Larval fish-induced phenotypic plasticity of coexisting *Daphnia*: an enclosure experiment

RANDALL J. BERNOT, WALTER K. DODDS, MICHAEL C. QUIST* AND CHRISTOPHER S. GUY†
Division of Biology, Kansas State University, Manhattan, KS, U.S.A.
*Present address: U.S. Geological Survey-Biological Resources Division, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY, U.S.A.
†Present address: U.S. Geological Survey-Biological Resources Division, Montana Cooperative Fishery Research Unit, Department of Ecology, Montana State University, Bozeman, MT, U.S.A.

SUMMARY

1. The indirect effects of predators on lower trophic levels have been studied without much attention to phenotypically plastic traits of key food web components. Phenotypic plasticity among species creates phenotypic diversity over a changing environmental landscape.
2. We measured the indirect effects of planktivorous larval walleye (*Stizostedion vitreum*) on phytoplankton biomass through their effects on the dominant herbivore species, *Daphnia pulicaria* and *D. mendotae*.
3. Fish had no effect on phytoplankton biomass or overall *Daphnia* density. We observed a compensatory response to predation by functionally comparable species within a trophic level in the form of shifting dominance and coexistence of *Daphnia* species. We hypothesized that this phenotypically plastic response to predation decoupled a potential trophic cascade in this freshwater pelagic system. *Daphnia pulicaria* density decreased over time with fish predation, but *D. mendotae* density increased over time with fish predation.
4. Phenotypically plastic life history trait shifts and reproductive rates differed between species in fishless and fish enclosures, accounting for population trends. *Daphnia pulicaria* were also proportionally higher in walleye larvae stomachs than in the enclosures, indicating that walleye preferred to feed on *D. pulcaria* over *D. mendotae*. The resultant shift in dominance may partially explain the overall benign effect of fish on grazers and supports the hypothesis that trophic level diversity can decouple a trophic cascade.

Keywords: *Daphnia*, life history, phenotypic plasticity, *Stizostedion vitreum*, trophic cascade

Introduction

The ability of a given genotype to respond to distinct environmental conditions, termed phenotypic plasticity, has been studied extensively by evolutionary biologists (Pigliucci, 2001). Phenotypically plastic traits have been documented in practically all major groups of organisms at every trophic level including aquatic taxa of *Daphnia* (Tollrian & Dodson, 1999),

snails (Crowl & Covich, 1990), tadpoles (Relyea, 2001) and mayfly larvae (Peckarsky *et al.*, 2002) among others. Organisms may have plastic behaviours, morphologies, and life histories that reflect trade-offs in the costs and benefits associated with factors such as predation risk (Relyea, 2001), resource acquisition (Tessier, Leibold & Tsao, 2000), or other environmental gradients (Pigliucci, 2001). Recently, the consequences of plastic trait shifts have also become the focus of ecological research (Bernot & Turner, 2001; Werner & Peacor, 2003).

The relative roles of top–down and bottom–up forces in ecological communities depend on the

Correspondence: Randall J. Bernot, Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, U.S.A. E-mail: bernot.1@nd.edu

spatial and temporal scale of study (Brett & Goldman, 1996; Polis & Strong, 1996; Persson, 1999), the productivity of the system (Leibold *et al.*, 1997; Persson *et al.*, 2001) and the system of study (Chase, 2000; Halaj & Wise, 2001; Shurin *et al.*, 2002). A given population may shift in top–down or bottom–up limitation seasonally (Leibold *et al.*, 1997; Schmitz, Hambäck & Beckerman, 2000), annually (Schmitz *et al.*, 2000), or apparently not at all (Polis *et al.*, 2000). From a community ecology standpoint, the indirect effect of predators on resources (i.e. the trophic cascade) extends the concept of top–down control (Carpenter & Kitchell, 1993). Trophic cascades in which predators exert top–down control on prey which in turn influences prey resources, have been illustrated in both aquatic and terrestrial systems (Chase, 2000; Shurin *et al.*, 2002). In aquatic systems, the extent to which predators release resources from herbivore grazing pressure depends in part on the productivity of the system, with the trophic cascade effects weakening as productivity increases (Leibold *et al.*, 1997; Steiner, 2001). Overall, fish may have positive (Carpenter & Kitchell, 1993), negative (McQueen & Post, 1988), or no net effect on phytoplankton (Ramcharan, France & McQueen, 1996). Fish can influence algae directly through nutrient regeneration (Threlkeld, 1987; Vanni & Findlay, 1990) and indirectly through impacts on zooplankton populations (Pace *et al.*, 1999).

While the relative importance of top–down and bottom–up limitation has been debated, the mechanisms by which limitation or trophic cascade decoupling occurs have received far less attention (Persson, 1999). In one example, Leibold *et al.* (1997) linked weakening top–down control of herbivores to inedible algal species. Thus, the response of a given trophic level to environmental changes will depend on diversity within the trophic level and the phenotypic traits of its species (Bernot & Turner, 2001; Duffy, 2002).

