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Disjunct distributions of two aquatic predators[1]

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Abstract

Two planktonic predators found in high altitude ponds of the Rockies are distributed locally in a disjunct fashion. Larvae of *Chaoborus americanus* are well known planktivores and can eliminate the semipredacious copepod *Diaptomus shoshone* from a pond; but in spite of the close proximity of many of these ponds, early instars of *Chaoborus* are rarely found in the presence of *D. shoshone*, and the densities are extremely low in the few cases of coexistence. Feeding experiments show that *D. shoshone* adults prey on early instar *Chaoborus*, but the later the midge instar, the greater its survivorship in the presence of *D. shoshone*. The copepods are in turn preyed upon by 4th instar midge larvae. The life cycles of the two species are offset so that midge eggs hatch in the presence of *D. shoshone* adults. It is suggested that reciprocal predatory interactions such as this one are unstable.

Following the pioneering work of Hrbáček et al. (1961) and Brooks and Dodson (1965), many investigators have helped establish the importance of vertebrate predators in aquatic communities. More recently, invertebrate predators have become recognized as having equally important influences on coexisting species (Dodson 1974; Kerfoot 1977, 1978; Li and Li 1979) in terms of distribution and adaptation. One invertebrate predator often studied is the larva of *Chaoborus* sp.—the phantom midge—a well known and common planktivore.

In the past few years copepod predation has also been recognized as important (Kerfoot 1977). *Diaptomus shoshone* Forbes is a large copepod found in the Rocky and Sierra Nevada Mountains (Wilson 1959), first reported as predatory by Anderson (1967). It preys on coexisting herbivorous zooplankton (Sprules 1972; Dodson 1974), but Sprules showed that it is not an obligate predator. These copepods have other influences as well, as Sprules first recognized, since *D. shoshone* adults can prey on *Chaoborus* larvae.

The faunal communities in subalpine ponds of northwestern Wyoming typically contain, among other species, *D. shoshone* and larvae of *Chaoborus americanus* (Joh.); although most ponds contain one or the other, they rarely contain both. A disjunct distributional pattern always suggests the presence of strong biological interactions between the two species. Dodson (1974) does speak of the occasional coexistence of *D. shoshone* and *C. americanus* in the Colorado ponds he and Sprules studied, but the midge larvae were "very rare" in the only case mentioned.

Different associations of herbivorous zooplankton are found in the presence of each predator, as would be expected from the principles first recognized by Hrbáček et al. (1961) and Brooks and Dodson (1965). *Chaoborus* larvae can eliminate some species, including *D. shoshone*, from a community by feeding on them, and *D. shoshone* may exert both competitive and predatory pressures on other species (Dodson 1970; Sprules 1972). The exact distributions of these two species and the full interactions producing the disjunct pattern have not, however, been fully described.

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Methods

The study was conducted in the Beartooth Mountains of northwestern Wyoming, where both *C. americanus* and *D. shoshone* are found. Heavy snow accu-

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mulates on what may be an exhumed peneplain of granite gneiss (Hughes 1933), and snowmelt trapped by glacial and erosional features creates many ponds with highly variable characteristics. Since 1973 I have been following the distribution of the fauna in many of these ponds (Williams 1976, unpubl.).

Plankton samples were collected with a 15-cm-diameter conical tow net with No. 20 fine (80-μm opening) nylon monofilament mesh (Turtox). To establish the five feeding experiments, I transferred individuals as soon after capture as possible by pipette into 120-ml jars filled with 110-ml filtered water from the source pond for *D. shoshone*. Replicate samples were also taken on each date and preserved with 4% formaldehyde for later measurements and life history determinations.

The sources for the experimental animals were ponds in similar terrain 5.6 km apart which have relatively dense populations of each species. Pond A1 (elevation, 3,045 m; max depth, 2.2 m; surface area, 0.7 ha) served as the source for *D. shoshone,* and pond E1 (2,920 m; 0.8 m; 0.2 ha) (Williams 1976) served for *Chaoborus*. The ponds are indistinguishable in total hardness and nitrate levels, but E1 has lower specific conductance (16–37 μmhos$\cdot$cm^{-1}) and lower pH (about 6.7–7.4). E1 generally thaws in late June or early July, 3 days before A1.

