Predation, Body Size, and Composition of Plankton

The effect of a marine planktivore on lake plankton illustrates theory of size, competition, and predation.

John Langdon Brooks and Stanley I. Dodson

During an examination of the distribution of the cladoceran Daphnia in the lakes of southern New England, it was noted that large Daphnia, although present in most of the lakes, could not be found among the plankton of several lakes near the eastern half of the Connecticut coast. The characteristic limnetic calanoid copepods of this region, Epischura nordenskioldi and Diaptomus minutus, and the cyclopoid Mesocyclops edax were also absent. Small zooplankters were abundant, especially the cladoceran Bosmina longirostris and the copepods Cyclops bicupispidatus thomasi and the small Tropocyclops prasinus (1).

All of these lakes lacking large zooplankters have sizable "landlocked" populations of the herring-like Alosa pseudoharengus (Wilson) = Pomolobus pseudoharengus (Fig. 1), known by several common names including "alewife" and "grayback" (2). This is originally an anadromous marine fish, breeding populations of which have become established in various bodies of fresh water, including Lake Cayuga, New York, and the Great Lakes (3).

The marine populations live in the coastal waters of the western Atlantic, from the Gulf of St. Lawrence to North Carolina, and ascend rivers and streams to spawn in springtime. The young return to the sea in summer and autumn (4). The seven Connecticut lakes (Fig. 2) with self-perpetuating populations of alewives are within about 40 kilometers of the present coastline, and each is drained directly, by a small stream or river, or indirectly, through the estuaries of the larger Connecticut or Thames rivers, into Long Island Sound (Fig. 3). As such streams and rivers are normally ascended by marine alewives, it is assumed that the establishment of these self-sustaining populations in the lakes is natural.

The "alewife lakes" are diverse in area and depth. Although we have not examined the food of the alewives in these Connecticut lakes (alewives are difficult to catch), studies in other lakes have revealed that planktonic copepods and Cladocera are the primary food. The indifferece of alewives to non-floating food is not surprising in view of the adaptation of the parent stock to feeding on zooplankton in the open waters of the sea (5).

The dominant crustaceans in the plankton of all the alewife lakes are the same small-sized species, Bosmina longirostris (or Ceriodaphnia lacustris) being most numerous; Cyclops bicuspidatus thomasi and Tropocyclops prasinus, present in varying ratios, are also numerous. By contrast, in the non-alewife lakes Diaptomus spp. and Daphnia spp. are always dominant, usually accompanied by the larger cyclooids Mesocyclops edax and Cyclops bicuspidatus thomasi. The absence of all but one of these last-named larger zooplankters from the lakes inhabited by the planktivorous-alewife may be due to differential predation by the alewives. The elimination of these pelagic zooplankters allows the primarily littoral species, such as Bosmina longirostris, to spread into the pelagic zone, from which, we conclude, they would otherwise be excluded by their larger competitors.

Changes in Crystal Lake Plankton

An opportunity to test this hypothesis was provided by the introduction into a lake in northern Connecticut of Alosa aestivalis (Mitchell), "gilt herring," a species closely related, and very similar, to Alosa pseudoharengus (6). The plankton of Crystal Lake had been quantitatively sampled by one of us in 1942 before Alosa was introduced. At that time the zooi plankton was dominated by the large forms (Daphnia, Diaptomus, Mesocyclops) expected in a lake of its size (see Table 1). Resampling 10 years after Alosa had become abundant should reveal plankton similar in composition to that common in the lakes with natural populations of Alosa pseudoharengus and unlike that characteristic of Crystal Lake before Alosa became abundant.

