THE EFFECTS OF INTRODUCED RAINBOW SMELT (*OSMERUS MORDAX*) ON THE INDIGENOUS PELAGIC FISH COMMUNITY OF AN OLIGOTROPHIC LAKE

by

Duncan B. Wain

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Theology 0469

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- Archaeology 0324
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- General 0310
- Accounting 0272
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Canadian Studies 0385
Economics
- General 0501
- Agricultural 0503
- Commerce-Business 0505
- Finance 0508
- History 0509
- Labor 0510
- Theory 0511

Folklore 0358
Geography 0366
Gerontology 0351
History
- General 0578
- Ancient 0579
- Medieval 0581
- Modern 0582
- Black 0328
- African 0331
- Asia, Australia and Oceania 0332
- Canadian 0334
- European 0335
- Latin American 0336
- Middle Eastern 0333
- United States 0337

History of Science 0585
Law 0398
Political Science
- General 0615
- International Law and Relations 0616
- Public Administration 0617

Recreation 0814
Social Work 0452
Sociology
- General 0626
- Criminology and Penology 0627
- Demography 0938
- Ethnic and Racial Studies 0631
- Individual and Family Studies 0628
- Industrial and Labor Relations 0629
- Public and Social Welfare 0630
- Social Structure and Development 0700
- Theory and Methods 0344

Transportation 0709
Urban and Regional Planning 0999
Women's Studies 0453

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BIOLOGICAL SCIENCES
Agriculture
- General 0473
- Agronomy 0285
- Animal Culture and Nutrition 0475
- Animal Pathology 0476
- Food Science and Technology 0359
- Forestry and Wildlife 0478
- Plant Culture 0479
- Plant Pathology 0480
- Plant Physiology 0817
- Range Management 0777
- Wood Technology 0746

Biology
- General 0306
- Anatomy 0287
- Biostatistics 0308
- Botany 0309
- Cell 0379
- Ecology 0329
- Entomology 0353
- Genetics 0369
- Limnology 0793
- Microbiology 0410
- Molecular 0307
- Neuroscience 0317
- Oceanography 0416
- Physiology 0433
- Radiation 0821
- Veterinary Science 0778
- Zoology 0472

Biophysics
- General 0786
- Medical 0760

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Biogeochemistry 0425
Geochemistry 0996
Geodesy 0370
Geology 0372
Geophysics 0373
Hydrology 0388
Mineralogy 0411
Paleobotany 0345
Paleoecology 0426
Paleontology 0418
Paleozoology 0985
Palynology 0427
Physical Geography 0368
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Environmental Sciences 0768
Health Sciences
- General 0566
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- Chemotherapy 0992
- Dentistry 0567
- Education 0350
- Hospital Management 0769
- Human Development 0758
- Immunology 0982
- Medicine and Surgery 0564
- Mental Health 0347
- Nursing 0569
- Nutrition 0570
- Obstetrics and Gynecology 0380
- Occupational Health and Therapy 0354
- Ophthalmology 0381
- Pathology 0571
- Pharmacology 0419
- Pharmacy 0572
- Physical Therapy 0382
- Public Health 0573
- Radiology 0574
- Recreation 0575
- Speech Pathology 0460
- Toxicology 0383

Home Economics 0386

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Pure Sciences

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- General 0485
- Agricultural 0749
- Analytical 0486
- Biochemistry 0487
- Inorganic 0488
- Nuclear 0738
- Organic 0490
- Pharmaceutical 0491
- Physical 0494
- Polymer 0495
- Radiation 0754

Mathematics 0405
Physics
- General 0605
- Acoustics 0986
- Astronomy and Astrophysics 0606
- Atmospheric Science 0608
- Atomic 0748
- Electronics and Electricity 0607
- Elementary Particles and High Energy 0798
- Fluid and Plasma 0759
- Molecular 0609
- Nuclear 0610
- Optics 0752
- Radiation 0756
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Statistics 0463

Applied Sciences

Applied Mechanics 0346
Computer Science 0984

Engineering
- General 0537
- Aerospace 0538
- Agricultural 0539
- Automotive 0540
- Biomedical 0541
- Chemical 0542
- Civil 0543
- Electronics and Electrical 0544
- Heat and Thermodynamics 0348
- Hydraulic 0545
- Industrial 0546
- Marine 0547
- Materials Science 0794
- Mechanical 0548
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Geotechnology 0428
Operations Research 0796
Plastics Technology 0795
Textile Technology 0994

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General 0621
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  - Anciennes 0294
  - Comparée 0295
  - Mediévale 0297
  - Moderne 0298
  - Africaine 0316
  - Américaine 0591
  - Anglaise 0593
  - Asiatique 0305
  - Canadienne (Anglaise) 0352
  - Canadienne (Française) 0355
  - Germanique 0311
  - Latino-américaine 0312
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  - Physique 0327
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  - Commerce-Affaires 0505
  - Économie agricole 0503
  - Économie du travail 0510
  - Finances 0508
  - Histoire 0509
  - Théorie 0511
- Études américaines 0323
- Études canadiennes 0385
- Études féministes 0453
- Folklore 0358
- Géographie 0366
- Gérontologie 0351
- Gestion des affaires
  - Généralités 0310
  - Administration 0454
  - Banques 0770
  - Comptabilité 0272
  - Marketing 0338
- Histoire
  - Histoire générale 0578
  - Ancienne 0579
  - Médiévale 0581
  - Moderne 0582
  - Histoire des noirs 0328
  - Africaine 0331
  - Canadienne 0334
  - États-Unis 0337
  - Européenne 0335
  - Moyen-orientale 0333
  - Latino-américaine 0336
  - Asie, Australie et Océanie 0332
- Histoire des sciences 0585
- Loisirs 0814
- Planification urbaine et régionale 0999
- Science politique
  - Généralités 0615
  - Administration publique 0617
  - Droit et relations internationales 0616
- Sociologie
  - Généralités 0626
  - Aide et bien-àtre social 0630
  - Criminologie et établissements pénitentiaires 0627
  - Démographie 0938
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- Transports 0709
- Travail social 0452

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  - Physiologie végétale 0817
  - Sylviculture et faune 0478
  - Technologie du bois 0746
- Biologie
  - Généralités 0306
  - Anatomie 0287
  - Biologie (Statistiques) 0308
  - Biologie moléculaire 0307
  - Botanique 0309
  - Cellule 0379
  - Écologie 0329
  - Entomologie 0353
  - Génétique 0369
  - Limnologie 0793
  - Microbiologie 0410
  - Neurologie 0317
  - Océanographie 0416
  - Physiologie 0433
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  - Zoologie 0472
- Biophysique
  - Généralités 0786
  - Medicale 0760

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- Géochimie 0996
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- Géographie physique 0368
- Géologie 0372
- Géophysique 0373
- Hydrologie 0388
- Minéralogie 0411
- Océanographie physique 0415
- Paléobotanique 0345
- Paléoécologie 0426
- Paléontologie 0418
- Paléozoologie 0985
- Palynologie 0427

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- Sciences de l'environnement 0768
- Sciences de la santé
  - Généralités 0566
  - Administration des hipitaux 0769
  - Alimentation et nutrition 0570
  - Audiologie 0300
  - Chimiothérapie 0992
  - Dentisterie 0567
  - Développement humain 0758
  - Enseignement 0350
  - Immunologie 0982
  - Loisirs 0575
  - Médecine du travail et thérapie 0354
  - Médecine et chirurgie 0564
  - Obstétrique et gynécologie 0380
  - Ophtalmologie 0381
  - Orthophonie 0460
  - Pathologie 0571
  - Pharmacie 0572
  - Pharmacologie 0419
  - Physiothérapie 0382
  - Radiologie 0574
  - Santé mentale 0347
  - Santé publique 0573
  - Soins infirmiers 0569
  - Toxicologie 0383

SCIENCES PHYSIQUES

Sciences Pures

- Chimie
  - Généralités 0485
  - Biochimie 487
  - Chimie agricole 0749
  - Chimie analytique 0486
  - Chimie minérale 0488
  - Chimie nucléaire 0738
  - Chimie organique 0490
  - Chimie pharmaceutique 0491
  - Physique 0494
  - PolymÇres 0495
  - Radiation 0754
- Mathématiques 0405
- Physique
  - Généralités 0605
  - Acoustique 0986
  - Astronomie et astrophysique 0606
  - Electronique et électricité 0607
  - Fluides et plasma 0759
  - Météorologie 0608
  - Optique 0752
  - Particules (Physique nucléaire) 0798
  - Physique atomique 0748
  - Physique de l'état solide 0611
  - Physique moléculaire 0609
  - Physique nucléaire 0610
  - Radiation 0756
- Statistiques 0463

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- Informatique 0984
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  - Agricole 0539
  - Automobile 0540
  - Biomédicale 0541
  - Chaleur et ther modynamique 0348
  - Conditionnement (Emballage) 0549
  - Génie aérospatial 0538
  - Génie chimique 0542
  - Génie civil 0543
  - Génie électronique et électrique 0544
  - Génie industriel 0546
  - Génie mécanique 0548
  - Génie nucléaire 0552
  - Ingénierie des systàmes 0790
  - Mécanique navale 0547
  - Métallurgie 0743
  - Science des matériaux 0794
  - Technique du pétrole 0765
  - Technique minière 0551
  - Techniques sanitaires et municipales 0554
  - Technologie hydraulique 0545
- Mécanique appliquée 0346
- Géotechnologie 0428
- Matières plastiques (Technologie) 0795
- Recherche opérationnelle 0796
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PSYCHOLOGIE

- Généralités 0621
- Personnalité 0625
- Psychobiologie 0349
- Psychologie clinique 0622
- Psychologie du comportement 0384
- Psychologie du développement 0620
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- Psychologie industrielle 0624
- Psychologie physiologique 0989
- Psychologie sociale 0451
- Psychométrie 0632

THE EFFECTS OF INTRODUCED RAINBOW SMELT (<u>Osmerus mordax</u>) ON THE INDIGENOUS PELAGIC FISH COMMUNITY OF AN OLIGOTROPHIC LAKE

BY

DUNCAN B. WAIN

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

MASTER OF SCIENCE

ABSTRACT

Wain, D.B. 1993. The effects of introduced rainbow smelt (*Osmerus mordax*) on the indigenous pelagic fish community of an oligotrophic lake.

The effects of introduced rainbow smelt on the pelagic fish community of an oligotrophic lake were investigated. Population characteristics, niche dimensions and niche overlap of cisco (*Coregonus artedi*), lake whitefish (*C. clupeaformis*), yellow perch (*Perca flavescens*), emerald shiner (*Notropis atherinoides*) and spottail shiner (*Notropis hudsonius*) were compared between Sandybeach Lake which contained rainbow smelt and Little Vermilion Lake which did not contain rainbow smelt. Fish distributions for the period of dusk to dawn during summer stratification were determined using replicated sets of deep pelagic gill nets and overlaps in habitat utilization were assessed. Stomach contents of preserved fish were examined to determine the extent of overlap in diet between species and size-classes. Population characteristics (abundance, size-class distributions, relative condition and recruitment) were compared between native species in sympatry and allopatry with rainbow smelt. Cisco abundance, recruitment, condition, sex ratio and habitat utilization decreased or were negatively affected in response to the presence of very abundant rainbow smelt in Sandybeach Lake. The overlap in habitat and diet between juvenile cisco in allopatry with rainbow smelt, combined with the selective and efficient feeding strategies of rainbow smelt have resulted in rainbow smelt dominance in the sympatric environment. Similarly the low habitat niche breadth and the high overlap in primary habitat utilization of juvenile lake whitefish in allopatry with rainbow smelt corresponds with the disappearance of juvenile lake whitefish in the sympatric environment. Yellow perch in the allopatric environment were the most abundant species in the epilimnion, however in the sympatric community yellow perch apparently were forced into the littoral zone by the abundant rainbow smelt in the epilimnetic zone. Emerald and spottail shiner were unaffected by the presence of rainbow smelt, probably due to specialization and low overlap in habitat and diet.

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Finally, I wish to acknowledge the support received from my family, friends and fellow students at the Department of Zoology and at the Natural Resources Institute during the course of this study.

TABLE OF CONTENTS

LIST OF TABLES

Table

LIST OF FIGURES

Figure

FORWARD

In 1989 and 1990 a study was undertaken to determine the extent of the distribution of rainbow smelt in the area draining into Hudson Bay, specifically those areas in northwestern Ontario draining into Hudson Bay via the Winnipeg river. Results of this study and a discussion on the potential consequences of further spread can be found in a paper titled "Present distribution and potential for dispersal of rainbow smelt in North Dakota and in Hudson Bay drainage waters of northwestern Ontario and Minnesota" by Franzin et al. (1990) and in a Master of Natural Resource Management practicum entitled "An assessment of the potential impact of the rainbow smelt on the fishery resources of Lake Winnipeg" by Richard A. Remnant (1991). Observational data obtained from that study provided the null hypotheses that were the basis for this thesis. These null hypotheses were:

H_0: Rainbow smelt do not prey on larval cisco and lake whitefish.

H_0: Rainbow smelt do not overlap significantly with cisco or lake whitefish in diet or habitat utilization.

H_0: Population parameters of indigenous pelagic species are not affected by the presence of rainbow smelt (i.e. condition, size, sex and age-class structure and relative recruitment).

INTRODUCTION

Rainbow smelt (*Osmerus mordax*) have dispersed or have been introduced widely throughout North America since their initial introduction in Crystal Lake, Michigan in 1912. Interactions of introduced rainbow smelt with native species have ranged from beneficial, such as increased growth rates of predators (Evans and Loftus 1987), to highly detrimental, including extirpation of native species (Christie 1974). Negative interactions of native fishes with rainbow smelt have occurred most frequently with coregonid species, particularly cisco (*Coregonus artedi*) and lake whitefish (*C. clupeaformis*). The high correlation between declines of cisco and lake whitefish following introduction or invasion of rainbow smelt often has been confounded by environmental or manmade disturbances, such as eutrophication, introductions of other non-native species or excessive exploitation (Christie 1972; 1974). Nevertheless, because of the similarity in niche between rainbow smelt and coregonids, several authors have suggested that predation by rainbow smelt on coregonid larvae or competition for food and space has played an important role in the coregonid declines (Anderson and Smith 1971a; Crowder 1980; Evans and Waring 1987).

The results of studies on the decline of cisco and lake whitefish which have focused on predation by rainbow smelt as the most important mechanism generally have been inconclusive or only relevant to specific environmental conditions. Anderson and Smith (1971a) found that rainbow smelt consumed up to 17% of cisco larvae produced in Nipigon Bay, Lake Superior where cisco recruitment was good, but none at all in the Apostle Islands area where cisco recruitment was poor. They concluded from these results that predation was not an important factor in cisco abundance. Similarly, Selgeby et al. (1978) reported that when local populations of rainbow smelt and cisco larvae were in close contact in Lake Superior the rainbow smelt preyed upon cisco larvae, but when densities of each species were lower and contact less direct, no cisco larvae were found in rainbow smelt stomachs. Loftus and Hulsman (1986) found that rainbow smelt consumed large numbers of cisco and lake whitefish larvae in Twelve Mile Lake, Ontario in early spring. They concluded that predation by rainbow smelt may inflict serious damage on coregonid populations in small lakes where there is a high degree of spatial overlap between species. Predation, however, does not explain how rainbow smelt can establish themselves, expand in population and exclude other species from preferred habitat.

Menge and Sutherland (1976) suggested that competition, not predation, is the most important organizing factor in communities with few trophic levels, such as the pelagic fish community of an oligotrophic lake. Competition between rainbow smelt and native coregonids and other species has been implicated but not well researched. Most studies focusing on the interaction between cisco, lake whitefish and rainbow smelt have relied on circumstantial or correlative evidence whereby population data on each species have been compared from year to year. Evans and Waring (1987) inferred competition between rainbow smelt and lake whitefish in Lake Simcoe by the decline of lake whitefish during high rainbow smelt abundance. Similarly Evans and Loftus (1987) suggested that the negative correlation between the abundance of cisco and lake whitefish with rainbow smelt abundance, combined with the similar niche requirements of each species, implied competition. Crowder et al. (1981) examined overlap in habitat and diet among rainbow smelt, alewife (*Alosa pseudoharengus*), yellow perch (*Perca flavescens*), troutperch (*Percopsis omiscomaycus*) and spottail shiner (*Notropis hudsonius*) in Lake Michigan using bottom trawling techniques. They found that overlap between species along one resource gradient often would be high but would be low on a second resource gradient thus allowing for coexistence without competition. It was suggested by Crowder et al. (1981) that the disappearance of native cisco and emerald shiner (*Notropis atherinoides*) probably was due to high overlap along both resource gradients (habitat and diet) with introduced rainbow smelt and alewife respectively.

This thesis is an examination of the niche relationships between indigenous species in allopatry (not occurring together) and in sympatry (occurring together) with rainbow smelt in the pelagic fish communities of two oligotrophic lakes to determine the extent of competition along the resource gradients of diet and habitat. Because of the piscivorous nature of rainbow smelt, an attempt was made to determine if predation by rainbow smelt on indigenous fishes was a factor in native fish recruitment. Ideally a study examining the effects of an introduced species (or any other manipulation) on a community would involve replicated experimental and control ecosystems. For obvious economic, political and ethical reasons such studies are not feasible nor desirable. In this study the most feasible option was to compare a lake already undergoing the effects of an introduction with an undisturbed lake with similar physical and biological characteristics within the same region to maximize correlation (Carpenter 1989). In such an unreplicated ecosystem study, the determination of causality rests on ecological as opposed to statistical arguments (Hurlbert 1984).

In this study niche overlap was examined along the resource gradients of diet and habitat during mid-summer stratification. For pelagic species summer stratification provides habitat diversity based upon temperature and oxygen in addition to factors such as light and proximity to the surface or bottom which are common factors at all times of the year. The habitat delineations created by summer stratification reveal patterns of utilization by the various pelagic species, and provide a basis of comparison between sympatric and allopatric environments. These comparisons focused on changes in abundance, size, age and sex class structure, habitat and diet preferences and niche dimensions, as well as intraspecific and interspecific niche relations.

STUDY AREA

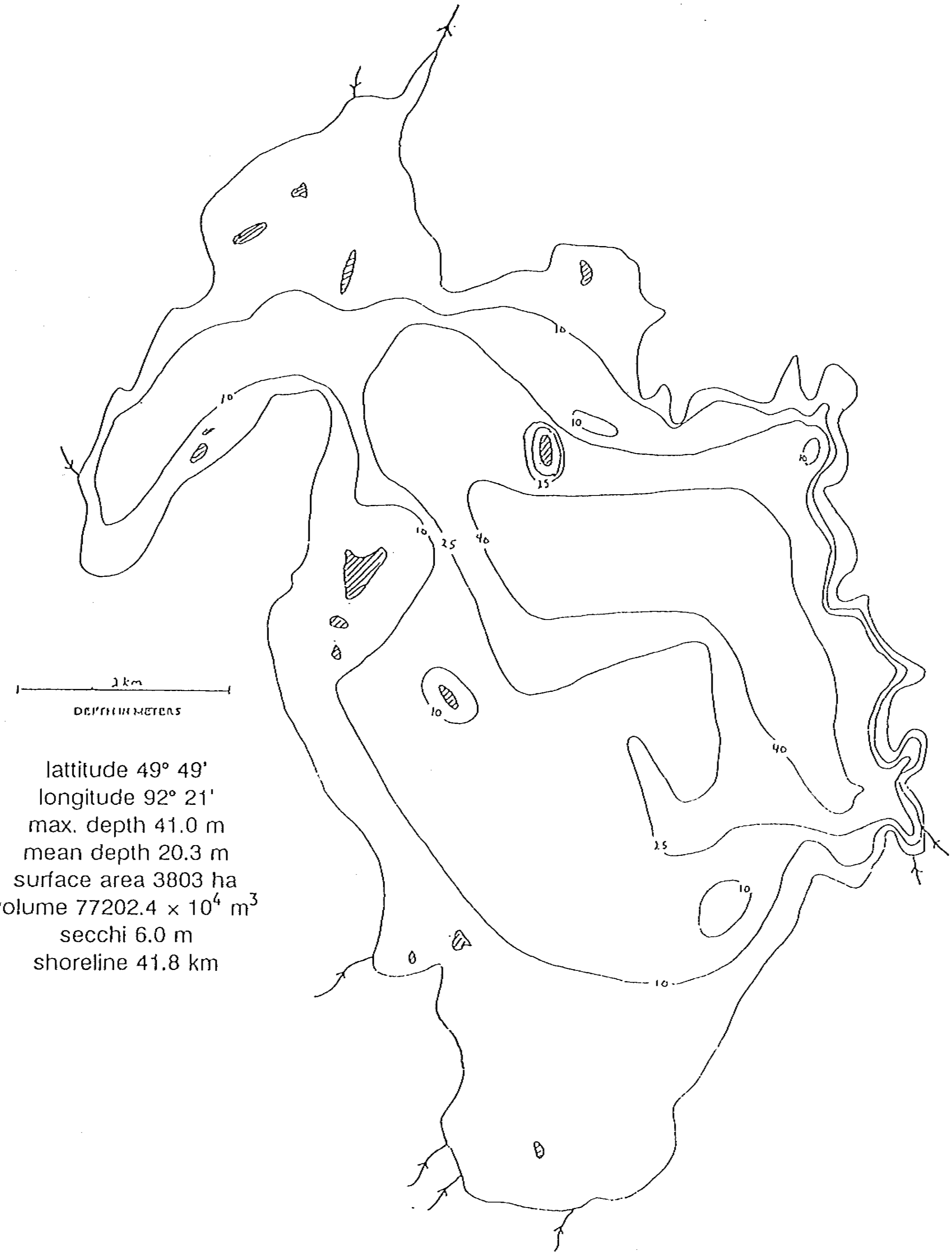
Sandybeach Lake (Fig. 1) and Little Vermilion Lake (Fig. 2), two oligotrophic lakes located within the English river drainage of northwestern Ontario, were examined in this study (Fig. 3). Both lakes are in headwaters and have similar fish species composition (Table 1) except that Sandybeach Lake contains introduced rainbow smelt. Species of the pelagic community of both lakes include cisco, lake whitefish, lake trout, yellow perch, emerald shiner, and spottail shiner.

METHODS AND MATERIALS

Spring Sampling

The purpose of spring sampling was to determine if rainbow smelt were preying upon juvenile or young-of-the-year coregonids and other pelagic species, and to examine the extent of habitat and diet overlap within Sandybeach Lake. In addition, population characteristics of cisco taken in the spring from Sandybeach and Little Vermilion lakes were compared.

Distributions of fishes were determined for the period from dusk to dawn (a 9-11 h period) immediately after ice-out for four sampling sites in Sandybeach Lake (6.1-, 11.4-, 22-, and 37.5-m depths). Sampling was accomplished using 5.2-m deep pelagic horizontal gill nets consisting of 6-m panels of 6.25-, 8-, 10-, 12.5- and 16-mm mesh; bar measure suspended at one level (0.9-m) at the 6.1-m deep site, two levels (0.9- and 6.1-m) at the 11.3-m deep site, four levels (0.9-, 6.1-, 11.3-, and 16.5-m) at the 22-m deep site and seven levels (0.9-, 6.1-, 11.3-, 16.5-, 21.7-, 26.9- and 32.1-m) at the 37.5-m deep site (Fig. 4). Because only two 5.2-m gangs were available during the spring sampling period the sets at each depth and site were randomized over the duration of the sampling period from May 15-25, 1990.



lattitude 49° 49'
longitude 92° 21'
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mean depth 20.3 m
surface area 3803 ha
volume 77202.4 × 10^4 m^3
secchi 6.0 m
shoreline 41.8 km

Fig. 1. Bathymetric map of Sandybeach Lake, Ontario

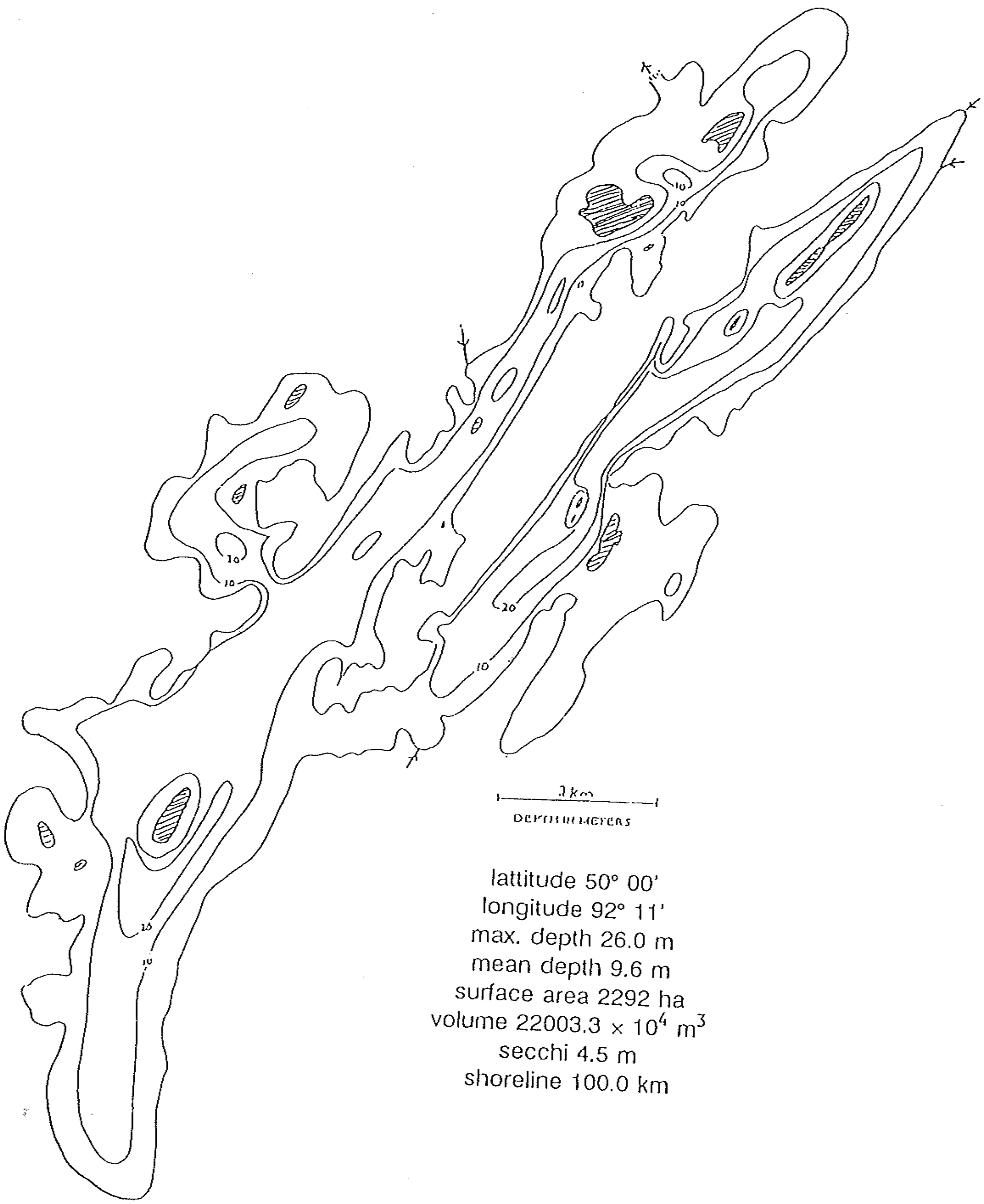


Fig. 2. Bathymetric map of Little Vermilion Lake, Ontario.

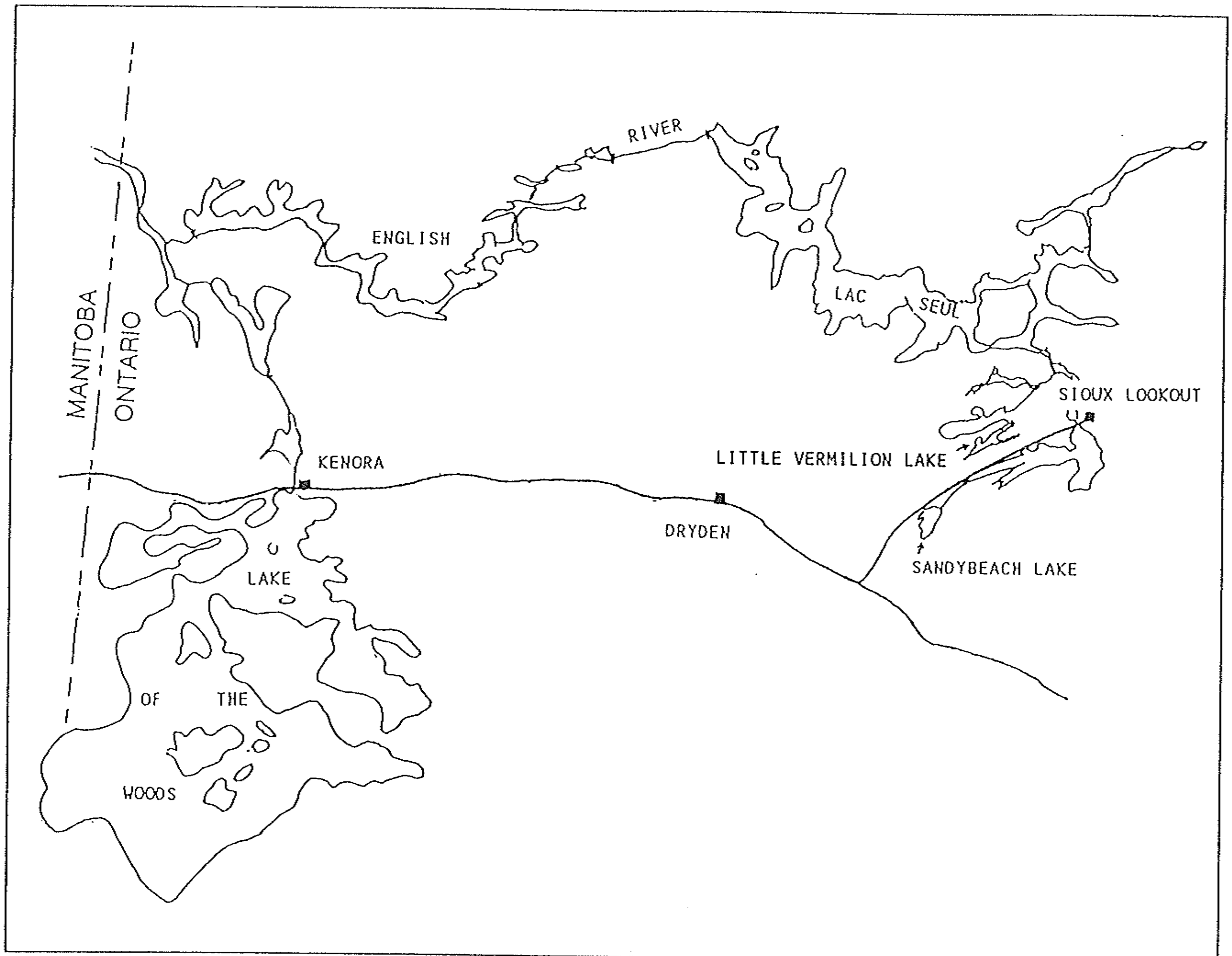


Fig. 3. Location of Sandybeach and Little Vermilion Lakes within Northwestern Ontario.

