TABLE 15 (*continued*)

Metanauplii, *1935*

Month Day	V 26	VI 6	VI 22	VII 10 day	VII 10 night	VII 20	VIII 11 day	VIII 11 night	IX 21
Depth in metres									
0	6.5	5.5	3.0	8.5	6.0	1.2	12.5	24.5	3.0
1	6.0	6.0	4.0	10.5	6.0	9.5	31.5	29.0	7.5
3	5.0	14.0	5.0	11.0	10.0	5.0	21.5	21.0	7.0
5	2.0	10.5	4.5	7.5	3.0	2.0	16.0	24.5	3.0
8	1.0	9.0	4.0	4.5	8.0	1.5	19.0	16.0	2.0
10	1.0	16.0	5.5	5.0	9.0	1.0	18.5	15.0	1.0
12	...	26.0	4.5	4.5	13.0	?	?	?	?

THE FOOD OF THE LAKE NIPISSING CISCO, *LEUCICHTHYS ARTEDI* (LE SUEUR) WITH SPECIAL REFERENCE TO THE UTILIZATION OF THE LIMNETIC CRUSTACEA

By

R. R. LANGFORD

(From the Department of Biology
University of Toronto)

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THE FOOD OF THE LAKE NIPISSING CISCO, *LEUCICHTHYS ARTEDI* (LE SUEUR) WITH SPECIAL REFERENCE TO THE UTILIZATION OF THE LIMNETIC CRUSTACEA

Abstract

Definite correlations were found between the nature and amount of plankton present at different depths, and the food taken by ciscoes caught in comparable strata. These correlations appeared when plankton trap catches were compared with detailed analyses of the stomach contents of between 5,000 and 6,000 ciscoes captured during the season of 1935.

Diurnal differences in feeding were determined in different localities, and from these differences the rate of digestion was ascertained and the daily intake evaluated. A determination of the relative amounts of different food taken by different size groups of the cisco population gave a measure of the value of the different food organisms in the production of this fish. A marked acceleration in growth of fish in the higher age classes appears to be a result of their being able to feed upon *Diaptomus oregonensis* in deep water during the summer. Cisco populations of certain Wisconsin lakes are considered in the light of generalizations arrived at from this study, and the differences in the rates of growth of the fish making up these populations are correlated with existing environmental conditions and food supply.

Introduction

The utilization of food in a lake is primarily dependent upon its quantity and availability. The availability and utilization of this food are in turn governed by the factors which determine its distribution in relation to that of the feeder, and by the factors which control the activities of the latter. Since these factors are many and varied, a measure of the utilization of the food present in a lake can be obtained only through an investigation of the distribution and habits of both food organisms and feeder.

It has been possible to investigate in some detail the utilization of the plankton crustacea by the cisco *Leucichthys artedi* (Le Sueur), which is probably the chief organism feeding upon these forms in lake Nipissing. Previous to 1935 Dr. F. E. J. Fry had obtained considerable data on the habits of the cisco population in the lake. In 1935 he began a study of the vertical distribution of this fish which made it possible to compare the plankton present and that taken by the fish at different depths. Advantage was taken of the opportunity offered at this time, of studying the food of the cisco to determine the utilization of the various plankters and their role in production.

The problem was attacked by determining the vertical distribution at comparable times, of both the plankton and the fish, and analysing the stomach contents of the latter. The primary data were thus concerned with the concentration of plankton in relation to depth, and the volume and nature of the stomach contents of fish caught at comparable depths. It will be appreciated that these data do not in themselves afford an expression of the quantitative relationship existing between food and feeding. The plankton samples within the limits of their error give a measure of the food present, but the stomach contents are not necessarily an absolute expression of the food taken. The stomach content is a resultant of rate of intake of food and the rate of digestion.

Certain questions arose in connection with the significance of stomach contents as a measure of food intake. Is feeding constant during the twenty-four hours? What is the rate of digestion of different foods under different temperature conditions? Does digestion continue after the fish is captured?

In order to answer these questions, the diurnal fluctuations have been investigated by determining the feeding during day and night. Also, it has been possible to obtain some idea of the rate of digestion by following its course with respect to certain indicator organisms taken by the fish, and the problem of digestion continuing after capture, has been attacked by lifting nets set for different periods of time.

In presenting the data it has been considered advisable to begin with the qualitative and quantitative changes in feeding during the season. These have been correlated with the changes in the plankton crustacea present in the water where the fish were caught. Organisms other than the plankton crustacea were taken by the fish, and their importance in the food necessitates a discussion of their utilization. Having gained a knowledge of the seasonal changes in the kind and amount of food taken, both in shallow and deep water, the changes in feeding during the day and night in those two areas are discussed. Using the results of this investigation of the diurnal changes in feeding and the index of digestion afforded by *Mysis relicta*, it is possible to obtain an estimate of the daily intake of food. The influence of factors other than food, particularly temperature, upon the feeding activities of the ciscoes, has been presented in some detail by Fry (1937), and is cited in this report. This gives us, in conclusion, a measure of the role of the limnetic crustacea in the production of the ciscoes of the lake, and an indication of the importance of physical and chemical conditions affecting production.

ACKNOWLEDGEMENTS

The utilization of the plankton crustacea by the cisco *Leucichthys artedi* (Le Sueur), was investigated in co-operation with Dr F. E. J. Fry who was making a study of that species. I am especially indebted to him, and it is a pleasure to acknowledge his assistance both in the field and in discussion of the results here given.

METHODS

The fish were sampled by gill netting. With the exception of one or two sets on bottom, most of the fishing was carried out by setting a gang of nets obliquely from bottom to surface. A discussion and a diagram illustrating this type of set are given by Fry (1937). By this procedure, each 15 foot stratum was fished with a net of $1\frac{1}{2}$, $2\frac{1}{4}$ or $2\frac{1}{2}$, and 3 or $3\frac{1}{4}$ inch stretched mesh. The numbers of specimens obtained in these oblique series are given by Fry (1937) in tables 7, 8, and 9.

Vertical series of plankton trap samples were taken at the period at which oblique sets were made for ciscoes, and in the same locality (Langford, 1938). The zooplankters in the total trap sample were enumerated, and the "settled volumes" were determined for each form appearing in the food of the ciscoes. The average settled volume of each form was then calculated for each interval of depth. A comparison is made between this "food present" and the "food taken" by the ciscoes in different strata. Both the ciscoes and the plankton were sampled at two stations in lake Nipissing, one in deep water (45 metres), and the other in shallow water (15 metres). The positions of these stations are given on maps published in Fry (1937), and also in Langford (1938).

The stomach contents of measured fish were analysed and the state of the alimentary tract was recorded. To obtain a reliable average, large numbers of stomachs were examined (between 5,000 and 6,000 in all). The volumes of the stomach contents were measured as the settled depth in alcohol in 20 x 60 mm. vials, and the percentages of the different organisms were estimated by microscopic examination. The results are expressed as the average volume of food in those stomachs which contained more than a "trace". Fish that were feeding but which had little or nothing in the stomach proper, were not included in the average, because it was considered that such very small volumes were largely a result of digestion taking place after the fish had been captured. Also, during the examination of the fish it was noticed that in certain cases some were completely empty throughout the length of the alimentary tract. It was felt that these individuals had not been feeding *for some time* previous to capture, and could be considered as a group of fish to which the food present was not available.

It was noticed throughout the investigation that fish of different sizes reacted differently to environmental conditions. It was also clear that size groups differed in the kind and amount of food which they ingested. Consequently, in the analysis, the cisco population has been divided into three quite arbitrary size groups in order to show these differences in behaviour. These groups consist of (1) "small" fish (less than 20 cm. in length), (2) "medium" fish (between 20 cm. and 25 cm. in length), and (3) "large" fish (over 25 cm. long).

VERTICAL DISTRIBUTION OF CISCOES

The seasonal variation in the vertical distribution of the cisco population in lake Nipissing is discussed in detail by Fry (1937) and a brief review is given here. In general the ciscoes in lake Nipissing migrate progressively from shallow to deeper water during the months of May, June, and July. During August they are concentrated in the restricted hypolimnion. In September and October they penetrate the thermocline and reappear in the shallow water. This migration is not a simple mass movement, but rather a case of the oldest fish leaving the epilimnion earlier in the spring

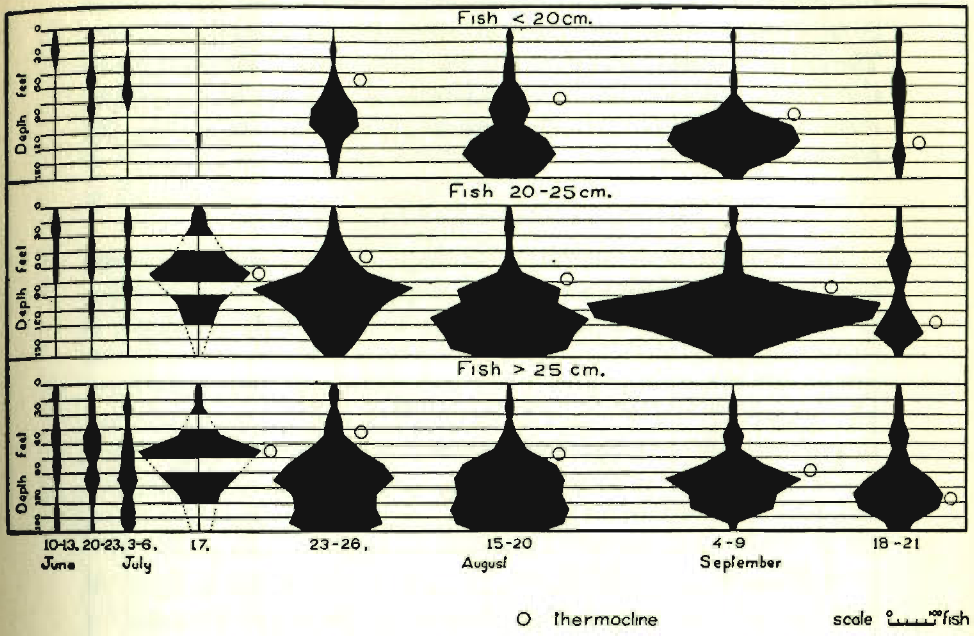


FIGURE 1.—Vertical distribution of ciscoes of different sizes at station I, throughout the season 1935. (After Fry, 1937.)

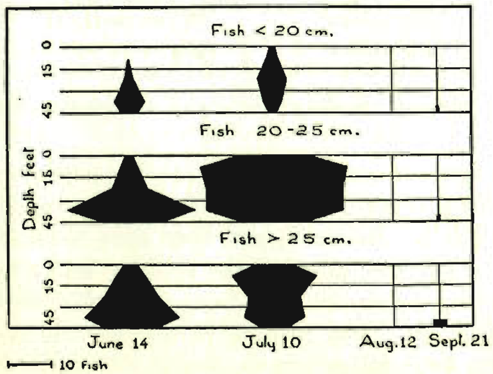


FIGURE 2.—Vertical distribution of ciscoes of different sizes at station II, throughout the season 1935. (After Fry, 1937.)

and returning to it later in the autumn. Fish of the younger age groups are progressively later in migrating to the hypolimnion. The order in leaving is complex. The movement of three arbitrary size groups is illustrated by figure 1 (after Fry, 1937) which depicts their abundance in different strata at the deep-water station (station I) in 1935.

