Ecology of Limnetic Bluegill (Lepomis macrochirus) Fry in Crane Lake, Indiana[1]

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ABSTRACT: In Crane Lake, Indiana, bluegill fry (*Lepomis macrochirus* Raf.) abandon littoral spawning areas shortly after yolk sac absorption and migrate to the limnetic zone of the lake. The ecology of the fry during their residence in the limnetic zone was studied utilizing data derived from fry captured in plexiglass fry traps. The distribution of the fry in the epilimnion is patchy, suggesting that they are aggregated, possibly in schools. They feed upon crustacean zooplankters, selecting copepods in preference to other plankters. They demonstrate a diel periodicity in their activity with low activity during the day, peak activity at dusk, low activity at night, and a secondary peak of activity at dawn. They remain in the limnetic zone for approximately a month and a half, growing at a rate of 0.4 mm/day. After achieving a size of 22 to 25 mm, they return to the littoral zone. In 1965 the brief period of limnetic residence for bluegill fry suggested that the duration of successful spawning had been very short, although nest-building activity extended from May to August.

INTRODUCTION

Evidence is gradually being accumulated which indicates that species of fish from quite different taxonomic groups undertake precocious migrations (Faber, 1967; Hart, 1930; Heard, 1965; Hubbs, 1921; McCart, 1967; Pritchard, 1930). Such larval migrations result in marked changes in habitat, which must be accompanied by concomitant adjustments in the ecology of the fish, particularly with regard to their feeding habits, behavior, predators and growth rates. Unfortunately, too little attention has been paid to the ecology of the fry during these shifts in habitat, even though such information may be of considerable value in explaining the fluctuations in year-class size noted in many fish populations.

In conjunction with a study on the ecology of the bluegill sunfish (*Lepomis macrochirus* Rafinesque) during its first summer the discovery was made that bluegill fry are among the group of fishes that undergo a migration early in their lives (Werner, 1967). The migration consists of a movement by postlarval bluegills from spawning areas in the littoral zone of the lake to the limnetic region, followed several weeks later by a return to the littoral zone. The ecology of the fry during their period of limnetic residence was of particular interest since so little is known of the ecology of limnetic larvae in general and nothing is known for the bluegill in this regard.

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DESCRIPTION OF STUDY SITE

This investigation was conducted on Crane Lake, a small eutrophic lake near the headwaters of the Tippecanoe River, Noble Co., Indiana. It has an elongate basin of 11.1 ha and a maximum depth of 11 m near the midpoint of the lake.

The lake was thermally stratified during the course of the study (Fig. 1). The epilimnion ranged from a depth of 2.0 m early in May to 4.0 m in September 1965; in July and August it was approximately 3 m thick. All of the water below 6 m was in the hypolimnion.

Light penetration was determined by the use of an underwater photometer. The 1% level of light penetration ranged from 3.5 m in May and June to 2.5 m in July and August.

Dissolved oxygen, *p*H, total alkalinity, and free carbon dioxide determinations were made at frequent intervals throughout the summer, following the procedures suggested in the Eleventh Edition of Standard Methods for the Examination of Water and Wastewater (American Public Health Association, 1960). Crane Lake has a *p*H of approximately 8.4 with a total alkalinity, based on titrations with methyl orange, ranging from 2.68 meq/l to 3.10 meq/l. Free carbon dioxide, as determined by titration, reaches 16 mg/l in the hypolimnion, but it is so rapidly used by algal photosynthesis that it is undetectable in the upper 2 m of the epilimnion. Dissolved oxygen was measured every week, generally at midday. Its vertical distribution followed a typical clinograde pattern (Fig. 1). The concentration was high, frequently supersaturated, in the epilimnion. In the hypo-

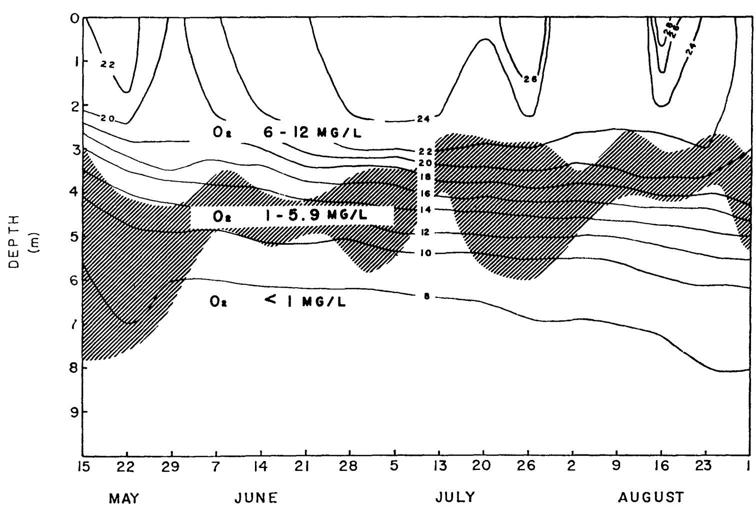

Fig. 1.—Depth isotherms (°C) and dissolved oxygen concentration (mg/l) at midday in Crane Lake, summer 1965.

limnion, on the contrary, the oxygen was reduced and during the latter part of the summer the deeper water was almost devoid of oxygen.

METHODS

Bluegill fry were collected by use of plexiglass fry traps arranged in a horizontal transect across the lake. The traps and their location have been described previously (Werner, 1967).