TABLE 1. Fish species composition of Sandybeach and Little Vermilion Lakes as determined by OMNR surveys and this study. A=Abundant, B=Common, C=Occasional, D=Rare, O=Absent or unknown.

Fish species	Common name	Sandybeach Lake	Little Vermilion Lake
Ambloplites rupestris	rock bass	C	C
Catostomus commersoni	white sucker	A	A
Coregonus artedi	cisco	A	A
Coregonus clupeaformis	lake whitefish	A	A
Coregonus zenithicus	shortjaw cisco	D	O
Cottus bairdi	mottled sculpin	B	B
Cottus cognatus	slimy sculpin	C	C
Esox lucius	northern pike	B	C
Esox masquinongy	muskellunge	D	C
Etheostoma exile	Iowa darter	C	C
Etheostoma nigrum	johnny darter	A	A
Lota lota	burbot	A	A
Luxilis cornutus	common shiner	B	B
Micropterus doloieui	smallmouth bass	C	B
Moxistoma anisurum	silver redhorse	C	O
Myoxocephalus thompsoni	deepwater sculpin	D	D
Notropis atherinoides	emerald shiner	A	A
Notropis heterolepis	blacknose shiner	B	B
Notropis hudsonius	spottail shiner	A	A
Osmerus mordax	rainbow smelt	A	O
Perca flavescens	yellow perch	A	A
Percopsis omiscomaycus	troutperch	A	A
Pungitius pungitius	nine-spine stickleback	A	A
Salvelinus namaycush	lake trout	B	B
Semotilus atromaculatus	creek chub	C	B
Stizostedion vitreum	walleye	D	D

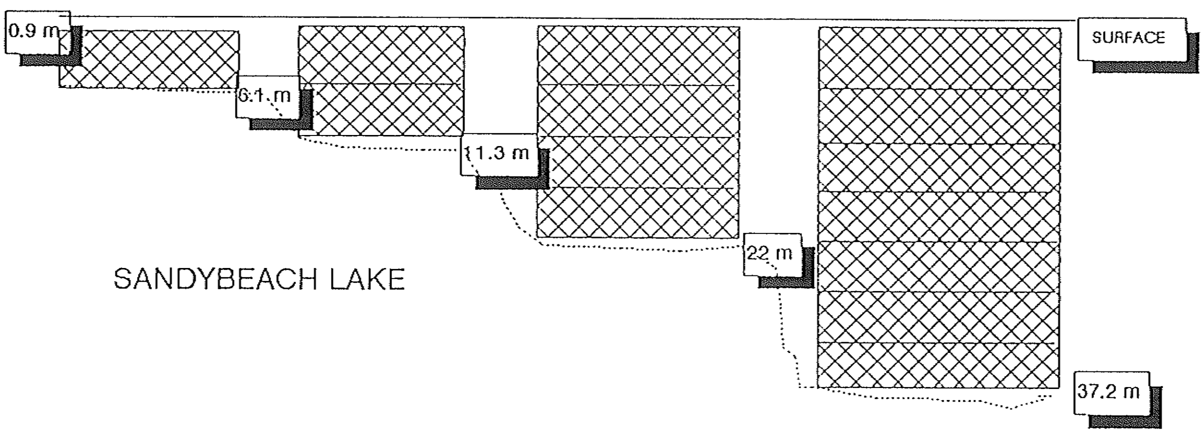


Fig. 4. Deep pelagic gill net sets as related to depth and site in Sandybeach Lake in May 1990.

In addition, two longer duration sets, an 18 h set on May 22 and a 24 h set on May 24, 1990, were made with 1.8-m deep gill nets consisting of 2 gangs of 25-m panels of 8, 10, and 13 mm mesh; bar measure, bottom set at 10 to 25-m depth to capture additional specimens for diet and population parameter analysis. These two gangs also were set in Little Vermilion Lake overnight (12 h) on May 25, 1990 to acquire specimens from that lake for population parameter analysis.

Summer Sampling

The purpose of summer sampling was to determine the utilization patterns of each of the pelagic species within the two lakes for the different habitats created within the water column during summer stratification, and to examine overlap in resource use among species and size-classes of species between and within the two lakes. Preference for dietary items and overlap among species and size-classes of species between and within the two lakes also were determined as well as comparisons of population parameters of key pelagic species between the two lakes.

Distributions of fishes were determined for the 8 h period from dusk to dawn during summer stratification for three sites in Sandybeach Lake (11.4-, 22-, and 37.5-m) and one site in Little Vermilion Lake (22-m). Sampling was accomplished using 5.2-m deep pelagic gill nets (mesh and panels as previously described) suspended at one level (32.1-m) at the 37.5-m deep site, at two levels (0.9- and 6.1-m) at the 11.3-m deep site, and four levels (0.9-, 6.1-, 11.3-, and 16.5-m) at the 22-m deep sites (Fig. 5). Sites and depths were chosen to sample as much of the different pelagic habitats as possible while optimizing effort. Note that the stratum from the surface to 0.9 m depth was not sampled using gill nets to provide for clearance for power boat users.

The 22-m site in Sandybeach Lake was chosen as the basis for distributions

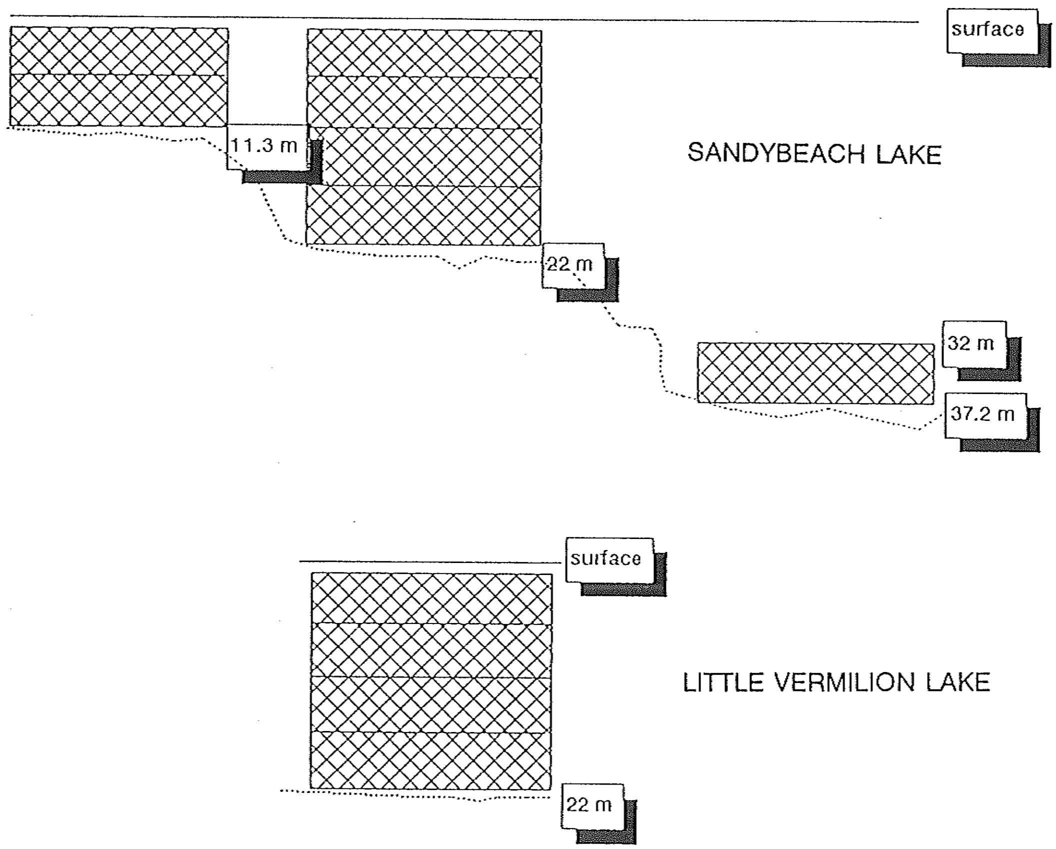


Fig. 5. Deep pelagic gill net sets as related to depth and site in Sandybeach and Little Vermilion Lakes in July 1990.

because it contained all of the stratified layers (i.e. epilimnion to hypolimnion) and these depth strata were available habitat within 75% of the area of the lake. Depths from 22-m to 37.5-m made up less than 10% of the area of the lake, however below 30-m there was a layer of cold water less than 8°C that was not available to be sampled at the 22-m deep site. In addition evening and night observations on a Micronar M-700 video echo-sounder suggested that there was a concentration of fish associated with the bottom at 37.5-m; therefore, the layer from 32.1 to 37.3-m was sampled as an additional pelagic habitat. The layer of water between 22-m and 32.1-m was not sampled because little additional data would have been collected for the effort. Temperatures and fish distributions observed on an echo-sounder in this layer did not differ from those observed within the hypolimnion at the 22-m deep site.

The 11.3-m deep site was chosen to ascertain the effects of the bottom or proximity to shallow water fishes (such as northern pike) on fish distributions by comparing with the top 11.3-m layer in the 22-m site. The 22-m site in Little Vermilion Lake covered all of the available layers within this lake (i.e. the maximum depth of Little Vermilion Lake is 25-m). A shallow site was not utilized in Little Vermilion Lake because the distributions of fishes in Sandybeach Lake did not differ between the 11.3-m site and the top 11.3-m of water at the 22-m site ($p > 0.5$).

Sets were replicated 6 times (Craig et al. 1986) for a total of 48 h of netting effort at each site at all depths. Because only three 5.2-m deep pelagic gill nets were available during the summer sampling period, sets were replicated systematically over the period of July 9-23, 1990 in Sandybeach Lake and July 24-31, 1990 in Little Vermilion Lake (Appendix 1). Weather and the depth of the thermocline were consistent over the entire sampling period in Sandybeach and Little Vermilion lakes (Appendix 2).

Additional overnight (12 h) bottom sets were made with 1.8-m deep nets in

Sandybeach Lake to acquire specimens (primarily cisco and lake whitefish) for analysis of population characteristics (i.e. age, size and sex-class structure) during different nights of the summer sampling period (Table 2). In addition 2 h sets were made with these 1.8-m deep nets to acquire fresh specimens for stomach content analysis. Overnight sets of 1.8-m gill nets were also utilized in Sandybeach Lake in 1991 to confirm size distributions of cisco and lake whitefish catches from 1990.

In Little Vermilion Lake in July 1990 an overnight set of these 1.8-m deep gill nets was used to ascertain whether juvenile whitefish were utilizing the bottom or shallow water habitats.

A seine haul was conducted on a sandy beach in less than one meter of water using a 3-m seine with 3 mm oval mesh at 2130 hrs on July 20, 1990 in Sandybeach Lake to acquire young-of-the-year rainbow smelt.

Fish sampling techniques

Fish caught in the 5.2-m deep pelagic gill nets were enumerated based on mesh size as well as being in one of four horizontal panel divisions within each net to assist in identifying the depth at which they were caught. All rainbow smelt, cisco and lake whitefish caught during the spring sampling period were retained, labelled to indicate in what mesh and depth they were captured, and preserved in a 10% formalin solution. All fish from at least three replicates of the summer sampling period were labelled and preserved; additional specimens were sub-sampled from large catches (in the case of rainbow smelt in Sandybeach Lake and cisco and yellow perch from Little Vermilion Lake) with infrequently caught sizes or species being retained. Catches of species in 1.8 m deep nets set in shallow water in Sandybeach Lake other than rainbow smelt, cisco or lake whitefish were not retained due to the limited scope of the study at the time. As such there are no data other than habitat utilization for yellow perch from Sandybeach Lake.

TABLE 2. Sampling regime using 1.8-m deep gill nets in Sandybeach and Little Vermilion Lake in July 1990 and June 1991.

lake	date	# of hrs set	panel range (mm)	# of panels	depth of set (m)	type of set
SBL	90/07/10	12	6.25 - 16	8	25	bottom
SBL	90/07/11	2	6.25 - 16	5	8 - 25	bottom
SBL	90/07/13	2	6.25 - 16	5	25 - 32	bottom
SBL	90/07/14	2	6.25 - 16	5	6 - 18	bottom
SBL	90/07/15	12	6.25 - 16	5	13 - 28	bottom
SBL	90/07/16	12	6.25 - 16	5	2 - 9	bottom
SBL	90/07/18	12	6.25 - 127	10	35 - 40	bottom
LVL	90/07/27	12	6.25 - 16	4	3 - 19	bottom
SBL	91/06/18	12	8 - 13	6	10 / 22	suspended
SBL	91/06/18	12	6.25 - 16	8	22	bottom

Preserved fish were transferred to 70% ethanol after one month. Fork lengths of preserved fish were measured to the nearest millimetre. Fresh specimens of rainbow smelt and cisco were measured for total and fork lengths and total, standard and fork lengths respectively before and after preservation to provide fresh versus preserved length ratios (Appendix 3). Weight was measured to the nearest 0.1 gram on a Mettler PJ4000 balance. The sex of mature cisco, lake whitefish, emerald and spottail shiner and mature spring caught rainbow smelt was determined by gross examination of gonads. Rainbow smelt caught in summer could not be sexed consistently. Some specimens of cisco from Sandybeach Lake were noted to have atypical morphological characteristics e.g. they had subterminal mouths, larger eye diameters and greater head to body length ratios than the typical ciscoes captured. Total gillraker counts on the first gill arch were taken from selected cisco from Sandybeach Lake that had the lower jaw included in the upper jaw (subterminal mouth). Counts were also done on a similar number of cisco with typical *C. artedi* characteristics (terminal mouth) from Sandybeach and Little Vermilion lakes. Total gillraker counts of cisco from Sandybeach Lake with the lower jaw included in the upper ranged from 35 to 40 with a mean of 37.1. This indicated that there was a sympatric population of shortjaw cisco (*Coregonus zenithicus*) coexisting with typical cisco in Sandybeach Lake (Clarke 1973; Scott and Crossman 1973; Becker 1983). Cisco exhibiting typical *C. artedi* characteristics in Sandybeach and Little Vermilion lakes had mean total gillraker counts of 41.6 and 42.2 respectively (Table 3) which were not significantly different from each other but were significantly different from shortjaw cisco ($p < 0.0001$) found in Sandybeach Lake. Shortjaw cisco made up 8.2% of the total catch of cisco in the deep pelagic nets (15 of 182 fish) in Sandybeach Lake and exhibited similar dietary preferences to that of typical cisco. Because this species was identified in the laboratory after other analyses were completed, any habitat preferences that may have been apparent could not be distinguished from those

TABLE 3. Counts of gillrakers on the first arch for cisco from Sandybeach and Little Vermilion lakes.

	Sandybeach cisco Subterminal mouth	Sandybeach cisco Terminal mouth	Little Vermilion cisco Terminal mouth
Mean	37.13	41.63	42.17
Std dev	1.55	1.89	1.53
Minimum	35	39	40
Maximum	40	46	45
Number	15	16	12

of typical cisco. Shortjaw cisco were therefore included with analyses for cisco taken from Sandybeach Lake in respect to diet and habitat utilization, however they were not included in ANCOVA comparisons of weight at length between cisco in each of Sandybeach and Little Vermilion Lakes.

Stomachs were removed from all preserved cisco and shortjaw cisco and lake whitefish, most yellow perch, emerald and spottail shiner, and a random selection of size ranges of rainbow smelt, particularly those with full stomachs. Stomach contents were removed from the oesophagus to the pyloric caeca in the case of cisco and shortjaw cisco, lake whitefish and rainbow smelt. Stomach contents in yellow perch, emerald and spottail shiner were removed from the oesophagus to the pyloric sphincter. Contents were distributed in a uniform layer in the bottom of a gridded 88 mm diameter petri dish and examined under a dissecting microscope. The occurrence of dietary items in fish stomachs was recorded and the volume percentage of dietary items within a stomach was determined by the points method of Hynes (1950). This was considered to be the most efficient method because of the small volumes being examined as well as the homogeneity of the contents of most stomachs. Only stomachs containing clearly definable contents were included in the results (this comprised over 95% of stomachs examined).

Scales and otoliths were removed from different size-classes of each species and placed in labelled scale envelopes. Rainbow smelt scales were removed immediately posterior to the dorsal fin and were examined under a drop of water at 100× magnification and aged according to the shiny scale method of McKenzie (1958) and Bailey (1964). Scale reading was deemed unreliable for cisco and shortjaw cisco taken from Sandybeach Lake in 1990 due to formalin deterioration. However scale ages were taken from a number of fresh cisco specimens captured in 1991 to corroborate age estimates based upon length-frequency. Age-classes of cisco from Little Vermilion Lake were discernable by length frequency distributions.

Zooplankton sampling

A Schindler (1969) plankton trap with a capacity of 28.7 litres was used to capture plankton at depths of 0.25-, 3.5-, and 8.5-m at the 11.3-m deep site, at 0.25-, 3.5-, 8.5-, 13.7- and 19-m at the 22-m deep site and 34.7-m at the 37.5-m deep site. Each haul was replicated twice (which were combined in the field for logistical reasons) with samples sieved through a 75 μm mesh and stored in a 5% formalin solution. Hauls were conducted approximately one half hour after dusk so as to capture plankton in habitat coincidentally with fish feeding activity (sonar observations of fish distributions during the late evening were consistent with gill net catches). Schindler trap hauls were conducted on July 13 and July 21 in Sandybeach Lake and July 27, 1990 in Little Vermilion Lake. Total counts of large (>1.5 mm body length minus setae) and small (1 to 1.5 mm body length minus setae) calanoid copepods, large (>1 mm body length minus setae) cyclopoid copepods, large (>1 mm head plus carapace length) and small (0.5 to 1 mm head plus carapace length) cladocerans were made of the two combined Schindler traps taken at each depth on the different dates. Species or groups were identified using the keys of Edmondson (1966).

Analyses

The extent of niche overlap can be determined by resource data; i.e. the amounts of total resources utilized by each species in each of a number of resource categories (Zaret and Rand 1971). Thus if there are n resource types, resource utilization by five species can be specified by a 5 by n matrix, whose entries p_{ij} represent the amount of resource j consumed or occupied by an individual of species *i* in some specified time period, or the proportion of total utilization by species *i* that is of type *j* (Abrahms 1980). In most studies the resource categories *n* are subdivided into smaller units of resource states which have ecologically equivalent degrees of distinctness (Slobodchikoff and Schulz 1980).

Habitat types in the pelagic zone are not readily observable in comparison to most other environments where there are usually visually distinctive differences. However there are physical and chemical differences within the water column that can influence the ecology of a fish species. These include temperature, oxygen, light, pH, total dissolved solids, turbidity, alkalinity and proximity to the surface or bottom. These in turn affect a fish species' physiology and its interaction with other species including competitors, predators and prey. In this study catches of pelagic fish species in the 5.2-m nets during the summer sampling period were tabulated as to being in one of nine habitat resource states (Fig. 6). These habitat states were determined by subjective interpretation based on known and observed ecoclines within the water column. These primarily were based on temperature and proximity to the surface or bottom. A further subdivision was created within temperature whereby proximity to a different zone was considered a separate habitat (i.e. an "edge").

Diet was divided into eleven resource states based on what was available in the environment and utilized by the fish examined. These were large calanoid copepods (primarily *Limnocalanus macrurus* and *Epischura lacustris*), small calanoid copepods, large cladocerans (*Daphnia longiremis*), small cladocerans, large cyclopoid copepods (*Cyclops vernalis*), amphipods (*Pontoporeia affinis*), chironimid larvae, *Mysis relicta*, insects other than chironimids (mostly *Hexagenia* sp. nymphs or adult dipterans), algae and fish. Note that all categories and identified genus or species were available and identified in both Sandybeach and Little Vermilion Lakes.

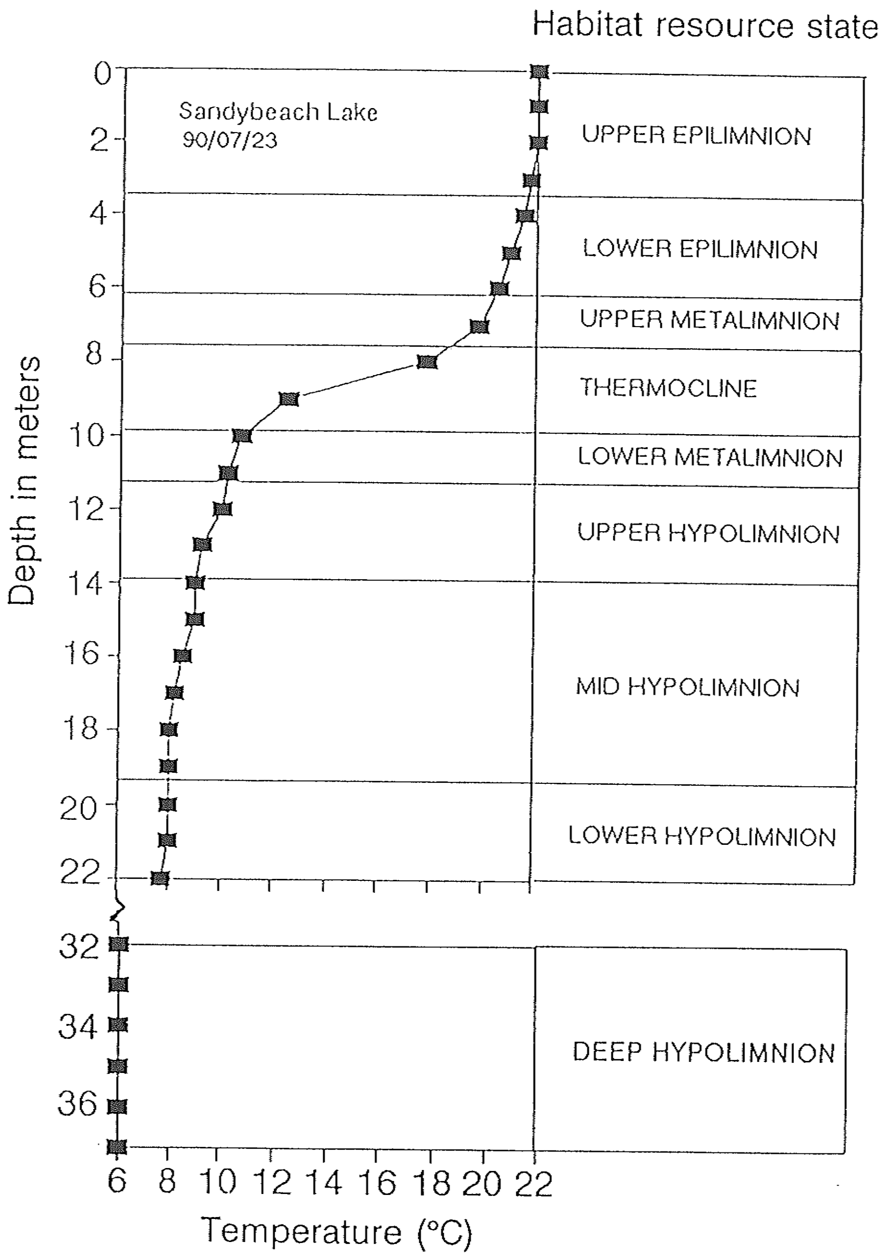


Fig. 6. Habitat resource states in relation to temperature profile of Sandybeach Lake on July 23, 1990.

Levins (1968) index was used to determine niche breadths (B_i) of habitat and diet for each species or size-class of fish. This index is taken as:

$$B_i = 1 / p_{ij}^2$$

where p_{ij} equals the proportion of the individuals of species i which is associated with resource state j. B_i is maximized when an equal number of individuals of species i are associated with each of the resource states. This implies that species i requires or prefers each resource state equally and thus has the broadest possible niche, with respect to those resource states. B_i is minimized when all individuals of species i are associated with one resource state.

Mohan and Sankaran's (1988) weighted resultant index (R_w) was used to determine the proportional importance of dietary items to each species or size-class of fish. This index incorporates both percentage volume and percentage occurrence into a formula and takes into account their relative significance. This index is taken as:

$$R_w = Q(v_i^2 + o_i^2)^{½} / \Sigma Q(v_i^2 + o_i^2)^{½} \times 100\%$$

where v_i is the percentage volume, o_i is the percentage occurrence. Since v_i and o_i can be considered as co-ordinates of a point in an X,Y plane, the line extending from this point to the origin would have both length and direction (Mohan and Sankaran 1988). Q is a weighting factor correcting for deviations of this line from the centre (ie $\theta = 45$). $Q = (45 - |\theta - 45|)/45$ where θ is the direction and is taken as $tan^{-1} (o_i / v_i)$.

Niche overlap between two species can be estimated by comparing the distribution of the individuals of the two species among the resource states of the matrix (Colwell and Futuyma 1971). If the distributions are identical, then the two niches overlap completely. If the two species share no resource states, then their niches do not overlap at all with respect to the resource states in the matrix. There are at least eight types of niche overlap indices that are in common use. These have been examined critically elsewhere (Hurlbert 1978; Abrahms 1980;

Slobodchikoff and Schulz 1980; Zaret and Smith 1982; Linton et al. 1989; Manly 1990). Hurlbert (1978) proposed a number of criteria which the ideal niche overlap index should contain. These criteria are:

[1] Easy to calculate.

[2] Free of assumptions about the nature of the competitive process if essentially nothing is known about it.

[3] Should facilitate inter-community comparisons.

[4] Should not be changed by the subdivision of resource states which are not distinguished by the competitors.

The only index to meet all of these criteria is the proportional similarity index of Schoener (1970). This index was used in this study to determine overlap of habitat and dietary item use between species and size-classes of fish between and within Sandybeach and Little Vermilion lakes. This index is taken as:

$$\alpha = 1 - 0.5(\Sigma\, p_{ij} - p_{ik}) \times 100\%$$

where p_{ij} is the proportional importance of item i to species j and p_{ik} is the proportional importance of item i to species k. Ross (1986) considered overlap values less than 40% to indicate substantially different resource utilization. In the present study values exceeding 50% were considered relevant in that this indicated overlap that could only be explained by resource partitioning on a second resource gradient (in the case of sympatric overlap), a non-limiting resource (in sympatric overlap), or implying previous competition for the resource(s) (in allopatric overlap). Also relevant are overlaps among species pairs or size-classes of the same species in allopatry where overlap in at least one resource does not exceed 50%. Such values imply substantially different resource utilization related to the degree of resource availability which may be due to different resource types or the intensity of competition for resources. Overlap values less than 50% among other species pairs or size-classes were not considered important in the context of this study unless they bore a relationship to the pairings described above. For community interactions, overlap values, niche breadth,, relative abundance, class structure, habitat and diet utilization were considered together to quantify relationships.

ANOVA procedures were performed on catch data using the $\log_{10}(1+x)$ transformation which adjusts for data with standard deviations greater than the mean. Regression analysis, ANOVA, ANCOVA and multiple comparison procedures and accompanying figures were conducted in SAS and SASGraph version 6.06. Additional graphics were prepared using Quattro Pro version 3.01.

RESULTS

Spring Sampling

Gill net sampling in Sandybeach Lake during May 1990 yielded 546 rainbow smelt, 132 yellow perch, 58 cisco, 41 spottail shiner, 28 troutperch, 17 emerald shiner, 12 nine-spine stickleback, 6 burbot, 6 white sucker, 3 lake trout, 3 mottled sculpin, 2 lake whitefish and 1 northern pike. The same gear yielded 57 cisco, 18 lake whitefish, 9 yellow perch, 6 nine-spine stickleback, 1 northern pike, 1 mottled sculpin and 1 deepwater sculpin from Little Vermilion Lake. Particulars for catches of fish in 1.8-m deep gill nets for each lake are provided in Appendix 4.

Rainbow smelt caught in the 5.2-m deep nets in overnight sets were primarily distributed in the top 11.3-m of water or associated with the bottom in most sites but were caught in significantly greater numbers in the shallow (6.1-m and 11.3-m) sites (Table 4) where surface temperatures were 9.5°C and 7°C respectively, compared to 5°C in the deeper sites. Rainbow smelt probably were present in these areas due to the warm inshore temperatures as opposed to spawning activity since the rainbow smelt examined were in a post-spawning condition and had full stomachs, indicating feeding activity. Too few cisco were captured to discern any distributional pattern. Yellow perch were caught only in the 6.1-m deep site, and all were males in ripe spawning condition.

Rainbow smelt

Rainbow smelt caught in the spring from Sandybeach Lake ranged in fork length from 66 to 135-mm but were comprised predominantly of two size-classes, with modes at 72-mm (range 66-80-mm) and 95-mm (range 82-110-mm) (Fig. 7). These size-classes corresponded roughly to the selectivity of the gill nets; the 6.25-

TABLE 4. Catch of fish in relation to depth in 5.2 m gill nets in May 1990 in Sandybeach Lake. Effort 10-11 h for all sets.

