AN ABSTRACT OF THE DISSERTATION OF

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Abstract approved:

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There is increasing awareness that human activities are altering the ways that natural systems operate and that local shifts in species composition and abundance can lead to abrupt and irreversible global change. Therefore, understanding the processes that buffer biological communities from critical shifts and how our actions affect natural stabilizing feedbacks are important goals of ecology. One human activity with far reaching consequences for global ecosystems is the introduction of exotic species outside of their native ranges. Introduced predators, whose effects may be exacerbated by lack of shared evolutionary history with native prey, can have particularly strong effects on recipient communities. As trophic interactions play a central role in both population regulation and community persistence, it is essential to determine the extent to which introduction of novel predators can alter the function of stabilizing mechanisms.

The goals of this dissertation were to use a combination of manipulative field experiments and theoretical modeling to explore how introduced predators influence invaded communities through their effects on the processes that naturally maintain bounded prey population dynamics and promote community coexistence. Densitydependent predation can regulate prey populations by providing a negative feedback in response to changes in population size. In my first experiment (Chapter 2), I investigated the effects of invasive Indo-Pacific red lionfish (Pterois volitans) on density-dependent mortality patterns previously documented to regulate a common native Atlantic prey species, the fairy basslet (Gramma loreto) on coral reefs in the Bahamas. By repeating a pre-invasion density-manipulation experiment, now in the context of predation by both native piscivores and lionfish, I demonstrated that per capita loss of fairy basslet remained density-dependent in the presence of lionfish, but the overall magnitude of loss was substantially greater compared to pre-invasion rates. Per capita loss was higher in 13 out of 16 basslet populations with an average increase of over 60% in the presence of the invader. The before-and-after design provided no evidence for a change in the intensity of density dependence between experiments, indicating the addition of destabilizing density-independent mortality caused by lionfish.

In my second experiment (Chapter 3), I employed a split-plot, cross-factored experimental design, manipulating both fairy basslet density and lionfish presence/absence such that differences in per capita loss rates were attributable only to predation by the invader. Over four weeks, mortality of fairy basslet was far greater on lionfish reefs compared to reefs with only native predators, displaying 2.4 times higher net loss on recruitment-enhanced fairy basslet populations and a five-fold increase in net loss at unmanipulated prey populations. Per capita loss was density-dependent in both predator treatments, but high mortality rates at low prey density on lionfish reefs resulted in extirpation of 15% of unmanipulated fairy basslet populations. In contrast, no prey populations were extirpated on reefs with only native predators.

In addition to field experiments, this dissertation includes a theoretical model (Chapter 4) that explored the effects of predator novelty on the coexistence of an intraguild predation web with adaptive antipredator defense in the shared prey. Adaptive prey responses can promote multi-predator coexistence by creating a stabilizing tradeoff in the allocation of predator-specific defense effort. Yet to date, all such theory has assumed that prey have accurate perception of predation risk and appropriate antipredator responses, assumptions that may not be justified when considering a novel predator. The model showed that the parameter region of IGP coexistence is dramatically reduced by an exotic predator but that effects of novelty on community persistence are complex and context-dependent. Specifically, the model predicts that predator novelty can weaken the effect of adaptive defense, causing exclusion of native predators that would persist in the absence of novelty. Coexistence is predicted to be more sensitive to the effects of suboptimal defense compared to naïveté and differentially leads to exclusion of native predators in highly productive environments and when defense costs are low. Moderate novelty of the

omnivore can increase resource density via a trophic cascade, while consumer novelty can either lead to omnivore exclusion or facilitate three-species coexistence by providing a subsidy to the otherwise excluded native omnivore. The results suggest that models of adaptive defense are sensitive to assumptions regarding predator-prey eco-evolutionary experience and that predator novelty has significant implications for food web dynamics.

Overall, the research described in this dissertation illuminates the mechanisms by which introduced predators can disrupt the boundedness and persistence of otherwise stable systems and provides insight into how predator novelty can alter biological communities via novel trophic and non-trophic interactions. As natural systems across the globe face multiple stressors that can alter their functioning, it is increasingly vital to understand the stabilizing mechanisms that buffer these systems from change, and how species introductions may modify the capacity for communities to respond to natural and human-caused disturbance. ©Copyright by Kurt E. Ingeman July 28, 2016 All Rights Reserved

Effects of Predator Introductions on Population and Community Dynamics

by Kurt E. Ingeman

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APPROVED:

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Kurt E. Ingeman, Author

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Effects of Predator Introductions on Population and Community Dynamics

Chapter 1— General Introduction

From its earliest beginnings, the science of ecology has focused on identifying the factors that produce and maintain stability of natural systems at multiple levels of organization. By stability in the general sense, I refer to the tendency to resist and return from change, as in common usage and which includes more rigorous concepts of resistance, resilience, persistence, and equilibrium stability. Even preceding the organization of ecology as a distinct scientific discipline, Charles Darwin (1859) was struck by the constancy in the abundance of animal and plant populations relative to what their intrinsic growth rates would potentially allow. The importance of biotic and abiotic factors in maintaining populations that neither increase nor decrease without bound was the basis of one of the longest-running and most contentious debates in 20th century ecology (Andrewartha and Birch 1954, Lack 1954, Nicholson 1954, Ehrlich and Birch 1967, Strong 1986, Murdoch 1994, Hixon et al. 2012). While this debate focused on regulation at the single-population level, a parallel research avenue sought the mechanisms producing another kind of stability at the community-level, often framed in terms of mechanisms that promote long-term coexistence of competing species (Hutchinson 1959, MacArthur and Levins 1964, Paine 1966, Schoener 1974, Caswell 1978, Chesson 1983). To explain the observation that natural food webs persist through time, researchers through the decades have invoked the stabilizing (or destabilizing) effects of species richness (MacArthur 1958, May 1973), omnivory (Pimm and Lawton 1978), interaction strengths (McCann 2000, Neutel et al. 2002), food web structure (Allesina et al.

2008), and myriad other factors. Fundamentally, each putative stabilizing mechanism represents an attempt to identify processes that counteract the inherent volatility of complex and stochastic biological systems, as well as to explain the observation that radical changes in population sizes or community composition are the exception rather than the rule (McCann 2011). Contemporary views on stable biological systems at all levels of organization (population, community, and ecosystem) have shifted away from constant steady states and point equilibria toward a fuzzier (yet defined) range of deviations around a long-term mean through time. Nevertheless, the maintenance of systems within a bounded state requires the presence of stabilizing negative feedbacks, such that when perturbed by external forces, the system does not follow a trajectory toward an entirely different state (Lenton and Watson 2011).

There is the increasing awareness that human-caused change is presently altering the ways that natural systems operate (Chapin III et al. 2000) and that local transitions to alternative states can lead to abrupt and irreversible global change (Barnosky et al. 2012). Therefore, it remains a vital goal of both basic and applied ecology to understand how various stabilizing mechanisms can buffer biological communities from critical shifts, and especially how human actions can alter important feedbacks that have heretofore prevented natural systems from undergoing radical change.

One human activity with far reaching consequences for biological communities is the introduction of exotic species outside of their native range (Vitousek et al. 1997, Meyerson and Mooney 2007). Although many species introductions either fail to establish viable populations or persist at low population levels (Mack et al. 2000), some introduced species become invasive, undergoing outbreaks that cause severe ecological change, including alteration of community structure and ecosystem function and precipitating native species loss (Gurevitch and Padilla 2004, Pimentel et al. 2005). Introduced predators can have particularly strong effects on recipient communities (Paolucci et al. 2013) and, once established, can form complex networks of interactions with native species, complicating predictions regarding their effects and effective management (Shea and Chesson 2002, Glen and Dickman 2005). Effects of invasive predators may be exacerbated by lack of shared evolutionary history with native prey (Cox and Lima 2006), especially if the invaders are behaviorally or morphologically dissimilar from native predators (Carthey and Banks 2014). Prey naïveté can thus lead to high consumption rates when prey fail either to recognize predator cues or to respond appropriately to predation risk (Carthey and Banks 2014). As a result, invasive predators have been linked to severe declines and even extinction of native prey (Blackburn et al. 2004), responses that necessarily imply an alteration of the processes that regulated prey populations prior to the invasion. As trophic interactions play a central role in both population regulation and community stability, it is therefore essential to determine whether novel trophic interactions alter important stabilizing mechanisms.

Regulation that keeps populations bounded above zero must occur at some spatial and temporal scale for a population to persist indefinitely (Murdoch 1994, Turchin 1999). To avoid a random-walk to extinction, populations must be subject to a negative feedback in response to changes in population size, such that they are constrained between upper and lower bounds and have a tendency to return toward an intermediate population size when they approach these extremes (Murdoch 1994, Hixon et al. 2012). Thus, regulation is intimately tied to the concept of demographic density dependence, whereby, as population density increases, the per capita loss rate (mortality and/or emigration) increases and/or the gain rate (birth and/or immigration) decreases in ways that bound population size. Predation can add density dependence to prey population dynamics through the functional, numerical, behavioral, or developmental responses by which the per capita consumption rate and/or local predator density increases directly with prey abundance (Murdoch and Bence 1987). However, the interactive effects of multiple predators can qualitatively change the relationship between density and mortality (Hixon and Carr 1997) so the addition of a new predator to an existing community has the potential to weaken or destroy population regulation. Therefore, examining the predatory effects of an introduced predator across a range of prey densities would be an important step towards determining the ultimate effects of the invader on native prey population regulation. In addition, such an experiment can provide insight into the effects of invasive predators on prey populations that are vulnerable to extirpation as a result of small local abundances, a key applied question in the conservation of threatened species.

However, introduced predators do not interact with prey alone. Rather, the insertion of a new predator into an existing food web may create a variety of novel competitive and predatory interactions, and these interactions may alter the processes that maintained coexistence among species of the native community. Stabilizing mechanisms at the community-level are those factors that promote coexistence by causing community constituents to have stable long-term population sizes that can

recover from perturbation (Chesson 2000). Essentially, these processes prevent species exclusion by decreasing the relative strength of negative interactions among species, such as interspecific competition, or by increasing the strength of indirect positive interactions (Matsuda et al. 1996). For example, frequency-dependent predation, wherein generalist predators switch among prey based on their density, yields a density-dependent feedback in prey dynamics such that each species can return from low abundances (Oaten and Murdoch 1975). This stabilizing process relies on an implicit tradeoff: predators cannot maximize predation on all prey simultaneously and thus predation rates among prey species negatively co-vary (Gendron 1987). By creating an indirect positive interaction among prey species, switching can promote the coexistence of competing species and can decrease the strength of apparent competition between non-competing prey (Matsuda et al. 1996). Critically, prey switching assumes that predators are less effective at capturing prey due to reduced encounter rates or increased pursuit times at low densities (Matsuda et al. 1993). Yet, introduced predators may have higher prey consumption rates even at low prey densities (Saul and Jeschke 2015), reducing the necessity of prey-switching and potentially disrupting this community stabilizing mechanism.

An equally important stabilizing mechanism in multi-predator communities that may work in concert with frequency-dependent predation is adaptive antipredator defense (Abrams 2000). In this process, prey employ predator-specific defenses (via phenotypic or behavioral trait modification) that reduce consumption rates of predator species based on the relative risk of predation posed by each (Abrams 1992). Similarly to frequency-dependent predation, the inability of prey to maximize defense simultaneously against multiple predator species yields a stabilizing tradeoff that can produce coexistence among predators (Kondoh 2007). However, this interaction is strongly influenced by the ability of prey to accurately evaluate predation risk, thereby potentially yielding competitive advantage to an introduced predator to which a native prey species is naïve. If prey fail to recognize an introduced predator, the introduction can disrupt the stabilizing effect of adaptive defense, potentially causing exclusion of native predators. Conversely, a novel predator that does elicit effective prey defense may indirectly benefit native predators via a predator-specific defense tradeoff. It is therefore of interest to examine the potential for novel predators to alter the potential for coexistence of native communities by circumventing adaptive defense in prey.

The overarching goals of this dissertation, then, are to understand how and to what extent an introduced predator may (*i*) disrupt the functioning of predatormediated population regulation of native prey and (*ii*) alter the stabilizing tradeoffs that lead to coexistence in webs of interacting species. Specifically, for goal (*i*), I conducted a series of manipulative field experiments to quantify the effects of an invasive marine predator, the Pacific red lionfish (*Pterois volitans/miles*, hereafter "lionfish") on the local population dynamics of native prey fish on Bahamian coral reefs. My goal was to understand how the invader may alter patterns of regulating density-dependent mortality caused by native predators, documented prior to the invasion. For goal (*ii*), I followed these population-level experiments with a theoretical exploration of the effects of an introduced predator on native community

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persistence, examining the role of prey naïveté and ineffective prey defense on native predator exclusion.

First documented off the coast of Florida in the 1980's (Semmens et al. 2004), lionfish have undergone dramatic increases in population densities and geographical range since the early 2000's (Schofield 2009, 2010). Their current invaded range encompasses the tropical and subtropical western Atlantic, Caribbean, and Gulf of Mexico regions extending year-round north to Cape Hatteras and south to Brazil. Lionfish possess a suite of morphological and behavioral traits that are unique in their invaded range (Albins and Hixon 2013, Côté et al. 2013). Camouflaged by cryptic coloration and possessing feather-like pectoral fins, lionfish do not resemble native Atlantic predators and may not induce effective prey defensive responses (Lönnstedt and McCormick 2013, Black et al. 2014, Kindinger 2015, Anton et al. 2016). Further, lionfish feed uniquely by herding small prey with their large pectoral fins while hunting, and employing a unique "blowing" behavior, effectively positioning and possibly disorienting prey prior to a rapid strike (Albins and Lyons 2012). Partially owing to these predatory traits, lionfish in the Atlantic display have strong negative effects on native prey-sized fishes via consumption (Albins and Hixon 2008, Morris Jr and Akins 2009, Green et al. 2012, Albins 2013, 2015) and have reached densities orders of magnitude higher than those reported from their native range (Green and Côté 2009, Kulbicki et al. 2012). Coinciding with the spread and subsequent increase in local density of lionfish, dramatic declines in native reef fish abundance and density have been observed in the invaded range (Lesser and Slattery 2011, Green et al. 2012).

Despite such evidence for the direct negative effects of lionfish on native prey population sizes, it is unknown how lionfish alter the patterns of density-dependent mortality by which native predators have been documented to regulate the local population dynamics of native prey (e.g., Hixon and Carr 1997, Webster 2003, Forrester and Steele 2004, among others). Therefore, in Chapter 2, I measured lionfish-induced changes in the mortality patterns of a common Atlantic reef and aquarium fish, the fairy basslet (*Gramma loreto*), by replicating a field manipulation of prey density that was originally conducted on Bahamian coral reefs prior to the invasion (Webster 2003). Using the same fairy basslet populations employed in the pre-invasion experiment, I experimentally manipulated the densities of local prev populations and compared demographic rates across a gradient of prey densities, now in the context of predation by both lionfish and native predators. I used the resulting cumulative per capita loss rates over the eight-week experimental to determine (1) whether or not per capita loss remained density-dependent following the lionfish invasion, (2) how the invader altered magnitude of prey mortality, and (3) any changes in the intensity of stabilizing density dependence.

Because of the before-after, natural experiment design described in Chapter 2, I could not unequivocally attribute the altered mortality patterns to lionfish, since the presence of the invader was confounded by possible environmental or biotic changes (e.g., increased native predator abundance and/or consumption rates) during the interval between experiments. Therefore, in Chapter 3, I conducted a controlled, cross-factored field experiment on natural coral reefs in the Bahamas, manipulating both prey density and invasive predator presence such that differences in per capita loss rates were attributable to predation by the invader alone. On reefs with and without invasive lionfish, I compared the immediate post-settlement and cumulative changes in density over the four-week experimental period: the magnitude of per capita loss due to predation by lionfish vs. native predators, and the presence or absence of density dependence in populations of fairy basslet prey.

In Chapter 4, I complement the field experiments described above with a theoretical exploration of the effects of novel predators on the persistence of native food webs using and intraguild predation model. Intraguild predation occurs when an omnivore both preys on and competes with an intermediate consumer for a shared resource. I consider separately two invasion scenarios in which an introduced predator alters the stabilizing tradeoff provided by adaptive antipredator defense: (i) a functionally similar invader that induces suboptimal defense, and (*ii*) a truly novel invader to which prey display reduced defensive response as a result of naïveté. I examine each of the above invasion scenarios for both an introduced top predator and an introduced intermediate consumer and evaluate the persistence of the community across gradients of productivity and defense cost. For each model variation, the primary goals are to examine the conditions that lead to native predator exclusion and to track changes in the abundance of the native predators and prey in response to predator novelty. By determining both coexistence criteria and population densities, I provide insight into the effects of an introduced predator on two different metrics of stability: community persistence and equilibrium density of species.

This dissertation employs a combination of natural and controlled field experimental studies, as well as theoretical studies to examine how an introduced 10

predator can alter the processes that produce stable population and community dynamics. While differing in methodology (experimental versus theoretical) and level of biological organization (population- versus community-level), the studies herein are linked by the conceptual view that various definitions of stability share a common underpinning in their reliance on negative feedback mechanisms that keep stable systems bounded. In asking how and to what extent introduced predators alter these stabilizing processes, this research provides insight into the mechanisms by which predator introductions can profoundly change their recipient communities. In a time of unprecedented ecological change from local to global scales, understanding the effects of exotic species on the processes that promote stability is vital to improve biological forecasting and inform the management of increasingly imperiled natural systems.

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Chapter 2 — Native prey mortality increases but remains density-dependent following lionfish invasion

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Abstract

Predators can regulate prey population dynamics, so the introduction of novel predators may alter predation-mediated regulatory mechanisms, potentially destabilizing prey populations. Compensatory density dependence is an essential condition for population regulation. Thus, understanding whether and how introduced predators alter the relationship between prey density and mortality can aid in predicting the ecological consequences of invasion. Here we investigate the effects of invasive Indo-Pacific red lionfish (*Pterois volitans*) on density-dependent mortality patterns previously documented for a common native Atlantic prey species, the fairy basslet (*Gramma loreto*). By repeating a pre-invasion density manipulation experiment, now in the context of predation by both native piscivores and lionfish, we provide a before-and-after comparison evidencing changes in prey mortality since the introduction of lionfish. Per capita loss of fairy basslet remained density-dependent in the presence of lionfish, but the overall magnitude of loss was higher compared to pre-invasion rates. In the presence of lionfish, seven of 16 local basslet populations experienced greater than 50% loss over the eight-week study duration, but there was no evidence of a difference in the slope of the density-mortality curve between preand post-introduction experiments. Our experiment therefore revealed a densityindependent increase in per capita mortality rates since the start of the invasion. We conclude that local fairy basslet populations now experience an elevated risk of extirpation as a result of increased predation and suggest that different predator foraging behavior and/or prey naïveté may explain the altered prey mortality patterns observed after the lionfish invasion.

