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# 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 bicuspidatus 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 indifference of alewives to nonfloating 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 nonalewife lakes *Diaptomus* spp. and *Daphnia* spp. are always dominants, usually accompanied by the larger cyclopoids *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), "glut 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 zooplankton 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

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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 catawba*, *Mesocyclops edax*, *Epischura nordenskioldi*, 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 thomasi*, 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 thomasi*, all the characteristic zooplank-

Table 1. The relative frequency of planktonic Crustacea in lakes with and without *Alosa*. C, Cedar Pond; BA, Bashan Lake; BE, Beach Pond; G, Lake Gaillard; L, Linsley Pond; A, Amos Lake; Q, Lake Quonnipaug; R, Rogers Lake. Relative frequencies expressed in percentages.

| Organism | Lakes without alewives | | | | Crystal Lake | | Natural alewife lakes | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | C | BA | BE | G | 1942 (No *Alosa*) | 1964 (*Alosa*) | L | A | Q | R |
| Cladocera | | | | | | | | | | |
| *Leptodora kindtii* | | * | | | * | | | | | |
| *Holopedium* spp. | | * | 6 | | | * | | | | 5 |
| *Diaphanosoma* spp. | | * | | * | 5 | | * | | * | |
| *Daphnia galeata* | 59 | | | | | | | | | |
| *Daphnia catawba* | | * | 7 | 11 | 14 | | | | | |
| *Ceriodaphnia lacustris* | | | | | | * | * | * | 43 | * |
| *Bosmina coregoni* | | | * | 13 | | | | | | |
| *Bosmina tubicens* | | | * | | | | | | | 5 |
| *Bosmina longirostris* | * | | | | | 34 | 39 | 44 | 16 | 10 |
| Copepoda | | | | | | | | | | |
| *Epischura nordenskioldi* | | * | * | * | * | | | | | |
| *Diaptomus minutus* | | 84 | 76 | | 52 | | | | | |
| *Diaptomus pygmaeus* | * | | | 50 | * | | * | 6 | * | 5 |
| *Mesocyclops edax* | 21 | | | }12 | | | | | | |
| *Cyclops bicuspidatus* | * | | | | | }29 | 34 | | | 35 |
| *Tropocyclops prasinus* | | | | | | | * | 11 | 9 | 20 |
| *Orthocyclops modestus* | | | | | | | | | 16 | |
| Nauplii | 11 | 13 | 10 | 12 | 11 | 28 | 7 | 30 | 8 | 18 |
| Rotifera | | | | | | | | | | |
| *Asplanchna priodonta* | | | | | | * | 17 | 6 | * | |
| Dimensions | | | | | | | | | | |
| Area (hectares) | 9 | 112 | 158 | 440 | 80 | | 9 | 42 | 45 | 107 |
| Maximum depth (m) | 5 | 14 | 19 | 20 | 14 | | 14 | 14 | 14 | 20 |
| Mean depth (m) | 3 | 5 | 6 | | 7 | | 7 | 6 | 4 | 6 |

* 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 bicuspidatus 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 *Cylops bicuspidatus 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 calanoides* (2.7 mm) is present only at depths below 80 meters. This numerical ascendancy 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*).