SEASONAL FEEDING AT STATION II

Previous to their migration through the thermocline, ciscoes were taken in shallow water in lake Nipissing. Their distribution at station II, where depths of 45 feet were regularly obtained, is

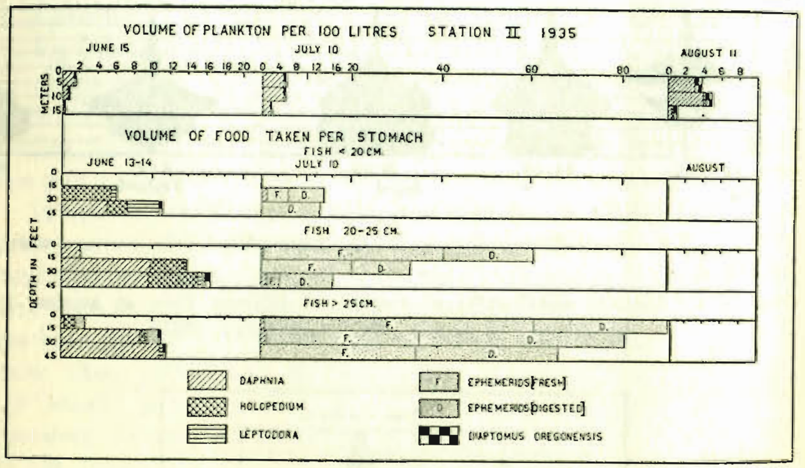


FIGURE 3.—Seasonal food and feeding of ciscoes at station II, 1935.

indicated in figure 2 (after Fry, 1937). They were quite evidently becoming concentrated in this area, since comparable numbers were not taken in similar strata over deep water, at station I. The failure to capture them in the shallow water area in August was expected in view of their great concentration below the thermocline after July 23. The feeding in this area is considered first, as it precedes their migration to deeper water at station I during July.

The vertical distribution at station II, of the species of plankton

commonly eaten by the cisco in lake Nipissing, is given in the upper panel of figure 3. The plankton collections were made at times comparable to those when the fish were sampled by oblique settings of gill nets. The average volume of food taken by "feeding" fish, subdivided into the volumes of constituent organisms, is indicated in the three lower panels. Practically all fish taken in the shallow water were found to be feeding.

Food Present, Station II

It may be seen from figure 3 that even as late as mid-June the volume of food available to the cisco was small, and this consisted principally of *Daphnia longispina*. Very few *Diaptomus oregonensis* were found in the shallow water, and *Cyclops* group and *Diaptomus minutus* were utilized only by fish under 10 cm. in length. By July 10 a marked change occurred in the food available for consumption. No great change was observed in the plankton crustacea, although *Daphnia* had increased somewhat, but at this time there was a great nocturnal emergence of ephemerid nymphs of the genus *Hexagenia*. By August 12 this emergence had been completed, and the population of limnetic crustacea had increased slightly.

Feeding, Station II

In June when the plankton was not abundant, the diet was heterogeneous. Some forms seem to have been selected as they appeared in the stomachs in greater relative proportions than in the water. It is clear from figure 3 and table 1 (p. 184), that neither *Holopedium* nor *Leptodora* were collected incidentally in random straining by feeding fish. Considerable amounts of *Daphnia* were consumed by all sizes of fish.

Although the plankton population underwent no marked change by July 10, the same cannot be said of the food taken by any size group of ciscoes, as the cisco population as a whole was gorged with ephemerids at this time.

The great increase in number of ciscoes in the hypolimnion at station I occurred about July 17 in 1935, and after July 27 there was no further noticeable migration of medium or large fish to deep water. This appears to indicate that medium and large fish had moved from shallow to deep water and thus, although the plankton food was increasing in the shallow water, very little of it was utilized by ciscoes after the middle of July.

FEEDING ACTIVITY OF CISCOES DURING THE SEASON

Fry (1937) states in summary (p. 77):

> Profound changes in the feeding activity of the population are correlated with the summer migration. Fish apparently stop feeding just prior to migrating below the thermocline and do not begin feeding again immediately. The length of time during which they do not feed varies with the time at which they migrated. Fish migrating early may begin feeding about a week after entering the hypolimnion. The last migrants may not feed for a period of six weeks or even longer.
>
> When the fish first leave the hypolimnion in the autumn, they again stop feeding for an undetermined period of time.

The feeding activity during the season as reflected in the results of the analysis of alimentary tracts is indicated in figure 4 (after Fry, 1937). This series of diagrams gives the vertical distribution of the fish obtained at the deep-water station, I (Fry's station 4) in 1935. It should be mentioned that the first three series of diagrams are plotted on three times the scale used for the later series. This has been done to show up the relationships within the three small catches in June and early July (see Fry, 1937, appendix 1).

The population in each 15 foot stratum has been divided into two groups: (1) fish with "full" stomachs, *i.e.* those having at least a trace of food in the stomach proper; (2) fish with "empty" stomachs, *i.e.* those having no food in the stomach. Fish with full stomachs are indicated in the diagrams by black, those whose stomachs were empty, by white rectangles. The greater percentage of fish in the latter groups were classified as "empty throughout" (p. 10) and they are considered as constituting a group to which the food present was not available. Fry considers the movement of the cisco population into the hypolimnion to be a result of an intolerance to high temperatures obtaining in the epilimnion. The cessation of feeding is therefore probably associated with this intolerance. The portion of the population which does feed in the hypolimnion in summer is thus largely made up of a group which migrated early and which in that summer probably did not feed on the mayfly rise in shallow water.

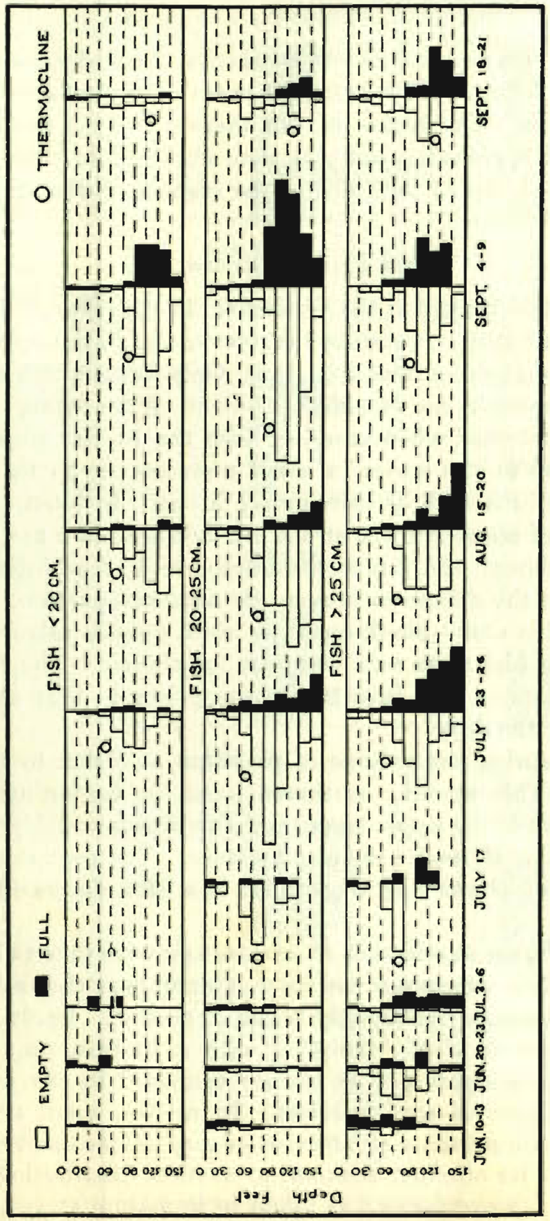


FIGURE 4.—Vertical distribution of ciscoes with full and empty stomachs at station I, 1935. (After Fry, 1937.)

SEASONAL FEEDING AT STATION I

Station I was selected as representative of the deep-water area of the lake. A depth of 150 feet or 45 metres was regularly obtained at this station. The region of the thermocline on the different dates on which plankton samples were obtained in this study, is indicated by circles to the right of the respective diagrams in the figures.

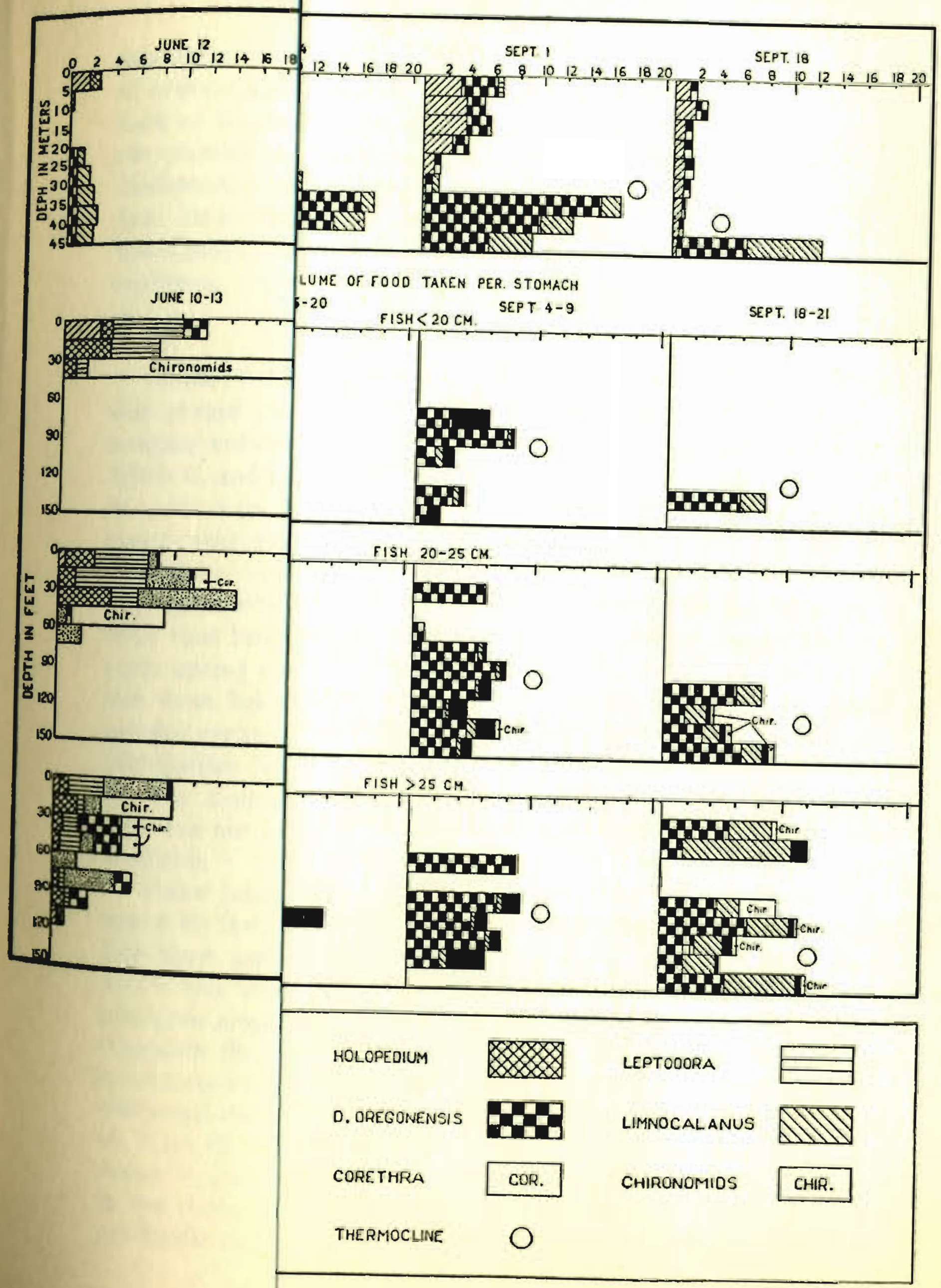
Food Present, Station I

The seasonal change in the volume of the constituent plankters in the different strata at station I is represented in the upper panel of figure 5 and given in table 2 (p. 185). Only forms which appeared in stomach contents are included. Not all of the forms taken by the fish are detected when sampling with the 10 litre trap, due to their presence in the water in small numbers, or to their being bottom organisms such as chironomid larvae. In illustrating the distribution of plankters, the strata are indicated in 5 metre intervals, and although the fish were sampled in 15 foot intervals, at no point does the difference prevent detailed comparison.

During this study plankton series were usually taken at midnight, on the night the nets were set for ciscoes. The plankton catches of June 12 and July 19 are exceptions in that they were taken during the day.

In early spring the volume of plankton available to the cisco was small. This scarcity continued until the beginning of July when *Daphnia* of the upper layers and *Diaptomus* and *Mysis* below the thermocline showed a definite increase. The peculiar vertical distribution of *Diaptomus oregonensis* has been discussed (Langford, 1938).