	37.5 m site		22 m site		11.3 m site		6.1 m site	
Depth	Smelt	Cisco	Smelt	Cisco	Smelt	Cisco	Smelt	Perch
0.9	11	1	1		15		39	
	12	2	4		2		47	
	1				7		26	
	2						44	128
6.1					14	1		
	1		1		11	1		
					13	1		
		1	1		61	1		
11.3	1							
	1							
	1							
	3		3					
16.5			1	1				
	1	3	3	1				
	2	2	6	1				
			24					
21.7	3	1						
		1						
	1							
26.1								
	1							
32.1	1							
37.3	3	1						

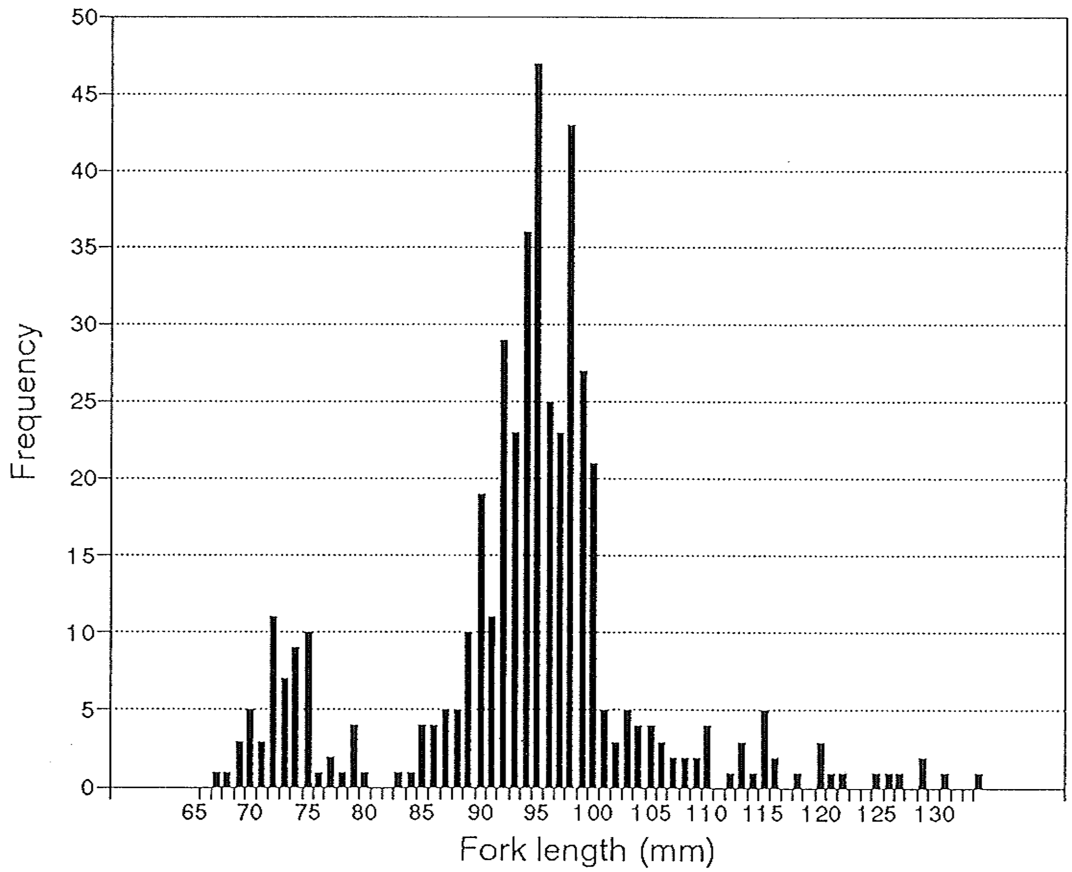


Fig. 7. Length frequency distribution of rainbow smelt caught in Sandybeach Lake in May 1990.

mm mesh selectively caught rainbow smelt at a modal fork length of 72-mm while the 8-mm mesh selectively caught rainbow smelt at a modal fork length of 95-mm.

The diet of rainbow smelt over 85-mm in fork length caught in the spring was determined by the weighted resultant index method and consisted of 91% large calanoid copepods and 9% insects (primarily *Hexagenia* sp nymphs). None of the rainbow smelt examined contained fish remains (Fig. 8).

Cisco

Cisco caught in Sandybeach Lake in May 1990 ranged in fork length from 112 to 241-mm while those taken in Little Vermilion Lake ranged from 79 to 184-mm. Analysis of covariance of weights of cisco ranging in fork lengths from 118 to 154-mm from both Sandybeach and Little Vermilion lakes indicated that cisco from Little Vermilion Lake had a significantly greater weight ($p < 0.0001$) for a given length (condition) than those of Sandybeach Lake (Fig. 9). Cisco with a fork length of 134-mm from Little Vermilion Lake had a mean weight of 25.0 grams while cisco of the same length from Sandybeach Lake had a mean weight of 23.4 grams (standard error of estimate 1.024). The diet of cisco in Sandybeach Lake, which consisted entirely of large calanoid copepods, overlapped to a large extent with that of rainbow smelt. The diet of cisco from Little Vermilion Lake overlapped with that of Sandybeach Lake rainbow smelt to an even greater extent with large calanoid copepods making up 95% of the diet and insects (primarily *Hexagenia* sp nymphs) making up the remaining 5% (Fig. 10).

Lake whitefish

The two lake whitefish caught in Sandybeach Lake in May 1990 (from a total of 16 gill net sets, 6 of which were set on bottom) were mature females over 250-

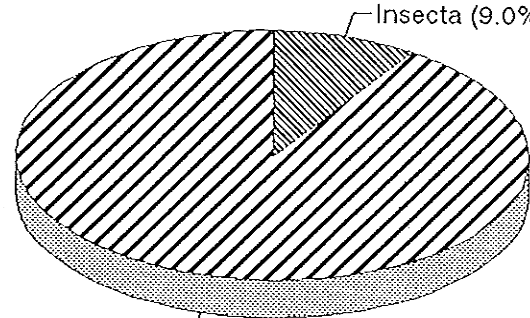


Fig. 8. Diet of 210 rainbow smelt (>85 mm FL) caught in Sandybeach Lake in May 1990.

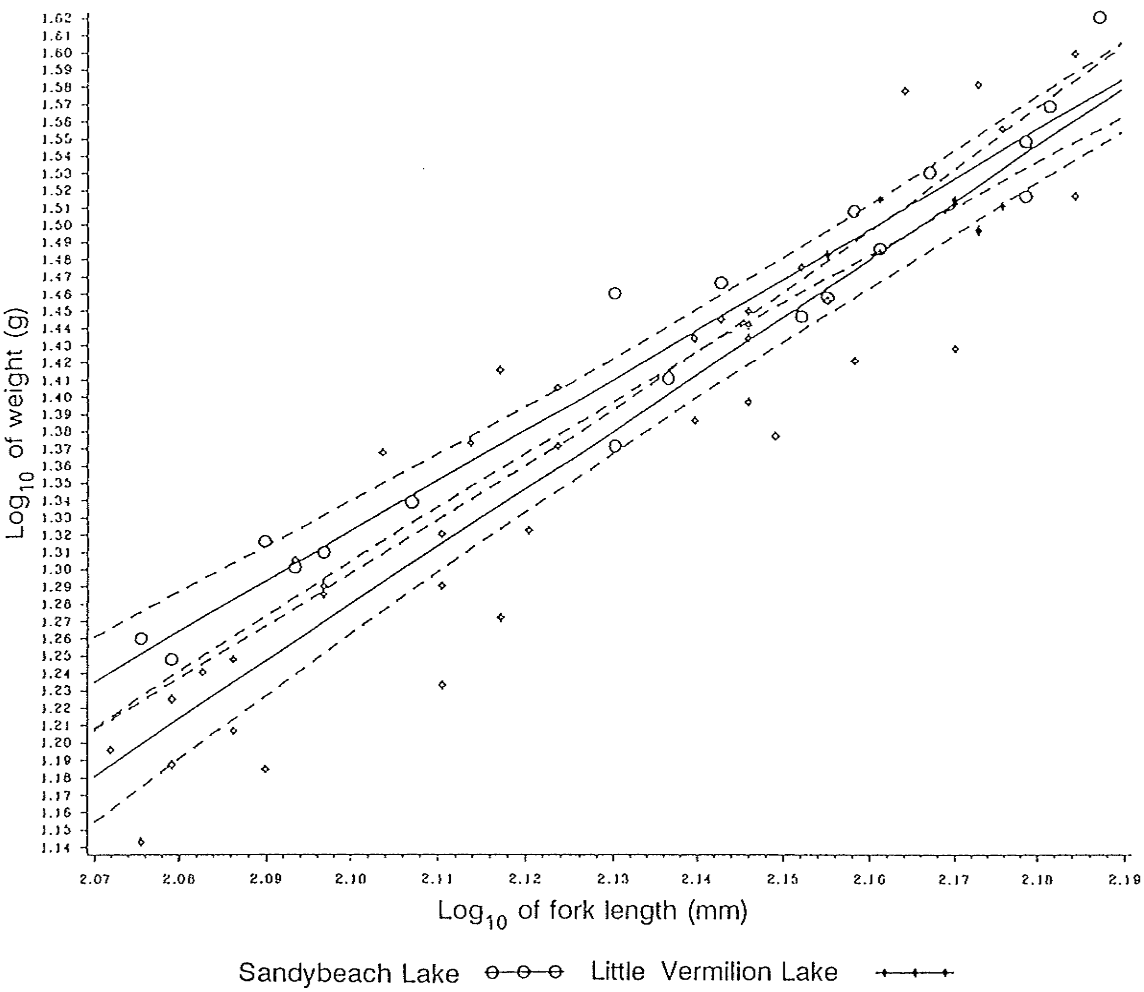


Fig 9. Plot of length-weight relationship of cisco 118-154 mm FL from Sandybeach and Little Vermilion Lakes caught in May 1990. ANCOVA estimate of lake effect 0.0275, std. error of estimate 0.0105, $p<0.0112$. Dotted lines indicate 95% confidence intervals.

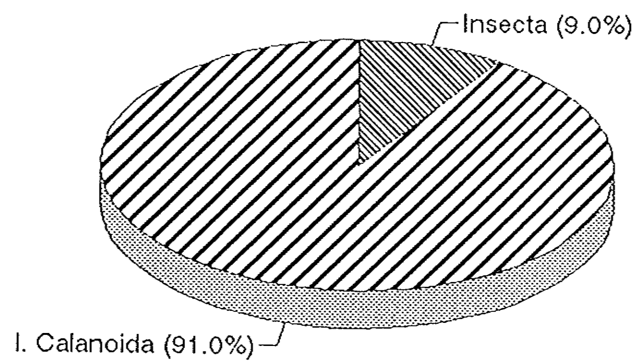


Fig. 10. Diet of 37 cisco from Little Vermilion Lake caught in May 1990.

mm fork length whereas the eighteen lake whitefish caught in Little Vermilion Lake (from only 2 bottom set gill net sets) consisted of 12 immature females and 6 immature males ranging in fork length from 107 to 178-mm. Identifiable stomach contents of lake whitefish from both lakes consisted of benthos, primarily chironimidae larvae and *Pontoporeia affinis* (Amphipoda).

Summer Sampling

Total catches of fish in Sandybeach and Little Vermilion Lake in July 1990 (Table 5) do not represent equivalent efforts but were total catches in all gill nets for each lake. A small proportion of the total catch in each lake was in 1.8-m deep gill nets (Appendix 5).

Total catches of pelagic fish species or size-classes of species in Sandybeach Lake from the 5.2-m deep gill nets at the 11.3-m site (Table 6) did not differ significantly ($p > 0.5$) in distribution or abundance with the equivalent 11.3-m column of water within the 22-m site (upper epilimnion to lower hypolimnion) combined with the 37.5-m site (deep hypolimnion) in Sandybeach Lake (Table 7). Rainbow smelt was the numerically dominant pelagic species at all sites in Sandybeach Lake with 6037 specimens compared to only 182 cisco and shortjaw cisco captured in the deep pelagic nets. Total catches of pelagic species or size-classes of species by habitat resource state at the 22-m site in Little Vermilion Lake (Table 8) are equivalent in effort to those from Sandybeach Lake in the 22 m site. Cisco was the dominant pelagic species and was much more abundant in this lake compared to Sandybeach Lake with 1368 specimens taken. Yellow perch was the next most abundant pelagic species; 734 specimens were taken which contrasts with the absence of yellow perch in the pelagic community of Sandybeach Lake. Juvenile lake whitefish also were present in the pelagic community of Little Vermilion Lake but absent in Sandybeach Lake. Emerald and spottail shiner were

TABLE 5. Total catch of fish species in all gill nets in Sandybeach and Little Vermilion Lake in July 1990.

Species	Sandybeach Lake	Little Vermilion Lake
rainbow smelt	6255	0
cisco	264	1418
shortjaw cisco	15	0
lake whitefish	25	27
yellow perch	98	736
emerald shiner	547	184
spottail shiner	46	19
troutperch	138	0
mottled sculpin	26	0
slimy sculpin	0	10
deepwater sculpin	2	0
lake trout	9	1
northern pike	8	1
white sucker	5	0
silver redhorse	4	0
johnny darter	2	1
smallmouth bass	0	2
creek chub	0	1
nine-spine stickleback	0	9

TABLE 6. Total catch of pelagic fish species or size classes in 5.2 m gill nets for the 11.3 m site in Sandybeach Lake in relation to habitat resource state.

	Species			
Habitat resource state	Rainbow smelt	Cisco species	Emerald shiner	Spottail shiner
Upper Epilimnion	279	0	173	22
Lower Epilimnion	447	2	37	1
Upper Metalimnion	310	6	5	0
Thermocline	943	10	2	0
Lower Metalimnion	325	1	0	0
Total Catch Per 48 h	2304	19	217	23

TABLE 7. Total catch of pelagic fish species or size classes in 5.2 m gill nets for the 22 and 37. 5 m sites in Sandybeach Lake in relation to habitat resource state.

	Species			
Habitat resource state	Rainbow smelt	Cisco species	Emerald shiner	Spottail shiner
Upper Epilimnion	153	0	113	20
Lower Epilimnion	334	1	11	3
Upper Metalimnion	327	6	0	0
Thermocline	1625	16	0	0
Lower Metalimnion	440	5	0	0
Upper Hypolimnion	204	7	0	0
Mid Hypolimnion	344	24	0	0
Lower Hypolimnion	202	34	0	0
Deep Hypolimnion	104	70	0	0
Total Catch Per 48 h	3733	163	131	23

TABLE 8. Total catch of pelagic fish species or size classes in 5.2 m gill nets for the 22 m site in Little Vermilion Lake in relation to habitat resource state.

	Species or size class						
Habitat resource state	Cisco 50-70 mm FL	Cisco 100-125 mm FL	Cisco 130-175 mm FL	Lake whitefish	Yellow perch	Emerald shiner	Spottail shiner
Upper Epilimnion	2	1	1	0	295	177	9
Lower Epilimnion	1	2	3	0	334	7	10
Upper Metalimnion	10	2	2	11	75	0	0
Thermocline	292	51	18	11	11	0	0
Lower Metalimnion	77	25	23	0	4	0	0
Upper Hypolimnion	32	179	153	0	7	0	0
Mid Hypolimnion	8	117	225	0	6	0	0
Lower Hypolimnion	0	20	124	0	2	0	0
Total catch per 48 hours	422	397	549	22	734	184	19

present in both lakes and catches of these species did not differ significantly between lakes ($p > 0.5$). One way ANOVA of catch by species for the six replicates of each depth strata at all sites and within and between each lake indicated that there were no significant differences in catches between replicates ($p > 0.5$). This confirmed the viability of utilizing the deep pelagic nets to assess pelagic fish distributions.

The following are descriptions of population characteristics of fish species from each lake's pelagic community, interactions between fish species within each community and a comparison of the pelagic zooplankton communities between lakes.

Rainbow smelt

Rainbow smelt caught in all gill nets in Sandybeach Lake in July 1990 ranged in fork length from 64 to 166-mm (Fig. 11). An additional 100 young-of-the-year rainbow smelt were caught in a beach seine also in July. These varied in total length from 23 to 29-mm. Scale ages of 30 rainbow smelt of various sizes (Table 9) indicated that there were three dominant age groups in the lake which overlapped in length frequency. Rainbow smelt were most susceptible to the 6.25-mm mesh at a modal fork length of 79-mm (up from 72-mm in May) and to the 8-mm mesh at a modal fork length of 95-mm (the same as in May) while the remaining mesh sizes caught an insignificant number of rainbow smelt of various lengths (Fig. 12). Rainbow smelt were the most abundant species in all habitats at all sites in Sandybeach Lake, however they were most prevalent in the thermocline as indicated by a larger percentage of the catch in that layer in each of the 11.3-m (Fig. 13) and the combined 22-m and 37.5-m sites (Fig. 14). Echo-sounder observations also confirmed large numbers of fish ascending into the thermocline with the onset of darkness, at times creating a layer thick enough to

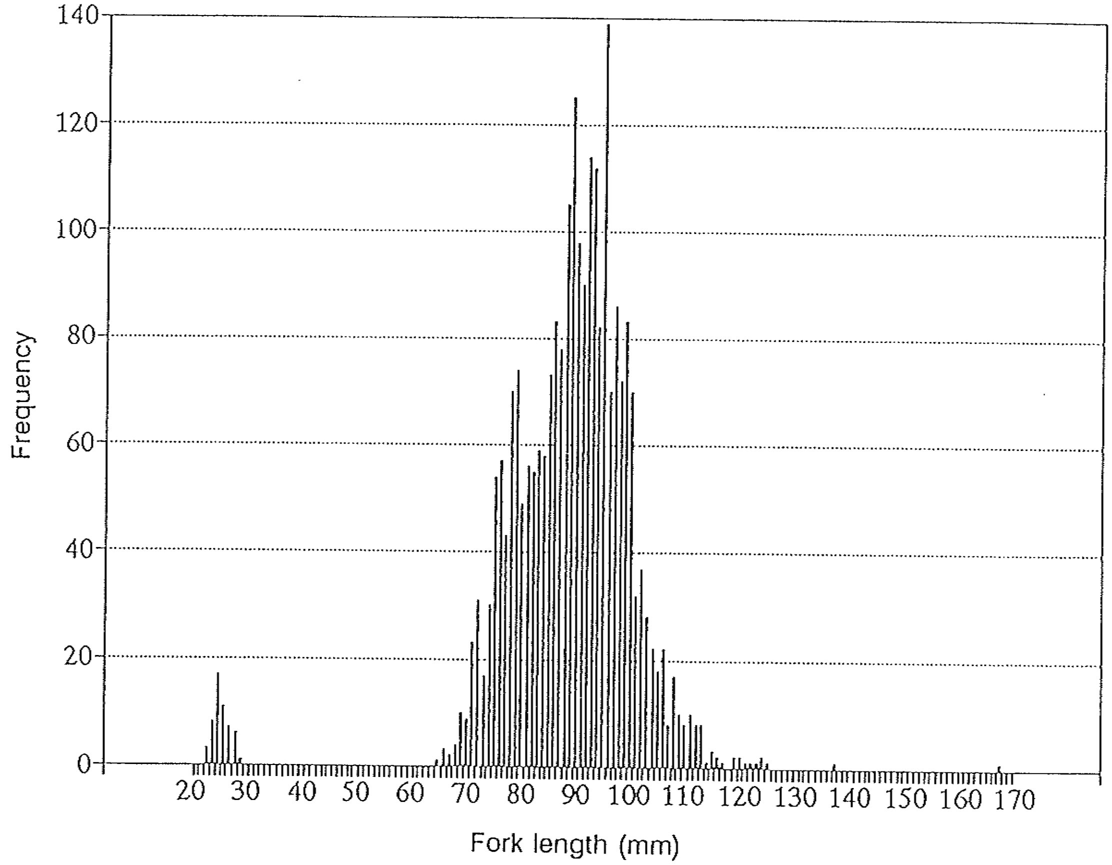


Fig. 11. Length frequency distribution of rainbow smelt caught in Sandybeach Lake in July 1990.

TABLE 9. Length (mm) at age of 30 rainbow smelt caught in Sandybeach Lake in July 1990.

Age 1+	Age 2+	Age 3+
78	85	119
83	89	119
84	90	120
86	95	120
87	95	121
88	97	122
88	102	123
89	105	124
90	110	125
91	112	125
$x = 86.4$	$x = 98.0$	$x = 121.8$
$s = 3.86$	$s = 9.05$	$s = 2.35$

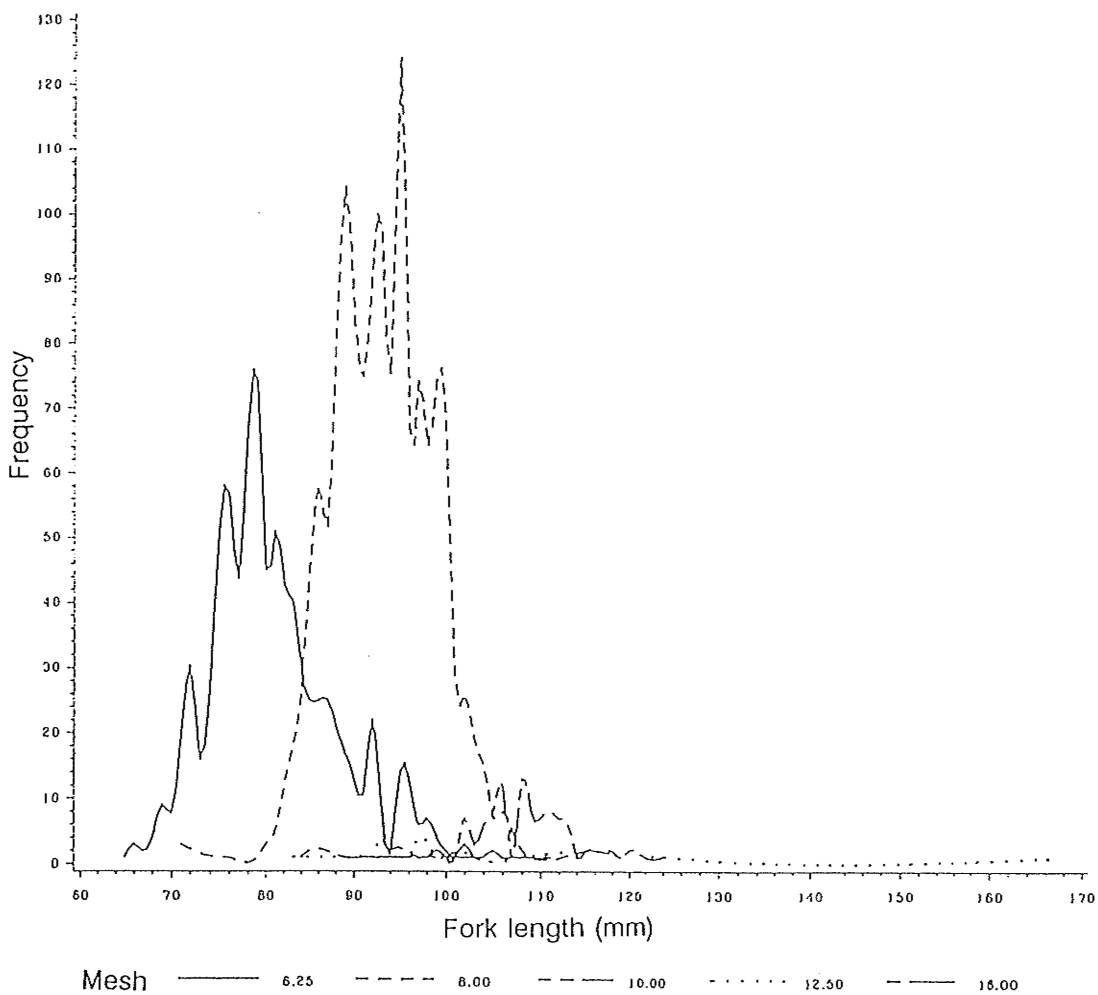


Fig. 12. Length frequency distribution of rainbow smelt caught in each gill net mesh size in Sandbeach Lake in July 1990.

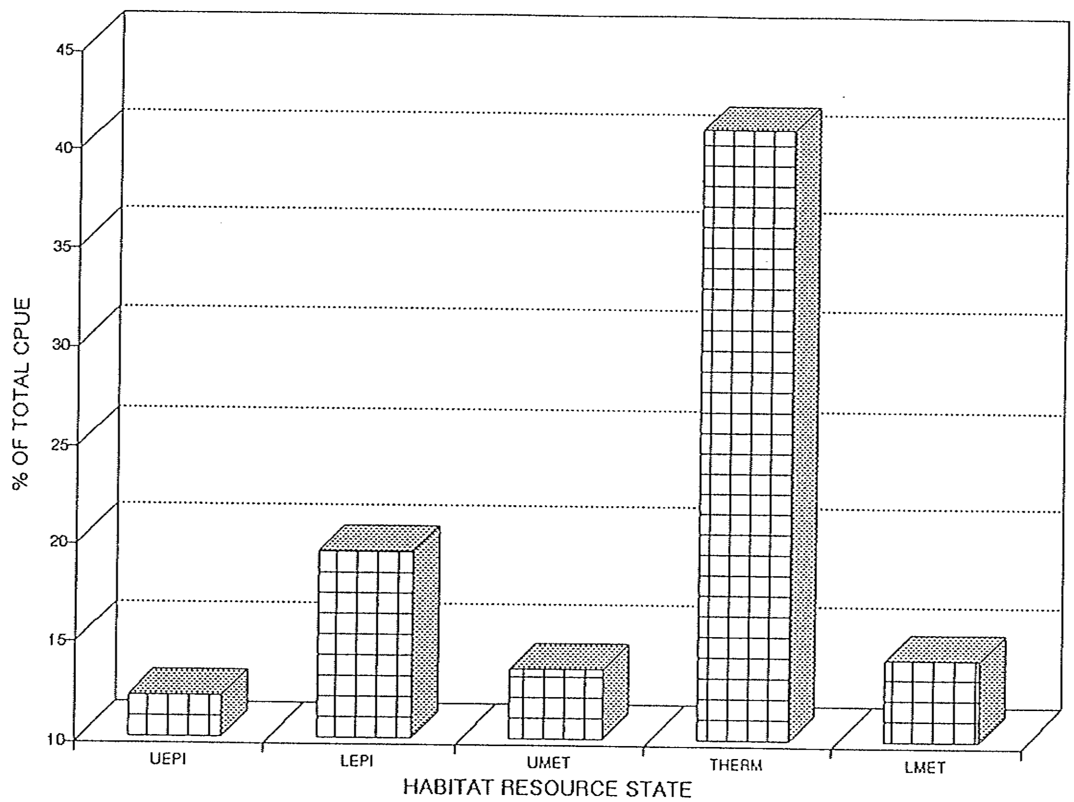


Fig 13. Proportional habitat utilization by rainbow smelt during the period of dusk to dawn during summer stratification for the 11.3 m site in Sandybeach Lake.

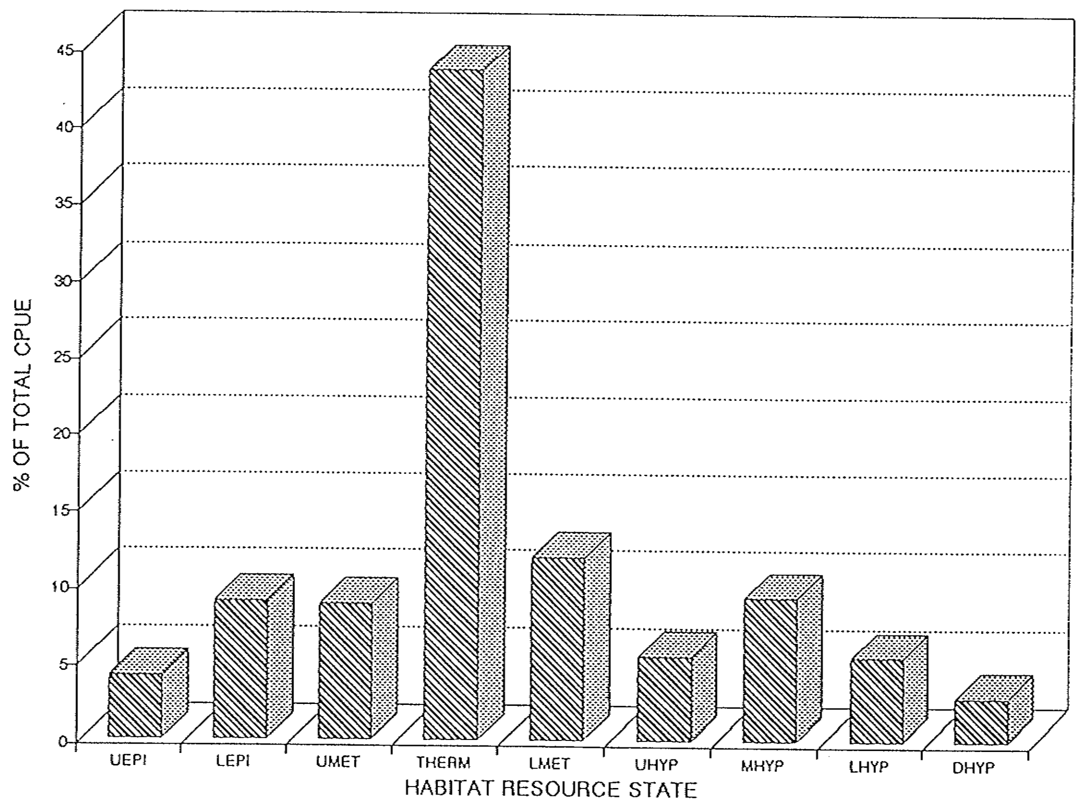


Fig. 14. Proportional habitat utilization by rainbow smelt during the period of dusk to dawn during summer stratification for the combined 22 and 37.5 m sites in Sandybeach Lake.

cause the sounder to indicate a false bottom. Overall habitat utilization by rainbow smelt was wide with a habitat niche breadth at 4.24, the highest value for a pelagic species recorded in either lake. Rainbow smelt 69-84-mm FL principally fed on small calanoid copepods and to a lesser extent on large calanoid copepods (Fig. 15). However, they had a dietary niche breadth of 1.71 which implied a fairly specialized diet in comparison to other species. Rainbow smelt 85-125-mm FL primarily fed on large calanoid copepods, occasionally taking insects and large cladocerans (Fig. 16). They had a dietary niche breadth of 1.04 which was even more specialized or selective than that of the smaller rainbow smelt.

Cisco species

The cisco species caught in Sandybeach Lake in July 1990 ranged in fork length from 92 to 230-mm (Fig. 17). Most of the catch occurred around a modal fork length of 146-mm which also was the modal length of cisco and shortjaw cisco caught most frequently in 16-mm mesh. Ages of cisco species caught in July 1990 could not be obtained reliably by scale readings, however ages of fresh specimens taken from Sandybeach Lake in June 1991 indicated that the portion of the catch occurring about the 146-mm mode consisted of age 3+ individuals.