The vertical distribution of the fry was studied by placing fry traps in a specially designed frame. The ¼" plexiglass frame was 2 m high, and had runners spaced at 0.5 m intervals to hold the traps in place. When the frame was placed vertically, it spaced the traps at 0, 0.5, 1.0, 1.5, and 2.0 m below the surface. The vertical position was maintained by securing a styrofoam float to the top of the frame and attaching an anchor to the bottom. Most often two frames were used to obtain duplicate trapping results, but at times one frame was placed

TABLE 1.—Aggregative tendency of limnetic bluegill fry determined by a comparison of the distribution of the catch between traps with a Poisson distribution

	Date	No. of fry	$\bar{x}$	Variance	I*	P**
July	15	14	2.33	14.67	31.43	0.001
	16	1	0.17	0.17	5.00	0.50
	17	2	0.33	0.26	4.00	0.70
	18	6	1.00	1.60	8.00	0.20
	19	17	2.83	7.37	13.00	0.05
	20	24	4.00	42.80	53.50	0.001
	21	22	3.67	31.47	42.91	0.001
	22	13	2.17	4.97	11.46	0.05
	23	31	5.17	20.97	20.29	0.01
	24	21	3.50	17.90	25.57	0.001
	25	10	1.67	2.67	8.00	0.20
	26	8	1.33	1.46	5.50	0.50
	27	49	8.17	42.57	26.06	0.001
	28	29	4.83	4.97	5.14	0.50
	29	9	1.50	3.50	11.67	0.05
	30	10	1.67	3.07	9.20	0.20
	31	41	6.83	61.37	44.90	0.001
Aug.	1	61	10.17	80.97	39.82	0.001
	2	187	31.17	1042.17	167.19	0.001
	3	66	11.00	19.60	8.91	0.20
	4	72	12.00	67.60	28.17	0.001
	5	123	20.50	121.90	29.73	0.001
	6	57	9.50	102.70	54.05	0.001
	7	43	7.17	86.96	60.67	0.001
	8	45	7.50	179.10	119.40	0.001
	9	36	6.17	103.76	84.14	0.001
	10	102	17.00	491.20	144.47	0.001
	11	22	3.67	12.27	16.73	0.01
	12	77	12.83	114.16	44.48	0.001

below the other in order to extend the trapping range to 4.5 m. This spaced the 10 traps in a vertical series at depths of 0, 0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0, and 4.5 m.

Biweekly limnetic plankton samples were taken in Crane Lake throughout the summer of 1965. With the exception of the collections made on 20 July, and 2 and 16 August, all sampling was done with a Juday plankton trap. A plankton tube (Pennak, 1962) was used on those dates. In the laboratory the samples were filtered and total counts of the crustacean zooplankters were made.

The stomach contents of 491 limnetic bluegill fry were analyzed. The composition of their diet was determined by the points method of analysis suggested by Hynes (1950) and supplemented by the occurrence and dominance methods. The period of active feeding was outlined by visually estimating the degree of fullness of stomachs taken from fish trapped at all hours. Percentage values were assigned according to the following set of arbitrary standards: A value of 100%

TABLE 1.—(continued)

Date		No. of fry	$\bar{x}$	Variance	I*	P**
	13	45	7.50	157.50	105.00	0.001
	14	40	6.67	86.00	64.40	0.001
	15	22	3.67	18.67	25.45	0.001
	16	28	4.67	19.47	20.86	0.001
	17	33	5.50	23.50	21.36	0.001
	18	26	4.33	25.46	29.38	0.001
	19	12	2.00	2.80	7.00	0.30
	20	10	1.67	2.27	6.80	0.30
	21	9	1.50	7.90	26.33	0.001
	22	13	2.17	2.97	6.85	0.30
	23	36	6.00	96.40	80.33	0.001
	24	5	0.83	0.56	3.40	0.70
	25	42	7.00	217.60	155.43	0.001
	26	26	4.33	37.47	43.23	0.001
	27	58	9.67	317.47	164.21	0.001
	28	76	12.67	737.46	291.11	0.001
	29	6	1.00	2.40	12.00	0.05
	30	23	3.83	5.37	7.00	0.30
	31	2	0.33	0.27	4.00	0.70
Sept.	1	16	2.67	4.67	8.75	0.20
	2	1	0.17	0.17	5.00	0.50
	3	2	0.33	0.27	4.09	0.70
	4	10	1.67	7.07	21.20	0.001
	5	2	0.33	0.27	4.09	0.70
	6	1	0.17	0.17	5.00	0.50

* Index of Dispersion (I) $= \frac{\text{variance}}{\text{mean}} \times (\text{N-1})$

** Derived from Chi-square with 5 df. Values of P given are the larger of the two bracketing values in the table.

was given only to stomachs which were distended to twice normal size; a stomach completely full, but not distended, was assigned a value of 50%; and an empty stomach, of course, received a value of 0%. All gradations in between were judged according to their relation to these three easily distinguished standards. In addition, two experiments were conducted: one to ascertain whether bluegill fry could feed in the dark, and the other to estimate the rate at which food passed through their stomachs.

RESULTS

LIMNETIC DISTRIBUTION OF BLUEGILL FRY

The results of the horizontal limnetic trapping for the period from 15 July through 6 September 1965 were analyzed to determine if the fish were randomly distributed in the epilimnion, using the variance/mean ratio (Greig-Smith, 1957:58). If the fry were randomly distributed, the variance between the catch in the limnetic traps, when divided by the mean catch for all limnetic traps should be approximately one, the variance/mean ratio of a Poisson distribution. If it were significantly greater than one, the fish would be patchily distributed. The significance of the difference between the actual variance/mean ratio and the expected ratio was tested using Chi-square.

