THE UNIVERSITY OF MANITOBA

GROWTH, FEEDING AND DISTRIBUTION OF YELLOW PERCH FRY, *PERCA FLUVIATILIS FLAVESCENS* (MITCHILL), DURING THEIR FIRST SUMMER IN WEST BLUE LAKE

by

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ABSTRACT

Growth, feeding habits and distribution of yellow perch during their first summer of life in West Blue Lake, Manitoba were investigated. When fry reached a length of approximately 9 mm in early July they dispersed from the shallows to occupy the 0 to 6 m zone in the lake. After reaching a length of approximately 30 mm in early August they moved inshore again to take up a littoral mode of life. During the epilimnetic stage, they exhibited a diel migration pattern; approaching the surface at night and descending to deeper water (5 m) during the day. In the months of July and August, young perch tripled their length and their weight increased ninefold. Throughout the summer, perch fed on small crustaceans, primarily *Daphnia pulex* and to a lesser extent, copepods. This low diversity in stomach contents reflected the low species diversity of West Blue Lake zooplankton. Size-selective feeding was prominent in young perch ranging in length from 9 to 20 mm. They changed from dependence on nauplii to copepods and then to *Daphnia* with increasing age. Older fry fed on all sizes of *Daphnia*. Size-selective feeding in younger fish was closely related to mouth size.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

In recent years, increasing attention has been centered upon the early life histories of many commercial and game fishes (Hunts and Carbine 1951; Kramer and Smith 1960; Faber 1963; Forney 1966; Houde 1967, 1969; Frank 1967; Siefert 1968). Investigations in this field have expanded the knowledge of fish populations in relation to year-class-strength, growth, production and management (Pycha and Smith 1954; Gerking 1966; Nelson 1968). Yellow perch, _Perca flavescens_ (Mitchill), is of minor importance as a commercial and game fish in Manitoba and their fry have not been studied intensively. Consequently their general ecology is relatively unknown.

Young perch, which hatch out in late spring, are abundant in the surface waters of West Blue Lake, Manitoba during the summer. In July, they are frequently seen near the surface in both the epilimnetic and littoral zones, while in August, encounters with these young fish are limited to the littoral zone.

The role of larval perch in freshwater ecosystems differs from that of the adults. They rely on zooplankton as their primary food source (Allen 1934; Smyly 1952) and in turn serve as forage for organisms higher on the food chain such as walleye (Forney 1966; Maloney and Johnson 1957). This appears to be the case in West Blue Lake, because during the summer, they are the major food of walleye (Kelso MS 1972) which accomplish most of their annual growth in this period (Glenn MS 1969). The food spectrum of larval perch is simple and unlike older fish which feed on a large variety of food organisms (Falk MS 1971). The relatively simple and discrete function of larval perch in this lacustrine ecosystem lends itself well to trophic studies. In West Blue Lake the theme of research is to describe the trophic relationships and ecology of the dominant components of the ecosystem. An examination of the role of these young fish in this context is a necessary step towards the overall understanding of the ecosystem.

The objective of this study was to examine the general ecology of larval perch during their first summer in West Blue Lake. Specifically, the goals were to determine growth rates, seasonal changes in distribution and food habits of larval perch.

LITERATURE REVIEW

The yellow perch, a spiny-rayed fish, is a member of the family Percidae, which includes the walleye, the sauger and darters. The subspecies *Perca fluviatilis flavescens* (Mitchill) is the equivalent of the European *Perca fluviatilis fluviatilis*, and the Russian intermediate form in the Kolyma River basin of Siberia (McPhail and Lindsey 1970).

The American yellow perch ranges from the Lesser Slave Lake of the Mackenzie River Basin and the Hudson Bay drainage, east to Nova Scotia, south to South Carolina, and west to Kansas (Hubbs and Lagler 1967).

Yellow perch are found in most lakes, and in the backwaters and impoundments of larger rivers, as well as in sluggish streams in the north temperate zone. Being very adaptable, perch occupy a wide variety of habitats, but they thrive in lakes with abundant open water and moderate amounts of vegetation (Herman *et al* 1959).

Perch usually reach maturity in about two years. In Lake Mendota, some males may mature a year after hatching, while those further north may take two to three years (Herman *et al* 1959). Sexual development in females occurs a year or two later than in males (Alm 1954). The size of perch at maturity varies from population to population. Males in a stunted population are about four inches long at maturity, compared to seven inches for fast growing fish (Alm 1954; Le Cren 1951). Sex ratios differ considerably between populations but females are generally more numerous than males (Eschmeyer 1938).

Spawning normally occurs in spring, from early April to late May, depending on the temperature of the water. In most lakes, an inshore migration commences as the water warms from 2 to 7 C (Muncy 1962). General activity of perch reaches a peak during this inshore spawning migration (Maloney and Johnson 1957). Males migrate first and most remain in the shallows until the end of the breeding season. Gravid female stay on the spawning grounds just long enough to breed. They then move offshore (Herman _et_ _al_ 1959).

Spawning takes place at temperatures between 7 and 11 C. Females deposit their eggs on gravel, rubble, vegetation and sunken logs and branches (Herman _et_ _al_ 1959). The spawning grounds are normally located in water 3 to 10 ft deep, where each female lays from 3,000 to 60,000 eggs (average 23,000 eggs), depending on size and condition (Sheri and Power 1969). Eggs are deposited in strands measuring from 2-7 ft long and from 2-3 in wide. The spawning period may last for a month or more depending on the rate of warming of the lake (Coots 1956; Muncy 1962).

Sac fry about 5.1 mm long hatch after an incubation period of from 8-15 days, depending on temperature (Herman _et_ _al_ 1959). Larval fish lose their yolk-sacs when they are slightly over 7 mm long (Fish 1953). In Oneida Lake, mortality differed little among years during the limnetic period and fluctuations in year class strength were the result of the success of hatching and survival during the prolarval stage (Nobel 1968).

There is some disagreement concerning the movements and habitats of larval fish during the summer. Turner (1920) suggested that young perch from 26 to 50 mm long, in Lake Erie, were generally found near shore at depths of from 2-5 ft. By comparing catches in 42 localities around Bass Island, he came to the conclusion that young fry have a general and rather uniform distribution along the shore with no apparent choice in habitat characteristics.

Echo (1954), in his study of perch spawning habits in Thomson Lake, Montana, observed that after hatching, when larval fish reached a length of 0.6 in, they schooled near the surface in hundreds over spawning areas from 3-6 ft deep. In July he also reported an almost continuous band of perch fry about 4 ft wide and approximately a mile in length along the margin of Middle Lake.

Maloney and Johnson (1957) gave a similar account of the distribution of young perch. They stated that perch and walleye, during their first summer of life, usually inhabit shallow waters near shore. Faber (1967), however, showed that the young stages of some freshwater fish in North Wisconsin Lakes are limnetic during May and early July and that perch fry are the dominant species in this zone when the water temperature is between 13 and 17 C.

Nobel (1968) found that pelagic yellow perch were not uniformally distributed, but occupied, primarily, the upper 20 ft of the epilimnion. During calm conditions, they concentrated in the upper 5 ft, while under conditions of sustained winds of 12 mph or over, they shifted down to depths between 5 and 15 ft (Nobel 1968).

Houde (1969) caught most perch (6 mm and over) in Oneida Lake at depths between 2 and 3 m, about 500 m off shore. He showed that they maintained themselves at depths between 2 and 3 m and were not affected by winds under 10 mph. Examination of horizontal distribution data indicated that perch fry in Oneida Lake did not form discrete sub-populations. Priegel (1969) also described perch fry as being dispersed throughout the lake horizontally in the summer, however, they were concentrated temporarily in the shallows near the mouth of a river early in May.

Despite disagreement concerning the distribution of perch fry in spring and early summer, it is agreed that in the fall they move into deeper water following the same pattern as the year-old and older fish (Allen 1934).

One of the most convenient methods of determining the distribution of aquatic animals is that of acoustic sampling. Objects with different acoustic properties to those of the medium (water) are detected by echosounders. The greater the difference in acoustic properties, the more readily will the objects be detected. Aquatic animals with gas bubbles or swim bladders (present in many freshwater fish) are model targets for acoustic studies.

The difficulties in the interpretation of echograms is the main drawback of the method. The "blip" (or image form) of an object as recorded on the trace is dependent on size and shape, the acoustic property, the swimming speed of the target, and its position within the cone-shaped field of wave pulses transmitted fromthe transducer (Cushing 1957). Complications also arise in interpretation when the animal under study intermingles with other animals of the same or different species. To some extent, animals of different sizes can be recognized in the echo trace by the size of the blips and by selecting transducers of suitable frequency or wave length. Tracings of animals with a diameter far smaller than the wave length of the sounder are not recorded in the form of a discrete spot (blip). Tracings of clumped accumulations of these animals, however, will be recorded by a low frequency sounder in the form of a diffuse "haze" on the tracing. The reflective strength of an object reaches a maximum when the acoustic diameter of the object is equal to the wave length of the transducer or a multiple (McNaught 1968). Low frequency sounders (10-30 kcs) are generally used for the fish study. High frequency sounders (200-1000 kcs), sensitive to objects as small as 1-3 mm, are preferred in zooplankton studies (McNaught 1968; Boden 1962).

Another method for studying the vertical distribution of small limnetic animals uses data obtained from meter tow net catches. This method is especially effective for animals with low swimming speeds. Good swimmers like most limnetic fish and fish larvae can actively avoid capture by outswimming or escaping through the sides of the net (Taylor 1968). Net avoidance is much more pronounced in daytime than at night, and this behavior has been attributed to the ability of fish to see the nets during the day (Isaacs 1964). The vulnerability of many limnetic fish to nets is highest at sunset and not during the period of minimal light (0100-0300 hr). It has been suggested that with rapid setting of the sun, some fish may experience a period of partial night-blindness before dark adaptation can take effect (Ali 1959).

Generally, the swimming speed of larval fish renders the low speed meter net unsuitable for quantitative and qualitative studies (Bridger 1956). Comparison of various open water fry sampling procedures demonstrates the need for an accurate quantitative method (Noebl 1968; Colten *et al* 1961). For qualitative studies, sampling error can be reduced by increasing towing speed, sample size and limiting sampling periods to the evening when the larval fish are more vulnerable. Furthermore, nets can be towed between two boats (Johnson 1956), or pushed in front of a boat (Faber 1963) to avoid unnecessary disturbance to the fish. These nets have been effective in studying the distribution of young sockeye salmon (Johnson 1956).

Growth of fish is generally estimated from the length, weight and age composition data from the population in question (Tesch 1968). The age of temperate water fish is normally determined by enumerating annuli formed in the bony parts of the body. Some frequently used bony structures are scales, otolighs, spines, opercular bones and the cleithrum (Tesch 1968). In the case of young of the year fish, age is determined by date of collection relative to hatching date, which, in wild fish, is seldom precisely known (Forney 1966). The length of young fish caught on a given date can also indicate age, because length at hatching for a species does not vary greatly.

Fish growth is generally determined directly from changes in length or weight during a specified period. Growth rate is, in temperate areas, highest in July for both young and older perch (Muncy 1962). Growth rate of female perch is greater than that of males, including the young of the year (Eschmeyer 1937).

Perch fry grow from a length 0.6 in in May to 3.0 in in September (Maloney and Johnson 1957). Similarly, Pycha and Smith (1954) found that perch reach lengths between 45 and 60 mm in September. Their length weight relationship is expressed by the equation:

$$W = 0.6198 \times 10^{-5} L^{3.1251} ,$$

where W and L are weight (gm) and length (mm) respectively.

Adult perch utilize a variety of organisms as forage (Ewer 1934; Langford and Martin 1940); however, as young fry, they feed on a narrow range of food organisms. Newly hatched perch larvae may feed on algae and copepods, then switch to cladocerans, small insect larvae or pupae, and finally to amphipods and other bottom fauna, as they increase in size (Turner 1920; Allen 1935). The range of food items ingested by young perch is limited by the size of individual items. The dimensions of ingested items relative to fish mouth size has been investigated (Northcote 1964; Hartman 1958). Northcote (1964) demonstrated that *Cottus rhotheus*, with a larger mouth than *C. asper* of same body length, ingested larger prey. Similarly Hartman (1958) showed that sizes of ingested food were dependent on predator mouth size. Even for a single food species, it has been established (Shelbourne 1962) that small fish are restricted to smaller prey, and that as they grow, so their feeding versatility increases to include all sizes of the same prey species. For perch fry, Smyly (1952) suggested that there was no definite relationship between the size of a crustaceans ingested and fry size, but there was a tendency for larger fry to feed more frequently on larger crustaceans.

A variety of quantitative methods are used to study feeding in freshwater fish. The applicability of these methods in determining minute quantities of food in small fish was reviewed by Hynes (1950). He selected the point method to describe the feeding habits of stickleback. Food items were assigned units according to their size and weight. This method is subjective and fails to provide a common quantitative unit for comparison with the results of other studies. Total stomach weights, a common and effective method to describe seasonal changes in stomach contents, was selected by Smyly (1952) in his study of the food of young perch. By pooling stomach contents, he overcame the difficulties in dealing with minute quantities of food in individual fish, but in the same process, the feeding habits of individuals was ignored.

METHODS

Description of the Area

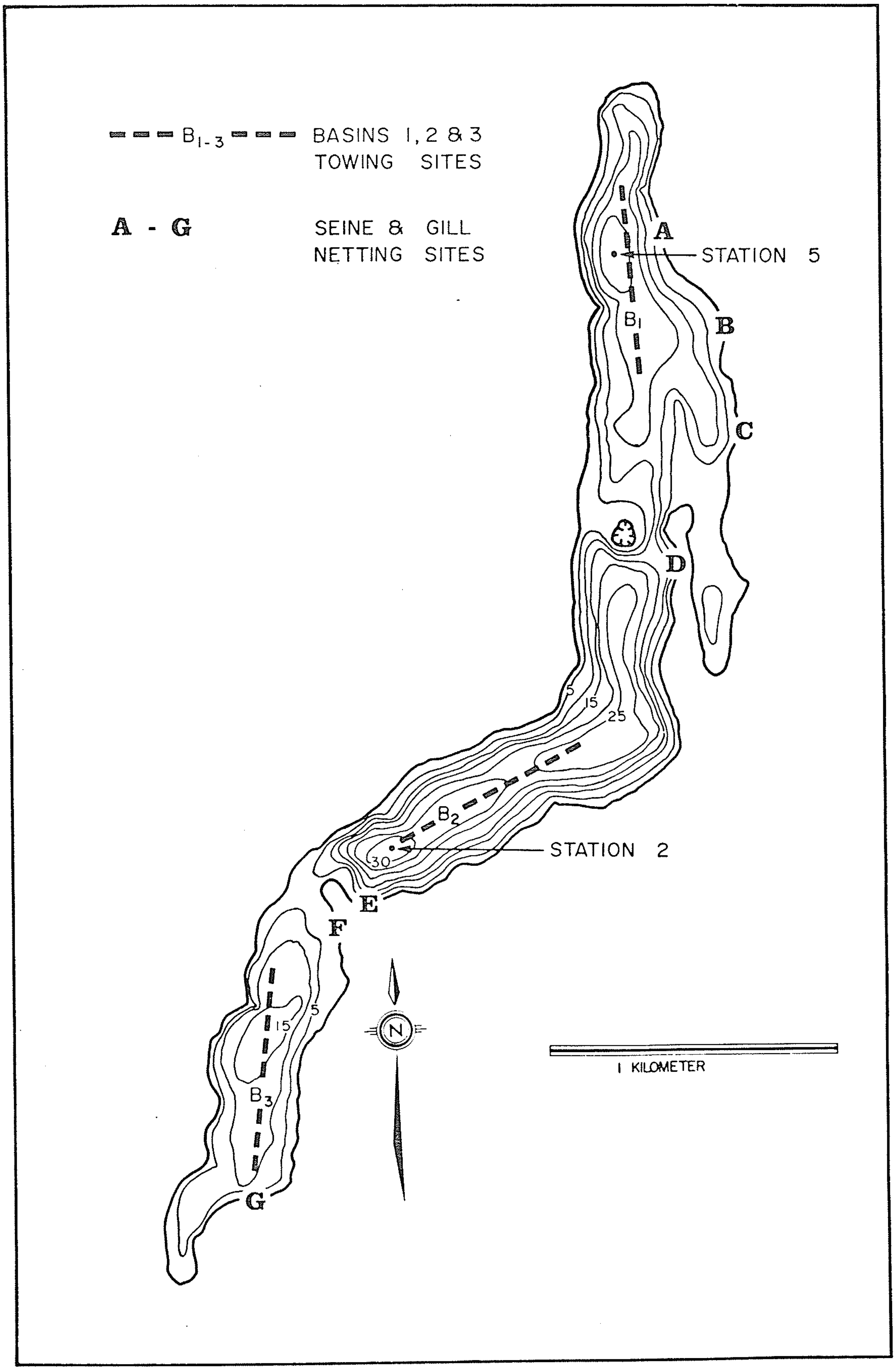
West Blue Lake (Fig. 1), situated in Duck Mountain Provincial Park in west-central Manitoba (lat. 51°36', long. 100°55' and altitude 670 m), is a 'channel' lake with a multibasin configuration. A clear lake with steeply sloping shores, West Blue Lake is essentially a closed system with mean depth of 11.3 m and an area of 160 ha (Bell and Ward 1970).

