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Invasive predator tips the balance of symmetrical competition between native coral-reef fishes

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Abstract. The importance of competition and predation in structuring ecological communities is typically examined separately such that interactions between these processes are seldom understood. By causing large reductions in native prey, invasive predators may modify native species interactions. I conducted a manipulative field experiment in The Bahamas to investigate the possibility that the invasive Pacific red lionfish (*Pterois volitans*) alters competition between planktivorous fairy and blackcap basslets (*Gramma loreto* and *Gramma melacara*, respectively). Competition between these coral-reef fishes is known to have symmetrical effects on the juveniles of both species, whereby the feeding positions under reef ledges and growth rates of these individuals are hindered. Following baseline censuses of local populations of competing basslets, I simultaneously manipulated the abundance of lionfish on entire reefs, and the abundance of basslets in local populations under isolated ledges within each reef, resulting in three treatments: unmanipulated control populations of both basslets, reduced abundance of fairy basslet, and reduced abundance of blackcap basslet. For eight weeks, I measured the change in biomass and feeding position of 2–5 cm size classes of each basslet species and calculated the growth rates of ~2 cm individuals using a standard mark-and-recapture method. Experimental populations were filmed at dusk using automated video cameras to quantify the behavior of lionfish overlapping with basslets. Video playback revealed lionfish hunted across all ledge positions, regardless of which basslet species were present, yet lionfish differentially reduced the biomass of only juvenile (2 cm) fairy basslet. Predation reduced the effects of interspecific competition on juvenile blackcap basslet as evidenced by corresponding shifts in feeding position toward coveted front edges of ledges and increases in growth rates that were comparable to the response of these fish in populations where competition was experimentally reduced. Thus, an invasive marine predator altered the outcome of interspecific competition via differential predation, which tipped the balance of competition between native prey species from symmetrical to asymmetrical effects on juveniles. This study reveals a newly demonstrated context in which predation can indirectly facilitate prey, further broadening our understanding of the interactive effects of predation and competition in the context of invasive species.

Key words: coral reefs; facilitation; indirect effects; interspecific competition; invasive species; lionfish; marine fishes; predation; prey; species interactions; symmetry.

Introduction

As ecosystems continue to be progressively altered at a global scale (Vitousek et al. 1997, Pereira et al. 2010, Hautier et al. 2015), understanding the processes that regulate biodiversity and ecosystem functioning is of ever-increasing importance. Ecologists have long recognized the importance of competition in structuring ecological communities, yet the inability of this process to entirely account for observed patterns led to the recognition of the dramatic effects predation can also have on species diversity (Mittelbach 2012). The interaction between competition and predation can produce a range of theoretical outcomes that structure ecological communities depending on the nature and intensity of both processes (Chesson and Huntly 1997, Abrams 2001, Chase et al. 2002, Chesson and Kuang 2008), yet empirical studies typically examine these processes separately such that their interactive effects are seldom understood (reviews by Sih et al. 1985, Gurevitch et al. 2000).

Sources of mortality that decrease the population size of competitors are expected to moderate competition as resources become less limiting until mortality reaches levels large enough to cause competition to cease altogether in local populations (e.g., intermediate disturbance hypothesis; Connell 1971). Predators that exhibit switching behavior and consume whichever species occurs in greater abundance (Murdoch 1969, Roughgarden and Feldman 1975) could prevent either prey species from competitively excluding the other (Kuang and Chesson 2010). Differential predation could moderate or intensify competition between prey species, depending on whether the dominant or subordinate competitor (respectively) is disproportionately consumed. For example, keystone predators can prevent the exclusion of subordinate competitors by preferentially consuming prey that are competitively dominant (reviews by Power et al. 1996, Eisenberg 2010, Terborgh and Estes 2010).

Predation by invasive species can have particularly large effects on prey that are typically stronger than the effects of native predators (Salo et al. 2007, Paolucci et al. 2013). Such predation often results in large declines in native species (reviews by Pitt and Witmer 2007, Gallardo et al. 2016), which in extreme cases can lead to local or global extinction (reviews by Clavero and García-Berthou 2005, Woinarski et al. 2015). By causing such substantial declines in native

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prey, invasive predators likely modify interactions among native species. Beyond direct reductions in taxa, however, little is understood regarding the ability and mechanisms by which invasive predators indirectly influence native communities and ecosystems (Parker et al. 1999, White et al. 2006, Ehrenfeld 2010, Simberloff 2011, Ricciardi et al. 2013).

