THE UNIVERSITY OF MANITOBA

Growth, Mortality, Production and Feeding of Yellow

Perch Fry, *Perca fluviatilis flavescens* (Mitchill)

and Their Effect on the *Daphnia pulicaria* Forbes
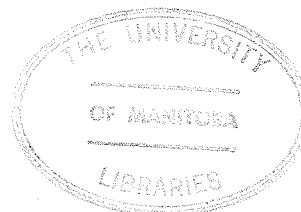
of West Blue Lake

by

MICHAEL A. HENDERSON

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

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GROWTH, MORTALITY, PRODUCTION AND FEEDING OF YELLOW
  PERCH FRY, PERCA FLUVIATILIS FLAVESCENS (MITCHILL)
  AND THEIR EFFECT ON THE DAPHNIA PULICARIA FORBES
                OF WEST BLUE LAKE"

                        by

               MICHAEL A. HENDERSON

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

               MASTER OF SCIENCE

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ABSTRACT

Distribution, mortality, growth, production and
feeding habits of perch fry and their effect on the
Daphnia pulicaria population of West Blue Lake was
investigated.   Perch hatched in the littoral zone
in early June and moved into the pelagic zone
7 to 14 days later when they were 9 - 10 mm in length.
Perch fry remained in the pelagic zone until they
reached a length of approximately 25 - 30 mm in mid-July,
and then returned to the littoral area.   Instantaneous
daily mortality rates ranged from .017 in areas of low
perch fry abundance to .140 in areas of high perch fry
abundance.

From hatching until mid-August perch fry increased
in length and dry weight by a factor of 10 and 2616
respectively.   Growth occurred in two distinct stanzas.
The first stanza, from hatching until the beginning of
the pelagic phase, was characterized by a low level of
feeding and a slow growth rate, while the second stanza,
lasting for the remainder of the summer, was characterized
by a high level of feeding and a fast growth rate.
Variation in the energy intake and growth of perch fry in
different parts of the lake was directly dependent upon the
abundance of *Daphnia pulicaria*.

Changes in the proportion of carbon, nitrogen and water and in the calorific value of perch fry tissues occurred from hatching through metamorphisis. The initial proportion of carbon, 547.9 ug mg dry weight^{-1}, decreased rapidly following hatching while the low levels of nitrogen at hatching, 70.6 ug mg dry weight^{-1}, increased, indicating that growth occurred at the expense of the accumulation of high energy compounds. Throughout the pelagic phase the proportion of carbon and nitrogen in the tissues increased concomitantly and later decreased when the fry returned to the littoral zone. Calorific values declined from 6727 cal mg dry weight^{-1} at hatching to approximately 5000 cal mg dry weight^{-1} at the end of the pelagic period. They gradually increased during the littoral phase to 5760 cal mg dry weight^{-1} by mid-August. Following an initial increase after hatching to 90%, the water content of the tissues decreased to approximately 81% by mid-August.

Perch fry initially fed on copepods and nauplii. On entering the pelagic zone *Daphnia pulicaria* became the dominant food source and remained so in most of the lake for the remainder of the summer. At one location during the littoral phase *Bosmina longirostris* became the dominant food source as the result of the very low

abundance of *Daphnia pulicaria*. Size selective feeding

was prominent in fish less than 20 mm in length but

older fry fed on all size-classes of *Daphnia pulicaria*.

Size selective feeding also occurred on a diel basis

with the largest *Daphnia pulicari* being consumed at

night. Total daily consumption of *Daphnia pulicaria*

by perch fry ranged from less than .1% to greater than

5.8% of the standing crop during the pelagic phase.

Predation was heaviest in the area with the highest

abundance of perch fry and contributed to the collapse

of the *Daphnia pulicaria* population at this location and

their replacement by *Bosmina longirostris*. Decreases in

the abundance of *Daphnia pulicaria* in areas of the lake

with low numbers of perch fry indicated that these

populations may decline independently of fish predation.

Mean whole lake production of perch fry was .08

mg C m^{-2} day^{-1}.

ACKNOWLEDGEMENTS

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INTRODUCTION

Yellow perch, *Perca fluviatilis flavescens* (Mitchill), are found throughout much of Canada, and combined with the Eurasian perch, have an almost circumpolar distribution in freshwaters of the northern hemisphere (Scott and Crossman 1973). As a result of their commercial and recreational importance there is a considerable body of literature available on age, growth and production of juvenile and adult forms in Canadian habitats (Harkness 1922, Carlander 1950, Lawler 1953, Coble 1966, Sheri and Power 1969, Falk 1971). Yet, little is known about the role of the 0+ age group beyond their general ecology (Keast and Webb 1966, Wong 1972).

The most important energy source for perch fry of West Blue Lake is the cladoceran, *Daphnia pulicaria* which comprises over 90% of their daytime energy intake (Wong 1972). In turn, perch fry are a major forage for juvenile and adult walleye of West Blue Lake (Glenn and Ward 1968, Kelso 1973) and account for approximately 30% of annual production in the walleye population (Ward and Robinson 1974). Annual variations in growth of young perch in Oneida Lake during their demersal stage is

1

highly correlated with *Daphnia* sp. abundance (Noble
1975) and growth and production in the walleye
population is directly related to abundance and
production of young perch (Forney 1965).

Qualitative aspects of the impact of predation
by planktivorous fish on zooplankton populations have
been well documented by Brooks and Dodson (1965) and
Galbraith (1967). In both cases, changes occurred to
the genus *Daphnia* which is a common and important food
source for most freshwater planktivorous fish (Ivlev
1961). Both studies indicated that the presence of
a planktivorous fish population affected size and species
composition of local zooplankton populations. More
recently, Noble (1975) has shown that young yellow
perch in their demersal stage have little effect on
the *Daphnia* sp. population of Oneida Lake.

In West Blue Lake the theme of the research is
to describe the trophic relationships and ecology of
the dominant components of the ecosystem and to evaluate
the importance of these relationships in defining the
productivity of the major components. The objectives
of the present study are (1) to quantify patterns of
growth, mortality, feeding and production in young perch
and (2) to determine their effect on the *Daphnia pulicaria*
population of West Blue Lake.

MATERIALS AND METHODS

Description of Area

West Blue Lake, situated in the Duck Mountain Provincial Park in west central Manitoba (latitude 51°36', longitude 100°55' and altitude 670 m) is a channel lake with a multibasin configuration (Fig. 1). It is essentially a closed lake with a maximum depth of 31 m, a mean depth of 11.3 m, and a total area of 160 ha (Bell and Ward 1970).

The zooplankton is composed of three dominant species, *Daphnia pulicaria*, *Cyclops bicuspidatus*, and *Diaptomus siciloides* and associated species *Mesocyclops edax*, *Epischura lacustris*, and *Bosmina longirostris*. The Rotifera are represented by *Keratella cochlearis*, *Keratella quadrata*, *Felinis longiseta* and *Asplanchna* sp. (Wong 1972).

The fish community of the lake consists of yellow perch, *Perca fluviatilis flavescens*; walleye, *Stizostedion vitreum vitreum*; five-spined stickleback, *Culea inconstans*; northern pike, *Esox lucius*; and lake trout, *Salvelinus namycush*. Also, two minnows, *Pimephales promelas* were caught in 1966 and two common white suckers, *Catostomus commersoni*, were caught in 1974.

Figure 1.   A contour map of West Blue Lake showing

sampling sites (depths in metres).

T₁₋₄ TOW LOCATIONS 1-4

D₁₋₃ DIP NET LOCATIONS 1-3

● ZOOPLANKTON SAMPLING
STATIONS 2,4,6,7,8,9,10 AND 11

D₁

BASIN I

T₄

4
10

D₂
BAY
11
6

5 15 25

BASIN 2

T₃

30
9
2

D₃
7
8

N

1 KILOMETER

15 5

T₂

BASIN 3
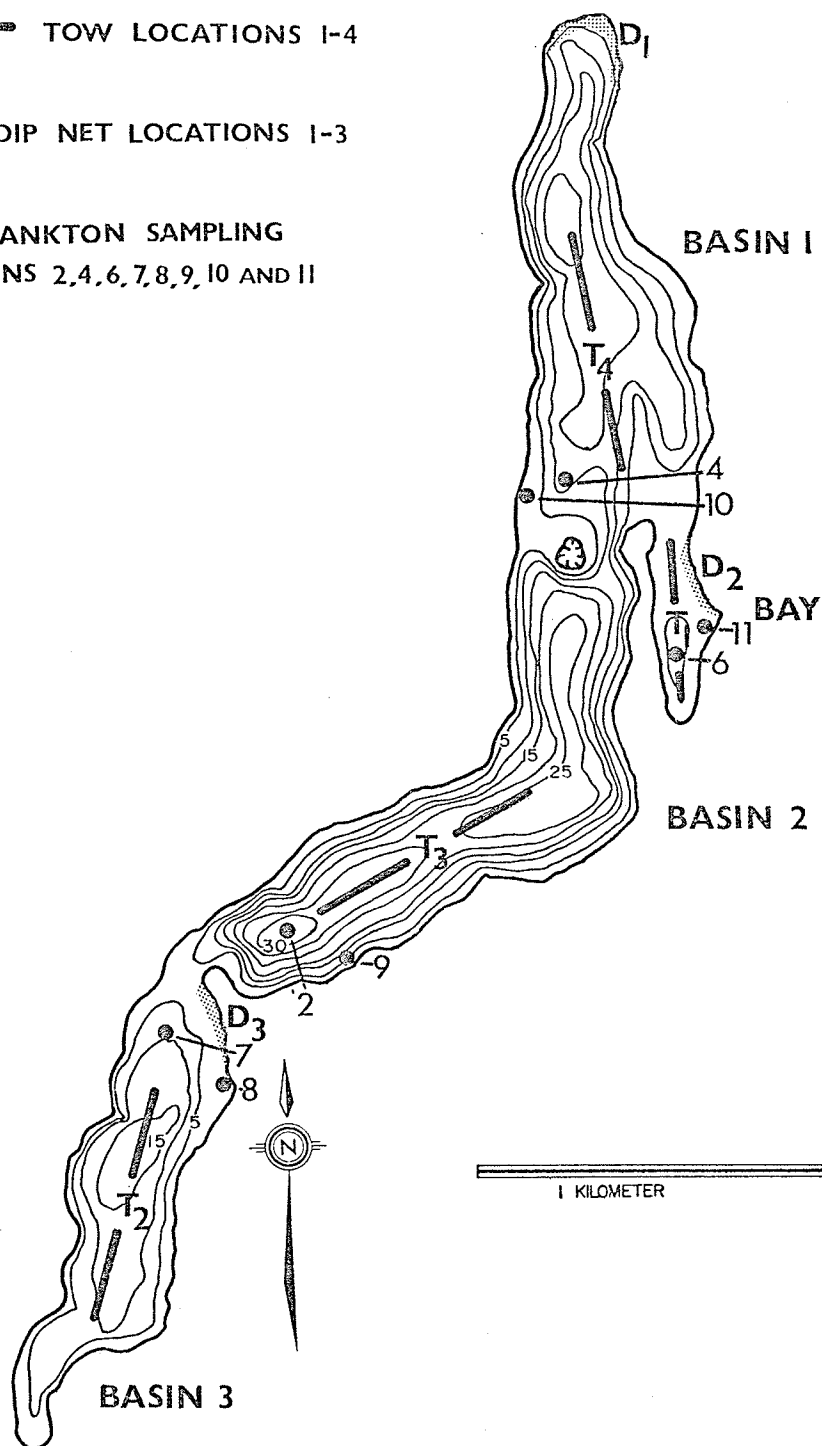
Sampling of Perch Fry

Date of initiation of spawning by adult perch, spawning locations, water temperatures at spawning sites, number of spawning sites over defined areas of the lake and date at which eggs became eyed were recorded in 1975.

Samples of perch fry were collected from different parts of West Blue Lake at regular intervals from early June until mid-August in 1974 and 1975. Perch fry used for determining lengths and weights were collected from basins 1, 2 and 3 and the bay. Those used for gut analysis were collected from basin 2 and the bay. Carbon, nitrogen and calorific estimates were based on samples collected from basins 1, 2 and 3 and the bay in 1974 and from basin 2 in 1975. These samples were collected using dip nets, half metre tow nets and seine nets.

In 1975 samples of perch less than 1 h old were collected from aquaria in which fertilized eggs had been reared. The aquaria, equipped with a flow-through water system, were kept at natural temperatures by supplying them with lakeshore water.

During the first days after hatching, perch fry were collected near shore (Fig. 1) at night by hanging an artificial light source over the side of the boat and dipping them out as they rose to the surface. Later, when they became pelagic,

a half-metre tow net was the main sampling method. The
sampling procedure was the same as that described by
Wong (1972).

In the middle of the summer, when the perch fry
returned to the littoral zone, collections were made
using a seine net with .63 cm (stretched measure) mesh.
The seine net was set about 7 m offshore and pulled in
slowly. Fish trapped were then removed with a dip net.
All seining was done during daylight hours.

Pelagic perch fry were also sampled using Miller
high-speed trawls (Miller 1961) between June 25 and July
15, 1975 to quantitatively estimate their abundance.
The translucent trawls, constructed with 1000 um Nitex
screening and plexiglass, were pulled at speeds of 11-12
kmh^{-1} using a towing cable attached to the transon of
a 4.9 m fibreglass boat (Noble 1970). Trawls were made
in basin 2 and the bay with four samples being taken
at each depth of 0, 2 and 4 m. All sampling was done
between 23:00 and 01:00 h and the distances over which
the trawls were made was determined using an Isurumi-
Seiki-kosakusho flow meter.

Samples were washed from the catch buckets and
immediately killed and preserved in 5% formalin. In
the laboratory the samples were placed in sorting pans
where perch fry were separated from zooplankton and counted.

Perch fry were collected at 2 h intervals over a 24 h period in basin 2 and the bay on June 28-29 and July 8-9 and in the bay on July 15-16. All samples were collected with a half-metre tow net at depths of 3-5 m during daylight and at the surface from dusk until dawn. A minimum of 10 perch fry were collected in each sample and immediately killed and preserved in 5% formalin for later gut analysis.

Experiments were conducted at the same time the 24 h sampling was in progress to determine the passage rate of food through the guts of the perch fry. Twenty to 30 perch fry were collected at each of four equal time intervals over the 24 h period using a half-metre tow net. The perch fry were immediately placed in feeding chambers containing zooplankton at natural concentrations. After 30 min the fry were transferred to chambers containing zooplankton stained with Bismark Brown Y. Through serial sacrifice the median time from initiation of feeding to initiation of evacuation of the stained food source was determined.

Sampling of *Daphnia pulicaria*

Daphnia pulicaria were collected at eight stations (Fig. 1) at weekly intervals from May 14 to August 13, 1975, using a 15 l Schindler-Patalas trap (Schindler 1969).

Station 2 was sampled at 0, 1, 3, 5, 7, 12, 17, 20, 25
and 30 m; station 4 at 0, 1, 3, 5, 7 and 12 m and
station 6 and 7 at 0, 2, 4, 6 and 8 m. Stations 8, 9,
10 and 11 were located within 3 m of the shoreline and
sampled at the surface in 1.0-1.5 m of water. Station
2 was always sampled first, at 10:00 h, with the remaining
stations being completed by 14:00 h. Samples were
immediately killed and preserved in formalin. They
were counted at a later date using a Zeiss inverted
microscope to determine the number of *Daphnia pulicaria*
present. The number of *Daphnia pulicaria* present at
intermediate depths was obtained by interpolation and
results were converted into the number under 1 m^2 of water.
The number of *Bosmina longirostris* under 1 m^2 of water
was determined for stations 2 and 6 at bi-weekly intervals
from July 3 to August 13 using the same samples and
counting procedure. At each station on each sampling
date a temperature profile was obtained.

Length-frequency distributions of the *Daphnia
pulicaria* population were determined at weekly intervals
from May 13 until August 15, 1975, for stations 2 and 6.
Vertical tows were taken at station 2 from 30-0 m and at
station 6 from 8-0 m using a Birge net constructed of
72 μm Nitex screening. Discrete samples were collected

weekly at station 2 at 2.5, 8, 15 and 20 m using a 15 h
Schindler-Patalas trap.   Samples from both stations
were collected at 10:00 h except on July 10 at station 2
and July 11 at station 6 when additional samples were
taken at 2.5 m at 24:00 h.   In most cases a minimum of
200 *Daphnia pulicaria* were collected and measured as
described by Wong (1972).

Seasonal Growth of Perch Fry

Perch fry used to estimate growth in 1974 were
collected from June 9, when they were 1-3 days old, until
August 19.   In 1975 they were collected from May 31, when
they were 1 day old, until August 12.   In 1975 lengths
and weights were obtained for perch within 1 h of hatching from
aquaria reared eggs.   Lengths and wet weights were determined
as described by Wong (1972).   Dry weights were obtained by
placing perch fry in a drying oven set at 100 C for 24 h.
Mean lengths and weights were calculated for all samples
and used to estimate seasonal growth (Chapman 1967) and
length-weight relationships (Tesch 1968).   Instantaneous
growth rates (Ricker 1975), measured as change in dry weight,
were estimated for both years.

Calorific, carbon and nitrogen estimates for perch
fry were obtained for a series of dates in 1974 and 1975.

Fry used for calorific work were measured and dried at 100 C for 24 h.   The remains were ground into a fine powder and frozen in a sealed container.   At a later date, samples were burned in a Phillipson Microbomb Calorimeter.

Perch fry used for carbon and nitrogen estimates were treated in a similar manner except care was taken to ensure that all surfaces touching the fry contained no residual carbon.   All instruments used in the manipulation of perch fry and containers used to store their remains had previously been soaked in dichromate acid for 30 min and rinsed six times in distilled water.   Carbon and nitrogen determinations were made on a Perkin-Elmer 240 Elemental Analyzer.

Perch fry production in terms of carbon and calories was estimated during the pelagic period using the method described by Allen (1951).   This is a method for estimating production graphically in which mean carbon or calorific content of the perch fry is plotted against population numbers at given times over the pelagic period. The area beneath the resulting curve was measured to estimate production.

Stomach Analysis of Perch Fry

Perch fry were collected over the spring and summer of 1974 and 1975 to determine number, type and size of prey being consumed. Guts of perch fry were examined using a binocular microscope. For fry with undifferentiated guts (total length < 23 mm), the entire digestive tract was examined. When the stomach became differentiated (total length > 23 mm), it alone was examined. The main taxonomic groups of prey were copepods and cladocerans. Copepods were classified as nauplii or adults (copepodids and mature adults) while the dominant cladoceran, *Daphnia pulicaria* was classified into one of 28 length classes (.1 mm intervals). The number of *Bosmina longirostris* and *Chaoborus flavicans* was also recorded. Calorific values of the prey species were based on the work of Snow (1972) for *Daphnia pulicaria*, Patrick (Department of Zoology, University of Manitoba, Winnipeg, Man., unpublished) for *Cyclops bicuspidatus*, Lysack (1976), for *Chaoborus flavicans* and Schindler, et al. (1971) for *Bosmina longirostris*.

The number of *Daphnia pulicaria* consumed by perch fry m^{-2} day^{-1} during the pelagic phase in basin 2 and the bay was determined in 1975. These estimates were obtained by multiplying the number of perch fry under 1 m^2 of water by the daily consumption of *Daphnia pulicaria* per perch fry.

Daily consumption of *Daphnia pulicaria* per perch fry was estimated by apportioning the average frequency distribution of *Daphnia pulicaria* found in perch fry stomachs, determined from samples collected at 2 h intervals over a 24 h period, into intervals equal to the time required for one *Daphnia pulicaria* to pass through the digestive system of a perch fry. The midpoint of each interval was determined and the corresponding number of *Daphnia pulicaria* in the gut. These estimates were summed over the 24 h period to determine daily consumption of *Daphnia pulicaria* by a perch fry. In equation form:

$$C_T = C_F \, X \, F$$

and $\quad C_F = \Sigma \, (D_{1-X})$

where C_T = total number of *Daphnia pulicaria* consumed m^{-2} day^{-1} by perch fry

C_F = number of *Daphnia pulicaria* consumed per perch fry day^{-1}

F = number of perch fry m^{-2}

D = number of *Daphnia pulicaria* in guts of perch fry at the midpoint of each evacuation interval

and X = number of evacuation intervals day^{-1}.

Estimates for dates between the 24 h samples were obtained by interpolation. Daily consumption of *Cyclops bicuspidatus*, *Bosmina longirostris* and *Chaoborus flavicans* by perch fry was estimated using the same procedure. Elevtivity indices for different size-classes of *Daphnia pulicaria* were calculated according to Ivlev (1961).

RESULTS

Perch Fry Distribution and Abundance

Adult perch began to spawn on May 13 in 1975 in water temperatures of 7.1 C (Table 1). The duration of spawning activity varied in different parts of the lake, but did not exceed 13 days from the initiation of spawning. Heaviest spawning activity occurred in the bay at dip net location 2 (Fig. 1). The first eggs became eyed on May 28 when embryos had a mean length of 4.37 mm. The time required for hatching of perch eggs at dip net location 2 was 20 days when the mean daily water temperature was 10.9 C. During this time water temperature varied from 7.1 - 13.0 C.

The first hatching of eggs reared in aquaria occurred on June 2 in 1975 when the fry had a mean length of 5.49 mm. The first fry were caught in the lake on June 9 in 1974 and June 2 in 1975 with mean lengths of 5.60 mm and 5.96 mm respectively.

Observations made on hatching perch fry in aquaria showed that on emerging from their eggs they passively sank to the bottom of the aquarium and laid on their side. At 2-3 min intervals during the first 3 h they would point their head towards the surface and wiggle vigorously, moving 3-5 cm off the bottom of the aquarium. At this point they would stop moving and sink to the bottom of the aquarium, resting on their side. Within 5 h of hatching the fry were able to

Table 1.   Observations of perch spawning sites in 1975.

Date	Dip Net Location 1			Dip Net Location 2			Dip Net Location 3		
	Temp (C)	No. of Spawning Sites	Eggs Eyed	Temp (C)	No. of Spawning Sites	Eggs Eyed	Temp (C)	No. of Spawning Sites	Eggs Eyed
May 13	+*	0		7.1	3	NO	+	0	
May 15				11.8	17	NO	10.8	1	NO
May 16	9.3	0							
May 18	8.3	3	NO	9.5	26	NO	9.5	4	NO
May 20	10.0	5	NO	11.0	32	NO	9.5	13	NO
May 26	10.5	5	NO	10.5	33	NO	10.0	18	NO
May 28	10.5	5	NO	12.5	29	YES	12.0	14	NO
May 30	10.0	4	YES	11.0	26	YES	10.5	12	NO
June 1	10.5	4	YES	12.0	31	YES	12.0	13	YES
June 2	10.5	4	YES	13.0	24	YES	12.0	11	YES

*+ temperature not available.

swim 10-12 cm off the bottom of the aquarium.   On
reaching this height they would again become inactive
and start sinking, but only until they came in contact
with another surface at which time they would resume
their swimming activity.

Perch fry remained in shallow water, near the
spawning sites, for approximately 1 wk following hatching
(Table 2).   They were easily caught at night with small
dip nets during this period as they would actively swim
towards an artificial light source shone on the surface
of the water.   By the end of the first wk they began to
move away from the shore and within 2 wk of hatching they
had moved into the pelagic zone (Tables 3 and 4).   This
transition occurred at a time when the surface water
temperature ranged from 13.0 - 19.0 C.

The smallest perch fry found in the pelagic zone
(9.17 mm) was caught on June 16 in 1975.   During this
phase of their life surface water temperatures ranged
from 16.0 - 22.0 C.   The fry were most readily caught in
the evening in the surface waters using a half-metre tow net.
Relative abundance of perch fry varied in different areas of
the lake and was always highest in the bay (tow location
1 in Table 4).

Tow catches declined rapidly in mid-July while
increasing numbers of perch fry were found in the littoral
zone.   The first fry were seen inshore on July 15 in 1974

Table 2. Catch per standard dip net haul of perch fry near the spawning sites in 1974 and 1975.