The zooplankton is composed of the three dominant species, *Daphnia pulex*, *Cyclops biscuspidatus* and *Diaptomus siciloides*, and the associated species, *Epischura lacustris* and *Mesocyclops edax* (Patalas, personal communication). The Rotifera are represented by *Keratella cochlearis*, *K. quadrata*, *Felinia longiseta* and *Asplanchna* sp. (Fernando, personal communication).

The littoral benthos is more luxuriant and diversified (Biette MS 1969) but many of the organisms have not been identified. Species of special importance in this study are the amphipods *Gammarus lacustris* and *Hyalella azteca*.

The fish community of the lake consists of Yellow Perch, *Perca flavescens*; Walleye, *Stizostedion vitreum vitreum*; Five-spined stickleback, *Culaea inconstans*;

FIGURE 1. West Blue Lake showing sampling sites.


B_{1-3} BASINS 1, 2 & 3 TOWING SITES
A - G SEINE & GILL NETTING SITES
A
STATION 5
B
B_1
C
D
5
15
25
B_2
STATION 2
30
E
F
5
15
B_3
G
N
1 KILOMETER

Northern Pike, *Esox lucius* and Lake Trout, *Salvelinus namaycush*.

Sampling Perch Fry and Zooplankton

Samples of Age 0 perch were taken from different parts of West Blue Lake between the middle of June and the beginning of September in 1969 and 1970 (Fig. 1). Various methods were employed in collecting fry. Throughout the main part of the summer, bi-weekly collections were made using either a tow or seine net. When these methods were unsuccessful, samples were collected using dip or gill nets.

Between July 1 and August 10, when young fish were pelagic, the meter tow net was the main sampling method. This cone shaped net was constructed of duPont nylon, 0.63 cm (stretched measure) netting in the forward section (1.8 m), 0.47 cm mesh for the middle section (0.9 m) and 0.32 cm mesh for the last section (0.9 m) of the net. A 280 ml nalgene bottle was secured at the apex. This arrangement minimized damage to the delicate fish during towing. The meter net was towed by two boats at the surface (Johnson, 1956) at a speed of approximately 3.9 km per hour. Five minutes tows were conducted over the deepest water along the length of each basin (Fig. 1). Tows were made in the evening, and especially at dusk (1900 to 2400 hr), when perch fry were abundant near the surface. Some samples were collected in the shallows during the day. In these cases a dip net made of 500 μ monofilament nylon screen was used.

From the end of July to the end of August, when fish inhabited the litteral zone, collections were made with a small mesh nylon seine 13.7 m long and 1.8 m deep. Seining was conducted by setting the net about 5 m off shore and drawing it slowly shoreward to form a bag. Fish trapped in the bag were removed with a dip net. Shore areas with gentle slopes were chosen as sites. In West Blue Lake, where the volume development is close to unity, such sites were limited (Fig. 1). To avoid local depletion, sites were fished in rotation. As in the case of towing, the chief seining periods were in the evenings. In late August and in the beginning of September, additional samples were collected by gill net. A gill net (1.27 cm, stretched measure) was set at an approximate 90° angle to the shore in depths from 2.5 to 5.5 m. The net was examined at two hour intervals.

All collected fish were immediately killed and preserved in 5% formalin. Preserved samples were examined in connection with growth and feeding studies.

Zooplankton samples were collected at stations 2 and 5 (Fig. 1) throughout the summer, using either a 4 liter Van Dorn sampler or a plankton net made of 70 μ nitex screen. Samples for quantitative studies were collected every two weeks at station 2, at 5 m intervals starting from the surface to the bottom using the Van Dorn sampler.

Samples for energy determinations were collected at station 2 and 5 using a plankton net hauled vertically through the water column. Several hauls were generally made on each sampling date.

Diel Vertical Distribution of Perch and Zooplankton

Diel changes in the vertical distribution of limnetic perch fry were investigated with a Furuno 50 kc/sec echo-sounder and a meter tow net, used singly or concurrently. Areas studied were also areas sampled regularly with the meter tow net (Fig. 1). The transducer of the sounder was mounted on the side of the boat. Echograms were recorded at a 3.5 gain setting and with the boat travelling at speed of approximately 3.9 km per hour.

The meter net was modified to tow at depths of approximately 3 and 5 m by adding lead weights and a depressor fin in the front of the net. The depth of the net, when towed at a fixed speed, could be regulated by adjusting the angle of the depressor. The actual depth of the net was judged by the angle of the tow lines and the ability of the net to pick up objects which were suspended at known depths.

Diel vertical perch migration were investigated on 22 July, 1969 and 29 June, 1970. In 1969, surface tows and concurrent echograms were made in all three basins (Fig. 1) between 0900 and 2430 hr. In 1970, the test was restricted to Basin 2, but tows were made at 0, 3 and 5 m with the echosounder operating. Fish in each collection were counted so that catches made at each depth could be compared to traces on the appropriate echogram. Collections at all three depths and concurrent echograms were made at two hour intervals for 24 hours. Zooplankton samples were also collected from the water column (see above) so that possible relationships between perch and zooplankton movements could be examined.

Seasonal Growth

A total of 1251 fish, collected by tow and seine nets between July 1 and August 31, 1969, were used to estimate growth. The total length of each fish (from the anterior extremity of the head to the tip of the caudal fin) was measured to the nearest 0.1 mm for fish under 20 mm using a dissecting microscope fitted with a measuring eye piece and a stage micrometer. Larger fish were measured to the nearest 0.5 m with a ruler graduated in millimeters.

Fish were blotted dry with paper towels and then their wet weights determined with a balance precise to the nearest 0.05 mg. Perch fry under 20 mm were weighed in groups, while the larger ones were measured individually. Gape width (Hubbs and Lagler 1967) of perch fry was measured with a copper cone (11°25' taper, calibrated in 0.2 mm increments). Gape width was the distance between the angles of the jaws with the mouth fully distended by the inserted cone.

Mean lengths and weights were calculated for all samples, and were used to estimate seasonal growth (Chapman 1967) and length-weight relationships (Tesch 1968)

$$W_t = W_o e^{kt}$$

$$\mathrm{Log}_{10} W_t = a + b\mathrm{Log}_{10} L_t$$

where W_o is the wet weight of larval perch at time 'o', W_t is the wet weight of larval perch at time 't', L_t is the length of larval perch at time 't' and a, b and k are constants. Weekly specific growth rates were calculated following Swift (1955),

$$(\mathrm{Ln}\ L_2 - \mathrm{Ln}\ L_1)/T_2 - T_1$$

where L_1 and L_2 are length of perch at time T_1 and T_2 respectively. Coefficients of condition (K_n) for perch fry were calculated according to Kramer and Smith (1960),

$$K_n = W/W_1$$

where W is the wet weight of larval fish and W_1 is the wet weight calculated from the length weight relationship.

Stomach Analysis

Only fish collected between 1900 and 2400 hr were used to study feeding habits. On the average, about 45 guts of fish from weekly samples were examined. Stomach contents were identified using a dissecting microscope. In the smallest fish, prior to the formation of the stomach, the full length of the digestive tract was examined, but in older fish only the esophagus and the stomach were examined. Regurgitation occurred in some fish when killed with formalin. Regurgitated food was examined in the same manner as the stomach contents and results were included in totals.

Food items found in perch stomachs were identified to genera (and species when possible) and enumerated. Food fragments (except animal heads) were not counted. To facilitate the estimation of food value, items were separated into taxonomic groups and size classes. The main taxonomic groups were copepods, cladocerans (*Daphnia pulex*) and amphipods. Copepods were divided into two size classes, juveniles (nauplii) and adults (copepodids and mature copepods). Cladocerans and amphipods, which increased considerably in size with age, were further divided into length classes. The cladocerans were separated into 14 classes (0.2 m intervals) and the amphipods into 12 size classes (0.5 m intervals). The length of *Daphnia pulex* was measured from the center of the eye to the base of the caudal spine (Ward *et al* 1970), while their depth was the maximum dorso-ventral measurement along the median sagittal plane. Both length and depth measurements were made using a microscope fitted with a measuring eyepiece. Amphipod lengths were measured from the center of the eye to the tip of the telson, with the animal straightened. These features were selected as reference points for length measurement since they were readily recognized even in semidigested animals. The sizes of damaged animals were estimated from the mean size of intact animals of the same taxonomic group found in stomachs in the same sample of fish.

The different taxonomic groups and size classes of food organisms were assigned predetermined calorific and organic carbon content values. The energy content of these food organisms was determined from fresh samples collected in the lake. This method of estimating the food value was dependent on the number and size of food organisms in the stomach and was unaffected by degree of digestion. Quantitative stomach contents were estimated by converting the food organisms found in the perch stomach into calorific and organic carbon content values. The relationship between stomach contents and the size of larval perch was expressed by the following equation

$$C_t = aW_t^b$$

where C_t is the stomach contents in calories, W_t is the calorific content of the fish and a, b are constants.

Energy Content of Food

The energy and organic carbon content of food organisms found in perch fry was determined from collections of fresh specimens from the lake. Copepods, obtained from zooplankton samples, were separated from most of the larger zooplankers by screening samples through a 600 μ monofilament nylon screen. Other zooplankters of similar size were removed from the filtrate with a pair of fine forceps under a dissecting microscope. Copepods were then separated from the phytoplankton by filtering samples onto a glass fiber filter (Whatman GF/C). Copepods were gently washed off the filter leaving the phytoplankton entangled in the fiber filter. This process was repeated until no phytoplankters were observed on the filter using a microscope. Nauplii were separated from adults by filtration through a 75 µ screen. Microscopic examination of copepods revealed that animals which passed through the screen were mainly nauplii; whereas those retained on the screen were mostly copepodids and adults. Cladocerans in this study were Daphnia pulex. Daphnia were collected individually from zooplankton samples with an eye dropper. To keep them alive, they were handled individually and kept moist during the sizing and sorting procedure described previously. Amphipods were collected, using a dip net, from the weedy shallows of the lake. To straighten the animals for measurement, they were exposed to freezing temperatures (-25 C) for a few seconds until the surface moisture froze and the animal were either paralysized or killed. They could then be straightened for measuring while thawing at room temperature.

The organic carbon content of live or freshly frozen food organisms was determined by wet combustion (Strickland and Parson 1968). Organic carbon values for Daphnia pulex were obtained from a previously determined relationship between length and organic carbon content

(Ward et al 1970). Calorific determinations were carried out with a modified Phillipson oxygen microbomb calorimeter (Wiegert-Gentry Instruments, Aiken, S. C.) which measures temperature rises with a series of thermocouples in contact with the bomb. Changes in temperature were recorded on a potentiometer (Honeywell Elektronic Ser. 19 potentiometric recorder). The calorimeter was calibrated using thermochemical standard benzoic acid (Phillipson 1964). This apparatus can be adjusted to measure to the nearest 0.1 cal increases in heat energy. Samples for calorific determination were oven dried to constant weight at 105 C for at least 24 hr and then stored in a desiccator. They were made into pellets ranging in weight from 1.5 to 30 mg. Pellets were weighed on a balance (Mettler Micro. MSSA Gramatic Balance) with precision to the nearest 2.5 μg. No attempt was made to determine the ash content of the samples.

RESULTS

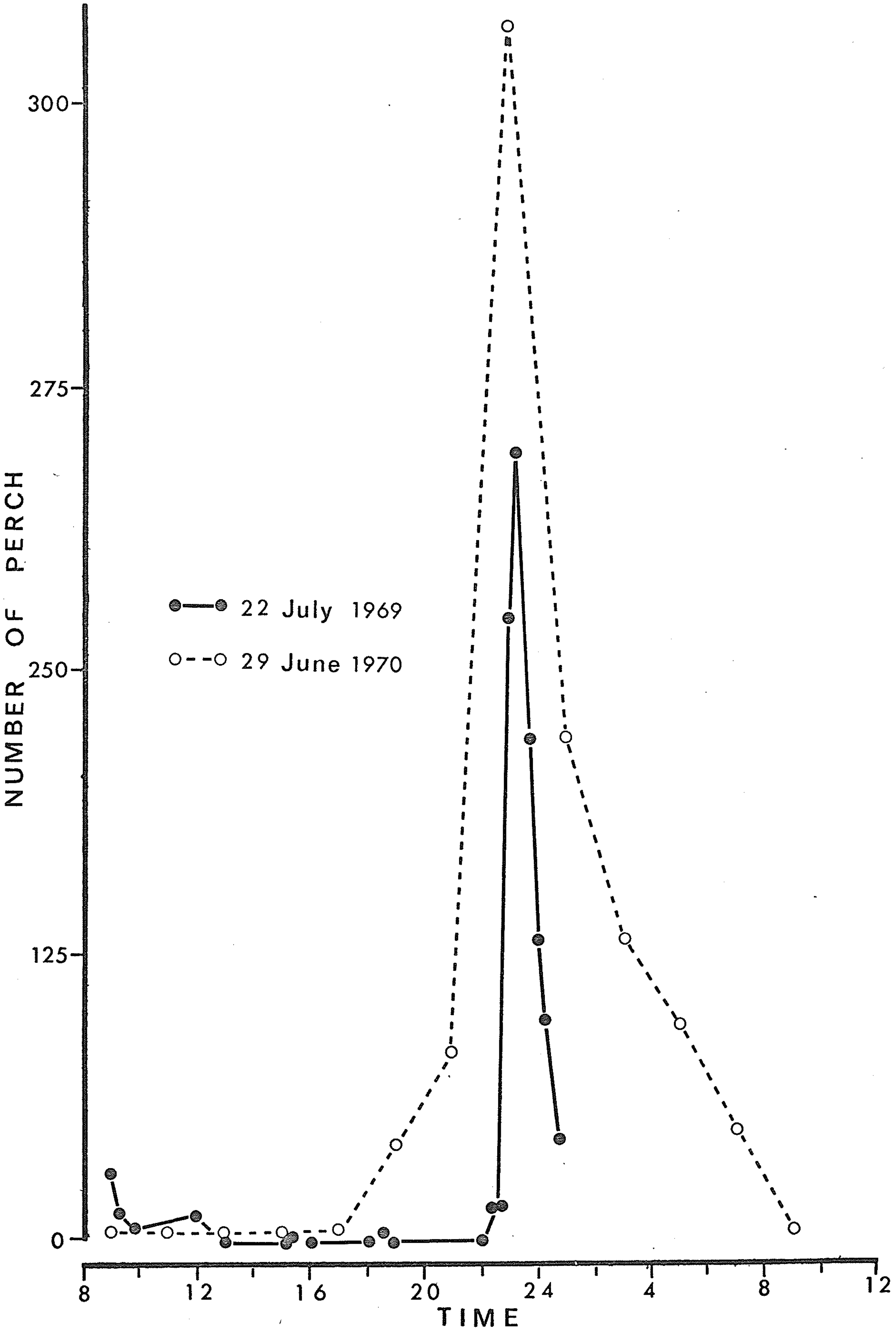
Descriptions of the seasonal horizontal and diel vertical distributions of larval perch depend in part on the interpretation of echosounder tracings. Consequently, in following sections, characteristics of echograms are interpreted in terms of catches of fry and zooplankton.

Interpretation of Echosounder Tracings

Surface perch fry catches by meter net were always much larger at night than during the day, as seen in the July 22, 1969 catches (Fig. 2). Echosounder tracings recorded simultaneously with tow netting disclosed a dark band at 5 m (Fig. 3) during the period of low surface catches (0900 to 2200 hr). During the period of sharp increases in surface catches (2200 to 2430 hr), this band became diffuse and seemed partially merged with the transmission line.

To demonstrate that this dark band, located at about 5 m during the day, indicated aggregations of perch fry, tows were made at 0, 3 and 5 m in conjunction with echo sounding on June 29, 1970. From 1100 to 1700 hr, the layers observed in the echograms (Fig. 4) seemed to coincide with depths at which a high proportion of perch fry were caught by the tow net (Fig. 5). For example at 1500 hr, there

FIGURE 2. Diel catches of perch fry made by surface tow netting.