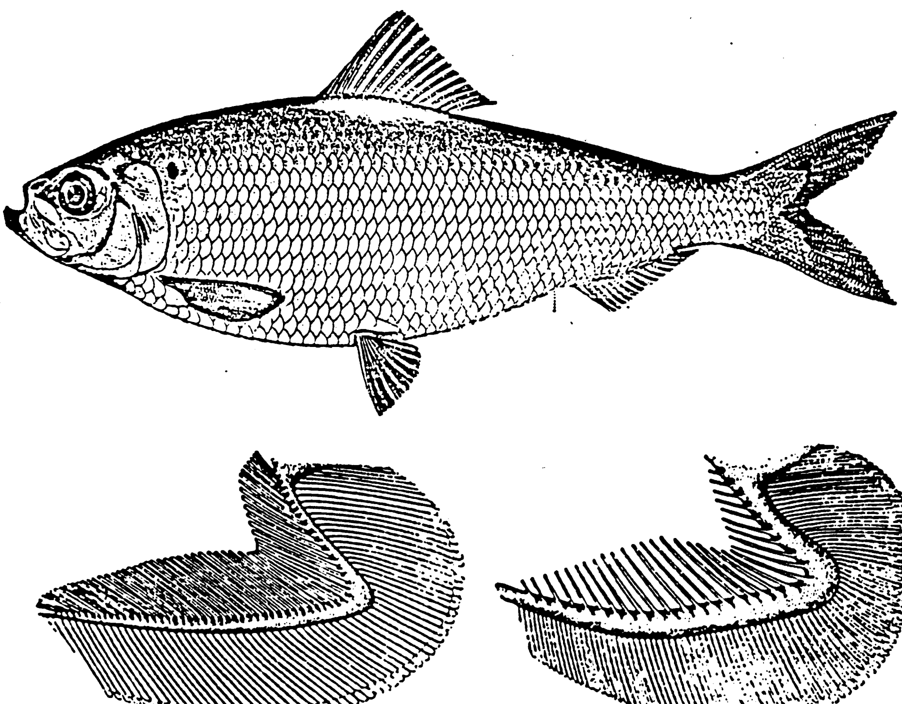

Fig. 1. *Alosa* (= *Pomolobus*) *pseudoharengus* (Wilson). Top, mature specimen, 300 mm long. Note that mouth opens obliquely. Bottom left, first branchial arch, with closely spaced gill rakers that act as a plankton sieve. Compare with (bottom right) the widely spaced gill rakers of *A. mediocris*, a species that feeds primarily upon small fish. [After Hildebrand (*4*), with the permission of the Sears Foundation for Marine Research, Yale University]

## 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 nannoseston.

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 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*).

## 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 $\mu$) 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).

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 nannoseston 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-