		C A T C H	
Date	Location 1	Location 2	Location 3
1974			
June 9		14	7
10	4	7	
12		3	
1975			
May 30	0	0	0
June 1	0	0	0
2	0	7	0
3		14	
4	0		4
5		32	
6	0		50
8		+*	
9	+		+
11	+		+
13		+	
14	0	0	0

*+ perch fry were caught but the numbers were not recorded.

Table 3.   Presence (+)/Absence (-) of perch fry as determined by surface
            tows in 1974.

Date	Two Location 1	Tow Location 2	Tow Location 3	Tow Location 4
June 18	+			
June 24		+	+	+
July 1		+	+	+
July 4		+	+	+
July 8		+	+	+
July 15	+	+	+	+
July 22	-	-	-	+
July 25	-	-	-	-

Table 4. Catch per standard tow of perch fry in 1975.

Date	Tow Location 1	Tow Location 2	Tow Location 3	Tow Location 4
June 10	0			
June 12	0			
June 16	+*			
June 17	+			
June 20	+			
June 21	+			
June 22	17.3	5.6	5.7	0.8
June 25	43.5	12.7	4.4	2.2
June 29	18.0	7.3	16.3	9.6
July 4	12.7	5.6	3.2	3.5
July 7	3.8	0	0.5	1.3
July 11	1.4	0	0	0
July 14	7.1	0	0	0.6
July 22	0	0	0	0

*+ perch fry were caught but the numbers were not recorded.

Table 5.   Catch per standard seine haul of perch fry in 1974.

Date	Bay	Basin 1	Basin 2	Basin 3
			CATCH	
July 15	0	0	0	0
July 22	19	1	.5	2
July 25	32	0	19.5	9
July 29	0	0	0	.3
Aug. 1	0	0	.5	0
Aug. 5	0	7	65	0
Aug. 8	0	1.5	7	0
Aug. 15	0	0	0	0
Aug. 17	0	0	0	0

Figure 2.   Growth of perch fry in length (●) and dry
             weight (▨) for 1974 and 1975.   Open
             points are estimates from the bay.
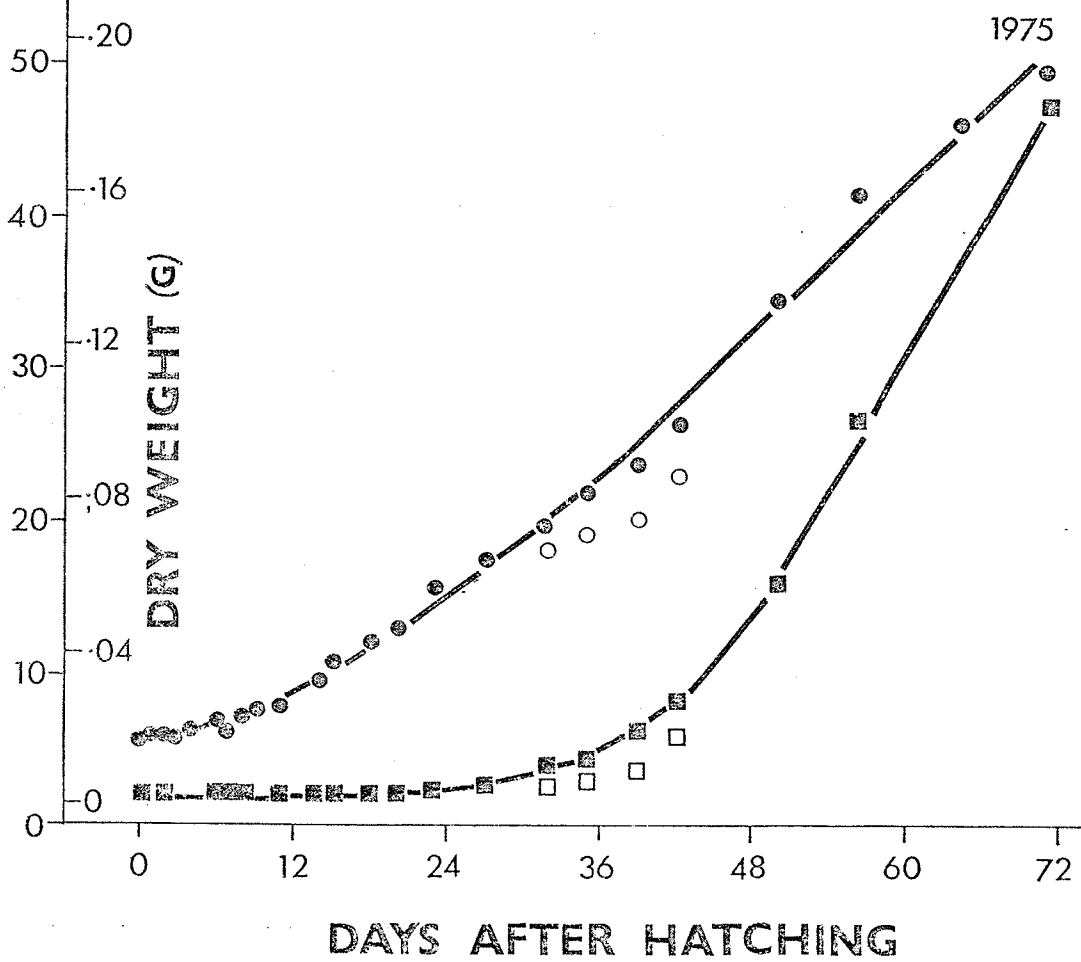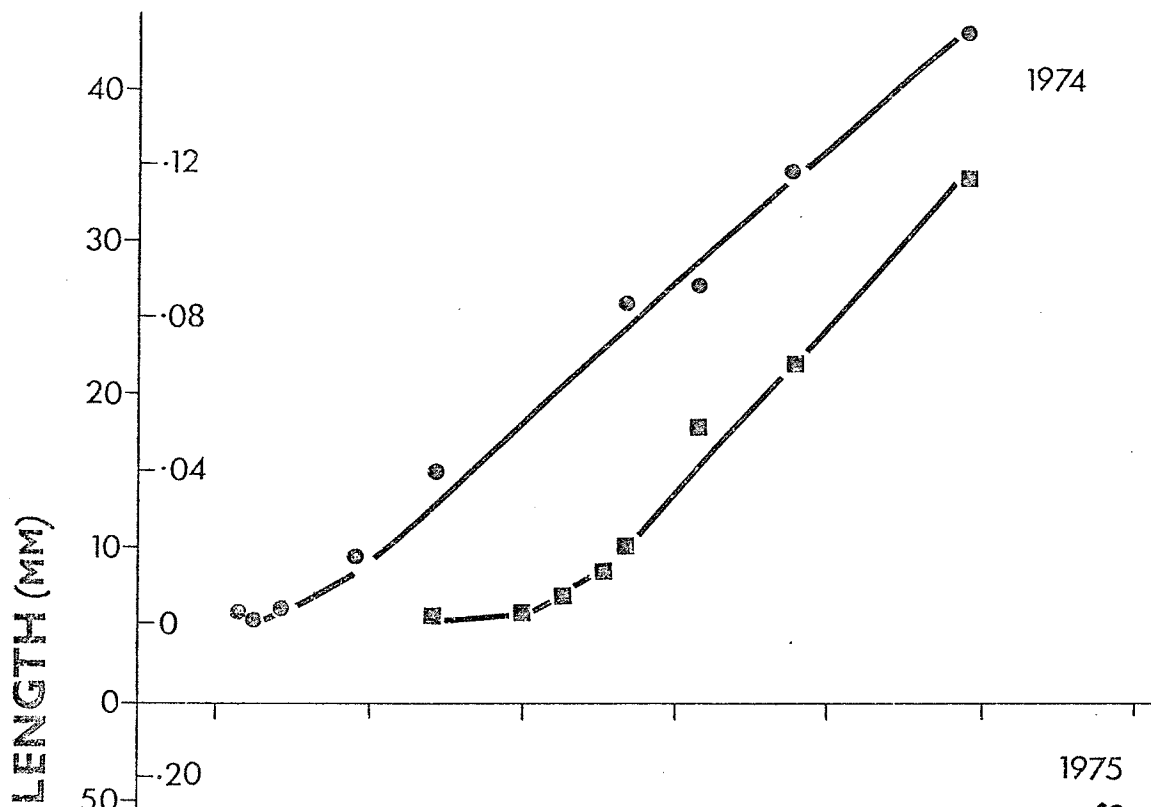
Figure 3.   Growth stanzas of perch fry in length (◉)

and dry weight (▦) for 1974 and 1975.
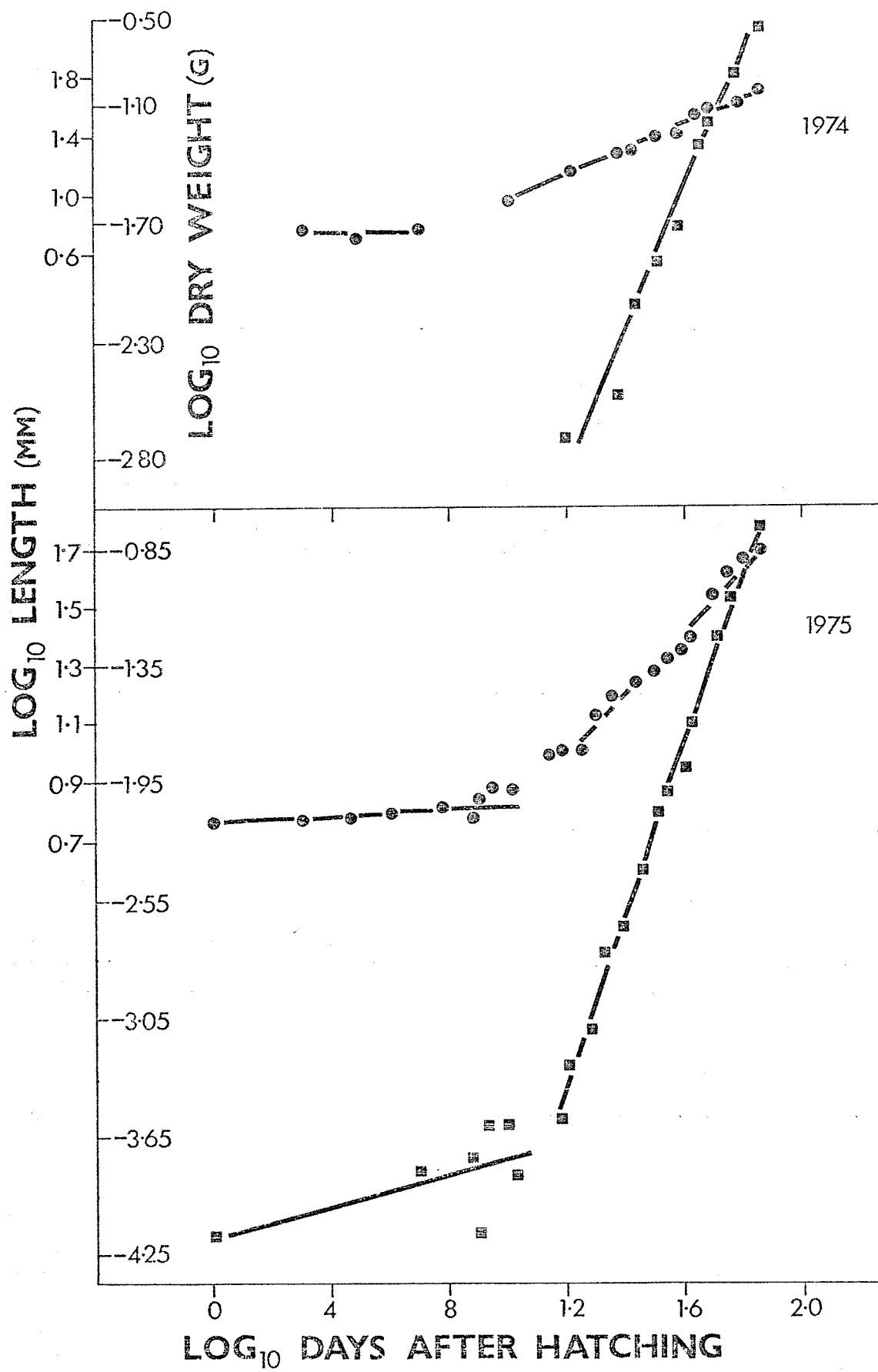
they moved into the pelagic zone.   Growth during this
stanza was slow and described as:

$$Log_{10} \text{ length} = .748 + .097 (Log_{10} \text{ days after hatching}); \quad r = .776 \ (P < .05)$$

and
$$Log_{10} \text{ dry weight} = .457 (Log_{10} \text{ days after hatching}) - 4.201; \quad r = .683 \ (P > .05)$$

in 1975.   The second stanza started at the beginning of
the pelagic phase and lasted for the remainder of the
summer (Fig. 3).   Growth during this stanza was rapid
and described as:

$$Log_{10} \text{ length} = .833 (Log_{10} \text{ days after hatching}) - .152; \quad r = .955 \ (P < .01)$$

and
$$Log_{10} \text{ dry weight} = 3.453 (Log_{10} \text{ days after hatching}) - 7.063; \quad r = .990 \ (P < .01)$$

for 1974 and Log_{10} length $= .989 (Log_{10}$ days after hatching)
$- .167; \quad r = .989 \ (P < .01)$

and
$$Log_{10} \text{ dry weight} = 3.913 (Log_{10} \text{ days after hatching}) - 7.982; \quad r = .997 \ (P < .01)$$

for 1975.

Regression lines describing the growth in terms of
length and in terms of dry weight were calculated for each
basin in 1974 and each basin and the bay in 1975.   Analysis
of covariance indicated the lines within a year were not
significantly different (P > .05) and therefore the results
from each sampling date were pooled.

In 1975 it was found that the size of perch fry caught in the bay during the pelagic phase was consistently smaller than those caught in other parts of the lake indicating the presence of a sub-population. Size estimates of fry captured in the bay are shown in Fig. 2 as open points. Although analysis of covariance indicated growth curves were similar for different parts of the lake, these points for the length growth curve fell well outside the 95% confidence intervals when they were omitted from the pooled data of the three basins.   The results are as follows:

Date	95% C.I. for Log_{10} length based on pooled data for basins 1, 2 and 3	Log_{10} length in the bay
July 4	$L_1 = 1.3487$	1.2596
	$L_2 = 1.3014$	
July 7	$L_1 = 1.3875$	1.2856
	$L_2 = 1.3401$	
July 11	$L_1 = 1.4343$	1.3043
	$L_2 = 1.3867$	
July 14	$L_1 = 1.4765$	1.3626
	$L_2 = 1.4289$	

As a result, these values were omitted from the common growth line. The same procedure was used for the dry weight growth curve. It showed that the dry weight values from the bay did not fall outside the 95% intervals when based on the

pooled data from the three basins, due mainly to the large confidence intervals. Although there was no statistical difference it was decided to omit these four values from the dry weight growth curve as there was a significant difference in their length and also, as the dry weight values from the bay were always lower than those from other parts of the lake during this period.

Length-dry weight relationships for 1974 and 1975 were described as:

Log_{10} dry weight - 3.838 (Log_{10} length) - 7.243;
r = .993 (P < .01)

for 1974 and Log_{10} dry weight = 3.713 (Log_{10} length) - 6.966;
r = .993 (P < .01)

for 1975 (Fig. 4). Values for each date were pooled as analysis of covariance indicated the length-dry weight relationships were similar for all parts of the lake in 1974 and 1975.

Length-weight relationships for carbon and nitrogen were similar in 1974 and 1975 (Fig. 5). The carbon curve was described as:

ln C = 3.527 (ln length) - 9.417; r = .997 (P < .01)

and the nitrogen curve as: lnN = 3.680 (ln length) - 11.364;
r = .993 (P < .01).

Instantaneous growth rates (Ricker 1975) of perch fry for 1974 and 1975, measured as dry weight, are shown in Fig. 6. In 1974, determinations of dry weight did not

Figure 4.   Length-dry weight relationship of perch
fry for 1974 and 1975.

Axis labels (vertical, left outer): DRY WEIGHT (G)

Top panel:
- Vertical axis (inner): LOG₁₀ DRY WEIGHT (G) — LOG_{10} DRY WEIGHT (G)
- Left weight scale: ·23, ·20, ·15, ·10, ·05, 0
- Log scale: −0.5, −1·3, −2·1, −2·9
- Label: 1974

Bottom panel:
- Left weight scale: ·19, ·15, ·10, ·05, 0
- Log scale: −0·5, −2·1, −3·7, −4·5
- Label: 1975

Horizontal axes:
- LOG_{10} LENGTH (MM): 0·6, 1·0, 1·5, 1·8
- LENGTH (MM): 0, 20, 40, 60
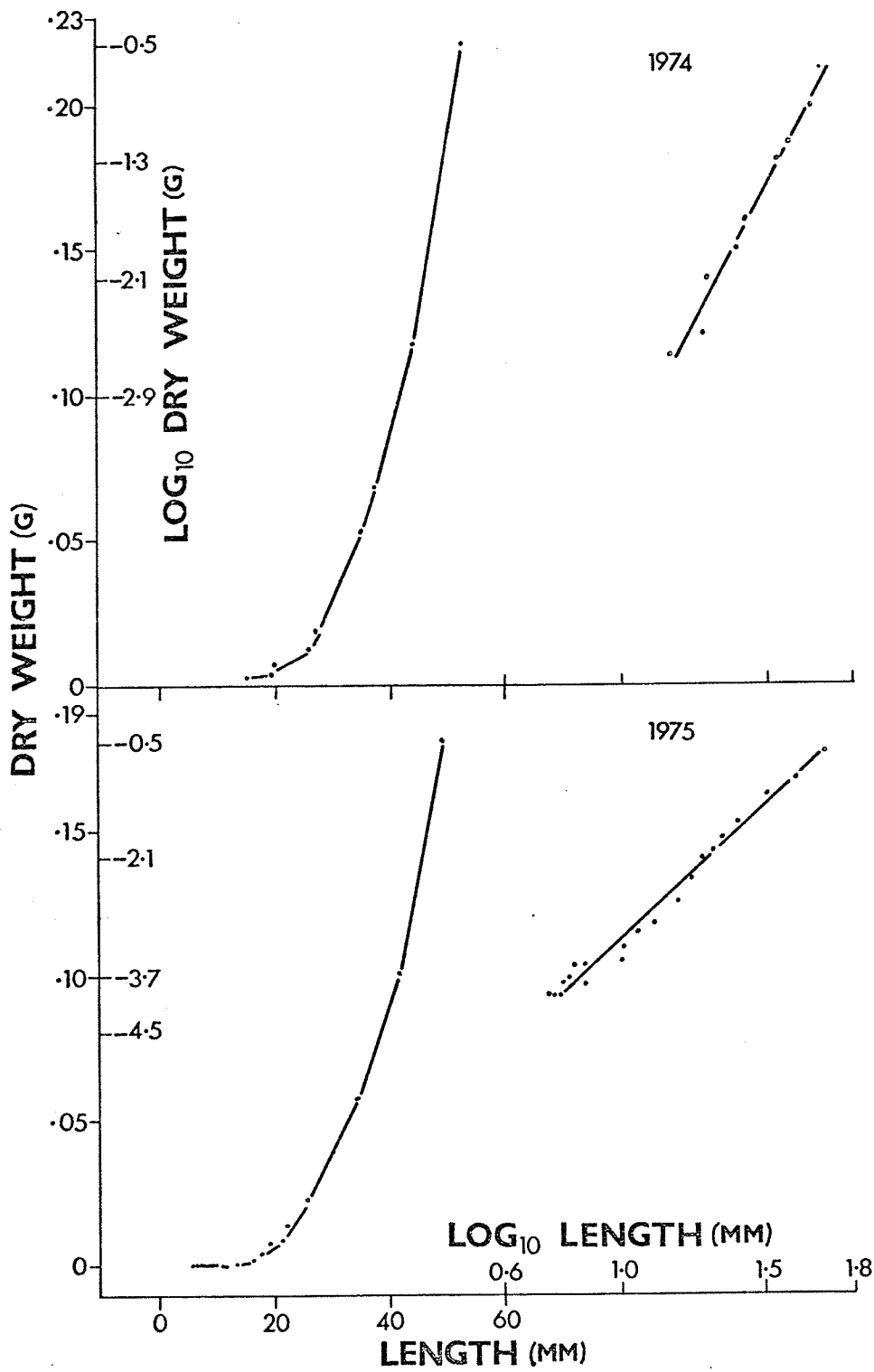
Figure 5.   Length-carbon and length-nitrogen

relationships of perch fry for 1974
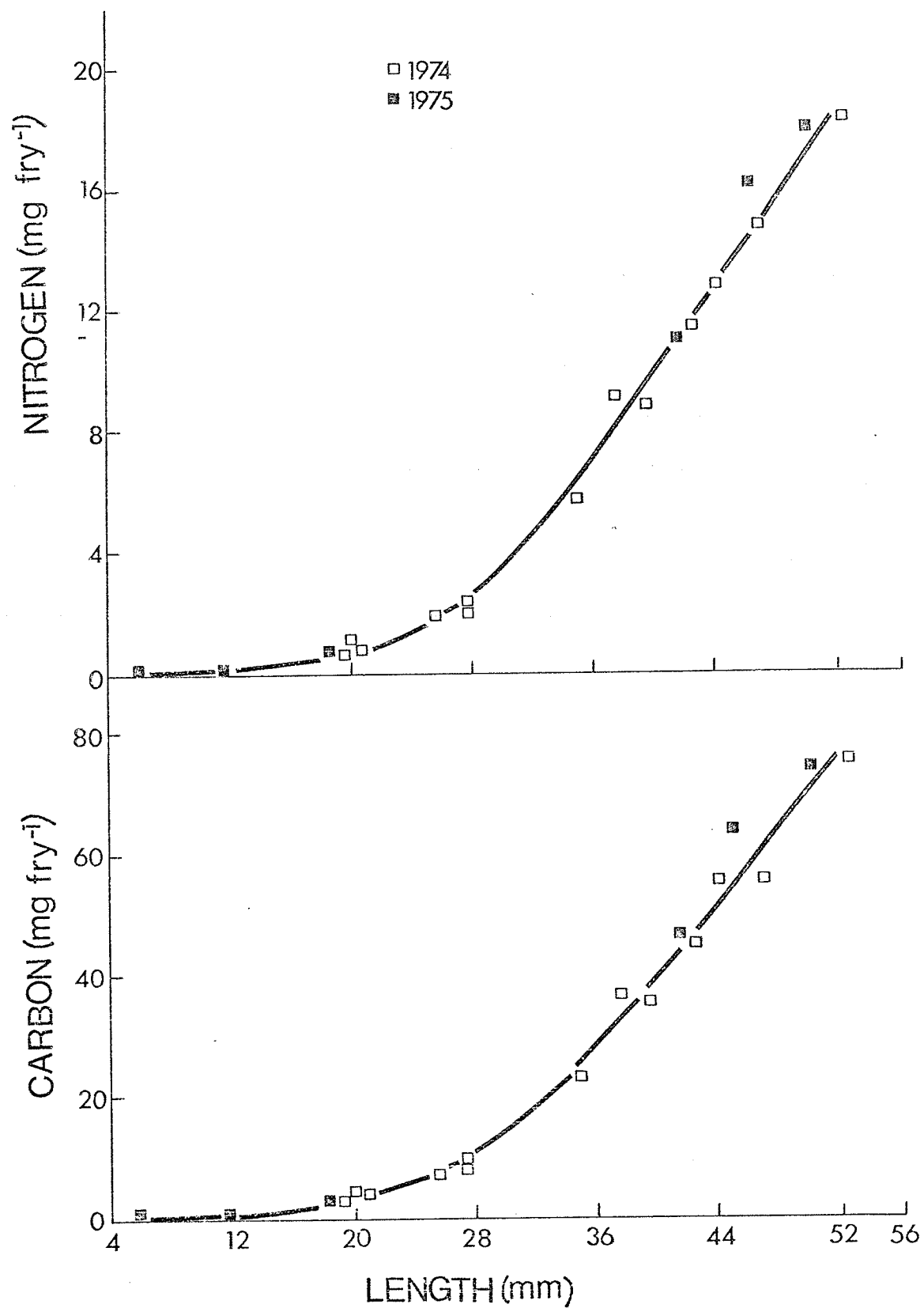
and 1975.