300
275
250
125
0
NUMBER OF PERCH
22 July 1969
29 June 1970
8
12
16
20
24
4
8
12
TIME

FIGURE 3. Echo sounding traces of Basins 1, 2 and 3, West Blue Lake, made on July 22, 1969.

22 JULY 1969

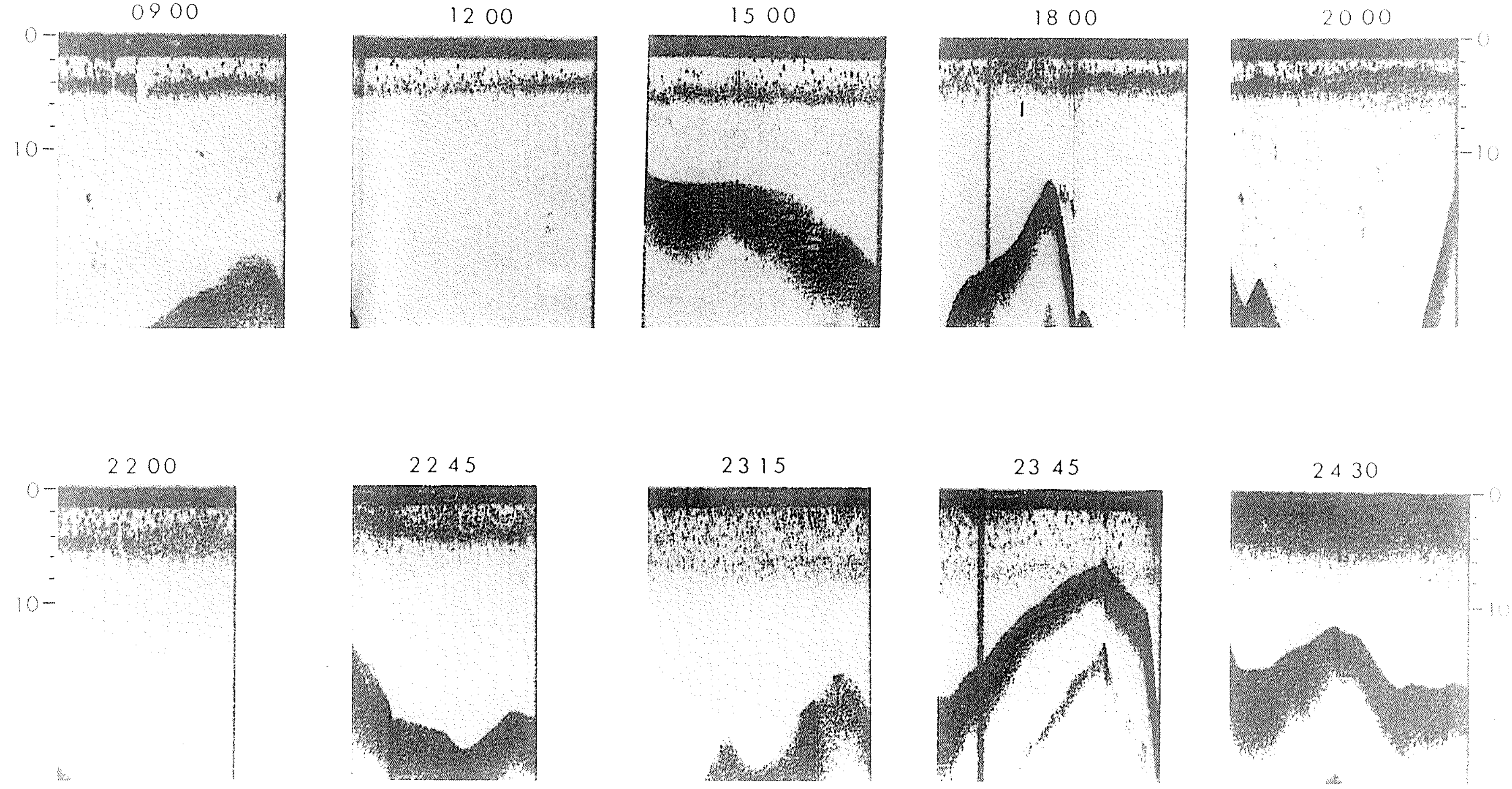
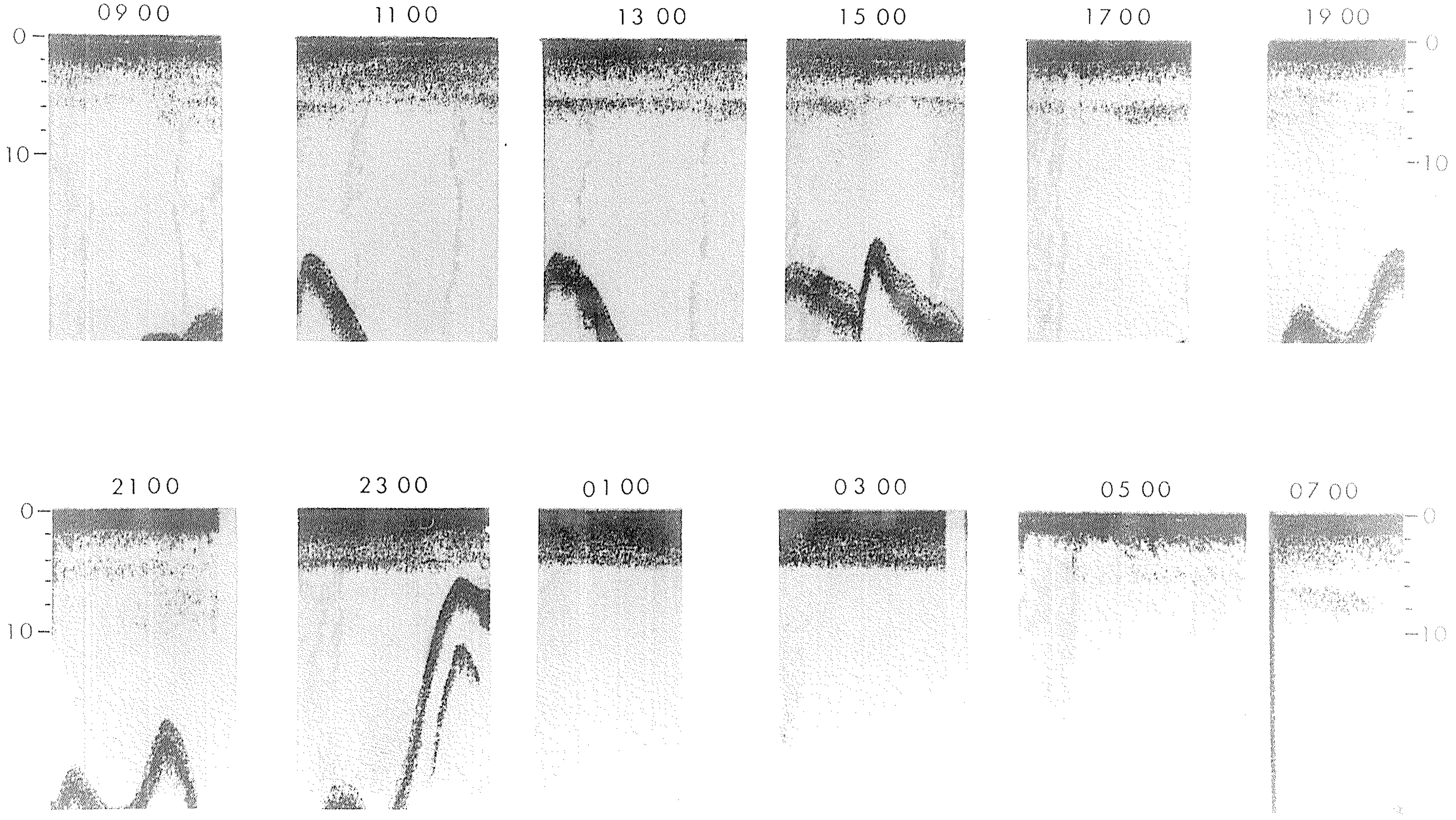

09 00
12 00
15 00
18 00
20 00
22 00
22 45
23 15
23 45
24 30
0
10
0
10
0
10
0
10

FIGURE 4. Echo sounding traces of Basin 2, West Blue Lake, made on July 29, 1970.

29 JUNE 1970


09 00
11 00
13 00
15 00
17 00
19 00
21 00
23 00
01 00
03 00
05 00
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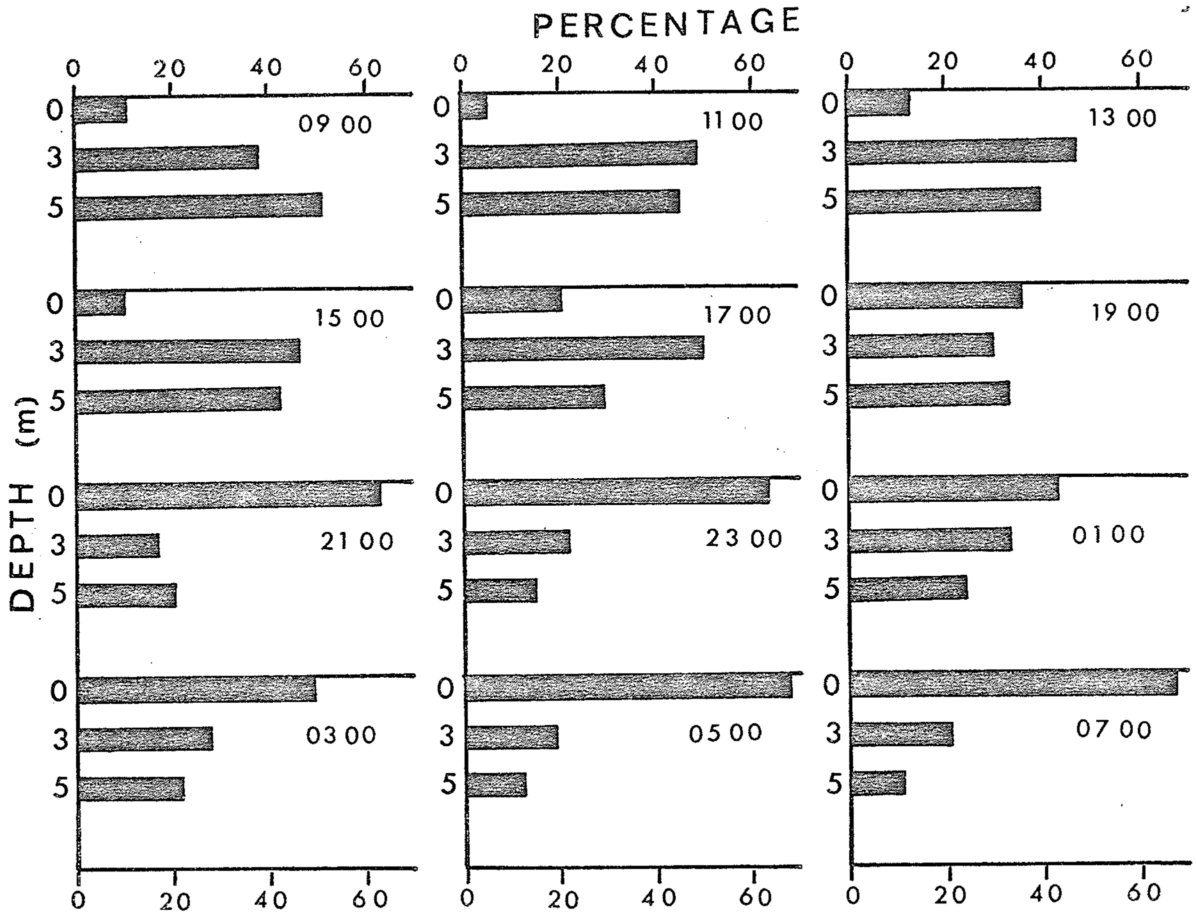


FIGURE 5. Percentage of perch fry caught at three depths by tow nets on June 29, 1970.

were distinct layers between 2-3 and 5-6 m (Fig. 4) which were the approximate depths at which most perch were caught (Fig. 5). Higher surface catches (Fig. 5) were made between 2300 and 0300 hr, when the transmission line apparently became about 4 m thick.

Although these results demonstrated that daytime perch fry aggregations were responsible for the observed near surface layers on the echograms, they failed to demonstrate that the objects producing the echoes were solely or mainly perch fry. It has been well established that aggregation of zooplankton are readily detected by echosounders with frequencies as low as 20 kc/sec (Boden 1962). The echoes recorded during daytime by the sounder used in this study (50 kc/sec) could be caused by aggregations of larval perch and zooplankton.

Zooplankton samples were also collected on June 29, 1969 in conjunction with sounding and towing. The main zooplankters in West Blue Lake likely to be detected by the sounder were _Daphnia_ and _Chaoborus_. During the day, the concentration of _Daphnia_ was at 10 m or deeper (Fig. 6), while _Chaoborus_ maintained themselves mainly at a depth of about 10 m (Table 1). Similar distributions of _Chaoborus_ were also reported by Teraguchi and Northcote (1966). Because no obvious layer of echoes were recorded on the tracings at these depths (Fig. 4), it can be concluded that during the day these zooplankters were not sufficiently

FIGURE 6. Diel vertical distribution of _Daphnia_ in West Blue Lake on June 29, 1970.

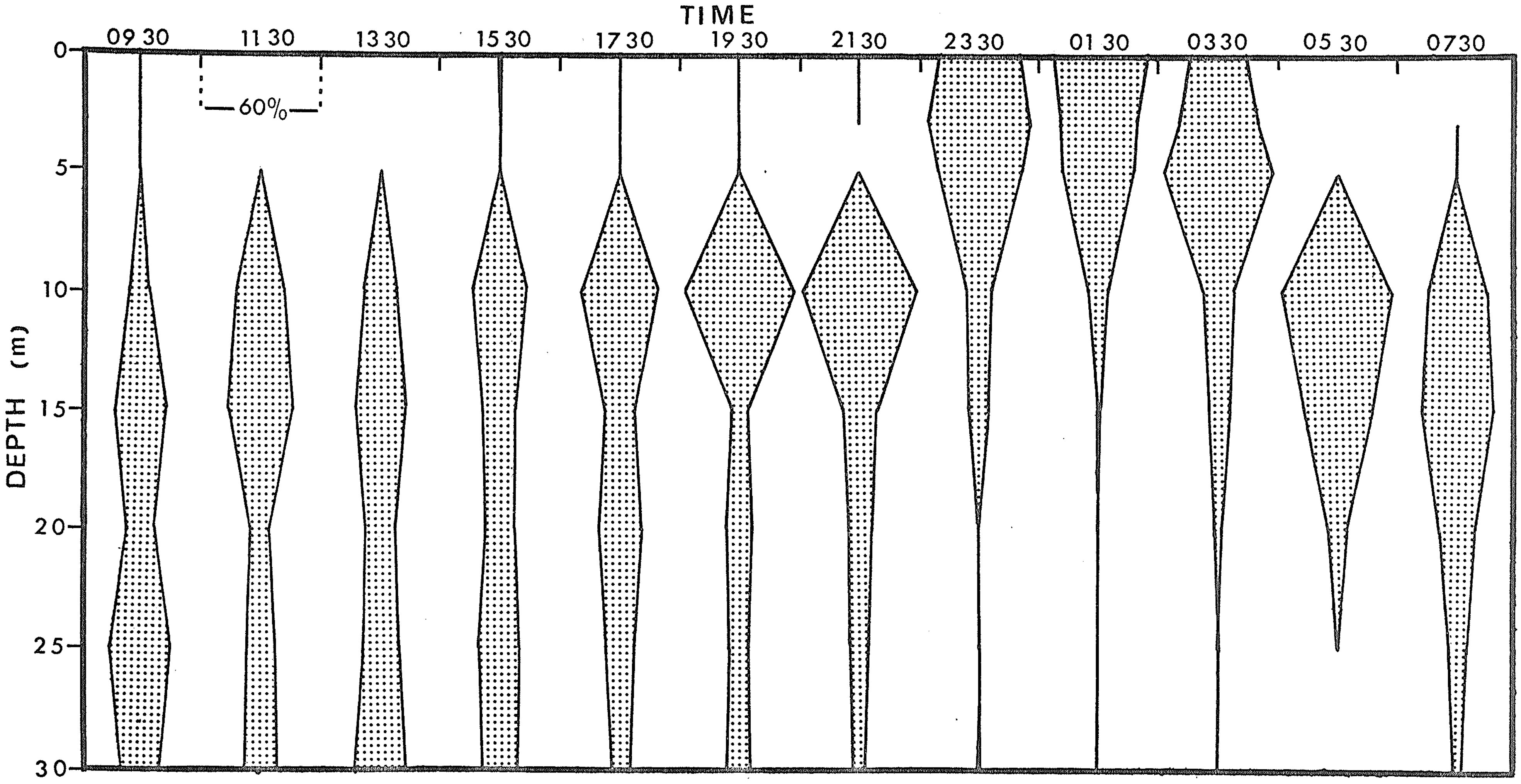

TIME
09 30
11 30
13 30
15 30
17 30
19 30
21 30
23 30
01 30
03 30
05 30
07 30
60%
DEPTH (m)
0
5
10
15
20
25
30

Table 1. Diel distribution of *Chaoborus* in West Blue Lake on June 29, 1970. Cathces of *Chaoborus* in Van Dorn sampler were shown by '*'. Catches in tow samples were shown by numbers.