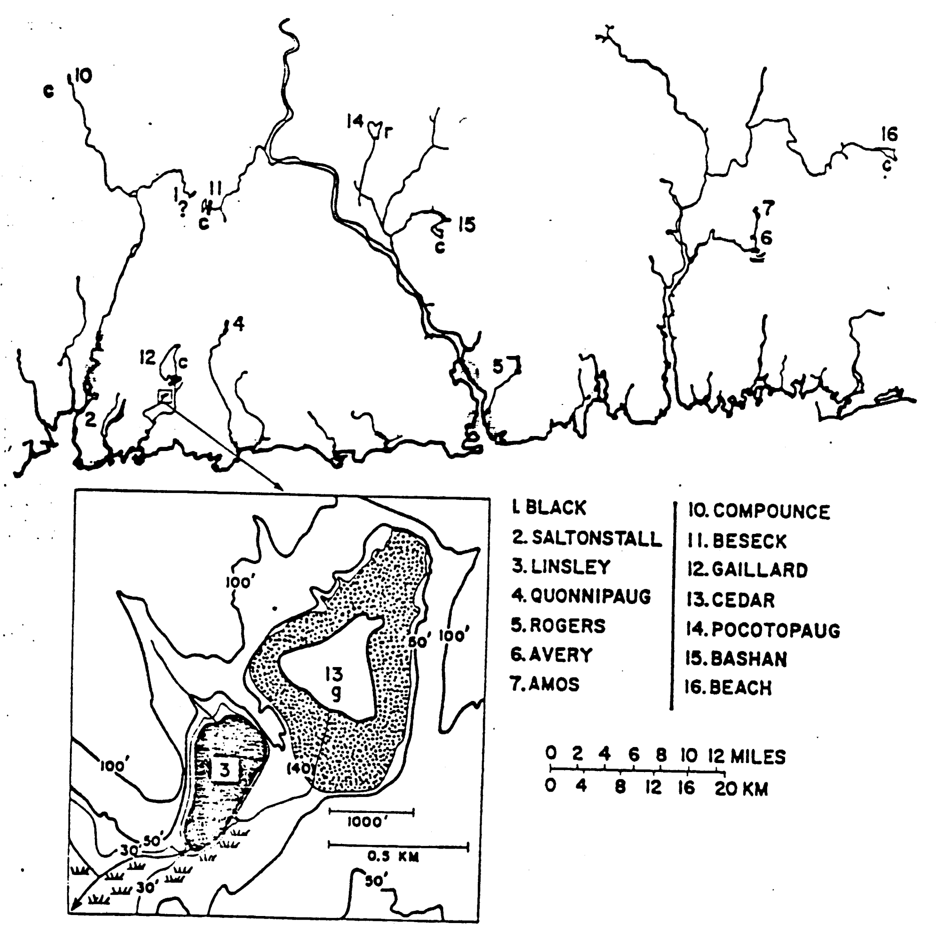


Fig. 2. The coastal strip of eastern Connecticut with the lakes (1–7) known to have natural "landlocked" populations of *A. pseudoharengus*. For the comparable lakes without *Alosa* (10–16), the species of openwater *Daphnia* present are indicated by the following symbols: *c*, *D. catawba*; *g*, *D. 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).

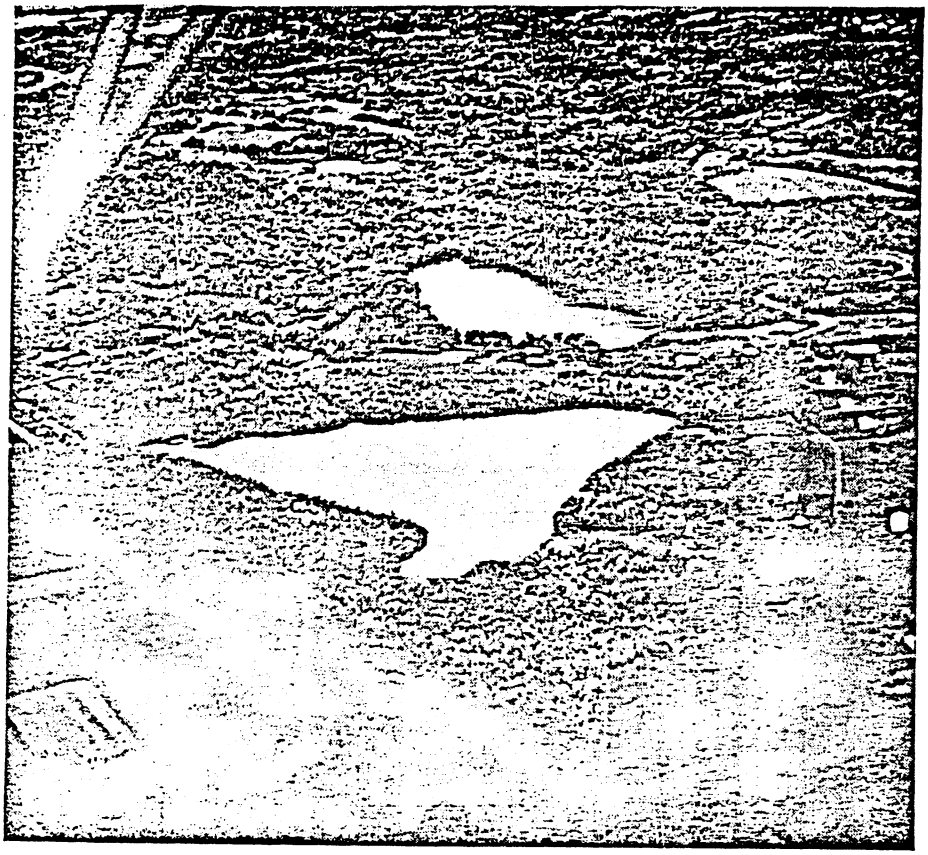

Fig. 3. Aerial view of Cedar and Linsley ponds (Branford, Connecticut). Cedar, in the foreground, lacks alewives, although they are common in Linsley, into which the outflow from Cedar drains through the surrounding bog forest (lighter in hue). Linsley in turn drains through a short meandering stream 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 Sushtchenia 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 panktonic 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 (Procházka) with a large fish stock. Poltruba drains through a screened outlet. The biomasses (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-

