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Zooplankton Community Structure in Arctic Ponds: Shifts Related to Pond Size

W. JOHN O'BRIEN[1] and CHRIS LUECKE[2]

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ABSTRACT. A multi-year experiment in which zooplankton species were manipulated in 12 ponds indicated that the presence of the carnivorous copepod *Heterocope septentrionalis* eliminated *Daphnia pulex* whenever *H. septentrionalis* became established. In contrast, the congener *D. middendorffiana* was able to persist only in ponds where *H. septentrionalis* became established. The fact that *Daphnia middendorffiana* could not successfully colonize ponds that did not contain *H. septentrionalis* indicates that this predator was necessary for *D. middendorffiana* to thrive. These results suggest that *D. pulex* is able to outcompete *D. middendorffiana* when *H. septentrionalis* is absent. Pond size was a key determinant of colonization success, in that *H. septentrionalis* and *D. middendorffiana* were able to persist only in ponds with volumes greater than 10 m^3. Results of these investigations support the pattern of zooplankton community composition observed in ponds in the western Nearctic and provide insight into the mechanisms responsible for these observations.

Key words: competition, predation, *Daphnia*, Arctic zooplankton, pond experiment

RÉSUMÉ. Une expérience échelonnée sur plusieurs années dans le cadre de laquelle les espèces de zooplancton de 12 étangs ont été manipulées a permis de déterminer que la présence du copépode carnivore *Heterocope septentrionalis* a éliminé le *Daphnia pulex* lorsque le *H. septentrionalis* s'était établi. En revanche, le congénère *D. middendorffiana* n'a pu persister que dans les étangs où *H. septentrionalis* s'était établi. Le fait que *Daphnia middendorffiana* n'a pas réussi à coloniser les étangs qui ne renfermaient pas *H. septentrionalis* indique que la présence de ce prédateur s'avérait nécessaire pour que *D. middendorffiana* puisse prospérer. Ces résultats laissent croire que *D. pulex* est capable de déplacer *D. middendorffiana* lorsque *H. septentrionalis* est absent. La taille de l'étang représentait un déterminant-clé en matière de réussite de la colonisation, en ce sens que *H. septentrionalis* et *D. middendorffiana* n'ont réussi à persister que dans les étangs dont le volume était supérieur à 10 m^3. Les résultats de ces enquêtes viennent appuyer le modèle entourant la composition de la communauté de zooplancton observé dans les étangs néarctiques occidentaux et permettent de comprendre les mécanismes responsables de ces observations.

Mots clés : compétition, prédation, *Daphnia*, zooplancton arctique, expérience dans les étangs

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INTRODUCTION

Our understanding of the role of biotic interactions in shaping the community structure of ponds and lakes generally derives from laboratory experiments (Anholt and Werner, 1995; McPeek, 1998) or from field enclosures (Sih et al., 1985). The abundant small ponds in the Arctic provide the opportunity to examine the role of predation and competition in shaping zooplankton communities by manipulating the species composition of entire ponds. This approach provides more insight into ecological processes than short-term, small-scale enclosure experiments, in that the experimental manipulations can be followed for the long periods of time that organisms need to express their complete life histories. In addition, the small number of species of crustacean zooplankton in Arctic ponds makes interpretation of the results of whole-system species manipulation more straightforward. In the Toolik Lake region of Alaska, there are only nine known crustacean zooplankton species (O'Brien et al., 2004). Zooplankton communities in small ponds of this region are even more species-poor, with five species dominating the assemblage (Luecke and O'Brien, 1983). Four of these five species occur in both ponds and lakes, whereas *Daphnia pulex* is restricted exclusively to ponds and is typically found in very small ponds throughout the region (Stross et al., 1980). The mechanisms that restrict *D. pulex* to ponds have not been established. Zooplankton of ponds in this region are typical of ponds throughout the western Nearctic. *Heterocope septentrionalis* is absent from the eastern High Arctic of North America, as well as from large sections of the Palearctic (Hebert and Hann, 1986).

