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# Warming Strengthens the Ecological Role of Intraspecific Variation in a Predator

David C. Fryxell<sup>1</sup> and Eric P. Palkovacs<sup>1</sup>

**Recent work shows communities and ecosystems can be shaped by predator intraspecific variation, but it is unclear whether the magnitude and direction of these influences are context-dependent. Temperature is an environmental context of strong ecological influence and widespread relevance given global warming trends. Warming should increase per capita predator effects on prey through increases in predator metabolic rate, potentially exacerbating intraspecific differences in ecological effects. Here, we used two populations of the potent pelagic freshwater predator, Western Mosquitofish (*Gambusia affinis*), to test how experimental pond temperature mediates the differences between their ecological impacts. Mosquitofish introduction induced a strong pelagic trophic cascade, causing a large reduction of crustacean zooplankton biomass, an increase in phytoplankton biomass, and changes to ecosystem-level response variables. Warming (+2°C above unwarmed treatments) exacerbated fish-induced reduction of zooplankton biomass, but moderated the cascade to phytoplankton, primary productivity, and nutrient concentrations. Effects of intraspecific variation were apparent only on zooplankton, and only at warmed environmental temperatures. The traits underlying this divergence may be related to the population source thermal environments. Overall, results show that warming may increase the ecological importance of predator intraspecific variation. In general, extrinsic environmental drivers, such as those associated with climate change, may reshape the effects of intraspecific trait variation on ecosystems.**

INTRASPECIFIC trait variation in ecologically important species is becoming a widely recognized potential driver of community—and ecosystem—level characteristics and processes (reviewed in Whitham et al., 2003; Hairston et al., 2005; Fussmann et al., 2007; Bailey et al., 2009a; Post and Palkovacs, 2009; Bolnick et al., 2011; Matthews et al., 2011; Schoener, 2011). Intraspecific effects can be strong even contrasted with traditional ecological factors like presence of a dominant species (Bailey et al., 2009b; Palkovacs et al., 2015; Gómez et al., 2016) and habitat size (Farkas et al., 2013). A typical study design is a “common gardening” experiment (*sensu* Matthews et al., 2011), in which one tests the ecological impacts of intraspecific trait variants in a common environmental context (e.g., Schweitzer et al., 2004; Palkovacs and Post, 2009; Ingram et al., 2011; Lundsgaard-Hansen et al., 2014; Fryxell et al., 2015; Rudman and Schluter, 2016). However, the role of environmental context in determining the strength and direction of intraspecific effects is not well known. Some studies find intraspecific effects depend on biotic context (i.e., presence of another species or another species’ particular phenotype; Palkovacs et al., 2009; Ingram et al., 2012; Rudman et al., 2015), but few studies evaluate how intraspecific effects may depend on the abiotic environment, especially in animals (but see El-Sabaawi et al., 2015; Lajoie and Vellend, 2015; Tuckett et al., this volume, 2017). Because abiotic context strongly shapes ecological interactions (Chamberlain et al., 2014), impacts of intraspecific variation likely also depend on abiotic context.

Temperature is an abiotic variable with profound impacts across levels of biological organization. The ecological influence of temperature is fundamental in that it shapes organismal metabolism (Gillooly et al., 2001; Brown et al., 2004), which itself may help explain higher-level ecological patterns such as biodiversity and carbon-flow through ecosystems (Allen et al., 2002; Schramski et al., 2015).

Temperature is highly variable across space and through time, and has been increasing rapidly on average across the globe in recent history (IPCC, 2014). Because of its pervasive ecological role and immediate relevance, it is important to understand how temperature may mediate the ecological role of intraspecific variation.

Metabolism increases exponentially with temperature within the range of temperatures typically encountered by an organism (Gillooly et al., 2001), so small increases in body temperature can greatly increase metabolic demand. This increased demand must be met by increased ingestion rates at the individual level (Rall et al., 2012), which, in consumers and predators, could contribute to the widely observed warming-induced strengthening of top-down effects on ecosystems (Sanford, 1999; Barton and Schmitz, 2009; Barton et al., 2009; O’Connor et al., 2009; Hoekman, 2010; Harley, 2011; Kratina et al., 2012; Shurin et al., 2012). If feeding-related trait variation occurs among populations, warming-induced increases in per capita feeding rates could increase the ecological effects differences between populations of ectotherm predators.

