

Predator Group Composition Indirectly Influences Food Web Dynamics through Predator Growth Rates

Kate L. Laskowski,^{1,2,*} Marta M. Alirangues Nuñez,³ Sabine Hilt,³ Mark O. Gessner,⁴ and Thomas Mehner¹

1. Department of Biology and Ecology of Fishes, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany; 2. Department of Evolution and Ecology, University of California, Davis, California 95616; 3. Department of Ecosystem Research, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany; 4. Department of Experimental Limnology, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Alte Fischerhütte 2, 16775 Stechlin, Germany; and Department of Ecology, Berlin Institute of Technology, Ernst-Reuter-Platz 1, 10587 Berlin, Germany

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ABSTRACT: Considerable theoretical work predicts that intraspecific trait variation can have profound ecological consequences by altering species interactions. Because of their high flexibility, behavioral traits may be especially relevant in mediating how species respond to one another, thus affecting food web dynamics and ecosystem functioning. However, empirical evidence supporting this idea is limited. Here, we generated predator groups where we manipulated the composition of behavioral types within the groups to assess effects on predator growth rates, prey communities, basal resources, and ecosystem functioning in replicated outdoor ponds. Using European perch (*Perca fluviatilis*), we created three types of predator populations: two where all individuals expressed either bold or shy phenotypes and one that contained a mix of individuals of the two behavioral types. Bold perch grew faster in mixed populations, indicating that predator growth depends on each individual's behavioral type and that of its group members. However, there was no evidence that the behavioral composition of the perch population directly altered the dynamics of lower trophic levels. Instead, final perch biomass, not behavioral composition, had the strongest influence on lower trophic levels. Thus, the central question may not be whether predator behavior matters at all for trophic dynamics but rather when behavioral effects will predominate over effects of other influences, such as predator biomass variation.

Keywords: animal personality, behavioral type, ecosystem processes, predation, species interactions, trophic cascades.

Introduction

Individual traits ultimately mediate species interactions. Variation among individuals in traits such as sex, age, and

size are well-known modulators of such interactions. Body size, for example, has long been recognized as a critical trait determining the dynamics and structure of food webs (Woodward et al. 2005). However, more labile traits, such as those involved with behavior or physiology, also have the potential to affect interactions among individuals and thus also interactions among species. The relative flexibility in these traits may be especially important in allowing individuals to respond or alter their responses to each other. For example, predator-prey interactions are critical for structuring food webs and the behavior of both predator and prey will determine encounter rates, recognition, and responses to one another (Lima and Dill 1990). It has been argued that the presence of intraspecific trait variation, including in behavioral traits, can have profound consequences on the strength and type of interactions that occur among individuals and species and thus deserves explicit consideration (Bolnick et al. 2011; Violle et al. 2012; Wolf and Weissing 2012; Des Roches et al. 2018). Indeed, individual specializations are well documented within predator populations (Araújo et al. 2011) and can have important consequences for predator-prey interactions by influencing an individual predator's foraging effort (Riechert and Hedrick 1993), prey selection (Estes et al. 2003), and shape of functional response (Toscano and Griffen 2014). Despite this, more labile traits, such as behavioral traits, have traditionally been described and measured primarily at the population level rather than the individual level (Cohen and Stephens 1978; Inouye 2005).

There are many aspects of individual behavior that may influence the outcome of predator-prey interactions. Variation

* Corresponding author. Present address: Department of Evolution and Ecology, University of California, Davis, California 95616; email: klaskowski@ucdavis.edu.

ORCID: Laskowski, <https://orcid.org/0000-0003-1523-9340>.

in individual activity and habitat use (Kobler et al. 2009; Cote et al. 2010), aggression (Winandy and Denoël 2015), or response to risk or novelty (Magnhagen 2006; Wilson and Godin 2009) can influence a predator's likelihood to encounter, recognize, and consume prey. Consistent individual variation in behavior, sometimes called "behavioral types" or "personalities," is now well documented across the animal kingdom (Bell et al. 2009). Such stable behavioral differences among individuals of a predator population can have knock-on effects on lower trophic levels if predator behavior alters the direct consumption of intermediate prey (Schmitz et al. 1997; Trussell et al. 2006) or prey behavior in response to predation risk (i.e., trait-mediated effects; Bolker et al. 2003; Werner and Peacor 2003; Sommer and Schmitz 2020). For example, the behavior of an individual predator has been shown to predict the behavior of the prey that predator consumes (McGhee et al. 2013; Toscano and Griffen 2014). Individual predator behavior can also influence movement and dispersal at larger scales (Fraser et al. 2001; Cote et al. 2010; Chapman et al. 2011) and the use of risky habitats (Griffen et al. 2012), which themselves may differ in resource availability compared with less risky habitats (Houtman and Dill 1998; Hernández and Laundré 2005). Altogether, current evidence suggests that individuals within a given predator population cannot be considered equivalent, as the behavior of an individual predator can alter their foraging decisions (reviewed in Toscano et al. 2016), generating the potential for profound consequences on prey populations, lower trophic levels, and ecosystem functioning.

Prey species rarely experience only a single predator at a time whether predators belong to different species (Turner et al. 1999) or to different behavioral types within a single population (Start and Gilbert 2019). Therefore, the composition of behavioral types within a predator population may also influence the strength and direction of species interactions. There is indeed growing evidence from theoretical analyses that explicit consideration of within-population behavioral variation can alter the outcome of predator-prey interactions (Okuyama 2008), population dynamics (Okuyama 2011), and the coexistence of species (Schreiber et al. 2011; Hart et al. 2016). If "bold" and active individual predators use a large fraction of a given habitat, then these individuals may have especially strong effects on lower trophic levels (Guariento et al. 2014). Recent work claimed that the presence of an active individual predator strengthens trophic cascades in simplified aquatic food webs (Start and Gilbert 2017; but see correction published on article). However, much less is known about the effects of variation in individual predator behavior when multiple individuals with different behavioral types are present in a population. On the one hand, intraspecific variation within a predator population comprising both active and inactive individuals might

be expected to interact with a greater range of prey species, thus depleting whole prey communities more effectively (i.e., "increased degree" [Bolnick et al. 2011]; e.g., as claimed in Royauté and Pruitt [2015], but see the editorial note on this article) and creating stronger trophic cascades. On the other hand, consumption by predators of more and different prey species could result in overall decreased interaction strengths. Additionally, rates of attack as the first step of predation are generally considered as curvilinear (concave) processes, so intraspecific variation in predation rates may instead lower the theoretically expected predation rate through Jensen's inequality, weakening effects on lower trophic levels (Okuyama 2008; Bolnick et al. 2011). It is also unclear how individual predators differing in individual behavior will interact with each other, for example, through aggressive interactions, and what effects this may have on their own success and on lower trophic levels. Empirical work is needed to uncover whether within-population behavioral variation has as strong and universal effects on species interactions as predicted by theory (Okuyama 2008, 2011; Bolnick et al. 2011 and references therein; Schreiber et al. 2011; Guariento et al. 2014; Hart et al. 2016).