	Time											
Depth (m)	0900	1100	1300	1500	1700	1900	2100	2300	0100	0300	0500	0700
0								276*	381*	285	14	
3							5	218*	544	162*	25	
5							*	197	472*	58*	2	
10	*	*		*	*	*		*	*		*	*
15			*									
20						*						
25												

30

concentrated to be detected by the sounder at the gain setting used.

Chaoborus and large Daphnia were also caught in the tow net on June 29, 1970. Many were captured during the night at 0, 3 and 5 m (Table 1) but few or none were caught at these depths during the day. The daytime absence of zooplankters at 3 and 5 m further indicated that the layer of echoes recorded at these depths and at this time were mainly echoes from aggregations of perch fry.

At night (0100 to 0500 hr), tracings showing echo layers were more difficult to interpretate. A dark band, including the transmission line, measuring 4 m in depth was recorded at the surface during this period (Fig. 4). This dark surface band was probably caused by concentrations of zooplankton and, of course, by the transmission line, as well as by perch fry (Fig. 5). Bell and Ward (1970) reported dense concentrations of Daphnia pulex at the surface of West Blue Lake at night as I also found (Fig. 6). Similarly, I have found Chaoborus near the surface at night (Table 1) as did Northcote (1964). Thus, these tracings recorded at night failed to disclose the precise location of perch fry within the first 4 m of water. In conclusion, only the layers seen beneath and clearly distinct from the transmission line (between 2 and 6 m) during the day (between 1100 to 1700 hr) could interpreted as aggregations of perch fry.

Distribution of Perch Fry

The smallest perch fry (7.9 mm) was caught on June 24, 1969 in the shallows with a dip net. The smallest individual caught with a meter tow net was 8.6 mm and was part of the collection obtained in Basin 1 on June 11, 1970 (Appendix I). Prolarval fish (Hubbs 1943) were never encountered in sampling. Fry over 10 mm (postlarvae) were readily caught on the lake surface by a meter tow net throughout the early summer (Appendix I). During this period, fry were also observed in the shallow water, although only the smaller fish could be caught with a dip net.

In early August, tow catches declined rapidly (Table 2), whilst increasing numbers of fry were observed in the shallows. After August 8, seining became a more effective means of sampling than tow netting. Echo layers (between 2-6 m during the period from 1100-1700 hr), interpretated as concentrations of perch fry, were prominent on echograms recorded in June and July (Fig. 3 and Fig. 4) and in the beginning of August, for example in the trace for August 1 (Fig. 7). The disappearance of these layers by the middle of August, for example August 15 (Fig. 7), indicated that perch fry gradually abandoned the epilimnetic zone. At this time they were approximately 30 mm in length.

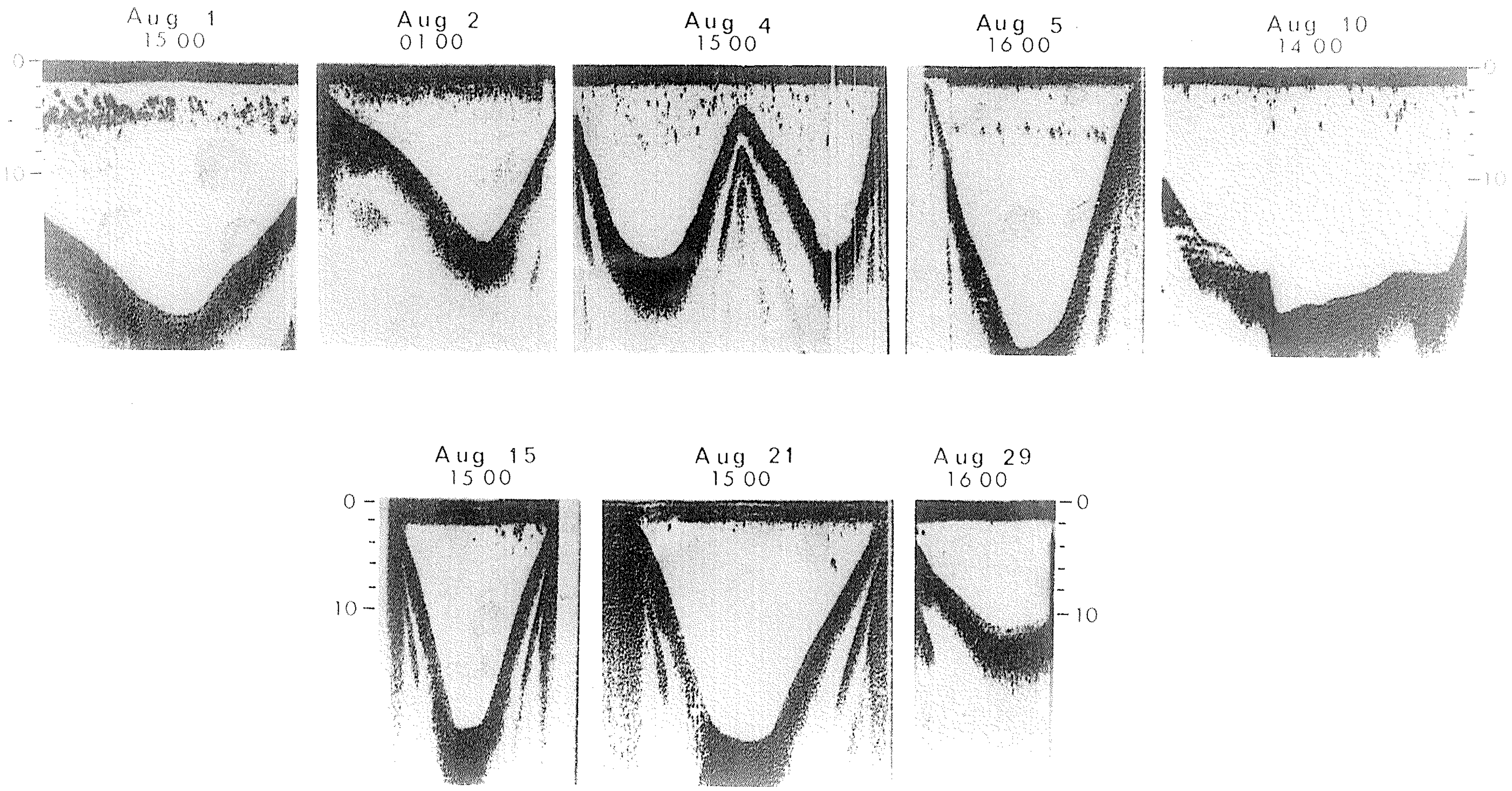
In August, schools of perch fry were conspicuous along the shore. The fish caught in the shallows at this time all had the characteristic vertical color bands of the

Table 2. Catch per unit effort of perch fry by surface tows in 1969

Date	Catch/5 min Tow
July 1	42
July 2	38
July 4-27	> 50
July 30	49
August 1	34
August 3	42
August 6	23
August 8	10
August 10	5
August 15	0

FIGURE 7. Echo sounding traces of Basin 1, 2 and 3 in West Blue Lake made in August 1969.

Aug- Sept 1969


Aug 1 15 00

Aug 2 01 00

Aug 4 15 00

Aug 5 16 00

Aug 10 14 00

Aug 15 15 00

Aug 21 15 00

Aug 29 16 00

adult. By the end of August it became increasingly difficult to catch fry by seining (Table 3) in the shallows, but in deeper water, gill nets were more successful. Frequently, older perch were caught with the young of the year in the gill nets (Table 4). Although schools composed exclusively of first summer perch were usually observed, older perch were also seen in some of these schools.

TABLE 3. Catch per unit effort for perch fry caught by seine nets in 1969.

Date	Catch/seine haul
July 29	19.0
August 1-18	< 20.0
August 21	16.0
August 27	9.7
August 30	2.5

TABLE 4. Gill net catches of yellow perch fry in 1969.

Date	Catch/per set	
	Fry (10+)	Older (1+)
August 27	11	0
August 30	14	1
August 31	20	0
September 6	17	2

Maximum tow catches were generally made shortly after sunset. Catches then declined throughout the night. This catch pattern was clearly defined by samples collected on July 22, 1969, when the maximum catch, during the period 0900 to 2430 hr, occurred at 2300 hr (Fig. 2).

Similar observations were made in the subsequent diel collection made on June 29, 1970. The peak surface catch occurred at the same time, 2300 hr (Fig. 2). Nigh catches at all depths (0, 3 and 5 m) were much larger than day catches (Table 5). The proportion of the total catch of a given hour made at each depth varied according to the time of the day. Generally, a greater proportion of perch fry were caught at the surface during the night and in deeper water during daytime. The percentage caught at the surface was lowest at mid day, but steadily increased from mid afternoon until 2300 hr when it reached a maximum. Surface catches then dropped slightly throughout the night and picked up again just prior to dawn (0700 hr), after which they declined sharply reaching the noon minimum (Fig. 8).

Echo layers were never recorded on echosounder tracings below a depth of 6 m (Fig. 3, 4 and 7). Large 'blips' were most likely echoes from large fish. The absence of echo layers below 6 m demonstrated that perch fry during the epilimnetic period generally aggregated within the top 6 m of the lake. From comparisons of echograms recorded on July 22, 1969 (Fig. 3) with those made

Table 5. The number of perch caught by tow netting (5 min) at 0, 3 and 5 m on June 2, 1970.

Time	Depths 0 m	 3 m	 5 m	Total
0900	4	14	19	37
1100	4	36	33	73
1300	5	19	16	40
1500	5	22	20	47
1700	5	12	7	24
1900	42	35	39	116
2100	83	22	27	132
2300	532	188	129	849
0100	220	168	120	508
0300	134	78	61	273
0500	97	27	19	143
0700	48	15	8	81

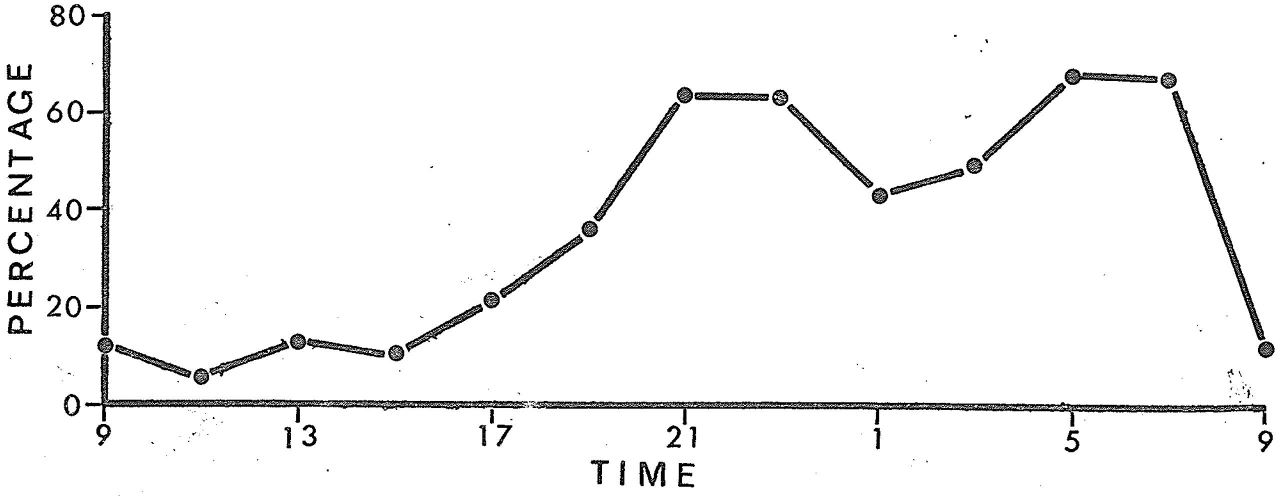


FIGURE 8. Percentage of perch fry caught at the surface at different times of the day.

on June 29, 1970 (Fig. 4), it can be concluded that older perch fry (at the end of July) formed tighter schools near the surface than the younger fish did at the end of June.

Growth and Feeding

Fish collected by meter and seine nets were used to study seasonal growth. Fish caught by other sampling methods were probably not representative of the population.

Differences in selectivity by seine and meter nets undoubtly occured, but they were less pronounced and fairly constant in nature. To cover the main growing season, both methods were included in this study of growth. Fish in seine samples were generally greater in length than those in tow samples caught on the same day (with exception of fish in the samples of August 6, 1969). It is not certain that the difference in size was mainly a result of gear selectivity (extrinsic factor) or because the older fish were becoming littoral while the younger fish were still limnetic (intrinsic factor). Since there was no basis for judging which samples provided the best growth estimates, all tow and seine catches were combined (Houde 1969).

Growth data determined from 1251 fish collected from July 1 to August 31, 1969 (Fig. 9), indicated that perch fry more than tripled their length and increased their weight by a factor of nine. The average increments in length and weight during this period were 37.55 mm and 1807.4 mg. The growth with time was typically exponential

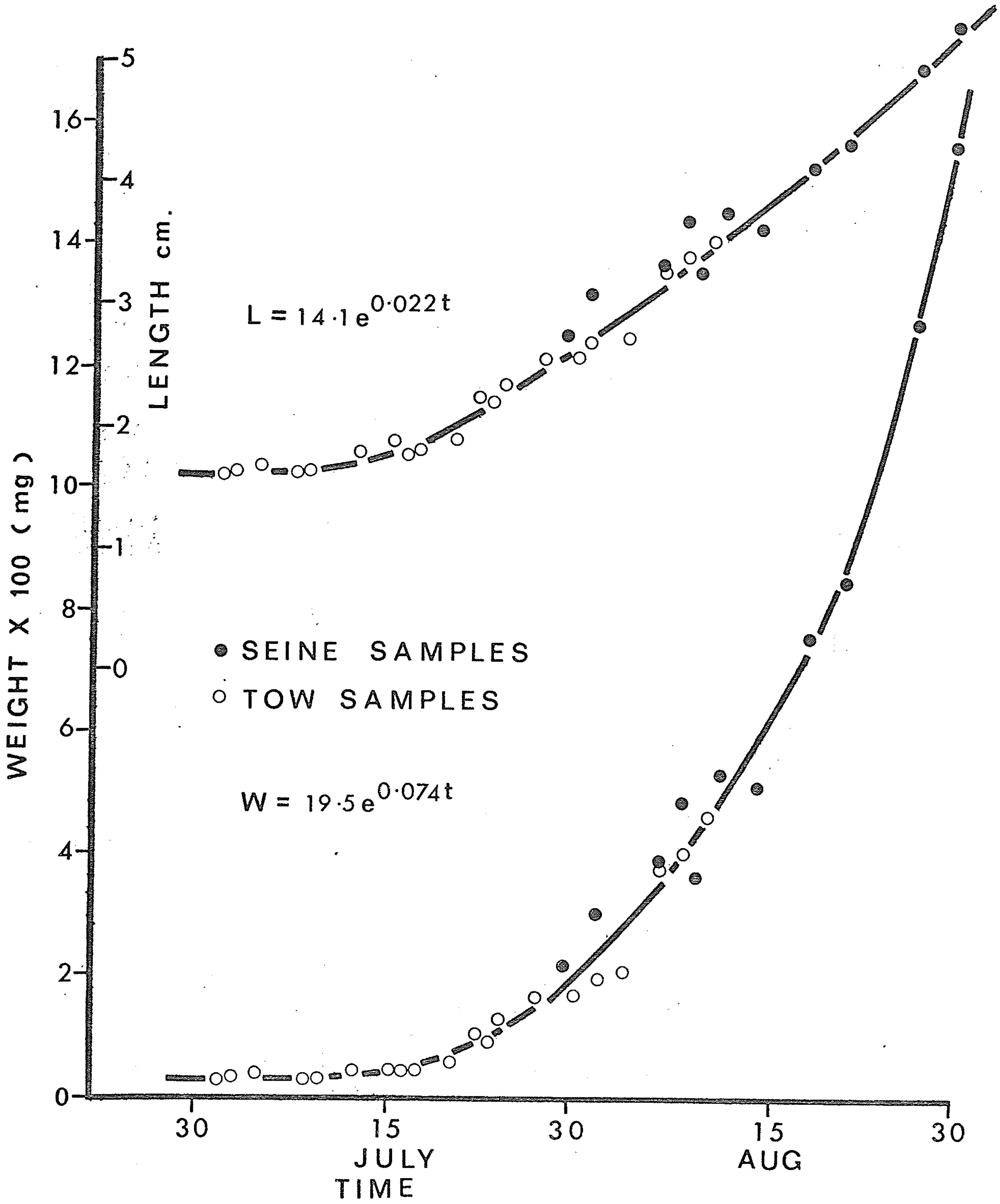


FIGURE 9. Growth of perch fry in West Blue Lake in 1969.

