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# Long Term Effects of Climate on Two Pond Predators

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# Long Term Effects of Climate on Two Pond Predators

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Abstract.—This study assessed the influence of annual snowpack on long term changes in the predatory regime of four high elevation ponds in the mountains of northwest Wyoming. Over 36 y of observation, in two ponds the primary predator alternated between phantom midge *Chaoborus americanus* larvae and *Diaptomus shoshone* predatory copepods, whereas the predatory regime did not change in the other two shallower ponds. Switching of predators correlated with extreme amounts of winter snow, either high or low, which determined the depth at which drying or complete freezing of the pond occurred. *Chaoborus americanus* colonized ponds after the wettest years and disappeared after the driest years. The results provide an unusual long term perspective of the effects of weather on predator dominance.

## Introduction

Responses of freshwater communities to the effects of vertebrate and invertebrate predators can be extensive and complex (Brooks & Dodson, 1965; Lynch, 1979; Kerfoot & Sih, 1987; Black & Hairston, 1988; Riessen *et al.*, 1988; Hanazato & Yasuno, 1989; Brett & Goldman, 1996). Phantom midge larvae (*Chaoborus* spp.) are important invertebrate predators in many lake and pond communities, feeding on rotifers, cladocera, and copepods (Elser *et al.*, 1987; Luecke, 1988) and exerting varying effects on different zooplankton species (MacKay *et al.*, 1990). Another group of invertebrate predators, large diaptomid copepods, also affect coexisting cladocera and copepods wherever they are found (O'Brien, 2001), even though these copepods may not be obligate predators (Kling *et al.*, 1992). One such species, *Diaptomus shoshone* Forbes, is widespread in alpine and subalpine lakes of western North America (Anderson, 1971; Stoddard, 1987; Larson *et al.*, 2009) and predaceous on crustacean zooplankton (Anderson, 1967; Williams, 1980). Large diaptomids like these exert strong effects on the communities of high elevation oligotrophic bodies of water, where food webs are usually simple (Hebert & Hann, 1986; Paul *et al.*, 1995; O'Brien, 2001).

A study by Williams (1976) of the zooplankton in lakes and ponds of the Beartooth Mountains, WY, revealed several distinct communities, each associated with one primary predator and with the distribution of predators determined primarily by physical characteristics of the water body. Planktivorous *Chaoborus americanus* (Johannsen) larvae were found in fishless pothole ponds (*see* Kurek *et al.*, 2010) with soft bottoms and extensive growth of sedges around the margins, and the copepod *Diaptomus shoshone* was found in shallow, hard-bottomed ponds. Fourth instar *C. americanus* fed heavily on *D. shoshone* in soft-bottomed pothole ponds (Williams, 1976, 1980), and *D. shoshone* adults fed on first instar *C. americanus*; consequently, the predators displayed a disjunct distribution (Williams, 1980). *Chaoborus americanus* have been found by others as well to significantly reduce the abundance of diaptomid copepods (MacKay *et al.*, 1990), though less has been reported about reciprocal predation.

Several ponds in the original study were marginal in the physical characteristics of typical *Chaoborus americanus* ponds, and midge larvae occurred in them in some years but not in others (Williams, 1976). To assess the influence of weather on changes in the predatory

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TABLE 1.—Summary of long term sampling of four ponds in the Beartooth Mountains, northwest Wyoming, from 1974 through 2009. Physical characteristics and the presence of *Diaptomus shoshone* (*Ds*) and *Chaoborus americanus* (*Ca*) are shown

| Pond | Elev (m) | Surface area (ha) | Max depth (m) | Latitude | Longitude | Years sampled | Years with | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | *Ca* | *Ds* | Both |
| G2 | 3021 | 0.24 | 0.5 | 44°55′34″E | 109°33′00″N | 31 | 19 | 7 | 5 |
| G3 | 3022 | 0.13 | 0.3 | 44°55′35″E | 109°33′04″N | 32 | 2 | 29 | 1 |
| G5 | 2908 | 0.33 | 0.4 | 44°56′05″E | 109°31′50″N | 30 | 0 | 28 | 2 |
| G6 | 2906 | 0.07 | 0.4 | 44°56′05″E | 109°31′47″N | 29 | 8 | 14 | 7 |

regime, I continued sampling two pairs of ponds for predator shifts over the next 36 y. I expected to find that heavy snowpack would increase water depth and make a pothole pond more suitable for *C. americanus*, which must overwinter as larvae, while low snow pack would decrease water depth and make a marginal pond more likely for dominance by *Diaptomus shoshone*, which overwinter as encysted eggs. Thus, winter weather, a factor external to the community, would determine the form of the predatory regime.

