Reports

Large effects of consumer offense on ecosystem structure and function

Michael F. Chislock,[1] Orlando Sarnelle,[2] Brianna K. Olsen,[1] Enrique Doster,[1,3] and Alan E. Wilson[1,4]

[1]*Department of Fisheries and Allied Aquacultures, Auburn University, Auburn, Alabama 36849 USA*
[2]*Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824 USA*
[3]*Department of Animal Sciences, Auburn University, Auburn, Alabama 36849 USA*

Abstract. Study of the role of within-species adaptation in ecological dynamics has focused largely on prey adaptations that reduce consumption risk (prey defense). Few, if any, studies have examined how consumer adaptations to overcome prey defenses (consumer offense) affect ecosystem structure and function. We manipulated two sets of genotypes of a planktonic herbivore (*Daphnia pulicaria*) in a highly productive ecosystem with abundant toxic prey (cyanobacteria). The two sets of consumer genotypes varied widely in their tolerance of toxic cyanobacteria in the diet (i.e., sensitive vs. tolerant). We found a large effect of tolerant *D. pulicaria* on phytoplankton biomass and gross primary productivity but no effect of sensitive genotypes, this result stemming from genotype-specific differences in population growth in the presence of toxic prey. The former effect was as large as effects seen in previous *Daphnia* manipulations at similar productivity levels. Thus, we demonstrated that the effect of consumer genotypes with contrasting offensive adaptations was as large as the effect of consumer presence/absence.

Key words: arms race; Daphnia; eco-evolutionary dynamics; harmful algal blooms (HABs); local adaptation; Microcystis; *nutrient enrichment; primary productivity; toxic cyanobacteria; trophic cascades.*

Introduction

Traditionally, ecologists have assumed that adaptive evolutionary change is much slower than ecological dynamics (Thompson 1998). This assumption implies that species traits can be treated as fixed with respect to understanding how species affect community and ecosystem dynamics (Chase and Leibold 2003). The concept of species as packages of more or less fixed traits has been fundamental to ecological research on trophic cascades (Leibold 1989, Brett 1994, Cottingham et al. 2004), biodiversity–ecosystem function (Hooper et al. 2005), and food web analysis (Tilman 1982).

In contrast, accumulating evidence shows considerable malleability in the ecological traits of many species over short time scales (Hairston et al. 1999, Grant and Grant 2002). Much of this evidence comes from the study of phenotypic plasticity (Tollrian and Harvell 1999), but more recently ecologists have begun to appreciate how heritable adaptive traits within a species