The plankton of the entire water column of Crystal Lake was sampled quantitatively on 30 June 1964 (7). All the crustacean zooplankters caught in the 1942 and 1964 collections (a total of 6623 specimens) were
identified, and those belonging to each species were enumerated. As the nauplii of all species were lumped and merely enumerated as "nauplii," the figures for copepods given in Table 1 indicate only the percentages of adults and copepodids. The copepodid stages of some coexisting cyclopoids were so similar that differentiation of species was sometimes uncertain. For these species a lumped total is given in the table. The plankton of four lakes with natural populations of Alosa was sampled for comparison with that of Crystal Lake in 1964, and the plankton of four lakes, without Alosa, in the "alewife" region of southern Connecticut was sampled for comparison with the Crystal Lake plankton of 1942. All these lakes were sampled between 5 June and 7 July 1964 (8). The relative frequencies of those crustacean zooplankters which comprise 5 percent or more of the total are given in Table 1. The relatively large predaceous rotifer Asplanchna priodonta, the only noncrustacean recorded in Table 1, was remarkably numerous in some of the alewife lakes. The plankton of Crystal Lake in 1964, when Alosa aestivalis was abundant, was quite like that of the natural alewife lakes, and not at all like the plankton of Crystal Lake before Alosa was a significant element in the open-water community. Crystal Lake in 1942 resembled the lakes without alewives in that its plankton was dominated by Diaptomus and Daphnia. It might be added that resampling (9) of a majority of the other Connecticut lakes after the same 20-year interval has not revealed such a major change in the composition of the zooplankton anywhere else.

In order to examine more carefully the differences in body size between the dominants of alewife and those of non-alewife lakes, the size range of each species was determined. Body size was measured as body length, exclusive of terminal spines or setae. (The posterior limit of measurement for each genus is shown on the drawings of Fig. 4.) A summation of the numbers of each dominant that fell within each size interval yields a size-frequency diagram for the crustacean zooplankters. Although such diagrams were prepared for each lake, only those for Crystal Lake in 1942 and 1964 are presented here (Fig. 4). As size intervals represented by less than 1 percent of the population sample were left blank, the histogram does not indicate the presence of large but relatively rare forms. In Crystal Lake in 1942, specimens of the genera depicted occurred up to a length of 1.8 millimeters, and the predaceous Leptodora kindtii was represented by a few specimens between 5 and 10 millimeters. In 1964, by contrast, no zooplankters over 1 millimeter long could be found, although in other Alosa lakes there were occasional specimens up to 1.25 millimeters. The nauplii and metanauplii were counted but not measured, so that the totals of measured specimens are decreased by these amounts (see Table 1). The histograms (Fig. 4) show that the majority of the zooplankton are less than about 0.6 millimeter in length when Alosa is abundant, whereas the majority of specimens of the dominant species in the same lake before Alosa became abundant were over 0.5 millimeter long. The modal size in the presence of Alosa was 0.285 millimeter, whereas the modal size in the absence of Alosa was 0.785 millimeter. This seems clear evidence that predation by Alosa falls more heavily upon the larger plankters, eliminating those plankters more than about 1 millimeter in length.

Effects of Predation by Alosa

Whether or not a species will be eliminated (or reduced to extreme rarity) by Alosa predation will in good part depend upon the average size of the smallest instar of egg-producing females; a sufficient number of females must survive long enough to produce another generation. To assess the significance of this critical size, specimens approximating the average size of the smallest mature instar of the dominant species of both years were drawn to scale and appropriately placed on the size-frequency histograms. The smallest mature females of Daphnia catawha, Mesocyclops edax, Epischura nordenstadii, and certainly Leptodora kindtii are too large to have a reasonable chance of surviving long enough to produce sufficient young. However, the elimination of Diaptomus minutus (depicted in Fig. 4) but not of Cyclops bicuspidatus thorami, indicates that for species maturing at a length between 0.6 and 1.0 millimeter, factors other than size (such as escape movements, spatial distribution) are also of significance. Aside from Cyclops bicuspidatus thorami, all the characteristic zooplank-

Table 1. The relative frequency of planktonic Crustacea in lakes with and without Alosa.