The results (Table 1) show that the fry were patchily distributed ($P < 0.05$) on 35 of the 54 days that they were abundant in the epilimnion of Crane Lake. Of the remaining 19 days, 13 had total catches for the six traps which were 10 or less and did not show a significant deviation ($P > 0.05$) from the Poisson. This leaves only six days out of 54 in which the catch was greater than 10 and yet not significantly different from a Poisson. Thus it appears that for the most part the fish are moving in the epilimnion of Crane Lake in aggregations. This conclusion was supported by the only two observa-

TABLE 2.—Vertical distribution of limnetic fry in Crane Lake during July and August, 1965, reported as the mean number of fry taken per trap every 24 hours

Depth (m)	Date 7/13 - 7/29[1]	7/29 - 8/2
0	5.9	9.8
½	6.7	19.0
1	4.2	11.6
1½	3.7	7.4
2	1.3	7.2
2½	......	7.4
3	......	2.0
3½	......	1.2
4	......	0
4½	......	0

[1] No observations below 2 m during this sampling period.

tions of limnetic fry which it was possible to make. In both cases the fry were aggregated moving in schools.

The vertical distribution of the fry in the limnetic zone was determined by trapping at 0.5-m intervals, using the vertical frames. Initially only the upper 2 m of the epilimnion were trapped. The traps were run once a day from 13 to 29 July 1965. The fry were common in the upper 2 m of the epilimnion (Table 2), showing some preference for the upper meter. The complete vertical extent of the habitable zone was determined next by placing one frame between 0 and 2 m and the other between 2.5 and 4.5 m. This trapping indicated that the fry were restricted to the upper 3.5 m, with the majority occurring above 3 m.

The habitat of the fry at this time was the upper 3-m stratum of water, bounded laterally on all sides by the littoral. This layer was characterized by having a temperature ranging from 22.3 to 21.7 C, and dissolved oxygen concentrations of 9.7 mg/l at the surface to 8.4 mg/l at 3 m. Below the region inhabited by the fry the values changed drastically. The dissolved oxygen dropped to 4.1 mg/l at 4 m, and 0.7 mg/l at 5 m. The temperature was 16.9 C at 4 m and the 1% level of light penetration was at 2.5 m. Which, if any, of these factors determines the vertical distribution of the fry is unknown, but it is apparent that the fry are restricted to the epilimnion during their limnetic residence. They were never found in any part of the metalimnion.

FEEDING

The results of an analysis of the stomach contents of 127 limnetic fry demonstrated that they fed almost exclusively on planktonic crustaceans (Table 3). The only noncrustacean food resources were *Chaoborus* sp. and an occasional rotifer. Conspicuously absent were algal cells and copepod nauplii. The two most important food organisms are *Daphnia galeata* and copepods, which between them comprise about 86% of the total quantity of food eaten by the fry. The remainder of the diet is provided by *Ceriodaphnia lacustris* (6.0%), *Bosmina longirostris* (3.7%), and *Chaoborus* sp. (3.9%).

TABLE 3.—Composition of the diet of limnetic bluegill fry as determined by the occurrence, dominance and point methods (Hynes, 1950)

Food organism	Frequency of occurrence (%)	Frequency of dominance (%)	Proportion of total points allocated (%)
Daphnia galeata	55.1	48.9	36.8
Ceriodaphnia lacustris	16.5	6.1	6.0
Bosmina longirostris	16.5	1.0	3.7
Copepoda	53.5	42.8	49.4
Chaoborus sp.	10.2	1.0	3.9
Empty	22.8	....	....

The suggestion has been made several times (Ball, 1948; Gerking, 1962) that adult bluegills are selective in their feeding habits. Since data were available on zooplankton concentrations both before and after a 12-day period of intensive trapping, electivity indices (Ivlev, 1961) were calculated for limnetic fry feeding on zooplankton, according to the following formula:

$$E = \frac{(r - p)}{(r + p)}$$

where E is the electivity index, r is the proportion of an organism in the stomach contents of the fry, and p is the proportion of that organism in the plankton population. Determinations of p were made from the relative proportions of the food species noted above that were found in the plankton collections taken on 2 and 16 August 1965. Stomach analyses of randomly selected fry taken at all hours during a 12-day period from 3 through 14 August 1965 were used to calculate r. E was calculated for the first half of the 12-day trapping period using the p derived from the 2 August plankton collection, and E for the second half used the plankton collected on 16 August 1965.

If one assumes that the p determined from the plankton samples is an adequate representation of the relative proportion of food organisms available to the fry; that each prey organism in the epilimnion is equally accessible to the fry; and further that the diet of the fry at this time consisted of only these five organisms, then the following conclusions can be made: Copepods were utilized more intensively than any other food source ($E = +0.40$ to $+0.54$). Conversely, *Daphnia* ($E = -0.32$ to -0.39) was not consumed by the fry as frequently as they must have been encountered, judging by their abundance. Although small numbers of *Bosmina* and *Ceriodaphnia* were taken in both the stomachs and plankton samples, electivity indices of $+0.33$ to $+0.37$ and $+0.67$ to -0.44, respectively, were calculated for them. *Chaoborus* was so rarely taken in the plankton that electivity indices could not be determined for it. These data suggest that bluegill fry select the organisms that they feed upon, preferring copepods and *Bosmina* to *Daphnia*.

