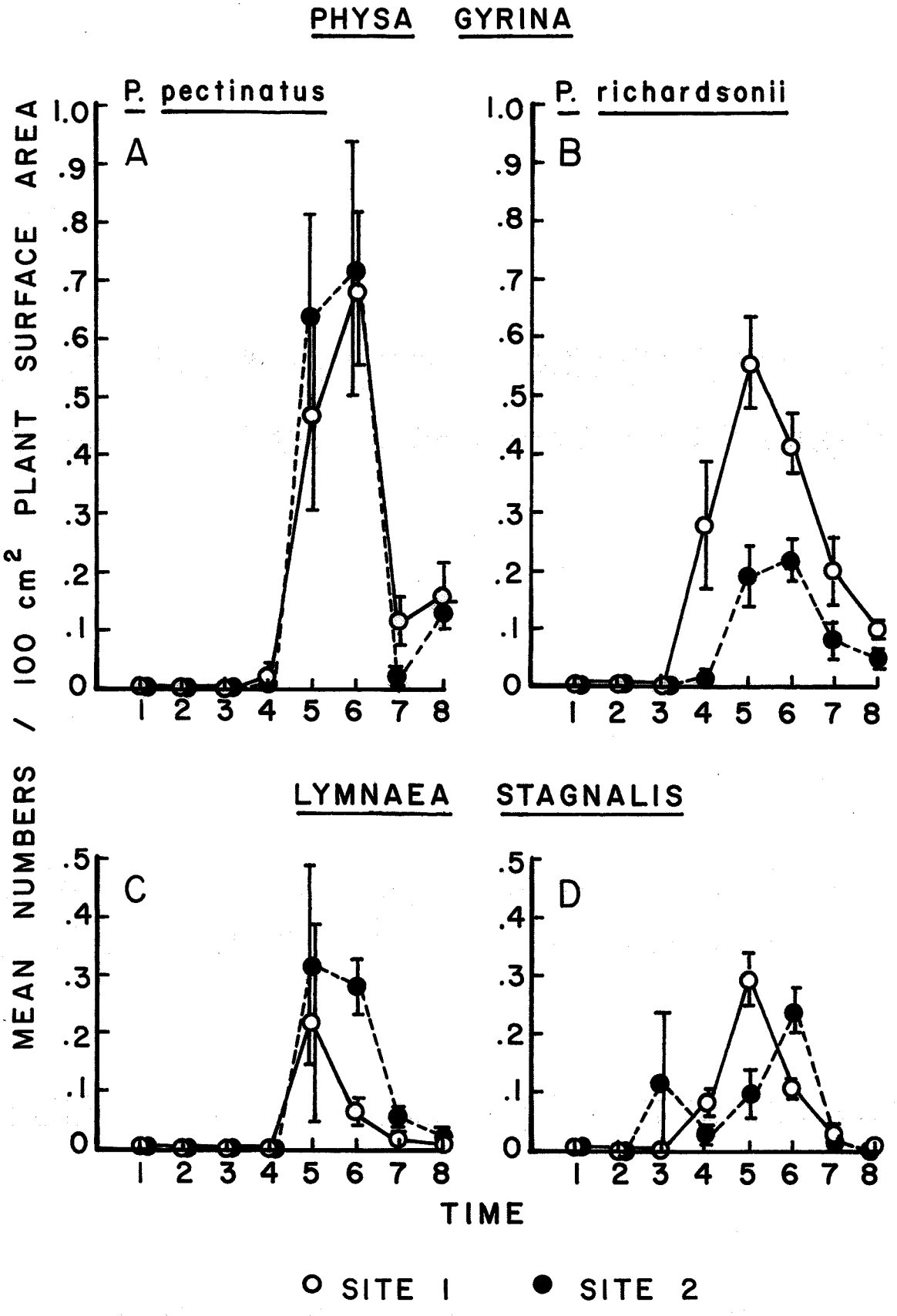

PHYSA GYRINA
P. pectinatus
A
P. richardsonii
B
LYMNAEA STAGNALIS
C
D
MEAN NUMBERS / 100 cm² PLANT SURFACE AREA
TIME
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
1 2 3 4 5 6 7 8
SITE 1
SITE 2

TABLE XXIX. Mean numbers per 100 cm^2 of plant surface area of *Fossaria modicella* and *Stagnicola palustris* (combined)(A), *Helisoma trivolvis* (B) and *Promenetus exacuous* (C) in the respective stands at sites 1 and 2. Values in parentheses represent standard errors.

A. *Fossaria modicella* and *Stagnicola palustris* (combined)

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0.06 (0.04)	0.21 (0.06)	0.01 (0.01)	0.01 (0)
5	0.85 (0.39)	0.52 (0.07)	2.44 (0.62)	0.25 (0.05)
6	1.83 (0.25)	0.47 (0.15)	2.18 (0.71)	0.27 (0.03)
7	0.62 (0.26)	0.06 (0)	0.27 (0.09)	0.01 (0)
8	0.06 (0.03)	0	0.04 (0.01)	0

B. *Helisoma trivolvis*

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0.02 (0.01)	0	0.01 (0)
5	0.02 (0.02)	0.04 (0.01)	0.01 (0)	0.21 (0.07)
6	0.03 (0.01)	0.02 (0)	0.05 (0.02)	0.10 (0.02)
7	0.02 (0.02)	0.02 (0)	0.01 (0)	0.01 (0)
8	0.01 (0)	0	0	0.01 (0)

C. *Promenetus exacuous*

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	0	0	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0.02 (0)	0	0
5	0	0.01 (0)	0	0.03 (0)
6	0	0.01 (0)	0	0.01 (0)
7	0	0	0	0
8	0	0	0	0

v. Snail biomass

At both sites values for the mean live weight of P. gyrina per quadrat sample (Fig. 81A and B) were greater in P. richardsonii than in P. pectinatus stands. At site 1, this difference was significant ($p < .01$-$.05$, n=10) at times 4-6 and 8, and was due in large part to the sparse nature of the P. pectinatus stands. At site 2 the difference in snail biomass between the two types of stands was not significant. The patterns were synchronous in both P. pectinatus stands. In P. richardsonii stands the maximum value at site 1 was observed at time 6 while at site 2 the peak was diffused over times 6 and 7.

The patterns for mean live weight of L. stagnalis per quadrat sample (Fig. 81C and D) were out of phase in the P. richardsonii stands at the two sites. At site 1 the maximum occurred at time 5 and at site 2 it was observed at time 6. Values in P. pectinatus stands were lower than those in P. richardsonii stands; at site 1 this difference was significant ($p < .001$-$.05$, n=10) during times 4-6 while at site 2 it was significant ($p < .05$, n=10) at time 6.

The mean live weight patterns of P. gyrina per unit dry plant weight (Fig. 82A and B) were highly correlated ($p < .001$, n=8) in the P. pectinatus stands at the two sites throughout the season. Values in the P. richardsonii stands were not correlated. At site 1, values were only slightly higher in P. pectinatus than in P. richardsonii stands at time 6 while at site 2 this difference was significant ($p < .02$, n=10).

The mean live weight patterns for L. stagnalis per unit dry plant weight (Fig. 82C and D) were asynchronous in the P. richardsonii stands at the two sites, while those in P. pectinatus stands were

Figure 81. Mean total live weight (g) of Physa gyrina (A and B) and Lymnaea stagnalis (C and D) per quadrat sample (1525 cm^2 bottom area) in stands of Potamogeton pectinatus and P. richardsonii respectively at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.

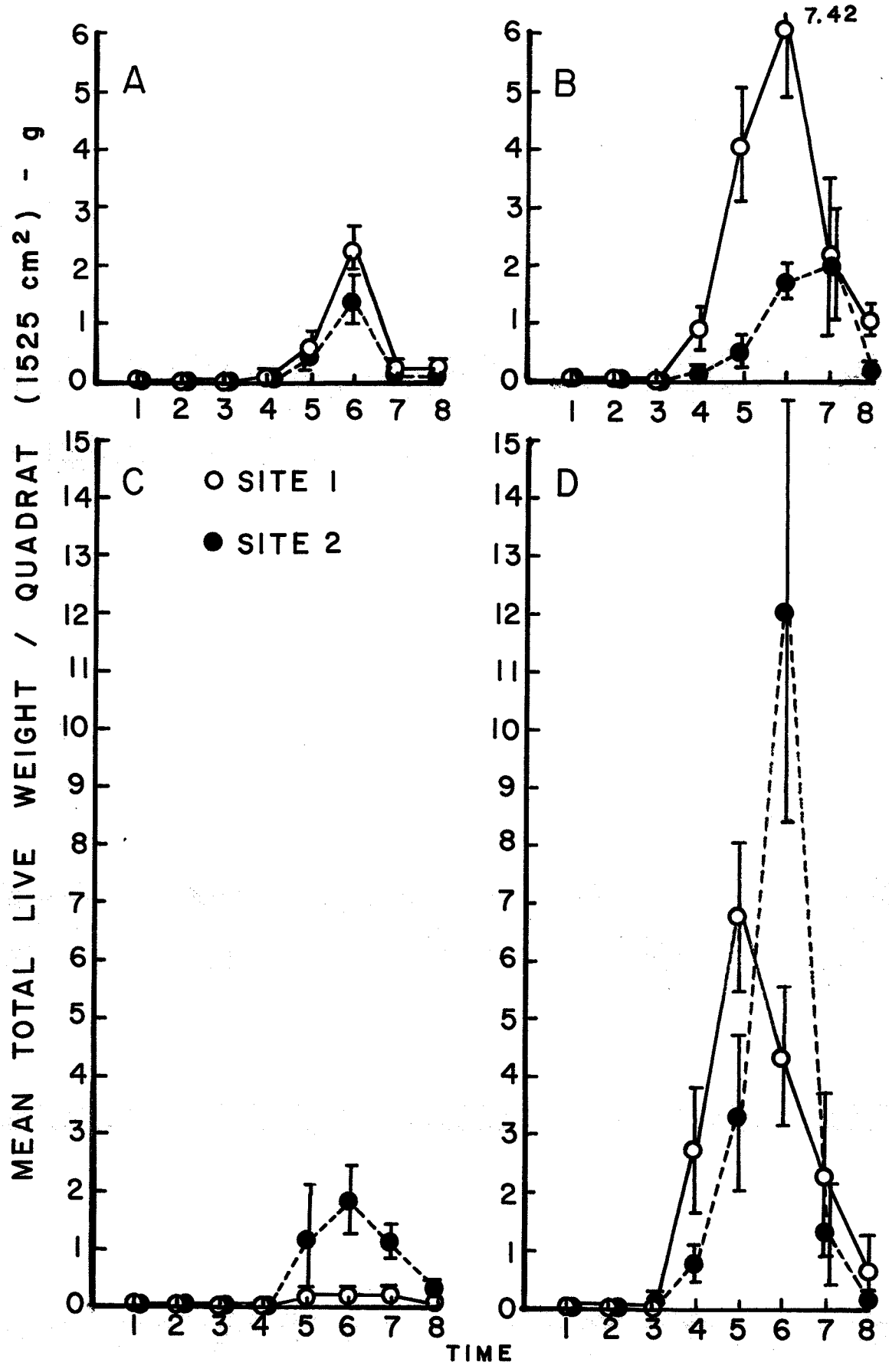

A
B
C
D
7.42
SITE 1
SITE 2
MEAN TOTAL LIVE WEIGHT / QUADRAT (1525 cm²) - g
TIME

Figure 82. Mean live weight (g) of Physa gyrina (A and B) and Lymnaea stagnalis (C and D) per gram dry weight of Potamogeton pectinatus and P. richardsonii respectively at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.

synchronous, with maxima occurring at time 5 at both sites, although the values at site 1 were much reduced. Significantly ($p < .01$-$.05$, n=10) greater values were observed in P. richardsonii stands at site 1 during times 4-6, and at site 2 ($p < .05$, n=10) at time 4.

The mean live weight patterns for P. gyrina per unit surface area of P. pectinatus (Fig. 83A) were correlated at the two sites while those in P. richardsonii stands (Fig. 83B) were not.

The mean live weight patterns of L. stagnalis per unit plant surface area (Fig. 83C and D) were asynchronous in P. richardsonii stands and correlated in time in the P. pectinatus stands. Values were significantly ($p < .001$-$.05$, n=10) greater in P. richardsonii stands at site 1 during times 4-6 while at site 2 the differences were not significant.

Thus, the associations expressed in terms of live weight of snails generally confirmed the results expressed in terms of snail numbers.

vi. Size class distributions

At site 1, P. gyrina first appeared on the plant shoots at time 4, when mean axial length (Fig. 84A and B) was slightly greater in P. pectinatus than in P. richardsonii stands. At this time a limited amount of hatching had occurred in P. richardsonii stands, as well as in those of P. pectinatus (Fig. 85), since by time 5 the young had advanced to several higher size classes in both types of stands. After time 4, the mean axial length decreased more sharply in the P. pectinatus stands, largely because of the smaller numbers of adults that were present. After time 5, a large cohort of young emerged in the P. pectinatus stands, as well as a smaller one in the P.

Figure 83. Mean live weight (g) of Physa gyrina (A and B) and Lymnaea stagnalis (C and D) per 100 cm^2 surface area of Potamogeton pectinatus and P. richardsonii respectively at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.

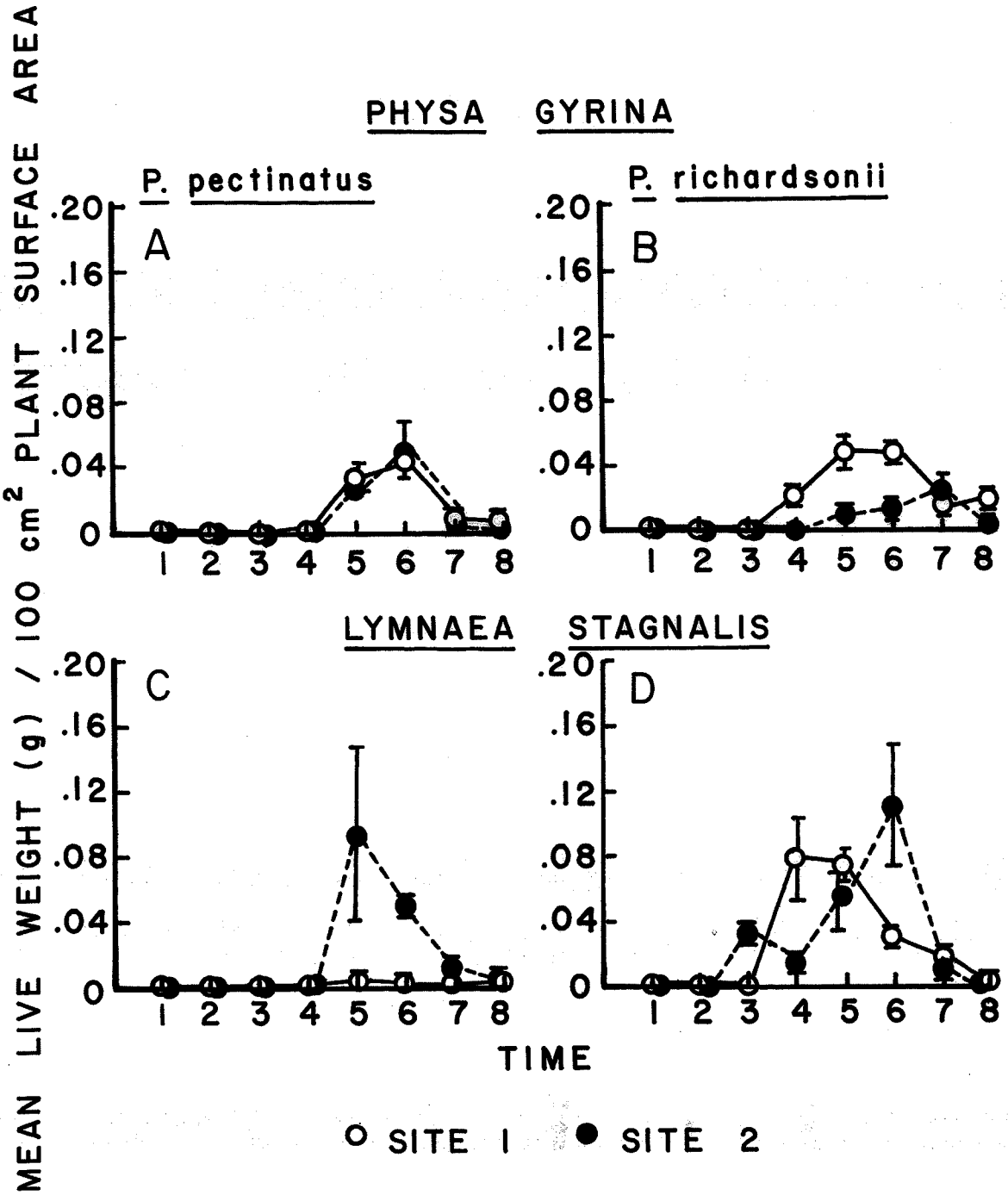
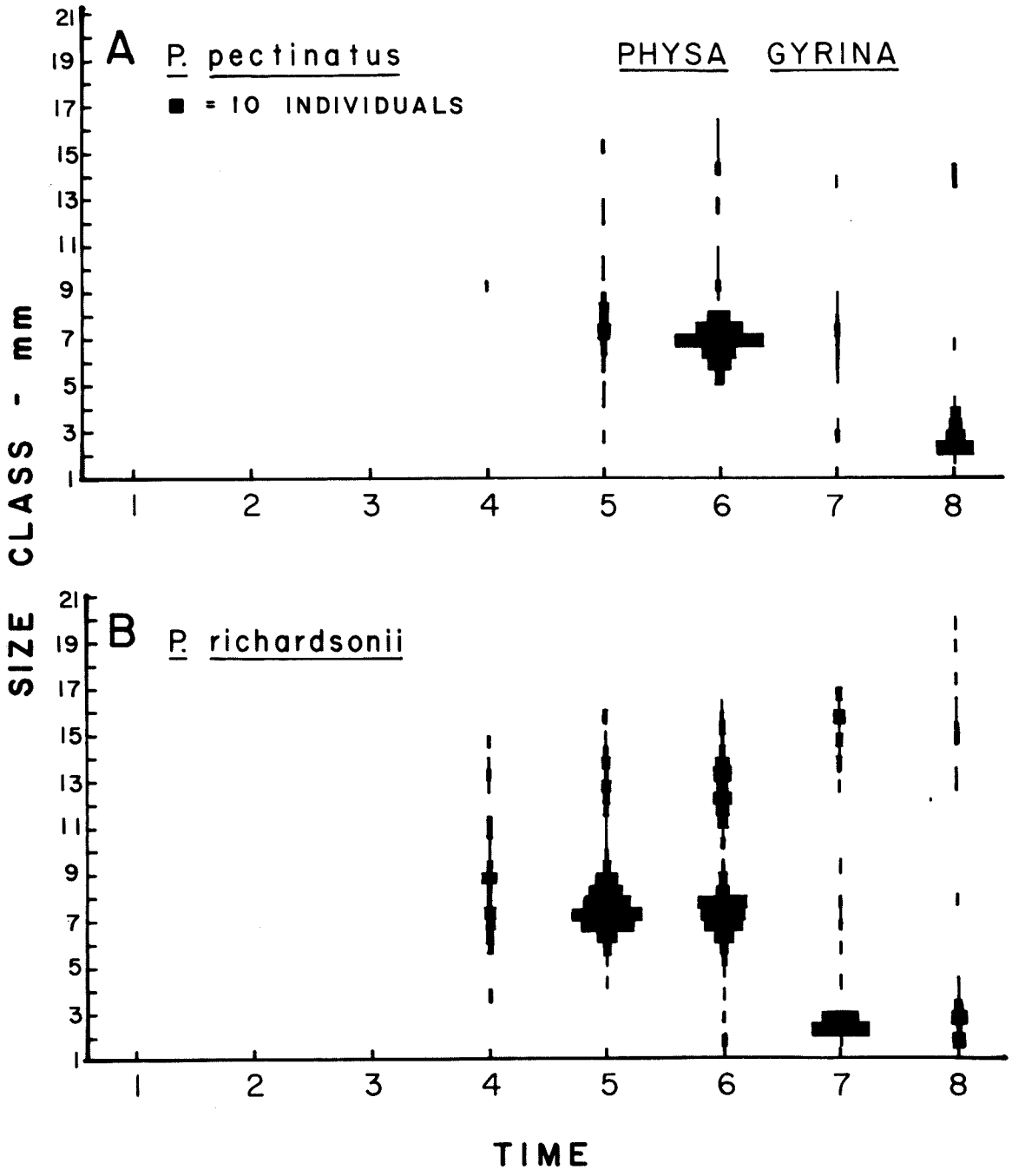

PHYSA
GYRINA
P. pectinatus
P. richardsonii
A
B
LYMNAEA
STAGNALIS
C
D
.20
.16
.12
.08
.04
0
1 2 3 4 5 6 7 8
MEAN LIVE WEIGHT (g) / 100 cm² PLANT SURFACE AREA
TIME
SITE 1
SITE 2

Figure 84. Mean axial length (mm) of Physa gyrina (A and B) and Lymnaea stagnalis (C and D) in stands of Potamogeton pectinatus and P. richardsonii respectively at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.

Figure 85. Size class distribution of Physa gyrina in stands of Potamogeton pectinatus (A) and P. richardsonii (B) at site 1 during the 1974 season. Values represent the total numbers of individuals recorded in five sample quadrats (7625 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.


A
P. pectinatus
■ = 10 INDIVIDUALS
PHYSA
GYRINA
B
P. richardsonii
SIZE CLASS - mm
TIME
1
3
5
7
9
11
13
15
17
19
21
1
2
3
4
5
6
7
8

richardsonii stands. Hatching was still evident at time 6 in the latter stands but mean axial length was greater in these stands because a smaller proportion of this subpopulation was composed of young, compared with that in the P. pectinatus stands. At time 7, mean axial length decreased in the P. richardsonii stands as a large cohort hatched in these stands; a secondary period of hatching was observed in the P. pectinatus stands at time 8. A period of high mortality followed time 6, particularly in the P. pectinatus stands, since little remained of the large groups of juveniles that had been present at times 5 and 6. The numbers of individuals in Fig. 85 were greater in the P. richardsonii stands because the values were expressed in terms of bottom area and were not related quantitatively to the host plants.

At site 2, time 4 (Fig. 84A and B), mean axial length of P. gyrina was again higher in the P. pectinatus stands but these values decreased after time 4 as young appeared (Fig. 86). The mean axial length increased in the P. richardsonii stands as smaller proportions of young were present and by time 7 these subpopulations contained very few young while those in P. pectinatus stands contained very few adults. By time 8 adults were rare in both types of stands. A secondary period of reproduction occurred prior to time 8 and was largely restricted to the P. pectinatus stands. As at site 1, mortality was high after time 6, particularly in the P. pectinatus stands.

The mean axial length of L. stagnalis at site 1 (Fig. 84C and D) decreased at time 5 due to hatching of young (Fig. 87), which occurred only once during the season. Both adults and young occurred

Figure 86. Size class distribution of Physa gyrina in stands of Potamogeton pectinatus (A) and P. richardsonii (B) at site 2 during the 1974 season. Values represent the total numbers of individuals recorded in five sample quadrats (7625 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.

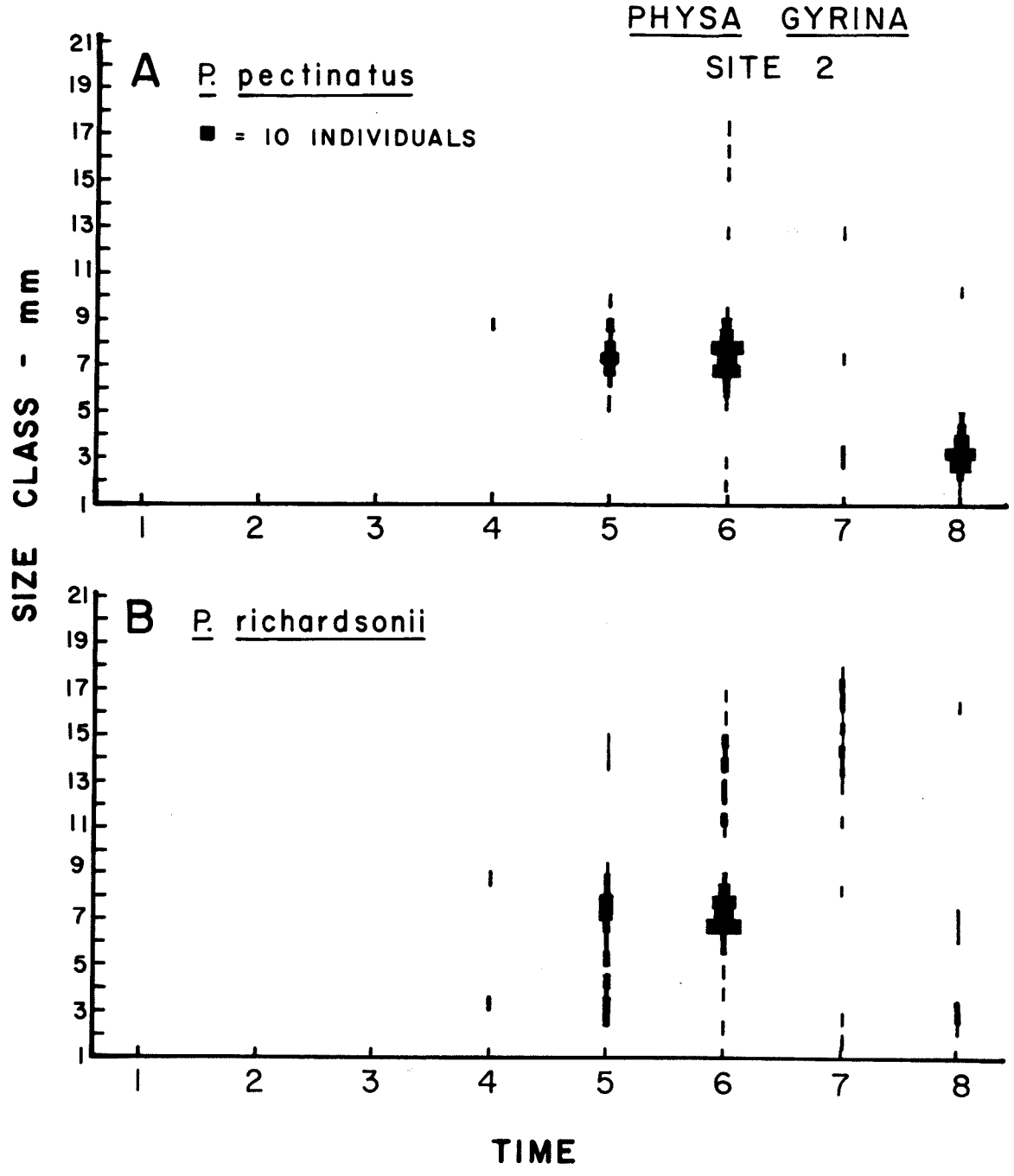
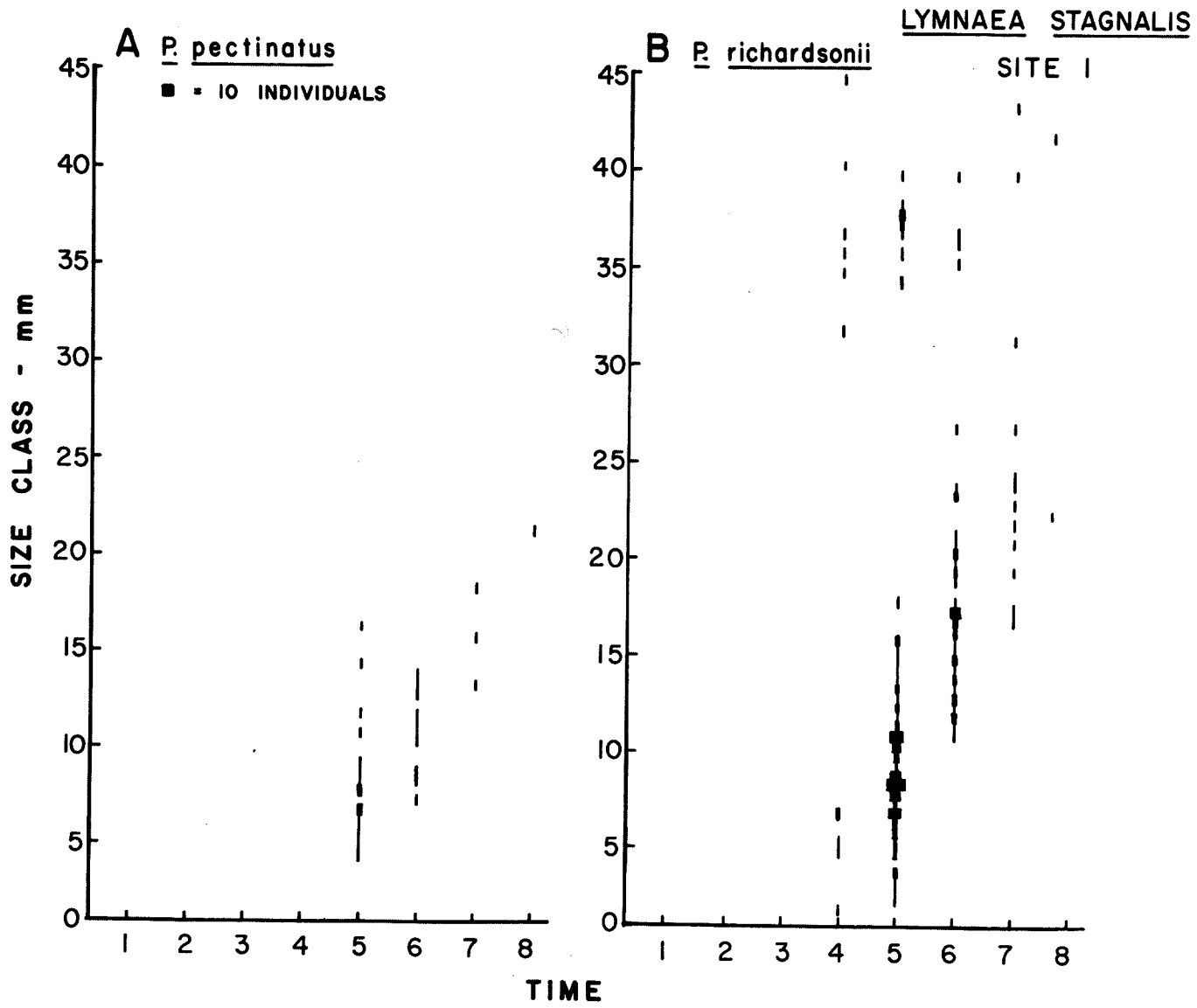

PHYSA GYRINA
SITE 2
A P. pectinatus
■ = 10 INDIVIDUALS
B P. richardsonii
SIZE CLASS - mm
TIME
1
3
5
7
9
11
13
15
17
19
21
1
2
3
4
5
6
7
8

Figure 87. Size class distribution of Lymnaea stagnalis in stands of Potamogeton pectinatus (A) and P. richardsonii (B) at site 1 during the 1974 season. Values represent the total numbers of individuals recorded in five sample quadrats (7625 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.


LYMNAEA STAGNALIS
A P. pectinatus
■ = 10 INDIVIDUALS
B P. richardsonii
SITE I
SIZE CLASS - mm
TIME
0
5
10
15
20
25
30
35
40
45
1
2
3
4
5
6
7
8

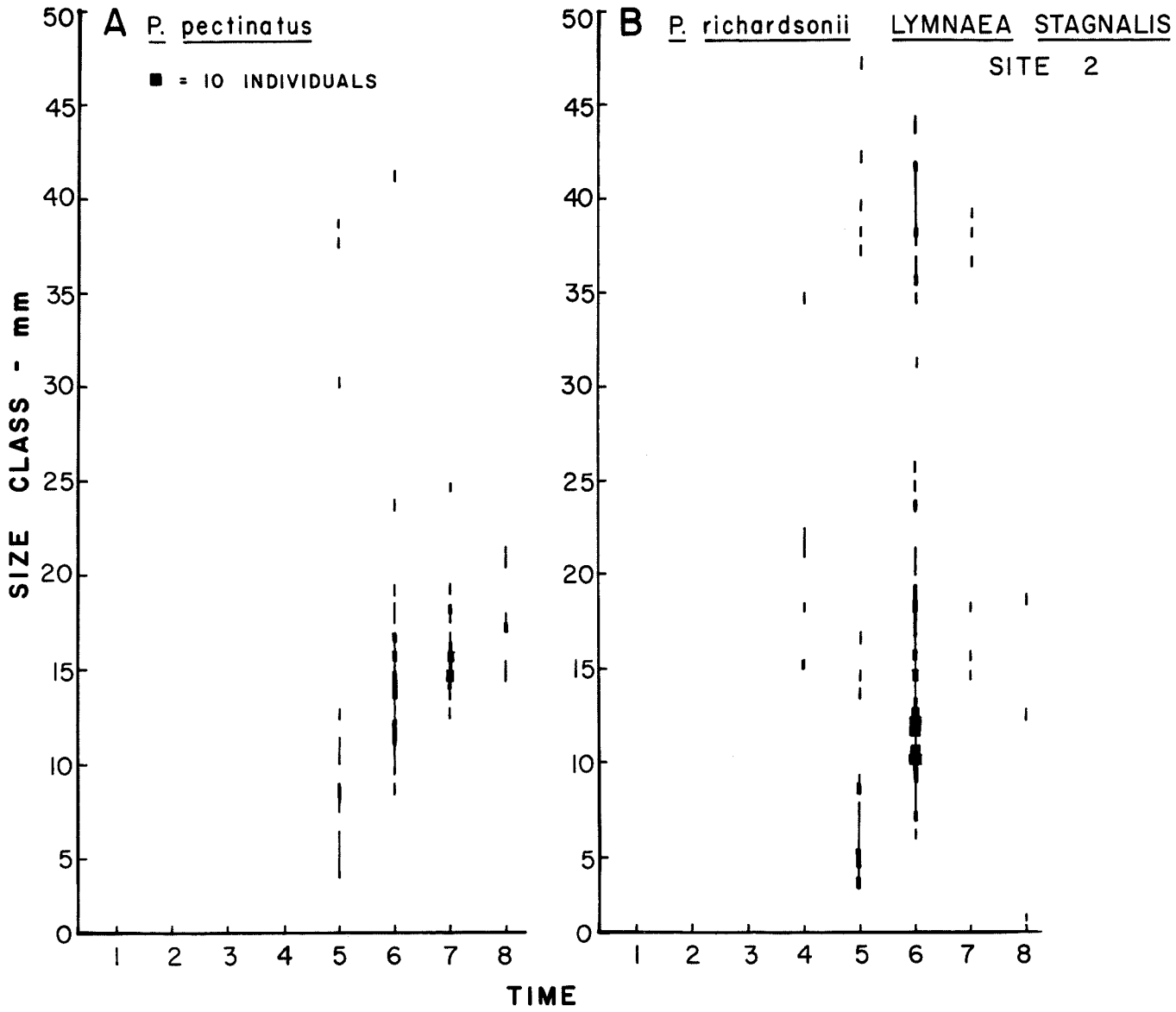
predominantly in the P. richardsonii stands and hatching appeared to commence earlier in these stands since the young were already observed here at time 4 and by time 5 the cohorts had advanced slightly farther in the P. richardsonii than in the P. pectinatus stands.

At site 2 (Fig. 84C and D), mean axial length again decreased at time 5 when the first young appeared but the bulk of hatching occurred after time 5 in the P. richardsonii stands (Fig. 88), unlike the situation at site 1, where most of the hatching occurred after time 4. Again, reproduction occurred only once during the season.

Thus, the size class distribution data showed the following features:

1. As in 1973, the timing of hatching was apparently related to the growth of the host plants and appeared to coincide with the early stages of increased growth of the preferred macrophytes.
2. Like that of the macrophytes, reproduction by the two gastropods was noticeably curtailed during the 1974 season, suggesting that conditions were suboptimal.
3. Because of high mortality and low natality during the 1974 season, it was difficult to assess the relative growth rates of the snails in the two types of stands. The high mortality after time 6 may have been related to proliferation of Lemna which obscured the water surface and led to accelerated decay of the submerged macrophytes.

Figure 88. Size class distribution of Lymnaea stagnalis in stands of Potamogeton pectinatus (A) and P. richardsonii (B) at site 2 during the 1974 season. Values represent the total numbers of individuals recorded in five sample quadrats (7625 cm^2 bottom area). Size classes were constructed at 0.5 mm intervals.


A P. pectinatus
■ = 10 INDIVIDUALS
B P. richardsonii LYMNAEA STAGNALIS
SITE 2
SIZE CLASS - mm
TIME
0
5
10
15
20
25
30
35
40
45
50
1
2
3
4
5
6
7
8

Discussion

During the 1973-4 seasons, snail numbers and biomass per unit plant dry weight and surface area showed a significant tendency for Physa gyrina to occur in stands of Potamogeton pectinatus, while Lymnaea stagnalis tended to occur in P. richardsonii stands. The mean numbers of these snails per unit dry plant weight and surface area were not constant but showed well-defined peaks in association intensity which occurred during periods of active growth of the host plants.

During both the 1973 and 1974 seasons, the association patterns of P. gyrina were syntonic at sites 1 and 2 in the P. pectinatus stands, whose growth was also synchronous at the two sites, but were incompletely correlated in the P. richardsonii stands, whose growth was out of phase. The association patterns of L. stagnalis during both the 1973 and 1974 seasons were out of phase by approximately two weeks in the P. richardsonii stands at sites 1 and 2 and were correlated with the growth of these plants. The association patterns of L. stagnalis for the small subpopulations present in the P. pectinatus stands at the two sites were syntonic and correlated with the synchronous growth of these plants. Thus the population dynamics of the two major grazers tended to follow the growth patterns of the host plants. The reason for the asynchronous growth of the P. richardsonii stands at sites 1 and 2 is not known.

Both plant dry weight and snail density per unit bottom area often continued to increase after the association peak, but the association intensity decreased because the plants outgrew the snails.

With senescence of the plants at the end of the season, the differential snail distributions disappeared.

The two major associations persisted despite the flood conditions in 1974 which resulted in altered community composition. The abundance of P. pectinatus fluctuated more from year to year than did that of P. richardsonii; such fluctuations of the former species have also been noted by Southwick and Pine (1975) and Zhadin (1956). The latter worker noted the sensitivity of P. pectinatus to flooding and suggested that the reduced abundance and vigor of this plant during periods of high water levels may be due to reduced light intensity (cf. Meyer et al, 1943).

Because the association peaks were composed of young snails as well as adults, the associations must be examined in terms of factors which: a) influence the distribution of adults and b) influence reproduction.

The differential distribution of adults between the two types of macrophyte stands could not be correlated with any of the monitored environmental parameters. Boerger (1975a) suggested that some distributional differences may result from passive distribution by wind-induced surface currents of snails which have come to the surface for air. Such distributions would be expected to show a greater density of all snail species to leeward; i.e. at sites 1 and 2 the prevailing westerly winds would be expected to push snails to the eastern portions of the sites into the P. pectinatus stands. However:

1. the P. richardsonii stands showed greater densities of some species than those of P. pectinatus at sites 1 and 2, and
2. differential distributions between the two types of stands

were observed at site 4 even though here the stands were intermixed and wind-induced currents were very strong.

Although L. stagnalis appears to be quite sensitive to heat budgets (van der Schalie and Berry, 1973) and exhibits negative thermotaxis from areas of high temperatures (Bovbjerg, 1975), the optimum being 20 C (McDonald, 1973), this factor did not appear to account for the differential distributions because no significant temperature differences could be detected at comparable depths between the two types of stands at each site. Sankurathri and Holmes (1976) reported higher densities of P. gyrina in an area of Lake Wabamun, Alberta heated by thermal effluents, where temperatures occasionally exceeded 30 C than in the unheated control area where temperatures during midseason reached only 20 C. These workers found that numbers of snails per unit dry plant weight showed a well-defined seasonal peak in the warmer area when the macrophytes were growing actively, despite the fact that reproduction in this area could continue on a year-round basis; no peak was observed in the colder area. Although these results may have largely been due to temperature effects, the significance of the difference in the respective plant communities was not explored; it is interesting that the colder area contained, among other species, Potamogeton richardsonii but not P. pectinatus, while in the warmer area the reverse was true.

The differential distributions of different gastropods in various macrophyte stands have been noted by several other workers (e.g. Krecker, 1939; Rosine, 1955; DeCosker and Persoone, 1970; Calow, 1973; Higler, 1976). It has been suggested (e.g. Shelford, 1918; Wieser, 1951; Calow, 1973) that structural differences between

different types of plants may account for differential snail distributions. Shelford (1918) and Frohne (1956) implied that plants were only vehicles of surface and Wieser (1951) postulated that under equal environmental conditions the numbers of organisms occurring on marine plants were directly dependent on the surface area. Andrews and Hasler (1943) believed that the abundance and diversity of the associated fauna was directly correlated with the degree of leaf dissection of the host macrophytes. Rosine (1955) attempted to test this viewpoint by examining the communities of several types of macrophyte stands on the basis of surface area. He found that seasonal variations existed in the distributions of animals over given areas of plant surfaces and concluded that the results did not support Wieser's (1951) hypothesis. An earlier study by Entz (1947) had also shown differences in the density of organisms in terms of surface area of macrophytes, which, however, he interpreted to be representative of varying ecological conditions. Calow (1973) and Bishop and Bishop (1973) continued to subscribe to the view that preference by snails for different plant stands was dependent upon plant morphology.

Since the morphology of the filiform P. pectinatus differs greatly from that of the broadleaved P. richardsonii, plant form appeared to be a valid question to which the following arguments could be addressed:

1. According to the view that plants with the most finely dissected leaves support the densest macrofauna, P. pectinatus would be expected to support the greater numbers of snails of all species. However, only P. gyrina and one or two (depending on the season) other gastropods were associated with P. pectinatus in greater

numbers, and the occurrence of association peaks and seasonal distributions would not be expected since the plants retain the same morphology throughout the season.

2. According to the view that surface area determines the density of organisms, all snail species would be expected to occupy both plant species in equal densities per unit surface area, since both plants were equally available for population. However, snail densities on the basis of plant surface area continued to show significant distributional affinities for certain macrophytes at certain times of the growing season.

It might be argued that smaller species, such as P. gyrina, would find adequate mechanical support on the thin stems of P. pectinatus, while the larger species, such as L. stagnalis, would require support from huskier species. During the 1973 season, the small Fossaria modicella was indeed associated with P. pectinatus, but so was the large Helisoma trivolvis. During the 1974 season, H. trivolvis was associated with P. richardsonii, but the large Stagnicola palustris was associated with P. pectinatus. The very small Promenetus exacuous was associated only with P. richardsonii. Furthermore, this theory would not explain why the associations were time-dependent.

Related to this argument is the hypothesis that differential distributions within a single water body may be related to differential oxygen consumption, since with increasing body weight, more oxygen is required by gastropods (Boerger, 1975b). According to this view, smaller species would have distributions different from those of larger species. However, large and small species occurred in both types of stands.

When dissolved oxygen levels are high, proportionately less surface breathing is required (Cheatum, 1934; McDonald, 1973). L. stagnalis has been reported at depths of up to 15-25 m in Starnbergesee (Pauly, 1877 in Cheatum, 1934) and even at 250 m in Lake Geneva (Forel, 1869 in Cheatum, 1934), while P. gyrina has been reported at depths of up to 7 m in Lake Mendota, Michigan (Muttkowski, 1918 in Cheatum, 1934). At such depths, as well as in winter, surface breathing does not occur and oxygen requirements are met by diffusion through the air-water interface at the pulmonary cavity and by skin respiration, which may comprise more than 50% of the total respiration (Jones, 1961). Under conditions of higher temperature and correspondingly reduced oxygen tensions, proportionately more time is spent breathing at the surface (McDonald, 1973). Sankurathri and Holmes (1976) suggested that, aside from the need for food, snails were closely associated with macrophytes because the latter provided an avenue of ascent to the surface for breathing. Although macrophytes do provide such an avenue, both plant species are equally suitable since both reach the surface and this explanation sheds no light on differential associations. These workers also explained the presence of hatchlings on plants by suggesting that the latter provide an avenue of descent which "may be essential for hatchlings to escape the surface tension" (Sankurathri and Holmes, 1976). What is meant by this statement is unclear because the young of both Lymnaea (Cheatum, 1934) and Physa (DeWitt, 1954) have the pulmonary cavity filled with water and do not ascend to the surface for some time after hatching.

Oxygen levels measured at site 1 during the 1972 season showed that concentrations remained at or above saturation levels

during most of the growing season. It is likely that in such situations surface breathing for non-hatchlings would be most important during midseason when temperatures are high and during the latter part of the season when body weight has increased. Since both species of macrophytes reach the surface at approximately the same time, this factor could not account for differential distributions at the study sites.

The role of behavioral factors in snail distribution has been discussed by several workers (e.g. Townsend, 1974; Thomas et al, 1975). Snails often follow mucus trails laid by individuals of the same, but not of another, species (Dawson, 1911; Townsend, 1974) significantly more frequently than would be expected due to chance after initial contact with the trail. Wells and Buckley (1972) and Townsend (1974) found that these trails contain directional information since snails follow these trails for longer periods of time when proceeding in the same direction as that in which the trail was laid. Chemoreception appears to be involved in trail following; Wilson (1968) found that the trails of Lymnaea truncatula contain free glucose, 5 protein fractions, 16 amino acids, ammonia, esterified and free fatty acids and cholesterol. Although trail following has the advantages that locomotion is facilitated and the chances of meeting a prospective mate are increased (Townsend, 1974), it is unlikely that trails contribute to large-scale differential distributions because the information contained in the trails is short-lived and disappears within less than an hour after the trail has been laid (Wells and Buckley, 1972; Townsend, 1974). The highest recorded instantaneous speed for snails is 528 cm/hour (Clampitt, 1970); however since

snails do not travel in straight lines nor at constant speeds, the rates of dispersal are generally an order of magnitude below that of the maximum instantaneous speed; the maximum net rate of dispersal recorded for P. gyrina in situ is 27.1 cm/hour and the maximum recorded net distance travelled is 18.5 m in 14 days (Clampitt, 1970). Thus trail-following behavior could not account sufficiently for differential distributions unless the different types of stands were in close proximity to each other, as at site 4. But even at site 4, one must still explain why the pioneer snails laid the trails.

Aside from trail-following, the recorded rates of dispersal would in themselves be sufficient to account for active travel of snails over the distances separating the two types of stands at sites 1 and 2.

Thus the results lead to agreement with Rosine (1955) that such distributions are "strongly suggestive of a direct influence of plants . . . even possibly on animals in the water around them."

Because a large proportion of newly hatched young comprised the association peaks, reproduction played a significant role in the association patterns. The time of reproduction was assumed to have preceded the association peak by approximately two weeks, or one sampling period. The developmental time required for eggs of L. stagnalis from the study sites was approximately 14 days at 20 C. in the laboratory; this value agreed with the value of 12-14 days at 20 C. reported by Levina (1973) for U.S.S.R. populations, although van der Steen et al (1969) found that development of eggs from populations in the Netherlands could require as little as 7 days at 20 C. under conditions of constantly renewed water supply. The developmental time

required for eggs of P. gyrina was slightly longer than that of L. stagnalis; Sankurathri and Holmes (1976) found that 16-18 days at 20 C. were required for eggs from Alberta populations, but DeWitt (1954) reported that eggs from Michigan populations required 7-8 days at 20-23 C.; this shorter time may have been influenced by the slightly higher temperatures since the rate of development is proportional to temperature (DeWitt, 1954; Levina, 1973) but may have been influenced by other factors as well.

Since the egg-cases are usually attached to plants (Levina, 1973), the latter may influence hatching by providing oxygen; plant exudates may also affect hatching since it has been suggested that these may stimulate hatching of mosquito (Aëdes trivittatus Coquillett) eggs (Abdel-Malek, 1948).

The factors that govern oviposition are complex and incompletely understood. According to DeWitt (1967), temperature rather than photoperiod is the primary factor that stimulates oviposition in both physids and lymnaeids; a rise in temperature above 10 C. induces oviposition in P. gyrina (DeWitt, 1954, 1955). Levina (1973) found that in L. stagnalis spawning commences in the spring when water temperatures rise to 15-16 C., although reproduction may continue in the fall until temperatures decrease to 10-12 C. Temperatures at all of the study sites during the time of major reproduction in 1973 were well above 10 C., while in 1974 they were approximately 25 C. Although reproduction per unit host plant was greater in stands of the preferred species, respectively, no temperature differences were detected between the stands. Since the fecundity of L. stagnalis increases with linear shell size and body weight (Levina, 1973), differences in the latter

two parameters between the two types of stands may have affected the relative magnitude of reproduction in the stands but could not account for the discrepancies in timing of reproduction between different stands and different sites. Apparently reproduction at these sites was also dependent on other factors once the threshold value for temperature had been exceeded.

Imhof (1973) and van der Steen (1967) found that lengthening of the photoperiod also stimulates spawning in lymnaeids, provided that the specific threshold values for temperature were exceeded. Photoperiod as a significant factor in the current study was rejected because of: a) the discrepancy between the sites for reproduction during 1973, b) the lag between sites 1 and 2 for L. stagnalis in the P. richardsonii stands but not in the P. pectinatus stands during 1973-4, c) the discrepancy in the time of reproduction between 1973 and 1974, and d) snails from the study sites continued to reproduce throughout the winter under conditions of natural photoperiod in indoor aquaria stocked with cultures of the respective macrophytes (unpublished).

Russell Hunter (1961) suggested that, aside from environmental factors, some populations may be genetically programmed to a particular pattern of reproduction. This factor was also probably not significant in the current study since the proximity of sites 1 and 2, with their consequent periodic contact during times of high water levels facilitated the interchange of population members. During the spring flood of 1974, the two sites were united for several weeks, yet the lag period between the subpopulations in the P. richardsonii stands persisted.

The occurrence of secondary periods of reproduction in pulmonates within a single season has been reported by several workers (e.g. DeWit, 1955; DeWitt, 1955; Duncan, 1959; Clampitt, 1970; Levina, 1973; Young, 1975; Sankurathri and Holmes, 1976) and appears to be related to the growth rates of the young. Since reproductive maturity is attained at a certain size (Levina, 1973), the magnitude of which varies with the genetic makeup and environmental conditions, the earlier in the season that the first hatching occurs, the more likely is the occurrence of a second period of reproduction during the same season (Young, 1975). Accordingly, the conditions which regulate the timing of the first period of reproduction also decide to a large extent whether more than one generation will be produced during the season. At sites 1 and 2, secondary periods of reproduction in L. stagnalis did not occur during the 1974 season because the young of the year emerged too late to reach reproductive maturity while environmental conditions were still suitable for oviposition.

The growth rates can be correlated with rate of food intake (Thomas et al, 1975) and are influenced by the type and abundance of primary production (Hunter, 1975a), temperature (Imhof, 1973; Levina, 1973) and the proximity of other feeding snails (Mooij-Vogelaar and van der Steen, 1973; Thomas et al, 1975). Why the growth rates of both Physa and Lymnaea were higher in stands of P. richardsonii during the second half of the 1973 season is not known. The maximum size attained by P. gyrina at both sites 1 and 2 was in excess of 27 mm; the largest specimen of this species previously recorded from

the Canadian Interior Basin had a length of 24.1 mm (Clarke, 1973). The latter worker suggested that exceptional size in this species may have been related to the absence of high concentrations of the metabolites of other snails, as well as to other factors.

Certain individuals of both P. gyrina and L. stagnalis appeared to survive beyond the second summer; Levina (1973) reported old-timers of L. stagnalis that were up to 5 years old. At site 3, very few individuals of Physa survived even one winter and complete replacement of the population occurred during the summer; such a pattern has also been reported for P. fontinalis L. (DeWit, 1955).

The reproductive patterns observed in the current study could not be correlated with any of the monitored physical variables; although the two-week lag period between sites 1 and 2 in the seasonal patterns of molybdenum-blue phosphorus during the 1973 season showed some promise of correlating with the growth of P. richardsonii, this possibility had to be discarded after the 1974 season.

The most obvious remaining factors were the plants themselves. Bretshneider (1948 in DeWitt, 1954) reported that oviposition in L. stagnalis was stimulated by renewal of aquarium water and the addition of Hydrocharis shoots. Nieuwenhaven and Lever (1946 in DeWitt, 1954) suggested that oviposition was stimulated by the oxygen produced by Hydrocharis; however the snails had to come into contact with the leaves before oviposition could occur. DeWitt (1954) found that Elodea had no effect on oviposition in P. gyrina. Young (1975), Hunter (1975a and b) and Sankurathri and Holmes (1976) suggested that the reproductive patterns of molluscan grazers may be related to the nature and extent of the primary producers, and these workers as well

as Eisenberg (1966) postulated that such a mechanism may operate through limitation of food. Thomas et al (1975) conjectured that other plant factors such as indole acetic acid may influence growth and natality rates by acting directly on the snails.

The controversy surrounding the question of whether submerged macrophytes are grazed upon has had a long history and confusion has persisted until recent times. Shelford (1918) stated that "one could probably substitute glass structures of the same form and surface texture without greatly affecting the immediate food relations". Welch (1935) wrote that "it is now certain that (Shelford's) statement is not well grounded; that these higher aquatic plants serve directly as food for a considerable array of animals, the quantities of the plants consumed sometimes being great". Rosine's (1955) work which cited Shelford (1918) stimulated Frohne (1956) to argue that macrophytes, particularly species of Potamogeton (Moore, 1915 in Frohne, 1956) sustain extensive direct grazing pressure from invertebrates. Robson (1968) resurrected the problem by stating that "weeds are seldom eaten while growing but when they die they provide one of the main sources of nutrients for much of the animal life of freshwater". Westlake (1975) suggested that grazing of submerged communities may occur but considered only the chordate grazers.

That the snails do eat living vascular plant tissue has been demonstrated in the current study through observation of the lesions produced by snail grazers as well as Warner's (1976) observations that lesions reflect relative feeding frequencies. The normal diets of physids and lymnaeids have been reported to consist of higher plant tissue, as well as small amounts of unicellular algae, detritus and

carrion (Graham, 1955; Monakov, 1972). The feeding behavior of grazing snails has been described in detail by several workers (e.g. Hubendick, 1957; Dawkins, 1974).

The behavioral patterns of L. stagnalis and P. gyrina show a positive kinesis towards aggregation on vegetation (Bovbjerg, 1975; Warner, 1976). The distance perception of vegetation is unlikely to be primarily optical since the eyes in L. stagnalis are believed to function largely for monitoring light intensity and direction (Stoll and Bijlsma, 1973) although their precise functions are incompletely understood (Stoll, 1973). Pulmonates exercise chemoreception of plant chemicals (Townsend, 1973; Calow, 1973) at variable distances and can apparently distinguish among quantitative levels of a single food source to the extent that they can adjust their feeding densities to conform to the available food levels (Warner, 1976). Since snails also appear to distinguish between different types of food (Bovbjerg, 1968, 1975), the evidence strongly suggested that the plants were active participants in the inception of the associations and perhaps held the key to the phenomenon of differential seasonal snail distributions.

SECTION III:

The biochemical status of the macrophytes

Introduction

Because the association peaks of Physa gyrina and Lymnaea stagnalis appeared to be correlated with the growth patterns of Potamogeton pectinatus and P. richardsonii respectively, and because the macrophytes were grazed upon by the snails, the objective of this portion of the study was to assess the seasonal composition of the macrophytes in terms of selected biochemical variables. At the very least, such an assessment would provide basic information on the quality of the plant tissues as food at different times of the season, and at most, it might provide a factor that could be correlated with the association patterns.

At the outset, the following classes of compounds were examined:

1. Total soluble carbohydrates.
2. Total titratable acids.
3. Total extractable proteins.
4. Carotenoid compounds.

Classes 1 and 2 were examined because of their nutritional value and because their solubility suggested that they were likely components of plant exudates. Class 3 was examined because, according to Boyd (1970), total protein is an important index of the nutritive quality of primary producers. Class 4 was examined because these compounds are necessary for photosensitivity in snails and originate from plant tissues (Benjamin and Walker, 1972).

Materials and methods

During the 1972-4 seasons, plant shoots were collected by hand on each sampling day from points scattered throughout each site. The shoots were rinsed in the field and immediately placed in iced, lightproof containers and were frozen within 6 hours of collection. The frozen plants were subsequently freeze-dried under liquid nitrogen and ground in an electric mill using a 1 mm mesh screen. The powder was stored in airtight glass containers in a freezer. Only above-ground vegetative parts were used.

I. Season I (1972)

A. Total soluble carbohydrate

A 0.5 g sample of plant powder was placed in a small erlenmeyer flask with 20 ml 80% ethanol. The flask was swirled for one minute and the suspension was transfered to a 50 ml centrifuge tube. The flask was rinsed with an additional 10 ml 80% ethanol which was added to the centrifuge tube. The suspension was centrifuged at 5000 rpm for 5 minutes. The supernatant was decanted and made up to a volume of 30 ml with 80% ethanol: the volume lost in the pellet and through evaporation was less than 5 ml. To minimize evaporation, the procedure was performed at 4 C. The extract was stored in airtight glass vials in a freezer.

The total soluble carbohydrate in the extracts was estimated using the method of Roe (1955). To a 0.1 ml aliquot of extract in a test tube were added 0.9 ml distilled water and 4.0 ml anthrone reagent (100 mg anthrone and 1.0 g thiourea in 100 ml 75% H_2SO_4,

stored in dark at 4 C), and shaken well. The solution was heated for 15 minutes in a water bath at 100 C. After cooling, the optical density of the solution was measured in a spectrophotometer at 620 nm against a blank that had been treated in the same way as the unknown but contained distilled water in place of the extract. This procedure was repeated for 3 aliquots of each extract. The carbohydrate concentrations were determined from a calibration curve for glucose, and results were expressed in terms of equivalent glucose concentrations.

B. Total titratable acids

Fractionation of the plant material was carried out according to the method described by Cook and Bieleski (1968). A 100 mg sample of plant powder was suspended in 2 ml MCW (methanol/ chloroform/ water, 12/5/3 by volume). The suspension was centrifuged at 1000g for 5 minutes and the pellet was extracted twice more using 2 ml MCW each time. The 3 MCW extracts were pooled and to these were added 2 ml chloroform and 2 ml distilled water. The solutions were mixed and transfered to a 10 ml separatory funnel where the two phases were allowed to separate. The chloroform layer, containing lipids, oils, phospholipids and pigments was discarded and the aqueous layer, containing organic acids, amino acids and phosphate esters was used for titration.

The volume of the aqueous fraction (ca. 4.5 ml) was made up to 6 ml with MCW. The small chloroform fraction that separated was discarded. A 1 ml volume of the aqueous fraction was made up to a volume of 10 ml with distilled water. This solution was titrated with 0.001 N NaOH until pH 8.3, the beginning of the indicator range

for phenolphthalein (Wood, 1952), using a pH meter. A control was made by separating 6 ml MCW into aqueous and chloroform fractions as described above and using 1 ml of the aqueous fraction made up to 10 ml with distilled water for titration. The results were expressed as meq/g titratable acidity. According to Wood (1952), the value of acidity obtained by titration is proportional to the total organic acids present in the extract.