<table>
<thead>
<tr>
<th>Organism</th>
<th>Lakes without alewives</th>
<th>Crystal Lake (1942)</th>
<th>Crystal Lake (1964)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C         BA       BE     G</td>
<td>L          A        Q         R</td>
<td></td>
</tr>
<tr>
<td>Cladocera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lepidora kindtii</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Holopedium spp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diaphanosoma spp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daphnia galeata</td>
<td>59</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daphnia catawha</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ceriodaphnia lacustris</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bosmina coregoni</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bosmina rubens</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bosmina longirostris</td>
<td>34</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copepoda</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Epischura nordenstadii</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diaptomus minutus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diaptomus pygmaeus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mesocyclops edax</td>
<td>21</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclops bicuspidatus</td>
<td>12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tropocyclops prasinus</td>
<td></td>
<td>29</td>
<td></td>
</tr>
<tr>
<td>Orthocyclops modestus</td>
<td></td>
<td>11</td>
<td>9</td>
</tr>
<tr>
<td>Nauplii</td>
<td>11</td>
<td>13</td>
<td>10</td>
</tr>
<tr>
<td>Rotiferina</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Asplanchna priodonta</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| Dimensions          |                        |                     |                     |
| Area (hectares)     | 9                      | 112                  | 158                  | 440                  | 80                    |
| Maximum depth (m)   | 5                      | 14                   | 19                   | 20                   | 14                    |
| Mean depth (m)      | 3                      | 5                    | 6                    | 7                    | 3                     |

* Present, but comprising less than 4.5 percent.
ters of *Alosa* lakes mature at lengths of less than 0.6 millimeter.

Since *Alosa*, except during spawning, avoids the shores, its predation falls more heavily upon, and may eliminate, "lake species" of zooplankton that tend to avoid the shore, allowing littoral or "pond species" to thrive. Among the Cladocera, for example, a large *Daphnia* (*D. catawba*, *D. galeata*) usually occurs as a dominant in the zooplankton of lakes over 5 meters deep, while *Bosmina longirostris* is a common dominant in shallower bodies of water. When *Alosa* is present, any population of large *Daphnia* is eliminated or severely reduced, and *Bosmina longirostris*, relatively spared by its smaller size and the more littoral habits of a large part of its population, replaces *Daphnia* as the open-water dominant. The differential predation due to the tendency of *Alosa* to feed in open water away from the bottom (5) can also be seen among the medium-sized copepods. Of the species usually dominant in lake plankton, *Diaptomus minutus*, the smallest, is eliminated by *Alosa* in small lakes, and in those lakes the larger *Cyclops bicuspisatus thomasi* (see Fig. 4) achieves a dominance that it seldom enjoys otherwise. This differential predation is probably due to the fact that adult *Diaptomus minutus* are primarily epilimnetic in summer, while the adult *Cyclops bicuspisatus thomasi* tend to be heavily concentrated in the inshore and bottom waters, only the immature being found in the open water. *Diaptomus pygmaeus*, intermediate between the above two species both in size at the onset of maturity and in spatial distribution of adults, often survives in *Alosa* lakes as a minor component of the plankton.

The alewife lakes of Connecticut are small. It is, therefore, of interest to examine the plankton of larger lakes into which *Alosa* has been introduced. *Alosa* has long been abundant in Lake Cayuga, the largest of the Finger Lakes of New York, with an area of 172 square kilometers and a maximum depth of 132 meters. The plankton of Cayuga is dominated by *Bosmina longirostris* (or *Ceriodaphnia sp.*). Large Cladocera, such as *Daphnia*, *Leptodora*, and *Polyphemus*, are never common, and *Diaptomus* is scarce. The calanoid *Senecella calmoides* (2.7 mm) is present only at depths below 80 meters. This numerical ascendency of the smaller zooplankters in the upper waters is consistent with the concept of size-dependent predation by *Alosa*. The persistence of large zooplankters in the Laurentian Great Lakes indicates that *Alosa* has had a less dramatic effect on the plankton of these immense lakes (10).

