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Arctic Zooplankton Community Structure: Exceptions to Some General Rules

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ABSTRACT. Commonly accepted theories of zooplankton species distribution hold that: 1) large-bodied zooplankton species are excluded by fish predation and so are found only in lakes and ponds without fish; and 2) because small-bodied species are unable to compete successfully against large ones and also are preyed upon heavily by invertebrate predators, they exist primarily in lakes with fish. This pattern is not followed in a group of lakes and ponds in arctic Alaska. Some of these lakes were found to support both large and small zooplankton species along with populations of facultative planktivorous fish. Other lakes that had no fish had a small-bodied zooplankton species co-existing with a more typical large-bodied community. Close analysis of these unusual distributions reveals that the mechanisms affecting zooplankton community dynamics are more subtle and complex than generally recognized, particularly in such harsh environments as the Arctic.

RÉSUMÉ. La théorie géneralement reconnue sur la repartition des espèces de zooplancton assure que

1) les poissons prédateurs excluent les espèces de zooplancton de grand taille et donc qu'on ne les trouve que dans les lacs et etangs sans poisson.

2) Du fait que les espèces de petite taille sont incapables de subsister avec les grandes et que d'autre part les prédateurs invertebrés font leur proie de ces dernieres, elles existent surtout dans les lacs poissoneux. Ce schema n'est pas valable pour un groupe de lacs et d'etangs de l'Alaska arctique. Il se trouve que certains de ces lacs sont riches à la fois en espèces de zooplancton de grande et petite taille, tout en ayant des colonies de poissons planctivrores, à l'occasion. D'autres lacs sans poisson, possédent des espèces de zooplancton de petite-taille, en coexistance avec des colonies typiques de grande taille. Une analyse precise de cette repartition inhabituelle revéle que les méchanismes affectant le dynamique des communautés de zooplancton, sont plus subtils et complexes qu'on le croyait généralement, en particulier dans un environnement aussi rigoureux que l'Arctique.

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Freshwater zooplankton community structure has received a great deal of study almost from the beginning of the science of limnology (Birge, 1895, 1898; Wesenberg-Lund, 1904); however, only recently have major unifying principles begun to emerge. Hrbacek (1962), Brooks and Dodson (1965), and others have clearly demonstrated that many zooplankton communities fall into two broad categories: 1) Small-bodied communities, with individuals rarely exceeding 1.5 mm in length, and generally found in the presence of planktivorous fish; and 2) large-bodied communities, with many individuals exceeding 2 mm and adults rarely smaller than 1.5 mm, generally found in the absence of visual-feeding vertebrate planktivores.

The ecological mechanism creating and maintaining the small-bodied zooplankton communities has been widely shown to be differential feeding by

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planktivorous fish on the large-bodied zooplankton in both temperate (Grygierek *et al.*, 1966; Galbraith, 1967; Hall *et al.*, 1970; Wells, 1970) and arctic environments (Nilsson and Pejler, 1973; O'Brien, 1975). Several different explanations of the tactic by which fish actually feed upon the larger prey have been offered (Werner and Hall, 1974; Confer and Blades, 1975; O'Brien *et al.*, 1976), but there is no disagreement as to the importance of fish predation to zooplankton community structure.

The ecological mechanisms creating and maintaining large-bodied zooplankton communities in the absence of visual-feeding planktivores have been more widely debated. Brooks and Dodson (1965) suggested competitive exclusion of small zooplankton species by large species as the causal mechanism, whereas more recently Dodson (1972, 1974) has suggested that differential feeding by invertebrate planktivores on small-bodied zooplankton acts to eliminate them from zooplankton communities where planktivorous fish are absent. Hall *et al.* (1976) invoke both of these explanations.

Whatever mechanisms are responsible, two distinct zooplankton communities are generally found, and have been reported in many arctic areas (Tash, 1971a, b; Nilsson and Pejler, 1973) and in temperate lakes. The zooplankton species distribution in the lakes and ponds of the Noatak River valley in arctic Alaska is a particularly clear example (O'Brien, 1975). Shallow ponds lack a fish population and have a distinctive large-bodied zooplankton community composed of *Daphnia middendorffiana* and *Heterocope septentrionalis*. Deep lakes with planktivorous fish have only small-bodied zooplankton, primarily *Daphnia longiremis* and *Bosmina longirostris*. Rarely if ever do the species of these two communities co-occur in the lakes and ponds studied in the Noatak River valley.