can influence community and ecosystem dynamics (Pennisi 2012, Weis and Post 2013). To date, the consequences of intraspecific adaptive variation for trophic interactions have been examined largely from the perspective of prey (both plants and animals) responding to changes in consumption or consumption risk (i.e., prey defense; Rhoades 1985, Karban and Agrawal 2002). In contrast, adaptations by consumers to overcome prey defenses (i.e., consumer offense) are less studied (Sotka and Whalen 2008) and the consequences of consumer adaptations for ecosystem dynamics are relatively unknown. This bias, in part, follows from the "life–dinner" argument: asymmetrical fitness outcomes of consumer–prey encounters should promote stronger selection on prey than on consumers (Dawkins and Krebs 1979). One important exception to this argument, however, is "dangerous" prey that can produce toxins that can harm or even kill consumers (DeMott et al. 1991, Brodie and Brodie 1999, Hansson et al. 2007). The most profitable systems in which to pursue the consequences of consumer offense should be those in which prey can have negative effects on consumer fitness. Thus, we have chosen to investigate the ecosystem-level consequences of adaptation by
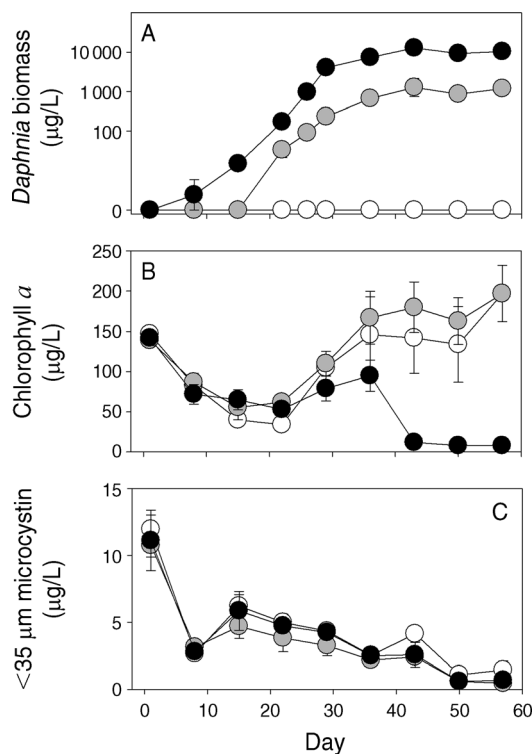
FIG. 1. Dynamics of (A) *Daphnia pulicaria* biomass, (B) chlorophyll *a*, and (C) <35 μm microcystin concentration. Data represent means ± SE. Open symbols denote controls (no *Daphnia*), gray symbols indicate *D. pulicaria* genotypes that are sensitive to toxic cyanobacteria, and black symbols indicate *D. pulicaria* genotypes that are tolerant of toxic cyanobacteria. Note that the *y*-axis of panel A is on a log-scale. ANOVA results are: for *Daphnia* biomass, $F_{2,7} = 313.927$, $P < 0.0001$; for chlorophyll *a*, $F_{2,7} = 32.378$, $P < 0.0001$; and for <35 μm microcystin, $F_{2,7} = 1.640$, $P > 0.250$.

Daphnia pulicaria (see Plate 1), a consumer that adapts to prey that are dangerous (toxic cyanobacteria) (Hairston et al. 1999, Sarnelle and Wilson 2005). *Daphnia* is well known to have dramatic effects on the total biomass and productivity of primary producers (phytoplankton), with effects being larger in more productive systems (Sarnelle 1992, Mazumder 1994). Indeed, the presence of *Daphnia* is essential for a strong trophic cascade in lakes (Carpenter et al. 1985, Leibold 1989).

Currently, the few experiments that have measured the effects of intraspecific variation in consumer traits on ecosystem structure or function have reported effects that are statistically significant but smaller than the effects of species presence/absence (Post et al. 2008, Bassar et al. 2010, Pennisi 2012, Walsh et al. 2012, Weis and Post 2013). In none of these studies, however, was the consumer adaptation offensive in nature. We asked whether the effect of different *D. pulicaria* genotypes having contrasting offensive ability (i.e., tolerant or sensitive to toxic prey; Appendix A, Appendix B: Table B1) was as large as the effect of *D. pulicaria* presence/absence with a field experiment conducted in an

environment with high concentrations of toxic cyanobacteria.

MATERIALS AND METHODS

We assessed the effects of sensitive vs. tolerant *D. pulicaria* genotypes on ecosystem structure and function (phytoplankton biomass and productivity) with a limnocorral experiment. We then conducted smaller-scale experiments to determine whether (1) toxic cyanobacteria were driving the poor performance of sensitive genotypes (cubitainer experiment) and (2) to compare the relative abilities of sensitive and tolerant genotypes to graze on phytoplankton (phytoplankton mortality experiment).

Limnocorral experiment

The experiment was conducted in limnocorrals (3100 L) suspended from a floating PVC frame anchored in an aquaculture pond at Auburn University (Auburn, Alabama, USA). Limnocorrals were filled on 28 August 2012 (day 1) by pumping water from a nearby highly enriched pond through a 75-μm mesh net to exclude any resident large zooplankton, including native *Daphnia*. Three treatments were established in the limnocorrals with four replicates of each: no-*Daphnia* control, sensitive *D. pulicaria*, and tolerant *D. pulicaria*. Two enclosures were damaged at the beginning of the experiment (one control, one tolerant). As a result, there were only three replicates for the no-*Daphnia* control and tolerant *D. pulicaria* treatments.