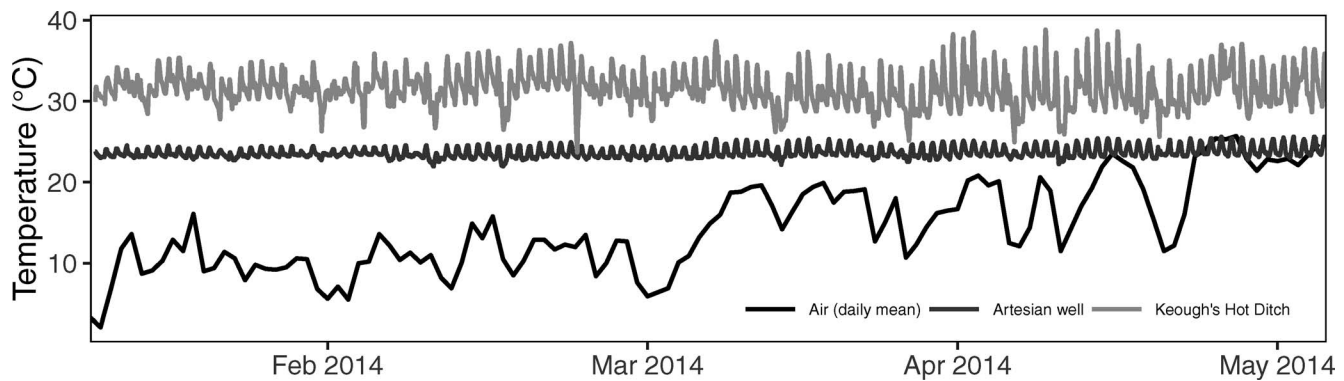
Here, we test the prediction that predator intraspecific differences have stronger effects for freshwater communities in a warmed versus an unwarmed environment. We test this prediction using Western Mosquitofish, *Gambusia affinis*, which prey heavily upon crustacean zooplankton in the pelagic zone of ponds (Hurlbert and Mulla, 1981; Pyke, 2005), causing trophic cascades whereby producer biomass increases, primary productivity increases, and nutrient concentrations decline (Hurlbert et al., 1972; Fryxell et al., 2016). Mosquitofish have been spread globally (Pyke, 2008) and today inhabit a wide diversity of environments to which they have acclimated and adapted (Pyke, 2005). There is considerable trait variation within and among Mosquitofish populations. Body size variation and sex ratio variation are common and can mediate a population’s ecological effects. An increasing proportion of females, which are generally

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**Fig. 1.** The temperature profiles of both fish sources used in the study. “Cool-source” fish were taken from the artesian well and “warm-source” fish were taken from Keough’s Hot Ditch, both in Bishop, California, USA. Daily average air temperatures are plotted from the Bishop Airport weather station, Bishop, California (Station ID GHCND:USW00023157), measured over the same period. In these geothermal systems, air temperature has little influence on water temperature.

larger, can induce stronger trophic cascades (Fryxell et al., 2015). Morphological differences among Mosquitofish populations can emerge via evolutionary responses to predation pressure (Langerhans et al., 2004). Mosquitofish are also known to exhibit rapid evolution of life history traits in response to habitat size variation (Stearns, 1983) and temperature (Stockwell and Weeks, 1999). Such contemporary trait change might also have community and ecosystem effects.

In this experiment, we used wild-caught Mosquitofish from two recently divergent populations of different thermal environment. We crossed three fish treatments (fishless, cool-source, warm-source) with two ecosystem temperature treatments (unwarmed, warmed) to test our predictions that 1) warming exacerbates top-down effects of fish introduction and 2) warming exacerbates the ecological differences between warm- and cool-source fish. Specifically, we expect 1) fish will more strongly suppress zooplankton at warmed versus unwarmed temperatures, which should cascade to affect phytoplankton, productivity, and nutrients, and 2) the ecological differences between populations for these same response variables will be larger at warmed versus unwarmed temperatures. Our use of recently divergent wild-caught fish from populations of different source temperatures may additionally allow us to address how predator trait variation generated along the temperature axis interacts with thermal context to shape ecological conditions.

## MATERIALS AND METHODS

**Source populations.**—We used Mosquitofish from two geothermal sites near Bishop, California, USA. The “warm-source” site was Keough’s Hot Ditch (37°15′33.6″N, 118°22′18.5″W), which has a mean temperature of 31.6°C, and the “cool-source” site was an unnamed dammed artesian well (37°21′02.1″N, 118°19′35.7″W), which has a mean temperature 23.7°C, as measured over the same period (Fig. 1). Mosquitofish were introduced to California from a common source population in Texas, USA in 1922 (Lenert, 1923). Fish have occupied these particular sites since at least 1980, though gene flow could have occurred until as recently as 2001, when the translocation of Mosquitofish among sites was discontinued by the Owens Valley Mosquito Abatement Program (Bob Kennedy, pers. comm.). There is little potential for natural gene flow between these sites because they are aquatic islands in a desert landscape and are both dammed

pools upstream from separate geothermal tributaries of the Owens River watershed.

**Mesocosm setup.**—We established 36 experimental ponds (1136 L Rubbermaid® stock tanks) in a 6 × 6 array at Long Marine Laboratory in Santa Cruz, California, USA. On 5 August 2013, we filled tanks with city water, evenly spread 19 L of sand each across their bottoms, and placed two cinderblocks (9.3 × 19.0 × 39.3 cm<sup>3</sup>) adjacently in the center of each. We placed a smaller cinderblock (6.0 × 8.5 × 16.0 cm<sup>3</sup>) between the two larger cinderblocks in the center of all ponds as cover and habitat structure for Mosquitofish. On 20 August 2013, we established a biological community in each pond by introducing a 4 L aliquot of a homogenized sediment sample and even aliquots of a large zooplankton sample taken from Antonelli Pond (36°57′18.6″N, 122°03′37.8″W), Santa Cruz, California, USA. The zooplankton community was dominated by crustacean zooplankton *Daphnia*, *Ceriodaphnia*, *Bosmina*, calanoid copepods, and cyclopoid copepods.

**Design and treatment application.**—We assigned treatments in our 3 × 2 factorial design (fishless, cool-source, warm-source × unwarmed, warmed) to the 6 × 6 mesocosm array using latin-squares random assignment. We initiated warming on 12 August 2013 using 300-watt heaters (Fluval Aquatics®) placed on the small central cinderblock in ponds assigned the warmed treatment. Similar warming methods have been used in other experiments, and had maintained a ~3°C temperature above unwarmed treatments, with similar patterns of temperature variation between treatments (Kratina et al., 2012; Shurin et al., 2012). This temperature increase is within the range of those expected globally over the next century (IPCC, 2014).