The maximum numbers of *D. oregonensis* were taken about the middle of July. *Mysis* reached its maximum near the end of July when *D. oregonensis* had already begun to decline. Because of the small numbers of *Mysis*, sampling with a 10 litre trap was inaccurate. This inaccuracy is further increased in the graph by the large volume of the organism. In reality, then, the graph denotes only its presence or absence in trap catches and does not delimit either its absolute seasonal or vertical distribution. To a large extent *Limnocalanus* was taken in immature stages, so that



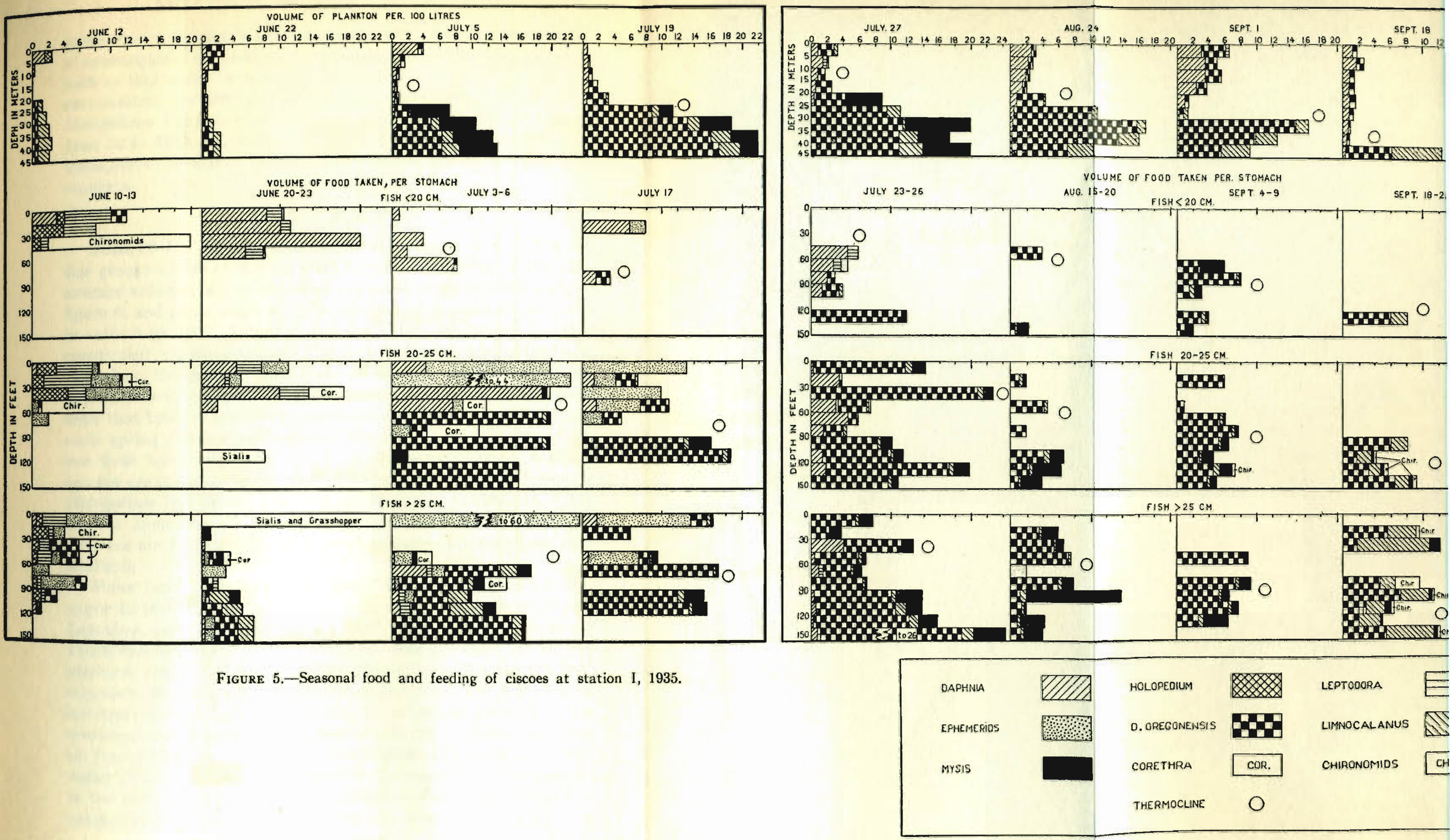


FIGURE 5.—Seasonal food and feeding of ciscoes at station I, 1935.

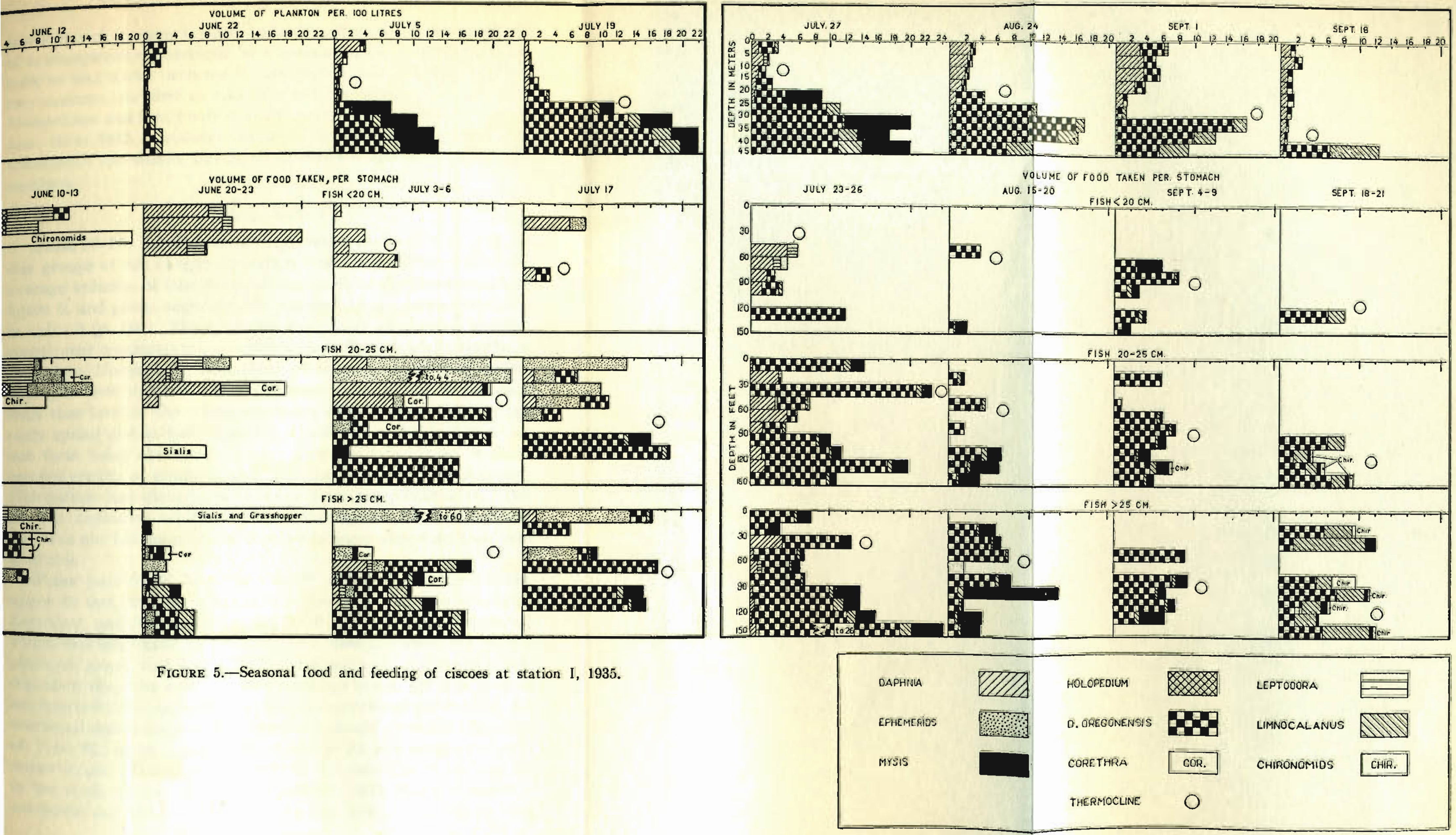


FIGURE 5.—Seasonal food and feeding of ciscoes at station I, 1935.

any apparent increase is likely to be due either to the development of unrecognized metanauplii, or a concentration of the population such as that which occurred in late September. *Daphnia* showed two maxima, the first in mid-July and the second in September. *Holopedium* was found only in early spring and had disappeared by June 22 in 1935. *Leptodora* occurred in the samples sporadically throughout the season, but at no time did it appear in significant numbers.

Feeding, Station I

June 10-13. An analysis of the stomach contents of each of the size groups of fish caught at station I on these dates yielded the average volumes of food taken as indicated in the lower panels of figure 5, and given, together with numbers of stomachs examined, in table 3 (p. 186). These volumes have been sub-divided into the constituent organisms taken, which include the following: *Daphnia*, *Leptodora*, *Holopedium*, *Diaptomus oregonensis*, chironomid larvae, and ephemerid nymphs. A comparison of the feeding at this date with that later in the spring emphasizes the heterogeneity of the early spring diet in lake Nipissing which was probably due to no one form being abundant. Later, when certain forms had increased greatly in numbers, they were fed upon almost exclusively. *Holopedium* had disappeared entirely from the plankton by June 22, but *Leptodora*, which continued throughout the summer and fall, was not fed upon at the time when more abundant food was available.

From June 10-13, when the "small" fish were restricted to the upper 45 feet, they were found to be feeding chiefly on *Daphnia*, *Leptodora*, and *Holopedium* in the 15-30 foot stratum. *Leptodora*, which was important in the food here, does not show up in the plankton graph, and was probably selected as it is a much larger organism than the others. The plankton graph for this date is constructed from daylight sampling, as mentioned above, but the nocturnal distribution of *D. oregonensis* should correspond to that of June 22, which would make possible its consumption in the upper strata. *Daphnia* was found in the stomachs of fish caught in the upper 15 feet only. It is probable that they underwent a nocturnal migration to this level at this time. *Holopedium* was found at the 1 metre level only, when sampling; therefore, either this organism or the cisco must have moved vertically during the feeding period investigated. It seems reasonable to believe that the single fish caught in the 30-45 foot stratum had obtained the small chironomids near bottom in shallow water since no "small" fish were taken below 120 feet until after July 17, and since chironomid larvae have never been taken as plankters in this lake. Because of the small number of fish taken, it is deemed inadvisable to attempt any interpretation of the relative volumes of food taken in different strata.

"Medium" fish were found to be feeding throughout their range in depth, selecting *Leptodora* as did the "small" fish. One fish had also obtained chironomid larvae. Several had obtained ephemerid nymphs. Again insufficient numbers of fish were taken to afford a reliable average for each depth.

"Large" fish were distributed from top to bottom and occurred in numbers large enough to give some indication of relative consumption of food organisms at different depths. *Daphnia* was not of importance in their food. *Holopedium* was found in fish taken at all depths but to a greater extent in those from the upper layers. *Leptodora* was again selected, as were ephemerids. The large fish showed a preference for *D. oregonensis* even at this early date when the latter were quite scarce in the lake. Chironomid larvae were again taken, but found only in fish above 60 feet. Feeding dropped off considerably below 90 feet and the fish caught below 120 feet had no food in their stomachs. On June 6 there were no fish near bottom in this deep water. Therefore these fish have arrived in this stratum recently.

June 20-23. "Small" fish were feeding almost exclusively upon *Daphnia*, and were finding it possible to obtain a fair quantity of food. Some were still selecting *Leptodora* as part of their diet.

"Medium" fish were also utilizing the *Daphnia* population and selected *Leptodora*, ephemerids, and *Corethra*. These fish were taken in the upper 60 feet. One fish caught in the 105-120 foot stratum had fed in shallow water on *Sialis* larvae, but all fish taken in the deeper strata were empty.

