

Research article

Native fish grows faster in the presence of a potential introduced competitor

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Abstract

Biotic resistance, through competition from native species, can limit the success of invasive species. Similarly, invasive species can impact natives when they reduce shared resources. Alternatively, some invaders may benefit natives if they either directly or indirectly increase resource acquisition by natives. I predicted that the native California killifish, *Fundulus parvipinnis* would reduce the fitness of the morphologically similar introduced sailfin molly, *Poecilia latipinna* in a California estuary. A field experiment found no effect of competition; increasing the density of the native killifish did not affect sailfin molly growth. However, there was an unanticipated positive association of female sailfin molly density on growth of native killifish. Unlike any other native fish in the estuary, the introduced molly is a live bearer and I hypothesize that the presence of female mollies may have generated a novel food source (newborn fish) for the native competitor. This potential food source could have overcompensated for any potential competition for other resources. The positive effect was not mutual, i.e., the presence of killifish did not increase the growth of adult mollies (killifish are oviparous and lay eggs on the substrate). While killifish may not limit mollies through competitive effects, they could provide partial resistance to invasion by preying on juvenile mollies. Additional experiments designed specifically to test whether juvenile mollies increase killifish growth would confirm the mechanism and potentially reveal the importance of this in nature. Considering the role of all life stages of an invader is a key step when evaluating interactions with natives and determining the success and impacts of introduced species.

Key words: biotic resistance, competition, predation, *Poecilia latipinna*, *Fundulus parvipinnis*

Introduction

Introduced species compete with, consume and are eaten by other species in the communities they invade and the net result of these interactions will determine their success and their impacts in novel communities. Biotic resistance occurs when native species in a community reduce the establishment success or performance of introduced species. While biotic resistance rarely completely prevents invasion, interactions with resident species can often reduce population growth and spread of invaders (Levin 2008). Competition is a central focus for biotic resistance to invasion (Levine et al. 2004), however, other processes, such as predation (deRivera et al. 2005), herbivory (Parker et al. 2006), and parasitism (Torchin et al. 2002) can also limit the abundance of introduced species. While some interactions between native and introduced species are readily apparent (e.g., predation by brown tree snakes in Guam, infection by the chestnut blight fungus in North America) others are not and depend on the spatial and temporal scale at which the inter-

actions are observed. Field experiments using caged animals which measure the effect of density on individual growth over a set period of time are a common approach for evaluating competitive effects between native and introduced species. However, these experiments generally only capture interactions over a set life history stage and limited time period. Nevertheless, evaluating the role of competition between native and introduced species through experimentation has played an increasingly crucial role in our understanding of ecology (Byers 2000; Levine et al. 2004; Bruno et al. 2005).

Importantly, invaders may exert both positive and negative effects on natives (Stachowicz 2001; Bruno et al. 2005) and evaluating the net impact of introduced species can require an evaluation of interactions at various life stages and across different spatial and temporal scales. Interspecific interactions may be negative at one spatial or temporal scale or life history stage and be positive at another. For example, while introduced bullfrogs, *Rana catesbeiana*, compete with native frogs for algal resources as larvae

(Kupferberg 1997), they often prey on native frogs as adults (Wu et al. 2005). In this case, the native frogs may negatively affect the invader during the larval stage, but they may benefit the invader, by serving as prey, as adults. Understanding the net impacts of these interactions would require an integration of the above studies.

The sailfin molly, *Poecilia latipinna* Lesueur, 1821, a widely introduced fish, is native to fresh, brackish and salt waters along the coast from North Carolina, USA to the Yucatan peninsula, Mexico (Lee et al. 1980; McGinnis 1984). It was introduced to southern California, probably through aquarium releases, and populations of the sailfin molly now occur in several coastal wetlands (Swift et al. 1993). In some estuaries, mollies co-occur in the same habitats with the morphologically similar native California killifish, *Fundulus parvipinnis* Girard, 1856 (Williams et al. 1998; West and Zedler 2000). However, while the distributions of these fishes overlap, killifish tend to be more common in large channels and sailfin mollies tend to be more restricted to smaller channels within the marsh (Williams et al. 1998). While killifish are oviparous, sailfin mollies are live bearers which presents a novel life history in California estuaries. Both killifish (Love 1996; West and Zedler 2000) and mollies (Harrington and Harrington 1961) are omnivorous although mollies are reported to be predominantly herbivorous in some habitats (Alkahem et al. 2007). However, gut content analyses from estuarine habitats, similar to Ballona Wetlands, indicate that both species ingest a high proportion of invertebrates (specifically insects and copepods) (Harrington and Harrington 1961; West and Zedler 2000) relative to other food items, including plant material. This suggests that their niche overlap is sufficiently high to expect that they potentially compete for resources. To evaluate whether native killifish reduced the fitness of the invader through competitive effects (biotic resistance), I conducted a field experiment to determine if increased killifish density reduced sailfin molly growth.