We collected experimental fish from both sites using seine and hand nets on 22 August 2013. We transported fish to Santa Cruz, California and immediately introduced a random subsample of ten individuals to each experimental pond following treatment assignments. This density of Mosquitofish was equivalent to densities used in prior mesocosm experiments, which reflect approximate natural summertime densities (Fryxell et al., 2015, 2016).

**Mesocosm sampling.**—We took repeated samples for water temperature, crustacean zooplankton (hereafter zooplankton) biomass, and phytoplankton biomass. Water tempera-

ture was monitored continuously at 15-minute intervals using HOBO Pendant (Onset Corporation®) data loggers. We sampled mesocosm water for zooplankton and phytoplankton two and four weeks following fish introduction. We collected zooplankton from a 1 L water sample using a 40  $\mu\text{m}$  sieve and preserved them in ethanol. Later, each zooplankton was identified to the lowest taxonomic group possible at 100X magnification and measured to get the body length using the “Live measurements” module of Leica Microsystems® Application Suite. Lengths were converted to mass by using published length-weight relationships for each taxonomic group (Bottrell et al., 1976), and masses of all zooplankton within a mesocosm sample were summed to get biomass. We collected phytoplankton from 1 L water samples filtered through Whatman GF/F® filters (pore size 0.7  $\mu\text{m}$ ). Filters were placed into a  $-20^{\circ}\text{C}$  freezer for later analysis. Chlorophyll *a* was extracted with acetone for 24 hours at  $4^{\circ}\text{C}$  and its concentration analyzed using the non-acid module on a Trilogy Fluorometer (Turner Designs®). Chlorophyll *a* concentration was used as a proxy for phytoplankton abundance.

We took final time point (week 4) samples for net primary productivity (NPP) and phosphate concentrations. NPP was estimated as the change in dissolved oxygen concentration between dusk and the previous dawn (as in Harmon et al., 2009). Phosphate (soluble reactive phosphorus) was measured from 60 mL water samples filtered (0.7  $\mu\text{m}$  pore size), frozen, and then thawed and analyzed on a LaChat® flow injection analyzer following standard methods (Rice et al., 2012).

After ecological sampling was complete, we removed fish and euthanized them with an overdose of tricaine methanesulfonate. Thereafter, fish were measured for length, counted to get population growth (number of offspring), weighed to get total fish biomass per mesocosm, and sexed to get the adult sex ratio (proportion males).

**Analyses.**—We used ANOVA to test the significance of warming, fish introduction, and intraspecific variation for each response variable. The “Warming” effect is the difference between the ‘warmed’ and ‘unwarmed’ treatments. Separate ANOVA analyses were used for the independent contrasts of interest—the “fish introduction effect” (FI) and the “intraspecific variation effect” (IV). The FI effect used all treatments but coded both populations as a single “fish present” factor level. The IV effect used only the treatments with fish to test for differences between the effects of the populations. Specifically, we used MANOVA of repeated measures for zooplankton and phytoplankton responses to account for correlations between sampling points, and used ANOVA for NPP and phosphate. All ecological responses were  $\log_{10}$  transformed before analyses to improve adherence to ANOVA assumptions, though zooplankton biomass was  $\log_{10}(1+x)$  transformed to avoid losing a replicate due to a 0 value. We used Bartlett’s tests to ensure approximate equality of variances for the FI effect, since it was an unbalanced comparison (6 replicates without fish, 12 with fish). For zooplankton, we additionally performed *post hoc* MANOVA tests for warmed and unwarmed treatments separately. We used principal components analysis (PCA) on correlations of the four transformed ecological responses at the final sampling point to understand how treatments arranged themselves in multivariate space. PCAs were run on data from all treatments, and then for warmed and unwarmed treatments separately.

We calculated standardized effect sizes (Hedge’s *G*) for the effects of FI and IV separately for unwarmed and warmed treatments to compare the magnitude of effects between community-level responses variables. Effect sizes were calculated across all data (i.e., including data from both time-points). Effect sizes and confidence intervals were calculated using the “cohen.d” function with arguments “hedges.correction=T” and “pooled=T” in the package “effsize” (Torchiano, 2016) on the R platform (R Core Team, 2015).

To associate population traits with effects, we performed a number of tests. First, we used a t-test to test for population differences in sex ratio at the start of the experiment. Next, we tested how temperature and source population affected final fish biomass and population growth using ANOVA. Lastly, we tested how initial sex ratio, final fish biomass, and population growth may have affected zooplankton biomass using standard least-squares linear regressions, separately for unwarmed and warmed ponds. All ANOVA- and regression-related analyses, and PCAs were performed in JMP Pro 12 (SAS Institute®).