In the present study, we experimentally manipulated the zooplankton communities in ponds in order to examine the roles of predation and competition in structuring zooplankton communities. In ponds near the Toolik Lake

[1] Department of Biology, University of North Carolina-Greensboro, Greensboro, North Carolina 27402, USA; deceased
[2] Department of Watershed Sciences, Utah State University, Logan, Utah 84322, USA; chris.luecke@gmail.com

Field Station, when *D. pulex* is present in a pond, the only other species found are the two ubiquitous Arctic copepods *Cyclops scutifer* and *Diaptomus pribilofensis*. A second very common Arctic daphnid, *D. middendorffiana*, also occurs in ponds but is never found with *D. pulex*. *Daphnia middendorffiana* also occurs in many lakes in the Toolik Lake region, often in conjunction with the predaceous calanoid copepod *Heterocope septentrionalis*. This distributional pattern of *D. pulex* occurring alone and *D. middendorffiana* and *H. septentrionalis* occurring together in most other ponds and many lakes has been noted by several other researchers (Hebert and Loaring, 1980; Stross et al., 1980; Luecke and O'Brien, 1983; Dodson, 1984; O'Brien and Luecke, 1988).

Prior research has investigated some of the possible mechanisms behind this distribution. In laboratory predation experiments, *H. septentrionalis* preyed more heavily on *D. pulex* than on *D. middendorffiana* (Hebert and Loaring, 1980; Luecke and O'Brien, 1983; Dodson, 1984). Previous experiments in isolated ponds have shown a similar outcome: when *H. septentrionalis* was added to ponds, *D. pulex* was eliminated (O'Brien and Luecke, 1988; O'Brien, 2001). These results indicated that *D. pulex* is quite vulnerable to predation by *H. septentrionalis*.

It is not known, however, why *D. middendorffiana* does not occur in ponds containing *D. pulex*. Dzialowski and O'Brien (2004) presented evidence from laboratory studies that *D. pulex* outcompetes *D. middendorffiana* in the absence of the predator. The large energy costs incurred by *D. middendorffiana* in producing a stronger carapace to reduce predation from *H. septentrionalis* may be the reason for the competitive advantage of *D. pulex* in the absence of such predation (Dodson, 1981; Riessen, 1992; Dawidowicz and Wielanier, 2004). Why *H. septentrionalis* does not colonize the shallow ponds harboring *D. pulex* remains unclear, and definitive studies indicating that such introductions have failed have not been reported. In this study, we report on the outcome of experimental introductions of the invertebrate predator *H. septentrionalis* into ponds of different sizes.

In 1997, a number of ponds that contained only *D. pulex* were found in a small area north of the Toolik Lake Field Station. These ponds were very close to the Dalton Highway and thus offered a practical opportunity to address pond community composition experimentally by introducing *H. septentrionalis* and *D. middendorffiana* into the ponds and tracking the distribution patterns over time.

MATERIALS AND METHODS

Site Description

The ponds used in this experiment are located on a disturbed stretch of tundra about 20 km north of the Toolik Lake Field Station and just off the north side of the Dalton Highway. Estimates from Google Earth of geographic coordinates for the middle of the area covered by the ponds are 68°41′21.08″ N and 149°04′51.33″ W. There are approximately 35 ponds in a 4–5 hectare area of a previous glacial moraine where much rock was removed during pipeline construction in the early 1970s. The ponds resulted from soil slumping caused by the melting of underlying permafrost and ice wedges and are now persistent features of the landscape. The ponds range in size from very small (0.3 to 1 m wide) to large (8 to 12 m wide). The deepest is 1.6 m deep, but most are less than 0.5 m deep. Catchment areas of each pond are very small (< 1 ha) resulting in low conductivities (160 to 360 μS/cm). We surveyed 29 ponds in the area on 19 July 1997. In 15 of these ponds, *D. pulex* was the only crustacean zooplankton present, and 12 of those ponds were used in this experiment. The other 14 ponds either had no Cladoceran zooplankton or had a community consisting of *D. middendorffiana* and *H. septentrionalis*.

Experimental Design

Four treatments with three replicates each were established in the 12 ponds in early summer of 1998 to assess the impact of *H. septentrionalis* and *D. middendorffiana* on the abundance *of D. pulex*. The four treatments were (1) addition of *H. septentrionalis* alone, (2) addition of *D. middendorffiana* alone, (3) addition of both *H. septentrionalis* and *D. middendorffiana*, and (4) no addition of zooplankton species (the reference treatment). Three replicates of each treatment were stratified by pond size so that each treatment contained a small, a medium, and a large pond. The small ponds were around 1 m^3, medium 2–14 m^3, and large 22–46 m^3. The number of individual *H. septentrionalis* and *D. middendorffiana* added varied by pond size: 8 individuals were added to the small ponds, 16 to the medium ponds, and 32 to the large ponds. The *D. middendorffiana* that were added all had parthenogenic eggs or embryos. Zooplankton additions were made on 28 June 1998. Subsequent sampling indicated that *H. septentrionalis* did not establish new populations in the small and medium ponds. To assure initial colonization of both introduced species, *H. septentrionalis* was added again on 7 July 1999 and 6 July 2000 to ponds that had received treatments 1 and 3. Both *H. septentrionalis* and *D. middendorffianna* were added on 12 July 2002 to the ponds that had received treatments 2 and 3.