Of the "large" fish, two caught in the 0-15 foot stratum had

fed on *Sialis* and grasshoppers. One fish in the 15-30 foot stratum had obtained *Mysis*, and in the 30-45 foot stratum one had eaten a few *Daphnia*, and another had taken *Corethra*. There is a marked contrast in feeding between these "large" fish and "small" and "medium" fish in similar positions. Presumably these "large" fish had difficulty in obtaining *Daphnia* in satisfactory amounts.

Between 45 and 90 feet, feeding was varied and fairly unprofitable. Below 90 feet, the food taken by "large" fish increased, and this was correlated with the greater number of food organisms present in this region. *Limnocalanus* and *D. oregonensis* predominated in the food taken by these fish, and since *Limnocalanus* did not appear above 65 feet at this time, these fish must have fed in the strata where they were captured. Some ephemerid nymphs appeared to be selected, but the other food was taken in proportion to its abundance. Differential digestion of such diverse forms as mayflies and entomostraca may, of course, be responsible for the apparent selection of the former.

At the time of sampling the plankton, there was a considerable volume of food in the 0-10 metre stratum which was not utilized by any of the fish caught in this stratum. It is possible that this concentration consisting mostly of *D. oregonensis*, which was no doubt due to diurnal migration, did not continue long enough to allow it to show up in stomach analyses.

July 3-6. By July 5, a definite thermocline had been formed between 45 and 60 feet. The staple forms of food had increased and were regionally separated by the thermocline. *Daphnia* had increased in the epilimnial layers, while the *D. oregonensis* population there consisted of only a few mature individuals. Below the thermocline, immature *D. oregonensis* had increased greatly and bulked large as a food organism. *Limnocalanus* was also restricted to the hypolimnion, and *Mysis* was taken for the first time during the season in this region.

The "small" ciscoes continued to feed almost exclusively upon *Daphnia*. Only one such fish was taken in the 0-30 foot stratum and only one in the region of the thermocline. More were taken immediately above and below the thermocline, and feeding was greatest at the 60-75 foot level. It is interesting to note that a small amount of *D. oregonensis* was taken by "small" fish below the thermocline where this crustacean was most abundant.

In the upper 30 feet the food of "medium" fish was chiefly emergent mayflies. These fish were probably lateral migrants from shallow water where the mayfly rise was occurring. From 30 feet to the thermocline their food was principally *Daphnia*. A striking change in diet occurred below the thermocline where *D. oregonensis* became the predominant plankter taken. Since the number of the "medium" feeding fish taken was not great, the absolute volumes of stomach contents recorded are not in themselves especially significant. Only one fish was captured in the 105-120 foot stratum and only one in the 120-150 foot stratum. There was a great apparent difference in feeding in these two strata which was likely due to insufficient data. However, all of the twenty feeding fish taken at this time were obtaining considerably more food than previously.

The "large" fish above the thermocline were not feeding, with the exception of two fish feeding at the surface which were gorged with emergent mayflies, probably obtained over shallow water. In the region of the thermocline, mayfly nymphs were taken but feeding was slight and varied. Again, as in the case of "medium" fish, the diet in the hypolimnion was in marked contrast to that above the thermocline. Numerous fish were feeding, some partly on the large *Daphnia* which remained in the colder water, but again immature *D. oregonensis* made up the bulk of the food. The greatest volumes of *D. oregonensis* were taken where its population was most concentrated. The variety of forms taken in the upper hypolimnion seems to indicate a scarcity in the supply of *D. oregonensis* and a selection of such forms as *Mysis*, *Limnocalanus*, *Daphnia*, and *Leptodora*.

It is evident that fish feeding below the thermocline did not move up into the epilimnion. The increase of *Daphnia* above the thermocline, together with the rise of the mayflies in shallow water and the increase of *D. oregonensis* in the hypolimnion, were of great importance in the increase in food taken at this date.

July 17. A complete series of net settings was not made at this date. Gaps therefore occur in the distribution graphs of the

ciscoes and of stomach contents. The steepest gradient of temperature occurred between 72 and 84 feet at this time. *D. oregonensis* had increased greatly in numbers below the thermocline. The numbers of *Daphnia* were probably similar to those found on July 5, but *Limnocalanus* showed an increase which was likely due to the development of unidentified nauplius stages.

Figure 5 indicates the *daylight* distribution of plankters on this date. This might affect the correlation between "food present" and "food taken", for mature *D. oregonensis* sometimes migrate to the surface at night. *Daphnia* also showed a slight diurnal migration at some periods during the season. Immature *D. oregonensis* were, however, restricted below the thermocline both day and night.

Little can be said about the feeding of "small" fish on this date. In upper layers they had taken *Daphnia*, and at 75 feet some *Daphnia* and *D. oregonensis*.

"Medium" fish in the upper layers were taking mayfly emergents as on July 3-6, although in smaller amounts. There was a decrease in the feeding upon *Daphnia*, and mature *D. oregonensis* were obtained in the upper layers correlated with the increase in their numbers there. No fish were obtained in either the 75-90 foot or 120-150 foot strata, but between 90 and 120 feet feeding was similar to that of two weeks previous.

Of the "large" fish above 60 feet, some were still obtaining mayfly emergents and some *Daphnia*, and some had begun to feed upon mature *D. oregonensis*. Evidently mature *D. oregonensis* had not been numerous enough to be utilized previously, or at least to be recognized in the stomachs. No large fish were taken, however, in the 30-45 foot stratum. Below 60 feet the food of the "large" fish was predominantly immature *D. oregonensis*. Feeding here had also increased, and this fact was correlated with the increase of this organism present in the water. *Mysis* and *Limnocalanus* present in the stomachs were probably captured incidentally.

July 23-26. By July 27 the thermocline, which had been present at 75-90 feet on July 19, had disappeared and another had been formed between 30 and 45 feet. The mature forms of *D. oregonensis* were concentrated in the upper 2 metres of water and the immature forms remained below the thermocline. Some *Limno-*

calanus were found in the upper 5 metre stratum, but maximum numbers were found from 25 metres to bottom. This is exceptional for no nocturnal migration of this form occurred later in the season. *Mysis* was collected only in the hypolimnion but may have been present in small numbers above the thermocline. *Daphnia* was found at all depths but was scarce in the lower hypolimnion.

"Small" fish in the epilimnion and in the region of the thermocline were not feeding. In the upper hypolimnion *Daphnia* was the predominant organism taken, together with some *Limnocalanus*. In the lower hypolimnion *D. oregonensis* predominated in the food. Between these extremes there appeared to be a gradual transition correlated with the numbers of these two staple food organisms. The correlation was, however, modified by an apparent selection of the larger organisms. In the 60-75 foot stratum *Daphnia* was scarce, and *D. oregonensis* abundant, yet no *D. oregonensis* was taken. Larger forms, *i.e.*, *Daphnia*, *Leptodora*, and mayfly nymphs made up the stomach contents.

"Medium" fish in the epilimnion were obtaining considerable amounts of mature *D. oregonensis*. *Limnocalanus* and *Mysis* were also taken above the thermocline at this date. In the hypolimnion, food taking was similar to that of small fish. The selection of *Daphnia* was not so marked in the upper hypolimnion but appeared to be greater in the lower strata. It is peculiar that in the epilimnion, although *Daphnia* was present in maximum numbers, it was taken as food by less than 50 per cent. of the feeding fish, and in small amounts. *Mysis* and *Limnocalanus* did not appear to have been selected below the thermocline, although selection may have been responsible for their occurrence in the food taken in the epilimnion. *D. oregonensis* made up 75 per cent. of the food taken by medium fish at this time.

"Large" fish in the epilimnion and region of the thermocline were feeding upon mature *D. oregonensis*, some *Daphnia*, and some *Mysis*. Below this depth immature *D. oregonensis* made up 80 per cent. of the food taken. *Mysis* and *Limnocalanus* were taken in amounts comparable to their relative abundance, and *Daphnia* appeared to have been taken only incidentally.

The population of "feeding" fish collected the greatest volumes of purely planktonic material at this time. The composition of

this food material contrasted greatly with the composition of comparable volumes obtained during the earlier part of the month. The mayfly emergence being completed, this food organism, previously so important to part of the fish population, practically disappeared from the diet. Mature *D. oregonensis* took the place of the mayfly food in the epilimnion, while the immature forms became by far the most important food in the hypolimnion. *Daphnia* again increased in importance in the diet of "small" and "medium" fish.

August 15-20. On August 18, the thermocline lay between 45 and 60 feet. In the epilimnion *Daphnia* had increased greatly, and the numbers of mature *D. oregonensis* had decreased. In the region of the thermocline there was a minimum of food present. In the hypolimnion *Daphnia* was distributed in diminishing numbers from the thermocline to the bottom. Immature *D. oregonensis* was most abundant in the upper hypolimnion, but *Limnocalanus* reached maximum numbers at the bottom. *Mysis* was trapped only in smaller numbers from surface to bottom. The numbers of immature *D. oregonensis* did not appear to be materially lessened except in the lower strata.

"Small" fish had practically ceased to feed at this time. One fish caught in the region of the thermocline appeared to have fed below the thermocline. Two fish were captured in the 135-150 foot stratum, and had fed slightly on organisms present there.

"Medium" fish above 105 feet were feeding to a limited extent, and only three feeding fish were captured in these strata. Below 105 feet the amount of food taken was small, although several feeding fish were captured.

"Large" fish in the epilimnion, and region of the thermocline, had been feeding to some extent. In the hypolimnion, feeding upon *D. oregonensis* decreased with depth, in marked contrast to food taking on July 23-26. The taking of *Mysis* increased greatly, and it appears to be definitely selected here.

The decrease in the average volume of the stomach contents observed in this series was very marked. This is probably because there had been a migration of certain groups of ciscoes to the epilimnion (Fry, 1937). These fish were in all likelihood those which had previously been feeding very heavily in the hypolimnion. It is significant that the ciscoes caught in the epilimnion and in the region of the thermocline had all fed upon immature *D. oregonensis* which they could have obtained only in the hypolimnion. In the case of the "large" fish, it is also possible that intense sampling had reduced the numbers of the heavy feeding group. The small volume of the stomach contents of the feeding fish at this time is thus considered to be a consequence of the commencement of feeding by previously fasting fish and the loss of previously feeding fish. These fish which had begun to feed were not yet feeding very heavily.

In the middle of August it appears that the volume of food taken by the ciscoes depends more upon the peculiar activities of that fish than upon the amount of plankton present. No ciscoes were feeding in the epilimnion even when present there, and therefore the increase of *Daphnia* in this region was not utilized by them. In the hypolimnion *Limnocalanus* had increased in numbers, but the ciscoes remaining there were not feeding to any extent at this time, and were not eating as many *Limnocalanus* as they had previously, when the numbers of that form had been fewer. The numbers of *D. oregonensis* had decreased somewhat, but there was, for the time being, a much more marked decrease in the feeding activity.

September 4-9. By September 9 the thermocline had been depressed to 90 feet. Correspondingly the *Daphnia* distribution was lowered in the epilimnion. Immature *D. oregonensis* occurred in maximum numbers just below the thermocline in the 30-35 metre stratum, and decreased in abundance from there to bottom. *Limnocalanus* was also numerous only in the restricted hypolimnion.

As discussed elsewhere (Fry, 1937), there was an increase in the numbers of "small" fish feeding at this date. With the exception of the 75-90 foot stratum, this increase was due principally to fish which had only a trace of food. The fish in the 75-90 foot stratum had evidently secured their food in the hypolimnion and were actively migrating above the thermocline. In the hypolimnion only five fish were captured with more than a trace of food in their stomachs. It is quite clear that these fish were just beginning to feed.

The great increase in the numbers of "medium" fish feeding at this date was in contrast to the large number of "small" fish which had only a trace of food. In the epilimnion twenty-six fish contained considerable food (figure 5). The absence of *Daphnia* from these stomachs, and the presence of immature *D. oregonensis* in them, indicate that these fish were feeding below the thermocline and were migrants to the epilimnion. The massed numbers of feeding fish immediately above the thermocline, where food was relatively scarce, bear out this assumption. Below the thermocline the increase in numbers feeding was also greater and volumes of food taken were comparable to those above the thermocline.