In the present study we experimentally tested in a realistic outdoor setting whether and how the composition of behavioral types of a predator population influences trophic cascades and ecosystem functioning. We used a simple aquatic food web with European perch (*Perca fluviatilis*) as the top predator, macroinvertebrate prey as intermediate consumers, and periphyton and leaf litter as basal resources to test whether the composition of behavioral types of predator populations influences (1) predator success as measured by individual growth rates, (2) prey community mass and size distribution, and (3) basal resource dynamics and thus ecosystem functioning. We manipulated the composition of behavioral types within predator populations so that some populations were composed of only individuals characterized as "bold and active," some were composed of only "shy and inactive" individuals, and some were mixed groups where half the individuals were bold and half were shy. If bolder and more active individuals exhibit greater predation rates and these effects are additive, then we predicted that predator populations with all bold individuals would have the strongest effects on lower trophic levels, followed by populations with half as many bold individuals, and predator populations with only shy individuals. Alternatively, if increasing behavioral variation (bold and shy) within a predator population allows the population as a whole to interact with more prey, then we predicted that populations with a mix of bold and shy individuals would exert the strongest pressure on lower trophic levels, with predator populations of only one type of individual (bold or shy) having weaker effects.

Methods

Perch Behavioral Typing

All animal care and experimental protocols complied with local and federal laws and guidelines and were approved by the appropriate governing body in Berlin, Germany, the Landesamt für Gesundheit und Soziales (G-0115/14). We used sink nets in March 2016 to capture 1–2-year-old perch (*Perca fluviatilis*) from Lake Müggelsee, a shallow eutrophic lake at the edge of the city of Berlin. Perch, a common fish in many northern temperate lakes (Mittelbach and Persson 1998), are fairly generalist predators. Their specific diet is largely dependent on their size; small perch eat exclusively zooplankton, graduating to larger invertebrates and eventually fish prey as they grow. The perch used in our experiment were on average 13.1 cm in length (range: 11.2–15.0 cm), meaning that macroinvertebrates would have composed most of their diet (Persson 1983), making them suitable top predators for our simplified aquatic food webs. We immediately anesthetized the fish with 50 mg/L clove oil in a 9:1 ethanol-to-clove-oil emulsion to implant a unique passive integrated transponder in the body cavity for permanent individual identification. This procedure could be completed in less than 1 min, after which the fish were allowed to individually recover in a dark, well-aerated bucket of freshwater until resuming normal swimming activity; all recovered within ~20 min. Fish were then placed in large square holding tanks (350 L with ~15 fish each) that contained several plastic plants for shelter to limit animal stress and acclimated to laboratory conditions for 2 months. During the whole duration of the laboratory acclimation and measurements, the fish were housed in a large walk-in climate chamber maintained at 15°C ($\pm 1^\circ\text{C}$) and a 12L:12D cycle. The fish were fed daily ad lib. with a mixture of thawed frozen bloodworms (chironomid larvae containing hemoglobin) and live chironomid larvae. Fish health and welfare were checked daily; water quality was checked weekly, and water was changed at least weekly by trained personnel. There was no mortality or signs of ill health after the tagging procedure or during the acclimation period.

We measured perch behavior in two standardized assays: one designed to measure baseline activity and the second designed to measure response to risk (“boldness”). We had 24 observation arenas available (37-L glass aquariums) and kept a single perch in each, which allowed us to measure the behavior of 24 individual perch in 1 day. The arenas contained gravel and two plastic plants and were covered in opaque cloth to limit disturbance of the fish. We used overhead webcams (Logitech HD Pro C920) to observe each individual. Fish acclimated in the observation arenas for 2 days and were not fed for 24 h before the start of observations to standardize hunger levels.

Each arena had a grid drawn on the bottom to divide the tank into six equally sized sections. We counted the number of sections crossed by the fish in 10 min as our measure of baseline activity. Subsequently, a small number (7–10) of thawed bloodworms were added to the center of the arena. Once the fish started foraging (which they all did), we dropped a weight suspended above the tank into the water. This universally elicited a response from the fish where they stopped swimming and hid under the plastic plants. We then measured the time (s) until the fish resumed swimming, up to 20 min, as our measure of response to risk. One cohort of 24 fish was observed per day; observations were performed in a random order. In total we observed five cohorts of 24 fish, though camera malfunctions prevented us from collecting data on five fish, resulting in behavioral observations on a total of 115 individuals.

We previously assessed the repeatability of perch behavior using a separate cohort of 38 perch from the same population that was used for other pilot experiments. These fish were observed three times over the course of a week in the same assays described above (1 day in between observations). Repeatability of both activity and latency to resume swimming was high (activity $R: 0.59, P < .001$; latency $R: 0.62, P < .001$; see table S1; tables S1–S11 are available online), and these behaviors were strongly negatively correlated with each other (Spearman correlation between individual average behavior = $-0.78, P < .001$; table S1). Previous work has demonstrated that perch also maintain individual differences in behavior over the course of a year in the wild (Nakayama et al. 2016) and across social contexts (Magnhagen and Staffan 2005; Magnhagen and Bunnefeld 2009). Thus, we are confident that our single observations of individual perch in the present study accurately captured each individual’s behavioral type while enabling us to observe the necessary number of fish within an appropriate time frame before placing the perch in outdoor ponds (see below). Perch behavior could not be determined at the end of the experiment, as we needed stomach contents (see below), which must be collected immediately after catching the fish to prevent continued prey digestion and was a lethal sampling.

Experimental Design

We used six experimental outdoor ponds located at the Leibniz Institute of Freshwater Ecology and Inland Fisheries in Berlin, Germany (fig. S1; figs. S1–S7 are available online). Each rectangular pond measured 12 m \times 5 m, with the sides uniformly sloping down to a depth of 1.5 m. The bottom and sloping sides of each pond were covered in open-cell cement pavers. To limit potentially confounding effects of among-pond habitat variability, we split each pond into four quadrats using 1-cm wire fencing to create

replicate quadrats but prevent perch from moving among quadrats. The fencing excluded the areas directly next to the inflow and outflow pipes to ensure no fish escaped. We floated a 100 × 60-cm foam board in each quadrat and placed four black plastic artificial plants underneath to act as refuge for perch and allow for habitat choice (which may influence foraging).

On the basis of their behavior in the laboratory assays, perch were split into replicate populations, each consisting of six individuals. The perch within each population consisted of individuals characterized as either all shy/inactive behavioral types (“shy” predator treatment) or all bold/active behavioral types (“bold” predator treatment) or a mix of both (three individuals each; “mixed” predator treatment). Thus, four predator treatments (bold, shy, mixed, and no-predator control) were randomly assigned to the four quadrats within each pond, resulting in a randomized block design with a replication level of six ($N = 108$ fish; seven fish that had been assigned to behavioral types were not used in the pond experiment). Before we placed them in the ponds, the fish were individually weighed to the nearest 0.1 g (wet mass) while keeping them in a bucket of water to avoid the need for anesthesia. The total fish body mass per quadrat was 181 ± 17 g (mean \pm SD), corresponding to an average fish biomass of 15–20 g/m², mimicking fish biomass found in highly productive lakes (Downing and Plante 1993) and ensuring that invertebrates in each quadrat experienced sufficient predation pressure to detect any existing effects of predator behavior.