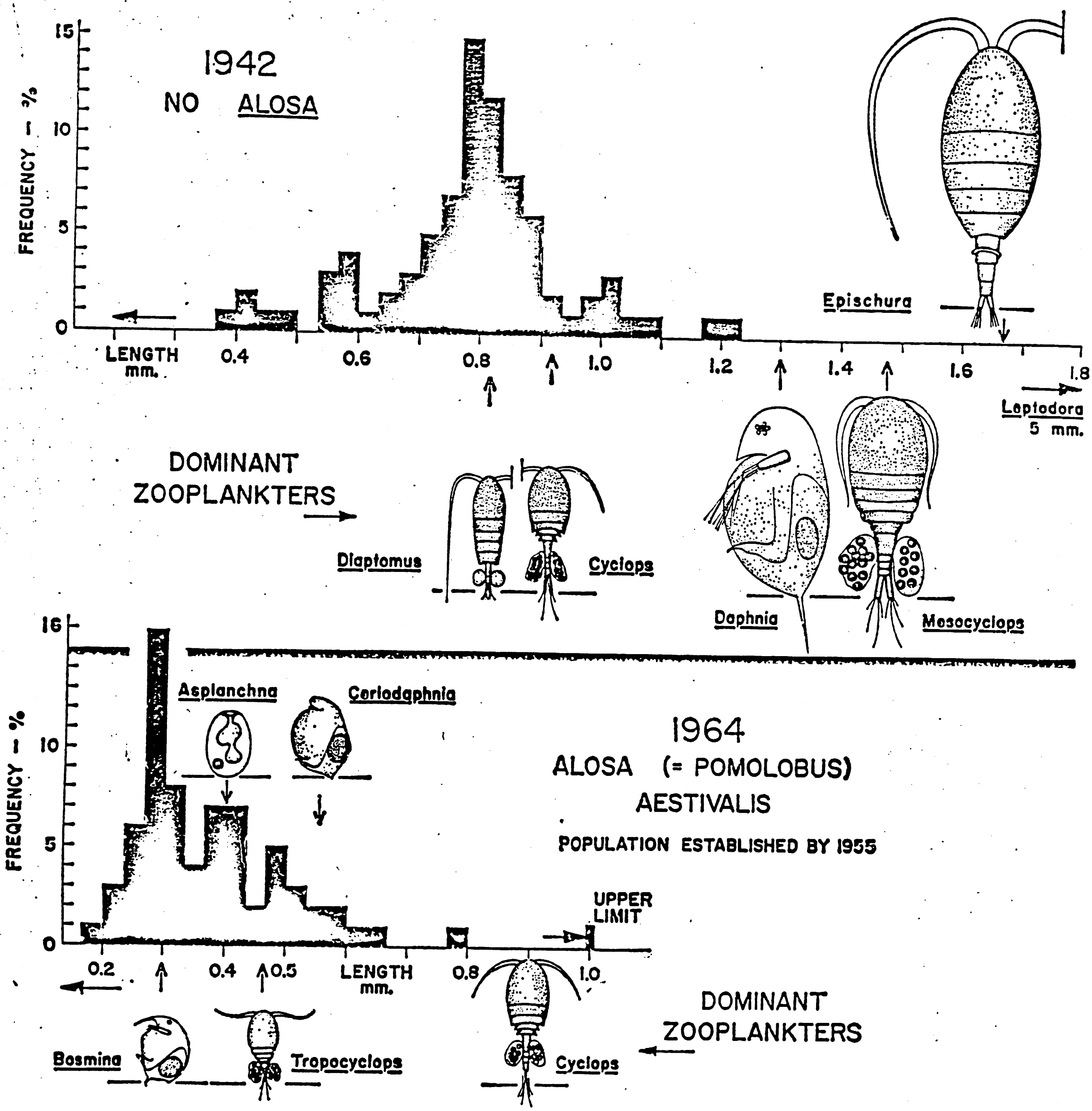


Fig. 4. The composition of the crustacean zooplankton of Crystal Lake (Stafford Springs, Connecticut) before (1942) and after (1964) a population of *Alosa aestivalis* had become well established. Each square of the histogram indicates that 1 percent of the total sample counted was within that size range. 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.

ticles alone, leaving these small particles to small-sized congeneric competitors (*25*).

On the contrary, many coexisting congeneric 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 $\mu$) 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 clupeoid *Alosa pseudoharengus* ("alewife") upon lake zooplankton, the usual large-sized crustacean dominants (spp. 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 $\mu$). 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 zooplankters.