The "medium" fish in the hypolimnion were feeding on the plankton organisms present there. Although these fish were feeding more actively than those on August 15-20, they were not obtaining as much food as did fish of similar size in July. Feeding seems to have been fairly uniform throughout the hypolimnion.

"Large" fish above the thermocline showed feeding habits similar to those of "medium" fish. Few fish with food were caught above 75 feet (figure 5). In the 75-90 foot stratum the average of sixteen feeding fish showed a volume and percentages of forms similar to those of fish captured in the hypolimnion.

In the upper hypolimnion, food taken corresponded with the plankton available, with the possible exception of some selection of *Mysis*. In the 120-135 foot stratum, however, feeding differed in that the amount of *D. oregonensis* decreased and the selection of *Mysis* was more marked. In the 135-150 foot stratum no feeding fish were captured. This phenomenon was dependent upon two facts: (*a*) the numbers of *D. oregonensis* had decreased in the lower 10 metres, and (*b*) the fish population had migrated out of the lower hypolimnion (Fry, 1937). The conditions noted in the August 15-20 series, indicating an upward migration of the individuals which feed early after their arrival in the hypolimnion, are seen to be more marked in early September. More ciscoes with stomach contents were taken above the thermocline. The complete contents of all the stomachs of these fish were of hypolimnial origin. The definite increase in the numbers of feeding individuals among the small fish apparent on this date is correlated with a low average stomach content. "Medium" fish which showed this increase in feeding activity by the date of the previous series were now taking more food per fish.

September 18-21. By September 18 the thermocline had been still further depressed, lying in the 105-120 foot stratum. The *Daphnia* were distributed, in decreasing numbers, from the surface to the thermocline. Maximum numbers of immature *D. oregonensis* were limited to the 40-45 metre stratum but showed no dense concentration, large numbers having penetrated the thermocline. *Limnocalanus*, on the other hand, showed a concentration of the population below 40 metres.

The average stomach volume of only two "small" fish appears in the graph (figure 5). These were feeding upon immature *D. oregonensis* and *Limnocalanus* in the 120-135 foot stratum.

"Medium" fish, which had fed, were captured from 90 feet to bottom. All had fed below the thermocline, even those captured in the epilimnion. In each of the three lower strata, a few of the fish had fed upon chironomid larvae.

"Large" feeding fish were captured in the 15-45 foot stratum, and from 105 feet to bottom. All had been feeding in the very restricted hypolimnion, as they contained large amounts of *Limnocalanus* which is confined to this region. It would appear that this form had not been sufficiently concentrated earlier to make it an important item of diet. Chironomid larvae were also taken by "large" fish.

None of the fish captured at this season had been feeding on *Daphnia*. All showed definitely that they had obtained their food in the hypolimnion. The fish that had previously risen from the hypolimnion, together with those leaving at this date, did not appear either to begin or to continue feeding when they reached the epilimnion. This could hardly be due to lack of food for similar fish utilized *Daphnia* to a considerable degree when this organism was present in comparable numbers earlier in the season.

SUMMARY OF FEEDING AT STATION I AND STATION II

From the preceding detailed analysis of the seasonal feeding, certain general facts become noticeable, *viz.*:

(1) The diet was heterogeneous at certain times when no single utilizable form occurred in easily available quantities.

(2) The greatest amount of purely planktonic material and probably of food in general was taken by feeding fish in middle or late July, and this corresponds to the maximum observed in numbers of *D. oregonensis*. Since the feeding fish represent only a minor portion of the population at this time, this maximum amount of food taken by feeding fish does not necessarily indicate the maximum amount of food taken by the population as a whole.

(3) At certain periods of the season certain forms were found in the stomachs in greater relative numbers than in the plankton collections. It is evident that these forms must have been definitely selected by the ciscoes rather than taken incidentally in random straining. It is also rather improbable that they were located by sight as all catches were obtained at night. Whatever the means of sensing the presence of such organisms, the results of this selection are evident.

(4) A great decrease in the amount of food taken by feeding fish occurred after July 27. This has been considered due to a migration from the hypolimnion of fish feeding there in July, and the commencement of feeding by previously non-feeding fish, at which time they probably take very little food. This phenomenon was most marked in the August series.

(5) *Diaptomus oregonensis* was the most important purely planktonic food organism of fish over 20 cm. in length. Its peculiar distribution practically restricted its utilization to fish in the hypolimnion. Fish less than 20 cm. in length utilized this organism only to a very slight degree. Previous to July 17 this was due to the fact that these "small" fish were not present in the hypolimnion, later because they were not feeding to any extent.

This organism was not taken as a principal food until its numbers in the plankton become considerably higher than those of any other organism present.

(6) The taking of *Daphnia* was in contrast to that of *D. oregonensis* in that *Daphnia* was not utilized to any extent by "large" fish but was the primary food of those below 20 cm. in length, and was fed upon to a large extent by "medium" fish.

The seasonal abundance of *Daphnia* was also in contrast to that of *D. oregonensis*. It reached a maximum early in the summer and decreased rapidly, as a result of the feeding activity of "small" and "medium" fish. When "small" and "medium" fish ceased feeding in the epilimnion and subsequently migrated to the hypolimnion, *Daphnia* regained a maximum abundance in the epilimnion. When the ciscoes migrated from the hypolimnion later, they did not feed in the epilimnion and this maximum persisted.

(7) *Holopedium*, taken in plankton trap catches and in stomachs only in the spring, was of importance in the food of each of the three size groups before other forms became abundant.

(8) *Leptodora* was of importance as food only in the spring owing to the lack of other forms in abundance at that time. It was taken in plankton collections in comparatively equal numbers throughout the season.

(9) *Mysis* was taken by the ciscoes in increasing amounts throughout the season, reaching a maximum in August. It is not known whether or not this corresponded with their maximum abundance in the plankton population.

(10) *Limnocalanus* was taken in small amounts throughout the season. A great increase in its consumption occurred when it was concentrated by the depressed thermocline in September.

(11) Other organisms were present in the plankton population, but were not utilized by fish of the sizes discussed. *Diaptomus minutus*, the *Cyclops* group, *Bosmina*, nauplii, and metanauplii are included in this unused portion of the plankton population. These forms are all smaller than any of the forms taken by the fish, and evidently were not strained out by the gill rakers of fish of these sizes. They were, however, found in the stomachs of ciscoes from 5 cm. to 7 cm. in length.

(12) *Corethra* was taken in the early part of the season when it was evidently planktonic.

(13) Chironomid larvae were utilized in early spring, and were evidently picked up on or near bottom in shallow water. In September they were again taken, but at this time in deep water below the thermocline, although they were found in stomachs of fish caught in the epilimnion.

(14) Ephemerid nymphs were important in the food of "medium" and "large" fish early in the season. At the time of

the peak emergence in shallow water in July, sub-imagos and rising nymphs are of extreme importance in the food of "medium" and "large" fish in the epilimnion.

THE SIGNIFICANCE OF STOMACH ANALYSIS

The *average* volume of food in the stomachs of "feeding" fish, which has been discussed previously, is, however, not a complete expression of the intake of food at any season. Sampling was not continued over the complete twenty-four hour period of the diurnal cycle, and the daily intake of food is not known. A few studies made indicate that there were at times great differences in feeding during day and night.

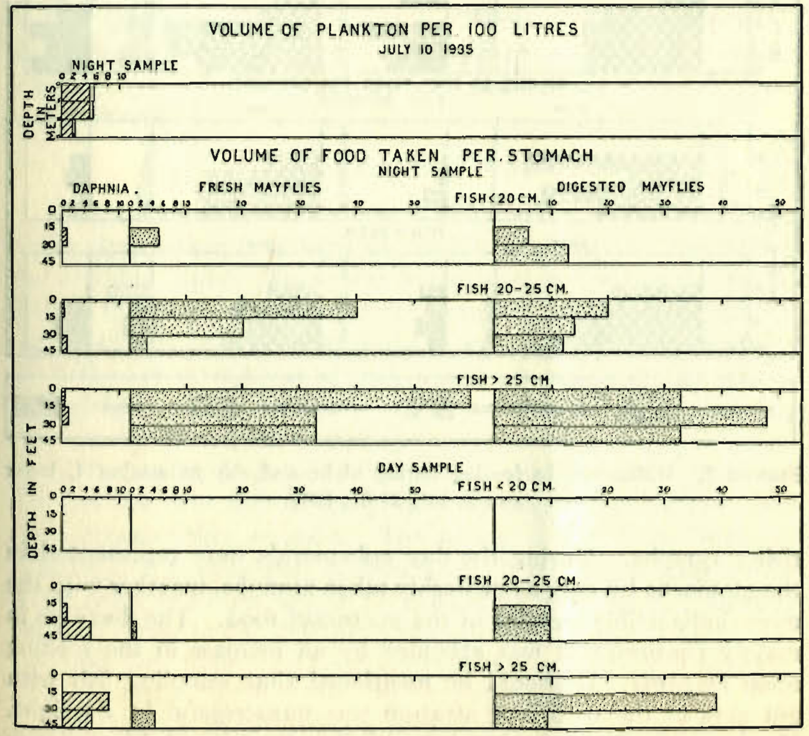


FIGURE 6.—Differences in feeding during night and day at station II, July 10, 1935.

Diurnal Differences in Feeding

On July 10 sets were made in daylight and in darkness at station II. This was the period at which mayflies bulked so large in the food. The relation between the feeding in the two periods is indicated in figure 6 and the data are tabulated in table 1 (p. 184). At night when the mayflies were actively rising to the surface, they were the dominant food organism and were taken as sub-imagos and

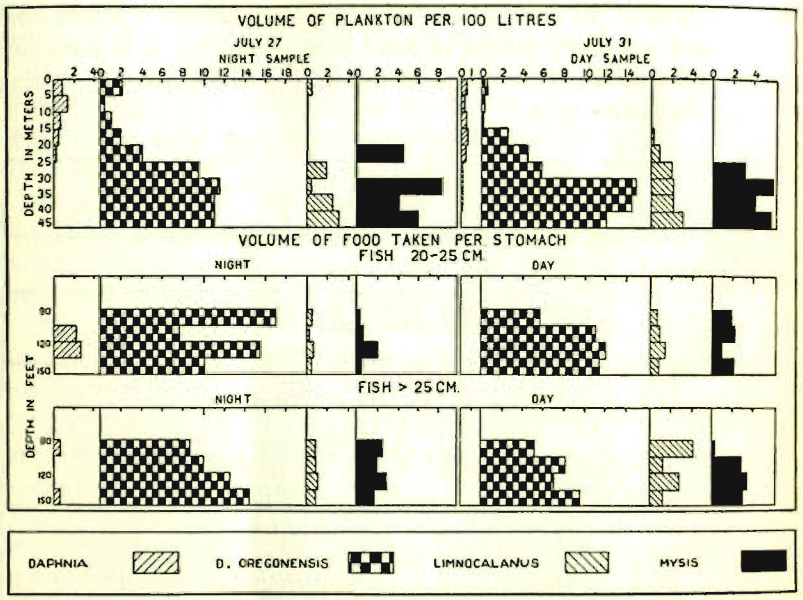


FIGURE 7.—Differences in feeding during night and day at station I, lower strata, July 27-31, 1935.

rising nymphs. During the day ephemerids were represented in the stomachs by only a few freshly taken nymphs, together with the more indigestible remains of the nocturnal food. The decrease in mayfly consumption was attended by an increase in the feeding upon *Daphnia*. It should be mentioned that sampling fish with gill nets in the 0-15 foot stratum was unsuccessful in daylight. However, considerable numbers of "medium" and "large" fish were obtained in the lower strata.

In contrast to the above type of diurnal feeding is that illustrated in figure 7, the data for which are given in table 4 (p. 189). On July 31, 3-inch mesh nets were set obliquely between 120 and 150 feet during the day. On July 23-26 a series of oblique settings had been made between these depths at night. The "food taken" by "large" and "medium" fish caught in the 3-inch mesh nets during this period is compared to that of fish obtained during daylight on July 31. The "food taken" by these fish cannot, however, be compared to that illustrated in figure 5, since, due to the larger mesh of the net, the larger "medium" fish are selected in the case discussed here. Feeding in deep water was at this time confined to the plankton crustacea.