C. Total protein

A 0.10 g sample of plant powder was suspended in approximately 30 ml of 1 N NaOH by shaking vigorously and was centrifuged at 10,000 rpm for 5 minutes. The supernatant was decanted and made up to a volume of 50 ml with 1 N NaOH. Protein content of this solution was estimated using the method of Lowry et al (1951). A 0.3 ml aliquot of the solution was made up to 0.5 ml volume with 1 N NaOH. To this was added 2.5 ml of alkaline copper sulphate solution (50 ml 2% Na_2CO_3 in 0.1 N NaOH and 1 ml 0.5% $CuSO_4 \cdot 5H_2O$ in 1% Na tartrate, mixed just before use), and the solution was allowed to stand for 10 minutes, after which time 0.5 ml Folin reagent (50% aq. Folin-Ciocalteu phenol reagent) was added and the solution was mixed. After 30 minutes the optical density of the solution was measured in a spectrophotometer at 500 nm. This procedure was repeated for 3 aliquots of each extract. For the control, distilled water was used in place of the extract. The protein content was estimated from a calibration curve for bovine serum albumin and was expressed as mg protein/g.

D. Carotenoids

Carotenoids were extracted using the method described by Goodwin (1955). A 0.5 g sample of plant powder was mixed in a mortar with 0.5 g of acid-washed silica sand and 1.5 g each of anhydrous Na_2SO_4 and acid-washed alumina until the mixture was homogeneous. The mixture was transfered to a 1 x 16 cm glass column containing a mixture of equal weights of anhydrous Na_2SO_4 and acid-washed alumina. A 50 ml volume of 2% acetone in n-hexane was flushed through the column under light suction with a syringe. The volume of the effluent was measured and the optical density was determined at 436 nm in a spectrophotometer against a blank of 2% acetone in n-hexane. The concentration was calculated from Goodwin's (1955) formula:

$$C = \frac{O.D. \times V \times 454}{196 \times L \times W} \quad \ldots\ldots\ldots (15),$$

where C= carotene concentration (mg/g tissue), V = final volume of effluent at the time of reading (ml), L = light path length (cm), and W = weight of tissue sample (g).

According to Goodwin (1955), 95% of the active carotenes present in the tissue are extracted by this method and consist largely of beta-carotene although some alpha-carotene is present as well.

II. Seasons II and III (1973-4)

During the 1973-4 seasons, the extraction and estimation of total soluble carbohydrate were made as described above (p. 273). The 80% ethanol extracts were separated on ion-exchange columns

(Wang, 1960; Canvin and Beevers, 1961) using Dowex -50W (50 x 8)(H^+; 200-400 mesh) and Dowex -1 (1 x 10) (Cl^-; 200-400 mesh). The resins were prepared in bulk (Atkins and Canvin, 1971). Dowex -50W was boiled with 2 N HCl and poured into 1 x 16 cm glass columns plugged at the bottom with glass wool. Dowex -1 was converted to the formate form by treating with 1 N sodium formate in a large column until the effluent gave a negative test for chloride with $AgNO_3$. The treated resin was poured into 1 x 16 cm glass columns as described above and each column was washed with 10 ml 0.1 N formic acid. Both types of columns were then washed with distilled water until the pH of the effluent was stable. Immediately prior to use, the columns were flushed with at least 2 bed volumes of distilled water.

Each ethanol extract was dried under an air jet and the residue was redissolved in 2 ml 80% ethanol. This solution was placed on a Dowex -50W column and flushed with 100 ml distilled water. The effluent (Fraction 1) was dried under an air jet; it contained organic acids, sugars and sugar phosphates (Canvin and Beevers, 1961; Cossins and Beevers, 1963). Amino acids remained in the column and were eluted with 100 ml 4 N NH_4OH (Fraction 2). The residue of Fraction 1 was redissolved in 2 ml 80% ethanol, placed on a Dowex -1 column and flushed with 100 ml distilled water. The effluent (Fraction 3) was dried under an air jet and contained sugars. Sugar phosphates and organic acids remained in the column and were eluted with 80 ml of 4 N formic acid followed by 20 ml of 6 N HCl (Fraction 4).

The residue of Fraction 3 was redissolved in 1 ml of 10% isopropanol. Two replicate 30 microliter aliquots of each solution were spotted adjacent to each other on a 46 x 57 cm sheet of Whatman

No. 1 filter paper. Markers were prepared by spotting 10 microliter samples of known sugars (1% in 10% isopropanol) on each sheet. Chromatograms were run for 48 hours in a descending solvent of n-butanol/acetic acid/water (52/13/35 by volume) (Putman, 1957). After the chromatogram had dried, it was cut into strips to separate replicate samples. One of each sample pair was developed by dipping into a tray containing aniline diphenylamine phosphate solution (10 vol. of 1% aniline and 1% diphenylamine in acetone combined with 1 vol. of 85% phosphoric acid, immediately prior to use)(Bacon and Dickinson, 1957; Smith, 1960), and heating the chromatogram for a few minutes at 95 C. Undeveloped portions of the chromatograms were compared with developed portions. Positions on the former that corresponded to locations of sugars on the latter were cut out and eluted individually with 5 ml of 10% isopropanol. The elute was dried under an air jet and the residue was redissolved in 1 ml of 10% isopropanol. The sugar present in this solution was quantified using the anthrone method of Roe (1955) described on p. 273.

Results

I. Season I (1972)

The total soluble carbohydrate content (Fig. 89A) of Potamogeton pectinatus tissues at site 1 fluctuated regularly with a period of approximately 4 weeks. During the first part of the season, maxima in P. pectinatus coincided with minima in P. richardsonii. The peak at time 4 in P. pectinatus coincided with the time of maximum density of Physa gyrina per unit bottom area in these stands and the time of the greatest numbers of young of this snail. Also the greatest net difference in carbohydrate levels between the two macrophytes was observed at this time. At time 5 a minimum occurred in P. pectinatus but a maximum in P. richardsonii, coinciding with the time of maximum density of Lymnaea stagnalis per unit bottom area in stands of the latter plant.

The total titratable acidity (Fig. 89B) showed the greatest observed net difference between the two macrophytes at time 6. The greatest observed net differences in total protein content (Fig. 89C) were seen at the beginning and end of the season.

Carotene content (Fig. 89D) showed a general increase during the season, and except for time 7, values were generally higher in P. richardsonii tissue. At time 8, a marked decrease was observed in P. pectinatus while in P. richardsonii carotene levels continued to rise.

At site 5 (Table XXXA), total soluble carbohydrate levels in Myriophyllum exalbescens were high at the beginning of the season and the first oviposition in P. gyrina occurred at time 2. After

Figure 89. Total soluble carbohydrate (mg eq. glucose/g dry tissue)(A), total titratable organic acids (meq. titratable acid/g dry tissue x 10^{-3})(B), total extractable protein (mg/g dry tissue)(C) and carotene (mg/g dry tissue)(D) content of Potamogeton pectinatus (O) and P. richardsonii (●) tissues at site 1 during the 1972 season.

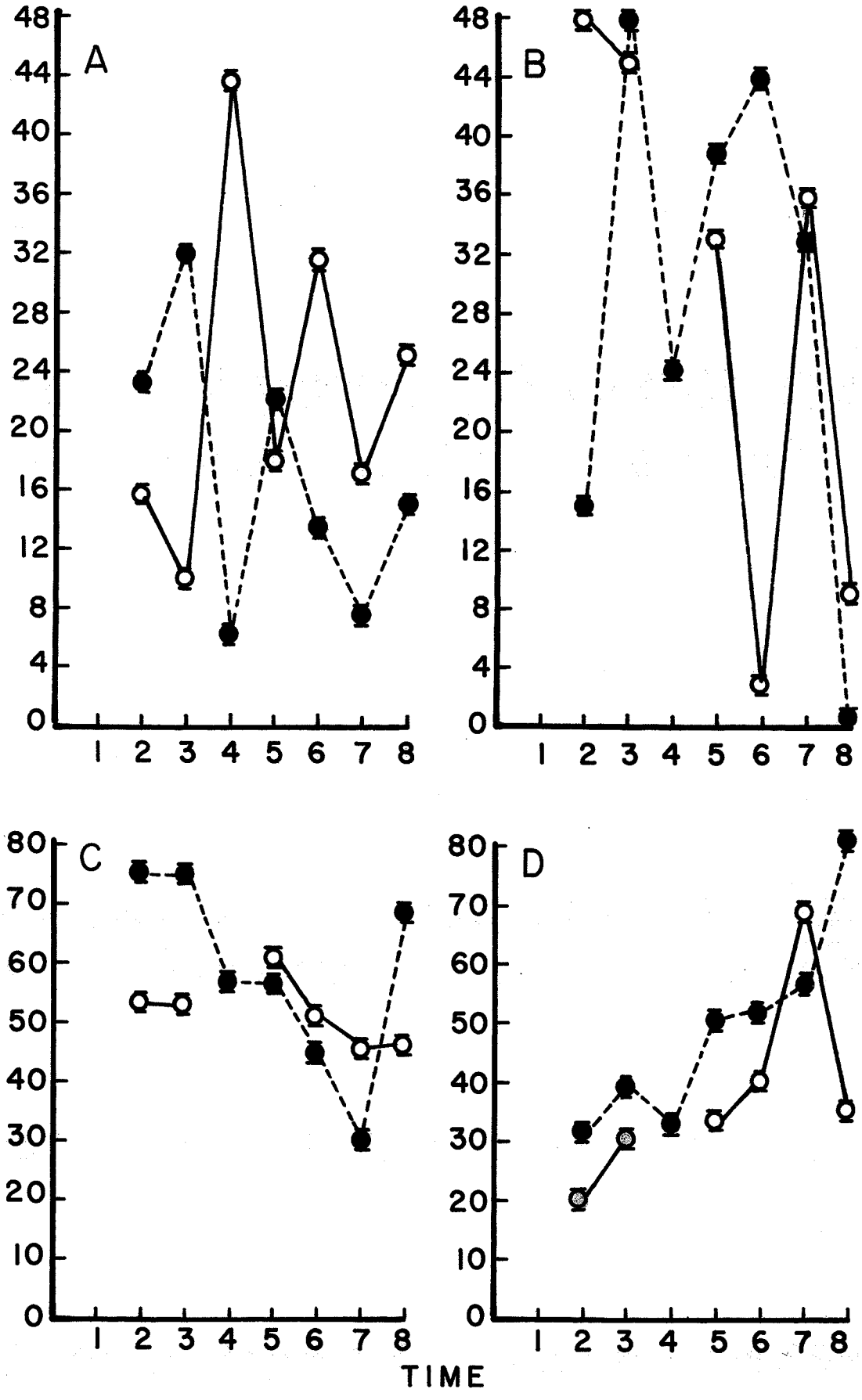

A
B
C
D
48
44
40
36
32
28
24
20
16
12
8
4
0
80
70
60
50
40
30
20
10
1 2 3 4 5 6 7 8
TIME

TABLE XXX. Mean total soluble carbohydrate (mg eq. glucose/g tissue) (A) and mean total soluble protein (mg/g tissue)(B) content of tissues of Myriophyllum exalbescens at site 5 and Potamogeton pectinatus at site 6 respectively, during the 1972 season.

A. Total soluble carbohydrate

Time	site 5	site 6
1	26.6	-
2	21.6	21.0
3	-	36.4
4	8.1	24.5
5	13.4	18.2
6	20.8	10.5
7	16.3	30.6
8	13.4	22.2

B. Total soluble protein

Time	site 5	site 6
1	45.2	-
2	58.5	46.5
3	-	30.0
4	46.5	43.5
5	61.5	43.5
6	44.0	121.0
7	43.5	45.0
8	6.8	76.5

hatching of the young at time 3, a quiescent period followed with no reproduction and carbohydrate levels in the plant tissues decreased. Oviposition resumed at time 5, when carbohydrate levels began to rise and continued until after time 6, when carbohydrate levels again began to decrease. In general, carbohydrate levels in M. exalbescens at both sites 1 and 5 were lower than those in P. pectinatus at site 1.

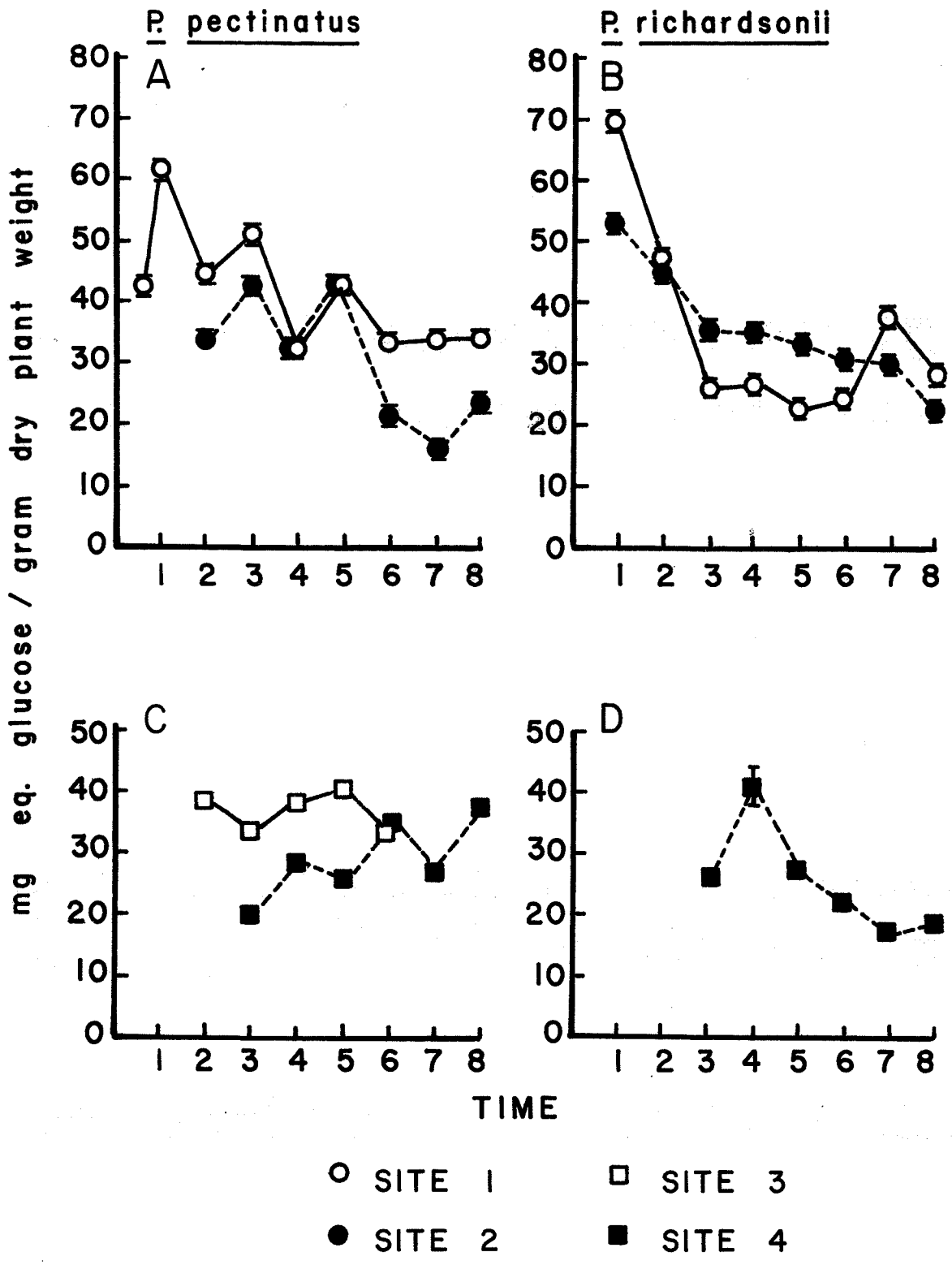
At site 6 (Table XXXA), carbohydrate levels in P. pectinatus reached maxima at times 3 and 7, coinciding with maxima in densities of Amnicola limosa and A. (=Probythinella) lacustris per unit bottom area in these stands.

Maxima in total soluble protein (Table XXXB) were observed at times 2 and 5 at site 5, while at site 6 an abrupt peak occurred at time 6, followed by a decrease at time 7 and another increase at time 8.

II. Seasons II and III (1973-4)

The total soluble carbohydrate levels in P. pectinatus tissues at sites 1 and 2 during the 1973 season (Fig. 90A) continued to fluctuate regularly with a period of approximately 4 weeks and the patterns were synchronous at these two sites. The maximum observed in these plants at time 3 coincided with decreases in the carbohydrate levels in P. richardsonii (Fig. 90B). However at site 2 the net difference between the two macrophytes was much smaller than at site 1 and may have contributed to the reduced intensity of association of snails with P. pectinatus at site 2. At time 2, the projected time of oviposition in P. gyrina, carbohydrate levels in P. richardsonii were decreasing while those in P. pectinatus had reached a minimum

Figure 90. Total soluble carbohydrate (mg eq. glucose/g dry tissue) content of tissues of Potamogeton pectinatus at sites 1 and 2 (A) and sites 3 and 4 (C), and of P. richardsonii at sites 1 and 2 (B) and site 4 (D) during the 1973 season. Vertical bars represent standard errors.


P. pectinatus
P. richardsonii
A
B
C
D
mg eq. glucose / gram dry plant weight
TIME
SITE 1
SITE 2
SITE 3
SITE 4

and increased again after time 2. The timing of reproduction at both sites was such that the young emerged during a peak in the carbohydrate content of P. pectinatus. Although the association patterns of P. gyrina appeared to be related to the carbohydrate content of P. pectinatus, those of L. stagnalis did not appear to be related to the total carbohydrate content of P. richardsonii.

At site 4 (Fig. 90C), carbohydrate values in P. pectinatus also fluctuated regularly with a period of approximately 4 weeks. The fluctuations were apparently two weeks out of phase with those observed at sites 1 and 2 and corresponded with the lag period seen for the association peak for P. gyrina at this site. The carbohydrate peak at time 4 coincided with the association maximum for P. gyrina with this plant. Unlike the situation at sites 1 and 2, the amplitude of the oscillations in carbohydrate content increased instead of decreased as the season progressed and the differences between the two macrophytes at site 4 became most pronounced towards the end of the season. This may have contributed to the fact that the bulk of reproduction in P. gyrina at this site occurred towards the end of the season. At time 4, carbohydrate values were higher in P. richardsonii (Fig. 90D) despite the association peak with P. pectinatus; after time 5 values in the former plant declined while those in the latter increased, creating a situation analogous to that seen at time 2 at sites 1 and 2. However oviposition at time 5 did not occur because by this time the previous year's adults had died out after reproducing at time 3 and the first young of the year had not yet reached reproductive maturity. Some reproduction occurred at time 6 when some young began to mature, and by time 7, when carbohydrate

levels in P. pectinatus were about to increase again, large-scale reproduction occurred which resulted in emergence of a large cohort of young at time 8 when carbohydrate levels were maximal. Because plant mass per unit bottom area was large at this time, this did not result in as pronounced an association peak in terms of snail numbers per unit plant as did the earlier peak, although in terms of snail density per unit bottom area, this gave the seasonal maximum.

Association peaks for L. stagnalis in P. richardsonii stands were observed at site 4 at times 4 and 6 but carbohydrate values for this macrophyte showed a maximum only at time 4.

At site 3, hatching of P. gyrina commenced at time 3, but the association peak occurred at time 4, suggesting that the majority of the oviposition occurred at time 3, when carbohydrate levels were about to increase in the P. pectinatus (Fig. 90C). At this site carbohydrate values did not fluctuate at regular intervals although the levels were similar to those observed at site 2.

During the 1974 season total carbohydrate levels were synchronous in P. pectinatus after time 2 at sites 1 and 2 (Fig. 91A), but values were higher than those observed during the 1973 season, particularly at site 1. At this site values were greater in P. pectinatus than in P. richardsonii (Fig. 91B) tissues during the first half of the season and during the association peak for P. gyrina at time 6, while at site 2 values were greater in P. pectinatus at times 5 and 6. As in 1973, the largest part of oviposition in P. gyrina occurred following a peak in carbohydrate levels in P. pectinatus and was timed so that it preceded another peak. Thus, by the time hatching had occurred, the host P. pectinatus had reached another peak in

Figure 91. Total soluble carbohydrate (mg eq. glucose/g dry tissue) content of tissues of Potamogeton pectinatus (A) and P. richardsonii (B) at sites 1 and 2 during the 1974 season. Vertical bars represent standard errors.

carbohydrate levels, coinciding with the association peak. As in 1973, the total carbohydrate levels in P. richardsonii were not correlated with the population dynamics of L. stagnalis.

The total soluble carbohydrates in both macrophytes were composed of fructose, glucose and sucrose (Tables XXXI and XXXII). These findings agreed with Hodgson's (1966) observations for P. pectinatus shoots that were more than 10 days old. However the relative proportions of these sugars followed different patterns in the two macrophytes.

During the first part of the 1973 season, the soluble carbohydrates in P. pectinatus were composed largely of fructose and glucose, while P. richardsonii contained high levels of sucrose which often exceeded the sum of the glucose and fructose concentrations in this plant (Table XXXIII). Hodgson (1966) found that sucrose/glucose/fructose ratios in P. pectinatus shoots averaged 14/3/3 regardless of age. However his results were based upon plants grown in artificial environments under constant conditions. At site 1, during the association peak with P. gyrina at time 3, the combined values of the glucose and fructose concentrations in P. pectinatus were 8.6 times greater than those in P. richardsonii, while at site 2 they were 2.3 times greater in P. pectinatus at time 3. At site 4, during the association peak at time 4, P. pectinatus contained 2.0 times as much glucose and fructose as did P. richardsonii. During the projected time of oviposition at site 1, time 2, combined glucose and fructose values were 1.9 times greater in P. pectinatus than in P. richardsonii; at site 2, these values were 1.3 times greater, while at site 4, time 3, these

TABLE XXXI. Fructose, glucose and sucrose content (mg eq. glucose/ g tissue) of Potamogeton pectinatus and P. richardsonii tissues at sites 1-4 during the 1973 season.

A. Site 1

	POTAMOGETON PECTINATUS			POTAMOGETON RICHARDSONII		
Time	Fructose	Glucose	Sucrose	Fructose	Glucose	Sucrose
1a	3.16	1.60	1.32	-	-	-
1	-	-	-	3.20	2.92	7.00
2	4.24	2.75	1.70	2.12	1.50	4.75
3	6.70	2.60	3.00	0.80	0.28	1.11
4	2.59	2.22	2.18	4.39	1.42	4.16
5	5.24	6.45	3.63	0.98	0.58	5.76
6	2.40	1.66	5.32	2.51	2.00	3.02
7	2.52	1.36	6.80	4.00	1.58	10.47
8	3.04	2.27	6.88	1.42	1.98	0

B. Site 2

	POTAMOGETON PECTINATUS			POTAMOGETON RICHARDSONII		
Time	Fructose	Glucose	Sucrose	Fructose	Glucose	Sucrose
1	-	-	-	28.39	0	4.35
2	6.69	5.09	9.26	6.19	2.75	4.02
3	6.36	1.78	3.18	1.28	2.31	3.52
4	0.82	2.47	1.58	2.03	0.22	4.11
5	0.23	2.60	4.22	1.12	0.12	3.34
6	1.76	0.86	0.92	1.76	1.34	1.64
7	1.51	1.76	2.86	1.64	1.48	7.35
8	3.32	2.15	1.87	1.30	0.87	6.08

continued . . .

TABLE XXXI.(continued)

C. Site 3

	POTAMOGETON PECTINATUS		
Time	Fructose	Glucose	Sucrose
1	-	-	-
2	6.09	3.25	3.34
3	0.20	1.04	0
4	0.65	1.65	0.89
5	1.40	1.51	1.34
6	0.72	1.92	4.80
7	-	-	-
8	-	-	-

D. Site 4

	POTAMOGETON PECTINATUS			POTAMOGETON RICHARDSONII		
Time	Fructose	Glucose	Sucrose	Fructose	Glucose	Sucrose
1	-	-	-	-	-	-
2	-	-	-	-	-	-
3	3.49	1.78	1.78	1.15	1.17	2.07
4	3.12	2.52	0	1.64	3.27	5.89
5	1.50	1.88	1.88	1.16	1.98	5.10
6	1.75	3.66	2.94	1.14	1.55	4.80
7	1.34	1.92	5.15	1.87	1.56	3.30
8	0.76	1.56	6.42	1.51	1.34	2.78

TABLE XXXII. Fructose, glucose and sucrose content (mg eq. glucose/ g tissue) of Potamogeton pectinatus and P. richardsonii tissues at sites 1 and 2 during the 1974 season.

A. Site 1

	POTAMOGETON PECTINATUS			POTAMOGETON RICHARDSONII		
Time	Fructose	Glucose	Sucrose	Fructose	Glucose	Sucrose
1	-	-	-	-	-	-
2	12.96	8.32	3.60	10.60	7.64	0.20
3	27.20	24.20	15.84	15.00	12.40	14.54
4	14.94	41.34	19.07	26.87	11.96	7.35
5	23.78	5.63	5.08	15.82	13.37	7.30
6	23.50	16.08	6.38	11.02	8.57	5.86
7	5.95	4.41	3.27	9.99	6.24	4.01
8	7.15	2.62	1.73	11.47	5.62	2.13

B. Site 2

	POTAMOGETON PECTINATUS			POTAMOGETON RICHARDSONII		
Time	Fructose	Glucose	Sucrose	Fructose	Glucose	Sucrose
1	-	-	-	-	-	-
2	1.20	8.94	10.07	40.00	0	2.40
3	1.29	0.48	0.08	1.22	0.67	0.57
4	10.00	5.34	7.94	1.50	5.92	19.14
5	3.11	6.91	8.66	1.40	4.00	5.30
6	3.43	4.96	11.07	4.27	3.50	6.14
7	4.44	2.43	6.12	3.06	2.62	5.80
8	3.87	2.18	2.06	0.55	0.51	1.74

TABLE XXXIII. Sucrose to combined fructose and glucose ratios in *Potamogeton pectinatus* and *P. richardsonii* tissue at sites 1-4 during the 1973 season.

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1a	0.28	-	-	-
1	-	1.14	-	0.15
2	0.24	1.31	0.79	0.45
3	0.32	1.03	0.39	0.98
4	0.45	0.72	0.48	1.83
5	0.31	3.69	1.49	2.69
6	1.31	0.67	0.35	0.53
7	1.75	1.88	0.87	2.36
8	1.30	0	0.34	2.80

	site 3	site 4	
Time	*P. pectinatus*	*P. pectinatus*	*P. richardsonii*
1	-	-	-
2	0.36	-	-
3	0	0.32	0.89
4	0.39	0	1.20
5	0.46	0.56	1.62
6	1.82	0.54	1.78
7	-	1.58	0.96
8	-	2.77	0.98

values were 2.3 times greater.

Sucrose levels were generally greater in P. richardsonii than in P. pectinatus tissues during the association peaks of L. stagnalis (site 2, time 4, 2.6 times greater; site 4, time 4, no sucrose in P. pectinatus, and at time 6, 1.6 times greater), except at site 1, time 3, where sucrose levels in P. richardsonii were lower than those in P. pectinatus. However during the projected time of oviposition, sucrose levels were greater in P. richardsonii tissues at all sites: site 1, time 2, 2.8 times; site 2, time 3, 1.1 times; site 4, times 3 and 5, 2.3 and 1.1 times greater). Although association peaks occurred at time 2 for L. stagnalis in P. pectinatus stands at sites 1 and 2, these were not the result of reproduction.

At site 1, sucrose values were already high in P. richardsonii tissues at time 1 and continued to increase until time 2, when oviposition occurred. The latter ceased after time 4 when sucrose levels declined and did not resume despite the sucrose increase at time 5, perhaps because most of the adults had disappeared. At site 2, sucrose levels in P. richardsonii stands were low at the beginning of the season and oviposition did not occur until time 3 when sucrose levels had increased. Oviposition ceased after time 5 when sucrose levels began to decline although a fair proportion of adults was still present at this site during the second half of the season.

At site 4, the first oviposition occurred at times 2 and 3 in P. richardsonii stands, when sucrose levels were increasing. A second period of oviposition occurred at times 5 and 6 when sucrose values were still increasing but declined at time 7.

At site 3, the proportions of sucrose to combined glucose and fructose were similar to those observed for P. pectinatus tissues at other sites. The first young of P. gyrina emerged at time 3 when no measurable levels of sucrose could be detected in the macrophytes. The major association peak followed at time 4 when the proportions of glucose and fructose were still high. However the sugar concentrations in these plants did not explain the magnitude of the association peak. No well-defined period of reproduction was observed for L. stagnalis at this site.

During the 1974 season, again P. pectinatus generally contained proportionately more glucose and fructose than P. richardsonii (Table XXXIV). During the association peak of P. gyrina at times 5 and 6, P. pectinatus contained 1.01 and 2.02 times, respectively, more glucose and fructose than P. richardsonii at site 1, while at site 2 these values were 1.86 and 1.10 times, respectively. At site 1 the ratio of sucrose to combined glucose and fructose increased until time 4 and oviposition in P. gyrina did not commence until after time 4 when sucrose levels declined. At site 2, the first decrease in sucrose levels occurred after time 2 but adult snails did not appear on the plants until time 4, after which oviposition occurred. Another period of oviposition was observed at time 7 in P. pectinatus stands at both sites 1 and 2 as fructose and glucose levels remained high. Values for fructose and glucose in P. richardsonii tissues were greater at site 1 than at site 2 and reproduction of P. gyrina was also greater in these stands at site 1. Thus during both 1973 and 1974, reproduction of P. gyrina appeared to be related to high fructose and glucose levels,

TABLE XXXIV. Sucrose to combined fructose and glucose ratios in *Potamogeton pectinatus* and *P. richardsonii* tissue at sites 1 and 2 during the 1974 season.

	site 1		site 2	
Time	*P. pectinatus*	*P. richardsonii*	*P. pectinatus*	*P. richardsonii*
1	-	-	-	-
2	0.17	0.01	0.99	0.06
3	0.31	0.53	0.05	0.30
4	0.34	0.19	0.52	2.58
5	0.17	0.25	0.86	0.98
6	0.16	0.30	1.32	0.79
7	0.32	0.25	0.89	1.02
8	0.18	0.12	0.34	1.64

or to minima in the sucrose to combined fructose and glucose ratios.

Sucrose levels were higher in P. richardsonii than in P. pectinatus tissues during the association peak of L. stagnalis at site 1 (time 5) but not at site 2 (time 6). The first oviposition began at site 1 at time 3 when sucrose levels in P. richardsonii were relatively high and continued until time 4; oviposition at site 2 commenced at time 4 when sucrose levels had increased and continued until time 5. In both cases oviposition followed increases in the relative proportions of sucrose.

In general, as the carbohydrate levels declined, so did the intensities of the associations. During the second half of the season the snails appeared to lose interest in discriminating between the macrophytes. The sucrose to combined fructose and glucose ratios, although usually higher in P. richardsonii tissues during midseason, often became greater in P. pectinatus tissues towards the end of the season.

Discussion

During the 1972 season, the total protein content of the plant tissues showed little correlation with the population dynamics of the two major gastropods. The nutritive quality of P. richardsonii tissue in terms of soluble protein was greatest at the beginning and end of the season, while that of P. pectinatus showed a midseason maximum. The identities of the amino acids were not pursued since Boyd (1970) had shown that the relative amino acid composition of total protein is very similar for aquatic vascular macrophytes of different species, ages and sites, although the magnitudes may differ.

Carotene content did not appear to be correlated with the association patterns. Carotenes, carotenoproteins and xanthophylls, particularly beta-carotene and lutein, occur in the tissues of Lymnaea (Fox, 1966) and probably in Physa as well, and are believed to be derived from plant tissues. Benjamin and Walker (1972) separated 7 carotenoid fractions from Lymnaea and suggested that the carotenoid prosthetic group in herbivorous gastropods may be a reflection of the plant diet. The function of carotenoids in snail tissues is not clear although they appear to be important as mediators in light sensitivity; they are already present in newly hatched young where they are believed to originate from plant substances via material in the eggs (Benjamin and Walker, 1972). However in the present study hatching neither coincided with nor succeeded periods of elevated carotenoid levels in the respective host plants.

The total titratable acids did not appear to be correlated with the association patterns. However at this point individual

organic acids cannot be discounted as factors biologically important to snails because of their solubility, and their identities warrant further study.

The total soluble carbohydrate levels in P. pectinatus appeared to be correlated with the association pattern of Physa gyrina. The differential concentrations of sucrose, glucose and fructose in P. pectinatus and P. richardsonii during the 1973 and 1974 seasons suggested a possible mechanism through which differential snail distributions might arise.

Since the plants are highly active metabolically before and during the times of densest snail occupation, they may produce soluble exudates which may act as specific attractants. According to Wetzel (1969a and b), macrophytes excrete significant amounts of dissolved organic compounds into the surrounding medium; secretion rates under various conditions may vary from 0.05 to 100% of the carbon fixed, although most values do not exceed 10% (Wetzel and Manny, 1972). The dense stands and polar distribution of the macrophytes at sites 1 and 2, combined with the absence of turbulence, would favor the existence of chemical differences in the regions of the different stands. Although it is likely that chemical gradients would be rapidly destroyed by bacteria (Wetzel and Manny, 1972), perhaps sufficient amounts could persist to act as attractants. At site 4, the intermixed nature of the two types of stands could still result in differences along the interfaces between stands. In areas with only one type of stand, differences would occur between vegetated and bare areas.

Several workers (e.g. Kohn, 1961; Bovbjerg, 1968, 1975) have noted the importance of chemoreception in food selection, particularly in experiments with plant tissues (Townsend, 1973). Bovbjerg (1968) observed a 50% response of Lymnaea stagnalis to P. richardsonii filtrate at dilutions of 1:500, and control levels of response were reached at dilutions of 1:1200. Such levels could easily exist within the study sites, and would be enhanced by the escape of plant tissue fluids from the lesions already made by grazing snails.

A quantitative study by Jager (1971) showed that low molecular weight carbohydrates stimulate eating responses in L. stagnalis and that this snail can distinguish between various types of sugars. The low threshold concentration of -3.5 log molar for sucrose led Jager (1971) to suggest that "sucrose is a biologically important compound for L. stagnalis". Since sucrose levels were generally higher in P. richardsonii than in P. pectinatus tissues during active growth of the macrophytes, this may explain in part why L. stagnalis tended to associate with P. richardsonii.

In general, for L. stagnalis, disaccharides are more effective than monosaccharides in inducing eating responses, suggesting that enzymatic splitting of disaccharides may occur at the receptor sites in this snail; however the snails can also distinguish between the monosaccharides fructose, glucose and galactose (Jager, 1971). The responsiveness of P. gyrina to various carbohydrates warrants investigation since the results of the current study suggest that fructose and glucose may be biologically important compounds for this snail.

The nature of the chemoreceptor sites in basommatophoran snails is not well understood. Michelson (1960) suggested that the extrapallial osphradium was the major site for this function in Biomphalaria glabrata, but Bailey (1968 in Townsend, 1973) and Bailey and Benjamin (1968 in Townsend, 1973) were unable to show chemoreception by this organ in a related species, Planorbarius corneus. The observations of Bovbjerg (1968) suggested that the tentacles and general surface of the head and foot appear to contain chemoreceptor sites for plant and animal food, although the two types of food elicit different responses, apparently due to perception differences. Related to this problem are the findings of Zylstra (1972), who suggested that the epidermal cells of L. stagnalis may also possess a digestive function, and that these snails may be able to take advantage of dissolved nutrients through selective uptake.

The relationships between carbohydrate intake and blood sugar levels in snails have been discussed by Goddard and Martin (1966). Friedl (1971) and Veldhuijzen (1975a) found that glucose concentration in the haemolymph increases after the snails have been fed on a carbohydrate-rich diet. Concomitant with this increase is a drop in ammonia output, which indicates a reduction in protein metabolism (Friedl, 1975). Apparently the role of lipids as an energy source in pulmonates is limited and the metabolism of these snails is carbohydrate oriented (Veldhuijzen and van Beek, 1976).

Reproduction causes a large demand for carbohydrate (Veldhuijzen, 1975a and b; Veldhuijzen and Dogterom, 1975). Veldhuijzen (1975a) has suggested that an increase in the haemolymph

glucose concentration is the stimulus for the start of reproduction and growth under constant environmental conditions. Veldhuijzen and Cuperus (1976) have proposed a detailed physiological model for this process. According to these workers, a dietary-induced increase in haemolymph glucose levels stimulates the endocrine cells of the lateral lobes to release a neurohormone which stimulates the dorsal bodies, attached to the cerebral ganglia, to release the dorsal body hormone (Geraerts and Algera, 1972; Geraerts and Bohlken, 1976; Geraerts and Joosse, 1976) into the haemolymph. This hormone may possibly influence galactogen synthesis in the albumen glands directly, or it may stimulate the reproductive organs to produce a gonadal factor which is essential for the stimulation of galactogen synthesis. Since glucose is the precursor of galactogen, this process lowers the haemolymph glucose concentration. Thus, according to this model, a decrease in carbohydrate content of the food would reduce the rate of replenishment of haemolymph glucose levels per unit of feeding effort. Veldhuijzen and Cuperus (1976) have also suggested that low temperatures inhibit the release of neurohormones and this may explain why a temperature threshold must be exceeded for reproduction to occur.

Thus a key to the phenomenon of time-dependent plant-snail associations may repose in such a mechanism, because we have seen that reproduction generally followed a high carbohydrate concentration in the host plant tissues, and reproduction was an important event in the setting up of association peaks.

The results from site 5 suggested that the population

dynamics of P. gyrina in vegetated habitats other than those of the two Potamogeton species also appeared to be correlated with carbohydrate levels in the host plants. Apparently differential snail distributions were not as stringently dependent upon the specific identity of the macrophytes as upon their biochemical status. The results from site 6 were interesting in that, although the amnicolids Amnicola limosa and A. (=Probythinella) lacustris probably do not feed to a significant extent on vascular plant tissues, they nonetheless may be affected by plant exudates since they occur often on the plants. This effect may work directly on the snails, or it may be manifested through a higher carbohydrate content of the periphyton ingested by the snails, and may thus stimulate reproduction.

The carbohydrate energy derived from plant tissue is not limited to the soluble fractions; according to Monk (1976) and Nielsen and Marshall (1973 in Thomas et al, 1975), pulmonates contain high activity levels of cellulases and polysaccharidases which increase the efficiency of plant food utilization.

Although carbohydrates appear to be influential factors in governing differential snail distributions, other factors cannot at present be excluded. Bousfield (personal communication) has found that plant-originated compounds active in attracting Biomphalaria glabrata have relatively low molecular weights (less than 500) and preliminary observations indicate that in this organism fatty acids may be more potent than amino acids or even sugars. Possibly other plant-originated substances may come to light as well with further study and it is likely that differences in sensitivity to various compounds may exist

between different gastropod species.

Both P. pectinatus and P. richardsonii contain a variety of complex compounds whose effects, if any, on snail grazing are unknown. Su and Staba (1972) found that Potamogeton species contain various alkaloids and flavonoids. Of the latter class, both P. pectinatus and P. richardsonii contain flavonols; the former species also contains flavonones while catechin has been detected in the latter. Potamogeton richardsonii contains tannins and the steroid, beta-sitosterol, has been tentatively identified in tissues of this plant.

By feeding on plant tissues, snails derive many other factors necessary for growth. The importance of carotenoids has already been discussed above. Shell formation is an important physiological process in pulmonates. Although aquatic gastropods can absorb calcium directly from the external medium, calcium obtained from food is also utilized (van der Borght and van Puymbroeck, 1966). Boycott (1936) and Macan (1950 in Greenaway, 1971) found that L. stagnalis requires a minimum concentration of 0.5 millimolar Ca/l in the water; according to Greenaway (1971), calcium uptake above this level requires little energy, although uptake can continue at smaller external concentrations with more energy expenditure. At sites 1, 2 and 3, calcium activity decreased below this level during part of the growing season and it is likely that calcium originating from food was more important at these times for all gastropods. However it is unlikely that calcium hunger contributed to differential distributions since calcium was not a limiting factor at site 4 yet the associations were still observed.

Thus far the discussion has centered on the effects of plants on snails. However the closeness of the associations must entail some effects of snails on plants. In grazing, the snails remove some of the periphyton which constitutes a portion of the ingested material (Bovbjerg, 1968) and calcium carbonate deposits on the leaves may also be ingested. Wounding of the plants during grazing may enhance the extrusion of plant metabolites into the medium, which may in turn attract more snails, and this may affect the growth of the plants. Snail-originated compounds may also affect the plants; for example Thomas et al (1975) suggested that carbohydrases and exogenous cellulases may be produced by snails. Wright and Ronald (1972) found that water conditioned by Stagnicola palustris contained amino acids; MacInnis et al (1974) found that water conditioned by Biomphalaria glabrata contained 19 amino acids, a peptide fraction and other unidentified groups. Compounds of snail origin may originate from waste products and from mucus, although amino acids may also be released from epithelial cells in the process of osmoregulation (Potts, 1967 in MacInnis et al, 1974). These compounds may enrich the medium and be absorbed by plant shoots, which in submerged macrophytes are the main sites of nutrient absorption (Arens, 1933; Steeman Nielsen, 1951; Lowenhaupt, 1956). Wetzel and McGregor (1968) observed that the presence of Amnicola in cultures of Chara stimulated the growth of this plant.

The provision of carbon dioxide by respiration of snails is probably of minor importance since a large proportion of breathing occurs at the surface. Some carbon dioxide from the body fluids of pulmonates may be fixed into intermediates of the citric acid cycle

within the body and may be later released by decarboxylation of oxalo-acetate and converted to carbonate and bicarbonate by carbonic anhydrase (Timmermans, 1969) which is present in the mantle of pulmonates and which accelerates calcium deposition (Freeman, 1960; Timmermans, 1969).

The participation of plants in the regulation of the population dynamics of their grazers is an interesting concept but it must be remembered that mechanisms of such complexity, based upon physiological processes, provide for a wide range of variation, and ultimately of flexibility within the system. Several workers (e.g. Bovbjerg, 1968; Jager, 1971; McDonald, 1973) have noted the individualistic natures of behavioral responses in snails subjected to the same sets of external stimuli; perhaps such plasticity within closed populations in nature provides a means for further evolution and adaptation of the system in the face of changing environmental pressures.

INTEGRATION OF SECTIONS I, II AND III

This portion of the study has demonstrated that differential, time-dependent distributions of gastropods existed with respect to different macrophyte stands, and that the population dynamics of the snails were related to the growth patterns of the host plants. The particular systems that showed this behavior were those of Physa gyrina and Potamogeton pectinatus, and Lymnaea stagnalis and P. richardsonii. The two associations functioned independently of each other when coexisting within the same water body.

At this point, the plant-snail association model could be formulated by the following statements:

1. Physa gyrina and L. stagnalis appeared to respond to slightly different exudates from different food sources: these may have involved fructose and glucose in the former and sucrose in the latter, or products resulting from microbial activity which altered the identity of the original compounds.
2. Potamogeton pectinatus produced higher levels and proportions of fructose and glucose than did P. richardsonii during a large part of the season; P. richardsonii produced higher proportions of sucrose.
3. During the early part of the growing season, a large part of each respective snail population migrated to the preferred plants; taxis may have been based on differential concentrations of specific carbohydrates or other plant-originated factors.
4. The snails grazed on the plants. The first rise in sugar levels in the host plant tissues raised the haemolymph glucose concentrations in the snails.

5. Provided that the temperature threshold had been exceeded, the increased haemolymph glucose levels stimulated reproduction which occurred on the respective plants.
6. Because carbohydrate levels in the plants fluctuated with time, oviposition occurred during a decrease in carbohydrate levels in the plants which followed the first peak that had raised the haemolymph glucose levels. The eggs hatched by the time the plant carbohydrate levels had again increased.
7. Reproduction ceased because: a) carbohydrate levels in the host plants decreased, or b) the adults disappeared. Reproduction resumed later in the season because temperatures still exceeded the threshold value and the young of the year had reached reproductive maturity. The second period of reproduction was often preceded by an increase in the carbohydrate levels in the host plants.

These associations were not obligatory in that the specific components of this model could be exchanged for alternate species, provided that the plants produced higher proportions of the respective attractants and that the snails were responsive to these substances.

The evolution of such a system has the advantages that the young emerge at a time when the substrate is richer in energy and their chances for survival are enhanced, and the differential resource partitioning within a closed environment minimizes interspecific competition for food and space.

The precise mechanisms that govern the operation of dynamically related plant-snail associations can at this point only

be speculated upon, pending a better understanding of submerged macrophyte ecophysiology and snail physiology and behavior. In particular, subsequent studies should be directed at the composition of plant exudates under various environmental conditions, the concentrations of these compounds and their persistence in the medium and the responsiveness of different gastropods to various plant fractions. It is likely that other associations will be brought to light, for such systems are probably widespread.

PART II.

A SURVEY OF SUBMERGED PLANT-SNAIL COMMUNITIES AND ASSOCIATIONS

Introduction

I. Objectives

The quantitative study of submerged macrophyte communities in Part I had shown that two major plant-snail associations existed within the study areas; these appeared to be persistent from year to year despite varying environmental conditions. Because the study in Part I was confined to a small geographical region, it provided little information regarding the extensity of these associations on a wider topographical or environmental scale, while the limited numbers of species present at the study sites reduced the potential for the development of other associations.

Accordingly, a study with a time-limited, space-unlimited approach was constructed having the following objectives:

1. To assess the extensity of the potential for development of the Potamogeton pectinatus - Physa gyrina and Potamogeton richardsonii - Lymnaea stagnalis associations in terms of selected environmental parameters within a portion of the geographical ranges of these species.
2. To estimate the extensity of the potential for development of other plant-snail associations in terms of selected environmental parameters within the geographical area in (1).
3. To study the species composition of the plant and snail communities, respectively within which the potential associations of (1) and (2) tend to occur.

These problems were approached in the following ways:

1. An ecological tolerance spectrum was estimated for each species by recording the range of values for each selected parameter within which the species occurred at a large number of sites under natural conditions. The range of values for sites at which the species was recorded was compared with that for sites from which the species appeared to be absent.
2. An examination was made of the significance of the tendency for:
   a) Potamogeton pectinatus to occur jointly with Physa gyrina and for P. richardsonii to occur jointly with Lymnaea stagnalis within the same site, and
   b) all other possible plant-snail combinations to each occur jointly within the same site.
3. The significance of the tendency for all possible plant combinations and all possible snail combinations to each occur jointly within the same site was examined.

II. Literature review

A. Aquatic macrophyte associations

Much of the current knowledge regarding the composition of submerged macrophyte communities with regard to environmental factors is the result of fairly recent investigations. Spence (1967) sampled more than 100 sites in Scotland for macrophytes and collected water samples from approximately 50 of these. He identified several plant associations which could be correlated with defined ranges of pH and alkalinity. Seddon (1972) combined the observations of several workers for a total of 70 lakes in Wales with respect to the

occurrence of macrophytes and constructed floristic lists which were ordinated using principal component analysis (e.g. Orloci, 1966). Water from 22 sites was examined by Seddon (1972) for the parameters of pH, conductivity, total dissolved solids, total alkalinity, color and unspecified cations, anions and trace elements. This study identified some plant associations and showed that the distributions of some macrophytes appeared to be confined within certain ranges of hardness and conductivity; however the small numbers of sites for which water chemistry was known precluded more definitive conclusions.

Crum and Bachmann (1973) conducted a survey of the submerged macrophytes in 6 lakes in Dickinson County, Iowa and were able to correlate community composition and distribution with Secchi disc transparencies. Reynolds and Reynolds (1975) studied the macrophytes of 12 lakes in the Chilcotin region of British Columbia in relation to the parameters of water temperature, conductivity, Secchi disc transparency and dissolved oxygen. These workers suggested that plant distribution in some areas may be correlated with the dominant anion, whose effect upon the composition of the submerged plant communities may in turn affect that of the associated invertebrate fauna.

Malme (1975) distinguished 7 association groups among the submerged communities of 26 lakes in western Norway using phytosociological techniques. He found that the associations showed wide tolerance ranges with respect to the parameters of pH, conductivity, chloride, color, dichromate, total phosphorus, nitrate, calcium, magnesium and sodium. Krausch (1976) described several submerged plant communities in Germany following the phytosociological methods

of Braun-Blanquet (1927, in Kershaw, 1973); he recognized several plant associations and concluded that their tolerance to environmental conditions depended upon the species involved.

On a more limited scale, surveys of submerged macrophyte communities have been conducted within single river systems (e.g. Southwick and Pine, 1975; Holmes and Whitton, 1975a and b) and estuaries (e.g. Verhoeven, 1975). Studies restricted to particular taxa in relation to water chemistry have been made: for example, Hutchinson's (1970) study of 3 species of Myriophyllum using Lohammar's (1938 in Hutchinson, 1970) data, and Hellquist's (1975) outstanding study of the genus Potamogeton at 321 sites in New England. The latter worker examined the distribution of the genus Potamogeton with respect to the parameters of total alkalinity, nitrate, chloride, free carbon dioxide and dissolved total phosphate and found that the latter two parameters were of little value in influencing community composition while total alkalinity, and to a lesser extent, nitrate and chloride appeared to exert significant effects.

B. Aquatic gastropod associations

Gastropod associations have been little studied aside from qualitative examination of species lists. Baker (1928) noted that certain species of molluscs often tended to occur with each other and with certain submerged macrophytes. La Rocque (1966) compiled and examined qualitatively the species lists of several workers. Clarke (1973) conducted a survey of the aquatic molluscs of the Canadian Interior Basin; he noted that certain species often occur together but provided no quantitative data. A survey conducted by Grimm (1975)

of 9 lakes in Quebec showed that recognizable assemblages appeared to exist but the number of sites examined was too small to show significant association tendencies.

C. Plant-snail associations

Aside from Baker's (1928) pioneering observations, the distribution of plant-snail associations has been little studied. Pip and Paulishyn (1971) qualitatively examined the plant and snail communities within which Promenetus exacuous occurred at several sites in southern Manitoba with respect to sulphate levels in the water. Ghestem et al (1974) conducted a phytosociological study of several sites in France in an effort to define, in terms of macrophytes, the biotopes characteristic of Lymnaea truncatula.

D. Analysis of association

Forbes (1907) was the first worker to study associations quantitatively on the basis of the frequency of joint occurrence of two species in a number of samples. Some subsequent workers (e.g. Malme, 1975; Krausch, 1976) have made use of phytosociological methods (see section A above) in describing plant associations but the subjective nature of such analysis has limited its value in comparative studies. Cole (1949) based his measurements of interspecific association on the Chi-square test for the significance of the frequency of two species to occur jointly in a series of samples. The Chi-square test has since been widely used in association analysis (e.g. DeVries, 1953; Goodall, 1953; Welch, 1960; Agnew, 1961). Modifications of association analysis for restricted application, such as inverted indices (Duke and Terrell, 1964) and Fager's affinity

index (in Fahy, 1975), still require the application of the Chi-square test to determine association significance.

III. Study area and site selection

The survey was conducted within the area bounded by 47°N and 54°N, and 94°W and 106°W. This region lay well within the distributional ranges of Potamogeton pectinatus and P. richardsonii (Gleason, 1952) as well as those of Physa gyrina and Lymnaea stagnalis (Baker, 1928; Clarke, 1973). The heterogeneity of this area in terms of geology and the abundance of permanently submerged habitats provided a large diversity of aquatic environments.

According to Weir (1960), the surface deposits of the region east of approximately 96°W to the eastern boundary of the study area are composed predominantly of Precambrian granites and granitic gneisses, often massed in large outcrops, although south of approximately 50°N these are replaced by deposits of sand. The region west of 96°W to 98°W in the extreme south and as far as 99°W in the area south of Lake Manitoba is characterized by heavy surface deposits of silts and clays, while the region from the western shore of Lake Winnipeg to approximately 100°W, north of the southern shore of Lake Manitoba, contains extensive deposits of limestone, which grade locally into dolomite and gypsum, and are often interspersed with fragmented granitic materials. The region west of 100°W and south of approximately 50°N contains deposits of sand and sandy loams, although these are locally interrupted in the south, particularly around the Pembina River valley, by shales and limestone. The region west of 100°W and north of approximately 50°N contains surface

deposits of shales and limestone which are interspersed locally with silts and clays. Weir (1960) has summarized the general climate and vegetation of much of this region.

The sites selected within this region had the following features:

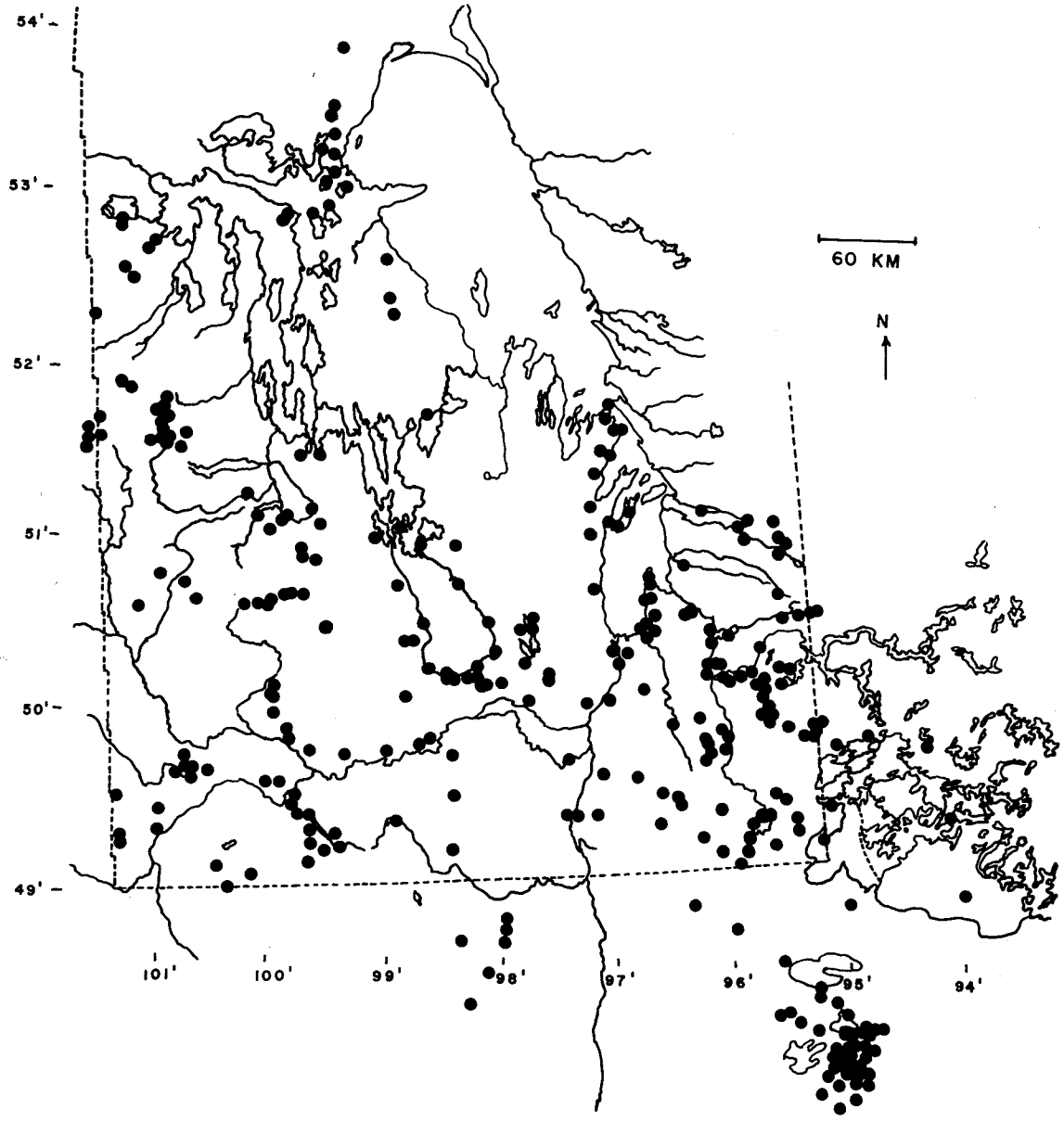
1. The sites were permanent, i.e. they contained areas that were submerged throughout the year.
2. The sites appeared to be free from the effects of herbicides and insecticides and showed no evidence of dumping.
3. In the case of artificially excavated basins, the sites were believed to be sufficiently established in time to have already provided opportunity for colonization by aquatic biota. This was assessed on the basis of:
   a. the presence of established shore flora,
   b. the absence of disturbed bare areas of soil indicating recent excavation,
   c. the presence of macroscopic aquatic biota, and
   d. dating the site by inquiry of local residents, if possible.
4. The sites were accessible by passenger car or four-wheel drive vehicle.

Sampling was conducted during the May to September, 1974-6 seasons; each site was visited only once.

A total of 305 sites was included in the survey. The distribution of the sites within the study region is shown in Fig. 92; their locations and descriptions are given in Appendix II.

Of the sites examined, 47.5% were lakes for which the area of open water exceeded 10 hectares, 6.9% were rivers for which the

Figure 92. Distribution of the sites within the study region. Sites 205 and 206 are not represented but lie farther to the west in Saskatchewan.


54'
53'
52'
51'
50'
49'
101'
100'
99'
98'
97'
96'
95'
94'
60 KM
N

depth of the major channel exceeded 2 m, and 8.9% were creeks for which the depth of the major channel did not exceed 2 m. The remaining 36.7% of the sites were closed, generally lentic bodies for which the area of open water did not exceed 10 hectares; this heterogeneous group included oxbows, natural ponds, bog pools, springs and artificial excavations.

Materials and methods

I. Biotic sampling

All species of plants that were at least partially submerged and directly accessible to grazing by aquatic snails, and all species of snails, including specimens in drift lines, that were seen at each site were recorded. Sites that were small enough to be searched within one hour, either by wading or by canoe, were explored completely, while in those that were larger, the sampling region was limited to an area of the submerged macrophyte zone that could be traversed by canoe in one hour. The size of this area was dependent on degree of exposure, weather, current velocity and visibility beneath the water surface. Submerged stands that were beyond reach were sampled by using a garden rake. In areas where visibility was poor and drift lines were absent, a bottom sample was obtained using the method described by Pip and Paulishyn (1971) and was filtered in the field through a 1 mm mesh sieve.

II. Environmental measurements

A surface water sample was collected at each site in an airtight bottle which was immediately placed in ice in a lightproof container. All water samples were frozen within a maximum of 48 hours after collection. The pH of the surface water was measured in the field with a pH meter.

The water samples were analyzed, after thawing, for total filtrable residue, total alkalinity, chloride, estimated total nitrate and nitrite, sulphate and molybdenum-blue phosphorus, and

an index for dissolved organic matter was determined using methods recommended by the American Public Health Association (1971) which have been described on p. 17.

Results

I. Macrophytes

A. Systematics

The 305 sites yielded a total of 2116 species lots of macrophytes that were wholly or partly submerged at the time of sampling. These were composed of 69 species or groups of species whose relative frequencies of occurrence within the study region (not related to frequencies within individual sites) are given in Table XXXV. Nomenclature was followed according to Gleason (1952), Scoggan (1957), Boivin (1968-69), Hotchkiss (1972) and Haslam et al (1975).