Figure 6.   Instantaneous growth rates (measured as dry
            weight) of perch fry for 1974 and 1975.
            Arrows indicate transition times from the
            spawning sites to the pelagic zone (A) and
            from the pelagic zone to the littoral zone
            (B).
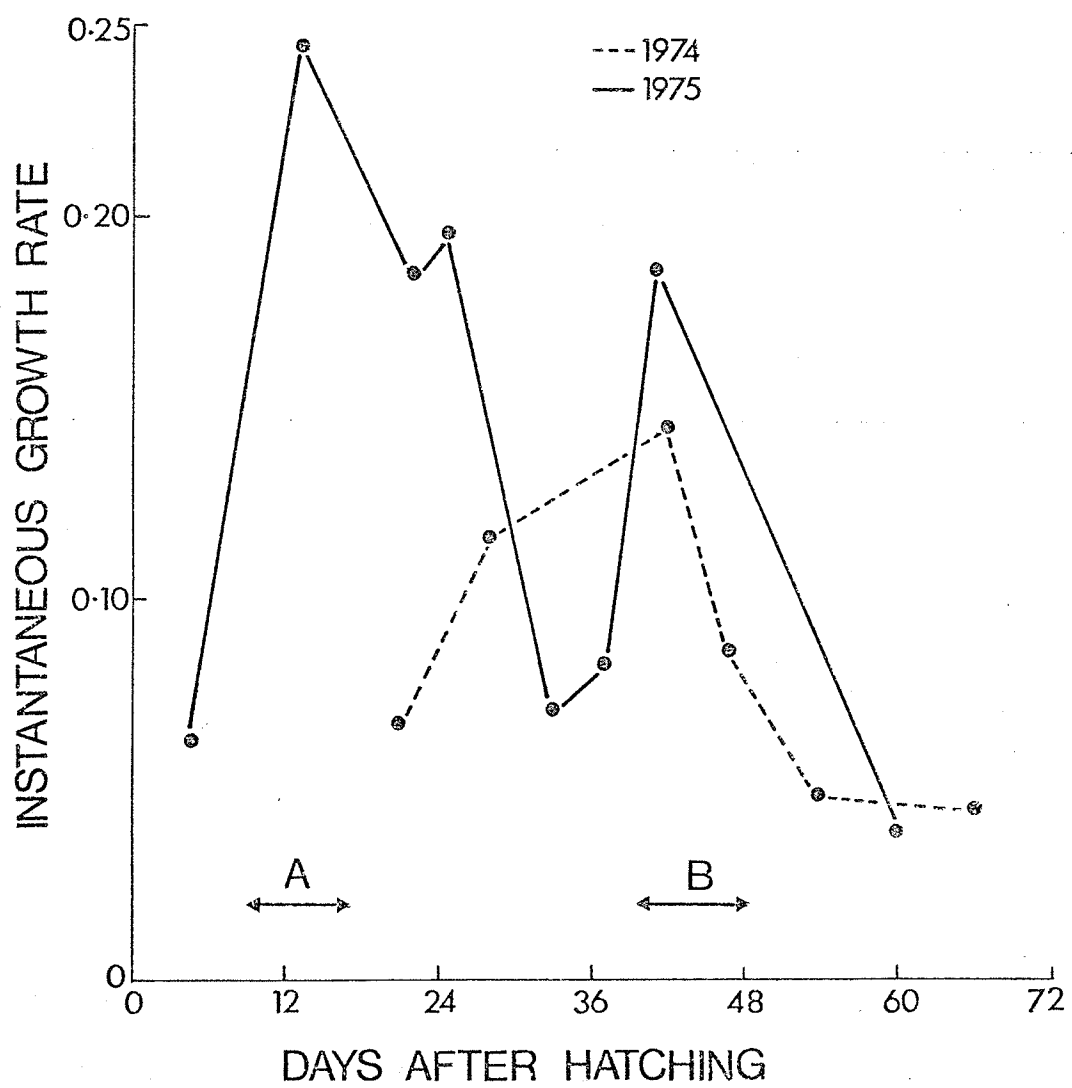
start until 21 days after hatching. In 1975, the instantaneous growth rate increased rapidly from hatching to a peak which coincided with the time of transition from a littoral to a pelagic habitat. It decreased while the fry were in the pelagic habitat and later developed a second peak in 1974 and 1975. The second peak coincided with the time of transition from a pelagic to a littoral habitat. The instantaneous growth rate then declined through the remainder of the littoral phase.

Seasonal changes occurred in the amount of carbon and nitrogen mg dry weight^{-1} in perch fry (Fig. 7). Both curves were fitted using a three point moving average. The fry had 547.9 ug C mg dry weight^{-1} on hatching. This value declined rapidly during the first 3 wk following hatching and was accompanied by an increase in nitrogen from 70.6 ug N mg dry weight^{-1} on hatching to 105.7 ug N mg dry weight^{-1} by the end of the pelagic phase. The amount of carbon and nitrogen mg dry weight^{-1} reached a peak just after the fry moved into the littoral zone at a length of 36-40 mm, after which both decreased sharply.

The highest carbon to nitrogen ratio (7.8) occurred immediately after hatching (Fig. 8). Following hatching there was a rapid decline to approximately four by the time

Figure 7. Proportion of carbon and nitrogen in perch

fry expressed as µg mg dry weight^{-1} relative

to growth in length for 1974 and 1975. The

standard deviation is shown (Arrows as

previously indicated).
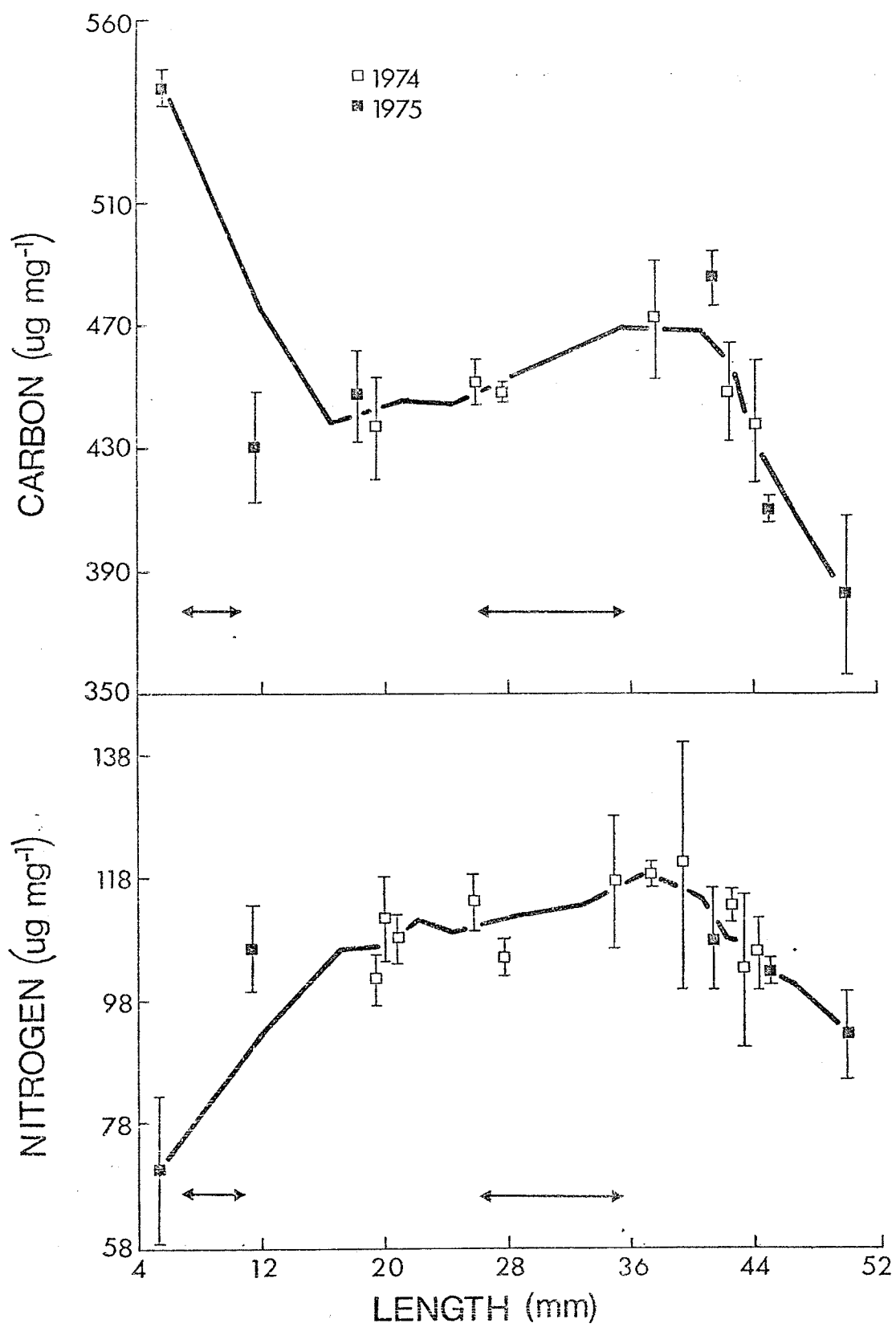
Figure 8. Carbon to nitrogen ratio of perch fry
relative to growth in length for 1974
and 1975. (Arrows as previously indicated).
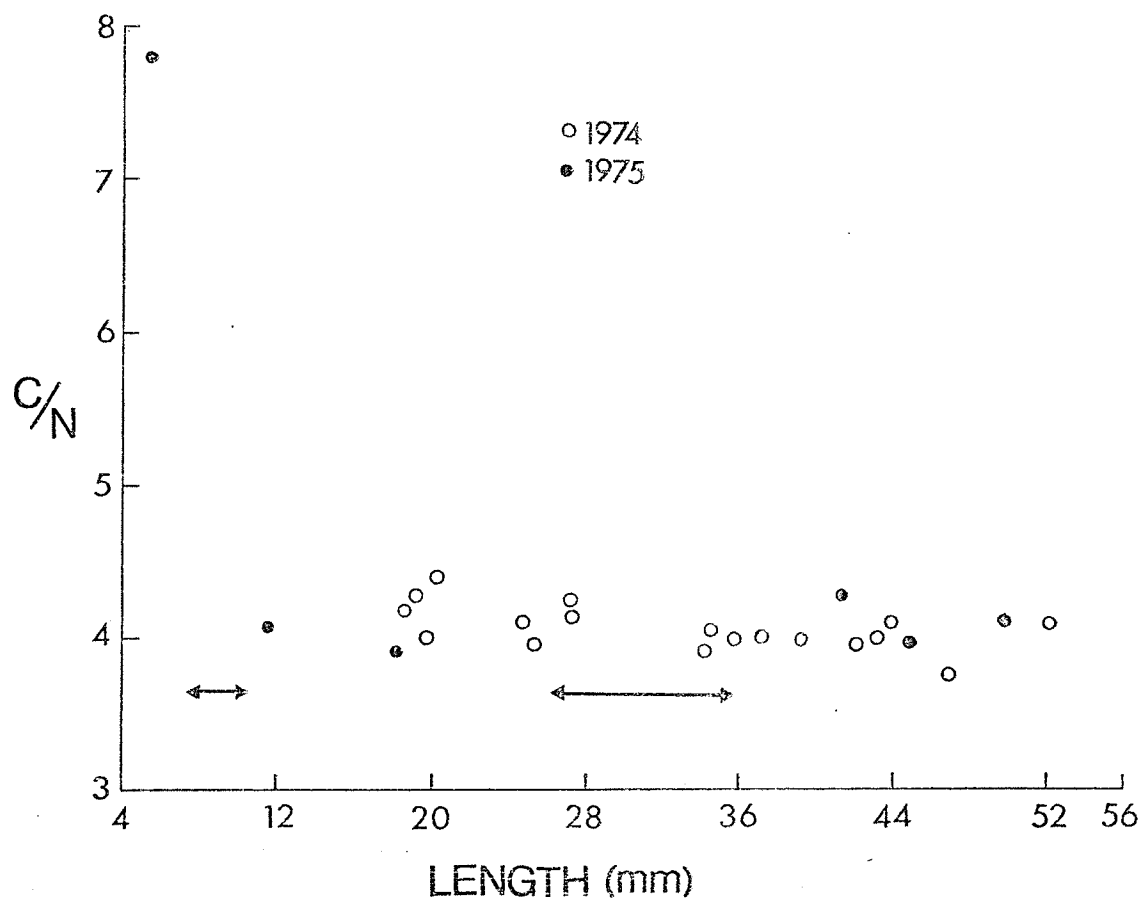
the fry were 11.5 mm in length. This value remained relatively constant for the rest of the season and the slope of a fitted regression line was not significantly different from zero (P > .05).

The highest seasonal calorific value for perch fry (6726.6 cal g dry weight^{-1}) was obtained from fry less than 1 h old, and declined rapidly, reaching a minimum (4947.1 cal g dry weight^{-1}) when the fry were 15 mm in length (Fig. 9). During the remainder of the summer there was a gradual increase in the calorific values, the greatest increase occurring after the fry had attained a length of 26 mm, which corresponds with the time of transition from a pelagic to a littoral habitat.

A large proportion of the wet weight of fish is made up of water. It was found that this value changes with time in perch fry (Fig. 10). The large degree of variation in fry 6-8 mm in length (1.79 to 2.08 as natural logs in Fig. 10) was the result of varying degrees of water absorption by recently hatched fry. Early growth was, in fact, largely the result of water absorption (Fig. 11). Prior to the initiation of feeding wet weight more than doubled but there was no perceptible increase in dry weight of the fry. Both curves in Fig. 11 were fitted by eye. Following the hatching period, the water content stabilized at approximately 89% of the total wet weight. It remained at this level

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Figure 9. Calorific value of perch fry relative to
growth in length for 1974 and 1975. The
standard deviation is shown. (Arrows as
previously indicated).

KCAL. G^{-1}

7·0

6·6

6·2

5·8

5·4

5·0

4·6

□ 1974
▣ 1975

*

4   12   20   28   36   44   52   56
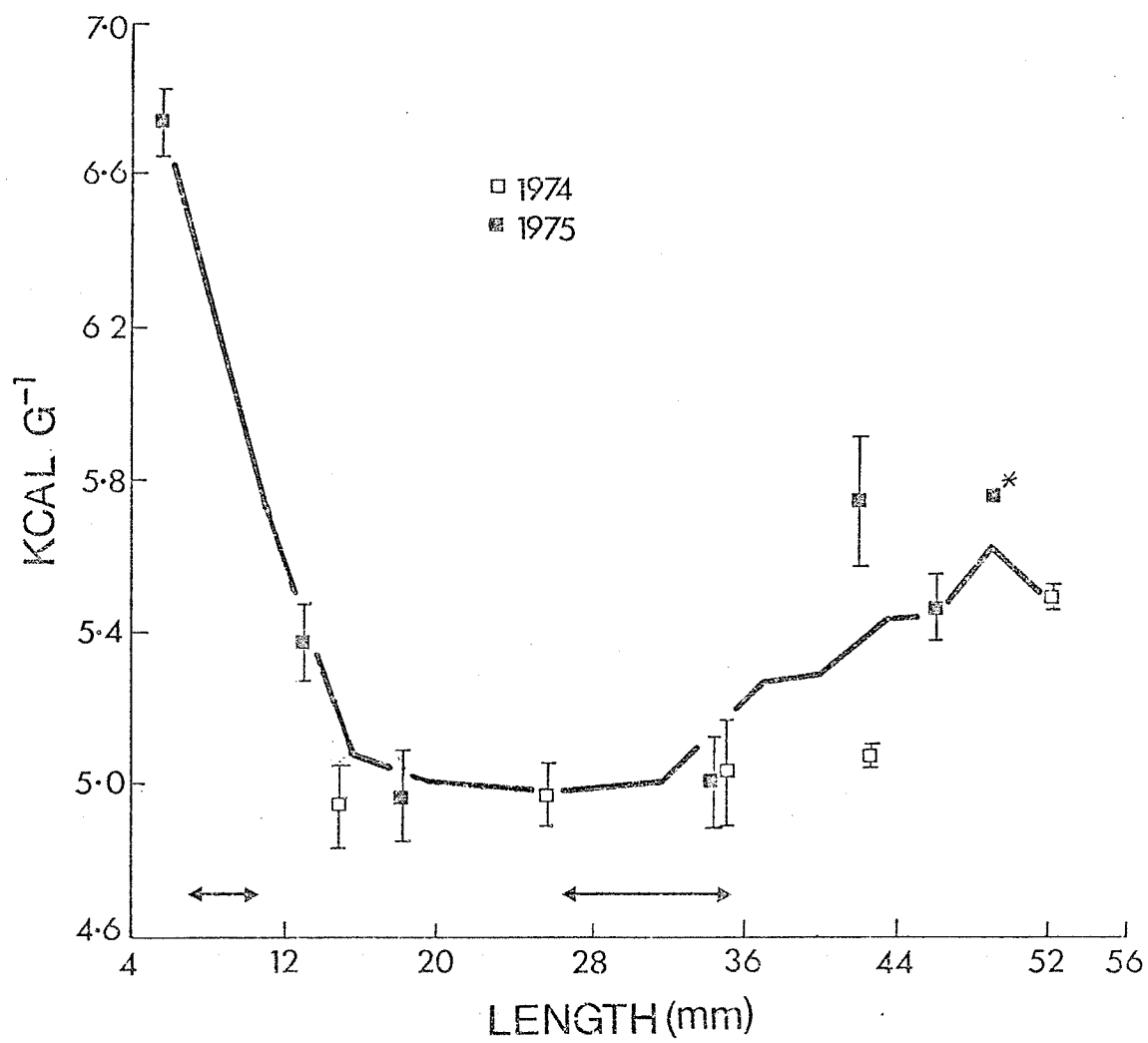
LENGTH (mm)

Figure 10.   Water content of perch fry relative to

growth in length for 1974 and 1975.

(Arrows as previously indicated).
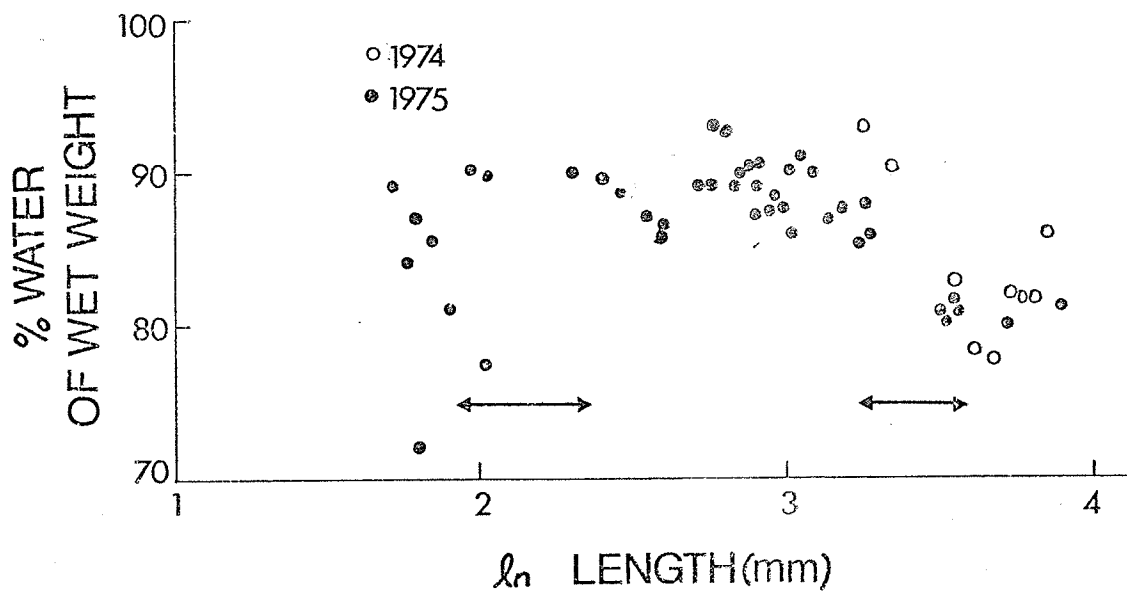
Figure 11. Wet weight (●) and dry weight (○) of

perch fry during early growth. The dotted

line indicates the approximate length at

first feeding.
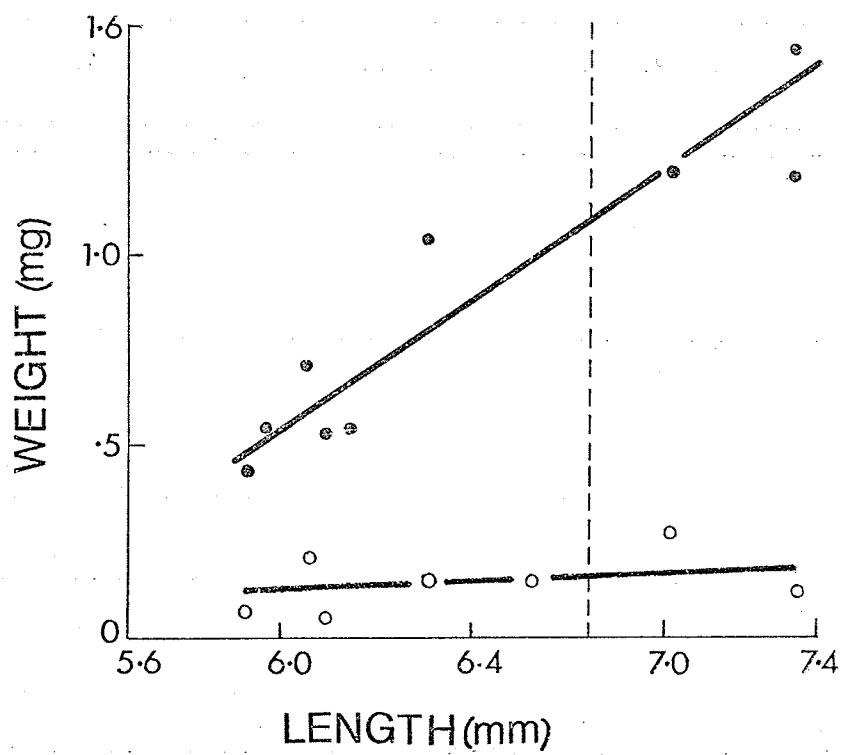
until the end of the pelagic phase and then decreased to
approximately 81% for the remainder of the sampling
period.

Feeding of Perch Fry

During the 1974 and 1975 growing seasons, perch
fry utilized a narrow range of food items consisting
entirely of planktonic organisms.   The relative importance
of different prey organisms was examined seasonally in
1974 and 1975.   The seasonal contribution (percent in terms
of calories) by different food items in the diet of perch
fry was similar in both years so only the 1975 results will
be discussed in detail.

Perch fry began to feed while the yolk sac was still
present, 6 days after hatching.   During the first 3-4 days
of feeding algae was present in the guts along with adult
copepods, copepodids, nauplii, and other unidentifiable
material (Table 6).   The importance of algae rapidly
declined while the adult copepods, copepodids and nauplii
remained the major food source prior to the fry moving into
the pelagic zone.   *Daphnia pulicaria* was first found in the
guts of fry in mid-June, shortly after the transition from
the littoral to the pelagic zone.   They quickly became
the dominant energy source for fry in basin 2 and the bay

Table 6. Seasonal contribution (percent in terms of calories) by different food items to the diet of perch fry caught in basin 2 and the bay in 1975. The mean total calorific value of the stomachs is shown.