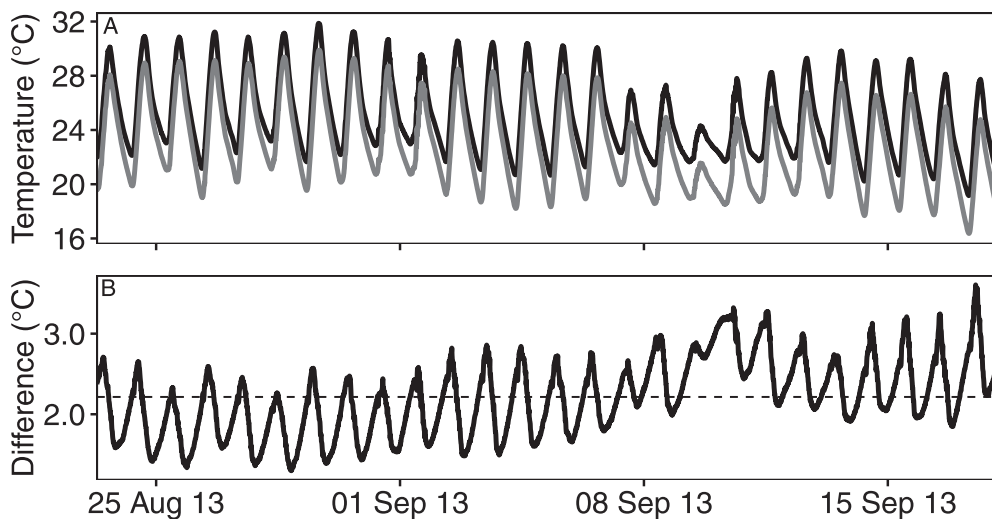
## RESULTS

Warmed treatments (overall mean  $25.0^{\circ}\text{C}$ ) were an average  $2.21^{\circ}\text{C}$  warmer than unwarmed treatments (overall mean  $22.8^{\circ}\text{C}$ ) and tracked unwarmed diel temperature patterns closely (Fig. 2A). The treatment difference did vary with time, from as little as  $1.30^{\circ}\text{C}$  to as much as  $3.60^{\circ}\text{C}$ , over the course of the experiment (Fig. 2B). Diel patterns in the magnitude of warming also emerged, where treatment warming was strongest in morning as temperatures naturally rose, and treatment warming was weakest in the evenings as temperatures naturally cooled (Fig. 2).

Fish introduction (FI) effects were significant at community and ecosystem levels, though there was little evidence for a FI x Warming interaction in most cases. Bartlett’s test identified no violations ( $P > 0.01$ ) of the heteroscedasticity assumption of ANOVA (Supplemental Appendix 1; see Data Accessibility), allowing us to proceed with FI tests. FI and Warming reduced zooplankton biomass (FI:  $F_{1,32} = 2.70$ ,  $P < 0.0001$ ; Warming:  $F_{1,32} = 7.03$ ,  $P = 0.0124$ ; Fig. 3A, B), without a FI x Warming interaction ( $F_{1,32} = 1.06$ ,  $P = 0.3104$ ; Fig. 3A, B). Univariate tests revealed a reduction in the FI effect through time (Time x FI:  $F_{1,32} = 8.42$ ,  $P = 0.0067$ ), which was dominated by the unwarmed treatment (*post hoc* unwarmed only Time x FI:  $F_{1,16} = 9.18$ ,  $P = 0.008$ ; *post hoc* warmed only Time x FI:  $F_{1,16} = 1.08$ ,  $P = 0.3143$ ; Fig. 3A, B), though the three-way interaction was nonsignificant (Time x FI x Warming:  $F_{1,32} = 2.13$ ,  $P = 0.1540$ ). We found evidence of a trophic cascade associated with FI, as phytoplankton biomass greatly increased with fish introduction ( $F_{1,32} = 38.04$ ,  $P < 0.0001$ ; Fig. 3C, D). Warming increased phytoplankton ( $F_{1,32} = 6.06$ ,  $P = 0.0194$ ; Fig. 3C, D), without an interaction with the FI effect ( $F_{1,32} = 0.9645$ ,  $P = 0.3334$ ; Fig. 3C, D), despite the result that the FI effect was weaker on average at warmer temperatures (Fig. 3C, D). NPP increased as a result of both FI and Warming, though Warming weakened FI effects (FI x Warming:  $F_{1,32} = 7.56$ ,  $P = 0.0097$ ; Fig. 4A). Lastly, FI reduced phosphate concentrations ( $F_{1,32} = 10.2826$ ,  $P = 0.0030$ ; Fig. 4B), and Warming may have moderated this impact (Warming:  $F_{1,32} = 3.4948$ ,  $P = 0.0707$ ; FI x Warming:  $F_{1,32} = 2.7594$ ,  $P = 0.1065$ ; Fig. 4B).

Zooplankton biomass was affected by intraspecific variation (IV), though this effect only emerged at warmed