Feeding experiments were begun at different times in July and August of 1977 and 1978 to test the ability of different sizes of *Chaoborus* larvae (different ages and instars) to prey on or to survive the presence of *D. shoshone* adults. Each experiment included an experimental series of 12 jars with *D. shoshone* and *C. americanus* combined and a separate control series of 6 jars for each species alone. The densities were about six times those in nature, but the relative proportions of the animals were as in nature. The jars were kept in the field, subject to ambient light and temperature. Each experimental jar contained five *D. shoshone* adults and either ten *C. americanus* 2nd instars, five *C. americanus* 3rd instars, five *C. americanus* new 4th instars, or two *C. americanus* old 4th instars.

The jars were observed every few daylight hours to determine relative rates of survival. Each individual was scored as alive, dead, injured, partially ingested, or wholly ingested. Occasionally a midge larva would regurgitate a partially digested copepod, but these copepod remnants were easily distinguished from newly killed individuals. Since *Chaoborus* larvae are quite transparent and *D. shoshone* is heavily pigmented, I could follow the rate of digestion within the *Chaoborus* gut. All dead individuals were collected from the jars for later examination; injured individuals were collected after they had died.

Because of possible difficulties in interpretation of experiments run at higher than normal densities, I also ran a smaller experiment using liter jars. Eight jars contained two *D. shoshone* and three 3rd instar midge larvae; additional jars served as controls.

To determine the dependence of *Chaoborus* feeding rate on the concentration of prey, I established a series of 220-ml jars with one *C. americanus* old 4th instar and either one, three, or nine *D. shoshone* adults. The seven replicates of each were observed every few daylight hours. As soon as a copepod had been eaten or otherwise killed, it was replaced with a fresh individual. The experiment was run for 10 days for a long term estimate of feeding rates.

Chaoborus was considered new if it had spent less than half the usual duration in a given instar and old if it had spent more than half. Old 4th instars are those that have survived the previous winter. *Diaptomus* was identified from Wilson (1959) and *Chaoborus* from Johannsen (1934) and Saether (1970).

Results

Life histories—Diaptomus shoshone eggs hatch as soon as there is open water during the spring thaw and the young reach maturity within 3 weeks. Nauplii may be found even before the ice on a

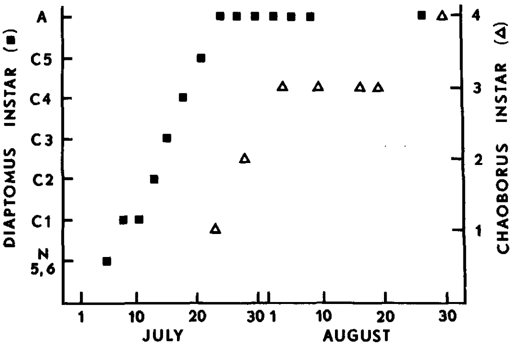

Fig. 1. Life cycles of *Chaoborus americanus* and *Diaptomus shoshone* from Ponds E1 and A1. Most abundant instar is shown for each date in 1978, excluding diaptomid nauplii 1–4 (N—nauplius; C—copepodite; A—adult). Pond E1, with *Chaoborus,* thaws 3 days before A1, so if these species inhabited the same pond their life cycles would be offset even more.

pond finally disappears. *Diaptomus shoshone* is univoltine, and after reaching maturity the copepods produce egg clutches through the rest of the open water season.

Midge eggs hatch, on the other hand, weeks after the thaw and generally reach the final instar 6 or 7 weeks later. Most, but not all, individuals emerge as adults the following summer. Although the body is flexible and its growth somewhat continuous, growth of the head capsule is discontinuous; thus the maximum size of ingestible prey also changes in a step-like fashion.

Because each species responds at a different rate to the spring thaw, their life cycles are offset (Fig. 1), though within a given year the timing of each species' life cycle depends on prevailing climatic conditions. For example, summer 1977, which followed a winter of record low snow accumulations, began unusually early and the development of both species was advanced by more than 3 weeks.