The species of the genera Chara, Sparganium, Eleocharis, Callitriche and Sagittaria (except S. rigida Pursh) were each grouped together because of the difficulty of identifying individual species only on the basis of vegetative characters, since reproductive structures were often not present at the time of sampling. Submerged mosses were also grouped into a single category; these belonged largely to the genera Leptodictyum and Drepanocladus.

Alisma gramineum Gmel. was not considered to be distinct from A. triviale Pursh, following the convention of Gleason (1952) who believed that the former morph fell within the limits of variation of the latter.

The following were first records for Manitoba: Potamogeton amplifolius Tuckerm., P. spirillus Tuckerm., P. obtusifolius Mert. & Koch. and Eriocaulon septangulare With.; Zosterella (=Heteranthera)

TABLE XXXV. Percent relative frequency within the study area of macrophytes at least partially submerged at the time of sampling, based upon a total of 2116 species lots examined from 305 sites. Species below the dotted line were recorded at fewer than 5 sites.

Species or species group	% relative frequency
Myriophyllum exalbescens Fern.	7.6
Potamogeton richardsonii (Benn.)Rydb.	5.7
P. pectinatus L.	4.8
Utricularia vulgaris L.	4.7
Ceratophyllum demersum L.	4.1
Chara spp.	3.6
Sagittaria spp. (except S. rigida)	3.6
Lemna minor L.	3.4
L. trisulca L.	3.2
Sparganium spp.	3.0
Potamogeton gramineus L.	2.9
P. natans L.	2.9
Polygonum amphibium L. var. stipulaceum (Coleman)Fern.	2.9
Nuphar variegatum Engelm.	2.9
Potamogeton zosteriformis Fern.	2.7
Sium suave Walt.	2.3
Elodea canadensis Michx.	2.3
Alisma triviale Pursh	2.1
Hippuris vulgaris L.	2.0
Submerged mosses	2.0
Potamogeton praelongus Wulfen	1.9
Najas flexilis (Willd.)Rostk. & Schmidt	1.8
Potamogeton pusillus L.	1.7
P. friesii Rupr.	1.6
Vallisneria americana Michx.	1.6
Potamogeton foliosus Raf.	1.5
P. vaginatus Turcz.	1.5
Eleocharis spp.	1.4
Spirodela polyrhiza (L.)Schleid.	1.4

continued. . .

TABLE XXXV. (continued)

Species or species group	% relative frequency
Potamogeton amplifolius Tuckerm.	1.2
Zizania aquatica L. var. interior Fassett	1.1
Potamogeton epihydrus Raf. var. nuttalli (C.&S.)Fern.	1.0
P. filiformis Pers.	1.0
Utricularia intermedia Hayne	1.0
Megalodonta beckii (Torr.)Greene	1.0
Ranunculus aquatilis L. var. capillaceus (Thuill.)DC.	0.9
Ruppia maritima L. var. occidentalis (Wats.)Graebn.	0.8
Callitriche spp.	0.8
Nymphaea odorata Ait.	0.7
Calla palustris L.	0.6
Utricularia minor L.	0.6
Nymphaea tetragona Georgi ssp. leibergii (Morong) Porsild	0.6
Nuphar microphyllum (Pers.)Fern.	0.5
Mentha arvensis L. var. villosa (Benth.)Stewart	0.5
Zosterella dubia (Jacq.)	0.5
Sagittaria rigida Pursh	0.3
Potamogeton alpinus Balbis var. tenuifolius (Raf.)Ogden	0.3
P. robbinsii Oakes	0.3
P. spirillus Tuckerm.	0.3
Nymphaea tuberosa Paine	0.3
Brasenia schreberi Gmel.	0.3
Riccia fluitans L.	0.2
Potamogeton obtusifolius Mert.&Koch.	0.2
Caltha palustris L.	0.2
Myriophyllum verticillatum L. var. pectinatum Wallr.	0.2
.....	.....
M. alterniflorum DC.	<0.2
Ranunculus sceleratus L.	<0.2
Najas gracillima (A.Br.)Magnus	0.1
Polygonum coccineum Muhl.	0.1

continued. . .

TABLE XXXV. (continued)

Species or species group	% relative frequency
Ranunculus circinatus Sibth. var. subrigidus (Drew) Benson	0.1
R. gmelini DC. var. hookeri (Don)Benson	0.1
Myriophyllum heterophyllum Michx.	0.1
Zannichellia palustris L.	<0.1
Potamogeton illinoense Morong	<0.1
P. strictifolius Benn. var. rutiloides Fern.	<0.1
Ranunculus flabellaris Raf.	<0.1
R. reptans L.	<0.1
Eriocaulon septangulare With.	<0.1
Utricularia geminiscapa Benj.	<0.1

dubia Jacq. was previously first reported from Manitoba by Pip and Paulishyn (1971). Rydberg (1932 in Scoggan, 1957) first reported Brasenia schreberi Gmel. from Manitoba, but Scoggan (1957) excluded this species from the flora of the province because of the lack of verifiable specimens. This species was found at several localities within the province during the present survey and must be reinstated in the flora of Manitoba.

Representative specimens of the macrophytes collected during this survey have been deposited in the herbarium of the University of Manitoba. A list of the sites where each species or species group was recorded is given in Appendix IIIA.

Myriophyllum exalbescens (Table XXXV) was the most frequently encountered species within the study region; it was recorded at 161 sites and comprised 7.6% of the total species lots examined. Potamogeton richardsonii and P. pectinatus were the next most frequent species, and were recorded at 121 and 101 sites respectively, comprising 5.7% and 4.8% of the total species lots. The most important generic group was Potamogeton, whose 18 species within the study region comprised a total relative frequency of 31.65% of the macrophyte groupings. A revised key to the species of the genus Potamogeton occurring within the study region is given in Appendix IV. All of these species were recorded in Manitoba during the present survey, except for P. illinoense; however Scoggan (1957) reported the latter species from the province.

The relative frequencies of some emergent species, e.g. Polygonum coccineum and emergent members of Ranunculus, were

deceptively low since these values did not reflect the true frequencies of occurrence but indicated the frequencies with which these taxa were found in an at least partially submerged condition.

B. Ecology

The mean values for each of the 8 parameters for water chemistry at the sites where each species or species group that occurred more than once was present and where it was absent (Figs. 93-100) showed that many species appeared to occur more frequently in waters where low or high values of certain parameters prevailed. The significance of the difference of these means between sites where each taxon was present and where it was absent was tested using unpaired t-tests. The results (Table XXXVI) showed that many significant ($p < .05$, $n=305$) distributions appeared to exist. The parameters could be correlated with distribution of the taxa, based on numbers of species or species groups showing significant tests, in the following order of importance: total alkalinity, total filtrable residue, pH, dissolved organic matter, estimated total nitrate and nitrite, molybdenum-blue phosphorus, chloride and sulphate. Significantly lower values for total alkalinity were observed for 24 groups, including 9 species of Potamogeton; Ruppia maritima was the only species that tended to occur at sites with significantly higher values for this parameter. Significantly lower values for total filtrable residue were observed for 21 taxa, including 8 species of Potamogeton, while Ruppia maritima, Potamogeton pectinatus and P. vaginatus tended to occur at sites with significantly higher values. Total alkalinity and total filtrable residue appeared to be related

Figure 93. Mean values for pH at sites where each macrophyte species or species group was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. *Chara* spp.
2. *Riccia fluitans*
3. *Sparganium* spp.
4. *Ruppia maritima*
6. *Potamogeton alpinus*
7. *P. amplifolius*
8. *P. epihydrus*
9. *P. filiformis*
10. *P. foliosus*
11. *P. friesii*
12. *P. gramineus*
14. *P. natans*
15. *P. obtusifolius*
16. *P. pectinatus*
17. *P. praelongus*
18. *P. pusillus*
19. *P. richardsonii*
20. *P. robbinsii*
21. *P. spirillus*
23. *P. vaginatus*
24. *P. zosteriformis*
25. *Najas flexilis*
26. *N. gracillima*
27. *Alisma triviale*
28. *Sagittaria rigida*
29. *Sagittaria* spp. (except *S. rigida*)
30. *Elodea canadensis*
31. *Vallisneria americana*
32. *Zizania aquatica*
33. *Eleocharis* spp.
34. *Calla palustris*
35. *Lemna minor*
36. *L. trisulca*
37. *Spirodela polyrhiza*
38. *Polygonum amphibium*
39. *P. coccineum*
40. *Ceratophyllum demersum*
41. *Nymphaea odorata*
42. *N. tetragona*
43. *N. tuberosa*
44. *Nuphar microphyllum*
45. *N. variegatum*
46. *Brasenia schreberi*
47. *Caltha palustris*
48. *Ranunculus aquatilis*
49. *R. circinatus*
52. *R. gmelini*
53. *R. sceleratus*
54. *Callitriche* spp.
55. *Myriophyllum alterniflorum*
56. *M. exalbescens*
57. *M. heterophyllum*
58. *M. verticillatum*
59. *Hippuris vulgaris*
60. *Sium suave*
61. *Mentha arvensis*
62. *Utricularia intermedia*
63. *U. minor*
64. *U. vulgaris*
66. *Megalodonta beckii*
68. *Zosterella dubia*

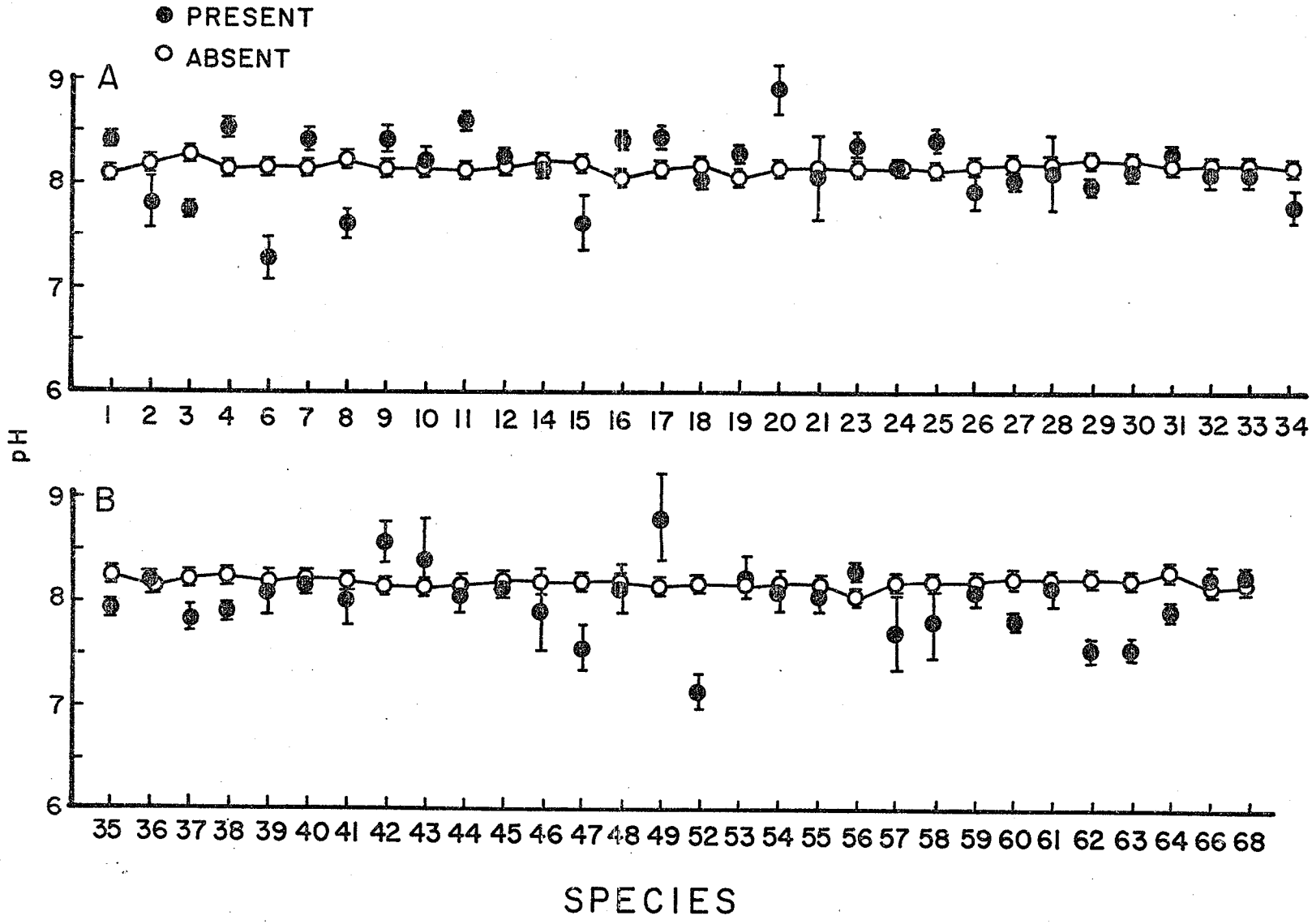

PRESENT
ABSENT
A
B
pH
9
8
7
6
1 2 3 4 6 7 8 9 10 11 12 14 15 16 17 18 19 20 21 23 24 25 26 27 28 29 30 31 32 33 34
35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 52 53 54 55 56 57 58 59 60 61 62 63 64 66 68
SPECIES

Figure 94. Mean values for total filtrable residue (g/l) at sites where each macrophyte species or species group was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. Chara spp.
2. Riccia fluitans
3. Sparganium spp.
4. Ruppia maritima
6. Potamogeton alpinus
7. P. amplifolius
8. P. epihydrus
9. P. filiformis
10. P. foliosus
11. P. friesii
12. P. gramineus
14. P. natans
15. P. obtusifolius
16. P. pectinatus
17. P. praelongus
18. P. pusillus
19. P. richardsonii
20. P. robbinsii
21. P. spirillus
23. P. vaginatus
24. P. zosteriformis
25. Najas flexilis
26. N. gracillima
27. Alisma triviale
28. Sagittaria rigida
29. Sagittaria spp. (except S. rigida)
30. Elodea canadensis
31. Vallisneria americana
32. Zizania aquatica
33. Eleocharis spp.
34. Calla palustris
35. Lemna minor
36. L. trisulca
37. Spirodela polyrhiza
38. Polygonum amphibium
39. P. coccineum
40. Ceratophyllum demersum
41. Nymphaea odorata
42. N. tetragona
43. N. tuberosa
44. Nuphar microphyllum
45. N. variegatum
46. Brasenia schreberi
47. Caltha palustris
48. Ranunculus aquatilis
49. R. circinatus
52. R. gmelini
53. R. sceleratus
54. Callitriche spp.
55. Myriophyllum alterniflorum
56. M. exalbescens
57. M. heterophyllum
58. M. verticillatum
59. Hippuris vulgaris
60. Sium suave
61. Mentha arvensis
62. Utricularia intermedia
63. U. minor
64. U. vulgaris
66. Megalodonta beckii
68. Zosterella dubia

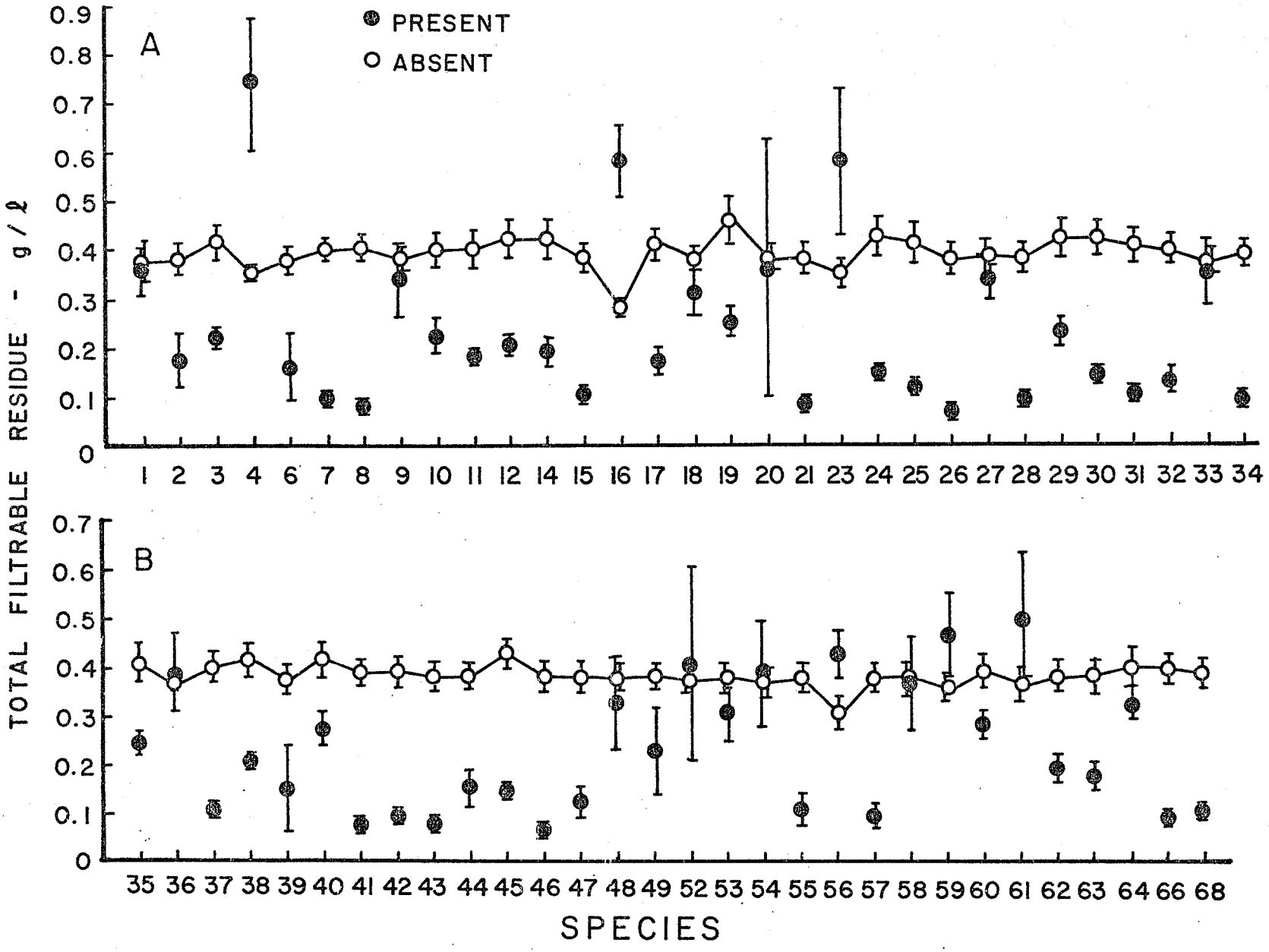

A
B
PRESENT
ABSENT
TOTAL FILTRABLE RESIDUE - g / ℓ
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1 2 3 4 6 7 8 9 10 11 12 14 15 16 17 18 19 20 21 23 24 25 26 27 28 29 30 31 32 33 34
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 52 53 54 55 56 57 58 59 60 61 62 63 64 66 68
SPECIES

Figure 95. Mean values for total alkalinity (mg/l $CaCO_3$) at sites where each macrophyte species or species group was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. *Chara* spp.
2. *Riccia fluitans*
3. *Sparganium* spp.
4. *Ruppia maritima*
6. *Potamogeton alpinus*
7. *P. amplifolius*
8. *P. epihydrus*
9. *P. filiformis*
10. *P. foliosus*
11. *P. friesii*
12. *P. gramineus*
14. *P. natans*
15. *P. obtusifolius*
16. *P. pectinatus*
17. *P. praelongus*
18. *P. pusillus*
19. *P. richardsonii*
20. *P. robbinsii*
21. *P. spirillus*
23. *P. vaginatus*
24. *P. zosteriformis*
25. *Najas flexilis*
26. *N. gracillima*
27. *Alisma triviale*
28. *Sagittaria rigida*
29. *Sagittaria* spp. (except *S. rigida*)
30. *Elodea canadensis*
31. *Vallisneria americana*
32. *Zizania aquatica*
33. *Eleocharis* spp.
34. *Calla palustris*
35. *Lemna minor*
36. *L. trisulca*
37. *Spirodela polyrhiza*
38. *Polygonum amphibium*
39. *P. coccineum*
40. *Ceratophyllum demersum*
41. *Nymphaea odorata*
42. *N. tetragona*
43. *N. tuberosa*
44. *Nuphar microphyllum*
45. *N. variegatum*
46. *Brasenia schreberi*
47. *Caltha palustris*
48. *Ranunculus aquatilis*
49. *R. circinatus*
52. *R. gmelini*
53. *R. sceleratus*
54. *Callitriche* spp.
55. *Myriophyllum alterniflorum*
56. *M. exalbescens*
57. *M. heterophyllum*
58. *M. verticillatum*
59. *Hippuris vulgaris*
60. *Sium suave*
61. *Mentha arvensis*
62. *Utricularia intermedia*
63. *U. minor*
64. *U. vulgaris*
66. *Megalodonta beckii*
68. *Zosterella dubia*

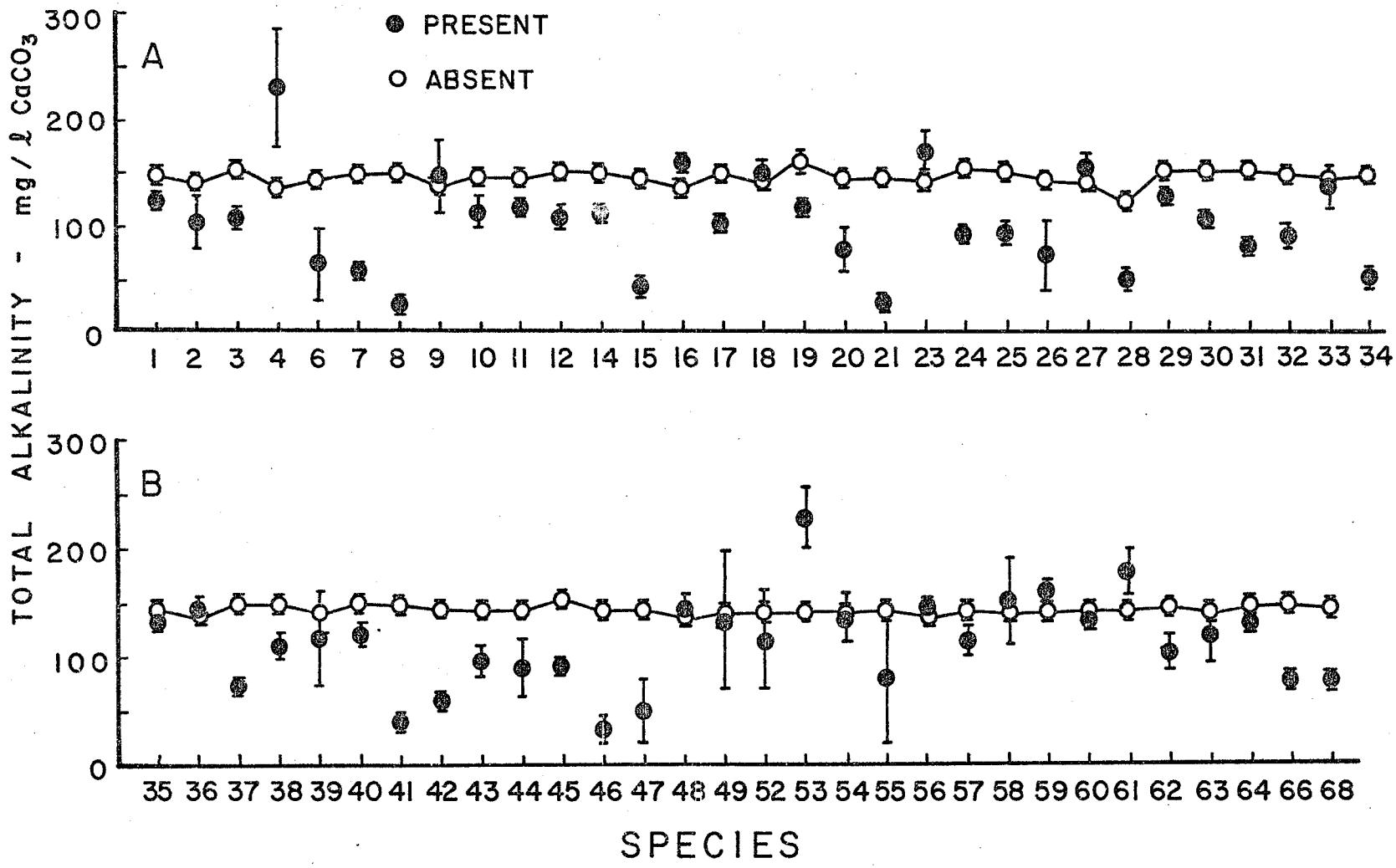

PRESENT
ABSENT
A
B
TOTAL ALKALINITY - mg/l CaCO3
300
200
100
0
1 2 3 4 6 7 8 9 10 11 12 14 15 16 17 18 19 20 21 23 24 25 26 27 28 29 30 31 32 33 34
35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 52 53 54 55 56 57 58 59 60 61 62 63 64 66 68
SPECIES

Figure 96. Mean values for chloride (mg/l) at sites where each macrophyte species or species group was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. *Chara* spp.
2. *Riccia fluitans*
3. *Sparganium* spp.
4. *Ruppia maritima*
6. *Potamogeton alpinus*
7. *P. amplifolius*
8. *P. epihydrus*
9. *P. filiformis*
10. *P. foliosus*
11. *P. friesii*
12. *P. gramineus*
14. *P. natans*
15. *P. obtusifolius*
16. *P. pectinatus*
17. *P. praelongus*
18. *P. pusillus*
19. *P. richardsonii*
20. *P. robbinsii*
21. *P. spirillus*
23. *P. vaginatus*
24. *P. zosteriformis*
25. *Najas flexilis*
26. *N. gracillima*
27. *Alisma triviale*
28. *Sagittaria rigida*
29. *Sagittaria* spp. (except *S. rigida*)
30. *Elodea canadensis*
31. *Vallisneria americana*
32. *Zizania aquatica*
33. *Eleocharis* spp.
34. *Calla palustris*
35. *Lemna minor*
36. *L. trisulca*
37. *Spirodela polyrhiza*
38. *Polygonum amphibium*
39. *P. coccineum*
40. *Ceratophyllum demersum*
41. *Nymphaea odorata*
42. *N. tetragona*
43. *N. tuberosa*
44. *Nuphar microphyllum*
45. *N. variegatum*
46. *Brasenia schreberi*
47. *Caltha palustris*
48. *Ranunculus aquatilis*
49. *R. circinatus*
52. *R. gmelini*
53. *R. sceleratus*
54. *Callitriche* spp.
55. *Myriophyllum alterniflorum*
56. *M. exalbescens*
57. *M. heterophyllum*
58. *M. verticillatum*
59. *Hippuris vulgaris*
60. *Sium suave*
61. *Mentha arvensis*
62. *Utricularia intermedia*
63. *U. minor*
64. *U. vulgaris*
66. *Megalodonta beckii*
68. *Zosterella dubia*

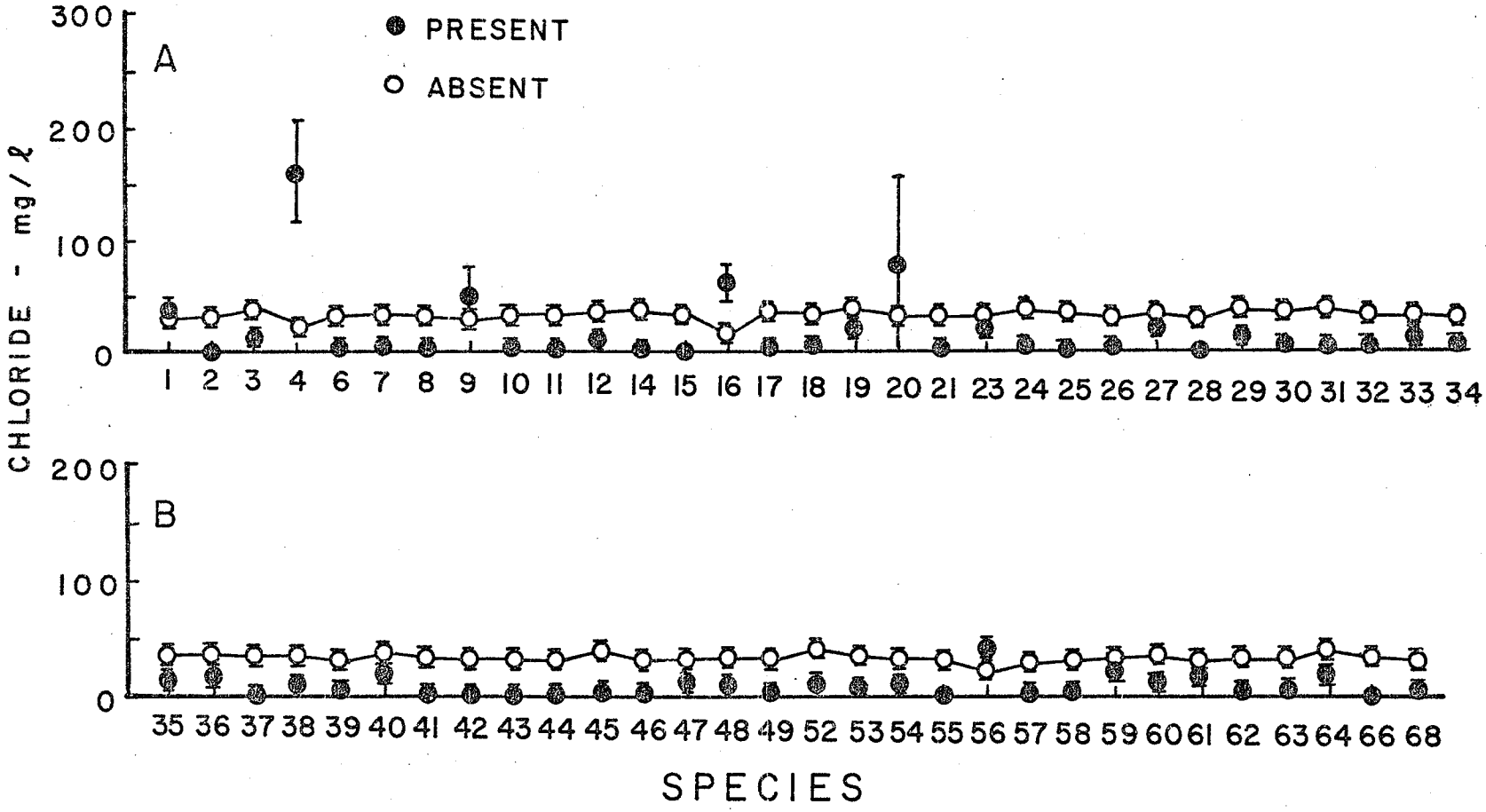

PRESENT
ABSENT
A
B
CHLORIDE - mg / ℓ
300
200
100
0
200
100
0
1 2 3 4 6 7 8 9 10 11 12 14 15 16 17 18 19 20 21 23 24 25 26 27 28 29 30 31 32 33 34
35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 52 53 54 55 56 57 58 59 60 61 62 63 64 66 68
SPECIES

Figure 97. Mean values for sulphate (mg/l) at sites where each macrophyte species or species group was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. Chara spp.
2. Riccia fluitans
3. Sparganium spp.
4. Ruppia maritima
6. Potamogeton alpinus
7. P. amplifolius
8. P. epihydrus
9. P. filiformis
10. P. foliosus
11. P. friesii
12. P. gramineus
14. P. natans
15. P. obtusifolius
16. P. pectinatus
17. P. praelongus
18. P. pusillus
19. P. richardsonii
20. P. robbinsii
21. P. spirillus
23. P. vaginatus
24. P. zosteriformis
25. Najas flexilis
26. N. gracillima
27. Alisma triviale
28. Sagittaria rigida
29. Sagittaria spp. (except S. rigida)
30. Elodea canadensis
31. Vallisneria americana
32. Zizania aquatica
33. Eleocharis spp.
34. Calla palustris
35. Lemna minor
36. L. trisulca
37. Spirodela polyrhiza
38. Polygonum amphibium
39. P. coccineum
40. Ceratophyllum demersum
41. Nymphaea odorata
42. N. tetragona
43. N. tuberosa
44. Nuphar microphyllum
45. N. variegatum
46. Brasenia schreberi
47. Caltha palustris
48. Ranunculus aquatilis
49. R. circinatus
52. R. gmelini
53. R. sceleratus
54. Callitriche spp.
55. Myriophyllum alterniflorum
56. M. exalbescens
57. M. heterophyllum
58. M. verticillatum
59. Hippuris vulgaris
60. Sium suave
61. Mentha arvensis
62. Utricularia intermedia
63. U. minor
64. U. vulgaris
66. Megalodonta beckii
68. Zosterella dubia

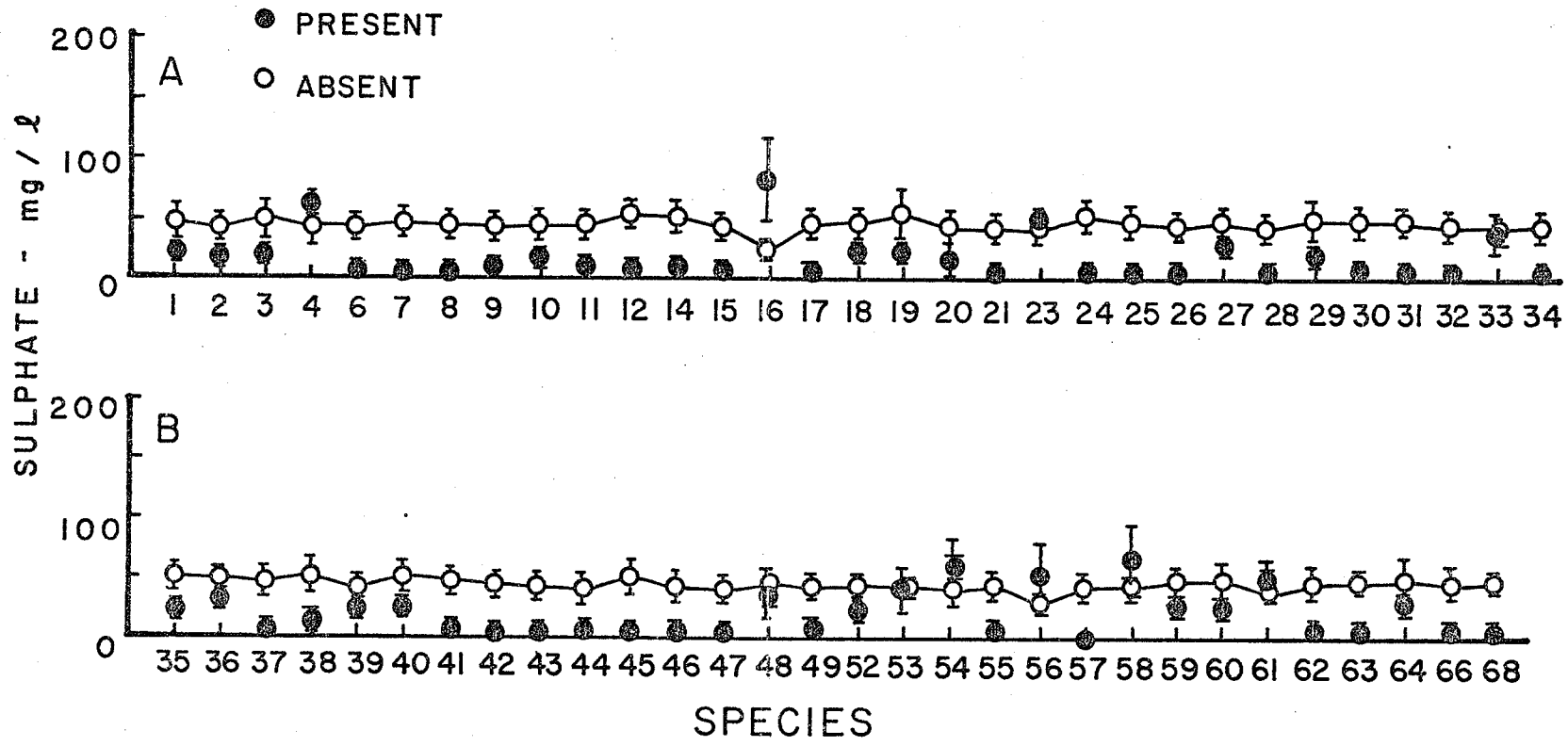

PRESENT
ABSENT
A
B
200
100
0
SULPHATE - mg / ℓ
1 2 3 4 6 7 8 9 10 11 12 14 15 16 17 18 19 20 21 23 24 25 26 27 28 29 30 31 32 33 34
35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 52 53 54 55 56 57 58 59 60 61 62 63 64 66 68
SPECIES

Figure 98. Mean values for estimated total nitrate and nitrite (mg/l) at sites where each macrophyte species or species group was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. Chara spp.
2. Riccia fluitans
3. Sparganium spp.
4. Ruppia maritima
6. Potamogeton alpinus
7. P. amplifolius
8. P. epihydrus
9. P. filiformis
10. P. foliosus
11. P. friesii
12. P. gramineus
14. P. natans
15. P. obtusifolius
16. P. pectinatus
17. P. praelongus
18. P. pusillus
19. P. richardsonii
20. P. robbinsii
21. P. spirillus
23. P. vaginatus
24. P. zosteriformis
25. Najas flexilis
26. N. gracillima
27. Alisma triviale
28. Sagittaria rigida
29. Sagittaria spp. (except S. rigida)
30. Elodea canadensis
31. Vallisneria americana
32. Zizania aquatica
33. Eleocharis spp.
34. Calla palustris
35. Lemna minor
36. L. trisulca
37. Spirodela polyrhiza
38. Polygonum amphibium
39. P. coccineum
40. Ceratophyllum demersum
41. Nymphaea odorata
42. N. tetragona
43. N. tuberosa
44. Nuphar microphyllum
45. N. variegatum
46. Brasenia schreberi
47. Caltha palustris
48. Ranunculus aquatilis
49. R. circinatus
52. R. gmelini
53. R. sceleratus
54. Callitriche spp.
55. Myriophyllum alterniflorum
56. M. exalbescens
57. M. heterophyllum
58. M. verticillatum
59. Hippuris vulgaris
60. Sium suave
61. Mentha arvensis
62. Utricularia intermedia
63. U. minor
64. U. vulgaris
66. Megalodonta beckii
68. Zosterella dubia

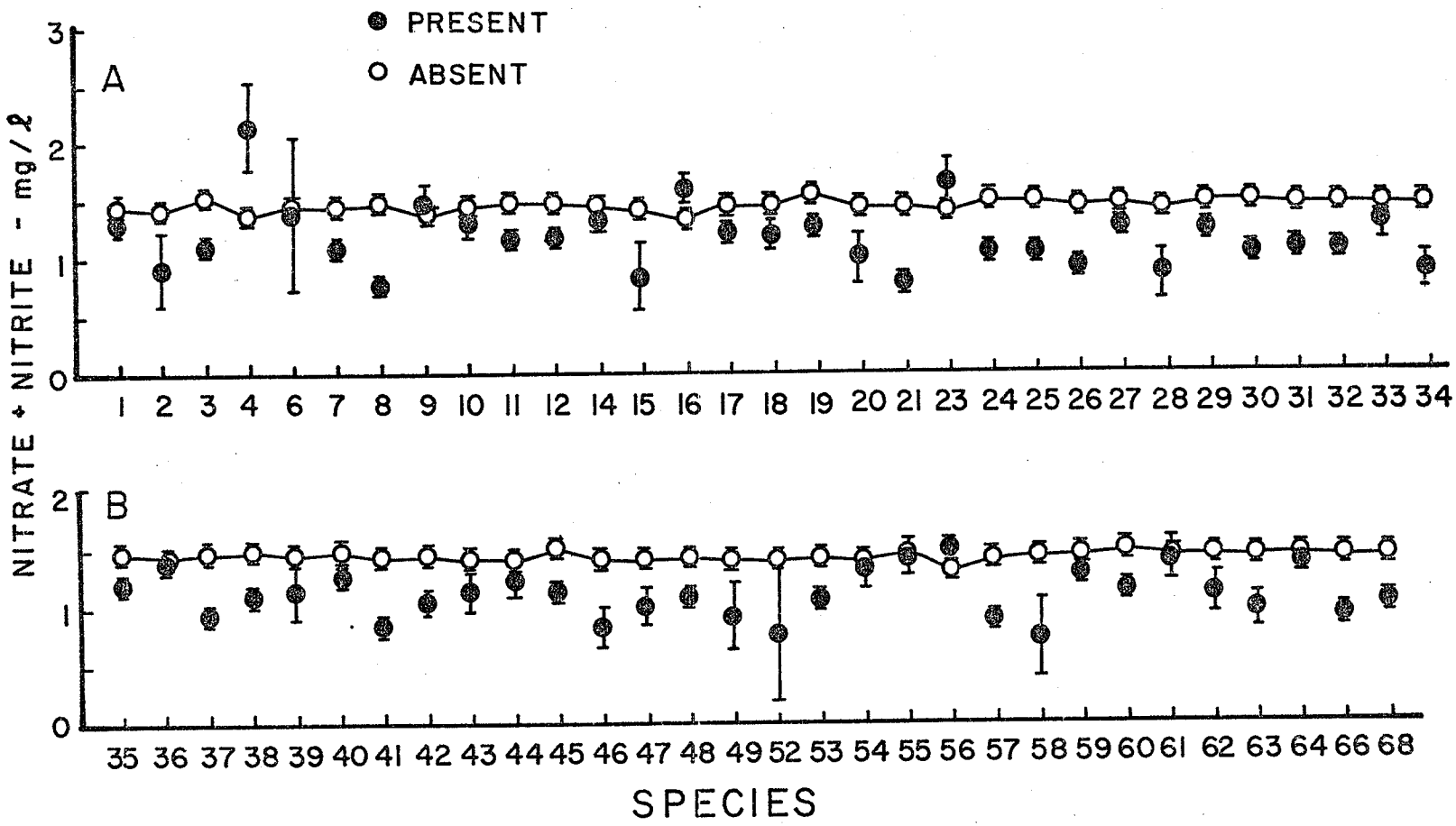

PRESENT
ABSENT
A
B
NITRATE + NITRITE - mg/ℓ
0
1
2
3
1 2 3 4 6 7 8 9 10 11 12 14 15 16 17 18 19 20 21 23 24 25 26 27 28 29 30 31 32 33 34
35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 52 53 54 55 56 57 58 59 60 61 62 63 64 66 68
SPECIES

Figure 99. Mean values for organic indices (optical density at 275 nm) at sites where each macrophyte species or species group was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. Chara spp.
2. Riccia fluitans
3. Sparganium spp.
4. Ruppia maritima
6. Potamogeton alpinus
7. P. amplifolius
8. P. epihydrus
9. P. filiformis
10. P. foliosus
11. P. friesii
12. P. gramineus
14. P. natans
15. P. obtusifolius
16. P. pectinatus
17. P. praelongus
18. P. pusillus
19. P. richardsonii
20. P. robbinsii
21. P. spirillus
23. P. vaginatus
24. P. zosteriformis
25. Najas flexilis
26. N. gracillima
27. Alisma triviale
28. Sagittaria rigida
29. Sagittaria spp. (except S. rigida)
30. Elodea canadensis
31. Vallisneria americana
32. Zizania aquatica
33. Eleocharis spp.
34. Calla palustris
35. Lemna minor
36. L. trisulca
37. Spirodela polyrhiza
38. Polygonum amphibium
39. P. coccineum
40. Ceratophyllum demersum
41. Nymphaea odorata
42. N. tetragona
43. N. tuberosa
44. Nuphar microphyllum
45. N. variegatum
46. Brasenia schreberi
47. Caltha palustris
48. Ranunculus aquatilis
49. R. circinatus
52. R. gmelini
53. R. sceleratus
54. Callitriche spp.
55. Myriophyllum alterniflorum
56. M. exalbescens
57. M. heterophyllum
58. M. verticillatum
59. Hippuris vulgaris
60. Sium suave
61. Mentha arvensis
62. Utricularia intermedia
63. U. minor
64. U. vulgaris
66. Megalodonta beckii
68. Zosterella dubia

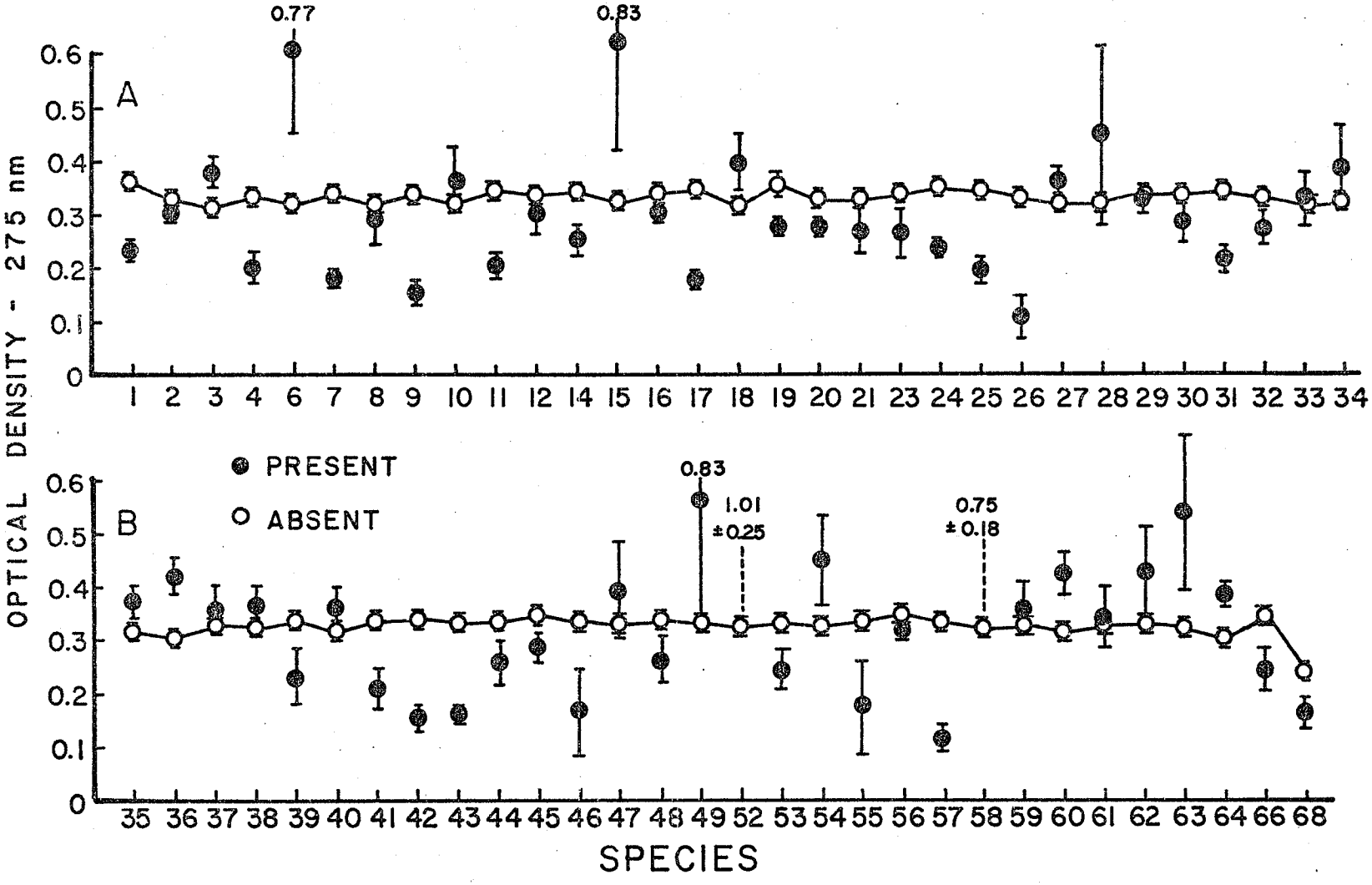

0.77
0.83
A
0.6
0.5
0.4
0.3
0.2
0.1
0
OPTICAL DENSITY - 275 nm
1 2 3 4 6 7 8 9 10 11 12 14 15 16 17 18 19 20 21 23 24 25 26 27 28 29 30 31 32 33 34
PRESENT
ABSENT
B
0.83
1.01
±0.25
0.75
±0.18
35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 52 53 54 55 56 57 58 59 60 61 62 63 64 66 68
SPECIES

Figure 100. Mean values for molybdenum-blue phosphorus (mg/l) at sites where each macrophyte species or species group was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. Chara spp.
2. Riccia fluitans
3. Sparganium spp.
4. Ruppia maritima
6. Potamogeton alpinus
7. P. amplifolius
8. P. epihydrus
9. P. filiformis
10. P. foliosus
11. P. friesii
12. P. gramineus
14. P. natans
15. P. obtusifolius
16. P. pectinatus
17. P. praelongus
18. P. pusillus
19. P. richardsonii
20. P. robbinsii
21. P. spirillus
23. P. vaginatus
24. P. zosteriformis
25. Najas flexilis
26. N. gracillima
27. Alisma triviale
28. Sagittaria rigida
29. Sagittaria spp. (except S. rigida)
30. Elodea canadensis
31. Vallisneria americana
32. Zizania aquatica
33. Eleocharis spp.
34. Calla palustris
35. Lemna minor
36. L. trisulca
37. Spirodela polyrhiza
38. Polygonum amphibium
39. P. coccineum
40. Ceratophyllum demersum
41. Nymphaea odorata
42. N. tetragona
43. N. tuberosa
44. Nuphar microphyllum
45. N. variegatum
46. Brasenia schreberi
47. Caltha palustris
48. Ranunculus aquatilis
49. R. circinatus
52. R. gmelini
53. R. sceleratus
54. Callitriche spp.
55. Myriophyllum alterniflorum
56. M. exalbescens
57. M. heterophyllum
58. M. verticillatum
59. Hippuris vulgaris
60. Sium suave
61. Mentha arvensis
62. Utricularia intermedia
63. U. minor
64. U. vulgaris
66. Megalodonta beckii
68. Zosterella dubia

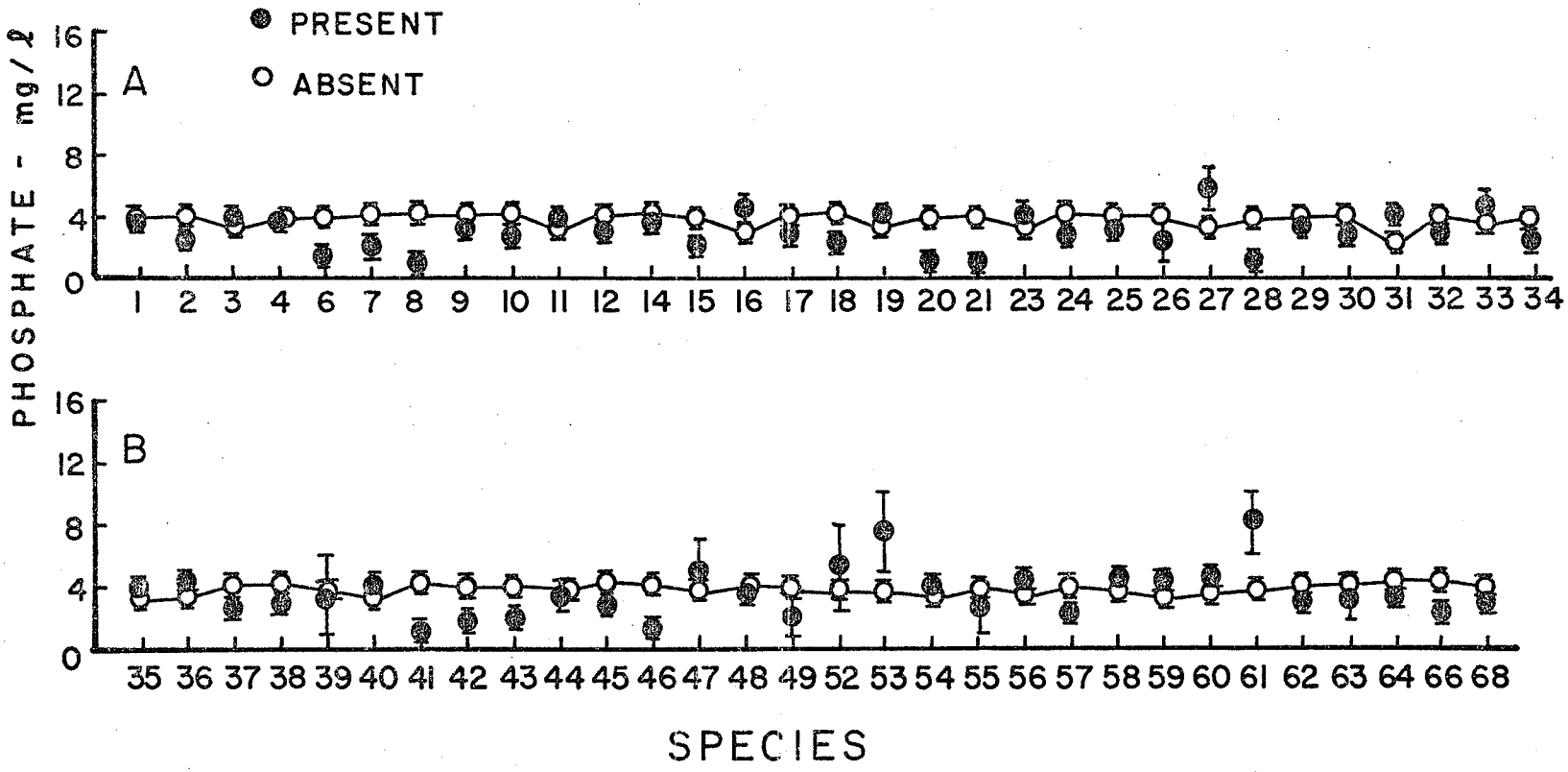

PRESENT
ABSENT
A
B
PHOSPHATE - mg/l
16
12
8
4
0
1 2 3 4 6 7 8 9 10 11 12 14 15 16 17 18 19 20 21 23 24 25 26 27 28 29 30 31 32 33 34
35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 52 53 54 55 56 57 58 59 60 61 62 63 64 66 68
SPECIES

TABLE XXXVI. Significance of the distribution of macrophytes with respect to 8 water chemistry parameters. Symbols indicate that the mean values for the sites at which each taxon was recorded were significantly ($p < .05$, n=305) higher (+) or lower (-) than the mean for the sites at which the taxon was not recorded; 0 indicates no significant difference. Taxa in parentheses were recorded only once. Parameter 1= pH, 2= total filtrable residue, 3= total alkalinity, 4= chloride, 5= sulphate, 6= total nitrate and nitrite, 7= dissolved organic matter, 8= molybdenum-blue phosphorus.

Species or species group	Parameter 1	2	3	4	5	6	7	8
1. *Chara* spp.	+	0	0	0	0	0	-	0
2. *Riccia fluitans*	0	0	0	0	0	0	0	0
3. *Sparganium* spp.	-	-	-	0	0	-	0	0
4. *Ruppia maritima*	+	+	+	+	0	+	0	0
(5. *Zannichellia palustris*)								
6. *Potamogeton alpinus*	-	0	0	0	0	0	+	0
7. *P. amplifolius*	0	-	-	0	0	0	-	-
8. *P. epihydrus*	-	-	-	0	0	-	0	-
9. *P. filiformis*	0	0	0	0	0	0	-	0
10. *P. foliosus*	0	0	0	0	0	0	0	0
11. *P. friesii*	+	-	0	0	0	0	-	0
12. *P. gramineus*	0	-	-	0	0	-	0	0
(13. *P. illinoense*)								
14. *P. natans*	0	-	-	-	0	0	-	0
15. *P. obtusifolius*	0	0	-	0	0	0	+	0
16. *P. pectinatus*	+	+	0	+	+	0	0	+
17. *P. praelongus*	+	-	-	0	0	0	-	0
18. *P. pusillus*	0	0	0	0	0	0	0	0
19. *P. richardsonii*	+	-	-	0	0	-	-	0
20. *P. robbinsii*	+	0	0	0	0	0	0	0
21. *P. spirillus*	0	0	-	0	0	0	0	0
(22. *P. strictifolius*)								
23. *P. vaginatus*	0	+	0	0	0	0	0	0
24. *P. zosteriformis*	0	-	-	0	0	-	-	0
25. *Najas flexilis*	+	-	-	0	0	-	-	0
26. *N. gracillima*	0	0	0	0	0	0	0	0
27. *Alisma triviale*	0	0	0	0	0	0	0	+
28. *Sagittaria rigida*	0	0	-	0	0	0	0	0
29. *Sagittaria* spp. (except *S. rigida*)	-	-	0	0	0	0	0	0
30. *Elodea canadensis*	0	-	-	0	0	-	0	0
31. *Vallisneria americana*	0	-	-	0	0	-	-	0
32. *Zizania aquatica*	0	-	-	0	0	0	0	0
33. *Eleocharis* spp.	0	0	0	0	0	0	0	0

continued. . .

TABLE XXXVI. (continued)

Species or species group	Parameter 1	2	3	4	5	6	7	8
34. Calla palustris	0	0	-	0	0	-	0	0
35. Lemna minor	-	-	0	0	0	0	0	0
36. L. trisulca	0	0	0	0	0	0	+	0
37. Spirodela polyrhiza	-	-	-	0	0	-	0	0
38. Polygonum amphibium	-	-	-	0	0	-	0	0
39. P. coccineum	0	0	0	0	0	0	0	0
40. Ceratophyllum demersum	0	-	0	0	0	0	0	0
41. Nymphaea odorata	0	-	-	0	0	-	0	-
42. N. tetragona	0	0	-	0	0	0	-	0
43. N. tuberosa	0	0	0	0	0	0	0	0
44. Nuphar microphyllum	0	0	0	0	0	0	0	0
45. N. variegatum	0	-	-	-	0	-	0	0
46. Brasenia schreberi	0	0	-	0	0	0	0	0
47. Caltha palustris	0	0	0	0	0	0	0	0
48. Ranunculus aquatilis	0	0	0	0	0	0	0	0
49. R. circinatus	0	0	0	0	0	0	0	0
(50. R. flabellaris)								
(51. R. reptans)								
52. R. gmelini	-	0	0	0	0	0	+	0
53. R. sceleratus	0	0	0	0	0	0	0	0
54. Callitriche spp.	0	0	0	0	0	0	0	0
55. Myriophyllum alterniflorum	0	0	0	0	0	0	0	0
56. M. exalbescens	+	0	0	0	0	0	0	0
57. M. heterophyllum	0	0	0	0	0	0	0	0
58. M. verticillatum	0	0	0	0	0	0	+	0
59. Hippuris vulgaris	0	0	0	0	0	0	0	0
60. Sium suave	-	0	0	0	0	-	+	0
61. Mentha arvensis	0	0	0	0	0	0	0	+
62. Utricularia intermedia	-	0	0	0	0	0	0	0
63. U. minor	-	0	0	0	0	0	+	0
64. U. vulgaris	-	0	0	0	0	0	+	0
(65. U. geminiscapa)								
66. Megalodonta beckii	0	-	-	0	0	-	0	0
(67. Eriocaulon septangulare)								
68. Zosterella dubia	0	0	-	0	0	0	-	0
69. Submerged mosses	0	0	0	0	0	0	0	0

in that 18 of the above taxa showed significant, similarly inclined preferences for both parameters. Significantly lower values for pH were observed for 12 groups, including only 1 species of Potamogeton (P. epihydrus), while significantly higher values were observed for 9 taxa of which 5 were Potamogeton species. Twelve groups, including 7 Potamogeton species, tended to occur at sites with significantly lower organic matter indices, while 8 taxa, including 2 Potamogeton species, tended to occur at sites with significantly higher indices. Fifteen taxa tended to occur at sites with significantly lower total nitrate and nitrite values, but this parameter was important for only 4 species of Potamogeton. Only Ruppia maritima tended to occur at sites with significantly higher values for this parameter. Molybdenum-blue phosphorus and chloride were important to only 6 and 4 groups respectively, while sulphate was important only for Potamogeton pectinatus. For the species of Potamogeton, these results agreed with the observations of Hellquist (1975) who found that total alkalinity was of great importance in influencing community composition within this genus, while nitrate, chloride and dissolved total phosphate were of lesser importance.