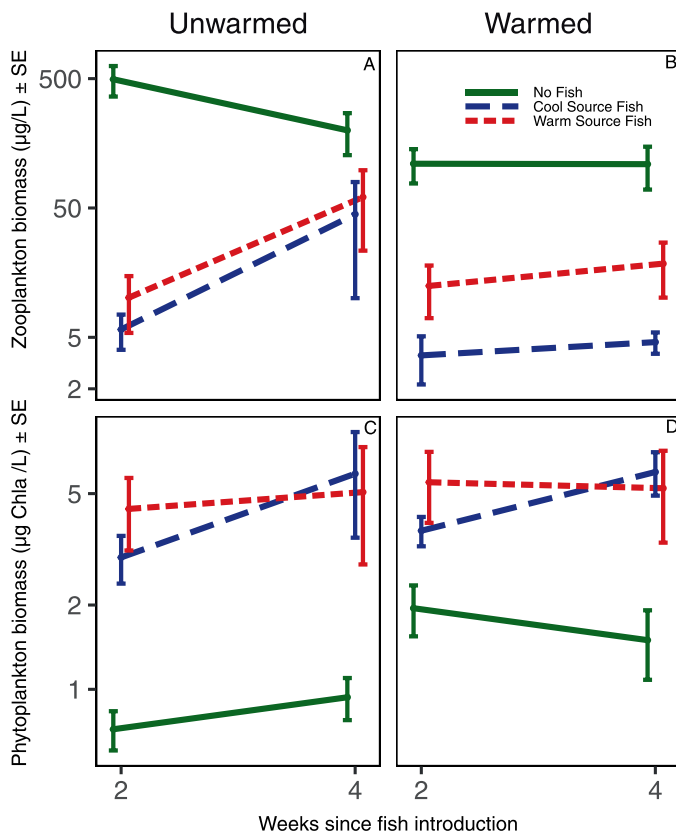


**Fig. 2.** (A) The mean of each logged temperature for both the warmed (black) and unwarmed (gray) treatments. (B) The difference between treatment means at each time-point, with the hatched line showing the overall mean temperature increase in the warming treatment: 2.21°C.

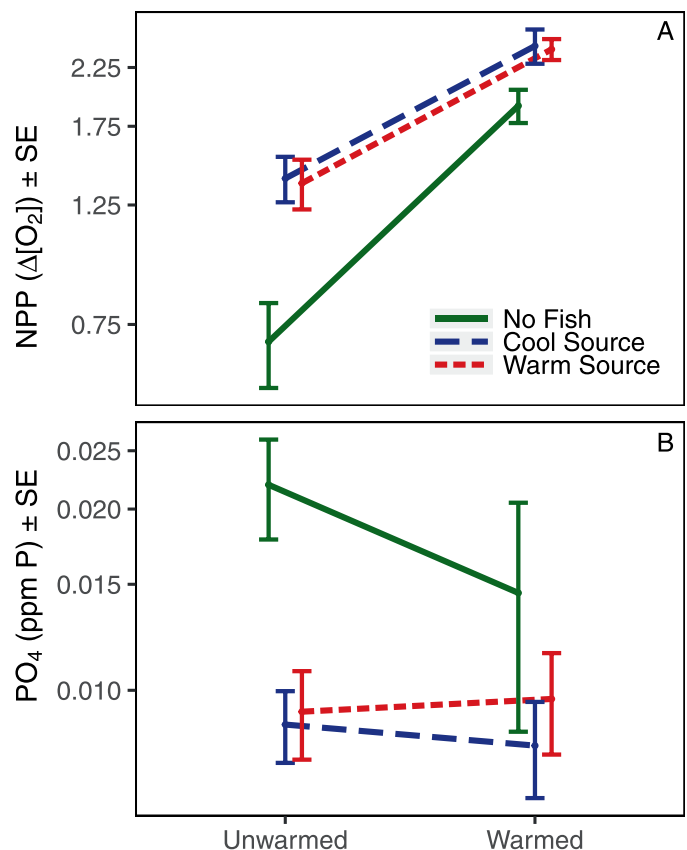
temperatures (IV:  $F_{1,20} = 2.92$ ,  $P = 0.1031$ ; *post hoc* unwarmed only:  $F_{1,10} = 0.2634$ ,  $P = 0.6189$ ; *post hoc* warmed only:  $F_{1,10} = 6.04$ ,  $P = 0.0338$ ; Fig. 3A, B). We did not detect cascading impacts of this effect, as IV effects were nonsignificant for phytoplankton biomass (IV x Warming:  $F_{1,20} = 0.03$ ,  $P = 0.8571$ ; IV:  $F_{1,20} = 0.001$ ,  $P = 0.9717$ ; Fig. 3C, D), NPP (IV x Warming:  $F_{1,20} = 0.01$ ,  $P = 0.9067$ ; IV:  $F_{1,20} = 0.04$ ,  $P = 0.8531$ ; Fig. 4A, B), and phosphate concentration (IV x Warming:  $F_{1,20} = 0.22$ ,  $P = 0.6406$ ; IV:  $F_{1,20} = 0.42$ ,  $P = 0.5244$ ; Fig. 4C, D).

The first principal axes of the three PCAs (across all mesocosms, or for warmed and unwarmed mesocosms

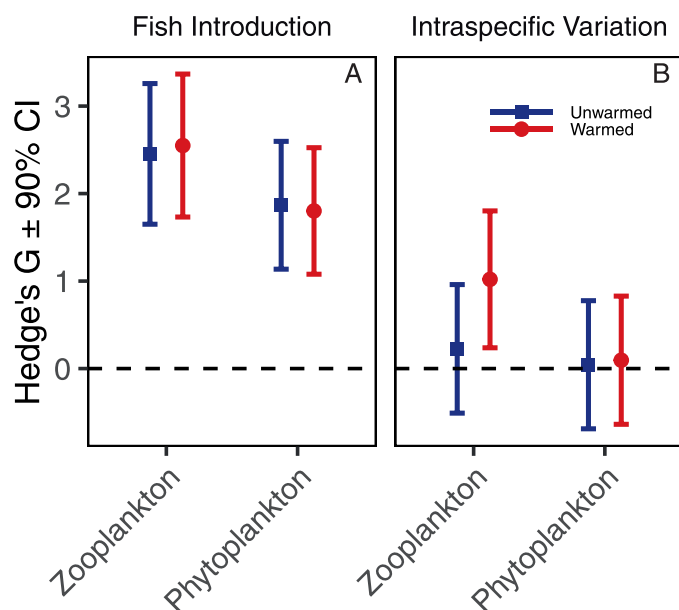
separately) each explained ~60% of the variation in the data, while the second principal axes explained ~20% of the variation. Phytoplankton and NPP had positive loadings on the first axis, while phosphate and zooplankton had negative loadings on the first axis. The second principal axes showed variable loadings across PCAs, suggesting different relationships among responses due to warming. PCAs showed spatial separation of fish from fishless treatments, but significant overlap of the two treatments with fish (Supplemental Appendix 2; see Data Accessibility).