INTRODUCTION

Species introductions have been identified as one of the greatest threats to global biodiversity (Wilcove et al. 1998, Mack et al. 2000, Sax and Gaines 2008) and can drastically alter population, community, and ecosystem-level properties of invaded systems (Gurevitch and Padilla 2004). Invasive predators, in particular, can have strong population-level impacts on native prey (Salo et al. 2007), effects that may be exacerbated by prey naïveté and/or novel hunting strategies of the invader that render anti-predator defenses ineffective (Sih et al. 2010). This lack of coevolution between introduced predator and native prey can lead to rapid and severe declines in prey populations (Simberloff 1995). As predators may regulate prey population dynamics, it is important to determine whether novel predators alter predation-mediated regulatory mechanisms, potentially destabilizing prey regulation. An essential condition for population regulation is demographic density dependence where, as population density increases, the per capita loss rate (mortality and emigration) increases and/or the gain rate (birth and immigration) decreases (review by Hixon et al. 2002). These compensatory processes can affect the bounded fluctuations and return-tendency necessary for long-term persistence of a population (Murdoch 1994b). Thus, understanding how introduced predators can alter the relationship between prey density and mortality is important for understanding the possible ecological consequences of invasion.

In reef-associated fishes, local population sizes are often sensitive to changes in the rate of post-settlement mortality caused by predation (Almany and Webster 2006). In many cases examined, predation causes density-dependent mortality in early post-settlement reef fishes (reviews by Hixon and Webster 2002, Osenberg et al. 2002, Hixon and Jones 2005, White et al. 2010). Density-dependent predation in fishes can be mediated by the interplay of multiple factors, including competition (Carr et al. 2002, Hixon and Jones 2005), availability of prey refuge (Forrester and Steele 2004), parasitism (Forrester and Finley 2006), behavioral responses by predators (Anderson 2001, Webster 2003), the synergistic effects of multiple suites of predators (Hixon and Carr 1997), spatial scale of observation (White and Warner 2007), and the relative scales of predator and prey habitat use (White et al. 2010). Because the predatory response to prey density is mediated by the identity and behavior of predators, it is difficult to predict how prey population dynamics will be altered by the introduction of an invasive predator, particularly when they share little or no evolutionary history.

Previous work comparing the functional responses of native and invasive freshwater and marine invertebrates in a laboratory setting has demonstrated that the high predatory impact of non-native predators can be attributed, at least in part, to higher per predator consumption rates (Hooff and Bollens 2004, Bollache et al. 2008, Haddaway et al. 2012). Dick et al. (2014) demonstrated experimentally that invasive bloody red shrimp (*Hemimysis anomala*) had higher prey consumption rates than native analogues and that the invader displayed a potentially destabilizing Type II functional response. To our knowledge, however, no previous study has compared the density-mortality relationship in prey before and after a predatory invasion using paired field experiments. Here, we use such an approach to explore the predatory effects of a recent and especially harmful introduced predator, the Indo-Pacific red lionfish (*Pterois volitans*).

Lionfish were first reported in the coastal waters of Florida in the 1980's (Morris and Whitfield 2009) and have spread rapidly throughout the tropical and subtropical western Atlantic and greater Caribbean regions (Whitfield et al. 2002, Schofield 2009, 2010). Within their invaded range, lionfish have reached much higher densities than those reported from the Indo-Pacific (Kulbicki et al. 2012). Their arrival in the region has precipitated large-scale declines in prey biomass (Green et al. 2012). Having high consumption rates and a generalist diet (Albins and Hixon 2008, Morris and Akins 2009, Côté and Maljković 2010), lionfish can drastically reduce recruitment of native species of reef fish (Albins and Hixon 2008, Albins 2013). Their direct and indirect effects on other species may substantially alter native reef fish communities (Albins and Hixon 2013, Côté et al. 2013).

A popular aquarium fish and common native species of that Caribbean that is now prey to invasive lionfish is the fairy basslet (*Gramma loreto*) (Morris and Akins 2009). Before the lionfish invasion, Webster (2003) demonstrated experimentally that local basslet populations in the Bahamas are regulated by temporal densitydependent mortality due to predation by small groupers and other native mesopredators. As predators provide a key mechanism of basslet population regulation, it is likely that fairy basslet dynamics are sensitive to the addition of a novel predator. Therefore, to detect and quantify potential changes to the densitydependent processes observed after the invasion, we repeated an important component of Webster's fairy basslet density manipulation subsequent to the arrival of lionfish to the Bahamas. By replicating the original density manipulations at the same reef locations, now in the context of predation by both native piscivores and lionfish, we present an unprecedented before-and-after comparison of density-dependent mortality patterns, providing insight into a novel predator-prey interaction and its potential to disrupt prey regulation. Specifically, we tested (1) whether fairy basslet mortality rates have increased, (2) whether mortality in fairy basslet has remained density-dependent, and (3) whether and how density dependence (the intercept and slope of the density-mortality curve) has been altered following invasion by lionfish.

MATERIALS AND METHODS

Study Species

The fairy basslet forms local populations of juveniles and adults inhabiting the undersides of distinct reef ledges (Böhlke and Randall 1963, Böhlke and Chaplin 1994, Asoh 1996). Isolated aggregations are demographically open via pelagic larval dispersal, yet movement of juveniles and adults among reef ledges is sufficiently rare that they can be considered local populations (Webster 2003). Local populations form size-structured social hierarchies whereby larger individuals have first access to passing planktonic food by positioning themselves at the outermost opening of the ledge (Webster and Hixon 2000). Intraspecific aggression forces smaller fish to the backs of ledges (Webster 2004) where they are subject to greater mortality from native mesopredators such as graysby and coney groupers (*Cephalopholis cruentata* and *C. fulva*). This mortality by native mesopredators at the backs of ledges is

density-dependent, contributing to between-generational regulation of local population sizes (Webster 2003).

Density Manipulation — Pre-invasion

Prior to the lionfish invasion, Webster (2003) conducted a controlled field experiment at two sites on natural reefs near Lee Stocking Island, Bahamas. This experiment involved 16 local fairy basslet populations initially ranging in size from eight to 55 individuals. Basslet populations were paired by habitat similarity (ledge size, rugosity, substrate, etc.) with one from each of eight pairs being randomly assigned to receive an increase in the density of new basslet recruits while the other being left as an un-manipulated control. Prior to density manipulations, all fish were tagged subcutaneously with elastomer pigment to differentiate these fish from subsequent settlers and to allow demographic rates (recruitment, mortality, immigration, and emigration) to be measured separately. Divers then enhanced basslet recruitment by transplanting new settlers (< 2 cm total length) to populations > 20 m from their natal reefs. Censuses commenced 24 hours after recruit manipulations to allow transplanted fish to recover from any handling effects, and weekly censuses of each population continued for 50 days.

Density Manipulation — Post-invasion

From 4 July to 2 September 2011, we partially replicated the density manipulations described above, adjusting fairy basslet populations at the same time of the year and on the same 16 reef ledges studied by Webster (2003). On ledges that received enhanced recruitment, we achieved densities nearly identical to the pre-invasion manipulations, with a mean of 13.82 fish/m² and a range of 10.59 to 23.57

fish/m² (compared to a pre-invasion mean of 13.35 fish/m² and range of 10.93 to 22.17 fish/m²). Unmanipulated population densities of fairy basslet were lower than those reported by Webster (2003), with a mean of 4.17 fish/m² and a range of 2.02 to 7.41 fish/m² (compared to a pre-invasion mean of 8.09 fish/m² and range of 4.44 to 11.78 fish/m²). This substantial decrease in population density is consistent with the findings of Green et al. (2012) who reported on average 65% declines in biomass across 42 native prey species contemporaneous with the ongoing invasion by lionfish.

We conducted a complete census of each basslet population weekly for two months, recording the total number of fairy basslet individuals at each experimental ledge. Due to logistical constraints, we were unable to individually mark priorresident fish prior to density manipulations, in contrast to the pre-introduction experiment. Therefore, we were prevented from tracking separate demographic rates of each fairy basslet population. Rather, at the end of the eight-week study period, we calculated net per capita loss of basslet for each population: the proportional change in abundance from the beginning to the end of the experiment. Loss, an aggregate measure of population change, differs from mortality in that it is inflated by emigration and reduced by natural settlement and immigration. Therefore, we reanalyzed Webster's pre-introduction data to calculate per capita loss in order to compare identical metrics of density-dependence across experiments. It is likely that loss patterns reflect similar patterns of mortality for the following reasons: 1) previous work on these same populations showed that rates of emigration, while density-dependent, were negligible compared to mortality, such that loss of individuals from a population was overwhelmingly driven by post-settlement

mortality (Webster 2003); 2) both immigration and recruitment were shown to be independent of fairy basslet density, so patterns of loss would not be systematically biased by experimentally inflated recruitment.

Predator Observations

Webster (2003) employed automated video monitoring on paired basslet populations to document density dependence in the presence of and amount of time spent actively hunting by native predators (i.e., an aggregative response). In the postinvasion experiment, we recorded the number, species, and total length of any predator within 2 m of the study ledges at the time of each weekly census. This approach allowed us to index the relative abundance of predators and to detect any aggregative response to local increases in prey density by lionfish or native predators.

Statistical Analysis

To quantify changes in fairy basslet mortality patterns since the introduction of lionfish, we employed a series of paired t-tests comparing per capita loss both between and within experiments. First, to test for the presence of density dependence in each experiment we compared per capita loss rates between control and recruitment-enhanced populations using Webster's original population pairs. For this comparison, higher loss rates in the recruitment-enhanced populations would indicate (compensatory) density dependence. Second, to quantify changes in the mortality rates for each treatment group across experiments, we compared loss rates at identical ledges before and after the arrival of lionfish. Because we sought simultaneous inferences regarding the resulting four (non-independent) pairwise comparisons, a Holm-Bonferroni correction was employed to account for the inflation of Type I error probability.

Natural variation in the unmanipulated densities of fairy populations created a continuous density gradient. Our recruitment enhancement extended this continuous range. We therefore used regression to quantify changes in the slope and/or intercept of the density-dependent mortality curve using initial fairy basslet densities as a continuous predictor of per capita loss. We employed a linear mixed-effects model (LMM) with one continuous and one categorical explanatory variable—basslet density and lionfish presence, respectively—as well as a two-way interaction between those terms as fixed effects. A significant interaction between basslet density and lionfish presence would represent an alteration in the slope in the presence of lionfish (i.e., a change in the direction or intensity of density dependence). We also incorporated a ledge term as a random effect in order to account for positive correlations in the response of identical basslet populations between experiments (non-independence).

We tested the significance of fixed effects using F-tests and estimated parameters of the final model using restricted maximum likelihood estimation (Zuur 2009). Likelihood ratio testing (LRT) with a correction for "testing-on-theboundary" (Pinheiro and Bates 2000) indicated that inclusion of random ledge resulted in better fit than a fixed-effects only model (L-ratio = 16.35027, p = 0.010, LRT). A test for heterogeneity provided no evidence to reject the null hypothesis of equal variance (L-ratio = 1.529, p = 0.22) and visual inspection of the residuals indicated that all other assumptions of linear mixed-effects model had been met.

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We measured relative predator abundance by recording the number, species identity, and total length of each individual predator with 2m of an experimental basslet population during each weekly censuses. These counts were then averaged across the total number of censuses to provide a metric of relative species encounter frequency throughout the post-invasion experiment. The authors acknowledge that individual predators are likely to have been counted in multiple censuses and therefore cumulative counts do not provide a direct measure of absolute abundance of predators in the study area. Rather, time-of-census predator observations provide an index of relative predator abundance and species encounter rates.

To determine whether native predators and/or lionfish displayed aggregative responses toward higher densities of fairy basslet prey, we employed mixed-effects logistic regression models (GLMM with logit link function) with the presence or absence of predators at the time of census as function of the basslet population density (fixed effect). In order to account for repeated measures at the basslet population level, we included ledge as a random effect. Likelihood ratio tests (z-statistic) were used to test the significance of basslet density as a predictor of predator presence, (i.e., an aggregative response). "Predator presence" was defined as one or more individual predators within 2m of the focal fairy basslet population at the time of census. For the small number of events (n=9) where multiple native or multiple lionfish predators were observed on the same ledge during the same census, all individuals were recorded but for the purposes of the logistic regression, the response was collapsed to "present." GLMMs were conducted separately for native predators and lionfish. All statistical analyses were conducted using R 3.1.3 (R Development

Core Team 2015) using packages nlme (Pinheiro et al. 2007) and lme4 (Bates et al. 2007) for analysis of mixed effects models.

RESULTS

Predator Observations

Potential predators were observed within 2m of fairy basslet populations on 50 out of 140 censuses. A total of 8 piscivore species from 4 families were observed (Table 2.1). During post-invasion censuses, lionfish were the second most commonly observed predator species (observed at 16 censuses) while the most common native predators were coney grouper *C. cruentata* (26 censuses) and graysby grouper *C. fulva* (12 censuses).

We found inconclusive evidence for aggregative behavior by native predators (GLMM LRT; Z = 1.77, p = 0.076) and by lionfish (GLMM LRT; Z = -1.65, p = 0.098). Notably, while these tests did not provide strong evidence, we observed opposing trends in aggregative behavior between native and non-native predators. On average, the odds of observing lionfish *decreased* with increasing basslet density, a multiplicative change of 0.80 for each individual/m² increase in fairy basslet density (odds-ratio).

Density Manipulation

After experimental manipulation of post-invasion populations, initial fairy basslet densities at recruitment-enhanced populations were not different from those of the pre-invasion experiment (t = 1.302, df = 7, p = 0.23, two-sided paired t-test). In

contrast, unmanipulated fairy basslet populations had substantially lower initial densities in the post-invasion experiment (t = -3.885, df = 7, p = 0.006, two-sided paired t-test). Between experiments, mean basslet density decreased by 3.92 fish/m², an average decrease of 43.5%.

Per Capita Loss

Across experiments, per capita loss in fairy basslet over eight weeks ranged from -0.27 (negative value reflecting population growth over the study duration) to 0.91. Seven of the 16 populations in the post-invasion experiment experienced greater than 50% loss over eight weeks, including two unmanipulated control populations. At one ledge, loss approached 100% during the study period despite a moderate initial basslet density. In contrast, prior to the lionfish invasion only two populations experienced per capita loss greater than 30%.

Across Experiment Comparisons

Compared with pre-invasion rates, per capita loss was higher in 13 out of 16 basslet populations and in all eight recruitment-enhanced populations (Figure 2.1). Comparing unmanipulated control populations before versus after the lionfish invasion, we observed on average 1.7 times higher per capita loss in the presence of lionfish (Figure 2.2). However high variability in loss rates among populations meant that loss rates in basslet controls were not different between experiments (t = 0.35, p = 0.74; df = 7, two-sided paired t-test). In contrast, recruitment-enhanced populations experienced higher per capita loss with lionfish present (t = 5.87, p = 0.002; df = 7, two-sided paired t-test). On average, per capita loss on manipulated ledges increased 1.6 times from 33.2% \pm 7.61% (mean \pm SE) pre-invasion to 53.8% \pm 6.62% in the presence of lionfish.

Within Experiment Comparisons

Re-analyzing Webster's pre-invasion data to calculate per capita loss did not qualitatively alter the results obtained by analyzing mortality; loss rates were higher in recruitment-enhanced populations compared to paired controls (t = 2.953, p = 0.021; df = 7, two-sided paired t-test), indicating density dependence in fairy basslet loss rates. Prior to the invasion, per capita loss was approximately six times higher at recruitment-enhanced populations versus pre-invasion controls (33.2% \pm 7.6% versus 5.50% \pm 6.25%). Further, per capita loss remained strongly density-dependent in the post-invasion experiment, with recruitment-enhanced populations experiencing higher loss rates than paired control populations (t = 5.81, p = 0.002; df = 7, two-sided paired t-test). Loss at control populations averaged 9.35% \pm 11.2% compared to 53.8% \pm 6.62% at enhanced populations, a ratio nearly identical to the 6-fold increase between control and recruitment-enhanced populations observed in the pre-invasion experiment (Figure 2.2).

Changes in Density-Dependent Curve

The linear-mixed effects model selection procedure indicated significant terms for both *basslet density* (LMM, F = 11.3, p = 0.0047; df = 14, *F*-test), and *lionfish presence* (LMM, F = 21.0, p < 0.001; df = 14, *F*-test), confirming that per capita loss remained density-dependent -- albeit at higher magnitude -- in the post-invasion experiment. Per capita loss was positively correlated with initial prey density. On average, per capita loss increased 0.051 for each unit increase in fairy basslet density. After accounting for basslet density, loss rates increased by 0.142 compared to preinvasion rates, a density-independent increase. However, we found no evidence to include an interaction term between *experiment* and *basslet density* factors (LMM, F= 0.25, p = 0.62; df = 13, *F*-test), suggesting that lionfish had not altered the slope of density dependence in fairy basslet loss (Figure 2.3). While a single basslet population was identified as highly influential due to the value of initial basslet density (see Fig 2.3), its omission did not alter the conclusions of the analysis.

DISCUSSION

Since the introduction of Indo-Pacific red lionfish to Atlantic coral reefs, per capita loss rates of native prey fishes have increased greatly (Albins and Hixon 2008, Green et al. 2012, Albins 2013). Our field experiments, repeated before and after the arrival of this novel mesopredator, reveal a density-independent increase in loss of fairy basslet compared to a pre-invasion experiment. They thereby provide circumstantial evidence that lionfish add substantially to post-settlement mortality of fairy basslet but have not, as yet, altered the direction or intensity of densitydependent loss.

Attributing mortality increase to lionfish

Although the marginal difference in loss between experiments cannot be attributed unambiguously to the invader because other sources of mortality may have changed before vs. after the lionfish invasion, additional evidence strongly implicates lionfish as a primary driver of increased post-settlement mortality. First, our predator observations at the time of censuses indicated that lionfish are now the second most abundant predatory fish on experimental reefs. Second, we observed that natural, unmanipulated densities of fairy basslet populations were nearly halved contemporaneously with the arrival and subsequent population explosion of lionfish. A three-year pre-invasion time series indicates that basslet population levels were tightly regulated and, after accounting for seasonal cycles, showed little year-to-year variability (Webster 2003). Therefore, an average reduction of 3.92 fish/m^2 at the identical reefs over the same period falls well outside of the expected range of interannual variability. Additionally, our observed increase in prey mortality is corroborated by the results of previous lionfish manipulation experiments that have measured both drastic reductions in average abundances of small native fishes and declines in species richness in the presence of lionfish. In predator manipulations on natural and artificial patch reefs, Albins and Hixon (2008) observed 79% reductions in the recruitment of native prey-sized caused by the presence of a single lionfish. A subsequent experiment (Albins 2013) demonstrated > 90% reductions in native prev compared to predator-free controls, a predator effect 2.5 times greater than that of the native coney grouper. Our observed increase in prey loss also substantiates observations by Green et al. (2012) demonstrating 65% reductions in the biomass of prey-sized fishes, including fairy basslet, at nine locations in the Bahamas coinciding with a rapid increase in local lionfish abundance. Likewise, a comparison of the fish assemblage prior (2003 - 2006) and subsequent to (2009) the arrival of lionfish on mesophotic reefs (30 - 150 m) in the vicinity of our experimental reefs documented major reductions in abundance and species richness (Lesser and Slattery 2011). Thus, our observations, combined with previously published small-scale lionfish manipulation experiments and large-scale observations, implicate invasive lionfish as a dominant driver of changes in fairy basslet mortality.