Cisco and shortjaw cisco caught in the deep pelagic nets in Sandybeach Lake were most prevalent in the deep hypolimnion (Fig. 18). Cisco and shortjaw cisco utilized all pelagic habitats resulting in a wide niche breadth of 3.8, however their diet consisted almost entirely of large calanoid copepods, occasionally including *Mysis relicta* and algae (Fig. 19). This resulted in a narrow dietary niche breadth of 1.04.

Cisco caught in Little Vermilion Lake in July 1990 ranged in fork length from 49 to 180-mm with three distinct size-classes, one at 50-70-mm FL, another at 100-125-mm FL and a third at 130-175-mm FL (Fig. 20). These size-classes

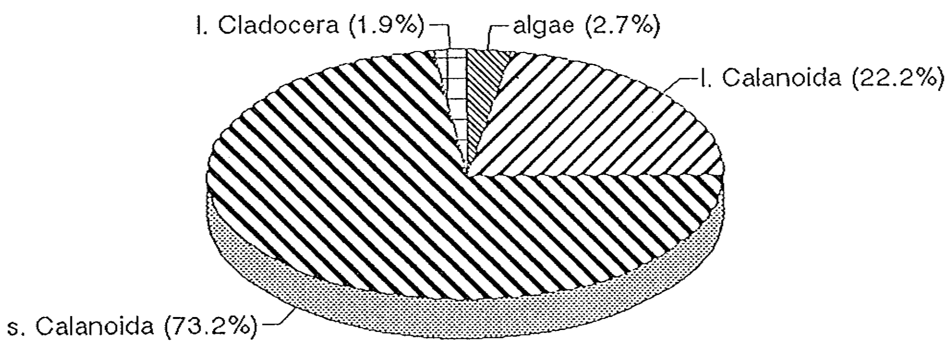


Fig. 15. Diet of 28 rainbow smelt 69-84 mm FL from Sandybeach Lake caught in July 1990.

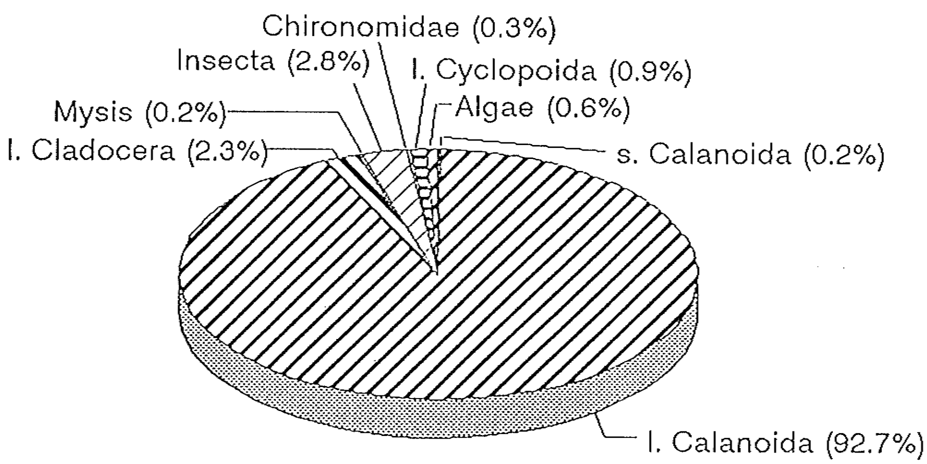


Fig. 16. Diet of 91 rainbow smelt 85-125 mm FL caught in Sandybeach Lake in July 1990.

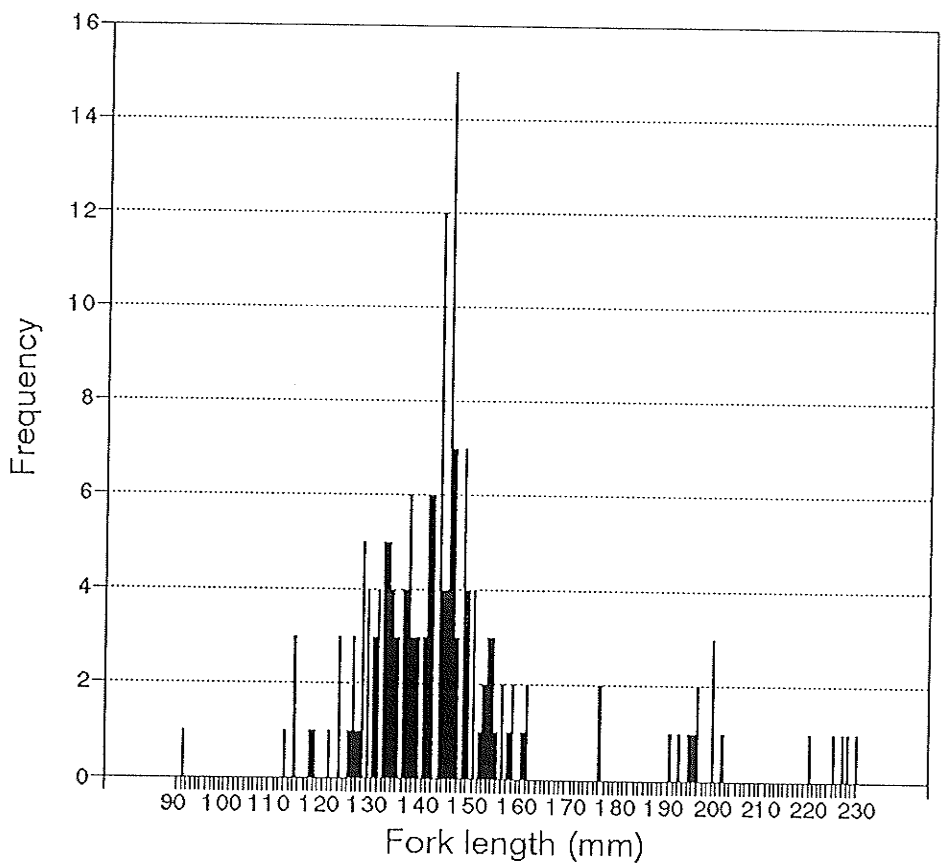


Fig. 17. Length frequency distribution of cisco species caught in Sandybeach Lake in July 1990.

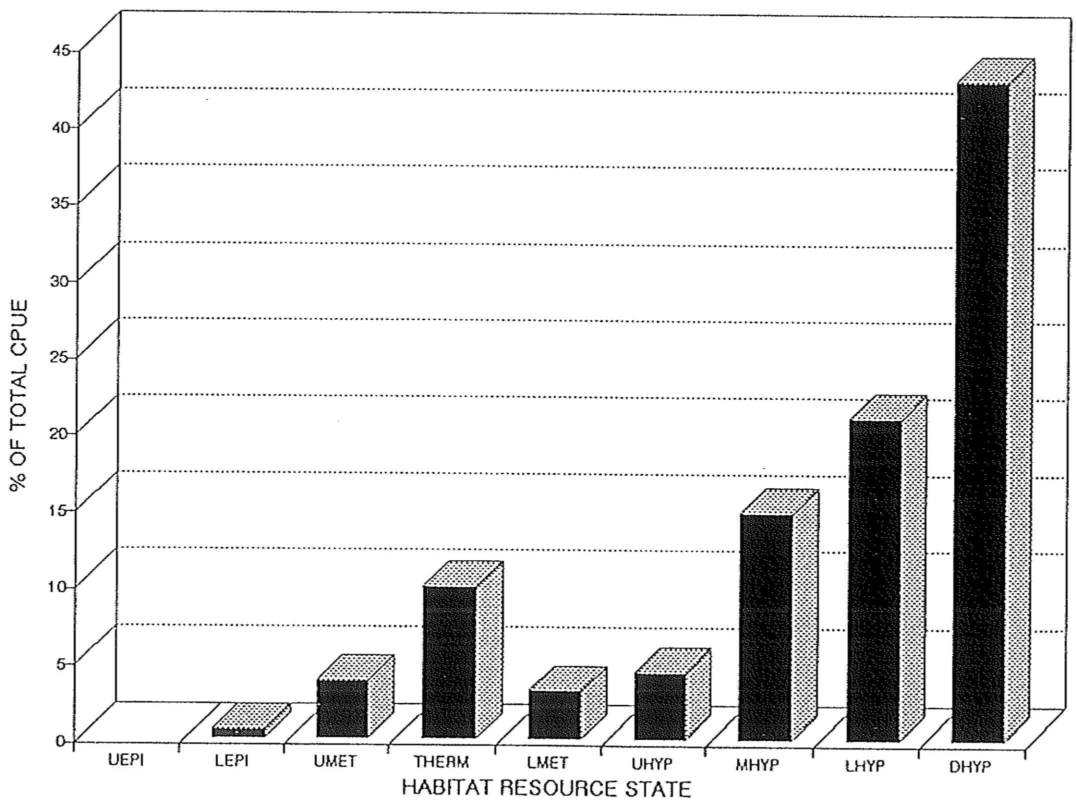


Fig. 18. Proportional habitat utilization by cisco species during the period of dusk to dawn during summer stratification for the combined 22 and 37.5 m sites in Sandybeach Lake.

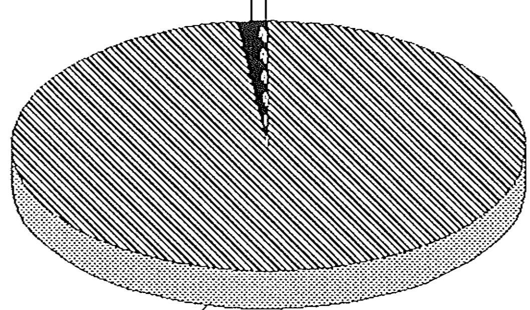


Fig. 19. Diet of 40 shortjaw cisco and cisco from Sandybeach Lake caught in July 1990.

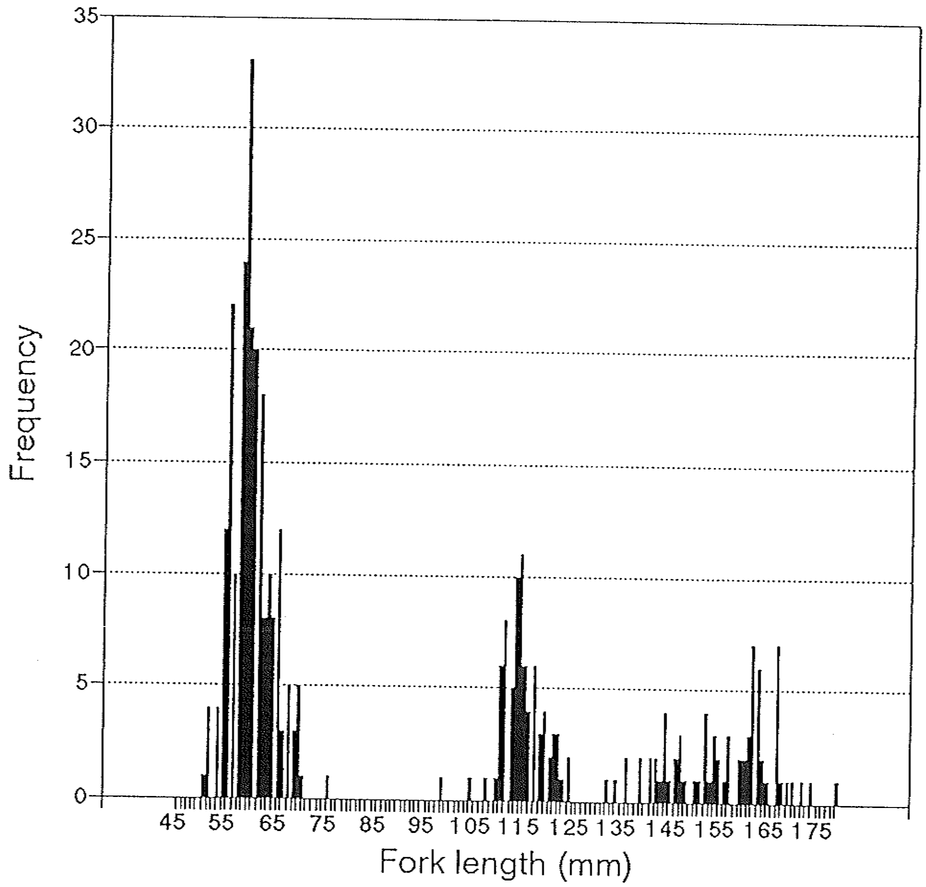


Fig. 20. Length frequency distribution of cisco caught in Little Vermilion Lake in July 1990.

corresponded to age 1+, 2+, and 3+ respectively. The first two of these size-classes were absent from catches from Sandybeach Lake. Modal fork lengths of catches of cisco by each mesh size in Little Vermilion Lake were: 60-mm for the 6.25-mm mesh, 66-mm for the 8-mm mesh and 115-mm for the 12.5-mm mesh. The 10-mm mesh caught relatively few cisco and the 16-mm mesh, as in Sandybeach Lake, caught a wide range of cisco greater than 120-mm FL.

Cisco of 50-70-mm FL were present in all pelagic habitats of Little Vermilion Lake except the lower hypolimnion, but were scarce in the lower metalimnion and epilimnion and thus had a relatively narrow habitat niche breadth of 1.93. These small cisco were primarily distributed within the thermocline (Fig. 21) which they dominated numerically in Little Vermilion Lake. Cisco 50-70-mm FL had a wide dietary niche breadth of 2.45, and fed primarily on large cyclopoid copepods followed by small calanoid copepods and small cladocerans (Fig. 22).

Cisco of 100-125-mm FL were present in all habitats in Little Vermilion Lake resulting in a wide niche breadth of 3.19. These cisco were most prevalent in the upper hypolimnion where they were the most abundant size-class or species (Fig. 23). Cisco of 100-125-mm FL had a wide dietary niche breadth of 2.58, feeding on large cladocerans and small calanoid copepods with algae, small cladocerans, large cyclopoid copepods and amphipods (*Pontoporeia affinis*) making up most of the rest of the diet (Fig. 24).

Cisco of 130-175-mm FL were present in all habitats in Little Vermilion Lake and thus had a wide niche breadth of 3.33. These cisco were the most abundant species, and size-class of cisco, in the mid and lower hypolimnion but primarily occupied the mid-hypolimnion (Fig. 25). Cisco of 130-175-mm FL had a narrow dietary niche breadth of 1.24 and fed primarily on large calanoid copepods (Fig. 26).

Analysis of covariance of weights of cisco from Sandybeach and Little Vermilion Lake caught during July 1990 ranging in fork length between 120 and

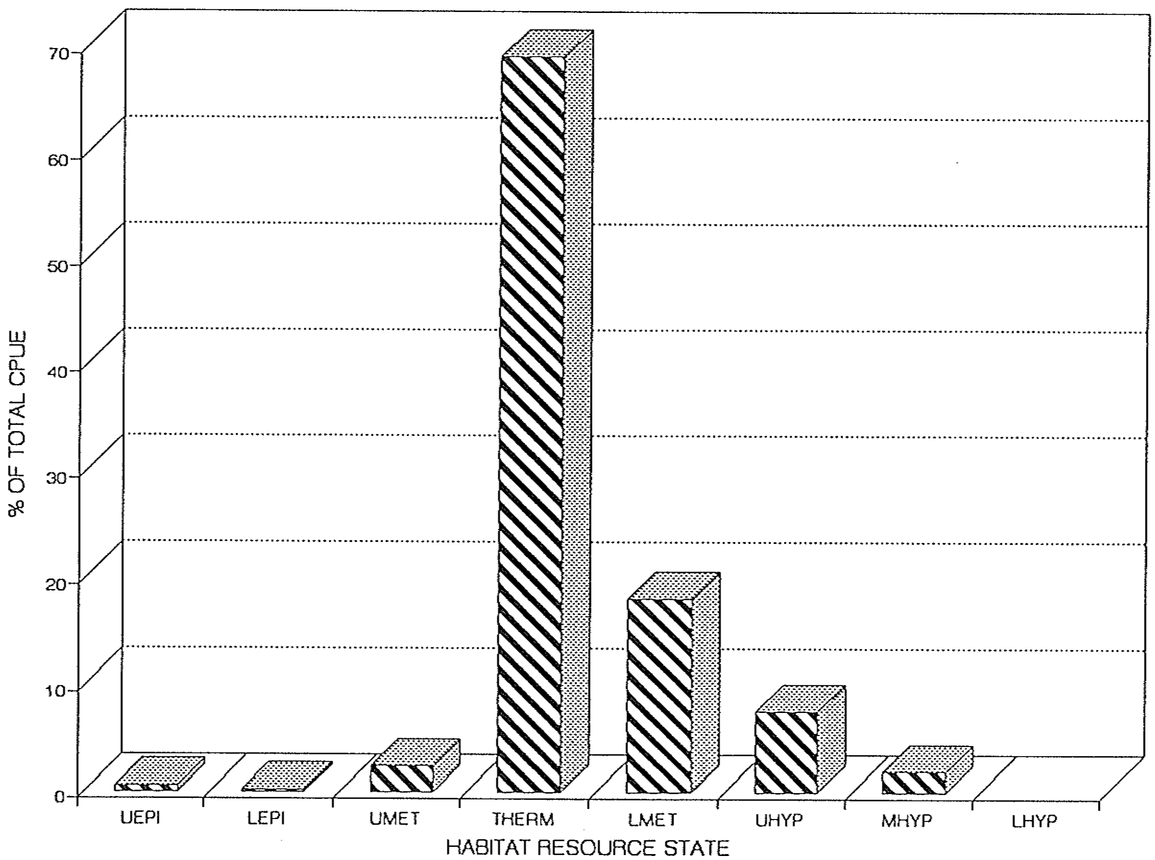


Fig. 21. Proportional habitat utilization by cisco 50-70 mm FL during the period of dusk to dawn during summer stratification for the 22 m site in Little Vermilion Lake.

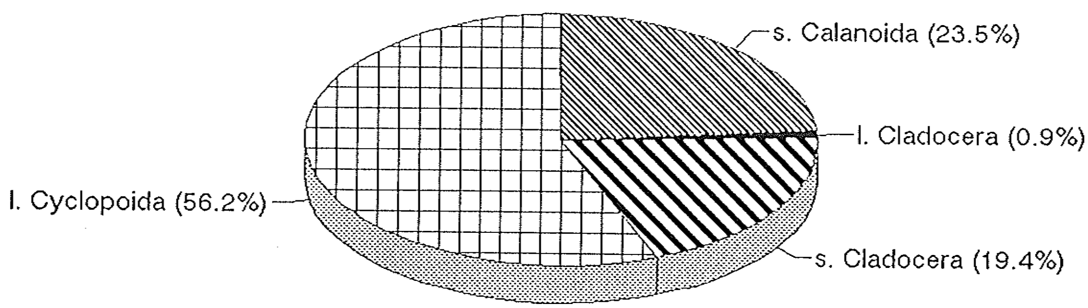


Fig. 22. Diet of 20 cisco 50-70 mm FL from Little Vermilion Lake caught in July 1990.

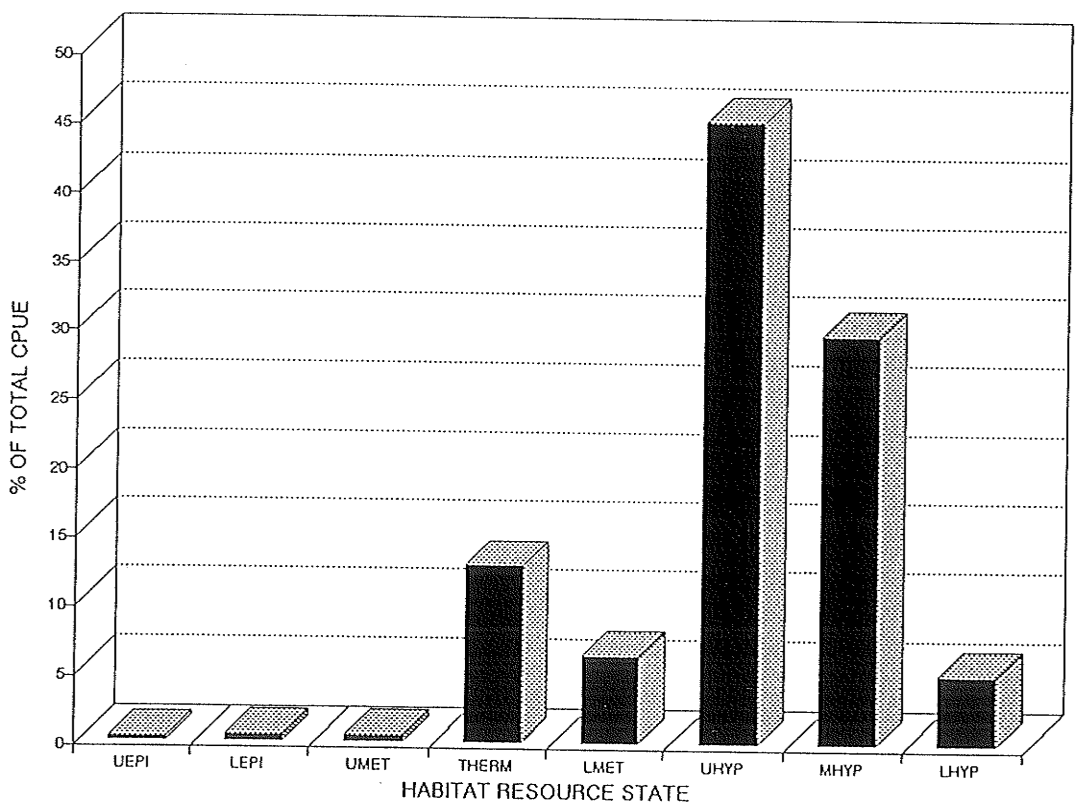


Fig. 23. Proportional habitat utilization by cisco 100-125 mm FL during the period of dusk to dawn during summer stratification for the 22 m site in Little Vermilion Lake.

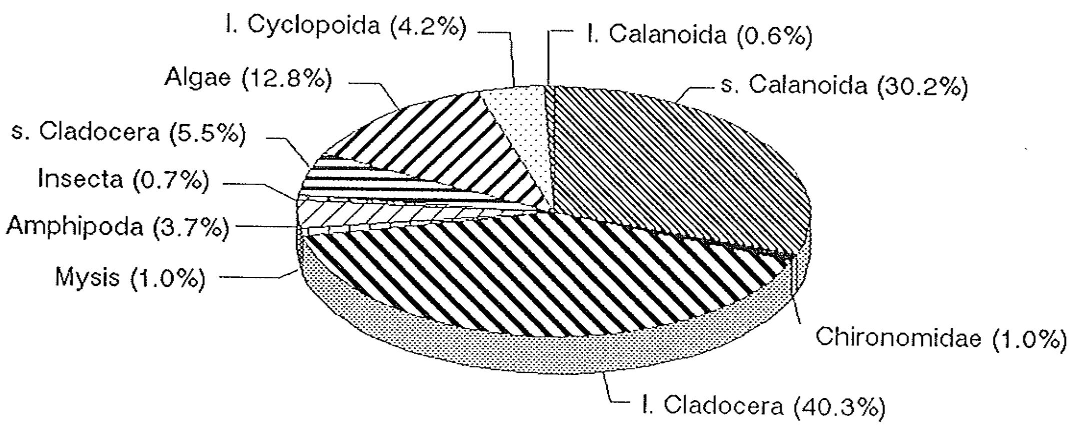


Fig. 24. Diet of 35 cisco 100-125 mm FL from Little Vermilion Lake caught in July 1990.

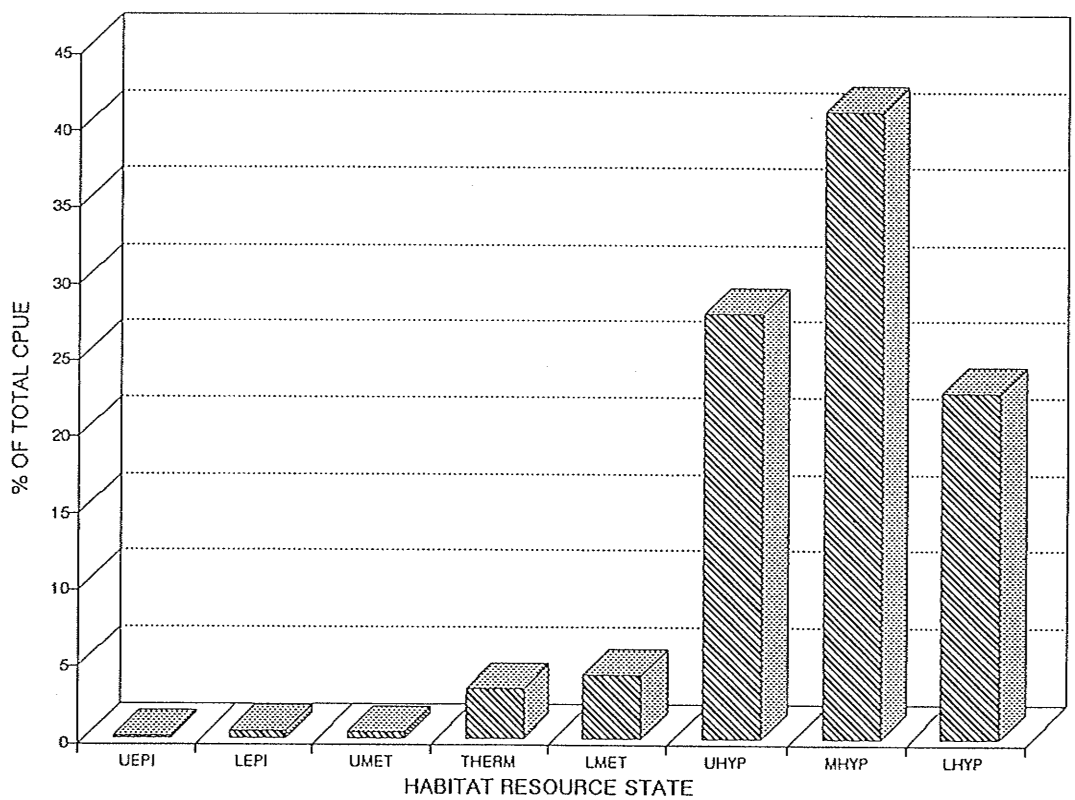


Fig. 25. Proportional habitat utilization by cisco 130-175 mm FL during the period of dusk to dawn during summer stratification for the 22 m site in Little Vermilion Lake.

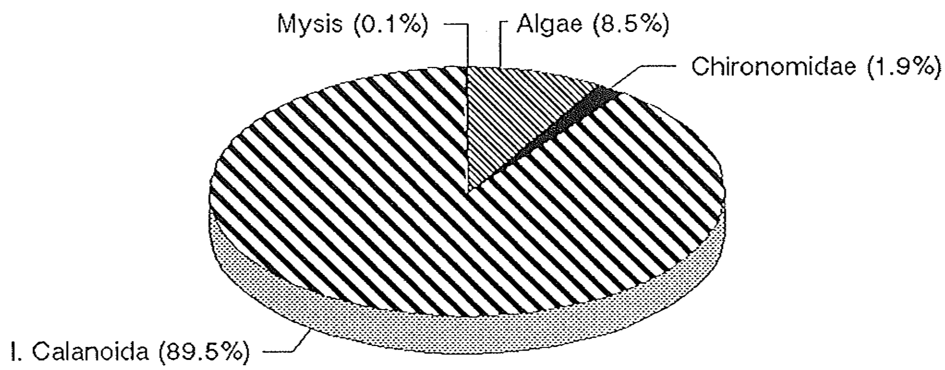


Fig. 26. Diet of 25 cisco 130-175 mm FL from Little Vermilion Lake caught in July 1990.

155-mm indicated that cisco from Little Vermilion Lake had a significantly ($p < 0.0001$) greater weight for a given length than those of Sandybeach Lake (Fig. 27). Covariance analysis indicated that cisco with a fork length of 138-mm from Little Vermilion Lake had a mean weight of 28.4 grams, whereas a cisco with a fork length of 138-mm from Sandybeach Lake had a mean weight of 26.2 grams (standard error of estimate 1.016).

Sex composition of cisco from Sandybeach and Little Vermilion lakes differed significantly ($p < 0.0001$). Of 261 cisco taken in Sandybeach Lake in May and July 1990 86.6% were female (Table 10). In Little Vermilion Lake 59% of 139 cisco captured in May and July 1990 were female.

Lake whitefish

No lake whitefish were caught in Sandybeach Lake in the 5.2-m deep pelagic gill nets and thus no lake whitefish were captured in the pelagic zone. However lake whitefish ranging in fork length from 364 to 454-mm were captured using bottom set gill nets with larger size mesh. These lake whitefish fed on *Pontoporeia affinis*, Chironimidae larvae and 33.3% (5 of 15 of lake whitefish stomachs with identifiable contents) contained rainbow smelt.

In contrast to Sandybeach Lake, lake whitefish ranging in fork length from 79 to 90-mm were present in the metalimnion and thermocline of Little Vermilion Lake. This narrow habitat utilization resulted in a very narrow habitat niche breadth of 2.00, implying a high degree of habitat specialization. Juvenile lake whitefish in Little Vermilion Lake had a wide dietary niche breadth of 3.07, but fed mostly on small calanoid copepods and large cladocerans (Fig. 28).