In contrast, the zooplankton communities in the lakes and ponds of the Toolik Lake region of arctic Alaska present no such orderly situation. In these lakes and ponds, the relationship between size distribution of zooplankton and planktivirous fish, competitive zooplankton species, and invertebrate predators is not obvious nor typical. This paper examines the unusual combinations of species and predators in these lakes and suggests some possible reasons for their occurrence.

METHODS

The Toolik Lake region is located 68° 37′N and 149° 35′W along the oil pipeline haul road 25 km north of the Brooks Mountains in Alaska. It is generally a morainal area, with several deep lakes (10 to 25 m maximum depth) and a large number of shallower lakes, many of which appear to be kettle basins. Within 5 km of Toolik Lake there are at least 30 ponds ranging from 0.1 to 4.5 m in maximum depth.

The ponds generally become ice-free in the first two weeks of June and the lakes slightly later. Freeze-up begins in early September. During summer days the ponds often warm to 16 to 18° C although there is considerable diel fluctuation. In the summers of 1975 and 1976, the lakes thermally stratified and reached maximal epilimnetic temperatures of around 15° C. Lake and pond water is generally well oxygenated and mildly alkaline, with other water chemistry parameters typical of undisturbed arctic waters (review by Hobbie, 1973).

Most zooplankton samples were collected during the day on: 1) 14 July 1975 from the series S ponds (those ponds and lakes south and west of Toolik Lake); 2) 15 July 1975 from series N (those ponds and lakes north and west of Toolik); and 3) 18 July 1975 from series NE (those ponds and lakes northeast and north of Toolik). Three large lakes, Toolik, N-1, and Oil Lake, were sampled several times during the summer of 1975.

Most of the samples were taken from a small inflatable raft by towing a 10-cm diameter No. 25 net several times from the deepest portion of the pond to the surface. On a few occasions tows were made from shore by casting the net out and retrieving it. The samples were preserved with a mixture of 95% alcohol with 8% formalin mixed half and half with the sample. In the laboratory the entire sample was scanned and species were identified utilizing Edmondson (1959) and the *Daphnia* key of Brooks (1957).

The maximum depth of the ponds was determined by sounding at the time of sampling, however, only Toolik, N-1, N-2, and NE-2 have been thoroughly sounded using sonar equipment. The presence of fish was determined in Toolik, N-1, and N-2 using an experimental gill net in July of 1976, whereas angling confirmed fish presence in the other lakes, and fish are suspected in lakes deeper than 3 to 4 m in the Toolik area which have an outflow during the summer.

In August of 1977 a field crew from the Alaskan Fish and Game Department of Wildlife sampled the fish population structure in Toolik Lake using several experimental gill nets set from the western shore into the lake. The stomachs from the 47 fish captured in the three days these nets were set were preserved and the contents noted. The gut contents were identified to species where possible and some attempt to estimate abundance in the gut was made.

RESULTS AND DISCUSSION

The species distribution of zooplankton in the 24 ponds and lakes sampled, the maximum depth of each pond or lake and the presence or absence of fish are listed in Table 1. The species found are generally typical of arctic Alaskan zooplankton assemblages (Reed, 1962, 1963; Tash, 1971a, b; O'Brien, 1975). However, the species composition of the ponds does not seem as rich as that of the ponds near Barrow, Alaska (Dodson, 1975), or the Cape Thompson area (Tash, 1971a), probably because of the general paucity of emergent macrophytic vegetation in the Toolik area lakes and ponds.

The most striking aspect of the zooplankton distribution is the occurrence of both large and small forms within the same communities. Deep lakes with populations of fish often have considerable populations of large-bodied zooplankton species (e.g., N-1, NE-1, Toolik, Oil Lake, and Itigaknit) and on occasion lack some or all of the small-bodied species common to arctic lakes

TABLE 1. Distribution of fish and pelagic zooplankton in lakes and ponds of the Toolik Lake region, Alaska. Lakes and ponds are grouped by the absence or suspected or known presence of fish, and zooplankton species according to the average adult body size and feeding habits.