Large-bodied grazers such as *Daphnia* species often give way to smaller-bodied grazers such as *Bosmina* later in the spring and summer during temperate lake seasonal succession (Cáceres, 1998). Functionally, *Daphnia* can filter (up to 14 mL water animal L^{-1} day L^{-1}; Kasprzak, Vyhnalek & Straskraba, 1986) food much more rapidly than *Bosmina* (0.5 mL water animal L^{-1} day L^{-1}; Haney, 1973). Additionally, *Daphnia spp.* constitute the majority of zooplank-

ton biomass in most assemblages (Dumont, Van de Velde & Dumont, 1975). Different *Daphnia* species have comparable (within the same order of magnitude) filtering rates and biomass (Hu & Tessier, 1995). Thus, the trophic effects of different *Daphnia* species are similar, making them functionally comparable such that replacement of one species by another should have little trophic effect.

Here, we propose an additional mechanism in potentially weakening the top–down effects of fish on algae that considers the species composition and phenotypically plastic life history traits of herbivores. Specifically, according to trophic cascade theory, increased fish predation on *Daphnia* may lead to population declines, thereby releasing algae from grazing pressure leading to higher algal population densities. We first tested whether zooplanktivorous fish larvae have positive, negative, or no net effect on phytoplankton biomass by adding larval fish to experimental bag enclosures. Then we measured the life history traits of two dominant herbivore (*Daphnia*) species to test the idea that larval fish induce phenotypically plastic trait shifts that can lead to coexistence and a shift in dominance. Using our results, we discuss the role of plastic trait shifts in weakening a potential trophic cascade.

Methods

Enclosure experiment

We performed an enclosure experiment in the shallow water portion of the Milford Supply Lake located below the dam at Milford reservoir in Kansas to test if fish affected zooplankton and algal abundance. Milford Supply Lake is a mesotrophic to eutrophic 41 ha reservoir used primarily as a water source for fish hatchery operations, but is also a recreational fishery (Quist, Guy & Stephen, 2003). We anchored two frames each holding four cylindrical translucent polyethylene plastic bags (1 m diameter, 2 m deep; $N = 8$). Enclosures were held open by plastic rings at the top, middle and bottom of each bag. Enclosures were filled by sinking them on 20 April 2001 during the day, thus enclosing <6.28 m^3 of reservoir water (bags were not filled to the top of the cylinder) with the natural zooplankton and phytoplankton composition. On 21 April, we pulled a 1 m diameter plankton net (500 µm mesh) from the bottom to the

top of each enclosure four times to remove any larval fish (none were found). On 23 April, we collected zooplankton from each enclosure by taking a full water column sample with a plankton net (30 cm diameter, 64 μm mesh). We also took a full water column tow from the lake outside the enclosures to assess the enclosure effects on the zooplankton and algal communities. Samples were fixed in 4% sugar formalin, then preserved in 70% ethanol.

Chlorophyll *a* concentration was used to estimate algal biomass in water samples collected from 0.5 m below the surface of each enclosure and outside the enclosure. Water samples were filtered through a glass fibre filter (Whatman GF/F) and immediately frozen and brought to the laboratory for chlorophyll *a* concentration analysis. To estimate chlorophyll *a*, pigments were extracted for 5 min in 90% ethanol at 78 °C (Sartory & Grobbelaar, 1984). After 24 h of refrigeration, samples were centrifuged and chlorophyll *a* pigment concentration in liquid was estimated using a fluorometric procedure corrected for phaeophytin (Welschmeyer, 1995; Greenberg, Clesceri & Eaton, 1998).

Twenty larval walleye (*Stizostedion vitreum*, 3.18 fish m^{-3}, 8 mm standard length) were stocked into four of the eight enclosures on 23 April after initial zooplankton and chlorophyll samples were taken. Zooplankton and chlorophyll *a* samples were subsequently collected every 2 days until 11 May by taking one full water column sample with a Wisconisn plankton net (30 cm diameter, 64 μm mesh). At the conclusion of the experiment, a 1 m diameter (500 μm mesh) plankton net was pulled from bottom to top of each enclosure eight times to collect the surviving walleye. After collection, walleye were immediately preserved in 4% formalin and transported to the laboratory for stomach content dissection and analysis.

Zooplankton taxa were enumerated in 5 mL subsamples. On four sampling dates (23 April, 25 April, 1 May and 11 May) the lengths of at least 20 individuals of all adult zooplankton taxa were measured. Previously published length–weight relationships were used to calculate the dry biomass of each taxon (Dumont *et al.*, 1975). At least 50 specimens of *D. pulicaria* and *D. mendotae* were counted and measured from the top of the eyespot to the base of the spine. Eggs were counted from at least 50 egg-bearing females of each species. If fewer than 50 egg-bearing

females were found, then all egg-bearing females were included in the analysis. Size at first reproduction (SFR) was estimated by determining the size class in which >50% of the maximum percentage of egg-bearing females was reached (Stibor & Lampert, 1993). Clutch size was estimated by regressing egg number against female body length, and is reported here as a standardised clutch size (not including females producing ephippia) for females 1.3 mm in body length. We also estimated ephippial production as the number of ephippia-producing (EP) females in each sample. While many ephippia were found in samples, resting eggs from each species could not be distinguished.