## MATERIALS AND METHODS

Ponds in the Beartooth high lakes district of northwest Wyoming (Table 1) were sampled in mid to late summer from 1974 through 2009. These four ponds occur as pairs in close proximity; one pond of each pair was shallower with a harder bottom, so it could be compared to the other with a softer bottom. All sampling over the 36 y was done using the same procedures and by the same person, so despite the length of time, the techniques were consistent from the first to the last sampling. A few years were missed during this 36 y span, so the number of years actually sampled ranged from 29 to 32, depending on the pond (Table 1). The location of each pond was calculated using Google Earth (Google Earth, 2010), and surface areas were determined from ImageJ (Rasband, 2009) analysis of Google Earth images. In the first years of the study, the depth of each pond was measured on each sampling date directly by meter stick in the deepest area.

The invertebrate predators *Diaptomus shoshone* and *Chaoborus americanus* were sampled with a 15.2 cm diameter conical townet with #20 fine nylon monofilament mesh. Each pond was sampled by making horizontal throws with the net at the end of a calibrated 10 m line and recording the actual length of the tow to the nearest half meter. Generally the samples from three different throws were combined. Occasionally, a pond was too shallow to obtain a quantitative sample, so the net was hauled quickly near the surface to obtain a nonquantitative sample. Samples were preserved by adding 95% ethyl alcohol in the field and then later transferring the contents to 70% ethyl alcohol with glycerin. Numbers of *D. shoshone* and *C. americanus* were counted from each sample under a Nikon SMZ-10 dissecting microscope at 15× magnification. The species were identified in the original study (Williams, 1976) using Wilson & Yeatman (1959) for *D. shoshone* and Johannsen (1934) and Saether (1970) for *C. americanus*.

Because the filtration efficiency of plankton nets (the volume of water actually filtered compared to the calculated volume) depends on the design of the net as well as how it is used (Tranter & Smith, 1968; McQueen & Yan, 1993), the percent efficiency of the net used in this study was determined with a General Oceanics Digital Flowmeter, model 2030, with both R and R6 (low speed) rotors. To determine the net's efficiency, the field sampling techniques were mimicked in an indoor swimming pool by making tows with the meter both inside and outside the net. The counts on the flowmeter recorded from 10 tows inside and 10 outside (comparison of counts from the two locations: $t_{18} = 12.094$, $P < 0.001$) yielded an efficiency of 58.9% (95% CI = 54.8% to 63.1%). All calculated densities of *Diaptomus shoshone* and *Chaoborus americanus* were adjusted accordingly.

Records of snow pack (SNOTEL data as water equivalence) were obtained from the NRCS National Water and Climate Center (NRCS, 2010) for the Beartooth Lake pillow (site 326), which reports data from 1981 on. The study ponds are less than 4 km from this recording station. Statistical analysis was with PASW Statistics 19 (SPSS, 2010), using independent samples *t*-test for comparisons, univariate general linear model (ANOVA) for analysis of the aggregated data, and regression analysis to examine the reciprocal densities of the two predators.

## RESULTS

The original survey (Williams, 1976) showed pond G2 to be intermediate in depth and softness between characteristic soft-bottomed *Chaoborus americanus* and hard-bottomed *Diaptomus shoshone* ponds, and *D. shoshone* and *C. americanus* dominated communities have occurred in this pond as alternative states during the 36 y study period. From 1974 through 1988, *C. americanus* was the only predator in G2, in densities from 0.01–1.41/L; in contrast, *D. shoshone* was abundant from 1989 through 1997, at densities from 0.13–1.07/L, with a single chaoborid found in the samples during these 9 y (Fig. 1). The community switched back to *C. americanus* dominance from 1998 through 2009, with densities up to 1.41/L. However, when *C. americanus* declined in 2002 and 2004 to its lowest abundance, *D. shoshone* reappeared (Fig. 1). Snowpack was not significantly different when comparing the sets of years in which each predator was dominant ($t_{20} = 1.087$, n.s.), but the changes in predatory regime occurred after years of snowpack extremes. The switch to *D. shoshone* occurred after the low snowfall year of 1987 (2.5 cm, the lowest depth recorded on May 15 during 1981–2009), and *D. shoshone* reappeared in the pond after the low snowfall year of 2001 (22.4 cm, the second lowest amount recorded for 1981–2009). The change towards *C. americanus* dominance took place after the heavy snowpack years of 1996 and 1997 (99.6 and 87.6 cm; during the same 1981–2009 period, these were the 2 y with the deepest snow). In comparing extreme conditions, there are too few replicates for statistical analysis, but the differences were dramatic: the lowest snowpack values correlated with a shift to *D. shoshone,* whereas the highest recorded values correlated with the shift to *C. americanus.*