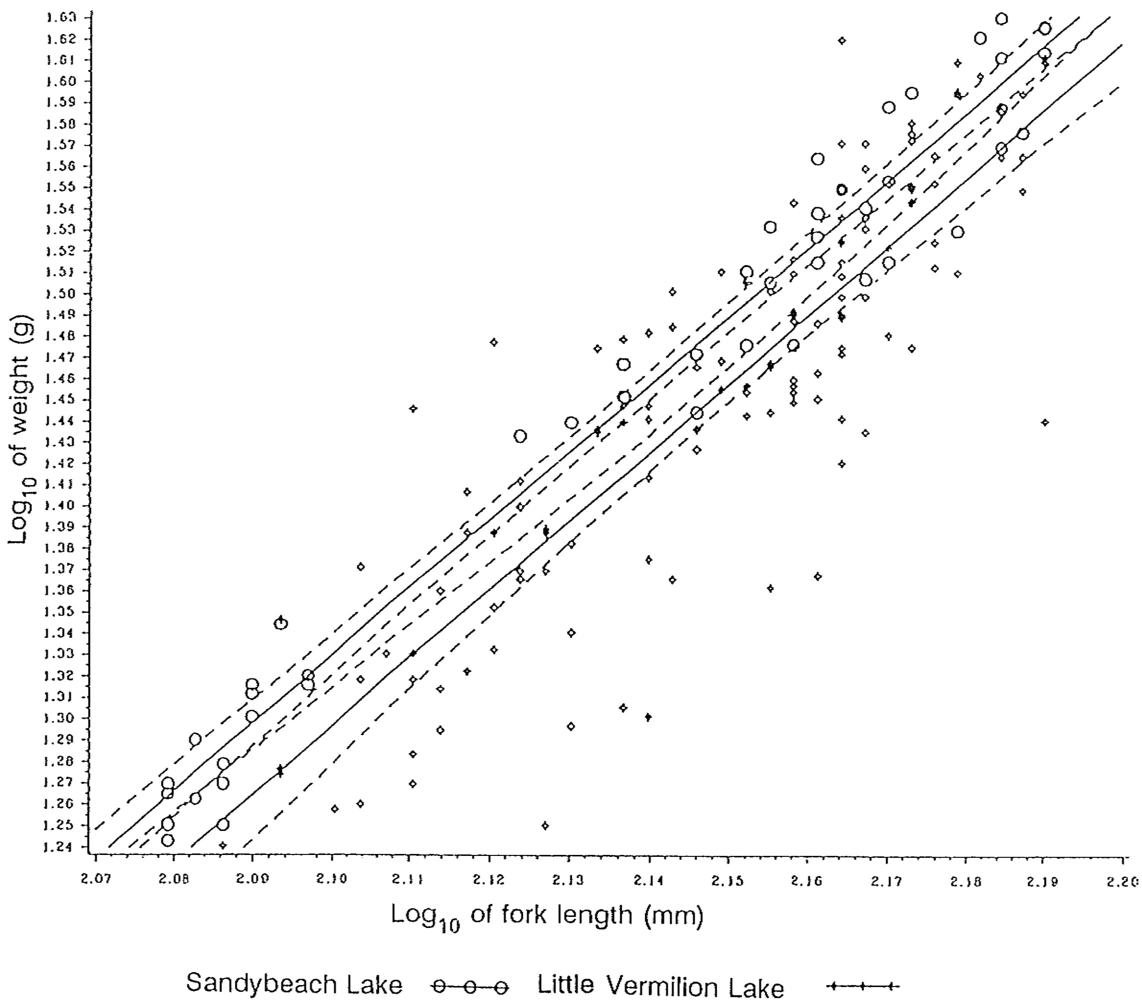


Fig 27. Plot of length-weight relationship of cisco 120-155 mm FL from Sandybeach and Little Vermilion Lakes caught in July 1990. ANCOVA estimate of lake effect 0.0319, std. error of estimate 0.0073, $p<0.0001$. Dotted lines indicate 95% confidence intervals.

TABLE 10. Sex composition of mature cisco and shortjaw cisco from Sandybeach Lake and cisco from Little Vermilion Lake.

Lake	% Female	% Male	n
Sandybeach	86.6	13.4	261
Little Vermillion	59.0	41.0	139

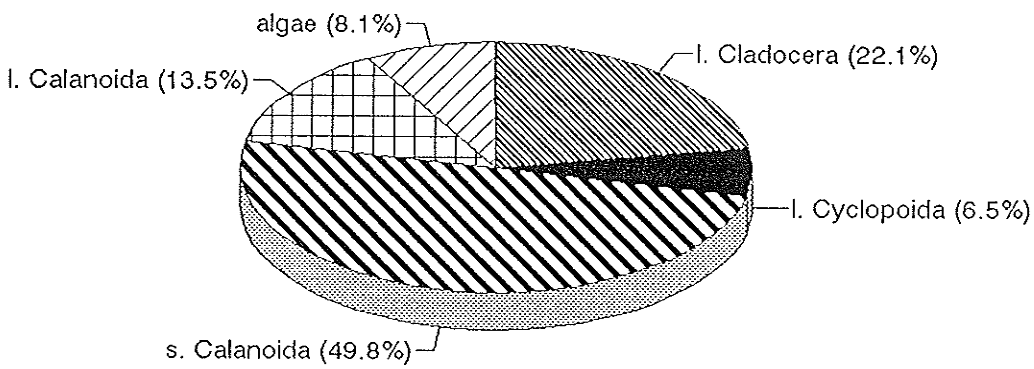


Fig. 28. Diet of 12 lake whitefish 79-90 mm FL from Little Vermilion Lake caught in July 1990.

Yellow perch

Yellow perch were present in Sandybeach Lake but were caught only in shallow littoral areas at depths less than 9-m (Appendix 5: Sets 19 & 27). Unfortunately none of these yellow perch were retained for analysis (Sandybeach Lake was sampled first and the lack of yellow perch in the pelagic zone was not recognized as being important or related to the presence of rainbow smelt at the time). As such no population characteristics of Sandybeach Lake yellow perch (i.e. length frequency, condition) were determined other than habitat utilization for comparison with Little Vermilion Lake yellow perch.

Yellow perch in Little Vermilion Lake utilized both the littoral and pelagic zones and had a wide habitat niche breadth of 2.11, occurring in all pelagic habitats to some extent. Yellow perch were the most abundant species in the upper and lower epilimnion and upper metalimnion in Little Vermilion Lake but primarily occupied the epilimnion (Fig. 29). Yellow perch caught in Little Vermilion Lake ranged in fork length from 34 to 115-mm and were caught in gill nets at the following modal fork lengths for each mesh size: 43-mm for the 6.25-mm mesh, 68-mm for the 8-mm mesh, 77-mm for the 10-mm mesh and 101-mm for the 12.5-mm mesh with no perch being caught in the 16-mm mesh. There were three distinct size-classes at 35-50-mm, at 60-80-mm and at 95-115-mm (Fig. 30) which were separated for diet analysis. Yellow perch 35-50-mm FL had a narrow dietary niche breadth of 1.29 and fed primarily on large calanoid copepods (Fig. 31). Yellow perch 60-80-mm FL had a more varied diet with a dietary niche breadth of 2.10 and fed primarily on insects and large calanoid copepods. Small and large cladocerans made up the rest of their diet (Fig. 32). Yellow perch 95-115-mm FL fed exclusively on fishes, mostly small *Notropis* and *Coregonus* species. These were the only pelagic fishes examined in this study that were piscivorous.

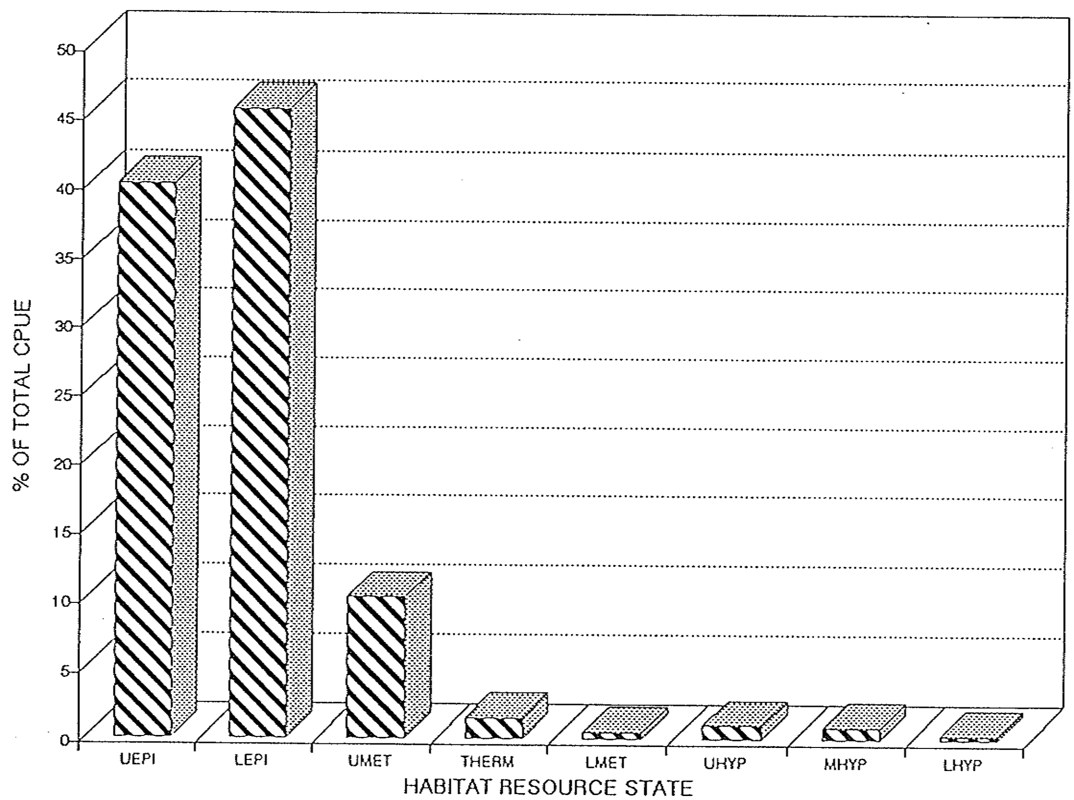


Fig. 29. Proportional habitat utilization by yellow perch during the period of dusk to dawn during summer stratification for the 22 m site in Little Vermilion Lake.

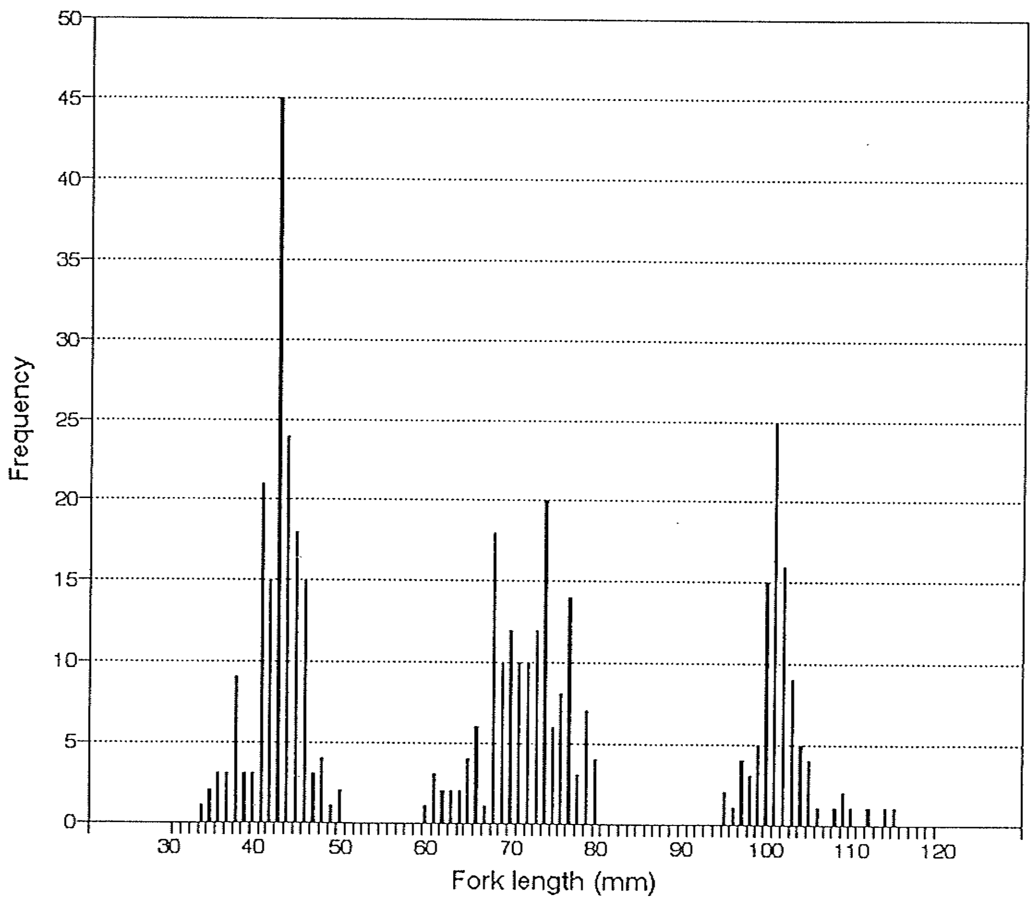


Fig. 30. Length frequency distribution of yellow perch caught in Little Vermilion Lake in July 1990.

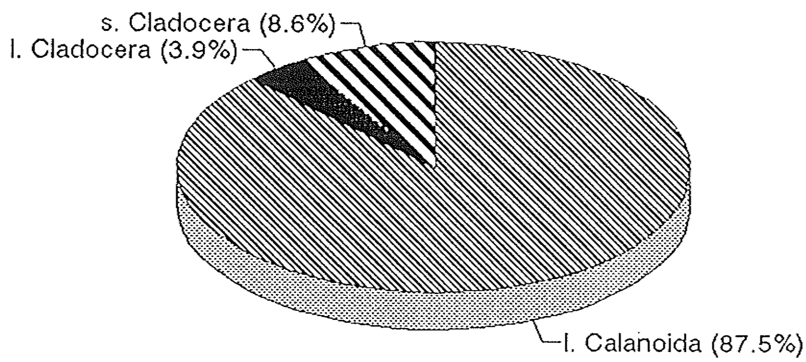


Fig. 31. Diet of 25 yellow perch 35-50 mm FL from Little Vermilion Lake caught in July 1990.

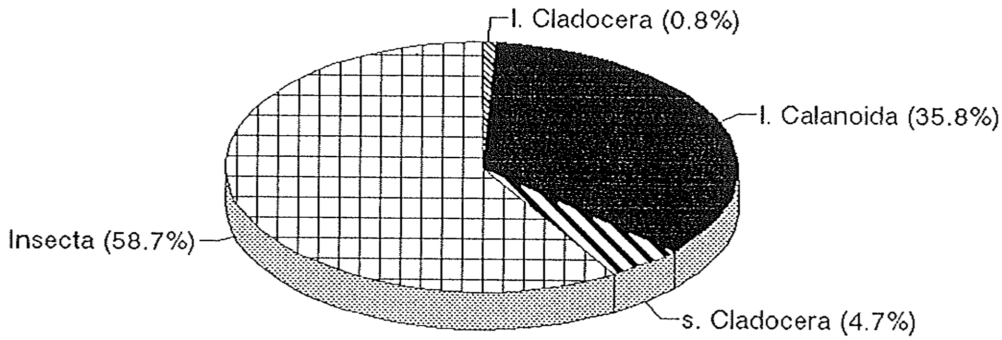


Fig. 32. Diet of 23 yellow perch 68-80 mm FL from Little Vermilion Lake caught in July 1990.

Emerald shiner

Emerald shiners were caught in the upper and lower epilimnion of both Sandybeach and Little Vermilion lakes and also utilized the upper metalimnion in Sandybeach Lake (Fig. 33). They primarily occupied the upper epilimnion resulting in a narrow habitat niche breadth of 1.33 and 1.08 in Sandybeach and Little Vermilion lakes respectively. Emerald shiners had a very narrow dietary niche breadth of 1.23 and 1.00 in Sandybeach and Little Vermilion lakes respectively, and fed primarily on insects in Sandybeach Lake (Fig. 34) and exclusively on insects in Little Vermilion Lake.

Analysis of covariance of weights of emerald shiner from Sandybeach and Little Vermilion lakes ranging in fork length from 82 to 105-mm FL indicated that Sandybeach Lake emerald shiners weighed less for a given range of lengths (Fig. 35). No covariate estimate could be made as the slopes of the length-weight relationships were not parallel (interaction significant, $p < 0.0043$). The emerald shiner populations in each lake were in spawning condition and thus weight differences may have been related to this activity.

Spottail shiner

Spottail shiners were caught in the upper and lower epilimnion of both Sandybeach and Little Vermilion lakes (Fig. 36). They had habitat niche breadths of 1.29 and 2.00 for Sandybeach and Little Vermilion lakes respectively (Note that the apparent significant difference in breadth is related to only a few individual fish, a consequence of low catches of spottail shiners in the pelagic zone). Spottail shiner had a very narrow dietary niche breadth in each lake, 1.00 and 1.93 respectively for Sandybeach and Little Vermilion lakes. They fed exclusively on insects in Sandybeach Lake and on algae and insects in Little Vermilion Lake (Fig.

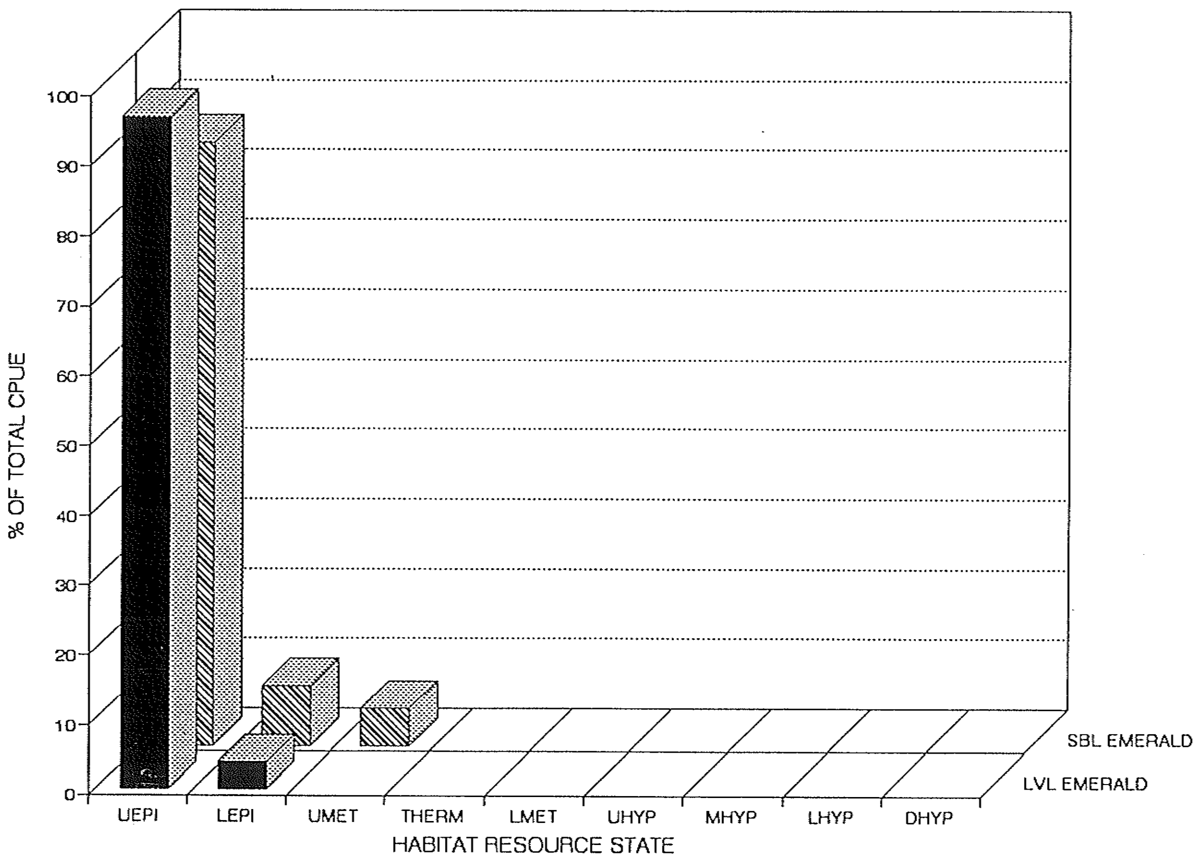


Fig. 33. Proportional habitat utilization by emerald shiner during the period of dusk to dawn during summer stratification for the combined 22 m and 37.5 m sites in Sandybeach Lake and the 22 m site in Little Vermilion Lake.

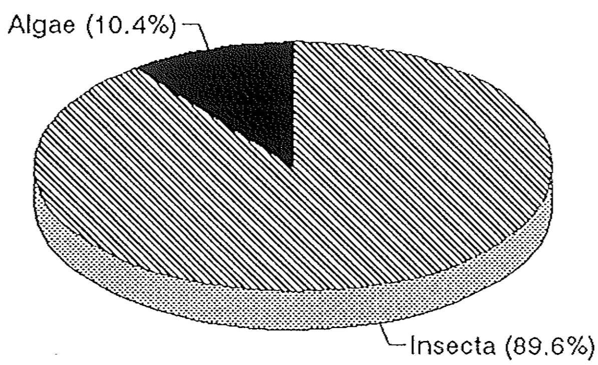


Fig. 34. Diet of 22 emerald shiner from Sandybeach Lake caught in July 1990.

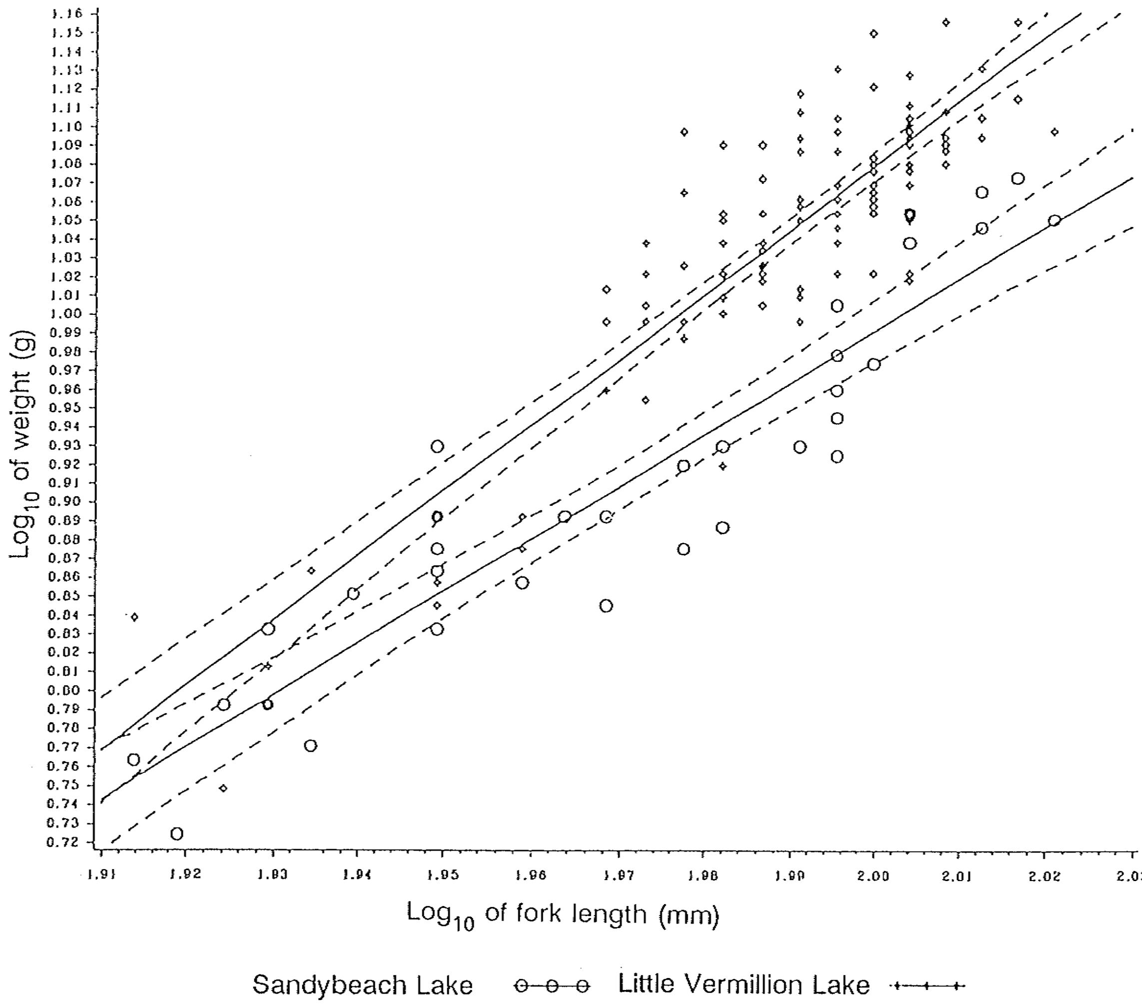


Fig 35. Plot of length-weight relationship of emerald shiner 82-105 mm FL from Sandybeach and Little Vermilion Lakes caught in July 1990. r^2 for common slope = 0.373. Dotted lines indicate 95% confidence intervals.

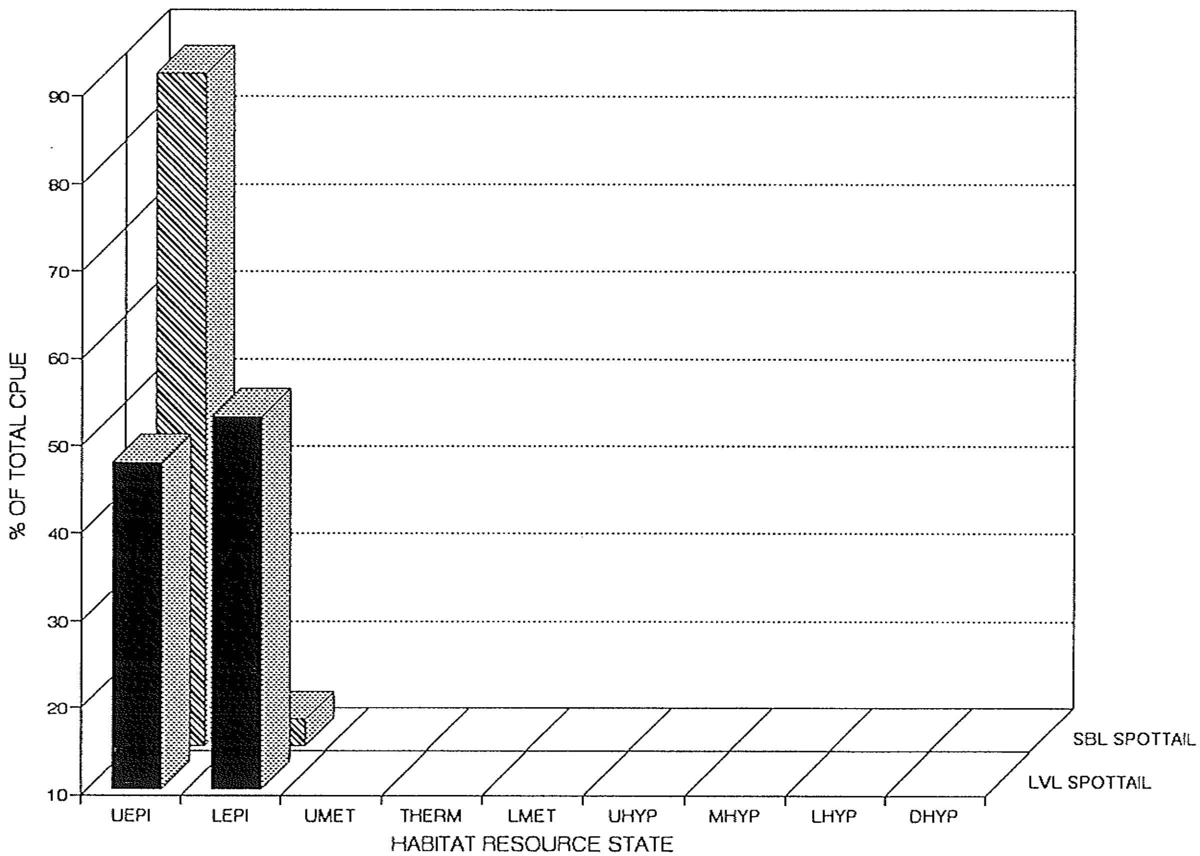


Fig. 36. Proportional habitat utilization by spottail shiner during the period of dusk to dawn during summer stratification for the combined 22 m and 37.5 m sites in Sandybeach Lake and the 22 m site in Little Vermilion Lake.

37). The low numbers of spottail shiner in the open waters of each lake suggests that this species may not be important in the pelagic community of these lakes.

Community Interactions:

Sympatric Niche Overlap in Sandybeach Lake

In Sandybeach Lake rainbow smelt 69-84 mm FL overlapped 100% with rainbow smelt 85-125 mm FL in habitat but only 24.9% in diet (Table 11) and had a slightly more varied diet than the larger smelt as indicated by a larger diet niche breadth (Fig. 38). This difference in prey utilization related to the size of the rainbow smelt, with larger rainbow smelt consuming predominately large calanoid copepods.

Rainbow smelt 69-125 mm FL overlapped 38.9% in habitat with cisco and shortjaw cisco, principally due to fact that both groups had a very wide habitat niche breath. However rainbow smelt were most prevalent in the thermocline while cisco and shortjaw cisco were most prevalent in the deep hypolimnion, which coincidentally was the least utilized habitat of rainbow smelt (Fig. 39). Rainbow smelt 69-84 mm FL overlapped in diet with cisco and shortjaw cisco 22.6% while smelt 85-125 mm FL overlapped almost completely in diet with cisco and shortjaw cisco at 93.3%. This related to a similar preference for large calanoid copepods.

Rainbow smelt overlapped 19.4% in habitat with emerald shiner, with rainbow smelt 69-84 mm FL overlapping 2.7% in diet and rainbow smelt 85-125 mm FL overlapping 3.4% in diet. Emerald shiner primarily utilized the upper epilimnion which contrasted with rainbow smelt which where most prevalent in the thermocline. Emerald shiner had a very narrow habitat niche breadth compared to rainbow smelt implying a greater degree of specialization.

Rainbow smelt overlapped 13.0% with spottail shiner in habitat with the smaller smelt not overlapping at all in diet and the larger smelt overlapping only

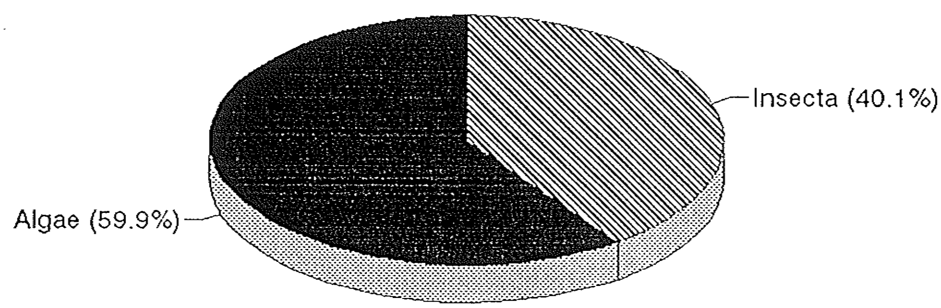


Fig. 37. Diet of 11 spottail shiner from Little Vermilion Lake caught in July 1990.