**Size and Food Selectivity**

To assess the significance of *Alosa* predation it is necessary to consider the importance of the size of food organisms throughout the open-water community. To simplify the discussion we shall consider the open-water community of a lake to comprise four trophic levels. Level four, the piscivores, consists chiefly of fish, even though their fry are planktivorous and thus belong to the third trophic level, planktivores. On the third level, also, fish are quantitatively most important (11). Level two consists of the herbivorous zooplankters. (Some zooplankters are predators and therefore on level three, but are quantitatively usually negligible.) The planktonic herbivores feed upon the microphytes—the larger algae (net phytoplankton) and the small algae (nannoplankton)—that comprise level one in the open waters, together with bacteria and a variety of nonliving organic particles. The nannoplankton, together with all the other particles that can pass through a 50-micron sieve, will be called nanoseston.

Animals choose their food on the basis of its size, abundance, and edibility, and the ease with which it is caught. However, there is a fundamental difference between food selection by herbivorous zooplankton and that by the predators of higher levels. For planktivores and piscivores, other things being equal, the least outlay of energy in relation to the reward is required if a smaller number of large prey, rather than a larger number of small ones, are taken (12). When the environment provides a choice, therefore, natural selection will tend to favor the predator that most consistently chooses the largest food morsel available. At the highest trophic levels, where the number of available prey is often low, a predator must often take either a small morsel or none at all. The variety (13) and abundance of the zooplankton, however, usually provide the planktivore with an array of sizes from which to choose. One would expect, therefore, that planktivores would prey upon larger organisms more consistently than do the piscivores. It should further be

---

Fig. 1. *Alosa* (= *Pomolobus*) *pseudoharengus* (Wilson). Top, mature specimen, 300 mm long. Note that mouth opens obliquely. Bottom left, first branchial arch, with closely spaced gill rakers that act as a plankton sieve. Compare with (bottom right) the widely spaced gill rakers of *A. mediocris*, a species that feeds primarily upon small fish. [After Hildebrand (4), with the permission of the Steers Foundation for Marine Research, Yale University]
noted that visual discrimination is indispensable in the feeding of piscine planktivores, even of those such as the alewife, whose gill-rakers serve as plankton strainers (Fig. 1) (14).

In the selection of food by herbivorous zooplankters, on the other hand, visual discrimination plays a negligible role; indeed, the absolute dimensions of both herbivore and food particle may well determine the restricted role of vision (15). The lower limit of food-particle size for planktonic herbivores is determined by the mechanism that removes these particles from a water current flowing over a part of the body near the mouth. Studies of feeding in rotifers, cladocerans, and calanoid copepods have demonstrated that all can secure particles in the 1- to 15-micron range. This represents the entire range that can be taken by most herbivorous rotifers, while the upper size limit of particles that can also be taken by large cladocerans and calanoids probably accords roughly with the body size of the zooplankter, and commonly includes particles up to 50 microns (16). Among food particles of usable size, both rotifers and calanoids can exercise selection by rejecting individual particles, apparently on the basis of chemical or surface qualities, but the chief control that cladocerans exert is by varying the rate of the feeding movements (17).

4) But when predation is intense, size-dependent predation will eliminate the large forms, allowing the small zooplankters (rotifers, small Cladocera), that escape predation to become the dominants.

5) When predation is of moderate intensity, it will, by falling more heavily upon the larger species, keep the populations of these more effective herbivores sufficiently low so that slightly smaller competitors are not eliminated.

The data supporting this hypothesis are summarized below.

The view that the small particles present in open waters are the most important food element for all planktonic herbivores is supported by the following: Rotifers and large Cladocera (Daphnia) and calanoids (for example, Eudiaptomus) are all able to collect particles of the 1- to 15-micron range, as noted above. Particles in this range are heterogeneous (algae, bacteria, organic detritus, organic aggregates) and therefore constitute a relatively constant and demonstrably adequate source of food. Also, they are more digestible than many of the net phytoplankton (such as diatoms) which have a covering that impedes digestion and assimilation (18).

The competitive success of the larger planktonic herbivores is probably due to (i) greater effectiveness of food-collection; and (ii) relatively reduced metabolic demands per unit mass, permitting more assimilation to go into egg production.