### References and Notes

1. For classification and distribution of North American *Daphnia*, see J. L. Brooks, *Mem. Conn. Acad. Arts Sci.* 13, 1 (1957). Identifications and nomenclature of Cladocera, Calanoida, and Cyclopoida in this article accord with accounts by J. L. Brooks, M. S. Wilson, and H. C. Yeatman in *Fresh Water Biology*, W. T. Edmondson, Ed. (Wiley, New York, ed. 2, 1959).
2. C. W. Wilde, *A Fisheries Survey of the Lakes and Ponds of Connecticut* (Connecticut State Board of Fisheries and Game, Hartford, 1959). Although the term "landlocked" is commonly used to refer to self-sustaining freshwater populations of typically marine fish, not all of these populations are barred from returning to the sea, 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 *Vertebrates of the United States* (McGraw-Hill, New York, 1957). Opinion is similarly divided on the use of English names. Hildebrand favors "grayback" for *A.* (= *P.*) *pseudoharengus*, whereas the American Fisheries Society suggests "alewife." J. Hay [*The Run* (Doubleday, 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 Cape Cod area of Massachusetts and along the central portion of the Maine coast. [For references to pertinent surveys see J. L. Brooks and E. S. Deevey, Jr., in *Limnology in North America*, D. G. Frey, Ed. (Univ. of Wisconsin Press, Madison, 1963), pp. 117–62.] Permanent natural populations of *A. pseudoharengus* are known from several freshwaters of northeastern U.S. in addition to the Connecticut lakes. There are resident breeding populations of both this species and *A. aestivalis* (Mitchell) in the lower Mohawk River, New York, and in a few small lakes, different for each species, tributary thereto [*N.Y. State Dept. Conserv. Biol. Surv. Suppl. Ann. Rept.* (1935)]. There is a difference of opinion as to whether the *A. pseudoharengus* population of Lake Ontario is natural or has been artificially established [see R. R. Miller, *Trans. Am. Fisheries Soc.* 86, 97 (1956)]. Regardless of its origin in Lake Ontario, it has spread into the other Great Lakes through man-made waterways. By the latter part of the 19th century, it had spread from a tributary of Lake Ontario via canals into Lake Cayuga and thence into the two adjoined Finger Lakes, Seneca and Keuka.
4. S. F. Hildebrand, "Fishes of the Western North Atlantic, Part III," *Mem. Sears Found. Marine Res.* 1, 111 (1963).
5. For food habits in freshwater populations, see T. T. Odell, *Trans. Am. Fisheries Soc.* 64, 118 (1934); A. L. Pritchard, *Univ. Toronto Biol. Ser. 38* (1929), p. 390. For a summary of food in sea, see S. F. Hildebrand (*4*).
6. *Alosa* (= *Pomolobus*) *aestivalis* (Mitchell) is referred to by several common names, among them "glut herring" which we shall use, and "blueback herring" or "blueback" which are preferred by Hildebrand (*4*). In a previous fisheries survey *Alosa* had not been found in Crystal Lake. See L. M. Thorpe, *Conn. State Geol. Nat. Hist. Surv. Bull. 63* (1942). For the 1955 survey that found *Alosa*, see C. W. Wilde (*2*). 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, with which a few glut herring could have been intermixed, from the Connecticut River, some 15 miles away.
7. Sampled with Forest-Juday 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 meters apart horizontally) were taken at each depth interval.
8. Beach and Bashan lakes were sampled by the method used in sampling Crystal Lake in 1964 (*7*); the others were sampled by vertical tow-nettings, bottom to surface. All specimens taken in each trap series were counted. Subsamples from net collections were counted until a total of 350 to 600 specimens was reached for each lake.
9. J. L. Brooks, unpublished data.