Date	Days after hatching	*Daphnia pulicaria* B2	Bay	*Bosmina longirostris* B2	Bay	Copepods B2	Bay	Nauplii B2	Bay	*Chaoborus flavicans* B2	Bay	Total (cal.) B2	Bay
June 8	6	algae, copepods, copepodids, nauplii and other unidentifiable material present in guts											
9	7												
10	8												
13	11	0		0		98.12		1.88		0		.0533	
17	15	0		0		75.28		24.72		0		.0089	
21	19		3.48		0		93.50		3.02		0		.0431
22	20	2.77		0		96.30		.93		0		.0973	
23	21		29.37		0		70.49		.15		0		.1209
24	22	67.92		0		31.97		.11		0		.1780	
30	28		75.72		0		22.39		.05		1.84		.2175
July 1	29	94.97		0		4.98		.05		0		.2087	
7	35	96.80	84.95	0	0	3.20	15.03	0	.02	0	0	.2380	.2432
14	42	97.62	99.15	0	0	2.38	.85	0	0	0	0	.1431	.7510
23	51	29.98	61.25	0	23.33	69.53	15.42	0	0	.49	0	2.1455	1.9912
30	58	59.21	24.97	0	18.89	30.82	52.45	0	0	9.97	3.64	.6323	1.1387
Aug. 6	65	79.05	9.15	0	46.07	19.49	44.78	0	0	1.46	0	4.1123	5.2748
12	71	88.37	1.27	0	58.57	11.63	40.16	0	0	0	0	6.5714	7.8953

for the remainder of the pelagic phase. At the time of
transition from the pelagic to the littoral zone in
mid-July there was a marked decrease in the importance of
Daphnia pulicaria to the total energy intake of the fry
with a corresponding increase in the importance of
copepods. This trend reversed itself in basin 2 in the
following weeks with *Daphnia pulicaria* again dominating
the diet. In the bay the decrease continued, until, on
August 12, *Daphnia pulicaria* comprised only 1.27% of the
total calories in the stomachs of the fry. *Bosmina
longirostris* was then the dominant food item at this
location.

Abundance of *Daphnia pulicaria* and *Bosmina longirostris*
in the water column as well as their importance to the diet
of perch fry is shown in Fig. 12. At station 2 (Fig. 1)
Bosmina longirostris never became very abundant and were
never present in stomachs of the fry collected in basin 2.
At station 6 the *Daphnia pulicaria* population decreased to
a very low level after mid-July and was replaced by
Bosmina longirostris. A similar trend was found in
stomach contents of fry collected from this location.
Abundance of *Daphnia pulicaria* and their importance to the
diet of perch fry in basins 1 and 3 was similar to that of
basin 2. Weekly samples taken at stations near the shore
(Fig. 1) showed that the abundance of all zooplankton species
was very low in shore waters.

Figure 12.   Abundance of *Daphnia pulicaria* (●) and

Bosmina longirostris (O) in plankton (——)

and their percent contribution to the total

stomach calories of perch fry (-----) in

basin 2 and the bay for 1975.
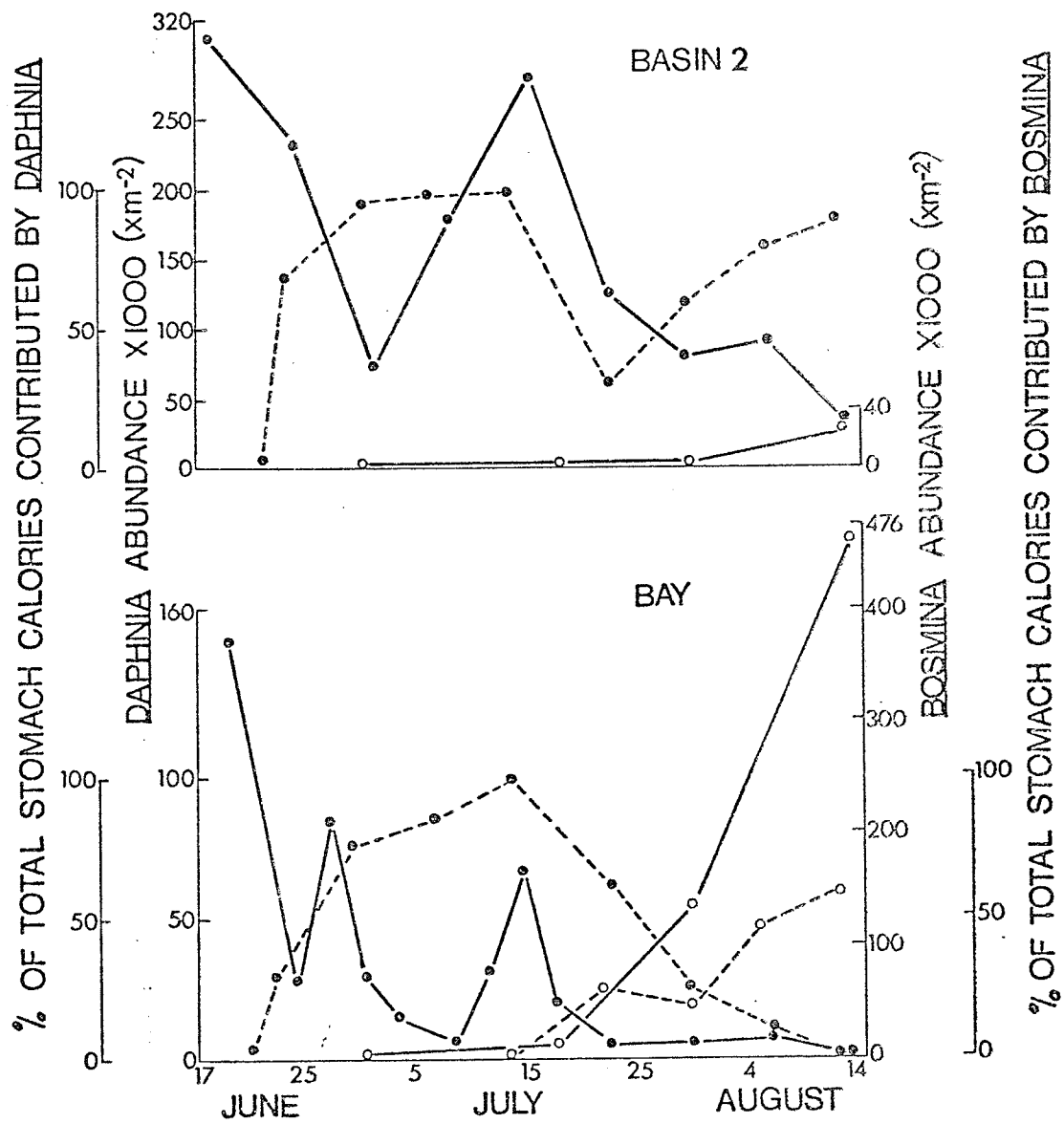
When comparing the mean length of *Daphnia pulicaria*
in stomachs of perch fry with the mean length in plankton
collections it was necessary to carefully consider the
length-frequency distribution of *Daphnia pulicaria* at
various depths.   On a typical mid-summer day the mean
length of *Daphnia pulicaria* was smallest at 8 m and largest
at 15 and 20 m with the 0-30 m integrated sample falling
in between (Fig. 13).   *Daphnia pulicaria* was absent from
the 2.5 m sampling depth during daylight hours after June 26
and did not reappear until September 4.

Perch fry of West Blue Lake remain in the region of
the metalimnion during the daylight hours (Wong 1972).
Therefore, the length-frequency distribution of *Daphnia
pulicaria* in stomachs of perch fry was compared to the
length-frequency distribution of *Daphnia pulicaria* at 8 m
at station 2 (Fig. 14).   The length-frequency distribution
of *Daphnia pulicaria* in stomachs of perch fry caught in the
bay was compared to the integrated length-frequency
distribution at station 6.   Early postlarval fry fed on
small *Daphnia pulicaria* but as they grew their prey increased
in size.   Following the end of the pelagic phase the mean
length of *Daphnia pulicaria* ingested was restricted to the
mean length of *Daphnia pulicaria* at the 8 m depth at station
2 and in the 0 - 8 m integrated sample at station 6.

Figure 13.   Length-frequency distribution of *Daphnia*

pulicaria for various depths at station 2

on a typical mid-summer day.   Samples were

collected at 10:00 h.
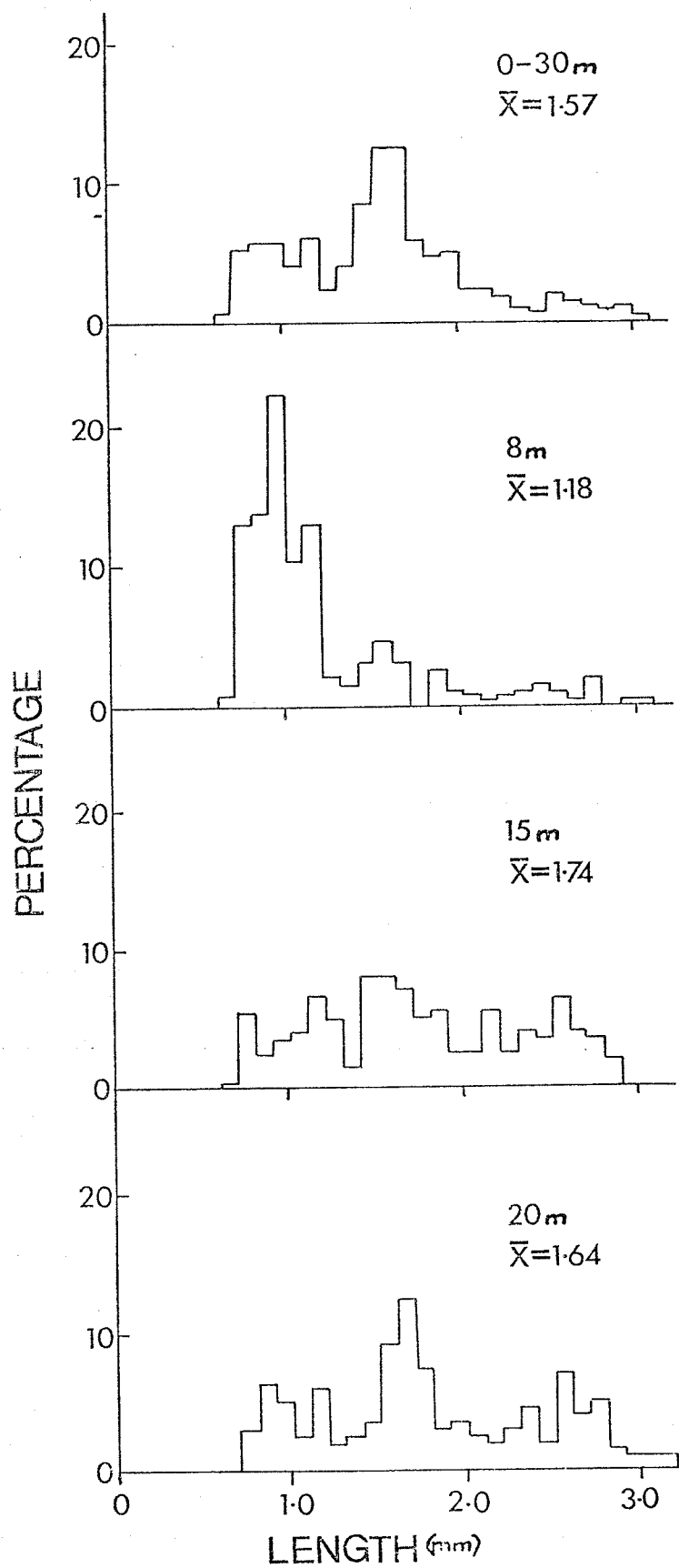
Figure 14.   Mean length of *Daphnia pulicaria* in perch
fry stomachs (▲) and in plankton samples
from 0-30 (●——— - ——●), 8 (●-----●) and 15 m
(●———●) in basin 2 (station 2) and from
0-8 m (●———●) in the bay (station 6)
for 1975.
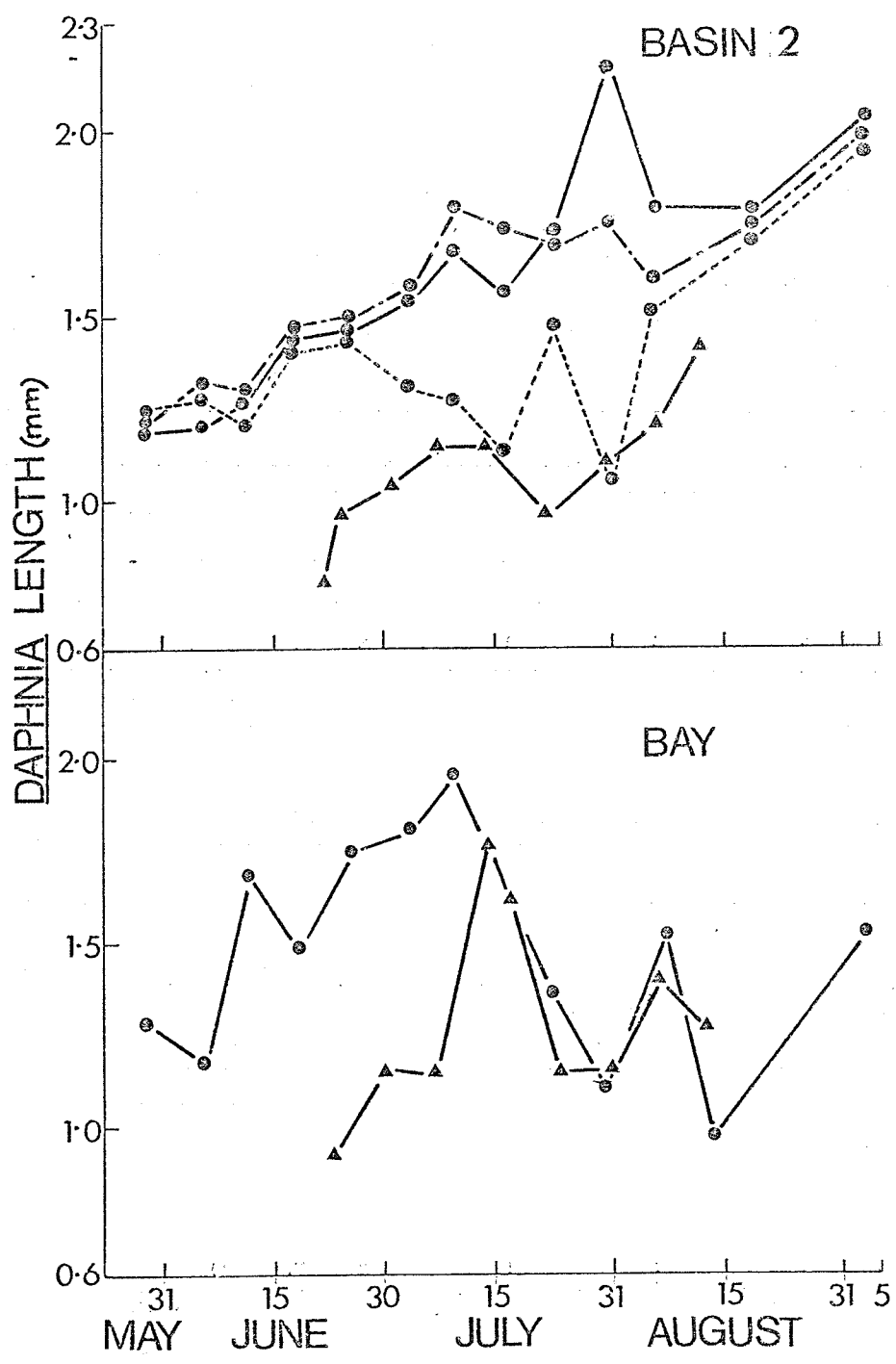
Differences in the mean length of *Daphnia pulicaria* at 8
and 15 m, in the 0-30 m integrated sample and in the
stomachs of perch fry are shown in Fig. 14.   The 20 m
samples, which were omitted for clarity, followed the
same pattern as the 15 m samples.

The importance of various utilizable length-classes
of *Daphnia pulicaria* to perch fry was dependent upon the
relative abundance of the different length-classes in the
plankton.   On July 4 and July 10 small *Daphnia pulicaria*
were not very abundant at either the 8 or 15 m depths
($\simeq$ 0 - .5 animals l^{-1}) (Fig. 15).   At the same time,
the mean length of *Daphnia pulicaria* in the stomachs of
the perch fry increased from 1.04 mm on July 1 to 1.15 mm
on July 7 (Fig. 14).   Between July 10 and July 17 a large
number of new *Daphnia pulicaria* were produced and were in
greatest abundance at the 8 m depth ($>$ 2 animals l^{-1}).   This
coincided with a decrease in the mean length of *Daphnia
pulicaria* in stomachs of perch fry from 1.15 mm on July 7
to 1.11 mm on July 14 to .97 mm on July 23.   By August 6
all size-classes of *Daphnia pulicaria* were in very low
abundance at station 2 and most were being used as a food
source.

Mean length and range in length of *Daphnia pulicaria*
in a reproductive condition were based on the 0-30 m and
0-8 m integrated samples for stations 2 and 6 respectively
(Fig. 16).   On August 1 at station 6, there were no

Figure 15.   Abundance of different length-classes of

Daphnia pulicaria at 8   and 15 m at

station 2 for 1975.
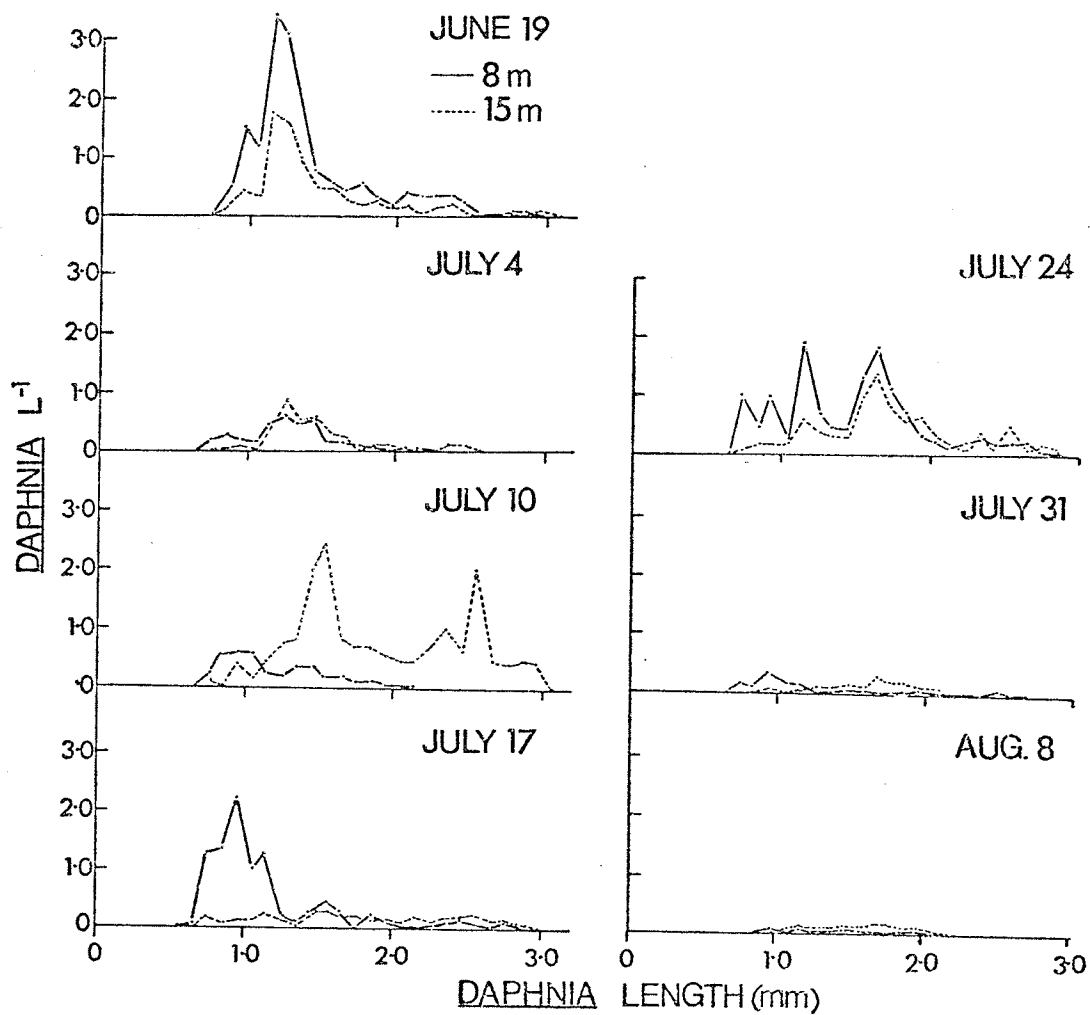
Figure 16.   Length-frequency distribution of

Daphnia pulicaria in stomachs of

perch fry collected from basin 2 and

the bay in 1975.   Mean length and range

in length of *Daphnia pulicaria* in a

reproductive condition are shown by

the arrows.

BASIN 2   BAY

PERCENTAGE

DAPHNIA LENGTH (mm)
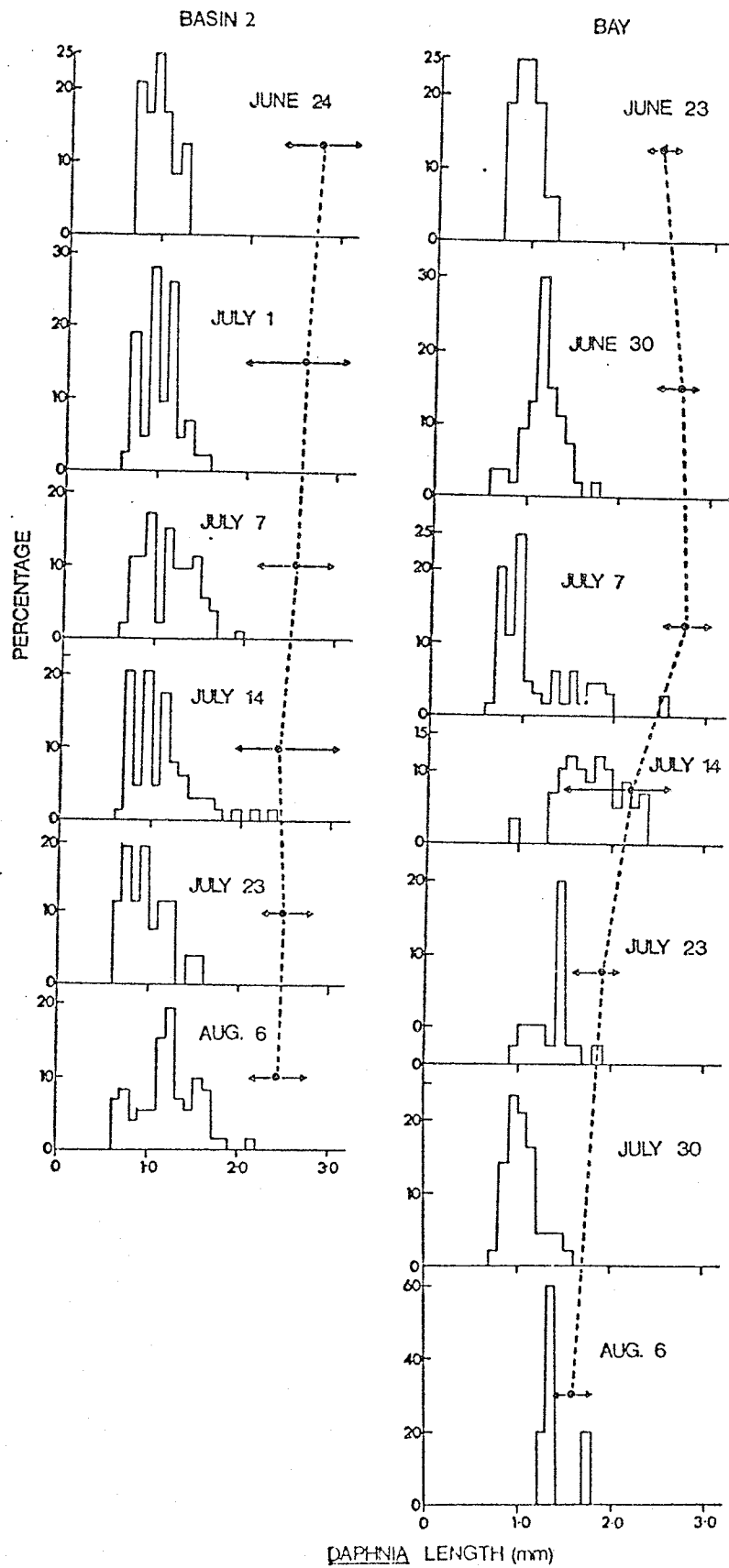
Daphnia pulicaria in a reproductive condition in the water column. The reproductive *Daphnia pulicaria* at station 2 were not affected by the predation of perch fry as they were larger than the size being utilized by the fry. The situation was the same at station 6 until mid-July. At this time there was a rapid decrease in the mean length of *Daphnia pulicaria* in a reproductive condition, and *Daphnia pulicaria* as small as 1.37 mm in length were found bearing eggs and embryos. For the remainder of the summer, in the bay, there was an almost complete overlap between the length of reproductive *Daphnia pulicaria* in the plankton and the length being consumed by perch fry.