Materials and methods

To evaluate the potential for biotic resistance to introduced mollies, I conducted a field experiment to determine the effect of killifish density on sailfin molly growth in an area where the native and introduced fishes co-occur in the

Ballona Wetlands in Los Angeles County, California, USA. For this, I used a randomized design, caging ambient densities of sailfin mollies (approx. $3.5/m^2$) in cylindrical enclosures (1.1 m diameter \times 0.75 m high, approx. benthic surface area = $0.95 m^2$) within four treatments; 0, ambient ($2/m^2$) and twice ambient ($4/m^2$) densities of killifish, as well as one treatment with ambient densities of killifish but without sailfin mollies (as a control for killifish growth). Ambient densities of fishes were estimated by seining a predetermined area within a marsh channel using blocking nets at two different locations. The number of fish caught was divided by the area seined to estimate ambient densities of each fish species. It is worth noting that killifish densities may have been different prior to sailfin molly invasion. However, killifish densities vary both temporally and spatially within coastal wetlands. For example, Brooks (1999) found densities ranging from 0-13 fish/ m^2 in another California estuary. The cages were made of Vexar mesh (7 \times 7mm mesh size) to allow water and food exchange, but prevent fish (except for new born mollies) from escaping. The caging method, modified from Brooks (1999), was designed to maintain the two fish species in an area within the marsh where they normally co-occur without altering their access to natural food items. The cages were buried approximately 5 cm below the surface and the mud was allowed to acclimate for one week prior to stocking fish.

The four treatments were replicated six times and cages were placed side by side in the middle of a marsh channel where the water did not drain completely at low tide. Total length (mm) of each fish was measured at the beginning and end of the experiment for both sailfin mollies and killifish. While on average, initial size of killifish was slightly larger than sailfin mollies, I attempted to match sizes of killifish and mollies in the cages, using the most common adult size classes caught (55-65mm for killifish and 45-60mm for mollies). The experiment was run from 28 September 2000 to 8 December 2000. At the end of the experiment, killifish in two of the cages were missing and thus the replicates were not used in the analyses. To test whether killifish reduce molly growth (biotic resistance), I used a least squares general linear model to examine the effect of killifish density (0, ambient, and $\times 2$ ambient), total number of fish per treatment and the interaction term on average molly growth within a cage.

While I was monitoring the experiment, I noticed that several of the female mollies were pregnant. After evaluating the results which suggested that killifish grew more in replicates with female mollies compared to those with no mollies or male mollies, I hypothesized that female mollies may contribute extra resources for killifish growth. Since the experiment was not designed to specifically evaluate the effect of female mollies on killifish growth, I used a stepwise general linear model to examine the extent to which the number of female mollies, male mollies and killifish per cage and interaction terms explained variation in average killifish growth across the replicates in the experiment. Non-significant ($P > 0.05$) interaction terms were removed from the final analysis. Both the original data and residuals were normally distributed for molly growth (Shapiro-Wilk $W = 0.94$, $P = 0.29$, $W = 0.94$, $P = 0.29$, respectively) as well as killifish growth (Shapiro-Wilk $W = 0.90$, $P = 0.08$, $W = 0.93$, $P = 0.23$, respectively) and data met the assumptions of the parametric tests. All analyses were conducted in JMP (SAS Institute Inc.). To evaluate whether killifish ate newly born sailfin mollies, I maintained killifish in 10 ten-gallon aquaria and fed them a diet of flake fish food ad libitum. Pregnant female sailfin mollies were maintained separately. Newly born sailfin mollies were collected and placed in aquaria with killifish to allow direct observation of predation by killifish.

Results

Competition

Over the course of the experiment, sailfin mollies grew an average of 4.8% in the control and 5.8% in the low and high density treatments, such that killifish density did not significantly affect molly growth rates ($P = 0.99$, $F = 0.00$, $n = 18$). Similarly, there was no effect of total fish density ($P = 0.12$, $F = 2.69$, $n = 18$) on molly growth (Figure 1). This is contrary to the expectation for competing fish species and suggests that killifish do not significantly reduce resources for mollies under the cage conditions.

Predation

During the course of the experiment, killifish grew an average of eleven percent of their initial total length (range = 8 to 14%) across the different treatments. The presence of several

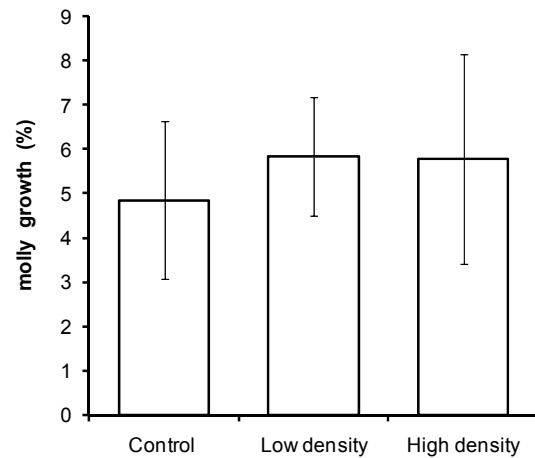


Figure 1. Percent growth (change in total length) of sailfin mollies in the three experimental treatments. Control had no killifish, low density had two killifish and high density had 4 killifish per cage. Error bars are 95% confidence intervals.