TABLE 11. Sympatric niche overlaps (%) among pelagic species and size classes in Sandybeach Lake for habitat/diet. Bold values indicate species combinations where overlap exceeds 50% in at least one resoure. Smelt1=69-84 mm FL, Smelt2=85-125 mm FL, Cisco species=Cisco and Shortjaw cisco.

	Smelt 1	Smelt 2	Cisco species	Emerald shiner
Smelt 2	**100** **24.9**	-	-	-
Cisco species	38.9 22.6	**38.9** **93.3**	-	-
Emerald shiner	19.4 2.7	19.4 3.4	4.3 0.2	-
Spottail shiner	13.0 0	13.0 1.4	0 0	**94.7** **44.8**

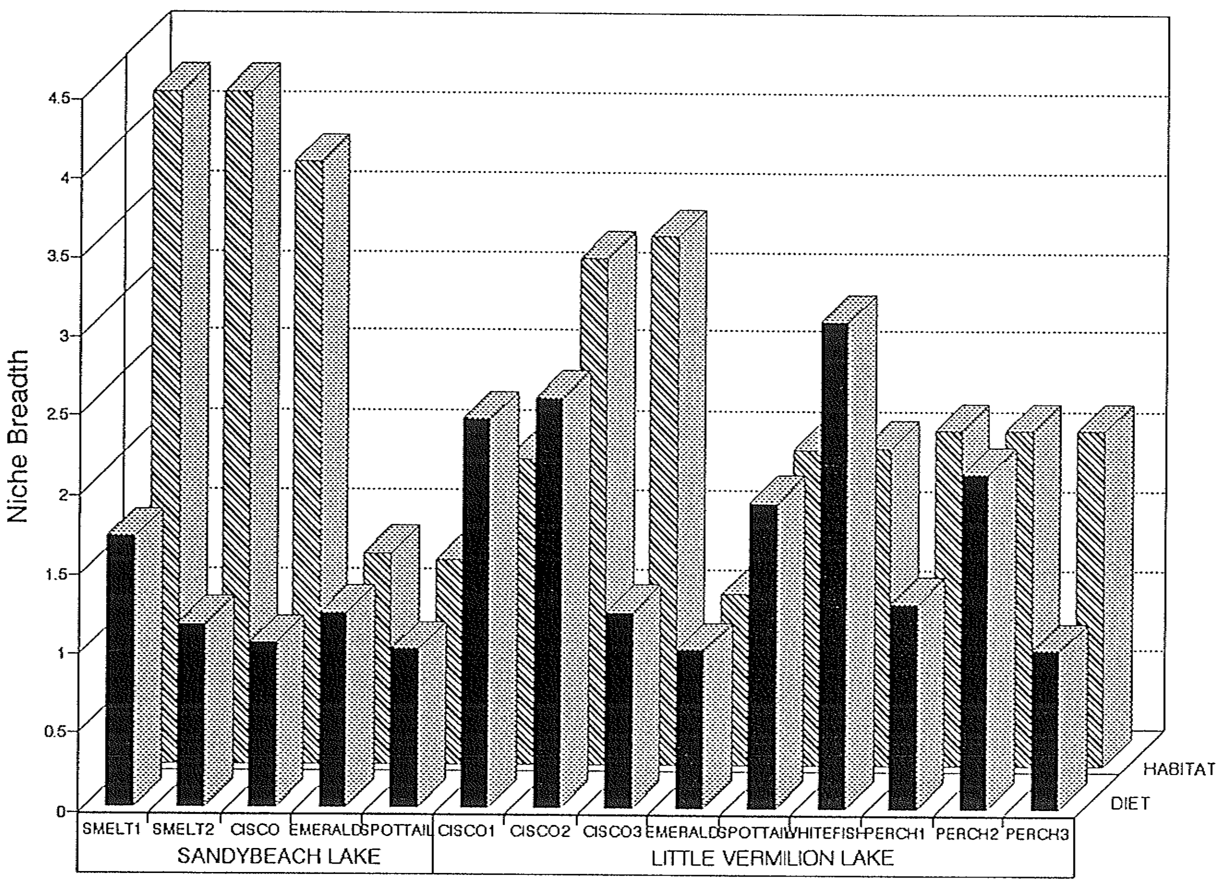


Fig. 38. Habitat and diet niche breadths of pelagic fish species caught in Sandybeach and Little Vermilion Lake in July 1990. Note that smelt1=69-84 mm FL, smelt2=85-125 mm FL, cisco1=50-70 mm FL, cisco2=100-125 mm FL, cisco 3=130-175 mm FL, perch1=35-50 mm FL, perch2=60-80 mm FL, perch3=95-115 mm FL.

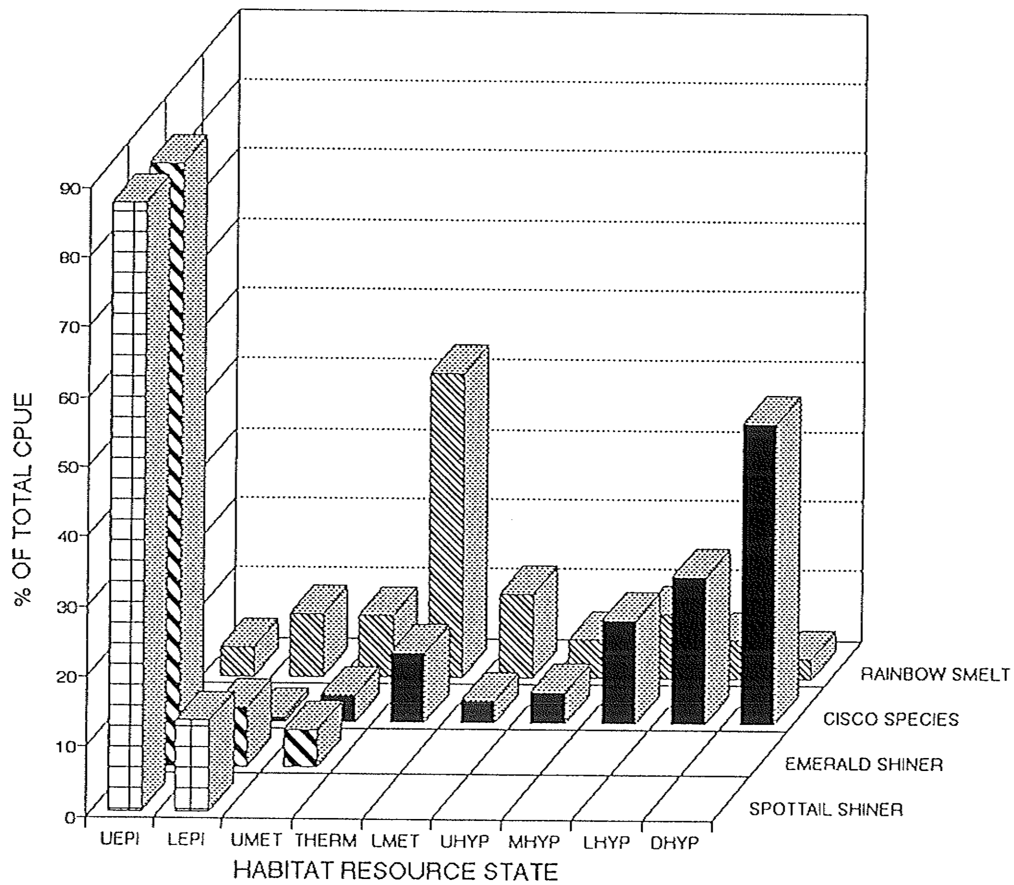


Fig. 39. Proportional habitat utilization by pelagic fish species during the period of dusk to dawn during summer stratification for the combined 22 and 37.5 m sites in Sandybeach Lake

1.4%. Like emerald shiner, spottail shiner had a relatively narrow habitat niche breadth compared to rainbow smelt.

Emerald and spottail shiner overlapped 94.7% in habitat and 44.8% in diet and had similar habitat distributions and habitat and diet niche breadths indicating that these two species shared a similar niche when utilizing the pelagic zone.

Sympatric Niche Overlap in Little Vermilion Lake

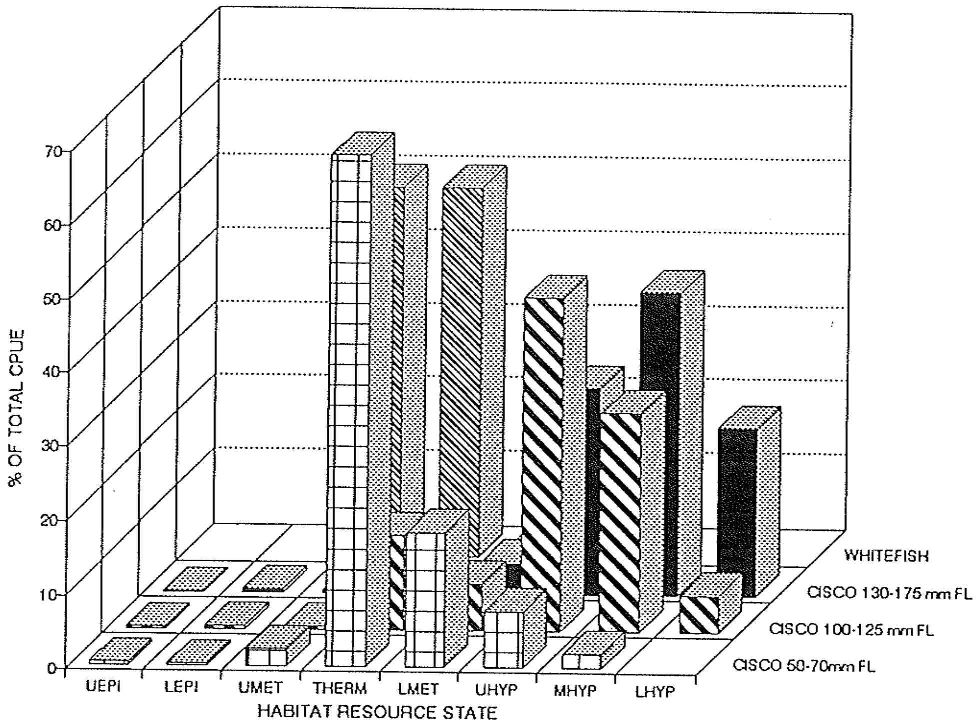
Niche overlap among size-classes in the cisco population in Little Vermilion Lake decreased with increasing length differential between groups (Table 12). The trend in the cisco population in Little Vermilion Lake was for the smaller cisco to occupy the layers closer to the surface with progressively larger cisco occupying deeper layers (Fig. 40a). Diet showed a similar trend: an increase in cisco length corresponded with a diet consisting of larger prey. The two largest cisco size-classes had relatively wide habitat niche breadths compared to the smallest cisco, while the two smaller size-classes of cisco had relatively wide diet niche breadths compared to the largest cisco. Overall, cisco size-classes were segregated to some extent in both habitat and diet.

Cisco of 50-70 mm FL overlapped with juvenile lake whitefish 53.4% in habitat and 15.5% in diet. The high overlap in habitat related to the distribution of each group primarily within the thermocline, while the low overlap in diet related to the more varied diet of the juvenile lake whitefish and the utilization of larger prey items. Juvenile lake whitefish shared many of the same prey items with cisco 100-125 mm FL; however cisco utilized deeper habitat and as they got larger they shared fewer prey species.

Cisco of all size-classes were segregated from yellow perch in habitat utilization (overlap in habitat was only 0.7%) because yellow perch utilized the warmest surface waters whereas cisco occupied the thermocline and the layers

TABLE 12. Sympatric niche overlaps (%) among pelagic species and size classes from Little Vermilion Lake for habitat/diet. Bold indicates species combinations where overlap exceeds 50% in at least one resource. Cisco1=50-70 mm, Cisco2=100-125 mm, Cisco3=130-175 mm, Whitefish 79-90 mm, Perch1=35-50 mm, Perch2=60-80 mm, Perch3=95-115 mm.

	Cisco 1	Cisco 2	Cisco 3	White-fish	Perch 1	Perch 2	Perch 3	Emerald shiner
Cisco 2	29.6 / 17.1	-	-	-	-	-	-	-
Cisco 3	17.8 / 0	**70.1 / 5.1**	-	-	-	-	-	-
White-fish	**52.4 / 15.5**	13.3 / 32.3	3.7 / 10.8	-	-	-	-	-
Perch 1	0.7 / 4.8	0.8 / 5.0	0.7 / 43.8	0 / 8.7	-	-	-	-
Perch 2	0.7 / 2.8	0.8 / 3.4	0.7 / 17.9	0 / 7.2	**100 / 20.7**	-	-	-
Perch 3	0.7 / 0	0.8 / 0	0.7 / 0	0 / 0	**100 / 0**	**100 / 0**	-	-
Emerald shiner	0.7 / 0	0.8 / 0.4	0.7 / 0	0 / 0	**51.2 / 0**	**51.2 / 29.4**	**51.2 / 0**	-
Spottail shiner	6.9 / 0	5.4 / 6.8	5.2 / 4.3	0 / 4.1	44.0 / 0	44.0 / 20.1	44.0 / 0	**85.7 / 20.1**



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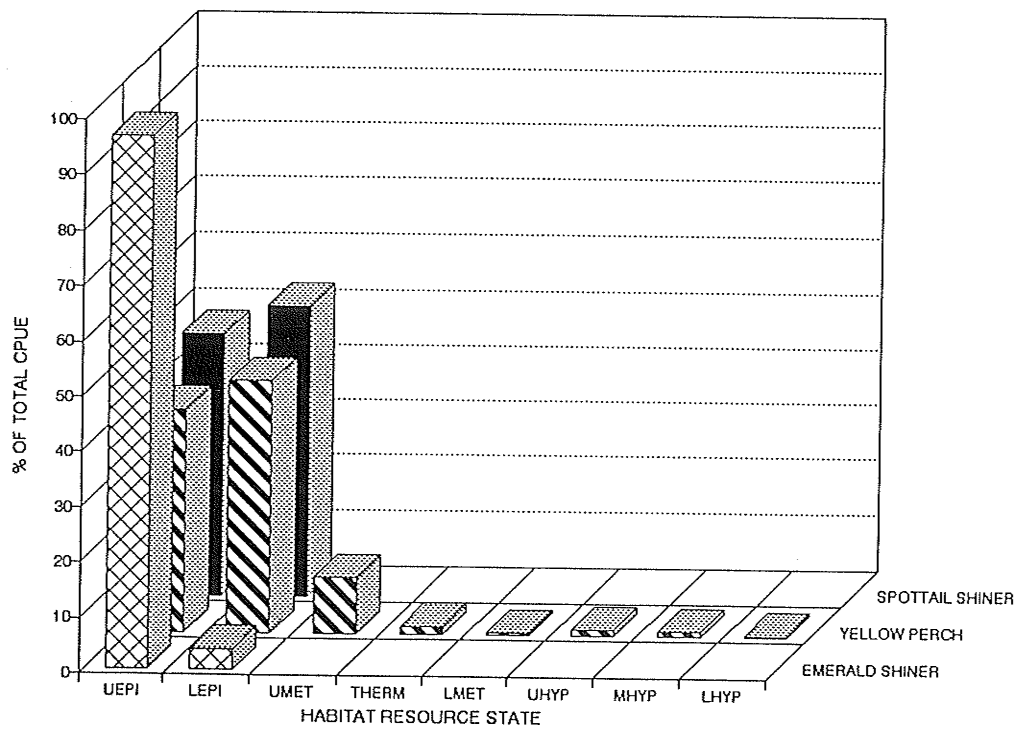

b

Fig. 40. Proportional habitat utilization by pelagic fish species during the period of dusk to dawn during summer stratification for the 22 m site in Little Vermilion Lake.

below. The smallest yellow perch utilized the largest planktonic prey and thus overlapped to a limited extent (43.8%) with the largest size-class of cisco.

Yellow perch of all size-classes overlapped in habitat with emerald shiner and spottail shiner to some extent (51.2 and 44.0% respectively) with all species prevalent within the warmer waters of the epilimnion (Fig. 40b), although emerald and spottail shiner were found closer to the surface. Only yellow perch 60-80 mm FL overlapped in diet with the shiners, with each species utilizing floating insects to some degree. This probably was a prey of opportunity rather than a limited resource as there were large emergences of insects during the course of the study.

Yellow perch of different size-classes shared the same habitat; however they utilized larger prey with increasing size, thus minimizing diet overlap.

Allopatric Niche Overlap between Sandybeach and Little Vermilion Lakes

Cisco of 50-70 mm FL from Little Vermilion Lake overlapped 65.8% in habitat with both size-classes of rainbow smelt from Sandybeach Lake but overlapped in diet only 24.3% with rainbow smelt of 69-84 mm FL and even less (1.7%) with rainbow smelt of 85-125 mm FL (Table 13). Rainbow smelt from Sandybeach Lake had high overlap in habitat with the smallest cisco from Little Vermilion Lake, primarily due to the distribution of the majority of individuals from each group within the thermocline (Fig. 41). Diet overlap between these two species related to a shared preference for larger zooplankton prey as both increased in size.

Rainbow smelt overlapped 52.3% in habitat with Little Vermilion Lake juvenile lake whitefish. Rainbow smelt 69-84 mm FL overlapped 67.9% in diet, but rainbow smelt 85-125 mm FL overlapped only 8.8% in diet with juvenile lake whitefish. Rainbow smelt had high overlap with lake whitefish due to the primary utilization of the thermocline by each species, although overall habitat distribution of these

TABLE 13. Allopatric niche overlaps (%) among pelagic species and size classes from Sandybeach and Little Vermilion Lakes for habitat/diet. Bold indicates species combinations where overlap exceeds 50% in at least one resource. Smelt1=69-84 mm, smelt2=85-125 mm, cisco species=cisco & shortjaw cisco, cisco1=50-70 mm, cisco 2=100-125 mm, cisco3=130-175mm, perch1=35-50 mm, perch2=60-80 mm, perch3=95-115 mm FL.

LVL SBL	Cisco 1	Cisco 2	Cisco 3	White -fish	Perch 1	Perch 2	Perch 3	Emerald shiner	Spottail shiner
Smelt 1	**65.8** **24.3**	40.1 35.4	27.2 24.9	**52.3** **67.9**	25.9 24.1	25.9 7.4	25.9 0	7.9 0	13.0 1.4
Smelt 2	**65.8** **1.7**	40.1 2.9	27.2 45.3	**52.3** **8.8**	25.9 44.9	25.9 19.7	25.9 0	7.9 1.4	13.0 1.7
Cisco species	21.7 0	45.0 1.0	47.2 45.0	13.5 6.7	0.6 43.8	0.6 17.9	0.6 0	0.6 0	8.4 0.2
Emerald shiner	3.1 0	1.3 5.6	1.1 4.3	5.3 4.1	**90.1** **0**	**90.1** **29.4**	**90.1** **0**	**75.6** **44.8**	**53.9** **25.3**
Spottail shiner	0.7 0	0.7 0.4	0.7 0	0 0	**90.8** **0**	**90.8** **29.4**	**90.8** **0**	**60.4** **100**	**53.2** **20.1**

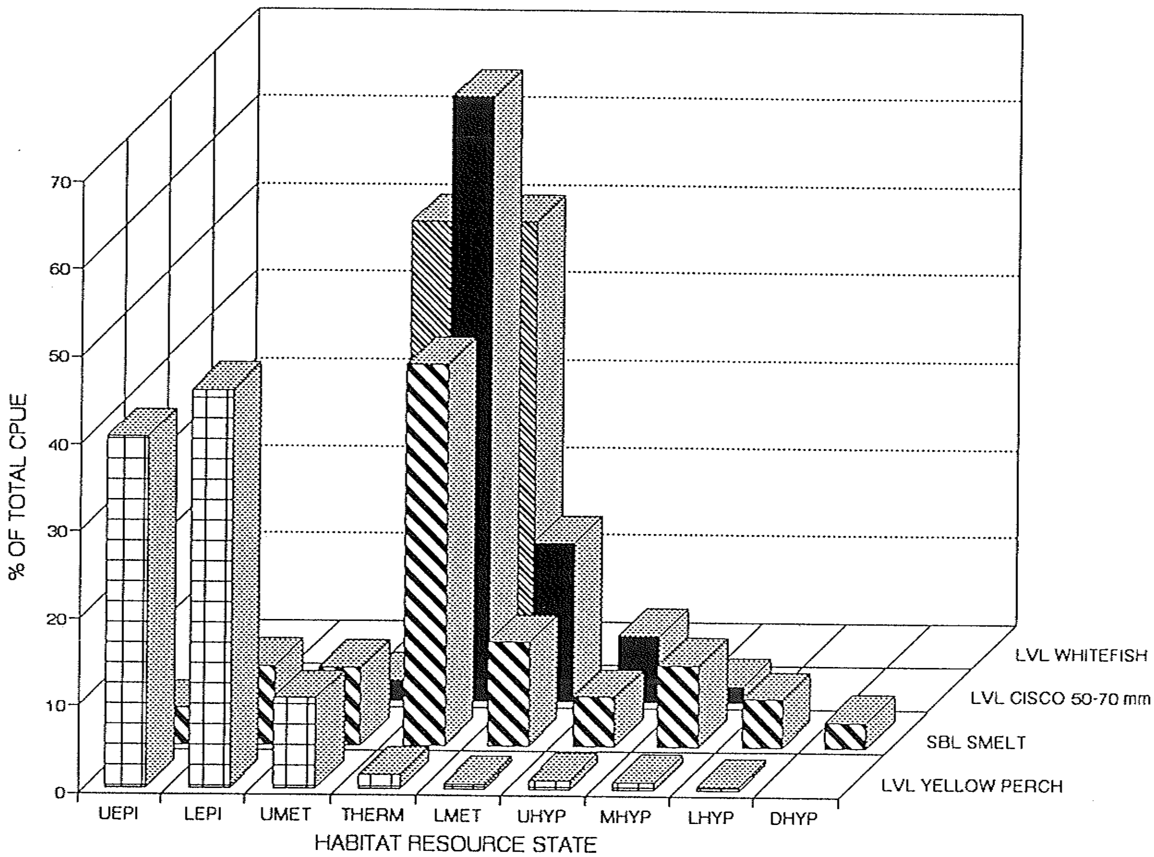

Fig. 41. Comparison of habitat utilization of rainbow smelt from Sandybeach Lake with cisco 50-70 mm FL, lake whitefish and yellow perch from Little Vermilion Lake during summer stratification.

species contrasted, with rainbow smelt having very high habitat niche breadth and lake whitefish having very low habitat niche breadth. Diet was very similar between smaller rainbow smelt and lake whitefish because both species utilized smaller zooplankton types.

The smaller yellow perch size-class in Little Vermilion Lake overlapped more with rainbow smelt in allopatry (25.9% in habitat and 24.1% in diet) than with any of the species with which they were sympatric in Little Vermilion Lake. This was primarily due to the utilization of the upper metalimnion and large zooplankton by both species.

The larger cisco and shortjaw cisco (the only size-class of cisco in Sandybeach Lake) overlapped to the greatest degree with the corresponding size-class of cisco from Little Vermilion Lake (47.2% in habitat and 45.0% in diet). However this overlap was less than would be expected because the cisco species in Sandybeach Lake utilized the deepest layers associated with the bottom, while cisco in Little Vermilion Lake primarily occupied the mid-hypolimnion which was not associated with the bottom (Fig. 42). Dietary differences between these two groups related to the percentage of various prey types consumed as opposed to the utilization of different prey types.

Sandybeach cisco species overlapped to a greater degree in habitat with lake whitefish in allopatry than did the corresponding size-class of cisco from Little Vermilion Lake did in sympatry (13.5% versus 3.7%). This related to a larger percentage of Sandybeach Lake cisco utilizing the thermocline compared to the same size-class of cisco in Little Vermilion Lake.

As in the sympatric overlap between cisco and yellow perch in Little Vermilion Lake, the cisco and shortjaw cisco in Sandybeach Lake inhabited colder, deeper water compared to the warmer water occupied by yellow perch and as a result overlap was low (0.6%). Utilization of the largest zooplankton types resulted in relatively high overlap in diet (43.8%) between Sandybeach Lake cisco species

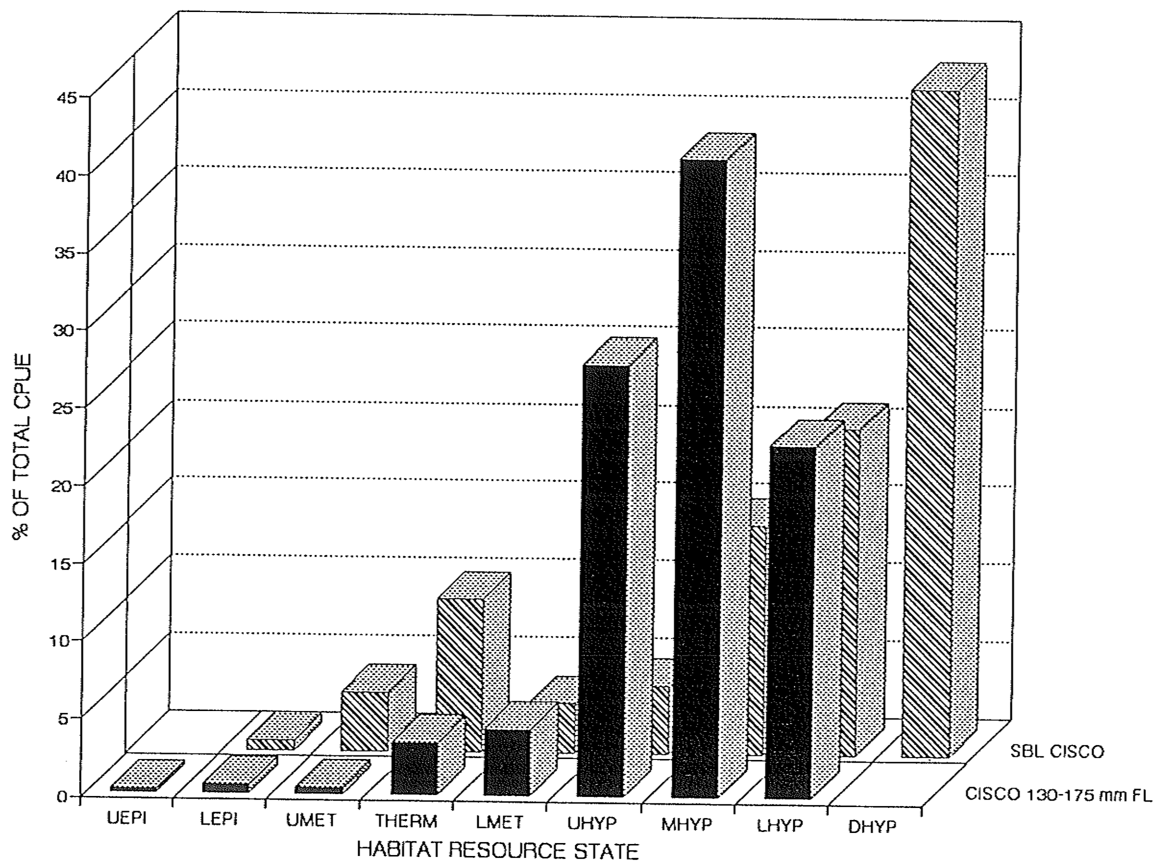

Fig. 42. Comparison of habitat utilization by cisco and shortjaw cisco in Sandybeach Lake and the largest size class of cisco (130-175 mm FL) from Little Vermilion Lake during summer stratification.

and small yellow perch of Little Vermilion Lake.

Allopatric overlap in habitat was high (90.1%) between emerald shiner from Sandybeach Lake and yellow perch from Little Vermilion Lake as it was in sympatry within Little Vermilion Lake. Diet overlap between yellow perch 60-80 mm FL and emerald shiner (29.4%) related to the utilization of emerging insects which were abundant on the surface of both lakes at the time this study was undertaken.

Emerald shiner from Sandybeach Lake overlapped 75.6% in habitat and 44.8% in diet with emerald shiner from Little Vermilion Lake. Habitat utilization of this species was almost identical between lakes, except that a few emerald shiner were caught in the upper metalimnion in Sandybeach Lake, a habitat primarily occupied by rainbow smelt in Sandybeach Lake and yellow perch in Little Vermilion Lake. Diet differed in the proportion of prey utilized as opposed to the type of prey.

Emerald shiner from Sandybeach Lake overlapped 53.9% in habitat and 25.3% in diet with spottail shiner from Little Vermilion Lake while emerald shiner from Little Vermilion Lake overlapped 60.4% in habitat and 100% in diet with spottail shiner from Sandybeach Lake. In the latter case both species were utilizing emerging insects (probably in an unlimited supply during the emergence) in the respective lakes resulting in complete diet overlap.

Spottail shiner from Sandybeach Lake overlapped 90.8% in habitat with pelagic yellow perch of all size-classes from Little Vermilion Lake. Spottail shiner shared a similar dietary preference for emerging insects with yellow perch 60-80 mm FL.

Spottail shiner from Sandybeach Lake overlapped 53.2% in habitat and 20.1% in diet with spottail shiner from Little Vermilion Lake. The identical habitats were used by this species in both lakes but in slightly different proportions, perhaps an artifact of low abundance. Dietary differences related to proportion of prey utilized as opposed to type of prey (emerging insects and algae).

Zooplankton

Zooplankton were counted from samples collected by a 28.7 litre capacity Schindler (1969) trap in Sandybeach Lake on July 13 and 21, 1990 and in Little Vermilion Lake on July 27, 1990 (Table 14). These limited data indicate that most of the large zooplankters in Sandybeach Lake on July 13, 1990 were concentrated near the surface (0.25-m) where 8 small calanoid copepods and 25 small cladocerans were captured, or near the bottom (19-m) where 25 small calanoid copepods, 15 large cladocerans and 20 small cladocerans were captured. A similar pattern of distribution occurred in Sandybeach Lake on July 21 but the abundance of zooplankton was lower. Five large calanoid copepods, 7 small calanoid copepods and 8 small cladocerans were captured at 0.25-m while 9 small calanoid copepods and 4 large cladocerans were captured at 19-m.