I tested whether and how an invasive predator modifies native interspecific competition by performing a manipulative field experiment in which I measured the response of each prey species in competitor-reduced and control populations, cross-factored with predator-reduced and control sites. Focal prey were congeneric fishes commonly found on coral reefs throughout the Caribbean region (Böhlke and Randall 1963, Starck et al. 1978) that are popular in the aquarium trade: fairy basslet (*Gramma loreto*) and blackcap basslet (*Gramma melacara*). Independent local populations of these planktivores inhabit the undersides of spatially isolated reef ledges, with negligible immigration and emigration of individuals among ledges (Webster and Hixon 2000, Webster 2003, 2004, Ingeman and Webster 2015, Kindinger 2016). Basslets are known to aggressively compete both within (Webster and Hixon 2000, Webster 2004) and between species (Kindinger 2016) for feeding positions under ledges, which maintains a size hierarchy among members of local populations. Larger basslets occupy prime locations at the fronts of ledges where individuals exhibit higher feeding rates, presumably due to increased access to passing zooplankton. Smaller fishes are found closer to the backs of ledges where they feed less (Webster and Hixon 2000, Kindinger 2016) and more often encounter resident predators (Webster 2004). Importantly, competition between fairy and blackcap basslets is known to have symmetrical effects on the juveniles of both species, whereby the presence of the competitor species in local populations results in affected individuals shifting in distribution further toward the backs of ledges where their feeding and growth rates are reduced (Kindinger 2016).

I investigated whether competition between native basslets is altered by an invasive predator, the Pacific red lionfish (*Pterois volitans*). The lionfish invasion is unprecedented for a marine fish in the extent of rapid geographical spread throughout the greater Caribbean region (including the Gulf of Mexico), successful establishment across numerous habitats, and strong predatory effects on native species (Albins and Hixon 2013, Côté et al. 2013). Invasive lionfish can cause substantial reductions in the abundance and species richness of native prey fishes that scale up from smaller patch reefs (Albins and Hixon 2008, Albins 2013, Green et al. 2014, Benkwitt 2015) to large coral reefs (Albins 2015). Importantly, both fairy and blackcap basslets have been found in the stomachs of invasive lionfish (Morris and Akins 2009), and a recent study by Ingeman (2016) demonstrated that, in only four weeks, invasive lionfish can increase the likelihood of local populations of fairy basslet reaching extirpation.

Given that competition between basslets has symmetrical effects on juveniles (Kindinger 2016) and that lionfish can extirpate local populations of fairy basslet (Ingeman 2016), I tested several alternative hypotheses regarding the effects of invasive lionfish on this native interspecific competition: (1) lionfish affects both basslet species substantially, thereby moderating interspecific competition; (2) lionfish differentially affects fairy basslet, thereby benefitting blackcap basslet; (3) lionfish differentially affects blackcap basslet, thereby benefitting fairy basslet; and (4) basslet populations are reduced in the presence of lionfish to the point in which one or both basslet species are extirpated.

METHODS

Experimental design

I conducted a field experiment from June through August of 2014 where I simultaneously manipulated the abundance of lionfish on reefs and the abundance of basslets under ledges within these reefs. Six large reefs (344–1,023 m^2) located off the southwest end of Eleuthera, The Bahamas were paired by similar habitat (depth, surface area, reef structure, etc.) and randomly assigned a low- or high-lionfish treatment ($n = 3$ reefs per treatment, Appendix S1: Table S1). All reefs were isolated by at least 150 m of open sand. Within each reef, I selected three local populations of competing basslets (Appendix S1: Table S2) under isolated reef ledges (≥4 m from all natural or experimental populations of basslets on reef).

I conducted baseline censuses of every population ($n = 18$), mapping the feeding position and visually estimating the total body length (TL) of each basslet to the nearest 0.5 cm. Following these initial observations, I manipulated the abundance of both the predator on reefs and competitor species in local populations, resulting in three treatments per reef: (1) unmanipulated populations of both basslets (control), (2) reduced abundance of fairy basslet, and (3) reduced abundance of blackcap basslet. I removed lionfish from low-lionfish reefs with hand nets and pole spears, and augmented the density of lionfish within naturally occurring limits by transplanting individuals onto high-lionfish reefs. Basslets were removed from populations with small aquarium hand nets and the fish anesthetic, quinaldine.

Throughout the experiment, mean lionfish densities differed between paired low- and high-lionfish reefs by about one order of magnitude or more (Appendix S1: Table S1). Although the biomass of competitor species were reduced relative to focal species within all competitor-removal populations, the respective ratios of competitor to focal species were not always less than those observed among control populations (Appendix S1: Table S2). This was accounted for in all analyses.

