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SOME ASPECTS OF THE ECOLOGY OF LIMNETIC ZOOPLANKTON IN LAKE WONONSKOPMUC, CONNECTICUT

Stephen Jay Warshaw

1971

A Dissertation Presented to the Faculty of the Graduate School of Yale University in Candidacy For the Degree of Doctor of Philosophy

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DISSERTATION SUMMARY

Section I

The effects of predation by alewives (Alosa pseudoharengus) on the limnetic zooplankton of Lake Wononskopomuc, Connecticut, were examined by sampling the zooplankton over a period of several years. Shifts in zooplankton composition and size distribution toward small forms had occurred eight years after alewives were introduced. A partial reversal of these effects, including an increase in the relative importance of large species and a size increase in at least one species (Daphnia galeata mendotae), followed an alewife die-off. After the die-off the recovery of a hypolimnetic species (Daphnia longiremis) was retarded relative to that of the epilimnetic Daphnia dubia, probably because of restriction of the former's reproductive rate by low hypolimnetic temperatures.

Section II

Two factors influencing natural estimates of Daphnia mortality made with the "egg ratio" method are considered: age-specific mortality influencing the egg-age distribution and horizontal variation in Daphnia population parameters. When mortality is concentrated among egg-bearing individuals of a computer model population, the egg-age distribution is skewed toward young eggs, and recruitment and mortality estimates made with the egg ratio method may be unacceptably high. Such estimates are less likely to be biased when mortality is concentrated among immature individuals. Horizontal variations in Daphnia abundance and in the ratio eggs:females (E) in Lake Wononskopomuc have been demonstrated, with both abundance and E being lower at stations 6 m deep than at deeper ones. In addition, Daphnia egg-age distributions in Wononskopomuc have been considered in light of the nature of potential mortality sources and the egg-age distributions likely to be produced by different predators.

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It is respectfully dedicated to Carol and Nancy.

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SECTION I: EFFECTS OF PLANKTIVOROUS ALEWIVES (*ALOSA PSEUDOHARENGUS*) ON THE ZOOPLANKTON OF LAKE WONONSKOPOMUC, CONNECTICUT

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INTRODUCTION

A predator's influence on a prey species association can be determined by comparing situations in which the predator is numerous to those in which it is rare or absent. The effects of vertebrate predators, mainly fish, on limnetic zooplankton communities are generally studied in this way, with comparisons being made between lakes (Anderson, 1968; Brooks and Dodson, 1965; Dodson, 1970; Hall et. al., 1970; Hrbáček and Hrbáčkova, 1966; Hutchinson, 1968), between different habitats of a single lake (Green, 1967; Zaret, 1970), or between different periods in the history of a lake (Brooks and Dodson, 1965; Galbraith, 1967; Hall et. al., 1970; Reif and Tappa, 1966; Wells, 1970). Without exception these studies support the generalization that the presence of a vertebrate planktivore tends to favor smaller or more cyclomophic forms because the predator selectively eats larger or less cyclomorphic ones.

Several of these studies concern the planktivorous alewife Alosa pseudoharengus (Wilson) or the closely related Alosa aestivalis (Mitchell). In small lakes (area <110 ha, maximum depth <21 m), Brooks and Dodson (1965) and Hutchinson (1968) find that, when alewives are present, the limnetic zooplankton is composed almost entirely of Bosmina longirostris, Ceriodaphnia lacustris or Holopedium sp., small cyclopoid copepods, and rotifers. Comparable lakes without alewives contain largely Daphnia spp., Diaptomus minutus, large cyclopoid copepods, and often Leptodora kindtii and Epischura sp.

Wells' study (1970) of the southern portion of Lake Michigan, where alewives increased markedly in the early 1960's, indicates that

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alewife-induced changes have been less extreme there. Leptodora kindtii, Daphnia spp., and large copepods, were less abundant in 1966 samples than in 1954 ones; but these forms were still collected in 1966, and Diaptomus minutus appeared not to have declined since 1954. Following a die-off of alewives in spring 1967, plankton samples in 1968 contained relatively more of all these forms. Other large lakes containing alewives (Bradshaw, 1964; Hall and Waterman, 1967) have zooplankton associations resembling that of Lake Michigan in 1966.

From these studies arise several questions that can only be answered by examining other lakes containing alewife populations. No previous study has precisely determined the period of time required for the zooplankton composition to change and stabilize in response to alewife predation. Secondly, Wells' hypothesis (1970) that effects of predation were partially reversed in Lake Michigan after the Alosa die-off should be examined with respect to other lakes, particularly since he based his interpretation on samples taken on only two dates in a single year. And Daphnia galeata mendotae and Mesocyclops edax, two species that declined in numbers in Lake Michigan from 1954 to 1966, did not increase in 1968 (Wells, 1970). So it seems likely that some species recover more quickly than others, and such differences between species should be explicable in terms of differences in species-specific characteristics such as reproductive capacity and physical conditions that prevail in the inhabited part of the water column.

The present study attempts to contribute toward answering these questions. Alewives (Alosa pseudoharengus) were artificially introduced into Lake Wononskopomuc, the study lake, during 1960-61. Large numbers of dead Alosa appeared following the ice-melt in the springs

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of 1966 and 1969, suggesting die-offs similar to that reported by Wells in Lake Michigan. Evidence that the dead fish of 1969 resulted from a general die-off similar to that in Lake Michigan, rather from the deaths of a numerically small, old or diseased portion of the population, is considered in the Results.

METHODS AND MATERIALS

All field data in this study were collected in the limnetic region of the study lakes. During the period 1968-69 temperature and dissolved oxygen concentration were measured with a Galvanic Cell Oxygen Analyzer (Precision Scientific Co., Model 68850), which was calibrated in the following way. An open bottle or beaker of water was agitated; the water was assumed to be 100% saturated with oxygen, and the measured oxygen concentration was used as a reference point. In 1970 temperature and oxygen concentration were measured with an Oxygen Meter (Yellow Springs Instrument Co., Model 51A), which included a calibration chamber that allowed calibration to be more precise. Determinations were made at the surface and at 1 m intervals to the lake bottom. Water transparency was measured on the shaded side of the boat with a white secchi disc.

Zooplankton samples were collected in essentially similar ways in the summers of 1941 and 1966-1969. A Juday plankton trap (capacity 10 l) bearing a nylon net (mesh aperture size 0.075 mm) was used to collect a vertical series of samples on each sampling date. Samples were collected at the surface and at 2 m intervals down through a depth of 24 m on all sampling dates except those in 1941 (when collections were made at the

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surface and at 3, 5, 8, 10, 12, 15, 20, and 25 m) and July 1, 1968 (when samples were collected at the surface and at 3 m intervals down through 24 m). Single samples were taken in 1941; all subsequent samples were taken in duplicate. They were preserved in 5-10% formalin in cork-stoppered 8 dram shell vials. Each sample was counted in a scored plastic petri dish with a dissecting microscope at 30X. Measurements were made with an ocular micrometer, from the anterior margin of the head to the tailspine base, or from the anterior margin of the eyespot to the tailspine base.

In summer 1970 plankton collections were made with a plankton net (G.M. Manufacturing Co.) of diameter 47 cm, length 175 cm, and mesh aperture size 0.075 mm. The net was lowered to 24 m, then pulled vertically at approximately 0.3 m/sec. Duplicate hauls were made on each of three sampling dates in 1970. Each sample was preserved in 5-10% formalin in a wide-mouthed plastic bottle (capacity 300 ml). For enumeration the volume of a sample was brought to 250 ml and the bottle was agitated; then two 2.5 ml subsamples were withdrawn with a wide-mouthed 10 ml pipette and counted in separate scored petri dishes.

A net with a large diameter was chosen to minimize the effects of possible differential net avoidance by different Daphnia spp. (Fleminger and Clutter, 1965) and of plankton patchiness (Wiebe, 1971; Wiebe and Holland, 1968) on net hauls. In order to determine the comparability of trap and net samples, several trap series and net hauls were made in July, 1970 (Table 1). The trap series were composed of duplicate samples at 3 m intervals from the surface down through 24 m, and all samples in a series were summed to give the Table 1 results; the net hauls were made from 24 m, and the results of two subsamples taken as above from each were summed for Table 1. At 10:30 p.m. on July 5 and 2:30 a.m.

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on July 6, one trap series and one net haul were made; and at 8:10 a.m. on July 6, one trap series and two net hauls were made. This study would probably have to be replicated several times for quantitatively accurate comparisons to be made among species. Since no extreme differences among species occur consistently in Table 1, however, 1970 collections are assumed to be comparable to those of previous years.

Additional vertical hauls were made in fall and winter of 1968-1970 with two nets, diameter 23 cm, length 80 cm, and mesh aperture sizes 0.100 mm (1968-69) and 0.055 mm (1969-70). Samples were preserved in 5-10% formalin in 8 dram shell vials. Later each sample was placed in a scored petri dish and approximately 200 specimens were counted; then the rest of the sample was examined for the presence of rare forms.

All the preceding samples were collected in Lake Wononskopomuc, Connecticut. A single trap series (one sample each at the surface and at 1 m intervals through 22 m) was also collected in East Twin Lake, Connecticut.

Fish were collected with gill nets of 1.0 in and 0.5 in mesh, set horizontally along the bottom in water 3-5 m deep and extended vertically from a styrofoam roller at the surface to the bottom (Lackey, 1968) in water 25-30 m deep. In 1969 nets were set at mid-afternoon and removed at mid-morning the following day, whereas in 1970 nets were set in the evening and removed 24 hrs later. Some alewives caught with 0.5 in gill nets in Aug. and Nov. of 1968 by the Connecticut Board of Fisheries and Game were also examined, as were some dead fish collected after the alewife die-off in 1969.

Total lengths of caught fish were measured to the nearest 0.5 cm, then stomachs of larger fish and whole bodies of smaller fish were pre-

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served in 10-20% formalin. Later stomach contents were enumerated in a scored petri dish with a dissecting microscope and measurements made as described previously. Only stomach contents in which the zooplankton genera were easily distinguishable were enumerated, and only prey items with intact carapaces were measured.

Egg developmental duration (D), defined here as the time between releases of consecutive broods by a female Daphnia, was determined in the laboratory for D. dubia, D. galeata mendotae, and D. pulex, at several temperatures. Live daphnids were collected from Wononskopomuc and cultured for several months prior to each experiment. Individuals of a species were then isolated singly in covered 8 dr. shell vials, and the resulting clones were maintained in filtered (0.055 mm mesh) spring water and an algal mixture dominated by Ankistrodesmus sp. Two individuals from each clone were isolated and grown as above at each experimental temperature in an environmental chamber (Honeywell) or in incubator (Coldspot). These experimental animals were checked twice daily, and all freely swimming young were removed with a pipette and recorded. A brood was released during some interval between two times at which the animals were examined; the midpoint of this interval was taken as the time of release, and D of the brood was estimated to be the period between its release and that of the preceding brood. It should be noted that such a determination of D includes the time between release of the previous brood and extrusion into the brood pouch.

RESULTS

Lake Wononskopomuc (Plate 1) is located in the town of Lakeville,

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Connecticut. Fig. 1 is a bathymetric map of the lake (Connecticut Board of Fisheries and Game, Work Projects Admin. O. P. 65-1-15-2388), and morphometric data based in part on Fig. 1 appear in Table 2. Soundings with a Heathkit Depth Sounder (Model MI-11A) in 1969 indicate this map to be accurate except that the isobaths are closer to the western shore (i.e. the lake is somewhat deeper there) than shown in Fig. 1. Its area (142.8 ha) and maximum depth (31 m) make Wononskopomuc slightly larger than the lakes studied by Brooks and Dodson (1965) and Hutchinson (1968).

Deevey (1942) characterized Wononskopomuc as a hard-water lake, poor in nutrients and low in phytoplankton productivity. His determinations of temperature, dissolved oxygen concentration, and secchi disc transparency, made in Aug., 1938, are given with comparable data for 1968-70 in Fig. 2. The decrease in transparency and in hypolimnetic dissolved oxygen concentration indicate that Wononskopomuc has become considerably more eutrophic during the past 30 years.

From 1876 until 1937, various species of fish were stocked rather indiscriminately in Wononskopomuc, according to stocking records of the Connecticut Board of Fisheries and Game. From 1937 until 1959, the lake was managed for rainbow trout (Salmo gairdneri), brown trout (Salmo trutta), and brook trout (Salvelinus fontinalis). In 1960 and 1961, a total of 1000 adult land-locked alewives (Alosa pseudoharengus) were introduced to provide a forage species for the trout populations. Since 1961 the State has continued to stock S. gairdneri and S. trutta, and in 1963 began stocking kokanee salmon (Onchorhynchus nerka).

Fig. 3 illustrates the thermal regime in Wononskopomuc during the period of thermal stratification. During May-Nov. 1969 the epilimnion

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extended from the surface to 4-6 m, and the hypolimnion, from 9-10 m to the bottom. The metalimnion, the zone in which temperature changed at least 1°C/m (Hutchinson, 1957), sometimes showed a temperature change >5°C/m. The epilimnetic temperature reached a maximum of 25-26°C in July and Aug.; the temperature of most of the hypolimnion was 4-6°C throughout the period.

Table 3 is a list of crustacean zooplankton collected in Wononskopomuc during this study. Members of the genus Daphnia were identified according to Brooks (1957) and other species were identified according to Edmondson (1959). There is some question about the identity of the species called Daphnia pulex, since it fits Brooks' description (1957) of Daphnia pulex L. and Hrbáček's description (1959) of Daphnia pulicaria F., which Brooks does not consider to occur in North America. Two of the characteristics that Hrbáček uses to distinguish the two species are present only in the male, and no males of the form in question have been found in Wononskopomuc collections or laboratory cultures. In the third characteristic, the structure of rostral cells in the female, the Wononskopomuc form resembles Hrbacek's D. pulicaria (Fig. 4). Until more material including males can be examined, however, the form will be referred to as D. pulex.

Changes in Composition

Table 4 shows that Bosmina and Daphnia were the most numerous cladocerans in samples collected during summer 1968. No Daphnia were collected in vertical hauls during the following fall and winter, when Bosmina and Chydorus were abundant. The large planktivorous cladoceran

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Leptodora was absent from 1968 collections. Various cyclopoids and the calanoid Diaptomus were the most numerous copopods during the summer; the cyclopoids remained abundant in the following fall and winter, but no Diaptomus individuals were collected during this period. None of the large calanoid Epischura were collected in 1968.

During 1969 the lake surface became ice-free on April 11, and thousands of dead Alosa appeared. Ninety-four of these fish were measured (Table 5) and varied from 6.5 to 21.0 cm in length. Forty-two fish were <8.0 cm long; although no age determinations were made, data from other studies (Hutchinson, 1968; Rothschild, 1965) indicate that these were young born the previous summer. It seems likely that dead fish >8.0 cm long represented most or all of the other year classes present in the lake, since other studies on land-locked Alosa (summarized in Fig. 6 of Hutchinson, 1968) report that fish five to seven years old are<20.0 cm. The large number of dead fish observed and probable representation of all or most year classes among them, are taken as evidence suggesting that a general die-off of the type reported in Lake Michigan by Wells (1970) had occurred. No direct measure of its effects on alewife population size in Wononskopomuc can be made, however, since efforts to census the fish population regularly did not begin until after the dead fish appeared. The cause of the die-off is not known; the dead fish did not appear to be decomposed, but might have died some time before the ice-melt and been preserved by the low water temperature beneath the ice.