No significant positive or negative preferences for any of the water chemistry parameters examined could be detected for Riccia fluitans, Potamogeton foliosus, P. pusillus, Najas gracillima, Eleocharis spp., Polygonum coccineum, Nymphaea tuberosa, Nuphar microphyllum, Caltha palustris, Ranunculus aquatilis, R. circinatus, R. sceleratus, Callitriche spp., Myriophyllum alterniflorum, M. heterophyllum and Hippuris vulgaris.

C. Plant associations

For positive associations whose members have different geographical or ecological tolerance ranges, the associations would be expected to occur within the region of range overlap between the two species; the size of this region would determine the ecological extensity of the associations. In practice, this area of overlap is difficult to ascertain, since each population possesses a unique set of genetically determined tolerance ranges whose expression is further modified by the particular set of environmental conditions characteristic of each habitat. Thus ideally the tolerance ranges for a species as a whole must be treated as the sum of the individual tolerance ranges of the populations that comprise the species.

Let us assume that the tolerance range T of species A for parameter 1 ranges from a minimum value of x_a to a maximum value of y_a; similarly that of species B ranges from a minimum of x_b to a maximum of y_b:

$$T_A = y_a - x_a \quad \ldots\ldots\ldots (16), \text{ and}$$

$$T_B = y_b - x_b \quad \ldots\ldots\ldots (17).$$

The overlap in tolerance spectra between species A and B would equal the difference between the smallest maximum value and the largest minimum value, regardless of whether one or both values were characteristic of only one species. If portions of the ranges of both species were equal to or exceeded the boundaries of the zone of overlap, i.e. if $y_a \leq y_b$, and $x_a \leq x_b$, then the zone of overlap (R) in one dimension would be:

$$R_{AB} = (y_a - x_b) \quad \ldots\ldots\ldots\ldots \quad (18).$$

If the range of one species fell entirely within the range of the other species, i.e. if $y_a \geq y_b$, but $x_a \leq x_b$, or conversely if $y_a \leq y_b$, but $x_a \geq x_b$, then

$$R_{AB} = (y_b - x_b) \quad \ldots\ldots\ldots\ldots \quad (19) \text{ and}$$

$$R_{AB} = (y_a - x_a) \quad \ldots\ldots\ldots\ldots \quad (20)$$

respectively.

Extending this argument to parameters 1 and 2,

$$T_A = (y_a - x_a)_1 \, (y_a - x_a)_2 \quad \ldots\ldots\ldots \quad (21) \text{ and}$$

$$T_B = (y_b - x_b)_1 \, (y_b - x_b)_2 \quad \ldots\ldots\ldots \quad (22).$$

The zone of overlap (R) between these two tolerance ranges in two dimensions would be equal to:

$$R_{AB} = (y_a - x_b)_1 \, (y_a - x_b)_2 \quad \ldots\ldots\ldots \quad (23),$$

where, for each parameter, $y_a \leq y_b$, and $x_a \leq x_b$ if the range of one species for each parameter does not lie entirely within the range of the other species. If, for any parameter, the range of one species lies entirely within the range of the other species, then, for that parameter, considerations (19) or (20) apply.

For n parameters, if

$$T_A = (y_a - x_a)_1 \, (y_a - x_a)_2 \cdot \ldots\ldots \cdot (y_a - x_a)_n \quad \ldots \quad (24)$$

and

$$T_B = (y_b - x_b)_1 \, (y_b - x_b)_2 \cdot \ldots\ldots \cdot (y_b - x_b)_n \quad \ldots \quad (25),$$

then the n-dimensional zone of overlap (R) would be:

$$R_{AB} = (y_a - x_b)_1 \, (y_a - x_b)_2 \cdot \ldots\ldots \cdot (y_a - x_b)_n \quad . \quad . \quad (26),$$

where, for each parameter, $y_a \leq y_b$ and $x_a \leq x_b$ if the ranges for these parameters are partially exclusive for both species. If not, then considerations (19) or (20) apply.

For more than two species, the overlap in tolerance ranges between the species would still equal the difference between the smallest maximum value and the largest minimum value for each parameter.

Positive associations between species A and B could occur only within the zone R defined by equation (26). Negative associations would be expected in the area outside the boundaries of this zone.

Since for each species the fundamental niche has an infinite number of dimensions, as pointed out by MacArthur (1968 in Williamson, 1972), the zone of overlap for the tolerance ranges between two species would also have an infinite number of dimensions, and thus could not be determined in practice. This value can only be approximated, poorly at best, by recording the values for selected parameters for a large number of populations and extracting the minimum and maximum values so obtained. For finite numbers of parameters, the expected range for positive associations could be estimated from the zone of overlap which would have to be further adjusted to the geographical ranges of the species.

In the present study, an 8-dimensional zone of overlap for all possible pairs of species was still not considered to be practicable. Instead, the study area was treated as a single unit, on the assumption that a large part of the 8-dimensional ecological range space would

overlap for at least the more common species. Thus the observed frequencies of joint occurrence were compared with values expected on the basis of randomness within the study area, and approximations of association extensity by this method were underestimates of the true values, since by this method some associations were expected in areas where they could not occur because the zone of ecological range overlap was exceeded.

In order to compare association frequencies on an environmental basis, the similarities in the significant preferences of each possible species or species group pair were graded by assigning a value of +1 when preferences of the two species for the same parameter were both significant and similarly inclined (both positive or negative); a value of -1 was assigned when the preferences were both significant but dissimilarly inclined (one positive and one negative). A significant preference shown by only one species was given a value of 0. These values were summed for the 8 parameters for each species pair, yielding the matrix in Table XXXVII. Negative values indicated net dissimilarity in habitat preference in terms of the parameters examined and reflected the likelihoods that the two species would not occur in the same habitat. Conversely, positive values indicated net similarity in habitat preference and predicted that the two species would occur together in the same habitat. Groups of species related by high positive values would be expected to form positive associations on the basis of selection for similar habitats.

The significance of the observed tendency for the members of each possible species or species group pair to occur jointly or

TABLE XXXVII. Net similarities in the significant parameter preferences for each possible macrophyte species or species group pair. Maximum possible is +8 for similarities and -8 for dissimilarities. Taxa which occurred only once were excluded. Species numbers represent the following taxa:

1. *Chara* spp.
2. *Riccia fluitans*
3. *Sparganium* spp.
4. *Ruppia maritima*
6. *Potamogeton alpinus*
7. *P. amplifolius*
8. *P. epihydrus*
9. *P. filiformis*
10. *P. foliosus*
11. *P. friesii*
12. *P. gramineus*
14. *P. natans*
15. *P. obtusifolius*
16. *P. pectinatus*
17. *P. praelongus*
18. *P. pusillus*
19. *P. richardsonii*
20. *P. robbinsii*
21. *P. spirillus*
23. *P. vaginatus*
24. *P. zosteriformis*
25. *Najas flexilis*
26. *N. gracillima*
27. *Alisma triviale*
28. *Sagittaria rigida*
29. *Sagittaria* spp. (except *S. rigida*)
30. *Elodea canadensis*
31. *Vallisneria americana*
32. *Zizania aquatica*
33. *Eleocharis* spp.
34. *Calla palustris*
35. *Lemna minor*
36. *L. trisulca*
37. *Spirodela polyrhiza*
38. *Polygonum amphibium*
39. *P. coccineum*
40. *Ceratophyllum demersum*
41. *Nymphaea odorata*
42. *N. tetragona*
43. *N. tuberosa*
44. *Nuphar microphyllum*
45. *N. variegatum*
46. *Brasenia schreberi*
47. *Caltha palustris*
48. *Ranunculus aquatilis*
49. *R. circinatus*
52. *R. gmelini*
53. *R. sceleratus*
54. *Callitriche* spp.
55. *Myriophyllum alterniflorum*
56. *M. exalbescens*
57. *M. heterophyllum*
58. *M. verticillatum*
59. *Hippuris vulgaris*
60. *Sium suave*
61. *Mentha arvensis*
62. *Utricularia intermedia*
63. *U. minor*
64. *U. vulgaris*
66. *Megalodonta beckii*
68. *Zosterella dubia*

TABLE XXXVII.

	1	2	3	4	6	7	8	9	10	11	12	14	15	16	17	18	19	20	21	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
1	x	0	-1	+1	-2	+1	-1	+1	0	+2	0	+1	-1	+1	+2	0	+2	+1	0	0	+1	+2	0	0	0	-1	0	+1	0	0	0	-1	-1	-1
2		x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3			x	-4	+1	+2	+4	0	0	0	+3	+2	0	-2	+1	0	+2	-1	+1	-1	+3	+2	0	0	+1	+2	+3	+3	+2	0	+2	+2	0	+4
4				x	-1	-2	-4	0	0	0	-3	-2	-1	+3	-1	0	-2	+1	-1	+1	-3	-2	0	0	-1	-2	-3	-3	-2	0	-2	-2	0	-4
6					x	-1	+1	0	0	-2	0	-1	0	-1	-2	0	-2	-1	0	0	-1	-2	0	0	0	+1	0	-1	0	0	0	+1	+1	+1
7						x	+3	+1	0	+2	+2	+3	0	-2	+3	0	+3	0	+1	-1	+3	+3	0	-1	+1	+1	+2	+3	+2	0	+1	+1	-1	+2
8							x	0	0	0	+3	+2	+1	-3	+1	0	+2	-1	+1	-1	+3	+2	0	-1	+1	+2	+3	+3	+2	0	+2	+2	0	+4
9								x	0	+1	0	+1	-1	0	+1	0	+1	0	0	0	+1	+1	0	0	0	0	0	+1	0	0	0	0	-1	0
10									x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11										x	+1	+2	-1	0	+1	0	+1	+1	0	-1	+2	+1	0	0	0	0	+1	+2	+1	0	0	0	-1	0
12											x	+2	+1	-1	+2	0	+3	0	+1	-1	+3	+3	0	0	+1	+1	+3	+3	+2	0	+2	+1	0	+3
14												x	0	-2	+3	0	+3	0	+1	-1	+3	+3	0	0	+1	+1	+2	+3	+2	0	+1	+1	-1	+2
15													x	0	0	0	0	0	+1	0	0	0	0	0	+1	0	+1	0	+1	0	+1	0	+1	+1
16														x	0	0	0	+1	0	+1	-1	0	0	+1	0	-2	-1	-1	-1	0	0	-2	0	-2
17															x	0	+4	+1	+1	-1	+3	+4	0	0	+1	0	+2	+3	+2	0	+1	0	-1	+1
18																x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19																	x	+1	+1	-1	+4	+5	0	0	+1	0	+3	+4	+2	0	+2	0	-1	+2
20																		x	0	0	0	+1	0	0	0	-1	0	0	0	0	0	-1	0	-1
21																			x	0	+1	+1	0	0	+1	0	+1	+1	+1	0	+1	0	0	+1
23																				x	-1	-1	0	0	0	-1	-1	-1	-1	0	0	-1	0	-1
24																					x	+4	0	0	+1	+1	+3	+4	+2	0	+2	+1	-1	+3
25																						x	0	0	+1	0	+3	+4	+2	0	+2	0	-1	+2
26																							x	0	0	0	0	0	0	0	0	0	0	0
27																								x	0	0	0	0	0	0	0	0	0	0
28																									x	0	+1	+1	+1	0	+1	0	0	+1
29																										x	+1	+1	+1	0	0	+1	0	+2
30																											x	+3	+2	0	+2	+1	0	+3
31																												x	+2	0	+2	+1	-1	+3
32																													x	0	+1	+1	0	+2
33																														x	0	0	0	0
34																															x	0	0	+2
35																																x	0	+2
36																																	x	0
37																																		x

continued . . .

TABLE XXXVII. (continued)

	38	39	40	41	42	43	44	45	46	47	48	49	52	53	54	55	56	57	58	59	60	61	62	63	64	66	68
1	-1	0	0	0	+1	0	0	0	0	0	0	0	-2	0	0	0	+1	0	-1	0	-2	0	-1	-2	-2	0	+1
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	+4	0	+1	+3	0	0	0	+3	+1	0	0	0	+1	0	0	0	-1	0	0	0	+2	0	+1	+1	+1	+3	+1
4	-4	0	-1	-3	-1	0	0	-4	-1	0	0	0	-1	0	0	0	+1	0	0	0	-2	0	-1	-1	-1	-3	-1
6	+1	0	0	0	-1	0	0	0	0	0	0	0	+2	0	0	0	-1	0	+1	0	+2	0	+1	+2	+2	0	-1
7	+2	0	+1	+3	+2	0	0	+2	+1	0	0	0	-1	0	0	0	0	0	-1	0	-1	-1	0	-1	-1	+2	+2
8	+4	0	+1	+4	+1	0	0	+3	+1	0	0	0	+1	0	0	0	-1	0	0	0	+2	-1	+1	+1	+1	+3	+1
9	0	0	0	0	+1	0	0	0	0	0	0	0	-1	0	0	0	0	0	-1	0	-1	0	0	-1	-1	0	+1
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	+1	+1	+1	0	0	+1	0	0	0	0	0	0	0	0	+1	0	-1	0	0	0	-1	0	0	+1	+1
12	+3	0	+1	+3	+1	0	0	+3	+1	0	0	0	0	0	0	0	0	0	0	0	+1	0	0	0	0	+3	+1
14	+2	0	+1	+2	+2	0	0	+3	+1	0	0	0	-1	0	0	0	0	0	-1	0	-1	0	0	-1	-1	+2	+2
15	+1	0	0	+1	0	0	0	+1	+1	0	0	0	+1	0	0	0	0	0	+1	0	+1	0	0	+1	+1	+1	0
16	-2	0	-1	-2	0	0	0	-2	0	0	0	0	-1	0	0	0	+1	0	0	0	-1	+1	-1	-1	-1	-1	0
17	+1	0	+1	+2	+2	0	0	+2	+1	0	0	0	-2	0	0	0	+1	0	-1	0	-2	0	-1	-2	-2	+2	+2
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	+2	0	+1	+3	+2	0	0	+3	+1	0	0	0	-2	0	0	0	+1	0	-1	0	+1	0	-1	-2	-2	+2	+2
20	-1	0	0	0	0	0	0	0	0	0	0	0	-1	0	0	0	+1	0	0	0	-1	0	-1	-1	-1	0	0
21	+1	0	0	+1	+1	0	0	+1	+1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+1	+1
23	-1	0	-1	-1	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-1	0
24	+3	0	+1	+3	+2	0	0	+3	+1	0	0	0	-1	0	0	0	0	0	-1	0	0	0	0	-1	-1	+3	+2
25	+2	0	+1	+3	+2	0	0	+3	+1	0	0	0	-2	0	0	0	+1	0	-1	0	-1	0	-1	-2	-2	+3	+2
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+1	0	0	0	0	0
28	+1	0	0	+1	+1	0	0	+1	+1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+1	+1
29	+2	0	+1	+1	0	0	0	+1	0	0	0	0	+1	0	0	0	-1	0	0	0	+1	0	+1	+1	+1	+1	0
30	+3	0	+1	+3	+1	0	0	+3	+1	0	0	0	0	0	0	0	0	0	0	0	+1	0	0	0	0	+3	+1
31	+3	0	+1	+3	+2	0	0	+3	+1	0	0	0	-1	0	0	0	0	0	-1	0	0	0	0	-1	-1	+3	+2
32	+2	0	+1	+2	+1	0	0	+2	+1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+2	+1
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	+2	0	0	+2	+1	0	0	+2	+1	0	0	0	0	0	0	0	0	0	0	0	+1	0	0	0	0	+2	+1
35	+2	0	+1	+1	0	0	0	+1	0	0	0	0	+1	0	0	0	-1	0	0	0	+1	0	+1	+1	+1	+1	0
36	0	0	0	0	-1	0	0	0	0	0	0	0	+1	0	0	0	0	0	+1	0	+1	0	0	+1	+1	0	-1
37	+4	0	+1	+3	+1	0	0	+3	+1	0	0	0	+1	0	0	0	-1	0	0	0	+2	0	+1	+1	+1	+3	+1

continued . . .

TABLE XXXVII. (continued)

	38	39	40	41	42	43	44	45	46	47	48	49	52	53	54	55	56	57	58	59	60	61	62	63	64	66	68
38	x	0	+1	+3	+1	0	0	+3	+1	0	0	0	+1	0	0	0	-1	0	0	0	+2	0	+1	+1	+1	+3	+1
39		x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40			x	+1	0	0	0	+1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+1	0
41				x	+1	0	0	+3	+1	0	0	0	0	0	0	0	0	0	0	0	+1	-1	0	0	0	+3	+1
42					x	0	0	+1	+1	0	0	0	-1	0	0	0	0	0	-1	0	-1	0	0	-1	-1	+1	+1
43						x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
44							x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45								x	+1	0	0	0	0	0	0	0	0	0	0	0	+1	0	0	0	0	+3	+1
46									x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+1	+1
47										x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48											x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49												x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52													x	0	0	0	-1	0	+1	0	+2	0	+1	+2	+2	0	-1
53														x	0	0	0	0	0	0	0	0	0	0	0	0	0
54															x	0	0	0	0	0	0	0	0	0	0	0	0
55																x	0	0	0	0	0	0	0	0	0	0	0
56																	x	0	0	0	-1	0	-1	-1	-1	0	0
57																		x	0	0	0	0	0	0	0	0	0
58																			x	0	+1	0	0	+1	+1	0	-1
59																				x	0	0	0	0	0	0	0
60																					x	0	+1	+2	+2	+1	0
61																						x	0	0	0	0	0
62																							x	+1	+1	+1	0
63																								x	+2	0	-1
64																									x	0	-1
66																										x	0
68																											x

apart was tested by means of a Chi-square test using the Watfiv program constructed for one data set in Appendix VA. All species that were recorded at fewer than 5 sites were excluded from the analysis.

The results of the Chi-square tests (Table XXXVIII) revealed 278 significant ($p < .05$, $n=305$) positive associations and 9 significant negative associations. These have been ranked in Table XXXIXA and B respectively, in descending order of significance according to the magnitude of the Chi-square values. Potamogeton zosteriformis appeared in 5 of the 10 most significant positive associations, while P. amplifolius, Vallisneria americana, Nymphaea odorata and Megalodonta beckii each appeared twice within the top 10 positive associations. The positive association of Potamogeton pectinatus and P. richardsonii, although significant, ranked only 113th in overall significance. The most important positive association of P. richardsonii was with P. zosteriformis and ranked 4th in overall significance. The most important association of P. pectinatus was with Myriophyllum exalbescens and ranked 65th in overall significance. However the nonassociation of P. pectinatus with Sparganium spp. formed the most significant of the negative associations.

Besides showing the most highly significant positive associations, Potamogeton zosteriformis also showed the greatest number of significant positive associations (29) (Table XL), followed by Nuphar variegatum with 25, P. richardsonii with 23, Najas flexilis with 21 and Megalodonta beckii with 20. Potamogeton pectinatus showed the greatest number of significant negative associations (5), followed

TABLE XXXVIII. Results of Chi-square tests for the significance of the discrepancy between theoretical frequencies and the observed frequencies for the members of each possible pair of macrophytes to occur together (+) or apart (-) ($p < .05$, $n=305$) within the same site; 0 indicates no significant difference. Symbols in parentheses indicate significant positive associations where joint occurrences were observed at fewer than 5 sites. Symbols followed by exclamation points (!) indicate significant positive or negative associations that did not coincide with net similarities or dissimilarities, respectively in significant environmental preferences (Table XXXVII). All taxa that were recorded at fewer than 5 sites have been deleted. Species numbers represent the following taxa:

1. *Chara* spp.
2. *Riccia fluitans*
3. *Sparganium* spp.
4. *Ruppia maritima*
6. *Potamogeton alpinus*
7. *P. amplifolius*
8. *P. epihydrus*
9. *P. filiformis*
10. *P. foliosus*
11. *P. friesii*
12. *P. gramineus*
14. *P. natans*
15. *P. obtusifolius*
16. *P. pectinatus*
17. *P. praelongus*
18. *P. pusillus*
19. *P. richardsonii*
20. *P. robbinsii*
21. *P. spirillus*
23. *P. vaginatus*
24. *P. zosteriformis*
25. *Najas flexilis*
27. *Alisma triviale*
28. *Sagittaria rigida*
29. *Sagittaria* spp. (except *S. rigida*)
30. *Elodea canadensis*
31. *Vallisneria americana*
32. *Zizania aquatica*
33. *Eleocharis* spp.
34. *Calla palustris*
35. *Lemna minor*
36. *L. trisulca*
37. *Spirodela polyrhiza*
38. *Polygonum amphibium*
40. *Ceratophyllum demersum*
41. *Nymphaea odorata*
42. *N. tetragona*
43. *N. tuberosa*
44. *Nuphar microphyllum*
45. *N. variegatum*
46. *Brasenia schreberi*
47. *Caltha palustris*
48. *Ranunculus aquatilis*
54. *Callitriche* spp.
56. *Myriophyllum exalbescens*
59. *Hippuris vulgaris*
60. *Sium suave*
61. *Mentha arvensis*
62. *Utricularia intermedia*
63. *U. minor*
64. *U. vulgaris*
66. *Megalodonta beckii*
68. *Zosterella dubia*
69. Submerged mosses

TABLE XXXVIII.

	1	2	3	4	6	7	8	9	10	11	12	14	15	16	17	18	19	20	21	23	24	25	27	28	29	30	31	32	33	34	35	36	37
1	x	0	-	0	0	+	0	+	0	+	(+)	!+	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0	0	0	0	-
2		x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(+)!
3			x	0	(+)	0	+	0	0	0	0	0	0	-	0	0	0	0	(+)	0	+	0	0	0	0	+	0	0	+!	0	0	0	+
4				x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6					x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7						x	+	0	+!	0	+	+	0	0	+	0	0	(+)	!0	0	+	+	0	0	0	+	+	0	0	0	0	0	0	0
8							x	0	0	0	0	0	(+)	-	0	0	0	0	(+)	0	+	0	0	0	0	0	0	0	0	0	0	0	+
9								x	0	0	+!	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10									x	0	+!	0	(+)	!0	0	0	0	0	0	0	+!	+!	0	(+)	!0	+!	0	0	0	(+)	!0	0	0
11										x	+	+	0	+!	+	0	+	0	0	0	+	+	0	0	0	+	0	0	0	0	0	0	+!
12											x	0	0	0	0	0	0	0	0	0	+	+	+!	0	0	0	+	0	0	0	0	0	0
14												x	0	0	+	0	+	0	0	0	+	+	0	0	+	+	0	+	0	0	0	+!	0
15													x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(+)	0	0	0
16														x	0	-!	+!	0	0	+	+!	0	-	0	0	0	0	0	0	0	0	0	0
17															x	0	+	(+)	0	0	+	+	0	0	0	+	+	+	0	0	0	0	0
18																x	0	0	0	0	0	0	+!	0	0	0	0	0	0	0	0	0	0
19																	x	0	0	0	+	+	+!	0	+!	+	+	+	0	0	0	+!	+
20																		x	0	0	0	0	0	0	0	0	(+)	!0	0	0	0	0	0
21																			x	0	0	0	0	0	0	0	(+)	0	0	0	0	0	0
23																				x	0	0	0	0	0	0	0	0	0	0	0	0	0
24																					x	+	-!	(+)	!+	+	+	+	0	+	0	+!	+
25																						x	0	0	0	+	+	+	0	+	0	0	0
27																							x	0	0	0	+	+	0	0	0	0	0
28																								x	0	0	0	0	+!	0	0	0	0
29																									x	0	0	0	0	(+)	0	0	0
30																										x	+	0	+	0	+	+!	+
31																											x	+	+	0	0	0	+
32																												x	+	0	0	+!	+
33																													x	0	0	0	0
34																														x	+!	0	+
35																															x	+!	+
36																																x	+!
37																																	x

continued . . .

TABLE XXXVIII. (continued)

	38	40	41	42	43	44	45	46	47	48	54	56	59	60	61	62	63	64	66	68	69
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(+)!0		0	(+)!0		0
3	+	0	0	0	0	+!	+	0	0	0	+!	0	0	+	0	+	0	+	0	0	+
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(+)	0	0	0	0	0
7	0	0	+	+	(+)!0		+	+	0	0	0	0	0	0	0	0	0	0	+	+	0
8	0	0	(+)	0	0	0	+	+	0	0	0	0	0	0	0	+	0	+	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(+)!0		0	0	0
11	0	+	0	+	0	0	+	0	0	0	0	+	0	0	0	0	0	0	+	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	+	+	(+)	0	0	+	+	0	0	0	+!	0	0	0	0	0	+	+	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(+)!(+)0			0	0	0
16	0	+!	0	0	0	0	0	0	0	0	0	+	0	-	0	0	0	0	0	0	0
17	0	+	+	+	0	0	+	0	0	+!	0	0	0	0	0	0	0	0	+	+	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+!	0	0	0
19	+	+	0	0	+!	+!	+	0	0	+	0	+	0	0	0	0	0	+!	+	+	0
20	0	0	(+)!+)!+)!0				(+)!0		0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	(+)(+)		0	(+)!+		0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	+!	+!	0	0	0	0	0	0	0	0
24	+	+	+	+	+!	0	+	0	0	0	0	+!	0	0	0	0	0	+!	+	+	0
25	0	+	+	+	+!	+!	+	0	0	0	0	0	0	0	0	0	0	0	+	+	0
27	0	0	0	0	0	0	-!	0	0	0	+!	0	0	+!	+	0	0	0	0	0	0
28	0	0	0	(+)	0	(+)!0		0	0	0	0	0	0	0	0	0	0	0	(+)	0	0
29	+	+	0	0	0	+!	+	0	0	0	0	0	+!	+	0	0	0	0	0	0	0
30	0	+	0	0	+!	0	+	0	0	0	0	0	0	0	0	0	0	0	+	+	0
31	0	+	0	0	+!	0	+	0	0	0	0	0	0	0	0	0	0	0	+	+	0
32	0	+	0	0	+!	0	+	0	0	+!	0	0	0	0	0	0	0	+!	+	0	0
33	0	0	0	0	0	0	0	0	0	+!	0	0	0	+!	0	0	0	0	0	0	0
34	0	0	0	0	0	0	+	0	(+)!0		0	0	0	0	0	0	0	+!	0	0	0
35	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	+!	+!	0	0	+!	0	+!	0	0	0	+!	+!	0	0	0	0	0	+	+!	0	0
37	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	+	0	0

continued . . .

TABLE XXXVIII. (continued)

	38	40	41	42	43	44	45	46	47	48	54	56	59	60	61	62	63	64	66	68	69
38	x	0	0	0	0	0	0	0	0	0	0	+!	0	0	0	0	0	0	0	0	0
40		x	0	+!	0	0	+	0	0	0	0	0	0	0	0	0	0	+!	+	+!	0
41			x	+	0	0	+	+	0	0	0	0	0	0	0	0	0	0	+	0	0
42				x	+!	0	+	+	0	0	0	0	0	0	0	0	0	0	+	0	0
43					x	0	0	0	0	+!	0	0	0	0	0	0	0	0	+!	+!	0
44						x	+!	0	0	0	0	0	0	0	0	0	0	0	0	0	0
45							x	+	0	0	0	0	0	0	0	0	0	+!	+	+	0
46								x	0	0	0	0	0	0	0	0	+!	0	0	0	0
47									x	0	0	0	0	(+)!	0	0	0	0	0	0	0
48										x	0	0	0	0	0	0	0	0	0	0	0
54											x	0	0	0	0	0	0	0	0	0	0
56												x	0	0	0	0	0	0	0	0	0
59													x	+!	0	0	0	0	0	0	+
60														x	+!	0	0	0	0	0	0
61															x	0	0	0	0	0	0
62																x	+	+	0	0	0
63																	x	0	0	0	+
64																		x	0	0	+
66																			x	+!	0
68																				x	0
69																					x

TABLE XXXIX. Significant ($p < .05$, $n=305$) positive (A) and negative (B) macrophyte associations ranked in descending order of significance according to decreasing Chi-square values. All taxa that were recorded at fewer than 5 sites have been deleted. Species numbers represent the following taxa:

1. *Chara* spp.
2. *Riccia fluitans*
3. *Sparganium* spp.
4. *Ruppia maritima*
6. *Potamogeton alpinus*
7. *P. amplifolius*
8. *P. epihydrus*
9. *P. filiformis*
10. *P. foliosus*
11. *P. friesii*
12. *P. gramineus*
14. *P. natans*
15. *P. obtusifolius*
16. *P. pectinatus*
17. *P. praelongus*
18. *P. pusillus*
19. *P. richardsonii*
20. *P. robbinsii*
21. *P. spirillus*
23. *P. vaginatus*
24. *P. zosteriformis*
25. *Najas flexilis*
27. *Alisma triviale*
28. *Sagittaria rigida*
29. *Sagittaria* spp. (except *S. rigida*)
30. *Elodea canadensis*
31. *Vallisneria americana*
32. *Zizania aquatica*
33. *Eleocharis* spp.
34. *Calla palustris*
35. *Lemna minor*
36. *L. trisulca*
37. *Spirodela polyrhiza*
38. *Polygonum amphibium*
40. *Ceratophyllum demersum*
41. *Nymphaea odorata*
42. *N. tetragona*
43. *N. tuberosa*
44. *Nuphar microphyllum*
45. *N. variegatum*
46. *Brasenia schreberi*
47. *Caltha palustris*
48. *Ranunculus aquatilis*
54. *Callitriche* spp.
56. *Myriophyllum exalbescens*
59. *Hippuris vulgaris*
60. *Sium suave*
61. *Mentha arvensis*
62. *Utricularia intermedia*
63. *U. minor*
64. *U. vulgaris*
66. *Megalodonta beckii*
68. *Zosterella dubia*
69. Submerged mosses

TABLE XXXIX.

A. Significant positive associations

1. 24 x 30
2. 41 x 46
3. 24 x 66
4. 19 x 24
5. 41 x 42
6. 31 x 66
7. 7 x 25
8. 11 x 24
9. 7 x 31
10. 24 x 45
11. 7 x 41
12. 24 x 31
13. 30 x 31
14. 14 x 45
15. 7 x 46
16. 17 x 45
17. 19 x 30
18. 25 x 31
19. 7 x 42
20. 30 x 66
21. 24 x 25
22. 17 x 25
23. 14 x 24
24. 31 x 46
25. 1 x 14
26. 25 x 42
27. 19 x 31
28. 45 x 66
29. 7 x 24
30. 31 x 68
31. 36 x 40
32. 30 x 40
33. 7 x 68
34. 31 x 43
35. 14 x 17
36. 24 x 37
37. 8 x 21 > equal
38. 43 x 66 >
39. 35 x 36
40. 27 x 60
41. 11 x 14
42. 29 x 38
43. 17 x 24
44. 35 x 37
45. 30 x 68
46. 25 x 68
47. 42 x 46
48. 7 x 66
49. 24 x 42
50. 29 x 36
51. 11 x 25
52. 19 x 40
53. 25 x 30
54. 31 x 45
55. 24 x 29
56. 3 x 33
57. 17 x 19
58. 42 x 45
59. 66 x 68
60. 7 x 43
61. 45 x 46
62. 3 x 60 > equal
63. 21 x 41 >
64. 32 x 45
65. 16 x 56
66. 19 x 45
67. 42 x 66
68. 29 x 45
69. 25 x 40
70. 29 x 37 > equal
71. 36 x 66 >
72. 37 x 66
73. 19 x 25
74. 28 x 34
75. 19 x 32
76. 25 x 66
77. 34 x 37
78. 31 x 40
79. 20 x 43
80. 30 x 32
81. 25 x 45
82. 30 x 43
83. 24 x 32
84. 3 x 8
85. 7 x 45
86. 33 x 48
87. 41 x 45
88. 29 x 32
89. 11 x 17
90. 63 x 69
91. 7 x 12
92. 23 x 59
93. 35 x 38
94. 41 x 66
95. 24 x 36 > equal
96. 14 x 42 >
97. 1 x 9
98. 21 x 31
99. 7 x 30
100. 19 x 29
101. 29 x 35
102. 19 x 56
103. 40 x 68
104. 8 x 62
105. 24 x 43
106. 35 x 40
107. 37 x 40
108. 9 x 12 > equal
109. 24 x 68 >
110. 31 x 32
111. 17 x 31
112. 10 x 28
113. 16 x 19
114. 21 x 45 > equal
115. 14 x 46 >
116. 8 x 46
117. 32 x 66
118. 11 x 19
119. 44 x 45
120. 37 x 38
121. 7 x 17
122. 40 x 45 > equal
123. 19 x 66 >
124. 47 x 60
125. 1 x 12
126. 36 x 37
127. 31 x 44
128. 3 x 45
129. 19 x 68
130. 23 x 56
131. 3 x 44
132. 36 x 56
133. 32 x 43
134. 30 x 45
135. 14 x 25
136. 3 x 37
137. 36 x 43
138. 25 x 32
139. 60 x 61
140. 11 x 45
141. 7 x 8
142. 2 x 37
143. 33 x 60
144. 18 x 27
145. 14 x 66
146. 40 x 64
147. 28 x 66
148. 12 x 25
149. 17 x 41
150. 7 x 20

continued . . .

TABLE XXXIX. (continued)

151. 27 x 54
152. 17 x 30
153. 29 x 40
154. 26 x 66
155. 11 x 42
156. 1 x 11
157. 1 x 25
158. 12 x 27
159. 14 x 29
160. 10 x 15
161. 12 x 24
162. 3 x 62
163. 27 x 33
164. 15 x 34 ⟩ equal
165. 15 x 63 ⟩
166. 34 x 47 ⟩
167. 32 x 40
168. 17 x 68
169. 21 x 44 ⟩ equal
170. 43 x 68 ⟩
171. 38 x 56
172. 29 x 30
173. 3 x 69
174. 10 x 12
175. 11 x 56
176. 31 x 37
177. 11 x 40 ⟩ equal
178. 8 x 41 ⟩
179. 14 x 32
180. 8 x 37
181. 29 x 60
182. 24 x 38
183. 20 x 42 ⟩
184. 21 x 42 ⟩ equal
185. 42 x 43 ⟩
186. 19 x 48 ⟩ equal
187. 3 x 54 ⟩
188. 7 x 10
189. 19 x 43
190. 17 x 42
191. 17 x 66
192. 14 x 41
193. 45 x 68
194. 11 x 30
195. 28 x 44
196. 46 x 63
197. 25 x 34
198. 24 x 64
199. 27 x 61
200. 24 x 56
201. 14 x 64 ⟩ equal
202. 45 x 64 ⟩
203. 36 x 45
204. 20 x 31
205. 32 x 37
206. 16 x 24
207. 64 x 69
208. 6 x 62
209. 3 x 64
210. 19 x 27 ⟩ equal
211. 36 x 54 ⟩
212. 16 x 40
213. 17 x 40
214. 20 x 41
215. 28 x 42
216. 7 x 14 ⟩ equal
217. 14 x 43 ⟩
218. 20 x 45 ⟩
219. 14 x 30 ⟩ equal
220. 19 x 36 ⟩
221. 19 x 37
222. 14 x 40
223. 25 x 41
224. 32 x 64
225. 17 x 48
226. 17 x 32
227. 3 x 21
228. 10 x 30 ⟩ equal
229. 34 x 35 ⟩
230. 32 x 36
231. 59 x 69
232. 11 x 66
233. 14 x 19 ⟩ equal
234. 19 x 38 ⟩
235. 8 x 64 ⟩ equal
236. 63 x 64 ⟩
237. 40 x 66
238. 25 x 43
239. 24 x 34
240. 18 x 64
241. 12 x 31
242. 19 x 64
243. 36 x 64
244. 3 x 38
245. 10 x 24
246. 24 x 28
247. 59 x 60
248. 17 x 20
249. 37 x 64
250. 14 x 36
251. 36 x 38
252. 30 x 37
253. 34 x 45
254. 3 x 6
255. 3 x 24
256. 11 x 12 ⟩ equal
257. 11 x 16 ⟩
258. 8 x 24 ⟩
259. 10 x 25
260. 1 x 7
261. 2 x 62 ⟩ equal
262. 8 x 15 ⟩
263. 15 x 62
264. 2 x 66
265. 25 x 44
266. 11 x 37
267. 24 x 41
268. 40 x 42
269. 29 x 59
270. 16 x 23
271. 29 x 44
272. 34 x 64
273. 10 x 63 ⟩ equal
274. 10 x 34 ⟩
275. 3 x 29 ⟩ equal
276. 32 x 48 ⟩
277. 19 x 44 ⟩ equal
278. 14 x 56 ⟩

B. Significant negative associations

1. 3 x 16
2. 24 x 27
3. 16 x 60
4. 16 x 18
5. 8 x 16
6. 1 x 37
7. 27 x 45
8. 16 x 27
9. 1 x 3

TABLE XL. Total numbers of significant positive and negative associations observed for each macrophyte species or species group, and the numbers of these associations that did not coincide (N.C.) with net similarities or dissimilarities, respectively in significant preferences for the monitored environmental parameters. All taxa that were recorded at fewer than 5 sites have been deleted.

Species or species group	Positive		Negative	
	Total	N.C.	Total	N.C.
1. *Chara* spp.	6	1	2	0
2. *Riccia fluitans*	3	3	0	0
3. *Sparganium* spp.	15	3	2	0
4. *Ruppia maritima*	0	0	0	0
6. *Potamogeton alpinus*	2	0	0	0
7. *P. amplifolius*	18	3	0	0
8. *P. epihydrus*	11	0	1	0
9. *P. filiformis*	2	1	0	0
10. *P. foliosus*	9	9	0	0
11. *P. friesii*	15	2	0	0
12. *P. gramineus*	9	4	0	0
14. *P. natans*	19	2	0	0
15. *P. obtusifolius*	5	2	0	0
16. *P. pectinatus*	6	4	5	1
17. *P. praelongus*	17	1	0	0
18. *P. pusillus*	2	2	1	1
19. *P. richardsonii*	23	7	0	0
20. *P. robbinsii*	7	6	0	0
21. *P. spirillus*	7	1	0	0
23. *P. vaginatus*	3	2	0	0
24. *P. zosteriformis*	29	7	1	1
25. *Najas flexilis*	21	3	0	0
27. *Alisma triviale*	7	6	3	2
28. *Sagittaria rigida*	6	3	0	0
29. *Sagittaria* spp. (except *S. rigida*)	15	4	0	0
30. *Elodea canadensis*	17	2	0	0
31. *Vallisneria americana*	16	2	0	0
32. *Zizania aquatica*	16	4	0	0
33. *Eleocharis* spp.	4	4	0	0
34. *Calla palustris*	10	4	0	0
35. *Lemna minor*	6	2	0	0
36. *L. trisulca*	15	14	0	0
37. *Spirodela polyrhiza*	17	3	1	0

continued . . .

TABLE XL. (continued)

Species or species group	Positive		Negative	
	Total	N.C.	Total	N.C.
38. Polygonum amphibium	8	2	0	0
40. Ceratophyllum demersum	19	5	0	0
41. Nymphaea odorata	12	1	0	0
42. N. tetragona	15	3	0	0
43. N. tuberosa	13	13	0	0
44. Nuphar microphyllum	7	7	0	0
45. N. variegatum	25	4	1	1
46. Brasenia schreberi	7	1	0	0
47. Caltha palustris	2	2	0	0
48. Ranunculus aquatilis	5	4	0	0
54. Callitriche spp.	3	3	0	0
56. Myriophyllum exalbescens	8	5	0	0
59. Hippuris vulgaris	4	3	0	0
60. Sium suave	7	5	1	0
61. Mentha arvensis	2	1	0	0
62. Utricularia intermedia	7	2	0	0
63. U. minor	5	2	0	0
64. U. vulgaris	14	7	0	0
66. Megalodonta beckii	20	4	0	0
68. Zosterella dubia	11	3	0	0

by Alisma triviale with 3 and Sparganium spp. and Chara spp. with 2 each.

Of the 278 significant positive associations, 185 or 66.5% (Table XXXVIII) coincided with net similarities in significant environmental preferences (Table XXXVII). The remaining 93 associations could not be explained on the basis of net similarity in preferences, at least for the parameters that were examined. Of the 9 significant negative associations, 3 could not be explained on the basis of net dissimilarity of preference for the parameters examined.

The proportions of unpredicted positive associations with regard to environmental preferences varied with the taxa, and almost all species or species groups showed some unpredicted associations (Table XL). All of the positive associations shown by Riccia fluitans, Potamogeton foliosus, P. pusillus, Eleocharis spp., Nymphaea tuberosa, Nuphar microphyllum, Caltha palustris and Callitriche spp. did not coincide with net similarities in significant environmental preferences because these taxa did not show any significant preferences. However more than half of the positive associations shown by Potamogeton pectinatus, P. robbinsii, P. vaginatus, Alisma triviale, Lemna trisulca, Ranunculus aquatilis, Myriophyllum exalbescens, Hippuris vulgaris and Sium suave could not be explained on the basis of net similarities in preferences. Two of the 3 negative associations shown by Alisma triviale and one of the 5 shown by Potamogeton pectinatus could also not be explained on the basis of net dissimilarities.

In an effort to rank the similarities of preferences for other species, a similarity index (S) was calculated for the

significant positive associations shown by the members of each possible species or species group pair:

$$S = \frac{2c}{a+b} \quad \ldots\ldots\ldots\ldots (27)$$

where a and b are the numbers of significant positive associations shown by species A and B respectively, and c is the number of significant positive associations that are common to both species A and B. Only positive associations where joint occurrences were observed at 5 or more sites were considered. It is important to note that this index was not used to denote the similarity of the respective communities, in the sense of Bray and Curtis (1957) and Loucks (1962), since individual communities were not compared at this level, but this index rather reflected the similarity of the species groupings within which each of the species tended to occur significantly frequently.

The association similarity values for each possible species or species group pair are given in Table XLI. Species pairs with high association similarity indices would be expected to occur frequently with each other and within similar communities. The two most important species groupings in terms of association similarity ($S > .70$) are abstractly represented in Fig.101. The distances between the species are theoretically the reciprocals of the Chi-square values that tested the significance of the frequency with which the members of the respective pairs were observed to occur jointly; the relative positions of the species within the multiple cluster cannot be represented in two dimensions and the distance values are only

TABLE XLI. Macrophyte association similarity indices for possible species or species group pairs. Only significant positive associations where the joint occurrences were observed at 5 or more sites were considered. Species for which all joint occurrences were observed at fewer than 5 sites have been deleted. Species numbers represent the following taxa:

1. *Chara* spp.
3. *Sparganium* spp.
7. *Potamogeton amplifolius*
8. *P. epihydrus*
9. *P. filiformis*
10. *P. foliosus*
11. *P. friesii*
12. *P. gramineus*
14. *P. natans*
16. *P. pectinatus*
17. *P. praelongus*
18. *P. pusillus*
19. *P. richardsonii*
21. *P. spirillus*
23. *P. vaginatus*
24. *P. zosteriformis*
25. *Najas flexilis*
27. *Alisma triviale*
29. *Sagittaria* spp. (except *S. rigida*)
30. *Elodea canadensis*
31. *Vallisneria americana*
32. *Zizania aquatica*
33. *Eleocharis* spp.
34. *Calla palustris*
35. *Lemna minor*
36. *L. trisulca*
37. *Spirodela polyrhiza*
38. *Polygonum amphibium*
40. *Ceratophyllum demersum*
41. *Nymphaea odorata*
42. *N. tetragona*
43. *N. tuberosa*
44. *Nuphar microphyllum*
45. *N. variegatum*
46. *Brasenia schreberi*
48. *Ranunculus aquatilis*
54. *Callitriche* spp.
56. *Myriophyllum exalbescens*
59. *Hippuris vulgaris*
60. *Sium suave*
61. *Mentha arvensis*
62. *Utricularia intermedia*
63. *U. minor*
64. *U. vulgaris*
66. *Megalodonta beckii*
68. *Zosterella dubia*
69. Submerged mosses

TABLE XLI.

	1	3	7	8	9	10	11	12	14	16	17	18	19	21	23	24	25	27	29	30
1	x	0	0.27	0.14	0.25	0.56	0.29	0.40	0.24	0.17	0.36	0	0.21	0	0	0.29	0.32	0.15	0.10	0.35
3		x	0.21	0.53	0	0.11	0.21	0.09	0.25	0.11	0.14	0.13	0.39	0.14	0	0.29	0.13	0.30	0.43	0.27
7			x	0.17	0.22	0.38	0.58	0.40	0.57	0.09	0.56	0	0.41	0.12	0	0.59	0.69	0.09	0.26	0.55
8				x	0	0.33	0.27	0.25	0.31	0.15	0.26	0.22	0.27	0.25	0	0.29	0.23	0	0.36	0.33
9					x	0.29	0.24	0.18	0.10	0	0	0	0	0	0	0	0.19	0.22	0	0
10						x	0.40	0.43	0.33	0.18	0.38	0	0.21	0	0	0.24	0.33	0.17	0.20	0.27
11							x	0.25	0.59	0.38	0.58	0	0.58	0.13	0.22	0.60	0.53	0.18	0.47	0.56
12								x	0.36	0.27	0.40	0	0.31	0	0	0.28	0.43	0	0.08	0.46
14									x	0.40	0.69	0.10	0.62	0.10	0.09	0.68	0.68	0.08	0.41	0.61
16										x	0.36	0	0.28	0.29	0	0.24	0.32	0.15	0.29	0.35
17											x	0	0.62	0.12	0	0.64	0.80	0.09	0.45	0.73
18												x	0.16	0	0	0.07	0	0	0	0
19													x	0.08	0.15	0.71	0.52	0	0.53	0.70
21														x	0	0.06	0	0	0.12	0.12
23															x	0.13	0	0	0.11	0
24																x	0.72	0.11	0.47	0.71
25																	x	0.15	0.41	0.72
27																		x	0.18	0.08
29																			x	0.44
30																				x

continued . . .

TABLE XLI. (continued)

	31	32	33	34	35	36	37	38	40	41	42	43	44	45	46	48	54	56	59
1	0.29	0.20	0	0.17	0	0.10	0.09	0	0.24	0.27	0.50	0	0	0.27	0.40	0	0	0.29	0
3	0.29	0.37	0.12	0.42	0.32	0.50	0.34	0.29	0.31	0.18	0.17	0.11	0.22	0.27	0.12	0.13	0	0.19	0.35
7	0.52	0.53	0	0.27	0	0.26	0.31	0.08	0.57	0.64	0.54	0.29	0.19	0.60	0.30	0.11	0	0.17	0
8	0.36	0.38	0.18	0.62	0.15	0.36	0.27	0.40	0.31	0.38	0.35	0.17	0.33	0.26	0.36	0	0.20	0.13	0
9	0.12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0.50	0.32	0	0.36	0	0.10	0.19	0.15	0.25	0.43	0.40	0.40	0	0.28	0	0	0	0.15	0
11	0.67	0.69	0	0.38	0.19	0.53	0.32	0.35	0.65	0.58	0.56	0.30	0.20	0.46	0.21	0.22	0	0.35	0
12	0.25	0.26	0.15	0.27	0	0.08	0.16	0.12	0.29	0.33	0.42	0.29	0.14	0.30	0.15	0	0.17	0.24	0
14	0.59	0.67	0	0.32	0.24	0.53	0.57	0.37	0.68	0.57	0.62	0.33	0.25	0.74	0.26	0.18	0.09	0.30	0.09
16	0.29	0.30	0	0.17	0.17	0.38	0.27	0.43	0.24	0.13	0.38	0.36	0.18	0.27	0	0.22	0	0.57	0.20
17	0.65	0.60	0.10	0.27	0.09	0.45	0.50	0.17	0.69	0.56	0.69	0.38	0.29	0.70	0.40	0.11	0	0.33	0
18	0	0.13	0.33	0.25	0	0.12	0.11	0	0.10	0	0	0	0	0.08	0	0	0.40	0	0
19	0.63	0.65	0.15	0.34	0.34	0.63	0.56	0.32	0.76	0.38	0.48	0.29	0.21	0.64	0.15	0.08	0.15	0.39	0.07
21	0.12	0.14	0	0.28	0	0.12	0	0	0.10	0.20	0.18	0	0.34	0	0.40	0	0	0	0
23	0	0	0	0	0	0.11	0	0.18	0.09	0	0	0	0	0	0	0	0	0.18	0
24	0.56	0.62	0.06	0.24	0.35	0.56	0.64	0.33	0.72	0.38	0.47	0.24	0.30	0.77	0.25	0.13	0.13	0.33	0.06
25	0.65	0.55	0	0.16	0.16	0.41	0.51	0.15	0.63	0.50	0.62	0.33	0.25	0.70	0.35	0.18	0	0.30	0
27	0.18	0.10	0.18	0	0	0.18	0.09	0.13	0.08	0	0	0.17	0.17	0.06	0	0.40	0	0.13	0.18
29	0.53	0.55	0.21	0.38	0.38	0.60	0.58	0.52	0.53	0.25	0.32	0.40	0.30	0.46	0.21	0.11	0.22	0.43	0.11
30	0.75	0.71	0	0.35	0.26	0.63	0.48	0.32	0.72	0.54	0.67	0.27	0.36	0.63	0.29	0.20	0	0.32	0.10
31	x	0.62	0	0.38	0.19	0.53	0.39	0.26	0.53	0.50	0.56	0.30	0.20	0.56	0.21	0.22	0	0.17	0
32		x	0	0.50	0.40	0.62	0.60	0.45	0.79	0.52	0.58	0.53	0.42	0.63	0.22	0.24	0.12	0.36	0.11
33			x	0	0	0	0.10	0.17	0	0	0	0	0.22	0.07	0	0	0.29	0	0
34				x	0.17	0.48	0.27	0.43	0.48	0.40	0.38	0.18	0.18	0.20	0.20	0	0	0.14	0
35					x	0.38	0.45	0.43	0.24	0	0.13	0	0.18	0.27	0	0	0.22	0.29	0.20
36						x	0.58	0.52	0.59	0.33	0.40	0.20	0.30	0.41	0.21	0.11	0	0.35	0.11
37							x	0.50	0.63	0.16	0.31	0.48	0.38	0.70	0	0.11	0.21	0.42	0.10
38								x	0.44	0.12	0.11	0.46	0.46	0.31	0	0.18	0.36	0.38	0.17
40									x	0.50	0.48	0.42	0.33	0.70	0.17	0.18	0.09	0.46	0.09
41										x	0.74	0.14	0.14	0.48	0.46	0.17	0	0.24	0
42											x	0.13	0.13	0.53	0.57	0.15	0	0.33	0

continued . . .

TABLE XLI. (continued)

	59	60	61	62	63	64	66	68	69
1	0	0	0	0	0	0.11	0.35	0	0.40
3	0.35	0.21	0.13	0.13	0.27	0.38	0.20	0.17	0.12
7	0	0	0	0.11	0	0.28	0.61	0.54	0
8	0	0.15	0	0.20	0.22	0.40	0.33	0.35	0.36
9	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0.11	0.36	0.53	0
11	0	0	0	0	0	0.43	0.63	0.64	0
12	0	0.13	0.18	0	0	0.09	0.38	0.42	0
14	0.09	0.08	0	0	0	0.38	0.63	0.07	0
16	0.20	0	0	0	0	0.32	0.35	0.38	0
17	0	0	0	0	0	0.41	0.85	0.69	0
18	0	0.25	0.50	0	0	0	0	0	0
19	0.07	0.14	0.08	0	0	0.39	0.65	0.48	0.07
21	0	0	0	0	0	0.14	0.12	0.18	0
23	0	0.22	0	0	0	0	0	0	0.29
24	0.06	0.12	0	0.13	0	0.49	0.71	0.47	0.13
25	0	0	0	0	0	0.44	0.78	0.62	0
27	0.18	0.15	0.22	0	0	0.20	0.08	0.12	0
29	0.11	0.19	0.12	0	0	0.64	0.56	0.40	0.21
30	0.10	0.09	0	0	0	0.47	0.76	0.67	0
31	0	0	0	0	0	0.43	0.69	0.72	0
32	0.11	0.10	0	0	0	0.52	0.71	0.75	0
33	0	0.40	0.67	0.29	0	0.12	0	0.25	0
34	0	0	0	0	0	0.32	0.35	0.38	0
35	0.20	0.17	0	0	0	0.42	0.26	0.13	0
36	0.11	0.10	0	0	0	0.43	0.44	0.40	0
37	0.10	0.18	0	0.21	0	0.55	0.48	0.46	0.20
38	0.17	0.29	0	0.18	0	0.48	0.32	0.22	0.17
40	0.09	0.08	0	0	0	0.44	0.78	0.55	0.09
41	0	0	0	0	0	0.27	0.54	0.63	0
42	0	0	0	0	0	0.35	0.67	0.70	0

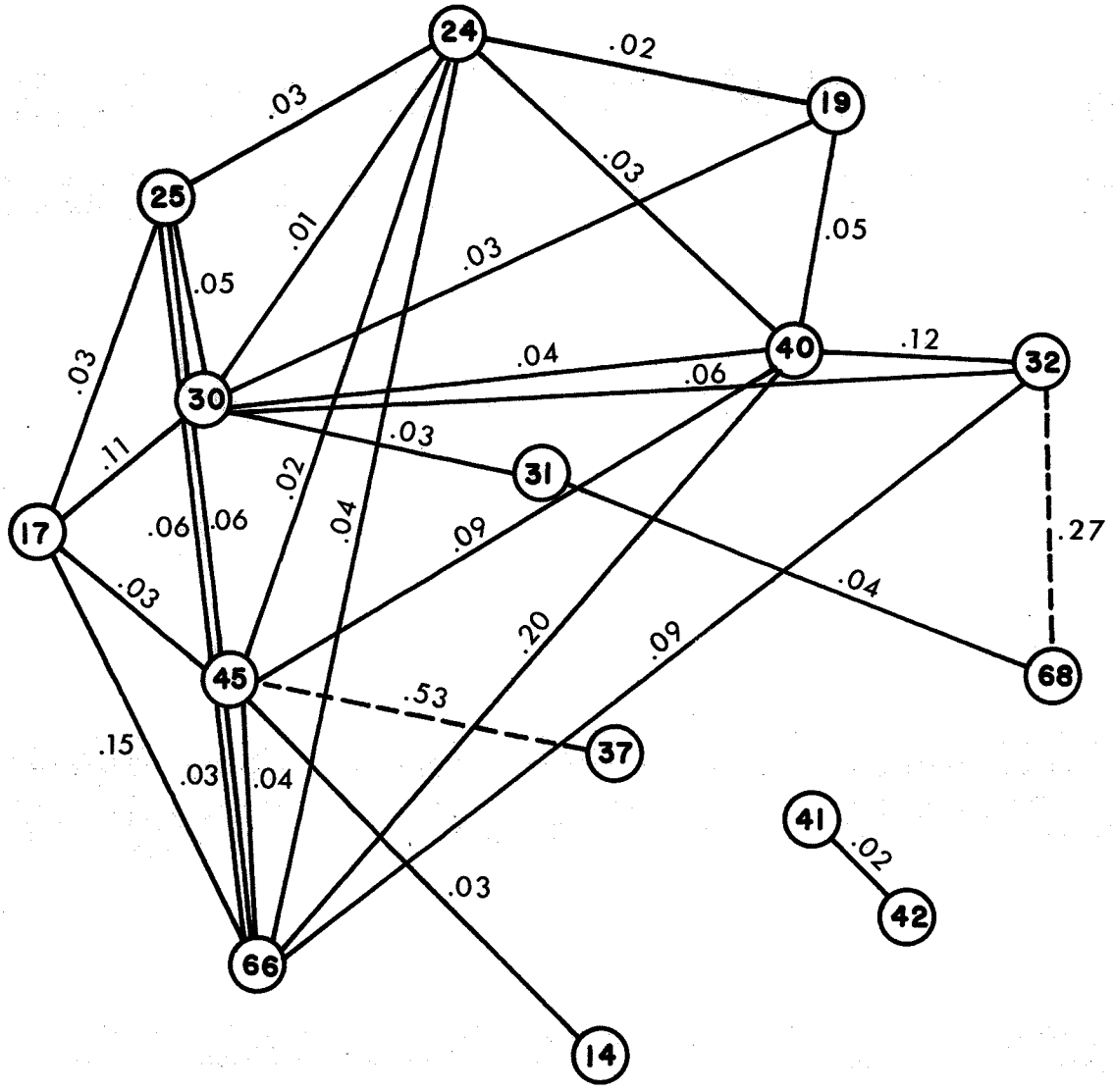
continued. . .

TABLE XLI. (continued)

	43	44	45	46	48	54	56	59	60	61	62	63	64	66	68	69
43	x	0.40	0.34	0	0.25	0.25	0.46	0	0	0	0	0	0.18	0.45	0.53	0
44		x	0.28	0.22	0.25	0	0.15	0.22	0.36	0	0.25	0	0.33	0.27	0.40	0.22
45			x	0.21	0.15	0.15	0.31	0.07	0.13	0	0.15	0	0.49	0.73	0.53	0.14
46				x	0	0	0.17	0	0	0	0	0	0.24	0.38	0.29	0
48					x	0	0.18	0	0.11	0	0	0	0.13	0.20	0.31	0
54						x	0.18	0	0.22	0.40	0.33	0	0.25	0.10	0	0.29
56							x	0	0	0	0	0	0.38	0.40	0.22	0
59								x	0.20	0.33	0	0.33	0.12	0	0	0
60									x	0.25	0.22	0	0.11	0	0	0.40
61										x	0	0	0	0	0	0
62											x	0	0.25	0	0	0.29
63												x	0.13	0	0	0
64													x	0.53	0.35	0.12
66														x	0.67	0
68															x	0
69																x

Figure 101. An abstract representation of the interrelations between macrophyte species for which the association similarity index exceeded a value of 0.70. Species joined by solid lines were themselves significantly ($p < .05$, $n=305$) positively associated, while those joined by broken lines were not significantly associated although the similarity index was greater than 0.70. Species not joined by lines showed association similarity indices that were less than 0.70. Values along the lines represent approximations of the theoretical distances between the species and are the reciprocals of the Chi-square values that tested the significance of the frequency with which the members of the respective pairs were observed to occur jointly. Species numbers represent the following taxa:

14. Potamogeton natans
17. P. praelongus
19. P. richardsonii
24. P. zosteriformis
25. Najas flexilis
30. Elodea canadensis
31. Vallisneria americana
32. Zizania aquatica
37. Spirodela polyrhiza
40. Ceratophyllum demersum
41. Nymphaea odorata
42. N. tetragona
45. Nuphar variegatum
66. Megalodonta beckii
68. Zosterella dubia


24
19
25
30
40
32
31
17
45
68
37
41
42
66
14
.02
.03
.03
.01
.05
.03
.05
.03
.04
.06
.12
.03
.11
.02
.04
.06
.06
.09
.27
.04
.03
.20
.09
.53
.15
.03
.04
.03
.02

approximations of the true values owing to the many sources of error.