The mean clutch size of *Daphnia pulicaria* (number of eggs per egg-bearing female) changed over the season but the pattern was not the same at stations 2 and 6 (Table 7). The largest clutch sizes occurred in the spring and declined into early July at both locations. At station 2 the decline stabilized at early July levels while at station 6 there was an increase in the mean clutch size of *Daphnia pulicaria* over the remainder of the season.

The length of *Daphnia pulicaria* consumed by perch fry was also found to change on a diel basis, during the pelagic stage (Fig. 17). On June 28-29 and July 8-9 the mean length of *Daphnia pulicaria* in stomachs, determined from

Table 7.   The mean clutch size of *Daphnia pulicaria*
(number of eggs per egg-bearing female) at
stations 2 and 6 in 1975.

| | Mean Clutch Size | |
Date	Station 2	Station 6
May 13	11.65	
19	15.35	
29	15.78	
	11.80	
June 5		
6		8.00
12	5.73	
13		6.05
19	4.36	
20		3.67
26	3.67	
27		2.33
July 3	2.57	
4		2.50
10	2.29	
11		3.56
17	2.50	
18		2.00
24	1.83	
25		3.08
31	2.00	
Aug. 1		+*
8	2.50	
9		3.38
14	+	
15		4.06
Sept.4	1.28	+

*+ no *Daphnia pulicaria* in a reproductive condition.

Figure 17. Diel variation in mean length of

Daphnia pulicaria in stomachs of

perch fry during the pelagic phase

in 1975.
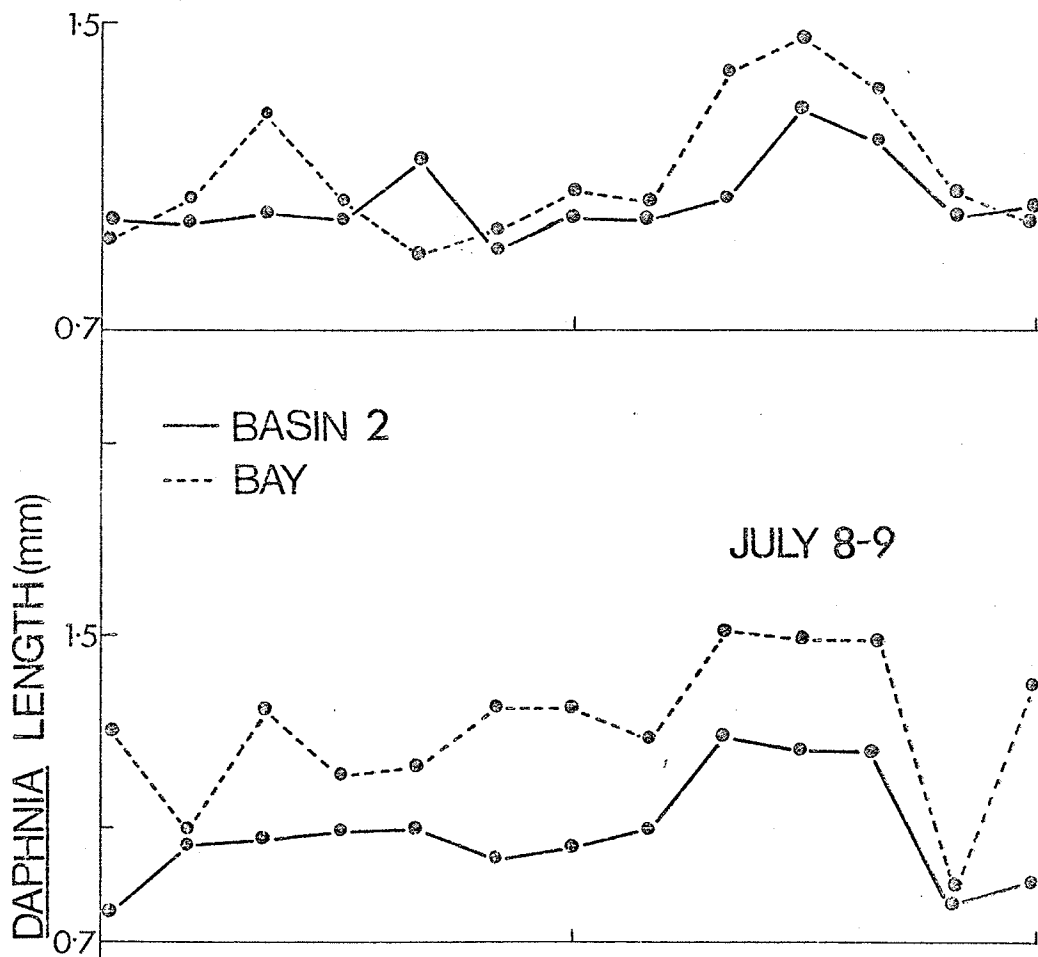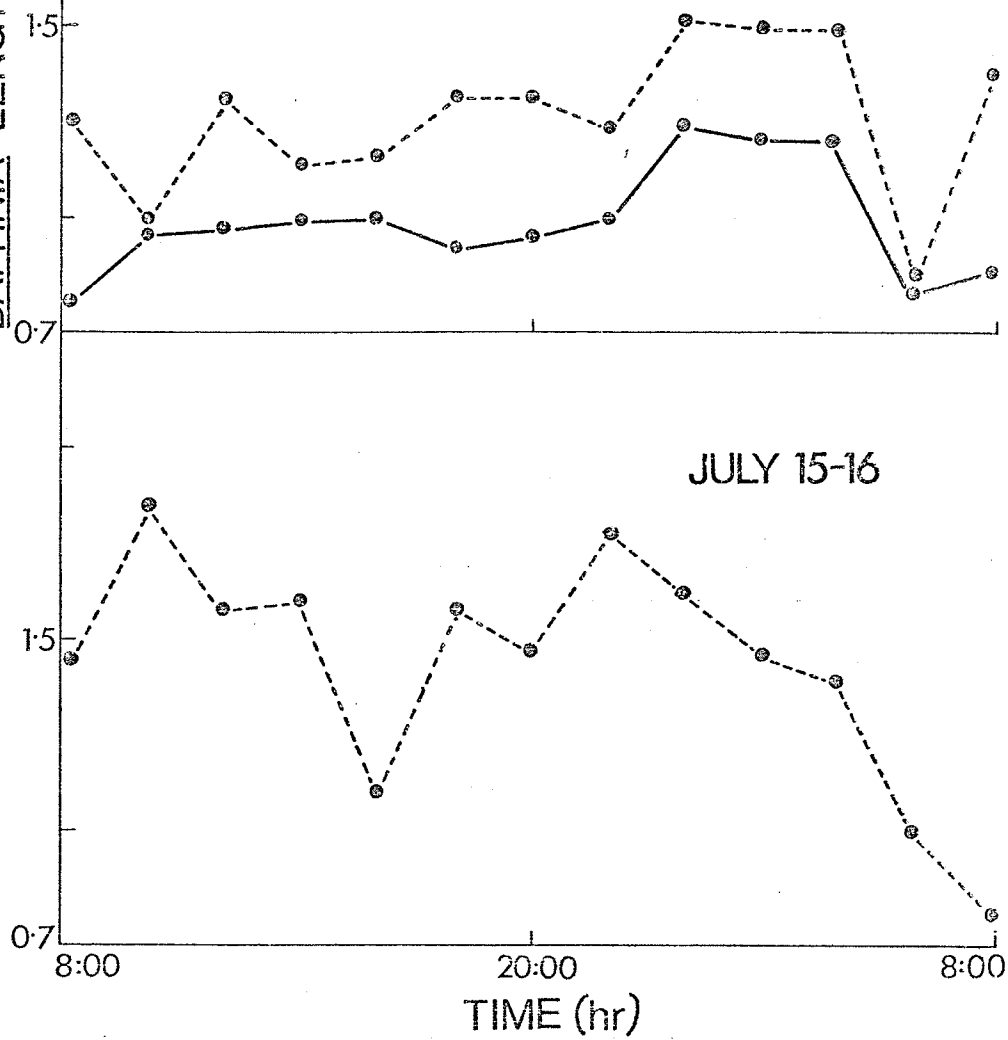
fry samples taken at 2 h intervals over a 24 h period,
was greatest at night between 24:00 and 04:00 h and
smallest in the morning between 06:00 and 08:00 h.
There was no apparent pattern in the bay on July 15-16.
The nighttime increase in the length of *Daphnia pulicaria*
consumed by perch fry coincided with an increase in the
mean length of *Daphnia pulicaria* in the feeding zone.
The *Daphnia pulicaria* of West Blue Lake are known to
undergo a diel vertical migration during the spring and
summer being generally below 5 m during the day (06:00 -
22:00 h) and forming dense concentrations near the surface
at night (22:00 - 06:00 h) (Bell and Ward 1970, Wong 1972).
The migration of *Daphnia pulicaria* changes their length-frequency
distribution in the feeding zone over the day (Fig. 18).
During the day, in basin 2, perch fry were feeding on a
Daphnia pulicaria population with a length-frequency
distribution approximated by the 8 m sample from station 2.
At night, perch fry and the entire *Daphnia pulicaria*
population rose to the surface (Wong 1972) increasing the
proportion of large *Daphnia pulicaria*, and their mean
length in the feeding zone (2.5 m).   The pattern was the
same in the bay where very few *Daphnia pulicaria* were
present in the upper 5 m of water during the day but became
very abundant in the surface waters at night with a

Figure 18.   Length-frequency distribution of

Daphnia pulicaria at station 2 on

July 10 and at station 6 on July 11,

1975.

STATION 2   STATION 6

PERCENTAGE

8 m 10:00 h
$\bar{X}$=1·27 mm

0-30 m 10:00 h
$\bar{X}$=1·67 mm

0-8 m 10:00 h
$\bar{X}$=1·96 mm

2·5 m 24:00 h
$\bar{X}$=1·64 mm

2·5 m 24:00 h
$\bar{X}$=2·02 mm

DAPHNIA LENGTH (mm)
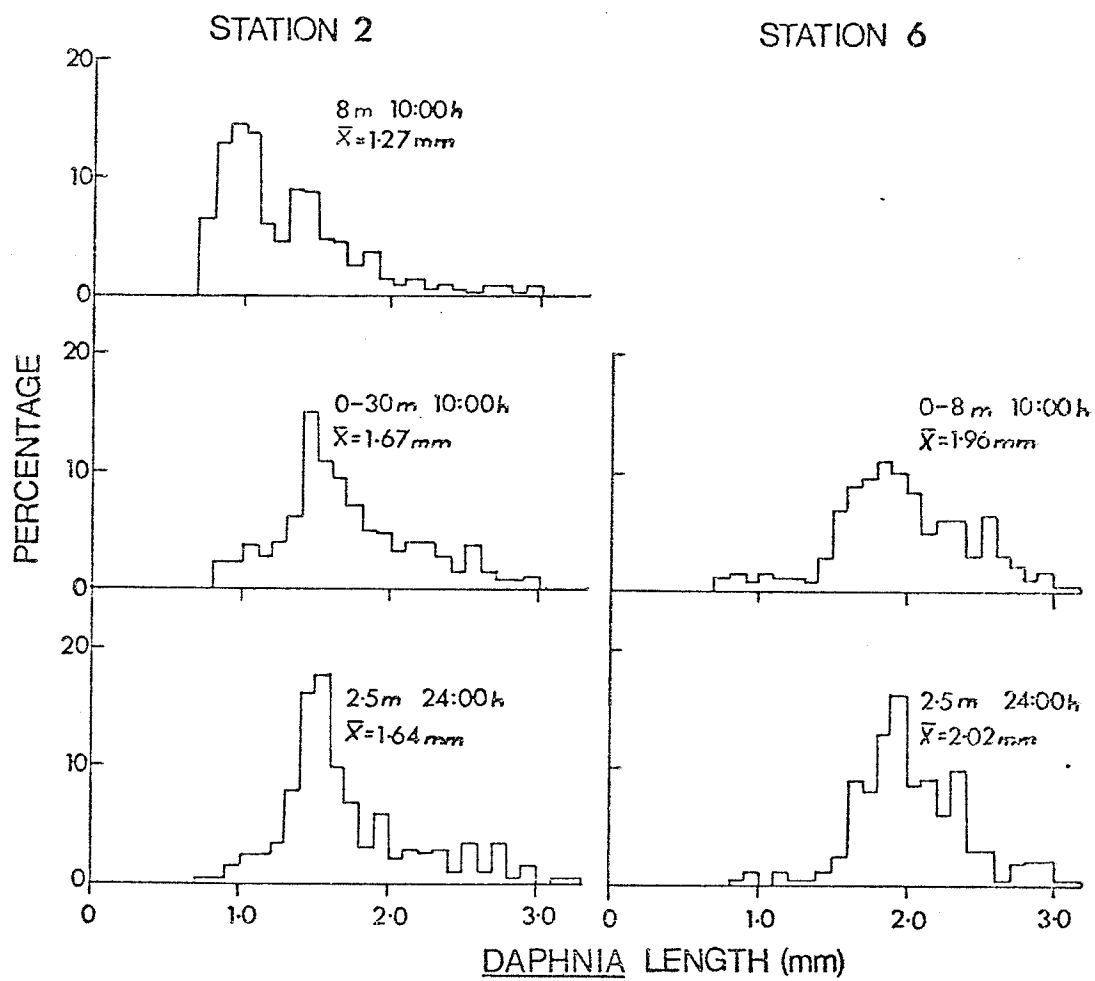
length-frequency distribution similar to that of the
0-8 m integrated sample collected at 10:00 h (Fig. 18).

The daytime vertical distribution of the *Daphnia*
pulicaria at station 2 isolated much of the population
from the effects of predation by perch fry.   In the
spring, the population was distributed throughout the
water column, while in the summer it was concentrated
below the thermocline (Fig. 19).   Abundance profiles were
often bimodal with peaks occurring at 3 and 20 m in the
spring and at 17 and 25-30 m in the summer.   The pattern
of the profiles was similar at station 6 although in the
summer it was more often unimodal.   The bimodality was
most evident during periods of high reproduction in the
Daphnia pulicaria population and was the result of high
densities of young near the surface and high densities of
older animals near the bottom of the water column.

Food Consumption, Mortality and Production of Perch Fry
During the Pelagic Stage

Although large differences occurred in the abundance
of *Daphnia pulicaria* between basin 2 and the bay during the
pelagic phase of perch fry (Fig. 12) they were the principle
daytime energy source for the fry at both locations (Table 6).
Copepods were also important in the bay, contributing as
much as 22.4% of the total daytime stomach calories while

Figure 19.   Vertical abundance distribution of

Daphnia pulicaria at 10:00 h at station

2 on July 17 and July 16 and at station

6 on July 13 and July 15, 1975.
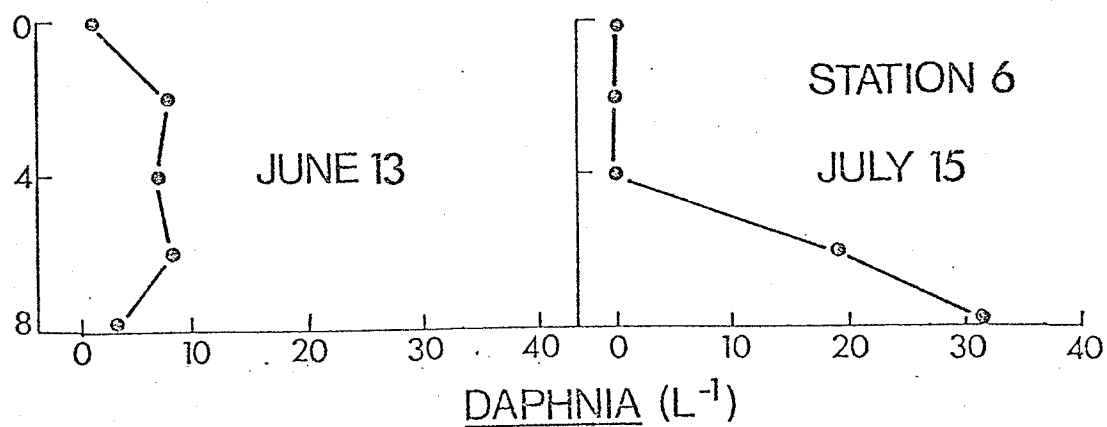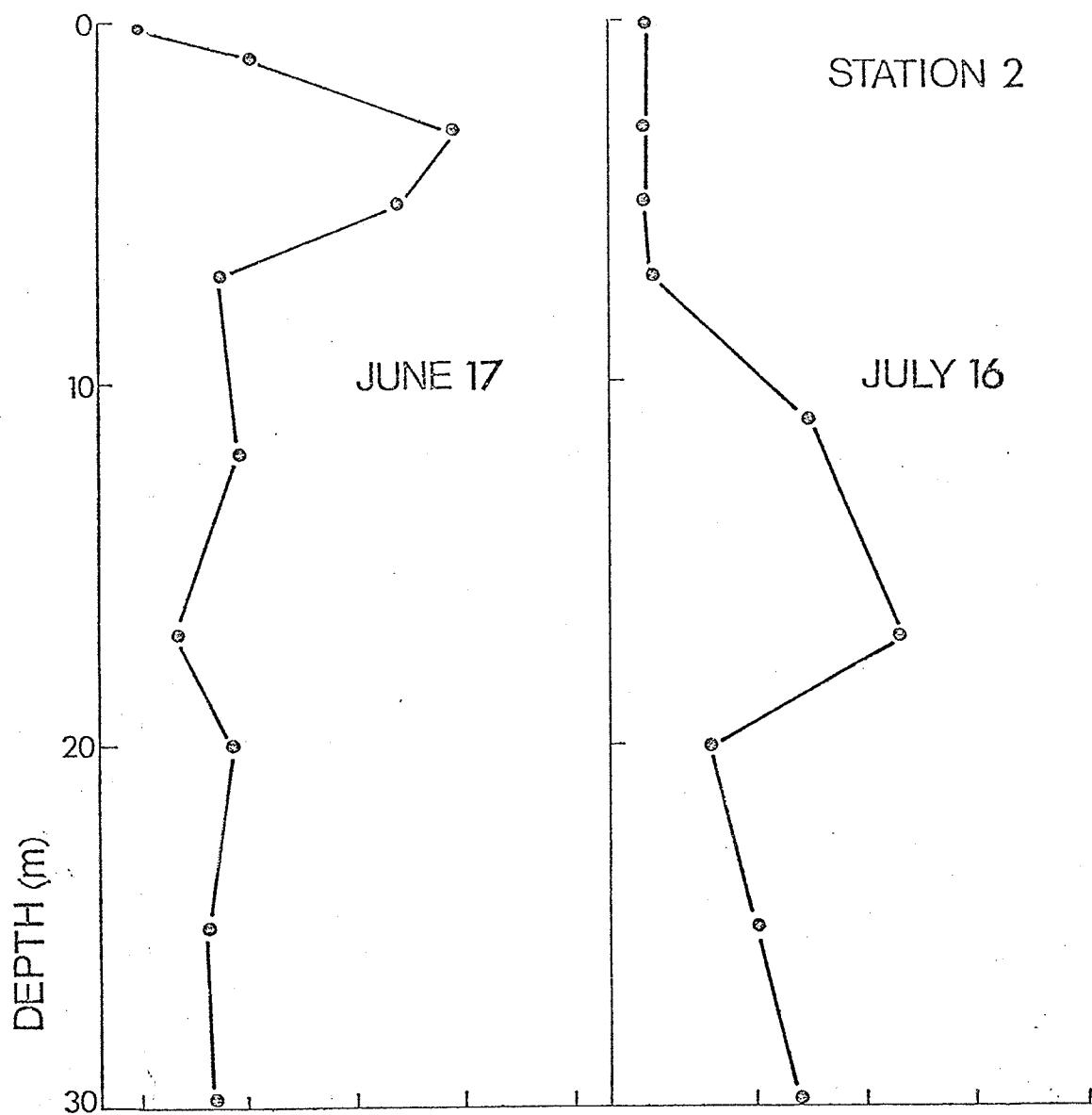
Table 8.   Average daily contribution (percent in terms of calories) of different food items in the diet of perch fry caught in basin 2 and the bay during the pelagic phase in 1975.   The mean total calorific value of the stomachs is shown.

Time (h)	Daphnia pulicaria		Bosmina longirostris		Copepods		Chaoborus flavicans		Total (cal.)	
	B2	Bay	B2	Bay	B2	Bay	B2	Bay	B2	Bay
08:00	56.36	67.12	0	1.83	.58	14.93	43.06	16.11	.6050	.2946
10:00	64.48	78.19	.84	.23	13.94	6.81	20.74	14.79	.4865	.2796
12:00	93.11	74.27	0	.61	4.58	14.08	2.31	11.03	.3386	.5449
14:00	92.91	43.89	0	.18	1.81	54.01	5.28	1.92	.4047	.2909
06:00	93.26	33.05	0	.46	.53	20.88	6.21	45.60	.4560	.5349
18:00	96.88	66.25	0	.42	.52	33.33	2.60	0	.4036	.3707
20:00	95.75	73.57	0	1.67	.78	22.03	3.47	2.72	.5652	.4890
22:00	97.72	77.09	0	.09	.44	17.86	1.84	4.96	.4891	.4179
24:00	83.88	85.79	0	0	14.89	9.81	1.23	4.40	.5705	.6838
01:00	98.88	100.00	0	0	1.12	0	0	0	.4702	.4830
04:00	100.00	99.91	0	.09	0	0	0	0	.2900	.315
06:00	73.32	41.79	0	.56	1.13	36.84	25.55	10.40	.6994	.3293
08:00	69.32	54.47	0	.09	.67	21.83	30.01	23.61	.3863	.4928
Ave.	85.84	68.88	.06	.48	3.15	19.42	10.95	10.43	.4742	.4251

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in basin 2 they never comprised more than 5% of the total.
As *Daphnia pulicaria* were always more abundant at station
2 than at station 6, this indicated a lower consumption of
secondary food items when the *Daphnia pulicaria* abundance
was high.

The contribution of different food items (percent in
terms of calories) to the diet of perch fry was determined
at 2 h intervals over a 24 h period on two dates in basin 2
(June 28-29; July 8-9) and on three dates in the bay
(June 28-29; July 8-9; July 15-16).   Values for the first
two dates at each location were averaged giving a
representative diel feeding pattern for this period (Table 8).

The importance of the energy contribution of
Daphnia pulicaria to perch fry changed within the day and
between the two locations.   The percent of the total
stomach calories of the fry in basin 2 contributed by
Daphnia pulicaria was lowest between 06:00 and 08:00 h
when copepods and *Chaoborus flavicans* became more important.
It was relatively high and constant for the rest of the day,
reaching a peak at 02:00 - 04:00 h when other prey organisms
were absent from the stomachs of perch fry.   In the bay,
the percent of the total stomach calories contributed by
Daphnia pulicaria was lowest in the early morning (06:00 -
08:00 h) and in the mid-afternoon (14:00 - 16:00 h) and
peaked at night (02:00 - 04:00 h). Over the 24 h period
Daphnia pulicaria contributed an average of 85.84 and 68.88%
of the total stomach calories in basin 2 and the bay
respectively.

Copepods contributed more to the total daily energy intake of perch fry in the bay than they did in basin 2. The increase in the importance of copepods was accompanied by a corresponding decrease in the importance of *Daphnia pulicaria*. *Chaoborus flavicans* contributed an average of 10.95 and 10.43% of the total daily energy intake in basin 2 and the bay respectively. The importance of *Bosmina longirostris* was negligible at both locations during this period.

The total calorific value of the stomach peaked in the early morning (06:00 - 08:00 h) and in the evening (20:00 - 24:00 h) in basin 2 (Table 8). The lowest value was recorded at night (04:00 h). Estimates for the total calorific value of stomachs of perch fry from the bay were more variable and not as clearly defined although they tended to be lowest between 04:00 and 10:00 h.