Sampling Procedures

The ponds were sampled two to three times each in the summers of 1998 to 2004 using small (10 × 13 cm) dip nets with a 400 μm mesh. Each pond had a designated net that was used only for that pond and was dried after each sampling effort. Six tows of similar length were made in each pond. These samples were returned immediately to the laboratory at the Toolik Lake Field Station, and all the zooplankton in each sample were identified and enumerated. The shallow morphology and heterogeneously distributed macrophytes in the ponds made it difficult to sample

TABLE 1. The presence (+) and absence (0) of *D. pulex*, *H. septentrionalis*, and *D. middendorffiana* in each pond at the end of the experiment in late summer of 2004. Parentheses after pond size (small, medium, or large) indicate maximum depth (m) and surface area (m^2) of each pond. Four treatments are noted: (1) addition of *H. septentrionalis*, (2) addition of *D. middendorffiana*, (3) addition of *H. septentrionalis* and *D. middendorffiana*, and (4) Reference (no additions).

Treatment and Pond Size	Species Present		
	D. pulex	*H. septentrionalis*	*D. middendorffiana*
Heterocope septentrionalis added:			
Small (0.37, 2.2)	+	0	0
Medium (0.39, 11.8)	0	+	0
Large (0.75, 36.0)	0	+	+
D. middendorffiana added:			
Small (0.27, 5.2)	+	0	0
Medium (1.0, 14.0)	+	0	0
Large (0.39, 64.1)	+	0	0
Heterocope septentrionalis and *D. middendorffiana* added:			
Small (0.24, 4.6)	+	0	0
Medium (0.26, 16.3)	+	0	0
Large (0.70, 65.7)	0	+	+
Reference ponds:			
Small (0.15, 6.7)	+	0	0
Medium (0.36, 11.1)	+	0	0
Large (0.35, 68.8)	0	+	+

quantitatively, so we present data on the presence, absence, and relative abundance of *D. pulex*, *D. middendorffiana*, and *H. septentrionalis*. The other crustacean zooplankton that were sometimes present in these ponds, *C. scutifer* and *D. pribilofensis*, were noted during the examination but are not reported here. The maximum depth and approximate surface area of each pond were estimated using a meter tape.

RESULTS

In the small and medium reference ponds, with no species additions, *D. pulex* maintained its presence across the eight years as expected (Table 1). The large reference pond was colonized independently by *H. septentrionalis*, which was first identified in samples collected from that pond in 2001, and later by *D. middendorffiana*, first identified in 2002. The addition of *H. septentrionalis* alone led to its colonization in the medium and large ponds, with the anticipated decline or exclusion of *D. pulex* in those ponds. In the large pond, *D. middendorffiana* independently colonized in 2001, when *D. pulex* densities had declined. Although added on four separate occasions across six years, *H. septentrionalis* never survived in the small ponds, and *D. pulex* maintained robust populations in those ponds. When *D. middendorffiana* was added alone, it failed to become established in any size pond. When both *H. septentrionalis* and *D. middendorffiana* were added, they colonized only the large pond, excluding *D. pulex* in the process.

The relative abundance of these three zooplankton species at the end of the experiment is shown in Figure 1. *Daphnia pulex* was the only species present in each of the small ponds and in three of four medium-sized ponds. In the larger ponds, *D. middendorffiana* became numerically abundant whenever *H. septentrionalis* was present. The large reference pond was inhabited by all three species, with *D. middendorffiana* as the numerical dominant.

The change in the relative abundance of the three zooplankton species over time was consistent among the treatments once *H. septentrionalis* became established (Fig. 2). The decline in *D. pulex* and the increase in *D. middendorffiana* began within a year after the appearance of *H. septentrionalis*. *Daphnia pulex* was nearly eliminated from ponds within four years of the establishment of *H. septentrionalis*. Five years after the establishment of *H. septentrionalis*, the crustacean zooplankton assemblage was composed of *D. middendorffiana* (75% by number), *H. septentrionalis* (20%), and *D. pulex* (5%).