Among the Cladocera, Daphnia became abundant and Bosmina decreased during summer 1969 (Table 6). Daphnia was the only cladoceran collected in vertical hauls in the following fall and winter. Leptodora was present in small numbers in most collections made in the summer. Cyclopoids were

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the most numerous copepods during the period May 1969-Feb. 1970; Epischura and Diaptomus were collected during the summer, and Diaptomus occurred in fall and winter samples as well.

Table 7 shows the relative abundance of the five Daphnia species collected in the summers of 1941 and 1966-70. In 1941 Daphnia pulex and a single D. galeata mendotae specimen were collected. During the period 1966-68 D. pulex was the least numerous Daphnia sp., and D. longiremis was the most numerous. In 1969, after the spring die-off of Alosa, D. pulex again occurred in small numbers, and the large D. longiremis population of previous years was absent. D. dubia was numerically dominant, and D. parvula was collected in the lake for the first time. In 1970 D. pulex was collected in considerably greater numbers than in 1966-69, D. longiremis was once again abundant, and no D. parvula occurred among the individuals counted.

The daytime vertical distribution of each of the five Daphnia species during summer 1969 is indicated in Table 8, which gives the number of animals counted from each of three strata (0-4 m, 4-10 m, and 10-24 m) on each of eight dates. All except D. pulex, which was scarce during much of the summer, were concentrated in the upper 10 m on June 5. By June 20 the distributions of D. longiremis and D. parvula had shifted downward, while D. dubia and D. galeata mendotae were still abundant in the epilimnion. This pattern was maintained through the rest of the summer, with D. pulex increasing in abundance in the hypolimnion in Aug.

Size Distribution

Fig. 5 indicates the cladoceran size distribution in each of the

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three strata in Wononskopomuc in summer 1968-69. The smallest size class includes Bosmina, Ceriodaphnia, small Daphnia, and Chydorus, whereas larger size classes contain only Daphnia. Small animals predominated in 1968; in all cases except the 4-10 m stratum on July 1, >80% were <1 mm long. During 1969 on all dates except June 5, the size distribution was considerably less skewed toward small animals.

Size distribution changes were due in part to composition changes and in part to shifts within individual species' size distributions. In order to indicate the cumulative influence of Alosa predation on an individual species, measurements were made of D. galeata mendotae collected in Wononskopomuc in Aug., 1966, 1968, and 1969, and in East Twin Lake in Aug., 1968 (Fig. 6). This species was chosen because it exhibited a wide size range, was abundant enough in plankton samples to give reliable data, and was numerous in Alosa stomachs collected Aug. 15, 1968. In Wononskopomuc the species was much smaller in 1968 (size range 0.45-1.60 mm, minimum egg-bearing size 0.80 mm) than in 1966 (size range 0.55-2.15 mm, minimum egg-bearing size 1.10 mm). In 1969 after the alewife die-off D. galeata mendotae size increased (size range 0.65-2.60 mm, minimum egg-bearing size 1.70 mm). In 1968, when dwarf forms predominated in Wononskopomuc, D. galeata mendotae individuals in nearby East Twin Lake, which lacks alewives, varied from 0.55 to 2.10 mm in size, with a minimum egg-bearing size of 1.45 mm.

Nineteen alewives varying in length from 11.0 to 22.0 cm were collected with gill nets during this study. Table 8 summarizes the results of examination of the stomach contents of 13 Alosa collected Aug. 15, 1968. Each prey species was classified as >100 present, 21-100, 5-20, 1-4, or absent. A more quantitative measure of abundance was deemed in-

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appropriate due to the deteriorated state of some of the material. Cyclopoid copepods and Daphnia were the most numerous forms in the fish stomachs (Table 9), whereas cyclopoids and Bosmina were most abundant in plankton samples collected in late summer 1968 (Table 4). Epischura occurred in three fish stomachs but was not detected in plankton samples. Among Daphnia, D. galeata mendotae predominated in fish stomachs, whereas D. longiremis was numerous in plankton samples collected during the period (Table 7).

The contents of three stomachs were relatively undigested, and the electivity index of Ivlev (1961) was used to compare the size distributions of Daphnia prey in these stomachs to those of individuals in plankton samples. This index is $\frac{(r_i - p_i)}{(r_i + p_i)}$ where r_i is the concentration of size class i in the stomach and p_i is its concentration in plankton samples. The index theoretically ranges in value from +1.0 (maximal selection) to -1.0 (maximal avoidance), with a value of 0.0 indicating that an item is eaten in the frequency of its occurrence.

Fig. 7 summarizes the results of this analysis. D. galeata mendotae individuals predominated in one stomach, so their size distribution (200 individuals measured) was compared to that of the same species in the 16-19 m stratum, where it was concentrated (Fig. 7) and, presumably, where the fish had been feeding. The other two stomachs contained largely D. longiremis prey, whose size distributions (51 and 47 individuals measured, respectively) were compared to that of D. longiremis in the 17-20 m stratum where it was concentrated (Fig. 7). The results suggest that Daphnia <0.75 mm were avoided and that individuals 0.75-1.35 mm were eaten approximately in the frequency of their occurrence. Values for individuals >1.35 mm are unreliable because few such animals

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were found in stomachs or plankton samples. D. galeata mendotae exhibited a broader size range (0.45-1.65 mm) than did D. longiremis (0.45-1.15 mm), so several of the values in Fig. 7 are based only on the former species.

The stomachs of three Alosa collected Nov. 15, 1968, contained only cyclopoid copepods. Stomachs of dead fish collected after the 1969 die-off contained no identifiable remains. A single fish collected Aug. 14, 1969, contained mainly Leptodora and small fish. And two fish collected Nov. 12, 1969, contained mainly Daphnia pulex and Epischura lacustris.

Evidence is strong that egg developmental rate (D^{-1}) in Daphnia is mainly a function of temperature (Esslová, 1959; Hall, 1964; MacArthur and Baillie, 1929). Laboratory determinations of D^{-1} for several Daphnia species at different temperatures are given in Table 10, and are plotted together with comparable determinations by other workers in Fig. 8. Only values from studies at more than one temperature appear in Fig. 8. A Figure summarizing copepod egg developmental rates is given in Burgis (1970), from which values for the stenothermal cyclopoid Cyclops scutifer are reproduced here.

DISCUSSION

Alosa was introduced in Wononskopomuc in 1960-61 and was first known to be abundant in spring 1966 when a die-off occurred. Daphnia and Diaptomus, common forms in summer 1968, did not occur in plankton samples collected during late fall and winter of 1968-69 or in alewife stomachs taken in Nov., 1968; Bosmina, Chydorus, and cyclopoid copepods predominated during fall and winter of 1968-69, as they have in other

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small lakes with dense Alosa populations. Thus eight years after its introduction Alosa had altered the zooplankton species composition considerably.

The shift in D. galeata mendotae size distribution and minimum egg-bearing size during 1966-68 is consistent with findings elsewhere (Anderson, 1968; Green, 1967; Hrbáček, 1960; Wells, 1970) that, within a given zooplankton species, increased fish predation favors dwarf forms whose growth increment per instar is less than that when predatory pressure is less. Other factors that might be suggested to account for the size decrease noted in the present study include a shift in age distribution unrelated to predation, or a decrease in the amount of available food in 1968 compared to 1966. The first of these can be eliminated, since it cannot account for the decline in minimum egg-bearing size. Both growth increment and brood size in D. magna (Green, 1954) and D. galeata mendotae (Hall, 1964) have been shown to depend on the amount of available food; so the second hypothesis cannot be ruled out, although the proportion of D. galeata mendotae adults bearing eggs was greater in 1968 than 1966 (Fig. 6).

Several additional facts suggest that Alosa predation, rather than a food decrease, caused the 1968 size decrease. The 1968 D. galeata mendotae size distribution in East Twin Lake, a nearby lake lacking alewives, resembled that of the 1966 Wononskopomuc population. And D. galeata mendotae size increased in Wonoskopomuc following the spring 1969 fish kill.

The increases of large zooplankters (Daphnia, Leptodora, Epischura) and shift in cladoceran size in 1969 relative to 1968 constitute support for the hypothesis that a partial reversal of alewife-induced changes in the zooplankton follows an Alosa die-off. Unfortunately no independent

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estimate of the die-off's effect on Alosa population size in Wononskopomuc is available; netting at approximately weekly intervals during May-Sept., 1969, yielded only three alewives, but too little netting was done prior to fish kill to allow comparison of 1968 and 1969 alewife population sizes. So one can only say that what is known of events there in 1966-69 parallels Wells' interpretation (1970) of events in Lake Michigan.

D. longiremis, which is largely confined to the hypolimnion in Wononskopomuc (Table 8) and other lakes (Hutchinson, 1967), was the most numerous Daphnia species in summers of 1966-68 and 1970 (Table 6). During the summer following the fish die-off, however, the epilimnetic D. dubia predominated. It seems likely that, following the disappearance of Daphnia species in fall 1968, D. longiremis recovered more slowly than the epilimnetic forms in part because of restriction of its reproductive rate by the low hypolimnetic temperature (Fig. 3). Eighty-three percent of the eggs carried by D. longiremis females in 1969 samples occurred in the 10-24 m stratum, the mean temperature of which was 5.1°C for 13 dates from May 22 through Sept. 11. Although no determinations of D. longiremis D^{-1} (egg developmental rate) were made, such determinations are available for several Daphnia species and Cyclops scutifer, which resembles D. longiremis in its dependence on low temperatures and distribution in North America (Elgmork, 1967). If D. longiremis D^{-1} varies with temperature in a similar way to that of the species in Fig. 8, its D^{-1} at 5.1°C probably falls within 0.05-0.02/day, so that a clutch of D. longiremis eggs would have required 20-50 days to develop during the summer 1969 in Wononskopomuc.

The events following the spring 1969 die-off did not appear to

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occur after that of spring 1966. D. longiremis was the most numerous daphnid (Table 7) and Diaptomus minutus the most numerous copepod (Table 11) in summer 1966 samples, whereas neither was abundant in 1969. No collections were made immediately prior to summer 1966, so there is no direct dvidence as to whether Daphnia and other large forms became rare prior to the first Alosa die-off as they did prior to the second. If temperatures characteristic of the Wononskopomuc hypolimnion restrict D. longiremis reproductive rate as they do that of the forms in Fig. 8, however, then it seems likely that there was a large overwintering D. longiremis population in 1965-66, which produced the summer 1966 population.

Thus the present study supports the following conclusions. Shifts in zooplankton composition and size distribution caused by alewife predation had occurred eight years after the fish was introduced and two years after it was known to be abundant. A partial reversal of these effects, including an increase in the relative importance of large species and a size increase in D. galeata mendotae, followed an alewife die-off, as found by Wells (1970) in Lake Michigan. Following the fish kill the increase of Daphnia longiremis was retarded relative to that of the epilimnetic dominant, D. dubia, probably because of restriction of the former's reproductive rate by low hypolimnetic temperatures.

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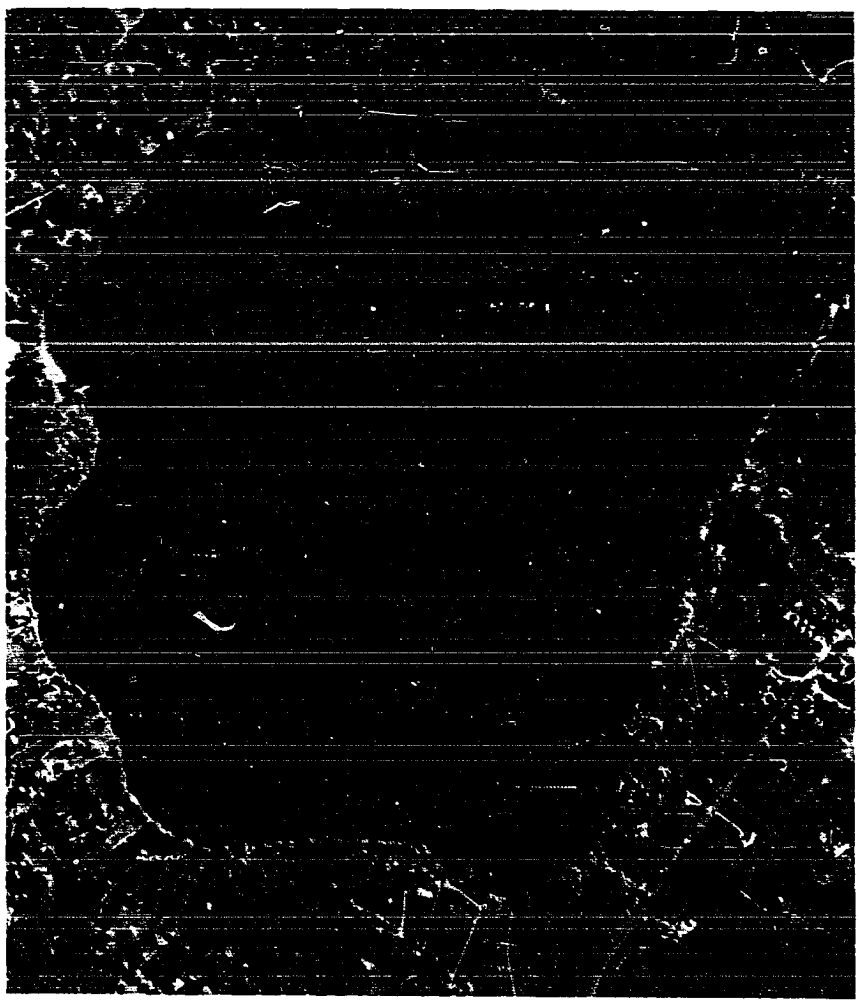

PLATE 1. LAKE WONONSKOPOMUC

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Table 1. Individuals/10 l caught with Juday trap and net in water column between surface and 24 m. Abbreviations: Dpul Daphnia pulex, Dgal D. galeata mendotae, Ddub D. dubia, Dlon D. longiremis, Lept Leptodora dindtii.

Time	Method	Total Daphnia	Dpul	Dgal	Ddub	Dlon	Lept
10:30 p.m. July 5, 1970	trap	494	88	46	39	321	1
	net	681	127	53	40	462	2
2:30 a.m. July 6, 1970	trap	303	82	27	25	170	1
	net	330	84	37	24	187	2
8:10 a.m. July 6, 1970	trap	470	109	27	19	316	1
	net	465	88	43	27	307	2
	net	530	79	21	17	409	1

Table 2. Morphometric data for Wononskopomuc (from Deevey, 1941)

Area (ha)	142.8
Mean depth (m)	11.1
Maximum depth (m)	31.0
Volume (m^3)	
0-4 m stratum	4635×10^3
4-10 m stratum	7560×10^3
10-24 m stratum	3267×10^3

Table 3. Crustacean zooplankton collected in Wononskopomuc in 1941, 1966-70.