10. E. B. Henson, A. S. Bradshaw, D. C. Chandler, *Mem. Cornell Univ. Agri. Exp. Sta. 378* (1961). Studies of Cayuga plankton: W. C. Muencher, *N.Y. State Dept. Conserv. Biol. Surv. Suppl. Ann. Rept.* (1928), p. 140; A. S. Bradshaw, *Proc. Intern. Assoc. Theor. Appl. Limnol.* 15, 700 (1964). Bradshaw also gives data on the plankton of Lake Erie. For other references to plankton of the Laurentian Great Lakes, as well as a general summary, see A. M. Beeton and D. C. Chandler in *Limnology in North America*, D. G. Frey, Ed. (Univ. of Wisconsin Press, Madison, 1963), p. 535.
11. This is not to deny that predation by various invertebrates, such as phantom midge larvae (*Chaoborus* spp.) and true plankton predators (*Leptodora*, polyphemids) can be significant in some lakes. However, as predators they are almost certainly not as important as fish.
12. For the significance of size and number in biotic communities, see C. S. Elton, *Animal Ecology* (Sidgwick and Jackson, London, 1927). Analyses of the factors influencing food selection by various freshwater fish are given by V. S. Ivlev, *Experimental Ecology of the Feeding of Fishes*, D. Scott, Transl. (Yale Univ. Press, New Haven, 1961).
13. The ease with which zooplankters are passively dispersed makes it probable that most species present in any continental area will be introduced into a given lake within a reasonably short time (10 to 25 years).
14. M. Kozhoff, *Lake Baikal and Its Life* (Junk, The Hague, 1963); V. S. Ivlev (see *12*).
15. The aberrant cladoceran *Polyphemus pediculus*, although rare, is the smallest widespread member of the open-water community to have an eye sufficiently complex to form a distinct image. This species uses its relatively large, movable, many-lensed eye to locate prey that are 100 to 300 $\mu$ in length (or larger). While medium-sized herbivorous zooplankters are the same size as *Polyphemus*, the particulate food they collect is one-tenth the size of the food particles seen and seized by *Polyphemus*.
16. Information on food size in planktonic rotifers is summarized by W. T. Edmondson, *Ecol. Monographs* 35, 61 (1965). Although *Polyarthra* (150 $\mu$ long) can take particles up to 35 $\mu$, this does not vitiate the general statement that 15 $\mu$ is the characteristic upper size limit for the food of 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 (*Chlorella, Chlamydomonas* spp.) less than 10 $\mu$ in length. Most analyses reveal that most of the gut content is unidentifiable small particles, several microns in diameter. Over half the gut content of two large cladoceran species, *Daphnia galeata* and *D. catawba*, from a Maine lake was unidentifiable fine particulate material [D. W. Tappa, *Ecol. Monographs* 35, 395 (1956)]. The identifiable algae present in the guts of both species were quantitatively similar and represented the forms, up to about 75 $\mu$, that occurred in the water. The only times during the two summers included in the study by Tappa when this fine particulate material constituted less than half of the gut contents was during a *Dinobryon* bloom in July 1961, when the guts of both species were full of (the tests of) *Dinobryon*. *Dinobryon* sp. (single or in small clusters up to about 25 $\mu$) was the most frequent identifiable alga in the guts of both species for the two years, and the diatom *Stephanodiscus* sp. (about 50 $\mu$) was the second most abundant, being the dominant alga about one quarter as frequently as *Dinobryon*. Aside from the short period when the guts were full of *Dinobryon*, there were never more than 20 identifiable algal cells per gut; the mean for each species for all 26 dates during the two summers is less than 10 algal cells per *Daphnia*.