GROWTH

A first approximation of growth rate of bluegill fry was made by measuring the total length of fry raised in a hatchery pond located several miles east of Crane Lake.

Adult bluegills were stocked in a pond that had been poisoned and was devoid of fish. The males began nest-building almost immediately and spawning took place several days after the introduction of fish. Since very little variation existed in the size of the individuals taken each day from the ponds (Table 4), it was assumed that a single spawning had occurred and that the mean length of the daily catch would give a reliable estimate of the growth rate of the fry.

These data showed that the rate was approximately 0.4 mm/day. This agrees with published estimates. Krumholz (1949) assessed the growth rates of bluegill fry from 12 to 25 mm total length at 0.1 mm/day in ponds where slow growth predominated, and at 0.6 mm/day in ponds conducive to faster growth. Lux (1960) determined that the daily increase in mean total length of young-of-the-year bluegill varied from 0.2 to 0.5 mm/day in the 11- to 39-mm size range.

If 0.4 mm/day is an adequate approximation of the growth of limnetic fry in Crane Lake, one can estimate the duration of their stay in the limnetic zone. Evidence presented in an earlier paper (Werner, 1967) suggested that the bluegill fry moved into the limnetic region when they were 6 mm long. They left after they had grown to a size of 22 to 25 mm. Thus, during their limnetic residence they grew 16 to 19 mm. At a growth rate of 0.4 mm/day, the bluegill fry in Crane Lake must have spent approximately 40 to 47.5 days during their first summer in the limnetic region.

With this information, we can summarize the sequence of events occurring during the early life of the bluegill in Crane Lake. The eggs

TABLE 4.—Growth rate of bluegill fry raised in hatchery ponds

Days after hatching	No. of fish	Mean total length (mm)	Std. dev.	Range (mm)
16	3	12.3	0.59	12-13
17	7	13.3	0.51	13-14
18	8	13.3	0.71	12-14
19	14	13.3	0.71	12-14
20	76	13.8	0.57	13-15
21	77	14.5	0.60	13-15
22	149	15.1	0.61	13-16
23	134	15.8	0.89	12-18
24	5	16.2	0.84	15-17
25	9	16.8	1.09	16-19
26	5	16.8	0.45	16-17
27	4	18.8	0.48	18-19
28	2	19.0	1.41	18-20
29	3	18.3	0.59	18-19
30	1	21.0	..	21
31	4	21.3	0.96	20-22
35	4	22.0	1.41	21-24
36	4	22.3	0.95	21-23
37	2	21.5	0.71	21-22
38	7	23.0	2.17	20-26
39	2	22.0	..	22
40	11	24.2	2.04	21-27
43	3	27.3	1.53	26-29
44	4	24.8	1.53	23-26
46	1	25.0	..	25

hatch in littoral nests about two days after fertilization (Morgan, 1951). The prolarvae begin exogenous feeding before yolk sac absorption approximately eight days after fertilization (Toetz, 1966). The yolk is absorbed by the 10th day and the 6-mm postlarvae leave the nest and begin their movement to the limnetic zone. The fry remain in the limnetic region for approximately a month and a half, grow to 22 to 25 mm, and then return to the littoral zone for the remainder of the summer.

A plot of the number of fry taken in the limnetic traps over the summer (Fig. 2) shows that 94.4% of the catch was taken between 15 July and 6 September, a period of 54 days. The similarity in the duration of time taken by fry to grow to the size at which they leave the limnetic zone (40 to 47.5 days) and the actual time spent in the limnetic zone as indicated by the trapping results suggests that the period of successful spawning is quite short.

Nest-building activity was evident in Crane Lake from May until August, yet there was not a continual stream of fry entering the limnetic region as one might have expected. Instead, it appears that only a small portion of the nest-building resulted in new recruits, due either to the fact that the nest-building was not accompanied by spawning, or spawning occurred but the eggs and prolarvae suffered extensive mortality.

DIEL PERIODICITY

The activity of the fry in the 0- to 3-m zone throughout the diel cycle was monitored by sampling the population every four hours. The trapping periods were designed to include overlapping time spans

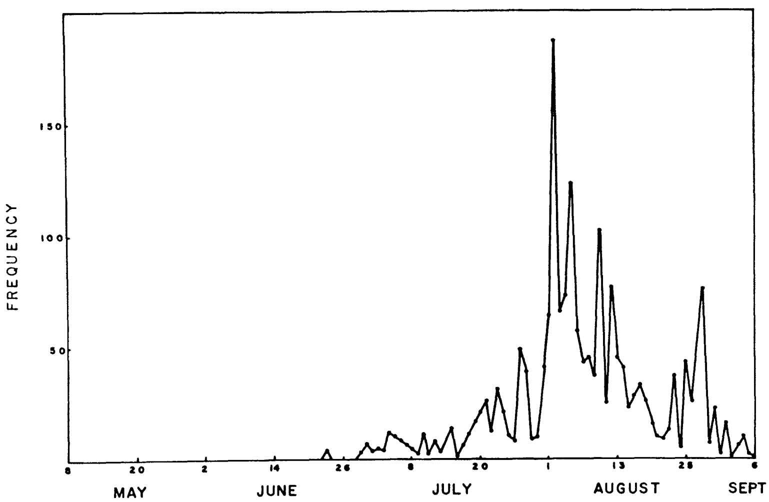

Fig. 2.—Numbers of bluegill fry trapped in limnetic zone of Crane Lake, summer 1965.

on consecutive days. For example, the traps were run on the first day at 0800, 1200, 1600, 2000, 2400, and 0400. On the second day the trapping period began at 0900, making the sequence 0900, 1300, 1700, 2100, 0100 and 0500. On the third day the trapping period began at 1000 hours, and so on. Every fourth day the cycle had been completed and had returned to the 0800 sequence. The traps were run in this fashion for 12 days, accumulating three replicates of each four-hour period.