			Small		Medium		Large	Predators			
Lake	Depth	Fish Present or Absent	*Daphnia longiremis*	*Bosmina longirostris*	*Holopedium gibberum*	*Diaptomus pribilofensis*	*Daphnia middendorffiana*	*Heterocope septentrionalis*	*Cyclops cappulatum*	*Cyclops scutifer*	*Polyphemus pediculus*
S-1	0.3	A		X							X
S-2	0.3	A		X							X
S-3	4.5	A		X	X	X	X	X	X	X	X
S-4	0.2	A		X		S	X				X
S-5	0.1	A		X		S	X				X
S-7	2.5	A		X		X		X		S	
NE-3	3.5	A				X	X	X		S	
NE-4	2.2	A				X	X	X		S	
NE-5	0.2	A				X				S	
NE-7	2.2	A				X	X	X		S	
NE-8	2.0	A				X	X	X		S	
NE-9	2.0	A				X	X	X		S	
NE-10	3.5	A				X	X	X		S	
S-6	7.0	P	X*	X		X		X	X		
N-1	11.0	P				X	X	X	X	X	
N-2	10.0	P*	X	X		X				X	X
N-3	5.0	P		X		S		X		X	
N-4	4.0	P		X		X		X		X	
NE-1	—	P		X		X	X	X		X	X
Ne-2	4.0	P	X*	X	X	X		X		X	X
Toolik	25.0	P	X*	X	X	X	X	X		X	X
Oil Lake	11.0	P			X	X	X	X		X	
Galbraith	6.0	P				X		X		X	
Itigaknit	6.0	P				X	X	X		X	

*Helmeted form.

(e.g., Lakes N-1, Oil Lake, Galbraith, and Itigaknit). Shallow ponds which lack fish sometimes have a very typical large-bodied zooplankton community (the NE series) but sometimes lack some of the large-bodied species and include a small-bodied species (e.g., S-1, S-2, and S-7). Thus in the Toolik region there are lakes and ponds that initially appear to contradict accepted ideas on the impact of predation and competition in creating and maintaining exclusively large- or exclusively small-bodied zooplankton communities.

TABLE 2. Fish gut contents from fish gillnetted on August 24, 25 and 26, 1977. The number of plus (+) signs is to indicate one or sparse presence for 1 plus, or considerable abundance with 2 pluses. The types of food are listed in an overall increase in size of the prey listed. Fish are grouped by species, size and sex.

	Arctic Grayling								Lake Trout														
Length (mm)	140	235	280	285	325	340	385	385	115	140	240	245	275	285	290	295	360	365	370	375	385	390	395
Weight (g)	30	150	330	290	430	460	680	650	20	25	140	140	220	230	230	250	470	490	530	540	620	610	670
Sex	im.	m. im.	f. ma.	f. ma.	m. ma.	f. ma.	f. ma.	m. ma.	im.	im.	f. im.	im.	m. im.	f. im.	m. im.	f. im.	f. im.	m. ma.	f. ma.	m. ma.	f. ma.	f. ma.	f. ma.
D. longiremis					+	+	+													+			+
Diaptomus						+						+											
Cyclops scutifer										+		+											
D. middendorffiana		+	+		‡	+	+			+	‡	‡	‡		‡	‡				+		‡	‡
Heterocope		‡	‡	+	‡	+	+		‡	+	+	+	+		+	+				+		+	+
Adult *Chiron.*	‡	+	+	+	‡	‡	‡	‡	+						+	+	+	‡		‡			
Snail *spp. 1*																+	+			+	+		
Snail *spp. 2*															+	+	+			‡	‡		
Clam																							
Trichoptera larvae																							
Small grayling																							
Grasshopper		+		+																			
Vole (*Microtus*)																							