(Fig. 9). The relation between length and weight during the same period is seen in Figure 10.

Growth of perch fry in the three basins (Fig. 1) was compared (Tables 6 and 7). The slope 'k' and the intercepts 'W_0' of the growth in weight equations were similar for the three basins. While the slopes 'k' of the growth in length equations were similar, their intercepts 'L_0' were different. The slope 'b' of the length weight relationship were also similar for the three basins but their intercepts differed (Table 8).

Table 6. Comparison of growth in weight of perch fry defined by $W_t = W_0 e^{kt}$, from the three basins

Basins	Intercepts W_0	Slopes k	Test for regression lines (H_o : $k \neq 0$) F	df	P
1	20.29	0.07368	534	1,29	<0.005
2	15.56	0.08151	408	1,13	<0.005
3	17.46	0.07829	346	1,16	<0.005
Pooled	19.50	0.07442	773	1,29	<0.005
F	1.633	0.268	Comparison of regression lines among the three basins.		
df	2,60	2,58			
P	N S	N S			

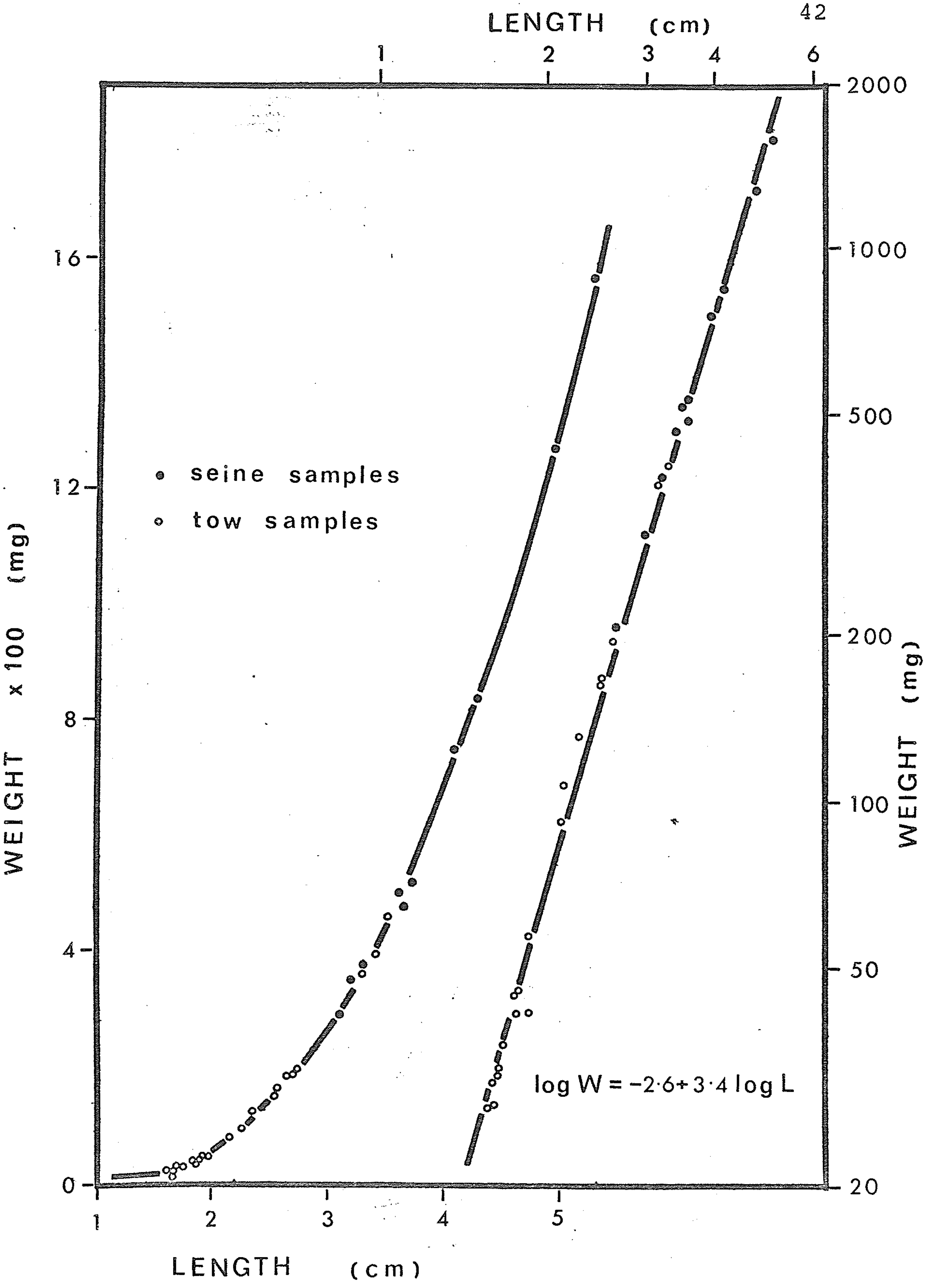


FIGURE 10. Length weight relationship of perch fry in 1969.

Table 7. Comparison of growth in length of perch fry defined by $L_t = L_0 e^{kt}$, from the three basins.

Basins	Intercepts L_0	Slopes k	Test for regression lines (H_o : $k \neq 0$) F	df	P
1	14.29	0.02118	617	1,29	<0.005
2	13.33	0.02326	356	1,13	<0.005
3	13.74	0.02281	233	1,16	<0.005
Pooled	14.13	0.02164	751	1,29	<0.005
F	3.83	0.1487	Comparison of regression lines among the three basins.		
df	2,60	2,58			
P	0.01	N S			

Table 8. Comparison of length weight relationships of perch fry Log$_{10}$ = a + bLog$_{10}$ L, from the three basins.

Basins	Intercepts a	Slopes b	Test for regression lines (H_o : $b \neq 0$) F	df	P
1	-2.6841	3.4609	4978	1,29	<0.005
2	-2.6810	3.4529	757	1,13	<0.005
3	-2.5719	3.3712	2102	1,16	<0.005
Pooled	-2.6350	3.4130	3703	1,29	<0.005
F	4.649	0.474	Comparison of regression lines among the three basins.		
df	2,60	2,58			
P	0.01	N S			

Because growth in weight which was similar in the three basins was of prime interest in this study and because the data were inadequate to consider separately perch fry captured in the three basins data were pooled.

During July, when perch fry were epilimnetic, their weekly specific rates of growth and coefficients of condition increased, but declined in the month of August, when perch became littoral (Fig. 11).

During the 1969 growing season, perch fry in West Blue Lake utilized a narrow range of food items and for most of this season they relied on planktonic animals as their source of food. Daphnia pulex, a major component of the zooplankton occurred in all but a few of the stomachs examined (99.9%). The second major food item was copepods (Cyclops biscuspidatus and Diaptomus siciloides), which occurred in 14-59% of the stomachs examined weekly (Table 9). Bottom fauna made up a small portion of stomach contents. Amphipods, which were the sole benthic animals found in perch fry stomachs, first appeared as a food source in August (Table 10).

During the prolarval stage, algae constitute a major portion of the perch fiet but their contribution declines rapidly during postlarval stages (Turner 1920). Plant traces were observed in the stomachs of some early postlarvae in West Blue Lake. The minute quantities present indicates that it is unlikely that they were actively or selectively ingested. Probably they were

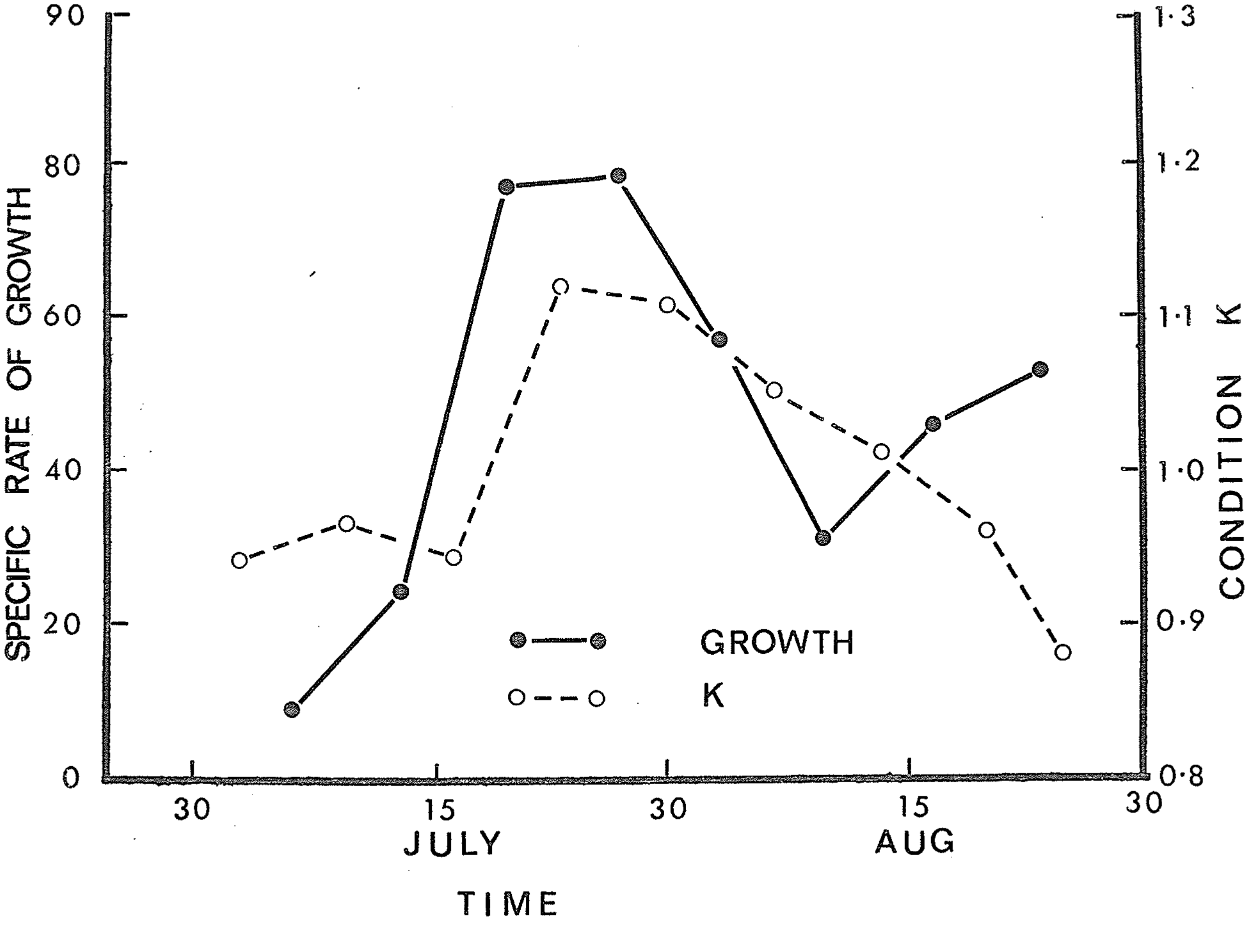


FIGURE 11. Weekly specific growth rates and condition coefficients of larval perch fry.

Table 9. Seasonal occurrence of different food items in the stomachs of perch fry.

Date	Daphnia %	Copepods %	Nauplii %	Amphipods %
1-5 July 1969	99.9	58.6	-	-
6-12 July 1969	100.0	26.8	-	-
13-19 July 1969	100.0	13.6	-	-
20-26 July 1969	100.0	23.3	-	-
27 July - 2 Aug. 1969	100.0	25.5	-	-
3-9 August 1969	100.0	38.7	-	-
10-16 August 1969	100.0	42.1	-	-
17-23 August 1969	100.0	25.0	-	65.6
24-30 August 1969	100.0	21.2	-	40.4
15-29 June 1970	100.0	100.0	100.0	-

Table 10. Seasonal contributions (per cent in terms of calories) by different food items in the diet of perch fry.

Date	Daphnia	Copepods	Nauplii	Amphipods
1-5 July 1969	86.9	13.2	-	-
6-12 July 1969	87.5	12.5	-	-
13-19 July 1969	91.3	8.7	-	-
20-26 July 1969	94.5	5.5	-	-
27 July - 2 August 1969	93.9	6.1	-	-
3-9 August 1969	94.0	6.0	-	-
10-16 August 1969	96.1	3.9	-	-
17-23 August 1969	92.3	2.6	-	4.5
24-30 August 1969	94.3	0.6	-	5.1
15-29 June 1970	77.1	19.2	3.7	-

taken along with zooplankters or were present in ingested zooplankters.

A few small dipteran pupae were found in perch fry stomachs during the first week of July, (less than 0.5% occurrence). One ostracod and the remains of only one fish were found.

Although _Daphnia_ made up about 90% of the diet in terms of energy contributed, not all sizes were fully utilized by the growing perch. Early postlarval perch fed on small _Daphnia_ but, as they grew, their prey increased in size too (Fig. 12). During their early life (less than 20 mm) the change in the mean size of _Daphnia_ ingested was directly proportional to gape width (Fig. 13) and not to fry length. Growth in mouth size during this period was relatively greater than growth in length (Fig. 14). The mean size of prey ingested by these older fish appeared to be restricted by the mean size of _Daphnia_ in the lake (Fig. 15).

Selection of copepods by their size was less obvious than in _Daphnia_ because of their comparatively limited size range. Nauplii (infrequent in 1969 samples) constituted a moderate portion of the stomach contents in early 1970 samples when some of the youngest larval fish were caught.

Perch fry food was expressed in terms of carbon content, calorific value and simply in terms of weight

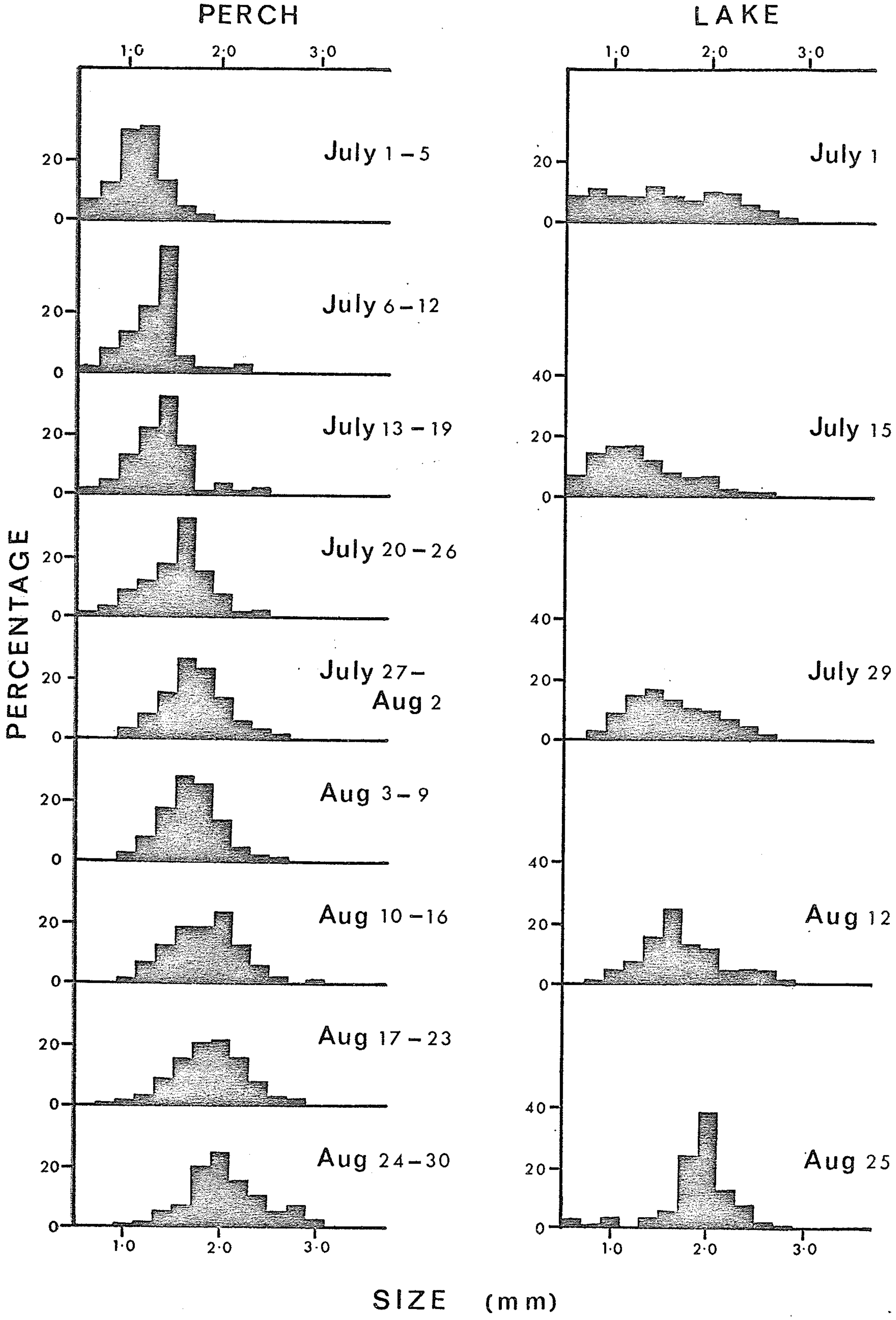


FIGURE 12. Length distribution of Daphnia in perch fry stomachs and in plankton collections during the summer.