While we observed an increase in loss on recruitment-enhanced populations compared to the identical populations in the pre-invasion experiment, per capita loss rates did not differ between experiments on unmanipulated basslet populations (Figure 2.2). Among these populations, mean per capita loss increased nearly 70% in the presence of lionfish—despite the fact that initial prey densities were somewhat lower in the post-introduction experiment—but high variability in both experiments meant that this difference was not statistically significant. Two different factors may underlie this result. First, absolute population sizes on unmanipulated populations rather than prey densities per se-tended to be small relative to the recruitmentenhanced populations. In a population with few individuals, a single predation event can substantially alter per capita loss. Thus, high variability in the per capita response among unmanipulated populations may be an artifact of their sensitivity to chance events. Secondly, the initial densities of these fairy basslet populations were much lower in the post-introduction experiment, which could bias loss rates downward. In order to replicate Webster's pre-lionfish manipulation as closely as possible, we allowed control populations to remain at their observed densities, which were on average 43% lower than those observed pre-introduction (Figure 2.3). As fairy basslet loss was strongly density-dependent in both experiments, lowered starting densities in the post-invasion experiment may have resulted in lower mortality than would have been observed had starting densities matched the pre-invasion

experiment. Indeed, the three populations that experienced *lower* loss rates in the post-introduction experiment (Figure 2.1– dashed lines with negative slope) were among those with the greatest decrease in initial prey density between experiments (ranked 1st, 3rd, and 4th), with an average 63% decrease in initial fairy basslet density.

Despite the potential bias of overall lower population sizes, we still observed a non-significant *increase* in per capita loss among fairy basslet control populations, an indication of the strength of lionfish direct effects. Indeed, the results of the linear model using initial prey density as a *continuous* predictor of basslet loss -- thus accounting for differences among pre- and post-introduction population starting densities -- indicated a change in intercept but not slope between experiments (Figure 2.3). In essence, we found that while the overall *magnitude* of basslet loss was higher in the presence of the invader, the *intensity* of the density-dependent mortality curve was unchanged between experiments. Thus, we can conclude that mortality rates have increased across the entire range of prey densities.

Potential behavioral mechanisms

A possible explanation for this cumulative density-independent increase in mortality rates is that lionfish themselves cause density-independent mortality that is simply added to the density-dependent mortality caused by native predators. Our experiment did not explicitly test behavioral mechanisms underlying our results, yet based on our anecdotal observations as well as known behavioral and morphological differences between native predators and lionfish, several non-mutually exclusive hypotheses could explain these results.

First, differences in spatial patterns of foraging between native and introduced predators could lead to differential prey mortality patterns. Over the short span of an eight-week field experiment, predators can cause density-dependent mortality only through (i) a Type III functional response, where individual (per predator) consumption rates are an accelerating function of increasing prey density (Holling 1959, Murdoch 1969); (ii) an aggregative response, where predator density is associated with higher prey concentrations (Hassell and May 1974); or (iii) a combination of both. Several studies of reef fishes have identified predator aggregation as a common behavioral mechanism leading to density dependence (Hixon and Carr 1997; Anderson 2001; Webster 2003; but see Overholtzer-McLeod 2006). In these same basslet populations prior to the invasion, data from automated time-lapse video cameras demonstrated that native predators were observed more frequently, and spent a greater proportion of their time actively hunting, near recruitment-enhanced basslet populations compared to controls (Webster 2003). This aggregative response led to the density-dependent mortality observed in the preinvasion experiment. In contrast, the current study demonstrated no such aggregative response by lionfish. In fact, lionfish presence was weakly associated with *lower* fairy basslet densities, a spatial distribution that would not, by itself, lead to densitydependent mortality. It should be noted that we found inconclusive evidence of an aggregative response in either category of predators using time-of-census predator observations. Diver observations may be less powerful than remote video surveys for capturing unbiased counts due to altered fish behavior in the presence of divers (Lindfield et al. 2014). An additional caveat is that lionfish activity levels and

foraging rates increase during the crepuscular period (Green et al. 2011, Cure et al. 2012); thus diurnal time-of-census observations may not capture spatial patterns of foraging, including potential aggregative responses. While we would not recommend drawing any strong conclusions from our predator observations, we suggest that lionfish foraging behavior may be an important mechanism driving differential predator effects and deserves further study.

The idea that different foraging behavior between native and invasive predators could lead to the observed prey mortality patterns is consistent with the scale-dependency advanced by White et al. (2010) for resolving contradictions in patterns of density-dependence observed in studies of reef fishes. While native ambush predators cause density-dependent mortality by aggregating at the scale of local basslet populations, lionfish foraging patterns may exceed the spatial scale at which basslet concentrations are clumped. Thus, lionfish predation could be causing density-independent mortality at the spatial scales of our study because their foraging effort is distributed more or less evenly across a large area of continuous reef containing multiple local basslet populations. Future studies comparing how the spatial scale of foraging patterns differ between native and introduced predators may lead to insight into their effects on prey dynamics.

A second potential mechanism for resolving the observed mortality patterns involves prey refuge availability and predator recognition. In reef fishes, the relative availability of predator-free shelter space can mediate the per capita risk of predation, thereby altering the slope of density-dependent mortality (Forrester and Steele 2004). Anti-predator defense in fairy basslet is characterized by individuals fleeing into

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small refugia within the ledges that they inhabit (Webster and Hixon 2000). In Pacific damselfishes at high conspecific density, competition for limited refuge can result in correspondingly high per capita mortality as some individuals are unable to secure adequate shelter (Holbrook and Schmitt (2002). In contrast, low-density populations experience higher relative refuge availability and are subject lower per capita mortality rates. However, antipredator responses are only effective if predation threats are recognized as such. Lionfish are morphologically and behaviorally unique in their invaded range (Albins and Lyons 2012) and may not present similar predator cues to those provided by native piscivores (Albins and Hixon 2008). Indeed, evidence from a controlled lab study demonstrated that even sympatric Pacific damselfish (Chromis viridis) that were conditioned to P. volitans olfactory cues displayed reduced antipredator responses and increased mortality compared to trials with other scorpaenid and serranid predators (Lönnstedt and McCormick 2013). If fairy basslet are naïve to the threat of lionfish predation and fail to respond appropriately, then lionfish may consume a large proportion of prey even when shelter is abundant at low prey density. Anecdotally, we observed many native prey fishes, including fairy basslet, showing a reduced flight response to approaching lionfish compared to native predators. Thus, predator crypsis or lack of recognition may allow lionfish to exploit prey equally effectively across the range of prey densities—despite differences in relative shelter availability—resulting in the observed pattern of increased density-independent mortality.

Key assumptions

Attributing the observed density-independent increase to lionfish requires the nontrivial assumptions that (1) native predators have not increased fairy basslet consumption rates, and (2) lionfish foraging neither interferes nor causes synergistic effects when combined with foraging by native predators. In evaluating the first assumption, an alternative explanation for our results is that the abundance and/or per capita consumption rates by native mesopredators have increased since the preinvasion experiment leading to greater basslet post-settlement mortality. However, several lines of evidence argue against this scenario. First, while we cannot directly compare predator abundance, encounter, or consumption rates between experiments due to the different nature of the two experiment's predator observations, regional trends in piscivore abundance over this time period offer circumstantial evidence. Observational data across the greater Caribbean from 1994 to 2008 indicate that the most commonly observed native mesopredators during the post-invasion experiment either show no temporal signal in abundance (C. fulva, C. cruentata) or a significant decline (Aulostomus maculatus) (Stallings 2009). More recently, observations from another location in the Bahamas demonstrated substantial declines in native mesopredators biomass coinciding with increases in lionfish abundance (Green et al. 2012). In addition to density-mediated changes in predation rates, removal of largebodied piscivores, such as Nassau grouper (*Epinephelus striatus*) can lead to behavioral release of smaller mesopredators (Stallings 2008), potentially increasing prey mortality rates. However, large-bodied Nassau grouper were abundant on study reefs, with the greatest biomass and second greatest abundance of native piscivores

observed during censuses. Also, while not enumerated during time-of-census surveys, large mobile predators, such as reef sharks (*Carcharhinus* spp.) and large jacks (Family *Carangidae*) were commonly observed throughout the study area, further reducing the likelihood of behavioral-release of small groupers. It therefore appears unlikely that either increased abundance or behaviorally-mediated release of native mesopredators could alone account for the observed increase in basslet mortality.

In order to evaluate the potential for compensatory or synergistic predation (interactive effects), an alternative experimental design with lionfish presence/absence and native predator presence/absence manipulated orthogonally would be required. While we were prevented from employing a cross-factor predator manipulation due to the mobility of predators in continuous reef habitat, this design has been conducted on small patch reefs with P. volitans and C. fulva as the focal predators (Albins 2013). The results of this study were consistent with compensatory predation. However, it should be noted that predator interactions on small patch reefs may play out differently than on large, continuous reefs where predator movement may be more important and where habitat characteristics may play a different role. For example, we observed native predators most often lurking toward the back of reef ledges in our study, while lionfish more frequently foraged along the outer edge of the reef (authors' pers obs). Thus, predator avoidance in response to native predators could make fairy basslet more susceptible to predation by lionfish, and vice-versa (synergistic predation, sensu Hixon and Carr 1997). As our study cannot directly

discriminate between additive versus non-additive predation future work should evaluate native and non-native predator interactions.

Implications for population regulation

This study provides evidence that an introduced predator can alter the densitymortality relationship derived from native interactions alone by raising per capita mortality rates across a range of prey densities. We found that, since the introduction of lionfish, mortality rates have increased substantially but remain density-dependent for local prey populations. The ultimate risk of such additional mortality is the extirpation or even extinction of native prey species. Subsequent field experiments with invasive lionfish have demonstrated cases of extirpation of local fairy basslet populations (Ingeman, unpublished manuscript), as well as declines in local species richness compared to lionfish-removal reefs (Albins 2015).

The large-scale effects of local extirpation remain uncertain. Extinctions in marine systems—where local populations may be continually recolonized by larval dispersal—are relatively rare and to date there are no known global marine fish extinctions (Dulvy et al. 2003). However, invasions by marine predatory fish are also rare and lionfish may represent an unprecedented scenario where the wide geographic range, extreme population densities, and morphological and behavioral novelty contribute to extremely high predation rates (Albins and Hixon 2013, Côté et al. 2013). Our observation that loss in fairy basslet remained density-dependent in the presence of lionfish means a potential regulatory mechanism remains intact. Despite increased predation rates, prey populations could achieve (dynamic) stability over time, albeit at lower average densities. However, a density-dependent demographic

rate is a necessary, but not *sufficient* condition of population regulation (Murdoch 1994b) and determining the long-term viability of prey populations would require monitoring of changes in recruitment rates as well. Further, from an invasion-wide perspective, there is no evidence that lionfish population densities have reached a maximum (Albins and Hixon 2013) and lionfish predation at the metapopulation-scale may lead to regional declines, eventually swamping any compensatory dynamics at the level of local prey populations.

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Figure 2.1 Change in per capita loss of fairy basslet in each local population across experiments. Comparing pre-invasion loss rates (on left) to values observed at the same populations after the introduction of lionfish (on right), fairy basslet loss rates overall were higher in the presence of lionfish. Thirteen out of 16 populations experienced higher rates in the post-introduction experiment, indicated by positive slopes for the majority of populations, including all eight recruitment-enhanced populations (solid black lines). Five of eight unmanipulated populations (dashed gray lines) also experienced increased per capita loss in the post-introduction experiment despite lower initial basslet densities.



Figure 2.2 Mean per capita loss of fairy basslet over eight weeks during field experiments conducted before (left, gray bars) and after (right, black bars) the lionfish invasion. Bars labeled "Cont" display average per capita loss in unmanipulated basslet populations in each experiment (n = 8 local populations per experiment); bars labeled "Inc" represent average per capita loss in populations that received enhanced recruitment (n = 8). Values with different letter labels are significantly different (Holm-Bonferroni corrected paired t-tests; familywise threshold p < 0.05). Within each experiment, per capita loss was density-dependent (i.e., greater per capita loss in increased-recruitment populations versus paired controls) (p = 0.043 for pre-invasion experiment; p = 0.002 for post-invasion experiment, two-sided paired t-tests). Comparing within basslet-density treatments between experiments, control populations were not different before versus after the lionfish invasion (p = 0.74, twosided paired t-test) while density-increase populations experienced higher per capita loss in the post-lionfish experiment (p = 0.002). Note: Error bars represent one standard error of the group means and are not reflective of significance based on the paired-sample tests.



Figure 2.3 Per capita loss of fairy basslet over eight weeks in field experiments as a linear function of initial density before (filled circles, solid line) and after the lionfish invasion (open circles, dashed line). Accounting for the effect of basslet densities, per capita loss was higher in the presence of lionfish (p < 0.001; *F*-test), yet the slopes of the pre-invasion and post-invasion curves were not statistically different (p = 0.62; *F*-test), suggesting that lionfish presence has not altered the intensity of density-dependence and has simply added density-independent mortality. Regression lines are fitted from linear mixed-effects model.



Supplement Figure 2.1 Time series of fairy basslet A) density, B) cumulative change in density, C) interval per capita loss (since previous census), and D) cumulative per capita loss (since initial census) at both recruitment-enhanced (black triangles and solid lines) and control populations (gray circles and dashed lines). Comparing panels A and C, it is evident that much of the loss in recruitment-enhanced populations was experienced early in the experiment when the absolute densities were highest. However, in the final censuses, after a short-term drop in per capita loss across both treatments (likely reflecting a natural recruitment pulse) loss is substantially higher in increase populations despite a moderate difference in prey density between treatments.

Table 2.1 Relative abundance of potential fairy basslet predators as observed during weekly censuses. "Total observations" are the number of individuals of each species observed at experimental ledges over the course of the survey period, while "Frequency" represents the average number of individuals of each predator observed per basslet population per census. As individual predators may have been observed during multiple censuses, these values represent an index of relative predator abundance. Introduced lionfish (bold) were the second most frequently observed resident predator in the study area. Large, mobile predators (e.g., jacks) were not recorded.

Rank	Scientific name	Common name	Family	Total obs.	Frequency (obs/census)
1	Cephalopholis fulva	coney	Serranidae	26	0.186
2	Pterois volitans	red lionfish	Scorpaenidae	16	0.114
3	Cephalopholis cruentata	graysby	Serranidae	12	0.086
4	Epinephelus striatus	Nassau grouper	Serranidae	12	0.086
5	Aulostomus maculatus	trumpetfish	Aulostomidae	4	0.029
6	Lutjanus apodus	Schoolmaster snapper	Lutjanidae	3	0.021
7	Liopropoma rubre	Peppermint basslet	Serranidae	1	0.007
8	Serranus tigrinus	Harlequin Bass	Serranidae	1	0.007

Chapter 3 — Lionfish cause increased mortality rates and drive local extirpation of native prey

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ABSTRACT

As predators play a central role in prey population regulation, predicting the impact of a novel predator requires determining how the invader affects the compensatory dynamics that underlie native prey persistence. The Indo-Pacific lionfish (*Pterois volitans*) is an invasive mesopredator that voraciously consumes native coral-reef fishes of the tropical Western Atlantic and Caribbean. The fairy basslet (*Gramma loreto*) is a common prey of lionfish, and pre-invasion research has demonstrated that basslet populations undergo regulating density-dependent mortality due to predation. To unequivocally measure lionfish effects on prey mortality and to test whether prey survival remained density-dependent when exposed to predation by the invader, I conducted a controlled field experiment wherein both fairy basslet settlement density and lionfish presence were manipulated by divers on natural coral reefs. On reefs with and without lionfish, I repeatedly censused fairy basslet populations over the 28-day experimental period and quantified mortality rates across a gradient of prey density. Per capita loss of fairy basslet was density-dependent on reefs with and without introduced lionfish; however the magnitude of this loss was significantly higher on reefs with the invader present. High mortality rates at low prey density resulted in local extinction of two of 14 fairy basslet populations exposed to the invader, a phenomenon observed only on lionfish reefs. Further, nine out of 14 lionfish-exposed prey populations showed loss rates of greater than 50% compared with just three prey populations with such rates on native-only reefs.

INTRODUCTION

Anthropogenic species introductions have been identified as a top conservation priority (Wilcove et al. 1998) as invasions can lead to altered community structure and ecosystem function and to native species loss (Gurevitch and Padilla 2004, Pimentel et al. 2005, Vilà et al. 2011). Invasive predators have caused some of the most severe impacts of introductions (Salo et al. 2007, Jones et al. 2008) and have precipitated numerous extinctions via strong, direct, consumptive effects (Blackburn et al. 2004, Kumschick et al. 2015). These invasive predatormediated extinctions necessarily imply a change in the processes that had previously ensured persistence of regulated prey populations. One condition of regulation is a compensatory response in one or more demographic rates to changes in prey density, causing populations to increase when rare and to decrease when abundant (Murdoch 1994, Hixon et al. 2002). Therefore, predicting the impact of a novel predator requires an understanding of whether and how the invader alters existing compensatory dynamics that underlie native population regulation.

Demersal marine fishes have been instrumental in the detection and quantification of such demographic density dependence as these populations are often amenable to the local-scale manipulations that can provide insight into the mechanisms behind density-mediated effects (Hixon and Webster 2002). Consensus has emerged that post-settlement mortality of demersal marine fishes often displays direct density dependence—a positive relationship between prey density and per capita mortality (Hixon 1998, Hixon and Webster 2002, White et al. 2010). Numerous studies have demonstrated that predation is often the proximate cause of
directly density-dependent (hereafter DD) mortality (Hixon and Carr 1997, Anderson 2001, Carr et al. 2002, Holbrook and Schmitt 2002, Hixon 2015) and that this mechanism can lead to temporal population regulation (Steele 1997, Carr et al. 2002, Webster 2003, Hixon et al. 2012).