Population growth rates (*r*; day^{-1}) were calculated from abundance (*N*) on two successive sampling dates (t_1 and t_2):

$$r = \frac{\ln(N_{t2}) - \ln(N_{t1})}{t_2 - t_1} \tag{1}$$

We used the egg ratio method to calculate birth rates (day^{-1}) for each species (Paloheimo, 1974):

$$b = \frac{\ln[(E/N) + 1]}{D} \tag{2}$$

based on the number of eggs per individual (*E/N*) and the temperature-dependent development time, *D*. Birth rates were calculated using both parthenogenic egg and EP females such that egg number for EP individuals was zero. Although each ephippium contains two eggs, they necessarily undergo a diapause stage, and are not included as part of the immediate population. For *D. pulicaria*, development times were calculated using data from Gulbrandsen & Johnsen (1990). Development times of *D. mendotae* were calculated using data from Hall (1964). Death rates, *d*, in each population were estimated using the difference between birth (*b*) and population growth (*r*) rates.

Walleye food habits were determined by removing the digestive tract and examining the contents under both dissecting and compound microscopes. Prey items were identified to lowest taxonomic level possible. Feeding selectivity of walleye was estimated as the electivity index E_i (Ivlev, 1961) from the proportion of food item *i* in the stomach (r_i) and the proportion of this item in the enclosures (p_i) by:

$$E_i = (r_i - p_i)/(r_i + p_i).$$

Statistical analyses

Differences in chlorophyll *a* concentration, *Daphnia pulicaria* and *D. mendotae* density, SFR, eggs per female, ephippial females and birth rates among enclosures before fish were added were analysed with one-way ANOVA ($n = 4$). Fish effects on these variables were analysed with repeated measures ANOVA, as each sampling date was an additional observation of each experimental unit ($n = 9$ sampling dates). We used a Geisser-Greenhouse adjustment (Geisser & Greenhouse, 1958) of the *P*-values for the repeated factors to account for a heterogeneous correlation structure among dates (Zar, 1996).

Results

Total *Daphnia* density, chlorophyll *a* concentration, and SFR, eggs per female, and birth rate of both *D. pulicaria* and *D. mendotae* did not differ in enclosures before fish were added ($F_{1,6} < 3.00$, $P > 0.13$). Chlorophyll *a* concentration ranged from 44.3 to 64.8 µg L^{-1} (mean $= 57.0$ µg L^{-1}, SE $= 2.3$) in fish enclosures, from 49.5 to 76.4 µg L^{-1} (mean $= 62.2$ µg L^{-1}, SE $= 2.9$) in no-fish enclosures, and from 55.3 to 71.2 µg L^{-1} (mean $= 62.1$ µg L^{-1}, SE $= 2.1$) outside of the enclosures. Water temperature rose steadily from 18.8 to 22.1 °C throughout the experiment. The number of *D. pulicaria* ephippial females did not differ before fish were added ($F_{1,6} = 0.36$, $P = 0.57$). No ephippial *D. mendotae* were found either before or after fish were added to enclosures.

Daphnia species together comprised over 80% of the total zooplankton biomass throughout the experiment (Fig. 1). *Daphnia pulicaria* biomass comprised over 70% of the overall zooplankton biomass in enclosures before walleye larvae were stocked (Fig. 1; 23 April) and 2 days after walleye were stocked (Fig. 1; 25 April). *Daphnia mendotae* biomass comprised less than 20% of total zooplankton biomass before fish were stocked and 2 days after fish stocking (Fig. 1). However, 8 days after stocking, *D. mendotae* biomass dominated in fish enclosures and outside enclosures (>72% of total biomass). In enclosures without fish, *D. pulicaria* comprised 47% and *D. mendotae* comprised 45% of the total biomass on 1 May. *Daphnia mendotae* biomass dominated total zooplankton biomass on the last day of the experiment in all treatments (Fig. 1, 11 May).
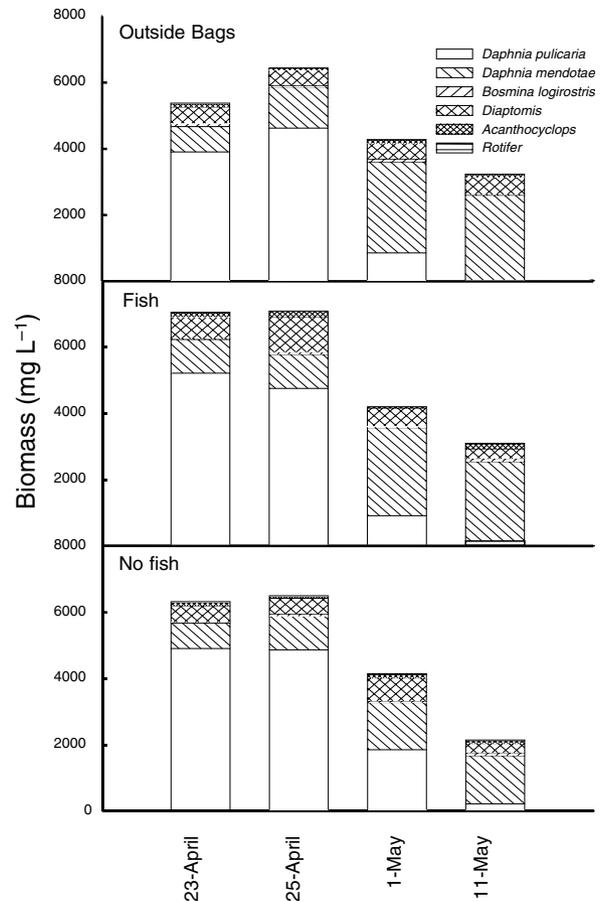