Zooplankters were more abundant in Little Vermilion Lake and more were large zooplankters, especially large calanoid copepods captured in the epilimnion and metalimnion. Catches in the two traps were as follows: at 0.25-m, 39 large calanoid copepods and 16 small cladocerans; at 3.5-m, 45 large calanoid copepods, 10 small calanoid copepods and 29 small cladocerans; at 8.5-m, 26 large calanoid copepods, 10 small copepods and 20 small cladocerans; at 12.7-m, 15 large calanoid copepods, 25 small calanoid copepods and 25 small cladocerans were captured and at 19-m, 19 large calanoid copepods.

TABLE 14. Zooplankton counts from Schindler (1969) trap samples taken in Sandybeach and Little Vermilion Lakes in July 1990. Each count represents two combined hauls.

		Sandybeach Lake	Sandybeach Lake	Little Vermilion
Depth (m)	prey type	July 13/90	July 21/90	July 27/90
0.25	l. Calanoida	3	5	39
	s. Calanoida	8	7	5
	l. Cladocera	0	0	0
	s. Cladocera	25	8	16
	l. Cyclopoida	2	2	4
3.5	l. Calanoida	0	1	45
	s. Calanoida	1	4	10
	l. Cladocera	0	0	0
	s. Cladocera	5	0	29
	l. Cyclopoida	0	0	6
8.5	l. Calanoida	6	0	26
	s. Calanoida	4	4	10
	l. Cladocera	0	0	0
	s. Cladocera	3	0	20
	l. Cyclopoida	1	0	3
13.7	l. Calanoida	4	0	15
	s. Calanoida	3	3	25
	l. Cladocera	0	0	0
	s. Cladocera	3	0	25
	l. Cyclopoida	0	0	5
19	l. Calanoida	3	1	19
	s. Calanoida	25	9	3
	l. Cladocera	15	4	0
	s. Cladocera	20	0	5
	l. Cyclopoida	0	0	2

DISCUSSION

This study compared the population dynamics and utilization of habitat and food resources of pelagic fish species and size-classes in two lakes, one in allopatry and the other in sympatry with rainbow smelt. The assumption governing these comparisons was that the fish community in Little Vermilion Lake (allopatric community) is representative of the fish community that existed in Sandybeach Lake (sympatric community) prior to rainbow smelt invasion. Carpenter (1989) suggested that regional correlations among lakes can substantially increase the sensitivity of ecosystem experiments since climatic factors and food web dynamics are the major source of variability that affect whole-lake experiments. In this study Little Vermilion Lake was found to be the most similar lake to Sandybeach Lake within the local region in terms of biological, chemical and physical characteristics. Both lakes are headwater lakes with virtually identical fish and zooplankton communities isolated from surrounding riverine species. Both lakes are deep, cold and clear with the same thermal regimes during summer stratification. Both lakes have limited human development and are only used for recreational purposes. Apparent differences between lakes involve physical geography, whereby Little Vermilion has much more shoreline development but less extensive littoral habitat and a lower mean and maximum depth in comparison to Sandybeach Lake. These differences may be important when considering vertical and horizontal distributions of pelagic fish species because of their impact on primary production (i.e. light penetration, nutrient cycling etc.).

Assuming that the pelagic community in Little Vermilion Lake is representative of that which occurred in Sandybeach Lake prior to rainbow smelt invasion, it is obvious that a number of dramatic transformations have taken place. The following discussion focuses on each species within each lake and the differences, if any, between lakes.

Rainbow smelt

Rainbow smelt dominated the pelagic community in Sandybeach Lake, both in abundance and in their use of available habitats. Rainbow smelt in Sandybeach Lake were relatively small for age at capture compared to populations in other oligotrophic communities (Bailey 1964; Saunders and Power 1970; Evans and Loftus 1987) and had a population structure dominated by the two most recent year classes. Very few large specimens were taken. This probably was not due to gear effects, because many rainbow smelt were caught by the teeth and larger and varied mesh sizes were utilized. A more likely explanation is a lack of older, larger specimens. This hypothesis would be consistent with the relatively recent arrival of rainbow smelt in Sandybeach Lake as they were only confirmed to exist there in 1989 (pers. comm. Dave Reid, OMNR Sioux Lookout). The recent colonization of Sandybeach Lake by rainbow smelt and their high abundance may explain why there are few older and larger rainbow smelt. Rainbow smelt are known to colonize lakes rapidly (Schmulbach 1985; McLain and Magnuson 1988) and are able to affect the size structure of the zooplankton community by size selective predation (Reif and Tappa 1966; Lammens et al. 1985; Seigfried 1987). The abundance of rainbow smelt in Sandybeach Lake appears to have reduced the numbers of larger plankton species, because their abundance in Sandybeach Lake was much lower than in Little Vermilion Lake. Rainbow smelt are obligate planktivores of marine origin and are able to utilize very small plankton in the absence of larger species (Zaret 1980), consequently there may be a bottleneck whereby the lack of an abundant large prey source has curtailed rainbow smelt growth, creating a "stunted" population (Werner and Gilliam 1984; Personn 1987). An analogous population explosion in bloater (*Coregonus hoyi*) occurred in Lake Michigan after the alewife (*Alosa pseudoharengens*) die-off in 1967. Brown et al. (1987) found that the growth and size at age of bloater decreased as a result of intense intraspecific competition for food and its subsequent depletion.

Rainbow smelt in Sandybeach Lake fed almost exclusively on zooplankton. Large calanoid copepods were the most prevalent and probably selected type because they were the largest zooplankton available (MacCrimmon et al. 1983). There was no evidence of predation by rainbow smelt on native fishes in Sandybeach Lake perhaps because of the small size of the rainbow smelt (Evans and Loftus 1987), sampling techniques (Crowder 1980) or low overlap or availability of suitable prey. The absence of fish in rainbow smelt stomachs probably was not an artifact of sampling procedures in this study because many of the specimens were captured live with stomach contents intact. Also, the low water temperatures during the spring sampling would have inhibited digestion after capture. The most likely explanation is a lack of prey availability or a preference of the relatively small rainbow smelt in Sandybeach Lake for smaller prey items. This lack of predation by rainbow smelt on larval fishes suggests that predation is not an important contributing factor to the interaction of rainbow smelt with the native coregonids or other species in Sandybeach Lake.

The spring distribution of rainbow smelt in the water column of the pelagic zone of Sandybeach Lake during the period from dusk to dawn was random but greater numbers were concentrated in nearshore areas. This was similar to the findings of Wells (1968) who indicated that rainbow smelt were scattered throughout the water column after spawning but were primarily in shallow water. Dahlberg (1981) also found that rainbow smelt remained in nearshore areas during the evening in the spring until temperatures in those areas exceeded 13°C.

During summer stratification, the distribution of rainbow smelt from dusk to dawn was in offshore areas primarily in the thermocline (10-16°C) but also in the epilimnion (up to 22°C) and scattered throughout the hypolimnion. Rainbow smelt were primarily distributed within the thermocline during this period but the large numbers of rainbow smelt in the lake has probably caused the rainbow smelt population to expand into marginal habitats, such as the epilimnion, in order to reduce intraspecific competition (Selander 1966). This high habitat niche breadth in the pelagic zone implies that rainbow smelt are a very plastic species. This would favour it over more specialized species if there were fluctuations in the amount of preferred resources (Moermond 1979). The distributions of rainbow smelt observed in this study were similar to those observed by Brandt et al. (1980), who found that thermal distribution of adult rainbow smelt in Lake Michigan during the summer months occurred at modal temperatures of 11-16°C. Ferguson (1965) found that rainbow smelt usually occupied the thermocline but often ascended into the epilimnion. Franzin et al. (1990) also noted that adult rainbow smelt had a greater tolerance to higher temperatures than is generally reported. They found rainbow smelt in waters at temperatures as high as 21°C in Two Island Lake, ON. in late summer. Distributions of rainbow smelt and other species were not limited by oxygen conditions which were satisfactory at all depths as demonstrated by catches in the deepest part of the lake and the formation of schools on the bottom during the daytime.

Cisco species

Cisco were dominant in the pelagic zone of Little Vermilion Lake (rainbow smelt absent) both in terms of abundance and breadth of habitat utilization. During summer stratification cisco were partially segregated based on the size-classes present, similar to the findings of Fry (1937) and Rudstam and Magnuson (1985). The small juvenile cisco predominated in the thermocline, the next largest cisco in the upper hypolimnion, and the largest cisco in the lower hypolimnion. The very low habitat niche breadth of juvenile cisco, primarily the thermocline and upper metalimnion, implies a high degree of specialization. This would make them susceptible to exclusion if confronted by a superior competitor (Moyle et al. 1986) with a similar temperature preference. The other two size-classes of cisco had relatively high habitat niche breadths and utilized most of the pelagic zone except for the warmest epilimnetic waters. This implies that they could avoid intraspecific or interspecific competition by shifting to the least contested habitat within their fundamental niche (Schoener 1974).

Segregation of cisco size-classes was enhanced by dietary differences which related to the size of zooplankton that were taken. Juvenile cisco took a variety of items including cyclopoid copepods, calanoid copepods, cladocerans and *Pontoporeia affinis*. Larger cisco fed primarily on calanoid copepods, algae, chironimid larvae and *Mysis relicta*. This diet was consistent with diets of cisco from other oligotrophic lakes (Dryer and Beil 1964; Anderson and Smith 1971b)

Two species of cisco occurred in Sandybeach Lake; the rare shortjaw cisco (*Coregonus zenithicus*), and the more abundant cisco (*C. artedi*). Anderson and Smith (1971b) noted that shortjaw cisco in Lake Superior fed primarily on *Pontoporeia affinis* and *Mysis relicta* with micro-crustaceans making up only a small percentage volume of the diet. Scott and Crossman (1973) further described shortjaw cisco as a deepwater species of cisco. These subtle differences may enable the adult shortjaw cisco to find refuge from rainbow smelt in the deep hypolimnion, since this was the least utilized habitat of rainbow smelt from the period of dusk to dawn during summer stratification. The ecology of larval and juvenile shortjaw cisco is unknown. If it is similar to that of cisco then the recruitment success of the species during this critical period also may be parallel. Shortjaw cisco in the Laurentian Great Lakes declined along with cisco after the introduction of rainbow smelt (Christie 1974; Houston 1988). Other than the morphological and meristic differences, there was no difference in diet between shortjaw and cisco noted during this study. Because this species was identified in the laboratory after other analyses were completed any differences in habitat utilization that may have been apparent could not be distinguished from those of cisco. As a result shortjaw cisco were lumped with cisco in describing the cisco population in Sandybeach Lake and for ecological comparisons with other species within and between lakes.

Cisco (shortjaw cisco and cisco) in Sandybeach Lake (sympatric with rainbow smelt) have suffered poor recruitment in recent years. The apparent absence of recent year classes, the low relative abundance of the year classes present, their poor relative condition and the high female to male sex ratio suggest that the cisco population in Sandybeach Lake is in decline. A similar rapid decline in cisco abundance occurred in Sparkling Lake, Wisconsin, a small oligotrophic lake where cisco were the most abundant species in 1981 but were replaced by rainbow smelt as the most abundant species by 1985 (McLain and Magnuson 1988). Since 1982 no young-of-the-year or yearling cisco have been captured in Sparkling Lake (McLain and Magnuson 1988).

In the present study very high niche overlap between juvenile cisco and rainbow smelt in allopatry was found. The lack of juvenile cisco in the sympatric environment suggests that rainbow smelt have excluded juvenile cisco either through interference or exploitation competition (Schoener 1974). Interference competition may be in the form of aggression by rainbow smelt, an avoidance reaction by cisco, or a niche shift by cisco caused by a change in the availability of preferred resources. The physical displacement of cisco by rainbow smelt has been implicated in previous studies. Anderson and Smith (1971a) suggested that concentrations of rainbow smelt on cisco spawning grounds in the Duluth area of Lake Superior during the spawning season may have crowded cisco off the grounds, thus impairing spawning. Rudstam and Magnuson (1985) found that young-of-the-year cisco moved out of the thermocline of Sparkling Lake into deeper water occupied by older cisco and sometimes even deeper. They suggested that the younger cisco may have been avoiding the rainbow smelt that were occupying the thermocline as one possible reason for this shift.

Exploitation competition is competition for limited resources that are utilized to some extent by each competitor (Schoener 1974). Anderson and Smith (1971a) believed that competition for copepods between adult rainbow smelt and larval cisco has contributed to the decline of cisco in western Lake Superior. They noted that larval cisco are dependent on copepods and suggested that this could be a limiting factor in cisco year-class success. Braum (1967) found that the coincidence of the shift from yolk to exogenous feeding with decreased food availability seems to be the most important factor causing high mortality rates of cisco larvae. Similarly, Rice et al. (1987) suggested that starvation or low food availability may indirectly contribute to mortality because reduced growth and swimming capability of young fish may result in increased or prolonged susceptibility to predation. Zooplankton sampling was not extensive in this study but data collected suggest that zooplankton were less abundant in the sympatric environment, particularly in the epilimnetic and metalimnetic strata where young cisco normally spend their first few years. The high abundance of rainbow smelt suggests that they have taken full advantage of the available food resources while excluding other pelagic species such as cisco.

Feeding strategy may be one of the mechanisms whereby rainbow smelt could prevail over cisco. Both rainbow smelt and cisco utilize gulping type strategies to feed on zooplankton (Janssen 1980). However an obligate marine planktivore such as rainbow smelt may be able to utilize filter feeding as an alternative strategy which would allow them to feed on smaller types of plankton to meet their energy needs (Crowder and Binkowski 1983). Janssen (1978) found that alewife, a marine planktivore like rainbow smelt introduced into freshwater environments, were able to use filtering as an alternative feeding method in the laboratory. Janssen (1978) believed that the inclusion of filtering in the alewife's repertoire probably meant that it could respond to a broader range of feeding conditions in the pelagic environment than non-filtering freshwater species such as cisco. If rainbow smelt are able to filter feed it would provide them with a competitive advantage over cisco when resources susceptible to gulping are in short supply.

A selective feeding strategy also may favour rainbow smelt over cisco in a small lake with a limited variety of food types. Engel (1976) found that cisco were non-selective feeders in Pallette Lake, Wisconsin. Janssen (1980) also found that gulping by cisco in darkness, when cisco feed (Emery 1973), was non-selective. Janssen (1980) concluded that continuous non-selective feeding would shorten the life expectancy of cladocerans, but that population growth rate and average age and size would not change. However size-selective feeding, such as that exhibited by rainbow smelt, would shift the population to a smaller body size, possibly creating a shift in competitive ability of a cladoceran species and possibly an overall shift in zooplankton community structure (Seigfried 1987; Reif and Tappa 1966). Lammens et al. (1985) found that high densities of introduced European smelt *Osmerus eperlanus* in Lake Tjeukemeer, The Netherlands, so depressed the average size of *Daphnia hyalina* that they were no longer retained by the gill rakers of native mature bream (*Abramis brama*) which consequently suffered poor growth and gonad development. Similarly, Crowder et al. (1987) and Miller et al. (1990) found evidence that the increase in alewife abundance in Lake Michigan severely reduced zooplankton size and resulted in poor recruitment of native bloater and yellow perch.

The adult cisco remaining in Sandybeach Lake did not have a different diet than rainbow smelt and had very high overlap in diet with introduced rainbow smelt over 85-mm FL, in contrast to cisco in Sparkling Lake, Wisconsin, which fed on insects while rainbow smelt fed on zooplankton (McLain and Magnuson 1988). The cisco in Sandybeach Lake may have reduced competition for food with rainbow smelt by utilizing areas close to the bottom in the deeper and colder part of the lake thereby minimizing overlap in habitat. Compared to allopatric cisco of the same size-class from Little Vermilion Lake, the Sandybeach Lake cisco may have shifted their habitat niche, as indicated by relatively low habitat overlap between lakes and the primary utilization of areas off the bottom by Little Vermilion Lake cisco. This difference in habitat utilization may have been related to the lower dissolved oxygen concentrations in Little Vermillion Lake (Appendix 6), although levels were above avoidance levels (Rudstam and Magnuson 1985), or to the differences in maximum depths of the two lakes. Sandybeach Lake had a maximum depth of 41.0 m while Little Vermilion Lake was only 26.0 m deep. However it appears that cisco in Sandybeach Lake are utilizing habitat colder than would be predicted based on preferences (Rudstam and Magnuson 1985). The greatest concentration of large zooplankton in Sandybeach Lake was captured in the lower and deep hypolimnion; thus it appears that by shifting habitat the cisco have benefitted by releasing themselves from interspecific competition with rainbow smelt while at the same time increasing dietary resource availability (Dill 1983). It is also possible that many of the cisco inhabiting deep water are shortjaw cisco. A higher survivorship of shortjaw cisco in the deep pelagic zone compared to cisco in shallower pelagic areas would make it appear that the overall cisco population had shifted to deeper water. A habitat shift by cisco (or higher survivorship of shortjaw cisco) in the presence of rainbow smelt is consistent with the competition theories of Moermond (1979), who indicated that the short-term effects of the addition of competitors to a community are a reduction in abundance or elimination of certain prey types. Subsequently this would result in an increase in the range of items included in the diet of the native species or cause them to restrict their foraging to habitat patches where the new competitor has had the least effect.

Although it appears that the sympatric adult cisco have reduced competition for food with rainbow smelt by shifting habitats from just below the metalimnion to the deep hypolimnion, it also seems that the overwhelming abundance of rainbow smelt has reduced food resources in Sandybeach Lake to the point that the condition (weight at length) of cisco is lower than that of cisco from Little Vermilion Lake. A lower population density would be expected to improve the condition of the remaining population because of increased resources released from intraspecific competition (Healey 1980; Henderson et al. 1983). However as the density of the cisco has decreased in Sandybeach Lake there has been a concomitant increase in rainbow smelt numbers fully exploiting available food resources and more than compensating for the decline in cisco abundance.

The prospects of a recovery of cisco in Sandybeach Lake appear to be remote. The high female to male ratio of the cisco in Sandybeach Lake is indicative of a population suffering from density dependent stress (Brown 1970; Brown et al. 1987). George (1977) suggested that the change in sex ratio in cisco species is under the control of the neuroendocrine system and represents a response to intraspecific and interspecific population density. Brown et al. (1987) indicated that the reproductive inefficiency that results from female predominance may result in a decrease in population via a decrease in fertilized eggs. The cisco spawning cycle involves as many as a dozen males following a single female early in the season, with two males to each female more normal late in the season (Scott and Crossman 1973). The female predominance in Sandybeach Lake, combined with low relative abundance and potentially low relative fecundity (as a consequence of low relative condition) suggests that spawning success of cisco in Sandybeach Lake may be poor. These factors combined would result in poor recruitment.

Low numbers of adult cisco in Sandybeach Lake may make them more susceptible to predation. Both cisco and smelt species form schools and occupy areas close to the bottom during the day (Dembinski 1976; Crowder 1980, Heist and Swenson 1983). Schooling fishes typically form schools of individuals of the same size range (Radovich 1979). Since the cisco were much larger than rainbow smelt in Sandybeach Lake in length and were broader in aspect they would be expected to form schools separate from rainbow smelt. Clarke (1974) suggested that the efficiency of schools for reducing predation would decrease as school size decreased. He suggested that beyond a critical point a small decrease in population size would result in a population collapse and possible extinction as a result of increased predation. Although the relative abundance of lake trout in Sandybeach Lake is not known, Evans and Waring (1987) demonstrated that lake trout have a dominant effect on the population structure of pelagic prey species such as rainbow smelt and cisco in Lake Simcoe. The larger size and greater susceptibility of cisco as a consequence of occurring in smaller schools and their shift to deeper habitat probably would make them the most attractive prey for lake trout in Sandybeach Lake. It was noted during the study that cisco entangled in the gill nets were the only target species of toothy predators (most likely lake trout or burbot) on at least 15 occasions where there were remains from attacks.

Although predation on larval cisco does not appear to be the mechanism for rainbow smelt dominance over cisco, it may be an additional factor that precludes recruitment success in the future. Previous studies have indicated that rainbow smelt are unlikely to overlap with pelagic larvae in the epilimnion (Evans and Loftus 1987). However in Sandybeach Lake rainbow smelt were utilizing the epilimnion in high relative abundance and occurred near the surface at temperatures as high as 22°C. Rainbow smelt are known to prey upon larval cisco in other waters (Anderson and Smith 1971b; Selgeby et al. 1978) and it is the contention of Loftus and Hulsman (1986) that high predation rates on larval coregonids by rainbow smelt would seriously affect the recruitment success of these fish in a small lake. Similarly Crowder (1980) suggested that predation by rainbow smelt on the early life history stages of cisco may have played an important role in their decline in the Laurentian Great Lakes.

Lake whitefish

Juvenile lake whitefish in Little Vermilion Lake, although not caught in abundance, primarily utilized the upper metalimnion and thermocline from dawn to dusk during summer stratification and fed on a variety of zooplankton including cladocerans and cyclopoid and calanoid copepods. These findings are consistent with those of Reckahn (1970) who found that schools of juvenile lake whitefish in South Bay of Lake Huron migrated to offshore areas but remained in relatively warm (17°C) water and fed primarily on cladocerans and other zooplankton. This high degree of habitat specialization (low niche breadth) of juvenile lake whitefish, combined with a low diet specialization (high niche breadth) probably allows the juvenile lake whitefish to coexist with young cisco. These species overlapped substantially in habitat but not in diet in Little Vermilion Lake. This dietary separation probably is related to the difference in length (and consequently particle size selection) between the species (Werner 1979). Lake whitefish were 30% larger than the cisco occupying the same habitat.

The low catch in relation to effort of juvenile lake whitefish in Little Vermilion Lake in comparison to juvenile cisco may have been caused by gill net selectivity whereby the size range of lake whitefish available may not have been susceptible to the mesh sizes presented. Small pelagic lake whitefish were caught in abundance in the thermocline in Lac Seul and Grassy Narrows Lake during research into rainbow smelt distributions in 1989. Over 100 were caught in one panel of an overnight gill net set suspended at the thermocline. These fish were caught in 8-mm mesh; bar measure, at a modal fork length of 65-mm (pers. obs.). This contrasts significantly with the length ranges encountered in Little Vermilion Lake (85-90-mm FL) which were caught in 10-mm bar mesh; bar measure.

No juvenile lake whitefish were caught in sympatry with rainbow smelt in Sandybeach Lake suggesting that they may have suffered a recruitment failure in the lake as a result of the introduction of rainbow smelt. Although there was a commercial fishery for lake whitefish on Sandybeach Lake a few years previous to this study (Appendix 7), it is doubtful that such a low intensity fishery would have reduced whitefish numbers to the point that there would be no recruitment. A more likely case might have been increased lake whitefish fecundity and the recruitment of smaller individuals into the system as a result of decreased intraspecific competition. The high overlap in habitat utilization and low habitat niche breadth of lake whitefish in allopatry with rainbow smelt suggests that in sympatry rainbow smelt may have eliminated juvenile lake whitefish from the contested space, apparently leaving the lake whitefish with no viable refugia. Evans and Waring (1987) suggested that age 0 rainbow smelt, being almost as large and more abundant than age 0 lake whitefish, probably placed an additional load on the food and space resources of the deep epilimnetic zone in Lake Simcoe in the 1970's. Competition for these resources may have caused the displacement of lake whitefish from their preferred habitat and resulted in higher mortality.

The diet of juvenile pelagic lake whitefish in allopatry seemed to be non-selective, indicating that whitefish would not affect the size or age distribution of their prey (Janssen 1980). The presence of selectively feeding rainbow smelt probably has affected the abundance of prey commonly used by lake whitefish, particularly the more readily caught cladoceran species (Drenner et al. 1978) that seemed to be lacking in the metalimnion of Sandybeach Lake.

The abundance of rainbow smelt has added an additional prey source for adult lake whitefish in Sandybeach Lake which they are exploiting. The addition of rainbow smelt, like the introduction of prey species in other systems, is negatively affecting recruitment of juvenile lake whitefish while potentially benefitting the adult population (Crossman and Larkin 1959; Li et al. 1976; Fast et al. 1982).

Potential predation by rainbow smelt on larval lake whitefish may preclude their successful comeback in Sandybeach Lake. Rainbow smelt were found to feed on larval lake whitefish in Twelve Mile Lake, Ontario (Loftus and Hulsman 1986) and it was believed that the high consumption rates on these larvae affected recruitment success. Populations of lake whitefish in Twelve Mile Lake previously had been under intensive recreational fishing pressure, and Loftus and Hulsman (1986) believed that predation would preclude any recovery after the fishery was closed.

Yellow perch

Yellow perch occupied the lower epilimnion and upper metalimnion of Little Vermilion Lake in the period from dusk to dawn during summer stratification where they were the most abundant species. Yellow perch often utilize the pelagic zone, usually in the warmer surface layers (Reckahn 1970, Engel and Magnuson 1976; Crowder and Magnuson 1982; Rudstam and Magnuson 1985). Small yellow perch forage in the pelagic zone where they have a competitive advantage over larger yellow perch (Persson 1987). Small yellow perch are efficient in catching micro-invertebrates due to their increased manueverability and their ability to see and to retain small prey (Persson 1987). Their ability to use the pelagic zone allows small yellow perch to escape from intraspecific and interspecific competition for micro-invertebrate prey in littoral areas of the lake (Persson 1987). The overall limitation of yellow perch to the epilimnetic waters of the pelagic zone is consistent with their preference for warmer water, usually temperatures of 19 to 21°C (Ferguson 1958; Brandt et al. 1980; Rudstam and Magnuson 1985). Yellow perch were caught in three size-classes (partially defined by gill net selectivity) which overlapped entirely in habitat niche breadth but, as found by Keast (1978), were separable based on diet, with the smaller yellow perch eating calanoid copepods, the next largest yellow perch eating insects and calanoid copepods, and the largest yellow perch eating fish.

Yellow perch seem to have been excluded from the pelagic zone of Sandybeach Lake in the presence of rainbow smelt. This is consistent with the findings of Rudstam and Magnuson (1985), who also noted the absence of yellow perch in the pelagic zone of Sparkling Lake, Wisconsin, a lake containing introduced rainbow smelt, even though yellow perch were known to occur in that lake. Small yellow perch in Little Vermilion Lake dominated the lower epilimnion, however in the sympatric community in Sandybeach Lake rainbow smelt were dominant in this habitat. This absence of intraspecific overlap between yellow perch allopatric and yellow perch sympatric with rainbow smelt implies a habitat shift by yellow perch in the environment sympatric with rainbow smelt from the pelagic zone into littoral areas. Persson and Greenberg (1990) using enclosure experiments, found that yellow perch (*Perca fluviatilis*) could be shifted from utilizing pelagic to benthic prey by increasing densities of roach (*Rutilus rutilus*), a competitor, like rainbow smelt, that feeds preferentially on pelagic resources. Yellow perch apparently were excluded from the pelagic lower epilimnetic habitat by rainbow smelt in Sandybeach Lake. However in Little Vermilion Lake, as in other lakes where yellow perch and cisco coexist, this warmer pelagic habitat probably was not contested by cisco because of differences in temperature preference between the two species (Engel and Magnuson, 1976; Rudstam and Magnuson 1985).

Small yellow perch, unlike juvenile cisco and lake whitefish, can occupy a refuge from rainbow smelt in littoral areas around macrophytes (Sandheinrich and Hubert 1984) and are opportunistic feeders (Scott and Crossman 1973). Sandybeach Lake had relatively extensive littoral areas compared to Little Vermilion Lake. Catches of yellow perch in shallow sets in Sandybeach Lake suggest that the realized niche of yellow perch in this lake was reduced or limited to the littoral areas of the lake. The reduction in the availability of pelagic habitats for small yellow perch in Sandybeach Lake would increase intraspecific and interspecific competition for resources available in littoral areas, and could shift the length frequency distribution of yellow perch in that lake to a few larger fish, since larger perch would be the superior forager in such areas (Persson 1987).

Emerald shiner

Emerald shiner in Sandybeach and Little Vermilion lakes occupied the surface waters of the upper epilimnion during the period of summer stratification from dusk to dawn. During this period they fed on algae or insects. Because of the masticating nature of cyprinid feeding, identification of dietary items was difficult and thus other items may have been taken but not identified. Scott and Crossman (1973) described adult emerald shiner as an open-water pelagic species that feeds on planktonic food such as micro-crustaceans, insects and algae on the surface at night. Emerald shiner had a very narrow niche breadth suggesting a high degree of specialization. Their morphology lends credence to this theory as they have very large eyes and large terminal mouth which is adapted for surface feeding. Specialization, combined with low overlap with rainbow smelt in habitat and diet probably gives a competitive advantage to emerald shiner over rainbow smelt in Sandybeach Lake in the upper epilimnetic waters. Distributions and catches of emerald shiners did not differ significantly between the two study lakes, suggesting little effect of rainbow smelt on this species. However emerald shiner weight at length was lower in Sandybeach Lake than in Little Vermilion Lake. This may have been a result of less abundant food as a result of competition from rainbow smelt, or may have been an artifact of the spawning activity of emerald shiner during that period.

Emerald shiner in Sandybeach Lake may be affected by predation from rainbow smelt. MacCrimmon and Pugsley (1979) found in Lake Simcoe that almost one third of the rainbow smelt examined contained emerald shiners. Frozen emerald shiner also were effective bait for catching rainbow smelt in the winter fishery. Evans and Loftus (1987) listed emerald shiner as a common prey of rainbow smelt. Beckman (1942) noted however, that emerald shiner have remained abundant in Crystal Lake, Michigan, despite continuous predation by rainbow smelt since their introduction in 1912. The utilization of shoreline areas by young emerald shiners in the summer (Scott and Crossman 1973) probably provides them with a refuge from rainbow smelt predation and competition.

Emerald shiner in Little Vermilion Lake overlapped substantially in habitat utilization with yellow perch, however diet overlap was low except with yellow perch 60-80 mm FL. This overlap was due to each species utilizing emerging insects which probably was a prey of opportunity that was in unlimited supply, albeit for a short duration during the emergence. From a competitive standpoint, emerald shiner are probably more effective in utilizing emerging insects or any prey source on the surface than are yellow perch due to their morphology. Emerald shiner may coexist with yellow perch by resource partitioning in diet and perhaps in habitat at a level not measured in this study (i.e. gill nets were not set from the surface to 0.9-m). Emerald shiner may have been feeding in forays up to or just below the surface with yellow perch in the layers down to the thermocline. Larger yellow perch in Little Vermilion Lake were feeding on unidentified *Notropis* species, probably emerald shiner, and thus predation by yellow perch in the allopatric community may be replaced by rainbow smelt predation in the sympatric community (although there was no evidence of such predation) as a controlling influence on emerald shiner abundance.