Of vital importance for understanding the implications of a predator introduction is characterizing the effects of multiple predators on patterns of prey mortality. Previous work on patch reefs has demonstrated emergent, synergistic effects of resident and transient predators on prey mortality patterns. Hixon and Carr (1997) showed that the effects of predators with differing hunting modes and scales of foraging (resident ambush piscivores versus transient pelagic hunters)—which separately caused density-independent (DI) mortality—interacted to produce DD mortality only when both predator types were present. Thus, the addition of a predator to an existing community has the potential to qualitatively alter the relationship between prey density and predation risk.

As the role of *native* predators in causing DD mortality is well understood in demersal fish communities, the introduction of a *novel* piscivore provides the opportunity to test how mortality patterns are altered by an invader. Theory predicts that DD (at some life stage and at some spatial scale) is a necessary condition for regulation (Murdoch 1994, Hixon et al. 2002), and simulations suggest that the effects of introduced predators on prey consumption rates may be particularly pronounced at low prey densities (Saul and Jeschke 2015), so the potential for a novel predator to weaken or even reverse DD demands study. Previously, Ingeman and Webster (2015) used manipulative field experiments—replicated before and after the introduction of the Indo-Pacific lionfish (*Pterois volitans*) to Western Atlantic marine habitats—to measure changes in the density-mortality patterns of a common reef fish, the fairy basslet (*Gramma loreto*). Per capita loss in fairy basslet remained DD after the invasion despite an increase in overall loss rates since the introduction of the novel predator (Ingeman and Webster 2015). However, the authors could not unequivocally attribute the altered mortality patterns to lionfish since the presence of the invader was confounded by possible environmental or biotic changes (e.g., increased native predator abundance and/or consumption rates) in the interval between experiments.

Therefore, in order to detect the effects of an invasive predator on the relationship between density and predation risk in native prey, I conducted a controlled field experiment on natural coral reefs in the Bahamas, manipulating both prey density and invasive predator presence, such that differences in loss rates are attributable to predation by the invader alone. On reefs with and without invasive lionfish, I compared (1) the immediate post-settlement and longer-term changes in density over the 28-day experimental period; (2) the magnitude per capita loss due to predation between repeated censuses; and (3) the presence or absence of DD in populations of fairy basslet prey.

METHODS

Study species

The fairy basslet (*Gramma loreto* Family Grammatidae) is a common aquarium fish inhabiting coral-reefs throughout the tropical Western Atlantic (Böhlke and Randall 1963). Like most reef fishes, the fairy basslet has a bipartite life-cycle with pelagic larvae and demersal juveniles and adults (Böhlke and Chaplin 1994). Fairy basslet are typically found on the ceilings of caves, outcrops, and open reef ledges (hereafter "ledges" collectively), where they feed opportunistically on passing plankton (Randall 1967). Individuals form dense aggregations with the largest individuals occupying prime feeding positions nearest the outer edge of the ledge (Freeman and Alevizon 1983). Population size at the local level is tightly regulated by high and density-dependent mortality caused by aggregating mesopredators (Webster 2003). Tagging studies have confirmed static membership of local aggregations and demonstrated that juveniles and adults rarely move farther than 3 m from their home ledge, such that post-settlement immigration is negligible and each ledge supports a distinct local population (Webster 2003).

The Indo-Pacific lionfish (*Pterois volitans/miles*), Family Scorpaenidae) is an invasive mesopredator introduced in the mid 1980's that has rapidly spread throughout the region from an invasion locus near Southeast Florida (Whitfield et al. 2002) and now inhabit most of the Western Atlantic and Caribbean, including the Gulf of Mexico (Schofield et al. 2010). These voracious, generalist predators have strong direct effects on native prey fishes via consumption of newly settled recruits and adults of small species (Albins and Hixon 2008, Albins 2013, 2015, Côté et al.

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2013, Benkwitt 2014, Ingeman and Webster 2015) and have the potential to alter invaded reef ecosystems directly through consumption of ecologically important native fishes and via the indirect effects of predation (Albins and Hixon 2013). To date, few biotic controls have been identified in the invaded range: Atlantic lionfish are relatively free of parasites (Sikkel et al. 2014) and do not experience increased mortality or emigration even at extreme densities (Benkwitt 2013). Lionfish possess an impressive array of traits that may render them difficult to detect and/or may confuse prey (Marsh-Hunkin et al. 2013, Lönnstedt & McCormick 2013, Black et al. 2014) and are themselves well-defended from predation by venomous dorsal spines (Halstead et al. 1955). As such, predation on lionfish in the invaded range, although reported, is irregular and thus far insufficient to control their densities (Hackerott et al. 2013), which have been reported as high as 393 individuals per hectare (Green and Côté 2009). Fairy basslet are common prey of the invader, which actively stalks juveniles and adults with large pectoral fins extended, herding individuals before striking rapidly (Albins & Lyons 2012). Anecdotally, fairy basslet individuals do not employ as robust an anti-predator response (fleeing into small refugia in the reef) to lionfish as toward native mesopredators. Experiments with other native Atlantic prey species have demonstrated a suboptimal response to the threat of predation by this novel predator (Black et al. 2014).

Study area

This study was conducted on coral patch reefs near the Cape Eleuthera Institute, Eleuthera, Bahamas. Patch reefs of highly variable structure occur on a 2-30 m deep shelf lining the 1500m deep Exuma Sound to the southwest of Cape Eleuthera. Prior to the initiation of the experiment, teams of divers on SCUBA identified 14 patch reefs ranging in surface area from 137 to 1290 m² at depths of 4-20 m, surrounded by sand and seagrass, and separated from all other hard substrate by at least 80 m. Experimental patch reefs were roughly cylindrical in shape and of variable diameter (10 to 30 m) and height (2 to 18 m). The benthos was dominated by small coral heads, algae, sponges, and soft corals of various species scattered over highly convoluted dead coral surfaces.

Experimental design

To determine the effects of invasive lionfish predation on prey densitymortality patterns, local fairy basslet populations were manipulated to create a range of prey densities on reefs with and without the introduced predator. Because the home ranges of adult lionfish span multiple local populations of fairy basslet prey, which restrict their movements to individual reef ledges, this study employed a splitplot design, whereby predator treatments where maintained at a larger scale (reef) than basslet density treatments (ledges within reef). Reefs were paired by proximity, as well as similarity in size, depth, vertical relief, and relative coral cover, to form 7 experimental reef pairs. One reef in each pair was assigned by randomization to receive periodic lionfish removals (with randomization constrained to avoid excessive clustering of this treatment; "native-only reef"); the other reef received variable levels of lionfish addition with the goal of achieving a standardized lionfish density ("lionfish reef"; see *Density Manipulations* next section). Within each reef, two fairy basslet populations were chosen based on similarity in initial population size, ledge area, proximity to reef margin, and orientation to prevailing currents. In order to

maximize demographic isolation of experimental fairy basslet populations, only discrete ledges that were > 3 m from other occupied ledges were chosen. Divers then performed an initial baseline census of all fairy basslet individuals on each experimental ledge and measured ledge surface area (0.4 to 1.5 m^2) to determine unmanipulated densities (6.3 to 18.9 fish m^{-2}). One fairy basslet population from each reef was then randomly chosen to receive artificially enhanced recruitment sufficient to increase density to levels commonly observed after a recruitment event (Webster 2003, Ingeman and Webster 2015). Fairy basslet additions rather than removals were employed to avoid artificially inflating extirpation rates by lowering prey density below ambient levels. Natural variation in the densities of unmanipulated populations created a continuous density-gradient that was thus extended by diver-enhanced artificial recruitment (manipulated population densities: 13.6 to 31.1 fish m⁻², see *Density Manipulations* next section).

Density manipulations

To maintain native-only reefs, divers conducted removals as needed, capturing lionfish using hand-nets where possible and employing pole spears where conditions made live-capture impossible. While the target for native-only reefs was complete removal of lionfish, the cryptic nature of this species, highly protected reef refugia, and occasional immigration resulted in low but non-zero densities on removal reefs. To maintain treatment densities on lionfish reefs, divers periodically captured juvenile and adult lionfish (8 to 38 cm TL) from native-only reefs and nonexperimental habitats then translocated them to distant (>500m) lionfish reefs. A target density of 300 lionfishhectare⁻² was chosen to represent a realistic average lionfish density based on observations of unmanipulated reefs in the region and other parts of the invaded range (Green and Côté 2009, Albins 2015). Transplant effects and variable emigration throughout the study duration necessitated repeated "stocking" of lionfish reefs. However, targeted censuses indicated a strong density gradient between predator treatment levels, with lionfish reefs maintaining approximately 6 times higher densities (240.4 ± 35.7 lionfish hectare⁻²) compared to native-only reefs (40.1 ± 18.3 lionfish hectare⁻²).

To enhance the natural range in fairy basslet density, recruits (approximately 1-2 weeks post-settlement and < 2.0 cm TL) were captured using dip nets and anesthetic clove oil, transferred into seawater-filled plastic bags, and translocated to target populations. Recruits were captured from distant locations to minimize emigration from study ledges. Small numbers of recruits (< 10) were added to a population during any single dive and additions were conducted over several days in order to simulate a natural recruitment pulse and to minimize immediate (pre-census) loss of basslet transplants to aggregating predators. Censuses for the experiment commenced 24 hours after recruit manipulations, thereby allowing a day for transplanted fish to recover from any handling effects and ensure that transplanted individuals did not suffer disproportionate mortality compared to resident fish.

Following the establishment of treatments and baseline censuses, a minimum of two divers re-censused each population after two days, four days and weekly thereafter, with a final census after four weeks. During each census, divers recorded the size of each fairy basslet individual, the total population size, and any predators within 2 m of the target basslet ledge. Observations of fairy basslet populations and individual sizes were highly congruent between divers, indicating that observation error was negligible.

Statistical analysis

All fairy basslet populations were censused prior to artificial recruitment enhancement and initial densities were checked for systematic bias by both predator treatment and assignment to recruitment-enhancement. Mean densities among treatment groups were compared using Welch's two-sample t-tests, with no assumption of equal variance. These comparisons were repeated for fairy basslet observations at the first post-manipulation census to ensure that a) mean fairy basslet density differed significantly among recruitment-enhanced versus unmanipulated populations and that b) differences in fairy basslet density were not biased among reefs with and without lionfish. Additionally, cumulative population-level effects of fairy basslet on prey density were assessed by comparing the four resulting categorical treatment levels created by cross-factoring predator treatment (lionfish versus native-only reefs, 7 reefs each) and fairy basslet recruitment regimes (enhanced versus unmanipulated, 14 ledges each, 28 ledges total).

Prey per capita loss was defined as the proportional change in abundance accumulated between intervals.

$$(1 - N_{t+1}/N_t)$$

Thus, positive values for per capita loss at a given time-step indicate that the total number of individuals decreased since the previous census, and this value is scaled to the previously observed abundance. Natural recruitment of fairy basslet was observed in between the 3^{rd} and 4^{th} censuses, indicated by reduced net loss and even

population increases on some ledges. Uncontrolled recruitment means that net loss (as an aggregate measure of population change) likely underestimates mortality but is not likely to systematically bias results since fairy basslet recruitment has been shown to be density-independent. I did not explicitly account for the difference in length of time intervals, which is likely to increase variability around estimates of per capita loss. However, time intervals were identical among treatment groups so this would not bias comparisons among groups or introduce a spurious effect of lionfish on patterns of mortality. To detect lionfish-induced changes in the magnitude of mortality and the presence of DD in fairy basslet per capita loss, I employed linear mixed effects models (LMMs) with 'ledge' nested within 'reef' as random effects; 'lionfish presence' and 'time-step' as categorical fixed effects; and 'prey density' (Note: this term represents the density at the beginning of each sampling interval and not the initial prey density) as a continuous fixed effect. In order to test the significance of lionfish presence on per capita loss at each census, I included a 'lionfish x time-step' (fixed) interaction term. A significant interaction between lionfish and time-step would indicate a lionfish-induced change in the magnitude of mortality in interval since the previous census. Further, to measure an effect of lionfish on the presence of DD, I incorporated a 'lionfish x basslet density' (fixed) term. This inclusion allows separately fitted slopes of the response of fairy basslet loss to prey density on lionfish and native-only reefs. A slope coefficient for lionfish reefs that does not differ from zero would be consistent with the hypothesis that lionfish predation eliminates regulating DD.

I fitted full models (including all fixed effects and interactions) with and without random effects using restricted maximum likelihood estimation (REML) and compared them using likelihood ratio test (LRTs) with an adjustment for testing-on the-boundary (Zuur et al. 2009). The inclusion of a random intercept at the 'ledge' level resulted in a better fit than a fixed effects only model (L-ratio = 9.43, p = 0.001). Visual inspection of the residuals of the resulting models showed no departures from the assumptions of homogenous variance and normality among populations. However, there was evidence of temporal autocorrelation in the residuals and inclusion of an AR1 structure substantially improved the model ($\Delta AIC >> 2$). Reexamination of the residuals indicated that all assumptions had been met. After selecting the optimum random effects and correlation structure, I refit the competing models using maximum likelihood (ML) and tested the significance of fixed effects using LRTs. Where LRTs indicated that interaction terms were not significant, they were dropped from the model and the main effects were tested using LRTs. Finally, I estimated parameters and effect sizes from the final model using REML (Zuur et al. 2009). All statistical analyses were conducted in the R language and software environment, v. 3.2 (R Development Core Team 2015) using add-on packages nlme v. 3.1-103 (Pinheiro et al. 2014).

RESULTS

Prior to diver manipulation, fairy basslet densities showed no systematic bias by lionfish treatment (t = -0.26, p = 0.79) nor by assignment to enhanced recruitment treatment (t = -0.73, p = 0.47). In contrast, during the initial census (24 hours post-

manipulation) fairy basslet population that received enhanced recruitment showed higher densities of 24.1 fish/m⁻² compared to 11.2 fish/m⁻² in unmanipulated populations (t = 25.0, p < 0.0001; Fig. 3.1: circles versus triangles at t = 0). Within each prey recruitment level, initial post-manipulation densities did not vary by predator treatment (t = -0.51, p = 0.62 and t = 0.80, p = 0.44 for unmanipulated and recruitment-enhanced fairy basslet populations, respectively; Fig. 3.1: open versus filled symbols at t = 0). Over four weeks and across all reefs, net change in fairy basslet population density ranged from -22.7 fish/m⁻² (negative values indicating a decrease in density) to 5.5 fish/ m^{-2} , with far greater average decreases observed on lionfish reefs compared to native predator only reefs. This pattern was true of both recruitment-enhanced fairy basslet populations—where decrease in density was approximately 140% greater on reefs with lionfish present (mean change in density -15.8 versus -6.6 fish/ m^{-2})—and at unmanipulated populations, with lionfish reefs experiencing 97% greater decreases compared to native-only reefs (mean change in density -3.62 with lionfish present versus -1.83 fish/m⁻² on native-only reefs). Over the course of four weeks and despite initial differences in prey density, fairy basslet populations on reefs with the invader were lower than those subject to predation by natives-only (Fig. 3.1: filled symbols versus open at t = 28).

Cumulative per capita loss of fairy basslet over 28 days was DD for both native-only reefs and those with lionfish present (Fig. 3.2; circles versus triangles). That is, recruitment-enhanced populations experienced greater per capita loss compared to unmanipulated basslet populations on both native-only reefs (24.8% versus 6.5% loss) and on lionfish reefs (60.0% versus 33.8% loss). However, the magnitude of this loss was substantially greater on lionfish reefs regardless of prey density (Fig. 3.2; filled versus open symbols). Notably, unmanipulated (low-density) fairy basslet experienced slightly higher mean loss rates on lionfish reefs even compared to recruitment-enhanced (high-density) populations at native predator only reefs (Fig. 3.2; filled circle versus open triangle). High mortality rates on lionfish reefs resulted in extirpation of two out of 14 fairy basslet populations; no fairy basslet populations on native-only reefs reached zero abundance. Further, nine out 14 prey populations exposed to the invader showed loss rates of greater than 50% over four weeks. In contrast, only three prey populations demonstrated such high mortality rates on native-only reefs.

Modeling interval per capita loss as a function of fairy basslet density using LMMs, there was a significant effect of 'prey density' (LRT, p < 0.001, see Table 3.1 for fixed effects selection criteria), indicating the presence of DD in per capita rates of prey loss (see Table 3.2 for parameter coefficients and variance). Further, I found no evidence to suggest that lionfish eliminated the presence of density dependence (LRT for the 'lionfish x prey density' interaction p = 0.98, Table 3.1). The coefficient for the effect of lionfish on the density-mortality relationship was small relative to the slope coefficient itself (0.008 and 0.021, respectively) and the confidence interval for this effect includes zero (Table 3.2). Together, these results indicate that prey loss was DD regardless of predator treatment. The effect of lionfish was mediated by time-step as indicated by a significant 'lionfish x time-step' interaction (LRT, p = 0.003) precluding the interpretation of the main effect of lionfish presence singularly across the duration of the experiment. However, in the

final model, after accounting for prey density, during time-steps four, five, and six (11, 18, and 28 days post-manipulation) per capita loss was higher on reefs with lionfish than without (Table 3.2).

DISCUSSION

Density dependence (DD) in vital rates represents a crucial component of population regulation and the detection of DD and the identification of the mechanisms that lead to DD remain relevant areas in population ecology (reviews by Lande et al. 2002, Osenberg et al. 2002, Hixon et al. 2002, Brook & Bradshaw 2006, White et al. 2010, Lebreton & Gimenez 2013, Thorson et al. 2015). As predation is often the proximate cause for this compensatory pattern in reef fishes (Hixon 2015), understanding how an introduced marine piscivore may alter patterns of densitymediated mortality in native prey is an important step in predicting the ultimate effects of invasion, including the risk of local or global extinction of native species. In this experiment, I found evidence that fairy basslet mortality remains DD in the presence of invasive lionfish. However, lionfish predation caused an overall increase in prey mortality and contributed to the local extinctions of two of 14 of prey populations. In contrast, no fairy basslet populations were extirpated on native-only reefs. Both extirpated populations began the experiment at low initial density, suggesting that, unlike native piscivores alone, the invader can cause high per capita loss rates at low prey density. Further, nine out 14 fairy basslet populations that were exposed to the invader—across a range of initial densities—had per individual predation risk over 50% across the experimental period compared with three prey

populations showing such mortality rates on native-only reefs. Thus, while patterns of fairy basslet mortality were qualitatively DD (per capita loss increasing with higher prey densities) regardless of predator treatment, lionfish nevertheless reduced the likelihood of local persistence of fairy basslet populations by increasing the magnitude of mortality across a broad range of prey densities.