**Fig. 3.** Responses of zooplankton (A, B) and phytoplankton (C, D) to warming and fish treatments for both sampling points. Y-axes are plotted on the log<sub>10</sub> scale.



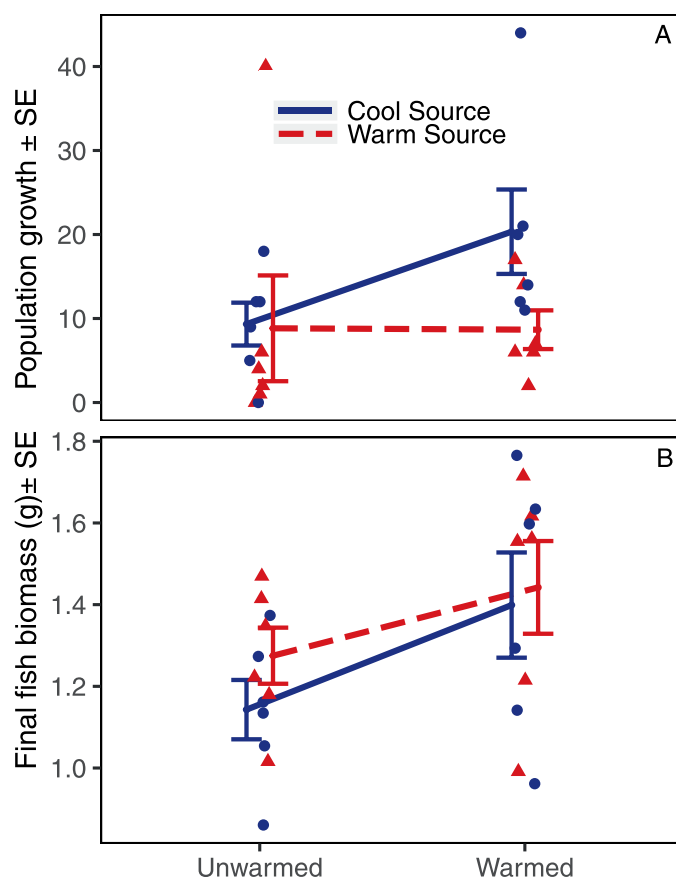
**Fig. 4.** Response of net primary production (A) and phosphate concentration (B) to warming and fish treatments at the final sampling point of the experiment—four weeks after fish introduction. Y-axes are plotted on the log<sub>10</sub> scale.



**Fig. 5.** The absolute value of effect sizes for all responses calculated over all sampling points, separately for (A) the fish introduction effect and (B) the intraspecific variation effect.

Effect size calculations showed very strong ( $>1$ ) effects of FI and little mediation of FI and IV effects by warming (Fig. 5A, B). For the IV effect, 90 percent confidence intervals overlap with zero except for effects on zooplankton in warmed environments (Fig. 5B). Effect sizes generally declined down trophic levels from zooplankton to phytoplankton.

Fish survival was high. Only 2 of the 240 individuals that were stocked at the start of the experiment died over the course of the experiment. Because of this high survival, and because few fish offspring reached maturity by the end of the experiment, we estimated initial sex ratio as the final adult sex ratio in experimental ponds. The cool-source population ( $M = 0.37$ ,  $SD = 0.16$ ) had a significantly higher proportion males than the warm-source population ( $M = 0.21$ ,  $SD = 0.16$ ;  $t_{22} = 2.34$ ,  $P = 0.0285$ ), though a range of 0.0 to 0.6 proportion males was present across mesocosms of both populations. Despite this, the cool-source population tended to have higher population growth ( $F_{1,18} = 9.90$ ,  $P = 0.0056$ , outliers removed; Fig. 6A), though this was apparent only after removal of two large, influential outlier values, or a log transformation (Supplemental Appendix 3; see Data Accessibility). Both populations had similar final fish biomasses ( $F_{1,20} = 0.78$ ,  $P = 0.388$ ; Fig. 6B). Warming increased fish biomass ( $F_{1,20} = 4.53$ ,  $P = 0.0458$ ; Fig. 6B) and population growth ( $F_{1,18} = 8.06$ ,  $P = 0.0109$ ; Fig. 6A), with no interaction with source population ( $F_{1,20} = 0.20$ ,  $P = 0.6599$ ;  $F_{1,18} = 0.06$ ,  $P = 0.9638$ ; Supplemental Appendix 3; see Data Accessibility). Lastly, our linear regressions of zooplankton biomass on sex ratio, fish biomass, and population growth found no significant effects on zooplankton biomass ( $P > 0.10$ ; Supplemental Appendix 1; see Data Accessibility). However, the variance in final zooplankton biomass explained by sex ratio (unwarmed:  $R^2 = 0.01$ ; warmed:  $R^2 = 0.03$ ), fish biomass (unwarmed:  $R^2 = 0.04$ ; warmed:  $R^2 = 0.16$ ) and population growth (unwarmed:  $R^2 = 0.02$ ; warmed:  $R^2 = 0.14$ ) was greater in warmed than unwarmed treatments. A summary of all



**Fig. 6.** Trait differences between populations at the end of the experiment. Fish population growth (A) was the number of offspring present at the end of the experiment, and total fish biomass (B) was the dry mass of all fish within a mesocosm at the end of the experiment. Means and standard errors were calculated without removing outliers (Supplemental Appendix 3; see Data Accessibility). Raw data points each reflect a mesocosm (triangles are warm-source, and circles are cool-source).

regression and ANOVA-related statistical tests is available in Supplemental Appendix 1 (see Data Accessibility).