In the multiple cluster in Fig.101, Potamogeton praelongus (sp. 17), Najas flexilis (sp. 25), Elodea canadensis (sp. 30), Nuphar variegatum (sp. 45), Megalodonta beckii (sp. 66), Potamogeton zosteriformis (sp. 24), P. richardsonii (sp. 19), Vallisneria americana (sp. 31) and Zizania aquatica (sp. 32) showed high similarities in their significant associations for other species and were also significantly positively associated with each other. This species group was characteristic of lakes and its members showed a significant preference for low values of total filtrable residue and total alkalinity. Of these two parameters, Ceratophyllum demersum (sp. 40) showed a significant preference only for low values of total filtrable residue while Zosterella dubia (sp. 68) showed a significant preference only for low values of total alkalinity. Although Zizania aquatica and Zosterella dubia showed a high association similarity index, they were not themselves significantly positively associated. Nuphar variegatum (sp. 45) showed a high similarity in associations to Spirodela polyrhiza (sp. 37) but these two species were not significantly positively associated, perhaps partly because of the latter's preference for waters of low pH.

The second most important species grouping in terms of association similarity was composed of Nymphaea odorata (sp. 41) and N. tetragona (sp. 42); these species were highly similar to each other in their significant associations with other species and were themselves significantly positively associated, despite the fact that they shared a common significant preference for only one

environmental parameter, that of total alkalinity.

Other, less similar and more complex association groupings may be obtained from Table XLI.

II. Gastropods

A. Systematics

A total of 1469 species lots was examined from the 305 sites; these were composed of 42 species whose relative frequencies within the study area are given in Table XLII. Nomenclature was followed according to F.C. Baker (1911, 1928, 1945); LaRocque (1968) and Clarke (1973). The systematics of many of these groups are currently in a state of flux. For the Physidae, F.C. Baker (1928) recognized several species of Physa but did not observe P. jennessi skinneri Taylor. Clarke (1973) recognized only 3 species within the Canadian Interior Basin: P. gyrina Say, P. jennessi Dall and P. johnsoni Clench. The latter species is known to occur in Alberta and falls outside the range of this survey. Clarke (1973) did not recognize P. integra Haldeman from the study area and left its status unresolved; however it does appear to occur in the study area, as LaRocque (1968) has suggested. Te (1975) recognized P. integra as a valid species, and this convention has been followed here.

The lymnaeid Pseudosuccinea columella Say, although previously reported from Manitoba (LaRocque, 1968; Mozley, 1938 and Dall, 1905 in Clarke, 1973), was not seen in this survey, despite a search of Brereton Lake and Lake Winnipeg, the localities of record. Clarke (1973) reported that this species was not collected during his survey. It is likely that this species no longer occurs in Manitoba. Stagnicola arctica Lea is known in Manitoba from the Churchill area which was not included in this study.

The sites at which each species was recorded are given in

TABLE XLII. Percent relative frequency of gastropods within the study area, based upon a total of 1469 species lots examined from 305 sites. Species below the dotted line were recorded at fewer than 5 sites.

Species	% relative frequency
Lymnaea stagnalis Linne, 1758 sspp. jugularis[1] Say, 1817; sanctaemariae Walker, 1892; ssp. ?[2]	13.3
Physa gyrina Say, 1821	12.9
Helisoma trivolvis Say, 1816 sspp. trivolvis Say, 1816; subcrenatum Carpenter, 1856	10.3
Stagnicola palustris Muller, 1774	10.0
Gyraulus parvus Say, 1817	9.3
Helisoma anceps anceps Menke, 1830	5.1
H. campanulatum campanulatum Say, 1821	4.4
Planorbula armigera Say, 1821	4.2
Amnicola limosa Say, 1817	3.9
Promenetus exacuous Say, 1821	3.4
Fossaria modicella Say, 1825	3.2
Valvata tricarinata Say, 1817	3.0
Gyraulus deflectus Say, 1824	2.3
Aplexa hypnorum Linne, 1758	2.1
Physa jennessi Dall, 1919 ssp. skinneri Taylor, 1953	1.9
Gyraulus circumstriatus Tryon, 1866	1.6
Cincinnatia cincinnatiensis Anthony, 1840	1.2
Ferrissia rivularis Say, 1817	1.0

continued. . .

[1] L. stagnalis lillianae F.C. Baker, 1910 appears to be a short-spired variant of L. s. jugularis; the two forms commonly coexist within the same population (Pip and Paulishyn, 1970; Clarke, 1973).

[2] This is a form characterized by an extremely slender spire and is known from 2 widely separated localities within the study area but its status requires further study.

TABLE XLII. (continued)

Species	% relative frequency
Stagnicola catascopium Say, 1817	
sspp. catascopium Say, 1817; nasoni	
F.C. Baker, 1906.	0.8
Bulimnea megasoma Say, 1824.	0.8
Armiger crista Linne, 1758	0.6
Marstonia decepta F.C. Baker, 1928	0.6
Valvata sincera Say, 1824	
sspp. sincera Say, 1824; helicoidea Dall, 1905. .	0.4
Fossaria exigua Lea, 1841.	0.4
Planorbula campestris Dawson, 1875	0.4
Promenetus umbilicatellus Cockerell, 1887.	0.4
Fossaria decampi Streng, 1896.	0.3
Marstonia gelida[1] F.C. Baker, 1921	0.3
Probythinella lacustris F.C. Baker, 1928	0.3
Stagnicola reflexa Say, 1821	0.2
Helisoma pilsbryi infracarinatum F.C. Baker, 1932. .	0.2
H. corpulentum corpulentum Say, 1824	0.2
Amnicola walkeri Pilsbry, 1898	0.2
Fossaria dalli F.C. Baker, 1907.	0.2
Acella haldemani "Deshayes" Binney, 1867	0.1
Stagnicola caperata Say, 1829.	0.1
Campeloma decisum Say, 1816.	0.1
Fossaria parva Lea, 1841	< 0.1
Ferrissia parallela Haldeman, 1841	< 0.1
Fossaria obrussa Say, 1825	< 0.1
Somatogyrus subglobosus Say, 1825.	< 0.1
Physa integra Haldeman, 1841	< 0.1

[1]This species is not known living and is believed to be a Pleistocene species which persists in drift lines (La Rocque, 1968).

Appendix IIIB.

The most frequent species within the study area (Table XLII) was Lymnaea stagnalis, which was recorded at 195 sites and comprised 13.3% of the total lots examined. Second in order of frequency was Physa gyrina, which was observed at 188 sites and comprised 12.9% of the total lots. Helisoma trivolvis, Stagnicola palustris and Gyraulus parvus were the next most frequent species. The relative frequencies of some species, e.g. Stagnicola caperata and Fossaria parva, as well as possibly others, were lower than the true frequencies of occurrence within the study region because these species tend to occur in semipermanent water bodies which were not represented in the present survey.

Teratological incidence within some of these populations has been discussed for site 4 (Pip, 1974), site 38 (Pip, 1975), site 217 (Pip, 1973), site 295 (Pip and Paulishyn, 1970) and site 304 (Pip, 1977).

B. Ecology

The mean values for each of the 8 parameters for water chemistry at the sites where each species was present and where it appeared to be absent are given in Figs. 102-105. The significance of the difference of these means was tested using unpaired t-tests; the results (Table XLIII) showed that some species appeared to occur significantly more frequently in waters characterized by low or high values for certain parameters.

The parameters could be correlated with distribution of the species, based on numbers of species showing significant tests, in

Figure 102. Mean values for pH (A) and total filtrable residue (g/l)(B) at sites where each gastropod species was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. Campeloma decisum
2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
6. M. gelida
7. Probythinella lacustris
8. Amnicola walkeri
9. A. limosa
11. Lymnaea stagnalis
12. Acella haldemani
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
16. S. caperata
17. S. reflexa
18. Fossaria decampi
19. F. exigua
20. F. modicella
22. F. dalli
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
28. Ferrissia rivularis
29. Helisoma trivolvis
30. H. pilsbryi
31. H. corpulentum
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
38. Armiger crista
39. Gyraulus parvus
40. G. circumstriatus
41. G. deflectus

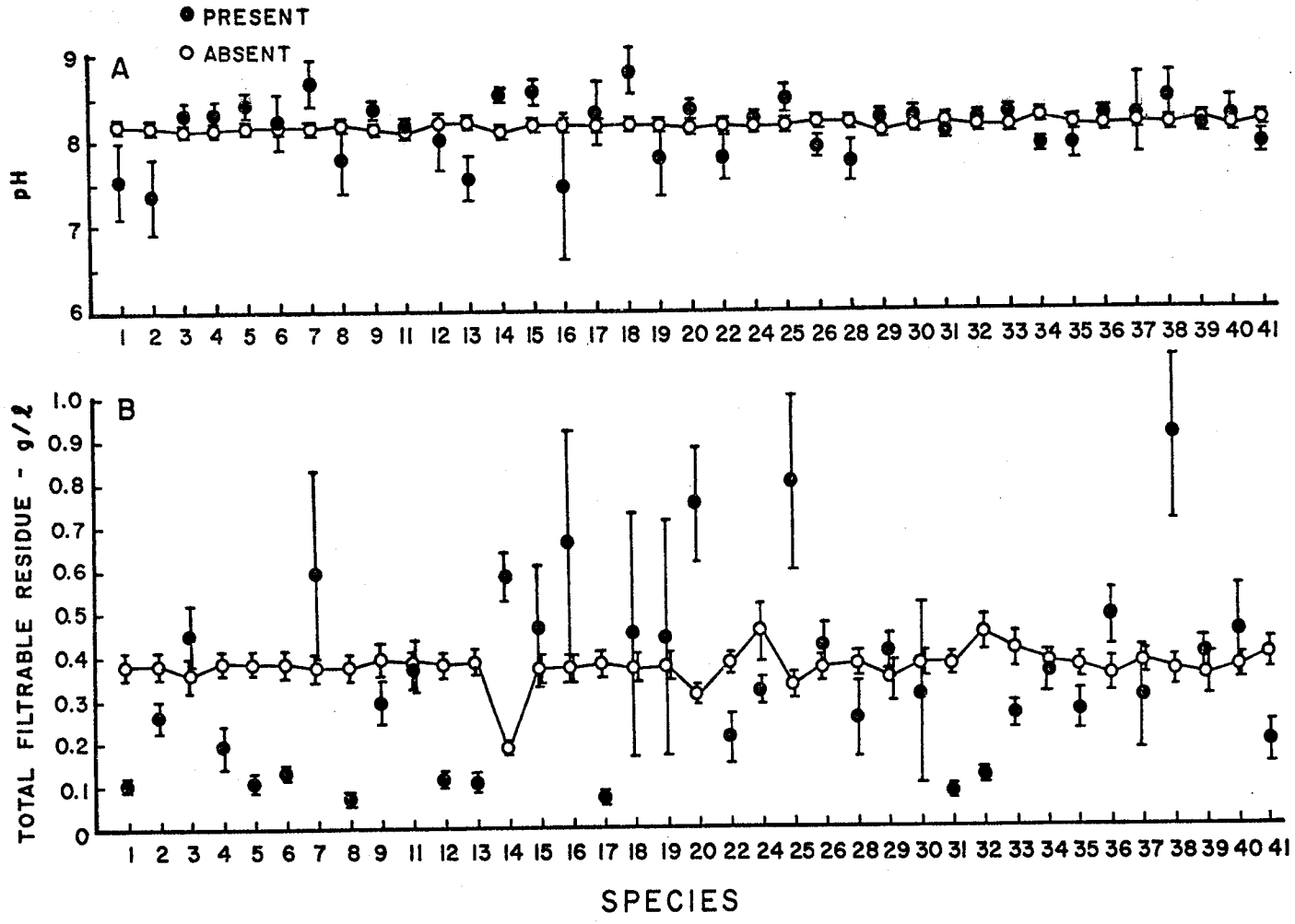

PRESENT
ABSENT
A
pH
9
8
7
6
1 2 3 4 5 6 7 8 9 11 12 13 14 15 16 17 18 19 20 22 24 25 26 28 29 30 31 32 33 34 35 36 37 38 39 40 41
B
TOTAL FILTRABLE RESIDUE - g/l
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1 2 3 4 5 6 7 8 9 11 12 13 14 15 16 17 18 19 20 22 24 25 26 28 29 30 31 32 33 34 35 36 37 38 39 40 41
SPECIES

Figure 103. Mean values for total alkalinity (mg/l $CaCO_3$)(A) and chloride (mg/l)(B) at sites where each gastropod species was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. Campeloma decisum
2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
6. M. gelida
7. Probythinella lacustris
8. Amnicola walkeri
9. A. limosa
11. Lymnaea stagnalis
12. Acella haldemani
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
16. S. caperata
17. S. reflexa
18. Fossaria decampi
19. F. exigua
20. F. modicella
22. F. dalli
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
28. Ferrissia rivularis
29. Helisoma trivolvis
30. H. pilsbryi
31. H. corpulentum
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
38. Armiger crista
39. Gyraulus parvus
40. G. circumstriatus
41. G. deflectus

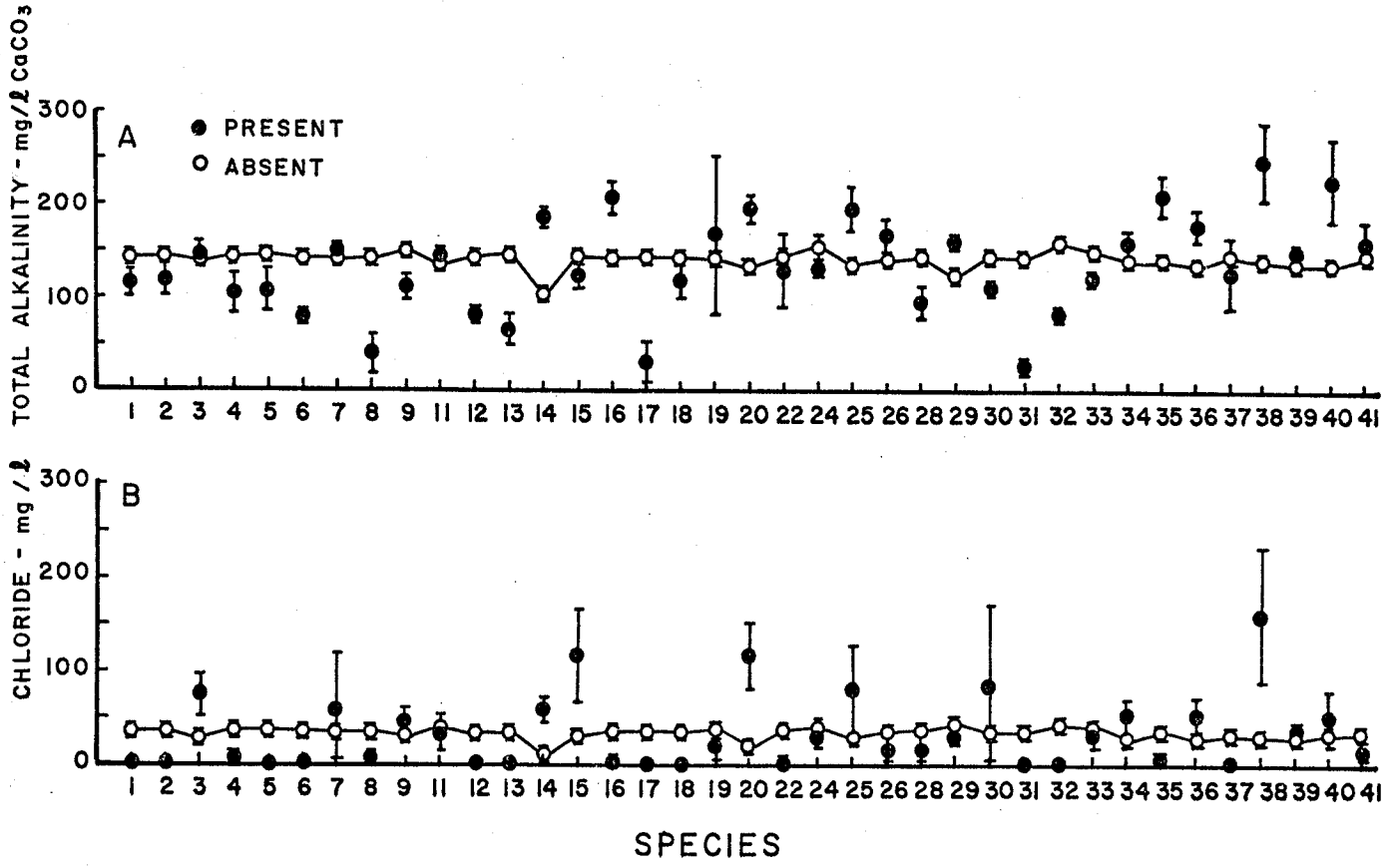

A
PRESENT
ABSENT
TOTAL ALKALINITY - mg/ℓ CaCO3
300
200
100
0
1 2 3 4 5 6 7 8 9 11 12 13 14 15 16 17 18 19 20 22 24 25 26 28 29 30 31 32 33 34 35 36 37 38 39 40 41
B
CHLORIDE - mg/ℓ
300
200
100
0
1 2 3 4 5 6 7 8 9 11 12 13 14 15 16 17 18 19 20 22 24 25 26 28 29 30 31 32 33 34 35 36 37 38 39 40 41
SPECIES

Figure 104. Mean values for sulphate (mg/l)(A) and estimated total nitrate and nitrite (mg/l)(B) at sites where each gastropod species was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. Campeloma decisum
2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
6. M. gelida
7. Probythinella lacustris
8. Amnicola walkeri
9. A. limosa
11. Lymnaea stagnalis
12. Acella haldemani
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
16. S. caperata
17. S. reflexa
18. Fossaria decampi
19. F. exigua
20. F. modicella
22. F. dalli
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
28. Ferrissia rivularis
29. Helisoma trivolvis
30. H. pilsbryi
31. H. corpulentum
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
38. Armiger crista
39. Gyraulus parvus
40. G. circumstriatus
41. G. deflectus

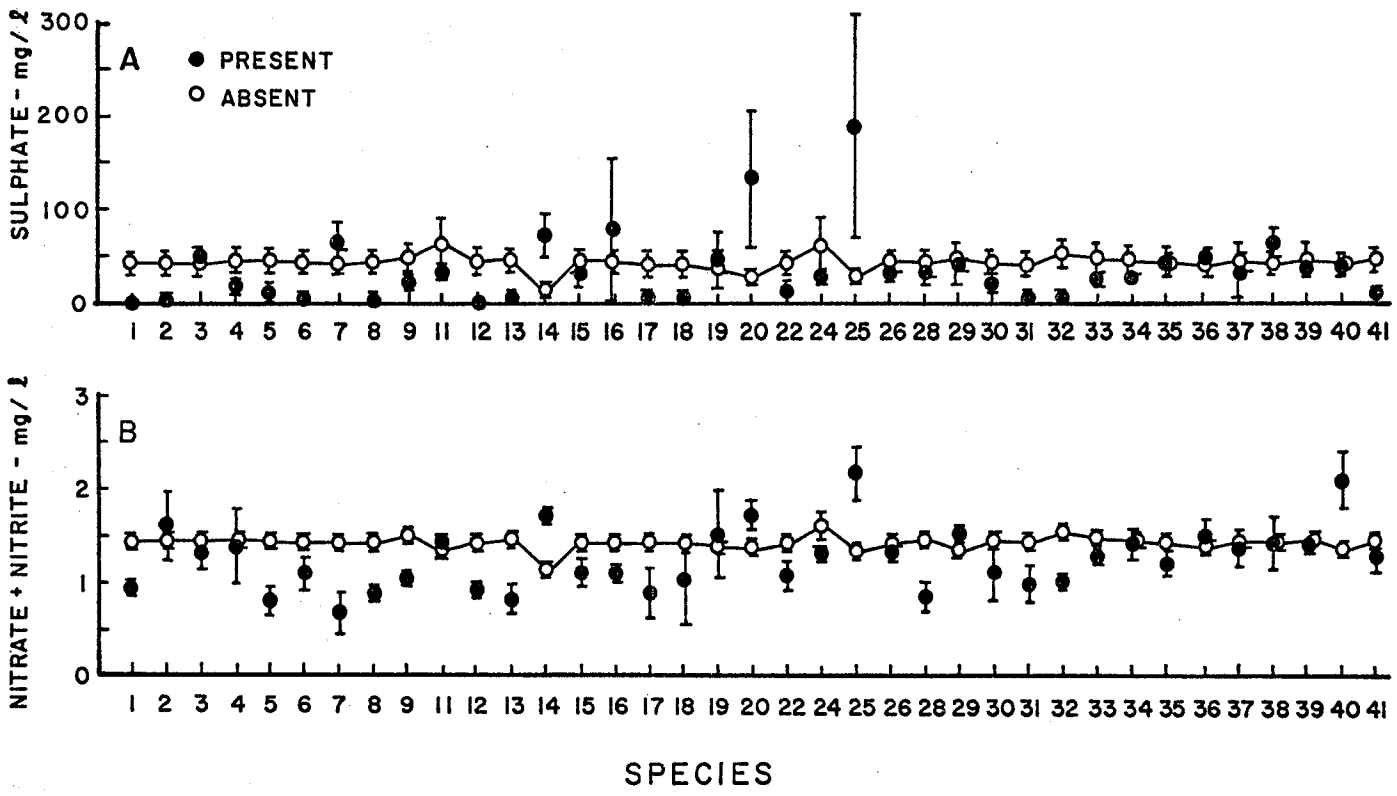

A
PRESENT
ABSENT
SULPHATE - mg/ℓ
300
200
100
0
1 2 3 4 5 6 7 8 9 11 12 13 14 15 16 17 18 19 20 22 24 25 26 28 29 30 31 32 33 34 35 36 37 38 39 40 41
B
NITRATE + NITRITE - mg/ℓ
3
2
1
0
1 2 3 4 5 6 7 8 9 11 12 13 14 15 16 17 18 19 20 22 24 25 26 28 29 30 31 32 33 34 35 36 37 38 39 40 41
SPECIES

Figure 105. Mean values for organic indices (optical density at 275 nm)(A) and molybdenum-blue phosphorus (mg/l)(B) at sites where each gastropod species was present and where it appeared to be absent. Vertical bars represent standard errors. Species which were recorded only once have been deleted. Species numbers refer to the following taxa:

1. Campeloma decisum
2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
6. M. gelida
7. Probythinella lacustris
8. Amnicola walkeri
9. A. limosa
11. Lymnaea stagnalis
12. Acella haldemani
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
16. S. caperata
17. S. reflexa
18. Fossaria decampi
19. F. exigua
20. F. modicella
22. F. dalli
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
28. Ferrissia rivularis
29. Helisoma trivolvis
30. H. pilsbryi
31. H. corpulentum
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
38. Armiger crista
39. Gyraulus parvus
40. G. circumstriatus
41. G. deflectus

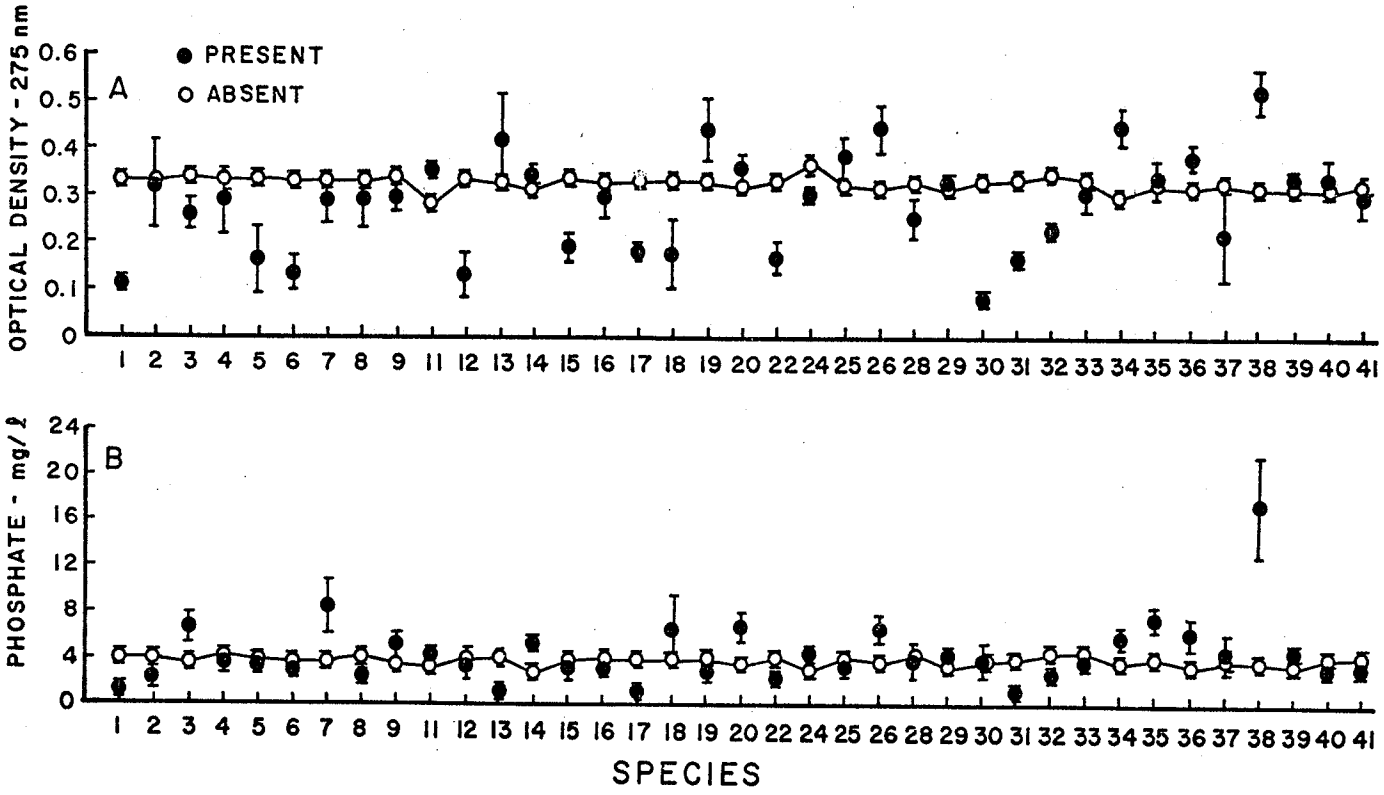

OPTICAL DENSITY - 275 nm
PRESENT
ABSENT
A
0.6
0.5
0.4
0.3
0.2
0.1
0
1 2 3 4 5 6 7 8 9 11 12 13 14 15 16 17 18 19 20 22 24 25 26 28 29 30 31 32 33 34 35 36 37 38 39 40 41
PHOSPHATE - mg/ℓ
B
24
20
16
12
8
4
0
1 2 3 4 5 6 7 8 9 11 12 13 14 15 16 17 18 19 20 22 24 25 26 28 29 30 31 32 33 34 35 36 37 38 39 40 41
SPECIES

TABLE XLIII. Significance of the distribution of gastropods with respect to 8 water chemistry parameters. Symbols indicate that the mean values for the sites at which each species was recorded were significantly ($p < .05$, $n=305$) higher (+) or lower (-) than the mean for the sites at which the species was not recorded; 0 indicates no significant difference. Taxa in parentheses were recorded only once. Parameter 1= pH, 2= total filtrable residue, 3= total alkalinity, 4= chloride, 5= sulphate, 6= total nitrate and nitrite, 7= dissolved organic matter, 8= molybdenum-blue phosphorus.

Species	Parameter 1	2	3	4	5	6	7	8
1. Campeloma decisum	0	0	0	0	0	0	0	0
2. Valvata sincera	-	0	0	+	0	0	0	0
3. V. tricarinata	0	0	0	0	0	0	0	+
4. Cincinnatia cincinnatiensis	0	0	0	0	0	0	0	0
5. Marstonia decepta	0	0	0	0	0	0	0	0
6. M. gelida	0	0	0	0	0	0	0	0
7. Probythinella lacustris	0	0	0	0	0	0	0	+
8. Amnicola walkeri	0	0	0	0	0	0	0	0
9. A. limosa	0	0	-	0	0	-	0	+
(10. Somatogyrus subglobosus)								
11. Lymnaea stagnalis	0	0	0	0	0	0	+	+
12. Acella haldemani	0	0	0	0	0	0	0	0
13. Bulimnea megasoma	-	0	-	0	0	0	0	-
14. Stagnicola palustris	+	+	+	+	+	+	0	+
15. S. catascopium	0	0	0	0	0	0	0	0
16. S. caperata	0	0	0	0	0	0	0	0
17. S. reflexa	0	0	0	0	0	0	0	0
18. Fossaria decampi	0	0	0	0	0	0	0	0
19. F. exigua	0	0	0	0	0	0	0	0
20. F. modicella	0	+	+	+	+	+	0	+
(21. F. parva)								
22. F. dalli	0	0	0	0	0	0	0	0
(23. F. obrussa)								
24. Physa gyrina	0	-	0	0	0	-	0	+
25. P. jennessi	+	+	+	+	+	+	0	0
26. Aplexa hypnorum	-	0	0	0	0	0	+	+
(27. Ferrissia parallela)								
28. F. rivularis	-	0	0	0	0	-	0	0
29. Helisoma trivolvis	0	0	+	0	0	0	0	+
30. H. pilsbryi	0	0	0	0	0	0	0	0
31. H. corpulentum	0	0	0	0	0	0	0	0
32. H. campanulatum	0	-	-	-	0	-	-	-
33. H. anceps	0	-	0	0	0	0	0	0

continued . . .

TABLE XLIII. (continued)

Species	Parameter 1	2	3	4	5	6	7	8
34. *Planorbula armigera*	-	0	0	0	0	0	+	+
35. *P. campestris*	0	0	0	0	0	0	0	0
36. *Promenetus exacuous*	0	0	+	0	0	0	0	+
37. *P. umbilicatellus*	0	0	0	0	0	0	0	0
38. *Armiger crista*	0	+	+	+	0	0	+	+
39. *Gyraulus parvus*	0	0	0	0	0	0	0	0
40. *G. circumstriatus*	0	0	+	0	0	+	0	0
41. *G. deflectus*	-	-	0	0	0	0	0	0
(42. *Physa integra*)								

the following order of importance: molybdenum-blue phosphorus, total alkalinity, total filtrable residue and pH and estimated total nitrate and nitrite (equal), chloride, organic matter and sulphate. Thus for both macrophyte and gastropod distributions total alkalinity was an important factor while sulphate was the least important. Whereas molybdenum-blue phosphorus was of minor importance for macrophytes, it appeared to be the most important factor for gastropods. Significantly ($p < .05$, $n=305$) higher levels of this parameter were observed for 12 species, including Lymnaea stagnalis, Physa gyrina, Fossaria modicella, Stagnicola palustris and Helisoma trivolvis, the grazers that had been studied in Part I. Two species, Bulimnea megasoma and Helisoma campanulatum, were significantly sensitive to high levels of molybdenum-blue phosphorus. Seven species tended to occur at sites with significantly higher values for total alkalinity, while 3 species, Amnicola limosa, Bulimnea megasoma and Helisoma campanulatum were significantly sensitive to high total alkalinity values. Significantly higher and lower values, respectively were preferred by 4 species for both total filtrable residue and estimated total nitrate and nitrite. Six species tended to occur at significantly lower pH values, while 2 species, Stagnicola palustris and Physa jennessi skinneri, tended to occur at significantly higher pH values. Five species preferred significantly higher chloride levels but only Helisoma campanulatum appeared to occur at significantly lower levels for this parameter. High organic matter indices were preferred significantly by 4 species but again only H. campanulatum appeared to occur at significantly lower levels. Only 3 species tended to occur in waters with significantly higher values for sulphate; these were Stagnicola palustris,

Fossaria modicella and Physa jennessi skinneri. No species appeared to be significantly sensitive to high levels of sulphate.

No significant positive or negative preferences for any of the parameters examined were shown by Campeloma decisum, Cincinnatia cincinnatiensis, Marstonia decepta, Amnicola walkeri, Acella haldemani, Stagnicola catascopium, S. caperata, S. reflexa, Fossaria decampi, F. exigua, F. dalli, Helisoma pilsbryi, H. corpulentum, Planorbula campestris, Promenetus umbilicatellus, Gyraulus parvus and Marstonia gelida. For many of these species significant preferences could not be detected because of the small numbers of sites at which they were recorded, while for the commoner species Cincinnatia cincinnatiensis, Marstonia decepta, Stagnicola catascopium, Fossaria exigua, Planorbula campestris, Promenetus umbilicatellus and Gyraulus parvus the absence of significant preferences probably reflected wide ecological tolerance ranges. For Marstonia gelida, the absence of significant environmental preferences was to be expected since this species is not known to be living.

The similarities in the significant environmental preferences of each possible species pair were graded by assigning a value of +1 when the preferences of the two species for the same parameter were both significant and similarly inclined (both positive or negative); a value of -1 was assigned when preferences were both significant but dissimilarly inclined (one positive and one negative). A value of 0 was assigned when one or none of the species showed a significant preference for the same parameter. The values for each species pair were summed, yielding the matrix in Table XLIV. Negative values indicated net dissimilarity in habitat preference in terms of the

TABLE XLIV. Net similarities in the significant parameter preferences for each possible gastropod species pair. Maximum possible is +8 for similarities and -8 for dissimilarities. Taxa which occurred only once were excluded. Species numbers represent the following taxa:

1. Campeloma decisum
2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
6. M. gelida
7. Probythinella lacustris
8. Amnicola walkeri
9. A. limosa
11. Lymnaea stagnalis
12. Acella haldemani
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
16. S. caperata
17. S. reflexa
18. Fossaria decampi
19. F. exigua
20. F. modicella
22. F. dalli
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
28. Ferrissia rivularis
29. Helisoma trivolvis
30. H. pilsbryi
31. H. corpulentum
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
38. Armiger crista
39. Gyraulus parvus
40. G. circumstriatus
41. G. deflectus

TABLE XLIV.

	1	2	3	4	5	6	7	8	9	11	12	13	14	15	16	17	18	19	20	22	24	25	26	28	29	30	31	32	33	34	35	36	37
1	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2		x	0	0	0	0	0	0	0	0	0	+1	0	0	0	0	0	0	+1	0	0	0	+1	+1	0	0	0	0	0	+1	0	0	0
3			x	0	0	0	+1	0	+1	+1	0	-1	+1	0	0	0	0	0	+1	0	+1	0	+1	0	+1	0	0	-1	0	+1	0	+1	0
4				x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5					x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6						x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7							x	0	+1	+1	0	-1	+1	0	0	0	0	0	+1	0	+1	0	+1	0	+1	0	0	-1	0	+1	0	+1	0
8								x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9									x	+1	0	0	-1	0	0	0	0	0	0	0	+1	-1	+1	+1	0	0	0	+1	0	+1	0	0	0
11										x	-1	+1	0	0	0	0	0	0	+1	0	+1	0	+1	0	+1	0	0	-2	0	+2	0	+1	0
12											x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13												x	-3	0	0	0	0	0	-2	0	-1	-2	0	+1	-2	0	0	+2	0	0	0	-2	0
14													x	0	0	0	0	0	+6	0	-1	+6	0	-2	+2	0	0	-5	-1	0	0	+2	0
15														x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16															x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17																x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18																	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19																		x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20																			x	0	-1	+5	+1	-1	+2	0	0	-5	-1	+1	0	+2	0
22																				x	0	0	0	0	0	0	0	0	0	0	0	0	0
24																					x	-2	+1	+1	+1	0	0	+1	+1	+1	0	+1	0
25																						x	-1	-2	+1	0	0	-4	-1	-1	0	+1	0
26																							x	+1	+1	0	0	-2	0	+3	0	+1	0
28																								x	0	0	0	+1	0	+1	0	0	0
29																									x	0	0	-2	0	+1	0	+2	0
30																										x	0	0	0	0	0	0	0
31																											x	0	0	0	0	0	0
32																												x	+1	-2	0	-2	0
33																													x	0	0	0	0
34																														x	0	+1	0
35																															x	0	0
36																																x	0
37																																	x

continued . . .

TABLE XLIV. (continued)

	38	39	40	41
1	0	0	0	0
2	+1	0	0	+1
3	+1	0	0	0
4	0	0	0	0
5	0	0	0	0
6	0	0	0	0
7	+1	0	0	0
8	0	0	0	0
9	0	0	-1	0
11	+2	0	0	0
12	0	0	0	0
13	-2	0	-1	+1
14	+4	0	+2	-2
15	0	0	0	0
16	0	0	0	0
17	0	0	0	0
18	0	0	0	0
19	0	0	0	0
20	+4	0	+2	-1
22	0	0	0	0
24	0	0	-1	+1
25	+3	0	+2	-2
26	+2	0	0	+1
28	0	0	-1	+1
29	+2	0	+1	0
30	0	0	0	0
31	0	0	0	0
32	-5	0	-2	+1
33	-1	0	0	+1
34	+2	0	0	+1
35	0	0	0	0
36	+2	0	+1	0
37	0	0	0	0
38	x	0	+1	-1
39		x	0	0
40			x	0
41				x

parameters examined while positive values indicated net similarity in preference. Species pairs showing positive values would be expected to occur together in the same habitats.

C. Gastropod associations

The significance of the tendency for the members of each possible species pair to occur jointly or apart was tested by means of a Chi-square test using the Watfiv program constructed for one data set in Appendix VA. All species that were recorded at fewer than 5 sites were excluded from the analysis.

The results of the Chi-square tests (Table XLV) revealed 71 significant ($p < .05$, $n=305$) positive associations and 4 significant negative associations. These have been ranked in Table XLVIA and B respectively, in descending order of significance according to decreasing Chi-square values. The association of Valvata tricarinata and Amnicola limosa was the most highly significant; each of these two species appeared three times within the 10 most significant positive associations, while Cincinnatia cincinnatiensis, Fossaria modicella, Helisoma campanulatum and Promenetus exacuous each appeared twice within the top 10 associations. Lymnaea stagnalis was most significantly associated with Helisoma trivolvis; this association ranked third in overall significance, while Physa gyrina was most significantly associated with Valvata tricarinata, an association 11th in overall significance. Physa gyrina and Lymnaea stagnalis were significantly associated with each other but this association ranked 45th in overall significance. The most significant negative association was that of Stagnicola palustris and Helisoma campanulatum.

TABLE XLV. Results of Chi-square tests for the significance of the discrepancy between theoretical frequencies and the observed frequencies for the members of each possible pair of gastropods to occur together (+) or apart (-)($p < .05$, $n=305$) within the same site; 0 indicates no significant difference. Symbols in parentheses indicate significant positive associations where joint occurrences were observed at fewer than 5 sites. Symbols followed by exclamation points (!) indicate significant positive or negative associations that did not coincide with net similarities or dissimilarities, respectively in significant environmental preferences (Table XLIV). All species that were recorded at fewer than 5 sites have been deleted. Species numbers represent the following taxa:

2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
6. M. gelida
9. Amnicola limosa
11. Lymnaea stagnalis
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
19. Fossaria exigua
20. F. modicella
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
28. Ferrissia rivularis
29. Helisoma trivolvis
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
38. Armiger crista
39. Gyraulus parvus
40. G. circumstriatus
41. G. deflectus

TABLE XLV.

	2	3	4	5	6	9	11	13	14	15	19	20	24	25	26	28	29	32	33	34	35	36	37	38	39	40	41
2	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3		x	+!	0	0	+	0	0	0	+!	0	+	+	0	0	0	+	0	+!	+	0	+	0	+	+!	0	0
4			x	0	(+)!	+!	0	0	0	0	0	0	+!	0	0	0	0	+!	0	0	0	0	0	0	0	0	+!
5				x	0	0	0	0	0	+!	0	0	0	0	0	0	0	+!	0	0	0	0	0	0	0	0	0
6					x	(+)!	0	0	0	0	0	0	0	0	0	0	0	(+)!	0	0	0	0	0	0	0	0	0
9						x	0	0	0	+!	0	0	+	0	0	0	0	+	+!	0	0	+!	0	+!	+!	0	+
11							x	0	+	0	0	0	+	0	0	0	+	0	0	+	0	+	0	0	+!	0	0
13								x	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+
14									x	0	0	+	0	+	+!	0	+	-	+!	0	+!	+	0	+	+!	0	0
15										x	0	+!	0	0	0	0	0	+!	+!	0	0	0	0	0	0	0	0
19											x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20												x	0	+	0	0	+	-	0	+	+!	+	0	+	0	0	0
24													x	+!	0	0	0	0	+	+	0	0	0	+!	+!	0	0
25														x	0	0	+	0	-	0	0	0	0	0	0	0	0
26															x	0	0	0	0	0	0	0	0	+	0	0	0
28																x	0	0	0	0	0	0	0	0	0	0	0
29																	x	0	0	0	0	+	0	+	+!	0	0
32																		x	+	0	0	0	0	0	0	0	+
33																			x	0	0	0	0	0	0	0	0
34																				x	0	0	0	+	0	0	0
35																					x	(+)!	0	0	0	0	0
36																						x	0	+	+!	0	+!
37																							x	0	0	0	0
38																								x	0	0	0
39																									x	+!	0
40																										x	0
41																											x

TABLE XLVI. Significant ($p < .05$, $n=305$) positive (A) and negative (B) gastropod associations ranked in descending order of significance according to decreasing Chi-square values. All taxa that were recorded at fewer than 5 sites have been deleted. Associations with species 6 are in parentheses because this species is not known living. Species numbers represent the following taxa:

2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
6. M. gelida
9. Amnicola limosa
11. Lymnaea stagnalis
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
19. Fossaria exigua
20. F. modicella
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
28. Ferrissia rivularis
29. Helisoma trivolvis
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
38. Armiger crista
39. Gyraulus parvus
40. G. circumstriatus
41. G. deflectus

TABLE XLVI.

A. Significant positive associations

1. 3 x 9	31. 9 x 39	61. 20 x 25
2. 9 x 32	32. (29 x 6)	62. 25 x 29
3. 11 x 29	33. 11 x 39	63. 9 x 33
4. 14 x 20	34. 3 x 39	64. 14 x 35
5. 32 x 41	35. 3 x 29	65. 5 x 15
6. 3 x 15	36. 13 x 41	66. 39 x 40
7. 3 x 4	37. 34 x 38	67. 4 x 41
8. 20 x 36	38. 3 x 38	68. 4 x 24
9. 4 x 9	39. 20 x 35	69. 24 x 38
10. 36 x 38	40. 26 x 38	70. 24 x 34
11. 3 x 24	41. 3 x 36	71. 36 x 41
12. 3 x 33	42. 35 x 36	
13. 36 x 39	43. 14 x 38	
14. 9 x 41	44. (4 x 6)	
15. 4 x 32	45. 11 x 24	
16. 14 x 26	46. 29 x 38	
17. 3 x 20	47. 9 x 15	
18. 20 x 38	48. 15 x 33	
19. 14 x 33	49. 11 x 14	
20. 5 x 32	50. 11 x 36	
21. 14 x 36	51. 11 x 34	
22. 9 x 36	52. 24 x 39	
23. 9 x 24	53. 9 x 38	
24. 24 x 33	54. 32 x 33	
25. 14 x 29	55. 14 x 25	
26. 24 x 25	56. 20 x 34	
27. 29 x 36	57. 15 x 20	
28. (9 x 6)	58. 15 x 32	
29. 29 x 39	59. 20 x 29	
30. 14 x 39	60. 3 x 34	

B. Significant negative associations

1. 14 x 32
2. 20 x 32
3. 13 x 14
4. 25 x 33

The associations shown by Marstonia gelida do not represent true affinities since this species is not known living; the association values reflect the types of communities currently existing in areas where this species occurred in the past. Although Berry (1943) observed that Amnicola limosa and Marstonia decepta appeared to be associated in Michigan lakes, no significant association between these species was found in the present survey.

Of the 71 significant positive associations, 36 or 50.7% could be correlated with net similarities in preferences for the monitored environmental parameters. The remaining 35 positive associations could not be explained on the basis of net similar habitat preferences. All 4 of the significant negative associations could be correlated with net dissimilarities in significant environmental preferences.

Valvata tricarinata and Amnicola limosa showed the highest number (11)(Table XLVII) of significant positive associations; Stagnicola palustris and Promenetus exacuous each showed 10 significant positive associations. All of the positive associations shown by Cincinnatia cincinnatiensis, Marstonia decepta, Stagnicola catascopium, Planorbula campestris, Gyraulus parvus and G. circumstriatus could not be correlated with similarities in habitat preferences because, except for G. circumstriatus, these species showed no significant preferences for any of the parameters. Stagnicola palustris and Helisoma campanulatum each showed two significant negative associations, both of which could be correlated with net dissimilarities in significant environmental preferences. Valvata sincera, Fossaria exigua, Ferrissia rivularis and Promenetus umbilicatellus showed no

TABLE XLVII. Total numbers of significant positive and negative associations observed for each gastropod species and the numbers of these associations that did not coincide (N.C.) with net similarities or dissimilarities, respectively in significant preferences for the monitored environmental parameters. All taxa that were recorded at fewer than 5 sites have been deleted.

Species	Positive		Negative	
	Total	N.C.	Total	N.C.
2. Valvata sincera	0	0	0	0
3. V. tricarinata	11	4	0	0
4. Cincinnatia cincinnatiensis	6	6	0	0
5. Marstonia decepta	2	2	0	0
6. M. gelida	(3)	(3)	(0)	(0)
9. Amnicola limosa	11	7	0	0
11. Lymnaea stagnalis	6	1	0	0
13. Bulimnea megasoma	1	0	1	0
14. Stagnicola palustris	10	4	2	0
15. S. catascopium	6	6	0	0
19. Fossaria exigua	0	0	0	0
20. F. modicella	9	2	1	0
24. Physa gyrina	9	4	0	0
25. P. jennessi	4	1	1	0
26. Aplexa hypnorum	2	1	0	0
28. Ferrissia rivularis	0	0	0	0
29. Helisoma trivolvis	8	1	0	0
32. H. campanulatum	7	4	2	0
33. H. anceps	6	4	1	0
34. Planorbula armigera	5	0	0	0
35. P. campestris	3	3	0	0
36. Promenetus exacuous	10	4	0	0
37. P. umbilicatellus	0	0	0	0
38. Armiger crista	9	2	0	0
39. Gyraulus parvus	8	8	0	0
40. G. circumstriatus	1	1	0	0
41. G. deflectus	5	2	0	0

significant positive or negative associations.

In order to rank the similarities of the significant positive associations for other species, a similarity index (equation 27, p. 354) was calculated for the members of each possible species pair. All positive associations where the two species occurred jointly at fewer than 5 sites and all negative associations were excluded. The values for the association similarity indices are given in Table XLVIII.

Four of the most important species groupings, in terms of high association similarity ($S > .60$) are shown in Fig. 106. The distances between the species are theoretically the reciprocals of the Chi-square values that tested the significance of the frequency with which the members of the respective pairs were observed to occur jointly. All the members of each group showed great similarities in their significant affinities for other species. However only Valvata tricarinata (species 3), Amnicola limosa (species 9) and Physa gyrina (species 24), and Stagnicola palustris (species 14), Helisoma trivolvis (species 29) and Promenetus exacuous (species 36) of group B (Fig. 106) and Fossaria modicella (species 20) and Armiger crista (species 38) of group C were themselves associated at a significant level. The remaining species in the four groups were not significantly associated with each other.

In group A (Fig. 106), Cincinnatia cincinnatiensis (species 4) and Stagnicola catascopium (species 15) were both characteristic of lakes although neither species showed any significant preferences with respect to the environmental parameters examined. These species were not positively associated, partly because S. catascopium was infrequent

TABLE XLVIII. Gastropod association similarity indices for possible species pairs. Only significant positive associations where the joint occurrences were observed at 5 or more sites were considered. Species for which all joint occurrences were observed at fewer than 5 sites have been deleted. Species numbers represent the following taxa:

2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
9. Amnicola limosa
11. Lymnaea stagnalis
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
19. Fossaria exigua
20. F. modicella
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
28. Ferrissia rivularis
29. Helisoma trivolvis
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
38. Armiger crista
39. Gyraulus parvus
40. G. circumstriatus
41. G. deflectus

TABLE XLVIII.

	2	3	4	5	9	11	13	14	15	19	20	24	25	26	28	29	32	33	34	35
2	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3		x	0.25	0	0.67	0.59	0	0.67	0.38	0	0.53	0.60	0.40	0	0	0.42	0.47	0.35	0.38	0
4			x	0.33	0.53	0.18	0.33	0	0.60	0	0.15	0.29	0.22	0	0	0.15	0.36	0.73	0.40	0
5				x	0.18	0	0	0	0.33	0	0	0	0	0	0	0	0	0.29	0	0
9					x	0.38	0.18	0.40	0.40	0	0.44	0.53	0.14	0	0	0.44	0.50	0.50	0.40	0
11						x	0	0.38	0	0	0.57	0.27	0.60	0.29	0	0.43	0	0.33	0.18	0.29
13							x	0	0	0	0	0	0	0	0	0	0.29	0	0	0
14								x	0.27	0	0.44	0.53	0.29	0	0	0.67	0.13	0	0.40	0
15									x	0	0.15	0.43	0.22	0	0	0.31	0.36	0.55	0.40	0
19										x	0	0	0	0	0	0	0	0	0	0
20											x	0.47	0.33	0.22	0	0.50	0.14	0.43	0.31	0.22
24												x	0	0	0	0.59	0.40	0.27	0.43	0
25													x	0.40	0	0.33	0	0.40	0.44	0.40
26														x	0	0.22	0	0.29	0	1.00
28															x	0	0	0	0	0
29																x	0	0.29	0.62	0.22
32																	x	0.29	0	0
33																		x	0.31	0.29
34																			x	0
35																				x

continued. . .

TABLE XLVIII. (continued)

	36	37	38	39	40	41
2	0	0	0	0	0	0
3	0.50	0	0.63	0.42	0.17	0.25
4	0.43	0	0.46	0.46	0	0.40
5	0	0	0	0	0	0.33
9	0.42	0	0.33	0.33	0.18	0.40
11	0.40	0	0.71	0.57	0.29	0.18
13	0.20	0	0	0	0	0
14	0.53	0	0.33	0.33	0.18	0.13
15	0.43	0	0.46	0.31	0	0.40
19	0	0	0	0	0	0
20	0.47	0	0.63	0.50	0	0.15
24	0.56	0	0.35	0.35	0.20	0.29
25	0.46	0	0.67	0.50	0	0
26	0.20	0	0.22	0.22	0	0
28	0	0	0	0	0	0
29	0.71	0	0.50	0.50	0.22	0.15
32	0.12	0	0.13	0.13	0	0.31
33	0.40	0	0.57	0.57	0	0.36
34	0.43	0	0.46	0.46	0	0
35	0.20	0	0.22	0.22	0	0
36	x	0	0.59	0.59	0.20	0.14
37		x	0	0	0	0
38			x	0.75	0	0.31
39				x	0	0.31
40					x	0
41						x

Figure 106. An abstract representation of the interrelations between gastropod species for which the association similarity index exceeded a value of 0.60. Species joined by solid lines were themselves significantly ($p < .05$, $n=305$) positively associated, while those joined by broken lines were not significantly associated although the similarity index was greater than 0.60. Species not joined by lines showed association similarity indices that were less than 0.60. Values along the lines represent approximations of the theoretical distances between the species and are the reciprocals of the Chi-square values that tested the significance of the frequency with which the members of the respective pairs were observed to occur jointly. Species numbers represent the following taxa:

3. Valvata tricarinata
4. Cincinnatia cincinnatiensis
9. Amnicola limosa
11. Lymnaea stagnalis
14. Stagnicola palustris
15. S. catascopium
20. Fossaria modicella
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
29. Helisoma trivolvis
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
38. Armiger crista
39. Gyraulus parvus

in the area where C. cincinnatiensis was abundant (in the extreme southeastern portion of the study region), while the latter species was infrequent in the area where S. catascopium was more frequent (in the central portion of the study region). Helisoma anceps (species 33) showed several significant associations common to those shown by C. cincinnatiensis but was not significantly associated with it, perhaps partly because the former species showed a significant preference for waters with a low total filtrable residue level while the latter did not.

In group B (Fig. 106), the cluster of Valvata tricarinata (species 3), Amnicola limosa (species 9) and Physa gyrina (species 24) represented an association grouping characteristic of lakes, with generally low values in the environmental parameters except for high levels in molybdenum-blue phosphorus. The bridge from this cluster to the next subgroup, composed of Stagnicola palustris (species 14), Helisoma trivolvis (species 29) and Promenetus exacuous (species 36), represented a transition zone formed by series of associations with relatively low association similarity indices (Table XLVIII) to the habitat type characteristic of this subgroup, i.e. small, lentic waters with high values of total alkalinity and molybdenum-blue phosphorus levels. Planorbula armigera (species 34) differed from the other species in group B in that it preferred significantly lower pH values. All of the species in group B were related by their significant preference for high molybdenum-blue phosphorus levels.

In group C (Fig. 106), Lymnaea stagnalis (species 11) showed many associations common to those of Fossaria modicella (species 20) and Armiger crista (species 38) but was not associated with the latter

two species largely because it was more flexible in terms of the habitats where it occurred. Fossaria modicella and Armiger crista were significantly associated with each other, and showed similar significant preferences for high values of total filtrable residue, total alkalinity, chloride and molybdenum-blue phosphorus. Both Lymnaea stagnalis and Armiger crista showed many associations common to those of Physa jennessi skinneri (species 25) but were not significantly associated with the latter which showed significant preferences for high values of six parameters (Table XLIII), all of which were not important to L. stagnalis and three of which were not important to A. crista. From Table XLIV, a strong similarity of associations would be expected between F. modicella and P. jennessi skinneri, but the value of the association similarity index for these species was only 0.33 (Table XLVIII). Although these species were themselves significantly positively associated as expected on the basis of the high value in net similarity of preferences for the environmental parameters, they did not share many common significant associations for other species. Gyraulus parvus (species 39) showed many associations common to those of A. crista but showed no significant preferences for any of the environmental parameters or habitat types examined.

The species in the binary group D (Fig. 106), Aplexa hypnorum (species 26) and Planorbula campestris (species 35), showed a similarity of significant associations but were not themselves significantly associated because the distribution of the latter species was limited to the southwestern portion of the study region while the former was distributed throughout the area. Planorbula

campestris showed no significant environmental preferences in terms of the monitored parameters while A. hypnorum preferred low values of pH and high levels of dissolved organic matter and molybdenum-blue phosphorus.

Other, more complex and less similar association groupings may be obtained from Table XLVIII.

III. Plant-snail associations

The significance of the tendency for the members of each possible plant-snail pair to occur together or apart was tested using a Chi-square test, calculated using the Watfiv program constructed for two data sets in Appendix VB. All plant or snail species or species groups that were observed at fewer than 5 sites were excluded from the analysis.

The results of the Chi-square tests (Table XLIX) revealed 161 significant ($p<.05$, $n=305$) positive associations and 31 negative associations. These have been ranked in Table LA and B respectively, in descending order of significance according to decreasing Chi-square values. The 10 most highly significant positive associations were formed by only two gastropod species: Helisoma campanulatum occurred in 7 and Amnicola limosa in 3 of the top 10 associations. Both of these gastropods showed a strong tendency to occur with Potamogeton richardsonii, P. zosteriformis and Elodea canadensis. Lymnaea stagnalis showed the strongest tendency to occur jointly with Myriophyllum exalbescens, but this association ranked 33rd in overall significance; the other plants with which this gastropod tended to occur significantly frequently were, in decreasing order of significance: Lemna trisulca (37th), Utricularia vulgaris (43rd), Potamogeton vaginatus (92nd), Sparganium spp. (107th) and Potamogeton richardsonii (137th). Physa gyrina did not occur significantly frequently with Potamogeton pectinatus; its strongest association was with P. zosteriformis, 69th in overall significance. This

TABLE XLIX. Results of Chi-square tests for the significance of the discrepancy between theoretical frequencies and the observed frequencies for the members of each possible plant-snail pair to occur together (+) or apart (-) ($p < .05$, $n=305$) within the same site; 0 indicates no significant difference. Symbols in parentheses indicate significant positive associations where joint occurrences were observed at fewer than 5 sites. Symbols followed by exclamation points (!) indicate significant positive or negative associations that did not coincide with net similarities or dissimilarities, respectively in significant environmental preferences (Tables XXXVI and XLIII). Only species from Tables XLI and XLVIII were considered. The taxa represented by the species numbers are listed on the opposite page.

TABLE XLIX. (explanation continued)

Species numbers represent the following taxa:

HORIZONTAL: MACROPHYTES

1. Chara spp.
3. Sparganium spp.
7. Potamogeton amplifolius
8. P. epihydrus
9. P. filiformis
10. P. foliosus
11. P. friesii
12. P. gramineus
14. P. natans
16. P. pectinatus
17. P. praelongus
18. P. pusillus
19. P. richardsonii
21. P. spirillus
23. P. vaginatus
24. P. zosteriformis
25. Najas flexilis
27. Alisma triviale
29. Sagittaria spp.
30. Elodea canadensis
31. Vallisneria americana
32. Zizania aquatica
33. Eleocharis spp.
34. Calla palustris
35. Lemna minor
36. L. trisulca
37. Spirodela polyrhiza
38. Polygonum amphibium
40. Ceratophyllum demersum
41. Nymphaea odorata
42. N. tetragona
43. N. tuberosa
44. Nuphar microphyllum
45. N. variegatum
46. Brasenia schreberi
48. Ranunculus aquatilis
54. Callitriche spp.
56. Myriophyllum exalbescens
59. Hippuris vulgaris
60. Sium suave
61. Mentha arvensis
62. Utricularia intermedia
63. U. minor
64. U. vulgaris
66. Megalodonta beckii
68. Zosterella dubia

VERTICAL: GASTROPODS

2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
9. Amnicola limosa
11. Lymnaea stagnalis
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
19. Fossaria exigua
20. F. modicella
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
28. Ferrissia rivularis
29. Helisoma trivolvis
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
38. Armiger crista
39. Gyraulus parvus
40. G. circumstriatus
41. G. deflectus

TABLE XLIX.