Basslet response

To quantify changes in biomass and/or shifts in feeding position of basslets, I conducted weekly censuses (already described) of each local population for eight weeks. Biomass was assessed to account for both the abundance and size of prey, which can influence both competition and predation. I used published length–mass parameters for fairy basslet (Sandin et al. 2008) to convert counts and size estimates of basslets to biomass, which was then divided by ledge area to further account for variance in size among reef ledges. Per week, I calculated the change in biomass from the baseline values ($\text{biomass}_{\text{week}(t)} - \text{biomass}_{\text{week}(0)}$) of 2–5 cm size classes (2 cm: 1.5–2.0 cm; 3 cm: 2.5–3.0 cm; 4 cm: 3.5–4.0 cm; and

5 cm: 4.5–5.0 cm) of each basslet species. Consistent with previous methods (Webster and Hixon 2000), I also measured the absolute feeding position (distance between fish and the front of the ledge) of every individual from the weekly maps and converted these values to relative feeding positions: 1 − (absolute position/ledge depth). For each population, I then calculated the weekly change in mean values ($\text{position}_{\text{week}(t)} - \text{position}_{\text{week}(0)}$) per size class (2–5 cm) of each basslet species.

To compare the growth of basslets among treatments, I used a standard mark-and-recapture method to measure the growth rates of small fish in every focal population (fairy basslet mean initial total length [TL], 2.29 ± 0.05 cm [mean ± SE]; blackcap basslet mean initial TL, 2.39 ± 0.05 cm). Each fish captured with small aquarium hand nets and the anesthetic quinaldine was measured to the nearest mm (TL) and injected with a unique visible tag of fluorescent elastomer (Frederick 1997) prior to release. After about a month (31–36 d in July–August), I recaptured and remeasured these tagged fish and calculated growth rates by dividing the change in TL by the number of days between initial and final measurements.

To assess the effects of the interaction between competition and predation on the response of basslets, I fitted linear mixed effects models (LMMs) to account for the varying spatial scales of treatments (Pinheiro and Bates 2000, Bolker et al. 2009, Zuur et al. 2009): all models included ledge (competitor treatment) nested within reef (predator treatment) as random effects. Full models of the change in biomass and feeding position of each size class of fairy and blackcap basslets (species analyzed separately) included the fixed effects, competition (comp) and time (weeks) as continuous variables, predation (pred; low- vs. high-lionfish reefs) as a categorical variable, and all potential interactions among these variables; full models of the growth rates of basslets did not include time. Competition was measured as the proportion of competitor biomass relative to the total biomass of all basslets within each local population; these measurements included basslets of all sizes. Because the effects of competition and predation can be density dependent, the total biomass of basslets within each local population was also included in all full models as a potential covariate to account for the range in biomass observed among populations.

Visual examination of residuals from full models indicated departures from the assumption of homogenous variance among reefs, therefore I included weighted terms allowing variance to differ among reefs. When plots of residuals from full models vs. time revealed patterns indicating temporal autocorrelation, further examination of partial autocorrelation function plots typically exhibited violations of independence at small lag distances; therefore, I also included AR-1 structures in models. I used likelihood ratio tests (LRTs) to test for a difference in fit between models with vs. without these terms of variance and/or temporal correlation structures in nested models (Zuur et al. 2009; Appendix S1: Table S3). I then refit models using maximum likelihood estimation and used LRTs (type I sums of squares) to compare models with vs. without each fixed effect, starting with interaction terms; variables that were not significant were sequentially dropped from models. Final models were refit using restricted maximum likelihood to estimate effect sizes and parameters (Pinheiro and Bates 2000, Zuur et al. 2009).

Lionfish behavior

To quantify the behavior of lionfish that overlapped with basslets, I filmed all experimental basslet populations on high-lionfish reefs with GoPro video cameras (GoPro, Inc., San Mateo, CA, USA). I simultaneously filmed all three basslet treatments in each reef twice for 2.5 to 3.5 h at a time, for a total of over 50 h of video footage. Invasive lionfish exhibit increased activity in conditions of lower ambient light during the crepuscular hours of the day, and in overcast cloudy conditions (Côté and Maljković 2010, Cure et al. 2012). Thus, I filmed focal ledges during the hours leading up to sunset (video start 16:00–16:31; video end 18:19–19:58; sunset 19:35–19:45), which was sufficient for observing lionfish hunting at these deeper depths (11.9–17.4 m).