Feeding experiments—Adult *D. shoshone* and different age and instar *Chaoborus* larvae were combined in replicate jars of pond water to observe the effect of each species on the other. When *Chaoborus* larvae are small (in early instars), their survival is much reduced (Fig. 2). Fourth instar *Chaoborus* survive as well as controls, however, and the copepods then have greatly reduced survivorship (Fig. 3). Only the 1978 results are pre-

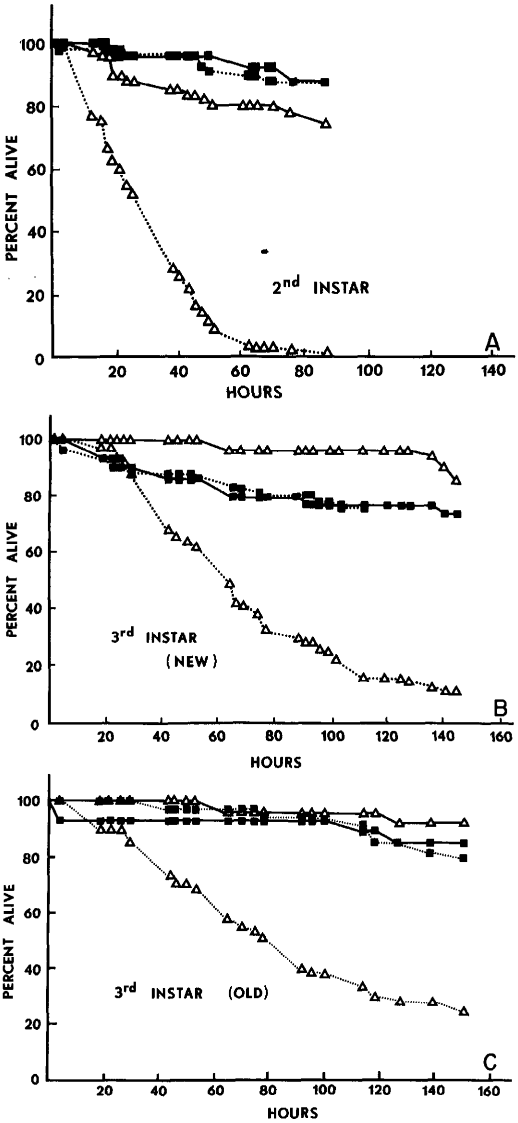

Fig. 2. Survivorship curves for experimental (dotted lines) and control (solid lines) 2nd, new, and old 3rd instar *Chaoborus americanus* (Δ) and adult *Diaptomus shoshone* (■). Percent individuals surviving at different times totaled from 12 replicate jars compared to percent surviving in set of 6 replicate controls.

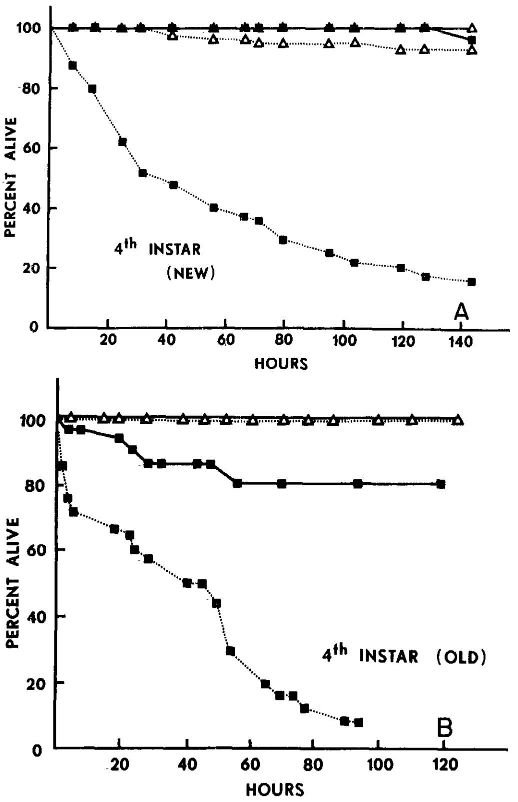

Fig. 3. As Fig. 2, but for new and old 4th instar animals.

sented here, but similar experiments run in 1977 had similar results.