## DISCUSSION

**Warming mediates fish effects.**—Mosquitofish have strong top-down impacts in pond ecosystems and show considerable trait variation within and among populations across their global range, making them good candidates for tests of the ecological effects of intraspecific trait variation (Pyke, 2005). As predicted, Mosquitofish introduction reduced crustacean zooplankton biomass, which induced a trophic cascade whereby phytoplankton bloomed, productivity spiked, and nutrient concentrations declined (Figs. 3, 4). These cascading impacts are consistent with prior studies of Mosquitofish-driven trophic cascades (Hurlbert et al., 1972; Hurlbert and Mulla, 1981; Fryxell et al., 2015, 2016) and set the stage for effects of intraspecific variation and their interaction with warming.

We predicted warming would increase the strength of the top-down effects of fish introduction. For zooplankton, this prediction was supported by the final time-point, despite the overall effect of fish introduction having no significant interaction with warming (Fig. 3A, B). This time-dependence was driven by changes in unwarmed treatments only, where fishless and fish present treatments converged through time.

In warmed treatments, fish effects were stable. This difference may reflect accelerated biological and ecological processes at warmed temperatures (Brown et al., 2004). Beyond four weeks, it is unclear whether zooplankton biomasses would have further converged in unwarmed treatments.

Despite warming-induced increases in fish introduction effects on zooplankton biomass, we did not find that warming increased pelagic trophic cascades from fish to phytoplankton, because warming directly increased phytoplankton biomass (Fig. 3C, D). This result is contrary to another warming study in pelagic freshwater systems, which showed strengthened trophic cascades from fish to phytoplankton under warming, and hence, enhanced top-down control (Kratina et al., 2012). However, in that experiment, warming did not enhance zooplankton biomass reduction by fish (Shurin et al., 2012). Perhaps fish excretion or zooplankton body size were primary drivers of the observed warming-induced trophic cascade in that study. Warming generally increases excretion rates (Vanni and McIntyre, 2016), which can increase nutrient supply for phytoplankton growth (Vanni and Layne, 1997). Zooplankton community size structure mediates trophic cascades through relationships between body size and grazing rates (Carpenter et al., 1985). In our study, increased fish excretion would not explain warming-induced phytoplankton blooms, as these effects were primarily seen in fishless treatments (Fig. 3C, D). Simultaneous warming-induced increases in phytoplankton and decreases in zooplankton in fishless ecosystems could occur if warming favored defended or toxic phytoplankton phenotypes (e.g., small phytoplankton, gelatinous-sheathed phytoplankton, cyanobacteria). These phenotypes may be favored via increased per capita predation by zooplankton (Peter and Sommer, 2012) and via some combination of nutrients (Vanni, 1987) and temperature (Rigosi et al., 2014; Yvon-Durocher et al., 2015). Without phytoplankton trait and/or community composition data, we are unable to directly address this hypothesis.

Increased productivity is a long-hypothesized (Carpenter et al., 1992) and common response to warming (Yvon-Durocher et al., 2015) and fish introduction (Carpenter et al., 1985). Ecosystem-level primary productivity is a process driven by metabolic rates of producers and producer standing stock, and is ultimately fueled by light and nutrient availability. As in similar studies (Shurin et al., 2012), we found warming and fish introduction increased NPP and decreased phosphate (Fig. 4). However, warming slightly reduced the effect of fish on these responses, perhaps because trophic cascades from fish to phytoplankton biomass were weaker with warming. Overall, we found support for our prediction that warming increases top-down effects of fish on zooplankton, but without cascading impacts for phytoplankton biomass and ecosystem characteristics. Bottom-up factors appear to have moderated this impact across trophic levels and to higher levels of organization.

**Warming mediates intraspecific effects.**—We predicted that ecological effects of intraspecific variation would be stronger with warming if top-down effects were stronger with warming. We found intraspecific variation had stronger effects at warmed versus unwarmed temperatures for crustacean zooplankton, but not other responses. Bottom-up factors at warmed temperatures likely prevented cascading effects of intraspecific variation, as they did for fish introduction. However, the effect size of intraspecific

variation was considerably smaller than fish introduction (Fig. 5B), so our power to detect its cascading influences was also smaller (Cohen, 1992). Even at warmed temperatures, the effect of intraspecific variation was less than half that of fish introduction (Fig. 5B), which is a notably weaker effect than found in many other studies (Palkovacs et al., 2015; Hendry, 2017).