DISCUSSION

The results of these experiments suggest that pond size is a key factor in the distribution of daphnids in the Arctic. *H. septentrionalis* and *D. middendorffiana* appear to be unable to persist in the small ponds that are the primary habitat for *D. pulex*. Of the four small and medium ponds to which *H. septentrionalis* was added, it was able to colonize in only one. This pond was in the mid-range of medium-sized ponds in terms of depth and surface area. By contrast, *H. septentrionalis* became established in both of the large ponds to which it was added for purposes of the experiment, as well as in the large reference pond where it successfully invaded. Once *H. septentrionalis* colonizes, it eliminates *D. pulex*, opening the opportunity for *D. middendorffiana* to colonize as well. After eight years, 11 of the 12 ponds had one of the two zooplankton population patterns typical

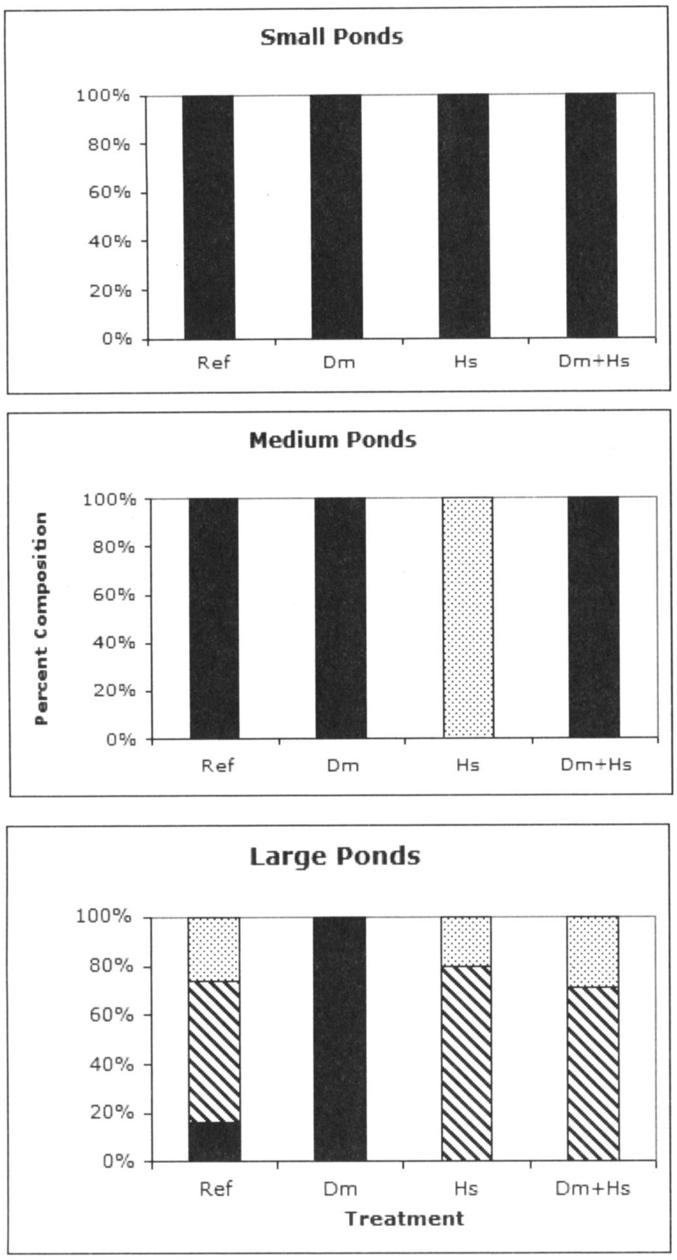

FIG. 1. The relative abundance of the three dominant crustacean zooplankton by number in small, medium, and large-sized ponds. In the bars, black represents *D. pulex*, obliques lines represent *D. middendorffiana*, and dots represent *H. septentrionalis*. For the treatments, Ref = reference, Dm = addition of *D. middendorffiana* alone, Hs = addition of *H. septentrionalis* alone, and Dm+Hs = addition of both species.

of Arctic ponds, either *D. pulex* alone or *H. septentrionalis* and *D. middendorffiana* together. Pond size differentiated these two outcomes.