The observation that lionfish lower the probability of local prey persistence corroborates previous experimental research from the invaded range. Albins (2013) demonstrated that, over eight weeks, a single lionfish on a small patch reef can reduce prey richness by nearly five species compared to predator-free controls, an effect nearly twice as large as that caused by native piscivores. Similarly, Benkwitt (2014) observed increases in native species richness over the summer recruitment period only on lionfish-free control reefs. In the presence of the invader species richness remained unchanged. Additionally, on large patch reefs and over multiple recruitment periods, Albins (2015) showed that lionfish reduced species richness and that the invader caused the greatest per capita effects on the rarest species. While increased mortality rates of native prey driven by lionfish is not itself a novel result, this study demonstrates how an introduced generalist predator can cause extirpation of rare species (or low-density population of a single species). By increasing loss rates even at the lowest prey densities-when prey populations are at their most vulnerable-predation by the invader heightens the likelihood that demographic stochasticity in local prey populations will result in local extinction.

The observation that lionfish remain effective predators at low prey density corroborates recent theory on differential effects of a novel predator. Saul and Jeshke

(2015) used mechanistic steady-state satiation equations (based on the predator functional response) to demonstrate that a novel predator with higher attack efficiency than natives and whose prey have low experience with the new predator will have higher consumption rates than natives across all prey densities. In such a scenario, the difference in consumption rate experienced by the prey will be most pronounced at low to intermediate prey densities (Saul and Jeshke 2015). Indeed, lionfish may have a lower threshold of prey density below which foraging becomes inefficient compared with native piscivores, a distinct possibility for a novel predator with no behavioral or morphological analogue in the Western Atlantic (Albins & Lyons 2012). While native piscivores often cause strongly DD mortality through an aggregative effect, spatially congregating and increasing attack rates in the vicinity of high prey densities (reviewed by White et al. 2010), there is thus far no evidence that lionfish do the same, continuing to hunt even as prey densities decline and native predators move on to richer patches where foraging is more efficient. Alternatively, lionfish may be less likely than other generalist native piscivores to employ prev switching at low densities of the target species. In either case, per capita predation rates caused by natives would fall with decreasing prey density but lionfish predation rates would remain high.

Another mechanism that could drive high predation rates at low prey density is naïveté, when prey fail to recognize and/or respond suboptimally to the threat of predation by a non-native predator, (Banks and Dickman 2007, Sih et al. 2010, Anson and Dickman 2013). DD mortality caused by native predators often relies on intense competition for predator-free shelter at high prey densities. In contrast, when prey are rare, shelter is plentiful and predation risk low (Forrester and Steele 2004a). However, if native prey are naïve to the risk of predation by this cryptic hunter with novel foraging behavior (Albins & Lyons 2012), lionfish would continue to consume prey at high rates even when shelter is abundant. Evidence of naïveté toward lionfish has been mixed in the invaded range. Recently, Anton (2016) demonstrated that the Atlantic grunt, *Haemulon plumierii*, maintains a greater approach distance from native predators than from lionfish. Similarly, Kindinger (2015) showed that territorial three-spot damselfish *Stegastes planifrons* that responded aggressively to all native fishes had reactions to captive lionfish that did not differ from the response toward empty controls. In contrast, Black et al. (2014) demonstrated, using another native Atlantic pomacentrid, S. leucostictus, that native prey can recognize and respond with anti-predator behavior in the presence of lionfish. However, this prey species did not modify their high-risk courtship behavior in the presence of the invader (Black et al. 2014), a result that suggests that other prey may similarly increase their risk predation when managing tradeoffs with foraging and/or reproductive demands.

Finally, differences in feeding behavior between lionfish and native predators could explain the observed mortality patterns in prey. Fairy basslet often occupy reef ledges where highest mortality rates occur toward the back of the ledges, the location at which native ambush hunters have the shortest pursuit distance (Webster and Hixon 2000). Larger, competitively dominant individuals that occupy the outer reaches of the ledge have access to passing plankton while remaining relatively near shelter leading to lower predation risk. Thus, these individuals may represent a partial prey population refuge, such that native predators alone rarely cause complete extirpation of a population. Anecdotally, lionfish often hunt in the open along the outer margins of reef ledges and do not rely on a high-velocity pursuit from a hidden location. They may therefore have access to prey individuals unavailable to native predators. While both native predators and lionfish employ variants of a hybrid "ramsuction" feeding behavior—combining a rapid burst of acceleration of the body (ram) with jaw protrusion and expansion of the buccal cavity to cause rapid flow of water into the mouth (suction) (Wainwright and Bellwood 2002)—common native predators of fairy basslet, such as serranids and aulostomids employ considerably more ram movement than lionfish, which may approach prey quite closely before initiating a strike (Muller and Osse 1984). Speculatively, lionfish may therefore employ a more effective capture method for prey that are very near shelter or those that occupy primary feeding positions near the outer margin of a reef ledge.

While the pre- and post-invasion experimental design employed in previous work could not unequivocally attribute the altered patterns of prey mortality to lionfish (Ingeman and Webster 2015), here I provide evidence that the increase in prey mortality observed between predator treatments is caused by the invader. However, while the cumulative effect of lionfish and native predators (the invasion scenario) represents an increase in prey mortality rates compared to native predators alone, it is possible that interactions with lionfish alter consumption patterns by native predators. The experimental design employed here cannot distinguish the singular and interactive effects of native and invasive predators and other studies of lionfish predatory effects have suggested non-additive effects of lionfish and native predators (Albins 2013). In all cases examined, the magnitude of lionfish effect has been greater than that of native predators and the cumulative mortality rates have been higher than those caused by either predator alone. Yet, the marginal difference in loss rates observed between predator treatments may represent an underestimate of the lionfish effect if native predators' consumption rates are reduced in the presence of the invader (compensatory mortality).

Another limitation of the study is the use of per capita loss (or its converse, survival) in quantifying density dependence. First, as an aggregate demographic measure, survival does not distinguish between the presence of a prior resident individual and a new recruit that has replaced a prior resident that was consumed in the interval between studies. In the latter case, both the effective prey density over the interval and the true mortality rate would be underestimated in calculating per capita loss. It is possible that natural recruitment rates in this study were not systematically biased by predator treatment, especially as native post-larval settlers have been shown to selectively avoid reefs with caged native predators but not reefs with lionfish (Benkwitt, unpublished data). Alternatively, in this study higher consumption of fairy basslet may have increased the level of conspecific, olfactory distress cues in the proximity of fairy basslet ledges on lionfish reefs, leading to reduced settlement and unreliable comparisons of basslet mortality. Notably, I observed that a natural recruitment pulse drove an increase in average fairy basslet population size (associated with a new moon soon after the third census) on native predator-only reefs. The absence of such an uptick in density on lionfish reefs is consistent with either reduced settlement or high post-settlement lionfish predation on uncensused fairy basslet recruits. In either case, measuring per capita loss as a function of previous population density may not capture the total effect of lionfish on density dependent dynamics.

In addition, if the underlying population dynamics follow a Beverton-Holt function as is commonly observed in reef fishes (Osenberg et al. 2002, Shima & Osenberg 2003), fitting per capita loss as a linear function of prey density may not be appropriate for identifying changes in the intensity of DD caused by the invader (C. Osenberg, pers. comm.). The mixed-effect model I employ here provides no evidence for lionfish-induced alteration of the intensity of DD (suggesting that lionfish could alter only the DI component of fairy basslet mortality). In contrast, an alternative analytical method assuming Beverton-Holt dynamics and using maximum likelihood parameter estimation for both recruitment and predator-specific mortality rates (Ingeman, unpublished data) suggests that lionfish in fact increase the DD component of mortality, albeit with wide confidence intervals around estimates of both DI and DD parameters. In the face of mixed evidence for changes in the intensity of DD and high variability in the data, I therefore refrain from making inference about lionfish changes to the DI or DD components of mortality based on these results. Future efforts should unambiguously measure demographic rates through tagging of prior resident fishes, and should adopt the appropriate dynamic model to infer effects of introduced predators on DD and DI mortality.

While I observed increased mortality rates and the local extinction of native prey populations, I do not conclude that fairy basslet is at high risk of global extinction as a result of this predator introduction; for this species, post-settlement

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demographics are largely disconnected from recruitment due to a pelagic larval phase and local populations are regularly replenished by density-independent larval settlement (Webster 2003). Further, this common species is buffered from the risk of global extinction by high-fecundity, large range size and fairly broad habitat tolerances (Böhlke and Chaplin 1994). Of greater conservation concern are rare species, those with demographically isolated populations, and species whose range is complete encompassed by the lionfish invaded range, such as the fairy basslet congener, G. dejongi (Victor and Randall 2010). This recently described basslet has been observed only in Cuba and the nearby Cayman Islands (Lohr et al. 2014) and its entire geographic and habitat range (reef walls 20-30m depth) are inhabited by lionfish. Another endemic coral-reef fish with a restricted range, the critically endangered social wrasse, Halichoeres socialis, has recently been documented as a primary prey item in lionfish diet contents in Belize (Rocha et al. 2015). As this study demonstrates, such native populations are no longer protected from high predator consumption rates by low local prey densities, a result that mangers should consider when designing and evaluating conservation and mitigation efforts throughout the invaded range.

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Figure 3.1 Time series of fairy basslet density (mean +/- SE) over the 28-day experimental period on reefs with lionfish (filled symbols and solid lines) and with native predators only (open symbols and dashed lines). Fairy basslet populations with artificially enhanced recruitment (triangles) began the experiment at higher densities compared to unmanipulated populations (circles). However, high and directly density-dependent mortality reduced the difference in final densities within each predator treatment. Further, prey populations on lionfish reefs (filled symbols, far right) achieved lower final densities than native-only reefs (open symbols, far right), regardless of initial density.



Figure 3.2 Cumulative per capita loss (proportional change in abundance) for crossfactored treatment groups over 28 days (group means +/- (mean +/- SE)). At both unmanipulated and recruitment-enhanced fairy basslet populations (circles and triangles, respectively), per capita loss was higher on reefs with lionfish compared to native only-reefs (closed versus open symbols). Per capita loss at unmanipulated prey populations subject to lionfish predation were similar to recruitment-enhanced populations on native-only reefs (comparing filled circle to open triangle) suggesting that lionfish cause high mortality at even low prey density.

Table 3.1 Selection criteria for fixed-effects. Likelihood ratio and associated pvalues comparing models with each potential explanatory variable (with all other fixed-effects and optimal random structure in place) to a reduced model without the focal parameter. ΔAIC indicates the change in model fit associated with retaining the variable in the model. P-values less than 0.05 (and negative ΔAIC values) provide evidence for retaining the variable. Fixed effects retained in final model are indicated in bold.

Explanatory variable	L. ratio	p-value	ΔΑΙC	
lionfish (presence)	8.330	0.004	-6.330	
prey density	11.124	< 0.001	-9.124	
lionfish x prey density interaction	0.018	0.975	1.982	
native predator biomass	0.867	0.352	4.017	
time step	13.274	0.021	3.274	
lionfish x time step interaction	11.197	0.003	- 1.197	

Effect	Value	Std. Error	df	t	Р
Intercept	-0.351	0.165	128	-2.12	0.035
prey density	0.021	0.008	128	2.48	0.014
lionfish	0.123	0.227	26	0.54	0.590
prey density:lionfish	-0.008	0.011	128	-0.711	0.478
time step 2	0.076	0.097	128	0.788	0.432
time step 3	0.069	0.097	128	0.716	0.475
time step 4	-0.05	0.097	128	-0.525	0.601
time step 5	0.057	0.097	128	0.588	0.557
time step 6	0.143	0.097	128	1.481	0.141
lionfish:time step 2	0.083	0.137	128	0.605	0.546
lionfish:time step 3	0.124	0.137	128	0.906	0.366
lionfish:time step 4	0.297	0.137	128	2.174	0.032
lionfish:time step 5	0.323	0.137	128	2.380	0.020
lionfish:time step 6	0.330	0.137	128	2.262	0.018

Table 3.2 Summary of fixed-effects for final model. Model coefficients and variance estimated using REML for all variables retained in final linear mixed effects model.

Supplementary Table 3.3 Selection criteria for random effects and autocorrelation structure. Random effects: None = no random effects; Reef = separate random intercepts at the reef-level; Ledge = separate random intercepts at the ledge-level. LRT results display likelihood ratio and associated p-value (corrected for testing-on-the-boundary) comparing the model with optimal random structure to a fixed-effects-only model. Optimum structure was chosen by AIC (Aikake's Information Criterion) and best fit model is indicated in **bold**.

<u>LRT</u> re	esults			
L. ratio	p-value	Random Effect	Autocorrelation Structure	AIC
		None	None	125.3
		Reef	None	120.1
		Ledge	None	118.1
		None	AR(1)	96.4
		Reef	AR(1)	126.9
9.28	0.0010	Ledge	AR (1)	87.6

Chapter 4 — Effects of predator novelty on intraguild predation community with adaptive prey defense

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ABSTRACT

Understanding coexistence within community modules such as intraguild predation (IGP), where an omnivore both preys on and competes with an intermediate consumer for a shared resource, has provided insight into the mechanisms that promote persistence of complex food webs. Adaptive, predator-specific defense has been shown theoretically to enhance coexistence of IGP communities when employed by shared prey. Yet to date, all such theory has assumed that prey have accurate perception of predation risk and appropriate antipredator responses, assumptions that may not be justified when considering a novel predator. We therefore consider the effects of an introduced predator on IGP coexistence, describing two invasion scenarios: suboptimal defense, whereby a similar invader elicits an ineffective antipredator response; and naïveté toward an unfamiliar invader, for which prey fail to accurately estimate predation risk. We examine predictions for native predator persistence across gradients of enrichment and defense costs using invasibility analysis methods. The model predicts that predator novelty can weaken the effect of adaptive defense, causing exclusion of native predators that would persist in the absence of novelty. Coexistence is predicted to be more sensitive to the effects of suboptimal defense compared to naïveté and differentially leads to exclusion of native predators in highly productive environments and when defense costs are low. Moderate novelty of the omnivore can increase resource density via a trophic cascade, while consumer novelty can either lead to omnivore exclusion or facilitate three-species coexistence by providing a subsidy to the otherwise excluded native omnivore. Our results suggest that models of adaptive defense are sensitive to

assumptions regarding predator-prey eco-evolutionary experience and that predator novelty has significant implications for food web dynamics.

INTRODUCTION

Factors affecting persistence of food webs are a fundamental concern in ecology, particularly as human activities continue to modify community composition and ecosystem function (Scheffer et al. 2001, Simberloff et al. 2013). Anthropogenic species introductions continue to rise (Levine and D'Antonio 2003) with the result that novel predator-prey interactions have become increasingly frequent across terrestrial, marine, and freshwater ecosystems (Ricciardi 2007). A key feature of predator introductions is a lack of shared evolutionary history between predator and prey (Cox and Lima 2006), which can result in strong effects if prey fail to recognize or effectively respond to novel predator cues (Sih et al. 2010). As exotic predators have been implicated in numerous species extinctions (Blackburn et al. 2004), it is of considerable theoretical interest to illuminate how predator introductions influence the persistence of native communities and to clarify the mechanisms by which their direct and indirect interactions can lead to native species loss.

One approach previously employed to predict invasion outcomes is to randomly generate large food webs and quantify the effects of species introduction on post-invasion properties (Lurgi et al. 2014). Such simulations have illuminated the role that species traits and web topology play in determining invasion success (Romanuk et al. 2009) and in mitigating the effects of invasion on loss of species, complexity, and other web properties (Lurgi et al. 2014). A complementary approach, which trades generality and food web-level inference for analytical tractability and mechanistic understanding, is to investigate the effects of invasion on the small community modules that comprise food webs. Community modules can isolate the key processes driving dynamics in more complex communities (Holt and Hochberg 2001). Furthermore, by allowing the specification of particular phenomena known to promote native species coexistence, they can provide detail on how predator introductions can alter the function of important stabilizing mechanisms, with implications for broader food web persistence (Kondoh 2008, Stouffer and Bascompte 2010).

One such stabilizing phenomenon is adaptive antipredator defense, whereby prey allocate defensive effort dynamically in response to a changing trophic landscape (Abrams 2000). Dynamic prey responses can promote multi-predator coexistence by creating a stabilizing tradeoff in the allocation of predator-specific defense effort (Kondoh 2007). Predator-induced morphological or behavioral defenses promote coexistence because prey defense reduces the target predator's feeding rate when predator abundance is high, resulting in a stabilizing negative feedback (Matsuda et al. 1996). Thus, adaptive responses to predator densities represent a stabilizing coexistence mechanism (Chesson 2000) that reduces the potential for competitive exclusion by introducing a positive interaction among predators, mediated through prey traits (Werner and Peacor 2003). A well-studied empirical example involves larval tadpoles of the genus *Rana*, which express different morphological adaptations when exposed to dragonfly larvae—increased fin depth to facilitate escape—than when exposed to gape-limited salamanders or fishes—"bulgy" heads that inhibit consumption (Van Buskirk and McCollum 1999). Importantly, each defensive response is predator-specific, allowing the alternate predator to maintain high consumption rates when predator species and defensive phenotype are mismatched (Kishida and Nishimura 2005).

Adaptive defense can dramatically alter the predictions for coexistence of community modules (Peacor and Cressler 2012) such as the intraguild predation (IGP) module, in which a top predator (hereafter, *omnivore*) both preys upon and competes with an intermediate predator (consumer) for a shared prey (resource) (Polis et al. 1989). IGP coexistence is sensitive to the effects of adaptive defense (Urbani and Ramos-Jiliberto 2010), so clarifying the effects of predator novelty on IGP coexistence represents key link in understanding how predator introductions can alter the function of this stabilizing mechanism. Further, because IGP features prominently in empirical food webs (Arim and Marquet 2004, Stouffer et al. 2007, Borrelli 2015) despite the fact that the coexistence of all three species is theoretically obtained under rather restrictive conditions (Holt and Polis 1997, Diehl and Feißel 2000), insight into the conditions that allow IGP coexistence is highly relevant for understanding how food webs more broadly respond to perturbations such as species exploitation, nutrient-enrichment, and global climate change. IGP systems have been studied extensively because they comprise a variety of ecological interactions (e.g. tri-trophic chain, apparent competition) and display a rich range of dynamical behaviors (Holt and Polis 1997). In classic Lotka-Voterra IGP models, predators do not experience self-limitation that could offset negative interspecific interactions and

promote coexistence (Polis et al. 1989). Coexistence is possible only through the tradeoff between superior competitive ability in the consumer and the availability to the omnivore of a second food source (Holt and Polis 1997). Adaptive defense by the resource has been theoretically shown to widen the parameter region of three-species coexistence by inducing a positive interaction between predators that strengthens this stabilizing tradeoff, relative to the magnitude of exploitative competition and IG predation (Nakazawa et al. 2010, Urbani and Ramos-Jiliberto 2010, Ikegawa et al. 2015).

