TRACING AN INVASION PARADOX ACROSS SCALES: PATTERNS AND TESTS FOR THE EFFECTS OF THE INTRODUCED PREDATORY GROUPER, *ROI* (*CEPHALOPHOLIS ARGUS*) IN HAWAIʻI

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAIʻI AT MĀNOA IN PARTIAL FULFULLMENT OF THE
REQUIRMENT FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

ZOOLOGY

April 2017

By

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DEDICATION

This dissertation is dedicated to my family, namely my parents Mary Nancy (Cavallo) Giddens and Craig Giddens. You always encouraged me to find my passion and follow it. You trusted in this process of discovery, even though the way was long and winding. Because your' parenting nurtured imagination and wonder about the world, I am forever a student of, and an advocate for the ocean, with an ever-growing love (*philo*) of knowledge (*sophy*). As Goethe said, "We are shaped and fashioned by what we love". This work has been shaped by a love of the sea.

In nature we never see anything isolated, but everything in connection with something else which is before it, beside it, under it and over it.

Johann Wolfgang von Goethe - 1893

ACKNOWLEDGMENTS

I would like to thank my committee members: Alan Friedlander, John N. Kittinger, Brian Bowen, Mark Hixon, and Tamara Ticktin. Your guidance and support has invited me to seek knowledge deeply, as well as broadly, and in so doing has opened up the world for discovery. Each one of you has contributed to this dissertation in your own unique way: Mark challenged me to think and communicate more clearly, Tamara encouraged positive and grounded work, Brian inspiration me to be creative and a story-teller, and Jack's enthusiasm is contagious, as is his drive to connect research with real-world problem solving in marine conservation. Alan has been a steadfast support. All have shaped who I now am as a scientist, and I am grateful for the opportunity to be your student.

I am grateful to Chuck Birkeland for being a mentor in the truest sense of the word. I would not be here without his guidance and investment in my academic path. Thank you for sharing your interest, insights, enthusiasm, and your music.

I would like to thank my lab-mates past and present at the Fisheries Ecology Research Lab (FERL). Mary Donovan, Kosta Stamoulis, Eva Schemmel, Hal Koike, Whitney Goodell, Alex Filous, Paolo Usseglio, Keith Kamakawa, and Kaylyn McCoy– your companionship made graduate school fun. And when it wasn't fun, well, at least we had each other. I would go to sea and embark on a project with each of you, and indeed I hope we have many more collaborations to come. I especially thank Mary Donovan. We met and became *roi* buddies, (as we studied the same animal), and soon turned into dive buddies, conference buddies, and so much more. Upon entering the graduate Program and right on up to the final defense, you were there with a smile of encouragement and with all of the things that I didn't even know that I needed yet.

The UH Zoology and Marine Biology programs are an *ohana*. I appreciate the collegiality and support across labs and programs. I especially would like to thank Chris Wall, Eileen Nalley, Courtney Couch, Lillian Tuttle, Rachel Dacks, and Chelsea Council for moral support and academic council. I also thank Nyssa Silbiger and Richard Coleman for their good advise on writing and presentations, and my cousin and colleague Steve Alexander for sharing his insight and expertise.

This dissertation research could not have been accomplished without The Nature

Conservancy Hawaii Marine Program (TNC). The tremendous fieldwork efforts and community outreach events were possible because of the leadership of Eric Conklin and the magic of Chad Wiggins. In particular, Chapter II and the initiation of Chapter III was a joint project between UH and TNC. Chapter III project management was carried through by TNC, and through all aspects of the dissertation research, the Marine Team has been crucial to its success. On a more personal note, Chad has been instrumental on my path as a marine conservation researcher in Hawaii. Chad introduced me to Puako – the place and the community – and through this partnership I found my way to graduate school and to my place as a scientist.

I thank the TNC marine field team for their comradery, excellence, and integrity beyond reproach. Specifically, I thank Russell Amimoto, Kydd Pollock, Zach Caldwell, Rebecca Most, Ryan Carr (yay Thursdays!), and Hank Lynch. Thank you to TNC Marine Fellows Ily Iglesias, Brad Wong, and Nahaku Kalei. Also, thank you to Joe Laughlin for teaching us the tow-board survey protocol for Chapter II. I thank Dwayne Minton for our coffee-shop conversations about the *roi* progress and the story unfolding.

This dissertation relied on the support of the Hawaii spear fishing community. Matthew Ramsey played a pivotal role in connecting this research with the wider community. Through Matt's work, I was able to connect with and learn from amazing people. Specifically, I would like to acknowledge Darrell Tanaka and all the DEADicated *roi* divers. I thank Kuhea Paracuelles, Kawika Auld, Rhinehart Jensen, Brian Thomas, Jake Merkel, Derek LeVault, Aaron Mickelson, Kimi Makaiau, and Kawika Duvauchelle. I also acknowledge the following organizations: Hilo Dive Club, Kawabanga Spears, Na Kane o Ke Kai, Selective Aloha, Tokyu Foundation, Topshot spearfishing, and All About Fish Maui. Further, I thank Skippy Hau and Linda Castro, Randy Clarke, John Kahiapo, Sierra Tobiason, Liz and Chelsea Morriss and Diesel. Michael Morris, your love of the ocean is a continued inspiration to us all.