The greater effectiveness of the larger zooplankters in collecting the nanosetton appears to be largely responsible for the replacement of small by larger species in nature, whenever circumstances permit (19). The probable basis for this greater effectiveness is the fact that in related species (with essentially identical food-collecting ap-

Size-Efficiency Hypothesis

To differentiate between these two types of feeding, the planktivores and piscivores can be called "food selectors," because they continuously make choices, in large part on the basis of size. The herbivorous zooplankters, on the other hand, can be called "food collectors," because the size range of their food is more or less automatically determined. The ecological implications of size-dependent predation upon the array of planktonic food collectors are outlined in what we shall call the "size-efficiency hypothesis":

1) Planktonic herbivores all compete for the fine particulate matter (1 to 15 μ) of the open waters;
2) Larger zooplankters do so more efficiently and can also take larger particles;
3) Therefore, when predation is of low intensity the small planktonic herbivores will be competitively eliminated by large forms (dominance of large Cladocera and calanoid copepods).

Fig. 2. The coastal strip of eastern Connecticut with the lakes (1-7) known to have natural "landlocked" populations of A. pseudoharenus. For the comparable lakes without Alona (10-16), the species of openwater Daphnia present are indicated by the following symbols: c, D. catawba; g, D. galeata; r, D. retrocurva. Large Daphnia are missing in all the "alewife" lakes. The bars at the outlets of lakes 11 and 12 indicate that they have been dammed by man. Major intertidal marshes are cross-hatched. The query next to Black Pond (1) indicates that the plankton has not been studied. Inset shows details of Linsley and Cedar ponds. Stippled area around Cedar Pond is bog forest (see Fig. 3).
Fig. 3. Aerial view of Cedar and Linsley ponds ( Branford, Connecticut). Cedar, in the foreground, lacks alewives, although they are common in Linsley, into which the outflow from Cedar drains through the surrounding bog forest (lighter in hue). Linsley in turn drains through a short meandering stream into Long Island Sound (Branford Harbor) which can be seen in the upper left corner (see Fig. 2). [Photograph by Truman Sherk]

paratus) the food-collecting surfaces are proportional to the square of some characteristic linear dimension, such as body length. In Crystal Lake, for example, the body length of *Daphnia catawba* is about four times that of *Bosmina longirostris*, so that the filtering area of the *Daphnia* will be about 16 times larger than that of *Bosmina*. Studies by Sushchenia have shown that the relative rates at which *Daphnia* and *Bosmina* filter Chlorella are, indeed, proportional to the squares of their respective body lengths, suggesting that in Cladocera the area of the filtering surfaces is a major determinant of filtration rate. In addition to this greater ability to collect particles in the 1- to 15-micron range, the larger species can also exploit larger particles not available to smaller species; this appears to be especially significant in the greater competitive success of large calanoid copepods (20).

There is some indication that both basal metabolic rate and at least a part of the ordinary locomotor activity may be lower per unit mass in the larger than in the smaller of related species of zooplankters, although the depression of the basal metabolic rate may be slight (21). Locomotor activity is difficult to relate to body size, but it is likely that for herbivores a considerable proportion of such work is done in overcoming sinking. The rate of passive sinking of zooplankton up to the size of *Daphnia galeata*, with a carapace length of 1.5 millimeters, is proportional to the square of the body length. However, in *D. pulex*, which are about 1 millimeter longer, the rate is almost proportional to the body length itself (22). Therefore, locomotor activity probably increases with no more than the square of the length, and in larger forms shows an even lower rate of increase.

Thus both greater efficiency of food collecting and somewhat greater metabolic economy explain the demonstrably greater reproductive success of the larger of related species. This, together with the fact that generation time is but little greater in large cladocerans than in small ones, undoubtedly underlies the rapidity with which dominance can shift in this group (23).

The size-efficiency hypothesis predicts that whenever predation by planktivores is intense, the standing crop of small algae will be high because of relatively inefficient utilization by small planktonic herbivores, and that of large algae will also be high because these cannot be eaten by the small herbivores. Whenever the intensity of predation is diminished and large zooplankters predominate, the standing crops of both large (net phytoplankton) and small algae (nannoseston) should be relatively low, because of the greater efficiency of utilization of nannoseston and because some of the net phytoplankton can also be eaten.