Crucially, effective antipredator defense relies on accurate perception of predation risk and appropriate antipredator response. Predator novelty can manifest in either of these components of the prey defense. Lack of eco-evolutionary experience with novel predators can result in reduced or missing antipredator response (hereafter, *naïveté*) or can result in a defense that is elicited but ineffective in reducing predation rates (hereafter, *suboptimal defense*) (Saul and Jeschke 2015). A naïve (lack of) antipredator response is predicted when prey have no evolutionary experience with predators of a similar archetype (Cox and Lima 2006), resulting in a mismatch between predator cues and the prey's recognition template (Carthey and Banks 2014). In contrast, an introduced predator that is similar to native predators may induce a prey antipredator response due to cue similarity, yet retain high predation rates due to key differences in predatory behavior (Lohrer and Whitlatch 2002). In the latter case, the consumptive effects (CEs) of predation are compounded by non-consumptive effects (NCEs) of costly defensive responses on prey fitness (Sih et al. 2010). It is difficult to predict *a priori* how each of these invasion scenarios
will affect persistence. Yet to date, models showing increased coexistence via adaptive defense within IGP systems have assumed that prey have perfect perception of predation risk and employ fully effective antipredator responses.

Here, we investigate the effects of predator novelty on the persistence of the IGP food web module. We consider two invasion scenarios: (i) suboptimal defense, whereby a similar invader (in terms of predator cues) elicits ineffective antipredator response; and (*ii*) naïveté toward an unfamiliar invader, for which prey fail to accurately perceive predation risk. Because of the role of resource productivity in shifting the relative importance of competition and predation and determining coexistence in IGP settings (Diehl and Feißel 2000), we examine naïveté and suboptimal defense across a basal enrichment gradient. Further, because the two invasion scenarios (naïveté and suboptimal defense) differ in the presence of NCEsthe magnitude of which depends greatly on the costliness of defense (Peacor et al. 2013)—we consider the effects of predator novelty over a range of defense cost levels. We consider both the situation in which the novel predator is the omnivore and the situation where the novel predator is the intermediate consumer, examining the conditions that lead to the exclusion of the native predator in each. We theoretically demonstrate that (i) predator introduction can cause exclusion of native predators by weakening the stabilizing feedback provided by adaptive defense, (ii) an introduced omnivore is predicted to exclude a native consumer over a wider parameter region than if predator origin is reversed, (iii) three-species coexistence is more sensitive to the effects of suboptimal defense than to naïveté and differentially leads to exclusion of native predators in highly productive environments and when

defense costs are low, (iv) moderate novelty of the omnivore—but not the consumer—can increase resource density by strengthening the tri-trophic chain within the IGP model, and (v) consumer novelty can facilitate three-species coexistence by providing a subsidy to an otherwise excluded native omnivore.

METHODS

We take as our starting point the IGP model of Nakazawa (2010), which assumes linear functional responses and adaptive, predator-specific defense. This model describes the interactions of the resource (R), consumer (N) and omnivore (P) by

$$\frac{dR}{dt} = R\left(r\ c\ -\frac{R}{k} - N\ a_{NR}\ d_N - P\ a_{PR}\ d_P\right) \tag{1a}$$

$$\frac{dN}{dt} = N(R a_{NR}b_{NR}d_N - P a_{PN} - m_N)$$
(1b)

$$\frac{dP}{dt} = P(R \ a_{PR} \ b_{PR} \ d_P + N \ a_{PN} \ b_{PN} - \ m_P).$$
(1c)

Parameter *r* is the resource's intrinsic growth rate and parameter *k* controls its density dependence, reflecting the system's basal productivity. Parameter a_{ij} is the attack rate of predator *i* on prey *j*, with b_{ij} representing the efficiency with which consumed *j* are converted to *i*. Parameter *c* denotes the resource's total cost of

allocating energy from growth towards defensive efforts and parameter d_i represents the effectiveness of the resource's defense in reducing predator *i*'s attack rate ($0 \le d_i$ ≤ 1). The realized attack rate owing to the defense effect is thus d_i times a_{ii} .

The resource's total cost of defense is comprised of the sum of its defensive efforts toward each predator,

$$c = 1 - \sum_{i=N,P} c_0 e_i$$
 (2)

where e_i represents the level of predator-specific defense effort that is allocated toward the *i*th predator. Parameter c_0 ($0 \le c_0 \le 1$) is a coefficient of cost (common to both predators) that converts defense effort into reduction in population growth rate in the resource. The magnitude of c_0 controls how costly the employment adaptive defense is to prey population growth and thus facilitates comparisons of invasion outcomes along a range of defense costliness from inexpensive (e.g., modestly reduced foraging with c_0 near zero) to very costly (e.g., morphological changes as c_0 approaches one). It is assumed that any effort allocated towards defense is thereby not allocated to growth and reproduction such that $0 \le e_N + e_P \le 1$. Defense effectiveness is similarly assumed to be linearly proportional to predatorspecific defense effort, e_b and a defense efficiency parameter, f, such that

$$d_i = 1 - e_i f. \tag{3}$$

The model assumes that prey allocate defense effort in such a way that resource fitness, w, defined as the resource per capita growth rate, w = 1/R dR/dt, is maximized. When the resource benefits from perfect perception of the trophic environment, resource fitness is given by

$$w = \left(\frac{1}{R}\right) \left(\frac{dR}{dt}\right) = r c - \frac{R}{k} - a_{NR} d_N - a_{PR} d_P.$$
(4)

Defensive efforts towards each predator, e_i , are specified as dynamic variables that respond to the trade-off that prey experience between predation risk and fitness gains, adaptively optimized in response to the trophic environment. The dynamics of effort allocation are described by the replicator equations,

$$\frac{de_i}{dt} = \nu e_i \left\{ \frac{\partial w}{\partial e_i} - \left(\sum_{x=N,P} e_x \frac{\partial w}{\partial e_x} \right) \right\},\tag{5}$$

such that effort toward the *i*th predator will increase when the gain in fitness of changing the effort, $\frac{\partial w}{\partial e_i}$, is higher than $\sum_{x=N,P} e_x \frac{\partial w}{\partial e_x}$ (Matsuda et al. 1996). The overall rate with which defensive efforts are able respond to a given fitness gradient is controlled by the adaptive rate, *v*.

We depart from earlier efforts by considering separately two invasion scenarios. First, we model an introduced predator that elicits defensive efforts in prey as a result of similarity with native predators, but to which antipredator defense yields reduced effectiveness (suboptimal defense). We do so by modifying the defense effectiveness equations to include a new parameter, φ ($0 \le \varphi \le 1$), which controls the efficiency of defense against the introduced predator relative to its effectiveness against the native predator:

$$d_{introduced} = 1 - e_{introduced} f_{native} \varphi.$$
⁽⁶⁾

Thus, $\varphi = 1$ reflects maximum defense effectiveness toward a novel predator while $\varphi = 0$ renders the resource's defense completely ineffective toward the invader.

Second, to consider an invader that fails to elicit defensive effort commensurate with its predation threat (naïveté), we incorporate the condition in which the resource incorrectly optimizes defensive allocation by maximizing "perceived fitness," w_p , whose difference from w, its true fitness, is determined by the resource's recognition level, ρ , of the invading predator ($0 \le \rho \le 1$). Thus, when the invader is the consumer we specify

$$w_p = r c - \frac{R}{k} - a_{NR} d_N \rho - a_{PR} d_P$$
(7a)

and when the invader is the omnivore we specify

$$w_p = r c - \frac{R}{k} - a_{NR} d_N - a_{PR} d_P \rho.$$
 (7b)

Prey naïveté modifies the perceived predation threat of the introduced predator in the fitness equation and hence alters the prey's adaptive response to changing predator density; $\rho = 1$ reflects perfect perception, while $\rho = 0$ reflects complete naïveté toward the introduced predator. Naïveté is propagated through the replicator equations (via perceived fitness) to reduce the level of defense effort allocated toward an unrecognized invader. We use invasibility analysis to determine the boundaries for three-species coexistence. The invasibility criterion for coexistence requires that each species can increase from low density in the presence of the remaining predator-prey community, a criterion that has been justified for a variety of models (Chesson 2000) and which provides a link between models and empirical tests of coexistence theory (HilleRisLambers et al. 2012). Note that our use of invasibility analysis techniques does not correspond only to an assessment of the conditions under which a non-native predator can invade the native predator and resource predator-prey system, but rather permits the assessment of the boundary conditions between the three-species coexistence and the exclusion of *either* the native or the non-native predator. Therefore, to avoid confusion with predator origin we henceforth employ the term "coexistence boundary" instead of the more commonly-used term "invasion boundary."

We first solve for the equilibria of the five-dimensional system of equations (three species plus two dynamical defense effort variables) by setting equations 1a-c and 5 to zero. We then evaluate the system's Jacobian matrix at each equilibrium and use the real part of its maximum eigenvalue (λ) to determine the parameter regions over which each equilibrium exhibits asymptotical stability ($Re(\lambda) < 0$). Because defensive effort towards a predator will vary dynamically only when that predator is present, each prey-effort-single predator system is three-dimensional, allowing us to determine the stable regions of these equilibria analytically.

We then determine the coexistence boundaries that describe the conditions under which each predator could invade an existing single-predator system. We rearrange coexistence boundaries in terms of basal productivity (k) because of the role of enrichment in determining the relative importance of interaction types (competition, apparent competition, and predation). Similarly, we examine coexistence boundaries in terms of defense cost (c_0) because of its importance in determining the relative magnitude of non-consumptive predator effects. Following previous efforts (Kimbrell et al. 2007, Nakazawa et al. 2010), we examine coexistence along these important gradients with respect to the strength of intraguild predation (a_{PN} , omnivore's attack rate on the intermediate consumer) because this parameter controls the degree to which the three-species system reflects a system of exploitative competition versus a trophic chain and provides a parameter with an unambiguous influence in shifting dominance between omnivore and consumer.

We determine how the resultant coexistence boundaries are altered by the consideration of suboptimal defense (decreasing φ) and naïveté (decreasing ρ) in order to generate predictions about what systems will be most sensitive to each type of invading predator. Finally, in the five-dimensional case where equilibria are not analytically accessible, we simulate population dynamics to determine the equilibrium densities of each species and levels of defense along gradients of novelty for each invasion scenario (suboptimal defense and naïveté).

Note that throughout the manuscript, we use *novel* and *novelty* as a general terms reflecting lack of eco-evolutionary experience with the invading predator that encompasses any part of the predator-prey interaction. A novel predator can therefore have unfamiliar traits that inhibit either recognition *or* effective defense. Thus, we employ the term *novelty parameters* to denote the parameters φ and ρ

collectively. When only one invasion scenario is being considered, we employ the more specific terms *naïveté* or *suboptimal defense*. Similarly, the term *predator* is employed in the general case that applies to either IG predator or IG prey. When a case applies to only one predator species individually, we specify using the terms *omnivore* or *consumer*.

RESULTS

Defense allocation and resource abundance and in single-predator case

For each combination of the resource and a single predator (either the putative omnivore or the consumer) there are exactly three feasible equilibria—one in which the resource's antipredator defense is zero, one in which antipredator defense is maximized at 1, and one in which antipredator defense remains at an intermediate value determined by parameter values and the consequent abundance of the predator. These three equilibria do not represent alternative stable states but rather feasibly exist and are stable along different parameter regions, including both productivity (as examined in Nakazawa et al. 2010) and defense cost gradients (Figure 4.1). When defense cost is zero, effort is maximized at one (Figure 4.1c), resulting in the highest possible equilibrium resource abundance (Figure 4.1a) and low abundance of the predator (Figure 4.1b). Effort remains maximized at one as costs increase to a threshold, causing both prey and predator abundances to decrease. Then, above a first threshold cost level separating maximized- and intermediate-defense equilibria (Figure 4.1a-c, grey vertical lines), the resource monotonically reduces defense allocation in response to the costs to growth associated with defense. The location of

this threshold is determined by specified parameters, including the attack rate of the focal predator on the resource, a_{iR} and its defense efficiency, f_i . Specifically, a higher attack rate or defense efficiency value will increase the cost threshold at which the resource reduces defense effort below the maximum. The predator's density increases linearly with the reduced allocation of defense (Figure 4.1b, positive slope). Beyond a second threshold cost level, the resource abandons defense allocation and neither resource nor predator densities vary with further increasing costs. The location of this second threshold is again determined by a combination of parameters that alter the balance between predation risk and defense cost. As intuition would suggest, in the absence of an alternative predator, the resource decreases defense effort unidirectionally along a gradient of increasing defense cost.

Conditions for coexistence of introduced and native predators

With adaptive defense, the coexistence boundary for an introduced predator (the boundary between exclusion and persistence) is not itself affected by novelty, regardless of whether the predator is the putative omnivore or the consumer. This is because the density of the introduced predator in the vicinity of this boundary is too low to elicit a defensive response from the resource. With no effort allocated toward defense against a novel predator there is no avenue for defense to be circumvented by novelty. Correspondingly, neither the defense efficiency parameter, φ , nor the naïveté parameter, ρ , is present in the coexistence boundary conditions of either introduced predator (Tables 4.1, 4.2).

In contrast, novelty can decrease (or in special cases, increase) the parameter region wherein a *native* predator coexists with the novel predator and shared resource.

Correspondingly, both novelty parameters occur in coexistence boundary conditions for native predators (Tables 4.1, 4.2). The model therefore predicts that the parameter space of novel predator coexistence does not depend on traits that induce naïveté or suboptimal defense. Rather, such invader traits alter the coexistence boundary and equilibrium density of the native predator through interactions mediated by both the resource density and its defense allocation, as described below.

Introduced omnivore

Native consumer coexistence along productivity gradient

With adaptive defense, increasing productivity does not simply decrease the IGP Strength (a_{PN}) at which the native consumer can persist (Figure 4.2a, blue curves). As observed by Nakazawa (2010), enrichment first reduces the parameter range of consumer coexistence (i.e., lowers the magnitude of a_{PN} at which the consumer can persist) by promoting increasing omnivore abundance, then facilitates greater coexistence range via increasing defense effort, and finally reduces the range of consumer persistence when defense toward the omnivore is maximized (parameter region of three species coexistence shaded and labeled "RNP" in Figure 4.2a-e). At maximum defense effort, increasing productivity causes the exclusion of the native consumer at a lower attack rate a_{PN} because resource defense can no longer compensate for increasing omnivore abundance.

The effect of suboptimal response toward an introduced omnivore is to reduce the level of a_{PN} at which the native consumer is excluded (Figure 4.2a-c). Because suboptimal defense results in reduced efficiency anytime defense is

employed, suboptimal defense promotes exclusion at both intermediate and high levels of enrichment and reduces native consumer coexistence to a narrow region parameter region of low productivity.

In contrast, naïveté causes exclusion of native consumer at intermediate, but not high, productivity (Figure 4.2d-e). Further, the overall effect of naïveté on the parameter region of coexistence is low relative to the effect of suboptimal defense (comparing Figure 4.2d-e to 4.2b-c). At intermediate productivity when defense effort is intermediate at levels determined by perceived omnivore density, naïveté results reduced defense effort, which in turn causes exclusion of the native consumer. At highest productivity, however, when effort toward introduced omnivore is maximized, defense continues to effectively reduce the abundance of the omnivore. Thus, the boundary of native consumer coexistence at high productivity (defense effort maximized) remains unchanged by naïveté.

Native consumer coexistence across range of defense cost

We first discuss the general effects of defense cost itself on IGP coexistence (ignoring novelty) as this gradient alone has itself not been explored in the previous literature. Similar to the effect of enrichment, increasing cost does not monotonically decrease the level of a_{PN} at which the native consumer can persist, but rather increases the three-species coexistence range over a portion of the cost gradient (Figure 4.3, positive slope of blue curves). However, unlike productivity, this increase does not occur when defense is intermediate but at the lowest cost range where defense against the omnivore is maximized at one (Figure 4.3b- c). The

mechanism for this positive relationship between resource defense cost and consumer persistence at maximized defense is mediated through resource density: increasing costs reduce the resource abundance available for the omnivore, thereby depressing the omnivore's ability to exclude the consumer via predation and exploitative competition. As cost increases further, the resource switches to intermediate levels of defense. The resulting effect of increasing costs is reduced defense effort, which enhances the omnivore's abundance and promotes the exclusion of the consumer via predation (Figure 4.3, negative slope of blue curves). Finally, at the highest defense costs, the resource abandons defense altogether and there is no effect of increasing cost on coexistence (Figure 4.3, blue curve of slope-zero). As observed by Ikegawa et al. (2015), in the absence of defense (here, at high cost) a region of bistability can exist wherein either predator can persist in the absence of the other and community composition depends on initial conditions.

Next, we examine the effects of suboptimal defense across a cost gradient. When effort is inexpensive and maximally employed, making defense less efficient leads to the higher abundance of the omnivore and promotes the exclusion of the native consumer (Figure 4.3b-c, reduced area of shaded RNP region). Less efficient defense also leads to the exclusion of the native consumer at intermediate levels of cost by causing the resource to rapidly reduce defense effort against the omnivore.

The effect of naïveté on coexistence across a gradient of defense costliness is modest compared to the effect of suboptimal defense (Figure 4.3d-e compared to Figure 4.3b-c). Further, naïveté toward an introduced omnivore causes exclusion of native consumer at intermediate defense cost but not at low cost. Despite naïveté,

when defense is inexpensive (at low productivity) defense effort toward the introduced omnivore remains fixed at one. This effectively inhibits the omnivore's abundance and allows for consumer persistence at low cost.

Equilibrium densities across a gradient of omnivore novelty

Both suboptimal defense and naïveté of the resource toward the omnivore increase equilibrium density of the resource (Figure 4.4, green curve) compared to resource density with perfect recognition and response (Figure 4, at the ordinate). This novelty-mediated increase in density is caused by strengthening the tri-trophic chain with the IGP model. The increase in resource density is limited to moderate levels of novelty as suboptimal defense and naïveté eventually lead to the abandonment of defense effort toward to invader (Figure 4.4, dashed red curves) and correspondingly low resource density. Further, the trajectory of defense effort directed toward each predator with low but increasing levels of novelty differs between the two invasion scenarios: suboptimal defense (Figure 4.4a) results in an initial increase in defense against the introduced omnivore (to compensate for reduced efficiency) and steadily decreasing effort toward the native consumer. In contrast, naïveté (Figure 4.4b) results in decreasing effort toward the unrecognized omnivore, causing the resource to shift allocation toward defense directed toward the native consumer.

Introduced consumer

Due to the asymmetrical nature of IGP, novelty of an introduced consumer affects only the coexistence boundaries of an IGP system under restricted conditions: where defense against the consumer is employed (see coexistence criteria in Table 4.2) and where reduction in effectiveness of defense (via novelty) can result in the consumer outcompeting the native omnivore for resources.