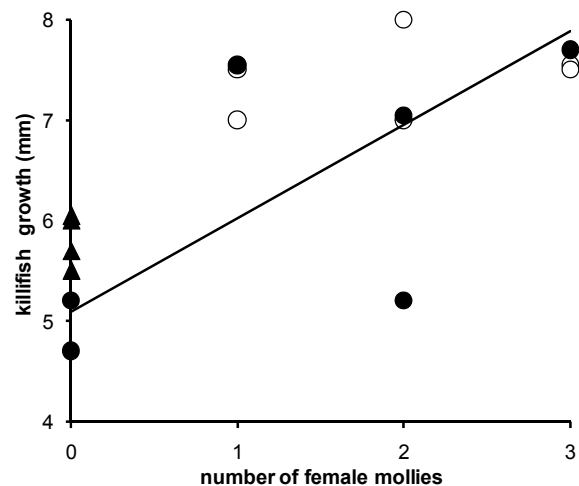


Figure 2. Association between killifish growth (average growth per fish (mm) across experimental cages) and number of female sailfin mollies ($r^2 = 0.49$, $P < 0.005$, $n = 16$). ▲ is the control (0 mollies, 2 killifish), ○ is the low density treatment (4 mollies, 2 killifish) and ● is the high density treatment (4 mollies, 4 killifish).

pregnant female mollies in the cages led me to hypothesize that they may be subsidizing killifish growth through predation of newborn mollies. The number of female mollies was significantly positively associated with killifish growth ($P = 0.002$, $F = 15.7$, $n = 16$, Figure 2). However, there was no effect of number of male sailfin mollies ($P = 0.38$, $F = 0.8$, $n = 16$) or

number of killifish ($P = 0.12$, $F = 2.7$, $n = 16$) on killifish growth. All interactions between the above factors were not significant ($P > 0.05$ for all). In the laboratory, all newly born mollies that were placed in the aquaria containing killifish were eaten by the killifish within a few minutes.

Discussion

I found no evidence that native killifish density reduced introduced sailfin molly growth suggesting that these similar species do not compete for food. While independent studies examining gut content of sailfin mollies and killifish suggest potential for diet overlap (Harrington and Harrington 1961; West and Zedler 2000), mollies are opportunistic feeders which are able to utilize a variety of food items depending on availability (Williams et al. 1998; Alkahem et al. 2007). I hypothesized that the faster growth of killifish in the presence of female sailfin mollies may have occurred because killifish preyed on the live young produced by female mollies. Because there are no native live bearing fishes in California estuaries, introduced mollies may provide a novel food source for killifish and, perhaps, other native fishes. Female mollies are highly fecund; capable of storing sperm and producing 10-140 young per brood several times per year (Lee et al. 1980; McGinnis 1984). It is important to add that it is not necessarily the fact that mollies are live bearers that allows killifish to benefit from their presence. Presumably, killifish could also feed on juvenile fishes that were hatched from eggs and locally developed from larvae. Similarly, mollies could conceivably eat killifish larvae. However, because newborn mollies initially emerge near their mothers, this potential effect was detectable on the scale of an experimental cage during the time scale of the experiment. An alternative hypothesis for this pattern is that male and female mollies compete differentially with killifish, where male mollies interfere with killifish growth, but female mollies do not, allowing normal growth in treatments with fewer males. Indeed, male sailfin mollies have been reported to exhibit aggressive behavior towards killifish in aquaria (Williams et al. 1998). However, the fact that male mollies had no effect on killifish growth and that killifish grew less in treatments without any sailfin mollies compared to those with mollies, including those with males

(Figure 1) suggests this is unlikely, but cannot be ruled out entirely.

While the effects of competition from native killifish may not limit the success of the introduced sailfin molly, predation of live-born mollies by killifish could provide partial biotic resistance in habitats where these species co-occur. For example, Taylor et al. (2001) demonstrated that mosquitofish, *Gambusia holbrooki* Baird and Girard, 1853 readily consumed sailfin mollies decreasing their survivorship over 70% in experimental mesocosms. However, in this study, it is still hypothetical since molly predation was not observed in the field and the effect of caging fishes could intensify encounter rates between killifish and new born mollies even though the mesh size of the cages was large enough for the new born fish to escape. For example, if female mollies give birth to young in different microhabitats this could reduce encounter rates. Indeed, Williams et al. (1998) found a greater proportion of juvenile sailfin mollies in marsh pans where killifish also occurred but were less common compared to channels. Experiments specifically designed to test the effect of killifish predation on introduced mollies are needed in order to reveal if this is in fact the mechanism that resulted in the pattern observed in this study. Future studies might also consider whether the positive effect of female mollies on killifish growth is significant at the scale of the killifish population in nature.

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