To start the experiment, we stocked three sensitive or three tolerant *D. pulicaria* genotypes (in approximately equal proportions) into each corresponding limnocorral at very low densities (~0.05 animals/L). A low initial density insured that *Daphnia* populations would have to increase greatly to suppress phytoplankton biomass, as would be the case in any natural system. All enclosures were fertilized approximately biweekly with sodium nitrate ($NaNO_3$) and sodium phosphate (Na_2HPO_4) at a rate of 10% of the ambient total nitrogen (TN) and phosphorus (TP) concentrations (TN ~3500 μg/L, TP ~500 μg/L) to maintain high densities of toxic cyanobacteria. The experiment was terminated after *Daphnia* populations had stabilized (Fig. 1; 24 October 2012).

Depth-integrated water samples for total phytoplankton biomass (as chlorophyll *a*), phytoplankton species composition, microcystin, and macrozooplankton biomass and species composition were collected with a tube sampler (inside diameter = 51 mm, 0.5 m deep) weekly from 30 August 2012 to 24 October 2012 and analyzed using standard limnological protocols (Chislock et al. 2013; Appendix A). We measured diel oxygen flux (measurements made at dawn, dusk, and the following dawn) at the beginning (there were no pretreatment differences; ANOVA $F_{2,7} = 0.192$, $P = 0.829$) and end of the experiment to estimate gross primary productivity (GPP; Wojdak 2005). We used repeated measures

analysis of variance (ANOVA, sampling date is a repeated measure) across all dates except the pretreatment sampling to compare *D. pulicaria* biomass, chlorophyll *a*, and microcystin concentrations for all treatments. We also used ANOVA to compare treatment effects on GPP at the conclusion of the experiment.

Cubitainer experiment

To verify that the relatively poor performance of sensitive *D. pulicaria* genotypes (Fig. 1) was driven by the phytoplankton rather than some other environmental factor, we conducted a small-scale field experiment toward the end of the limnocorral experiment. Juveniles of the same sensitive *D. pulicaria* genotypes were stocked into replicate 5-L cubitainers filled with either unaltered limnocorral water (pond water) or limnocorral water from which all phytoplankton were removed and replaced with a comparable biomass of the highly nutritious phytoplankter, *Ankistrodesmus falcatus* (good food; Appendix A). Microcystin concentrations (<35 μm) for the good food and pond water treatments were ~0.01 and 3.0 μg/L, respectively, at the start of the experiment. Cubitainers were incubated in the pond for 8 days at which point all *D. pulicaria* were counted, measured, and scored for fecundity (Appendix A).

Phytoplankton mortality experiment

We conducted a 24-hour grazing experiment at the end of the limnocorral experiment to compare the abilities of adult sensitive and tolerant *D. pulicaria* genotypes to inflict mortality on the phytoplankton present in the limnocorrals (Appendix A). Three treatments were established in replicate 100-mL glass bottles: no-*Daphnia* control, sensitive *D. pulicaria*, and tolerant *D. pulicaria*. Bottles were incubated for 24 hours in the dark on a plankton wheel in a climate controlled room (25°C), and we used ANOVA to compare treatment effects on chlorophyll *a* at the conclusion of the experiment.

RESULTS

Limnocorral experiment

At the start of the experiment, enclosures contained high levels of toxic cyanobacteria and the cyanobacterial toxin microcystin (Fig. 1C) with the genera *Oscillatoria*, *Microcystis* (see Plate 1), and *Cylindrospermopsis* accounting for >98% of total phytoplankton biomass. All three of these genera are known producers of microcystin (Carmichael 1992). Tolerant *D. pulicaria* increased more rapidly than sensitive genotypes and equilibrated at about 10-fold higher biomass (Tukey's test, $P < 0.0001$; Fig. 1). As a consequence of higher *D. pulicaria* biomass, total phytoplankton biomass (as chlorophyll *a*) during the last three weeks of the experiment was ~95% lower in the tolerant-*Daphnia* treatment than in either the no-*Daphnia* control (Tukey's test, $P < 0.002$) or the sensitive-*Daphnia* treatments ($P < 0.0001$). Phytoplankton biomass in the sensitive-*Daphnia* treatment was not
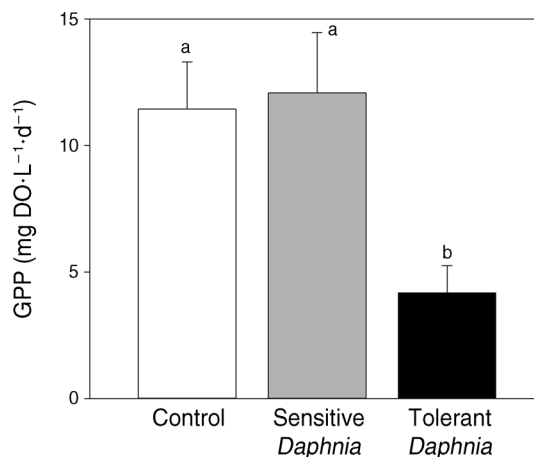