When this prediction is tested, it is important that the biomass of the standing crops of large and small zooplankters be more or less equal, and the only data that meet these requirements are those obtained by Hrbáček et al. from Bohemian fish ponds with low and high fish stocks (19). In this excellent study, the authors made a qualitative and quantitative comparison between the zooplankton, net phytoplankton, and nannoseston of Poltruba Pond in 1957, when the fish stock was low, and the situation in the same pond in 1955, when the fish stock was high. In 1957, Poltruba Pond was also compared with a pond of roughly similar size (Procházkova) with a large fish stock. Poltruba drains through a screened outlet. The biomass (measured as organic nitrogen) of the zooplankton in the three situations were roughly equivalent, but in Poltruba in 1957, a large *Daphnia* comprised 80 percent of the zooplankton, whereas in the other two situations *Bosmina longirostris* was dominant and rotifers and ciliates were common. Where fish stocks were high and *Bosmina* was dominant, the net phytoplankton (especially diatoms and Dinobryon) was much more abundant than when *Daphnia* was dominant. Moreover, in both situations with *Bosmina* dominant the standing crop of nannoseston was two to three times greater than in the presence of *Daphnia*. This was true for both its organic nitrogen and its chlorophyll content. (Photosynthesis of the nannoseston in the presence of *Bosmina* was about five times greater than in the presence of *Daphnia*, a clear indication that the increase in the nannoseston in the presence of *Bosmina* was not merely an increase in the amount of slowly dying algae or detritus.) This result is precisely what the size-efficiency hypothesis predicts.
Size of Coexisting Congeners

In both aquatic and terrestrial habitats, pairs of closely related species of food selectors living in the same community and exploiting the same food source often apportion the available size array of food bits, in rough accord with their own divergent body sizes; that is, the larger species takes the larger bits and the smaller one the smaller bits. This is such a common and well-known phenomenon among congeneric birds (coexisting species of which may differ principally in body size, beak size, and size of food taken) that specific instances thereof and its evolutionary significance do not require discussion here (24). We wish only to emphasize that food apportioning according to body size is a path to stable coexistence seldom available to planktonic food collectors. Only in rare circumstances could it be advantageous for a species of large planktonic food collectors to abandon the 1- to 15-micron size range in favor of large par-

---

**Fig. 4.** The composition of the crustacean zooplankton of Crystal Lake (Stafford Springs, Connecticut) before (1942) and after (1964) a population of *Alosa aestivalis* had become well established. Each square of the histogram indicates that 1 percent of the total sample counted was within that size range. The larger zooplankters are not represented in the histograms because of the relative scarcity of mature specimens. The specimens depicted represent the mean size (length from posterior base lines to the anterior end) of the smallest mature instar. The arrows indicate the position of the smallest mature instar of each dominant species in relation to the histograms. The predaceous rotifer, *Asplanchna priodonta*, is the only noncrustacean species included; other rotifers were present but not included in this study.

1 OCTOBER 1965
ticles alone, leaving these small particles to small-sized congenic competitors (25).

On the contrary, many coexisting congenic zooplankters are of roughly similar size, and presumably—according to the size-efficiency hypothesis—of similar efficiency in food collecting (26). This tendency towards similarity in body size can be illustrated by the association in European lakes of Daphnia galeata and D. cucullata, the latter almost certainly derived from the former. This pair is well suited to our purpose because the various populations of D. cucullata exhibit a range of body size unusually large for Daphnia. During midsummer, some pond populations of D. cucullata mature when the carapace is only about 500 microns long, whereas in lake populations the body size at the onset of maturity may be as much as 900 microns. There is, of course, a complete array of intermediate body sizes in other populations. At the onset of maturity in midsummer, females of Daphnia galeata are slightly larger than the largest D. cucullata, usually at least 1 millimeter. As all these populations can be passively disseminated, clones of large, intermediate, and small forms of D. cucullata have almost certainly been introduced many times into each of the lakes in which D. galeata lives. But, as Wagler (27) has pointed out after examining 87 European populations of D. cucullata, it is only the clones with the largest body size that are found coexisting with D. galeata. The dwarf D. cucullata would be competitively excluded by D. galeata from lakes, just as Hrbáček observed it to be eliminated from ponds by larger species of Daphnia, whenever decreased predation allows the larger species to exist. In fact, clones of dwarf forms (carapace length in midsummer less than 550 μ) were found only in ponds where they were associated with Bosmina longirostris. It is also clear from Hrbáček's studies of fish ponds that dwarf D. cucullata, like Bosmina longirostris, can dominate only when predation by planktivores is intense (28).