Fig. 1 Biomass of zooplankton taxa, in enclosures with larval walleye (*Stizostedion vitreum*), in enclosures without larval walleye and outside enclosures anchored in Milford Reservoir in 2001.

Fish had no effect on total *Daphnia* density ($F_{1,14} = 1.705$, $P = 0.21$). Total *Daphnia* density declined slightly inside and outside the enclosures (Fig. 2) over the course of the experiment, but this time effect was not significant ($F_{8,112} = 3.00$, $P = 0.10$). *Daphnia pulicaria* density generally declined over time (Fig. 2) with higher densities in enclosures without fish ($F_{1,6} = 24.55$, $P < 0.01$). However, a fish effect on *D. pulicaria* depended on the sampling date (fish × time: $F_{8,48} = 4.58$, $P = 0.02$). Conversely, *D. mendotae* density generally increased over time (Fig. 2) with higher densities in enclosures with fish ($F_{1,6} = 40.65$, $P < 0.01$). The fish effect on *D. mendotae* density also depended on sampling date (fish × time: $F_{8,48} = 14.17$, $P < 0.01$).
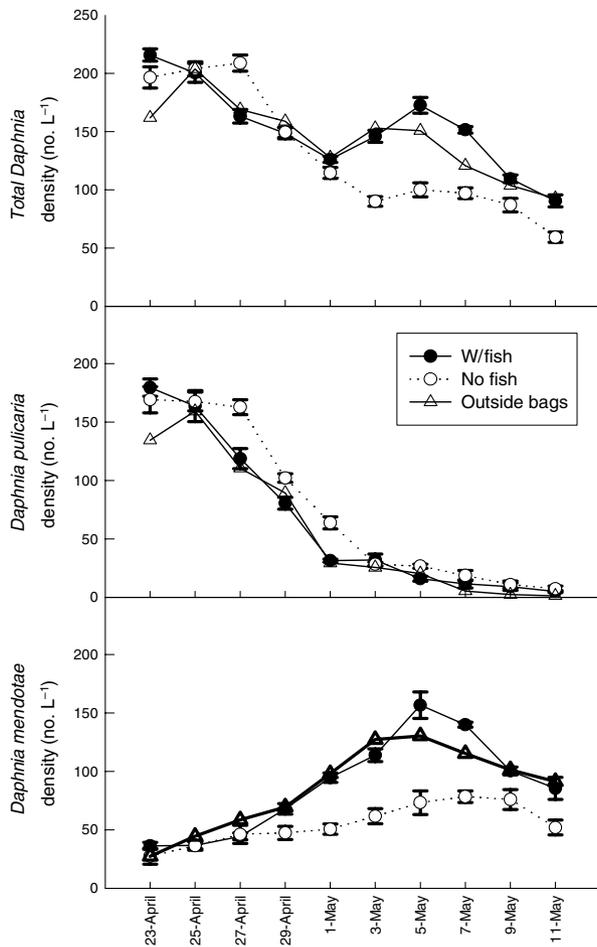
Fig. 2 Total *Daphnia* density, *D. pulicaria* density, and *D. mendotae* density in enclosures with larval walleye (*Stizostedion vitreum*), in enclosures without larval walleye and outside enclosures anchored in Milford Reservoir in 2001. Symbols represent mean value ± 1 SE.

Fig. 3 Size at first reproduction (SFR) of *Daphnia pulicaria* and *D. mendotae* in enclosures with larval walleye (*Stizostedion vitreum*), in enclosures without larval walleye and outside enclosures anchored in Milford Reservoir in 2001. Symbols represent mean value ± 1 SE.