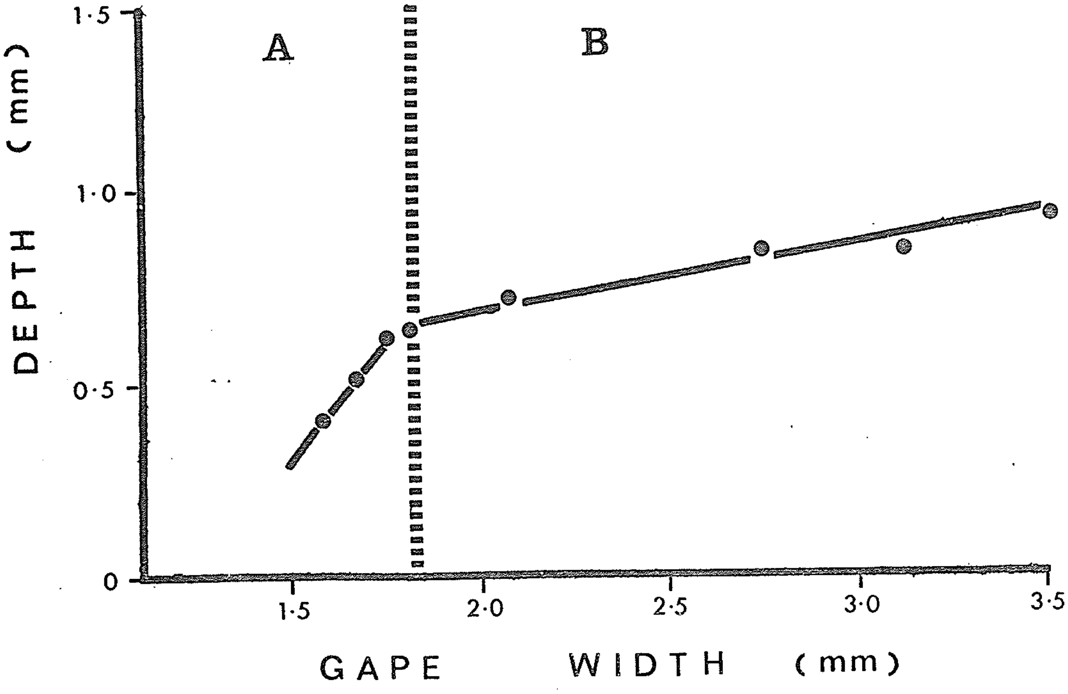


FIGURE 13. The relation of mean depth of ingested <u>Daphnia</u> to mean mouth sizes of perch fry during their life. Portion A, ingested prey size is directly related to the predator mouth size. Portion B, ingested prey size is related to the size of <u>Daphnia</u> in plankton collections.

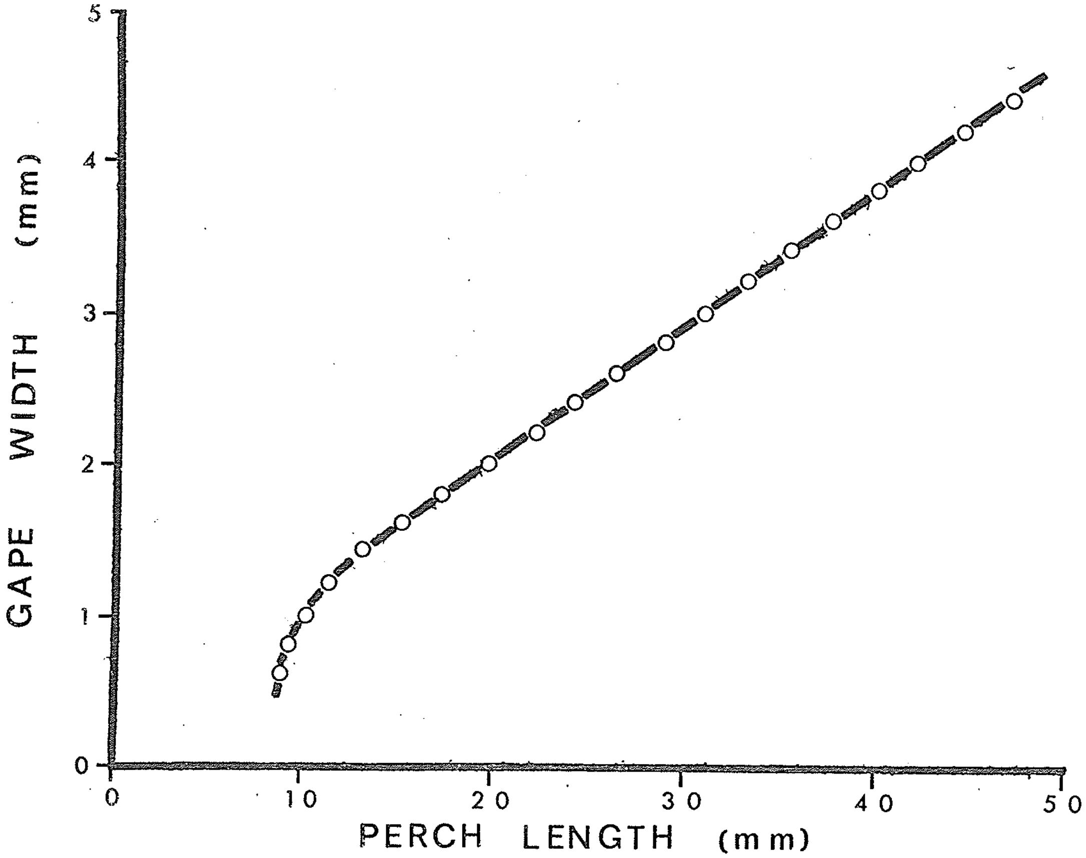


FIGURE 14. Growth in gape width of perch fry relative to growth in length.

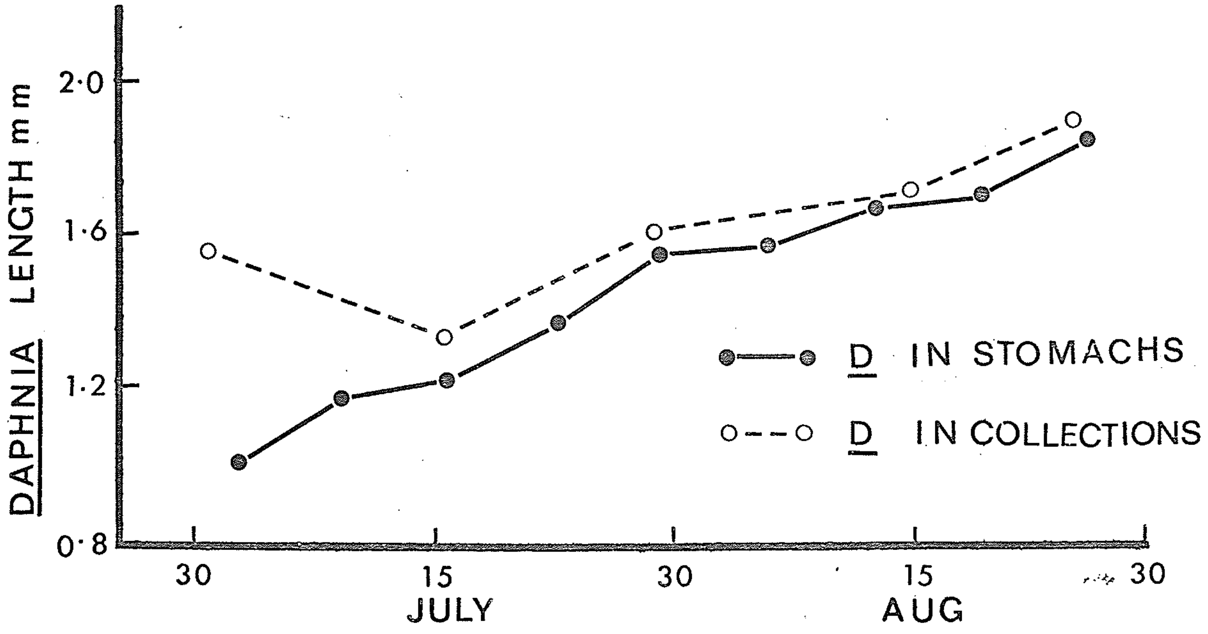


FIGURE 15. The mean length of Daphnia in perch fry stomachs and in plankton collections.

(Table 11). The calorific value of a given size of *Daphnia* was a direct function of its carbon content. A similar observation for freshwater crustaceans, including *Daphnia*, was made by Platt *et al* (1969). Since calorific values for *Daphnia* were determined for a limited size range and with smaller sample sizes than those used to determine carbon content, the mean calorific value of each size group of *Daphnia* was interpolated from the regression of carbon content on size:

$$\mathrm{Log}_{10}\, Y_{car} = 0.190 + 0.504\ X$$

$$Y_{cal} = 10.7\ Y_{car}$$

$$Y_{wt} = 2.17\ Y_{car}$$

where Y_{car}, Y_{cal} and Y_{wt} respectively, are the carbon values, calorific content and weight of *Daphnia* of size 'X'. The carbon contents and calorific values determined for the crustaceans and larval perch (Table 12) were in general agreement with the values in the literature (Vinogradov 1953; Maciolek 1962; Cummins 1967; Omori 1969).

The quantity of food in perch fry stomachs (between 1900 and 2400 hr) increased with increasing fish weight (Table 13). The relationship between fish weight (W_t expressed in calories) and the calorific value of stomach contents (C_t) was expressed by

$$C_t = 0.029\ W_t^{0.80}\ .$$

Table 11. Carbon contents and calorific values of the different food items and of perch fry.

Organisms	Calories per gram dry weight	Carbon (mg) per gram dry weight
Copepods	6695.06 ± 536.30	467.4 ± 37.4
Nauplii	6132.04 ± 393.64	508.9 ± 52.1
Cladocerans	4916.57 ± 418.94	460.7 ± 63.6
Amphipods	3629.67 ± 186.22	365.9 ± 30.3
Perch fry	4967.07 ± 55.16	421.7 ± 41.4

Table 12. Mean carbon and energy content of Copepods and amphipods relative to their size.

Organisms	Mean carbon contents per individual (ug)	Mean calories per individual	Mean dry weight per individual (ug)
Copepods			
adults	1.56	0.0224	3.34
nauplii	0.32	0.0038	0.62
Amphipods mm			
3.0 - 3.45	78.93	1.862	543
3.5 - 3.95	102.25	2.101	583
4.0 - 4.45	174.24	2.446	628
4.5 - 4.95	183.96	3.089	895
5.0 - 5.45	192.34	3.372	963
5.5 - 5.95	288.49	3.549	1044

Table 13. Stomach contents of perch fry during various stages of their life.

Date	Wet weight of fish (mg)	Stomach contents (cal)
1-5 July 1969	31.65	0.468
6-12 July 1969	34.62	0.620
13-19 July 1969	44.02	0.774
20-26 July 1969	94.09	0.839
27 July - 2 Aug. 1969	209.45	1.809
3-9 August 1969	370.66	3.150
10-16 August 1969	504.27	5.675
17-23 August 1969	796.76	7.304
24-30 August 1969	1353.00	12.240

The slope of the regression line was highly significant ($F = 75$, $p < 0.001$, df = 1,7). The percentage of stomach contents per unit fish when expressed in calories, carbon contents and weight showed little variation (Table 14).

Stomach contents (mean calorific value of stomach contents expressed as a percentage of the mean total calorific content of the fish) in July were generally higher than in August (Fig. 16). Stomach contents of larval perch remained above 1% of the body calorific value throughout the day (Fig. 17). To maintain this high level of stomach contents, perch fry would most likely feed continuously.

Table 14. Seasonal changes in quantities of stomach contents[a] of perch fry.

Date	Calories	Carbon	Weight
1-5 July 1969	1.20	1.16	1.17
6-12 July 1969	1.45	1.41	1.42
13-19 July 1969	1.43	1.40	1.41
20-26 July 1969	0.73	0.70	0.71
27 July - 2 Aug. 1969	0.70	0.69	0.70
3-9 August 1969	0.69	0.68	0.69
10-16 August 1969	0.92	0.90	0.92
17-23 August 1969	0.75	0.72	0.77
24-30 August 1969	0.74	0.72	0.76

[a] Stomach contents (calories, carbon and dry weight) are expressed as percentages of total body calories, carbon and dry weight.