Summary

In the predation by the normally marine clupeid Alosa pseudoharengus ("alewife") upon lake plankton, the usual large-sized crustacean dominants (sp. of Daphnia, Diaptomus) are eliminated, and replaced by small-sized, basically littoral, species, especially Bosmina longirostris. The significance of size in food selection by planktivores as opposed to planktonic herbivores is examined, and it is proposed that all planktonic herbivores utilize small organic particles (1 to 15 μ). The large species, more efficient in collecting these small particles and capable of collecting larger particles as well, will competitively exclude their smaller relatives whenever size-dependent predation is of low intensity. Intense predation will eliminate the large species, and the relatively immune small species will predominate. These antagonistic demands of competition and predation are considered to determine the body size of the dominant herbivorous zooplankton.

References and Notes


2. C. C. B. Wilde, A Fishery Survey of the Lakes and Ponds of Connecticut (Connecticut State Board of Fisheries and Game, Hartford, 1959). Although the term "landlocked" is now used to refer to self-sustaining freshwater populations of typically marine fish, not all of these populations are barren at certain times of the year, although low dams on most rivers probably isolate them from the anadromous marine stock. Opinions appear about equally divided between Alosa and Pomolobus as the generic name for the alewife. For example, Pomolobus is favored by S. F. Hildebrand, in "Fishes of the Western North Atlantic, Part III," Mem. Sears Found. Marine Res. 1, 111 (1963); "Alosa" by G. A. Moore in Vertebases of the U. S. (Washington, New York, 1957). Opinion is similarly divided on the use of English names. Hildebrand favors "sprat" for Alosa pseudoharengus, whereas the American Fisheries Society suggests "alewife." J. Hay [The Run (Double-day, New York, ed. 2, 1965)] discusses the ecology of anadromous alewives.

3. Anadromous marine alewives are common, at least during the summer, in many coastal lakes in the Great Lakes area and along the central portion of the Maine coast. For references to pertinent surveys see L. B. Brown and E. A. Dow, Jr., in Linnoimogy in North America, D. C. Frey, Ed. (Univ. of Wisconsin Press, Madison, 1963), pp. 117-62; Permanent natural popula- tion of Alosa pseudoharengus is known from several freshwater of northeastern U.S. in addition to the Connecticut lakes. There are records of occurrence in Lake Champlain and Lake Ontario, and records of its occurrence in Lake Ontario, it has spread into the other Great Lakes through man-made waterways. But now there are records of its occurrence in the Great Lakes. The species has been spread from a tributary of Lake Ontario via canals into Lake Cayuga and thence into the two adjoining Finger Lakes, Seneca and Keuka.


6. Alosa (Pomolobus) aestivus (Mitchell) is referred to by several common names, among them "glut herring" which we shall use, and "alewife" which are preferred by Hildebrand (4). In a previous fisheries survey Alosa had not been found in Connecticut, but in 1957 C. Thorpe, Conn. State Geol. Nat. Hist. Surv. Bull. 63 (1942). For the 1957 survey that found Alosa, see C. Thorpe, "The Connecticut State Board of Fisheries and Game suspects that the glut herring was inadvertently introduced into Crystal Lake by the dumping of live bait, and that the state of Connecticut River, some 15 miles away.

7. Samples with which mid-July plankton trap of 10-liter capacity in 1942 one sample was taken at each meter depth interval from the surface to just above the bottom. In 1964, two samples (2 m apart horizontally) were taken at each depth interval.