FIG. 2. Gross primary productivity (GPP; mean + SE) at the conclusion of the experiment (day 57). Different lowercase letters indicate significant treatment differences using Tukey's multiple comparisons ($P < 0.05$). ANOVA: $F_{2,7} = 7.407$, $P < 0.02$.

significantly different from controls ($P > 0.500$). By the conclusion of the experiment, tolerant *Daphnia* had suppressed the biomass of all the phytoplankton (Appendix C: Fig. C1) relative to the other two treatments and resulted in a shift in phytoplankton species composition toward cryptophytes and cyanobacteria (Fig. C1). The effect of tolerant *Daphnia* on phytoplankton biomass was as large as effects seen in previous *Daphnia* manipulations at comparable productivity levels (Sarnelle 1992). Thus, the magnitude of the *Daphnia*-genotype effect on primary producer biomass in our experiment was essentially the same as the effect of *Daphnia* presence/absence. The response of gross primary production was analogous to that of primary producer biomass (Fig. 2), although smaller in overall magnitude likely due to higher periphyton growth on limnocorral walls in the tolerant-*Daphnia* treatment (since light penetration was higher).

Cubitainer experiment

Survival and fecundity of sensitive *D. pulicaria* were both much lower in cubitainers containing unaltered limnocorral water relative to the treatment with *Ankistrodesmus* (Fig. 3). Thus, the phytoplankton in the limnocorrals was highly inhibitory to neonates of the sensitive genotypes, which can explain the relatively poor performance of sensitive *D. pulicaria* in the limnocorrals. Sensitive neonates showed extremely poor survival in the small-scale experiment (Fig. 3), yet in the limnocorrals there was some population growth by sensitive genotypes (although much lower than by tolerant genotypes) despite high concentrations of toxic cyanobacteria. This contrast probably stemmed from the fact that the initial inocula in the limnocorrals contained adults, combined with the demonstrated ability of adult *Daphnia* to phenotypically acclimate to
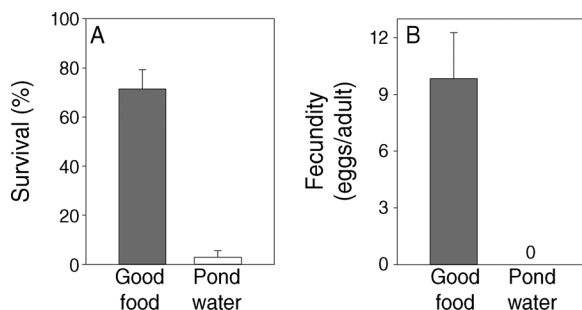
FIG. 3. (A) Survival and (B) fecundity of *Daphnia pulicaria* genotypes sensitive to toxic cyanobacteria in mesocosms containing either pond water or pond water filtered to remove toxic cyanobacteria and replaced with a similar quantity of the nutritious green alga *Ankistrodesmus* (good food). Error bars represent SE. Results of *t* test for survival, $t_{14} = 8.203$, $P < 0.0001$; for fecundity, $t_{14} = 10.820$, $P < 0.0001$. Zero reproduction in the pond-water treatment was a consequence of zero neonates reaching adult size.

toxic cyanobacteria and transfer some degree of tolerance to their offspring (Gustafsson et al. 2005).