Ponds were operated as flow-through systems in which water from the adjacent Lake Müggelsee (for water quality details, see Shatwell and Köhler 2019) was continuously pumped through a filter to remove large debris before entering the ponds. The ponds had been drained and fallen dry for ~1 year before starting the experiment. Two weeks before the start, we flooded the ponds to a depth of 1 m and added to each one 300 g fresh mass of benthic macroinvertebrates that had been collected from Lake Müggelsee and its tributaries. More than 90% of the total added biomass were gammarids (*Gammarus* and *Dikerogammarus* spp.). After adding the fish on June 1, 2016, we placed a basket with a 1-mm mesh under the inflow pipe of the ponds to prevent any additional large invertebrates from entering.

Assessment of Food Web Responses

We assessed responses to the different predator treatments across three trophic levels over the course of 6 weeks, a time frame similar to that of previous studies on trophic cascades in aquatic systems (e.g., Power 1990; Start and Gilbert 2017). At the predator level, we measured the relative gain in body mass of individual perch to estimate predator

growth. On the final sampling point after 6 weeks, we used nets to capture all of the perch and weighed them to the nearest 0.1 g (wet mass). Fish were then humanely euthanized by concussion as approved by the authorities. We then dissected the fish stomachs to analyze their contents and thus assess whether and how individual behavior may relate to foraging preferences. Whole stomachs were stored in 95% ethanol until sorting and identifying the ingested invertebrates. Using a dissecting microscope, we identified all extracted specimens larger than 1 mm to the lowest possible taxonomic level, which was typically family (Chironomidae, Gammaridae, Baetidae) or genus (*Gyrinus*, *Planorbis*, *Physa*, *Bithynia*). We recorded counts of each invertebrate taxon in each stomach but refrained from sizing them, as most were partially fragmented (Baker et al. 2014). Identification was performed blind to predator treatment and behavioral type.

To assess effects on invertebrate prey as well as on basal resources and ecosystem functioning, we determined the macroinvertebrate colonization of standard batches of leaf litter, as well as litter dry mass remaining, total periphyton dry mass, periphytic algal biomass as chlorophyll *a*, and the composition of macroinvertebrates associated with periphyton at three time points. We used two different plant species to assess leaf litter decomposition. Oak (*Quercus robur*) leaves tend to decompose slowly, whereas ash (*Fraxinus excelsior*) leaves decompose very quickly (Gessner and Chauvet 1994). We collected freshly fallen leaves of these species in a forested landscape 80 km north of Berlin, air-dried them, weighed batches of 3.0 ± 0.1 g, and placed them into litter bags (15 cm × 20 cm) made of 1-cm plastic mesh to allow macroinvertebrates access to the leaves. Six litter bags, three with oak litter and three with ash litter, were placed on the bottom of each of the quadrats the day before adding the predators to the ponds; these litter bags served both to determine rates of leaf litter decomposition and to sample invertebrate communities. We also added three polypropylene strips (100 mm × 22 mm × 0.3 mm; Ibico PolyClearView) to each quadrat, which is an established method to quantify total periphyton mass and algal biomass (Brothers et al. 2014; Kazanjian et al. 2018). The strips had previously been placed in Lake Müggelsee for 2 weeks to ensure colonization by periphyton (Roberts et al. 2003). In the lake, the strips were exposed at 50 cm below the water surface, suspended from a horizontal metal rod. In the ponds, the strips were also suspended from a horizontal metal rod but positioned at 10 cm above the bottom, corresponding to a water depth of 0.9 m.

Every 2 weeks for a total of three sampling dates we removed from each quadrat one periphyton strip and two litter bags, one each of oak and ash. We removed the leaves from each bag directly in the field and gently cleaned them individually of all invertebrates using distilled water. The

leaves were frozen and later freeze-dried to determine litter dry mass remaining. All invertebrates from a single quadrat were pooled and preserved in 95% ethanol for later identification. Specimens larger than 1 mm were identified to the lowest possible taxon (generally family or genus as above) under a dissecting microscope and sized to the nearest millimeter using an ocular micrometer. Identification was performed blind to predator treatment.

The retrieved periphyton strips were placed for 60 s into 50-mL Falcon tubes (Orange Scientific, Braine-l'Alleud, Belgium) containing 50 mL of carbonated water to remove macroinvertebrate grazers, which were preserved in 95% ethanol for subsequent counting. The samples were then transferred to a second 50-mL Falcon tube with 5 mL of filtered pond water to prevent drying. These samples were stored in a cooling box for transport to the laboratory, where periphyton was scrubbed from the polypropylene strips using a brush and filtered pond water. We homogenized each sample by manually stirring with a glass rod, and a 5-mL subsample was then filtered onto a pre-weighed 25-mm GF/F filter (Whatman, Maidstone, UK) and dried at 105°C to determine periphyton dry mass (Balance BP 210 D, Sartorius AG, Göttingen, Germany). To determine algal biomass in the periphyton, we measured the total chlorophyll *a* content in each sample. To this end, another 5-mL subsample was filtered onto a 25-mm GF/F filter and frozen at -80°C until high-performance liquid chromatography analysis as described in Woitke et al. (1994).

Data Analysis

We investigated how individual predator success, measured as growth rate, was influenced by both its own behavioral type and the treatment group it was placed in. For this, we used a linear mixed model with predator growth (measured as percentage of mass increase from the initial body mass) as the response and tested for the interaction between individual behavioral type (bold vs. shy) and predator treatment type, which we coded as either single (bold or shy predator treatments) or mixed (mixed predator treatment) for this analysis. This allowed us to test for the interaction between behavioral type and the type of predator population the animal was in (i.e., bold perch were never present in shy predator populations). We additionally included the random effects of pond and quadrat nested within pond.

We then investigated how predator treatment influenced lower trophic levels. We generated normalized size spectra to characterize body size distributions (Vidondo et al. 1997; Kerr and Dickie 2001) of the macroinvertebrate communities collected from the litter bags at each sampling date in each pond quadrat. Size spectra are useful

to characterize communities, since body size is a key trait affecting the structure and dynamics of food webs (Woodward et al. 2005). First, we used published length–dry mass relationships at the family or genus level (Calow 1975; Benke et al. 1999) to calculate macroinvertebrate biomass. Total biomass was binned into 12 \log_2 size classes from $\log_2(-6)$ (from 2^{-6} to 2^{-5} mg = 7.81×10^{-3} to 3.13×10^{-2} mg) to $\log_2(5)$ (16–32 mg). The biomass in each bin was then divided by the size range of the bin to estimate the normalized biomass in each bin. The resulting relationship between size class and normalized biomass within a given size class can be described by a line where the slope informs about the size distribution of the community. Shallow slopes have more large animals, often representing higher trophic levels, whereas steep slopes characterize communities with a predominance of small animals, presumably belonging to low trophic levels.