Native omnivore coexistence along productivity gradient

The effect of increasing productivity on the coexistence boundary for the native omnivore (Figure 4.5, red curve) is simpler than for native intermediate consumer: increasing productivity facilitates coexistence of the native omnivore with respect to IGP strength (a_{PN}) . However, novelty of an introduced consumer modifies the boundary of omnivore coexistence in complex ways because the consumer represents both a competitor and a resource for the omnivore. Whether suboptimal response to a consumer causes omnivore exclusion or facilitates consumer persistence depends on the relative contribution of energy to the native omnivore by each of its prey, which in turn depends on relative efficiencies of the indirect versus direct pathways. At lowest productivity, defense toward the consumer is minimized at zero and the coexistence boundary remains unchanged by novelty (Figure 4.5b-c and see coexistence criteria in Table 4.2). When adaptive defense is intermediate at a magnitude set by predator abundance (at intermediate productivity) decreasing defense efficiency results in an increase in consumer abundance (which promotes omnivore coexistence) but a decrease in the abundance of the resource (which promotes omnivore exclusion). Indeed, suboptimal defense can reverse the relationship between enrichment and omnivore coexistence when defense is intermediate (Figure 4.5c, positive slope of red curve at intermediate productivity). Similarly, when effort is fixed at one (high productivity) suboptimal response results

in reduced resource abundance but increased consumer abundance, and whether this leads to exclusion of the omnivore depends on the efficiency of pathways. As the majority of energy flux is through the indirect route at high productivity, suboptimal defense results in exclusion of native omnivore at a given level of a_{PN} (Figure 4.5a-c).

The effect of naïveté toward an introduced consumer on omnivore coexistence is modest compared to the effects of suboptimal defense (Figure 4.5d-e). Low levels of naïveté result in little change in coexistence boundaries (Figure 4.5d). However, there is a sharp threshold of naïveté above which the resource abandons defensive effort toward to consumer, resulting in omnivore exclusion across a broad range of productivity (Figure 4.5e). Repeated simulations at varying parameter values revealed that the location of this threshold is determined primarily by the attack rate of the consumer on the resource, a_{NR} , and the efficiency of resource defense toward the consumer, f_N (and see Table 4.2).

Native omnivore coexistence across a range of defense cost

Similar to the effect of productivity whether increasing cost of defense increases or decreases the range of native omnivore coexistence in the absence of novelty depends on relative efficiency of energy pathway (Table 4.2). When the indirect pathway is dominant and the omnivore primarily feeds on the intermediate consumer (e.g. at low productivity and high IGP strength), increasing costs of defense will first decrease then increase the parameter range omnivore persistence. In contrast, the omnivore persistence predictions are reversed for systems that are dominated by the direct pathway. Suboptimal defense yields a reduced parameter region of omnivore coexistence by reducing the availability of the resource at both low and intermediate cost (Figure 4.6a-c). There is no effect of suboptimal defense at high cost because defense is not employed. In contrast to suboptimal defense, naïveté does not have any effect on the coexistence region when cost is low and defense is maximally employed. Provided that defense remains maximally employed, it effectively reduces consumer predation of the resource and precludes competitive exclusion of the native omnivore. Naïveté does reduce the allocation of defense toward the consumer at intermediate cost, thereby increasing the magnitude of IGP strength at which the omnivore is excluded. As a whole, the effects of naïveté toward the consumer across a cost gradient are modest compared to the effects of suboptimal defense.

Equilibrium densities across a gradient of consumer novelty

Increasing novelty of an introduced consumer results in decreasing abundance of the resource (Figure 4.7; solid green lines). In contrast to the increased resource abundance observed with novelty of an introduced omnivore (via the tri-trophic chain), neither suboptimal defense nor naïveté toward the introduced consumer can increase resource abundance. In fact, since the consumer is also prey for the native omnivore, increasing novelty of the consumer can subsidize the omnivore, resulting in further reduced abundances of the resource. Density of the introduced consumer itself (Figure 4.7; solid blue curves) increases until naïveté results in abandonment of antipredator defense by the resource. Increasing novelty can result in exclusion of native omnivore (Figure 4.7; solid red curves) when omnivore persistence depends on the increased resource abundance provided by defense (at low productivity and low IGP strength). However, because of the consumer novelty can also facilitate persistence of a native omnivore (Figure 4.8) that would be otherwise excluded (in the absence of consumer novelty) by subsidizing the omnivore via the indirect route energy pathway. As resource defense toward the consumer becomes less efficient, the omnivore can invade the system subsidized by increasing abundance of an additional food resource (Figure 4.8, red curve).

DISCUSSION

In this study, we investigate the effects of an introduced predator on IGP community persistence. Previous work has identified adaptive defense as an important phenomenon that can contribute to food web maintenance (Kondoh 2007), yet to our knowledge, this is the first study to examine the effects of predator novelty on the functioning of this stabilizing coexistence mechanism in an IGP context. We find that a novel predator reduces the parameter region of three-species coexistence by excluding the native predator from a parameter space in which it could otherwise persist in the absence of novelty. This exclusion occurs when the stabilizing positive interaction between predators, mediated by predator-specific defense allocation in shared prey, is eroded by either reduced or ineffective defense toward the invader. Thus, while our model corroborates previous theory regarding the positive effect of adaptive defense on community persistence (Matsuda et al. 1996, Kondoh 2007, Nakazawa et al. 2010), we extend these findings by showing that persistence is

sensitive to the assumptions of perfect risk perception and effective defense that may not be justified for novel predators.

While both naïveté and suboptimal defense reduced the parameter region of coexistence, we found strong differences in the magnitude of changes caused by each invasion scenario. Specifically, holding other parameters constant, naïveté had far more modest effects on native predator persistence than suboptimal defense. The mechanism primarily driving differential effects on coexistence boundaries was not the presence of non-consumptive effects (NCEs) in suboptimal defense, as may have been expected. While simulations showed lower resource densities at comparable levels suboptimal defense of compared to naïveté (Figures 4 and 7), reduced prev availability (as a result of costly but ineffective defense) had little effect on native predator exclusion. Rather, dramatic differences in the parameter region of coexistence resulted from differences in the relationship between effort and effectiveness in the two invasion scenarios. Specifically, naïveté reduced the level of defensive effort that prey allocated to a novel predator, but allowed defense to remain maximally effective provided that it was employed. In contrast, suboptimal defense caused prey to *increase* effort in response to reduced defense efficiency, but the effectiveness of the defense toward the invader was eroded even at high levels of defense effort. This difference can be seen by examining which equilibria change with novelty: while naïveté alters only the equilibria corresponding to intermediate levels defense effort (when effort varies based on perceived predation threat), suboptimal defense changes the equilibria and hence the coexistence boundaries

associated with both intermediate and maximized defensive effort (Table 4.1 and Figures 4.2, 4.3, 4.5, 4.6).

Effects of introduced predators across productivity and defense cost gradients

Because the clearest differences between invasion scenarios arise when defense is maximally employed, and because defense investment changes along productivity and defense cost gradients, our model makes specific predictions for where along these gradients exclusion will occur in each scenario. First, our model predicts that highly productive systems will be more sensitive to an introduced predator that provokes suboptimal responses than to an unfamiliar predator to which prey are naïve. Productivity has long been recognized as one of the primary factors determining coexistence in IGP systems, shifting the importance of exploitative competition and predation and causing the exclusion of the omnivore and the consumer at low and high productivity, respectively (Holt and Polis 1997, Diehl and Feißel 2000). While adaptive defense can widen the productivity region at which three-species coexistence occurs, we show that this effect is sensitive to predator novelty, and that an introduced predator will alter IGP coexistence at different regions of productivity depending on whether it elicits suboptimal defense or reduced recognition by prey. In the case of an introduced omnivore, defense is maximally employed at the highest productivity region. Suboptimal defense therefore lowers the IGP strength at which the native consumer is excluded across a broad range of intermediate to high productivity. In contrast, because naïveté does not alter the effectiveness of defense provided that it is employed, native consumers can persist at the highest levels of productivity in this invasion scenario. It has been previously

demonstrated that, at low defense efficiency adaptive antipredator behavior can reinforce the paradox of enrichment (Rosenzweig 1971) by lowering the productivity levels at which oscillatory dynamics replace stable IGP coexistence (Urbani and Ramos-Jiliberto 2010). This is in line with our results regarding the effect of suboptimal response toward an introduced omnivore: coexistence at high levels of productivity was dramatically reduced by lowered defense efficiency (suboptimal response) but not by reduced recognition (naïveté).

In contrast to productivity, the effects of defense cost on communities with adaptive defense have been relatively understudied. Abrams and Fung (2010) compared IGP models with cost-free versus costly defense in terms of their responses to top-down and bottom-up effects. However, their treatment did not explore how varying levels of costliness alter the employment of defense, and hence to changes in coexistence across a defense cost gradient. Using a graphical model of adaptive trait change, Peacor et al. (2013) clarified the effects of higher or lower costs of adaptive trait change on fitness to identify when large NCEs should be expected. Specifically, they predicted that large NCEs will occur when defense has a high cost but the benefits outweigh the costs because predation in the absence of defense is high. Therefore, exploring the effects of novelty across a cost gradient, we expected the greatest differences between suboptimal defenses versus naïveté would occur in highcost situations because of the increased relative strength of NCEs. In contrast, we observed that the greatest differences occurred at low cost, when defense was maximally allocated. Specifically, neither suboptimal defense nor naïveté result in altered persistence in the high-cost region because defense is simply too expensive to

employ. Further, both components of novelty caused exclusion when costs are intermediate—in essence suboptimal response and naïveté always oppose the positive effect on coexistence provided by adaptive defense. The discrepancy between invasion scenarios appears at the lowest range of defense cost because when defense is essentially cost-free it will be employed regardless of reduced effectiveness or predation recognition. This employment of defense causes increased parameter range of exclusion in the case suboptimal defense but not naïveté. Thus, systems with lowcost defense are predicted to be more sensitive to the effects of an introduced predator that matches prey's recognition template than to the effects of an unfamiliar predator.

However, we observed that the relationship between defense cost and native predator coexistence depends on the identity of the introduced predator and the relative importance of the direct versus indirect energy pathway from resource to omnivore. As shown by Ikegawa et al. (2015), predictions about IGP coexistence across parameter gradients are strongly dependent on the relative strength of the direct versus indirect energy pathway. In the case of an introduced consumer, which competes with—but also provides a food resource for—the omnivore, the effects of increasing defense costs can either promote or preclude native omnivore coexistence. Thus, our model highlights the importance of quantifying interaction strengths in IGP systems as their response to defense cost will differ between communities that approximate a food chain compared to those that are more similar to pure exploitative competition (see also Stier et al. 2016).

Effects of novelty on resource abundance and native predator facilitation

Many of the predictions from our model align with and are explainable by the characteristic asymmetry inherent in IGP systems, including for example, that an introduced omnivore is more likely to exclude a native consumer than the converse. However, several counterintuitive predictions also emerge. For example, a resource that *inaccurately* assesses the predation threat posed by an introduced omnivore shows higher equilibrium density relative to a resource with perfect perception of the trophic landscape. This result occurs because, in maximizing its own per capita growth rate through defense allocation, the resource indirectly benefits the intermediate consumer by reducing the growth rate of the omnivore. Hence, perfect perception results in reduced prey density. Naïveté reduces the recognition of the predation threat posed by, and therefore the optimal level of effort toward, the omnivore, thereby increasing predation on the consumer and enhancing resource abundance. In other words, naïveté can increase the strength of the trophic cascade, resulting in higher prey abundance at lower prey perception. Thus, predator-specific adaptive defense which does not take into account indirect effects of multi-predator systems may not ensure maximum resource abundance. This observation raises questions regarding the degree to which prey adaptations for predation risk assessment and defense allocation are able account for multiple predators and the indirect effects among them.

The highest resource density is found at an intermediate novelty of the omnivore due to the strengthening of the trophic cascade via either suboptimal defense or naïveté. In contrast, increasing novelty of an intermediate consumer results only in reduced or unchanged resource abundance as there is no indirect mechanism by which reduced defense toward the consumer can benefit the resource. Therefore, our analyses predict that the introduction of putative omnivores can either increase or decrease resource abundance, but that the introduction of intermediate consumers can only reduce the abundance of their resource. In fact, since consumers also represent a second resource for the omnivore, novelty of a non-native consumer can facilitate the persistence of an omnivore that would otherwise be excluded. While this observation runs counter to simple intuition, increasing novelty weakens the effect of resource defense making consumers more abundant prey for the omnivore. Both suboptimal defense and naïveté toward an introduced consumer can promote increased consumer abundance in such a way that it acts as an energy subsidy for a native omnivore that would otherwise be unable to persist at the same parameter region in the absence of novelty. Indeed, empirical studies have shown that introduced prey can in fact benefit natives of higher trophic levels when native predators also had access to native prey (Pintor and Byers 2015), as was the case with our model.

Predator novelty and invasion success

Another prediction of the model is that predator novelty does not alter the coexistence boundary for the introduced predator itself. Rather, because the coexistence boundaries for the non-native predator necessarily occur in parameter regions where that predator represents a low predation threat, the resource does not allocate defensive effort toward he invader and defense can therefore not be circumvented by novelty. However, this result should not be interpreted to imply that

novel traits cannot alter initial invasion success (as defined by the establishment of a persistent self-sustaining population) for two reasons. First, we examined *equilibrium* coexistence conditions so the behavior of the system at an invasion (coexistence) boundary should not be equated with the transient dynamics likely to occur during the initial phases of an empirical invasion. Second, in our model, defense is allocated in such a way that it maximizes resource per capita growth in response to changes in predator population density; therefore prey do not allocate defense effort toward predator species at low equilibrium abundance. Yet, in nature, prey individuals may indeed display a defensive response to predators that pose an immediate predation risk, regardless of the predator population size. Further, local predator density may be uneven, leading to a patchy landscape for both predation risk and predator cues. For phenotypic and behavioral defenses, individual prey experience only the local trophic environment, which may differ from the aggregate mean predation risk at the population level. An individual invader could therefore experience a fitness gain if novel traits facilitated high predation rates by rendering prey defense ineffective, regardless of predator population density. We therefore conclude that predator traits may very well influence initial invasion success (Lurgi et al. 2014), but that the invader's coexistence boundaries at equilibrium will not vary based on its ability to circumvent prey defense.

Key assumptions of the model

Alternative modeling choices may alter the predictions from this model and should be explored in future work. First, in this effort we considered predatorspecific defenses only. While adaptive predator-specific defenses promote coexistence of multi-predator systems by allowing prey to allocate effort in response to dominant predators (Lima 1992, Matsuda et al. 1996, Kondoh 2008, Nakazawa et al. 2010), this stabilizing mechanism is not present with generalized defense (Matsuda et al. 1993, Kimbrell et al. 2007). Ikegawa (2015) showed that the joint use of predator-specific and generalized antipredator defense promotes three-species coexistence in IGP systems even at high productivity, and it would be informative to explore the effects of imperfect predator recognition or response in the context of generalized or joint-use defenses. For example, it is entirely possible for prey to be protected from attack by a novel predator—even one that is unrecognized as a predation threat—by a generalized defense that is elicited by recognition of a native predator alone.

Second, in order to facilitate analytical tractability, we assumed linear functional responses for all predator-prey interactions. Type-II functional responses are commonly observed in empirical studies (Jeschke et al. 2004) and are predicted to alter stability properties of IGP at high productivity levels (Diehl and Feißel 2000, Mylius et al. 2001, Křivan and Diehl 2005). Therefore, our predictions may be most applicable at low prey abundance where predator consumption rate is adequately approximated by a linear function. For the same reason, we also assumed a linear relationship between defense effort and effectiveness at reducing attacks rates by the target predator. A non-linear functional form may be more biological reasonable in many cases (e.g., a decelerating function that models diminishing returns of increased defense effort). However, Peacor et al. (2013) note that their qualitative predictions (regarding fitness optima) are identical when comparing linear and non-linear relationships between defense effort and reduced predation. We predict that such a non-linear functional form would likely lower the optimum defense effort compared to the linear case, but this model variation too merits future consideration.

We considered suboptimal defense and naïveté separately in order to compare the cases of similar predators (bearing cue similarity to natives) and predators representing a novel predator archetype to which prey are naïve. In nature, these two components of novelty are not mutually exclusive (Sih et al. 2010) and prey may respond to a single introduced predator with both reduced effort and lowered effectiveness of antipredator defense (Carthey and Banks 2014). The total effects of such a predator (combining strong CEs and weak NCEs) are predicted to be intermediate between that of a totally novel predator (CEs only) and that of a similar predator that elicits suboptimal defense (strong CEs and NCEs) (Sih et al. 2010). To facilitate clear predictions about the effects of introduced predators (of each type) on community coexistence, we chose to model the extreme cases. We expect that a novel predator to which prey display both naïveté and suboptimal response will cause exclusion of native predators over a large parameter range, primarily owing to the negative effects of suboptimal defense on native persistence over the entire parameter region in which it is employed.

We motivated this modeling effort with a well-known empirical example of induced antipredator defense and assumed that phenotypic plasticity provides the adaptive stabilizing mechanism promoting coexistence. Behavioral or evolutionary trait change each represent alternative stabilizing mechanisms (at shorter and longer time-scales, respectively, compared to induced defenses) that could be explored with

similar models. The adaptive rate of trait change (in our model, represented by the parameter v) provides a means to "tune" the rate of adaptation to the appropriate time-scale relative to population dynamics (Matsuda et al. 1996). In fact, slower adaptation rates in response to the introduced predator may provide an alternative means of modeling partial naïveté that should be explored. Over evolutionary scales, however, prey response to novel predators itself is not static, so our model may be most applicable to plasticity or behavioral dynamics. Future modeling scenarios that allow prey recognition and defense efficiency to evolve in response to selection would improve our understanding of the role of novelty in shaping invasion outcomes.

Implications for food webs

The effects of predator introductions on natural communities span the entire continuum from a failure to establish viable populations to causing a native food web to collapse (Mack et al. 2000). Understanding the interaction between predator traits and native community characteristics that determine which scenario plays out for given introduction remains a major goal of conservation ecology (Kolar and Lodge 2001, Mata et al. 2013). Here we demonstrate theoretically that predator novelty can lead to native species exclusion in an IGP module. In a broader food web context, such biodiversity loss may lead to lead to secondary extinctions (Lundberg et al. 2000). For example, an excluded predator could represent an important hub of interactions, making secondary extinctions likely (Dunne et al. 2002). Even in the absence of initial native predator exclusion, introduced predator novelty could alter food web stability by influencing the interaction strengths within the network.

Speculatively, invader traits that result in ineffective antipredator defense could facilitate subsequent invasions (Simberloff and Von Holle 1999), especially if they lead to increased resource availability, as was demonstrated in the case of an introduced omnivore.

Our study illuminates how introduced predators can influence the persistence of natural systems and provides insight the mechanisms by which predator novelty can alter biological communities via novel trophic and non-trophic interactions. As natural systems across the globe face multiple stressors that can alter the functioning of their basic ecosystem processes, understanding the effects of exotic species on stabilizing mechanisms is vital to improve biological forecasting and inform the management of increasingly imperiled natural systems.