From video playback, I recorded the behavior and ledge position of each lionfish, which was estimated by visually dividing each ledge into four equal sections from the back to the front. Lionfish behavior included resting (inactive, body against reef or seafloor); hovering (body off of substrata, but relatively stationary); swimming (directional movement across the reef); and hunting (characteristic posture of head facing prey and pectoral fins flared). These encompass the breadth of behaviors that invasive lionfish exhibit throughout diurnal and crepuscular hours of the day (Côté and Maljković 2010, Cure et al. 2012). For each basslet population, I calculated the proportion of time (per video) that lionfish displayed each behavior per ledge position.

Following the statistical procedures described above, I fitted LMMs to test if the proportion of time lionfish were observed correlated with the relative biomass of fairy and blackcap basslets (basslet treatment: measured as the proportion of fairy basslet relative to the total basslet biomass per population), ledge position of lionfish, lionfish behavior, and total biomass of basslets per population as a potential covariate. Basslet measurements were from censuses conducted during the same weeks that local populations were filmed. Visual examination of residuals indicated no violations in the assumption of homogenous variance, thus weighted terms were not included in models of lionfish behavior. In the instance of a significant correlation between behavior and response, I used Tukey's Honestly Significant Difference (HSD) method to conduct post-hoc pairwise comparisons of the proportions of time lionfish displayed each behavior. I also used a subset of observations in which lionfish were hunting to test for a correlation between the ledge position of lionfish and/or basslet treatment to assess potential hunting preferences of lionfish. All statistical analyses were conducted using R version 3.4.1 (*R* Core Team 2014) with associated packages, nlme (Pinheiro et al. 2014), AICcmodavg (Mazerolle 2017), and multcomp (Hothorn et al. 2008).

RESULTS

Basslet response

The results of the field experiment were consistent with the prediction that lionfish differentially affect fairy basslet, thereby benefitting blackcap basslet: lionfish decreased the biomass of 2-cm fairy basslet (Fig. 1A; Appendix S1: Fig. S1), and the feeding position and growth rate of ~2-cm

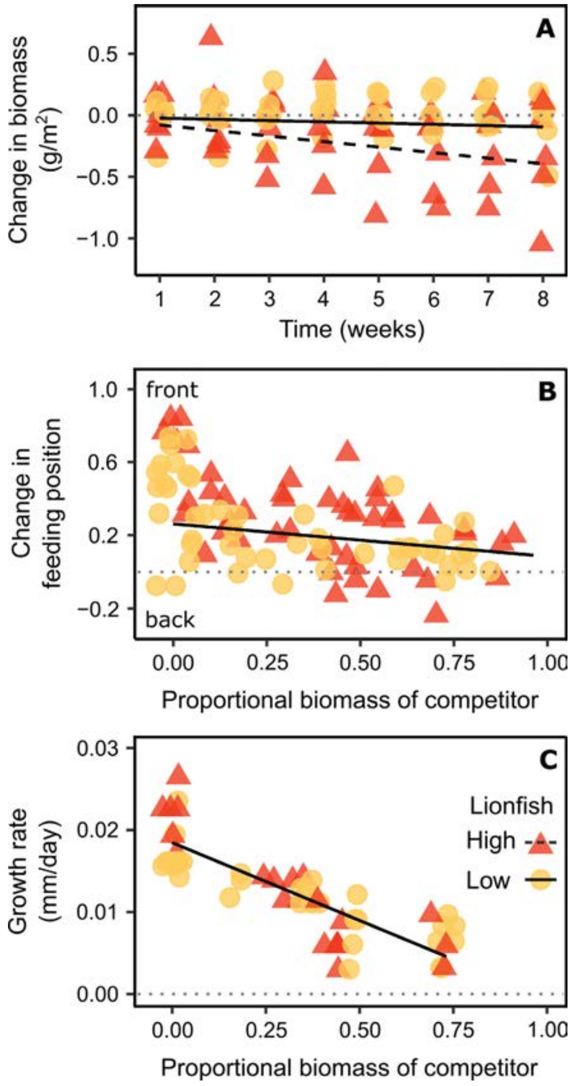

FIG. 1. Response of 2-cm fairy basslet in a manipulative experiment consisting of local populations with reduced abundances of blackcap basslet and unmanipulated controls resulting in a range of proportional competitor biomass within low- vs. high-lionfish reefs (lighter circles and solid lines vs. darker triangles and dashed lines, respectively). Lionfish affected the change in biomass through (A) time, whereas competitor biomass affected the change in (B) feeding position and (C) growth rate of fairy basslet. Intercepts and slopes of lines were estimated from linear mixed effects models fitted using restricted maximum likelihood.