The transition of feeding dominance from one species to the other is related to two factors: the maximum size of midge larvae that *D. shoshone* can catch, hold, and ingest, and the size of the *Chaoborus* feeding apparatus through which a copepod must pass. Larvae >3.5 mm (as measured between hydrostatic organs) are in general too large or too strong for *D. shoshone* to feed upon, while only 4th instar larvae have a large enough head capsule to ingest a copepod as large as an adult *D. shoshone*. The transition of greater survivorship from one species to the other is gradual, with new 3rd instar midges surviving better than 2nd instars and old 3rd instars better than new 3rd instars (Table 1).

Only 4th instar larvae were seen to ingest *D. shoshone*; often these larvae would regurgitate a copepod after partial digestion. In the feeding experiment shown in Fig. 3B, for example, 6 of 29 ingested *D. shoshone* were regurgitated. *Diaptomus shoshone* is probably the largest prey that *C. americanus* from the Beartooth Mountain area can ingest. This statement is not contradicted by the fact that 8% of the copepods in the presence of late 3rd instar larvae have mortality attributed to *Chaoborus* predation (Table 1). The experiment began with 3rd instar larvae, but during its 6-day course some molted and became new 4th instars, which were then able to feed upon the copepods.

Swift and Fedorenko (1975) stated that copepods 2.2 mm long are likely to be the largest that *C. americanus* can ingest, but they did not have copepods of this size to test. The cephalothorax of adult *D. shoshone* generally measures 2.1 mm in males and 2.3 mm in females, though

Table 1. Results of feeding experiments (*C*—*Chaoborus*; *D*—*Diaptomus*).

	Chaoborus			Predation actually observed (%)		Time to 50% survival (h)		Wilcoxon paired-sampled test†	
Begin date	Instar	Length* (mm)	*n*	*C*	*D*	*C*	*D*	*C*	*D*
28 Jul 78	2nd	1.8±0.3	33	20.0	0.0	27	‡	$P<0.001$	$P>0.05$
9 Aug 78	3rd new	3.2±0.5	43	8.3	0.0	64	‡	$P<0.001$	$P>0.10$
16 Aug 78	3rd old	3.4±0.4	54	3.3	8.3	79	‡	$P<0.001$	$P>0.02$
22 Aug 78	4th new	3.6±0.4	42	5.0	31.7	‡	36	$P<0.001$	$P<0.001$
8 Jul 77	4th old	4.1±0.5	71	0.0	48.3	‡	39	identical	$P<0.001$

* As measured between hydrostatic organs, $\bar{x}\pm$SD.

† Based on differences between experimental and control percentages, as given in Figs. 2 and 3. Test is from Zar (1974).

‡ Beyond length of experiment; no apparent difference from that of controls.

Maly (1973) has shown that the mean size may vary from year to year.

Adult copepods fed readily on 2nd instar larvae, less successfully on 3rd instars, and were only occasionally successful in feeding on new 4th instars. Late 4th instars are strong, voracious planktivores which no *D. shoshone* can harm, but new ones are sometimes vulnerable to the copepods. Only a small percentage of 3rd instars were fed upon by the copepods, yet while the feeding rate seemed to diminish, the appearance of injured individuals increased sharply to 18% of late 3rd instars. This may indicate that the copepods held onto the midge larvae for a shorter period and could not so readily ingest them, but they were effective in reducing the midge survival rate.

I saw no avoidance reactions by *Chaoborus* larvae of any size in the presence of *D. shoshone,* but the copepods do show avoidance behavior when a midge larva attacks and accelerate away from the point of contact.

The copepods generally began feeding on the posterior end of the midge larvae. In 23 cases in which the direction of feeding was known, 21 proceeded from the tail and only two from the head. The copepods rarely consumed an entire larva; often a *Chaoborus* head was seen floating afterward.