Pond G3 is 56 m away and lies in terrain identical to that of G2, but it is shallower, with a depth usually of only 0.3 m. Pond G3 is a characteristic hard-bottomed pond. *Diaptomus shoshone* was found here in 30 of 32 sampled years, at densities ranging from 0.02–2.40/L; *Chaoborus americanus* appeared only twice (1979 and 1986; Table 1) and at low densities (≤0.03/L). Only two midge larvae were found during their most recent appearance (1986), which was a heavy snowpack year (82.8 cm).

Ponds G5 and G6, the second pair of ponds, are situated 38 m apart and 1.7 km distant from G2 and G3; G6 is a little deeper and has a softer bottom. The hard-bottomed G5 maintained a *Diaptomus shoshone*-dominated community throughout the sampling period, with a few *Chaoborus americanus* present only in 1979 and 1981, which is when *D. shoshone* had low abundance (too shallow to be measured quantitatively). Since 1988 in pond G5, *D. shoshone* densities have been high, to over 4.2/L, and *C. americanus* have been absent.

The slightly greater depth and softer bottom of pond G6 have facilitated the more regular occurrence of *Chaoborus americanus* in this water body. For 14 y, including the low snowpack years of 1987 and 2001, only *Diaptomus shoshone* was present; for 8 y, including the heavy