Fish ($F_{1,6} < 4.00$, $P > 0.09$) and sampling date (fish × time: $F_{8,48} < 1.10$, $P > 0.40$) did not affect *D. pulicaria* SFR (Fig. 3) or egg number per female (Fig. 4). *Daphnia mendotae* SFR was smaller in enclosures with fish on the later sampling dates (fish × time: $F_{8,48} = 6.13$, $P < 0.01$; Fig. 4). Eggs per female of *D. mendotae* were higher in enclosures with fish on the later sampling dates (fish × time: $F_{8,48} = 3.11$, $P < 0.01$; Fig. 4). Significantly more *D. pulicaria* ephippial females were sampled on the later sampling dates (time: $F_{8,48} = 144.34$, $P < 0.01$; Fig. 5). More females generally produced ephippia in enclosures with fish (Fig. 5), but this effect was only marginally statistically significant ($F_{1,6} = 5.38$, $P = 0.06$). Birth rates of *D. pulicaria* depended on
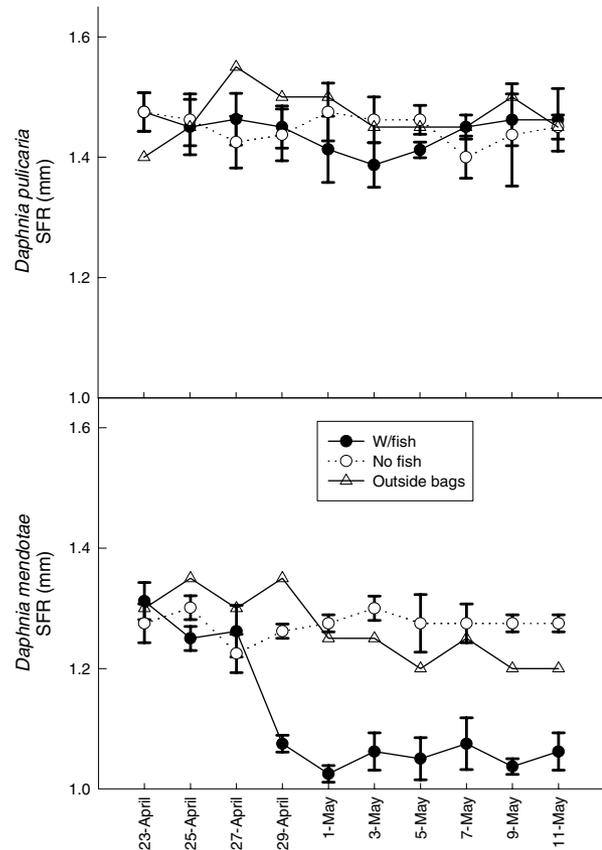
sampling date (time: $F_{8,48} = 270.51$, $P < 0.01$), but were not affected by fish (fish: $F_{1,6} = 0.01$, $P = 0.99$; Fig. 6). Birth rates of *D. mendotae* were higher in fish enclosures (fish: $F_{1,6} = 71.29$, $P < 0.01$), especially on later sampling dates (fish × time: $F_{8,48} = 7.74$, $P < 0.01$; Fig. 6). Death rates of *D. pulicaria* depended on sampling date (time: $F_{8,48} = 7.66$, $P < 0.01$), but were not affected by fish (fish: $F_{1,6} = 0.21$, $P = 0.67$; Fig. 7). Death rates of *D. mendotae* were higher in fish enclosures (fish: $F_{1,6} = 42.20$, $P < 0.01$), especially on later sampling dates (fish time: $F_{8,48} = 5.51$, $P < 0.01$; Fig. 7).

Fish did not affect chlorophyll *a* concentration (fish: $F_{1,6} = 2.91$, $P = 0.14$; fish × time: $F_{8,48} = 0.38$, $P = 0.79$). Larval walleye were recovered from all fish enclosures at the conclusion of the experiment. Three of the enclosures contained four surviving fish
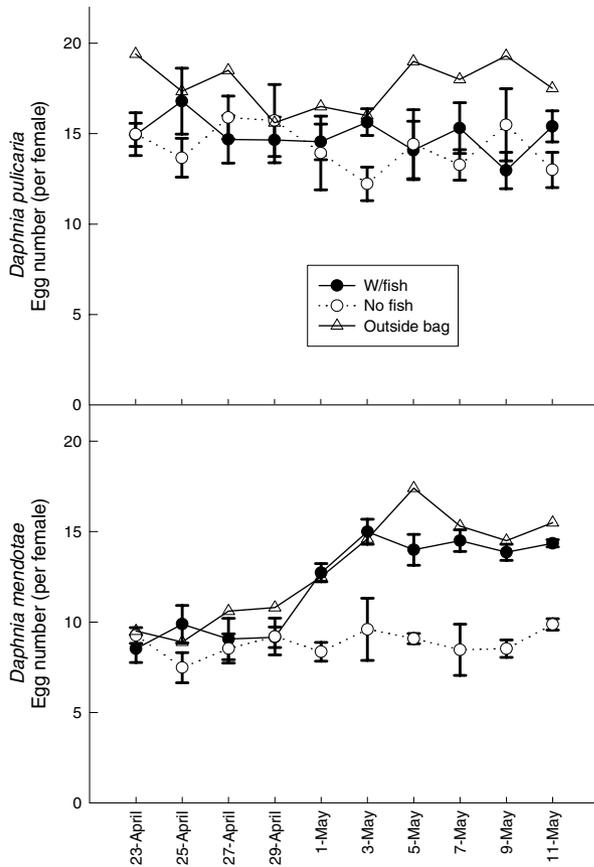
Fig. 4 Egg number per female of *Daphnia pulicaria* and *D. mendotae* in enclosures with larval walleye (*Stizostedion vitreum*), in enclosures without larval walleye and outside enclosures anchored in Milford Reservoir in 2001. Symbols represent mean value ± 1 SE.
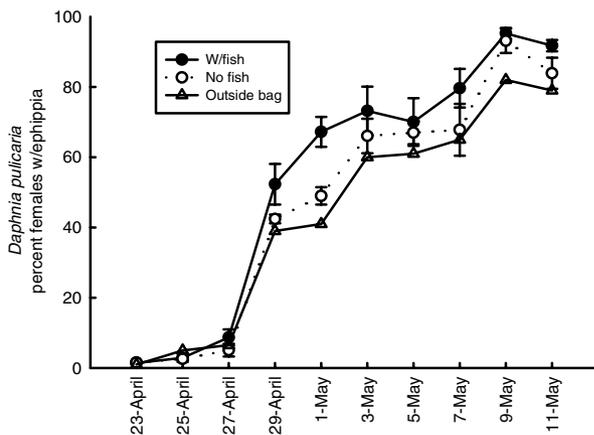