Feeding experiments conducted during the pelagic phase of the perch fry revealed that they fed continuously under natural conditions. Evacuation times for the entire digestive tract of smaller fry and for the stomach of larger fry are shown below:

Mean length (mm)	Temperature (C)	Total fry examined	Evacuation time (h)	
			Digestive Tract	Stomach
17.0	19.0	81	1.8	
22.1	19.5	77	2.7	
25.9	20.9	80		.8

It was not possible to determine the evacuation time of the stomachs of fry less than 23 mm in length as the stomach had not fully differentiated. The evacuation time increased steadily with the size of the fry. Since stomach (or intestinal) capacity increased proportionally with the size of the fry, effects of size of fry on the evacuation rate were confounded with the effects of meal size. Consequently, the slower evacuation rate of larger fry may also reflect the effects of the greater amount of food in the stomachs of larger fry and a decreasing absorptive surface relative to the total volume of the stomach.

The reduced growth of perch fry in the bay relative to basin 2 during the pelagic phase (Fig. 2) was positively correlated with *Daphnia pulicaria* abundance, indicating, that food may have been limiting the growth of fry in the bay. The number of *Daphnia pulicaria* consumed by a perch fry of any given length was always less in the bay (Fig. 20) as was the absolute (Fig. 12) and relative (Table 9) abundance of *Daphnia pulicaria*. This relationship may be somewhat fortuitous since differences in species composition and abundance, and in the length-frequency distribution of the *Daphnia pulicaria* population occurred between the two locations. Therefore, the total calorific intake of perch fry at both locations was compared for the period from June 28-29 to July 8-9. Estimates from July 8-9 to July 15-16 were only available in the bay because of the extended pelagic period at this location. The results were as follows:

Figure 20.   Daily consumption of *Daphnia pulicaria*

per perch fry relative to growth in

length for basin 2 and the bay in 1975.
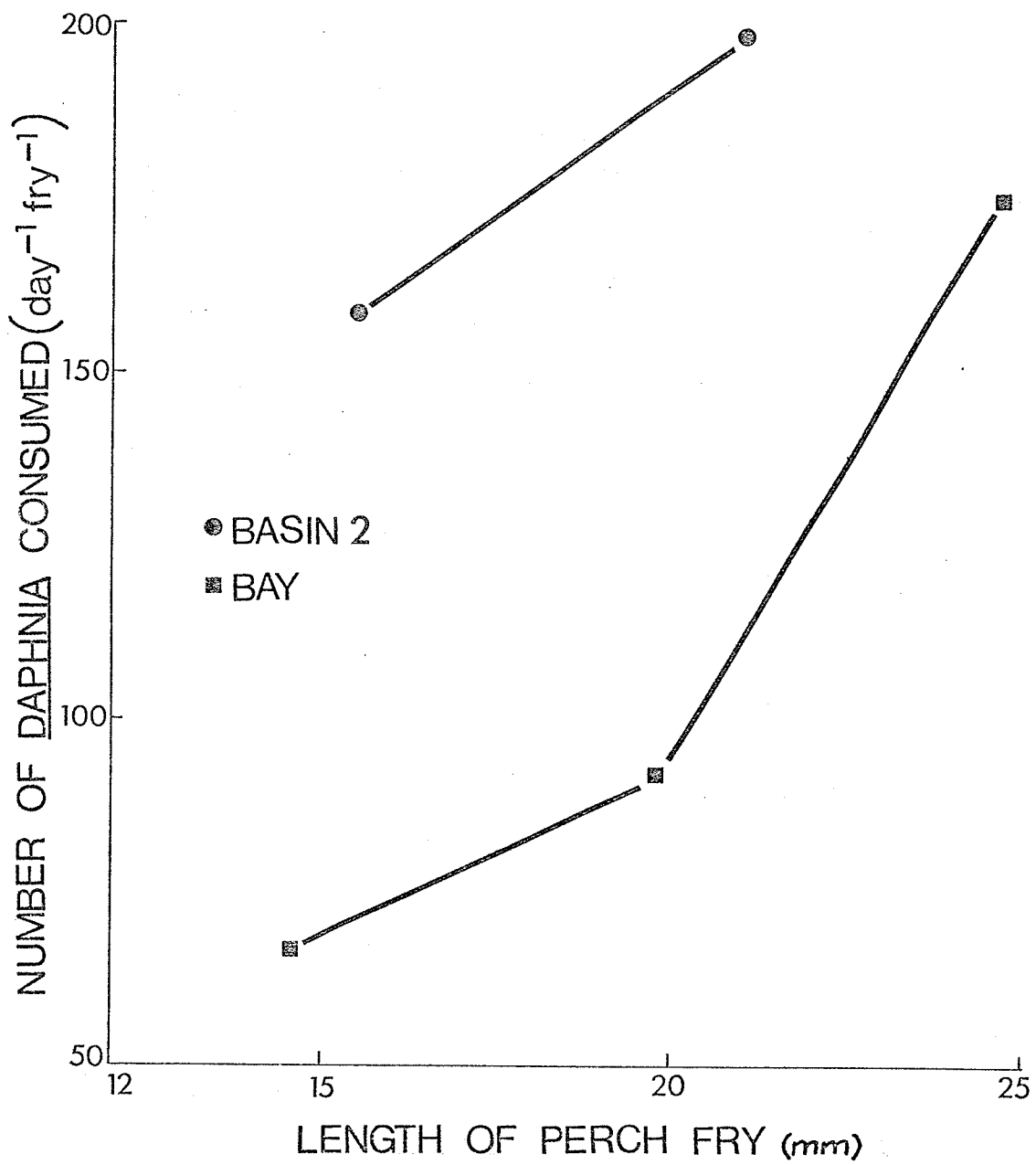
Table 9.   Mean *Daphnia pulicaria* abundance, and mean perch fry abundance during the pelagic phase of the perch fry in West Blue Lake and an index of availability of *Daphnia pulicaria*

Location	Mean *Daphnia pulicaria* Abundance (no. m^{-2})	Mean Perch Fry Abundance (no. m^{-2})	Index of Availability (no. of *Daphnia pulicaria* .1 perch fry^{-1})
Basin 1	42399	.22	19272
Basin 2	122953	.40	30738
Basin 3	36121	.42	8600
Bay	29836	10.56	282

Date	Location	Mean surface Temp. (C)	Calories consumed (fry^{-1})	Growth of fry (cal)	Food conversion Gross	Efficiency ($\%$)
June 28-29 – July 8-9	Basin 2	19.5	50.36	31.09	1.62	61.73
	Bay	20.5	42.47	23.52	1.80	53.39
July 8-9 – July 15-16	Bay	20.1	85.53	45.91	1.86	53.68

During the June 28-29 to July 8-9 period the greatest calorific intake per fry occurred in basin 2 where growth of the fry was also greatest. Food conversion efficiency during this period was highest in basin 2 and occurred at a time when the fry were increasing their dry weight at the rate of 10% day^{-1}. The food conversion efficiency did not appear to be closely related to the mean surface water temperature.

Abundance estimates of perch fry (Table 10) were based on catches from Miller high-speed trawls. Throughout the pelagic phase, perch fry were consistently much more abundant in the bay than in basin 2.

Differential mortality rates occurred between basin 2 and the bay during the pelagic phase with a much higher proportion of the population dying in the bay than in basin 2 (Table 10). The catch of perch fry in the bay declined steadily from 21.05 fry m^{-2} at the beginning of the pelagic period to 1.30 fry m^{-2} by the end of the pelagic period. In basin 2 the decline was not as rapid going from .44 fry m^{-2} at the beginning of the pelagic period to .35 fry m^{-2} by the end of the pelagic period.

Table 10. Estimates of the abundance of West Blue Lake perch fry during the pelagic stage for basin 2 and the bay.

Location	Day	Perch Fry Abundance (no. m^{-2})	95% C.I.
Basin 2	1	.44	$L_1 = .45$ $L_2 = .42$
	4	.42	$L_1 = .43$ $L_2 = .41$
	7	.40	$L_1 = .41$ $L_2 = .39$
	10	.38	$L_1 = .39$ $L_2 = .37$
	15	.35	$L_1 = .36$ $L_2 = .33$

In Abundance = -.017 (Day) -.798

Location	Day	Perch Fry Abundance (no. m^{-2})	95% C.I.
Bay	1	21.05	$L_1 = 23.64$ $L_2 = 18.74$
	6	10.40	$L_1 = 11.27$ $L_2 = 9.60$
	9	6.90	$L_1 = 7.37$ $L_2 = 6.44$
	13	3.90	$L_1 = 4.17$ $L_2 = 3.65$
	17	2.20	$L_1 = 2.39$ $L_2 = 2.02$
	21	1.30	$L_1 = 1.45$ $L_2 = 1.16$

In Abundance = -.140 (Day) -3.187

The mortality rate for each location was estimated from the slope of the regression of the natural logarithm of abundance on time. Sampling of perch fry with Miller high-speed trawls was stopped prior to the inshore movement of the fry so as to avoid any errors in the mortality data. Instantaneous daily mortality rates were .017 and .140 for basin 2 and the bay respectively.

The consumption rates of *Daphnia pulicaria* by perch fry were calculated for basin 2 (Table 11) and the bay (Table 12) during the pelagic period. They were based on daily consumption rates of *Daphnia pulicaria* per perch fry and perch fry abundance. The consumption rate was expressed as a percent of the total numbers and the total biomass of *Daphnia pulicaria* under 1 m^2 of water. Losses of *Daphnia pulicaria* to predation by perch fry in basin 2 were negligible, never exceeding .09% of the total number or .05% of the total biomass of *Daphnia pulicaria* m^{-2}. In the bay, the daily predation rates ranged from less than 1.0% of the total numbers and biomass to 5.25% of the total numbers and 2.19% of the total biomass of *Daphnia pulicaria* m^{-2}.

Effects of the predation by perch fry on various length-classes of *Daphnia pulicaria* was determined for basin 2 (Table 13) and the bay (Table 14). In basin 2 the percentage of any length-class consumed per day was

Table 11. Consumption of *Daphnia pulicaria* by perch fry in basin 2, 1975.

Date	Perch fry density (no.m^{-2})	Daily consumption per fry (no.)	Total daily consumption no. m^{-2}	mgC m^{-2}	*Daphnia pulicaria* density no. m^{-2}	mgC m^{-2}	% *Daphnia pulicaria* consumed no. m^{-2}	mgC m^{-2}
June 28	.42	158.0	66.4	.24	164320	1085.65	.04	.02
29	.42	162.0	68.1	.25	141640	935.81	.05	.03
30	.41	166.1	68.1	.25	118960	804.27	.06	.03
July 1	.40	170.1	68.1	.24	96600	668.31	.07	.04
2	.40	174.2	69.7	.25	73600	521.05	.09	.05
3	.39	178.2	69.5	.24	88652	642.23	.08	.04
4	.38	182.3	69.3	.24	103704	751.27	.07	.03
5	.38	186.3	70.8	.24	118756	900.86	.06	.03
6	.37	190.4	70.4	.24	133803	1038.64	.05	.02
7	.37	194.4	71.9	.24	148860	1209.98	.05	.02
8	.36	198.5	71.5	.24	163912	1363.36	.04	.02

Table 12. Consumption of *Daphnia pulicaria* by perch fry in the bay, 1975.

Date	Perch fry density (no. m^{-2})	Daily consumption per fry (no.)	Total daily consumption		*Daphnia pulicaria* density		% *Daphnia pulicaria* consumed	
			no. m^{-2}	mgC m^{-2}	no. m^{-2}	mgC m^{-2}	no. m^{-2}	mgC m^{-2}
June 28	13.80	66.4	916.3	3.92	84900	829.67	1.08	.47
29	12.00	66.9	802.8	3.48	66356	648.30	1.21	.54
30	10.40	71.4	742.6	3.26	47811	478.11	1.55	.68
July 1	9.10	73.9	672.5	3.00	29266	299.48	2.30	1.00
2	7.90	76.4	603.6	2.78	24410	249.79	2.47	1.09
3	6.90	78.8	543.7	2.46	19555	204.77	2.78	1.20
4	6.00	81.3	487.8	2.24	14700	157.51	3.32	1.42
5	5.30	83.8	444.1	2.07	12940	141.88	3.43	1.46
6	4.50	86.3	388.3	1.83	11180	125.44	3.47	1.46
7	3.90	88.8	346.3	1.66	9420	108.16	3.68	1.53
8	3.40	91.3	310.4	1.51	7660	90.00	4.05	1.68
9	3.00	103.3	309.9	1.59	5900	72.59	5.25	2.19
10	2.60	115.2	299.5	1.63	14378	185.22	2.08	.88
11	2.20	127.2	279.8	1.61	22856	301.33	1.22	.53
12	1.90	139.2	264.5	1.61	31333	403.65	.84	.40
13	1.70	151.1	256.9	1.64	43298	557.79	.59	.29
14	1.50	163.1	244.6	1.65	55263	711.92	.44	.23
15	1.30	175.1	227.6	1.62	67228	865.90	.34	.19

Table 13.   Consumption and electivity (E) of different
             size-classes of *Daphnia pulicaria* by perch
             fry in basin 2, 1975.

Size Class (mm)	June 28-29 % of size-class consumed day^{-1}	E	July 8-9 % of size-class consumed day^{-1}	E
.5-.6	-*		-	
.6-.7	.60	.89	1.49	.95
.7-.8	-		-	
.8-.9	.51	.85	.30	.75
.9-1.0	.35	.80	.26	.72
1.0-1.1	.22	.69	.12	.45
1.1-1.2	.06	.22	.10	.40
1.2-1.3	.05	-.27	.03	-.17
1.3-1.4	.01	-.49	.02	-.37
1.4-1.5	.01	-.72	.01	-.90
1.5-1.6	.01	-.87	.01	-.68
1.6-1.7	.01	-.53	.01	-.51
1.7-1.8	0	-1.0	.01	-.75
1.8-1.9	0	-1.0	.01	-.83
1.9-2.0	0	-1.0	.01	-.81
2.0-2.1	0	-1.0	.01	-.53
2.1-2.2	0	-1.0	0	-1.0
2.2-2.3	0	-1.0	.01	-.58
2.3-2.4	0	-1.0	0	-1.0
2.4-2.5	0	-1.0	0	-1.0
2.5-2.6	0	-1.0	0	-1.0
2.6-2.7	0	-1.0	0	-1.0
2.7-2.8	0	-1.0	0	-1.0
2.8-2.9	0	-1.0	0	-1.0
2.9-3.0	0	-1.0	0	-1.0
3.0-3.1	0	-1.0	0	-1.0
3.1-3.2	0	-1.0	0	-1.0
3.2-3.3	0	-1.0	0	-1.0

* size-class not present in plankton.

Table 14. Consumption and electivity of different size
classes of *Daphnia pulicaria* by perch fry in
the bay, 1975.

Size Class (mm)	June 28-29 % of size class consumed day^{-1}	E	July 8-9 % of size class consumed day^{-1}	E	July 15-16 % of size class consumed day^{-1}	E
.5-.6	-*		-		-	
.6-.7	-		-		2.80	0.78
.7-.8	-		64.10	.88	.30	-0.12
.8-.9	35.20	0.94	34.80	.79	.10	-0.58
.9-1.0	34.00	0.94	42.20	.82	.30	-0.12
1.0-1.1	43.20	0.95	11.60	.47	.50	-1.0
1.1-1.2	54.70	0.67	28.30	.75	.30	0.03
1.2-1.3	1.70	0.22	16.70	.60	.60	0.30
1.3-1.4	1.30	0.06	25.00	.72	1.80	0.68
1.4-1.5	.70	-0.21	8.90	.38	.80	0.43
1.5-1.6	.61	-0.19	5.10	.13	.90	0.45
1.6-1.7	.66	-0.24	2.40	-.26	.60	0.28
1.7-1.8	0	-1.0	1.70	-.23	.40	0.04
1.8-1.9	.22	-0.66	1.10	-.56	.20	-0.25
1.9-2.0	0	-1.0	1.30	-.51	.30	-0.10
2.0-2.1	0	-1.0	0.70	-.73	.20	-0.26
2.1-2.2	0	-1.0	1.20	-.51	.10	-0.27
2.3-2.4	0	-1.0	0	-1.0	.10	-0.52
2.4-2.5	0	-1.0	0	-1.0	0	-0.41
2.5-2.6	0	-1.0	0	-1.0	.10	-1.0
2.6-2.7	0	-1.0	0	-1.0	0	-0.66
2.7-2.8	0	-1.0	0	-1.0	0	-1.0
2.8-2.9	0	-1.0	0	-1.0	0	-1.0
2.9-3.0	0	-1.0	0	-1.0	0	-1.0
3.0-3.1	0	-1.0	0	-1.0	0	-1.0

* size-class not present in plankton.

low, never exceeding 1.5% of the total number of individuals. On June 28-29 and July 8-9, in the bay, the predation rate of perch fry on smaller length-classes of *Daphnia pulicaria* was high, with up to 64% of the number of individuals in a length-class being consumed daily. By July 15-16 the percentage of all small length-classes being consumed was reduced with no value exceeding 2.8% of the number of individuals present. Ivlev's (1961) electivity indices showed that on June 28-29 and July 8-9, at both locations, the smaller length-classes of *Daphnia pulicaria* were most strongly selected for, being much more concentrated in the guts of perch fry than in the plankton. On July 15-16 in the bay, the intermediate length-classes of *Daphnia pulicaria* were most strongly selected for by the perch fry.

Production of perch fry during their pelagic phase differed by an order of magnitude in different parts of the lake (Table 15). The highest average daily production occurred in the shallow waters of the bay where perch fry were very abundant (Table 4). Production for basins 1 and 3 was estimated by calculating the ratio of the mean catch of perch fry caught in standard tows in basins 1 and 3 between June 22 and July 4 (Table 4) to the mean catch in basin 2 over a similar period. As the tows in each basin were of identical duration, these ratios accurately

Table 15.   Estimates of mean daily production for
            West Blue Lake perch fry during their
            pelagic stage.

Location	Mean Production $(mgC\ m^{-2}\ day^{-1})$	Mean Production Calories $(m^{-2}\ day^{-1})$
Basin 1	.07	2.34
Basin 2	.07	2.22
Basin 3	.04	1.21
Bay	.71	20.42
Whole Lake	.08	2.61

reflected the relative number of fry in basins 1 and 3. The ratios were then multiplied by the total production estimate of basin 2 to obtain estimates for basins 1 and 3.

Production estimates for each basin and the bay were weighted according to the surface area of each location and summed to obtain an estimate of the mean whole lake production for perch fry (Table 15). Although production in the bay was very high relative to the rest of the lake, it had little effect on the mean whole lake estimate as it only comprised 4% of the total surface area of the lake, and contained only 14% of the total number of perch fry in the lake.

DISCUSSION

Seasonal Distribution, Abundance and Mortality

Beginning in mid-May, heaviest spawning activity was concentrated in the bay (dip net location 2 in Table 1) which was one of two areas with an extensive littoral zone (Fig. 1). This resulted in a greater initial abundance of perch fry along the shoreline of the bay than along the shoreline of other parts of the lake (Table 2).

In lakes with several species of pelagic fry, the appearance of a particular fry species in open water seemed to be related to the temperature of the lake (Faber 1967). In some northern Wisconsin lakes, perch fry became the dominant species in the pelagic zone from the end of May until the beginning of June when the water temperature was between 13 and 17 C. Noble (1968) has shown that perch fry of Oneida Lake moved into the pelagic zone when they were 9 mm long while Wong (1972) found that this transition in West Blue Lake occurred when perch fry were 9-10 mm long. Similar water temperature and size of perch fry at the time of transition from the spawning sites to the pelagic zone were found in this study. The similarity between this study and the others with regard to water temperatures

and size of perch fry when they moved into the pelagic
zone indicated that this movement was not based on
passive dispersion.

Although suitable temperatures (Ferguson 1958)
and lighting conditions (Privolnev 1958) for the perch
fry occurred in both the littoral and pelagic zones,
the pelagic environment was apparently the preferred
habitat for early life. As the littoral area of
West Blue Lake is very small (Fig. 1), there were
very high concentrations of perch fry in this zone of
very low food abundance following hatching. The pelagic
zone is much more extensive in size, so that movement
into this zone effectively reduced the density of perch
fry. It also provided the fry with a high density of
their preferred food, *Daphnia pulicaria* (Fig. 12).
Paloheimo and Dickie (1966) have shown, in a review of
the literature, that growth of fishes is reduced at
high densities even if the feeding rate per unit weight
is the same at all densities of fishes.

Differences in the growth rate between perch fry
from the bay and those from the rest of the lake (Fig. 2)
indicated there was little or no movement of the fry
into or out of the bay during the pelagic phase.
Observations at the mouth of the bay (Fig. 1) during
the pelagic phase also revealed no movement of the fry

into or out of the bay.   A wide sand bar, heavily

covered in aquatic vegetation, enclosed the mouth of

the bay.   The water depth here during the summer was

usually less than 60 cm.   This sand bar probably

acted as a barrier to perch fry which, during this stage,

preferred open, deep water.   Furthermore, the sand bar

and the surrounding high terrain made the bay a very

calm area.   As perch fry are strongly dependent on

wind generated water currents for their distribution

(Houde 1969), fry hatching in the bay were probably

restricted to that area until the post-pelagic period.

After mid-July tow catches declined rapidly

(Table 4) as perch fry completely abandoned the pelagic

zone and returned to littoral areas (Table 5).   Wong

(1972) found a similar movement of perch fry in West

Blue Lake in 1969.   During this second littoral stage,

large schools of perch fry were seen moving in and out

of the bay.   This caused a mixing of the different

populations of perch fry, so, that after this transition,

no differences in the growth rates of the fry from

different parts of the lake could be detected.

Factors which caused the movement of perch fry

from the pelagic to the littoral zone were not clear.

The transition occurred at a time when the mean temperature

in the upper 6 m of water was 18.0 C, the surface

temperature was 21.0 C and the shore temperatures
ranged from 21.3 - 23.5 C. The movement may have
been the result of more favourable water temperatures
in the littoral zone. Neil and Magnuson (1974)
found that young perch generally avoided temperatures
under 21 C and over 26 C, and preferred temperatures
were between 21 and 24 C. There was no evidence that
the time of transition was controlled by the length of
the fry, food preferences associated with the increased
size of the fry, or the vertical distribution of the
food organisms. The real causes of the changes in the
physiology and behaviour of perch fry at this time were
probably very complex and beyond the scope of this study.

Mortality rates for perch fry during the pelagic
period of 1975 were estimated from the decline in the catch
in Miller high-speed trawls. The negative exponential
model fitted to the catch data assumes that the mortality
rate at each location was constant over the sampling period.
This model has been generally applied to mortality data
since it implies a constant proportion of deaths rather
than a constant number of deaths.

Instantaneous daily mortality rates for perch fry
were .017 for basin 2 and .140 for the bay during the
pelagic stage (Table 9). Noble (1968) found that the
instantaneous daily mortality rates for perch fry in

Oneida Lake were .030 in 1965, .056 in 1966 and .051
in 1967, all lying between the two estimates for West
Blue Lake.

Few other mortality rates for pelagic fry of
warm water fishes are available in the literature,
but perch fry mortality rates were low in basin 2 and
comparable in the bay with the estimated mortality
rates of fry of several marine fishes. Sette (1943)
estimated instantaneous daily mortality rates of
larval Atlantic mackerel, *Scomber scombrus*, as .10 - .14
for larvae over 10 mm. Farris (1961) estimated
instantaneous daily mortality rate of jack mackeral
larvae, *Trachurus symmetricus*, 10 - 60 days after hatching
as .17 while Ahlstrom (1954) estimated a rate of .11 for
sardine, *Sardinops sagax*, from 8 - 20 mm - about 20 days
after hatching.

Avoidance of the Miller high-speed trawl by perch
fry did not appreciably bias the estimates of mortality
or abundance. Perch fry, sampled under the conditions
described here, do show a low level of avoidance to the
trawls although it is not very significant (Noble 1968).
Nevertheless, the estimates of abundance should be
regarded as minimal values, and the estimates of mortality
as maximal values.