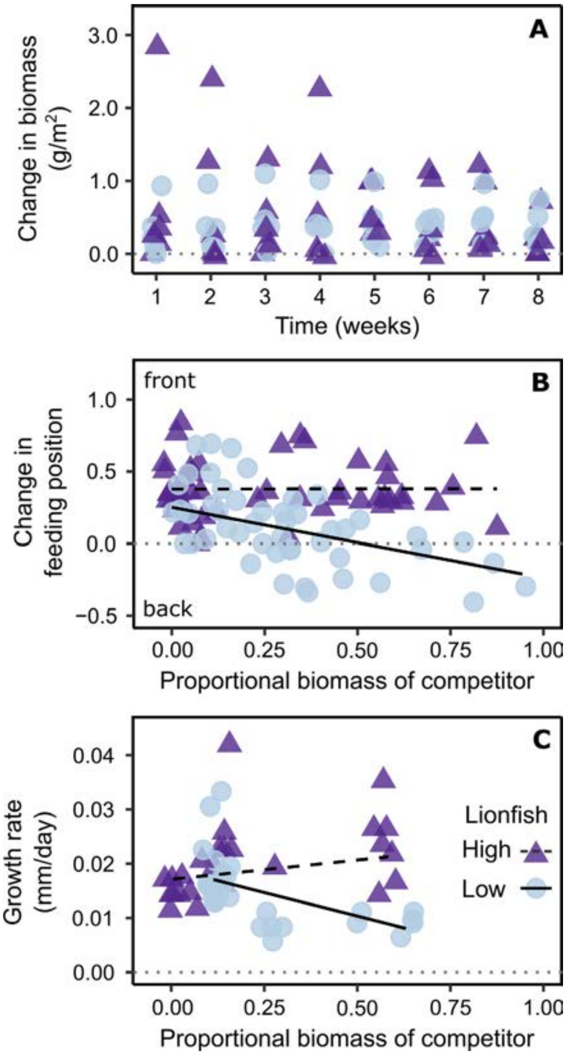

FIG. 2. Response of 2-cm blackcap basslet in a manipulative experiment consisting of local populations with reduced abundances of fairy basslet and unmanipulated controls resulting in a range of proportional competitor biomass within low- vs. high-lionfish reefs (lighter circles and solid lines vs. darker triangles and dashed lines, respectively). Competitor biomass and lionfish had no effect on (A) the change in biomass, but had interactive effects on the change in (B) feeding position and (C) growth rate of blackcap basslet. Intercepts and slopes of lines were estimated from linear mixed effects models fitted using restricted maximum likelihood.

blackcap basslet were enhanced (Fig. 2B, C; Appendix S1: Fig. S2). Despite greater mean biomass of blackcap vs. fairy basslets in reduced-competitor populations within the same reef (Appendix S1: Table S2), lionfish had an effect on the biomass of only 2-cm fairy basslet (pred × time LRT $P = 0.005$). The population biomass of these fish declined in high-lionfish reefs at an enhanced rate of on average 0.03 ± 0.01 g·m^{-2}·week^{-1} (mean ± SE) greater than in low-lionfish reefs (Fig. 1A).

The effect of competition on the feeding position of 2-cm blackcap basslet was dependent on the presence of lionfish (comp × pred × time LRT $P = 0.005$). As the proportion of competitor biomass increased, 2-cm blackcap basslet shifted closer to the backs of ledges (-0.50 ± 0.13 mean ± SEM) in low-lionfish reefs, whereas these fish shifted closer to the fronts of ledges (0.03 ± 0.14 mean ± SEM) in high-lionfish reefs (Fig. 2B). Similarly, the effect of competition on the growth rate of small blackcap basslet differed between lionfish treatments (comp × pred LRT $P = 0.010$) as expected if lionfish predation benefits this species. In low-lionfish reefs, the mean growth rate of these fish decreased -0.02 ± 0.01 mm/d as the proportional biomass of the competitor increased. In contrast, the mean growth rate of blackcap basslet increased 0.01 ± 0.01 mm/d with increasing competition in high-lionfish reefs (Fig. 2C).