Cladocera

Leptodora kindtii
Daphnia pulex
Daphnia galeata mendotae
Daphnia dubia
Daphnia longiremis
Daphnia parvula
Ceriodaphnia sp.
Diaphanosoma leuchtenbergianum
Sida crystallina
Simocephalus vetulus
Simocephalus serrulatus
Scapholeberis aurita
Scapholeberis kingi
Iliocryptus spinifer
Holopedium amazonicum
Bosmina longirostris
Latona setifera
Chydorus sphaericus
Acroperus harpae
Alonella excisa

Copepoda

Epischura lacustris
Diaptomus minutus
Cyclops scutifer
Cyclops vernalis
Mesocyclops edax

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Table 4. Percentage composition of zooplankton samples collected June, 1968-Feb., 1969. Abbreviations: Epis Epischura lacustris, Diapt Diaptomus minutus, cyclo cyclopoid copepods, Daph Daphnia spp., Cerio Ceriodaphnia sp., Bosm Bosmina longirostris, Diaph Diaphanosoma leuchtenbergianum, Chyd Chydorus sphaericus, Lept Leptodora kindtii. Symbol: + <1% of individuals counted.

Date	Jun 10	Jul 1	Aug 8	Sep 28	Oct 26	Jan 11	Feb 8
Total no.	23834	13972	10305	6652	188	199	201
Copepoda	29	30	28	49	16	30	62
Epis	0	0	0	0	0	0	0
Diapt	17	16	2	0	0	0	0
cyclo	11	14	26	49	16	30	62
Cladocera	71	70	72	51	84	70	38
Daph	30	64	21	3	0	0	0
Cerio	+	2	2	+	0	0	0
Bosm	41	2	51	46	84	63	35
Diaph	+	1	0	0	0	0	0
Chyd	+	0	+	2	0	7	3
Lept	0	0	0	0	0	0	0

Table 5. Total lengths of 94 alewives (Alosa pseudoharengus) collected from among dead fish after fish kill of spring 1969.

Length (cm)	No. of fish
19-20	10
17-19	15
15-17	5
13-15	14
8-9	8
6-8	42

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Table 6. Percentage composition of zooplankton samples collected May, 1969-Feb., 1970. Abbreviations: Epis Epischura lacustris, Diapt Diaptomus minutus, cyclo cyclopoid copepods, Daph Daphnia spp., Cerio Ceriodaphnia sp., Bosm Bosmina longirostris, Diaph Diaphanosoma leuchtenbergianum, Chyd Chydorus sphaericus, Lept Leptodora kindtii. Symbol: + <1% of individuals counted.

Date	May 22	Jun 5	Jun 20	Jul 3	Jul 18	Aug 3	Aug 15	Aug 29	Sept 12	Oct 7	Jan 31	Feb 18
Total no.	7805	16761	14022	8741	6158	5130	4810	5552	5082	201	200	208
Copepoda	89	57	64	76	79	52	61	71	71	65	24	73
Epis	+	+	1	1	1	1	1	2	2	0	0	0
Diapt	0	+	+	+	0	+	+	1	2	2	3	8
cyclo	89	57	62	75	78	51	59	69	67	63	22	65
Cladocera	11	43	36	24	21	48	39	29	29	35	76	27
Daph	1	17	27	23	20	47	39	29	29	35	76	27
Cerio	+	5	+	0	0	0	0	0	0	0	0	0
Bosm	9	20	9	1	1	+	+	+	0	0	0	0
Diaph	+	+	+	0	0	+	0	0	0	0	0	0
Chyd	1	1	+	+	0	0	+	+	0	0	0	0
Lept	0	+	+	+	+	+	+	+	+	0	0	0

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Table 7. Percentage composition within genus Daphnia in plankton samples collected summer 1941 and 1966-70. Abbreviations: ES early summer, MS mid-summer, LS late summer; Dpul Daphnia pulex, Dgal D. galeata mendotae, Ddub D. dubia, Dlon D. longiremis, Dpar D. parvula. Symbol: + 1% of individuals counted.

	Dpul			Dgal			Ddub			Dlon			Dpar		
	ES	MS	LS	ES	MS	LS	ES	MS	LS	ES	MS	LS	ES	MS	LS
1941	100	100	98	0	0	2	0	0	0	0	0	0	0	0	0
1966	+	+	4	17	23	26	+	1	33	82	76	36	0	0	0
1967		+	2		9	4		1	45		89	49	0	0	0
1968	+	+	4	25	5	26	11	5	+	63	90	70	0	0	0
1969	+	+	5	5	16	4	88	72	79	2	8	11	4	4	1
1970	18	11	8	3	3	1	3	2	8	76	84	83	0	0	0

	Numbers of individuals counted			Dates		
	ES	MS	LS	ES	MS	LS
1941	572	171	50	May 11	Jul 13	Aug 10
1966	9834	5847	1930	Jun 9	Jul 5	Aug 30
1967		11763	3630		Jul 6	Aug 29
1968	7078	4013	739	Jun 10	Jul 1	Aug 29
1969	2867	2063	2275	Jun 5	Jul 3	Aug 29
1970	2060	8661	2402	May 27	Jul 8	Aug 20

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Table 8. Numbers of individuals collected from three strata in 1969. Abbreviations: e 0-4 m, m 4-10 m, h 10-24 m; Dpul Daphnia pulex, Dgal D. galeata mendotae, Ddub D. dubia, Dlon D. longiremis, Dpar D. parvula.

		Jun 5	Jun 20	Jul 3	Jul 18	Aug 3	Aug 15	Aug 29	Sep 12
	e	2	6	0	1	1	0	0	4
Dpul	m	3	2	2	0	0	0	6	6
	h	2	8	5	7	28	34	104	72
	e	139	274	216	105	106	33	28	52
Dgal	m	18	152	84	38	47	77	52	9
	h	5	23	30	7	5	11	6	2
	e	2169	1610	1033	827	1130	330	924	512
Ddub	m	274	975	380	385	774	1013	798	451
	h	83	139	69	49	76	64	71	73
	e	15	1	4	10	5	1	2	2
Dlon	m	46	61	3	1	18	16	45	64
	h	9	90	157	206	203	252	211	200
	e	58	13	2	1	1	0	0	0
Dpar	m	53	112	28	5	1	2	1	2
	h	1	310	82	45	29	22	27	21

Table 9. Number of Alosa stomachs containing>100, 21-100, 5-20, 1-4, and 0 individuals of each form listed. Based on 13 fish collected Aug. 15, 1968, in Wononskopomuc. Abbreviations as in Table 4.

	>100	21-100	5-20	1-4	0
Copepoda					
Epis				3	10
Diapt		1	2	2	8
cyclo	10	2			1
Cladocera					
Daph	4	2	4	1	2
Dpul			1	4	8
Dgal	2	3	5	1	2
Ddub				1	12
Dlon	2			2	9
Cerio				3	10
Bosm			1	3	9
Diaph					13
Chyd					13
Lept					13
Ostracoda				1	12
Insecta					
Tendipes larvae				4	9
Chaoborus larvae				3	10

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Table 10. Laboratory determinations of incubation period (see text) at different temperatures. At 9°C D. dubia produced only ephippial eggs. Abbreviations: NA no. of experimental animals, NB no. of broods whose incubation period was measured, I avg. incubation period in days, SD standard deviation of I in days.

	Daphnia pulex				D. galeata mendotae				D. dubia			
T°C	NA	NB	I	SD	NA	NB	I	SD	NA	NB	I	SD
8	11	23	14.14	5.66								
9					8	22	8.88	1.38	17	--		
14	12	52	3.82	.32								
16					9	23	3.89	.96	15	59	4.01	2.16
19	12	56	2.32	.41					16	56	2.96	.43
22	12	70	1.79	.32	10	46	2.47	.64	16	79	2.23	.85

Table 11. Percentage composition of zooplankton samples collected June-July 1966. Abbreviations and symbol as in Table 4.

Date	Jun 9	Jul 5
Total no.	12910	9052
Copepoda	23	35
Epis	+	+
Diapt	15	19
cyclo	7	16
Cladocera	77	65
Daph	76	65
Cerio	0	0
Bosm	1	+
Diaph	+	0
Chyd	+	+
Lept	+	+

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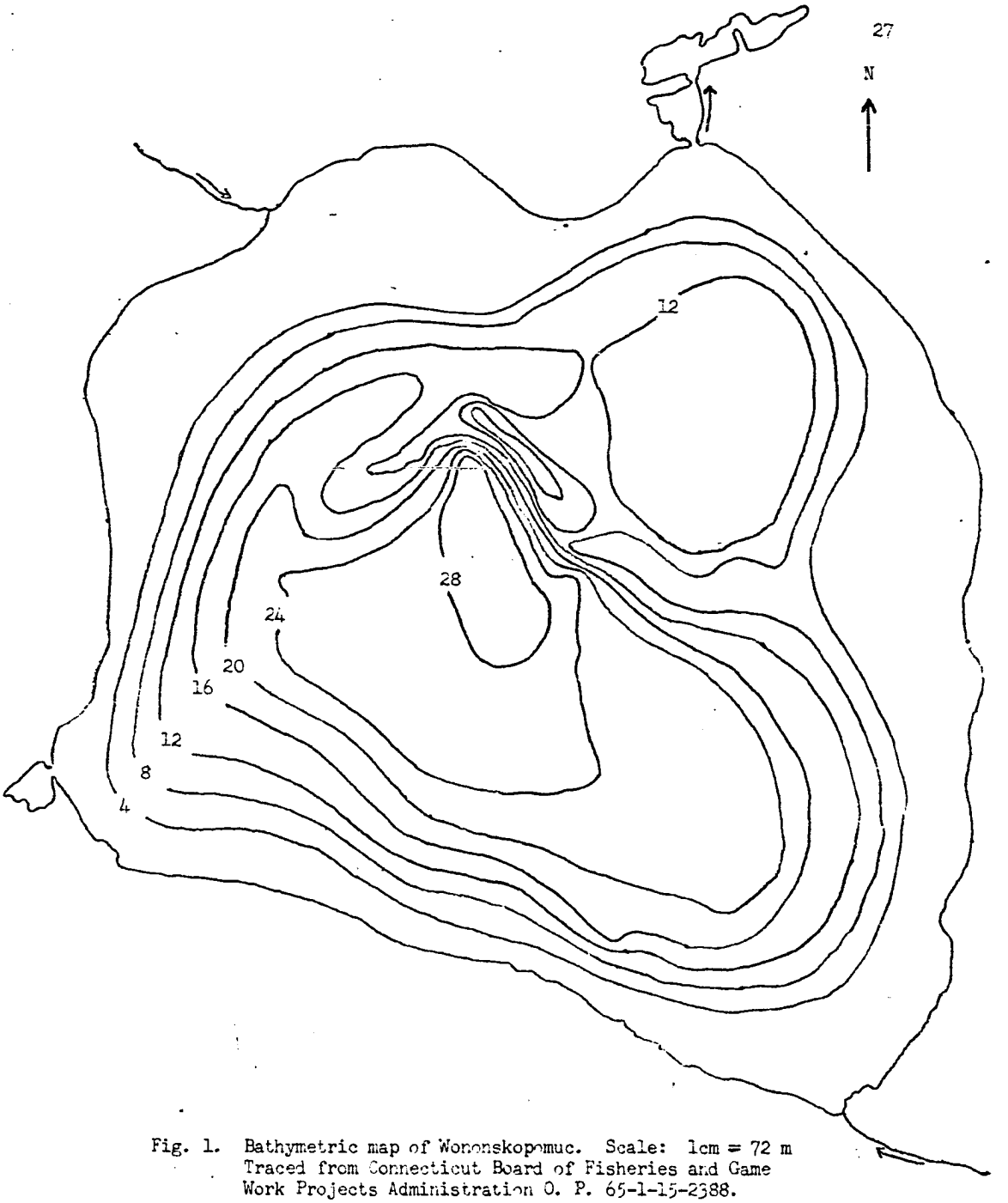

Fig. 1. Bathymetric map of Wononskopomuc. Scale: 1cm = 72 m
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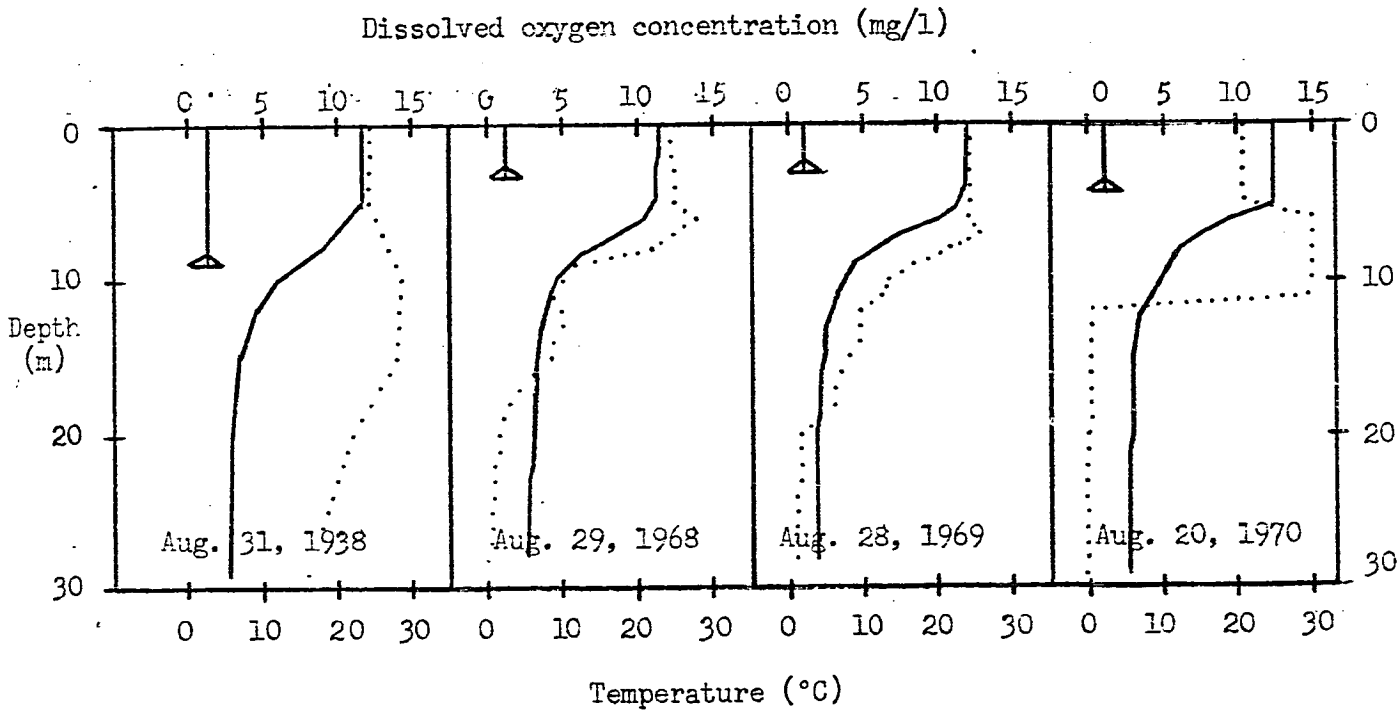

Fig. 2. Temperature (solid line), dissolved oxygen concentration (dotted line), and secchi disc transparency (triangle) in Wononskopomuc. Aug. 31, 1938 data from Deevey (1941).