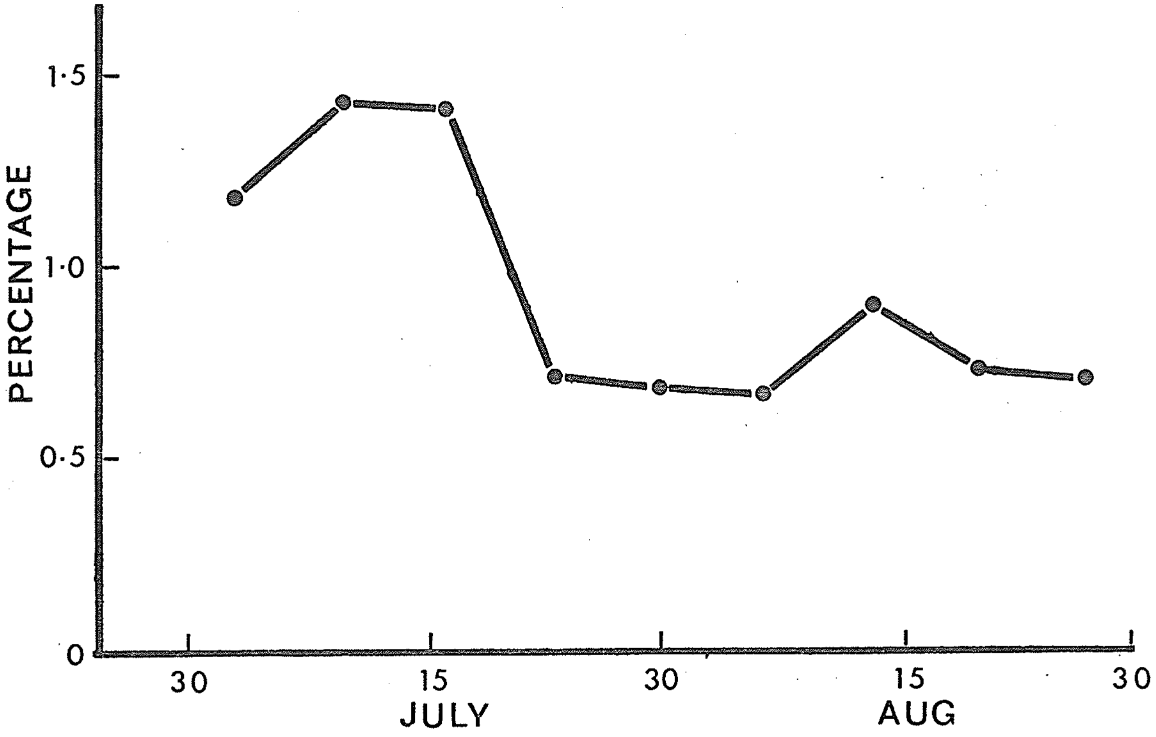
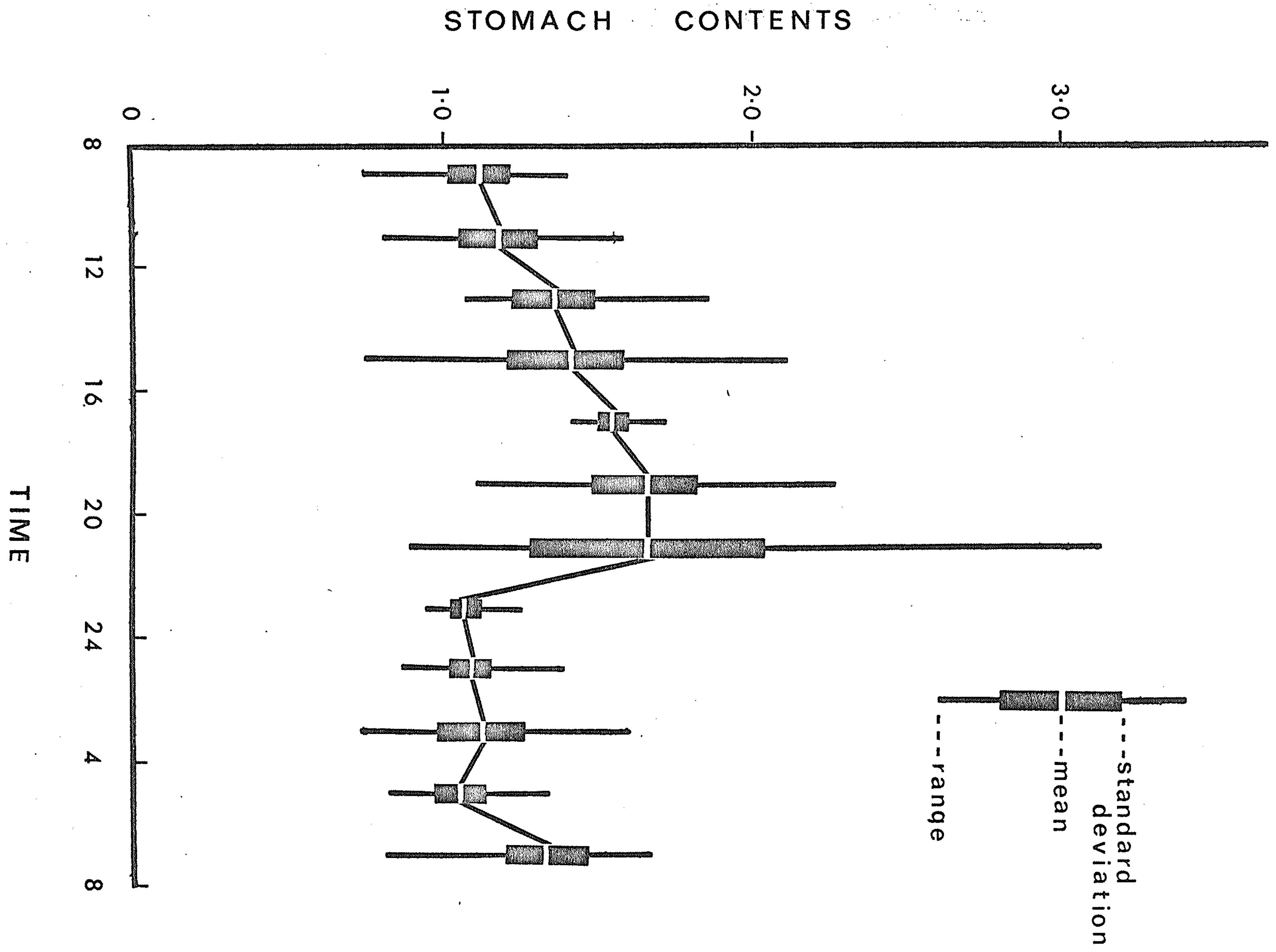


FIGURE 16. Seasonal changes in stomach contents (percentage of stomach calories to fish calories).

FIGURE 17. Diel variations in stomach contents of larval perch on June 29, 1970 (calorific value of stomach contents expressed as a percentage of the total calorific value of the fish).


STOMACH CONTENTS
0
1·0
2·0
3·0
TIME
8
12
16
20
24
4
8
standard deviation
mean
range

DISCUSSION

Seasonal Distribution

The distribution of perch fry in a lake seems to be variable. They have been reported to be mainly littoral (Turner 1920; Echo 1954; Maloney and Johnson 1957), but also, they have been described to be limnetic (Faber 1967; Nobel 1968). In West Blue Lake, perch fry were found in the top 5-6 m of water, both along the shore and in the open water in the month of July. Ambiguity concerning their mode of life seems to be the result of the differences in biological and morphometric characteristics of the lakes studied, and, to some extent, the result of differences in sampling methods.

Under sustained winds, in small lakes, perch fry tend to shift to deeper water (Nobel 1968). In contrast, in Lake Erie, because of its large area, wind action can generate strong currents, making the surface of open water unfavorable to perch fry. In this situation, perch fry either occupy the surface of protected inshore areas (Turner 1920) or, in open waters, move deeper (Fish 1932). The latter worker caught large numbers of young perch at a depth of 19 m.

In lakes with several species of limnetic fry, the appearance of a particular fry species in open waters seemed to be realted to the temperature of the lake (Faber 1967). In some North Wisconsin Lakes, perch fry become the dominant species in the limnetic zone from the end of May to the beginning of June, when the water temperature was between 13 and 17 C. At other temperatures, different species become dominant (Faber 1967).

West Blue Lake, a relatively small lake, is fairly well protected from high winds by the surrounding terrain. Populations of walleye and pike fry are relatively small in the epilimnion (only six larval fish other than perch were caught during the 1969 and 1970 sampling). Without large numbers of other species and adverse environment factors, such as high winds, perch fry spread throughout the surface waters. The epilimnetic period lasted from mid-June to the end of July when the surface water was from 12 to 21 C. Although this period differs from the one given by Faber (1967), the temperature when perch fry became abundant were similar. It has been reported that perch, when they reached 9 mm, become limnetic (Nobel 1968). Apparently in West Blue Lake, perch dispersed in the epilimnetic zone when they were about 9-10 mm long. The smallest fry that could be obtained in open water was 8.6 mm and the mean size of this sample was 10 mm. The coincidence in the temperature and size when perch fry became epilimnetic in these lakes indicate that movement towards epilimnion was not merely a passive dispersion. The cause of this dispersion is beyond the scope of this thesis.

Both the littoral and epilimnetic zones appear to be suitable habitats for young perch. Fingerling perch (exact size not given), when acclimated to temperatures from 8 to 20 C, prefer temperatures ranging from 18 to 23 C (Ferguson 1958). Furthermore, perch fry exhibit positive phototaxis (Privolnev 1958). Both preferred temperatures and suitable lighting occur in the epilimnion and the littoral zones, however, the relatively large volume of the epilimnion provided an important energy source in the form of zooplankton. Early in life perch fry were size-selective in their choice of prey. This limited them to only a portion of the standing crop of zooplankton. By inhabiting the epilimnion, this energy source too became available and crowding in the littoral zone may have been avoided. The translucent appearance of the larval fish further suggests that they are well suited to a pelagic mode of life.

At the end of July, tow catches decreased rapidly (Table 2). This decline could have been caused by two circumstances. Perch fry at the end of July were almost 30 mm long, and may have been able to avoid or outswim the tow net. On the other hand, they may have been slowly abandoning the area and moving to deeper water or towards the littoral zone.

The echo layers recorded during the day in July were representative of larval perch (see interpretation of echosounder tracing). These layers slowly disappeared

(Fig. 7) in August indicating that fry had left the epilimnion. Increased seine catches in the shallows (Table 3) further suggested an inshore migration. Aggregations of perch fry near shore at the end of July were also observed in the Thomson Lakes by Echo (1954).

As mentioned, the littoral zone was apparently as suitable as the epilimnetic zone for young perch but was more restricted (Fig. 1). Migration towards shore could create crowding and acute competition for food and space. The mortality of perch fry from 8 to 20 mm is between 54 and 71% (Nobel 1968). By the beginning of August, when perch fry were about 30 mm, a small fraction of the initial number would have survived and, consequently, an inshore migration might not have resulted in congestion. In addition, perch fry in early August had developed the characteristic dark vertical adult bands, making them very conspicuous in open waters and perhaps, subject to increased predation. In the shallows, littoral vegetation offered a sanctuary for the young perch. In this environment the dark bands might actually provide protection by blending with the vegetation.

It is highly unlikely that a change in temperature or day-length initiated the inshore movement, since day to day variations in temperature and day length were greater than average weekly changes during the period of inshore migration (Appendix II). Moreover, the migration did not seem to be related to feeding habits (Table 10). Young fish caught in open water (in July) and near shore (during most of August) all fed upon zooplankton, therefore, food would not seem to be a prime factor for the initiation of the inshore migration. The development of the characteristic adult banding at this time seemed to be the only apparent phenomenon associated with the inshore migration of young perch. Coincidence of the inshore migration with the formation of vertical bands suggests that the former is as much an innate characteristic of young perch as the latter. If both these characters are inborn, young perch will display these characteristics at a length of about 30 mm as in the case in West Blue Lake.

Diel Vertical Distribution

Sampling in 1969 indicated that perch were much more available for capture on the surface at night (Fig. 2). Sinclair (1968) concluded that an increase in the availability of young cottids (Cottus asper) occurred at night at the lake surface. The night time availability of age 0 perch may also indicate a diel vertical migration. During daylight young fish can actively avoid capture by means of visual clues (Isaacs 1964; Taylor 1968). The increased fraction of perch fry caught at 5 m during the day in contrast to the lower fraction caught at night (Fig. 5) indicated an active diel vertical migration which was not obscured by varying vulnerability to the net. This conclusion was supported by the converse comparison, the relative fractions caught on the surface during the day and at night (Fig. 5).

Echogram interpretations (Fig. 3) also supported the existence of a diel vertical migration. As shown, the upward movement of a layer of echoes which had been located at a depth of about 5 m during the day, coincided approximately with peak surface catches (Fig. 2).

The catch data of June 29, 1970, besides showing the diel change in distribution of perch fry, also revealed some interesting phenomena. The peak catch made by a tow net for all depths (0, 3 and 5 m) occurred a short time after sunset and not at the time of lowest light intensity (0100-0400 hr). Apparently, the catchability of perch fry depends on more than the absolute light intensity. At dusk, when light intensity drops rapidly and falls below the threshold of sensitivity of the cone cells of the eye, a partial night blindness results in sockeye salmon fry if the rate of dark adaptation is slower than the rate of decrease in light intensity (A-i 1959). A combination of partial night blindness and low efficiency of scotopic vision could explain the ease of capturing perch fry at night and also the occurrence of the maximum catch some time after sunset. No increase in catch was observed at dawn, when perch fry change from scotopic to photic vision. Light adaptation is generally faster in sockeye salmon fry than dark adaptation (Ali 1959), and fish can see before full light adaptation. To obtain an increase in the catch at dawn, timing would be of utmost importance. With Cottus, increased catches were sometimes observed at dawn (Sinclair 1968).

Another interesting phenomenon is that the catch of perch fry at the surface (compared to those caught at 3 and 5 m), resulted in two peaks, one at 2100 to 2300 hr and one at 0500 to 0700 hr (Fig. 8). The drop in percentage of perch at the surface seemed to indicate a dispersion of the perch to deeper water during the period 0100 to 0300 hr. Similar observation on the settling or dispersal of limnetic fish (larval sockeye salmon) after dark was reported (Johnson 1961). Perch fry, being positively phototactic, moved closer to the surface at dusk and dawn, forming a high concentration near the surface. Working on the assumption that partial night blindness did occur at about 2300 hr, perch fry would become disoriented at the surface and some would disperse into deeper water. In addition, with decreased light intensity, fish encounter increased difficulty in maintaining a tight school, until a certain intensity is reached when the schools actually break up (Hergenrader and Hasler 1968). At night, when light was minimal, perch fry could not be expected to form closely packed schools at the surface as seen at dusk and dawn. At minimal light intensity herring separate and hunt for food individually (Blaxter and Parrish 1965). In West Blue Lake, where food (Daphnia) is abundant from the surface to 10 m, it would then benefit the perch fry to disperse in search of food rather than maintain a tight school at the surface, as long as they avoided depths beyond the lower threshold of their scotopic vision.

The diel feeding habits of perch fry during the limnetic stage is inseparably related to their diurnal migration. Stomach contents of these fish steadily increased throughout the day, reaching a maximum at 2100 hr (Fig. 17). The rate of feeding was obviously greater than the rate of emptying of the stomach, allowing the accumulation of food in the stomach during this period. In sockeye fry, feeding rate was unaffected by the light intensity above the threshold of cone vision (Ali 1959). The movement of perch fry to the surface prior to 2100 hr could be an attempt to prolong feeding by photic vision. The rapid drop in stomach contents from 2100 to 2300 hr (Fig. 17) was perhaps caused by diminished rod vision and possibly, by partial night blindness. These factors may have jointly reduced the feeding rate below the rate of emptying of the stomach. As none of the fish examined contained empty stomachs between 2300 and 0300 hr and the stomach contents remained relatively constant or, in other words, ingestion was in step with assimilation and egestion, it was unlikely that there were any extended periods when perch fry abstained from feeding. The ability of perch fry to feed after dark could be because light intensity during this period was above their threshold of scotopic vision, or the concentration of food was high enough (Fig. 6) so that they could feed by chance encounters (Werner 1969). Unlike photic vision, the lower the light intensity in the range of scotopic vision, the lower the feeding rate in sockeye fry (Ali 1959; Hunter 1968). If perch and sockeye behaved similarly, the lower stomach contents would be expected to occur between 2300-0500 hr as was the case.

Although the advantages of vertical movements by larval perch seem apparent, the cause or causes of this behavior are not clear.The upward migration at dusk extended the period of photic vision and perhaps allowed more time for dark adaptation (Blaxter and Parrish 1965). The dispersion during the night increased their chance of encountering prey, which were abundant when the light intensity was minimal. Rising to the surface at dawn increased the visual acuity of larval perch when food became scarce.

Several theories have been put forward for vertical migration in fish. The main ones are that migration is a response to changes in light intensity, changes in distribution of food, temperature and oxygen changes, and combinations of all these factors. In fish with migration paths which cross the thermocline, changes in temperature and oxygen concentration seemed to have some minor influence on the migration (Alabaster and Robertson 1961). Unlike many vertically migrating fish, the amplitude of migration of larval perch is relatively short (6 m at most). Consequently, it would be highly unlikely that the rather minor diel changes in temperature and oxygen levels in the epilimnion would cause the perch to migrate when one considers the major day to day variation which can occur.

Planktonic food, which is generally abundant during the night in the surface water, has been cited as one of the major causes of the migratory response. Upward migration of white bass at night has been interpreted as the result of white bass following their primary prey, Daphnia (McNaught and Hasler 1960). In the case of perch fry, vertical migration occurs prior to the appearance of Daphnia at the surface. Furthermore, the gathering of perch at the surface at dawn when Daphnia were moving down to deeper water seemed to contradict the possibility that migration was mainly a response to the movements of this prey. Seemingly, a change in light intensity is the prime factor to which larval perch respond during migration, and other factors or combination of them play a minor role in their vertical migration.

Growth

The growth of young fish usually occurs in several stanzas (Tesch 1968). In this study, where the emphasis was placed on the short period of maximum growth, only one growth stanza seemed apparent in the length weight relationship and the growth curves. The growth season of young perch extended into September. This was observed in the growth curves (Fig. 9) where length and weight increased exponentially with time, indicating no decline in late August. Furthermore, the specific growth rate at the end of August was higher than in mid month (Fig. 11).

Differences in growth of perch fry in the three basins was slight (Tables 6 and 7). The similarity of slopes in length weight relationships and in growth rates suggested that growing conditions in the three basins were similar. In a small lake, like West Blue Lake, it is unlikely that prolonged differences in physical and biological factors could be maintained in different regions of the surface waters, where the mixing is most pronounced.

Differences in intercepts in the length weight relationships and for growth in length (Tables 7 and 8) were most probably the result of the difference in hatching times and initial growth. The spawning temperature of yellow perch ranges from 7-12 C (Herman et al 1959) and the duration of spawning period is dependent on the rate of warming of the lake. Considering the variations in spawning time, time required for hatching and initial grwoth, differences in intercepts were to be expected.