The intraspecific effect from our study could be relatively weak for many reasons. Our focal populations are recently divergent (~90 years maximum, likely less), with human-assisted gene flow possible until very recently. Many other studies of intraspecific effects in fishes compare traits variants with a much longer or larger divergence—e.g., Alewives at >300 years (Palkovacs et al., 2008), stickleback, which are post-Pleistocene incipient species (Rundle et al., 2000), and guppies, which are probably longer-derived, showing considerable within-drainage genetic divergence and incomplete phenotypic transformation after a 50-year-long transplant experiment (Willing et al., 2010). Second, populations of many fish species exhibit countergradient variation with respect to temperature—where natural selection favors phenotypic similarity across populations in different environments (Conover and Schultz, 1995; Angilletta, 2009). Countergradient variation may have minimized trait differences between our focal populations and minimized ecological effects differences despite potential genetic differences (Kinnison et al., 2015). Third, other experiments are designed with a more thorough understanding of the trait differences between populations (e.g., Alewives, guppies, stickleback), allowing implementation of methods aimed specifically at detecting or maximizing the ecological effects of the functional trait differences. Investigators might choose maximally divergent focal populations for ecological effects tests, might focus on contexts (i.e., experimental arenas) hypothesized to maximize effects, and/or might control for many aspects of ecologically relevant natural variation like sex ratio, body size, and density, so as not to “swamp out” intraspecific effects. Lastly, studies with incomplete knowledge of ecological effects of focal population differences tend to measure a large number of ecological responses, and may emphasize responses showing relatively large intraspecific effects.

The effect sizes we measure in this study may more accurately reflect general intraspecific effect sizes among populations in nature. With little understanding of specific trait differences between our focal populations, we were unable to cater our experimental arena for maximizing intraspecific effects. We chose to control only for initial fish density, so other sources of natural intraspecific variation were present. Lastly, we focused on measuring a few responses with well-known linkages and broad ecological relevance (i.e., trophic cascades). Using such a less biased strategy in picking focal populations and focusing on one or a few ecological mechanisms of general relevance may better inform as to how strong intraspecific effects are more generally in nature.

**Traits underlying intraspecific effects.**—After testing whether the populations diverged in ecological effects, we asked whether we could predict those effects from traits and attributes of known ecological relevance across experimental populations (i.e., mesocosms)—sex ratio, population growth (a reflection of life history and phenological differences), and final fish biomass. Temperature is known to have strong phenotypic effects on Mosquitofish traits like body size and

life history (e.g., Vondracek et al., 1988; Meffe, 1991; Meffe et al., 1995; Stockwell and Weeks, 1999; Stockwell and Vinyard, 2000), and may affect sex ratio via sex-specific responses to temperature (e.g., see Seebacher et al., 2015). In our experiment, cool-source fish ended with the same biomass of fish as warm-source populations, but had more male-biased initial sex ratios and had greater population growth overall (Fig. 6). Therefore, at a given temperature treatment, cool-source populations had the same biomass of fish but had more and smaller individuals. Nevertheless, initial sex ratio, population growth, and biomass were each independently not associated with final zooplankton biomass at either warmed or unwarmed temperatures. Despite these factors being nonsignificant predictors of zooplankton biomass, we did find stronger associations (i.e., explained variance) between them at warmed versus unwarmed temperatures, in line with our overall prediction.

We hypothesized that intraspecific effects would be greater at warmed versus unwarmed temperatures because of increased metabolic demand. This general prediction is an over-simplification. Metabolic demand does not increase exponentially over the range of all possible temperatures, and does not do so with the same rate across evolutionary lineages (Gillooly et al., 2001). Further, feedings rates and other ecological rates do not perfectly track this metabolic demand (Rall et al., 2012), usually increasing approximately linearly up until a performance maximum, beyond which performance declines (Angilletta, 2009). In this study, experimental temperatures were approximately at or below population source temperatures. Theory therefore predicts focal populations were tested within the range that performance should increase with increasing temperature. Cool-source fish were nearer the source temperature of their natural pond (23.7°C) in experimental treatments (unwarmed: 22.8°C; warmed: 25.0°C) than warm-source fish (31.6°C), and greater reduced zooplankton (Fig. 3A, B). Cool-source fish also greater suppressed zooplankton at warmed versus unwarmed temperatures, perhaps because organisms are commonly found to perform optimally at a temperature slightly above that to which they are acclimated or adapted (Angilletta, 2009). Intraspecific variation in thermal performance curves likely contributes to ecological effects differences at different temperatures.

**Eco-evo dynamics and global change.**—“Eco-evolutionary dynamics” is an emerging worldview that posits evolutionary trait change and ecological change can interact on contemporary timescales (Hendry, 2017). Trait responses to anthropogenic drivers can be particularly fast (Hendry et al., 2008), so eco-evolutionary dynamics may be important in the face of anthropogenic change (Lavergne et al., 2010; Norberg et al., 2012; Urban et al., 2016). A question recently posed by researchers is whether global change drives eco-evolutionary dynamics such that population trait responses buffer or exacerbate further ecological or environmental change (Palkovacs et al., 2012). Tuckett et al. (this volume, 2017) found that lake eutrophication causes trait changes in white perch that exacerbate nutrient loading. Urban et al. (this volume, 2017) found that adaptive responses of anuran prey to climate-induced predator range expansion mitigated the predator’s impact on prey survival. Trait responses may thus exacerbate or mitigate further change in the face of global change drivers. Our study focused on another potential global change driver of eco-evolutionary dynamics—temperature. We found the population from temperatures more

similar to experimental conditions more strongly affected prey community biomass. If trait differences reflected recent adaptation, these results may suggest that predator thermal adaptation can mitigate ecological change by maintaining top-down effects on prey across different temperatures. However, our study only shows how a presumably relatively adapted versus a relatively non-adapted population might impact prey in one temperature range (i.e., both experimental temperatures were near the “home” temperature of one of the populations). Future studies might profitably test whether predator populations recently adapted to different temperatures have ecological effects more similar in their specific respective “home” temperatures than in their “away” temperatures.

## DATA ACCESSIBILITY

Supplemental material is available at <http://www.copeiajournal.org/ce-16-527>.

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