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Fig. 3. Temperature in °C in Wononskopomuc during April 26-November 12, 1969. Dashed lines indicate interpolated values.

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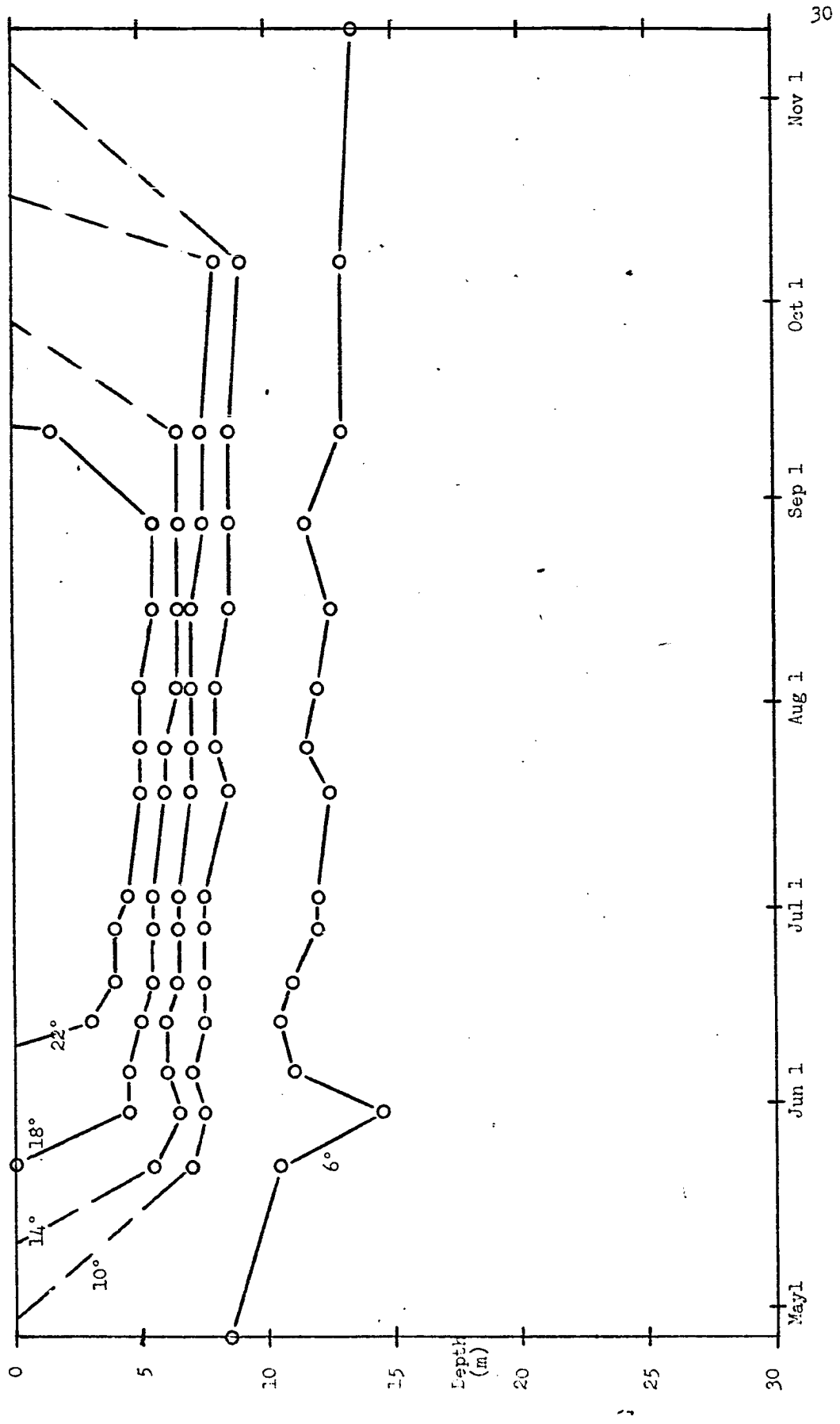

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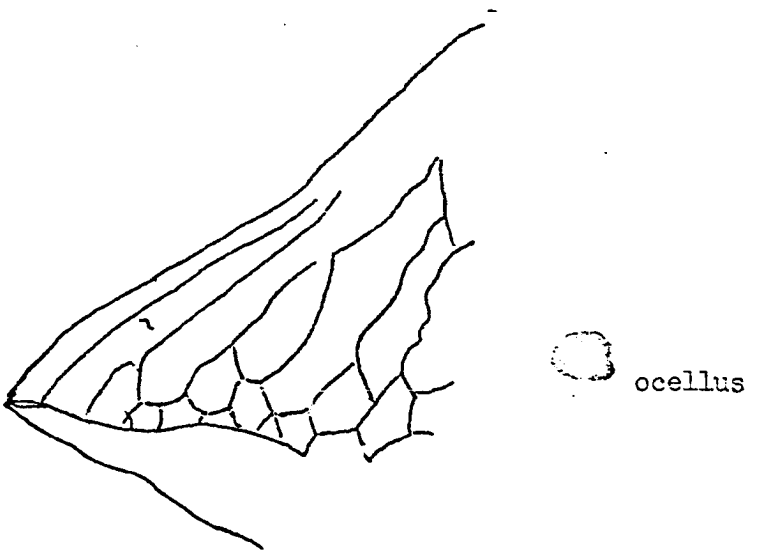

Fig. 4. Free-hand drawing of rostral cell arrangement of Wononskopomuc Daphnia pulex.

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Fig. 5. Cladoceran size distribution in Wononskopomuc during summer 1968 and 1969. Size classes are, left to right on each date, <0.75 mm, 0.75-1.00 mm, 1.00-1.25 mm, 1.25-1.50 mm, and >1.50 mm. Dashed line indicated a frequency of 50%. All measurements from anterior margin of eyespot to tailspine base.

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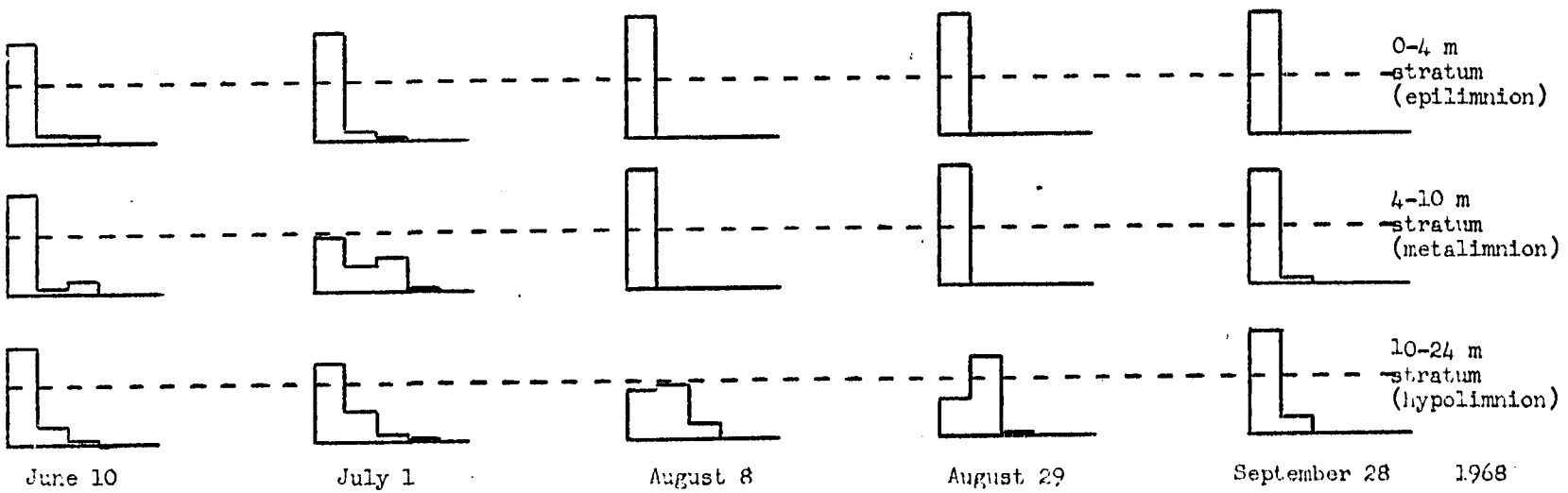

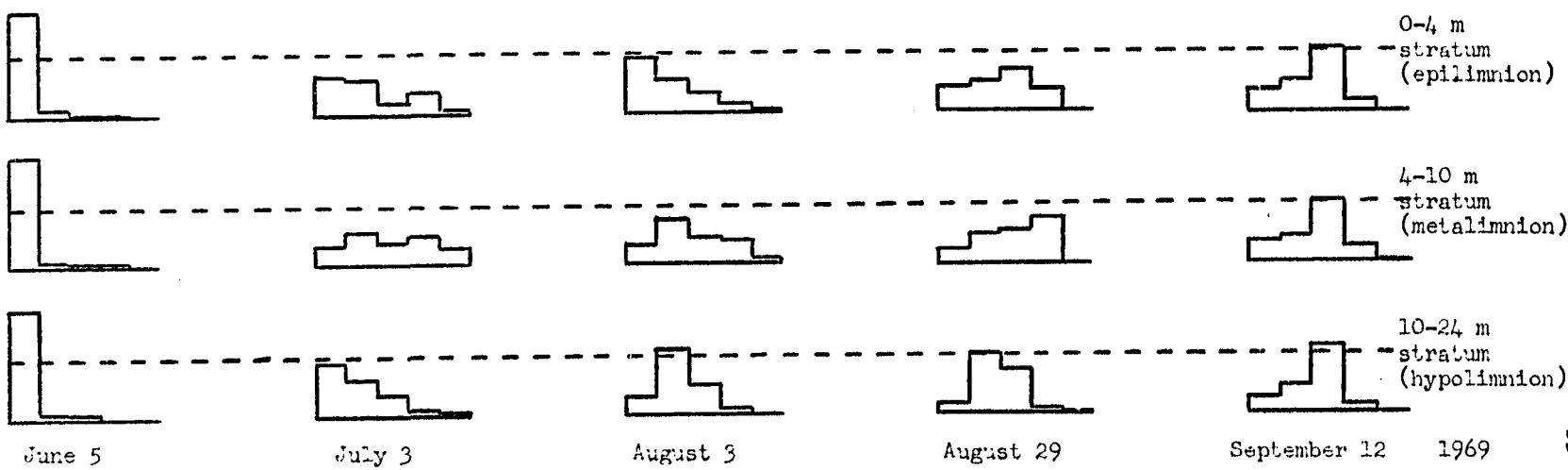

Fig. 6. Size-frequency distribution of Daphnia galeata mendotae in Wononskopomuc and East Twin Lake. Measurements from anterior margin of head to tailspine base. Darkened area indicates egg-bearing animals. Symbols: N number of animals measured, ↓ median size class.

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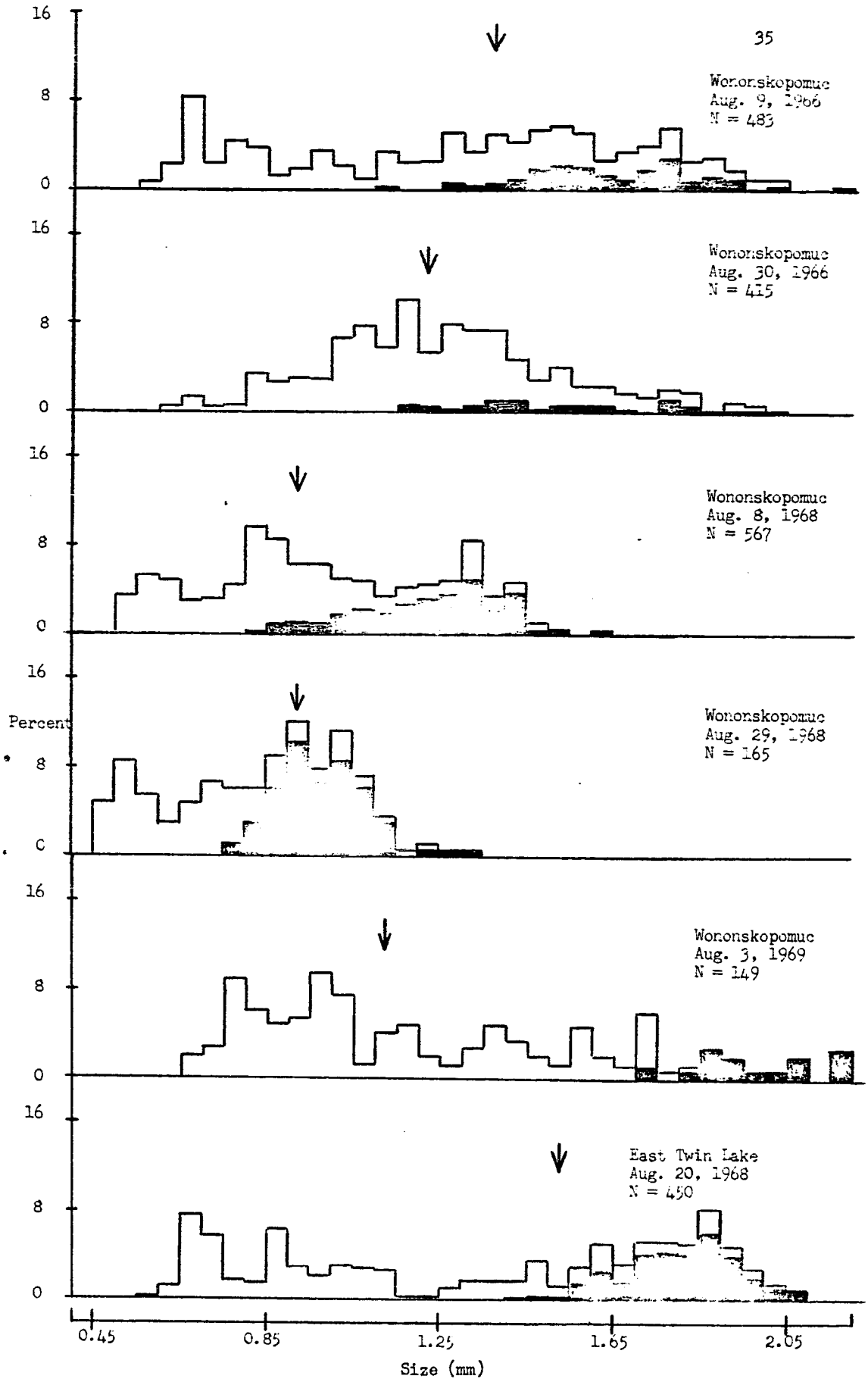

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Fig. 7. Electivity values of Daphnia in three stomachs of Alosa collected Aug. 15, 1968, and the vertical distributions of D. galeata mendotae and D. longiremis on that date. All measurements are from anterior margin of carapace to tailspine base. Symbols: open circles - values based only on stomach containing largely D. galeata mendotae, closed circles - average of three stomachs, one containing largely D. galeata mendotae and two containing largely D. longiremis, together with maximum and minimum values recorded among the three stomachs, * unreliable values based on very few specimens in stomachs and samples.