Although there was no marked migration of the plankton forms living below 120 feet, *Limnocalanus* and *Mysis* were taken to a slightly greater extent during daylight hours. This may possibly have been due to active selection by sight. Roughly speaking, however, the Entomostraca were fed upon equally during daylight and darkness.

Daily Intake of Food

To determine the food intake of fish feeding in the lower strata of the deep water, nets were set for four hour periods throughout the day and night. There was a variation in feeding during the period, the peak of consumption occurring about noon (figure 8 and table 5, p. 189). The volumes of organisms in the stomachs of fish collected at the end of each four hour period are plotted on the upright pillars. Connecting lines indicate the increase or decrease for the period following.

If we consider in detail only the food organism *Mysis*, indicated in black, we note that it was principally responsible for the maximum consumption at noon. The taking of this form decreased gradually to a minimum at 4.00 a.m. *Mysis* being large it was found possible to distinguish between fresh material and partially digested forms and to determine the relative volumes of each. The eyes appeared to be most resistant to digestive action and remained after the rest of the body had become shredded.

The change in the volume of partially digested *Mysis* in the stomachs is represented in white, immediately above that of fresh

Mysis. The greatest amount of partly digested *Mysis* was found four hours after the greatest intake of the form. Following along the cycle, although there was a constant decrease in the amount of *Mysis* taken, the effect of the great intake at noon is not lost until eight o'clock the next morning, after which a rapid decrease occurs until noon.

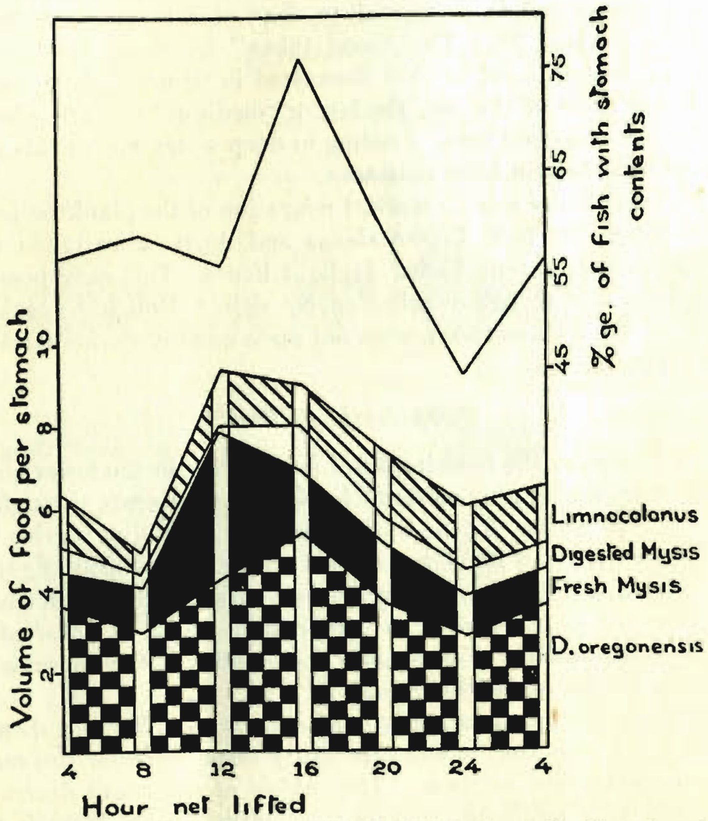


FIGURE 8.—Variation in feeding of ciscoes throughout the diurnal cycle at station I, lower strata, 1935.

It would therefore appear that within the eight hours from 4.00 a.m. until twelve noon, the stomach is practically cleared of *Mysis*, and considerable digestion and evacuation must take place in even four hours. As *Mysis* is the largest of the crustacea taken, it is possible that the smaller forms pass through the stomach in

approximately four hours. The average daily intake of food is, then, considerably higher than that indicated as the *average* stomach content. It is possible that the daily intake is four or even five times the average figures given in the previous discussions.

Digestion after Capture

A complete evaluation of the daily intake of food is not obtained even when consideration is given to diurnal changes in feeding. If the stomach contents of a fish which has been feeding continuously are preserved immediately after its capture, the volume of food present in the stomach represents the resultant of rate of intake and rate of digestion. If, however, a fish has remained alive in the net for a period of time before preservation, digestion and peristalsis may have continued, and the volume determined may be below the natural volume for feeding fish, since the captured fish will have ceased to feed. As the catch of any series is made up of fish caught at different times during the twelve-hour fishing period, many fish will have remained alive in the net for some part of this time. It was hoped that by eliminating the stomachs containing very small volumes, an average nearer that of the free population was obtained.

The above suppositions are borne out by the comparison of two different series given below. Three catches were taken, lifting the net every four hours, on the night of August 12-13, and a twelve-hour set was made on August 17-18. Both series were taken in the stratum between 120 and 150 feet inclusive at station I. In the four-hour catches 47 per cent. of the fish were empty; in the twelve-hour catch, 61 per cent. were empty. These series were taken within a short interval of time so that changes in the feeding habits of the population may be considered as negligible.

It is also probable that the amount of food being taken by the population will have an influence on the proportion of stomachs recorded as empty in any catch. In data obtained from fishing in shallow water in spring and early summer, it was seen that when ciscoes were feeding heavily the proportion of full stomachs was high. In May when food was scarce and stomach contents were of small volume, only 38 per cent. were found with contents. In June when the amount of food taken was higher, 88 per cent. were classified as "full", and in July when the fish were gorged with mayflies all were found with food except for one or two recorded as "empty throughout".

Two facts are clearly illustrated by figure 8. When the amount of food taken was at a minimum, the percentage of fish with stomach contents was comparatively low. The maximum percentage of fish with stomach contents lags behind the maximum consumption. It is believed that this lag indicates that fish caught early in the period of minimum consumption had practically emptied their stomachs before analysis, since they were unable to feed after capture. This appears to be consistent with the information obtained from samples taken in the eight to twelve o'clock period. On the other hand, the maximum percentage of fish with stomach contents was found four hours after maximum consumption. This seems to be the result of the larger amount of food present in fish at the beginning of the twelve to sixteen o'clock period. Owing to the presence of this large amount of food in the stomach, more of these fish still retained some at death.

The variation between the maximum and minimum percentage values for fish with stomach contents was from 44 to 77 per cent., and a regular relationship existed between amount of food taken and percentage of stomachs with food.

THE ROLE OF PLANKTON IN PRODUCTIVITY

The extreme complexity of the interrelation between the plankton and the cisco populations emphasizes the importance of precise information regarding the distribution of food and feeder, and the habits of both throughout the season. An analysis of stomachs of fish caught on bottom cannot be considered as an index of the food obtained by the population as a whole, for feeding has been shown to be dissimilar at the different levels in which the fish are distributed. Neither does a determination of the daylight distribution of plankton give a complete picture of the relation between food and feeder, for many of the plankton crustacea change their vertical distribution during the diurnal cycle. The fact that differences exist in the proportions of the cisco population which are feeding at different periods of the season must also be taken into consideration in the assessment of the rôle of the plankton in the production of this species.

In the previous discussion it has been shown that the amount of plankton present is not an absolute measure of its utilization. Food must necessarily be in close proximity to the feeder to be available. For this reason the availability is primarily governed by the relationship existing between the distribution of the plankton and the fish. For example, the second seasonal maximum of *Daphnia* in lake Nipissing is not utilized by the ciscoes since it occurs in the epilimnion at a time when the fish are confined to the hypolimnion. Indeed, it is possible that this second maximum is a result of the cessation of consumption of this form by the cisco.

Not only must the food be where it may be taken by the feeder but there must be a desire to feed on the part of the fish. From a study of the migratory habits and the consequent changes in feeding activity of the ciscoes in lake Nipissing, it is evident that the population is not a homogeneous whole with respect to its intake of nutritive material. Certain groups are able to feed in different localities and over longer periods than others, and differences exist in the kinds of food which they are able to obtain. Thus while there may be a relation between the volume of stomach contents of feeding fish and the abundance of plankton in a given locality, it is not always possible to determine the intake of food for the total population from the average stomach content of feeding fish, since these may form only a minor percentage of the total population present there. Neither is it justifiable to determine the average stomach content for the total population since, at times when large numbers of non-feeding fish are present, the food taking is not a random activity of the population as a whole, but is confined to a special group.

Although it was not possible to obtain absolute measurements of the food taken by the different size groups of the cisco population because of the very great complexity of interrelations between food and feeder, some generalizations may be given. Apparently the larger fish which migrate early to the hypolimnion are able to feed almost continuously from spring until the middle of September, upon food of high fat content, the plankton crustacea. At the peak of consumption these fish were obtaining an average of 80 mm.

of this food per twenty-four hours (as measured in 20 x 60 mm. vials). This is a calculation based on the average stomach content (16 mm.) multiplied by five since this material is apparently passed through the stomach in from four to five hours. This daily intake is about equal in volume to that obtained by fish in shallow water during the mayfly rise. Although mayflies bulk considerably larger in the stomach contents as measured, they are not digested as quickly as planktonic material. These fish in shallow water, however, begin a fast just previous to their migration to the hypolimnion, which may continue for six weeks or possibly longer.

It should be pointed out that the volumes given above are conservative estimates, for it has been shown that digestion probably takes place after the fish is captured. The average volumes observed in stomach contents are therefore lower than those of fish in the populations from which the samples were taken. This would be most marked in the case of planktonic food which is apparently digested quite rapidly.

Fish which feed in the hypolimnion possibly reflect the superior advantage of feeding there as evinced by a statement made by Fry (1937, p. 78):

> Certain individuals found to be feeding in the hypolimnion in July grow more quickly than individuals of the same age and sex which are not feeding in the hypolimnion at this time. The proportion of the members of a year class which feed in the hypolimnion in July increases as the year class becomes older. Correlated with this increase in feeding activity there is an acceleration in growth in the higher age groups.

This acceleration in growth may be due to a peculiar situation existing in the hypolimnion of lake Nipissing. This situation is a result of a marked concentration of immature *D. oregonensis* in the restricted hypolimnion, produced by adults in a considerable volume above, and the fact that of the concentration of ciscoes in the same restricted areas not over one-third are feeding during July and August. Those which feed are thus able to obtain large numbers of immature *D. oregonensis* which under other circumstances might not be available to them.

The utilization of the food materials in lake Nipissing is fortunately of such a nature as to be of great importance in the survival of both the cisco and of individual species of plankton crustacea.

The wide distribution of the ciscoes over the shallow water area of the lake in spring, before *D. oregonensis* increases in abundance, allows the economical utilization of *Holopedium*, *Daphnia*, and *Leptodora* at that time. Similarly, a large portion of the cisco population is able to utilize the mayfly rise in shallow water in July. When the migration of fish to the hypolimnion takes place late in July, the large concentration of immature *D. oregonensis* yields sufficient food for the feeding fish, and it protects the population of *Mysis* and *Limnocalanus* from depletion since the fish do not select these forms in the presence of large numbers of *D. oregonensis*. In September the *D. oregonensis* population becomes scattered in the epilimnion but the descending thermocline concentrates the *Limnocalanus* population so that it becomes a large part of the food taken at this period just previous to the time when the fish themselves become scattered again. Thus the crops of individual plankton forms are not unduly depleted at any period, and fish desiring to feed can at practically any time during spring, summer, and fall, obtain considerable amounts of nutritive material.

The above relationships may not hold in many deep lakes where the relative volume of hypolimnion to epilimnion is so large as to be poorly populated by plankton. In such lakes it is probable that rates of growth of such a plankton-feeding fish are retarded, at least in part, as a result of lack of food. That this may be true of Trout lake in north-eastern Wisconsin will be indicated later. In some shallow lakes the high temperatures may inhibit feeding activity, or be fatal to a part of the population of ciscoes comparable to that which migrates early to the hypolimnion in lake Nipissing. Such a condition would have an effect on the general growth rate of the population similar to the retardation in deep lakes. Although these are but conjectures, the explanation of certain observations on comparative growth rates of ciscoes in various lakes may lie in studies similar to this made on lake Nipissing.