We used linear mixed models to test for differences in the body size spectra of invertebrates, with normalized biomasses as the response variable and the \log_2 size classes, predator treatment, and sampling date included as fixed effects. Our main hypothesis was tested by including an overall three-way interaction among size class \times predator treatment \times sampling date, the significance of which would indicate that the prey community composition varied in the different treatments over time. We included an additional fixed effect of sun exposure (high vs. low), as the ponds were located near a tree line where half of the quadrats in each pond received less sun in the afternoon (assignment of predator treatments was balanced across sun level). Quadrats were nested within ponds as random effects to account for the experimental block design and repeated measurements. We also graphed each body size spectrum according to sampling date (see “Results”) to help with data visualization and ran another set of linear mixed models to investigate differences in size spectra within each sampling date separately. We included size class, predator treatment (and their interaction), and sun exposure in each model; pond identity was included as a random effect.

We further investigated potential effects of predator treatment on the invertebrate community composition in terms of taxonomic identity and functional feeding groups. We did this first by using permutational multivariate ANOVA (PERMANOVA) to test whether total biomasses of the different taxa (Chironomidae, Gammaridae, Baetidae, Ostracoda, *Gyrinus*, *Planorbis*, *Physa*, *Bithynia*) or functional feeding groups (scrapers, collector gatherers, shredders, predators) differed among the four predator treatments. We also tested, again with linear mixed models, whether the total invertebrate, gammarid, or chironomid biomass was affected by predator treatment and sampling date, with pond and quadrats (nested within ponds) treated as random effects. All biomass values were \log_{10} transformed to meet model

assumptions of normality and variance homogeneity of the residuals.

At the basal resource level, we also used linear mixed models to test for differences among predator treatments in leaf litter mass, periphyton mass (g/m^2), algal biomass (percentage of chlorophyll *a* in periphyton dry mass), and the number of macroinvertebrate scrapers on periphyton strips. Leaf dry mass remaining (oak and ash; data on ash were square root transformed to meet model assumptions), total periphyton dry mass, algal biomass, and the numbers of chironomids and snails were used as response variables. We included predator treatment, sampling date, the interaction of both, and sun exposure as fixed effects, and pond and quadrat (nested within pond) were included as random effects.

To assess whether the food web configuration was as expected, we tested whether biomass at the end of the experiment at a higher trophic level affected biomass at the next-lower trophic level. Thus, we tested whether final perch biomass in each quadrat affected total invertebrate biomass (\log_{10} transformed) and then whether final invertebrate biomass (\log_{10} transformed) affected oak litter mass (square root transformed), ash litter mass, periphyton dry mass, and algal biomass. Predator treatment and pond identity were included as fixed and random effects, respectively, in all models.

All linear models were run using the lme4 package (Bates et al. 2015) in R (ver. 3.6.0; R Development Core Team 2017), assuming a Gaussian error distribution as confirmed by visual inspection of residual plots (fitted values vs. residuals, residuals vs. predictors, quantile-quantile plots, etc.). We assessed the significance of the fixed effects using log likelihood ratio (LLR) tests where we compared the log likelihood of models with and without the effect of interest. Within each sampling date, we used Tukey's post hoc tests to determine differences among treatments. We additionally estimated marginal and conditional R^2 values for each model using the MuMIn package (Barton 2018); marginal R^2 values estimate the total variance explained by the fixed effects, whereas conditional R^2 estimates the total variance explained by the fixed and random effects combined. PERMANOVAs were run using the adonis function in the vegan package with 1,000 permutations (Oksanen et al. 2019).

Results

We confirmed in a separate cohort of perch from the same population that both baseline activity ($R = 0.59$, $P < .001$) and latency to resume swimming ($R = 0.62$, $P < .001$) are highly repeatable (table S1). In our experimental fish released in the ponds, the single measurements of baseline activity and latency to resume swimming after a dis-

turbance were significantly negatively correlated (Spearman $R_s = -0.55$, $P < .001$), supporting our classification of perch as either bold/active or shy/inactive. We classified fish as shy if they had a latency to resume swimming of greater than 20 min and crossed fewer than 20 sections in the activity assay (fig. S2), whereas fish considered bold resumed swimming in less than 20 min. There was no difference in body mass between bold and shy fish at the start of the experiment ($t_{106} = -0.74$, $P = .46$; fig. S3).

Trophic interactions occurring within ponds were as expected (fig. 1). Specifically, we found evidence that perch consumed invertebrates, as the final perch mass within quadrats was negatively related to the total mass of macroinvertebrates at the final sampling (estimate of perch mass in grams on \log_{10} invertebrate mass in milligrams; slope = -0.006 , LLR = 5.39, $P = .02$, $R_m^2 = 0.27$, $R_c^2 = 0.37$; fig. 1a). The final macroinvertebrate mass tended to be positively related to periphyton dry mass (slope = 23.4, LLR = 3.68, $P = .054$, $R_m^2 = 0.19$, $R_c^2 = 0.27$) and negatively related to the dry mass remaining of ash leaves (slope = -0.19 , LLR = 3.77, $P = .052$, $R_m^2 = 0.20$, $R_c^2 = 0.50$; fig. 1b, 1c). However, there was no indication that macroinvertebrate mass was related to oak leaf dry mass remaining (slope = 0.009, LLR = 0.02, $P = .90$; fig. 1d).

Contrary to our predictions, we did not find consistent evidence that the behavioral composition of the predator treatments affected lower trophic levels or ecosystem functioning. At the prey level, there was no evidence for a three-way interaction between invertebrate size class, predator behavioral composition, and date (LLR = 6.63, $P = .35$). When the data were analyzed separately for each sampling date, control quadrats without perch tended to exhibit size spectra with shallower slopes as expected, indicating higher invertebrate biomass in larger size ranges (fig. 2). There was evidence for an interaction between predator behavioral composition and size class after 4 and 6 weeks, indicating differences in slopes among the treatments (4 weeks: size class \times treatment LLR = 11.5, $P < .01$; 6 weeks: size class \times treatment LLR = 22.6, $P < .001$; for full model results, see table S2). However, these differences were not consistent over time: after 4 weeks, quadrats with bold predators showed the steepest decline in large invertebrate size classes, whereas at 6 weeks, quadrats with mixed and shy predators had the steepest declines (fig. 2). Similarly, PERMANOVA revealed that while control quadrats were often different from the quadrats that contained perch, there were no differences among predator treatments in the biomass of any invertebrate taxon (fig. S4; tables S3, S4) or functional feeding group (fig. S4; tables S5, S6). We also found no differences in total invertebrate, chironomid, or gammarid biomass in response to the predator treatments (table S7; fig. S5).