Plants	1	3	7	8	9	10	11	12	14	16	17	18	19	21	23	24	25	27	29	30	31	32	33	34	35
Snails																									
2	0	(+)	0	0	0	0	0	0	(+)!	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	+	+!	0	+!	0	0	+!	0	0	0	0	0	+!	0	0	0
4	+!	0	+!	0	0	0	0	0	0	+!	+!	0	+!	0	0	+!	+!	0	0	+!	+!	+!	0	0	+!
5	0	0	0	0	0	0	(+)!	+!	+!	0	+!	0	+!	0	0	+!	+!	0	0	0	0	0	0	0	0
9	0	0	+!	+	0	0	+!	0	0	0	0	0	+	0	0	+	+	-!	+!	+	+	+	0	+	0
11	0	+!	0	0	0	0	0	0	0	0	0	0	+!	-!	+!	0	0	0	0	0	0	0	0	0	0
13	0	0	0	(+)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(+)	0	(+)	0
14	0	0	-	0	0	0	-!	0	+!	+	-	0	+!	0	0	-	-	+	+!	+!	-	0	0	-	+!
15	+!	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(+)!	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	-	0	+	0	0	0	0	0	0	-	0	-	0	0	0	0	0	0
24	+!	0	0	0	0	0	0	0	+	0	0	0	-!	0	0	+	0	0	+	+	0	0	0	0	+
25	-!	0	0	0	0	0	0	-	-	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	+	0	0	0	0	+!	0	0	0	0	0	0	0	0	0	0
32	0	0	+	+	0	+!	+	0	+	0	+	0	+	0	0	+	+	0	+	+	+	+	0	+	0
33	+!	0	0	0	0	0	+	0	+	0	+	0	0	0	0	0	+	-!	0	0	0	+	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	(+)!	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	+!	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	0	0	+	+	0	+!	0	0	+	0	+!	0	+!	0	0	+	+!	0	0	+	+	+	0	+!	0

continued. . .

TABLE XLIX. (continued)

Plants	36	37	38	40	41	42	43	44	45	46	48	54	56	59	60	61	62	63	64	66	68
Snails																					
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	-!	+!	0	0	0	0	0	0	0	0	+!	0	-!	0	0	0	0	0	0
4	0	0	0	+!	0	0	(+)!	0	+!	0	0	0	0	0	0	0	0	0	0	(+)!	+!
5	0	0	0	+!	0	(+)!	0	(+)!	+!	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	+!	+	+	+!	0	+	0	0	0	0	-!	0	0	0	0	0	+	+
11	+	0	0	0	0	0	0	-!	0	0	0	0	+!	0	0	0	0	0	+	0	0
13	(+)!	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(+)	0	0	+	0
14	0	+!	+!	0	0	0	0	-!	-	0	0	0	0	0	0	+	0	0	0	-	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0	0	+	0	0	0	0	+	0	0	0	0	0	0	-!	0	0	0	0	0
25	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0	0	0	0	0	0	0	0	0	+!	+	(+)	0	0	+	0	0
28	0	(+)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	+!	0	0	+!	0	-	0	0	+!	0	0	0	+!	0	0	0	0	0	0	0	0
32	+!	+	+	+	+	+	+!	0	+	(+)	0	0	0	0	0	0	0	0	0	+	+
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-!	0	0	0	0	0	0
34	+	+	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	(+)!	0	0	0	0	0
36	0	0	0	+!	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	(+)!	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	-!	0	0	0	0	0	0	0	+!	+!	0	0	0	0	0	0	0
40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
41	+!	+	0	+	0	0	(+)!	0	+	0	0	0	0	0	0	0	0	0	+	+	+!

TABLE L. Significant ($p < .05$, $n=305$) positive (A) and negative (B) gastropod-plant associations ranked in descending order of significance according to decreasing Chi-square values. Only associations from Table XLIX have been included. The first number of each pair represents a gastropod, the second a macrophyte. The taxa referred to by the species numbers are listed on the opposite page.

TABLE L. (explanation continued)

Species numbers represent the following taxa:

FIRST NUMBER: GASTROPOD

2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
9. Amnicola limosa
11. Lymnaea stagnalis
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
20. Fossaria modicella
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
28. Ferrissia rivularis
29. Helisoma trivolvis
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
39. Gyraulus parvus
41. G. deflectus

SECOND NUMBER: MACROPHYTE

1. Chara spp.
3. Sparganium spp.
7. Potamogeton amplifolius
8. P. epihydrus
9. P. filiformis
10. P. foliosus
11. P. friesii
12. P. gramineus
14. P. natans
16. P. pectinatus
17. P. praelongus
19. P. richardsonii
21. P. spirillus
23. P. vaginatus
24. P. zosteriformis
25. Najas flexilis
27. Alisma triviale
29. Sagittaria spp.
30. Elodea canadensis
31. Vallisneria americana
32. Zizania aquatica
34. Calla palustris
35. Lemna minor
36. L. trisulca
37. Spirodela polyrhiza
38. Polygonum amphibium
40. Ceratophyllum demersum
41. Nymphaea odorata
42. N. tetragona
43. N. tuberosa
44. Nuphar microphyllum
45. N. variegatum
46. Brasenia schreberi
56. Myriophyllum exalbescens
59. Hippuris vulgaris
60. Sium suave
61. Mentha arvensis
62. Utricularia intermedia
64. U. vulgaris
66. Megalodonta beckii
68. Zosterella dubia

TABLE L.

A. Significant positive associations

1. 32 x 24	51. 13 x 37	101. 14 x 30
2. 9 x 30	52. 33 x 14	102. 41 x 45 ⟩ equal
3. 32 x 31	53. 3 x 40	103. 34 x 64 ⟩
4. 32 x 25	54. 14 x 14	104. 41 x 37
5. 32 x 32	55. 9 x 68	105. 36 x 40
6. 9 x 19	56. 26 x 64	106. 33 x 11
7. 32 x 19	57. 5 x 17	107. 11 x 3
8. 9 x 24	58. 26 x 60	108. 24 x 30
9. 32 x 30	59. 32 x 8 ⟩ equal	109. 24 x 35
10. 32 x 45	60. 13 x 62 ⟩	110. 24 x 45
11. 41 x 24	61. 33 x 1	111. 29 x 16
12. 32 x 66	62. 5 x 24	112. 14 x 66
13. 9 x 32	63. 32 x 34	113. 39 x 56
14. 9 x 31	64. 32 x 43	114. 4 x 1
15. 4 x 68	65. 4 x 17	115. 33 x 32
16. 32 x 7	66. 32 x 11	116. 14 x 35 ⟩ equal
17. 41 x 66	67. 41 x 68	117. 26 x 61 ⟩
18. 32 x 17	68. 5 x 14	118. 2 x 14
19. 32 x 42	69. 24 x 24	119. 9 x 11
20. 3 x 16	70. 41 x 14	120. 20 x 16
21. 41 x 32	71. 13 x 32	121. 41 x 43
22. 9 x 25	72. 13 x 34	122. 34 x 36
23. 3 x 19	73. 9 x 45	123. 14 x 38
24. 4 x 30	74. 34 x 38	124. 24 x 1
25. 32 x 40	75. 4 x 32	125. 41 x 10
26. 32 x 68	76. 37 x 42	126. 26 x 59
27. 9 x 43	77. 32 x 41	127. 5 x 45
28. 41 x 31	78. 41 x 25	128. 2 x 3
29. 41 x 30	79. 41 x 8	129. 4 x 66
30. 5 x 25	80. 41 x 19	130. 34 x 37
31. 41 x 34	81. 4 x 31	131. 15 x 31
32. 32 x 37	82. 41 x 64	132. 41 x 17
33. 11 x 56	83. 3 x 17	133. 13 x 36
34. 8 x 7	84. 14 x 16	134. 5 x 12
35. 14 x 27	85. 35 x 61	135. 32 x 46
36. 4 x 25	86. 24 x 40	136. 9 x 34
37. 11 x 36	87. 24 x 14	137. 11 x 19
38. 9 x 40	88. 24 x 29	138. 9 x 29
39. 9 x 42	89. 14 x 29	139. 3 x 24
40. 4 x 19	90. 4 x 24 ⟩ equal	140. 33 x 25
41. 41 x 40	91. 29 x 36 ⟩	141. 5 x 40
42. 33 x 17	92. 11 x 23	142. 29 x 23
43. 11 x 64	93. 9 x 41	143. 41 x 36
44. 9 x 66	94. 5 x 19	144. 32 x 10
45. 41 x 7	95. 29 x 40	145. 5 x 44
46. 32 x 14	96. 32 x 38	146. 13 x 8
47. 29 x 56	97. 3 x 56	147. 14 x 37
48. 32 x 29	98. 32 x 36	148. 26 x 27
49. 4 x 7	99. 5 x 11	149. 4 x 43
50. 4 x 40	100. 14 x 19	150. 39 x 59

continued. . .

TABLE L. (continued)

151. 9 x 8
152. 37 x 9
153. 4 x 35
154. 28 x 37
155. 29 x 45
156. 5 x 42
157. 14 x 61
158. 4 x 45
159. 39 x 10
160. 3 x 32
161. 15 x 1

B. Significant negative associations

1. 14 x 45
2. 13 x 66
3. 14 x 7
4. 14 x 25
5. 14 x 24
6. 14 x 31
7. 24 x 19
8. 14 x 17
9. 20 x 45
10. 9 x 27
11. 33 x 27
12. 14 x 11
13. 14 x 34
14. 20 x 29
15. 14 x 44
16. 9 x 59
17. 25 x 19
18. 11 x 44
19. 3 x 38
20. 24 x 61
21. 25 x 12
22. 39 x 41
23. 25 x 1
24. 20 x 25
25. 3 x 60
26. 33 x 60
27. 11 x 21 > equal
28. 29 x 42 >
29. 25 x 14 > equal
30. 25 x 45 >
31. 20 x 12

gastropod also formed significant positive associations with the following macrophytes: Ceratophyllum demersum (86th), Potamogeton natans (87th), Sagittaria spp. (88th), Elodea canadensis (108th), Lemna minor (109th), Nuphar variegatum (110th) and Chara spp. (124th). The most highly significant positive association shown by Potamogeton richardsonii was with Amnicola limosa (6th), while P. pectinatus was associated the most highly significantly with Valvata tricarinata (20th).

The most significant of the negative associations was that of Stagnicola palustris and Nuphar variegatum. The former species formed 6 of the 10 most highly significant negative associations. Bulimnea megasoma showed a strong tendency to occur in sites where Megalodonta beckii was absent; this negative association was second in overall significance. Physa gyrina and Potamogeton richardsonii were negatively associated and this combination was the most highly significant of the negative relationships shown by both of these species, ranking 7th in overall importance. Physa gyrina also showed a significant negative association with Mentha arvensis (20th in overall importance); this relationship is difficult to explain since both of these species showed a significant preference for higher levels of molybdenum-blue phosphorus and significant affinities for other parameters showed no conflicts. Lymnaea stagnalis showed significant negative associations with Nuphar microphyllum (18th) and Potamogeton spirillus (27th). Potamogeton pectinatus showed no significant negative associations with any of the gastropod species.

Of the 161 significant positive plant-snail associations

(Table XLIX), only 82 or 50.9% could be explained on the basis of net similarities in significant preferences for the environmental parameters examined (Tables XXXVI and XLIII), while of the 31 significant negative associations, 17 or 54.8% could be explained on the basis of net dissimilarities in significant environmental preferences.

Ceratophyllum demersum showed the highest number of significant positive associations with gastropods (9)(Table LI), followed by Potamogeton richardsonii with 8, and P. natans, P. zosteriformis, Zizania aquatica and Nuphar variegatum, each with 7 positive associations. All of the positive associations shown by Chara spp., Potamogeton filiformis, P. foliosus, P. gramineus, P. vaginatus, Nymphaea tuberosa, Nuphar microphyllum, Myriophyllum exalbescens and Hippuris vulgaris could not be correlated with net similarities in environmental preferences, although only Potamogeton foliosus, Nymphaea tuberosa, Nuphar microphyllum and Hippuris vulgaris showed no significant environmental preferences. No significant positive associations could be detected for Potamogeton pusillus, P. spirillus, Eleocharis spp., Ranunculus aquatilis, Callitriche spp. and Utricularia minor.

Nuphar variegatum showed the greatest number of significant negative associations with gastropods (3)(Table LI), all of which could be explained by net dissimilarities in significant environmental preferences. Potamogeton gramineus, P. richardsonii, Najas flexilis, Alisma triviale, Nuphar microphyllum and Sium suave each showed 2 significant negative associations; for

TABLE LI. Total numbers of significant positive and negative gastropod associations observed for each macrophyte species or species group and the numbers of these associations that did not coincide (N.C.) with net similarities or dissimilarities, respectively in significant preferences for the monitored environmental parameters. Only macrophytes from Table XLI were considered.

Species or species group	Positive		Negative	
	Total	N.C.	Total	N.C.
1. *Chara* spp.	4	4	1	1
3. *Sparganium* spp.	2	1	0	0
7. *Potamogeton amplifolius*	4	2	1	0
8. *P. epihydrus*	4	0	0	0
9. *P. filiformis*	1	1	0	0
10. *P. foliosus*	3	3	0	0
11. *P. friesii*	4	2	1	1
12. *P. gramineus*	1	1	2	0
14. *P. natans*	7	3	1	0
16. *P. pectinatus*	5	1	0	0
17. *P. praelongus*	6	4	1	0
18. *P. pusillus*	0	0	0	0
19. *P. richardsonii*	8	6	2	1
21. *P. spirillus*	0	0	1	1
23. *P. vaginatus*	2	2	0	0
24. *P. zosteriformis*	7	3	1	0
25. *Najas flexilis*	6	3	2	0
27. *Alisma triviale*	2	0	2	2
29. *Sagittaria* spp.	4	2	1	0
30. *Elodea canadensis*	6	2	0	0
31. *Vallisneria americana*	4	1	1	0
32. *Zizania aquatica*	7	2	0	0
33. *Eleocharis* spp.	0	0	0	0
34. *Calla palustris*	4	1	1	0
35. *Lemna minor*	3	2	0	0
36. *L. trisulca*	6	4	0	0
37. *Spirodela polyrhiza*	6	1	0	0
38. *Polygonum amphibium*	3	1	1	1
40. *Ceratophyllum demersum*	9	6	0	0
41. *Nymphaea odorata*	2	0	1	1
42. *N. tetragona*	4	2	1	0
43. *N. tuberosa*	4	4	0	0
44. *Nuphar microphyllum*	1	1	2	2
45. *N. variegatum*	7	3	3	0
46. *Brasenia schreberi*	1	0	0	0

continued. . .

TABLE LI. (continued)

Species or species group	Positive Total	Positive N.C.	Negative Total	Negative N.C.
48. Ranunculus aquatilis	0	0	0	0
54. Callitriche spp.	0	0	0	0
56. Myriophyllum exalbscens	4	4	0	0
59. Hippuris vulgaris	2	2	1	1
60. Sium suave	1	0	2	2
61. Mentha arvensis	3	1	1	1
62. Utricularia intermedia	1	0	0	0
63. U. minor	0	0	0	0
64. U. vulgaris	4	0	0	0
66. Megalodonta beckii	5	1	1	0
68. Zosterella dubia	4	2	0	0

Alisma triviale, Nuphar microphyllum and Sium suave these could not be explained on the basis of net dissimilarities in significant habitat preferences. Although Potamogeton spirillus showed no significant positive associations, it did show one significant negative association.

Of the gastropods, Helisoma campanulatum showed the greatest number (25) of significant positive associations with macrophytes (Table LII), followed by Gyraulus deflectus with 20, Amnicola limosa with 18 and Gincinnatia cincinnatiensis with 16. All of the positive associations shown by C. cincinnatiensis, Marstonia decepta, Stagnicola catascopium, Planorbula campestris, Promenetus exacuous, P. umbilicatellus and Gyraulus parvus could not be correlated with net similarities in environmental preferences because all of these species except P. exacuous showed no significant preferences. No significant positive associations were observed for Fossaria exigua, Physa jennessi skinneri, Armiger crista and Gyraulus circumstriatus.

Stagnicola palustris showed the greatest number (10) of significant negative associations with macrophytes, followed by Physa jennessi skinneri with 5; the bulk of these associations could be correlated with net dissimilarities in environmental preferences. Valvata tricarinata, Amnicola limosa, Lymnaea stagnalis, Physa gyrina and Helisoma anceps each showed two significant negative associations, both of which could not be correlated with net dissimilarities in habitat preferences.

In order to compare the similarities of the members of each possible pair of macrophytes in terms of their significant positive gastropod associations, a similarity index (equation 27, p. 354) was

TABLE LII. Total numbers of significant positive and negative macrophyte associations observed for each gastropod species and the numbers of these associations that did not coincide (N.C.) with net similarities or dissimilarities, respectively in significant preferences for the monitored environmental parameters. Only gastropods from Table XLVIII were considered.

Species	Positive		Negative	
	Total	N.C.	Total	N.C.
2. *Valvata sincera*	2	1	0	0
3. *V. tricarinata*	7	6	2	2
4. *Cincinnatia cincinnatiensis*	16	16	0	0
5. *Marstonia decepta*	11	11	0	0
9. *Amnicola limosa*	18	5	2	2
11. *Lymnaea stagnalis*	6	4	2	2
13. *Bulimnea megasoma*	7	1	0	0
14. *Stagnicola palustris*	10	7	10	2
15. *S. catascopium*	2	2	0	0
19. *Fossaria exigua*	0	0	0	0
20. *F. modicella*	1	0	4	0
24. *Physa gyrina*	8	1	2	2
25. *P. jennessi*	0	0	5	1
26. *Aplexa hypnorum*	5	1	0	0
28. *Ferrissia rivularis*	1	0	0	0
29. *Helisoma trivolvis*	6	5	1	0
32. *H. campanulatum*	25	3	0	0
33. *H. anceps*	6	1	2	2
34. *Planorbula armigera*	4	0	0	0
35. *P. campestris*	1	1	0	0
36. *Promenetus exacuous*	1	1	0	0
37. *P. umbilicatellus*	2	2	0	0
38. *Armiger crista*	0	0	0	0
39. *Gyraulus parvus*	3	3	1	1
40. *G. circumstriatus*	0	0	0	0
41. *G. deflectus*	20	8	0	0

calculated for pairs of macrophytes whose joint occurrence was observed at 5 or more sites; only associations with gastropod species that were recorded at 5 or more sites were considered. The gastropod association similarity indices for possible macrophyte species or species group pairs are given in Table LIII.

Macrophyte pairs with a similarity index greater than 0.70 formed the two groups in Fig. 107; the multiple group cannot be represented in two dimensions. The two groups were composed of 21 macrophyte species or species groups which showed a total of 51 interrelationships in terms of high similarity in associations with gastropods. For only 18 of these interrelationships were the members of the respective pairs not themselves significantly associated with each other.

When viewed with respect to common gastropod associations, the macrophyte groupings formed a system that was more complex than when viewed with respect to common associations for other macrophytes. All of the macrophyte taxa that had emerged in Fig. 101 on the basis of high similarities in significant associations for other macrophytes emerged again when compared in terms of significant associations with gastropods, except for Potamogeton natans. The latter species was highly similar (S = 0.74) in terms of common associations for other macrophytes to only one species, Nuphar variegatum; when viewed in terms of common associations with gastropods, the association similarity index for this species pair dropped to 0.62 (Table LIII). The remaining 14 species in Fig. 101 whose association similarity index in terms of other macrophytes had exceeded a value of 0.70, still exceeded this value when treated in terms of gastropod

TABLE LIII. Gastropod association similarity indices for possible macrophyte species or species group pairs. Only significant positive associations of macrophytes with gastropods were considered where the joint occurrences were observed at 5 or more sites. Species numbers represent the following taxa:

1. *Chara* spp.
3. *Sparganium* spp.
7. *Potamogeton amplifolius*
8. *P. epihydrus*
9. *P. filiformis*
10. *P. foliosus*
11. *P. friesii*
12. *P. gramineus*
14. *P. natans*
16. *P. pectinatus*
17. *P. praelongus*
18. *P. pusillus*
19. *P. richardsonii*
21. *P. spirillus*
23. *P. vaginatus*
24. *P. zosteriformis*
25. *Najas flexilis*
27. *Alisma triviale*
29. *Sagittaria* spp.
30. *Elodea canadensis*
31. *Vallisneria americana*
32. *Zizania aquatica*
33. *Eleocharis* spp.
34. *Calla palustris*
35. *Lemna minor*
36. *L. trisulca*
37. *Spirodela polyrhiza*
38. *Polygonum amphibium*
40. *Ceratophyllum demersum*
41. *Nymphaea odorata*
42. *N. tetragona*
43. *N. tuberosa*
44. *Nuphar microphyllum*
45. *N. variegatum*
46. *Brasenia schreberi*
48. *Ranunculus aquatilis*
54. *Callitriche* spp.
56. *Myriophyllum exalbescens*
59. *Hippuris vulgaris*
60. *Sium suave*
61. *Mentha arvensis*
62. *Utricularia intermedia*
63. *U. minor*
64. *U. vulgaris*
66. *Megalodonta beckii*
68. *Zosterella dubia*

TABLE LIII.

	1	3	7	8	9	10	11	12	14	16	17	18	19	21	23	24	25	27	29	30
1	x	0	0.25	0	0	0	0.29	0	0.40	0.22	0.40	0	0.31	0	0	0.36	0.40	0	0.25	0.40
3		x	0	0	0	0	0	0	0	0	0	0	0.20	0	0.67	0	0	0	0	0
7			x	0.86	0	0.57	0.57	0	0.20	0.22	0.60	0	0.62	0	0	0.73	0.80	0	0.50	0.80
8				x	0	0.67	0.67	0	0.44	0	0.44	0	0.50	0	0	0.60	0.67	0	0.57	0.67
9					x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10						x	0.33	0	0.44	0	0.44	0	0.31	0	0	0.40	0.44	0	0.29	0.44
11							x	0	0.44	0	0.44	0	0.31	0	0	0.40	0.67	0	0.57	0.44
12								x	0.29	0	0.29	0	0.20	0	0	0.25	0.29	0	0	0
14									x	0.18	0.67	0	0.67	0	0	0.62	0.67	0.25	0.60	0.67
16										x	0.36	0	0.43	0	0.29	0.33	0.18	0.29	0.22	0.36
17											x	0	0.67	0	0	0.77	0.83	0	0.20	0.50
18												x	0	0	0	0	0	0	0	0
19													x	0	0.18	0.88	0.67	0.18	0.62	0.80
21														x	0	0	0	0	0	0
23															x	0	0	0	0	0
24																x	0.77	0	0.55	0.77
25																	x	0	0.40	0.67
27																		x	0.33	0.25
29																			x	0.80
30																				x

continued. . .

TABLE LIII. (continued)

	31	32	33	34	35	36	37	38	40	41	42	43	44	45	46	48	54	56	59	60
1	0.25	0.40	0	0	0.50	0	0	0	0.31	0	0	0	0	0.36	0	0	0	0	0	0
3	0	0	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0	0	0.40	0	0
7	1.00	0.80	0	0.86	0.29	0.44	0.44	0.29	0.62	0.67	0.67	0.67	0	0.73	0	0	0	0	0	0
8	0.86	0.67	0	1.00	0	0.50	0.50	0.33	0.46	0.80	0.80	0.80	0	0.60	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0.57	0.44	0	0.67	0	0.50	0.50	0.33	0.31	0.40	0.40	0.40	0	0.40	0	0	0	0.29	0.40	0
11	0.57	0.67	0	0.67	0	0.25	0.25	0.33	0.31	0.80	0.80	0.80	0	0.40	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0.20	0	0	0	0	0.25	0	0	0	0	0	0
14	0.40	0.50	0	0.44	0.44	0.36	0.55	0.44	0.53	0.25	0.25	0.25	0	0.62	0	0	0	0	0	0
16	0.22	0.36	0	0	0.50	0.20	0.20	0.25	0.43	0	0	0	0	0.33	0	0	0	0.44	0	0
17	0.60	0.83	0	0.44	0.22	0.36	0.36	0.22	0.67	0.25	0.25	0.25	0	0.62	0	0	0	0.20	0	0
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0.62	0.67	0	0.50	0.50	0.43	0.43	0.33	0.78	0.36	0.36	0.36	0	0.75	0	0	0	0.31	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0.57	0	0	0.18	0	0	0	0	0.22	0	0	0	0.67	0	0
24	0.73	0.77	0	0.60	0.40	0.33	0.33	0.20	0.88	0.44	0.44	0.44	0	0.86	0	0	0	0.18	0	0
25	0.80	0.83	0	0.67	0.22	0.36	0.36	0.22	0.53	0.50	0.50	0.50	0	0.77	0	0	0	0.20	0	0
27	0	0	0	0	0.40	0	0.29	0.40	0	0	0	0	0	0	0	0	0	0	0.50	0.67
29	0.50	0.40	0	0.57	0.57	0.22	0.44	0.57	0.46	0.67	0.67	0.67	0	0.55	0	0	0	0	0	0
30	0.80	0.67	0	0.67	0.67	0.36	0.55	0.44	0.67	0.50	0.50	0.50	0	0.77	0	0	0	0	0	0
31	x	0.80	0	0.86	0.29	0.44	0.44	0.29	0.62	0.67	0.67	0.67	0	0.73	0	0	0	0	0	0
32		x	0	0.67	0.22	0.36	0.36	0.22	0.67	0.50	0.50	0.50	0	0.62	0	0	0	0	0	0
33			x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34				x	0	0.50	0.50	0.33	0.50	0.80	0.80	0.80	0	0.60	0	0	0	0	0	0
35					x	0	0.25	0.33	0.33	0	0	0	0	0.40	0	0	0	0	0	0
36						x	0.60	0.50	0.43	0.29	0.29	0.29	0	0.33	0	0	0	0.44	0	0
37							x	0.75	0.29	0.29	0.29	0.29	0	0.33	0	0	0	0	0	0
38								x	0.17	0.40	0.40	0.40	0	0.20	0	0	0	0	0	0
40									x	0.36	0.36	0.36	0	0.88	0	0	0	0.31	0	0
41										x	1.00	1.00	0	0.44	0	0	0	0	0	0
42											x	1.00	0	0.44	0	0	0	0	0	0

continued. . .

TABLE LIII. (continued)

	61	62	63	64	66	68
1	0	0	0	0	0	0
3	0	0	0	0.40	0	0
7	0	0	0	0.25	0.75	1.00
8	0	0	0	0.29	0.86	0.86
9	0	0	0	0	0	0
10	0	0	0	0.29	0.57	0.57
11	0	0	0	0	0.57	0.57
12	0	0	0	0	0	0
14	0.29	0	0	0.20	0.40	0.40
16	0.33	0	0	0	0.22	0
17	0	0	0	0.20	0.40	0.60
18	0	0	0	0	0	0
19	0.20	0	0	0.31	0.46	0.62
21	0	0	0	0	0	0
23	0	0	0	0.33	0	0
24	0	0	0	0.18	0.55	0.73
25	0	0	0	0.20	0.60	0.80
27	0.67	0	0	0.33	0	0
29	0.40	0	0	0	0.50	0.50
30	0.29	0	0	0.20	0.60	0.80
31	0	0	0	0.25	0.75	1.00
32	0	0	0	0.20	0.60	0.80
33	0	0	0	0	0	0
34	0	0	0	0.29	0.86	0.86
35	0.50	0	0	0	0	0.29
36	0	0	0	0.67	0.44	0.44
37	0.33	0	0	0.44	0.67	0.44
38	0.50	0	0	0.29	0.29	0.29
40	0	0	0	0.15	0.31	0.62
41	0	0	0	0	0.33	0.67
42	0	0	0	0	0.33	0.67

continued. . .

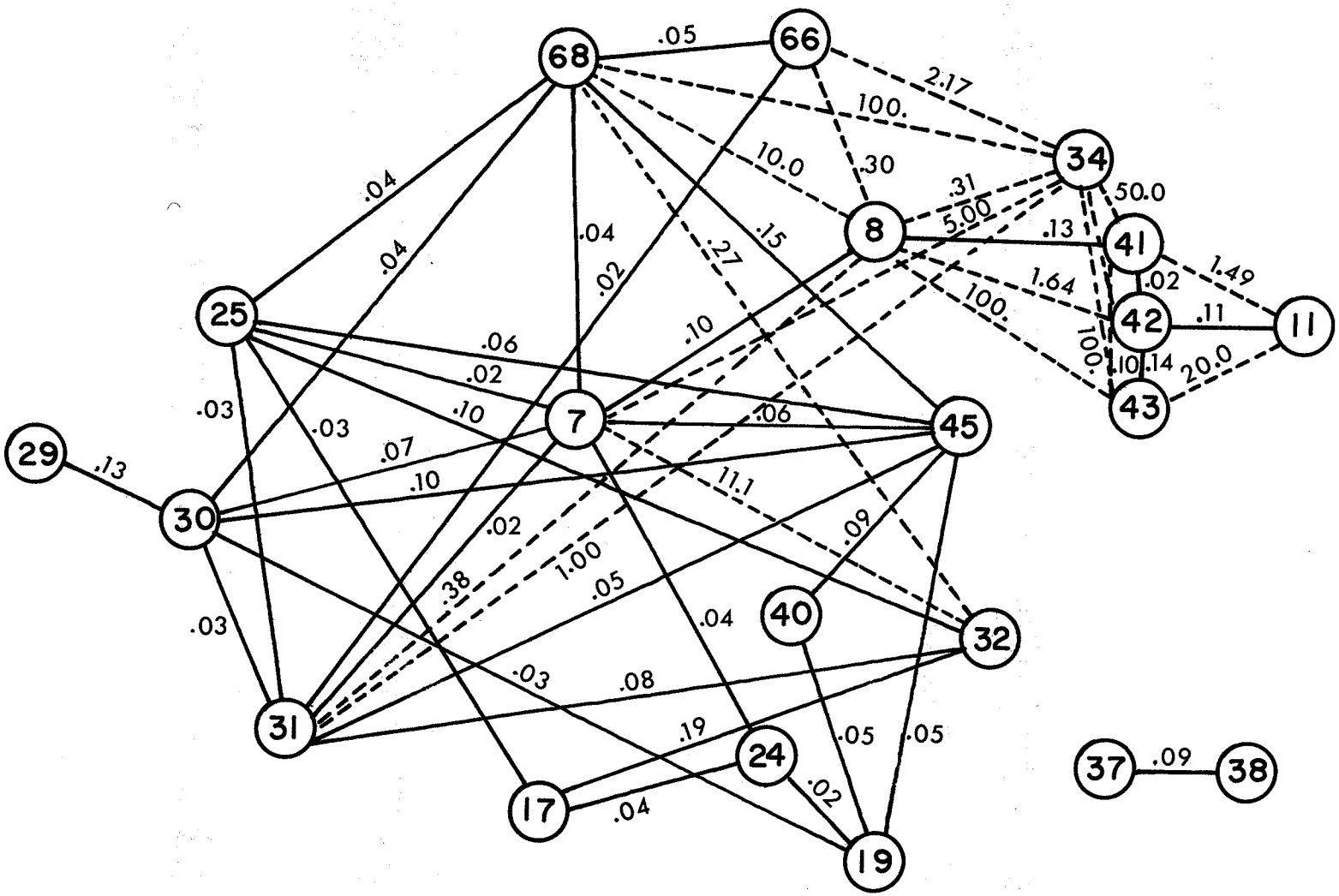
TABLE LIII. (continued)

	43	44	45	46	48	54	56	59	60	61	62	63	64	66	68
43	x	0	0.44	0	0	0	0	0	0	0	0	0	0	0.33	0.67
44		x	0	0	0	0	0	0	0	0	0	0	0	0	0
45			x	0	0	0	0.18	0	0	0	0	0	0.18	0.55	0.73
46				x	0	0	0	0	0	0	0	0	0	0	0
48					x	0	0	0	0	0	0	0	0	0	0
54						x	0	0	0	0	0	0	0	0	0
56							x	0.33	0	0	0	0	0.25	0	0
59								x	0.67	0	0	0	0.33	0	0
60									x	0	0	0	0.40	0	0
61										x	0	0	0	0	0
62											x	0	0	0	0
63												x	0	0	0
64													x	0.25	0.25
66														x	0.75
68															x

Figure 107. An abstract representation of the interrelationships between macrophyte species for which the association similarity index for significant gastropod associations exceeded a value of 0.70. Species joined by solid lines were themselves significantly ($p < .05$, $n=305$) positively associated, while those joined by broken lines were not significantly associated although the gastropod association similarity index was greater than 0.70. Species not joined by lines showed association similarity indices that were less than 0.70. Values for the theoretical distances between the species are equal to the reciprocals of the Chi-square values that tested the significance of the frequency with which the members of the respective macrophyte pairs were observed to occur jointly.

Species numbers represent the following taxa:

7. Potamogeton amplifolius
8. P. epihydrus
11. P. friesii
17. P. praelongus
19. P. richardsonii
24. P. zosteriformis
25. Najas flexilis
29. Sagittaria spp.
30. Elodea canadensis
31. Vallisneria americana
32. Zizania aquatica
34. Calla palustris
37. Spirodela polyrhiza
38. Polygonum amphibium
40. Ceratophyllum demersum
41. Nymphaea odorata
42. N. tetragona
43. N. tuberosa
45. Nuphar variegatum
66. Megalodonta beckii
68. Zosterella dubia


68
66
34
8
41
42
43
11
25
7
45
29
30
31
32
40
24
17
19
37
38
.05
2.17
100.
10.0
.30
.31
5.00
50.0
.13
.04
.04
.02
.27
.15
1.64
100.
1.49
.02
.11
20.0
.10
.14
100.
.06
.02
.10
.03
.03
.07
.10
.06
11.1
.09
.13
.02
1.00
.38
.05
.04
.03
.08
.19
.05
.05
.02
.04
.09

associations, although the members of the respective pairs for which this value was exceeded were often not the same. Thus, although the same species emerged again, the interrelationships among them were different. Spirodela polyrhiza (species 37), which was highly similar to Nuphar variegatum (species 45) in terms of plant associations but was not significantly associated with it (Fig. 101), formed a separate group with Polygonum amphibium (species 38) when compared in terms of gastropod associations (Fig. 107). The latter species, together with Potamogeton amplifolius (species 7), P. epihydrus (species 8), P. friesii (species 11), Sagittaria spp. (species group 29), Calla palustris (species 34) and Nymphaea tuberosa (species 43) were not present in the groupings in Fig. 101 because they showed no values for association similarity indices in terms of macrophyte associations that were greater than 0.70, but this value was exceeded by these species when treated with respect to gastropod associations. It is interesting that many species of macrophytes which showed high similarities in gastropod associations also tended to occur significantly frequently with each other.

Conversely, the similarities of the members of each possible pair of gastropods were compared in terms of their significant positive macrophyte associations by calculating a similarity index (equation 27, p. 354) for pairs of gastropods whose joint occurrence was recorded at 5 or more sites; only associations with macrophytes that were recorded at 5 or more sites were considered. The macrophyte association similarity indices for possible gastropod species pairs are given in Table LIV.

TABLE LIV. Macrophyte association similarity indices for possible gastropod species pairs. Only significant positive associations of gastropods with macrophytes were considered where the joint occurrences were observed at 5 or more sites. Species numbers represent the following taxa:

2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
9. Amnicola limosa
11. Lymnaea stagnalis
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
19. Fossaria exigua
20. F. modicella
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
28. Ferrissia rivularis
29. Helisoma trivolvis
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
38. Armiger crista
39. Gyraulus parvus
40. G. circumstriatus
41. G. deflectus

TABLE LIV.

	2	3	4	5	9	11	13	14	15	19	20	24	25	26	28	29	32	33	34	35
2	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3		x	0.57	0.53	0.32	0.31	0	0.24	0	0	0.25	0.27	0	0	0	0.46	0.32	0.31	0	0
4			x	0.55	0.63	0.10	0	0.33	0	0	0.13	0.55	0	0	0	0.30	0.58	0	0	0
5				x	0.38	0.14	0	0.22	0	0	0	0.50	0	0	0	0.29	0.44	0.43	0	0
9					x	0.08	0.10	0.21	0	0	0	0.38	0	0	0	0.17	0.86	0.25	0	0
11						x	0	0.13	0	0	0	0	0	0.20	0	0.50	0.13	0	0.40	0
13							x	0.17	0	0	0	0	0	0	0	0	0.15	0	0.33	0
14								x	0	0	0.18	0.44	0	0.14	0	0.13	0.35	0.13	0.29	0
15									x	0	0	0	0	0	0	0	0	0	0	0
19										x	0	0	0	0	0	0	0	0	0	0
20											x	0	0	0	0	0.29	0	0	0	0
24												x	0	0	0	0.29	0.38	0.14	0	0
25													x	0	0	0	0	0	0	0
26														x	0	0	0	0	0.25	0
28															x	0	0	0	0	0
29																x	0.20	0	0.20	0
32																	x	0.33	0.21	0
33																		x	0	0
34																			x	0
35																				x

continued. . .

TABLE LIV. (continued)

	36	37	38	39	40	41
2	0	0	0	0	0	0
3	0.25	0	0	0.18	0	0.38
4	0.13	0	0	0	0	0.67
5	0.22	0	0	0	0	0.52
9	0.11	0	0	0	0	0.70
11	0	0	0	0.20	0	0.24
13	0	0	0	0	0	0.19
14	0	0	0	0	0	0.28
15	0	0	0	0	0	0
19	0	0	0	0	0	0
20	0	0	0	0	0	0
24	0.22	0	0	0	0	0.37
25	0	0	0	0	0	0
26	0	0	0	0	0	0.09
28	0	0	0	0	0	0
29	0.29	0	0	0.20	0	0.24
32	0.08	0	0	0.07	0	0.84
33	0	0	0	0	0	0.32
34	0	0	0	0	0	0.26
35	0	0	0	0	0	0
36	x	0	0	0	0	0.10
37		x	0	0	0	0
38			x	0	0	0
39				x	0	0.09
40					x	0
41						x

Gastropod pairs with a similarity index greater than 0.60 formed the collinear species group in Fig. 108; this group was composed of four species interrelated by five similarity indices which exceeded a value of 0.60. It is noteworthy that these four species composed the 19 most highly significant positive associations with macrophytes (Table L). Although these gastropods were significantly associated with each other, only two of these, Cincinnatia cincinnatiensis (species 4) and Amnicola limosa (species 9), showed similarity indices greater than 0.60 when viewed with respect to associations with other gastropods (Fig. 106); however in terms of the latter criterion they showed a mutual similarity index of only 0.53 (Table XLVIII).

The greatest distance within the species group in Fig. 108 was between C. cincinnatiensis (species 4) and Gyraulus deflectus (species 41); the former species showed no significant habitat preferences in terms of the environmental parameters examined, while the latter tended to occur significantly more frequently in sites characterized by low levels of pH and total filtrable residue. These two species were highly similar (S = 0.67) in their significant positive macrophyte associations. Cincinnatia cincinnatiensis and A. limosa (species 9) were slightly less similar (S = 0.63) in their macrophyte associations but tended to occur with each other more frequently than did C. cincinnatiensis and G. deflectus: hence the smaller distance between the former two species. Cincinnatia cincinnatiensis was not significantly associated with Helisoma campanulatum (species 32), although the association similarity index for these two species in terms of plant associations was fairly high

Figure 108. An abstract representation of the interrelations between gastropod species for which the association similarity index for significant macrophyte associations exceeded a value of 0.60. Species joined by solid lines were themselves significantly ($p < .05$, $n=305$) positively associated. Values for the theoretical distances between the species are reciprocals of the Chi-square values that tested the significance of the frequency with which the members of the respective gastropod pairs were observed to occur jointly within the same site. Species numbers represent the following taxa:

4. Cincinnatia cincinnatiensis
9. Amnicola limosa
32. Helisoma campanulatum
41. Gyraulus deflectus

(S = 0.58). Amnicola limosa, H. campanulatum and G. deflectus were significantly associated with each other and were also highly similar in terms of plant associations. The sequence of these species reflected in some measure a progression in significant environmental preferences: A. limosa tended to occur significantly more frequently in sites characterized by low values for total alkalinity and estimated total nitrate and nitrite and high values for molybdenum-blue phosphorus; H. campanulatum tended to occur in sites characterized by significantly lower values of total alkalinity and estimated total nitrate and nitrite, as well as lower values of total filtrable residue, chloride, dissolved organic matter and molybdenum-blue phosphorus; G. deflectus occurred in sites with significantly lower values of total filtrable residue and pH; C. cincinnatiensis showed no significant environmental preferences.

Thus, when viewed in terms of common plant associations, the gastropods generally showed few similarities to each other. The similarities that did appear to exist were doubtless the complex product of similarities in habitat preferences, range overlap, dispersal factors and other, unknown elements whose relative contributions towards any given association cannot at present be defined.

Discussion

The association potentials demonstrated in this study reflected in very simplified form the complexities of sociological structure within the submerged plant-snail communities found within the study region. Significant positive and negative associations were observed among the macrophytes, among the gastropods, and among the macrophytes and gastropods. While many of these associations appeared to be sufficiently widely distributed to be commonplace, it is likely that many additional associations may have existed which were not detected during this survey. Accordingly the significance values presented here must be regarded as underestimates of the true values, since, while it was not possible to overestimate frequencies of occurrence of individual species, most of the values were almost certainly underrated because many species were overlooked, particularly at large sites, on account of limited search time and often poor visibility.

As has been pointed out in Part I of this study, and by Southwick and Pine (1975), submerged aquatic plant communities often vary greatly in species composition at a single site during different times of the season and from year to year. Steenis et al (1971 in Southwick and Pine, 1975) have suggested that changes in the plant communities may be precipitated by many unpredictable ecological factors, of which they believed turbidity to be the most important, since many submerged macrophytes have a light compensation point of approximately 2% of the ambient surface light (Meyer et al, 1943). Changes in the composition, abundance and vigor of macrophyte

communities may directly or indirectly affect the composition of the gastropod communities, or the latter may be subject to the same or related environmental factors that affect the plants. Thus the representativeness of a sample isolated from a given site at a single point in time is difficult to assess. The error inherent in single-point sampling with respect to both community composition and water chemistry may only be minimized by increasing the number of sites and sampling over a wide range of points in time, even though each site is visited only once.

Moyle (1945) was among the first workers to point out the importance of water chemistry parameters as ecological factors in the distribution of aquatic plants. These factors were recognized to be related to nutrient uptake, which in submerged macrophytes occurs in large part directly from the medium through the surfaces of the shoots (Arens, 1933; Steeman Nielsen, 1951; Lowenhaupt, 1956; Hynes, 1972), as well as from the substrate (Spence, 1972). The relative contributions of these two sites of absorption probably vary with the species and with different environmental conditions, but in general the nutrient status of the water is an important factor influencing the growth of submerged plants.

Spence (1967, 1972) suggested that the nutrient status of water was reflected by its alkalinity. Moyle (1945), Spence (1967, 1972) and Seddon (1972) found that the distributions of many macrophytes could be correlated with alkalinity and these workers classified water bodies as plant community habitat types in terms of this parameter. Hellquist (1975) found that total alkalinity was of

great importance in the distribution of Potamogeton. According to this worker, alkaline waters (> 90.0 mg/l $CaCO_3$) in New England were characterized by P. pectinatus; preference of this species for waters with high alkalinity was also reported by Spence (1967) and Seddon (1972). The results of the present survey agreed with these observations ($\bar{x}$ = 157.0 ± 8.2 mg/l $CaCO_3$, n=101), although the values at which this species occurred were not significantly higher than the values for sites from which this species appeared to be absent. Hellquist (1975) found that P. friesii and P. filiformis var. borealis were characteristic of waters whose alkalinity ranged from 61.0 to 90.0 mg/l $CaCO_3$ in northeastern Maine and western New England; the present survey showed that in the study region both of these species tended to occur in waters with much higher total alkalinity values than those reported by Hellquist (1975): P. friesii occurred at a mean value of 117.6 ± 7.2 mg/l $CaCO_3$ (n=34) while P. filiformis occurred at a mean value of 146.9 ± 33.8 mg/l $CaCO_3$ (n=21). Because these values were not significantly higher than those from sites where these species did not appear to occur, perhaps populations of these species are more tolerant of high total alkalinity values in regions where such waters are predominant. Spence (1967) noted that Scottish populations of P. filiformis often tended to occur in waters with high values of total alkalinity.

Hellquist (1975) found that moderately alkaline New England waters, for which total alkalinity ranged from 15.1 to 60.0 mg/l $CaCO_3$, were characterized by the taxa P. spirillus, P. epihydrus var. ramosus, P. gramineus, P. natans, P. zosteriformis and P. pusillus

var. tenuissimus. The present survey showed that, within the study region, all of these species, except P. pusillus, were significantly sensitive to high values of total alkalinity; the mean values at which these species occurred were (mg/l $CaCO_3$): P. spirillus, 29.3 ± 10.7 (n=6); P. epihydrus var. nuttallii, 26.4 ± 4.1 (n=21); P. gramineus, 109.2 ± 9.0 (n=62); P. natans, 111.3 ± 6.8 (n=60); P. zosteriformis, 91.2 ± 5.4 (n=57); P. pusillus, 146.9 ± 14.7 (n=36). Other taxa that tended to occur at sites with significantly lower total alkalinity values were: Sparganium spp., P. amplifolius, P. obtusifolius, P. praelongus, P. richardsonii, Najas flexilis, Sagittaria rigida, Elodea canadensis, Vallisneria americana, Zizania aquatica, Calla palustris, Spirodela polyrhiza, Polygonum amphibium, Nymphaea odorata, N. tetragona, Nuphar variegatum, Brasenia schreberi, Megalodonta beckii and Zosterella dubia. Although these species occurred significantly more frequently at lower values of total alkalinity, some, such as P. richardsonii, nonetheless had wide tolerance ranges for this parameter. Spence (1972) reported that P. praelongus was ubiquitous in Scotland in terms of alkalinity; the significant preference of this species for lower values of this variable in the present study may have been due to inherent differences in the tolerance ranges between the two groups of populations or it may have been related to other factors. For example, this species occurred consistently at the greatest water depths of the submerged macrophyte zone where most other species were unable to compete; sites where such depths were present were generally lakes and these water bodies tended to show relatively low values for total alikalinity.

The taxa characteristic of waters with a total alkalinity of less than 15.0 mg/l $CaCO_3$ in eastern New England (Hellquist, 1975) did not occur within the present study region, where no taxa appeared to be confined to such waters.

Ruppia maritima was the only species that tended to occur in waters with significantly higher values of total alkalinity ($\bar{x}$ = 232.6 ± 53.3 mg/l $CaCO_3$, n=17). Spence (1967, 1972) found that populations of Chara spp. and Ceratophyllum demersum tended to occur at ranges of high alkalinity values in Scotland, but the present study showed that these taxa occurred at a wide range of values within the study region. Again, these discrepancies may have been due to inherent tolerance range differences and/or to a variety of other factors such as temperature, with which alkalinity may act synergistically (Reynolds and Reynolds, 1975).

Total filtrable residue was found to be only slightly less important than total alkalinity in correlating with macrophyte distribution, and species that showed significant tests for both of these parameters also showed similarly inclined preferences. Ruppia maritima, Potamogeton pectinatus and P. vaginatus tended to occur in waters with significantly higher levels of total filtrable residue. Taxa which occurred in waters with significantly lower values of this parameter were: Sparganium spp., Potamogeton amplifolius, P. epihydrus, P. friesii, P. gramineus, P. natans, P. praelongus, P. richardsonii, P. zosteriformis, Najas flexilis, Sagittaria spp. (except S. rigida), Elodea canadensis, Vallisneria americana, Zizania aquatica, Lemna minor, Spirodela polyrhiza, Polygonum amphibium, Ceratophyllum

demersum, Nymphaea odorata, Nuphar variegatum and Megalodonta beckii.

Significantly higher levels of pH, the next most important factor, were observed for Chara spp., Ruppia maritima, Potamogeton friesii, P. pectinatus, P. praelongus, P. richardsonii, P. robbinsii, Najas flexilis and Myriophyllum exalbescens, while significantly lower pH values were observed for Sparganium spp., Potamogeton alpinus, P. epihydrus, Sagittaria spp. (except S. rigida), Lemna minor, Spirodela polyrhiza, Polygonum amphibium, Ranunculus gmelini, Sium suave, Utricularia intermedia, U. minor and U. vulgaris. The significantly lower values observed for Lemna minor and Spirodela polyrhiza agree with the findings of McLay (1976) and Hicks (1932). However, as Hutchinson (1970) has pointed out, this parameter must be regarded in conjunction with others since significant ecological effects of pH per se on macrophyte communities may be limited to acidic waters.

Hellquist (1975) found that nitrates were relatively less important than total alkalinity in the distribution of Potamogeton, although this factor could still be used to define the distributions of certain species. Holmes and Whitton (1975b) found that the local distribution of P. pusillus within a single river system in Britain was positively correlated with nitrate-nitrogen, but in the present survey this species showed no significant test for combined estimated nitrate and nitrite. Significantly higher values of this parameter were observed only for Ruppia maritima, while significantly lower values were recorded for Sparganium spp., Potamogeton epihydrus, P. gramineus, P. richardsonii, P. zosteriformis, Najas flexilis, Elodea

canadensis, Vallisneria americana, Calla palustris, Spirodela polyrhiza, Polygonum amphibium, Nymphaea odorata, Nuphar variegatum, Sium suave and Megalodonta beckii.

With respect to chloride, Hellquist (1975) found that Potamogeton pectinatus and P. pusillus var. tenuissimus were tolerant of high levels of chloride in New England waters. During the present survey, only P. pectinatus and Ruppia maritima tended to occur at significantly higher levels of this parameter, but P. pusillus showed no significant test, indicating a wide tolerance range. Rørslett (1975) found that Ruppia was tolerant of high salinity levels. Haller et al (1974) suggested that Vallisneria americana was relatively salt intolerant; during the present study, although this species was significantly sensitive to high levels of total alkalinity and total filtrable residue, it showed no significant test for chloride. Only Potamogeton natans and Nuphar variegatum tended to occur at significantly lower levels of chloride.

Reynolds and Reynolds (1975) suggested that macrophytes may tolerate much higher salinities where the dominant anion is sulphate than where it is carbonate or bicarbonate. The highest sulphate level (3403 mg/l) recorded in this survey was at site 205, a saline pond in Saskatchewan, where the concurrent chloride level was 1234 mg/l; this site supported populations of Potamogeton pectinatus and Myriophyllum exalbescens as well as the gastropods Stagnicola palustris, Physa jennessi skinneri, Fossaria obrussa and F. modicella. It is likely that the observation of Reynolds and Reynolds (1975) may be true for both macrophytes and gastropods. During the present survey, no macrophytes appeared to be significantly sensitive to high sulphate

levels and only Potamogeton pectinatus tended to occur at sites with significantly higher values of this parameter, which was the least important of the variables that were examined.

Molybdenum-blue phosphorus appeared to be relatively unimportant in the distribution of most macrophytes. Forsberg (1964a and b, 1965) found that growth of Chara was inhibited at high levels of phosphorus; during the present survey this plant showed no significant test for this parameter. Caines (1965) found that Myriophyllum alterniflorum and Potamogeton praelongus were phosphorus tolerant; within the study region these species occurred at a wide range of molybdenum-blue phosphorus levels and showed no significant tests for this parameter. Species that did significantly tend to avoid waters with high levels of molybdenum-blue phosphorus were: Potamogeton amplifolius, P. epihydrus and Nymphaea odorata. Potamogeton pectinatus, Alisma triviale and Mentha arvensis occurred at significantly higher levels of this parameter.

Dissolved organic matter also appeared to be a relatively unimportant factor in the distribution of macrophytes, and approximately equal numbers of taxa occurred at significantly higher or lower values of this parameter. Significant tests for dissolved organic matter often coincided with significant but oppositely inclined tests for pH; these two factors appeared to be related in that highly colored waters tended to be acidic. The influence of this parameter on plant distribution may have been due to its effect on light quality and intensity, or to related factors.

Thus for macrophytes, the parameters that were examined could be ranked in the following order of importance, based on

numbers of species or species groups that showed significant tests: total alkalinity, total filtrable residue, pH, dissolved organic matter, estimated total nitrate and nitrite, molybdenum-blue phosphorus, chloride and sulphate.

The effects of other chemical factors upon plant distribution have been little studied. Calcium levels have been correlated with the distribution of Myriophyllum (Hutchinson, 1970), Potamogeton and Zannichellia (Holmes and Whitton, 1975b). Reynolds and Reynolds (1975) and Holmes and Whitton (1975b) found that conductivity could not be correlated with macrophyte distributions.

In the distributions of gastropods, molybdenum-blue phosphorus appeared to be the most important factor. Valvata tricarinata, Probythinella lacustris, Amnicola limosa, Lymnaea stagnalis, Stagnicola palustris, Fossaria modicella, Physa gyrina, Aplexa hypnorum, Helisoma trivolvis, Planorbula armigera, Promenetus exacuous and Armiger crista tended to occur at significantly higher levels of this parameter. Bulimnea megasoma and Helisoma campanulatum occurred at significantly lower levels of molybdenum-blue phosphorus.

Total alkalinity was the second most important factor in gastropod distributions. Stagnicola palustris, Fossaria modicella, Physa jennessi skinneri, Helisoma trivolvis, Promenetus exacuous, Armiger crista and Gyraulus circumstriatus occurred significantly more frequently in waters with high total alkalinity values, while Amnicola limosa, Bulimnea megasoma and Helisoma campanulatum occurred at sites with significantly lower total alkalinity values.

Significantly higher levels of total filtrable residue, the next most important factor, were observed for Stagnicola palustris,

Fossaria modicella, Physa jennessi skinneri and Armiger crista; significantly lower values were observed for Physa gyrina, Helisoma campanulatum, H. anceps and Gyraulus deflectus. As had been the case for macrophytes, where significant tests were shown for both total alkalinity and total filtrable residue by the same species, these preferences were both similarly inclined.

The importance of total filtrable residue, pH and combined estimated nitrate and nitrite was equal, although many species showed significant tests for only one of the latter two parameters. Stagnicola palustris and Physa jennessi skinneri showed significant positive tests for both pH and nitrate/nitrite, while Fossaria modicella and Gyraulus circumstriatus showed significant positive tests only for the latter variable. Amnicola limosa, Physa gyrina, Ferrissia rivularis and Helisoma campanulatum tended to occur at significantly lower nitrate/nitrite levels while Valvata sincera, Bulimnea megasoma, Aplexa hypnorum, Ferrissia rivularis, Planorbula armigera and Gyraulus deflectus occurred at significantly lower pH values.

Cvancara et al (1976) suggested that high chloride levels may affect the occurrence of molluscs. The present survey showed that only Helisoma campanulatum was significantly sensitive to high levels of this parameter while Valvata sincera, Stagnicola palustris, Fossaria modicella, Physa jennessi skinneri and Armiger crista were observed at significantly higher levels of chloride.

Dissolved organic matter appeared to be a relatively unimportant parameter; only Helisoma campanulatum occurred at significantly lower levels of this parameter, while Lymnaea stagnalis, Aplexa hypnorum, Planorbula armigera and Armiger crista tended to

occur at significantly higher values.

As had been the case for macrophytes, sulphate was the least important factor in the distribution of gastropods. Only Stagnicola palustris, Fossaria modicella and Physa jennessi skinneri showed significant tests for this parameter, all of them tending to occur at significantly higher values.

In general, Stagnicola palustris, Fossaria modicella, Physa jennessi skinneri and Armiger crista tended to occur at significantly higher levels of most parameters, while Helisoma campanulatum was sensitive to high levels of most parameters. The sensitivity of Bulimnea megasoma to three of the parameters may be contributing towards the progressive disappearance of this species from the study area, particularly from localities of declining water quality (LaRocque, 1968; Grimm, 1975). However H. campanulatum continues to be distributed widely throughout the study area, despite its sensitivity to six of the parameters.

Thus for the gastropods, the parameters examined could be ranked in the following order of importance, based on numbers of species showing significant tests: molybdenum-blue phosphorus, total alkalinity, total filtrable residue and pH and combined estimated nitrate and nitrite (equal), chloride, dissolved organic matter and sulphate.

Of course, other factors may also be important in the distributions of molluscs, for example,potassium (Imlay, 1973), calcium (Greenaway, 1971) and substrate type (Cvancara et al, 1976).

Since each species would be expected to occur in the

habitats whose characteristics fall within the tolerance ranges of that species, provided that such habitats also fall within the geographical range of the species, absence of the species from such a habitat could be interpreted as a result of biotic factors or inefficient dispersal. Overland dispersal among isolated aquatic habitats is believed to occur primarily through accidental attachment of eggs and small snails to the legs and feathers of aquatic birds (Malone, 1965; Rees, 1965) and it is likely that plant propagules may be dispersed in the same way. F.C. Baker (1945) pointed out the similarities of the distributions of planorbid snails such as Promenetus exacuous to the migration routes of aquatic birds. Dispersal is now aided substantially by human activity; for example, the influx of sport fishermen complete with boats and equipment from Minnesota to the Duck Mountains and Whitefish Lake regions of Manitoba may account in part for the unusual species diversities of some of these lakes. Thus, the presence of Helisoma corpulentum in Whitefish Lake, in the Porcupine Provincial Forest, is almost certainly the result of human activity, since this species is otherwise confined to the Winnipeg River system and more southeasterly regions. In the north, it is likely that aquatic aircraft may be aiding in the dispersal of both plants and snails.

In terms of species diversity, the eastern portion of the study area was found to be richer than the western portion. Some species, such as Nymphaea tuberosa, Utricularia geminiscapa, Najas gracillima and Myriophyllum heterophyllum, and Acella haldemani and Somatogyrus subglobosus, were limited to the extreme southeastern portion of the study area and the sites where these species were

recorded probably represented the northwestern boundary of the ranges for these species.

The characteristically eastern species, Potamogeton amplifolius, P. epihydrus, P. robbinsii, P. spirillus, Brasenia schreberi and Zosterella dubia, and Marstonia decepta, Amnicola walkeri and Helisoma corpulentum were limited to the region east and south of Lake Winnipeg. Pseudosuccinea columella would also appear to belong in this category although at present it seems to be extinct from the study region. Bulimnea megasoma may be regarded as an eastern species since at present its most westerly point of known occurrence is on Hecla Island in Lake Winnipeg. Potamogeton obtusifolius at present has a very limited distribution within the study area, with foci in the region of Wallace Lake in southeastern Manitoba and near Beaver Creek on the western shore of Lake Winnipeg; these populations appear to be the result of initially accidental introduction. The range of Zizania aquatica may be regarded as eastern since the westernmost known natural population within the study area was recorded at Sewell Lake in the Spruce Woods Provincial Forest.

The macrophytes characteristic of the eastern region were, except for Potamogeton robbinsii, intolerant of high alkalinity levels and often of high total filtrable residue and combined estimated nitrate and nitrite levels. This sensitivity may be among the major factors that restrain the range expansion of these species beyond the granitic Shield region. Species such as P. amplifolius and P. spirillus have expanded their ranges westward fairly recently, judging from the absence of these species from previous reports, but

have remained within the limits of the Shield region. Although Zizania aquatica has spread beyond this region, it has selected for sites where the total alkalinity and total filtrable residue levels are significantly lower.

On the other hand, gastropods with characteristically eastern ranges, such as Marstonia decepta, Amnicola walkeri and Helisoma corpulentum did not show any significant preferences for any of the environmental parameters that were examined. Bulimnea megasoma was the only species limited to this region that showed significant sensitivities to high levels of water chemistry factors. Although larger samples for the eastern species may yet reveal sensitivities which were overlooked in the present study, it nonetheless appears that these species either do not disperse well overland or are sensitive to other factors.

Although no taxa were restricted to the western portion of the study area, species such as Ruppia maritima and Physa jennessi skinneri were much more frequent in this area, perhaps because they were tolerant of high levels of total alkalinity, total filtrable residue, pH, chloride and combined estimated nitrate and nitrite which were characteristic of much of the waters of this region.