The reasons why *H. septentrionalis* failed to become established in the small ponds remain unclear. These smaller ponds likely experienced different limnological conditions during winter compared to the larger ponds, where less extensive ice cover and more extensive free water may have produced an environment that allowed overwintering. Results of these experiments support previous findings indicating that *D. pulex* outcompetes *D.*

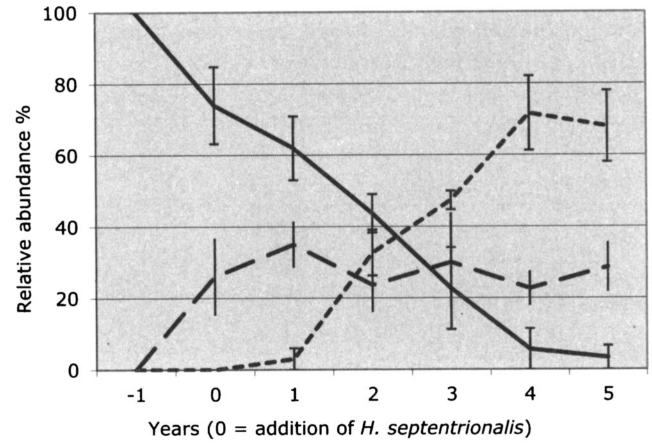

FIG. 2. The time sequence of changes in relative abundance after *H. septentrionalis* became established in four of the ponds. Black line = *Daphnia pulex*, dotted line = *D. middendorffiana*, and dashed line = *H. septentrionalis*. Vertical lines show the standard errors of these means. Numbers indicate years before and after the year when *H. septentrionalis* was introduced.

middendorffiana in western Nearctic ponds (Dzialowski and O'Brien, 2004).

DEDICATION

This manuscript is dedicated to the memory of Dr. W. John O'Brien, a great mentor, scientist, and lover of the Arctic. John was working on this manuscript at the time he was diagnosed with terminal cancer. His lifelong pursuit of the mechanisms explaining zooplankton community structure is perpetuated through the work of his many students and colleagues.

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REFERENCES

Anholt, B.R., and Werner, E.E. 1995. Interaction between food availability and predation mortality mediated by adaptive behavior. Ecology 76:2230–2234.

Dawidowicz, P., and Wielanier, M. 2004. Costs of predator avoidance reduce competitive ability of *Daphnia*. Hydrobiologia 526:165–169.

Dodson, S.I. 1981. Morphological variation of *Daphnia pulex* Leydig (Crustacea: Cladocera) and related species from North America. Hydrobiologia 83:101–114.

———. 1984. Predation of *Heterocope septentrionalis* on two species of *Daphnia*: Morphological defenses and their cost. Ecology 65:1249–1257.

Dzialowski, A.R., and O'Brien, W.J. 2004. Is competition important to Arctic zooplankton community structure? Freshwater Biology 49:1103–1111.

Hebert, P.D.N., and Hann, B.J. 1986. Patterns in the composition of Arctic tundra pond microcrustacean communities. Canadian Journal of Fisheries and Aquatic Sciences 43:1416–1425.

Hebert, P.D.N., and Loaring, J.M. 1980. Selective predation and species composition of Arctic ponds. Canadian Journal of Zoology 58:422–426.

Luecke, C., and O'Brien, W.J. 1983. The effect of *Heterocope* predation on zooplankton communities in Arctic ponds. Limnology and Oceanography 28:367–377.

McPeek, M.A. 1998. The consequences of changing the top predator in a food web: A comparative experimental approach. Ecological Monographs 68:1–23.

O'Brien, W.J. 2001. Long-term impact of an invertebrate predator, *Heterocope septentrionalis*, on an Arctic pond zooplankton community. Freshwater Biology 46:39–45.

O'Brien, W.J., and Luecke, C. 1988. The coexistence of a predaceous copepod and a daphnia: Weeding and gardening in the Arctic. Verhandlungen des Internationalen Verein Limnologie 23:2069–2074.

O'Brien, W.J., Barfield, M., Bettez, N.D., Gettel, G.M., Hershey, A.E., McDonald, M.E., Miller, M.C., et al. 2004. Physical, chemical, and biotic effects on Arctic zooplankton communities and diversity. Limnology and Oceanography 49:1250–1261.

Riessen, H.P. 1992. Cost-benefit model for the induction of an antipredator defense. The American Naturalist 140:349–362.

Sih, A., Crowley, P., McPeek, M., Petranka, J., and Strohmeier, K. 1985. Predation, competition, and prey communities: A review of field experiments. Annual Review of Ecology and Systematics 16:269–311.

Stross, R.G., Miller, M.C., and Daley, R.J. 1980. Zooplankton. In: Hobbie, J.E., ed. Limnology of tundra ponds: Barrow, Alaska. United States National Committee for the International Biological Program, Synthesis Series 13. Stroudsburg, Pennsylvania: Dowden, Hutchinson & Ross, Inc. 251–296.