Predation on perch fry of West Blue Lake during
their pelagic stage was probably very low. There are

no species of zooplankton capable of attacking the fry.   Juvenile and adult walleye and perch are the most important predators on the young perch, but perch fry do not appear in the stomachs of these fish during the early part of the pelagic period (Falk 1971, Ward and Robinson 1974).   Although perch fry contributed over 80% of the wet weight of walleye stomachs in mid-July of 1966 (Ward and Robinson 1974), it was not known if this was during the pelagic or post-pelagic period of the fry as the time of transition from the pelagic to the littoral zone varies from year to year (Wong 1972).   Walleye is the principle predator on the perch fry of Oneida Lake and this predation is primarily responsible for establishing the year-class abundance of the perch population.   But, the predation is restricted to the post-pelagic period of the perch fry (Forney 1971).   More recently, Kelso (1976), using ultrasonic tracking, has shown that the juvenile and adult walleye of West Blue Lake generally move along the shoreline and rarely cross into the pelagic zone when the lake is stratified.   The resulting habitat segregation of juvenile and adult walleye from much of the perch fry population would limit any effect the former had on perch fry.

The importance of walleye fry, the only other
potential predator on perch fry of West Blue Lake
during their pelagic stage, was negligible.   Although
perch fry have appeared in the guts of walleye fry
as small as 9 mm (total length) in Oneida Lake they
did not constitute a major food item for the walleye
fry while the perch fry were in the pelagic zone (Houde
1967).   Also, the abundance of walleye fry in West
Blue Lake in 1975 appeared to be very low as walleye
fry, which are known to be closely associated spatially
with perch fry (Houde 1969) were rarely caught.

Success or failure in feeding of perch fry will
depend on the searching power of the fry, their ability
to catch zooplankton and the abundance of suitable
zooplankton.   Assuming the first two parameters were
the same for perch fry in basin 2 and the bay, the
last, the abundance of suitable zooplankton may explain
the differential mortality rates observed at the two
locations (Table 9).

The high abundance of suitably sized *Daphnia*
pulicaria in basin 2 indicated mortality of perch fry
at this location was not the direct or indirect result
of an inadequate food source.   Therefore, the low
mortality rate observed must have been the result of
some other unknown cause.   Noble (1968) found dead

perch fry in samples from Oneida Lake that were of
normal size and in good condition except for the
degeneration of the caudal fin and caudal peduncle.
He also observed these symptoms just before death in
larger juvenile yellow perch held in the laboratory
but was unable to determine the cause.

The much higher mortality rate of perch fry in
the bay was probably the direct or indirect result of
an inadequate food source. The lower energy intake of
perch fry in the bay as well as the low relative abundance
of *Daphnia pulicaria* (Table 9) would support this argument
and indicate the density-dependent nature of the mortality.

In most fish populations the overwhelming majority
of the mortality occurs within the first few weeks following
hatching. At the same time the year-class strength is
usually fixed. Examples of both density-independent and
density-dependent mechanisms regulating the abundance
of fry populations exist, and it now appears that either
may act, depending on the conditions. Temperature has
often been cited as the most important factor regulating
fry survival (Christie 1963, Lawler 1965, Svardson and
Molin 1973, Christie and Regier 1975). Others have found
water turbidity (Doan 1942), rate of water warming and the
frequency of storms (Busch, et al. 1975) also to be important.
In salmonid populations, density-dependent mortality is

often of primary importance in regulating fry abundance
(LeCren 1962, 1965, 1973; Backiel and LeCren 1967).
LeCren (1973), based on a series of *in situ* experiments
found a high level of starvation in *Salmo trutta* in some
experiments and was able to show that this mortality was
proportional to the density of the fry.   Similarly,
Lyashenko (1961) reported starvation of young-of-the-year
zander (*Stizostedion lucioperca*) in Soviet reservoirs when
food became scarce.

Growth

The growth of young fish usually occurs in several
stanzas (Tesch 1968).   In this study, the first stanza,
characterized by a slow growth rate (Fig. 3), was divided
into two parts based on the feeding habits of the fry.
Early in the first stanza the fry did not feed and depended
entirely on the yolk for energy and structural material.
A doubling of the wet weight during this period was the
result of water absorption by the fry (Fig. 11).   Gray
(1928), Suyama and Ogino (1958) and Ishibashi (1974) have
shown a similar weight increase after hatching in brown
trout, *Salmo trutta*, rainbow trout, *Salmo gairdneri*, and
Tilapia sparmanii respectively.

Initial feeding of perch fry on small zooplankters (Table 6) occurred late in the first growth stanza. Algae was also present in the guts of the perch fry at this time but it was not possible to determine whether this was the result of passive or active uptake. Wong (1972) found traces of algae in the guts of perch fry during their pelagic stage in West Blue Lake, but he did not sample the fry at the time of initial feeding in their first growth stanza.

The second growth stanza, characterized by a high growth rate (Fig. 3), coincided with the start of intensive feeding by perch fry and a switch in diet to one which was dominated by *Daphnia pulicaria* (Table 6). The most important factors affecting growth of young fish are water temperature and food availability (Blaxter 1969). As there was no dramatic change in the water temperature at the time of transition from growth stanza one to growth stanza two, the increased growth rate in stanza two was the result of the increased food consumption by the fry.

The reduced feeding rate in the first growth stanza was probably caused by the inability of newly hatched fry to locate and handle prey and the distribution of the potential prey. On emerging from their eggs perch fry were very poor swimmers spending much of their time

passively sinking in the water column or laying on the
bottom, unable to actively hunt for prey. As well,
the mouth and jaws of hatching fry are poorly developed
and not able to handle food (Blaxter 1969). Although
the fry began to use an external food source 6 days
after hatching (Table 6), the fry were still very
limited while they remained near the spawning sites as a
result of the low abundance of zooplankton in the littoral
zone. Rosenthal and Hempel (1970) and Blaxter and Staine
(1971) have shown for marine fry that the success rate in
the capture of food particles was on the order of 1% of
encounters. Assuming a similar low success rate occurs
in the young perch fry and combining this with the very
low densities of food in the littoral zone would lead to
a very low level of food consumption by the fry in the
first growth stanza.

There were no detectable differences in the growth
of perch fry in the three basins in 1974 or 1975 (Fig. 2).
Similarity in the slopes of the length-weight relationships
(Fig. 4) and in the growth rates (Fig. 3) indicated that
growing conditions in the three basins were similar.
The mean temperature from 0 - 6 m was similar in each
basin and the *Daphnia pulicaria* abundance, although
showing a great deal of variation among the three basins
was very high in each basin relative to the number of

perch fry (Table 9). This indicated that *Daphnia pulicaria* abundance was at, or in excess of the level needed to maintain maximal growth under the given temperature regime.

The situation in the bay was different as the growth of perch fry at this location was significantly less ($P < .05$) than in the lake as a whole during the pelagic phase in 1975 (Fig. 2). The separation of the perch fry population in the bay from the rest of the lake and the differences in the mean clutch size (Table 7), and the average reproductive size (Fig. 16) of the *Daphnia pulicaria* population in the bay from that of the rest of the lake indicated that, from a biological point of view, the bay was essentially a separate lake. The mean temperature from 0 - 6 m in the bay was similar to that of the rest of the lake but the *Daphnia pulicaria* abundance relative to perch fry abundance was much lower, and resulted in an index of availability which was one to three orders of magnitude lower than for the rest of the lake (Table 9). Also, much of the *Daphnia pulicaria* population in the bay was larger than the size the fry could use (Fig. 14). This caused a lower consumption rate of *Daphnia pulicaria* per perch fry (Fig. 20) and a lower total energy intake during the pelagic period, resulting in reduced growth in the bay.

The dependence of growth in young fish on zooplankton abundance has been shown for chum salmon, *Oncorhynchus keta* (LeBrasseur 1969), yellow perch (Noble 1975), blueback herring, *Alosa aestivalis* (Burbidge 1974), and sockeye salmon, *Oncorhynchus nerka* (Johnson 1961). Increased growth in young fish has been related to the actual amount of zooplankton consumed in large-mouth bass, *Micropterus salmoides* (Kramer and Smith 1960) and in yellow perch (Noble 1975).

The highest instantaneous growth rates occurred at the time of transition from the spawning areas to the pelagic zone and later, at the time of transition from the pelagic to the littoral zone (Fig. 6). Condition coefficients for perch fry of West Blue Lake also peaked at the time of transition from the pelagic to the littoral zone (Wong 1972). The possible significance of these peaks is unknown.

Food conversion efficiencies for perch fry during their pelagic stage were over 50% in the bay and over 60% in basin 2. This indicated that over half of the energy consumed by the perch fry went directly into growth, while the remainder was being used for maintenance requirements or was excreted. The primary factors affecting food conversion efficiency in fish are age,

water temperature, photoperiod (Huh, et al. 1976) and
feeding rates (Andrews and Stickney 1972). As the
age of perch fry, water temperature and photoperiod
were the same in basin 2 and the bay, the observed
differences in efficiencies were likely caused by
differences in food abundance. The lower abundance
of the primary food, *Daphnia pulicaria*, in the bay not
only decreased the total energy intake during the
pelagic phase at this location relative to basin 2,
but probably increased the proportion of the total
energy intake used for food procurement. This resulted
in less energy for growth and hence lower food conversion
efficiency. The higher food conversion efficiency of
perch fry in basin 2 would further increase the difference
in growth rate between basin 2 and the bay beyond what
one would expect based on the differences in energy intake
alone.

Although there are no estimates of food conversion
efficiency for fish fry in the literature, the values shown
here are remarkably consistent with estimates determined
for fingerling yellow perch. Huh, et al. (1976)
determined for yellow perch that photoperiod was a more
important factor in controlling food conversion efficiency
than temperature. When they subjected fingerling perch
to a 16 h light - 8 h dark photoregime food conversion
efficiencies ranged from 52.4 - 69.6%. Although it

was not possible to compare food abundance of West Blue Lake with food abundance used in Huh, et al. (1976) studies, one would expect that under natural conditions the older fish (fingerlings) would have a lower food conversion efficiency (Phillipson 1966).

Changes in the chemical composition of perch fry occurred from hatching through metamorphisis. Throughout this period of growth all constituents increased in actual amounts but at different rates. Carbon values, which were largely a reflection of fats and carbohydrates (Ehrlich 1974a), were very high on hatching but decreased rapidly over the first 25 days (Fig. 7). The fat component provides nearly twice the calories per unit weight of protein (Winberg 1971) and was used as one of the initial energy sources for perch fry.

Increases in the proportion of nitrogen in tissues during early development similar to that shown for perch fry (Fig. 7) also occur in plaice, *Pleuronectes platessa* (Ehrlich 1974b), herring, *Clupea harengus* (Ehrlich 1974a), and grunion, *Leuresthes tenuis* (May 1971). This suggests that the conversion of much of the yolk material, of which protein is the dominant component (Blaxter 1969), and later of food obtained exogenously into growth rather than accumulated energy stores is probably advantageous

to newly hatched fry.   The deposition of protein in perch fry, as indicated by the increased proportion of nitrogen in the tissues (Fig. 7), would represent growth.

The importance of rapid growth during early developmental stages of perch fry has been clearly illustrated by Wong and Ward (1972).   They found that the maximum size food particle which a perch fry could ingest was dependent on the size of the mouth gape. As the mouth gape size increased rapidly with growth in length, rapid growth during early development would quickly increase the abundance of potential prey by widening the size spectrum of prey available to the fry.   This would be particularly important in years when food is scarce.

Following the movement of perch fry into the pelagic zone and initiation of active feeding on *Daphnia pulicaria*, the proportion of carbon in the body tissues increased and reached a peak during metamorphisis (Fig.7).   It then declined throughout the remainder of the summer.   Newsome and Leduc (1975) have shown an identical pattern in the percent variation in fat of 1+ and 2+ immature yellow perch in two Quebec lakes.   This indicated that the changing proportion of carbon in the tissues of perch fry over the season was a result of a changing percentage of the total weight composed of fat.

The carbon to nitrogen ratio remained relatively
constant, at approximately four, after the initially
high value at hatching (Fig. 8).   The close correlation
between the changing proportions of carbon and nitrogen
mg dry weight^{-1} may be the result of the requirement
for a certain amount of carbohydrate for the efficient
utilization of protein as was shown for carp, *Cyprinus*
carpio (Nagi and Ikeda 1971).

The time of metamorphisis of perch fry in West
Blue Lake was well defined, occurring 8 - 9 wk after
fertilization.   It took place at the same time that
fry moved from the pelagic to the littoral zone.   The
period of metamorphisis was marked by the transformation
of the silvery-coloured, tube shaped body of the fry to
the more compressed body shape of the adult form with
the characteristic orange and brown pigmentation.

The exact cause of the simultaneous decrease in
the amount of carbon and nitrogen mg dry weight^{-1} of
perch fry in the post-pelagic stage (Fig. 7) is unknown.
During this period the condition of perch fry decreases
rapidly (LeCren 1951, Wong 1972).   LeCren (1951) has
suggested that a shortage of zooplankton in the littoral
zone may lead to this decrease in condition.   Presumably
this food shortage would result in catabolization of
carbon and nitrogen compounds in tissues of perch fry

to supplement external energy source. Examination of guts of perch fry in West Blue Lake during the post-pelagic period did not indicate a shortage of food. Also, it was during the post-pelagic period that the calorific value of perch fry began to increase (Fig. 9), indicating that high energy compounds were accumulating in the tissues. This would not be expected to occur during a period of food shortage. More likely, decreasing amounts of carbon and nitrogen mg dry weight^{-1} were the result of the increasing mineral content of fry during and following metamorphisis. At this time there is a rapid development of scales, spines and skeletal structure all of which have a high mineral content (Van Oosten 1957).

Changes in the calorific value of perch fry g dry weight^{-1} over the growing season (Fig. 9) was the result of growth requirements and internal physiological changes. From hatching until metamorphisis the calorific value decreased, indicating energy was being diverted into growth and not accumulating in tissues as high energy compounds. Following metamorphisis there was a gradual increase in the calorific value of perch fry. The point of inflection from decreasing to increasing calorific content occurred when the fry reached a length of approximately 20 mm. It was at this size when the entire size spectrum of *Daphnia pulicaria* first became available as potential prey for the fry (Wong and Ward 1972)

and probably caused the change in metabolism towards the
increasing deposition of high energy compounds.   The
metabolism of herring (Ehrlich 1974a) and plaice fry
(Ehrlich 1974b) changed towards an increasing deposition
of fat when they reached a length which enable them to
capture a sufficiently wide size-range of food particles.

Decreasing proportions of water in perch fry
tissues during their early developmental stages (Fig. 10)
appears to be a general phenomenon in fish, occurring in
Oncorhynchus gorbuscha (Parker and Vanstone 1966),
Eptatretus stouti (Mung and Morris 1965), *Cyprinodon
macularis* (Kinne 1960), *Salmo salar* (Houston and Threadgold
1963), *Clupea harengus* (Ehrlich 1974a) and *Pleuronectes
platessa* (Ehrlich 1974b).   Rapidly dividing cells of
young fish cause large extracellular spaces which are
occupied by water, thus increasing the relative water
content of the tissues (Love 1970).   This is followed
by a period when cells increase in size with the increasing
length of the fish, decreasing the amount of extracellular
space and hence the water content of the tissues (Love
1958).

Feeding

Food selected at the initiation of feeding by various
freshwater fishes is similar (Keast and Webb 1966).   Fish
fry at this stage have small mouths and are weak swimmers.

To be potential food, an organism must be small enough
for the fry to ingest, slow enough for the fry to catch,
and in the immediate vicinity of the fry.   To satisfy
these needs, most larval fish, including perch, utilize
zooplankton as their initial food source.

Various species of Copepoda, Cladocera, insect
larvae and pupae have been documented as the prey of
perch fry (Turner 1920, Allen 1934, Smyly 1952, Siefert
1972 and Wong 1972).   In West Blue Lake where the species
composition of zooplankton is simple, *Daphnia pulicaria*
and *Cyclops bicuspidatus* made up most of the diet of the
perch fry with *Bosmina longirostris* and *Chaoborus*
flavicans being secondarily important (Table 6).
Organisms from the genus *Daphnia* were the preferred
food for perch fry as is the case for most freshwater
fry (Brooks 1968).

The importance of *Daphnia pulicaria* and
Bosmina longirostris to the diet of perch fry was
dependent on the abundance of these prey species
(Fig. 12).   The abundance of *Daphnia pulicaria* in
basin 2 although variable, was high throughout the spring
and summer and with the exception of August 6 occurred
in 100% of the stomachs of fry after June 23.   *Daphnia*
pulicaria also accounted for most of the calorific value
of stomachs after June 23 (Table 6).   *Bosmina longirostris*
never became abundant in basin 2 or significant in the
diet of perch fry caught there (Fig. 12).

In the bay, the abundance of *Daphnia pulicaria*
and their contribution to the total stomach calories of
the perch fry was high until the end of the pelagic period
(Fig. 12). During the post-pelagic period there was a
rapid decline in the abundance of *Daphnia pulicaria* and
in their contribution to the diet of perch fry. Coincidentally,
the increasing abundance of *Bosmina longirostris* was reflected
in the increased contribution they made to the diet of fry.

Towards the end of July there was an abrupt increase
in the importance of copepods to the diet of perch fry
(Table 6). A similar change in diet was shown by Lin
(1975) for perch fry of Oneida Lake. As in West Blue
Lake, the change occurred shortly after the transition
from the pelagic to the littoral zone and he attributed
it to a vertical change in the distribution of perch fry
at the transition time which brought them to a depth
dominated by copepods. The switch in diet to one
dominated by copepods lasted only 1 wk in basin 2,
after which *Daphnia pulicaria* again became the most
important food item (Table 6). In the bay, copepods
continued to make up more than 40% of the calorific
value of the stomachs of perch fry caught at this
location for the remainder of the post-pelagic period.
This, as well as the increasing importance of *Bosmina*
longirostris to the diet of perch fry was the result
of the low abundance of *Daphnia pulicaria* in the bay
(Fig. 12).

There is an obvious advantage to perch fry in being able to utilize more than one preferred food source. By having a large scope of potential prey species fry have a large potential energy source available, therefore, reducing the possibility of starvation resulting from fluctuations in the abundance of the primary food source.

Selection of different prey species on the basis of their availability has been documented for several species of young fish. Burbidge (1974) has shown that young-of-the-year blueback herring, selected copepods and *Bosmina* sp. in relation to their relative abundance in the environment. When copepods were more abundant in the plankton than *Bosmina* sp. they were eaten to a greater extent than the latter. The reverse was true when *Bosmina* sp. was more abundant in the plankton. Given prey of suitable size LeBrasseur (1969) found that juvenile chum salmon selected prey in proportion to their abundance, while Feller and Kaczynski (1975) found that the same fish were selecting epibenthic prey on the basis of its availability.

As in the seasonal studies, *Daphnia pulicaria* was the principle component of the diet of the perch fry on a diel basis during the pelagic phase in both basin 2 and the bay (Table 8). Copepods were not an important food source in basin 2 as most of the population was below

the feeding zone of the perch fry throughout the day
(P. H. Patrick, Department of Zoology, University of
Manitoba, Man., personal communication).

In the bay, where fry were able to move throughout
most of the water column, there was no refuge for the
copepods and hence, they contributed significantly to
the diet of the fry.

The importance of *Chaoborus flavicans* to the diet
of perch fry was largely confined to the early morning
hours (Table 8) and was probably controlled by their
vertical distribution.   In the early evening, between
22:00 and 23:00 h both *Daphnia pulicaria* and *Chaoborus
flavicans* moved to the surface of the lake where they
remained for several hours (Wong 1972).   While both
were present in high densities the fry continued to
feed on their preferred food, *Daphnia pulicaria*.
Between 04:00 and 05:00 h all of the *Daphnia pulicaria*
population moved from the surface strata into deeper
water.   *Chaoborus flavicans* which started their downward
migration at the same time were slower and large numbers
were still present in the surface waters between 05:00
and 07:00 h (Lysack 1976).   With the decreasing abundance
of their preferred food, the perch fry became opportunistic
feeders taking advantage of the large number of *Chaoborus
flavicans* still present in the surface waters of the lake.

The importance of *Bosmina longirostris* to the
diet of the perch fry during the pelagic phase was negligible
at both locations (Table 8). Their average daily
contribution accounted for less than 1% of the total
calories consumed.

Generally, maxima in the total calorific value
of stomachs of perch fry in basin 2 occurred in the
morning (06:00 - 08:00 h) and the evening (20:00 -
24:00 h) (Table 8). Wong (1972) found a similar
pattern in the stomach contents of the perch fry from
West Blue Lake in 1969. In the bay, the pattern of
feeding was not as clearly defined. This was probably
the result of differences in the relative vertical
distribution of the perch fry and their prey.

At first feeding fish fry usually consume small
zooplankters. A change in feeding preference towards
the consumption of larger zooplankters with increasing
size of the fry has been shown for white suckers,
Catostomus commersoni, bluegills, *Lepomis macrochirus*,
emerald shiners, *Notropis atherinoides*, rainbow smelt,
Osmerus mordax (Siefert 1972), large-mouth bass (Kramer
and Smith 1960) and yellow perch (Allen 1934, 1935,
Siefert 1972, Wong 1972). The interspecific selection
of zooplankton by perch fry of West Blue Lake showed
that they first fed on small copepods and nauplii and

later, as they grew, they began to utilize the larger

Daphnia pulicaria and *Chaoborus flavicans* (Table 6).

Intraspecific differences were also found in the

size of prey consumed by perch fry as progressively

larger *Daphnia pulicaria* were found in stomachs of fry

as they grew during the pelagic stage (Fig. 12).   Wong

and Ward (1972) found a similar pattern of intraspecific

feeding for perch fry of West Blue Lake.

When examining the possible size selectivity of

a predator for a particular prey, it is essential to

know the size of the prey in the feeding zone of the

predator.   There have been no detailed studies reported

in the literature on seasonal changes in size or age of

a single zooplankton species with depth.   Patrick

(Department of Zoology, University of Manitoba, Man.,

unpublished) found that older individuals of the *Cyclops*

bicuspidatus population of West Blue Lake were generally

in deeper water in the spring and summer with younger

individuals above.   Hall (1964) found that for

Daphnia galeata mendotae, population size structure in

relation to depth showed little variation among upper,

middle and lower water strata although juveniles were

slightly more frequent in the upper and middle strata

during the summer.   Applegate and Mullan (1969)

casually observed that in populations of *Daphnia galeata*

mendotae, Daphnia retrocurva and *Daphnia parvula* there

was no tendency for juveniles to occur in strata
overlying the adults.   Stavn (1974) has shown that
individuals from populations of *Daphnia parvula* and
Daphnia ambigua tend to be smaller in upper positions
of the water column in July in lakes in North Carolina.

At station 2 in West Blue Lake the smaller
Daphnia pulicaria were most abundant in the upper water
strata (Fig. 13) during the summer.   Consequently,
the size-frequency distribution of *Daphnia pulicaria*
in perch fry stomachs from basin 2 was compared with
the 8 m size-frequency distribution sample at station 2.
In the bay, perch fry were able to move throughout
most of the water column; therefore, the size-frequency
distribution of *Daphnia pulicaria* in perch fry stomachs
was compared with the 0 - 8 m integrated sample at station
6 (Fig. 13).   At both locations, size of the largest
Daphnia pulicaria consumed by the fry increased as they
grew but the fry also continued to make use of the
smaller size-classes (Fig. 16).   The apparent non-size
selective behaviour of older fry may be of survival value.
Galbraith (1967) stated that removal of only a certain
size-class of daphnids would increase the turnover time
of the whole population beyond that expected if removal
of individuals was proportional to their frequency of
occurrence in various size-classes (turnover time was

defined as the time it takes to completely replace

the population). By increasing the turnover time,

the *Daphnia pulicaria* population would be subjected

to predation over a longer period and hence, would be

more adversely affected by predation of perch fry.

Wong and Ward (1972) have shown that for perch

fry up to 20 mm in length the size of *Daphnia pulicaria*

consumed was restricted by the predator's mouth size.

This size was reached around July 14 in 1975. Prior

to this time, the mean size of *Daphnia pulicaria*

consumed by perch fry was smaller than the mean size of

Daphnia pulicaria in the feeding zone (Fig. 14). The

rapid growth of the mouth gape of perch fry (Wong and

Ward 1972) during the first few weeks of life is

undoubtedly of survival value as it increases the size

spectrum, and therefore the abundance of potential prey.