Fig. 5 Percentage of *Daphnia pulicaria* females with ephippia in enclosures with larval walleye (*Stizostedion vitreum*), in enclosures without larval walleye and outside enclosures anchored in Milford Reservoir in 2001. Symbols represent mean value ± 1 SE.

Fig. 6 Birth rates (day^{-1}) of *Daphnia pulicaria* and *D. mendotae* in enclosures with larval walleye (*Stizostedion vitreum*), in enclosures without larval walleye and outside enclosures anchored in Milford Reservoir in 2001. Symbols represent mean value ± 1 SE.
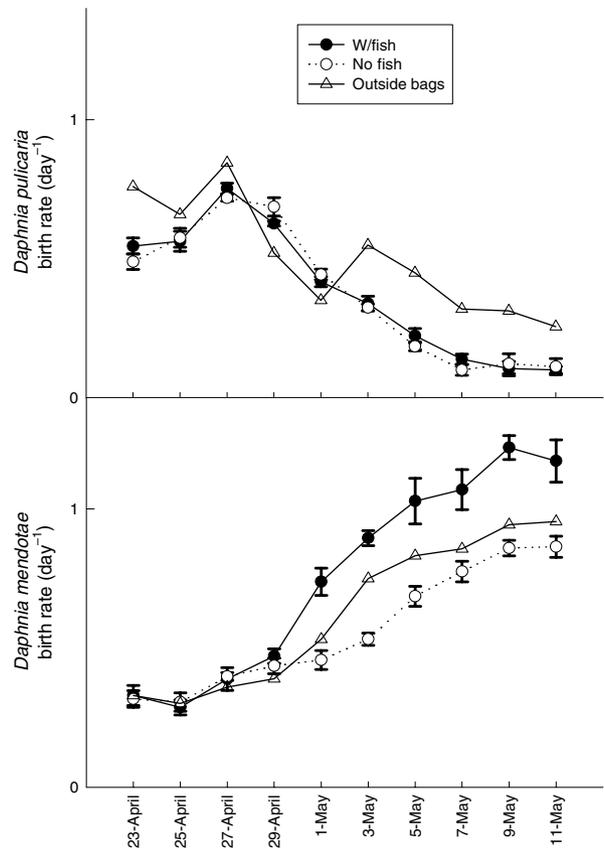
while the remaining enclosure contained seven fish. The main food items of walleye larvae in the enclosures on the final experimental day were *Bosmina longirostris* (32.5% of prey abundance) and copepod nauplii (27.6%), whereas *Daphnia spp.* were eaten in lower proportions (Fig. 8). Walleye strongly preferred *D. pulicaria* (Ivlev's electivity = 0.75), *B. longirostris* (Ivlev's = 0.54), and copepod nauplii (Ivlev's = 0.37). In contrast, *D. mendotae* (Ivlev's = −0.63) and adult copepods (Ivlev's *Diaptomis pallidus* = −0.06; *Acanthocyclops vernalis* = 0.25) were negatively selected or eaten according to their densities in enclosures (Fig. 8). Rotifers were not found in walleye stomachs.