Phytoplankton mortality experiment

Interestingly, the inability of sensitive genotypes to suppress phytoplankton biomass in the presence of toxic cyanobacteria (Fig. 1) did not seem to be driven by an inability of adults to graze on the phytoplankton in the limnocorrals. Sensitive and tolerant *D. pulicaria* genotypes inflicted statistically indistinguishable mortality on the phytoplankton as a whole, reducing chlorophyll *a* by >75% (Fig. 4). Thus, the inability of sensitive *Daphnia* to control phytoplankton biomass was probably more the result of poor neonate survival (and perhaps reduced fecundity) leading to reduced population growth, not an inability of individuals to kill toxic phytoplankton. In support of this conclusion, another limnocorral experiment conducted in a productive pond with low levels of toxic cyanobacteria showed no differences in the ability of these same *D. pulicaria* genotypes to increase and greatly suppress phytoplankton biomass (Appendix A; Appendix D: Fig. D1).

DISCUSSION

Our results may help to explain an apparent paradox with respect to phytoplankton responses to fertilization in low-nutrient systems vs. responses to top-down manipulation in high nutrient systems. When released from the predation pressure of zooplanktivores, *Daphnia* typically strongly suppress cyanobacteria-dominated phytoplankton in high nutrient lakes (Lynch and Shapiro 1981, Shapiro and Wright 1984, Vanni 1984, Reinertsen et al. 1990, Sanni and Waervagen 1990, Vanni et al. 1990, Sarnelle 1993). In contrast, *Daphnia* often fail to prevent phytoplankton biomass from increasing when low-nutrient systems are experimentally enriched, with failure attributed to escape from *Daphnia* control by dangerous cyanobacteria (Carpenter et al. 1995, 2001,

Brett and Goldman 1997, Ghadouani et al. 2003). This contrast might be explained by postulating the presence (or absence) of sensitive vs. tolerant *Daphnia* genotypes in low- vs. high- nutrient systems. Enrichment studies (and global change studies, in general) tend to measure short-term responses (Schindler et al. 2008, Carlsson et al. 2009) relative to the time scales of heritable adaptive change (Weider et al. 1997). The long-term responses of ecosystems to eutrophication (a major agent of global change) may depend not only on the presence of particular consumer species (such as *Daphnia*) but also on the evolution of consumer adaptations to overcome prey defenses. The response of primary producers to enrichment has been a major focus in food web research (Rosenzweig 1971, Oksanen et al. 1981, Persson et al. 1988, Leibold 1989, McCauley et al. 1989, Sarnelle 1992, Mazumder 1994) but the role of consumer adaptation in regulating that response remains to be understood.

It has been suggested that intraspecific trait variation be incorporated into studies of species interactions only when that variation has large consequences for communities/ecosystems (Agrawal 2003). In our experiment, the effect of contrasting genotypes of a single species on ecosystem structure and function was of the same magnitude as the effect of presence/absence of that species. Thus, in this system, adaptation can be as important a driver of ecosystem dynamics as species identity. This result has major implications for community and ecosystem ecology since adaptation (particularly by consumers) is usually ignored in studies of food-web interactions. Our results add to accumulating evidence about the importance of adaptation in ecological dynamics and argue for more attention to adaptation in studies of species responses to global change
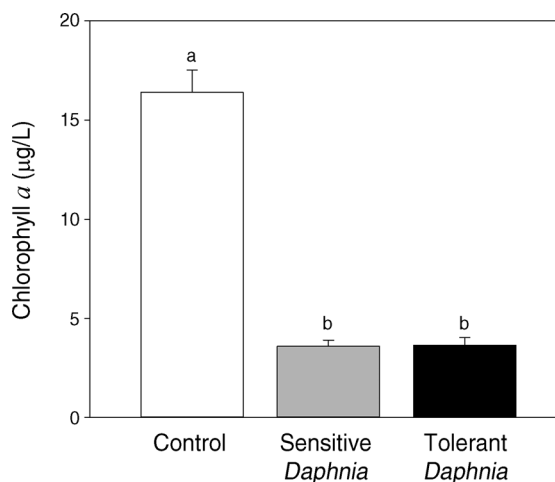