Because the entire flora and fauna of a single water body was regarded as a single ecological unit, following Seddon's (1972) viewpoint, the significantly frequent occurrence of two species jointly within the same water body was interpreted as positive association. Although many of these associations could be correlated with net similarities in significant environmental preferences, a large proportion could not. Although some members of the latter

group could perhaps be explained in terms of similarities in preferences for other, unknown environmental variables, this explanation was not generally satisfactory since the members of some of the most highly significant associations showed no net similarities in terms of the known parameters and the wide distributions and frequent occurrence of such species made selectivity for obscure elements unlikely.

Species of both macrophytes and gastropods that occurred at significantly lower levels of several parameters tended to form more highly significant associations than did species that occurred at significantly higher levels of several parameters. In general, the most common species did not form the most highly significant associations.

The macrophyte species groupings that emerged in terms of similarities of possible species pairs with respect to significant positive associations with other macrophytes showed that species highly similar to each other in terms of other associations often tended to be significantly positively associated with each other. These groupings, when viewed in terms of similarities of each macrophyte pair with respect to significant gastropod associations, were again composed of largely the same macrophyte taxa, although the interrelationships between them were different.

The species groupings of gastropods that emerged in terms of the similarities of the members of possible species pairs with respect to significant positive associations with other gastropods showed little relationship to each other in terms of mutual association but rather reflected transitions in the characteristics

of the habitats within which the species tended to occur. When possible gastropod pairs were examined with respect to similarity in significant macrophyte associations, few species showed high similarity indices; the species for which these indices were relatively high also composed the most highly significant positive associations with macrophytes. The impracticability of defining the ecological range overlap between any two species and the large number of unknown factors made interpretation of these interrelationships in the light of environmental factors difficult.

Significantly frequent joint occurrences within the same sites provided no indication of whether the two species were indeed directly associated since the species may have been segregated into different subcommunities in the manner observed in Part I, and thus may not have been truly associated. Conversely, the absence of significantly frequent joint occurrences within the study region may not have excluded the possibility for the existence of positive association at the sites where joint occurrence did take place. For example, Physa gyrina did not occur jointly with Potamogeton pectinatus at an acceptable significance level within the study region, yet at sites 1-4 (Part I) these species were seasonally associated. However, since Lymnaea stagnalis was significantly frequently associated with P. richardsonii within the study area, the extensity of the potential for this association to develop was greater. This still did not preclude the possibility that this gastropod may have been associated more strongly with other macrophytes that also occurred within the sites where both it and P. richardsonii were present.

Evidence of grazing by gastropods was found on the submerged leaves of all species of Potamogeton except in P. natans; in the latter species the submerged leaves are reduced to petioles and grazing was difficult to assess. The abundance of grazing lesions in various taxa suggested that direct plant-snail associations may occur across a broad spectrum of macrophyte types.

The results of this survey suggested that specific plant-snail associations are not obligatory, and where alternate macrophytes occur the snails may adapt relatively successfully to alternate food sources. However the large proportion of negative plant-snail associations which could not be explained in terms of net dissimilarities in significant environmental preferences for the monitored environmental parameters suggested that adaptability was not unrestricted among all macrophyte taxa. Because of the variability of the plant communities within which the gastropods occurred at different sites, the development of specific associations within each site was probably dependent upon a combination of factors involving the species present and their respective physicochemical attributes relative to each other and to the environment. It is likely that many of the associations within a given site were seasonal and may have varied from year to year. Thus association analysis where the biota of an entire site is treated as a single ecological unit can only be used to predict the potential for the development of particular associations, but the types and intensities of the associations actually present must be examined quantitatively within the respective subcommunities present at each site.

INTEGRATION OF PARTS I AND II

The varied types of plant-snail associations that may exist within a single water body are not constant in time and space but depend upon a large array of biotic and environmental factors. Different plant-snail associations may coexist within the same water body relatively independently of each other through segregation within distinct subcommunities. Snails may be associated with certain macrophytes only at certain times of the season that are unrelated to the growth cycles of either member of the association, or the growth cycles of both members may be highly synchronized in order to maximize the survival of each. In the latter types of associations, the young may hatch on the plants at times when the latter are comparatively richer in energy, and are best capable of sustaining a grazing load. In such associations, a highly complex system of biochemical controls may be operating wherein the host plants may be participating in the regulation of the reproductive cycles of their grazers. Where several such systems coexist, they minimize competition for food and space among the different species of grazers.

The large numbers of potential plant-snail associations are probably based upon a relatively small number of basic mechanisms for which many specific variations may be possible. Because of the plasticity of plant-snail associations, the adaptability of gastropods to alternate food sources may be an important factor in the survival of these species, and such adaptability is perhaps a strong contributory factor in the wide distributions of many of the large grazers.

The large numbers of alternate, significant plant-snail associations suggest that the particular combination of association patterns operating within the communities present at a given site is peculiar to each water body, depending upon the particular set of environmental and biotic conditions prevalent therein. Although joint occurrences within a single site provide no information regarding the degree of interaction between the species, it is likely that many of these potential associations may function on a system as complex as that involving biochemical regulation. The incunabula of such systems may take place during the early stages of colonization of a water body when only a small number of species is present; the complexities of the interactions may be modified and refined as species diversity increases. The role of imprinting of the young, which hatch in greater numbers upon the preferred macrophytes, in the subsequent selection by adults of plants for oviposition is not known, but could conceivably become significant through progressive generations. The evolution of such systems within a set of communities is indicative of the high degree of interaction between the members of the respective associations, and changes that reflect upon the species abundance or community composition may have profound effects upon the equilibrium of the entire aquatic unit.

Not all aquatic gastropods are significant macrophyte grazers and not all macrophytes are suitable snail fodder; plant-snail associations composed of species which do not appear to participate in direct grazing relationships to any significant extent may reflect requirements of the gastropods for shelter,

epiphytes, exudates or other, unknown factors. The interpretation of plant-snail associations is complicated by the tendencies of the members of the respective plant and snail communities to associate among themselves; furthermore the role of preferences for certain environmental variables shown by certain members of these communities cannot be disregarded.

Thus the remarkably intricate interrelationships between the members of submerged plant-snail communities and other biota, together with the effects of environmental factors, are at present difficult to envisage, much less to isolate and quantify. So little work has been done in this field, and so many dimensions remain unexplored, that the information already gained is lost among the vastness of what continues to be unknown.

"Felix qui potuit rerum cognoscere causas".
Vergil

SUMMARY

In Part I of this study, some quantitative relations between macrophytes and molluscs in submerged aquatic communities were examined. During the 1972 season, sites 1, 5 and 6 in the Delta Marsh on the southern shore of Lake Manitoba were sampled by Ekman dredge at approximately two-week intervals during May to August. The results showed that at the three sites many species of molluscs tended to occur significantly more frequently in areas occupied by stands of submerged vegetation than in bare areas. Differential distributions were observed for both live and dead shells, and the greater accumulations of the latter in vegetated areas could not be satisfactorily explained by passive distribution, since graveyard indices, based on the numbers of dead land shells found in the sediment samples, suggested that in the majority of cases passive redistribution was not significantly different between the various habitat types within a single site to account for polar distributions.

At site 1, Physa gyrina tended to occur significantly more frequently in stands of Potamogeton pectinatus than in the other habitat types while Lymnaea stagnalis tended to occur significantly more frequently in stands of P. richardsonii than in any other habitat type. Besides these two major gastropods, associations with these macrophytes on a reduced scale were observed for Fossaria modicella, Stagnicola palustris and Helisoma trivolvis. Live counts of snails observed on the macrophytes in situ supported the results of the bottom sampling. At site 5, where only Myriophyllum exalbescens was present in the sampling area, strong associations with this

plant were observed for P. gyrina and F. modicella. At site 6, where only P. pectinatus was present in the sampling area, Amnicola limosa and Pisidium casertanum were observed to occur significantly more frequently in areas occupied by vegetation stands than in bare areas. The associations, in terms of snail density per unit bottom area, were time-dependent and peaks were related to reproduction by the snails. The differential snail distributions could not be correlated with any of the monitored environmental parameters.

During the 1973 season, sites 1, 2 and 3 in the Delta Marsh and site 4 in the Big Grass Marsh west of Langruth, Manitoba were studied; during the 1974 season only sites 1 and 2 were sampled. At these sites, apparently homogeneous stands of P. pectinatus and P. richardsonii were sampled quantitatively using a modified macrophyte sampler. The results showed that during both seasons the growth of P. pectinatus was synchronous in terms of increase of mean dry shoot weight per unit bottom area, while the growth of P. richardsonii was out of phase at these two sites by approximately two weeks. The associations of the five gastropod species that had shown significant affinities for vegetation at site 1 during the 1972 season were found at sites 1, 2 and 4 and could be expressed in terms of snail numbers per unit host plant weight and surface area. The associations of P. gyrina and L. stagnalis could also be demonstrated in terms of snail biomass per plant unit. The mean numbers of the latter two snails per plant unit showed well-defined seasonal peaks which were due to reproduction and occurred during periods of active growth of the host plants. The timing of the peaks appeared to be related to the growth patterns of the preferred

macrophytes at the respective sites: the association peaks of P. gyrina were synchronous in the P. pectinatus stands at sites 1 and 2 while those of L. stagnalis were approximately two weeks out of phase in the P. richardsonii stands at these sites. Size class distribution patterns of snails in the two types of stands at each site showed that reproduction in the stands of preferred macrophytes often slightly preceded that in stands of alternate plants. At site 3, where only P. pectinatus was present in the sampling area, P. gyrina and F. modicella showed an intense association with this plant. The associations shown by F. modicella, S. palustris and H. trivolvis, although significant, were not consistent from year to year and the density patterns of these snails did not appear to be related in time to the growth of the host plants. Promenetus exacuous was present on the macrophytes only during the 1974 season, when it occurred only on P. richardsonii shoots.

The density of grazing lesions sustained by the plants at different times of the season could be correlated with the total numbers of gastropods present per plant unit during the preceding sampling period. The differential distributions of the respective gastropods and timing of reproduction did not appear to be directly related to any obvious environmental factors.

The macrophytes collected during the 1972 season were examined for total soluble carbohydrates, total titratable acids, total extractable protein and carotenoid compounds. The seasonal patterns of total soluble carbohydrate in tissues of the two Potamogeton species from site 1 suggested that this factor may have been related to the differential snail distributions. Plant material

collected at the study sites during the 1973-4 seasons was extracted, fractionated on ion-exchange columns and examined chromatographically. The results showed that P. pectinatus contained higher levels of fructose and glucose than did P. richardsonii, while the latter species contained proportionately more sucrose than did the former. These results, combined with physiological data from the literature, suggested that a complex physiological system may be operant in the regulation of snail distributions. The adult snails may be attracted to the respective macrophytes by particular plant-originated compounds. Elevated sugar levels in the plant tissues would in turn raise the haemolymph glucose levels of the grazing snails. Increased levels in the haemolymph glucose would give rise to a series of hormonal responses which would stimulate reproduction, provided that the temperature threshold had been exceeded; reproduction would give rise to an association peak. The young often emerged at times when carbohydrate levels in the host plants were elevated.

In Part II of this study, 305 sites in southern Manitoba and the peripheral regions were surveyed with respect to water chemistry and the presence of submerged macrophytes and gastropods. The macrophytes present within the study region were grouped into 69 taxonomic categories; several new records for macrophytes in Manitoba were established. The gastropods found within the study region were composed of 42 species. Many species of both macrophytes and gastropods tended to occur in sites characterized by significantly higher or lower values of certain environmental parameters. For the macrophytes, these parameters could be ranked in the following

order of importance, based on numbers of taxa showing significant tests: total alkalinity, total filtrable residue, pH, dissolved organic matter, estimated total nitrate and nitrite, molybdenum-blue phosphorus, chloride and sulphate; for gastropods this order was: molybdenum-blue phosphorus, total alkalinity, total filtrable residue and pH and combined estimated nitrate and nitrite (equal), chloride, dissolved organic matter and sulphate.

Within the study region, the three most common macrophytes were Myriophyllum exalbescens, Potamogeton richardsonii and P. pectinatus. The plant communities showed 278 significant positive and 9 significant negative associations, a large portion of which could not be explained on the basis of net similarities or dissimilarities, respectively in significant preferences for the monitored environmental variables. In general, the most common species did not show the most highly significant associations. Potamogeton zosteriformis showed the most highly significant positive associations as well as the greatest number of significant positive associations. Potamogeton pectinatus and P. richardsonii were significantly positively associated within the study region but this association ranked 113th in significance among the positive associations. A comparison of possible species pairs with respect to similarities in the significant positive associations with other macrophytes revealed groups of species which were highly similar to each other in their positive associations and were also significantly associated with each other.

The three most frequently encountered gastropods within the study region were Lymnaea stagnalis, Physa gyrina and Helisoma

trivolvis. The gastropod communities showed 71 significant positive and 4 significant negative associations. Valvata tricarinata and Amnicola limosa showed the most significant positive associations as well as the greatest numbers of significant positive associations. Physa gyrina and L. stagnalis were significantly positively associated with each other but this association ranked 45th in significance among the positive associations. A comparison of possible species pairs with respect to their similarities in the significant positive associations with other species revealed several groups of species which appeared to represent different habitat types.

An examination of plant-snail associations revealed 161 significant positive and 31 significant negative associations, many of which could not be explained on the basis of net like or unlike significant preferences for the environmental parameters examined. Helisoma campanulatum and Amnicola limosa showed the most highly significant associations with macrophytes. Ceratophyllum demersum showed the highest number of significant positive associations with gastropods while H. campanulatum showed the greatest number of significant positive associations with macrophytes. A comparison of possible plant-snail species pairs with respect to their similarities in the significant positive associations with gastropods, and a comparison of possible gastropod species pairs with respect to their similarities in the significant positive associations with macrophytes, revealed species groupings which were often bound by significant positive associations with each other.

The results of the survey suggested that the potential for

many plant-snail associations within the study area is great and that the particular set of associations which develops within a given site is dependent upon a complex array of biotic and environmental factors. The evolution of differential distribution patterns within a single site may serve to minimize competition for food and space among gastropods. However the associations are quite flexible in their specificities and such plasticity may be important in the survival of gastropods and their utilization of alternate food sources.

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APPENDIX I

A Method for Fitting Population Data to a Matrix Model when the Growth Rate is Unknown.

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A Method for Fitting Population Data to a Matrix Model when the Growth Rate is Unknown

Abstract

A simple method is presented for fitting any size class data to a matrix model when the growth rate of the population is not known. Fixed values are set for the probability of recruitment (p) from the ith to the $(i + 1)$ class by $(t + 1)$ and the corresponding mean probability of remaining in the $(i + 1)$ class (r) is determined for each value of p. The mean r value exhibiting the least variance and its corresponding p value are taken as the optimal fit. Total fecundity can be estimated from the data once the optimal p and r values are known, facilitating use of the model in prediction. Sample data are presented for *Physa gyrina* (Mollusca: Gastropoda).

Matrix models are particularly useful in the description of population growth since their dynamic properties can be adapted to reflect the growth, survival and fecundity of populations under a variety of conditions. Because knowledge of the latter three parameters is essential for the operation of a matrix model of a population, such as that proposed by LEFKOVITCH (1965), the initial construction of the matrix depends upon the availability of this information, often procured by experimental means. However, it is sometimes desirable to construct a matrix from size class data obtained for populations where none of the three parameters are known. Under certain conditions the elements required for a projection can be estimated from the data, allowing for the construction of a tentative model which can be subsequently improved when additional information becomes available.

If a population of organisms, where size is dependent on age, is subdivided into several classes at repeated time intervals, the data so obtained represents the flux of numbers of individuals present in each class with progression in time. Let us consider two consecutive size classes, i and $(i + 1)$, each containing the numbers of individuals present in that class at successive times.

$$i = (n_t, n_{t+1}, n_{t+2} \ldots n_{t+n}) \tag{1}$$

$$(i + 1) = (n_t, n_{t+1}, n_{t+2} \ldots n_{t+n}) \tag{2}$$

The numbers of individuals present in class i at time t will have, by time $(t + 1)$, either recruited to the $(i + 1)$ class, remained in the ith group, or died (LEFKOVITCH, 1965). Thus a value in the $(i + 1)$ group at time $(t + 1)$ is composed of recruits from the ith class at time t and remnants from the $(i + 1)$ class at time t:

$$n_{(i+1),(t+1)} = pn_{i,t} + rn_{(i+1),t} \tag{3}$$

where p is the probability of recruiting from the ith class to the $(i + 1)$ class by $(t + 1)$, and r is the probability of remaining in the $(i + 1)$ class by $(t + 1)$. It can be seen that

$$p = \frac{n_{(i+1,(t+1)} - rn_{(i+1),t}}{n_{i,t}} \tag{4}$$

and

$$r = \frac{n_{(i+1),(t+1)} - pn_{i,t}}{n_{(i+1),t}} \tag{5}$$

When r equals zero then

$$p = \frac{n_{(i+1),(t+1)}}{n_{i,t}} \tag{6}$$

Let us consider an example where class $i = (250, 200, 150, 100, 50, 10, 5, 0)$ and class $(i + 1) = (100, 100, 80, 60, 40, 20, 4, 2)$. The values of p and r may be obtained by solving equations for two unknowns. Alternatively a series of fixed values may be set for p, and r solved for each pair of $n_{i,t}$, $n_{(i+1),(t+1)}$ values. When the various fixed values of p are plotted against the calculated mean values of r the relationship shown by the closed circles in Fig. 1 is obtained. When the variance of each series of calculated r values (each series corresponding to a single fixed value of p) (Table 1), is plotted

Table 1. Fixed p values, mean calculated r values and variance of r for examples 1 and 2. In the calculations the predicted numbers of individuals contributed through p and r have been treated as integers. The range of values may be extended in either direction by introducing additional fixed values of p.

Example 1			Example 2		
p	r	s_r^2	p	r	s_r^2
0.30	0.14	0.0078	0.30	0.32	0.0072
0.31	0.12	0.0059	0.31	0.30	0.0056
0.32	0.11	0.0047	0.32	0.29	0.0044
0.33	0.10	0.0034	0.33	0.28	0.0033
0.34	0.09	0.0024	0.34	0.27	0.0024
0.35	0.06	0.0023	0.35	0.25	0.0021
0.36	0.05	0.0016	0.36	0.24	0.0015
0.37	0.04	0.0008	0.37	0.23	0.0008
0.38	0.03	0.0004	0.38	0.22	0.0004
0.39	0.01	0.0001	0.39	0.21	0.0001
0.40	0.00	0.0000	0.40	0.20	0.0000
0.41	0.02	0.0001	0.41	0.18	0.0001
0.42	0.03	0.0004	0.42	0.18	0.0002
0.43	0.04	0.0009	0.43	0.16	0.0007
0.44	0.05	0.0016	0.44	0.15	0.0012
0.45	0.08	0.0017	0.46	0.13	0.0022
0.47	0.10	0.0037	0.47	0.11	0.0033
0.48	0.11	0.0047	0.48	0.11	0.0042
0.49	0.13	0.0064	0.49	0.09	0.0056
0.50	0.14	0.0078	0.50	0.07	0.0044

against the associated value of p, this gives the relationship shown by the closed circles in Fig. 2. The minimum variance of r occurs at $p = 0.40$; at this value $r = 0$.

Let us consider a second example where class $i = (250, 200, 150, 100, 50, 10, 5, 0)$ and class $(i + 1) = (100, 120, 104, 81, 56, 31, 10, 4)$. In this case a plot of fixed values of p versus calculated mean values of r yields the relationship shown by the open circles in Fig. 1. The variance of each mean value of r plotted against the corresponding value of p (Table 1), gives the curve shown by the open circles in Fig. 2. Here the minimum variance occurs when $p = 0.40$ and from Table 1 it can be seen that at this p value $r = 0.20$. Hence it is apparent that the variance of r reaches a minimum value at the point of best fit with the given data. The accuracy of fit increases as both the numbers of individuals and the number of time intervals under consideration are increased.

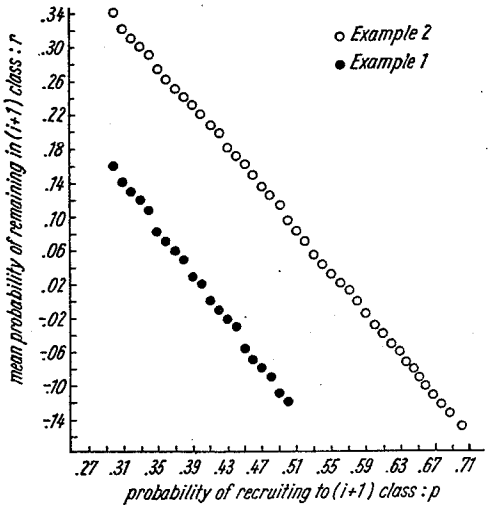

Fig. 1. Relationship between p and r values for Examples 1 and 2. In the calculations predicted numbers of individuals were considered as integers.

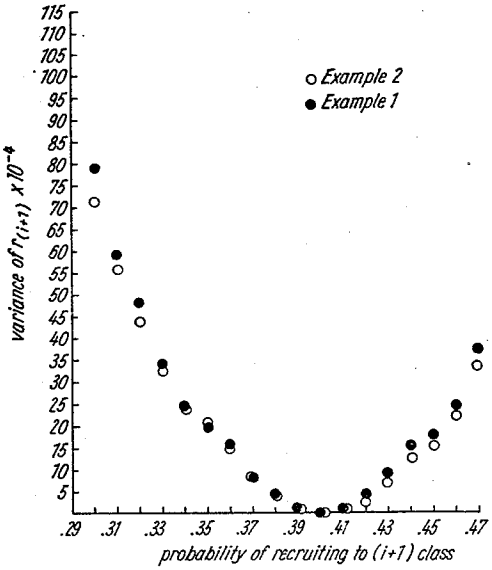

Fig. 2. Variance of r plotted against the respective values of p for Examples 1 and 2. In the calculations predicted numbers of individuals were considered as integers.

Application of the Method to Field Data

Data for a closed population of the freshwater snail *Physa gyrina* (SAY) (Mollusca: Gastropoda) is presented as an example. The population was sampled in a closed shallow ditch in the Delta Marsh on the southern shore of Lake Manitoba. Sampling was carried out with a rapid guillotine-type submerged macrophyte sampler at two week

Table 2. Numbers of individuals present in each size class grouping at successive time intervals

Time / Size (mm)	1.5—5.0	5.5—7.0	7.5—9.0	9.5—11.0	11.5—12.5	13.0—17.0
t_0	157	88	59	16	0	0
t_1	386	236	73	18	1	0
t_2	180	316	216	58	6	0
t_3	22	128	298	126	32	1
t_4	12	23	173	134	77	58
t_5	1	1	57	122	28	92

intervals. The area encompassed by the total number of samples at each time was 1.525 m^2. The axial length of the snails present in the samples was measured to the nearest 0.5 mm. The classes were more or less arbitrarily combined so that in general $n_{i,t} \geqq n_{(i+1),(t+1)}$. This gave the values in Table 2, t_0 corresponding to early June of 1973.

The first value in the first column of Table 2 was evidently incomplete and did not contribute to the calculations. The values of p and r were calculated using the above approximations for minimum variance. The values in the higher size classes become increasingly inaccurate because of the diminishing number of individuals and time intervals.

The applied matrix model was modified after LEFKOVITCH (1965):

$$\begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_{n-1} & f_n \\ p_0 & r_1 & 0 & \cdots & 0 & 0 \\ 0 & p_1 & r_2 & \cdots & 0 & 0 \\ 0 & 0 & p_2 & r_3 \cdots & r_{n-1} & 0 \\ \cdot & \cdot & \cdot & & \cdot & \cdot \\ \cdot & \cdot & \cdot & & \cdot & \cdot \\ \cdot & \cdot & \cdot & & \cdot & \cdot \\ 0 & 0 & 0 & \cdots & p_{n-1} & r_n \end{bmatrix} \cdot \begin{bmatrix} n_{t,0} \\ n_{t,1} \\ n_{t,2} \\ n_{t,3} \\ \cdot \\ \cdot \\ \cdot \\ n_{t,n} \end{bmatrix} = \begin{bmatrix} n_{t+1,0} \\ n_{t+1,1} \\ n_{t+1,2} \\ n_{t+1,3} \\ \cdot \\ \cdot \\ \cdot \\ n_{t+1,n} \end{bmatrix} \tag{7}$$

where f represents the class-specific fecundity, p the probability of recruitment from i to $(i+1)$ by $(t+1)$ and r the probability of remaining in the $(i+1)$ class. Substitution of the obtained values in this model yields the following matrix:

$$\begin{bmatrix} f_0 & f_1 & f_2 & f_3 & f_4 & f_5 \\ 0.80 & 0.01 & 0 & 0 & 0 & 0 \\ 0 & 0.85 & 0.15 & 0 & 0 & 0 \\ 0 & 0 & 0.56 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.41 & 0.19 & 0 \\ 0 & 0 & 0 & 0 & 0.81 & 1.00 \end{bmatrix}$$

The fecundity was not known; approximations of the total number of new individuals added were made from Table 2 since the values of p and r were known. These estimates were substituted for the first element in each successive column vector applied to the model since in effect this element equals the total number of new individuals added to the first size class. Using sigma notation (cf. CAMPBELL, 1965),

$$n_{t+1,0} = \sum_{k=1}^{n} f n_t \tag{8}$$

where the new individuals added to the first size class ($n_{t+1,0}$) at $t+1$ equals the sum of the products of the fecundity and the number of individuals present (n_t) at time t.

Repeated application of this model, commencing with a column vector corresponding to t_1 in Table 2 and subsequently utilizing the successive vectors generated by the model, gives good agreement between the predicted and the observed values (Fig. 3).

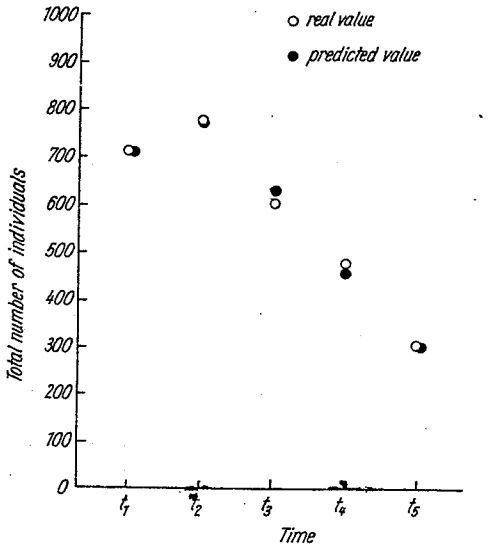

Fig. 3. Real and predicted values for total number of individuals of *Physa gyrina*. The predicted values were generated commencing with a column vector corresponding to t_1 in Table 2.

Although fecundity remains unknown and environmental effects are disregarded, the model nonetheless provides an overview of the behaviour of the population over the total interval under consideration. Models describing the behaviour of the population at each particular time may be obtained by constructing a matrix using data from only that time period.

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APPENDIX II

Locations and descriptions of sampling sites and the dates on which they were visited.

Site	Location
1	Roadside ditch, immediately southeast of the University of Manitoba Field Station buildings, Delta Marsh, on the southern shore of lake Manitoba, Manitoba. Shallow ditch, silt/clay with organic matter. July 25, 1973.
2	Roadside ditch, immediately west of site 1, southeast of the University of Manitoba Field Station buildings, Delta Marsh, on the southern shore of Lake Manitoba, Manitoba. Shallow ditch, silt/clay with organic matter. August 8, 1973.
3	Drainage ditch at entrance to Inkster property, access via the east dyke road, along the eastern side of the Assiniboine River diversion channel, Delta Marsh, on the southern shore of Lake Manitoba, Manitoba. Shallow ditch, clay with organic matter. June 25, 1973.
4	Roadside ditch, 12.5 km west of Langruth on No. 265, Manitoba. Shallow ditch, sand/gravel. July 9, 1973.
5	Crescent Pond, Portage Country Club property, 1.6 km west of the University of Manitoba Field Station buildings, Delta Marsh, on the southern shore of Lake Manitoba, Manitoba. Exposed remnant of marsh drainage channel, silt with organic matter. July 11, 1972.
6	Lakeshore of Lake Manitoba, at the University of Manitoba Field Station, Delta Marsh, Manitoba. Large lake, sand/clay. August 10, 1972.
7	Sewell Lake, near Camp Shilo, Spruce Woods Provincial Forest, Manitoba. Exposed lake, peat/sand. July 10, 1974.
8	2 km east of junction No. 1 and No. 340, on No. 1, Manitoba. Small, almost stagnant river, silt with organic matter. July 10, 1974.
9	Oxbow of Assiniboine River at northern entrance to Spruce Woods Provincial Park on No. 258, Manitoba. Oxbow, silt with organic matter. July 10, 1974.
10	5 km east of junction No. 2 and No. 10, on No. 2, Manitoba. Pond, silt with organic matter. July 10, 1974.
11	Pelican Lake at No. 23, near Ninette, Manitoba. Inlet to lake, fractured shale with organic matter. July 10, 1974.
12	14.5 km west of Ninette, on No. 23, Manitoba. Pond, silt with organic matter. July 10, 1974.
13	Pembina River at No. 34, Manitoba. Slow river, fractured shale with organic matter. July 10, 1974.

14 Gravel pit 300 m from F.I.G. area center, Whiteshell Nuclear Research Establishment, near Pinawa, Manitoba. Shallow pond, sand. July 11, 1974.

15 2.5 km west of junction No. 11 and road 1.6 km south of Elma, Manitoba. Shallow pond, gravel/clay. July 11, 1974.

16 1 km north of junction No. 11 and No. 506, on No. 11, Manitoba. Shallow ditch, clay under peat. July 11, 1974.

17 1.5 km north of junction No. 254 and No. 255, on No. 254, Manitoba. Small pond, sand. July 16, 1974.

18 Northeast shore of Oak Lake, access via No. 254, Manitoba. Bay of lake, sand. July 16, 1974.

19 Game Refuge on east shore of Oak Lake, access via No. 254, Manitoba. Shallow ditch, silt with organic matter. July 16, 1974.

20 1.5 km east of public park on No. 254 at Oak Lake, Manitoba. Marsh, silt with organic matter. July 16, 1974.

21 Plum Creek at No. 254, Manitoba. Small creek, fractured shale. July 16, 1974.

22 Stony Creek at No. 83, Manitoba. Small creek, silt with organic matter. July 16, 1974.

23 Jackson Creek at No. 83, Manitoba. Small creek, silt with organic matter. July 16, 1974.

24 6.5 km west of junction No. 3 and No. 450, on No. 3, and 9.5 km south of No. 3, Manitoba. Pond, silt with organic matter. July 16, 1974.

25 Lake Metigoshe at No. 450, Manitoba. Lake, silt with organic matter. July 16, 1974.

26 Northwest shore of Lake Max, Turtle Mountain Provincial Park, Manitoba. Lake, sand. July 16, 1974.

27 Pond at junction No. 2 and No. 10, Manitoba. Pond, silt with organic matter. July 16, 1974.

28 La Salle River at No. 247, La Salle, Manitoba. Small river, clay. August 9, 1974.

29 Morris River at No. 75, Morris, Manitoba. Turbulent river, clay. August 9, 1974.

30 1.5 km east of junction No. 75 and No. 23, on No. 23, Manitoba. Small, almost stagnant creek draining into Red River, clay. August 9, 1974.

31 Marsh River at No. 23, Manitoba. Small, stagnant creek, clay. August 9, 1974.

32 2.5 km south of junction No. 10 and No. 25, on No. 10, Manitoba. Pond, silt with organic matter. August 27, 1974.

33 6.5 km south of junction No. 10 and No. 262, on No. 10, Manitoba. Pond, silt with organic matter. August 27, 1974.

34 1.5 km south of junction No. 10 and No. 262, on No. 10, Manitoba. Pond, silt with organic matter. August 27, 1974.

35 3.2 km south of junction No. 10 and No. 563, on No. 10, Manitoba. Pond, silt with organic matter. August 27, 1974.

36 Small lake at southern outskirts of Onanole, at No. 10, Manitoba. Small lake, silt with organic matter. August 27, 1974.

37 Small pond behind Wasagaming Marina, Clear Lake, Riding Mountain National Park, Manitoba. Small pond, gravel. August 27, 1974.

38 Lake Katharine, Riding Mountain National Park, Manitoba. Lake, gravel. August 27, 1974.

39 Swanson Creek at No. 19, Riding Mountain National Park, Manitoba. Small creek, organic. August 27, 1974.

40 Whirlpool Lake, Riding Mountain National Park, Manitoba. Small lake, gravel with undecomposed organic matter. August 27, 1974.

41 Tongue River near intersection of No. 5 and Pembina County Road No. 2, North Dakota. Small river, sand/silt. May 20, 1975.

42 0.5 km north of intersection of No. 18 and Walsh County Road No. 9, near Nash, North Dakota. Oxbow of Park River, clay/gravel. May 20, 1975.

43 Park River, near junction No. 17 and No. 18, on No. 18, Walsh County, North Dakota. Small river, sand/gravel. May 20, 1975.

44 3.5 km east of junction No. 32 South and No. 2, on No. 2, North Dakota. Pond, silt with organic matter. May 20, 1975.

45 East shore of Red Willow Lake, access via No. 1, North Dakota. Lake, gravel. May 20, 1975.

46 1.4 km south of junction No. 1 and No. 17, on No. 1, North Dakota. Pond, silt with organic matter. May 20, 1975.

47 1.5 km south of Douglas on No. 340, Manitoba. Pond, gravel. May 27, 1975.

48 Plum Creek at No. 21, Manitoba. Small creek, clay. May 27, 1975.

49 1.9 km south of junction No. 256 and No. 445, on No. 256, Manitoba. Pond, sand/silt with organic matter. May 28, 1975.

50 Graham Creek, 2.2 km north of junction No. 256 and No. 445, on No. 256, Manitoba. Excavation beside creek, gravel/ clay. May 28, 1975.

51 7.8 km south of junction No. 256 and No. 2, on No. 256, Manitoba. Pond, sand. May 28, 1975.

52 1.5 km south of Rossendale, on No. 242, Manitoba. Small pond, sand. May 30, 1975.

53 19.4 km south of junction No. 518 and No. 415 West, on No. 518, Manitoba. Farm pond, gravel. June 3, 1975.

54 7.0 km east of junction No. 229 and No. 518, on No. 229, Manitoba. Marsh ditch, gravel. June 3, 1975.

55 2.6 km east of No. 518, on road 5.3 km north of junction No. 518 and No. 415 West, Manitoba. Pond, gravel. June 3, 1975.

56 North Shoal Lake, 1.9 km north of junction No. 416 and No. 415, on No. 416, Manitoba. Lake, gravel. June 3, 1975.

57 8.0 km north of junction No. 518 and No. 6, on No. 518, Manitoba. Large pond, peat. June 3, 1975.

58 3.2 km north of junction No. 322 and No. 67, on No. 322, Manitoba. Shallow ditch, silt with organic matter. June 3, 1975.

59 8.0 km north of junction No. 8 and No. 101, on No. 220, Manitoba. Shallow ditch, silt. June 3, 1975.

60 1.6 km east of La Broquerie on No. 210, Manitoba. Ditch, fine sand. June 5, 1975.

61 Seine River at No. 210, Manitoba. Small river, fine sand. June 5, 1975.

62 2.9 km north of Rat River on No. 210, Manitoba. Pond, gravel. June 5, 1975.

63 1.3 km west of junction No. 12 and No. 310, on No. 12, Manitoba. Shallow ditch, gravel/peat. June 5, 1975.

64 3.0 km east of Williams on No. 11, Minnesota. Shallow ditch, gravel. June 5, 1975.

65 14.9 km south of Finland on No. 71, Ontario. Pond, peat. June 5, 1975.

66 Log River at No. 71, Ontario. River, gravel/fine sand. June 5, 1975.

67 45.0 km south of Kenora on No. 71, Ontario. Small river in black spruce community, gravel/clay. June 5, 1975.

68 Middle Lake, on road 6.2 km west of Keewatin, Ontario. Lake, gravel. June 6, 1975.

69 5.3 km south of No. 17 on Rush Bay Road, 15.8 km east of Manitoba-Ontario border on No. 17, Ontario. Beaver dam, gravel. June 6, 1975.

70 7.2 km west of junction No. 1 and No. 506 (western end), on No. 1, Manitoba. Pond, gravel. June 11, 1975.

71 1.5 km north of junction No. 506 (western end) and No. 1, on No. 506, Manitoba. Ditch, peat. June 11, 1975.

72 8.5 km north of junction No. 506 (western end) and No. 1, on No. 506, Manitoba. Pond, gravel. June 11, 1975.

73 10.4 km north of junction No. 506 (western end) and No. 1, on No. 506, Manitoba. Ditch, gravel with organic matter. June 11, 1975.

74 At junction No. 11 and No. 506, Manitoba. Pond, peat. June 11, 1975.

75 31.8 km east of junction No. 15 and No. 302 South, on No. 15, Manitoba. Ditch, gravel. June 11, 1975.

76 Limestone quarry pool, at Gillis Quarries on southeast side of junction No. 44 and No. 306, Garson, Manitoba. Limestone quarry, deep pool, rock flour and rubble. June 11, 1975.

77 10.9 km north of junction No. 12 and No. 208, on No. 12, near Zhoda, Manitoba. Pond, gravel. June 12, 1975.

78 16.8 km west of junction No. 308 and Moose Lake Road (southern end), on No. 308, Manitoba. Pond, gravel. June 12, 1975.

79 Northeast shore of Moose Lake, Northwest Angle Provincial Park, Manitoba. Lake, gravel. June 12, 1975.

80 Birch Point, Buffalo Bay, Lake of the Woods, Northwest Angle Provincial Forest, Manitoba. Lake, gravel. June 12, 1975.

81 Northwest Angle Resort, Lake of the Woods, Minnesota, access via Manitoba No. 308. Boat channel leading into lake, clay. June 12, 1975.

82 6.9 km east of junction No. 308 and Northwest Angle Road, on Northwest Angle Road, 49.8 km south of junction No. 308 and No. 503, on No. 308, Manitoba. Ditch, gravel. June 12, 1975.

83 24.2 km south of junction No. 308 and No. 503, on No. 308, Manitoba. Bog pool, peat. June 12, 1975.

84 10.4 km south of junction No. 308 and No. 503, on No. 308, Manitoba. Ditch, peat. June 12, 1975.

85 7.8 km east of junction No. 221 and No. 248, on No. 221, Manitoba. Shallow ditch, clay/gravel. June 18, 1975.

86 12.5 km east of junction No. 227 and No. 430, on No. 227, Manitoba. Shallow ditch, gravel. June 18, 1975.

87 0.8 km west of junction No. 227 and No. 430, on No. 227, Manitoba. Pond, gravel. June 18, 1975.

88 1.6 km west of junction No. 227 and No. 430, on No. 227, Manitoba. Pond, gravel. June 18, 1975.

89 3.2 km north of junction No. 11 and No. 307, on No. 11, Manitoba. Pond, clay/gravel. June 19, 1975.

90 Northern shore of Twin Lakes Beach, Lake Manitoba, access via No. 6, Manitoba. Excavation ditch draining directly into lake, gravel/clay. June 25, 1975.

91 Oak Point, Lake Manitoba, access via No. 6, Manitoba. Lake, gravel/clay. June 25, 1975.

92 3.2 km west of junction No. 419 and No. 418, on No. 419, Manitoba. Marsh pond, clay/gravel. June 25, 1975.

93 9.3 km east of junction No. 235 and No. 514, on No. 235, Manitoba. Pond, gravel/clay. June 25, 1975.

94 6.2 km west of junction No. 235 and No. 514, on No. 235, at southwest shore of Dog Lake, Manitoba. Marsh, gravel/clay with organic matter. June 25, 1975.

95 Lake Manitoba Narrows at No. 235, 28.8 km west of junction No. 235 and No. 514, westbound on No. 235, Manitoba. Lake, gravel. June 25, 1975.

96 32.5 km north of junction No. 278 and No. 50, on No. 278, Manitoba. Small river, gravel. June 25, 1975.

97 20.2 km north of Amaranth on No. 50, Manitoba. Pond, gravel. June 25, 1975.

98 Lee River at No. 313, east of Lac du Bonnet, Manitoba. River, granitic bedrock with organic matter in pockets. July 2, 1975.

99 Pointe du Bois, Winnipeg River, on No. 313, Manitoba. Large river, granitic bedrock/gravel/sand. July 2, 1975.

100 Cat Lake, at No. 314, 16.6 km north of junction No. 314 and No. 315, Manitoba. Lake, granitic bedrock with organic matter in pockets. July 2, 1975.

101 Lake, 32.0 km east of junction No. 315 and No. 314, on No. 315, Manitoba. Lake, granitic bedrock/gravel. July 2, 1975.

102 29.6 km east of junction No. 315 and No. 314, on No. 315, Manitoba, at Manitoba-Ontario border. Lake, granitic bedrock/gravel. July 2, 1975.

103 Bird Lake at No. 315, Manitoba. Lake, granitic bedrock/gravel/sand. July 2, 1975.

104 Bird River at No. 315, 8.8 km east of junction No. 315 and No. 314, on No. 315, Manitoba. River, granitic bedrock/gravel. July 2, 1975.

105 West shore of Sandy Lake, at Sandy Lake townsite, No. 250, Manitoba. Lake, sand/gravel. July 8, 1975.

106 4.3 km east of junction No. 470 and No. 354, on No. 470, Manitoba. Small lake, gravel/sand. July 8, 1975.

107 8.3 km east of junction No. 359 and No. 566, on No. 359, Manitoba. Pond, organic matter. July 8, 1975.

108 Rossman Lake, on No. 577 near Rossburn, Manitoba. Lake, gravel/sand. July 8, 1975.

109 Silver Beach, 2.2 km east of junction No. 254 and No. 476, on No. 254, Manitoba. Lake, sand. July 8, 1975.

110 6.9 km east of junction No. 478 and No. 4, on No. 478, Manitoba. Pond, sand with organic matter. July 8, 1975.

111 1.2 km south of junction No. 83 and No. 57, on No. 83, Manitoba. Small lake, peat. July 8, 1975.

112 Southwest shore of Childs Lake, at No. 367, Duck Mountain Provincial Park, Manitoba. Lake, sand/gravel. July 9, 1975.

113 North shore of Laurie Lake, at No. 367, Duck Mountain Provincial Park, Manitoba. Lake, sand/gravel. July 9, 1975.

114 South shore of Gull Lake, at No. 367, Duck Mountain Provincial Park, Manitoba. Lake, sand/gravel. July 9, 1975.

115 South shore of Beautiful Lake, at No. 367, Duck Mountain Provincial Park, Manitoba. Lake, sand/gravel. July 9, 1975.

116 West shore of Singoosh Lake, at No. 367, Duck Mountain Provincial Park, Manitoba. Lake, peat. July 9, 1975.

117 East shore of Elk Lake, at No. 366, Duck Mountain Provincial Park, Manitoba. Lake, gravel and rock. July 9, 1975.

118 North shore of East Blue Lake, at No. 366, Duck Mountain Provincial Park, Manitoba. Lake, sand/gravel. July 9, 1975.

119 West Blue Lake at University of Manitoba Field Station, at No. 366, Duck Mountain Provincial Park, Manitoba. Lake, sand/gravel. July 9, 1975.

120 Perch Lake, at No. 366, Duck Mountain Provincial Park, Manitoba. Lake, sand/gravel with organic matter. July 9, 1975.

121 North shore of Dragline Lake, at No. 366, Duck Mountain Provincial Park, Manitoba. Beaver dam, sand/clay with organic matter. July 9, 1975.

122 Two Mile Lake, at No. 366, Duck Mountain Provincial Park, Manitoba. Lake, gravel with organic matter. July 9, 1975.

123 Glad Lake, at No. 366, Duck Mountain Provincial Park, Manitoba. Lake, gravel. July 9, 1975.

124 Northwest shore of Wellman Lake, at No. 366, Duck Mountain Provincial Park, Manitoba. Lake, sand/gravel. July 9, 1975.

125 Whitefish Lake, at No. 279, Porcupine Provincial Forest, Manitoba. Lake, gravel. July 9, 1975.

126 6.1 km east of junction No. 10 and Pelican Rapids road, on Pelican Rapids road, Manitoba. River, clay. July 10, 1975.

127 25.6 km north of junction No. 10 and No. 277, on No. 10, Manitoba. Beaver dam, undecomposed organic matter. July 10, 1975.

128 South shore of Red Deer Lake, near Red Deer Lake townsite, Manitoba. Lake, coarse rock. July 10, 1975.

129 4.8 km north of Barrows, access via No. 277, Manitoba. Pond, clay with organic matter. July 10, 1975.

130 East shore of Steeprock Lake, Porcupine Provincial Forest, Manitoba. Lake, gravel. July 10, 1975.

131 North shore of Bell Lake, Porcupine Provincial Forest, Manitoba. Lake, gravel. July 10, 1975.

132 East shore of Cross Lake, on road west of Grand Rapids, Manitoba. Lake, limestone bedrock. July 15, 1975.

133 Limestone quarries west of hydroelectric dam, Grand Rapids, Manitoba. Limestone quarry pool, bedrock/clay. July 15, 1975.

134 Southeast shore of Little Limestone Lake, 64 km north of Grand Rapids on No. 6, Manitoba. Lake, limestone rubble. July 15, 1975.

135 Buffalo Lake, 30.4 km north of Grand Rapids on No. 6, Manitoba. Lake, gravel with organic matter. July 15, 1975.

136 Lake, 20.8 km north of Grand Rapids on No. 6, Manitoba. Lake, limestone rubble with organic matter. July 15. 1975.

137 Lake, 14.9 km north of Grand Rapids on No. 6, Manitoba. Lake, limestone rubble. July 15, 1975.

138 Eating Point Creek, 10.2 km north of Grand Rapids on No. 6, Manitoba. Small creek, undecomposed organic matter. July 15, 1975.

139 3.0 km west of No. 6, on road 9.6 km south of Grand Rapids on No. 6, Manitoba. Fast-flowing creek, limestone/clay. July 16, 1975.

140 25.3 km south of Grand Rapids on No. 6, and 1.5 km east of No. 6 on Manitoba Hydro right-of-way, Manitoba. Ditch, clay. July 16, 1975.

141 North shore of Katimik Lake, at No. 327, Manitoba. Lake, sand/clay/limestone rubble. July 16, 1975.

142 North shore of Kawinaw Lake, access via No. 327, Manitoba. Lake, clay. July 16, 1975.

143 Denbeigh Point, at end of Denbeigh Point Road, Lake Winnipegosis, access via No. 327, Manitoba. Lake, limestone bedrock. July 16, 1975.

144 3 km south of junction No. 327 and Denbeigh Point Road, on Denbeigh Point Road, Manitoba. Pond, organic matter. July 16, 1975.

145 113.6 km north of junction No. 6 and No. 513, on No. 6, Manitoba. Stagnant creek, clay. July 16, 1975.

146 East shore of Devils Lake, 77.1 km north of junction No. 6 and No. 513, on No. 6, Manitoba. Lake, rock rubble. July 16, 1975.

147 64.3 km north of junction No. 6 and No. 513, on No. 6, Manitoba. Shallow ditch, sand/gravel. July 16, 1975.

148 Northwest shore of Lake St. Martin, near Gypsumville, Manitoba. Lake, clay/gravel. July 16, 1975.

149 Brokenhead River at No. 15, Manitoba. River, sand/gravel with organic matter. July 21, 1975.

150 St. Ambroise Beach, Lake Winnipeg, at No. 430, Manitoba. Lake, sand/gravel. July 23, 1975.

151 6.7 km north of junction No. 430 and No. 227 East, on No. 430, Manitoba. Shallow ditch, clay with organic matter. July 23, 1975.

152 Lynch's Point, Lake Manitoba, at No. 242, Manitoba. Lake, sand/clay. July 23, 1975.

153 5.9 km north of Ste. Rose du Lac, on No. 276, Manitoba. River, clay. July 23, 1975.

154 Methley Beach, Dauphin Lake, access via No. 276, Manitoba. Lake, sand/gravel. July 23, 1975.

155 Toutes Aides, at No. 276, Manitoba. Marsh channel at inlet to Lake Manitoba, clay with organic matter. July 23, 1975.

156 6.7 km north of junction No. 481 and No. 364, on No. 481, Manitoba. Farm pond, gravel. July 23, 1975.

157 Northeast shore of Sarah Lake at Sarah Creek, Duck Mountain Provincial Forest, Manitoba. Lake, sand/gravel. July 24, 1975.

158 Ruby Creek, 3.2 km southeast of No. 586 on Sarah Lake road, Manitoba. Small creek, silt/sand. July 24, 1975.

159 8.3 km north of junction No. 83 and No. 57, on No. 83, Manitoba. Small lake, gravel/organic. July 24, 1975.

160 Pickerel Point, east shore of Madge Lake, Duck Mountain Provincial Park, Saskatchewan. Lake, clay/sand. July 24, 1975.

161 North shore of Batka Lake, Duck Mountain Provincial Park, Saskatchewan. Lake, sand/gravel. July 24, 1975.

162 2.6 km south of No. 57 on Batka Lake road, Duck Mountain Provincial Park, Saskatchewan. Lake, undecomposed organic matter. July 24, 1975.

163 Eleanor Lake, 1.5 km east of Whiteshell Provincial Park entrance on No. 307, Manitoba. Marshy bay of lake, gravel. July 31, 1975.

164 South shore of Eleanor Lake at No. 307, Whiteshell Provincial Park, Manitoba. Lake, silt with organic matter. July 31, 1975.

165 Dorothy Lake, at No. 307, Whiteshell Provincial Park, Manitoba. Lake, granitic bedrock and sand. July 31, 1975.

166 Opapiskaw campground, west of Nutimik Lake campground, on No. 307, Whiteshell Provincial Park, Manitoba. Lake, granitic bedrock and sand. July 31, 1975.

167 Rennie River at No. 307, Whiteshell Provincial Park, Manitoba. Marshy river, sand/peat. July 31, 1975.

168 Betula Lake, access via No. 307, Whiteshell Provincial Park, Manitoba. Lake, sand/gravel. July 31, 1975.

169 Whiteshell River, 2.6 km east of No. 309 on Lone Island Lake road, Whiteshell Provincial Park, Manitoba. River, undecomposed organic matter. July 31, 1975.

170 Big Whiteshell Lake, access via No. 309, Whiteshell Provincial Park, Manitoba. Lake, granitic bedrock/gravel/sand. July 31, 1975.

171 Green Lake, at No. 309, Whiteshell Provincial Park, Manitoba. Lake, granitic bedrock. July 31, 1975.

172 White Lake, at No. 307, Whiteshell Provincial Park, Manitoba. Lake, granitic bedrock/gravel/sand. July 31, 1975.

173 Jessica Lake, at No. 307, Whiteshell Provincial Park, Manitoba. Lake, gravel with organic matter. July 31, 1975.

174 Breezy Point, Red River, north of Selkirk on No. 320, Manitoba. River, clay. August 1, 1975.

175 8.0 km north of Selkirk city center on No. 320, Manitoba. Pond, clay. August 1, 1975.

176 5.1 km west of Libau, Manitoba. Shallow ditch, clay/sand. August 1, 1975.

177 Gull Lake, 1.5 km east of junction No. 219 and No. 59, on No. 219, Manitoba. Lake, sand/gravel. August 1, 1975.

178 Lake Winnipeg, 3.5 km west of junction No. 319 and No. 59, on No. 319, Manitoba. Bay of lake, clay. August 1, 1975.

179 Patricia Beach, Lake Winnipeg, access via No. 319, Manitoba. Lake, sand/gravel. August 1, 1975.

180 2.6 km south of junction No. 11 and No. 214, on No. 11, Manitoba. Shallow ditch, sand. August 11, 1975.

181 12.2 km south of junction No. 11 and McArthur Falls road, on No. 11, Manitoba. Pond, sand/granitic rock rubble. August 11, 1975.

182 1.4 km north of junction No. 11 and McArthur Falls road, on No. 11, Manitoba. Pond, fine silt and organic matter. August 11, 1975.

183 9.8 km west of junction No. 219 and No. 11, on No. 219, Manitoba. Pond, clay. August 11, 1975.

184 4.8 km west of junction No. 219 and No. 11, on No. 219, Manitoba. Shallow ditch, clay. August 11, 1975.

185 Birds Hill lake, Birds Hill Provincial Park, Manitoba. Lake, gravel/sand/clay. August 11, 1975.

186 West Hawk Lake, at No. 44, Whiteshell Provincial Park, Manitoba. Lake, granitic bedrock. August 12, 1975.

187 Hunt Lake, east of West Hawk Lake on No. 44, Whiteshell Provincial Park, Manitoba. Lake, granitic bedrock. August 12, 1975.

188 East shore of Caddy Lake, access via No. 312, Whiteshell Provincial Park, Manitoba. Lake, sand/silt. August 12, 1975.

189 Lake at Ingolf, at No. 312, Manitoba. Lake, sand/granitic bedrock. August 12, 1975.

190 5.4 km east of junction No. 312 and No. 44, on No. 312, Whiteshell Provincial Park, Manitoba. Inlet of creek into small lake, granitic bedrock. August 12, 1975.

191 The Lily Pond, at No. 44, Whiteshell Provincial Park, Manitoba. Small lake, granitic bedrock and peat. August 12, 1975.

192 2.2 km north of junction No. 307 and No. 44, on No. 307, near Brereton Lake, Whiteshell Provincial Park, Manitoba. Pond, granitic bedrock with undecomposed organic matter. August 12, 1975.

193 East shore of Brereton Lake, at No. 307, Whiteshell Provincial Park, Manitoba. Lake, granitic bedrock/sand. August 12, 1975.

194 North shore of Red Rock Lake, access via No. 307, Whiteshell Provincial Park, Manitoba. Lake, granitic bedrock/sand. August 12, 1975.

195 Small creek draining into south end of Brereton Lake, access via No. 307, Whiteshell Provincial Park, Manitoba. Small, almost stagnant creek, sand/peat. August 12, 1975.

196 O'Hanley River at No. 304, Manitoba. Excavation draining into river, gravel. August 13, 1975.

197 Southwest shore of Wanipigow Lake, access via No. 304, Manitoba. Lake, granitic bedrock/ sand/ silt. August 13, 1975.

198 North shore of Caribou (Quesnel) Lake, access via No. 304, Manitoba. Lake, granitic bedrock. August 13, 1975.

199 Red Rice Lake, 3.4 km south of junction No. 304 and Caribou Lake Road, on Caribou Lake Road, Manitoba. Lake, peat. August 13, 1975.

200 East shore of Long Lake, at No. 304, Manitoba. Lake, granitic bedrock and undecomposed organic matter. August 13, 1975.

201 9.5 km east of junction No. 304 and Wallace Lake road, on No. 304, Manitoba. Ditch, peat. August 13, 1975.

202 Lake 6.2 km east of junction No. 304 and Wallace Lake road, on No. 304, Manitoba. Lake, granitic bedrock and peat. August 13, 1975.

203 West shore of Wallace Lake, access via No. 304, Manitoba. Lake, granitic bedrock, sand. August 13, 1975.

204 Lake at San Antonio gold mine, Bissett, access via No. 304, Manitoba. Lake, granitic bedrock/sand. August 13, 1975.

205 7.5 km west of Elstow, on No. 14, Saskatchewan. Pond, gravel/ silt. August 21, 1975.

206 6.2 km west of Plunkett, on No. 14, Saskatchewan. Pond, sand. August 21, 1975.

207 4.2 km south of junction No. 8 and No. 324, on No. 8, Manitoba. Ditch, clay/gravel. August 28, 1975.

208 32.6 km north of junction No. 8 and No. 324, on No. 8, west of Riverton, Manitoba. Ditch, gravel/silt. August 28, 1975.

209 River at No. 234 draining into Washow Bay, Lake Winnipeg, north of junction No. 234 and No. 233, Manitoba. River, gravel/silt. August 28, 1975.

210 21.9 km south of Beaver Creek on No. 234, Manitoba. Creek, gravel/silt. August 28, 1975.

211 4.0 km south of Beaver Creek on No. 234, Manitoba. Spring fed pool, sand. August 28, 1975.

212 Beaver Creek at No. 234, Manitoba. Creek, sand/peat. August 28, 1975.

213 Shore of Lake Winnipeg opposite Matheson Island, at end of No. 234, Manitoba. Lake, limestone rubble. August 28, 1975.

214 10.6 km north of Pine Dock on No. 234, Manitoba. Ditch, peat. August 28, 1975.

215 Pine Dock Beach, at Pine Dock townsite, Lake Winnipeg, at No. 234, Manitoba. Lake, sand. August 28, 1975.

216 Lagoon behind Pine Dock Beach, at Pine Dock townsite, at No. 234, Manitoba. Pond, sand/peat. August 28, 1975.

217 Southwest side of Hecla Island causeway, on No. 233, Manitoba. Lake, clay. August 28, 1975.

218 4.0 km east of Hecla Island Provincial Park boundary on No. 233, Manitoba. Ditch, peat. August 28, 1975.

219 11.8 km east of Hecla Island Provincial Park boundary on No. 233, Manitoba. Bog pool, peat. August 28, 1975.

220 0.8 km south of junction No. 5 and No. 261, on No. 5, Manitoba. Fast flowing creek, sand. September 9, 1975.

221 River 8.5 km south of junction No. 480 and No. 582, on No. 480, near Laurier, Manitoba. Fast flowing creek, sand and gravel. September 9, 1975.

222 0.5 km south of junction No. 480 and No. 582, on No. 480, near Makinak, Manitoba. Shallow ditch, gravel. September 9, 1975.

223 Ochre Beach, southwest shore of Dauphin Lake, access via No. 20, Manitoba. Lake, gravel. September 9, 1975.

224 Channel behind Ochre Beach, southwest shore of Dauphin Lake, access via No. 20, Manitoba. Large ditch, silt. September 9, 1975.

225 8.9 km south of junction No. 362 and No. 267, on No. 362, Manitoba. Shallow ditch, gravel. September 9, 1975.

226 Oxbow of Vermilion River, behind Vermilion Hotel, Dauphin. Oxbow, gravel with organic matter. September 10, 1975.

227 12.6 km west of junction No. 5 and No. 582, on No. 5, Manitoba. Pond, gravel. September 10, 1975.

228 2.4 km west of junction No. 480 and No. 360, on No. 480, Manitoba. Marsh ditch, gravel with organic matter. September 10, 1975.

229 7.4 km east of junction No. 573 and No. 50, on No. 573, near Embury, Manitoba. Marsh ditch, gravel/clay. September 10, 1975.

230 9.8 km north of junction No. 240 and No. 2, on No. 240, Manitoba. Pond, silt. September 10, 1975.

231 Boyne River at No. 240, Manitoba. Oxbow, silt. September 10, 1975.

232 Colert Beach, Lake Minnewasta, west of Morden, at No. 434, Manitoba. Small lake, sand/clay. September 10, 1975.

233 Intake of Clay Boswell power plant, Mississippi River, at Cohasset, Itasca County, Minnesota. River, clay. September 26, 1975.