	Lake Trout (cont.)											Round Whitefish												
Length (mm)	415	420	420	425	450	455	455	465	470	470	475	310	315	320	325	325	340	390	395	410	420	420	425	450
Weight (g)	780	750	890	730	910	1060	1010	980	1190	1070	1110	300	330	310	360	340	470	820	760	830	850	980	880	1220
Sex	m. ma.	f. ma.	f. ma.	m. ma.	f. ma.	m. ma.	m. ma.	f. ma.	f. ma.	m. ma.	f. ma.	f. ma.	m. im.	m. im.	m. im.	f. ma.	f. ma.	f. ma.	f. ma.	f. ma.	f. ma.	f. ma.	f. ma.	f. ma.
D. longiremis																								
Diaptomus																								
Cyclops scutifer																								
D. middendorffiana				‡											‡									
Heterocope			+	+																				
Adult *Chiron.*		+		‡			+									+		+						
Snail *spp. 1*	‡	‡	‡	+		‡	‡	‡	‡		‡					+		+				‡	‡	‡
Snail *spp. 2*	+	+						+			‡		‡	‡	+	+		‡	‡	‡	+	‡	‡	‡
Clam														+							‡			
Trichoptera larvae												‡	+		+	‡								
Small grayling										+														
Grasshopper																								
Vole (*Microtus*)								+																

However, closer examination of the zooplankton community structure in the Toolik area ponds and lakes reveals predator-prey and competition mechanisms to be more subtle and complex than has heretofore been widely appreciated.

Fish Predation

Eleven of the lakes studied are known to support the facultative planktivores arctic grayling (*Thymalus arcticus*) and lake trout (*Salvelinus namaycush*) although Lake N-2 is thought not to have any lake trout. Toolik Lake also has a population of round whitefish (*Prosoprium cylindraceum*). Gut samples of the grayling and lake trout show them to feed on zooplankton although the larger lake trout feed primarily on benthic invertebrates (Table 2). Once lake trout reach 400 mm they appear not to feed on zooplankton. The round whitefish is almost totally benthagagic as its subterminal mouth would suggest (Table 2).

Lake trout, arctic grayling, and especially the planktivorous whitefish (*Coregonus clupeaformis*) are the species presumed to be responsible for the elimination of large-bodied zooplankton and maintenance of a small-bodied zooplankton community in the lakes of the Noatak region (O'Brien, 1975; O'Brien and Huggins, 1974). However, of the eleven Toolik area lakes with fish, only one (N-2) has a zooplankton community exactly comparable to that found almost universally in Noatak lakes with fish. Seven of the other 10 lack one or two of the common small zooplankton species, *Daphnia longiremis* and *Bosmina longirostris* (Table 1). All ten of the lakes have one or two representatives of the common large-bodied zooplankton species, *Heterocope septentrionalis* and *Daphnia middendorffiana* (Table 1).

Contingency tables comparing the presence or absence of fish with the presence or absence of *D. middendorffiana* or *H. septentrionalis* yield X^2 values of 1.39 and 2.74 respectively, showing no effect due to fish presence. Similar X^2 values for these same species in the ponds and lakes of the Noatak (O'Brien and Huggins, 1974) yielded values of 29.4 and 19.9 respectively. While the particular significance of a given chi square value varies with the degrees of freedom, generally, low values indicate no association between species and high values indicate strong negative or positive association between species.
between species.

Several factors can be proposed to account for the unusual distributions of zooplankton in Toolik area lakes with fish. First, it is likely that facultative planktivores such as lake trout and grayling are not efficient enough in their feeding to exclude large zooplankton in these lakes. Schmidt and O'Brien (in preparation) found that the distance at which all but the largest grayling could locate zooplankton of a given size was very short compared to some other planktivorous fish (Werner and Hall, 1974; Confer and Blades, 1975; Vinyard and O'Brien, 1976). For example, an 8.5 cm (SL) arctic grayling could locate 2 mm *D. pulex* no further than 11 cm away, whereas a comparable sized sunfish could locate a similar prey at more than twice that distance (Vinyard and O'Brien, 1976). Given the sparse zooplankton densities in lakes in the Toolik area, any fish would have to search intensively for food; the grayling's short reactive distance to zooplankton prey would therefore be a considerable handicap.

Secondly, the notched mouths of salmonids are not efficient in creating the powerful suction intake needed to feed effectively upon *H. septentrionalis* (Alexander, 1974; Drenner *et al.*, 1978), an abundant copepod in the Toolik area and an important invertebrate predator on zooplankton. In measuring capture rates, Kettle and O'Brien (1978) found that lake trout often failed in their efforts to capture *H. septentrionalis* which frequently could swim out of the fishes' suction intake. The copepod evaded 30% of the attacks from trout in laboratory experiments.