Competition and predation had no effects on the change in biomass of 2-cm blackcap basslet (Appendix S1: Table S5; biomass of these fish rarely decreased from baseline values

(n = 3 time points of one population, Fig. 2A). Competition did, however, cause a shift in 3-cm blackcap basslet closer to the backs of ledges (−0.09 ± 0.05 cm, comp × time LRT P = 0.048). Lionfish did not alter any of the effects of competition on fairy basslet (all LRT P values > 0.05 of interactions including both comp and pred, Appendix S1: Table S4). The 2- and 3-cm fairy basslet shifted closer to the backs of ledges as competitor biomass increased (−0.18 ± 0.08 mean ± SEM and −0.19 ± 0.07 mean ± SEM, respectively) regardless of lionfish treatment (comp × time LRT P < 0.001 and comp LRT P = 0.017, respectively). Similarly, competition was the only variable that affected the growth rate of ~2-cm fairy basslet (comp LRT P < 0.001). The larger size classes (4 and 5 cm) of both fairy and blackcap basslets were not affected by competition or predation (Appendix S1: Tables S4 and S5).

Lionfish behavior

Lionfish ranging in size from 15 to 35 cm TL were observed overlapping with experimental basslet populations 15% of the filmed time (7.59 out of 50.7 h). The proportion of time lionfish were observed did not significantly differ among basslet treatments (LRT P = 0.155) nor among ledge positions (LRT P = 0.509), but did vary among behaviors (LRT P = 0.005). Lionfish hunted more than any other behavior (Appendix S1: Table S6) except resting (rest vs. hunt P_{cor} = 0.776). When hunting, lionfish spent similar amounts of time along all ledge positions (LRT P = 0.410) across all basslet treatments (LRT P = 0.998), regardless of variance in total biomass among populations (LRT P = 0.787). Lionfish hunted both basslet species, but the respective amounts of time could not be accurately quantified from video footage, given the small size of prey (<8 cm TL).

Discussion

By consuming a dominant competitor, predators can indirectly enhance coexistence among competitors (e.g., Paine 1974, Menge et al. 1994). My study revealed that differential predation of an invasive marine predator alters symmetrical (rather than asymmetrical) competition, which is a newly demonstrated context in which an invasive predator facilitates a native prey species via predator-mediated competitive release. Lionfish affected only juvenile (2 cm) fairy basslet in local populations, thereby reducing the effects of competition on blackcap basslet as evidenced by a positive indirect effect on the feeding position and growth rate of juveniles. Specifically, predation by lionfish was sufficient to cause corresponding shifts in feeding position toward the fronts of ledges and increases in growth rates of juvenile blackcap basslet that were comparable to the response of these fish in populations where fairy basslet had been experimentally reduced in abundance (Fig. 3).

Obtaining feeding positions closer to the front of ledges can simultaneously decrease the predation risk of native predators (Webster 2004) and enhance food acquisition (Webster and Hixon 2000, Kindinger 2016), both of which likely contributed to the observed increase in growth rates of juvenile blackcap basslet. All of these factors may increase the overall likelihood of juvenile blackcap basslet reaching adulthood by the following annual recruitment season. In contrast, invasive lionfish cause an increase in mortality of fairy basslet, with high per capita loss rates that persist even at low basslet densities (Ingeman 2016). Therefore, even though local populations are replenished annually by density-independent recruitment of fairy basslet (Webster 2003), the likelihood of these larval fish surviving to the adult stage is reduced in the presence of invasive lionfish. Importantly, studies are needed to test the long-term effects of invasive lionfish across multiple generations of basslet populations to determine whether the demonstrated influence on early life stages of basslets ultimately scales up to affect the overall structure and perhaps even persistence of local basslet populations.

Very few studies have documented the indirect facilitation (Schoener 1993) of native species by invasive predators (Rodriguez 2006). An invasive marine crab in California preferentially consumes a competitively dominant clam due to its larger prey size, which results in increased abundances of other native and non-native benthic invertebrates (Grosholz et al. 2000, Grosholz 2005). And off the coast of California, introduced pigs provided abundant prey that enabled native Golden Eagles to newly colonize the Channel Islands and heavily consume the island fox, thereby releasing populations of a competitively inferior skunk (Roemer et al. 2002). Differential predation by the Golden Eagle is likely driven by underlying variation in natural histories among prey, in which the island fox is more vulnerable to predation given its smaller size and diurnal (rather than nocturnal) activity (Crooks and Van Vuren 1995).

Potential mechanisms underlying differential predation by invasive lionfish likely involve characteristic traits and behavior of both predator and prey that influence the probability of a prey item being encountered, attacked, and/or consumed (Sih and Christensen 2001). Invasive predators are expected to have comparable effects on congeneric prey species that are taxonomically and functionally similar (Diamond and Case 1986, Ricciardi and Atkinson 2004, Thomsen et al. 2011). Consistent with this prediction, invasive lionfish spent similar amounts of time hunting across all ledge positions and among all reef ledges. These observations imply the potential predation risk of this generalist predator (Morris and Akins 2009) is homogenous throughout local basslet populations; however, invasive lionfish had negative effects on only small fairy basslet located at the backs of ledges, which suggests the realized capture success of this predator varies across the landscape (both within and among reef ledges).