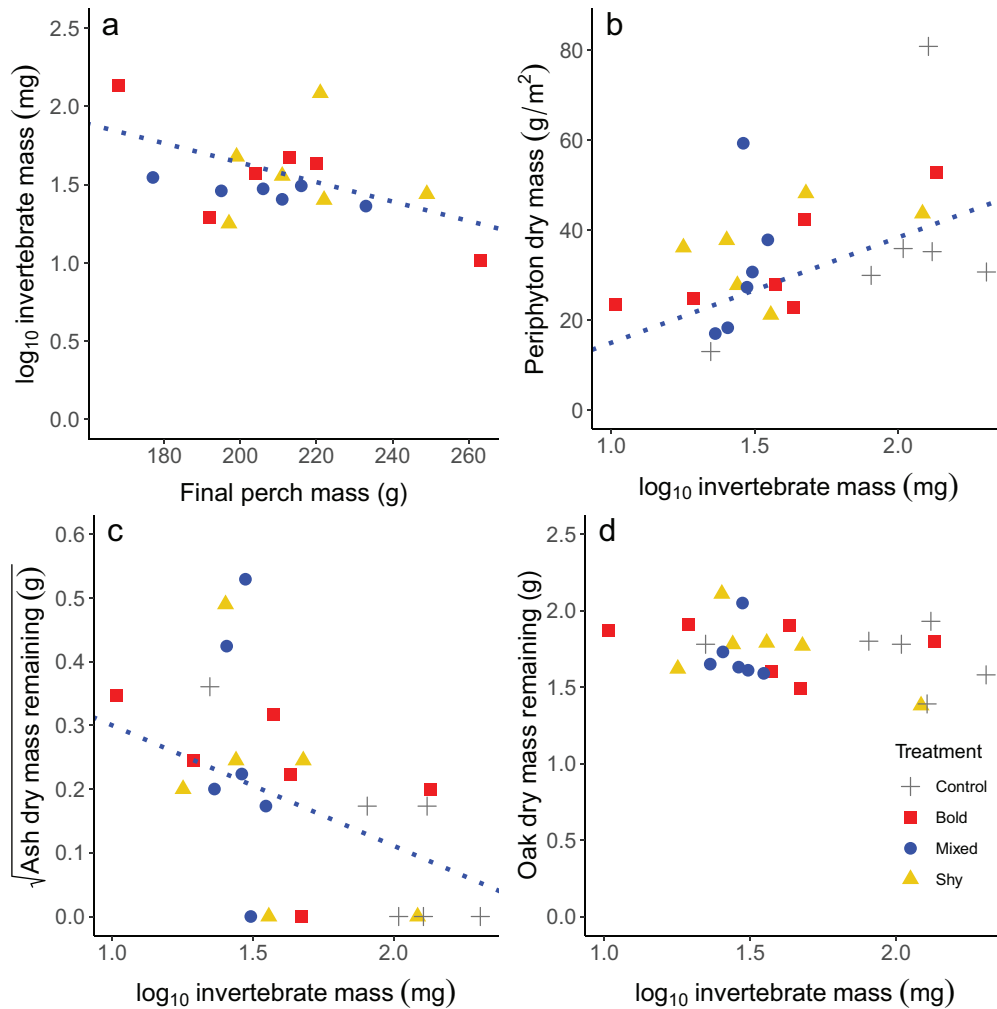


Figure 1: Relationships between the biomass of consumers (predatory fish and macroinvertebrates) at the final sampling date after 6 weeks and the dry mass at the trophic level below. Each point of the scatterplots represents data from one quadrat. For *a*, $N = 18$, as this included only quadrats that contained predators, and for *b–d*, $N = 24$. Significant relationships ($P < .05$) are indicated with a regression line.

Similarly, there was no evidence that the predator treatment affected the basal resource level and associated ecosystem functioning. Ash leaf litter decomposed at similar rates across all treatments (nonsignificant date \times treatment interaction; for results of the full model, see table S8), and while there was a significant effect of predator treatment (treatment LLR = 17.2, $P < .001$; table S8), post hoc tests revealed that the effect was driven by greater litter mass loss in the control quadrats (fig. 3*a*). For the more slowly decomposing oak leaves, there was no evidence for differences among the predator treatments (treatment LLR = 2.52, $P = .47$; table S8; fig. 3*c*). Finally, there was no evidence for an effect of predator behavioral composition on periphyton dry mass (treatment LLR = 4.77, $P = .19$; for results of the full model, see table S9; fig. 3*b*), periphytic

algal content (treatment LLR = 5.21, $P = .16$; table S9; fig. 3*d*), or the number of chironomids or snails found on or in the periphyton (fig. S6).

In contrast to the lack of effects on lower trophic levels, predator success measured as relative gain in body mass depended on both the perch's own behavioral type and the behavioral composition of the experimental predator population (behavioral type \times predator treatment type interaction = 5.75, $P = .016$). Specifically, bold perch grew faster in quadrats with both bold and shy individuals (mixed predator treatment) compared with shy perch in the mixed predator treatment (fig. 4; table S10). This effect was largely driven by two especially fast-growing bold individuals in mixed populations, as omitting these individuals from the analysis removed the significant effect