No cannibalism was observed in the copepods. *Chaoborus* larvae do occasionally feed on one of their own species, especially on 2nd instar larvae.

In the density experiment I paired old 4th instar *Chaoborus* (one larva in each 220-ml jar) with different densities of *D. shoshone* adults as prey for a 10-day period and continuously replaced dead individuals. With a density of five copepods per liter, the feeding rate was 0.21 ± 0.14 copepods per day; with 15 per liter, it was 0.33 ± 0.17; and with 45 per liter it was 0.44 ± 0.21. The results show part of the predator functional response curve. Although a Mann-Whitney test does not show statistical differences when these results are compared pairwise, there is the trend that one would expect of increased feeding rates in the presence of more prey. The smallness of the trend (feeding rate doubles while density increases nine times) indicates that the difference between natural and experimental densities may not be very important to the experimental results.

This conclusion is further substantiated by the results of the feeding experiments in liter jars. Where the experimental density was six times that in nature for the initial experiments, the density in the liter jars was half that in nature, and the feeding rates were of course lower. The copepods consumed about 0.6 *Chaoborus* per copepod per day for 2nd instar larvae and 0.2 for 3rd instar larvae. There was no mortality in the controls. One may presume, therefore, that the predatory interaction is sufficient at natural densities to account for the elimination of early midge instars from a pond.

I used animals in the above experiments fresh from their native habitat, to reduce any handling effects. An additional run was made with old 4th instar *Chaoborus* that had been isolated from visible prey for at least 4 days and thus starved. The time to 50% survivorship for *D. shoshone* was 54 h for a control with fresh *Chaoborus,* 35 h with starved *Chaoborus.*

Dynamics—A few ponds in the Beartooth Mountains contain *D. shoshone* in one year and *C. americanus* in the next, or, rarely, both species in the same year. Table 2 presents some sampling information from two such ponds over a 5-year period. In light of the experimental results it is significant that the two species were either never found together (Pond G3) or at very low densities when they did co-occur (Pond M2). The absence of a species from a pond might mean that it was there but at densities so low that it was not collected; however even with a low value of 50% net efficiency at least 50 liters of pond water were filtered for each sample.

Discussion

Chaoborus overwinters in larval form (Fedorenko and Swift 1972; Bradshaw

Table 2. Densities of *Chaoborus americanus* (*C*) and *Diaptomus shoshone* (*D*) in ponds G3 and M2, which have contained both species since 1974. Densities given as No.·liter^{-1}. No observations made in 1976.

		G3	M2
Elevation (m)		3,020	2,915
Depth (m)		0.4	0.4
1974	*C*	0.01	*
	D	0	*
1975	*C*	0	present†
	D	0.11	present†
1977	*C*	0	0.02
	D	present†	0.01
1978	*C*	0	0.24
	D	0.02	0.09
1979	*C*	0.02	0.01
	D	0	0.07

* Not observed.
† Densities unknown.

1973), usually in soft-bottomed ponds where the larvae can find a refuge from the winter freeze by burrowing into organic muck (Williams 1976). The copepods, on the other hand, overwinter as encysted eggs resistant to desiccation and low temperatures; thus, they can occur in ponds which are hard-bottomed and freeze completely or which dry up by the end of the summer. This difference determines the basic distributional pattern, but, in the absence of strong biological interactions, some overlap in habitat would be expected.

Samples taken from more than 100 ponds on the Beartooth Plateau during the past 6 years—many sampled each year—have with one exception never included individuals of these two species from the same pond. The sole exception is a broad, very shallow pond where a few individuals of each species can periodically be recovered; but these cannot be considered representatives of thriving, interacting populations. More specifically, of 71 shallow ponds in the 2,900–3,050-m elevational range, where the density of ponds is greatest and both species commonly occur, 33 ponds contained *D. shoshone*, 28 had *Chaoborus*, 9 had neither, and only the one just mentioned had both. A 2 × 2 contingency table shows that this distributional pattern is significantly different ($P \ll 0.005$, $\chi^2 = 41.58$, df = 1) from random.