In addition to the 10 traps in the two vertical frames, two individual traps were placed in deeper water, one at 2.5 m and one at 3.0 m. As a result, the entire habitable zone was sampled and primary emphasis placed on those strata in which the fish were most abundant.

Two general conclusions emerged from the 24-hour sampling: Firstly, the fact that fry are found exclusively in the epilimnion with the largest numbers appearing in the upper strata was confirmed (Table 5). Secondly, limnetic fry undergo a pronounced diel periodicity in their activity. This latter point can be illustrated by examining the trapping results for a composite day (*e.g.,* the trapping periods

TABLE 5.—Diel periodicity in the activity of limnetic bluegill fry as demonstrated by the number of fish caught in vertical traps during 4-hour trapping periods; results in each category are the total fry taken for the three replicates of each trapping period

Trapping period	Depth (m)							
	0	0.5	1	1.5	2	2.5	3	Total
0800 - 1200	0	10	0	9	3	0	0	22
0900 - 1300	0	0	1	3	0	10	0	14
1000 - 1400	0	2	3	5	1	1	0	12
1100 - 1500	8	0	0	0	0	1	0	9
1200 - 1600	0	0	1	14	8	0	0	23
1300 - 1700	0	2	0	41	0	2	0	45
1400 - 1800	1	0	1	0	0	0	0	2
1500 - 1900	3	21	12	23	9	0	0	68
1600 - 2000	3	11	11	3	0	0	0	28
1700 - 2100	221	109	96	35	16	7	1	485
1800 - 2200	157	60	19	11	7	0	0	254
1900 - 2300	175	99	60	19	4	1	0	358
2000 - 2400	76	37	14	16	12	0	0	155
2100 - 0100	2	1	0	2	0	1	0	6
2200 - 0200	1	2	1	0	1	0	0	5
2300 - 0300	5	0	0	1	2	0	0	8
2400 - 0400	2	3	0	2	1	0	0	8
0100 - 0500	7	9	23	13	18	1	0	71
0200 - 0600	4	0	2	4	7	2	0	19
0300 - 0800	1	5	12	51	12	0	0	81
0400 - 0900	10	2	12	8	10	39	0	81
0500 - 1000	36	18	53	5	6	20	1	139
0600 - 1100	0	14	8	1	3	0	0	26
Total	712	405	329	266	120	85	2	1919

beginning with 0900, 1300, 1700, 2100, 0100, and 0500 hours). During the day the fry are rarely taken at the surface and with only a slightly greater frequency in deeper water (Table 5). The catch at dusk (1700), however, contrasts sharply with the daylight catch, increasing more than tenfold over the total number caught during the previous trapping period. The disparity between the daylight and the dusk catch is greatest at the surface and decreases with depth. At night very few fry are collected throughout the water column, approaching the condition prevailing during daylight. As morning draws near, the catch shows a secondary increase, with a drop later in the morning to normal daytime lows. Because the traps are stationary and capture is dependent upon the movement of the fry, increased activity is assumed to be responsible for the high catch at evening twilight.

Unfortunately, these data do not demonstrate whether or not the increased twilight activity is accompanied by an upward movement of the fry. The data, while not contradictory, are still insufficient to establish vertical migration as fact. However, the almost complete absence of fry in the 0-m traps during exclusively daylight trapping periods (1100 to 2000) and the occurrence of the largest numbers at the surface in the twilight catch suggest the possibility that limnetic bluegill fry may undertake a diel vertical migration toward the surface at dusk.

A more detailed analysis of the occurrence of the twilight peak can be made by utilizing the overlapping trapping periods. Of the six periods that coincide with twilight (1600, 1700, 1800, 1900, 2000, 2100), 97.4% of the catch occurred in the four in the center (1700, 1800, 1900, and 2000). The catch for the trapping done prior to 2000, that is the 1600 to 2000 trapping period, was small, comprising only 2.2% of the total for the six periods. The remaining 0.4% was taken during the 2100 to 0100 trapping period. The hour between 2000 and 2100 is the only one common to all four periods in which a high catch occurred, suggesting that this hour is the hour of greatest activity. Sunset varied from 1956 hours to 1941 hours, and thus peak activity is probably taking place about one hour after sunset.

The same type of analysis can be made to ascertain the dawn peak. The critical time period is between 0400 and 0600. Sunrise ranged from 0537 to 0549. Consequently, the dawn peak is apparently occurring in the hour and a half before sunrise and the half-hour after sunrise.

DIEL PERIODICITY AND LIMNETIC ZOOPLANKTON

Since the fry feed predominantly on crustacean zooplankters at this stage, the periodicity in their activity with respect to the activity of the limnetic plankton is of particular interest. The basic pattern of vertical migration in planktonic crustaceans is well known (Bainbridge, 1961). A movement toward the surface occurs near twilight, frequently continuing into the night, with a return to deeper water either immediately after the upward migration or at dawn. The occurrence of this phenomenon by the plankton in Crane Lake was verified by sampling.