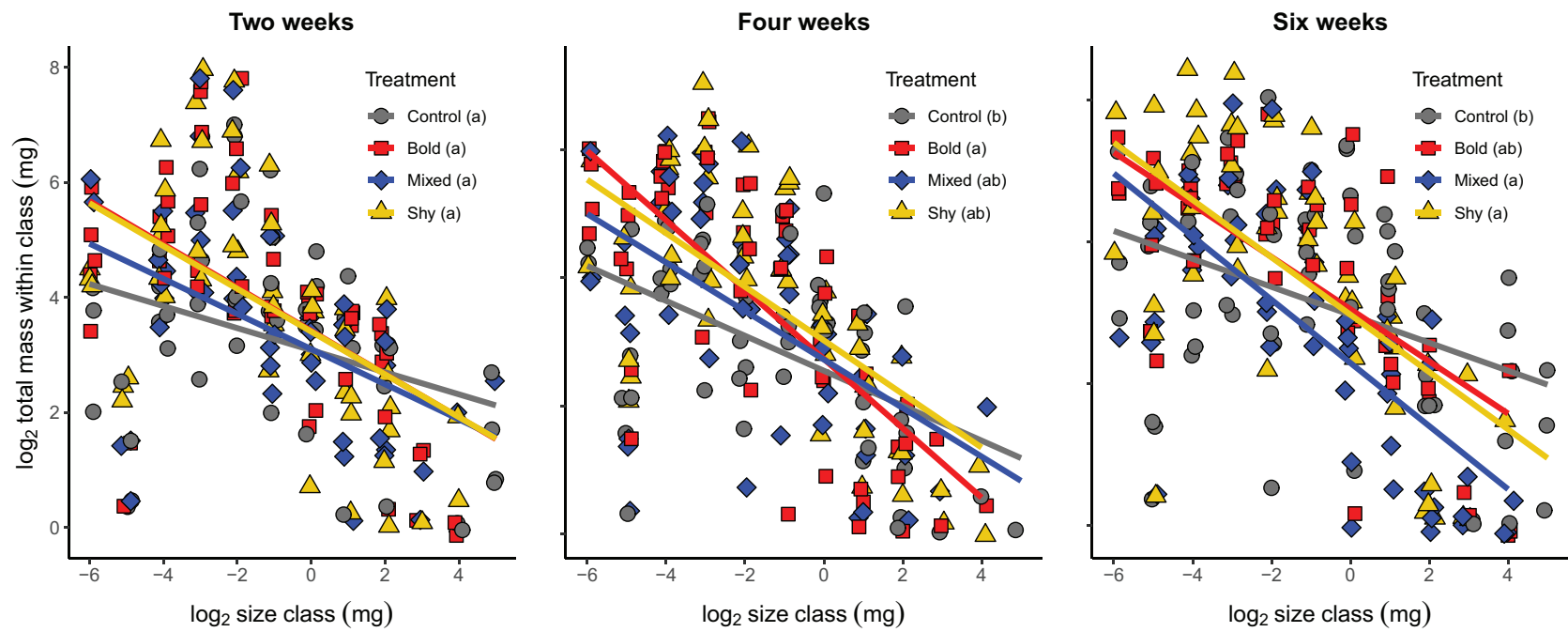


Figure 2: Macroinvertebrate body size distribution across the three sampling dates. Lines indicate relationships between \log_2 size class and \log_2 total invertebrate dry mass in each size class for four different predator treatments. Predator treatments sharing the same letter are not significantly different from each other ($P > .05$).

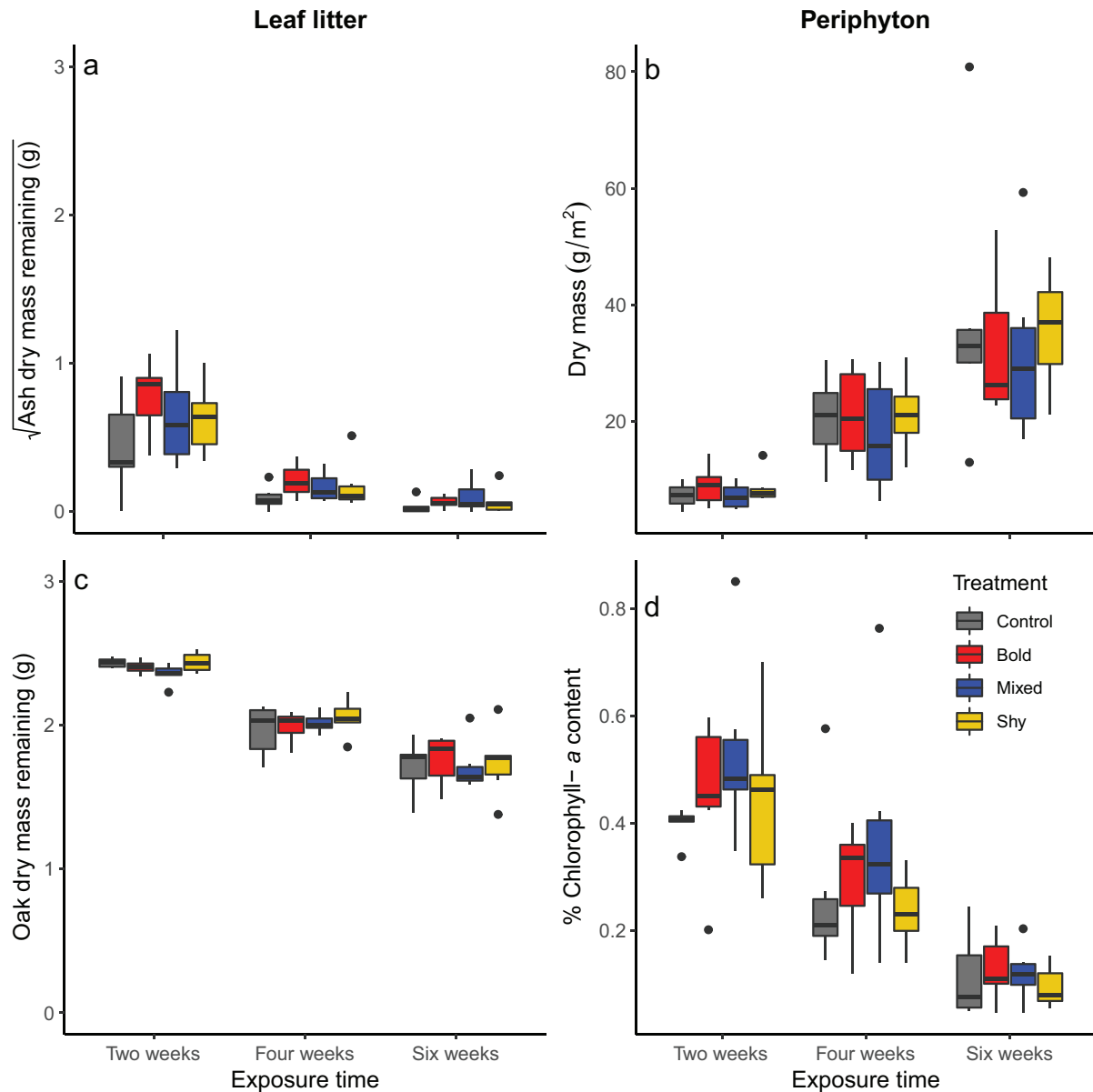


Figure 3: Response of basal resources to predator treatments. There were no differences in ash (a) or oak (c) leaf litter decomposition, periphyton dry mass (b), or periphytic algal biomass assessed as percentage of chlorophyll *a* in periphyton dry mass (d). Boxplots show medians (middle lines), upper and lower quartiles (boxes), and the 1.5 times interquartile ranges (whiskers); data points outside this range are indicated by points.

(LLR = 1.75, $P = .18$; table S10). Growth of shy perch, however, was independent of predator behavioral composition (fig. 4). Predator behavioral type alone did not predict the perch's growth rate (LLR = 0.19, $P = .66$). Finally, as inferred from stomach contents, there was no evidence at the end of the 6-week experiment that bold and shy predators showed major differences in prey types consumed (table S11). All data underlying these results and figures have been deposited in the Dryad Digital Re-

pository (<https://doi.org/10.25338/B8W610>; Laskowski et al. 2021).