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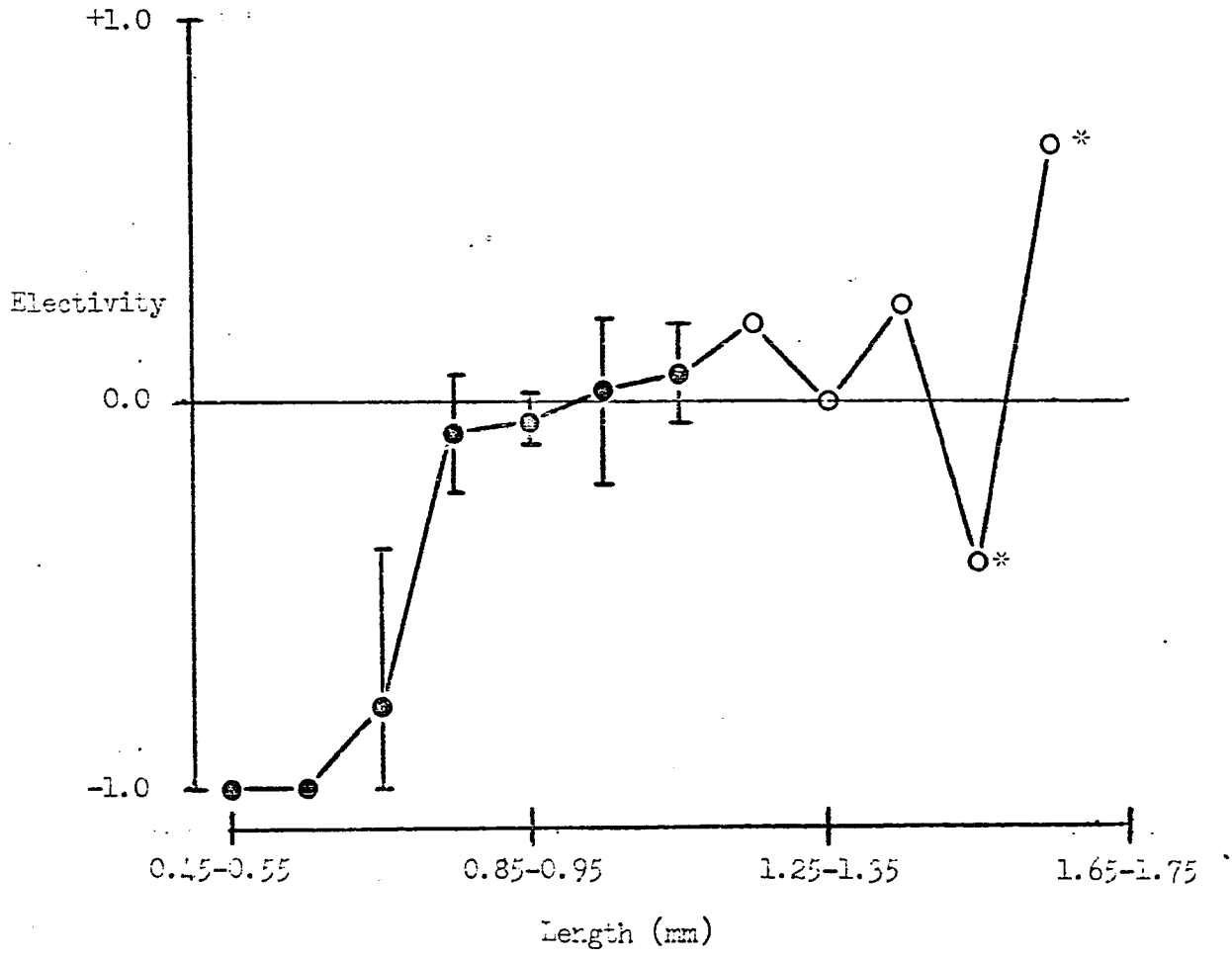

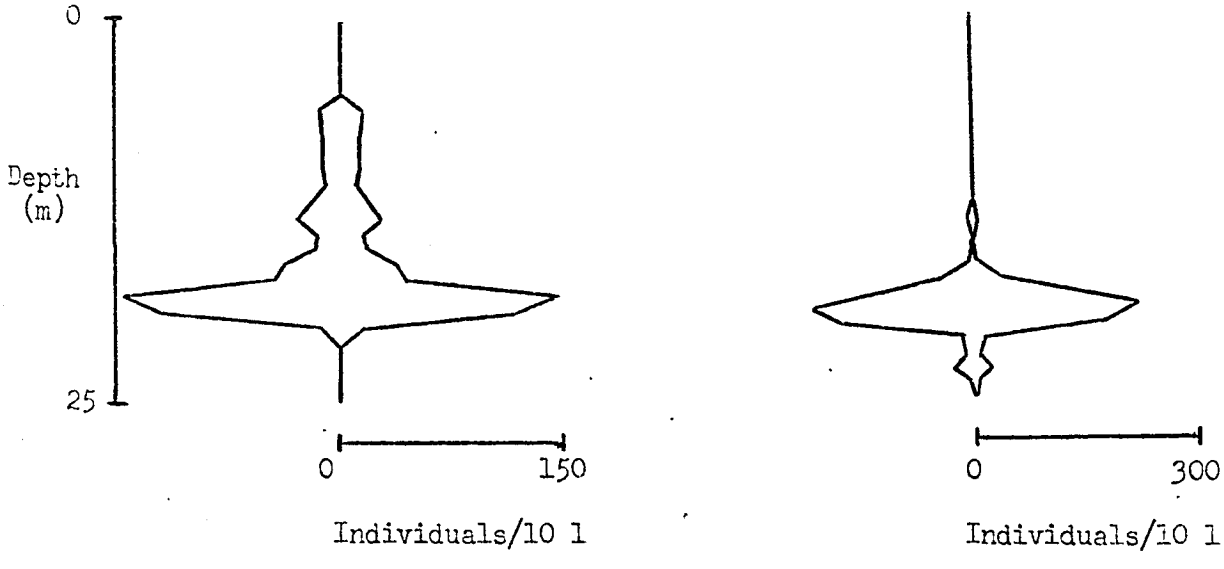

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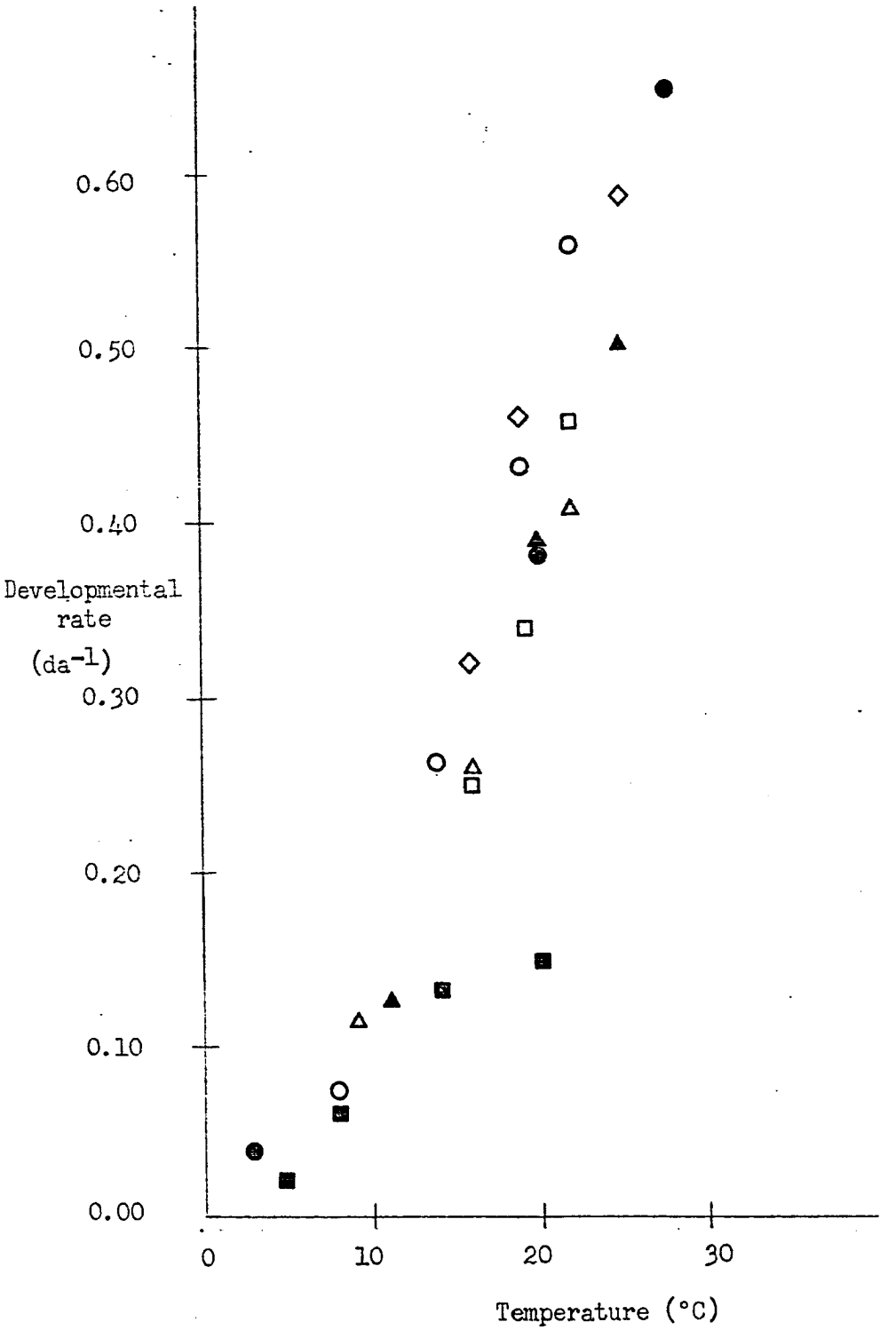

Fig. 8. Developmental rates of Daphnia spp. and Cyclops scutifer eggs as a function of temperature. Symbols: open circles D. pulex (present study), closed circles D. pulex (Esslová, 1959), open triangles D. galeata mendotae (present study), closed triangles D. galeata mendotae (Hall, 1964), open diamonds D. hyalina (Kořínek, 1970), open squares D. dubia (present study), closed squares Cyclops scutifer (Burgis, 1970).

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SECTION II: EFFECTS OF HORIZONTAL PATCHINESS AND EGG-AGE DISTRIBUTION ON *DAPHNIA* MORTALITY ESTIMATES

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INTRODUCTION

Edmondson's (1960) "egg ratio" method of estimating instantaneous mortality rates has frequently been applied to natural Daphnia populations (Costa, 1967; Hall, 1964; Tappa, 1965; Wright, 1965), since Daphnia species possess certain life history and population characteristics (carrying eggs in transparent brood pouches and, in most cases, having overlapping generations) that make the method an appropriate one. This paper gives the results of several studies undertaken to determine its usefulness for evaluating mortality rates of Daphnia in Wononskopomuc, a lake in northwestern Connecticut.

The method estimates an instantaneous mortality rate d' as $(b'-r')$, where b' is an approximation of the instantaneous birth rate and r', a measure of observed population growth. These values are determined from field samples as:

$$(1)\quad b' = \ln\left(\frac{E}{D} + 1\right), \text{ and}$$

$$(2)\quad r' = \frac{\ln(N_t) - \ln(N_0)}{t},$$

where E is the ratio eggs:females, D is the egg developmental duration, N_t is the female population size at time t, and N_0 is the initial female population size. In other words, an estimate of population recruitment is projected over some time interval, and mortality during the interval is approximated as the difference between projected and observed population changes. Use of the method presumes a stable age distribution of individuals and a uniform egg-age distribution during the interval.

Leigh (Edmondson, 1968) and Smith (Cooper, 1965: Appendix) have shown that b' is only an approximation of the birth rate for $D \neq 1$. The

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method is also subject to problems associated with projecting average values for reproductive and mortality rates, which probably vary continuously due to factors such as density (Frank, 1960). Yet it has yielded reasonable results when applied (Hall, 1964; Wright, 1965) to situations in which something was known of the temporal distribution of likely mortality sources. Thus the considerations in the present study can be used to determine when the egg ratio method is most likely to be useful, and to increase the accuracy of determinations made.

Two factors influencing mortality estimates made with Edmondson's method are considered here, age-specific mortality influencing the egg-age distribution and horizontal variations in zooplankton abundance. Edmondson (1968) examined the assumption of a uniform egg-age distribution with a computer model of a prey population having various reproductive schedules. d' was compared to:

$$(3)\quad d = \ln(N_t) - \ln(N_t - C)\ ,$$

where C is the number of deaths between t and (t+1). He assumed that d, based on actual counts of deaths, was a more direct mortality measure than d', and noted that d'>d when D>1. For all these schedules the population was increasing (r'> 0), so the egg-age distribution was skewed toward young eggs and the proportion of eggs hatching per day was $\frac{1}{D}$. He calculated the actual fraction of eggs hatching as a function of D, r', and d, and concluded that likely field values of r' led to young recruitment overestimates of <20% (his Table 6). As Cooper (1965) observed, however, young recruitment increment is a function of adult survivorship rather than of r' per se; so a non-uniform egg-age distribution can also occur in a stable population (r' = 0). A computer model simulating a Daphnia population exposed to several age-specific mortality

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patterns is used in the present study to determine the effects of a non-uniform egg-age distribution on the egg ratio method when population size is relatively stable.

Edmondson (1960) noted that accurate determinations of b' and r' require extensive collections to avoid errors associated with sampling the patchy spatial distributions of many zooplankton populations. Since it is ultimately temporal variation in d' that one wishes to measure, collections must be extensive in time as well as in space. Thus one should know the important factors contributing to horizontal variation in order to design an economical sampling program.

Horizontal patchiness may be small- or large-scale. The former has been carefully studied and is reviewed by Hutchinson (1967). Zooplankton populations in such studies are often characterized as superdispersed (individuals clumped), randomly dispersed, or infradispersed (individuals more or less uniformly spaced), with deviations from random attributed to hydrographic-behavioral factors (e.g. rheotactic movements in a Langmuir spiral) or to interactions among individuals (competition, social aggregation).