If lake trout and grayling are inefficient planktivores, it can be hypothesized that the whitefish in the Noatak area lakes controlled the zooplankton community structure there. A similar situation has been reported by Nilsson (1972) who found that salmonid fish did not exclude the large Eurasian copepod *Heterocope saliens* but that this species was replaced by a much smaller species after the introduction of whitefish.

One lake in the Toolik area (N-2), with no planktivorous whitefish, however, has a zooplankton community identical to that occurring in the lakes of the Noatak. Lake N-2 differs from others in the area primarily in that it lacks lake trout. Extensive gill netting in this lake during the summer of 1976 collected only grayling, and there have been no reports of sightings or captures of lake trout from this lake. The absence of lake trout may allow a higher density of small grayling which has then increased the predation pressure on large zooplankton (Table 2).

Thus it appears that the exclusion of large zooplankton by planktivorous fish is not automatic, as has often been inferred from the many temperate examples (Brooks and Dodson, 1965; Hrbacek, 1962; Galbraith, 1967; Hall *et al.*, 1970), but rather is relative to the types and densities of planktivorous fish in the lake.

Invertebrate Predation

The size-selectivity of most invertebrate predators is well accepted (Anderson, 1970; Smyly, 1970; Confer, 1971; Brandl and Fernando, 1975) and such predation has been suggested as the mechanism excluding small zooplankton species from large bodied zooplankton communities. Of those predators common in arctic waters, *Heterocope septentrionalis* is known to feed more heavily on small zooplankton species than on larger forms (O'Brien, *et al.*, 1979); the small cyclopoid copepods, which are about the size of *Bosmina longirostris*, likely feed on smaller organisms; and *Polyphemus pediculus* feeds more heavily on nauplii and small rotifers than on cladocerans (Haney, unpublished data).

Comparing the distribution of the predator *Heterocope septentrionalis* with that of the small-size *Bosmina longirostris* in the Toolik area ponds shows that in some cases this predator is unable to exclude this species. For example, in the S-series of ponds, *B. longirostris* and *H. septentrionalis* co-occur in two ponds without fish and one where fish are present (Table 1). There are five other lakes in the region where the two species can both be found. A contingency table of the presence or absence of *Bosmina* with that of *Heterocope* yields a X^2 value of 2.74, clearly showing no exclusion of the small prey by this predator.

It appears that *Bosmina* from Toolik Lake are preyed upon less heavily by *Heterocope* than would be expected from their size alone (O'Brien and Schmidt, 1979). Their mortality rate is closer to that typical of a 2 to 2.4 mm *D. pulex*, almost three times the size of the average *Bosmina*. A similar report of predation rate lower than predicted by size has been made by Kerfoot (1975, 1977) in studying *Bosmina* preyed upon by *Epischura*. The Toolik Lake *Bosmina* were also notable for having enlarged mucral spines and antennules, and it may be that these animals are more difficult for *Heterocope* to capture, handle and consume. Kerfoot (1977) has also suggested that *Bosmina* may be able to disguise their presence from tactile predators by passively sinking.

Competition

The size-efficiency hypothesis (Brooks and Dodson, 1965), in which it was proposed that larger species could effectively exclude smaller species from ponds and lakes without fish because they were energetically more efficient, has recently lost favor (Dodson, 1974), and indeed is not supported in the present situation. Three of the six S-series ponds without fish support a population of the small *Bosmina longirostris* but not of the large *D. middendorffiana*, and in the remaining three ponds of the series, both species are present. A contingency table of the presence or absence of *Bosmina* relative to that of *D. middendorffiana* yielded a X^2 value of 4.61, showing as much evidence for *Bosmina's* excluding *D. middendorffiana* as for the reverse. However, other than in Toolik Lake and a very few individuals of *Bosmina* in two other ponds (Table 1), these two species did not commonly co-occur throughout the area.

Predation and Competition

The S-series of ponds shows an example of the combined forces of invertebrate predation and competition which still are unable to exclude the small-bodied *Bosmina longirostris*. In pond S-3, *Bosmina* must face predation from *Heterocope septentrionalis* and competition from the large-bodied *Daphnia middendorffiana*, yet all three species co-exist (Table 1). In Toolik Lake both *Heterocope* and *D. middendorffiana* are present with *Bosmina* and another small-bodied zooplankter, *D. longiremis*; however, both small forms in Toolik Lake appear to have developed adaptations that reduce the impact of invertebrate predation (O'Brien, *et al.*, 1979).