After perch fry in basin 2 had exceeded 20 mm in

length, the mean size of *Daphnia pulicaria* in their

stomach was similar to the mean size at 8 m at station 2

(Fig. 14). Wong and Ward (1972) found that the mean

size of *Daphnia pulicaria* in stomachs of perch fry was

consistently about .1 mm less than the mean size of

an integrated sample from the water column after the fry

had reached 20 mm in length. The concluded this to be

an artifact and the result of distortion by the activities

of the alimentary canal. A more probable explanation now appears to be that the mean size of *Daphnia pulicaria* in the stomachs of perch fry was the same as that in the feeding zone of the fry but as already shown, the mean size in the feeding zone was less than that of the integrated sample during the summer.

Selection between different size-classes of *Daphnia pulicaria*, in a size range which perch fry could handle, was controlled by the abundance of different size-classes in the plankton. A comparison of Figs. 15 and 16 shows that in basin 2 the proportion of different size-classes of *Daphnia pulicaria* in the stomach of fry increased as their absolute abundance in the plankton of the perch fry feeding zone increased.

The increase in the mean size of *Daphnia pulicaria* consumed by perch fry at night in basin 2 (Fig. 17) coincided with an increase in the mean sizes of *Daphnia pulicaria* in the feeding zone (Fig. 18). The same relationship was found in the bay which indicated that the perch fry did not feed in the very bottom water layers where the larger *Daphnia pulicaria* were present during daylight hours. Results from both locations show that daytime samples of perch fry stomachs do not give a true indication of the maximum size of *Daphnia pulicaria* that can be consumed by the fry.

The bimodal size distribution of *Daphnia pulicaria* in stomachs of perch fry in the bay on July 15-16 (Fig. 17) represented the regular night peak plus an additional morning peak. Whether the morning peak was the result of sampling error or a true indication of the feeding pattern is unknown. Because the size-frequency distribution of the *Daphnia pulicaria* population in the bay at this time was strongly skewed towards larger animals (Fig. 14), the lack of a clearly defined diel size selective pattern may have been caused by the narrow size range of *Daphnia pulicaria* available.

Throughout the day on both June 28-29 and July 8-9 the mean size of *Daphnia pulicaria* in stomachs of perch fry was larger in the bay than in basin 2 (Fig. 17). This was the result of the greater proportion of large *Daphnia pulicaria* in the perch fry feeding zone in the bay (Fig. 14).

The progressive shift towards larger size classes of a prey species being consumed as light levels decreased (Fig. 17) has not to my knowledge been reported previously. Voigtlander and Wissing (1974) found a shift towards the consumption of larger prey species by juvenile white bass, *Morone chrysops*, as light levels decreased, but they made no observations on changes in the size of a single species consumed under the same conditions.

Whether the selection of *Daphnia pulicaria* by perch fry at night was based on a visual stimuli as it is during the day (Brooks 1968) or on a chance tactile stimuli is

unknown.   If selection was based on visual stimuli, it
seems that fry were still able to see the smallest
Daphnia pulicaria at night because the smallest *Daphnia
pulicaria* found in stomachs in daytime were also present
in night samples, although relatively less abundant.

Effects of continuous and non-continuous feeding
on the passage rate of food through the guts of young
fish has been shown for large-mouth bass (Laurence 1971)
and yellow perch (Noble 1973).   In both cases the passage
rate was faster for continuously feeding fish than for
those fed a single meal.   For fishes such as yellow perch
fry which feed continuously rather than on a single meal,
the conventional method of fasting, feeding a single meal
and holding for serial sacrifices to determine the passage
rate of food through the gut is clearly inadequate.
Fortunately, digestion in perch fry was so incomplete that
the passage of individual food items through the gut could
be followed.

Most estimates of digestion and passage rates in
yellow perch are restricted to adults (Pearse and Achtenberg
1920, Molnar, Jamassy and Tölg 1967, Ivanov 1968) and
consequently are not directly comparable.   Estimates of
the passage rate of food through the guts of continuously
feeding perch fry are available for Oneida Lake (Noble 1973)
and compare favourably with those reported here.   Noble
(1973) found that the median time for food to pass through

the entire digestive tract of continuously feeding perch
fry, 17-19 mm in length at 20 - 21 C, ranged from 2.1 -
2.9 h.   He also found that the median time for the
passage of food through stomachs of continuously feeding
perch fry with a mean length of 23 mm at 22 C ranged
from .6 - 1.1 h.   The similarity of the estimates of
food conversion efficiency (calories consumed fry^{-1}/
growth of fry) for the perch fry of West Blue Lake and
the perch fingerlings of Huh, et al. (1976) studies
further indicate the reliability of the passage rate
estimates.

Variation in growth of perch fry during the pelagic
stage between basin 2 and the bay (Fig. 2) was directly
attributable to differences in the abundance of *Daphnia
pulicaria* (Fig. 12).   These two areas of West Blue Lake
illustrate the relationship between the abundance of
Daphnia pulicaria, growth of perch fry and consumption
of *Daphnia pulicaria* by perch fry.   In basin 2 the high
abundance of *Daphnia pulicaria* resulted in a higher
consumption per fry (Fig. 2) and in a higher fry growth
rate (Fig. 2) than in the bay.   However, the low abundance
of perch fry in basin 2 (Table 10) resulted in a low total
consumption of *Daphnia pulicaria*.   On a daily basis they
never consumed more than .1% of the standing crop of
Daphnia pulicaria in terms of numbers or biomass (Table 10).
The effect of predation on any size-class was also negligible
(Table 13).

The mean production of *Daphnia pulicaria* in
West Blue Lake during the spring and summer of 1972,
1973 and 1974 was 28.3 mg C m^{-2} day^{-1} (F. J. Ward,
Department of Zoology, University of Manitoba, Winnipeg,
Manitoba, unpublished).   Similar abundance estimates of
Daphnia pulicaria and temperatures in West Blue Lake during
the spring and summer of 1975 indicated that production of
Daphnia pulicaria in this year was comparable to preceding
years.   Comparison of production estimates for *Daphnia
pulicaria* with the consumption rate by perch fry (Table 11)
again shows that the effect of predation by perch fry
was negligible and that the decline in abundance of
Daphnia pulicaria occurred independently of perch fry
predation.

In the bay, the lower abundance of *Daphnia pulicaria*
(Fig. 12) resulted in a lower consumption per fry (Fig. 20)
and a slower growth rate (Fig. 2).   However, the very high
abundance of perch fry resulted in a much higher total
consumption rate with up to 5.2% of the standing crop of
Daphnia pulicaria being consumed daily (Table 12).   The
size selective nature of feeding resulted in very heavy
predation on smaller size-classes with up to 64.1% of a
size-class being consumed daily (Table 14).   Very heavy
predation on smaller size-classes caused their virtual
elimination from the plankton, and subsequently from the
guts of perch fry by the end of the pelagic period (Fig. 16).

This resulted in a very low reproductive population for the next generation. Also, reproductive individuals in the bay during the post-pelagic period were subjected to predation by the fry (Fig. 16) which lead to a further decrease in the population and in recruitment into the next generation.

The data show the direct relationship of *Daphnia pulicaria* abundance to consumption and growth of perch fry; however causes of the variation in *Daphnia pulicaria* abundance appears to be more complex. Rapid declines in the abundance of *Daphnia pulicaria* from spring through summer in West Blue Lake were similar for each year between 1972 and 1975 (F. J. Ward, Department of Zoology, University of Manitoba, Winnipeg, Manitoba, unpublished) even though the year-class strength of perch fry likely experienced a great deal of variation from year to year (Forney 1971, Noble 1975). The spring-summer decline in abundance of *Daphnia* species even occurs in lakes which have no planktivorous predators (Kwick and Carter 1975) which suggests that these populations innately decline during this period. The additional stress of the high predation rate in the bay appeared to contribute to the decline of the *Daphnia pulicaria* population at this location.

Chaoborus flavicans, walleye fry, and juvenile and adult perch were also predators on the *Daphnia pulicaria* population of West Blue Lake, but none were very important.

Chaoborus flavicans do not prey heavily on *Daphnia pulicaria*
(Lysack 1976), and densities of walleye fry were very low.
For juvenile and adult perch, *Daphnia pulicaria* were a
secondary food source and were not consumed in great
numbers (Falk 1971).

Noble (1975) has shown that demersal perch fingerlings
in Oneida Lake consumed 0 - 17.2% of the standing crop of
Daphnia sp. daily from late July until the end of September.
Based on larval densities and their daily energy requirements
Thayer (1974) calculated that larval fish of the Newport
River estuary consumed approximately 10% of the standing
crop of zooplankton daily. Hall (1964) found a 25% loss
per day of *Daphnia galeata mendotae* through predation in
Base Line Lake and calculated that losses up to 36% could
occur without experiencing a decline in population abundance.
His model however did not include the effects of size
selective predation. Slobodkin and Richman (1956) have
shown in a population of *Daphnia pulicaria*, removal of
newborn animals at varying rates from 25 - 90% every 4
days markedly reduced the size of the residual population.
Smith (1963) concluded from Slobodkin and Richman's (1956)
data that removal of young individuals more effectively
reduces population abundance than does the removal of
adults.

Effects of fish predation on species composition
and structure of zooplankton populations has been
demonstrated for numerous freshwater lakes (e.g., Brooks
1968).   It is most commonly characterized by a decline
in abundance of the larger species of cladocerans and
their subsequent replacement with *Bosmina longirostris*
(Brooks and Dodson 1965, Grygierek 1966, Reif and Tappa
1966, Galbraith 1967, Brooks 1968, Hutchinson 1971,
Warshaw 1972, Ilkowska 1973).   A similar change in
abundance and species composition of zooplankton occurred
in the bay of West Blue Lake (Fig. 12) and again showed
that the *Daphnia pulicaria* population at this location was
experiencing heavy predation.   Two other changes associated
with fish predation, an increase in the egg to animal ratio
(Archibald 1975) and a decrease in the mean reproductive
size of zooplankton species experiencing predation
(Wells 1970, Warshaw 1972, Archibald 1975) also occurred
in the *Daphnia pulicaria* population in the bay (Table 7 and
Fig. 16).   Although these changes may be further evidence
of heavy fish predation they cannot be regarded as conclusive,
since both growth increment and brood size in *Daphnia magna*
(Green 1954) and *Daphnia galeata mendotae* (Hall 1964) have
also been shown to depend on the amount of available food.

Production of Perch Fry

Production estimates for perch fry are dependent
on both their growth and abundance. Variations in
estimates for different parts of West Blue Lake were
largely the result of differences in perch fry abundance
(Table 4). Growth rates of perch fry were identical
in each basin (Fig. 2) and abundance was similar resulting
in similar production estimates ranging from .04 - .07 mg
C m^{-2} day^{-1} during the pelagic phase (Table 14). Perch
fry production in the bay was an order of magnitude higher
than in the rest of the lake with a value of .71 mg C m^{-2}
day^{-1}. The reduced growth rate of perch fry in the bay
during the pelagic phase (Fig. 2), caused by a biomass of
fry which was disproportionately high in relation to the
primary food source, had little effect on the production
estimate as the result of the high abundance of fry at
this location (Table 9).

Mean whole lake production of perch fry during the
pelagic phase was .08 mg C m^{-2} day^{-1}. The relationship
between perch fry production and production of the other
components of the West Blue Lake ecosystem are shown
below:

	Production during spring-summer period (mg C m^{-2} day^{-1})	Year	Remarks	Source
Primary	350.00	1967-73		Ward and Robinson 1974
Daphnia pulicaria	28.30	1972-74		Ward (unpublished)
Cyclops bicuspidatus	6.92	1974		Patrick (unpublished)
Age 0 perch	.08	1975	15-25 cm	this study
Walleye	.12	1969-70 1974-75	> 25 cm	Kelso 1972 Schweigert 1976

Although the estimate of perch fry production may initially
appear low relative to other values, more careful consideration
of the part of the population being monitored reveals that
it agrees very well. Production in young fishes comprises
a large proportion of total fish production in a lake
(Chapman 1967), usually ranging from 10 - 50%. Nyber
(1976) found that 0+ production of yellow perch in two
Sweedish lakes from 1970-1973 averaged 4.0 kg out of a
total of 27.8 kg which was equivalent to 14% of total
perch production in the lake. Values ranged from 10.6 -
58.6%. Mathews (1971) studied production of bleak
(*Alburnus alburnus*), roach (*Rutilus rutilus*), gudgeon
(*Gobio gobio*), and dace (*Leuciscus leuciscus*) in the
Thames River during their first year and found that this
group accounted for 39 - 73% of total production for all
age groups. Assuming perch fry production in West Blue
Lake represented 10 - 50% of total perch production, estimates
of the latter would be .16 - .80 mg C m^{-2} day^{-1}. These

estimates are very reasonable in relation to other values for West Blue Lake and give a conversion factor between primary and perch production of .05 - .23%.

Although one would expect a general trend towards decreasing production proceeding from *Daphnia pulicaria* and *Cyclops bicuspidatus*, the food of perch, to perch, to walleye, the major predator on the perch, a direct relationship which is constant from year to year is unlikely to occur. The level of production in the 0+ age class will, in part, be controlled by the number of reproductive adults, spawning success, wind and water generated currents following hatching, and a number of other biotic and abiotic factors, none of which are necessarily related to production of predators on, or prey of the perch population.

The quantitative ecology of young fish and their effect on aquatic ecosystems as described here for perch fry is generally poorly understood for most freshwater species. The reason for this lack of understanding is attributable to two factors. First, young fish have proven extremely difficult to sample in a quantitative fashion using conventional fisheries techniques. With the exception of Noble's (1972) work on the Miller high-speed trawl, few attempts have been made to develop sampling techniques which can be used to derive quantitative estimates

of abundance of young fish. The indirect method of
estimating abundance of young fish on the basis of
the amount of roe deposited by spawning adults (e.g.,
LeCren 1962) is of little value because of the unknown
importance of various abiotic (Doan 1942, Christie 1963,
Lawler 1965, Christie and Regier 1973, Svardson and
Molin 1973, Busch, et al. 1975) and biotic (Regier, et al.
1969, Forney 1971, Noble 1972) factors in controlling
mortality during the post-hatching period. Secondly,
as young fish are not immediately valuable to commercial
or sport fisheries they tend to be ignored.

Probably the most important goal of applied
fisheries biology today is to rebuild depressed fish
stocks and fish stock complexes to, or above former levels
(Loftus 1976). One of the most potentially promising
ways to achieve this goal appears to be to innoculate
lakes with massive numbers of young fish in the hope
that future catches will be roughly proportional to the
number of fish planted. Despite the apparent spectacular
sources of some such programmes (e.g., Ward and Clayton
1974, Lawler, et al. 1974) there is still considerable
question about the long term advantages (Forney 1976,
Loftus 1976). If future attempts are made to rebuild
fish communities through fry stocking programmes it will
become essential to gain a greater understanding of the

quantitative requirements of young fish and their effect
on the ecosystem. More information will be needed on
the potential food producing capacity of "nursery" areas
to determine the number of fish, both natural and
introduced, it can support without reducing growth or
increasing mortality. Further, information will be
needed on the importance of various species specific
limnological and morphological parameters which affect
the growth and abundance of young fish.

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Appendix A

Total Length of Perch Embryos When They First Become
Eyed

Fish Number	Length (mm)
1	4.31
2	4.35
3	4.35
4	4.35
5	4.16
6	4.47
7	4.51
8	4.39
9	4.43
10	4.39
	Ave. = 4.37

Appendix B.   Sampling of Perch Fry in West Blue Lake - Length

Sampling Date	Sampling Method	Basin 1 Mean Length (mm)	Basin 2 Mean Length (mm)	Basin 3 Mean Length (mm)	Bay Mean Length (mm)	Pooled Mean Length (mm)
1974						
June 9	Dip Net	5.60			5.82	5.71
10	Dip Net	5.10			5.13	5.13
12	Dip Net				6.00	6.00
18	Tow				9.54	9.54
24	Tow	15.30	14.97	14.72		14.97
July 1	Tow	19.85	18.81	19.59		19.42
4	Tow	20.04	19.45	20.56		20.02
8	Tow	25.75	24.98	27.49		26.07
15	Tow	27.00	25.92	28.82	27.54	27.32
22	Seine	37.85	37.00	33.93	34.77	34.88
25	Seine		39.50	37.36	36.09	37.65
Aug. 5	Seine	47.20	43.30	42.45	42.20	44.29
19	Seine	52.50				52.50
1975						
May 31-June 2	Newly hatched from aquaria					5.49
June 2					5.96	5.96
3	Dip Net				5.96	5.91
4	Dip Net	6.16				6.16
5	Dip Net				6.08	6.08
6	Dip Net	6.39				6.39
8	Dip Net				6.66	6.66
9	Dip Net	6.12		7.35		6.69
11	Dip Net	7.64		7.35		7.50
13	Dip Net				7.65	7.65
16	Tow				9.84	9.84
17	Tow				10.83	10.83
20	Tow				11.47	11.47
22	Tow	13.42	12.98		13.10	13.10
25	Tow	15.62	15.40	15.90	16.43	15.84
29	Tow	17.42	16.75	18.08	17.32	17.39

Appendix B.   cont'd.   Sampling of Perch Fry in West Blue Lake - Length

Sampling Date	Sampling Method	Basin 1 Mean Length (mm)	Basin 2 Mean Length (mm)	Basin 3 Mean Length (mm)	Bay Mean Length (mm)	Pooled Mean Length (mm)
July 4	Tow	20.55	18.30	18.95	18.18	19.00
7	Tow	21.90	21.80	21.11	19.30	21.03
11	Tow	23.50	21.87	23.92	20.15	22.22
14	Tow	25.94	26.20	26.46	23.05	25.40
22	Seine	34.40	34.00	34.40	34.80	34.41
28	Seine	41.37				41.37
Aug. 5	Seine		45.75			45.75
12	Seine		48.85			48.85

Appendix C.   Sampling of Perch Fry in West Blue Lake - Weight

Sampling Date	Sampling Method	Basin 1 Mean Wet Weight (mg)	Mean Dry Weight (mg)	Basin 2 Mean Wet Weight (mg)	Mean Dry Weight (mg)	Basin 3 Mean Wet Weight (mg)	Mean Dry Weight (mg)	Bay Mean Wet Weight (mg)	Mean Dry Weight (mg)	Pooled Mean Wet Weight (mg)	Mean Dry Weight (mg)
1974											
June 24	Tow	21.6	2.1	20.7		17.4				19.9	2.1
July 1	Tow		3.8		3.0		3.5				3.4
4	Tow	80.0	4.4	55.9	4.0	85.6	4.4			73.8	4.3
8	Tow	162.1	10.9		10.1		15.4			162.1	12.1
9	Tow			164.3	15.7	201.2	17.9			182.7	16.8
15	Tow			157.5	13.8	254.2	22.6	207.9	20.6	206.5	19.2
22	Seine					271.7	50.8	308.8	52.0	290.2	51.4
25	Seine			354.0	78.9	319.0	71.5		57.0	336.5	69.1
Aug. 5	Seine	850.0	145.8	610.0	108.6	610.0	107.7	666.0	118.2	628.7	120.1
1975											
May 31-June 2	Newly hatched fry from aquaria									.43	.07
June 2	Dip Net							.55		.55	
3	Dip Net							.43	.07	.43	.07
5	Dip Net							.71		.71	
6	Dip Net	1.04	.15							1.04	.15
8	Dip Net							2.90	.17	.90	.17
9	Dip Net	0.53	.07			1.53				1.03	.07
11	Dip Net	1.20	.27			1.20	.12			1.20	.19
13	Dip Net							1.37	.14	1.37	.14
16	Tow							2.80	.28	2.80	.28
17	Tow							5.12	.57	5.12	.57
20	Tow							7.32	.78	7.32	.78
22	Tow	13.14	1.85	12.40	1.64			11.90	1.60	12.48	1.70
25	Tow	23.65	2.52	18.78	1.97	23.29	1.61	23.98	1.78	22.42	1.97
29	Tow	43.22	4.26	36.99	4.06	49.23	4.67	40.53	4.12	42.49	4.28

Sampling Date	Sampling Method	Basin 1		Basin 2		Basin 3		Bay		Pooled	
		Mean Wet Weight (mg)	Mean Dry Weight (mg)	Mean Wet Weight (mg)	Mean Dry Weight (mg)	Mean Wet Weight (mg)	Mean Dry Weight (mg)	Mean Wet Weight (mg)	Mean Dry Weight (mg)	Mean Wet Weight (mg)	Mean Dry Weight (mg)
July 4	Tow	82.23	11.40	59.86	6.64	63.10	7.40	51.44	6.56	64.16	8.00
8	Tow	114.99	11.48	112.98	11.04	104.80	9.30	63.00	7.84	100.19	9.91
11	Tow	130.4	17.5	111.1		131.3	15.1	72.9	9.0	111.4	13.84
14	Tow	181.8	25.1	196.7	23.4	195.5	27.4		17.9	192.2	23.52
22	Seine	294.2	56.98	288.8	55.39	305.7	56.7	321.5	60.4	302.55	57.38
28	Seine	513.1	101.5							513.1	101.5
Aug. 5	Seine			767.9						767.9	
12	Seine			987.0	183.2					987.0	183.2

Appendix D.　Carbon, Nitrogen and Calorific Estimates for Perch Fry.

Date	Length (mm)	Carbon (mg fry^{-1})	Nitrogen (mg fry^{-1})	Calories (g^{-1})
1974	14.97			4947.1
	19.50	2.62	0.61	
	20.00	4.08	1.02	
	20.60	3.50	0.80	
	24.86			4967.9
	25.70	7.08	1.79	
	27.50	8.06	1.95	
	27.50	9.00	2.12	
	34.80	23.02	5.70	
	34.88			
	37.40	36.44	9.14	5026.0
	39.50	35.19	8.75	
	42.50	45.07	11.42	
	44.29			5071.3
	44.20	55.61	12.81	
	47.20	55.43	14.82	
	52.50	75.38	18.32	5642.6
1975	5.49	0.03	0.01	6726.6
	11.47			5368.0
	11.50	0.33	0.08	
	17.99			4966.0
	18.30	2.97	0.75	
	34.00			5008.4
	40.71			5741.7
	41.40	46.85	10.96	
	45.10	64.01	16.22	
	45.31			5471.5
	48.85			5759.4
	50.10	74.16	18.03	

Appendix E.   *Daphnia pulicaria* Abundance at Deep Water Stations in 1975.

| Date | Station (no. m^{-2}) | | | |
	2	4	6	7
May 14	13335		333	
15		61633		5600
20	19337	34500	134	3933
28	148900	121853	5567	30733
June 4	145367	177267	36833	114533
7			127900	
10				29733
11	319527	241127	166337	
13			53666	
16			110733	
17	307020	196400		96933
19			149833	
25	232360	127933	28400	173400
28			84900	
July 1			29266	17333
2	73600	22966		
4			14700	
9	178967	44300	5900	11900
12			31333	
15			67228	
16	279627	136700		29533
18			4320	
23	124466	23000	4800	48733
30	81366	87267	5633	13967
Aug. 6	90933		6733	4000
13	24633	10367	1300	72567

Appendix F.   *Bosmina longirostris* Abundance at
Deep Water Stations in 1975.

Date	Station (no. m^{-2})	
	2	6
July 1		500
2	0	
16	532	
18		13167
30	2067	134100
13	24580	466600

Appendix G.   *Daphnia pulicaria* Abundance at Shallow Water Stations in 1975.

Date	Station (no. 1^{-1})			
	8	9	10	11
May 28	2.5	0.5	5.6	0
June 4	1.5	5.5	7.7	0.1
10				0.5
11	0.5	1.3	6.7	
13				6.1
16				0.7
17	0	0.3	6.0	
19				0
25	0.1	0.1	0.1	0.3
28				1.5
July 1				0.2
2	0	0.5	0.5	
4				0.3
9	0.9	0.4	0	0
12			0	0
15				0.1
16	1.5	2.3	0.3	
18				0.1
23	1.0	0.6	0.1	0.1
30	0	0.1	0.1	0
Aug. 6	0	0.1	1.7	0.1
13	2.3	0.2	0	0.1