Large-scale patchiness, the type considered in the present study, has been attributed to several different factors. Patalas (1969) considered differences in zooplankton concentration between eastern and western Lake Ontario to be due to different warming rates in the two regions. Langford and Jermolajev (1966) found that zooplankton of three small lakes were concentrated centrally on calm days and along the leeward shores on windy days. Dumont (1967) found no direct effect of wind on Bosmina coregoni in a shallow pond; he postulated a single large patch that was maintained by avoidance of littoral regions and

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broke up into smaller subpatches when it moved into shallower (<1m) waters. The phenomenon of littoral avoidance by limnetic zooplankton has been reported frequently; Hutchinson (1967) reviews early studies, and more recent ones include Anderson (1970), Gliwicz (1967), and von Siebeck (1964a, 1964b). In the present study zooplankton distribution is examined by analysis of variance to determine which factors should be considered in measuring E (eggs:females) and population size of Wononscopomuc Daphnia species.

METHODS

Computer model

The computer model simulates a prey species with four immature and eight mature instars, with each instar and D (egg developmental duration) equal in length to three days. All individuals are females. Thus an individual entering the fifth instar at time t acquires a brood that she releases at time (t+3) if she survives the interval. All mature females carry an equal number of eggs. At the end of the twelth instar an animal dies of "old age."

Values of E and age-specific predation rates are read in at t = 0. During each subsequent day prey are subtracted, after which the remaining animals carrying eggs three days old release their young as the population grows one day older. In order to avoid oscillating values of population parameters, three such populations are begun at one-day intervals (termed "pulsing" by Edmondson, 1968) and censused as a single population. The computer population is censused after the age distributions of eggs and individuals stabilize to two decimal places. It is difficult to determine b' and d in a population growing and dying in

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such a discontinuous fashion, because their values depend on when within the day the census is made. In the present study d is calculated from the population size immediately before predation, and the number of deaths during the day; r', b', and age distributions are calculated immediately after predation. Thus d is based on the number of individuals "exposed" to mortality, and b' is based on potential contributors to the next young recruitment increment.

For each model population three death rates are given. These are based, respectively, on actual counts of prey, actual counts of total deaths, and Edmondson's method of estimating total deaths. The values compared in Results are expressed as finite death rates rather than as instantaneous rates, and are calculated as follows:

(4) predatory death rate (PD) = $\frac{\text{prey eaten in a day}}{\text{population size at beginning of day}}$

(5) total death rate (TD) = $\frac{\text{deaths in a day}}{\text{population size at beginning of day}}$

(6) estimated total death rate (ETD) = $1 - e^{-d'}$

The formula for calculating ETD is derived from the exponential growth equation:

(7) $N_t = N_0 e^{(b-d)t}$.

We wish to find $\frac{C}{N_0}$ where C is the number of deaths from t = 0 to t = 1. For b = 0, the population size at the end of the day (N_1) will be the initial size diminished by C, so

(8) $\frac{N_0 - C}{N_0} = e^{(0-d)1}$

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$$(9)\ \frac{C}{N_0} = 1 - e^{-d}.$$

Field study

Zooplankton samples were collected with a 10 l Juday trap during summer 1969. Collections were made between 5:00 and 11:00 A.M. on each of eight dates at the 12 sampling stations in Fig. 1. This time of day was chosen to minimize the effects of wind, which generally blew from about 10:00 A.M. until late afternoon. Stations were located by maintaining the boat along a line between two fixed shore points and proceeding to the position of desired depth as measured with a Heathkit Depth Sounder (Model MI-11A). Single samples were taken at the surface and at 2 m intervals through 4 m (shallow stations), 14 m (intermediate), or 24 m (deep), for a total of 96 samples per date. The two transects were sampled in each of eight possible sequences (e.g. 1-2, 3-4; 3-4, 2-1) during the summer. Thus a balanced design was maintained except for eight samples not taken Aug. 3, when the trap failed to close properly. The following data were recorded from each sample: for each species, number of males, mature sexual females, and other females. This last category was divided into mature and immature females in the case of D. dubia. In addition eggs carried by D. dubia and D. galeata mendotae were assigned to four developmental categories (see below), and mature females were measured, for samples collected at 4 and 6 m depths.

During summer 1970 the zooplankton was sampled on four pairs of dates by vertical hauls. On each date hauls were made at the six stations along transect 1-2 (Fig. 1). A haul was made from 4 m to the surface at all stations, from 14 m to the surface at intermediate and deep

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stations, and from 24 m to the surface at deep stations. Each sample was preserved in 5-10% formalin in a wide-mouthed plastic bottle (capacity 300 ml). For enumeration the volume of a sample was brought to 250 ml and the bottle was agitated; then two subsamples were withdrawn (each 25 ml for 4 m hauls, 5 ml for 14 m hauls, and 2.5 ml for 24 m hauls) with a wide-mouthed pipette and counted. During counting of all subsamples the following data were recorded: for each species, number of males, mature sexual females, and other females. All eggs were assigned to developmental categories. Descriptions of sampling gear and the comparability of net and trap catches are given in Warshaw (1971).

Stomach contents of Wononskopomuc yellow perch (Perca flavescens) caught with gill nets of 1 in and 0.5 in mesh were analyzed to determine relative predatory pressure on different Daphnia species. In addition stomach contents of kokanee salmon (Onchorhynchus nerka) caught by hook and line during summer 1967 in Beach Pond, Connecticut, were examined, as were three vertical series of Beach Pond Juday trap samples (one sample each at the surface and at 3 m intervals through 15 m) collected during the same period. All daphnid measurements were from anterior margin of carapace to tailspine base.

Laboratory study

The duration of each egg developmental stage was determined by growing Daphnia eggs in vitro as described in Obreshkove and Frazer (1940). Eggs were observed at half-hour intervals at 23°C. The stages corresponded to those defined by Stross et.al. (1961) from Green's (1956) study of Daphnia magna egg development. Stage I extended from

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time of extrusion into the brood pouch to formation of fat cells; stage II, from that point until eye pigment was visible; stage III, from that point until straightening of the tailspine, which approximates time of release from the brood pouch (Obreshkove and Frazer, 1940). A fourth category for degenerate eggs was included in plankton sample counts.

RESULTS

Computer model

The computer model was applied to hypothetical populations having E values, respectively, of 0.30, 0.60, or 0.90. For a stable age distribution and uniform mortality of all age classes, a mature female in these populations carried, respectively, approximately one, four, or twelve eggs. For each E value three conditions of age-specific predatory mortality were imposed; predation either fell entirely on immature instars, was distributed uniformly over all ages, or fell entirely on mature instars. Since the model was designed to demonstrate that age-specific mortality affects mortality estimates based on the egg ratio method even when population size is relatively stable, predation rates were chosen so as to make r' very close to 0.

Several generalizations can be made from the results, shown in Table 1. When the predator removed only immatures (Examples 1, 2, 7, 8, 13, 14), the egg-age distribution (which reflects adult survivorship) was uniform, and the total death rate (TD) and death rate estimated by the egg ratio method (ETD) were similar (i.e. $\frac{TD}{ETD}$ was close to 1). When predatory mortality was shifted to egg-bearing animals (Examples

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5, 6, 11, 12, 17, 18), the egg-age distribution was skewed toward young eggs, and ETD was larger relative to TD. Except for the predation pattern in which the predator removed only immatures, increases in E increased the discrepancy between ETD and TD, since such increases in egg:females required an increase in the proportion of adults removed daily (increasing the skew of the adult survivorship curve toward young adults) in order to maintain $r' = 0$.

The discrepancy between ETD and TD was due mostly to a bias introduced into the calculation of ETD by violation of the assumption that the egg-age distribtuion was uniform (i.e. that the proportion of eggs hatching per day was $\frac{1}{D}$). The egg ratio method used to calculate ETD derives mortality as the difference between a projected population change, based on E, and the actual population change, over some interval. Skewing of the egg-age distribution toward young eggs resulted in a hatching rate $< \frac{1}{D}$, such that the actual number of births/female/day was $< \frac{E}{D}$. As shown below, the discrepancy between what the birth rate would be if the egg-age distribution were uniform, and the actual birth rate, accounts for most of the discrepancy between ETD and TD.

Example 9:

Assuming uniform egg-age distribution	Using Actual egg-age distribution
(0.60)(0.333) =	(0.60)(0.283) =
0.200 births/female/day	0.170 births/female/day

$$\frac{0.170}{0.200} = 0.850 \text{ compared to } \frac{TD}{ETD} = 0.870$$

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Example 17:

Assuming uniform egg-age distribution	Using actual egg-age distribution
(0.90)(0.333) =	(0.90)(0.090) =
0.200 births/female/day	0.081 births/female/day

$$\frac{0.081}{0.300} = 0.270 \text{ compared to } \frac{TD}{ETD} = 0.313$$

Thus the effect of egg-age distribution on natural recruitment estimates should be considered even when population size is relatively stable. Such estimates, and mortality determinations derived from them, are less likely to be biased when mortality is concentrated among immature individuals, which do not contribute to the young recruitment increment. Leptodora predation on Daphnia probably results in an age-specific mortality pattern of this type, since laboratory experiments (Mordukhai-boltovskaya, 1958; Moshiri and Cummins, 1969) indicate that Leptodora is only able to eat Daphnia <1 mm long. When mortality is concentrated among egg-bearing individuals, however, the egg-age distribtuion is proportionately skewed toward young eggs, and recruitment and mortality estimates may be unacceptably high (Table 1). Predation by certain fishes on Daphnia (Galbraith, 1967) probably exemplifies such a mortality pattern.

Field studies

The concentrations of abundant Cladocera and the large rotifer Asplanchna sp. in Wononskopomuc during summer 1969 are given in Table 2 and Fig. 2, the values for which are based on the average concentration in all samples collected on a given date. An exceptional date is

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Aug. 3, for which eight samples from the west half of transect 3-4 are missing, so that only samples collected on 1-2 and the east half of 3-4 are used. Data from collections made along 1-2 on May 22 are included in Fig. 2, but are not utilized in subsequent calculations.

Small cladocerans (Ceriodaphnia, Bosmina, Chydorus) and Asplanchna were abundant in early June and declined rapidly thereafter. Daphnia (D. dubia and D. galeata mendotae) was abundant throughout the summer and showed the mid-summer minimum found in the studies of Hall (1964) and Wright (1965). The planktivorous Leptodora peaked in mid-summer and then declined gradually.

The spatial and temporal distributions of Daphnia dubia and D. galeata mendotae were analyzed by analysis of variance, for which each observation (x) was transformed to $\log_{10}(1+x)$. The a priori model proposed to account for variation in the transformed observations included as major effects: sample depths, transects, and dates. In addition two interactions were considered: between sample depth and station depth (shallow, intermediate, deep), to measure the importance of station depth, and between sample depth and the order (time of day) in which the transects were sampled, to determine whether vertical migration occurred during the sampling period. The results are given in Table 3. The correlation coefficient (coefficient of product-moment correlation) significance was determined from Campbell's (1967) Table A18, and F-ratio significances were determined from Owen's (1962) Table 4.1.

The correlation coefficient (0.80) between the two species was highly significant ($p < 0.001$), indicating a strong positive linear relationship between D. dubia and D. galeata mendotae concentrations.

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Sample depth, or the depth to which the plankton trap was lowered to collect a sample, was significant for both species ($p < 0.005$), with their vertical distributions showing marked concentrations in the epilimnion (Warshaw, 1971). There were seasonal trends for both species (Fig. 3), with dates being more significant for D. galeata mendotae ($p < 0.005$) than for D. dubia ($0.010 < p < 0.025$). Transects (e.g. north half of 1-2, east half of 3-4) were significant for D. galeata mendotae ($p < 0.005$) but not for D. dubia ($p > 0.500$). The interaction measuring the importance of station depth was significant for both species ($p < 0.005$), with animals being less concentrated at shallow than at other stations (Table 4). The interaction between sample depth and time of day was not significant for both species ($p > 0.500$), indicating that vertical migration did not occur during sampling.

The effect of station depth on D. dubia was examined further by X^2 tests for a difference in proportions (Dixon and Massey, 1957) of individuals judged to be mature, at stations of different depths. Only animals collected in the 0-4 m stratum were considered in this analysis. Maturity was determined on the bases of presence or absence of eggs in the brood pouch, length of the first abdominal process (longer in mature animals; Brooks, 1957), and the shape of the postero-dorsal margin of the carapace (more rounded in mature animals). Table 5 shows that the proportion of adults was 9.2-11.2% greater at intermediate than at shallow stations, 7.1-9.1% greater at deep than at shallow stations, and 1.2-3.0% greater at intermediate than at deep stations (95% confidence intervals). D. galeata mendotae was omitted from this analysis because of the absence of good criteria of maturity. Thus D. dubia and D. galeata mendotae were significantly less concentrated,

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and the proportion of D. dubia adults was significantly smaller, at shallow than at other stations.

Planktivorous fish of Wononskopomuc include yellow perch (Perca flavescens), alewives (Alosa pseudoharengus), rainbow trout (Salmo gairdneri), and kokanee salmon (Onchorhynchus nerka), the latter two species being stocked yearly by the Connecticut Board of Fisheries and Game. Table 6 gives, for each species, the size range and number caught with vertical gill nets in the limnetic region during 1969-70. All fish were caught in the 0-14 m stratum.

The species compostion and size distribution of the Wononskopomuc zooplankton indicate that A. pseudoharengus predation greatly decreased after an alewife die-off in spring 1969 (Warshaw, 1971). Of the other three species, yellow perch were caught in greatest abundance, perhaps in part because their spines make them more susceptible to gill net fishing. Each of these three species preferentially selects large Daphnia prey (Table 7). In Galbraith's (1967) study, Daphnia >1.3 mm long comprised roughly half the individuals in plankton samples but 96% and 82%, respectively, of the Daphnia eaten by rainbow trout and yellow perch. In Wononskopomuc during summer 1969 Daphnia was the most abundant prey in P. flavescens stomachs (Table 8), and 98% were >1.3 mm (Table 7). Size-selective predation by kokanee salmon was evident upon examination of Beach Pond samples and O. nerka stomach contents during summer 1967. Individuals >1.3 mm comprised 89% of the Daphnia catawba in stomachs but only 39% of those in lake samples.

D. galeata mendotae is larger than D. dubia, as indicated by a comparison of their minimum egg-bearing sizes during summer 1969 (Table 9); so the former is subject to heavier fish predation (Table 10).

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Also, if fish predation is a major mortality source of either species in Wononskopomuc, then such mortality should be reflected in that species' egg-age distribution. This is because larger individuals are generally those in egg-bearing instars, whose mortality has the effect of skewing the egg-age distribution toward young eggs. D. galeata mendotae would be expected to illustrate this latter effect more strongly since it is more heavily preyed upon. The egg-age distribution must also be interpreted, of course, in the light of the population's r' (since skewing toward young eggs also occurs when the population is increasing) and of other mortality sources.