It has been well established that *Chaoborus* larvae can exclude *D. shoshone* from a pond through predation (Dodson 1970; Sprules 1972). However, the distributions are so precisely disjunct in the Beartooth area that the single interaction of predation by *Chaoborus* on the copepod is not sufficient to account for the distributional patterns. Because many of the ponds are close to one another and high winds may enhance the dispersal ability of these insects, adult midges might occasionally lay their eggs in a hard-bottomed, shallow pond. Though the larvae would not survive the next winter, they should sometimes occur in such ponds during summer.

An alternative explanation for the absence of early instar *Chaoborus* larvae in ponds with *D. shoshone* follows from the usual habitat differences of the two species. If adult midges are induced to deposit eggs only in ponds with certain characteristics, the dispersal postulated above would not occur, and eggs would never reach *D. shoshone* habitats. The difficulty with this reasoning is that ponds do not fall into two discrete categories. There are ponds with physical characteristics intermediate between those of typical *D. shoshone* and *C. americanus* habitats: they contain a small amount of organic sediment and are shallow, so that midge larvae might survive the winter in them in a wet year but not in a dry one. Dispersal by both species to such ponds is proven through year-to-year comparisons, yet in a single year only one species can be found. Typically the densities in these cases are low, since neither population has the chance to build up to high densities, but there may be enough individuals within the restricted confines of a small pond for one species to prey upon and eliminate the other.

How can shifts from one species to the other occur? *Diaptomus* is generally dispersed in late summer or fall, when encysted eggs are exposed at the margins of partially or wholly evaporated ponds and blown from place to place by the wind. Dispersal is also likely through the attachment of eggs to animals moving through the area. *Chaoborus,* on the other hand, is dispersed in early summer by the adults laying eggs. If a pond has neither species but in one season receives propagules of both (*Diaptomus* eggs from the previous fall and *Chaoborus* eggs during the summer), *D. shoshone* should dominate because it reaches the adult stage by the time of emergence of 1st instar *Chaoborus.* If a shallow pond with *Chaoborus* is subjected to a dry year, the pond may evaporate and the midge larvae within it will not survive the winter. That pond then becomes an open habitat ready for immigration.

The conversion of a *D. shoshone* pond to one with *Chaoborus* is more difficult to interpret. In one instance, during the spring melt, the 4th instars of *Chaoborus* were literally washed out of one pond into a neighboring *D. shoshone* pond 10 m away. In some instances the *D. shoshone* density may be low enough so that some early instar *Chaoborus* escape predation and survive to the 4th instar; this may have been the case in the one pond that contained very low densities of both. Some conversion from copepod to midge predation does apparently occur.

Predation may not be the only interaction of importance, of course, but the evidence points to it as the primary interaction in structuring the pond communities. Competition between *C. americanus* and *D. shoshone* is possible, as Sprules (1972) noted, but could not effect the changes as rapidly as they occurred (Pond G3 for example). The role of competitive interactions remains unclear. I have seen no other important predators in these ponds through 7 years of observations, so the interpretation of Dodson (1970) that *Chaoborus* occupies a "complementary feeding niche" could not apply here; there are no salamanders or axolotls to create a feeding role for *Chaoborus.*

Ponds are not homogeneous environments. Zooplankton concentrate in certain parts of a pond, even though vertical migration may be severely limited; the densities of organisms change during summer; and other biological and physical factors lend additional complexity to the pond habitat. These factors must be recognized in relating feeding experiments to nature; however, the distributional data for *C. americanus* and *D. shoshone* indicate the importance of direct interactions between these two species, despite the complexities of the natural environment.

Except when the population densities are extremely low, *C. americanus* and *D. shoshone* are distributed over space and over time in a precisely disjunct fashion. My experimental results indicate clearly a reciprocal predatory interaction between the two species and show that, at certain stages of their life cycles, each species can reduce to a significant degree the survivorship of the other. These results clarify the mechanisms involved in establishing the distributional precision seen in nature and allow the hypothesis that reciprocal predatory interactions such as this one are unstable.

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