234 South shore of Trout Lake, at No. 21, Itasca County, Minnesota. Lake, sand. September 26, 1975.

235 Little Sand Lake, at Itasca County Road No. 70, Minnesota. Lake, sand. September 26, 1975.

236 Swan Lake, at No. 65, Itasca County, Minnesota. Lake, gravel. September 26, 1975.

237 Snowball Lake, at No. 169, Itasca County, Minnesota. Lake, sand. September 26, 1975.

238 Pokegama Lake, at No. 169, Itasca County, Minnesota. Lake, sand. September 27, 1975.

239 Inlet of Pokegama Bay at Itasca County Road No. 17, Minnesota. Stream inlet into lake, clay. September 27, 1975.

240 Jay Gould Lake, near junction No. 63 and Itasca County Road "C", Minnesota. Lake, iron ore rubble and organic matter. September 27, 1975.

241 Loon Lake, at No. 63, Itasca County, Minnesota. Lake, sand. September 27, 1975.

242 Gile Lake, at No. 64, Itasca County, Minnesota. Lake, sand. September 27, 1975.

243 West shore of Little Rice Lake, at No. 64, Itasca County, Minnesota. Lake, clay with organic matter. September 27, 1975.

244 Little White Oak Lake, at Itasca County Road No. 11, Minnesota. Lake, undecomposed organic matter. September 27, 1975.

245 White Oak Lake, near Deer River townsite, Itasca County, Minnesota. Lake, gravel/sand. September 27, 1975.

246 Ball Club Lake, access via No. 2, Itasca County, Minnesota. Lake, sand. September 27, 1975.

247 Pike Bay, Cass Lake, Chippewa National Forest Recreation Area, at No. 2, Cass County, Minnesota. Lake, sand. September 27, 1975.

248 Cass Lake, rest area at No. 2, Chippewa National Forest Recreation Area, Cass County, Minnesota. Lake, gravel. September 27, 1975.

249 Pond at Cass Lake rest area, at No. 2, Chippewa National Forest Recreation Area, Cass County, Minnesota. Pond, clay with organic matter. September 27, 1975.

250 Bemidji Lake at Bemidji townsite, access via No. 2, Beltram County, Minnesota. Lake, sand/gravel. September 27, 1975.

251 Prairie Lake, Blandin Gunn Park, access via No. 38, Itasca County, Minnesota. Lake, sand/rock rubble. July 5, 1976.

252 Little Wabana Lake, at No. 49, Itasca County, Minnesota. Lake, sand. July 5, 1976.

253 Wabana Lake near Murphy's Landing, at No. 49, Itasca County, Minnesota. Lake, sand/gravel. July 5, 1976.

254 McKinney Lake at No. 38, Itasca County, Minnesota. Lake, sand. July 5, 1976.

255 Little Sugar (Little Siseebakwet) Lake, west of Sugar Lake, Itasca County, Minnesota. Lake, sand and undecomposed organic matter. July 5, 1976.

256 Sugar (Siseebakwet) Lake, Itasca County, Minnesota. Lake, sand. July 5, 1976.

257 Moose Lake, access via No. 19, Itasca County, Minnesota. Lake, sand. July 6, 1976.

258 Deer Lake at No. 19, Itasca County, Minnesota. Lake, sand. July 6, 1976.

259 Island Lake, access via Itasca County Road No. 48, Minnesota. Lake, sand with undecomposed organic matter. July 6, 1976.

260 Little Bowstring Lake, access via Itasca County Road No. 48, Minnesota. Lake, sand/gravel. July 6, 1976.

261 East Smith Lake, access via No. 49, Itasca County, Minnesota. Lake, sand with undecomposed organic matter. July 6, 1976.

262 West Smith Lake, access via No. 49, Itasca County, Minnesota. Lake, sand with undecomposed organic matter. July 6, 1976.

263 North Star Lake, access via No. 38, Itasca County, Minnesota. Lake, sand/gravel. July 6, 1976.

264 Bello Lake, access via No. 43, Itasca County, Minnesota. Lake, peat. July 6, 1976.

265 Big Turtle Lake, access via No. 43, Itasca County, Minnesota. Lake, sand. July 6, 1976.

266 Hatch Lake, access via No. 43, Itasca County, Minnesota. Lake, sand. July 6, 1976.

267 Little Turtle Lake, access via Itasca County Road No. 252, Minnesota. Lake, sand. July 6, 1976.

268 Big Jessie Lake, Itasca County, Minnesota. Lake, sand. July 6, 1976.

269 Northeast shore of Lake Winnibigoshish (Big Winnie), access via No. 46, Itasca County, Minnesota. Lake, sand. July 7, 1976.

270 Round Lake, access via No. 46, Itasca County, Minnesota. Lake, sand. July 7, 1976.

271 Dora Lake, access via No. 29, Minnesota. Lake, sand. July 7, 1976.

272 East shore of Lower Red Lake, at No. 1, north of Chippewa Beach, Minnesota. Lake, sand. July 7, 1976.

273 Island Lake, access via No. 46, Minnesota. Lake, sand. July 7, 1976.

274 Lansing A. Parker pool, Mud Lake, Agassiz National Wildlife Refuge, access via No. 7, Minnesota. Marsh ditch, silt with organic matter. July 7, 1976.

275 Bronson Lake, access via No. 59, Bronson State Park, Kittson County, Minnesota. Lake, sand. July 7, 1976.

276 7.2 km west of junction No. 265 and No. 50, on No. 265, Manitoba. Marsh pool, clay with organic matter. September 3, 1976.

277 Squirrel Creek at No. 350, Manitoba. Creek, clay/gravel. September 3, 1976.

278 1.9 km west of junction No. 461 and No. 242, on No. 461, Manitoba. Shallow ditch, silt. September 3, 1976.

279 Victoria Beach, Lake Winnipeg, access via No. 59, Manitoba. Lake, sand/gravel/rock rubble. September 6, 1976.

280 1.5 km south of Victoria Beach on No. 59, Manitoba. Marsh ditch, undecomposed organic matter. September 6, 1976.

281 2.2 km south of junction No. 59 and No. 219, on No. 59, Manitoba. Shallow ditch, undecomposed organic matter. September 6, 1976.

282 1.8 km west of junction No. 311 and No. 206, on No. 311, Manitoba. Large ditch, clay. September 16, 1976.

283 Creek in downtown Marchand at No. 210, Manitoba. Creek, sand/rock rubble. September 16, 1976.

284 7.2 km north of St. Labre on St. Labre road, access via No. 210, Manitoba. Pond, sand with organic matter. September 16, 1976.

285 18.3 km east of junction of Whitemouth Lake road and Vassar road, on Whitemouth Lake road, access via No. 308, Manitoba. Pond, clay. September 16, 1976.

286 Whitemouth River, 13.1 km east of junction of Whitemouth Lake road and Vassar road, on Whitemouth Lake road, access via No. 308, Manitoba. Creek, clay. September 16, 1976.

287 North shore of Whitemouth Lake, access via Whitemouth Lake road and No. 308, Manitoba. Lake, sand with organic matter. September 16, 1976.

288 15.5 km north of junction of Vassar road and No. 12, on Vassar road, Manitoba. Creek, clay with organic matter. September 16, 1976.

289 Sprague Creek at Vassar road, north of junction of Vassar road and No. 12, Manitoba. Stagnant creek, clay with organic matter. September 16, 1976.

290 East Pine Creek at No. 12, Manitoba. Fast flowing creek, sand/rock rubble. September 16, 1976.

291 0.6 km east of junction No. 311 and No. 200, on No. 311, Manitoba. Marsh pool, clay. September 16, 1976.

292 East beach, Grand Beach, Lake Winnipeg, access via No. 59, Manitoba. Lake, sand/gravel. September 19, 1976.

293 Lagoon behind east beach, Grand Beach, access via No. 59, Manitoba. Lake, sand. September 19, 1976.

294 11.2 km north of junction No. 59 and No. 219, on No. 59, Manitoba. Pond, sand. September 19, 1976.

295 Jackson Lake, 3 km southeast of Sidney, access via No. 352, Manitoba. Lake, sand. September 30, 1976.

296 5.0 km north of junction No. 344 and No. 23, on No. 344, Manitoba. Small lake, silt with organic matter. September 30, 1976.

297 4.3 km north of junction No. 344 and No. 23, on No. 344, Manitoba. Pond, sand with organic matter. September 30, 1976.

298 3.4 km south of junction No. 18 and No. 23, on No. 18, Manitoba. Pond, clay with organic matter. September 30, 1976.

299 11.9 km south of junction No. 18 and No. 23, on No. 18, Manitoba. Pond, clay with organic matter. September 30, 1976.

300 Killarney Lake, near Killarney townsite, access via No. 3, Manitoba. Lake, sand/gravel. September 30, 1976.

301 6.1 km west of junction No. 253 and No. 340, on No. 253, Manitoba. Pond, clay with organic matter. September 30, 1976.

302 3.2 km west of Glenora on No. 253, Manitoba. Pond, sand/gravel. September 30, 1976.

303 Northeast shore of Rock Lake, access via No. 342, Manitoba. Lake, fractured shale with organic matter. September 30, 1976.

304 475W, 100N F.I.G. grid, F.I.G. area, Whiteshell Nuclear Research Establishment, near Pinawa, Manitoba. Pond, gravel. July 14, 1975.

305 Portage Creek at No. 227, Manitoba. Creek, clay. May 28, 1973.

APPENDIX III

A. The sites at which each macrophyte species or species group was recorded. Locations of the sites are given in Appendix II. Species numbers represent the following taxa:

1. *Chara* spp.
2. *Riccia fluitans*
3. *Sparganium* spp.
4. *Ruppia maritima*
5. *Zannichellia palustris*
6. *Potamogeton alpinus*
7. *P. amplifolius*
8. *P. epihydrus*
9. *P. filiformis*
10. *P. foliosus*
11. *P. friesii*
12. *P. gramineus*
13. *P. illinoense*
14. *P. natans*
15. *P. obtusifolius*
16. *P. pectinatus*
17. *P. praelongus*
18. *P. pusillus*
19. *P. richardsonii*
20. *P. robbinsii*
21. *P. spirillus*
22. *P. strictifolius*
23. *P. vaginatus*
24. *P. zosteriformis*
25. *Najas flexilis*
26. *N. gracillima*
27. *Alisma triviale*
28. *Sagittaria rigida*
29. *Sagittaria* spp. (except 28)
30. *Elodea canadensis*
31. *Vallisneria americana*
32. *Zizania aquatica*
33. *Eleocharis* spp.
34. *Calla palustris*
35. *Lemna minor*
36. *L. trisulca*
37. *Spirodela polyrhiza*
38. *Polygonum amphibium*
39. *P. coccineum*
40. *Ceratophyllum demersum*
41. *Nymphaea odorata*
42. *N. tetragona*
43. *N. tuberosa*
44. *Nuphar microphyllum*
45. *N. variegatum*
46. *Brasenia schreberi*
47. *Caltha palustris*
48. *Ranunculus aquatilis*
49. *R. circinatus*
50. *R. flabellaris*
51. *R. reptans*
52. *R. gmelini*
53. *R. sceleratus*
54. *Callitriche* spp.
55. *Myriophyllum alterniflorum*
56. *M. exalbescens*
57. *M. heterophyllum*
58. *M. verticillatum*
59. *Hippuris vulgaris*
60. *Sium suave*
61. *Mentha arvensis*
62. *Utricularia intermedia*
63. *U. minor*
64. *U. vulgaris*
65. *U. geminiscapa*
66. *Megalodonta beckii*
67. *Eriocaulon septangulare*
68. *Zosterella dubia*
69. submerged mosses

Species	Sites
1:	4, 6, 7, 14, 15, 16, 22, 27, 28, 38, 70, 71, 72, 73, 74, 75, 77, 82, 89, 90, 95, 105, 114, 122, 133, 135, 138, 139, 140, 144, 146, 147, 148, 150, 155, 159, 161, 180, 181, 183, 184, 187, 190, 222, 227, 230, 234, 237, 238, 239, 241, 242, 243, 247, 248, 249, 252, 253, 256, 257, 258, 259, 260, 263, 264, 265, 266, 267, 269, 273, 274, 284, 285, 286, 295, 304.
2:	47, 167, 199, 230, 233.
3:	3, 42, 47, 48, 50, 52, 58, 59, 60, 61, 62, 65, 67, 68, 69, 72, 74, 80, 81, 82, 84, 85, 86, 97, 99, 100, 103, 104, 107, 112, 116, 126, 130, 131, 153, 163, 164, 173, 184, 188, 189, 190, 193, 203, 204, 209, 210, 213, 233, 235, 259, 261, 263, 267, 271, 280, 285, 288, 290, 291.
4:	45, 91, 95, 105, 109, 117, 141, 142, 143, 148, 150, 152, 160, 196, 238, 239, 296.
5:	232.
6:	80, 84, 201, 255, 257, 285.
7:	15, 100, 163, 170, 171, 187, 188, 194, 202, 235, 236, 238, 239, 241, 242, 249, 251, 252, 253, 255, 261, 262, 265, 267, 268.
8:	69, 81, 83, 100, 104, 163, 164, 166, 169, 186, 188, 189, 190, 191, 195, 197, 199, 202, 235, 254, 261.
9:	75, 88, 95, 114, 116, 124, 131, 133, 139, 141, 145, 146, 147, 160, 241, 256, 257, 258, 266, 267, 268.
10:	13, 20, 36, 120, 147, 168, 171, 180, 183, 184, 188, 192, 196, 199, 201, 210, 212, 241, 244, 249, 251, 252, 264, 267, 269, 274, 280, 282, 284, 300, 301, 304.
11:	9, 26, 38, 39, 40, 47, 98, 107, 114, 122, 125, 132, 135, 137, 144, 163, 170, 175, 181, 182, 216, 239, 251, 252, 253, 256, 259, 260, 263, 269, 271, 273, 295, 302.
12:	14, 15, 36, 38, 57, 58, 62, 68, 72, 74, 77, 81, 86, 93, 95, 116, 123, 125, 127, 131, 133, 135, 137, 140, 145, 146, 147, 151, 156, 165, 166, 169, 170, 171, 183, 184, 186, 188, 193, 194, 207, 210, 214, 217, 222, 225, 228, 234, 235, 237, 241, 249, 251, 252, 253, 254, 256, 263, 267, 268, 269, 295.
13:	233.
14:	4, 7, 9, 14, 16, 25, 31, 38, 40, 63, 71, 75, 81, 109, 112, 115, 121, 122, 123, 124, 126, 135, 137, 140, 144, 146, 149, 181, 184, 187, 191, 195, 196, 209, 213, 216, 233, 235, 239, 241, 242, 243, 245, 249, 253, 256, 258, 259, 260, 261, 262, 263, 264, 267, 271, 273, 285, 286, 288, 295.
15:	195, 201, 202, 212, 267.

Species	Sites
16:	1, 2, 3, 4, 5, 6, 7, 9, 11, 12, 14, 17, 18, 21, 26, 27, 28, 30, 31, 33, 34, 35, 36, 41, 47, 48, 50, 54, 55, 89, 90, 92, 93, 94, 96, 105, 106, 107, 108, 114, 116, 117, 119, 124, 135, 140, 144, 150, 154, 155, 159, 174, 175, 177, 178, 179, 181, 185, 205, 206, 209, 213, 216, 217, 218, 223, 224, 229, 230, 233, 235, 237, 239, 241, 242, 246, 249, 250, 251, 253, 257, 260, 268, 269, 270, 273, 274, 275, 276, 279, 280, 287, 292, 293, 295, 296, 297, 298, 300, 303, 305.
17:	7, 9, 25, 36, 40, 48, 50, 79, 80, 109, 112, 115, 116, 117, 118, 122, 124, 135, 146, 168, 172, 234, 235, 238, 239, 241, 245, 250, 251, 252, 253, 254, 255, 256, 259, 263, 265, 271, 287.
18:	24, 49, 53, 57, 65, 73, 76, 80, 83, 85, 98, 121, 123, 127, 129, 137, 139, 149, 151, 159, 162, 176, 181, 182, 184, 187, 195, 218, 231, 232, 234, 237, 243, 262, 277, 291.
19:	1, 2, 4, 6, 7, 9, 11, 22, 23, 25, 26, 28, 31, 32, 36, 39, 40, 81, 87, 90, 96, 97, 98, 99, 108, 112, 113, 114, 115, 116, 117, 118, 119, 124, 126, 128, 130, 131, 132, 134, 135, 137, 139, 149, 150, 152, 153, 154, 157, 161, 163, 164, 165, 166, 167, 168, 170, 172, 173, 175, 178, 179, 186, 188, 189, 197, 200, 203, 204, 208, 209, 210, 212, 213, 215, 216, 217, 223, 224, 232, 233, 234, 235, 236, 237, 238, 239, 241, 242, 243, 244, 246, 247, 250, 251, 253, 254, 255, 256, 257, 258, 260, 263, 265, 266, 267, 268, 269, 270, 271, 272, 273, 275, 279, 287, 291, 292, 293, 295, 298, 300, 303.
20:	98, 236, 253, 254, 255.
21:	173, 189, 190, 251, 254, 261.
22:	236.
23:	4, 19, 25, 33, 40, 48, 79, 93, 105, 107, 108, 111, 113, 117, 125, 126, 128, 132, 135, 137, 138, 143, 153, 161, 177, 233, 234, 276, 287, 295, 296, 298.
24:	7, 9, 25, 28, 40, 81, 98, 99, 116, 117, 120, 125, 126, 132, 135, 163, 164, 166, 169, 170, 173, 175, 187, 188, 199, 209, 213, 216, 217, 232, 233, 235, 236, 237, 238, 239, 241, 242, 243, 244, 245, 246, 251, 252, 253, 259, 260, 263, 264, 267, 268, 269, 271, 273, 280, 287, 295.
25:	7, 38, 107, 135, 146, 149, 167, 168, 170, 171, 173, 181, 193, 194, 199, 216, 234, 238, 239, 241, 242, 244, 246, 248, 250, 251, 252, 253, 255, 260, 263, 265, 267, 268, 270, 271, 275.
26:	238, 239, 261.
27:	4, 14, 22, 42, 46, 50, 52, 53, 58, 64, 77, 80, 82, 84, 85, 86, 88, 95, 129, 137, 139, 140, 145, 149, 151, 156, 157, 163, 167, 176, 180, 183, 184, 185, 207, 208, 222, 225, 226, 227, 231, 249, 254, 277.
28:	173, 188, 199, 200, 212, 264.

Species	Sites
29:	4, 7, 8, 9, 22, 23, 24, 25, 28, 31, 36, 39, 45, 66, 81, 90, 96, 97, 98, 99, 101, 103, 104, 107, 116, 120, 122, 123, 125, 128, 135, 140, 145, 149, 153, 157, 158, 161, 163, 164, 165, 166, 167, 169, 173, 176, 178, 190, 195, 197, 208, 209, 210, 213, 218, 224, 226, 231, 233, 242, 243, 244, 246, 249, 259, 260, 261, 265, 267, 270, 271, 273, 280, 282, 283, 286, 288, 293.
30:	9, 28, 30, 31, 40, 61, 98, 126, 164, 169, 170, 188, 197, 199, 209, 212, 216, 218, 223, 224, 233, 235, 236, 237, 238, 239, 241, 242, 243, 244, 245, 246, 247, 248, 251, 252, 263, 265, 269, 271, 272, 275, 280, 282, 286, 287, 291, 292, 293.
31:	9, 39, 98, 170, 171, 172, 173, 186, 187, 188, 189, 194, 203, 233, 234, 235, 236, 237, 238, 239, 241, 242, 243, 245, 246, 248, 250, 251, 254, 268, 270, 272, 273.
32:	7, 28, 31, 66, 68, 80, 81, 149, 169, 197, 200, 203, 204, 233, 234, 239, 243, 244, 251, 270, 271, 295.
33:	4, 7, 48, 50, 52, 58, 59, 61, 68, 74, 81, 85, 86, 89, 99, 100, 103, 114, 146, 151, 163, 186, 206, 207, 208, 212, 263, 270, 294.
34:	7, 67, 83, 98, 99, 122, 171, 173, 195, 199, 201, 264, 265.
35:	2, 8, 9, 11, 25, 26, 28, 30, 31, 36, 37, 44, 49, 50, 57, 63, 65, 66, 73, 74, 78, 80, 81, 89, 96, 98, 99, 103, 104, 107, 111, 121, 125, 136, 149, 157, 162, 167, 173, 174, 175, 176, 178, 179, 184, 194, 195, 201, 211, 214, 215, 216, 217, 226, 227, 240, 242, 249, 257, 260, 261, 264, 265, 270, 272, 274, 278, 280, 282, 284, 288, 289, 290.
36:	1, 2, 8, 9, 10, 22, 23, 24, 25, 26, 30, 31, 32, 33, 35, 36, 44, 48, 50, 63, 73, 78, 80, 81, 96, 98, 109, 121, 125, 136, 149, 153, 157, 162, 163, 164, 173, 176, 184, 188, 199, 202, 204, 210, 212, 213, 217, 218, 231, 233, 236, 239, 240, 242, 243, 244, 245, 259, 260, 267, 268, 273, 274, 278, 288, 291, 301, 302.
37:	9, 26, 66, 78, 98, 99, 103, 104, 163, 164, 167, 169, 173, 175, 178, 194, 195, 199, 201, 209, 213, 215, 217, 233, 240, 245, 270, 271, 273.
38:	36, 38, 57, 68, 69, 78, 81, 99, 103, 112, 114, 116, 117, 118, 120, 121, 122, 126, 127, 131, 138, 139, 144, 148, 157, 162, 164, 165, 166, 167, 170, 173, 176, 178, 201, 208, 209, 210, 212, 213, 216, 217, 218, 224, 230, 240, 249, 260, 262, 264, 267, 268, 270, 278, 280, 282, 286, 288, 290, 293.
39:	166, 174, 244.

Species	Sites
40:	1, 2, 7, 9, 13, 21, 24, 25, 26, 28, 30, 34, 37, 44, 45, 47, 63, 66, 73, 81, 84, 98, 99, 106, 107, 109, 124, 148, 153, 157, 162, 163, 164, 167, 169, 172, 173, 175, 176, 178, 184, 188, 193, 195, 196, 204, 210, 211, 212, 216, 217, 218, 223, 224, 226, 233, 234, 235, 237, 238, 239, 241, 242, 245, 246, 247, 248, 250, 251, 258, 259, 260, 263, 264, 265, 267, 268, 269, 271, 272, 274, 275, 295, 297, 300, 302, 303.
41:	66, 68, 100, 101, 173, 191, 235, 241, 251, 253, 255, 259, 261, 262.
42:	199, 242, 251, 253, 255, 259, 260, 261, 262, 263, 264, 268.
43:	233, 236, 239, 242, 243, 255.
44:	39, 68, 131, 135, 153, 171, 172, 173, 188, 190, 271.
45:	7, 9, 25, 36, 61, 73, 81, 96, 98, 99, 102, 104, 107, 116, 117, 122, 123, 126, 127, 135, 138, 149, 153, 161, 171, 172, 187, 188, 189, 190, 191, 196, 197, 200, 202, 204, 209, 210, 216, 233, 234, 235, 238, 239, 241, 244, 245, 251, 253, 254, 255, 259, 260, 261, 262, 263, 264, 271, 273, 288.
46:	171, 191, 235, 253, 261, 262.
47:	64, 67, 71, 81, 122.
48:	22, 32, 50, 58, 85, 135, 163, 186, 208, 233, 243, 251, 256, 265, 271, 275, 290, 294.
49:	98, 133, 156.
50:	78.
51:	145.
52:	62, 65, 211.
53:	50, 52, 60, 223.
54:	22, 32, 52, 72, 85, 131, 157, 158, 166, 173, 183, 184, 185, 193, 204, 212, 213.
55:	171, 186, 261, 278.
56:	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13, 15, 18, 20, 23, 25, 26, 30, 32, 33, 34, 35, 36, 38, 39, 40, 44, 45, 47, 48, 50, 54, 55, 57, 60, 69, 70, 74, 80, 82, 87, 90, 91, 92, 93, 95, 96, 97, 98, 99, 105, 106, 107, 108, 109, 112, 113, 114, 115, 116, 117, 119, 120, 121, 122, 123, 124, 126, 127, 128, 129, 130, 131, 132, 135, 136, 137, 139, 140, 143, 144, 146, 148, 149, 151, 153, 156, 157, 159, 160, 161, 162, 163, 164, 166, 170, 173, 176, 177, 181, 185, 187, 188, 195, 198, 205, 206, 208, 210, 212, 213, 216, 217, 218, 224, 227, 228, 234, 235, 236, 237, 240, 241, 242, 246, 247, 248, 252, 253, 255, 257, 258, 259, 260, 264, 268, 269, 270, 271, 273, 274, 276, 278, 279, 281, 285, 286, 287, 288, 291, 292, 293, 295, 296, 298, 299, 300, 301, 303, 305.

Species	Sites
57:	233, 238, 243.
58:	78, 84, 138, 158, 184.
59:	4, 24, 25, 27, 48, 54, 59, 60, 61, 67, 72, 78, 86, 90, 112, 113, 116, 117, 119, 121, 125, 128, 131, 135, 138, 139, 140, 153, 158, 161, 180, 185, 208, 210, 211, 228, 231, 248, 250, 265, 288, 295.
60:	22, 42, 45, 48, 50, 53, 54, 58, 60, 62, 63, 64, 65, 67, 68, 69, 77, 78, 81, 85, 86, 93, 98, 103, 104, 111, 122, 129, 139, 148, 149, 153, 156, 163, 167, 169, 171, 202, 208, 209, 210, 222, 224, 226, 231, 244, 246, 284.
61:	4, 42, 45, 48, 53, 62, 86, 136, 137, 144, 204.
62:	16, 67, 69, 75, 80, 107, 139, 140, 145, 180, 190, 191, 199, 202, 207, 212, 233, 261, 263, 276, 285.
63:	57, 86, 107, 139, 145, 180, 192, 201, 212, 214, 219, 235, 261.
64:	4, 7, 12, 13, 17, 18, 19, 21, 24, 30, 34, 44, 47, 49, 51, 54, 55, 57, 58, 60, 62, 63, 64, 65, 66, 68, 69, 72, 73, 75, 80, 81, 82, 83, 84, 94, 96, 98, 100, 101, 104, 105, 107, 109, 110, 111, 116, 121, 127, 132, 135, 137, 138, 139, 140, 146, 147, 148, 149, 155, 157, 162, 163, 169, 173, 176, 188, 190, 191, 195, 196, 199, 200, 201, 209, 211, 213, 216, 217, 229, 230, 233, 239, 243, 244, 245, 246, 253, 259, 263, 264, 267, 271, 274, 276, 284, 289, 291, 297.
65:	253.
66:	164, 173, 194, 199, 200, 202, 209, 233, 235, 236, 237, 238, 239, 243, 244, 245, 251, 253, 259, 260, 273.
67:	171.
68:	194, 204, 216, 234, 235, 236, 237, 238, 242, 265, 271.
69:	7, 19, 34, 49, 51, 55, 57, 61, 62, 65, 68, 72, 78, 96, 104, 107, 112, 113, 119, 123, 135, 137, 145, 153, 158, 164, 181, 183, 199, 202, 204, 211, 212, 219, 230, 235, 261, 283, 284, 288, 289, 290.

B. The sites at which each gastropod species was recorded. Locations of the sites are given in Appendix II. Species numbers represent the following taxa:

1. Campeloma decisum
2. Valvata sincera
3. V. tricarinata
4. Cincinnatia cincinnatiensis
5. Marstonia decepta
6. M. gelida
7. Probythinella lacustris
8. Amnicola walkeri
9. A. limosa
10. Somatogyrus subglobosus
11. Lymnaea stagnalis
12. Acella haldemani
13. Bulimnea megasoma
14. Stagnicola palustris
15. S. catascopium
16. S. caperata
17. S. reflexa
18. Fossaria decampi
19. F. exigua
20. F. modicella
21. F. parva
22. F. dalli
23. F. obrussa
24. Physa gyrina
25. P. jennessi
26. Aplexa hypnorum
27. Ferrissia parallela
28. F. rivularis
29. Helisoma trivolvis
30. H. pilsbryi
31. H. corpulentum
32. H. campanulatum
33. H. anceps
34. Planorbula armigera
35. P. campestris
36. Promenetus exacuous
37. P. umbilicatellus
38. Armiger crista
39. Gyraulus parvus
40. G. circumstriatus
41. G. deflectus
42. Physa integra

Species	Sites
1:	233, 241, 265.
2:	69, 267, 269, 285, 288, 295.
3:	1, 2, 5, 6, 7, 9, 28, 40, 45, 80, 91, 106, 107, 108, 113, 115, 135, 148, 150, 152, 154, 155, 160, 175, 215, 232, 234, 235, 239, 241, 250, 264, 265, 269, 272, 273, 274, 279, 292, 293, 295, 300, 303.
4:	28, 80, 174, 179, 197, 215, 234, 235, 238, 239, 241, 242, 260, 265, 269, 275, 303.
5:	41, 81, 135, 247, 250, 253, 263, 267, 271.
6:	234, 264, 265, 267.
7:	6, 152, 154, 179.
8:	66, 168, 236.
9:	1, 2, 5, 6, 7, 9, 28, 38, 39, 40, 45, 66, 68, 81, 90, 91, 98, 99, 100, 126, 150, 152, 166, 170, 186, 197, 199, 202, 212, 215, 223, 233, 234, 235, 236, 237, 239, 241, 242, 243, 244, 251, 255, 260, 263, 264, 265, 267, 268, 269, 270, 271, 272, 279, 292, 293.
10:	265.
11:	1, 2, 3, 4, 6, 7, 8, 10, 11, 12, 13, 14, 15, 16, 18, 19, 20, 21, 22, 23, 24, 25, 26, 28, 30, 31, 32, 33, 34, 35, 36, 38, 39, 40, 44, 46, 47, 48, 49, 50, 51, 54, 57, 60, 62, 63, 64, 66, 70, 71, 73, 74, 75, 77, 78, 79, 80, 81, 82, 83, 84, 87, 91, 93, 94, 96, 97, 98, 104, 105, 106, 107, 108, 109, 110, 111, 112, 113, 115, 116, 117, 118, 119, 121, 122, 123, 127, 128, 129, 132, 135, 136, 137, 139, 140, 145, 146, 147, 149, 150, 151, 152, 153, 155, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166, 169, 170, 175, 176, 177, 178, 180, 182, 183, 185, 187, 192, 199, 200, 201, 202, 207, 208, 209, 210, 211, 212, 213, 215, 216, 217, 218, 223, 224, 227, 228, 229, 230, 233, 234, 235, 236, 239, 240, 241, 242, 243, 244, 245, 246, 247, 248, 251, 253, 255, 256, 260, 263, 264, 265, 266, 267, 269, 272, 273, 274, 276, 278, 280, 285, 286, 287, 288, 289, 291, 292, 293, 294, 295, 296, 297, 298, 299, 302, 304.
12:	235, 241, 265.
13:	67, 169, 173, 199, 200, 202, 219, 233, 234, 240, 288.
14:	1, 2, 3, 4, 5, 6, 7, 10, 11, 13, 14, 15, 17, 18, 19, 20, 21, 22, 24, 26, 27, 28, 32, 33, 34, 35, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 53, 55, 56, 58, 59, 60, 62, 64, 70, 72, 73, 77, 80, 82, 85, 86, 87, 88, 89, 90, 91, 92, 93, 95, 97, 105, 106, 108, 109, 110, 117, 126, 128, 129, 131, 132, 137, 139, 140, 141, 142, 143, 144, 145, 146, 147, 148, 149, 150, 151, 152, 155, 156, 157, 158, 159, 160, 161, 162, 165, 175, 176, 177, 178, 179, 183, 185, 205, 206, 207, 209, 210, 212, 217, 220, 221, 222, 223, 224, 225, 227, 228, 229, 231, 232, 233,

Species	Sites
14: cont'd	239, 245, 246, 270, 272, 274, 278, 279, 280, 281, 285, 289, 292, 293, 294, 295, 296, 297, 298, 299, 301, 302, 304, 305.
15:	6, 80, 91, 143, 150, 155, 247, 248, 250, 269, 270, 272.
16:	48, 284.
17:	104, 188, 249.
18:	6, 115, 234, 265.
19:	14, 18, 32, 52, 82, 98, 284.
20:	1, 2, 3, 4, 5, 6, 11, 19, 28, 38, 46, 48, 49, 51, 56, 59, 60, 72, 80, 85, 89, 90, 91, 106, 126, 132, 145, 150, 152, 154, 155, 160, 175, 176, 182, 205, 206, 207, 215, 223, 276, 281, 286, 296, 297, 298.
21:	34.
22:	132, 139, 264.
23:	205.
24:	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 13, 16, 18, 19, 20, 21, 24, 25, 26, 28, 31, 35, 36, 38, 39, 40, 41, 42, 43, 44, 45, 47, 51, 60, 63, 64, 65, 67, 69, 71, 72, 73, 74, 75, 76, 77, 80, 81, 82, 85, 89, 90, 91, 96, 98, 99, 100, 102, 104, 105, 106, 107, 108, 109, 111, 112, 113, 114, 115, 116, 117, 118, 119, 120, 122, 123, 124, 126, 128, 132, 135, 138, 143, 146, 147, 148, 149, 150, 152, 153, 154, 157, 158, 160, 161, 162, 165, 166, 167, 174, 175, 176, 177, 178, 179, 180, 181, 182, 184, 185, 187, 188, 189, 190, 194, 197, 198, 199, 201, 202, 203, 207, 208, 209, 210, 211, 212, 213, 215, 216, 217, 223, 224, 226, 227, 228, 231, 232, 233, 234, 235, 236, 237, 239, 241, 242, 243, 245, 246, 247, 248, 249, 251, 252, 254, 258, 259, 260, 261, 263, 264, 265, 266, 267, 269, 272, 273, 274, 275, 277, 278, 279, 280, 281, 282, 283, 284, 285, 287, 288, 289, 292, 293, 295, 300, 304, 305.
25:	20, 23, 30, 32, 34, 37, 42, 48, 56, 85, 88, 110, 136, 142, 162, 201, 205, 206, 207, 218, 224, 229, 238, 276, 285, 298, 302.
26:	1, 6, 13, 26, 42, 44, 49, 51, 53, 56, 58, 60, 62, 64, 72, 73, 81, 82, 86, 108, 139, 158, 176, 185, 209, 210, 247, 248, 274, 284, 291, 297.
27:	233.
28:	6, 41, 42, 99, 108, 152, 191, 192, 194, 197, 198, 233, 245, 288.

Species	Sites
29:	1, 2, 3, 5, 6, 7, 8, 9, 10, 12, 13, 15, 18, 20, 21, 22, 24, 25, 26, 28, 30, 31, 32, 33, 34, 36, 37, 38, 39, 40, 42, 44, 45, 46, 48, 50, 51, 53, 54, 55, 56, 57, 60, 66, 69, 74, 77, 78, 81, 86, 87, 89, 93, 94, 97, 106, 107, 108, 109, 110, 113, 114, 115, 116, 117, 118, 120, 121, 124, 125, 129, 130, 132, 135, 136, 139, 145, 146, 149, 150, 151, 152, 153, 156, 157, 158, 159, 160, 161, 162, 163, 164, 169, 173, 174, 175, 176, 177, 178, 182, 184, 195, 199, 201, 202, 206, 209, 215, 223, 224, 226, 228, 230, 231, 232, 233, 234, 238, 239, 240, 241, 243, 245, 246, 247, 248, 251, 256, 265, 269, 271, 272, 274, 276, 278, 280, 281, 285, 286, 287, 292, 293, 295, 296, 297, 298, 299, 301, 302, 305.
30:	143, 241, 247.
31:	99, 125, 166, 186.
32:	7, 9, 36, 61, 66, 68, 69, 80, 81, 98, 99, 103, 115, 120, 122, 132, 149, 163, 164, 165, 166, 167, 168, 170, 188, 197, 199, 200, 201, 204, 233, 234, 235, 236, 237, 238, 239, 240, 241, 242, 243, 244, 245, 246, 247, 248, 250, 251, 253, 254, 256, 258, 260, 261, 262, 263, 264, 265, 266, 267, 268, 269, 270, 271, 273.
33:	1, 6, 7, 9, 16, 25, 38, 39, 40, 43, 47, 63, 65, 68, 69, 71, 73, 74, 75, 82, 83, 89, 91, 105, 106, 107, 108, 109, 112, 113, 115, 117, 119, 120, 125, 130, 135, 148, 154, 155, 160, 169, 177, 181, 182, 184, 187, 192, 196, 197, 203, 212, 214, 234, 235, 238, 239, 243, 247, 250, 251, 253, 254, 255, 256, 258, 264, 265, 266, 269, 270, 275, 283, 285, 288.
34:	1, 2, 5, 6, 7, 18, 21, 48, 57, 69, 72, 73, 80, 98, 103, 104, 115, 126, 127, 132, 140, 144, 148, 149, 150, 152, 155, 156, 164, 165, 166, 167, 169, 174, 176, 179, 207, 209, 210, 211, 211, 212, 213, 216, 221, 236, 240, 243, 244, 245, 246, 272, 273, 278, 284, 285, 286, 288, 289, 291, 303.
35:	45, 46, 51, 53, 207, 223.
36:	1, 2, 5, 6, 7, 13, 21, 28, 44, 45, 46, 48, 51, 55, 62, 68, 91, 98, 107, 109, 110, 122, 123, 145, 151, 152, 160, 162, 175, 176, 198, 203, 212, 216, 223, 224, 230, 233, 236, 244, 247, 265, 270, 296, 297, 298, 301, 305.
37:	133, 158, 260, 268, 295.
38:	1, 2, 5, 6, 20, 44, 51, 278.
39:	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 12, 13, 17, 18, 20, 22, 23, 24, 28, 32, 34, 35, 38, 39, 40, 42, 44, 46, 47, 49, 50, 55, 56, 57, 58, 62, 69, 72, 77, 80, 82, 84, 87, 91, 98, 103, 105, 107, 108, 111, 114, 116, 121, 122, 126, 129, 135, 136, 137, 145, 150, 151, 152, 155, 156, 158, 160, 161, 162, 163, 164, 165, 166, 167, 173, 175, 179, 181, 184, 185, 187, 192, 196, 197, 199, 201, 202, 207, 210, 216, 219, 221, 222, 223, 224, 226,

Species	Sites
39, cont'd	227, 230, 232, 233, 234, 236, 237, 239, 241, 242, 243, 245, 247, 249, 252, 263, 264, 267, 270, 274, 279, 280, 281, 282, 284, 285, 287, 288, 292, 293, 294, 295, 296, 297, 298, 300, 301, 302, 305.
40:	17, 18, 45, 48, 60, 69, 73, 74, 106, 110, 139, 141, 142, 144, 147, 173, 177, 209, 231, 255, 264, 269, 273, 280.
41:	7, 9, 13, 64, 68, 81, 98, 109, 114, 115, 141, 169, 173, 186, 187, 188, 195, 199, 200, 201, 212, 233, 235, 237, 238, 239, 242, 244, 253, 265, 267, 280, 295, 296.
42:	9.

APPENDIX IV

Key to species of the genus Potamogeton occurring within the study area, modified after Gleason (1952) and Scoggan (1957).

---

1. Submersed leaves 4 mm wide or wider.
    2. Base of submersed leaves cordate or auriculate.
        3. Stipules persistent and conspicuous, 10-50 mm long.
            4. Leaves 2-ranked, margins minutely serrulate, adnate at base to stipules. . . . . P. robbinsii.
            4. Leaves 10-25 cm long, boat-shaped at ends, free from stipules, margins not toothed, peduncles up to 40 cm long, stems up to 4 m long. P. praelongus.
        3. Stipules soon disintegrating and 1-2 cm long, leaves not boat-shaped at ends, peduncles 2-10 cm long. . . . . P. richardsonii.
    2. Base of submersed leaves not cordate nor auriculate.
        5. Stem flattened, leaves linear, with 1-3 main nerves and up to 30 small ones. . . . . P. zosteriformis.
        5. Stem round in cross-section, less than half as wide as submersed leaves.
            6. Stipules 4-12 cm long, leaves with 11-50 veins.
                7. Submersed leaves falcate-folded and usually very wide. . . . . P. amplifolius.
                7. Submersed leaves 2-5 cm wide, not falcate-folded. . . . . P. illinoensis.
            6. Stipules 1-3 cm long, submersed leaves with 3-14 veins.
                8. Lacunar strip of submersed leaves less than 0.5 mm wide (less than 4 rows of cells).
                    9. Leaves 8-14 cm long, margins of some specimens (particularly from Minnesota) may be finely crenulate and minutely toothed at the tips; floating leaves not sharply distinct from the short petioles. . . . . P. alpinus.
                    9. Leaves 3-8 cm long, floating leaves sharply distinct from elongate petioles. . P. gramineus.
                8. Lacunar strip of submersed leaves 1-3 mm wide, consisting of 9-18 rows of cells, submersed leaves up to 20 cm long. . . . P. epihydrus.
1. Submersed leaves less than 4 mm wide.
    10. Stipules free to base of leaves.
        11. Submersed leaves without blades, only floating leaves developed, attached to petioles by a joint up to 2 cm long. . . . . P. natans.
        11. Submersed leaves with blades.
            12. Submersed leaves with very many fine nerves, stem flattened. . . . . P. zosteriformis.
            12. Submersed leaves 3-7 nerved.
                13. Stipules fibrous, soon disintegrating to shreds.

14. Leaves 5-7 nerved, minutely cuspidate at tip. . . . . P. friesii.
14. Leaves 3- nerved, not cuspidate at tip P. strictifolius.

13. Stipules membranous.
15. Submersed leaves with lacunar strip 1-3 mm wide. . . . P. epihydrus.
15. Lacunar strip less than 4 cells wide, floating leaves absent.
16. Achene 3-4 mm long, leaves linear, 3-10 cm long, 2-4 delicate lateral nerves, rounded or minutely cuspidate at tip. . . . . P. obtusifolius.
16. Achene less than 3 mm long, leaves usually less than 5 cm long.
17. Achene with thin, undulate dorsal keel, glands absent at base of leaves, leaves 3-5 nerved, peduncle less than 1 cm long, spikes 2-5 mm long. P. foliosus.
17. Achene without dorsal keel, glands present at base of most leaves, leaves 3-nerved, peduncle more than 1 cm long. P. pusillus.

10. Stipules adnate at base to base of leaves.
18. Achene with conspicuous dorsal keel, floating leaves common and small. . . . . P. spirillus.
18. Achene without dorsal keel, floating leaves absent.
19. Stipular sheaths, particularly of primary leaves, loose and much wider than stem. . P. vaginatus.
19. Stipular shaths scarcely wider than stem.
20. Stem branched from most of nodes, achenes more than 2.5 mm long. . . P. pectinatus.
20. Stem branched chiefly at base, spikes often borne below water surface, achenes 1.5-3 mm long. . . . . P. filiformis.

Note: Floating leaves were rarely observed in P. richardsonii but do not appear to have been previously reported. When present, these retain the same morphology as that of the submersed leaves but are leathery in texture and the upper surfaces are water repellant. A petiole is absent.

Figure IV-1. Achenes of Potamogeton:

A, B : P. amplifolius

C, D : P. epihydrus

E, F, G : P. filiformis

H : P. friesii

I, J : P. foliosus

Numbers indicate sites from which the material originated.

Figure IV-2. Achenes of Potamogeton:

A, C : P. natans

B : P. gramineus

D, F : P. obtusifolius

E, G, H : P. pectinatus

Numbers indicate sites from which the material originated.

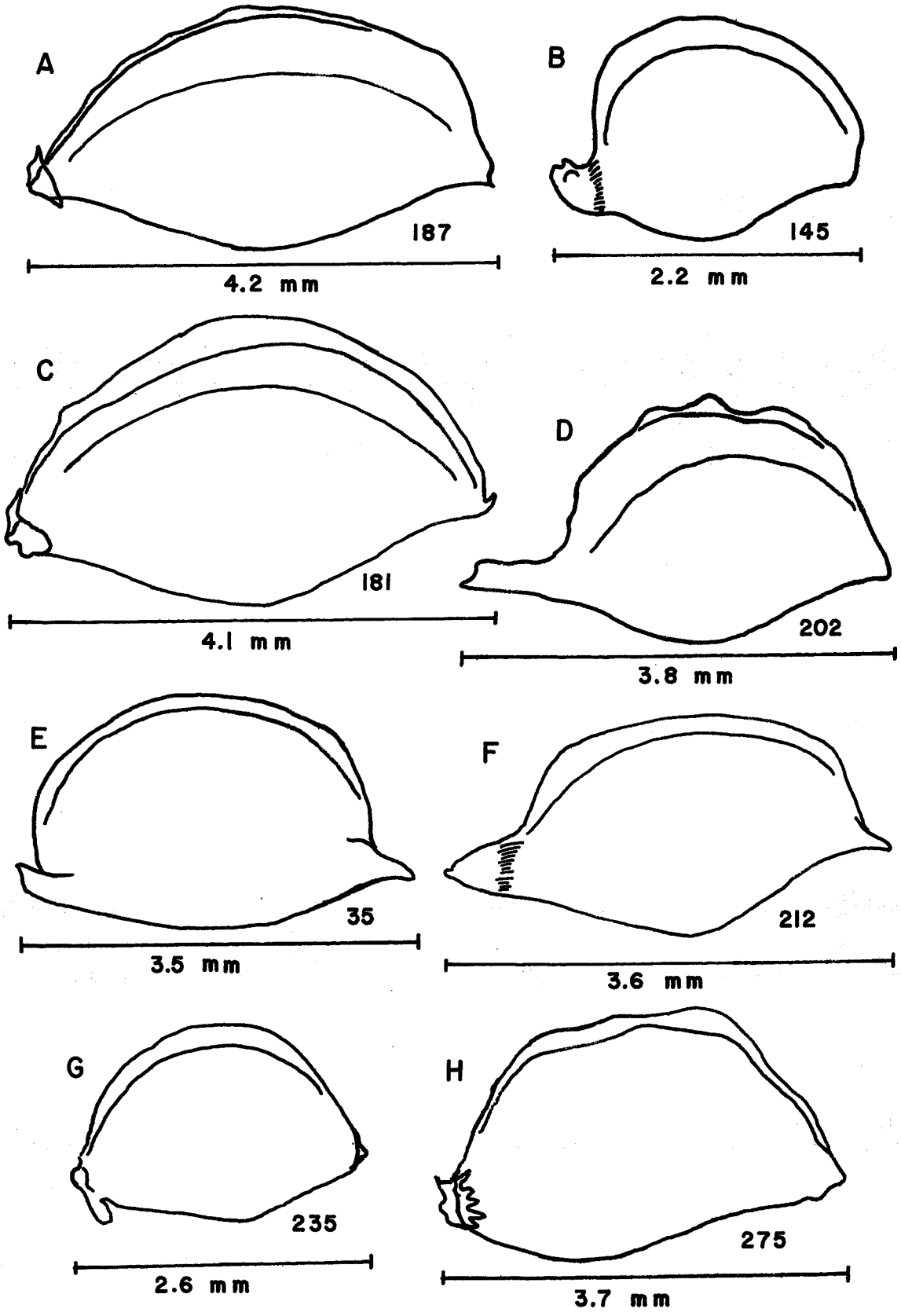
A
187
4.2 mm
B
145
2.2 mm
C
181
4.1 mm
D
202
3.8 mm
E
35
3.5 mm
F
212
3.6 mm
G
235
2.6 mm
H
275
3.7 mm

Figure IV-3. Achenes of Potamogeton:

A : P. praelongus

B : P. pusillus

C, D : P. spirillus

E : P. richardsonii

F, G : P. zosteriformis

Numbers indicate sites from which the material originated.

APPENDIX V

A. Chi-square program for one data set.

```
      $JOB WATFIV
      C-----------------------------------------------------------------
      C  THIS PROGRAM PERFORMS 2 OPERATIONS
      C    1) CALCULATES NO OF TIMES SINGLE SPECIES AND PAIRED SPECIES
      C       APPEAR IN A LIST OF COMMUNITIES.
      C    2) CALCULATES CHI-SQUARE FOR SPECIES.
      C
      C    PRINTOUTS ARE THEN PERFORMED FOR THESE TWO CALCULATIONS
      C    IN THE FORM OF TWO ARRAYS OF APPROPRIATE SIZE.
      C
      C  INPUT CONSISTS OF
      C   CARD(1)  NUMBER OF SPECIES (NSPES) AND
      C            NUMBER OF SITES (NOSITS)
      C            FORMAT(2I4)
      C    CARD(2)-(NOSITS)  SITE NUMBER THEN INTEGER DATA
      C                      FORMAT(I3,77I1)
      C
      C-----------------------------------------------------------------
 1          INTEGER DATA(x,y),NOSPRS(x,x)
 2          REAL CHISQU(x,x),CHI,FLOAT
 3          INTEGER A,B,C,D,TA,TB,IABS,BOT,TOP
 4          CHARACTER*40 HEAD
      C
      C  READ IN DATA AND PUT INTO ARRAY.
 5          READ(5,15,END=99)NSPES,NOSITS
 6          DO 6 J=1,NOSITS
 7            READ(5,8,END=99)SIGHT,(DATA(I,J),I=1,NSPES)
 8        6  CONTINUE
 9       15  FORMAT(2I4)
10        8  FORMAT(I3,77I1)
      C
      C  THIS PROGRAM SEGMENT DOES ALL CALCULATIONS.
      C
11          NUM=NSPES-1
12          DO 16 J=1,NUM
13            KK=J+1
14            DO 17  JJ=KK,NSPES
15              NA=0
16              NB=0
17              A=0
      C
      C    CALCULATION OF TOTALS.
      C
18              DO 18 I=1,NOSITS
19                TA=DATA(J,I)
20                TB=DATA(JJ,I)
21                NA=NA+TA
22                NB=NB+TB
23                A=A+(TA+TB)/2*1
24      18        CONTINUE
```

```
      C
      C  PLACEMENT OF TOTALS INTO ARRAY
      C
25              NOSPRS(J,J)=NA
26                NOSPRS(JJ,JJ)=NB
27                NOSPRS(J,JJ)=A
28                NOSPRS(JJ,J)=A
29                IF(A.EQ.0)GO TO 165
      C
      C    CALCULATION OF EXTRA VALUES FOR CHI-SQUARE CALCULATION
      C
30                B=NB-A
31                C=NA-A
32                D=NOSITS-(A+B+C)
33                NNB=C+D
34                NNA=B+D
35                N=NOSITS
      C
      C  CALCULATION OF CHI-SQUARE AND BUILDING ARRAY CHISQU(NSPES,NSPES)
36                NDIV=NA*NNA*NB*NNB
37                IF(NDIV.EQ.0)GOTO 165
38                CHI=((FLOAT(IABS(A*D-B*C))-.5*N)**2*N)/NDIV
39                GOTO 167
40     165        CONTINUE
41                CHI=0.0
42     167       CONTINUE
43                CHISQU(J,JJ)=CHI
44                CHISQU(JJ,J)=CHI
45       17     CONTINUE
46              CHISQU(J,J)=0.0
47       16   CONTINUE
48           CHISQU(NSPES,NSPES)=0.0
      C
      C  OUTPUT TOTALS
      C
49            HEAD='THE TOTALS ARE'
50            LIM=(NSPES+29)/30
51            BOT=1
52            TOP=(NSPES+LIM-1)/LIM
53            DO 20  LO=1,LIM
54              WRITE(6,10)HEAD,(I,I=BOT,TOP)
55              PRINT,' '
56              DO 50 J=1,NSPES
57                WRITE(6,40)J,(NOSPRS(I,J),I=BOT,TOP)
58        50        CONTINUE
59              BOT=TOP+1
60              IF(LO+1.EQ.LIM)THEN DO
*EXTENSION*   OTHER COMPILERS MAY NOT ALLOW IF-THEN-ELSE, DO CASE, WHILE,
                    EXECUTE, REMOTE BLOCK OR AT END STATEMENTS
61                TOP=NSPES
62              ELSE DO
63                TOP=(NSPES+LIM-1)/LIM*(LO+1)
```

```
64              END IF
65              HEAD=' '
66        20  CONTINUE
          C
67        10  FORMAT('1'//1X,A40//4X,30I4)
68        40  FORMAT(' ',I3,30I4)
          C
          C  OUTPUT CHI-SQUARE VALUES
          C
69            HEAD='CHI-SQUARE VALUES'
70            LIM=(NSPES+15)/16
71            TOP=(NSPES+LIM-1)/LIM
72            BOT=1
73            DO 30 LO=1,LIM
74              WRITE(6,22)HEAD,(I,I=BOT,TOP)
75              PRINT,' '
76              DO 60 J=1,NSPES
77                WRITE(6,70)J,(CHISQU(I,J),I=BOT,TOP)
78        60      CONTINUE
79              BOT=TOP+1
80              IF(LO+1.EQ.LIM)THEN DO
*EXTENSION*   OTHER COMPILERS MAY NOT ALLOW IF-THEN-ELSE, DO CASE, WHILE,
                      EXECUTE, REMOTE BLOCK OR AT END STATEMENTS
81                TOP=NSPES
82              ELSE DO
83                TOP=(NSPES+LIM-1)/LIM*(LO+1)
84              END IF
85              HEAD=' '
86        30  CONTINUE
          C
87        70  FORMAT(' ',I3,16F8.2)
88        22  FORMAT('1'//1X,A40//4X,16I8)
89            GO TO 100
90        99  PRINT ,'**ERROR** ON INPUT'
91       100  CONTINUE
92            STOP
93            END
```

B. Chi-square program for two data sets.

```
      $JOB WATFIV
      C-------------------------------------------------------------
      C
      C  THIS PROGRAM PERFORMS 2 OPERATIONS
      C    1) CALCULATES THE NO. OF TIMES TWO DIFFERENT TYPES OF SPECIES
      C       APPEAR SIMULTANEOUSLY IN A LIST OF COMMUNITIES
      C    2) CALCULATES CHI-SQUARE FOR SPECIES.
      C
      C    PRINTOUTS ARE THEN PERFORMED FOR THESE TWO CALCULATIONS
      C    IN THE FORM OF TWO ARRAYS OF APPROPRIATE SIZE.
      C
      C  INPUT CONSISTS OF TWO SETS OF DATA
      C   EACH CONSISTING OF
      C    1) CARD CONTAINING NO. OF SPECIES AND
      C       NO. OF SITES IN FORMAT(2I4).
      C    2) STACK OF DATA CARDS CONTAINING SITE NO.
      C       AND INTEGER DATA IN FORMAT(I3,77I1).
      C
      C-------------------------------------------------------------
 1          INTEGER DATA1(x,y),DATA2(z,y),NOSPRS(x,z)
 2          REAL CHISQU(x,z),CHI,FLOAT
 3          INTEGER A,B,C,D,TA,TB,IABS,BOT,TOP
 4          CHARACTER*40 HEAD
      C
      C  READ IN DATA AND PUT INTO ARRAY.
      C
 5          READ(5,15,END=99)NSPES1,NOSITS
 6          DO 6 J=1,NOSITS
 7            READ(5,8,END=99)SIGHT,(DATA1(I,J),I=1,NSPES1)
 8        6 CONTINUE
 9          READ(5,15,END=99)NSPES2,NOSITS
10          DO 7 J=1,NOSITS
11            READ(5,8,END=99)SIGHT,(DATA2(I,J),I=1,NSPES2)
12        7 CONTINUE
13       15 FORMAT(2I4)
14        8 FORMAT(I3,77I1)
      C
      C  THIS PROGRAM SEGMENT DOES ALL CALCULATIONS.
      C
15          DO 16 J=1,NSPES1
16            DO 17  JJ=1,NSPES2
17              NA=0
18              NB=0
19              A=0
      C
      C    CALCULATION OF TOTALS.
      C
20              DO 18 I=1,NOSITS
21                TA=DATA1(J,I)
22                TB=DATA2(JJ,I)
23                NA=NA+TA
24                NB=NB+TB
```

```
25                A=A+(TA+TB)/2*1
26        18      CONTINUE
                C
                C  PLACEMENT OF TOTALS INTO ARRAY
                C
27                NOSPRS(J,JJ)=A
28                IF(A.EQ.0)GO TO 165
                C
                C    CALCULATION OF EXTRA VALUES FOR CHI-SQUARE CALCULATION
                C
29                B=NB-A
30                C=NA-A
31                D=NOSITS-(A+B+C)
32                NNB=C+D
33                NNA=B+D
34                N=NOSITS
                C
                C  CALCULATION OF CHI-SQUARE AND BUILDING ARRAY CHISQU(NSPES,NSPES)
35                NDIV=NA*NNA*NB*NNB
36                IF(NDIV.EQ.0)GOTO 165
37                CHI=((FLOAT(IABS(A*D-B*C))-.5*N)**2*N)/NDIV
38                GOTO 167
39       165      CONTINUE
40                CHI=0.0
41       167      CONTINUE
42                CHISQU(J,JJ)=CHI
43        17     CONTINUE
44        16   CONTINUE
                C
                C  OUTPUT TOTALS
                C
45              HEAD='THE TOTALS ARE'
46              LIM=(NSPES1+29)/30
47              BOT=1
48              TOP=(NSPES1+LIM-1)/LIM
49              DO 20  LO=1,LIM
50                WRITE(6,10)HEAD,(I,I=BOT,TOP)
51                PRINT,' '
52                DO 50 J=1,NSPES2
53                  WRITE(6,40)J,(NOSPRS(I,J),I=BOT,TOP)
54         50         CONTINUE
55              BOT=TOP+1
56              IF(LO+1.EQ.LIM)THEN DO
*EXTENSION*   OTHER COMPILERS MAY NOT ALLOW IF-THEN-ELSE, DO CASE, WHILE,
                        EXECUTE, REMOTE BLOCK OR AT END STATEMENTS
57                TOP=NSPES1
58              ELSE DO
59                TOP=(NSPES1+LIM-1)/LIM*(LO+1)
60              END IF
61              HEAD=' '
62        20  CONTINUE
                C
```

```
      10  FORMAT('1'//1X,A40//4X,30I4)
      40  FORMAT(' ',I3,30I4)
C
C  OUTPUT CHI-SQUARE VALUES
C
          HEAD='CHI-SQUARE VALUES'
          LIM=(NSPES1+15)/16
          TOP=(NSPES1+LIM-1)/LIM
          BOT=1
          DO 30 LO=1,LIM
            WRITE(6,22)HEAD,(I,I=BOT,TOP)
            PRINT,' '
            DO 60 J=1,NSPES2
              WRITE(6,70)J,(CHISQU(I,J),I=BOT,TOP)
      60    CONTINUE
            BOT=TOP+1
            IF(LO+1.EQ.LIM)THEN DO
*EXTENSION*   OTHER COMPILERS MAY NOT ALLOW IF-THEN-ELSE, DO CASE, WHILE,
                    EXECUTE, REMOTE BLOCK OR AT END STATEMENTS
              TOP=NSPES1
            ELSE DO
              TOP=(NSPES1+LIM-1)/LIM*(LO+1)
            END IF
            HEAD=' '
      30  CONTINUE
C
      70  FORMAT(' ',I3,16F8.2)
      22  FORMAT('1'//1X,A40//4X,16I8)
          GO TO 100
      99  PRINT ,'**ERROR** ON INPUT'
     100  CONTINUE
          STOP
          END
```