Fig. 3 compares the population size (also given in Table 2) and egg-age distribution for the two Daphnia species during summer 1969. Egg-age distributions are based on samples from 4 and 6 m, where egg-bearing individuals of both species were most numerous; the values shown have been divided by the appropriate values for the proportion of D (egg developmental duration) spent in each developmental stage (Table 11), so that the bar graphs in Fig. 3 directly reflect what skewing, if any, was present for each species on each date.

D. dubia and D. galeata mendotae egg-age distributions did not differ from each other in a consistent way, with the bar graphs in Fig. 3 indicating a preponderance of stage II eggs. No theoretical age-specific mortality pattern can account for such a distribution if it is stable. It seems likely that the distributions are due in part to differential loss of eggs from brood pouches during collection. Table 12, which gives the age distributions of retained and loose eggs in 1970 samples, indicated that stage III eggs were dropped more often than those in stage I or II. Thus a correction for this bias, if it applies to summer

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1969 samples as well, would increase the proportion of stage III eggs in Fig. 3 relative to those in stages I and II.

DISCUSSION

Two factors that may bias mortality estimates made with the egg ratio method have been considered here. Horizontal variation in Daphnia abundance has been measured by a sampling program with an analysis of variance format, and significant differences between stations of different depths have been demonstrated. The effects of age-specific mortality on egg-age distribution and the Edmondson method have been examined with a computer model. In addition, Daphnia egg-age distributions in Wononskopomuc have been considered in light of the nature of potential mortality sources and the egg-age distributions likely to be produced by different predators.

The finding that D. dubia and D. galeata mendotae were less concentrated at 6 m stations than at deeper ones, together with frequent reports by other workers of littoral avoidance, imply that population size and E determinations should often be derived from samples at several stations of different depths. Study of limnetic zooplankton in a lake with a substantial littoral area should follow this sampling strategy; whereas towing a net through a large distance probably minimizes error due to small-scale patchiness (Wiebe, 1971), large-scale patchiness requires sampling areas of different depths.

The effect of age-specific mortality on egg-age distribution should be considered in determinations of natural recruitment and mortality. The computer model simulating a Daphnia population shows that skewing

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toward young eggs occurs and mortality rates are overestimated when deaths are concentrated among egg-bearing individuals. Departure of the egg-age distribution from uniformity in a population with asynchronous reproduction is a function of adult recruitment and mortality and of age-specific mortality of the developing eggs themselves. If the population rate of change (r') is known and developmental mortality is low, the egg-age distribution is an index of female age-specific mortality. It should be a particularly useful index when post-embryonic life stages are difficult to distinguish from one another, as in Daphnia.

Some data on egg-age distributions of natural Daphnia populations have been published. Edmondson (1955) gave the egg-age distribution of a synchronously reproducing D. middendorfiana (Brooks, 1957) population in an Arctic lake. The results reflected passage of the dominant cohort through a single generation and indicated relatively low adult mortality. Hall (1964) gave no data but stated he found little seasonal variation in D. galeata mendotae egg-age distribution. Stross et.al. (1961) also gave no data but stated that a comparison of Daphnia egg-age distribution to Green's (1956) laboratory results for a uniform egg-age distribution in D. magna revealed no differential egg mortality. Green (1956) found several instances of non-uniform egg-age distributions in D.magna and D. pulex;he suggested these might be due to occasional synchronization of reproduction or to apparent synchronization caused by sampling a population in which females at the same stage of instar were clustered.

One study suggests an egg-age distribution shift as a result of fish predation. Korinek (1966) found that D. pulicaria mortality rates, presumed to be due to carp predation, were highest during late June-July, when population size was relatively stable. The egg-age distribu-

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tion was more skewed toward young eggs and the proportion of total eggs in the population released per day as freely swimming young (determined from field experiments utilizing plastic bags) was lower during this period of high mortality than earlier in the summer.

Wononskopomuc Daphnia egg-age distributions during summer 1969 did not provide evidence that size-selective fish predation was an important mortality source since no skewing toward young eggs was noted. Leptodora probably accounted for some mortaltiy, since its population persisted through the summer, whereas potential cladoceran prey other than Daphnia were rare after June. Since Leptodora eats only small daphnids, deviation from uniformity of egg ages is unlikely to occur when it is the principal predator. Hall's (1964) statement that he found little seasonal variation in egg-age distribution of a D. galeata mendotae population heavily preyed upon by Leptodora is consistent with this hypothesis.

The preponderance of stage II eggs (Fig. 3) among Wononskopomuc Daphnia was probably due in part to a differentially high loss of stage III eggs from brood pouches during collecting. The under-representation of stage I eggs (as compared to a theoretical uniform distribution of egg ages), however, cannot be explained in this way. At least two hypotheses could account for these results. In the first place, it is possible that eggs extruded into the brood pouches of natural females were relatively older than those of females in laboratory studies of developmental stage durations; that is, in natural populations part of stage I might be traversed before the eggs enter the brood pouch. A second possibility is that natural reproduction may be synchronized as suggested by Green (1956), such that most eggs in the natural

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populations might pass through stage I at some time of day other than morning, when samples were taken. Egg developmental duration could still be temperature-dependent, but some stage of development would require cueing by an environmental factor that varied diurnally. No evidence concerning either hypothesis was collected in the present study.

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Table 1. Results of computer model simulating a Daphnia population. E is the ratio egg:females. Predation rate is the proportion of juveniles (j), juveniles and adults (u), or adults (a) removed by the predator per day. r' is the rate of population change; for a population increasing at a rate of 1% per day, r' = +0.01001. Egg-age distribution is given in order of increasing egg age. Text should be consulted for definitions of PD (predatory death rate), TD (total death rate), and ETD (estimated total death rate).

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	Egg age distr.	PD	TD	ETD	TD/ETD
Example 1	0.34	0.0708	0.0870	0.0855	1.02
E = 0.30	0.33				
pred. rate = 0.12j	0.33				
r' = +0.00596					
Example 2	0.33	0.0752	0.0928	0.0912	1.02
E = 0.30	0.33				
pred. rate = 0.13j	0.33				
r' = - 0.00036					
Example 3	0.36	0.0800	0.0842	0.0907	0.93
E = 0.30	0.33				
pred. rate = 0.08u	0.31				
r' = +0.00026					
Example 4	0.36	0.0890	0.0931	0.1006	0.93
E = 0.30	0.33				
pred. rate = 0.09u	0.30				
r' = -0.01066					
Example 5	0.45	0.0637	0.0637	0.0897	0.71
E = 0.30	0.32				
pred. rate = 0.28a	0.23				
r' = +0.00132					
Example 6	0.45	0.0653	0.0653	0.0922	0.71
E = 0.30	0.32				
pred. rate = 0.29a	0.23				
r' = -0.00143					
Example 7	0.34	0.1537	0.1629	0.1612	1.01
E = 0.60	0.33				
pred. rate = 0.20j	0.33				
r' = +0.00655					
Example 8	0.33	0.1588	0.1690	0.1673	1.01
E = 0.60	0.33				
pred. rate = 0.21j	0.33				
r' = - 0.00078					
Example 9	0.39	0.1408	0.1413	0.1622	0.87
E = 0.60	0.33				
pred. rate = 0.14u	0.28				
r' = +0.00539					
Example 10	0.39	0.1491	0.1496	0.1719	0.87
E = 0.60	0.33				
pred. rate = 0.15u	0.28				
r' = -0.00630					

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	Egg age distr.	PD	TD	ETD	TD/ETD
Example 11	0.59	0.0698	0.0698	0.1626	0.43
E = 0.60	0.28				
pred. rate = 0.53a	0.13				
r^1 = +0.00114					
Example 12	0.60	0.0733	0.0733	0.1694	0.43
E = 0.60	0.28				
pred. rate = 0.54a	0.13				
r^1 = -0.00291					
Example 13	0.33	0.2243	0.2299	0.2285	1.01
E = 0.90	0.33				
pred. rate = 0.26j	0.33				
r^1 = +0.00295					
Example 14	0.33	0.2296	0.2360	0.2348	1.01
E = 0.90	0.33				
pred. rate =0.27j	0.34				
r^1 = -0.00527					
Example 15	0.41	0.1906	0.1907	0.2283	0.84
E = 0.90	0.33				
pred. rate = 0.19u	0.26				
r^1 = +0.00136					
Example 16	0.41	0.1982	0.1982	0.2379	0.83
E = 0.90	0.33				
pred. rate = 0.20u	0.26				
r^1 = -0.00926					
Example 17	0.67	0.0723	0.0723	0.2307	0.31
E = 0.90	0.24				
pred. rate = 0.63a	0.09				
r^1 = +0.00334					
Example 18	0.67	0.0745	0.0745	0.2349	0.32
E = 0.90	0.24				
pred. rate = 0.64a	0.09				
r^1 = -0.00205					

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Table 2. Concentrations of abundant Cladocera in Lake Wononskopomuc during summer 1969. Small Cladocera include *Ceriodaphnia* sp., *Bosmina longirostris*, and *Chydorus sphaericus*. Abbreviations: $\bar{X}$ individuals/10 l in all samples taken on a date except for Aug. 3, as noted in text, s.d. standard deviation. Symbol: + present in small numbers.

		Jun 5	Jun 20	Jul 3	Jul 18	Aug 3	Aug 15	Aug 29	Sep 12
D. dubia	$\bar{X}$	102	110	93	42	97	77	84	59
	s.d.	27	13	36	8.4	22	40	31	10
D. galeata mendotae	$\bar{X}$	6.7	19	16	7.3	6.8	8.4	5.2	3.4
	s.d.	0.37	3.2	5.4	4.1	1.8	3.6	1.8	1.4
D. dubia and *D. galeata mendotae*	$\bar{X}$	108	130	109	49	103	85	89	62
	s.d.	27	16	41	7.5	24	41	32	12
Small *Cladocera* and *Asplanchna*	$\bar{X}$	352	60	3.1	+	+	+	+	+
	s.d.	87	16	0.64					
Leptodora kindtii	$\bar{X}$	0.073	1.1	1.4	0.96	0.46	0.38	0.20	0.10
	s.d.	0.051	0.16	0.46	0.47	0.00	0.19	0.062	0.024

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Table 3. ANOVAR results for Daphnia dubia and D. galeata mendotae during summer 1969. The correlation coefficient between the two species was 0.80 ($p < 0.001$). Abbreviations: ss sum of squares, df degrees of freedom, ms mean square, F f-ratio.

Daphnia dubia

	ss	df	ms	F	
transects	0.844	3	0.281	0.982	$0.500 < p < 0.750$
depths	138.682	2	69.341	244.	$p < 0.005$
dates	2.283	2	1.141	4.01	$0.010 < p < 0.025$
depths X station depths	32.626	4	8.156	28.7	$p < 0.005$
depths X times of day	0.638	6	0.106	0.374	$p > 0.500$
residual	210.100	739	0.284		

D. galeata mendotae

	ss	df	ms	F	
transects	2.972	3	0.991	5.01	$p < 0.005$
depths	59.658	2	29.829	151.	$p < 0.005$
dates	15.119	2	7.560	38.3	$p < 0.005$
depths X station depths	20.226	4	5.057	25.6	$p < 0.005$
depths X times of day	0.642	6	0.107	0.542	$p > 0.500$
residual	146.012	739	0.198		

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Table 4. Average concentrations of D. dubia and D. galeata mendotae in the 0-4 m stratum at stations of different depths during summer 1969.

	Jun 5	Jun 20	Jul 3	Jul 18	Aug 3	Aug 15	Aug 29	Sep 29
Daphnia dubia								
shallow	104.7	105.1	43.8	23.5	96.2	53.9	82.1	26.3
intermediate	273.2	143.8	199.0	101.2	173.2	108.7	102.8	130.4
deep	322.0	251.6	207.2	114.3	168.0	71.0	159.6	101.1
D. galeata mendotae								
shallow	8.8	16.5	8.3	4.5	2.6	5.0	1.8	1.0
intermediate	16.6	30.3	34.0	20.5	11.8	16.2	5.4	8.4
deep	19.2	41.8	35.5	18.5	19.0	6.9	6.8	8.8

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Table 5. Results of X^2 tests for difference in proportions of D. dubia adults in the 0-4 m stratum at stations of different depths during summer 1969. Abbreviation: p_x proportion of adults at stations of depth x.

Observations

	No. adults	No. juveniles	Total	%adults	%juveniles
Shallow stations	712	5427	6139	11.6	88.4
Intermediate stations	3113	11157	14270	21.8	78.2
Deep stations	3200	13033	16233	19.7	80.3

Tests

Shallow (s) v. intermediate (i)

$$0.116 - 0.218 - 1.96\sqrt{\frac{0.116(0.884)}{6139} + \frac{0.218(0.782)}{14270}} < p_s - p_i < 0.116 - 0.218 + 1.96\sqrt{\frac{0.116(0.884)}{6139} + \frac{0.218(0.782)}{14270}}$$

$$-0.112 < p_s - p_i < -0.092$$

Shallow (s) v. deep (d)

$$0.116 - 0.197 - 1.96\sqrt{\frac{0.116(0.884)}{6139} + \frac{0.197(0.803)}{16233}} < p_s - p_d < 0.116 - 0.197 + 1.96\sqrt{\frac{0.116(0.884)}{6139} + \frac{0.197(0.803)}{16233}}$$

$$-0.091 < p_s - p_d < -0.071$$

Intermediate (i) v. deep (d)

$$0.218 - 0.197 - 1.96\sqrt{\frac{0.218(0.782)}{14270} + \frac{0.197(0.803)}{16233}} < p_i - p_d < 0.218 - 0.197 + 1.96\sqrt{\frac{0.218(0.782)}{14270} + \frac{0.197(0.803)}{16233}}$$

$$0.012 < p_i - p_d < 0.030$$

Table 6. Fish caught with vertical gill nets in the limnetic region of Wononskopomuc during 1969-70.

	No. caught	Size range (cm)
Perca flavescens	89	8.9 - 28.0
Salmo gairdneri	2	16.5
Salmo trutta	2	23.0 - 24.1
Onchorhynchus nerka	3	19.0
Alosa pseudoharengus	3	11.7 - 21.0

Table 7. Evidence for size-selective predation on Daphnia by planktivorous fish species that occur in Wononskopomuc. All values refer to Daphnia measured from anterior margin of carapace to tailspine base. Symbol: * data from Galbraith (1967).

	No. fish examined	No. prey measured	Proportion of prey > 1.3 mm	Proportion of individuals in plankton > 1.3 mm
Salmo gairdneri*			0.96	0.50
Perca flavescens*			0.82	0.50
P. flavescens	12	1261	0.98	
Onchorhynchus nerka	6	318	0.89	0.39

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Table 8. Generic composition of Perca flavescens stomach contents from Wononskopomuc during the period May - Nov. 1969. Each value is number of stomachs containing >20, 19-5, 4-1, or 0, of the prey item.