L. M. Sushtchenia [*Nauchn. Dokl. Vysshei Shkoly Biol. Nauki* 4, 21 (1959)] notes that food particles about 3 $\mu$ are filtered more readily by *Bosmina*, *Diaphanosoma*, *Simocephalus* and *Daphnia* spp. than those 15 to 20 $\mu$.

The great differences in the methods of food gathering by various species of cyclopoids 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 (Eudiaptomus) gracilis* Sars, a common Eurasian calanoid species of medium size (adults about 1.2 mm long), consists of small algae (nannoplankton), and G. Fryer [*Schweiz. Z. Hydrol.* 16, 64 (1954)] also reported considerable amounts of fine detritus, apparently of vegetable origin, in the guts of this species in Lake Windemere. E. Nauwerck [*Arch. Hydrobiol.* 25, 393 (1962)] demonstrated that this species in culture could ingest and derive nourishment from particles of animal detritus between 0.1 and 10 $\mu$ in diameter. We will consider this well-studied species to be characteristic of most freshwater calanoids, although, of course, larger species are expected to ingest larger particles as well.

17. For observations of selectivity in rotifers on the basis of qualities other than size see works of W. T. Edmondson, especially *Ecol. Monographs* 35, 61 (1965). See also L. A. Erman, *Zool. Zh.* 41, 34 (1962).

Selectivity by *Diaptomus gracilis* in laboratory culture (see *16*) has been noted by A. G. Lowndes. [*Proc. Zool. Soc. London* 1935, 687 (1935)] and for cyclopoid copepods by G. Fryer (see *16*).

L. M. Sushtchenia, (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 magna* is controlled at various food concentrations by the rate of food collection and at high concentrations by rejection of the excess collected food from the food groove leading to the mouth [J. W. McMahon and F. H. Rigler, *Can. J. Zool.* 41, 321 (1963); see biblography of that paper for other references to feeding rates].

18. See J. W. G. Lund, *Proc. Intern. Assoc. Theor. Appl. Limnol.* 14, 147 (1961), for discussion of seasonal occurrence of microalgae in some English lakes. The quantitative importance of bacteria and detritus as food for planktonic herbivores has been mentioned too frequently for listing here. Detritus alone (although probably with some bacteria admixed) has been noted as food, but of poor quality, for *Diaptomus gracilis* (see Nauwerck, *16*) and for *Daphnia* [A. G. Rodina, *Zool. Zh.* 25, 237 (1946)]. Although organic aggregates have been most thoroughly investigated to date in the sea [see G. A. Riley, *Limnology and Oceanography* 8, 372 (1963)], their size range in the sea, 1 to 50 $\mu$, is probably also characteristic of fresh waters where they certainly occur (G. A. Riley and P. Wangersky, private communications).

The relative digestibility of flagellates, small green algae, and some bacteria as compared to *Scenedesmus*, *Raphidium*, and *Pediastrum* was noted by M. A. Kastal'skaia-Karzinkina [*Zool. Zh.* 21, 153 (1942)]. M. Lefevre [*Bull. Biol. France Belg.* 76, 250 (1942)], using egg production as a measure, assesses the nutritive value of 21 species of algae and shows that it is small size and fragile cell walls which make algae the most suitable as food.

19. For changes consequent upon alterations in fish stock in Bohemian ponds, see J. Hrbáček, M. Dvořakova, V. Kořínek, L. Procházková, *Proc. Intern. Assoc. Theor. Appl. Limnol.* 14, 195 (1961); J. Hrbáček, *Cesk. Akad. Ved, Rada. Mat. Prirod. Ved* 72, 1 (1962). W. Pennington [*J. Ecol.* 5, 29 (1941)] details rapid replacement of rotifers by *Daphnia* in tub cultures of microalgae.

20. Sushtchenia (see *17*), in her Table 3, provides data on the filtration rates of *Bosmina longirostris*, *Diaphanosoma brachyurum*, *Simocephalus vetulus*, and *Daphnia magna*, at several temperatures and concentrations of *Chlorella*. When these results are reduced to the approximate values of 19°C with a standard concentration of *Chlorella* cells, the relative filtration rates of these four species are 1 : 1 : 10 : 18. The relative body lengths (from her Table 2) are 1 : 1.5 : 3 : 4, while the squares of the body lengths are as 1 : 2 : 9 : 16. Thus the filtration rates of these four cladoceran species are approximately proportional to the squares of their respective body lengths.

Calanoid copepods may be quite unlike the Cladocera in the relationship between body length and rate of food collection, because of a compensatory decrease in the rate at which the head appendages beat. R. Schröder, *Arch. Hydrobiol. Suppl.* 25, 348 (1961) has shown that in a *Diaptomus* species 2.4 mm long the rate of beating was one-half that in a species 1.2 mm long.