Intraspecific competition appears to be stronger within fairy vs. blackcap basslets, with the smallest size classes affected the most by aggression (Kindinger 2016). Reduced access to the protective shelter of subordinate competitors is often a consequence of asymmetries in fighting ability, which ultimately enhances vulnerability to predation (Reynolds 2011, Forrester 2015). Therefore, the realized prey availability of small fairy basslet may be higher as individuals are outcompeted for refuge more frequently than intra- and interspecific competitors.

Patterns of hunting activity among visual predators are typically related to light conditions (Lima and Dill 1990). Crepuscular predators are active at twilight, but may continue to hunt in suitable light conditions during other times of day (e.g., periods of bright moonlight; Rich and Longcore

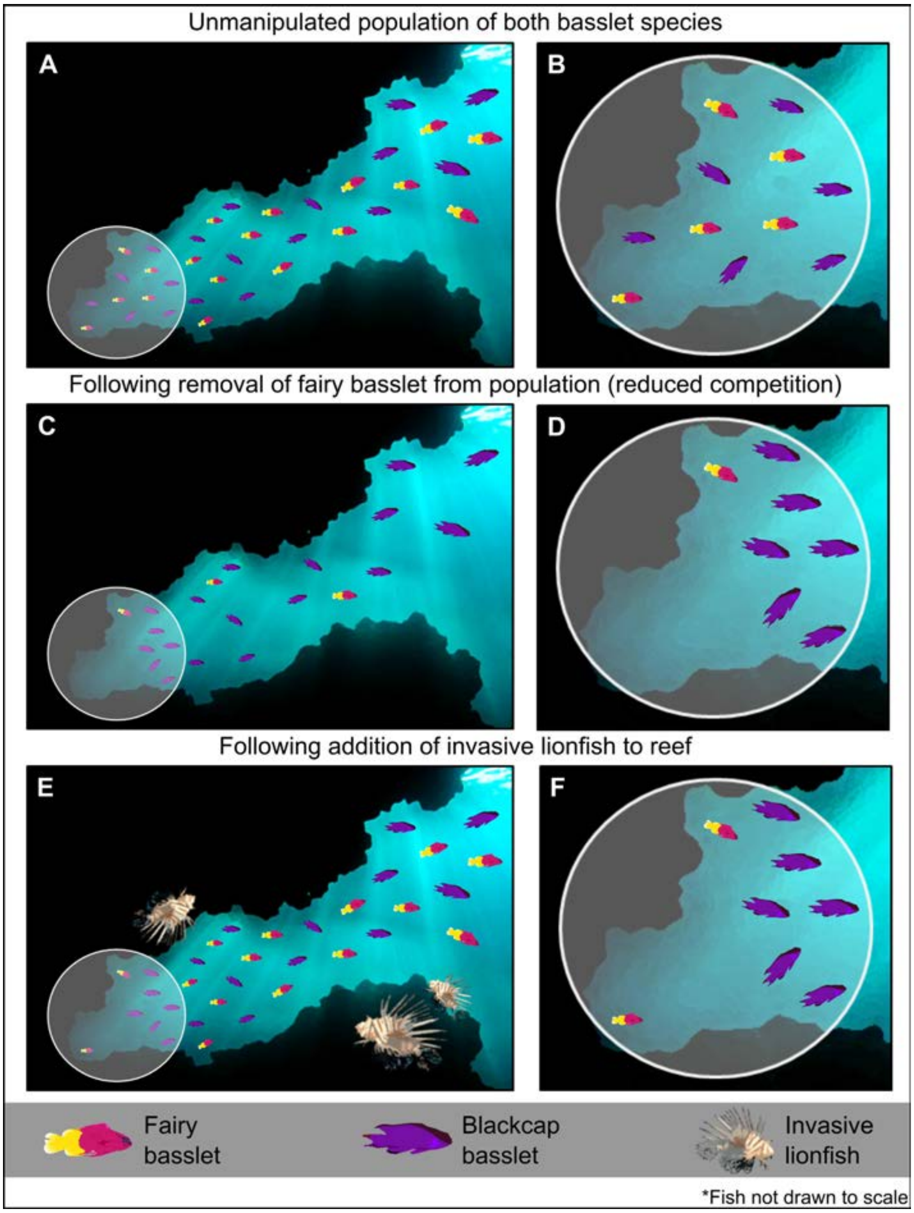

Fig. 3. Overview of how invasive lionfish alters symmetrical competition between native basslets via differential predation. Basslets are distributed in local populations based on a size hierarchy, whereby larger basslets occupy prime feeding positions at the fronts of ledges and smaller fishes are found closer to the backs of ledges (A, C, E). (A) In the absence of invasive lionfish, (B) interspecific competition inhibits the feeding position and growth rates of juveniles of both basslet species equally. (C) Following experimental reductions in fairy basslet, (D) juvenile blackcap basslet move closer to the fronts of ledges and grow faster. (E) Following the addition of invasive lionfish to reefs, (F) juvenile fairy basslet are reduced in abundance such that juvenile blackcap basslet shift closer to the fronts of ledges and exhibit increased growth rates. Therefore, the effect of invasive lionfish on interspecific competition is comparable to the effect of experimentally removing fairy basslet from populations.

2006, Mills 2008, Gaston et al. 2013). The Pacific red lionfish is a crepuscular predator that also spends a substantial amount of time hunting during the day in overcast, cloudy conditions (Cure et al. 2012) that likely result in a visual advantage over prey in lower levels of light (McFarland 1991). Assuming habitat complexity is similar along reef ledges, capture rates of lionfish may also increase as ambient light levels decrease from the fronts to the backs of ledges. The contrast in visual cues between basslet species may also be heightened in lower light levels since the fairy basslet is brighter in coloration and more active in terms of aggression than the competitor basslet (Kindinger 2016), both of which are factors that can enhance the detectability of prey to visually oriented predators (e.g., the oddity effect; Landeau and Terborgh 1986).