Spottail shiner

Spottail shiner were not caught in abundance in the pelagic zone in either lake, however they primarily utilized the upper and lower epilimnion from dusk to dawn during summer stratification and fed on algae and insects. Brandt et al. (1980) caught spottail shiners in Lake Michigan in bottom trawls in 15-20°C water; similar to the temperature of the epilimnion in this study. Spottail shiner overlapped substantially with emerald shiner in habitat, however they did not overlap to a great extent in diet in sympatry. Stomach contents of spottail shiner, like those of emerald shiner, were difficult to identify and they may have consumed a wider range of organisms. Spottail shiners differ in morphology from emerald shiners in that they have a moderate sized subterminal mouth. Dymond (1926) noted that spottail shiner fed on more planktonic organisms than emerald shiners in Lake Nipigon, with large cladocerans making up most of the diet. Similarly Anderson and Smith (1971b) found that spottail shiners in Lake Superior fed on amphipods, *Mysis relicta* and cladocerans. It is plausible that spottail shiners are occurring incidentally in emerald shiner or yellow perch schools in the pelagic zone while the majority of spottail shiner occur in the shoreline community. Scott and Crossman (1973) found that spottail shiner were susceptible to shore seining at night, and McPhail and Lindsey (1970) regarded spottail shiner as a shoreline community species. In Sandybeach Lake spottail shiner were observed around macrophytes close to shore, and were dipnetted by fishermen for use as bait. Spottail shiners apparently were not affected by the presence of rainbow smelt in Sandybeach Lake, similar to observations in other waters where they overlap (Crowder et al. 1981). Evans and Loftus (1987), however, listed them as a common prey species of rainbow smelt.

Zooplankton

Large calanoid copepods and small cladocerans were abundant throughout the water column of Little Vermilion Lake but were concentrated in the epilimnion and metalimnion. This probably related to the diel migrations of these groups (Engel and Magnuson 1976; Carter and Goudie 1986). Overall zooplankton abundance in Sandybeach Lake was substantially lower than in Little Vermilion Lake with few large calanoid copepods caught at any level. The most abundant zooplankton in Sandybeach Lake were small calanoid copepods and large and small cladocerans caught near the bottom. The disparity in numbers of large zooplankton between lakes probably is a result of the high abundance of rainbow smelt in the epilimnion and metalimnion of Sandybeach Lake and their selective feeding on the largest available prey. This reduction of large plankton species in the zooplankton community of Sandybeach Lake is consistent with rainbow smelt invasions into other systems. Gannon and Beeton (1971) suggested that rainbow smelt may have contributed to the large calanoid copepod *Limnocalanus macrurus* in Lake Erie. Such reductions in large plankton have resulted in effects ranging from poor growth of native fishes to eutrophication (Reif and Tappa 1966; Lammens et al. 1985; Seigfried 1987).

Conclusion

The results of this study clearly demonstrate the negative impact that rainbow smelt can inflict on indigenous planktivores in a small oligotrophic lake. The effects of rainbow smelt in other lakes or systems may not be as dramatic, however fisheries managers should focus on preventing expansion of this highly plastic species.

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APPENDIX 1

TABLE A1.1. Sampling regime using 5.2-m deep pelagic nets in Sandybeach Lake in July 1990.

date	site	set depth	replicate #
90/07/9	11.3	6.1	1
90/07/9	22	0.9	1
90/07/9	22	11.3	1
90/07/10	11.3	0.9	1
90/07/10	22	16.5	1
90/07/10	22	6.1	1
90/07/11	22	11.3	2
90/07/11	22	0.9	2
90/07/11	11.3	6.1	2
90/07/12	11.3	0.9	2
90/07/12	22	16.5	2
90/07/12	22	6.1	2
90/07/13	11.3	6.1	3
90/07/13	22	0.9	3
90/07/13	22	11.3	3
90/07/14	22	6.1	3
90/07/14	11.3	0.9	3
90/07/14	22	16.5	3
90/07/15	11.3	6.1	4
90/07/15	22	6.1	4
90/07/15	22	0.9	4
90/07/16	11.3	0.9	4
90/07/16	22	11.3	4
90/07/16	22	16.5	4
90/07/17	22	0.9	5
90/07/17	22	11.3	5
90/07/17	11.3	6.1	5

TABLE A1.1 cont'd. Sampling regime using 5.2-m deep pelagic nets in Sandybeach Lake in July 1990.

date	site	set depth	replicate #
90/07/18	22	6.1	5
90/07/18	22	16.5	5
90/07/18	11.3	0.9	5
90/07/19	37.5	32.1	1
90/07/19	37.5	32.1	2
90/07/19	22	16.5	6
90/07/20	37.5	32.1	3
90/07/20	11.3	6.1	6
90/07/20	37.5	32.1	4
90/07/21	37.5	32.1	5
90/07/21	37.5	32.1	6
90/07/21	22	0.9	6
90/07/22	22	16.5	6
90/07/22	22	6.1	6
90/07/22	11.3	0.9	6

TABLE A1.2. Sampling regime using 5.2-m deep pelagic nets in Little Vermilion Lake in July 1990.

date	site	set depth	replicate #
90/07/23	22	16.5	1
90/07/23	22	6.1	1
90/07/23	22	0.9	1
90/07/24	22	16.5	2
90/07/24	22	11.3	1
90/07/24	22	6.1	2
90/07/25	22	16.5	3
90/07/25	22	11.3	2
90/07/25	22	0.9	2
90/07/26	22	11.3	3
90/07/26	22	6.1	3
90/07/26	22	0.9	3
90/07/27	22	0.9	4
90/07/27	22	6.1	4
90/07/27	22	16.5	4
90/07/28	22	16.5	5
90/07/28	22	11.3	4
90/07/28	22	6.1	5
90/07/29	22	16.5	6
90/07/29	22	11.3	5
90/07/29	22	0.9	5
90/07/30	22	11.3	6
90/07/30	22	6.1	6
90/07/30	22	0.9	6

APPENDIX 2

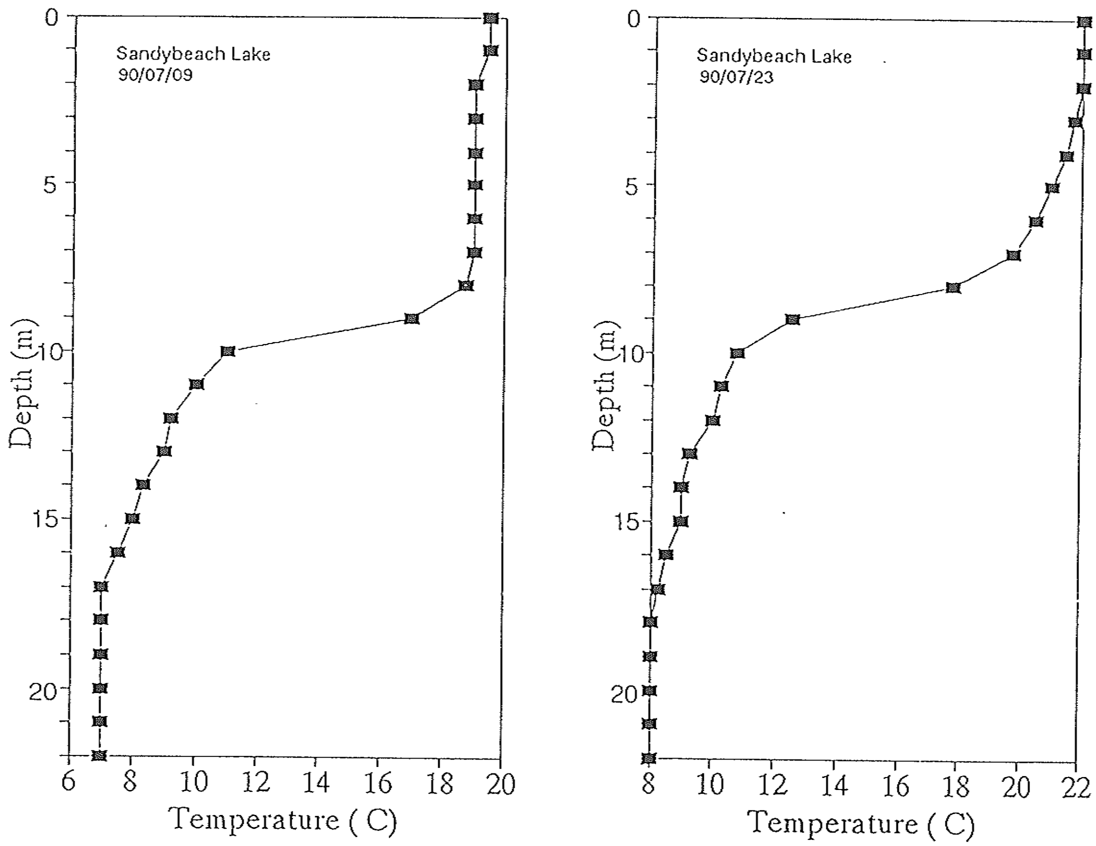

Fig. A1.1. Temperature profiles of water column down to 22 m for Sandybeach Lake on first and last day of gill net sampling in July 1990.

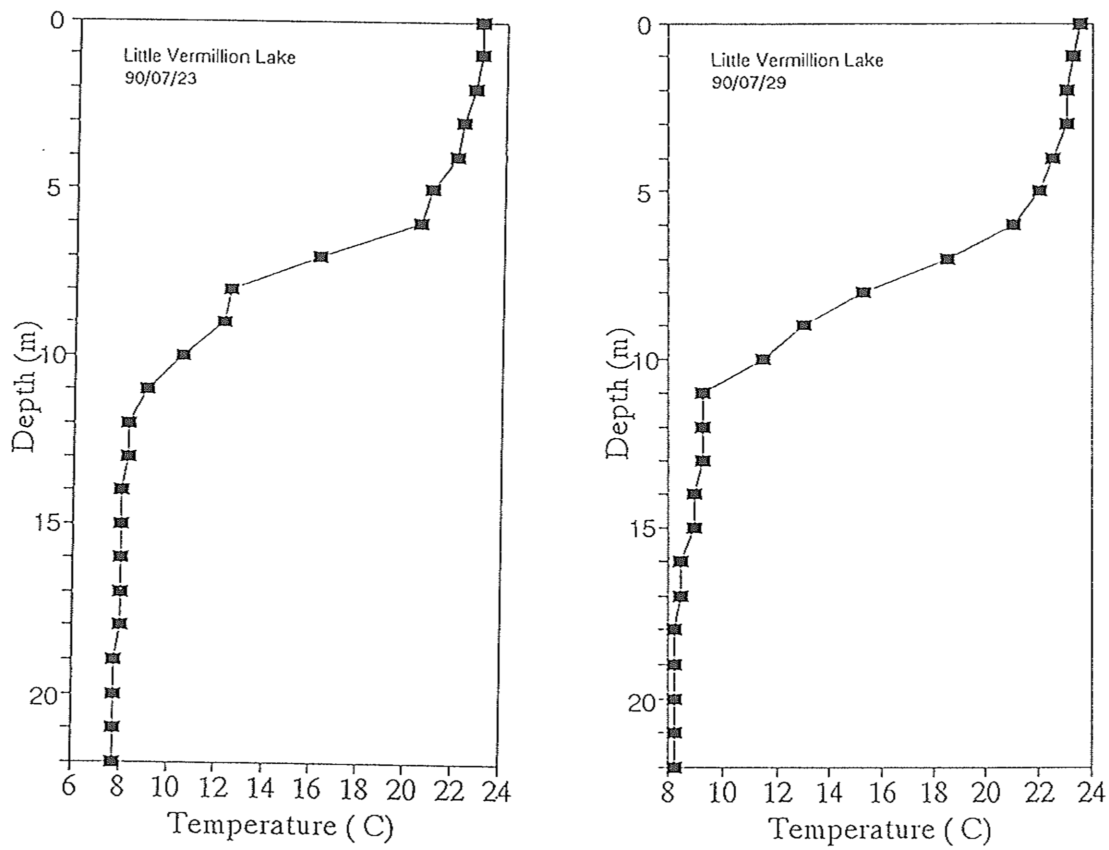

Fig. A1.2. Temperature profiles of water column down to 22 m for Little Vermillion Lake on first and last day of gill net sampling in July 1990.

APPENDIX 3

Weight-length relationships and conversions.

note that:
L = $\log_{10}$
FL = fork length in millimetres
TL = total length in millimetres
SL = standard length in millimetres
WT = weight in grams
All measurements are on preserved fish unless otherwise stated.
Probability > F value is 0.0001 for all of the regression equations provided below.

Rainbow smelt

Preserved length of 65 rainbow smelt from Sandybeach Lake in July 1991 (12 days 10% formalin solution, 45 days 70% ethanol solution) = 0.987 Fresh length (fresh frozen for 2 days) - 0.213. Adj r^2 = 0.8561 range 80 to 112 mm FL.

Total length : fork length ratio for 500 rainbow smelt from Sandybeach Lake.

TL = 1.104 FL - 0.273 adj r^2 = 0.9995 range 69 to 168 mm FL.

Weight - fork length relationship for 452 smelt caught in Sandybeach Lake in May 1990.

LWT = 2.834 LFL - 4.859 adj r^2 = 0.9412 range 66 to 135 mm FL.

Weight - total length relationship for 452 smelt caught in Sandybeach lake in May 1990.

LWT = 2.826 LTL - 4.961 adj r^2 = 0.9412 range 73 to 149 mm TL.

Weight - fork length relationship for 2414 smelt caught in Sandybeach Lake in July 1990.

LWT = 2.786 LFL - 4.704 adj r^2 = 0.9133 range 65 to 166 mm FL.

Weight - total length relationship for 2414 smelt caught in Sandybeach Lake in July 1990.

LWT = 2.778 LTL - 4.805   adj r^2 = 0.9133   range 71 to 183 mm TL.

Cisco

Preserved length of 59 cisco from Sandybeach Lake in June 1991 (12 days 10% formalin solution, 45 days 70% ethanol solution) = 0.975 Fresh length (fresh frozen for 2 days) - 0.101. Adj r^2 = 0.7821 range 136 to 179 mm FL.

Total length : fork length ratio for 59 cisco from Sandybeach Lake.

TL = 1.115 FL - 5.641   adj r^2 = 0.9918   range 140 to 244 mm FL.

Standard length : fork length ratio for 59 cisco from Sandybeach Lake.

SL = 0.909 FL + 1.683   adj r^2 = 0.9905   range 140 to 244 mm FL.

Weight - fork length relationship for 55 cisco caught in Sandybeach Lake in May 1990.

LWT = 3.086 LFL - 5.195   adj r^2 = 0.9447   range 110 to 240 mm FL.

Weight - total length relationship for 55 cisco caught in Sandybeach Lake in May 1990.

LWT = 2.985 LTL - 5.119   adj r^2 = 0.9947   range 117 to 262 mm TL.

Weight - fork length relationship for 170 cisco caught in Sandybeach Lake in July 1990.

LWT = 3.335 LFL -5.710   adj r^2 = 0.9530   range 89 to 229 mm FL.

Weight - total length relationship for 170 cisco caught in Sandybeach Lake in July 1990.

LWT = 3.229 LTL - 5.637   adj r^2 = 0.9528   range 94 to 250 mm TL.

Weight - fork length relationship for 59 cisco (fresh specimens) caught in Sandybeach Lake in June 1991.

LWT = 2.974 LFL - 4.900   adj r^2 = 0.9513   range 140 to 244 mm FL

Weight - total length relationship for 59 cisco (fresh specimens) caught in Sandybeach Lake in June 1991.

LWT = 2.897 LTL - 4.874   adj r^2 = 0.9641   range 150 to 266 mm TL.

Weight - standard length relationship for 59 cisco (fresh specimens) caught in Sandybeach Lake in June 1991.

LWT = 2.979 LSL - 4.805   adj r^2 = 0.9550   range 129 to 223 mm SL.

Weight - fork length relationship for 51 cisco caught in Little Vermilion Lake in May 1990.

LWT = 3.048 LFL - 5.085   adj r^2 = 0.9946   range 78 to 176 mm FL.

Weight - fork length relationship for 375 cisco caught in Little Vermilion Lake in July 1990.

LWT = 3.043 LFL - 5.055   adj r^2 = 0.9969   range 51 to 200 mm FL.

Weight - fork length relationship for 375 cisco caught in Little Vermilion Lake in July 1990.

LWT = 2.875 LTL - 4.832   adj r^2 = 0.9969   range 53 to 217 mm TL.

Lake whitefish

Weight - fork length relationship for 9 lake whitefish caught in Little Vermilion Lake in May 1990.

LWT = 3.011 LFL - 4.998   adj r^2 = 0.9917   range 107 to 176 mm FL.

Weight - fork length relationship for 23 lake whitefish caught in Little Vermilion Lake in July 1990.

LWT = 2.937 LFL - 4.857   adj r^2 = 0.8863   range 79 to 95 mm FL.

Weight - fork length relationship for 17 lake whitefish caught in Sandybeach Lake in July 1990.

LWT = 4.075 LFL - 7.698   adj r^2 = 0.8908   range 363 to 455 mm FL.

Yellow perch

Weight - fork length relationship for 174 yellow perch caught in Little Vermilion Lake in July 1990.

LWT = 2.751 LFL - 4.437   adj r^2 = 0.9918   range 39 to 115 mm FL.

Emerald shiner

Weight - fork length relationship for 12 emerald shiner caught in Sandybeach Lake in May 1990.

LWT = 2.361 LFL - 3.735   adj r^2 = 0.8582   range 88 to 103 mm FL.

Weight - fork length relationship for 131 emerald shiner caught in Sandybeach Lake in July 1990.

LWT = 3.041 LFL - 5.010   adj r^2 = 0.9126   range 72 to 110 mm FL.

Weight - fork length relationship for 45 emerald shiner caught in Little Vermilion Lake in July 1990.

LWT = 2.809 LFL - 4.627   adj r^2 = 0.9768   range 59 to 107 mm FL.

Spottail shiner

Weight - fork length relationship for 15 spottail shiner caught in Sandybeach Lake in May 1990.

LWT = 2.948 LFL - 4.765   adj r^2= 0.9860   range 58 to 98 mm FL.

Weight - fork length relationship for 24 spottail shiner caught in Sandybeach Lake in July 1990.

LWT = 2.958 LFL - 4.786   adj r^2 = 0.9868   range 38 to 85 mm FL.

Weight - fork length relationship for 13 spottail shiner caught in Little Vermilion Lake in July 1990.

LWT = 2.451 LFL - 3.845   adj $r^2 = 0.8825$ range 65 to 91 mm FL.

Troutperch

Weight - fork length relationship for 24 troutperch caught in Sandybeach Lake in May 1990.

LWT = 3.103 LFL - 5.015   adj $r^2 = 0.9587$ range 73 to 92 mm FL.

Nine - spine stickleback

Weight - total length relationship for 8 nine - spine stickleback caught in Sandybeach Lake in May 1990.

LWT = 1.841 LTL - 3.010   adj $r^2 = 0.8379$ range 57 to 76 mm TL.

APPENDIX 4

Gill net catches in 1.8 m deep nets.

SANDYBEACH LAKE - SPRING 1990

Set # 17: 2 gangs of 1.8 m deep gill nets on bottom at 10-30 meters.
Set @ 1745 hrs 90/05/22
Pulled @ 1130 hrs 90/05/23
Catch for each mesh:

- 8 mm: 8 rainbow smelt, 1 emerald shiner.
- 10 mm: 9 rainbow smelt, 4 spottail shiner, 1 emerald shiner, 1 cisco, 1 white sucker, 1 yellow perch, 2 burbot.
- 13 mm: 1 rainbow smelt, 5 cisco, 1 troutperch, 2 white sucker, 1 lake trout.
- 8 mm: 22 rainbow smelt, 1 nine-spine stickleback.
- 10 mm: 1 rainbow smelt.
- 13 mm: 2 cisco, 1 white sucker.

Set # 20: 2 gangs of 1.8 m deep gill nets on bottom at 10-30 meters.
Set @ 1230 hrs 90/05/23
Pulled @ 1330 hrs 90/05/24
Catch for each mesh:

- 8 mm: 55 rainbow smelt, 1 spottail shiner.
- 10 mm: 27 rainbow smelt, 17 spottail shiner, 1 emerald shiner, 1 yellow perch, 1 troutperch, 1 white sucker.
- 13 mm: 12 cisco, 1 troutperch, 3 mottled sculpin.
- 8 mm:31 rainbow smelt, 2 emerald shiner, 3 spottail shiner, 1 white sucker.
- 10 mm: 1 rainbow smelt, 1 troutperch.
- 13 mm: 6 cisco, 2 whitefish, 1 troutperch, 1 lake trout.

LITTLE VERMILION LAKE - SPRING 1990

Set # 22: 1 gang of 1.8 m deep gill net on bottom at 25 meters.
Set @ 1915 hrs 90/05/25.
Pulled @ 0745 hrs 90/05/26.
Catch for each mesh:

- 8 mm: 1 cisco, 1 yellow perch.
- 10 mm: 4 cisco, 1 whitefish.
- 13 mm: 4 cisco, 1 whitefish, 1 crayfish.

Set # 23: 2 gangs of 1.8 m deep gill nets on bottom at 7-20 meters.
Set @ 2015 hrs 90/05/25.
Pulled @ 0845 hrs 90/05/26.
Catch for each mesh:

8 mm: 6 nine-spine stickleback, 1 yellow perch.
10 mm: 15 cisco, 1 yellow perch, 5 lake whitefish, 2 deepwater sculpin.
13 mm: 10 cisco, 7 lake whitefish.
8 mm: 4 cisco, 2 lake whitefish, 1 yellow perch.
10 mm: 1 cisco, 1 yellow perch.
13 mm: 18 cisco, 2 lake whitefish, 1 northern pike, 1 mottled sculpin, 4 yellow perch.

APPENDIX 5

Gill net catches in 1.8 m deep nets

SANDYBEACH LAKE - SUMMER 1990

Set # 4: 2 gangs of 1.8 m deep gill nets on bottom at 25 meters.
Set @ 2100 hrs 90/07/10.
Pulled @ 1125 hrs 90/07/11.
Catch for each mesh:

- 8 mm: 65 rainbow smelt, 1 lake whitefish, 1 mottled sculpin.
- 10 mm: 8 rainbow smelt, 2 lake whitefish, 3 cisco, 5 mottled sculpin.
- 13 mm: 3 rainbow smelt, 22 cisco, 3 mottled sculpin, 1 lake trout.
- 6.25 mm: 13 rainbow smelt, 2 mottled sculpin.
- 8 mm: 28 rainbow smelt, 2 mottled sculpin.
- 10 mm: 1 rainbow smelt, 2 mottled sculpin.
- 12.5 mm: 1 rainbow smelt, 7 mottled sculpin.
- 16 mm: 1 rainbow smelt, 1 lake whitefish, 1 cisco.

Set # 8: 1 gang of 1.8 m deep gill nets on bottom at 8-25 meters.
Set @ 1940 hrs 90/07/11.
Pulled @ 2145 hrs 90/07/11.
Catch for each mesh:

- 6.25 mm: 1 rainbow smelt.
- 8 mm: 3 rainbow smelt.
- 10 mm: 1 rainbow smelt.
- 12.5 mm: 4 cisco.
- 16 mm: 4 cisco.

Set # 15: 1 gang of 1.8 m deep gill nets on bottom at 25-32 meters.
Set @ 1943 hrs 90/07/13.
Pulled @ 2135 hrs 90/07/13.
Catch for each mesh:

- 6.25 mm: 1 rainbow smelt.
- 8 mm: 1 rainbow smelt.
- 10 mm: 0
- 12.5 mm: 1 cisco.
- 16 mm: 3 cisco, 2 lake whitefish.

Set # 19: 1 gang of 1.8 m deep gill nets on bottom at 6-18 meters.
Set @ 1955 hrs 90/07/14.
Pulled @ 2155 hrs 90/07/14.
Catch for each mesh:

6.25 mm: 15 rainbow smelt.
8 mm: 9 rainbow smelt.
10 mm: 1 yellow perch, 5 troutperch.
12.5 mm: 2 rainbow smelt, 1 emerald shiner, 7 yellow perch, 6 troutperch.
16 mm: 36 yellow perch, 1 white sucker.

Set # 23: 1 gang of 1.8 m deep gill nets on bottom at 13-28 meters.
Set @ 1930 hrs 90/07/15.
Pulled @ 0750 hrs 90/07/16.
Catch for each mesh:

6.25 mm: 17 rainbow smelt.
8 mm: 42 rainbow smelt.
10 mm: 1 cisco.
12.5 mm: 6 cisco.
16 mm: 10 cisco, 1 lake whitefish.

Set # 27: 1 gang of 1.8 m deep gill nets on bottom at 2-9 meters.
Set @ 2035 hrs 90/07/16.
Pulled @ 0710 hrs 90/07/17.
Catch for each mesh:

6.25 mm: 3 yellow perch, 1 northern pike, 2 johnny darter.
8 mm: 73 emerald shiner, 8 yellow perch, 37 troutperch.
10 mm: 100 emerald shiner, 20 yellow perch, 55 troutperch, 2 white sucker.
12.5 mm: 1 rainbow smelt, 25 emerald shiner, 15 yellow perch, 35 troutperch, 2 white sucker.
16 mm: 5 rainbow smelt, 16 yellow perch, 4 silver redhorse, 1 northern pike.

Set # 34: 2 gangs of 1.8 m deep gill nets on bottom at 35-40 meters.
Set @ 2050 hrs 90/07/18.
Pulled @ 1000 hrs 90/07/19.
Catch for each mesh:

6.25 mm: 1 rainbow smelt.
8 mm: 5 rainbow smelt, 1 cisco.
10 mm: 2 cisco, 1 lake whitefish.
12.5 mm: 11 cisco, 2 mottled sculpin.
16 mm: 9 cisco, 1 lake trout, 1 deepwater sculpin.
38 mm: 20 cisco, 4 lake whitefish.

- mm: 4 cisco, 1 lake whitefish.
- mm: 2 lake whitefish, 1 lake trout.
- mm: 9 lake whitefish, 1 lake trout.

127 mm: 1 lake whitefish, 1 lake trout.

LITTLE VERMILION LAKE - SUMMER 1990

Set # 65: 1 gang of 1.8 m deep gill nets on bottom at 8 to 20 meters.
Set @ 2030 hrs 90/07/27.
Pulled @ 0730 hrs 90/07/28.
Catch for each mesh:

6.25 mm: 14 nine-spine stickleback, 1 cisco.
8 mm: 2 smallmouth bass, 5 nine-spine stickleback, 1 slimy sculpin.
10 mm: 2 yellow perch, 4 slimy sculpins, 2 cisco.
12.5 mm: 25 cisco, 5 slimy sculpins, 1 northern pike, 1 lake whitefish (over 250 mm FL).
16 mm: 22 cisco, 4 lake whitefish (over 250 mm FL).

SANDYBEACH LAKE - SUMMER 1991

Set # 1: 2 gangs of 1.8 m deep gill nets suspended at 10 m over 22 m bottom.
Set @ 2030 hrs 91/06/18.
Pulled @ 1045 hrs 91/06/19.
Catch for each mesh:

6.25 mm: none.
8 mm: 28 rainbow smelt.
10 mm: 3 cisco.
12.5 mm: 7 cisco.
16 mm: 37 cisco.
6.25 mm: 25 rainbow smelt.
8 mm: 94 rainbow smelt.
10 mm: 4 rainbow smelt.
12.5 mm: 7 cisco.
16 mm: 59 cisco.

Set # 2: 2 gangs of 1.8 m deep gill nets set on bottom at 22 m.
Set @ 2045 hrs 91/06/18.
Pulled @ 1300 hrs 91/06/19.
Catch for each mesh:

8 mm: 148 rainbow smelt.

10 mm: 190 rainbow smelt.
13 mm: 31 rainbow smelt, 6 cisco.
8 mm: 131 rainbow smelt.
10 mm: 26 rainbow smelt.
13 mm: 8 rainbow smelt, 2 emerald shiner, 2 lake whitefish (over 200 mm FL).

Note that none of the cisco caught in 1991 were less than 120 mm FL, thus confirming the lack of smaller year classes as found in 1990.

APPENDIX 6

TABLE A6.1. OMNR Lake Survey data for Sandybeach Lake taken on 27/08/81. Station located within 1 km of 37.5 m gill netting site for this study.

Depth (m)	Temp °C	D.O. mg L^{-1}	pH	Alk. mg L^{-1}	T.D.S. mg L^{-1}	Cell T. °C	Conductivity μmhos/cm
0	21.0						
1	20.5						
2	20.0	7.4	9.0	75.1	66.6	25.0	100.0
4	20.0						
6	20.0						
8	20.0						
9	16.5	7.8	8.0	68.4	88.6	22.0	125.0
10	12.0						
12	10.0						
14	9.0						
16	8.5						
18	8.5						
20	8.0						
22	7.0						
24	7.0						
26	6.5						
28	6.0						
30	6.0						
32	6.0						
34	6.0						
36	6.0						
38	6.0						
39	6.0	6.0	7.5	75.1	77.4	18.0	100.0
41	6.0						

TABLE A6.2. OMNR Lake Survey data for Little Vermilion Lake taken on 29/07/81. Station at same location as 22 m gill netting site for this study.

Depth (m)	Temp °C	D.O. mg L^{-1}	pH	Alk. mg L^{-1}	T.D.S. mg L^{-1}	Cell T. °C	Conductivity μmhos/cm
0	19.7						
1	19.7						
2	19.6	8.6	9.0	75.1	111.0	20.0	150.0
4	19.5						
6	19.4						
8	13.6	8.0	8.5	82.1	111.0	20.0	150.0
10	8.6						
12	6.9						
14	6.1						
16	5.8						
18	5.6						
20	5.3	4.0	7.5	75.1	116.2	18.0	150.0
22	5.2	3.8	7.5	75.1	116.2	18.0	150.0
24	5.0						

APPENDIX 7

TABLE A7.1. Commercial lake whitefish harvest in Sandybeach Lake from 1979 to 1986. Not fished from 1986 to present (OMNR - Sioux Lookout).

Year	Harvest (kg)
1979	2463
1980	not fished
1981	not fished
1982	1066
1983	847
1984	1452
1985	not fished
1986	4126