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Figure 4.1 Equilibrium values for resource abundance (a), defense effort (b), and abundance of a single predator (c) in the absence of the alternative predator along a gradient of defense costliness. Solid colored lines indicate equilibrium values in regions of stable equilibria. Vertical gray lines indicate transitions between equilibrium states. Between the ordinate and the left-most vertical gray line, defense effort remains maximized at one and increasing defense costliness results in decreasing predator abundance (negative slope of blue line in panel c). Between the thresholds indicated by vertical lines, defense effort is intermediate and decreases adaptively with increasing defense cost (monotonically decline of purple curve in panel c). In this same region, predator abundance increases and resource abundance decreases as a result of declining defense effort. Finally, to the right of the second threshold, defense effort is adaptively abandoned due to high cost; beyond this cost throeshold, predator and resource abundance does not vary with defense cost.



Figure 4.2 Coexistence conditions across gradients of productivity (x-axes) and IGP strength $(a_{PN}, y-axes)$ in the case of an introduced omnivore (circled in red in the IGP module). For all panels, gray regions labeled "RNP" indicate three-species coexistence. Areas labeled "RN" allow coexistence of resource (R) and consumer (N), but exclusion of the omnivore (P). The boundary between such regions and three-species coexistence regions are shown in red to indicate the boundary between omnivore coexistence and exclusion. Likewise, regions labeled RP indicate exclusion of the intermediate consumer (N) and blue curves indicate the boundary between consumer coexistence and exclusion. In (a) both novelty parameters are set to 1 (no naïveté or suboptimal defense) and the resulting coexistence region encompasses a large portion of the parameter space shown. Increasing productivity can both inhibit and promote coexistence of the native consumer (depending on the level of defense effort) as indicated by alternating positive and negative slopes of blue curves. Similarly to Figure 1, these changes in response along a gradient indicate transitions among equilibrium states with respect to optimized defense effort. Panels (b) and (c) display a reduced region of coexistence with increasingly suboptimal response to the omnivore ($\varphi = 0.75$ and 0.5, respectively). Panels (d) and (e) show coexistence/exclusion boundaries with naïveté towards the omnivore ($\rho = 0.75$, and 0.5, respectively). Compared to suboptimal defense (top row) the decrease in the parameter region of three-species coexistence caused by naïveté (bottom row) is more modest and localized at intermediate levels of productivity.


Figure 4.3 Coexistence boundaries across a range of defense costs (x-axes) and IGP strength (a_{PN} , y-axes) in the case of an introduced omnivore (circled in red in the IGP module). Color, shading, and labeling conventions are similar to Figure 4.2. Gray regions labeled "RNP" indicate parameter regions of three-species coexistence. In addition, bistability appears at high levels of defense cost and is indicated by light gray shading and labeled "RN/RP." Within these regions, either predator can coexistence with the resource excluding the alternate predator and the identity of the excluded predator depends on initial conditions. As with productivity (shown in Figure 4.2), increasing defense cost either inhibit or promote coexistence of the native consumer depending on whether defense effort is maximized, minimized, or intermediate (see Figure 4.1). In (a) both novelty parameters are set to 1 (no naïveté or suboptimal defense) and the resulting coexistence region encompasses a large portion of the parameter space shown. Panels (b) and (c) display a reduced region of coexistence with increasingly suboptimal response to the omnivore ($\varphi = 0.75$ and 0.5, respectively). Panels (d) and (e) show coexistence/exclusion boundaries with naïveté towards the omnivore ($\rho = 0.75$, and 0.5, respectively). Compared to suboptimal defense (top row) the decrease in the parameter region of three-species coexistence caused by naïveté (bottom row) is minor.



Figure 4.4 Equilibrium densities and defense effort levels across the full range of suboptimal defense (a) and naïveté (b) toward an introduced omnivore. Solid green, blue and red lines indicate equilibrium densities of the resource, consumer, and omnivore, respectively. Dashed lines indicate levels of defense effort directed toward each predator species (colors match predator identity). Suboptimal defense toward the omnivore (a) results in increased but ineffective defense effort toward the omnivore, eventually resulting in consumer exclusion. In (b) naïveté results in *decreased* effort toward an unrecognized omnivore. Defense effort is shifted toward the consumer, which is again excluded at higher levels of omnivore novelty. In both cases, the maximum resource abundance does not occur at perfect recognition and optimal defense ($\varphi = \rho = 1$) but rather at intermediate levels of omnivore novelty, due to a novelty-mediated release from consumer predation.



Figure 4.5 Coexistence conditions across gradients of productivity (x-axes) and IGP strength (a_{PN} , y-axes) in the case of an introduced consumer (circled in blue in the IGP module). Color, shading, and labeling conventions are similar to Figure 4.2. Gray regions labeled "RNP" indicate parameter regions of three-species coexistence. Increasing productivity promotes coexistence of the native of the native omnivore as indicated by the negative slope of red curves across all panels. In (a) both novelty parameters are set to 1 (no naïveté or suboptimal defense toward the consumer). Panels (b) and (c) display a reduced region of coexistence with increasingly suboptimal response to the consumer ($\varphi = 0.75$ and 0.5, respectively). Panels (d) and (e) show coexistence/exclusion boundaries with increasing naïveté towards the consumer ($\rho = 0.75$, and 0.5, respectively). Moderate naïveté (b) results in little change in coexistence; higher levels of naïveté (e) result in a substantial parameter region of native consumer exclusion.



Figure 4.6 Coexistence boundaries across a range of defense costs (x-axes) and IGP strength (a_{PN} , y-axes) in the case of an introduced consumer (circled in blue in the IGP module). Color, shading, and labeling conventions are similar to Figure 4.2. Gray regions labeled "RNP" indicate parameter regions of three-species coexistence. Coexistence occurs over the broadest range of IGP strength when defense is inexpensive (far right). Over much of the cost gradient, increasing defense cost promotes exclusion of the native omnivore as indicated by the positive slope of the red curve. At high cost levels, defense effort is abandoned and the level of IGP strength at which coexistence occurs does not vary with defense cost (red curve, zeroslope). In (a) both novelty parameters are set to 1 (no naïveté or suboptimal defense). Panels (b) and (c) display a reduced region of coexistence with increasingly suboptimal response to the omnivore ($\varphi = 0.75$ and 0.5, respectively). Panels (d) and (e) show coexistence/exclusion boundaries with naïveté towards the omnivore ($\rho = 0.75$, and 0.5, respectively).



Novelty Gradient

Figure 4.7 Equilibrium densities and defense effort levels across the full range of suboptimal defense (a) and naïveté (b) toward an introduced consumer. Solid green, blue and red lines indicate equilibrium densities of the resource, consumer, and omnivore, respectively. Dashed lines indicate levels of defense effort directed toward each predator species (colors match predator identity). Suboptimal defense toward the consumer (a) results in increased but ineffective defense effort toward the consumer, resulting in reduced resource densities and omnivore exclusion. In (b) naïveté results in *decreased* effort toward an unrecognized consumer. Defense effort is shifted toward the omnivore, which increases with increasing naïveté toward the consumer. In both cases, the maximum resource abundance occurs at perfect recognition and optimal defense ($\varphi = \rho = 1$) because there is no mechanism by which novelty of a consumer can indirectly facilitate resource abundance.



Figure 4.8 Consumer novelty can promote native omnivore coexistence. Equilibrium densities and defense effort levels across a restricted range of suboptimal defense (a) and naïveté (b) toward an introduced consumer. Solid green, blue and red lines indicate equilibrium densities of the resource, consumer, and omnivore, respectively. Dashed lines indicate levels of defense effort directed toward each predator species (colors match predator identity). Parameter values were chosen such that increasing consumer novelty permits the coexistence of an otherwise excluded omnivore. At perfect defense efficiency toward the consumer (far right) effective defense results in low consumer density and exclusion of the omnivore. Moving left-to-right, decreasing defense effectiveness allows the consumer to increase density providing and increased energy source for the omnivore, which can then persist (albeit at low density) despite reduced resource abundance. Note: this phenomenon only occurs under restricted parameter values (e.g., low resource productivity).

Invasion scenario	Predator	Defense Effort	Coexistence criteria (focal predator can persist when expression is > 0)
		0	$\frac{aPN \ bPN \ (aNR \ bNR \ k \ r - mN) + aNR \ aPR \ bPR \ k \ mN}{aNR^2 \ bNR \ k} - mP$
	Omnivore	int.	$\frac{r(aPN \ bPN \ c0 + aNR \ aPR \ bPR \ k \ (fN - c0))}{aNR \ fN} - mP$
		1	$\frac{aNR \ aPN \ bNR \ bPN \ (c0-1) \ (fN-1) \ k \ r - mN \ (aPN \ bPN + aNR \ aPR \ bPR \ (fN-1) \ k)}{aNR^2 \ bNR \ (fN-1)^2 \ k} - mP$
Suboptimal Defense	Consumer	0	$\frac{aPR \ k \ (aNR \ bNR \ mP - aPR \ bPR \ mN) + aPN \ (mP - aPR \ bPR \ kr)}{aPR^2 \ bPR \ k}$
		int.	$aNR \ bNR \ k \ r - \frac{c0 \ r \ (aPN + aNR \ aPR \ bNR \ k)}{aPR \ fN \ \phi} - mN$
		1	$\frac{aNR \ aPR \ bNR \ k \ mP \ (1 - fN\phi) + aPN \ (mP - aPR \ bPR \ (c0 - 1) \ k \ r \ (fN \ \phi - 1))}{aPR^2 \ bPR \ k \ (fN \ \phi - 1)^2} - mN$
Naïveté	Consumer	0	$\frac{aPR \ k \ (aNR \ bNR \ mP - aPR \ bPR \ mN) + aPN \ (mP - aPR \ bPR \ k \ r)}{aPR^2 \ bPR \ k}$
		int.	$\frac{aNR \ bNR \ (\frac{\sqrt{k}\sqrt{r}\sqrt{\rho(aPR \ bPR \ k \ r(c0 - fP)^2 + 4 \ c0 \ fP \ mP)} - 4 \ c0 \ fP \ mP}}{\sqrt{aPR} \ \sqrt{\rho}} - c0 \ k \ r + fP \ k \ r)}{2 \ fP} - \frac{aPN \ c0 \ r}{aPR \ fP \ \rho} - mN$
		1	$\frac{aPN (aPR bPR k r (c0 (-fP) + c0 + fP - 1) + mP) - aPR(fP - 1) k (aNR bNR mP + aPR bPR (fP - 1) mN)}{aPR^2 bPR (fP - 1)^2 k}$

 Table 4.1 Coexistence criteria for introduced omnivore and native consumer

Invasion scenario	Predator	Defense Effort	Coexistence criteria (focal predator can persist when expression is > 0)
		0	$\frac{aPR \ k \ (aNR \ bNR \ mP - aPR \ bPR \ mN) + aPN \ (mP - aPR \ bPR \ k \ r)}{aPR^2 \ bPR \ k}$
	Consumer	int.	$\frac{r (aPN c0 + aNR aPR bNR k (fP - c0))}{aPR fP} + mN$
		1	$\frac{aPN\left(aPR\ bPR\ k\ r\ (c0\ (-fP)+c0+fP-1)+mP\right)-aPR\ (fP-1)\ k\ (aNR\ bNR\ mP+aPR\ bPR\ (fP-1)\ mN)}{aPR^2\ bPR\ (fP-1)^2\ k}$
Suboptimal Defense	Omnivore	0	$\frac{aPN \ bPN \ (aNR \ bNR \ k \ r - mN) + aNR \ aPR \ bPR \ k \ mN}{aNR^2 \ bNR \ k} - mP$
		int.	$\frac{c0 r (aPN bPN - aNR aPR bPR k)}{aNR fP \phi} + aPR bPR k r - mP$
		1	$\frac{aPN \ bPN \ (aNR \ bNR(c0-1) \ k \ r \ (fP \ \phi - 1) - mN) + aNR \ aPR \ bPR \ k \ mN \ (1 - fP \ \phi)}{aNR^2 \ bNR \ k \ (fP \ \phi - 1)^2} - mP$
Naïveté	Omnivore	0	$\frac{aPN \ bPN \ (aNR \ bNR \ k \ r - mN) + aNR \ aPR \ bPR \ k \ mN}{aNR^2 \ bNR \ k} - mP$
		int.	$\frac{aPN \ bPN \ c0 \ r}{aNR \ fN \ \rho} - \frac{aPRbPR(-\frac{\sqrt{k}\sqrt{r}\sqrt{\rho} \ (aNR \ bNR \ k \ r \ (c0 - fN)^2 + 4 \ c0 \ fN \ mN) - 4 \ c0 \ fN \ mN)}{\sqrt{aNR}\sqrt{bNR}\sqrt{\rho}} + c0 \ k \ r - fN \ k \ r \)}{2 \ fN} - mP$
		1	$\frac{aNR \ aPN \ bNR \ bPN \ (c0-1) \ (fN-1) \ k \ r - mN \ (aPN \ bPN + aNR \ aPR \ bPR \ (fN-1) \ k)}{aNR^2 \ bNR \ (fN-1)^2 \ k} - mP$

 Table 4.2 Coexistence criteria for introduced consumer and native omnivore

Chapter 5 — General Conclusions

This dissertation has examined how introduced predators influence the recipient communities of their invaded range through their effects on the stabilizing processes that previously bounded prey population dynamics and promoted community coexistence. Using a combination of natural and manipulative experiments, I tested predictions regarding the effects of an introduced marine predator on the local population dynamics of a common prey species. Following this empirical work, I used theoretical approaches to generate testable hypotheses regarding the potential for an exotic predator to exclude native predators by circumventing the antipredator defense in shared prey.

The field experiment described in Chapter 2 showed that fairy basslet on natural coral reefs in the Bahamas displayed over 60% higher per capita loss over eight weeks compared to rates from the same reefs measured prior to the lionfish invasion. While the average loss rates were greater on both recruitment-enhanced and unmanipulated populations, per capita loss rates remained strongly densitydependent, with a nearly 6-fold increase in per capita loss between control and recruitment-enhanced populations. Despite the continuing presence of density dependence, the increased magnitude of mortality caused seven of 16 local basslet populations to experience greater than 50% loss over the eight-week study duration, compared to just two populations with similar rates prior to the invasion. These results suggest that, while one condition for population regulation (demographic density dependence) continues to operate on local fairy basslet dynamics, lionfish predation nevertheless increases the risk of extirpation by increasing post-settlement mortality across a broad range of prey densities. The presence of density dependence in the post-invasion experiment means that the stabilizing process by which fairy basslet populations were previously regulated has not been completely eliminated by lionfish predation. However, pre- and post-invasion comparisons of unmanipulated population densities (far lower on average since the arrival of lionfish) suggest that the regulating process provided by density-dependent predation has been altered by the invader, resulting in an overall increase in mortality across prey densities. Future work should experimentally test the hypothesized mechanisms by which lionfish alter mortality patterns. Specifically, direct comparisons of the functional and aggregative responses of both native and introduced predators would address the mechanisms behind these results. Consumption rates of introduced predators may have a different functional form than those of natives, or they may display altered spatial responses to prey aggregations, leading to altered prey density-mortality relationships. Directly testing the functional responses would require standardizing both native and introduced predator densities, a manipulation that was not feasible at the scale of this experiment but could conceivably be performed on smaller patch reefs.

The experiment described in Chapter 3 builds on the results of the previous chapter by complementing the before-after, natural-experiment design of the prior study with a cross-factored controlled experiment at another location in the Bahamas. By experimentally manipulating both the presence of lionfish and the population density of fairy basslet, this study unequivocally attributed the altered mortality patterns of prey to the invasive predator alone. This experiment corroborated the conclusions of the previous chapter: in the presence of lionfish, fairy basslet experienced higher yet still density-dependent per capita loss. In addition, this experiment documented the extirpation of two local fairy basslet populations on reefs with lionfish; no such extirpations occurred on lionfish-free reefs. The five-fold increase in mortality rates at unmanipulated fairy basslet populations observed in the presence of the invader suggests that lionfish remain efficient predators as prey become depleted, an alarming result because depleted populations are the most vulnerable to extirpation. While predation rates remained higher at populations with more prey, nevertheless the local population dynamics are clearly destabilized in the presence versus the absence of lionfish, as evidenced by the complete extirpation of local fairy basslet populations only on lionfish reefs. While persistence (one stability metric) and abundance were lower in the presence of lionfish, this study did not examine differences in population variability (another stability metric) among predator treatments, although the data suggest that variability may be higher on lionfish reefs. Future work should also examine the potential role of prey naïveté in allowing introduced predators to cause high predation rates at low prey density. An experimental design that can distangle the effects of prey density and refuge availability (confounded and unexamined in this study) would provide insight into the role prey naïveté plays in allowing introduced predators to consume prey even at low prey densities.

The theoretical study described in Chapter 4 examined an intraguild predation model with adaptive defense in the basal prey, and compared conditions for community coexistence when one of the predators is an introduced species. The model predicts that an introduced omnivore is more likely to exclude a native intermediate consumer than when predator origin is reversed, and that a functionally similar predator (i.e., one that elicits a defensive response by prey) causes exclusion over a great parameter region than a truly novel predator to which prey fail to respond. Further, the two invasion scenarios alter the predictions for coexistence along different regions of productivity and defense-cost gradients, suggesting that the differential effects of introduced predators based on their degree of novelty may be complex and context-dependent. Adaptive defense (and adaptive trait modification, more broadly) provides a mechanism of coexistence among competing species by creating an indirect positive effect that promotes stabilizing tradeoffs. By circumventing antipredator defense, an introduced predator reduces the strength of this tradeoff, allowing the negative interactions to cause exclusion. In this sense of stability (community persistence), novel predators are predicted to be destabilizing over the range of parameter space where adaptive defense otherwise prevents exclusion. Under very specific conditions, increasing consumer novelty can facilitate omnivore coexistence by subsidizing the native top predator, broadening the region of community persistence. Future work should clarify the conditions under which introduced predators will increase or decrease the stability of native communities, especially as they potentially represent both predator and prey in native food webs. Further, while this research examined the role of predator novelty in a small

community module, subsequent work should explore the consequences of ineffective antipredator responses in other food web configurations and in more speciose webs.

Overall, the research described in this dissertation illuminates the mechanisms by which introduced predators can influence the boundedness and persistence of otherwise stable systems and provides insight regarding how predator novelty can alter biological communities via novel trophic and non-trophic interactions. As natural systems across the globe face multiple stressors that can alter the functioning of their basic ecosystem processes, it is increasingly vital to understand the stabilizing mechanisms that buffer these systems from change, and how species introductions may modify the capacity for natural systems to respond to natural and human-caused disturbance.

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