Discussion

Theoretical models predict that intraspecific variation in behavior alters species interactions, with implications for trophic dynamics and ecosystem functioning (Okuyama 2008, 2011; Bolnick et al. 2011 and references therein;

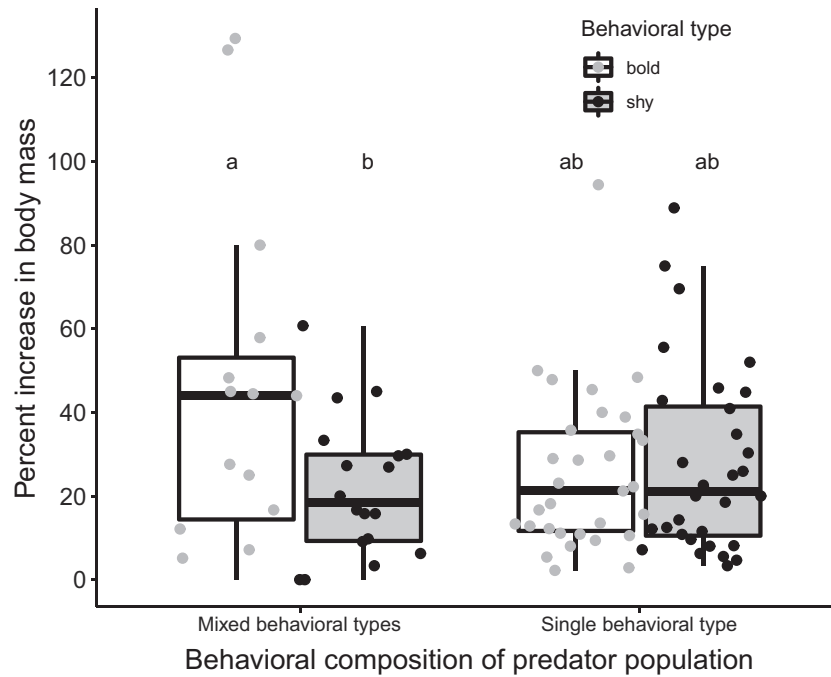


Figure 4: Bold perch in experimental populations with mixed predator personalities gained significantly more body mass on average than shy perch in mixed populations. Boxplots show the medians (middle lines), upper and lower quartiles (boxes), and 1.5 times the interquartile ranges (whiskers). All individual data points are depicted as gray or black dots. Groups that share the same letter (above the box) are not significantly different from each other ($P > .05$).

Schreiber et al. 2011; Guariento et al. 2014; Hart et al. 2016). Here, we find in a realistic replicated pond experiment that individual predator behavior and predator composition of experimental populations affects predator success; however, variation in the composition of behavioral types in the experimental predator populations did not alter cascading effects on macroinvertebrate prey and basal resources. Rather, differences in predator growth rates, potentially mediated by predator behavior, may play a larger role in contributing to trophic cascades. Overall, these results suggest that effects of intrapopulation behavioral variation may not be as strong, or at least not as influential, as variation in other functional traits, such as growth rate and body size.

Theoretical work has highlighted the possibility of individual predator behavior to influence prey communities and trophic cascades (Bolnick et al. 2011 and references therein). However, only a handful of studies have explicitly tested the effects of intraspecific behavioral variation in predators on species interactions across multiple trophic levels. Start and Gilbert (2017, 2019) indicated that the behavioral type of larval dragonfly predators altered zooplankton abundances and trophic cascades extending to phytoplankton. Similarly, Royauté and Pruitt (2015) reported that behavioral composition in small groups of

spiders altered invertebrate prey communities (note though that corrections for Royauté and Pruitt [2015] and Start and Gilbert [2017] call for caution in relying on these reports), but they did not test for cascading effects to lower trophic levels. Our present results suggest that effects of predator behavioral composition may not be universal, and even if not completely absent, they may be more subtle than, in particular, effects of variation in biomass.

We limited variation in initial predator biomass in our experiment (15–20 g/m² in all quadrats of our experimental ponds), and initial perch biomass did not relate to final invertebrate biomass (fig. S7). However, variation in individual perch growth resulted in greater variation in biomass at the end of the experiment (17–26 g/m²), and this final perch biomass did predict total invertebrate biomass at the end of the experiment (fig. 1). This suggests that differences in growth rates and/or foraging effort among the different perch may have contributed to the differences in perch biomass at the end of the experiment. So while the behavioral composition of the perch did not directly alter species interactions, the predators' behavioral types could be indirectly related to changes in biomass mediated through differences in growth. This means, however, that a direct link between behavioral variation and larger-scale species interactions may be difficult to find if this relationship is mediated

through other traits or processes. For example, Ingram et al. (2011) found that variation in the body size of sticklebacks explained individual prey consumption, which would be predicted to then lead to differences in prey communities. However, even when body size variation was empirically manipulated in a group of sticklebacks, there was little effect on prey community abundance and composition. Ingram et al. (2011) reasoned that the effects of predator body size on individual prey consumption as well as of prey consumption on prey community composition are relatively weak, making direct relationships between predator body size and prey community consumption hard to detect. Therefore, a central question to be explored in future theoretical and empirical work would be under which conditions behavioral effects predominate over other influences, such as predator biomass variation, or how dynamics change when multiple, potentially linked traits, such as growth rate and behavior, are manipulated concomitantly.

Predator behavioral variation was important for one of the key responses we assessed: the growth of the individual predators themselves. Bolder perch grew more but only when in groups of perch consisting of mixed behavioral types as opposed to groups comprising only bold perch. However, this effect was largely driven by two especially fast-growing bold individuals in mixed predator treatment ponds. These two individuals, which both gained more than 100% of their body mass over the course of the 6-week experiment, were some of the smallest at the start of the experiment (15 and 17 g), suggesting that their large scope to grow was instrumental. This only partly explains the positive growth effect of boldness because there were also shy individuals of similar initial size that did not achieve similarly high growth rates.

The interactive effect of predator behavioral type and the composition of the predator population that we observed highlights how the success of an individual is rarely absolute but will depend on both its own phenotype and that of other interacting individuals in the same population (McPeck 2017). Similar dependencies have been found in aquatic insects where the propensity to disperse was dependent not just on their own behavior but also on that of other individuals in their group (Kitchen and Chalcraft 2020). Given evidence that bolder, highly active individuals often show higher metabolic and growth rates (Stamps 2007; Biro and Post 2008; Careau et al. 2011), the bold perch in our experiment may have more easily met their energetic demands in the presumably less competitive environment encountered in the mixed groups, resulting in an overall greater allocation of resources to growth.

We did not find strong evidence from stomach content analysis to support the idea of major foraging differences between bold and shy perch (table S6). However, it is important to note that stomach contents were taken at the

end of the 6-week experiment, so they likely represent consumption only in the previous few days and not over the entire experimental period. It is possible that differences in consumption would have been detectable earlier in the experiment or with methods that provide information on consumption integrated over longer time frames (e.g., stable isotope analysis). Moreover, there are many factors that affect digestion and assimilation rates (Baker et al. 2014), so stomach content analyses may not always accurately capture the energy available to an individual. For example, even when ingesting similar types and amounts of food, some dragonflies are more efficient at extracting energy from their diet, which could lead to faster growth (McPeck et al. 2001). Thus, even if consumption rates did not differ among individual predators, differences in assimilation or growth efficiencies, or both, among individuals of different behavioral types could be important.

The indications we have suggest that our experimental pond system performed as expected: quadrats with greater perch biomass at the end of the experiment exhibited lower invertebrate biomass and therefore slower leaf litter decomposition. This indicates the presence of a trophic cascade from perch to leaf litter mediated through the intermediate macroinvertebrate consumers. Invertebrates, such as chironomids and gammarids, are an important food source for perch (Persson 1983; Rask and Hiisivuori 1985) and were commonly found in the stomachs of perch in our study (table S6). Both gammarids and chironomids were added in large numbers to the ponds, and gammarids in particular likely contributed to leaf litter decomposition (Baldy and Gessner 1997; Graça 2001; Worischka et al. 2018). Moreover, quadrats with greater invertebrate biomass also exhibited greater periphyton biomass, indicating that perch preferred macroinvertebrates not associated with periphyton. Accordingly, we found no evidence for differences in the number of snails on the exposed periphyton strips, and chironomid abundances were not reduced (fig. S6). Taken together, these data suggest that our experimental setting mimicked realistic aquatic communities and trophic relationships, with predatory perch preferentially exploiting benthic macroinvertebrates associated with leaf litter.