FIG. 4. Chlorophyll *a* concentrations at the conclusion of the lab experiment comparing the ability of high densities (>300 individuals/L) of cyanobacterial-sensitive vs. cyanobacterial-tolerant *Daphnia pulicaria* to kill phytoplankton from the pond. Error bars represent SE. Different lowercase letters indicate significant treatment differences using Tukey's multiple comparisons ($P < 0.05$). ANOVA: $F_{2,18} = 111.580$, $P < 0.0001$.

Tolerant *Daphnia pulicaria*   *Microcystis aeruginosa*   Sensitive *Daphnia pulicaria*
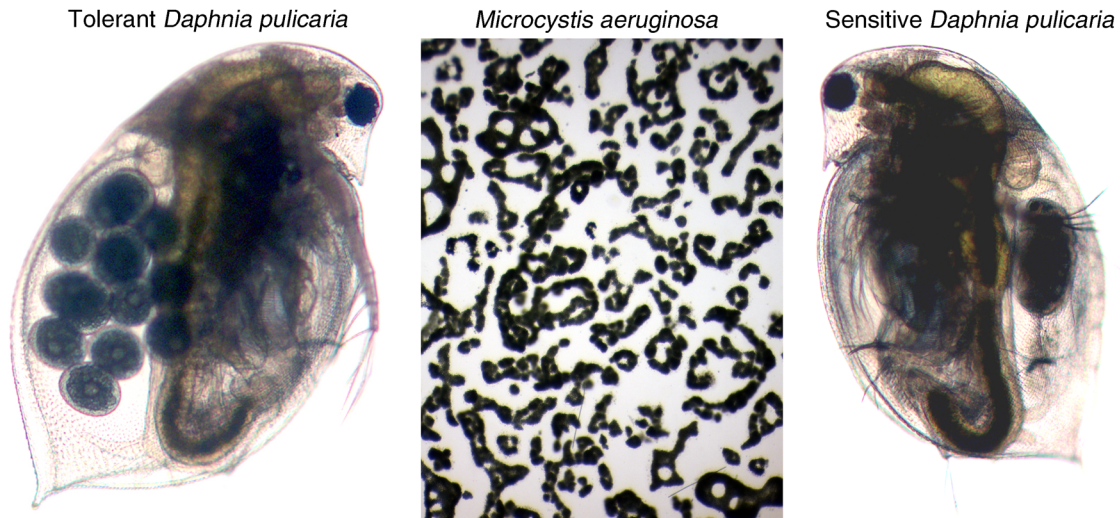

PLATE 1.   *Daphnia* are generalist herbivores that play a powerful role in the structure and function of lake ecosystems. When high levels of toxic cyanobacteria were present (center), the effect of *D. pulicaria* genotypes with contrasting offensive adaptations to toxic prey on phytoplankton biomass and gross primary productivity was as large as the effect of species presence/absence in an experiment using limnocorrals. This result is a direct effect of significantly higher survival and reproduction of cyanobacteria-tolerant (left) vs. cyanobacteria-sensitive *D. pulicaria* genotypes (right) when toxic cyanobacteria are abundant. Photo credits: O. Sarnelle (*Daphnia*); A. E. Wilson (*Microcystis*).

(Hairston et al. 1999, Sarnelle and Wilson 2005, Parmesan 2006, Lohbeck et al. 2012).

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Supplemental Material

Appendix A

Detailed methods (*Ecological Archives* E094-218-A1).

Appendix B

Juvenile survivorship and genetic discrimination using microsatellites for the six *Daphnia pulicaria* genotypes used in the experiments (*Ecological Archives* E094-218-A2).

Appendix C

Phytoplankton biomass and species composition for major taxa at the conclusion of the experiment (*Ecological Archives* E094-218-A3).

Appendix D

Daphnia and chlorophyll data from a related experiment where cyanobacteria and microcystin were lower in abundance (*Ecological Archives* E094-218-A4).