Since the upward movement of the plankton at dusk corresponds with the peak activity of the fry, it was surmised that this peak may be due to active feeding on the plankton by the fry. The data derived from an analysis of the stomachs of the fry does not support this contention, however.

An examination of the stomach contents of 204 limnetic fry, selected at random from the various sampling periods during the day, was undertaken in order to relate — if possible — the time of feeding of the fry, their diel activity cycle, and the movement of the crustacean component of the zooplankton population. The feeding period of the fry was determined by assessing the degree of fullness of their stomachs from each trapping period (Table 6).

The stomachs of the fry taken in the early hours of the morning are, almost without exception, empty. The first appearance of fry with substantially filled stomachs occurs in the 0800 catch, indicating that feeding probably resumed near sunrise. Considerable variation

TABLE 6.—Quantity of food in stomachs of limnetic fry during a typical 24-hour cycle

Time of trapping	Number of stomachs analyzed	Mean percent fullness
0800	10	38.5
0900	10	18.0
1000	11	26.4
1100	10	39.0
1200	10	10.0
1300	10	37.0
1400	10	27.0
1500	8	66.3
1600	10	10.0
1700	10	23.0
1800	2	25.0
1900	10	51.1
2000	10	44.5
2100	10	32.0
2200	10	25.5
2300	10	3.0
2400	10	5.0
0100	6	3.3
0200	5	9.0
0300	5	11.0
0400	7	0
0500	10	0
0600	10	0.5

in stomach fullness was encountered from 0800 to 2200, but the values were much higher on the average than those after 2200. Stomach fullness declined sharply at 2300, and most of the stomachs for the remainder of the night are empty.

The fry did not exhibit an increase in feeding between 2000 and 2100, when their activity was at its peak. In fact, the amount of food in the stomachs gradually declined from 1900 to 2200. If the fry were actively feeding at dusk, the fullest stomachs would be in the catches directly after 2100, and the effect of this feeding should be obvious late into the night. Studies conducted on fry sacrificed at regular intervals after a brief period of feeding indicate that the stomachs of the fry would be cleared, at the earliest, four hours after the last food had been ingested. In most individuals food was retained in the stomach for more than six hours. If these estimates can be applied to Crane Lake fry, the last food must have been ingested no later than 1800, two hours prior to the peak catch. Thus, it seems unlikely that the twilight activity peak is related to feeding. On the contrary, limnetic bluegill fry appear to be daylight feeders, depending upon sight for the capture of their food.

A preliminary experiment designed to test whether bluegill fry can feed without the aid of vision was conducted during the summer of 1966. Seventy limnetic fry were starved for 48 hours. At the end of the starvation period they were divided into seven lots of 10 fish each. One lot was sacrificed as a starved control. Three lots were placed in hatchery jars containing filtered lake water and put in a completely darkened room. One hour later zooplankton concentrates were added to each jar, creating known concentrations of food organisms for the fry. The final three lots were treated in exactly the same way except that they were under continual illumination. Four hours later all fish were sacrificed. The results (Table 7) indicate that in the jars containing zooplankton in concentrations less than 510 organisms/l, bluegill fry are not capable of feeding in the dark. At the higher concentration (4,160 organisms/l) the fry in the dark were

TABLE 7.—Results of an experiment designed to test the ability of bluegill fry to feed in the dark on varying concentrations of zooplankton

Light	Zooplankton concentration (no/1)	No. fish	Mean % stomach fullness	Standard deviation
No	4,160	10	30.5	11.7
No	510	10	1.2	2.1
No	50	10	0	....
Yes	4,160	10	69.5	13.8
Yes	510	10	24.5	9.6
Yes	50	10	9.5	7.6
Starved controls	....	10	0	....

able to feed, probably through the high frequency of chance tactile encounters with zooplankters, but still not as effectively as their lighted counterparts. Considering that the concentration of zooplankton in Crane Lake during the summer ranged from 18 to 300 organisms/l (Werner, 1966), it seems unlikely that limnetic bluegill fry could feed effectively at night. It seems even more unlikely when one considers the fact that during August, the period of maximum abundance of bluegill fry in the limnetic zone, the zooplankton concentration ranged from 18 to 65 organisms/l.

The twilight peak of activity is at a time (one hour after sunset) when the light is reduced to a point which probably does not allow for effective feeding by the fry. Consequently, it seems reasonable to relate the twilight peak to another, as yet undetermined, aspect of their behavior.

The fact that the fry are feeding throughout the day but are taken in large numbers only after the light has diminished at twilight suggests an avoidance of the traps by the fry during the day. If this were true, the fry taken at dusk could be accounted for not by an actual increase in activity, but by an overlap of their normal daytime activity with the decreased visibility of the traps. An attempt was made to evaluate this possibility by comparing the catch taken just before the twilight peak with the twilight catch itself. Since the traps in deeper water are less visible, one would expect an increase in the catch in these traps just prior to the twilight peak. As the light decreases at sunset the traps in the upper strata will become progressively less visible and the catch in them should increase correspondingly. This was not the case in Crane Lake. The data show that the catch just before evening twilight (1600 to 2000) is evenly distributed, with no increase in deeper water (Table 5). The increase at twilight (1700 to 2100) is pronounced, with most of the fish being taken at the surface. The decrease (2100 to 0100) is also quite abrupt. Although this does not completely disprove the idea that the fry see the traps and thus avoid them during the daylight, it suggests that this effect may be minimal. The catch at dusk is considered to be a true reflection of the activity of the fry. However, this still leaves unexplained the reason for the low daylight catch during a time when the fish are apparently feeding. Unfortunately, no evidence is available that bears on this point.