There are a number of potential explanations for why we failed to detect a strong effect of predator behavioral composition on lower trophic levels. There is ample evidence that intraspecific genetic variation (Treseder and Vitousek 2001; Wimp et al. 2005; Whitham et al. 2006; Hughes and Stachowicz 2009) and variation in traits other than behavioral traits (Harmon et al. 2009; Palkovacs and Post 2009) affect trophic dynamics and ecosystem functioning. For example, intraspecific variation in foraging-related morphology of alewives (*Alosa pseudoharengus*) drives community structure and trophic cascades in lakes (Post

et al. 2008). Morphological traits, however, are considerably less flexible than behavioral traits, implying that the perch might have adjusted their foraging behavior during our experiment to exploit the available invertebrates over time. Despite evidence that individual perch maintain differences in behavior over extended periods (Nakayama et al. 2016) and across social contexts (Magnhagen and Staffan 2005; Magnhagen and Bunnefeld 2009), changes in the behavior of individuals after release into the ponds could still have occurred (Dingemanse et al. 2010). This could be one reason for the lack of consistent effects of predator treatment on lower trophic levels. Another reason could be that other aspects of behaviors that we did not measure, such as aggression or exploration, might be more directly linked to predator foraging and the impact it has on lower trophic levels. Thus, the lack of strong differences among our predator treatments on lower trophic levels might have occurred because we failed to capture the ecologically most relevant behavioral variation or because predators changed their behavior in response to changes in their environment. However, even if individuals adjusted their behavior over the course of the experiment, their individual behavioral type, measured before releasing the fish in the ponds, remained predictive of their individual growth, indicating that our behavioral typing captured some important aspect of individual identity.

The possibility also remains that our experimental design did not provide sufficient statistical power to detect relatively subtle effects of predator behavior on food web function. A counterargument is, however, that based on effect sizes found in previous work (reductions of 50%–75% in prey species were reported in Royauté and Pruitt [2015] and Start and Gilbert [2017]), we would have expected up to 0.85 power to detect effects (though, again, caution is needed when using those studies as benchmarks, given their recent corrections). A promising area for future research would be to follow the behavior of the individual predators once they have been assigned to a given experimental group to explore how behavioral plasticity and behavioral interactions among predator individuals affect trophic relationships.

Finally, it is possible that our block design involving quadrats within ponds might have inadvertently limited our ability to detect the effects of predator behavioral composition on lower trophic levels. The coarse-mesh net separating the quadrats permitted both predator chemical cues and invertebrate movement. Conceivably, therefore, chemical predator cues shared across quadrats could have weakened differences in predation threat perceived by the invertebrates. Additionally, if prey were not influenced by (perceived) predation risk but instead dispersed randomly across the pond, a pattern could result where new prey from a different quadrat replace any prey eaten in a particular

quadrat. If such source-sink dynamics happened on a faster timescale than our sampling regime, any effects resulting from differential predation risk on lower trophic levels could have been overwhelmed. However, there is considerable evidence that intermediate consumers do in fact modulate their behavior according to the type and level of predator threat (Turner et al. 1999; Griffen et al. 2012; Carlson and Langkilde 2014; Breviglieri et al. 2017). This includes the dominant intermediate consumers in our ponds, gammarids (de Gelder et al. 2016; Mennen and Laskowski 2018) and chironomid larvae (Hölker and Stief 2005).

Indeed, prey behavior can also contribute to the strength of trophic cascades and consequent effects on ecosystem functioning, and not all prey species or individuals within the same species may respond to predation threat in the same way (Sommer and Schmitz 2020). Additionally, prey species perceive risk also by direct encounters with predators, and these were effectively constrained within the quadrats in our experiment. So if invertebrates moved among the quadrats in response to perceived predation risk, one would expect any effects of differential prey consumption related to behavioral type to be exaggerated rather than weakened. Overall, the interpretation thus remains that top-down control of invertebrates was not notably and/or consistently altered by variation in predator behavioral composition on the timescale of weeks, as in our experiment. Rather, variation in predator mass, potentially as a result of behaviorally mediated variation in growth rates, was more influential on lower trophic levels.

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Statement of Authorship

K.L.L. and T.M. designed the experiment; K.L.L., M.A., S.H., and M.O.G. collected the data; and K.L.L. performed the data analysis and drafted the manuscript. All authors contributed to revisions of the manuscript.

Data and Code Availability

All data and R code to reproduce analyses have been deposited in the Dryad Digital Repository (<https://doi.org/10.25338/B8W610>; Laskowski et al. 2021).

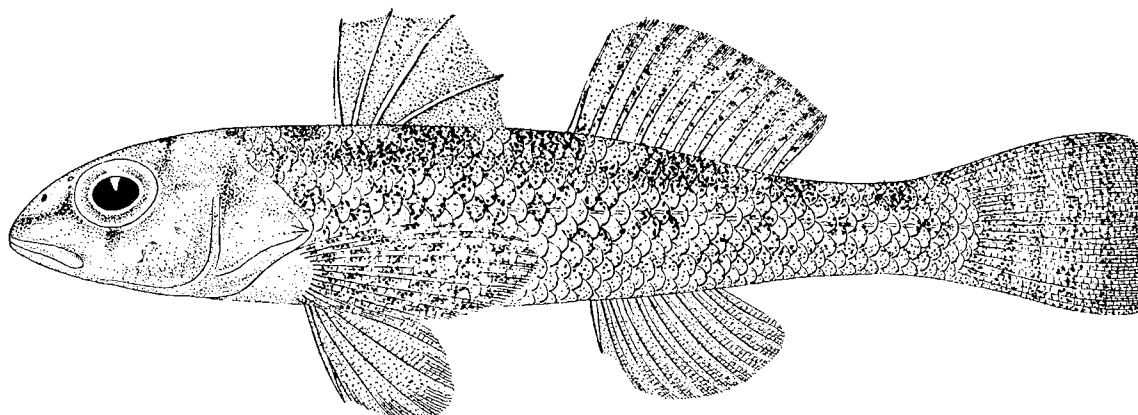
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“In view of the desideratum of definite records for the distribution of the different species in the various streams, lakes, etc., I have collected at a number of localities, and thus am able to offer nearly complete notes for some districts. . . . The accompanying figure represents a remarkable variation of fin-rays seen in an example I secured at Holmesburg, Philadelphia, September 11th, 1898.” Figured: “Variation of *Boleosoma nigrum olmstedii* (Storer).” From “Records of Pennsylvania Fishes” by Henry W. Fowler (*The American Naturalist*, 1907, 41:5–21).