Discussion

Larval walleye had no net effect on phytoplankton biomass over the course of this experiment although
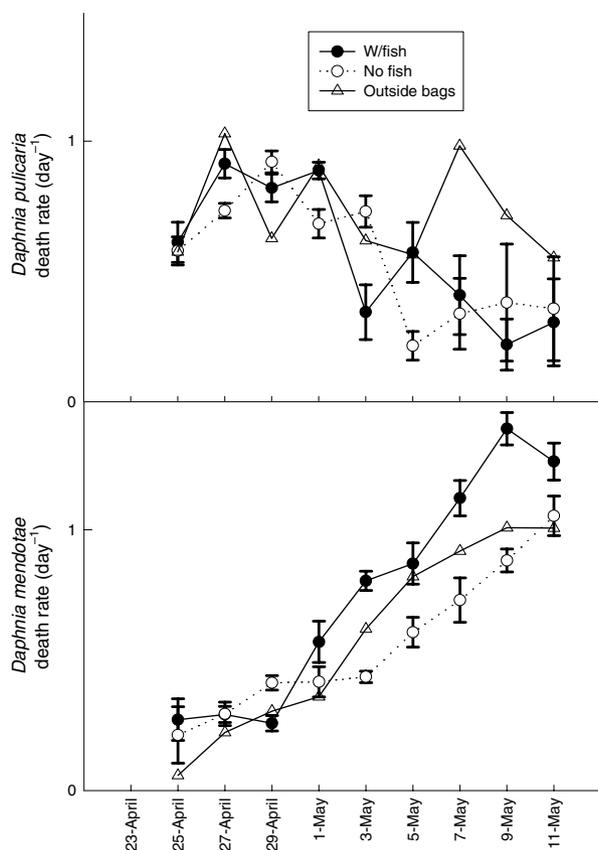
Fig. 7 Death rates (day^{-1}) of *Daphnia pulicaria* and *D. mendotae* in enclosures with larval walleye (*Stizostedion vitreum*), in enclosures without larval walleye and outside enclosures anchored in Milford Reservoir in 2001. Symbols represent mean value ± 1 SE.
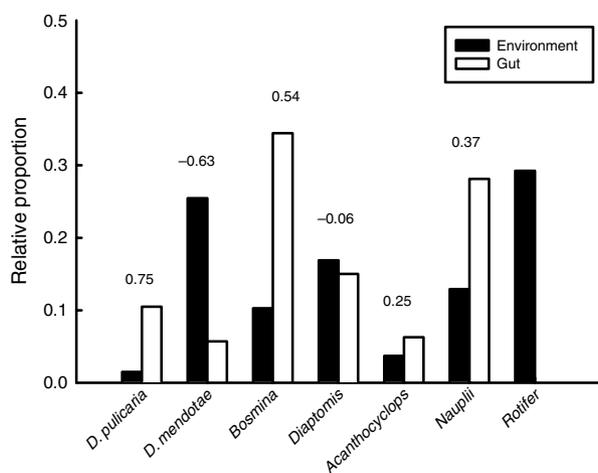

Fig. 8 Relative proportion of the zooplankton taxa observed in the environment and in the stomachs of walleye collected from enclosures anchored in Milford Reservoir in 2001. Numbers above bars are Ivlev's selectivity index values. Note that no rotifers were found in walleye stomachs.

they apparently altered zooplankton community structure. Overall *Daphnia* density declined over time, but was not affected by larval walleye presence. These results suggest that the trophic cascade was decoupled at the fish-zooplankton link and not necessarily the zooplankton–phytoplankton link as shown in a number of previous studies (McQueen & Post, 1988; Brönmark & Weisner, 1996). Whereas omnivory by top or mid-level predators eliminated other trophic cascades (Stein, Devries & Dettmers, 1995; Flecker, 1996; Romare, Bergman & Hansson, 1999), the food web reported here was simplified by having only the general fish–zooplankton–phytoplankton food chain. Moreover, the coexistence and seasonal dominance shift of the *Daphnia* species support the notion of diversity by seasonal replacement within trophic levels having dynamical consequences (Persson, 1999).

Numerous examples of chemically induced phenotypic plasticity have been documented, including dozens of studies with *Daphnia* (Tollrian & Dodson, 1999). In fact, in a companion study to the one presented here, both *D. pulicaria* and *D. mendotae* exhibited phenotypically plastic life history shifts in response to walleye chemical cues and higher water temperature (Bernot, 2003). *Daphnia pulicaria* responded to warmer temperatures by producing ephippia, but did not respond to fish chemical cues (Bernot, 2003). *Daphnia mendotae*, however, produced more eggs at smaller body sizes in the presence of fish cues and at higher water temperatures (Bernot, 2003). Estimates of *Daphnia* SFR, clutch size, and ephippia production in this study (Fig. 4) also indicate that *D. mendotae* exhibited higher clutch sizes and lower SFR in the presence of fish, suggesting phenotypically plastic responses. *Daphnia pulicaria* SFR and clutch size, however, did not differ in the presence and absence of fish, but produced ephippia late in the experiment (Fig. 5). *Daphnia pulicaria* produced ephippia in warmer water temperatures, resulting in a seasonal decline in abundance (Bernot, 2003). Thus, *D. mendotae* exhibited plasticity in response to fish cues, while *D. pulicaria* exhibited plasticity in response to warmer temperatures. The corresponding reproductive rates (Fig. 6) may account for the observed changes in *Daphnia* population sizes even in the absence of substantial direct mortality from fish predation.