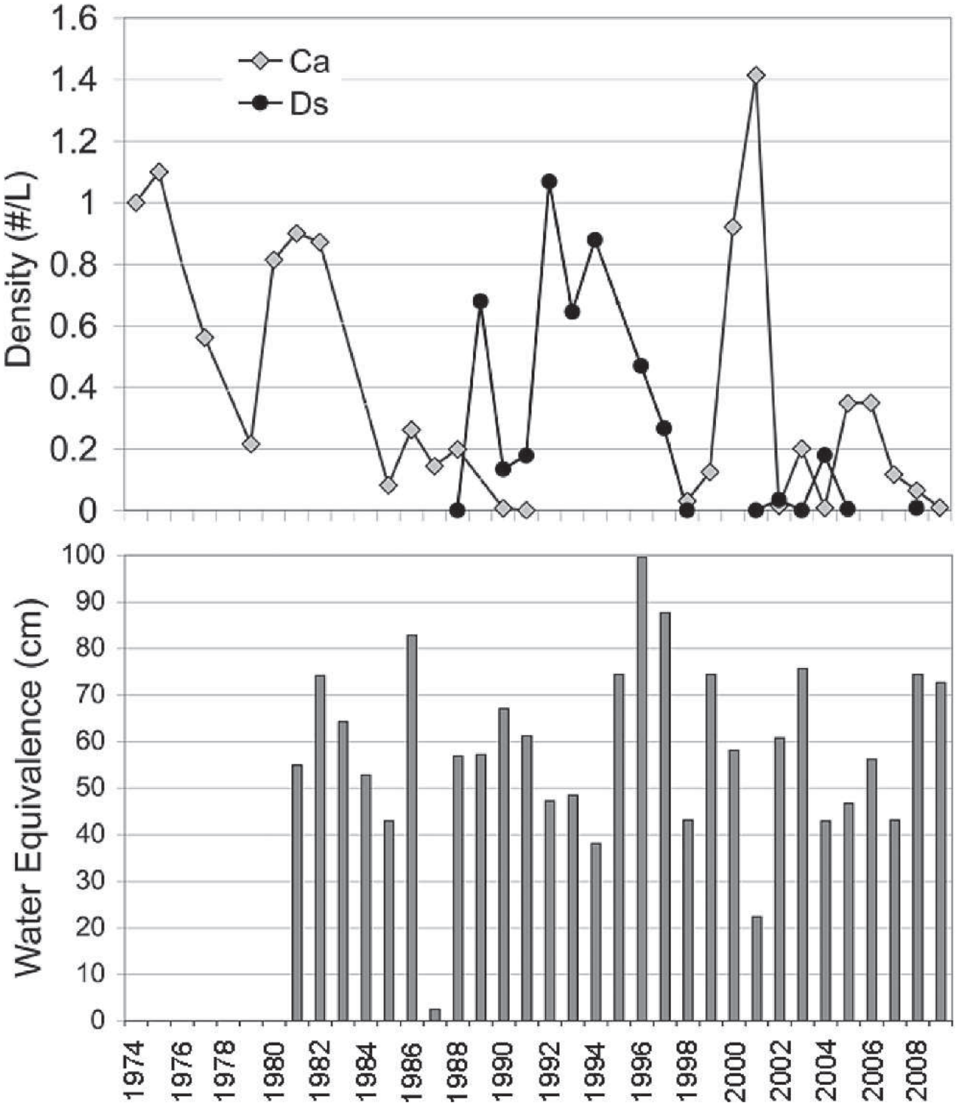


FIG. 1.—(top) Densities of *Chaoborus americanus* (*Ca*) and *Diaptomus shoshone* (*Ds*) in G2 pond; (bottom) snowpack on May 15 each year, shown as water equivalence in cm. *Ds* replaced *Ca* in G2 pond after a dry year (1987); *Ca* replaced *Ds* after 2 wet years (1996, 1997); and *Ds* reappeared after another dry year (2001)

snowpack years of 1996 and 1997, only *C. americanus* was present; and for 7 y, both invertebrate predators occurred together. For those years when *C. americanus* was the only predator, the snowpack on 15 May the previous year averaged 67.0 ± 19.1 cm (n = 8), and for those years when only *D. shoshone* was found, the snowpack on 15 May the previous year averaged 55.1 ± 24.1 cm (n = 14; mean ± SD). The difference in snowpack over these sets of years did not differ statistically ($t_{17} = 0.590$, n.s.). As with pond G2, extreme snowpack values

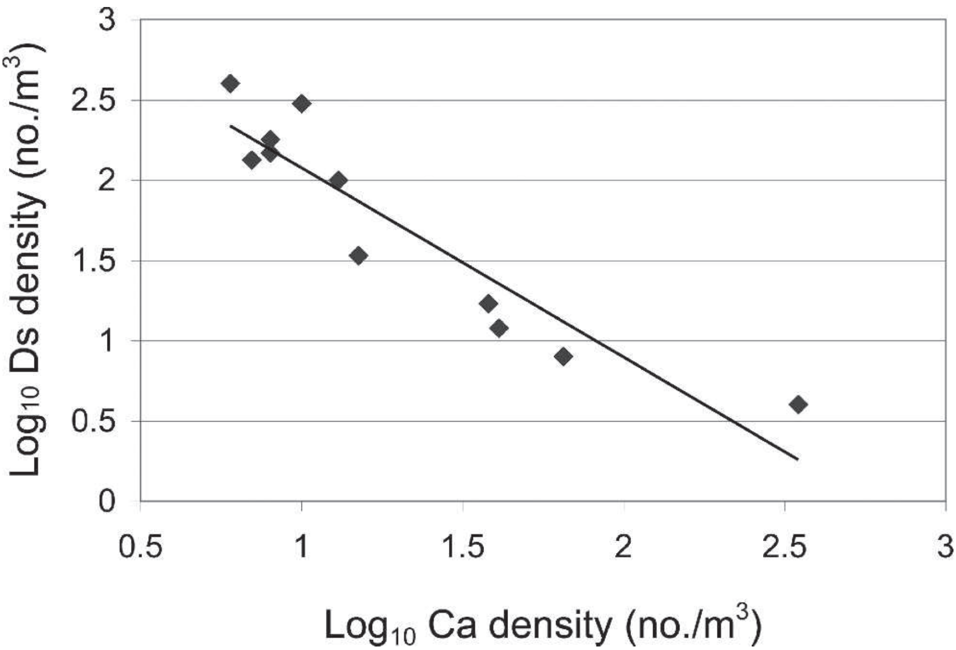


FIG. 2.—Densities of *C. americanus* (*Ca*) and *D. shoshone* (*Ds*) when found together in the same pond, showing reciprocal responses in density. Data from all 11 years in which the species were found together in ponds G2, G3 and G6

correlated with shifts in predator dominance: one year following the extremely low snowpacks of 1987 and 2001, the community shifted to *D. shoshone,* and following the extremely high snowpack years of 1996 and 1997, the community returned to *C. americanus* dominance. The difference in snowpack just missed significance when the data for ponds G2 and G6 were analyzed in aggregate ($F_{1,42} = 2.298$, one-tailed $P = 0.069$).