It may be that small forms such as *Bosmina* gain a competitive advantage in those ponds and lakes that have a population of *Polyphemus pediculus*, which preys more heavily on still smaller nauplii and rotifers than on cladocerans. Whatever the mechanism that is operating, however, it is clear that the forces of predation and competition, even combined, do not always result in exclusion of small-bodied zooplankton species from ponds and lakes without fish.

Another factor that may be contributing to the atypicalness of the zooplankton communities in the Toolik area is the alteration in the competitive balances once a population of an invertebrate predator such as *Heterocope septentrionalis* can be maintained. Large-bodied daphnids such as *D. middendorffiana* have been shown to be 10 to 20 times less susceptible to predation from *Heterocope* than smaller daphnids such as *D. longiremis* (O'Brien *et al.*, 1979). Thus the combined effect of inefficient fish predation on large-size zooplankters and efficient *Heterocope* predation on small forms may give *D. middendorffiana* an added competitive advantage. Interestingly, Lake N-2, which lacks the predatory copepod, also lacks *D. middendorffiana*.

Other Unusual Distribution Patterns

Heterocope septentrionalis: Throughout the Toolik area, *Heterocope* was found to occur only in ponds and lakes that are at least 0.3 m in maximum depth. Five ponds sampled are less than this depth, and in none of them was *Heterocope* found. Three of these ponds also lacked *D. middendorffiana*. In 18 of the other 19 ponds and lakes — the sole exception was Lake N-2 — *Heterocope* was found. This distribution may reflect the existence of some environmental extreme, such as high temperatures, in these very shallow ponds. It seems likely that these ponds often dry up during the summer and are filled again in spring by runoff. It may be that the ponds do not remain filled long enough for *Heterocope* and in some cases, *D. middendorffiana* to complete their life cycles to a diapause stage.

Rotifers: Rotifers are extremely sparse throughout the Toolik area. Through three summers of observation of Toolik Lake and the surrounding ponds, we have recorded individuals of only two genera, *Filinia* and *Conochilus*. The dense populations of cyclopoid copepods in Toolik Lake (100 to 200/l in deep water) may account for the paucity of rotifers there, as these predators feed on animals the size of planktonic rotifers. Likewise, the sparse phytoplankton densities may make it difficult for rotifers to compete with cladoceran filter feeders.

GENERAL DISCUSSION

Although the zooplankton distributions reported here do not fit the Hrbacek, Brooks, and Dodson paradigm, they are not unique. Reed (1963) commonly found *Bosmina longirostris* and sometimes *Daphnia longiremis* co-occurring with *Heterocope septentrionalis*. His report does not describe either pond depth or fish presence or absence, but it appears that *D. middendorffiana* did not occur in larger, deep lakes whereas *Heterocope* sometimes did.

It is quite unlikely that the results in the present study were confounded by sampling problems. All the ponds and lakes were sampled in a similar fashion by the same investigators within five days of one another. All were sampled during late morning or early afternoon at a time of continuous daylight. In addition, samples taken from the same ponds the following year showed similar distributions to those reported here.

It must therefore be concluded that the zooplankton community structure in many lakes and ponds of the Toolik area offer exceptions to some generally accepted rules of zooplankton distribution. Planktivorous fish do not always exclude large-sized zooplankton; instead, the population's density and feeding efficiency of the fish must be considered. Nor can invertebrate predators, either with or without fish predation and competition from other species, always eliminate small forms. It is becoming increasingly evident that size alone does not determine the ability of zooplankton species to withstand invertebrate predation (Kerfoot, 1975, 1977; O'Brien *et al.*, 1979; O'Brien and Schmidt, 1979). In harsh environments, such as the Arctic, where only a few species are able to survive, it appears that specially adapted morphs of these species develop in the presence of invertebrate predation. In more benign temperate areas, where a greater variety of species occur, such adaptations are less common than exclusion and replacement by another species. Continued studies of the lakes and ponds of the Toolik area will allow greater understanding of the subtle mechanisms operating to structure zooplankton communities.

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