Invasive lionfish may also exhibit higher capture rates at the backs of ledges simply because smaller basslets are located in these positions. Smaller-sized prey can be limited in escape ability due to their smaller ranges of perception for detecting predator cues (Stankowich and Blumstein 2005), less-effective performance traits (e.g., speed, maneuverability, etc.) and defenses (Bateman and Fleming 2008), greater energetic costs associated with antipredator response (Martín and López 2015), and increased risk of capture by gape-limited predators (Urban 2007). Smaller body size often also coincides with earlier life stages of prey that are typically more vulnerable to predation having had limited opportunities for learned recognition of predators (Healey and Reinhardt 1995, Brown and Chivers 2005, Lönnstedt et al. 2012).

A lack of evolutionary history with invasive predators can also result in suboptimal antipredator response by native prey (i.e., prey naivete; Diamond and Case 1986, Cox and Lima 2006, Freeman and Byers 2006). Lionfish is an invasive species that also uses a unique hunting strategy (Albins and Lyons 2012), and the extent of naivete appears to vary among native prey fishes in the presence of this novel predator (Marsh-Hunkin et al. 2013, Black et al. 2014, Kindinger 2015, Anton et al. 2016, Eaton et al. 2016). Naivete could vary between native basslet species, however, a lack of evolutionary history between predator and prey per se cannot independently explain differential predation within prey species (i.e., among size classes).

Most of our knowledge about the importance of interactions between predation and competition comes from terrestrial and freshwater systems and is rarely tested explicitly in marine systems (reviews by Sih et al. 1985, Osenberg and Mittelbach 1996, Gurevitch et al. 2000, Chase et al. 2002). This study provides strong evidence that an invasive marine predator can alter interspecific competition, whereby differential predation tips the balance of competition between native prey species from symmetrical to asymmetrical effects on juveniles. I have also demonstrated that an invasive predator can have negative direct and positive indirect effects on native prey, further broadening our mechanistic understanding of the interactive effects of predation and competition in the context of invasive species. Conceptual frameworks of invasions consistently highlight the need to incorporate both direct and indirect effects when predicting overall impact (Parker et al. 1999, Ehrenfeld 2010, Simberloff 2011, Ricciardi et al. 2013), yet indirect processes remain a neglected concept in empirical studies (White et al. 2006). As a result, unexpected consequences can arise following the strategic reduction or eradication of invasive consumers, often due to undocumented indirect positive interactions between invasive and native organisms (e.g., Murphy and Bradfield 1992, Bergstrom et al. 2009, Simberloff 2009, Kessler 2011). Therefore, demonstrating complex interactions between invasive and native species can greatly inform and enhance management and conservation initiatives (Zavaleta et al. 2001, Byers et al. 2002).

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