8. Beach and Basin lakes were sampled by the method described in 1964 (7); the others were sampled by vertical tow-nettings, bottom to surface. All samples for this study were enumerated, and subsamples from net collections were counted. Subsamples from net collections were counted until a total of 350 to 600 specimens were reached for each lake.


12. This is not to deny that predation by various invertebrates, such as phantom midge larvae (Chaoborus), may be important, but planktonic rotifers (Lepidophyta, polyphemidae) can be significant in some lakes. However, as predators these are not almost certainly almost as important as fish.

13. In the lake in which zooplankton with large pharyngeal papillae was found, 99% of the fish particles seen and counted were fish (26, 32). Thus, the passive dispersal makes it probable that most species present in any continental area will be conducted into a given lake within a reasonable period of time.


15. The planktonic luci, although rare, is the smallest widespread member of the open-water community to have a distinctive eye and a distinct eye. This species uses its relatively large, movable, many-lensed eye to locate prey between 100 and 300 μ in length (or larger). While medium-sized herbivorous plankters are the same size as Polyphemus, the particular they collect is one-tenth the size of the food particles seen and counted by Polyphemus.

16. Information on food size in planktonic rotifers is scattered. The Ecol. Monographs 35, 61 (1965). Although Polyvaria (150 μ long) can take particles up to 15 μ, this does not vitiate the general statement that large planktonic herbivorous species are limited to the size for the planktonic herbivorous rotifers.

Sources of information on the size of food of Cladocera are too numerous to list here. Large Daphnia, among the largest of the cladoceran herbivores, are cultured on bac-
teria or algae (Chorella, Chlamydomonas spp.) less than 10 μ in length. Most analyses reveal that most of the gut content is undistinguishable small particles, several microns in diameter, of various algae, components of two large cladoceran species, Daphnia galeata and C. caligata, from a Maine lake was undistinguishable fine particulate material (W. T. Tappu, Ecol. Monographs 35, 395 (1956)). The identifiable algae present in the gut of both species was similar and represented the forms, up to about 10 μ, that occurred in the water. The only times during the two summers included in the study by Tappu when this fine particulate material constituted less than half of the gut contents was during a Dinobryon bloom in July 1953. For the two years, the diatom Stephanodiscus spp. (about 10 μ) was the second most abundant, being the dominant one in June, as frequently as Dinobryon. Aside from the short period when the guts were full of fine detritus, the mean for each species for 26 dates during the two summers is less than 10 algae cells per Daphnia.

L. M. Suschitzka (Nauch. Dokl. Vysshel. Zhub. Biol. Nauk, 9 (1910) noted that fish food particles about 3 μ in diameter are readily disengaged from the gut walls by Bosmina, Diaphanosoma, Simocephalus and Daphnia spp. than those 15 to 30 μ in length.

The great differences in the methods of food gathering by various species of cladocerans makes their inclusion here impossible, but see G. Fryer, Proc. Zool. Soc. London 129, 1 (1957); J. Animal Ecol. 26 (1957). The nutrition of Diaptomus (Suchi- atomus) gracilis, a common fish food, was studied by S. K. Jones and J. A. Stewart (J. Exp. Zool. 16, 64 (1954)) also considered considerable amounts of fine detritus, apparently of vegetable origin, in the guts of Daphnia in Lake Windermere. E. Nauwerck (Arch. Hydrobiol. 25, 393 (1962)) demonstrated that Daphnia nigra ingest and digest the organic matter of the food they eat. We will consider this well-studied species to be representative of our other cladocerans without noting it here.

For observations of selectivity in rotifers on the basis of quality other than size see works of W. T. Edmondson, especially Ecol. Monographs 35, 61 (1956). See also L. A. Eason, Zoolog. J. 33, 119 (1963)


M. L. East (see 16), provides data on the rates at which four species of planktonic Cladocera filter suspensions of various algae. The rate of food ingestion in Daphnia moina (second instar) is given in Table 13 (1963).


M. L. East (see 16), provides data on the rates at which four species of planktonic Cladocera filter suspensions of various algae. The rate of food ingestion in Daphnia moina (second instar) is given in Table 13 (1963).