	>20	19-5	4-1	0
Copepoda				
Epischura		7	11	11
Diaptomus				29
cyclopoids			12	17
Cladocera				
Daphnia	27	1	1	
Ceriodaphnia		2	1	26
Bosmina			1	28
Diaphanosoma			1	28
Chydorus				29
Leptodora	2	1	3	23

Table 9. Length (mm) of smallest egg-bearing animal encountered for D. dubia and D. galeata mendotae in samples collected at 4 and 6 m during summer 1969.

	Jun 5	Jun 29	Jul 3	Jul 18	Aug 3	Aug 15	Aug 29	Sep 29
D. dubia	1.10	1.35	1.40	1.30	1.20	1.15	1.25	1.25
D. galeata mendotae	1.50	1.70	1.70	1.70	1.65	1.40	1.60	1.50

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Table 10. Relative proportions of three Daphnia species in P. flavescens stomach contents from Wononskopomuc during summer 1970. Number in parenthesis is number of examined stomachs containing Daphnia. Daphnia longiremis was abundant in plankton samples but occurred in only one stomach, so it was omitted from this analysis. Stomach sample proportions are mean frequencies for each date. Plankton sample proportions refer to the 0-14 m stratum, as no P. flavescens were collected below 14 m.

	Stomach samples			Plankton samples		
	Daphnia pulex	Daphnia galeata mendotae	Daphnia dubia	Daphnia pulex	Daphnia galeata mendotae	Daphnia dubia
25-27 May (17)	0.95	0.04	0.01	0.47	0.22	0.31
15-17 June (18)	0.39	0.60	0.01		no sample	
6-8 July (4)	0.40	0.54	0.06	0.30	0.43	0.27
27-29 July (3)	0.22	0.71	0.07	0.40	0.21	0.38
19-20 Aug (5)	0.31	0.30	0.39	0.12	0.09	0.79

Table 11. Duration of *D. dubia* and *D. galeata mendotae* egg developmental stages *in vitro*.

	Stage	No. determinations	Mean (hours)	Range (hours)	Proportion of total D
Daphnia dubia	I	3	12.1	11.9 - 12.4	0.254
	II	4	19.7	19.5 - 20.0	0.413
	III	4	15.9	14.7 - 16.5	0.333
D. galeata mendotae	I	7	15.6	14.5 - 16.6	0.300
	II	4	18.4	18.0 - 18.5	0.354
	III	4	18.0	17.4 - 18.6	0.347

Table 12. Retention by *D. dubia* and *D. galeata mendotae* of eggs of different developmental stages in plankton samples from 0-4 m during summer 1970. Abbreviations: pI proportion of eggs in first developmental stage, etc.

	No. eggs	pI	pII	pIII
Retained	7773	0.263	0.450	0.287
Loose	2724	0.226	0.352	0.421

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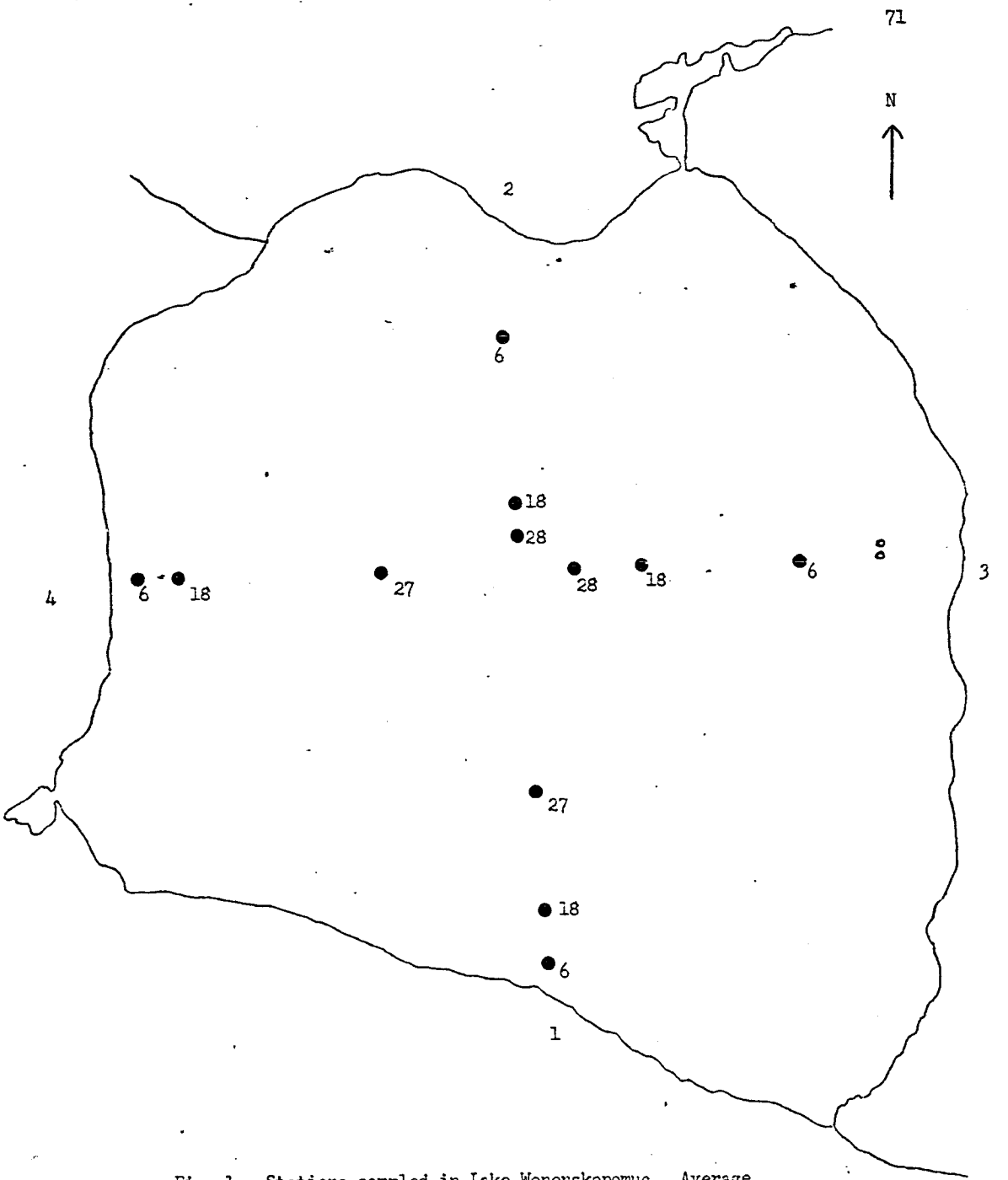

Fig. 1. Stations sampled in Lake Wononskopomuc. Average depth in m is given with each station. Numbers on shore refer to transects in text.

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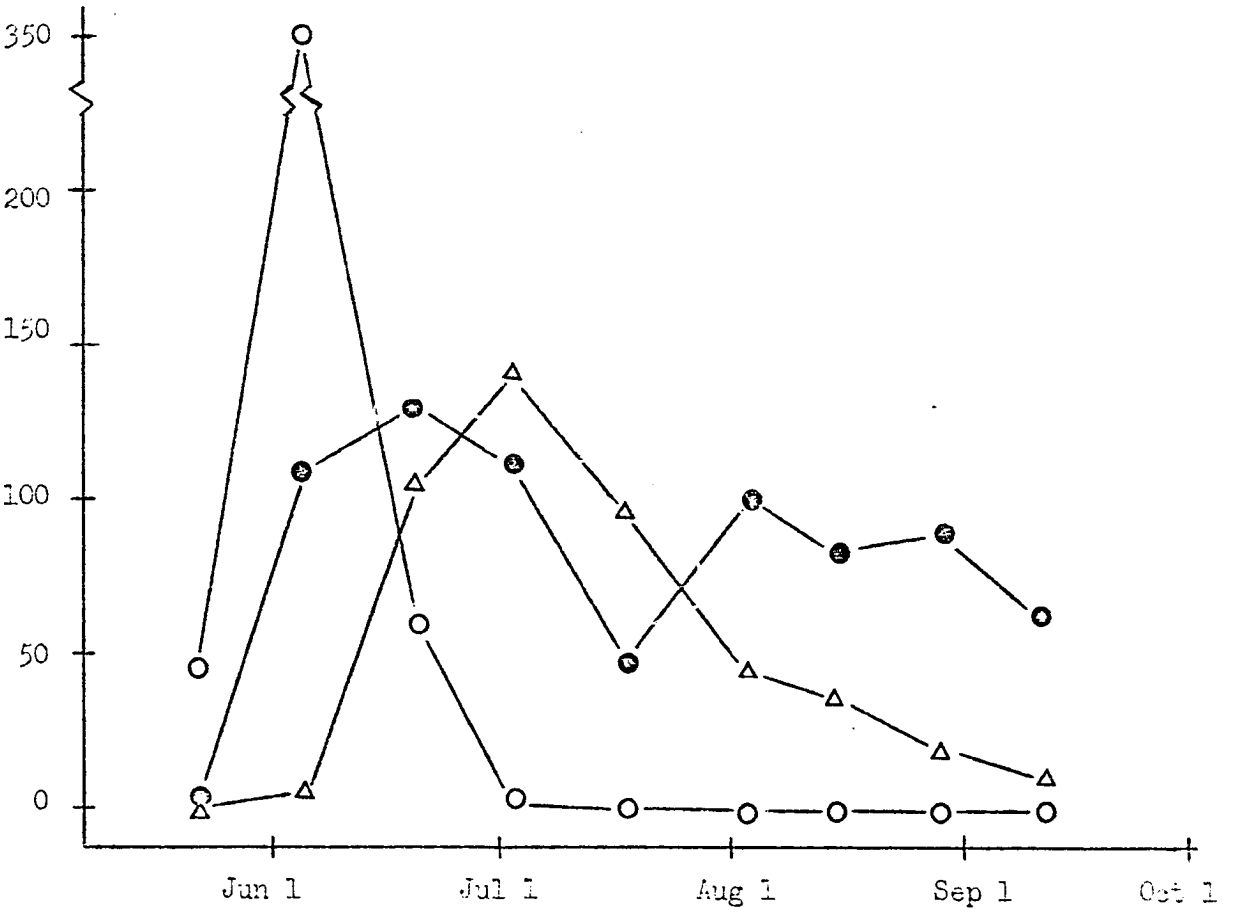

Fig. 2. Concentrations of numerically important zooplankton during summer 1969. Values refer to all samples collected on a date except for Aug. 3, as noted in text. All values are individuals/10 l except for Leptodora, which is individuals/1000 l. Symbols: open circles - small Cladocera (Ceriodaphnia, Bosmina, Chydorus) and the rotifer Asplanchna, closed circles - Daphnia (D. dubia and D. galeata mendotae), triangles - Leptodora.

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Fig. 3. Daphnia dubia and D. galeata mendotae concentrations and egg-age distributions, during summer 1969. Concentrations are individuals/10 l. Egg-age distributions refer to samples from 4 and 6m; the values shown have been divided by the appropriate values from Table 11 to reflect what skewing, if any, was present for each species on each date. For each sampling date and species stage I eggs are represented in the left bar graph, stage II in the center, and stage III on the right. Symbols: open circles - D. dubia, closed circles - D. galeata mendotae, N - number of eggs examined.

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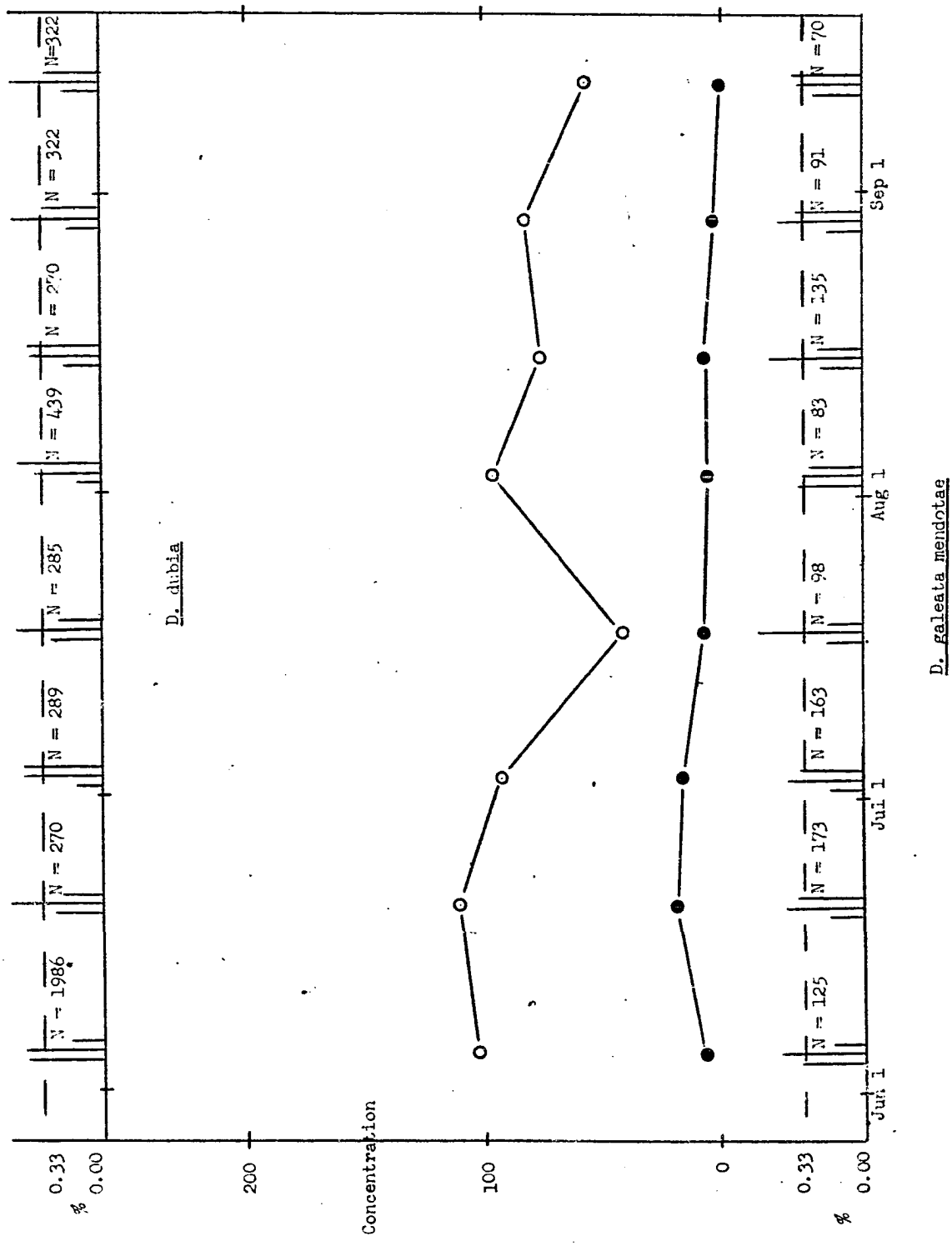

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