Leibold & Tessier (1998) studied a similar system where *D. pulicaria* coexisted with *D. mendotae* because of differential habitat preferences within the water

column. The dominant competitor, *D. pulicaria*, occupied the hypolimnion, whereas *D. mendotae*, the species more susceptible to predation, exhibited diel vertical migration preferring the epilimnion at night and the hypolimnion during the day (Leibold & Tessier, 1991). This trade-off allowed them to coexist and influenced the strength of the trophic cascade (Leibold & Tessier, 1998). In contrast, *Daphnia* did not segregate by depth in our study, but instead coexisted through phenotypically plastic life history shifts (Bernot, 2003) also altering a potential trophic cascade.

The prey items most prevalent in walleye stomachs were *B. longirostris*, *D. pallidus*, copepod nauplii, and *D. pulicaria*. Despite lower densities of *D. pulicaria* than *D. mendotae* in enclosures at the end of the experiment, the data also indicate that walleye elected to feed on *D. pulicaria* (Ivlev's = 0.75) over *D. mendotae* (Ivlev's = −0.63). *D. pulicaria* are larger (1.3–1.6 mm) and have more pigments (Hu & Tessier, 1995) than *D. mendotae* (1.1–1.4 mm) making them more conspicuous to visually foraging fish. The small cladoceran, *Bosmina* (0.5 mm), was the most abundant prey taxon in walleye stomachs and was probably a primary food source throughout the experiment as the walleye were gape-limited until they grew large enough to eat *D. pulicaria* (Graham & Sprules, 1992).

Rotifers were abundant in enclosures, yet none were definitively found in walleye stomachs. This is consistent with previous studies (e.g. Houde, 1967; Graham & Sprules, 1992) in which few, if any, rotifers were collected from larval walleye stomachs. The lack of evidence of rotifers in fish stomachs, however, does not preclude their presence and potential importance as rotifers do not have hard structures and are likely to be digested and assimilated quickly. The potential importance of rotifers to the growth and survival of young fish after coming off of the yolk sac and before their gape is large enough to swallow a *Daphnia* remains unclear.

The initial density of fish used in enclosures (3.18 m^{-3}) was well within natural density estimates (Fox & Flowers, 1990; Qin & Culver, 1992), but lower than other enclosure studies of larval walleye (Qin & Culver, 1992). The final density collected after the experiment (four fish from three enclosures and seven fish from one enclosure) was at worst 20% of the initial density (0.64 m^{-3}), indicating that substantial fish mortality occurred. Thus, overall predation pressure appeared to be low in fish enclosures. The

impact of larval fish on *Daphnia* is a function of *Daphnia* biomass and production, larval fish biomass and time of maximum predation (Post & Kitchell, 1997; Mehner et al., 1998). A critical fish biomass is required before declines in *Daphnia* are observed (Mills & Forney, 1983; Post & McQueen, 1987; Hülsmann & Mehner, 1997). However, the non-lethal effects of fish, such as chemical cue induced trait shifts, may occur at low levels of actual predation. Thus, although fish predation appeared to be low, shifts in life history and demographic rates because of the mere presence of fish led to declines in *D. pulicaria* abundance and increases in *D. mendotae* abundance.

An alternative explanation for shifting dominance between species is a change in algal quality, with *D. mendotae* better able to feed on these algae. However, a concurrent lab experiment in which both species were fed a common algal type (*Scenedesmus acutus*) resulted in similar shifts in life history traits and species dominance because of walleye chemical cues (Bernot, 2003). Thus, while changing algal quality may have played a part in *Daphnia* population trends, phenotypically plastic life history shifts likely played as least as great a role in the observed dominance shift.

Our results provide an interesting example of how phenotypic plasticity might potentially reduce the strength of a trophic cascade. However, our experimental design did not allow us to test this idea conclusively. An additional control treatment that had all species present (including larval walleye), but without *Daphnia* plasticity would be necessary to test the hypothesis that zooplankton plasticity can block a trophic cascade. Another limitation of our study given the highly productive conditions of Milford Reservoir, is that we probably should not expect a modest change in herbivory to have much impact on algal biomass. Larval fish effects on phytoplankton across different levels of productivity would be a useful comparison.

Debates about the relationship between biodiversity and ecosystem function have focused on the number of species within an ecosystem without, until recently, mechanistic understanding (Wardle et al., 2000; Duffy, 2002; Naeem, 2002). Functional redundancy within a trophic level can minimise the effect of species loss within a system (Walker, 1992). However, the extent to which species appear to perform the same function depends on the environmental context (Wellnitz &

Poff, 2001). Additionally, phenotypic variance (both intra- and interspecific) influences the biodiversity-ecosystem relationship (Norberg *et al.*, 2001; Duffy, 2002). The coexistence of *D. pulicaria* and *D. mendotae* may buffer the effects of the loss of one species on herbivore grazing. Importantly, phenotypic variance in life histories between species and within species (via phenotypic plasticity) led to seasonal replacement. The presence or absence of trophic cascades along with top–down or bottom–up forces depends on factors that vary from system to system (Strong, 1992; Carpenter & Kitchell, 1993; Polis & Strong, 1996). Thus, deeper knowledge of species' traits will lead to a better understanding of the nature of trophic cascades and the more complex food webs in which they are embedded.

Acknowledgments

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