The specific growth rates and condition coefficients of perch fry increased steadily during July but tended to decline in August (Fig. 11). The two periods were also, approximately, the periods when perch fry were, respectively, limnetic and littoral. This coincidence, suggested that the epilimnion was more favorable than the littoral for perch fry. In July, mean stomach contents was higher than in August (Fig. 16). This greater food intake could account for the observed high specific growth rates and condition factors in July. It also implied that the epilimnion, with it's relatively large volume, provided a greater energy source in the form of zooplankton than the littoral zone.

Margalef (1963) states, "Animals tend to spend their adult lives in more mature systems, but to reproduce in less mature ones and send larvae or reproductive elements into them." The littoral, with a wide species diversity, is a more mature system than the epilimnion (Werner 1969). The intralacustrine migration of larval perch in West Blue Lake and the similar migration of bluegill fry in Crane Lake (Werner 1969), is consonant with Margalef's (1963) hypothesis. Furthermore, increases in specific growth rates, condition coefficients and stomach contents in the epilimnetic phase of the life of perch fry demonstrated that the less mature system (epilimnion) was initially more favorable for perch fry than the littoral zone.

Feeding

Many larval fish, perch fry included, are planktivorous. Various species of Copepoda, Cladocera, insect larvae and pupae are documented as the prey of perch fry (Turner 1920; Allen 1934; Ewer 1934; Smyly 1952). In West Blue Lake, where the species composition of zooplankton is simple, Daphnia pulex, Cyclops biscuspidatus and Diaptomus siciloides made up most of the diet of young perch.

Daphnia, which were one of the largest and most abundant zooplankter, made up over 90% of the diet of perch fry through the summer (Table 10). The dependence of larval perch on *Daphnia* was obvious. The net energy gained in capturing a larger prey (*Daphnia*) is generally greater than in capturing several smaller ones (copepods), although in total, the smaller animals may be equal in energy content to the single larger animal, particularly when the larger form is abundant. Although copepods generally made up less than 10% of the diet (Table 10), large numbers were consumed by the perch fry, because of their small size. Copepods remained as the second main source of food until they were replaced by amphipods.

Younger fish larvae consume small zooplankters. A change from smaller to larger zooplankters with increasing fish size is clearly demonstrated in largemouth bass (Kramer and Smith 1960) and in yellow perch (Allen 1934, 1935). The simple species composition of the West Blue Lake zooplankton did not lend itself to identifying a trend similar to the one shown by Allen. Although a particular food species was not observed to be utilized by a discrete size range of perch fry, larger fry relied more heavily on larger zooplankton species (Table 10). As shown, smallest fry, early in the season, fed mostly on small copepods and nauplii and only later did they feed on *Daphnia* which were larger. At the time when

Daphnia became almost the sole food, copepods were still abundant in the lake.

Difference in size of food animals consumed by perch fry were intraspecific as well as interspecific. The mean depth of *Daphnia* consumed by fry between 10 and 20 mm increased linearly (45° angle) with the increasing mouth size of the fry (Fig. 14). A similar relationship between the size of juvenile plaice and the food organism *Oikopleura* has been observed (Shelbourne 1962). Unlike plaice, which did not consume the smallest *Oikopleura* after increases in their size, perch fry over 20 mm made full use of the whole size range of *Daphnia* (Fig. 12). The mean size of *Daphnia* in the stomachs of these perch during a given week was closely related to the estimated mean size of *Daphnia* in the lake (Fig. 15). The seemingly non size selective behavior of older perch fry when feeding on *Daphnia* may be of survival value. Size specific feeding by rainbow trout and adult perch in Sporley Lake, Michigan, resulted in the reduction in the mean size of *Daphnia* in the lake (from 1.4 to 0.8 mm) and the disappearance of *Daphnia pulex,* which was the largest species of *Daphnia* in the lake (Galbraith 1967).

The increase in size of prey ingested during the development of fry can be explained in terms of increased hunting ability, in swimming speed and mouth size. The effects of increases in swimming speed and hunting ability are difficult to interpret since these two factors were not measured in this study. The effect of changes in mouth size relative to feeding habits is clearly seen in perch fry between 10 and 20 mm in length. Increases in mean gape width and prey size were directly proportional (1:1 ratio) (Fig. 14). In other words, prey size was restricted by predator mouth size. Size selectivity of prey restricts the developing fry to a narrow variety of food items. The wellbeing of these developing fry may depend on the presence of the correct food items of an exploitable size at the right time. Insect larvae and pupae, which were abundant in July 1969 and served as food for older perch (Falk MS 1971), were generally too large to be ingested by perch fry. Only very small quantities of minute dipteran pupae served as energy source for the young fry. It might therefore, be disastrous to the survival of perch if the appearance of abundant small immature zooplankters did not coincide with hatching and dispersion of the fry.

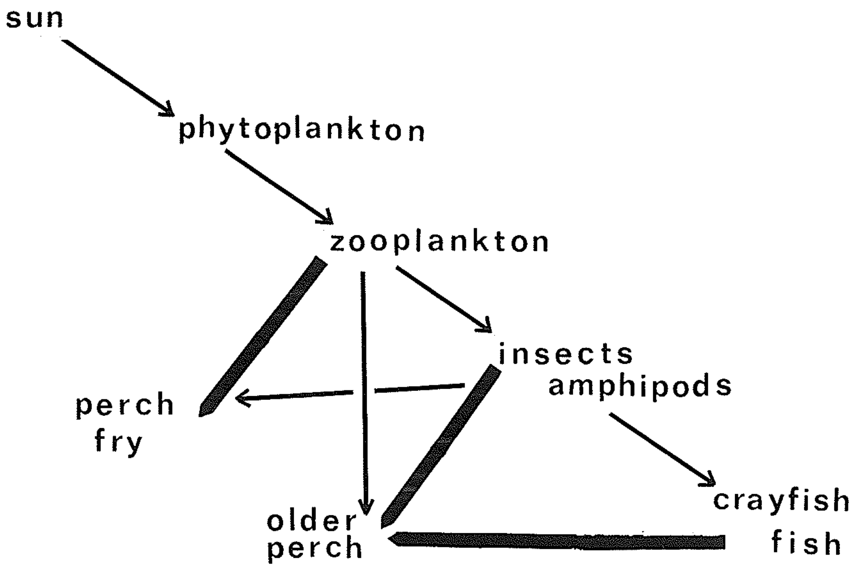
In year-old and older perch, the mouth size to body length is 8% (Keast and Webb 1966). A ratio (9.5%) was also observed for perch fry over 20 mm in West Blue Lake. The differences in the ratios were the result of differences in the method of measuring mouth size. In the early post-larval stage (10-20 mm), however, the ratio was lower. Growth in gape width was relatively higher than growth in length (Fig. 13). The accelerated growth in mouth size not only shortened the period of dependence on small immature zooplankters, but also enabled the larvae to utilize a greater range of prey sizes and species during this period. The accelerated growth in mouth size of small perch fry and their movement into the epilimnion helped to minimize their dependence on abundant small immature zooplankters and perhaps helped to minimize fluctuations in their year class strengths.

The average stomach content (dry weight) of larval perch was about 1% of the body weight (dry), which is in close agreement to values reported by Smyly (1952). The method used to determine stomach contents in this study was very similar to that of Ricker (1937). As well as assigning a predetermined mean value to a given food species, I went one step further. Energy values of fresh individuals of the various sizes of each food species were determined. The advantages of this modification to Ricker's procedure are threefold. Accurate estimates can be obtained for absolute stomach contents and for differences between fish. Thirdly, estimates of stomach contents are unaffected by digestion rate.

This modified Ricker method is apt to become tedious and impractical when applied to small fish which utilize a large spectrum of food species. In addition to the time consuming process of food value determinations, sampling for the correct specimens can further burden the method. With increases in the food spectrum, variations between stomach contents of individual fish increases too, which in turn increases the necessity for determining this variation in order to obtain quantitative estimates of stomach contents. Since the method is practical only for animals with a limited food spectrum, it is unable to provide an estimate of the variation between fish when the knowledge of this variation is most needed. Another limitation is that the method is only applicable if, during the digestive process, prey in the stomachs is not greatly distorted or fragmented, making measurement difficult or impossible. As mentioned, the mean size of Daphnia in the stomachs differed by less than 0.1 mm from that in the lake during the summer months (Fig. 15). Although the difference was very small, the mean size of Daphnia was consistently smaller in the stomachs of perch than in collections. It is unlikely that the Van Dorn sampler was more effective in capturing large Daphnia. A more realistic conclusion is that the Daphnia in the stomachs were slightly distorted by the activities of the alimentary canal. In other words, this method has a tendency to underestimate stomach contents. The degree of distortion was more pronounced with increase in perch size. For this reason no attempt was made to estimate the stomach contents of perch fry captured after the end of August.

Comparison of Age 'O' Fry with Older Fish

In contrast with adults, larval perch exhibit a different mode of life. During the period of rapid growth in their first summer, perch fry fed almost exclusively on small planktonic crustaceans. On the other hand, the diet of the adult perch comprises of a wide variety of food organisms (Fish 1953; Falk MS 1971). The difference in food requirements extended beyond the size and kind of organisms. In general fry in West Blue Lake obtained most of their energy from a lower trophic level than did older fish. For instance, in the diagram, the thick line between zooplankton and perch fry indicates a major utilization of zooplankton whereas thick lines between older perch and insects, amphipods and crayfish indicates a dependence on higher trophic levels.



The spatial distributions of the adult and the larval perch were also very different. Larval perch in this study occupied the first six meters of the surface water. Older perch, however, generally maintain themselves below this depth in West Blue Lake (Falk MS 1971) and in other lakes (Hasler and Bardach 1949). Furthermore, young perch as previously mentioned, undertook diel vertical migrations during the months June and July, whereas the adults, as shown by Falk (MS 1971), undertook diel horizontal migrations.

Young perch feed at a high rate throughout the day. The stomach contents reaches a maximum at 2100 hr. Older perch generally exhibit two peaks in feeding activity associated with their shoreward migrations at dusk and dawn (Keast and Welch 1968; Falk MS 1971).

Differences between fry and older perch in food and habitats enables a greater exploitation of available space and food, and a more efficient use of the natural resources of a lacustrine ecosystem. These advantages, associated with the departure of the general ecology of the young from that of the older fish are recognized in many fish species. For example, many salmon reproduce in the fresh water but mature in the ocean. Although the separation of young and older salmon is interlacustrine while that of young and older perch is intralacustrine, they both are consonant with Margalef's hypothesis (1963). The less obvious intralacustrine separation of the young from the adults are also observed in bluegill (Werner 1969) and perhaps in many other fresh water fish species.

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APPENDIXES

APPENDIX I

SAMPLING OF PERCH FRY IN WEST BLUE LAKE

Sampling Date	Sampling Methods	Basin 1 Mean Length (mm)	Basin 1 Mean Weight (mg)	Basin 2 Mean Length (mm)	Basin 2 Mean Weight (mg)	Basin 3 Mean Length (mm)	Basin 3 Mean Weight (mg)	Pooled Mean Length (mm)	Pooled Mean Weight (mg)
1969 July 1	Tow	15.92	26.38			16.32	28.45	16.22	27.94
2	Tow	16.40	31.19			16.43	33.44	16.41	31.92
4	Tow	16.75	35.60					16.75	35.60
8	Tow	16.04	27.85	16.31	29.51	17.05	27.98	16.41	28.71
9	Tow	16.63	34.77			16.50	31.78	16.59	33.69
12	Tow			17.71	41.43	17.85	42.32	17.79	41.94
15	Tow	18.62	41.81	19.08	40.08			18.77	41.25
16	Tow	17.96	44.71			17.24	45.32	17.69	44.94
17	Tow	18.42	47.87			16.14	35.86	18.01	45.71
20	Tow	19.21	57.27			18.73	57.06	18.93	57.15
22	Tow	23.45	134.71	22.38	102.94	23.12	130.18	22.43	106.15
23	Tow	22.04	101.54	21.70	79.37			21.89	91.68
24	Tow	23.48	138.23	21.30	112.44			23.46	131.24
27	Tow	25.67	172.87	25.29	153.24			25.49	163.71
29	Seine	27.32	207.32	27.42	207.81			27.37	207.83
30	Tow	25.54	175.64			25.74	165.79	25.67	169.37
Aug. 1	Tow	26.79	195.70			27.15	195.32	26.98	195.52

APPENDIX I (Continued)

Sampling Date	Sampling Methods	Basin 1		Basin 2		Basin 3		Pooled	
		Mean Length (mm)	Mean Weight (mg)	Mean Length (mm)	Mean Weight (mg)	Mean Length (mm)	Mean Weight (mg)	Mean Length (mm)	Mean Weight (mg)
1969 Aug. 1	Seine	30.52	289.89	31.14	314.19			30.83	303.74
3	Tow	27.19	209.18	27.05	201.91			27.13	205.73
6	Tow	32.89	380.66	32.68	373.85			32.84	379.04
6	Seine	33.21	382.94			33.42	395.33	33.27	386.40
8	Tow	33.80	401.75	34.19	410.55	34.21	400.67	34.00	404.42
8	Seine	36.78	544.51			36.80	428.36	36.95	486.43
9	Seine	32.37	353.88			32.52	370.21	32.44	361.18
10	Tow	35.18	471.18	33.00	377.52	37.40	552.25	35.19	467.78
11	Seine	37.23	548.59	37.31	526.50			37.27	532.54
14	Seine	36.17	509.49					36.17	509.49
18	Seine	41.26	778.71			41.20	734.20	41.23	755.88
21	Seine	42.74	818.91	43.96	917.27			43.23	846.36
27	Seine	46.39	955.85			54.86	1833.99	49.60	1276.35
30	Seine	52.95	1575.36					52.95	1575.36
1970 June 11	Tow	10.21	5.88					10.21	5.88
15	Tow	12.52	10.31					12.52	10.31
18	Tow			14.04	12.53			14.04	12.53
22	Tow					15.73	18.27	15.73	18.27
23	Tow					16.17	30.32	16.17	30.32
26	Tow	17.06	33.26					17.06	33.26

APPENDIX II

SEASONAL CHANGES OF SURFACE TEMPERATURE AND DAYLENGTHS FOR SUMMER 1969

June			July			August		
Date	Surface Temp. (C)	Day Length (hr)	Date	Surface Temp. (C)	Day Length (hr)	Date	Surface Temp. (C)	Day Length (hr)
1	11.5	14.50	1	13.5	15.00	1	19.5	14.75
2	10.5	14.25	2	15.0	15.25	2	20.0	13.50
3	11.5	14.50	3	16.5	16.00	3	22.0	13.50
4	11.5	14.75	4	16.5	15.00	4	22.0	13.75
5	11.5	14.25	5	14.5	16.25	5	21.0	15.00
6	11.0	13.75	6	16.0	16.00	6	21.0	13.25
7	11.5	14.50	7	16.0	16.00	7	20.5	14.00
8	12.0	15.00	8	16.0	15.75	8	20.5	14.00
9	12.5	15.00	9	16.0		9	20.5	14.25
10	12.5		10	16.0	15.75	10	21.0	14.75
11	13.0	14.25	11	17.5	16.00	11	21.0	14.75
12	11.5	14.25	12	18.0	15.00	12	21.0	14.75
13	11.5	15.50	13	19.0	14.25	13	21.0	14.25
14	12.0	14.50	14	18.0	16.00	14	21.0	14.25
15	12.5	14.00	15	18.0	15.75	15	19.5	
16	12.5	14.50	16	18.5	14.75	16	19.5	14.25
17	13.0	15.50	17	19.0	15.25	17	19.5	14.25

APPENDIX II (Continued)

June			July			August		
Date	Surface Temp. (C)	Day Length (hr)	Date	Surface Temp. (C)	Day Length (hr)	Date	Surface Temp. (C)	Day Length (hr)
18	13.0	15.25	18	19.5	15.25	18	19.5	14.25
19	12.5	16.00	19	19.5	14.50	19	19.5	14.50
20	12.5	15.25	20	19.5	15.25	20	19.5	13.75
21	12.5	15.00	21	19.5	13.75	21	20.0	12.75
22	13.5	16.00	22	20.0	14.50	22	21.0	13.50
23	15.0	15.25	23	19.5	14.50	23	21.0	13.25
24	15.0	15.50	24	19.5	15.50	24	21.0	13.00
25	15.0	16.00	25	19.5	16.00	25	20.5	13.00
26	13.5		26	20.5	15.50	26	20.0	13.25
27	13.5	15.00	27	19.5	14.75	27	20.5	
28	13.0	16.00	28	19.5	14.00	28		
29	15.0	14.50	29	20.5	14.25	29		15.00
30	13.0	15.00	30	21.0	13.25	30		14.25
			31	19.5	14.75	31		