21. A general treatment of the realtionship between size and metabolism is given in E. P. Odum, *Fundamentals of Ecology*, (Saunders, Philadelphia, ed. 2, 1959), pp. 56–59. For zooplankton see G. C. Vinberg, *Zh. Obshch. Biol.* 11, 367 (1950). Vinberg's "rule" states that decreasing the weight of a plankter by one decimal place increases its $O_2$ consumption per unit weight by 155 percent (transl. J. Hrbáček, see *19*). For summary of Crustacea in general, see H. P. Wolvekamp and T. H. Waterman in *Physiology of Crustacea*, T. H. Waterman, Ed. (Academic Press, New York, 1960), vol. 1.

22. J. L. Brooks and G. E. Hutchinson, *Proc. Nat. Acad. Sci. U.S.* 36, 272 (1950).

23. At 20°C the eggs of large limnetic *Daphnia*, such as *D. galeata*, develop into neonates in 2.5 days and become egg layers (in nonturbulent culture) in a week; see D. J. Hall, *Ecology* 45, 94 (1964). J. Green [*Proc. Zool. Soc. London* 126, 173 (1956)] gives data relating body size to egg size and clutch size in *Daphnia* and other Cladocera. The longer generation time and the complexity of the life cycle of copepods may obscure the effects of body size upon competition.

24. T. W. Schoener [*Evolution* 19, 189 (1965)] considers the ecological and evolutionary implications of this phenomenon in birds.

25. G. E. Hutchinson [*Ecology* 32, 571 (1951)] based his suggestion of food-size selectivity in relation to body size in calanoid copepods on Lowndes's observation (see *17*) of selectivity in the feeding of *Diaptomus gracilis*. Although selectivity is clearly demonstrated by this copepod, it seems likely that attributes other than size of the algae were the basis of this selection. G. Fryer (see *16*) adduced his observation of differential food habits of *Diaptomus gracilis* and *Diaptomus laticeps* in support of such a food-partitioning hypothesis. During February, March, and April, when diatoms are abundant in Lake Windemere, *D. laticeps* (1.6 mm) had their guts full of *Melosira italica*, whereas *D. gracilis* had apparently been feeding primarily on nannoplankton. That it is the larger copepod that takes a somewhat larger food particle is not surprising, but it does not necessarily mean that *D. laticeps* is incapable of feeding on nannoseston under other conditions. Comparison with the food habits of the *Daphnia* in Aziscoos Lake, Maine (Tappa, see *16*), may be useful. One might assume that *Daphnia galeata* is a selective feeder on the basis of the July 1961 samples at which time the guts were crammed with *Dinobryon*. However, at all other times during the open water season of 1961 and all of 1962, over half of the gut was filled with ingested nannoseston. While copepods can be highly selective feeders, their discriminations do not appear to be based primarily upon size. To summarize, at certain times in certain ecosystems a population of a large-sized calanoid may ingest large food particles not utilizable by a coexisting, small-sized, congener. But it does not necessarily follow that the larger species always feeds exclusively on such large particles.

26. Such a stable association of *Daphnia galeata* and *Daphnia catawba* is not uncommon in the lakes of central Connecticut (J. L. Brooks, unpublished). The nature of the association between these two species in a Maine lake has been carefully examined by D. W. Tappa (see *16*). K. Patalas [*Roczniki Nauk Rolniczych Ser. B* 82, 209 (1963)] presents data on the seasonal changes in the crustacean plankton of several Polish lakes and considers the relation of fish predation to the population size of the various competing zooplankters.

27. E. Wagler, *Intern. Rev. Ges. Hydrobiol. Hydrog.* 11, 41, 262 (1923).

28. For a possible relationship between the seasonal incidence of predation and seasonal changes of size and form in *Daphnia* (cyclomorphosis), see J. L. Brooks, *Proc. Nat. Acad. Sci. U.S.* 53, 119 (1965).

29. We thank the following for their assistance: D. W. Tappa for help with field work; Dr. S. Jacobson, New Haven Water Co., for permission to sample Lake Gaillard; J. Atz, American Museum of Natural History, for sharing his extensive knowledge of fish and their literature; G. E. Hutchinson and W. T. Edmondson for making translations of Erman and Sushtchenia available; and C. Goulden, G. E. Hutchinson, and G. A. Riley for critical perusal of the manuscript. S.I.D. was supported in part by the NSF Undergraduate Science Education Program at Yale University. The research of J.L.B. has been supported by grant GB1207 from the National Science Foundation.