DISCUSSION

Although the value of investigating the early life history of fishes has long been recognized (Fabre-Domerque and Bietrix, 1897; Hjort, 1914), the number of studies of larval freshwater fishes in the literature is quite small. The importance of understanding the ecology of larval fishes lies in the fact that although fishes are the most fecund vertebrate group, their survival rate during their first few weeks is extremely low (Ahlstrom, 1954; Hjort, 1914; Kramer and Smith, 1962; Le Cren, 1962; Sette, 1943). Nikolsky (1963) reports that the percentage of eggs that develop into mature adult fish ranges from

0.006 to 0.022% for the bream (*Abramis brama*) and from 0.13 to 0.58% for the chum salmon (*Oncorhynchus keta*). Frequently in those years in which larval survival is modestly increased, dominant year-classes are formed (Hjort, 1914; Kramer and Smith, 1962). Consequently it may be possible to explain population fluctuations, in part, by a high and variable early mortality. Knowledge of the ecology of larval fishes would clearly be a prerequisite to any such explanation.

This is particularly true for the bluegill. The young bluegill, by undertaking an early change in habitats, is exposed to two quite different environments. The littoral and limnetic habitats are ecologically distinguished by the number and kinds of predators and food organisms found in each. The littoral zone in Crane Lake is populated by species of *Hydra,* Haliplidae, Dytiscidae, Gyrinidae, Belostomatidae, Nepidae, Aeschnidae and Libellulidae. Each of these groups has been implicated as potential predators of larval fishes (Balfour-Browne, 1940; Dimmock, 1886; Ormerod, 1889; Usinger, 1963; Wilson, 1923). Such predators are not found in the limnetic zone. In contrast, studies comparing littoral *vs.* limnetic plankton populations (Pennak, 1966) suggest that the limnetic zone may contain considerably higher concentrations of zooplankton than does the littoral region. Thus, by moving from the littoral spawning area to the limnetic zone bluegill fry evade most potential invertebrate predators and enter a habitat that apparently offers an abundance of food resources.

The possibility that the availability of substantial food resources in the limnetic zone may have acted as an inducement to the evolution of the intralacustrine migration of bluegill fry is consonant with an idea discussed by Margalef (1963). The limnetic plankton community is considered to be relatively immature, exporting energy to all of the adjacent lacustrine communities, particularly the benthos. Margalef (1963) suggests several possible mechanisms by which such energy exchanges might be accomplished, of which one has a direct bearing on the present study. He states, "Animals tend to spend their adult lives in the more mature systems, but to reproduce in the less mature ones and send larvae or reproductive elements into them." A quotation from Lloyd in the same paper (pers. comm.) suggests that the habit of sending larvae into less mature systems has evolved as a result of the fact that the energy necessary for growth can be gathered more easily with less competition in the productive immature community.

The movements of bluegill fry into the limnetic zone and their feeding on the plankton community may represent a mechanism by which energy in the limnetic zone could be utilized by the fry and ultimately transported to the littoral zone. However, before either the direction or the magnitude of energy flow may be assessed, quantitative data will be needed contrasting the amount of energy transported into the limnetic region as small fish with that removed as larger fish returning to the littoral zone.

The effect of predation by bluegill fry on the composition of the limnetic zooplankton community should be investigated in the light of the recent work of Brooks and Dodson (1965). They have shown that in Connecticut lakes containing the plankton-eating alewife (*Alosa pseudoharengus*), the species composition of the plankton is different from that in those without the alewife. The difference is reflected most dramatically in the average size of the individual zooplankters. In alewife lakes the modal crustacean zooplankter size is 0.285 mm, whereas in the absence of alewives the mode is 0.785 mm.

The effect of feeding by the limnetic fry on the plankton population in Crane Lake has not been determined. Although the abundance of the plankton (Werner, 1966) follows the pattern found in most lakes, with a peak in spring, a decline in summer and another peak in the fall, the possibility that predation by limnetic fry may be contributing to the summer decline should be explored. Gerking (1962) noted a sharp decline in the entomostracan population in Wyland Lake and found that it could not be accounted for on the basis of predation by adult bluegills alone. They consumed only 13.6% of the total decrease in weight from July to August. This left more than 85% to be consumed either by other fish species (which *in toto* had a standing crop biomass only one-half that of the bluegill) or by some other unknown source of mortality. Gerking did not study bluegill fry, but it is interesting to speculate on what effect their predation may have had on the plankton population in Wyland Lake.

If predation by limnetic bluegill fry on plankton entomostraca accounted for even a fraction of the decrease noted in Crane Lake, the effect of fry predation would have to be considered in any analysis of the population dynamics of limnetic plankton. In addition, since it has been suggested that bluegill fry are selective in their feeding, they may also alter the species composition of the plankton, as Brooks and Dodson have demonstrated for the alewife.

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REFERENCES

AHLSTROM, E. H. 1954. Distributions and abundance of egg and larval populations of the Pacific sardine. *U.S. Fish and Wildlife Serv., Fish. Bull.*, **56**(93):83-140.

AMERICAN PUBLIC HEALTH ASSOCIATION. 1960. Standard methods for the examination of water and waste water. 11th ed. Prepared and published jointly by Amer. Pub. Health Assoc., Amer. Water Works Assoc., and Water Pollution Control Fed. 626 p.