Hile (1936) reports that in four lakes in north-eastern Wisconsin (Trout, Muskellunge, Silver, and Clear lakes) the respective cisco populations showed marked differences in amount and rate of growth both in length and weight. Their order in respect to growth rate in length from maximum to minimum was found to be: Clear lake, Muskellunge lake, Silver lake, Trout lake. The order with respect to growth in weight was: Clear lake, Silver lake, Muskellunge lake, Trout lake. The order of the four lakes with respect to the average condition of the fish from maximum to minimum was : Clear lake, Silver lake, Trout lake, Muskellunge lake. These facts are illustrated in the first three columns of table 6.

Hile discusses several factors which he considers may be responsible for the differences observed in the populations. The order of each of these is also indicated in table 6.

The approximate length of the growing season of the ciscoes (obtained from scale measurements) in each of the lakes is directly correlated with the order of the lakes with respect to growth rate in weight. The same is true of the density of population covering the entire growing season. Of this latter factor he states (p. 262):

> Although it is recognised that crowding itself may possibly impede growth to a certain extent independently of its effect in creating competition for food, and that various physical-chemical factors may affect growth rate directly, it is believed that the differences in growth rate in these four populations depend in large measure on the varying degrees of competition for food in the different lakes. It is further probable that variation in the intensity of competition for food from lake to lake may be related to the observed differences in the length of the growing season of the different stocks.

In an attempt to explain the peculiarities of the growth of these populations, Hile also discusses the biological productivity of these four lakes. Of this he states (p. 287):

> In general, the amount of bound CO_2 in a lake's waters is roughly indicative of the biological productive capacity of that lake. In view of this fact it would hardly be expected that the poorest growth of the cisco would occur in the lake with the greatest concentration of bound CO_2. This apparently paradoxical situation is explained, however, if it is assumed that an abundance of bound CO_2 makes not only for a greater production of food organisms, but also makes for a much greater abundance of the ciscoes themselves, and that the abundance of the ciscoes in turn determines their growth rates.

That the above-mentioned relationship does not hold with regard to the organic matter of the surface plankton of these four lakes is evident from the last two columns of table 6, and no data are given by Hile as to the relationship between bound CO_2 and the abundance of food organisms of the ciscoes of these lakes. It therefore seems impossible to obtain a correlation between these factors of bound CO_2, biological productivity of intermediate food, and the growth of the ciscoes in the respective lakes. In this regard Hile states (p. 292):

> Although the abundance of organic matter in surface samples of plankton may not serve as a wholly reliable index of the abundance of plankton forms most commonly taken by the ciscoes and in the strata of water inhabited by that species, the data do show that the cisco suffers the most rapid loss of condition with increase in length, and shows the poorest average condition in the lake (Muskellunge) with the most eutrophic environment, while the most rapid gain in condition and the best average condition are found in Clear Lake with the most oligotrophic environment [*see also table 6*, p. 48]. . . . While it is hardly to be inferred that a mere abundance of food causes loss of condition in the cisco or that a scarcity of food makes for better condition, *it is quite probable that the cisco does not thrive in the physical and chemical conditions most conducive to a large production of food organisms.* The eutrophic environment of Muskellunge Lake may, for example, force the cisco to live under such undesirable conditions of temperature and dissolved oxygen that it fails to thrive even in the presence of abundant food, while in Clear Lake favorable physical and chemical conditions may make it possible for the cisco to reach the best of condition on a substantially smaller basic abundance of food. [Italics are present author's.]

It is believed that the latter view is upheld in the results of the study of the cisco in lake Nipissing. If we carry those results to a consideration of the facts observed in the four Wisconsin lakes, it will be seen that the poorest growth occurred in a deep lake with an abundant hypolimnion making for a sparse zooplankton population. Together with this there is found a heavy cisco population, in fact the greatest density of population in the four lakes is found in Trout lake. In this lake there is an abundance of oxygen in the cold hypolimnion. It is possible that the growing season is cut short by the migration of the cisco from shallow water to the hypolimnion in July (see table 6, p. 190).

When we consider the ciscoes of Clear lake we find no great restriction of the population in midsummer. The hypolimnion is well oxygenated and remains quite cool. The growing season is long, running to late September, because the least dense cisco population is scattered through the hypolimnion which without doubt has a fairly good zooplankton population.

Silver lake which stands second in the series with respect to growth in weight, also stands next to Clear lake with respect to density of population. However, a marked difference occurs with respect to the distribution of that population. In August it occurs within sharp limits (between 10 and 15 metres) probably because of unfavourable conditions below that depth. The oxygen is considerably lower than in Clear lake, although the temperature of the hypolimnion is quite similar. The growing season is shorter than in Clear lake probably due to the restriction, and probably to the expulsion and cessation of feeding of part of the population in early fall.

Muskellunge lake shows still more severe conditions than does Silver lake. The condition factor of the cisco population is also the lowest of all the lakes studied. The population is most restricted in midsummer (between 11 and 13 metres), and the oxygen of the hypolimnion is lowest, while in temperature this water is the warmest. The growing season is shorter than in Silver lake, probably because of the more severe environmental conditions, which quite likely results in earlier cessation of feeding in this lake.

SUMMARY

Definitely different plankton populations are found in the shallow and deep water of lake Nipissing. The cisco *Leucichthys artedi* (Le Sueur) migrates from the shallow water to deeper strata during early summer, and the predominance of the respective plankton crustacea in their food differs in the two regions. In shallow water *Daphnia* is utilized to a large extent, and ephemerids are an important food as nymphs and sub-imagos. In deep water immature *Diaptomus oregonensis* is the predominant food organism taken.

There are marked differences in the feeding of the different size groups of ciscoes. These differences occur in the amount and kind of food obtained at different times during the diurnal as well as the seasonal cycle. These diurnal differences in feeding yielded a measure of the daily intake of food of feeding fish, which has been estimated as being from four to five times the average volume of the stomach contents of large numbers of fish taken at different depths.

The larger fish which migrate early to the hypolimnion are able to feed almost continuously from spring until the middle of September, upon food of high fat content, the plankton crustacea. Fish which remain longer in shallow water, however, obtain large amounts of mayfly emergents for a short time, but begin a fast just previous to their migration to the hypolimnion in early July, and this fast may continue for six weeks or possibly longer. The superior advantage of the fish which feed continuously during the summer on immature *D. oregonensis* is possibly reflected by an acceleration in growth of these older fish.

An explanation of the differences in the rates of growth of ciscoes in other lakes may quite possibly lie in studies similar to this made on lake Nipissing. In many deep lakes where the relative volume of hypolimnion to epilimnion is so large as to be poorly populated by plankton, rates of growth of ciscoes may be retarded, at least in part, as a result of lack of food. In some shallow lakes the high temperatures may inhibit feeding activity, or be fatal to a part of the cisco population comparable to that which migrates early to the hypolimnion in lake Nipissing. Such a condition would have an effect on the general growth rate of the population similar to the retardation in deep lakes. A discussion of the action of these environmental factors upon the cisco populations is given in a comparison of four north-eastern Wisconsin lakes studied by Hile in 1936.

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TABLE 1.—Feeding of ciscoes at station II, 1935. (Amounts are settled volumes in 20 x 60 mm. vials.)

	Depth in feet								
	0–15			15–30			30–45		
June 13-14	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
Number of stomachs	...	1	3	1	4	5	2	13	10
Daphnia	...	2.0	0.2	...	9.8	8.8	5.0	9.7	10.9
Holopedium	...	...	1.1	5.4	3.8	0.5	2.2	5.3	...
Leptodora	...	...	...	0.6	0.2	...	3.6	0.5	0.4
Mayflies	...	...	1.3	...	...	1.1	...	0.4	...
D. oregonensis	...	...	...	...	...	0.2	0.3	0.5	0.2
July 10 (night)									
Number of stomachs	...	17	7	7	17	5	3	12	5
Daphnia	...	0.2	0.5	1.0	...	1.1	...	0.5	...
Mayflies (fresh)	...	40.0	60.0	5.0	20.0	33.0	...	3.3	33.0
Mayflies (digested)	...	20.0	38.0	8.0	13.5	48.0	13.0	12.0	33.0
July 10 (day)									
Number of stomachs	...	...	...	...	3	1	...	15	14
Daphnia	...	...	...	...	1.3	10.0	...	5.5	4.4
Mayflies (fresh)	...	...	...	...	...	...	...	1.0	4.4
Mayflies (digested)	...	...	...	...	10.0	40.0	...	10.0	8.0

TABLE 2.—Relative volumes of plankton present in cc. per 100 litres at different depths, during the season, at station I, 1935.

	Depth in metres								
	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45
June 12 (day)									
Daphnia	1.5	0.1	...	...	...	...	...	...	...
Holopedium	1.0	...	...	...	...	...	...	...	...
D. oregonensis	...	...	...	...	0.5	0.5	0.5	0.6	0.4
Limnocalanus	...	...	...	...	0.6	1.2	1.5	1.7	1.7
June 22 (night)									
Daphnia	0.6	0.9	0.5	0.3	0.1	0.1	...	0.1	0.1
D. oregonenis	2.2	1.2	0.1	0.1	0.2	0.4	0.9	1.3	1.3
Limnocalanus	...	...	...	0.1	0.4	0.2	0.6	1.0	1.0
July 5 (night)									
Daphnia	3.1	1.0	0.5	0.3	0.2	0.3	0.5	0.1	0.1
D. oregonensis	0.4	0.7	0.3	0.3	0.5	1.8	4.4	6.0	6.0
Limnocalanus	...	...	...	...	...	0.2	1.0	1.6	2.2
Mysis	...	...	...	...	...	4.7	4.7	4.7	4.7
July 19 (night)									
Daphnia	0.5	0.6	0.6	0.7	0.5	0.1	+	+	+
D. oregonensis	...	0.2	0.5	1.2	2.3	8.6	13.0	16.0	17.0
Limnocalanus	...	...	...	...	0.2	1.0	1.7	2.6	4.0
Mysis	...	...	...	...	...	1.7	4.0	3.7	2.1
July 27 (night)									
Daphnia	0.8	1.6	0.8	0.4	0.2	...	...	...	...
Leptodora	...	0.4	...	...	...	...	...	...	...
D. oregonensis	2.1	0.2	0.9	2.1	4.1	9.4	11.5	11.0	11.0
Limnocalanus	0.1	...	...	...	...	1.8	0.2	2.8	3.3
Mysis	...	...	...	...	4.7	...	9.5	4.7	9.5
July 31 (day)									
Daphnia	0.5	0.3	0.4	0.7	0.4	0.05	0.05	0.05	...
D. oregonensis	0.4	0.2	0.05	2.6	4.5	5.8	14.8	14.5	12.1
Limnocalanus	...	...	...	0.2	0.8	2.0	2.4	2.4	3.2
Mysis	...	...	...	...	...	3.2	5.5	4.0	5.5
August 24 (night)									
Daphnia	2.5	2.3	2.0	1.7	1.0	0.6	0.4	0.2	0.2
D. oregonensis	0.8	0.8	0.7	0.8	3.2	9.5	14.8	13.3	6.8
Limnocalanus	...	...	...	...	0.2	1.0	1.2	2.5	3.2
September 1 (night)									
Daphnia	3.0	3.6	3.7	2.5	1.0	0.1	0.1	0.1	0.1
Leptodora	0.2	...	...	...	...	...	...	...	...
D. oregonensis	3.2	1.5	2.0	1.4	0.5	0.5	15.0	10.0	5.4
Limnocalanus	...	...	...	...	...	0.7	1.6	2.5	3.7
September 18 (day)									
Daphnia	1.2	1.8	0.8	0.7	0.9	0.8	0.5	0.4	0.3
D. oregonensis	0.7	1.0	0.7	0.8	0.7	0.5	0.4	0.4	6.0
Limnocalanus	...	...	...	...	...	...	...	...	6.0

TABLE 3.—Seasonal feeding of ciscoes at station I, 1935. (Amounts are settled volumes in 20 x 60 mm. vials.)