However, because these two invertebrate predators can eat each other, their densities displayed a reciprocal response. *Chaoborus americanus* densities were lower (0.02 ± 0.02/L) when both species were present than when the midge larvae were alone (0.13 ± 0.12/L); similarly, *Diaptomus shoshone* densities were lower (0.14 ± 0.16/L) when *C. americanus* was present than when it was absent (0.70 ± 0.83/L). Based on all observations when the species were found together from 1974 to 2009 (5 y in each of G2 and G6 ponds and once in G3), a reciprocal response in the logs of their densities was apparent (Fig. 2), with a significant negative correlation ($F_{1,9} = 57.17$, $P < 0.001$).

## DISCUSSION

An early study of high elevation ponds in this mountainous region found that, while bodies of water with inlets and outlets supported fish populations with distinct plankton communities, the pond communities represented two distinct types: those dominated by *Chaoborus americanus* and those characterized by the presence of *Diaptomus shoshone* (Williams, 1976). Because chaoborids must overwinter as larvae, they survive in ponds that retain water year round and have a layer of organic mud at the bottom. Williams (1976) showed that the mud provides a nonfreezing refuge during winter for chaoborid larvae.

These ponds are typically surrounded by a dense growth of sedges. In contrast, any pond that either dries fully by the end of summer or freezes completely to the bottom over winter cannot support overwintering *Chaoborus* larvae. Instead, *D. shoshone,* which overwinters as encysted eggs, are typically found in the plankton communities of these harder bottomed ponds. Encysted eggs can sometimes be found in the pond bottoms when dry (pers. obs.).

The effect of snowpack on predator dominance was most noticeable in pond G2. In average snowpack years, this pond retained enough water to avoid freezing completely or drying up, and in these years *Chaoborus americanus* was the dominant predator and *Diaptomus shoshone* was absent. Following the very low snowpack year of 1987, however, *D. shoshone* appeared. It reappeared again after another dry year (2001), when *C. americanus* density dropped dramatically. As expected, pond G3, close to G2 and shallower with a harder bottom, retained a *D. shoshone* predatory regime throughout the 36 y period. Similar results were found for the other pair of ponds, with the hard-bottomed G5 retaining dominance by *D. shoshone* while the softer-bottomed G6 changed in predatory regime. As with G2, the changes in G6 were associated with extreme snowpack levels. This study gives some evidence that, as hypothesized, weather influenced major shifts in the predatory regime of the invertebrate predators. The strongest result is that the effect was most obvious with extreme snowpack levels. Other effects of weather on pond communities have been documented by George (2000), who found an increase in algal growth with higher temperatures and thus increased zooplankton abundance, and by Drenner *et al.* (2009), who reported that drying in pond communities altered fish predation.

The occasional appearance of *Chaoborus americanus* in the four study ponds shows that flying adults can readily disperse their eggs to different bodies of water. Fourth instars exert stronger feeding pressure on the rest of the pond community than do earlier instars (Williams, 1980; Swift, 1992), so those midge larvae that survive the winter in a pond and then reach the large size of later instars become the most important predators during the following summer. After *C. americanus* has been eliminated from a pond through drying or complete freezing, *Diaptomus shoshone* may become reestablished through wind or water mediated dispersal of eggs or through hatching of diapausing eggs from what is the egg equivalent of a seed bank (Parker *et al.*, 1996). Feeding by *D. shoshone* adults on first instar chaoborids prevents the predatory regime from switching back. The feeding of these two invertebrate predators, *C. americanus* and *D. shoshone,* on each other leads to reciprocity of their densities when they occur together and to their frequently disjunct distribution, as shown here and reported initially in Williams (1980).

Weather is not the only factor that influences these pond communities. The study area is in a national forest (Shoshone N.F.), and late in the summer of some years, grazing sheep brought up to high elevations may contribute to nutrient loading of the drainage area of a pond. Increased nutrients may promote the growth of sedges, which add decaying organic matter and increase the softness of the pond bottom. This change, in turn, could facilitate overwinter survival of *Chaoborus* larvae and potentially alter the predatory regime of a pond community, but no examples were apparent in this study.

Few studies examine predatory effects for a time frame longer than several years (examples are Bell *et al.*, 2003; Findlay *et al.*, 2005), so the evidence presented here about dynamism in predatory regimes of high elevation ponds provides an unusual long term perspective of the effect of weather and the pattern of community responses. These results demonstrate the importance of extreme events, too; average snow depth did not lead to changes in the predators, but the years with the most and least snow did correlate with switching of predatory regimes. Climate change may lead to a long term decline in winter snowpack, so pond communities could shift towards predators and coexisting species that are more tolerant of drying.

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