BAINBRIDGE, R. 1961. Migrations, p. 431-463. *In* T. H. Waterman, The Physiology of Crustacea. Vol. II. Academic Press, New York.

BALFOUR-BROWNE, F. 1940. British Water Beetles, Vol. I. Ray Society, London. 375 p.

BALL, R. C. 1948. Relationship between available fish food, feeding habits of fish and total fish production in a Michigan lake. *Michigan St. Coll. Agr. Exp. Sta. (Zool.) Tech. Bull.,* **206**:1-59.

BROOKS, J. L. AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. *Science,* **150**:28-35.

DIMMOCK, G. 1886. Belostomidae and other fish-destroying bugs. *Bull. U. S. Fish Comm.,* **6**:353-359.

FABER, D. 1967. Limnetic larval fish in northern Wisconsin lakes. *J. Fish. Res. Bd. Canada,* **24**:927-937.

FABRE-DOMERQUE, P. AND E. BIETRIX. 1897. La periode critique postlarvaire des poissons marins. *Bull. Mus. d' Hist. Natur., Paris,* **3**:57-58.

GERKING, S. D. 1962. Production and food utilization in a population of bluegill sunfish. *Ecol. Monogr.,* **32**:31-78.

GREIG-SMITH, P. 1957. Quantitative plant ecology. Butterworths Sci. Publ., London. 198 p.

HART, J. L. 1930. The spawning and early life history of the whitefish, *Coregonus clupeaformis* (Mitchill), in the Bay of Quinte, Ontario. *Contrib. Can. Biol. and Fish., (Stud. from the Biol. Sta. of Canada),* **6**:167-214.

HEARD, W. R. 1965. Limnetic cottid larvae and their utilization as food by juvenile sockeye salmon. *Trans. Amer. Fish. Soc.,* **94**:191-193.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in light of biological research. *Conseil Perm. Internatl. Explor. Mer, Rapp et Proc-Verb.,* **20**:1-228.

HUBBS, C. L. 1921. An ecological study of the life-history of the fresh-water atherine fish *Labidesthes sicculus. Ecology,* **2**:262-276.

HYNES, H. B. N. 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of food of fishes. *J. Anim. Ecol.,* **19**:36-58.

IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven. 302 p.

KRAMER, R. H. AND L. L. SMITH, JR. 1962. Formation of year classes in largemouth bass. *Trans. Amer. Fish. Soc.,* **91**:29-41.

KRUMHOLZ, L. A. 1949. Rates of survival and growth of bluegill yolk fry stocked at different intensities in hatchery ponds. *Ibid.,* **76**:190-203.

LE CREN, E. D. 1962. The efficiency of reproduction and recruitment in freshwater fish, p. 283-296. *In* E. D. Le Cren and M. W. Holdgate, The exploitation of natural animal populations. John Wiley and Sons, New York.

LUX, F. E. 1960. Notes on first-year growth of several species of Minnesota fish. *Progr. Fish-Cult.,* **22**:81-82.

MARGALEF, R. 1963. On certain unifying principles in ecology. *Amer. Natur.,* **97**:357-374.

MCCART, P. 1967. Behavior and ecology of sockeye salmon fry in the Babine River. *J. Fish. Res. Bd. Canada,* **24**:375-428.

MORGAN, G. D. 1951. The life history of the bluegill sunfish, *Lepomis macrochirus,* of Buckeye Lake, Ohio. *Denison Univ. Bull., Sci. Lab.,* **42**:21-59.

NIKOLSKY, G. V. 1963. The ecology of fishes. Academic Press, New York. 352 p.

ORMEROD, E. A. 1889. *Ranatra linearis* attacking small fish. *Entomologist*, **11**:95, 119-126.

PENNAK, R. W. 1962. Quantitative zooplankton sampling in littoral vegetation areas. *Limnol. and Oceanogr.*, **7**:487-489.

———. 1966. Structure of zooplankton populations in the littoral macrophyte zone of some Colorado lakes. *Trans. Amer. Microscop. Soc.*, **85**:320-349.

PRITCHARD, A. L. 1930. Spawning habits and fry of the cisco (*Leucichthys artedi*) in Lake Ontario. *Contrib. Can. Biol. and Fish.* (*Stud. from the Biol. Sta. of Canada*), **6**:227-240.

SETTE, O. E. 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I. Early life history, including growth, drift, and mortality of the egg and larval populations. *U. S. Fish and Wildl. Serv., Fish. Bull.*, No. 38, **50**:149-237.

TOETZ, D. W. 1966. The change from endogenous to exogenous sources of energy in bluegill sunfish larvae. *Invest. Indiana Lakes and Streams*, **7**:115-146.

USINGER, R. L. (ed.). 1963. Aquatic insects of California. Univ. of California Press, Berkeley. 508 p.

WERNER, R. G. 1966. Ecology and movements of bluegill sunfish fry in a small northern Indiana lake. Ph.D. thesis. Indiana Univ., Bloomington. 74 p.

———. 1967. Intralacustrine movements of bluegill fry in Crane Lake, Indiana. *Trans. Amer. Fish. Soc.*, **96**:416-420.

WILSON, C. B. 1923. Water beetles in relation to pondfish culture, with life histories of those found at Fairport, Iowa. *Bull. U.S. Bur. Fish.*, **39**:231-345.

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