DEPTH IN FEET

	0—15			15—30			30—45			45—60			60—75			75—90			90—105			105—120			120—150		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
JUNE 10–13																											
Number of stomachs.*	1	5	11	4	5	7	1	5	6		2	9		1	4			5			2			1			
Av. vol. of food: *Daphnia*	3.0	0.4	0.3																					0.4			
Holopedium	1.2	2.6	0.9	4.0	1.4	2.0	1.0	4.5	0.7			0.6						0.5			1.0						
Leptodora	6.0	4.7	3.0	4.0	6.0	0.6	1.0	2.2	1.4			1.7						0.5			0.5						
Mayflies		0.7	5.3		3.1	1.3		8.2	0.1		0.8	1.1		2.0	2.0			4.2									
D. oregonensis	1.8	0.1	0.1		0.3				3.6		0.2	2.2						1.6			1.5			0.4			
Corethra					1.0																						
Chironomids						6.2	18.0		1.4		8.0	1.5									0.2						
Total	12.0	8.5	9.6	8.0	11.8	10.1	20.0	14.9	7.2		9.0	7.1		2.0	2.0			6.8			3.2			0.8			
JUNE 20–23																											
Number of stomachs	7	2	3	2	2	1	1	2	1	9	2	10			6			1			14		1	3			3
Av. vol. of food: *Daphnia*	8.1	4.4		9.9	3.0		20.0	9.9	0.2	5.6	2.0	0.1															0.2
Leptodora	2.0	3.3		1.1	0.5			3.6		2.4								0.4									
Mayflies		3.3			1.5							0.8			3.0						0.3						1.3
D. oregonensis										0.5		0.8						1.6			0.5			2.5			3.1
Limnocalanus																					2.8			2.5			1.8
Mysis						1.0						1.2									1.1						
Corethra	0.1							4.5				1.0															
Miscellaneous			23.0												3.0			2.0					8.0				
Total	10.2	11.0	23.0	11.0	5.0	1.0	20.0	18.0	0.2	8.5	2.0	3.9			6.0			4.0			4.7		8.0	5.0			6.4

TABLE 3—*Continued.*

DEPTH IN FEET

	0—15			15—30			30—45			45—60			60—75			75—90			90—105			105—120			120—150		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
JULY 3–6																											
Number of stomachs	1	4	2		3		8	1		1	3	5	9	1	9		5	11		1	10		1	12		1	12
Av. vol. of food: *Daphnia*	1.0	4.4					4.1	18.0		2.0	7.8	0.1	8.0		4.4			0.2			0.9			1.0			
Leptodora															0.6						0.7			1.2			
Mayflies		17.6	60.0		44.0						1.2	2.5			1.7		2.2	0.6			1.1						
D. oregonensis													0.2	18.0	7.0		2.2	8.8		18.0	4.3			5.0		16.0	15.0
Limnocalanus														1.0	1.5			0.4		1.0	2.7			4.2			1.2
Mysis								1.0				0.5		1.0	1.7			1.4		1.0	0.2		2.0	1.6			0.3
Corethra								1.0			3.0	1.4					6.6	2.8									
Total	1.0	22.0	60.0		44.0		4.1	20.0		2.0	12.0	4.5	8.2	20.0	16.9		11.0	14.2		20.0	9.9		2.0	13.0		16.0	16.5
JULY 16–17																											
Number of stomachs		6	6	2	5	1		1			6	4		5	3	4				7	39		7	13			
Av. vol. of food: *Daphnia*			2.0	6.0	1.4						1.8	0.7				1.7											
Mayflies		13.3	11.2	2.0	2.8			10.0			5.5	6.4		2.5													
D. oregonensis			2.5		2.7	5.7					3.6	1.5		2.5	16.6	1.7				12.9	12.1		17.6	13.4			
Limnocalanus			0.2		0.1	0.2						0.1			0.2					0.7	0.7		0.6	0.6			
Mysis			0.1			0.1						0.7			0.2					2.6	2.3		0.3	1.8			
Total		13.3	16.0	8.0	7.0	6.0		10.0			10.9	9.4		5.0	17.0	3.4				15.2	15.1		18.5	15.8			

TABLE 3—*Continued.*

DEPTH IN FEET

	0–15 Small	0–15 Medium	0–15 Large	15–30 Small	15–30 Medium	15–30 Large	30–45 Small	30–45 Medium	30–45 Large	45–60 Small	45–60 Medium	45–60 Large	60–75 Small	60–75 Medium	60–75 Large	75–90 Small	75–90 Medium	75–90 Large	90–105 Small	90–105 Medium	90–105 Large	105–120 Small	105–120 Medium	105–120 Large	120–135 Small	120–135 Medium	120–135 Large	135–150 Small	135–150 Medium	135–150 Large
JULY 23–26																														
Number of stomachs..		2	3		2	1		5	3	2	4	5	3	5	11	4	9	6	3	9	20		7	21	1	14	27		18	33
Av. vol. of food: *Daphnia*.......		0.2			3.8				4.3	4.5	3.3	0.7	2.9	4.8	1.1	2.2	1.8		1.3		0.5		1.6	0.7		2.0	0.3			1.0
Leptodora......										1.5			0.8		0.6															
Mayflies.......											0.2		0.9																	
D. oregonensis..		11.8	5.9		0.2	2.5		21.2	7.3		3.5	5.5		1.4	3.5	0.7	2.4	6.6	2.3	8.5	9.8		8.5	9.5	11.4	15.4	12.3		9.8	2.6
Limnocalanus..		0.8	0.2					0.6			0.1	0.3			0.1		0.3	0.2	0.2	0.2	0.6		0.1	1.1		0.6	1.1		0.4	1.5
Mysis.........		1.6	2.0			1.5		1.2	1.3		0.2	0.4			0.9			0.2		1.3	3.2		1.2	2.2	0.6	2.0	2.5		0.8	4.0
Total.........		14.4	8.1		4.0	4.0		23.0	12.9	6.0	7.3	6.9	4.6	6.2	6.2	2.9	4.5	7.0	3.8	10.0	14.1		11.4	13.5	12.0	20.0	16.2		11.0	9.1
AUGUST 15–20																														
Number of stomachs..					1	3			2	1	1	3			1		1	1			2		3	1		5	7	2	11	14
Av. vol. of food: *Mayflies*.......															2.0															
D. oregonensis..					1.4	3.8			5.5	4.0	4.4	7.5					2.0	6.0			1.2		4.2	1.5		2.5	0.9	0.5	1.0	1.3
Limnocalanus..					0.2	0.2			0.2		0.4	0.2						0.4			0.7		0.8	0.2		0.3	0.3	0.1	0.2	0.2
Mysis.........					0.4	1.8			1.1									1.6			12.0		1.6	0.3		4.0	3.1	1.6	2.9	2.5
Total.........					2.0	5.8			6.8	4.0	4.8	7.7			2.0		2.0	8.0			13.9		6.6	2.0		6.8	4.3	2.2	4.1	4.0
SEPTEMBER 4–9																														
Number of stomachs..					1						1	2	1	4		7	19	16	3	16	10		14	8	1	8	7	1	4	
Av. vol. of food: *D. oregonensis*..					6.0						1.0	8.5	3.0	5.6		7.5	6.8	7.4	1.5	5.2	5.2		2.9	6.2	3.2	4.7	2.7	1.0	3.8	
Limnocalanus..														0.3		0.4	0.5	0.3	0.6	0.1	0.2		0.1	0.3	0.4	0.7	0.4		0.1	
Mysis.........												0.5	3.0	0.1		0.1	0.4	1.6	0.9	1.0	1.2		1.6	1.3	0.4	1.8	3.1	1.0	1.0	
Chironomids....																										0.1				
Total.........					6.0						1.0	9.0	6.0	6.0		8.0	7.7	9.3	3.0	6.3	6.6		4.6	7.8	4.0	7.3	6.2	2.0	4.9	
SEPTEMBER 18–21																														
Number of stomachs..						3			2									3		2	3		5	16	2	7	9		3	11
Av. vol. of food: *D. oregonensis*..						5.4			1.8									4.3		6.0	7.0		1.8	2.9	6.0	3.3	1.9		6.3	5.3
Limnocalanus..						3.6			9.0									2.0		2.0	3.7		1.8	2.2	2.0	1.3	2.6		1.7	5.8
Mysis.........									1.0												0.3		0.2	0.7		0.5	0.2		0.4	0.4
Chironomids...						0.3												3.0			0.2		0.2	0.3		0.7	0.1		0.6	0.7
Total.........						9.3			11.8									9.3		8.0	11.2		4.0	6.1	8.0	5.8	4.8		9.0	12.2

*In tables of fish captured given by Fry (1937), fish with at least a trace of food were considered full. In the above table only fish with more than a trace have been included.

TABLE 4.—Differences in feeding during night and day, July 27-31, 1935, at station I, lower strata. (Amounts are settled volumes in 20 x 60 mm. vials.)

	Depth in feet: 90–105 Medium	90–105 Large	105–120 Medium	105–120 Large	120–135 Medium	120–135 Large	135–150 Medium	135–150 Large
July 27 (night)								
Number of stomachs......	3	17	5	15	12	20	14	28
Daphnia.........	...	0.7	2.2	...	2.5	...	...	0.7
D. oregonensis....	17.2	8.8	7.8	10.0	15.7	12.7	10.1	14.6
Limnocalanus.....	0.5	0.8	0.2	0.9	0.6	1.2	0.4	0.9
Mysis...........	0.3	2.6	0.7	2.0	2.1	3.0	0.5	1.8
Total..........	18.0	12.9	10.9	12.9	20.9	16.9	11.0	18.0
July 31 (day)								
Number of stomachs......	4	3	3	17	5	9	16	18
D. oregonensis.....	5.8	5.3	11.2	8.3	12.1	7.1	11.7	9.7
Limnocalanus.....	0.7	4.3	1.0	1.4	1.4	2.9	0.9	1.3
Mysis...........	1.9	0.3	2.3	2.8	0.9	3.5	2.1	3.0
Total..........	8.4	9.9	14.5	12.5	14.4	13.5	14.7	14.0

TABLE 5.—Variation in feeding of ciscoes throughout the diurnal cycle at station I, lower strata, 1935. (Amounts are settled volumes in 20 x 60 mm. vials.)

Date	Time net set o'clock	Number of fish caught	Number of full stomachs	Volume of *Limnocalanus*	Volume of digested *Mysis*	Volume of fresh *Mysis*	Volume of *D. oregonensis*	Average volume per full stomach
August 12..	12–16	109	84	1.0	1.1	1.5	5.4	9.0
	16–20	126	76	1.7	0.6	1.5	3.6	7.4
	20–24	104	46	1.6	0.6	1.0	2.8	6.0
August 13..	0–4	105	60	1.2	0.7	0.8	3.6	6.4
	4–8	49	29	0.6	0.3	1.1	2.9	4.9
	8–12	69	39	1.4	0.1	3.6	4.3	9.4

TABLE 6.—Order of four Wisconsin lakes with respect to certain phases of the life history of the cisco, and also with respect to certain physical and chemical conditions of the water. Order is from maximum to minimum. Data from Hile, 1936.

Lake	Growth of ciscoes		Condition of ciscoes	Length growing season	Density of cisco population entire season	Restriction of cisco population in midsummer	O_2 of hypolimnion in August	Temp. of hypolimnion in August	Organic matter in surface plankton	Bound CO_2
	Weight	Length								
Trout...........	4	4	3	4 3 mos. (end July)	1	4 (entire hypol.)	2	1 (7°-10°C.)	4 (0.7 mg./l.)	1
Muskellunge.....	3	2	4	3 4 mos. – (late Aug.)	2	1 (11-13 m.)	4	4 (10°-14°C.)	1 (1.16 mg/l.)	2
Silver...........	2	3	2	2 4 mos. + (early Sept.)	3	2 (10-15 m.)	3	3 (7°-11°C.)	2 (0.85 mg/l.)	3
Clear............	1	1	1	1 5 mos. (late Sept.)	4	3 (all parts small hypol.)	1	2 (8°-10°C.)	3 (0.84 mg/l.)	4