I have had the best of mentors throughout the years. I am very grateful to Dr. Bill Walsh and the Kona DAR *ohana*. Dr. Bill hired me as a fish surveyor in my undergraduate days, and has been a mentor ever since. Likewise, I met Dr. Ivor Williams diving with DAR, and have gone to Ivor for advise on analysis and reef fish ecology ever since. Megan Donahue led a working group on Bayesian analysis, and I am thankful for her sharing her expertise. Marc Nadon helped me clarify ideas during my Chapter II analysis, and shared his expert knowledge of fisheries models. Kyle Edwards taught the most useful class I have ever taken – advanced statistics, and was a great help in thinking through the BACI analysis in Chapter III. Mark Hixon led some of the best seminars for graduate students. I am grateful for the opportunity to not only be exposed to new exciting ideas, but also be challenged to put those ideas into words and affectively communicate the “aha” moments that they inspired.

I thank the funding sources that made all of this possible: NSF Graduate Research Fellowship (DGE-1329626); EA Kay (Biology Department); Yoshimoto and Maybelle Roth (EECB); ARCS Foundation; NOAA Hawaii Coral Reef Initiative (NA09NOS4260242); NOAA Coral Reef Conservation Program (NA10NMF463081); PADI (7886); and the UH Manoa Graduate Student Organization. I also thank Malia Chow, Jonathan Maritinez, and Patty Miller of the Humpback Whale National Marine Sanctuary for their support of my fellowship applications.

I thank the administrative and institutional support; the Biology Department (Audrey Shintani and Pia Dizon); UH Diving Safety Office (Dave Pence, Maria Laamang, Keoki Stender); Hawaii Coral Reef Initiative (Risa Minato); and the Office of Graduate Education (Patricia Cooper and Petra Kubalkova). Also thank you to the Hawaii Conservation Alliance for the Hawaii Conservation Conference every year. It is an integral part of professional development as a conservation scientist in Hawaii.

In addition to my own dissertation research, I had the honor of participating as a research assistant with the Coastal SEES (Science, Engineering, and Education for Sustainability) team, led by Dr. Tamara Ticktin. I learned so much about collaboration across disciplines and the joy of science. This project allowed me to work in vital places with beautiful communities, and I thank Haena and Kaupulehu for that time and everything learned and shared there.

I am fortunate to also have been involved with the National Geographic Society Pristine Seas mission and I thank my advisor and the Chief Scientist, Alan Friedlander, for opening up that opportunity. Thanks to Patrick Hare, Tatiana Faramarzi, and Sam Mendel. I thank Lida Teneva for developing the next great project with me, and I thank Don Kobayashi for helping it come to fruition through the NOAA Ecosystems Sciences

Division. Thank you to Ivor Williams for making the connection of the two.

I thank Jeff Kuwabara for being my oldest friend (not that you are old [you are], but that you are the first friend that I met in Hawaii). You have always given the wisest council, even when sometimes it was hard to hear. More generally, I thank the Marine Option Program and the Quantitative Underwater Ecosystem Survey Techniques (QUEST) programs for preparing me for a career in marine science. I thank Misaki Takabayashi and the very first *Ku*ʻ*ula* Traditional Hawaiian Marine Resource Management class. Our trip to *Pihemanu* (Midway atoll) resonates deeply in all the work that I do as a part of these Hawaiian ecosystems. I thank Sea Education Association, the SSV Robert C. Seamans, class 184, and I thank the winds and sails for bringing me to Hawaii.

My Hawaii *ohana* has made the time here special and meaningful as we celebrate the seasons turning and all the ups and downs of life: Mary Donovan and Joey Lecky, Eva Schemmel and Brian Nielsen, Chris and Megan Wall, you are the best community to share it with. Thank you to Mindy and Don Wallace for welcoming me to Oahu (Hibiscus place!) and making me feel at home.

Matthew John Iacchei– you are the light of my world. With you by my side there is no doubt or fear, only love, and that’s what makes life so beautiful. This dissertation owes its existence to your steadfast support through all the aspects of the work, and is as much a testament to your patience, persistence, and devotion as my own.

Finally, I thank you Hawaii, for the '*Āina* (that which feeds us). In particular, I am grateful for ‘walking and thinking’ meditations in Kohanaiki, Leahi, and Laniakea to Papailoa. Of course, dear Puako, you are loved. Mark Twain wrote that Hawaii is “the loveliest fleet of islands that lies anchored in any ocean”, and I couldn’t agree more. I am grateful everyday be able to live, learn, grow and work here.

ABSTRACT

Theory, observation, and experimental studies in invasion ecology have led to what is known as the ‘invasion paradox’, where both the factors that determine the invasability of ecosystems, and the invasiveness of species are context specific. As the patterns observed and the underlying processes are sensitive to the extent and resolution of inquiry, paradox can best be understood by tracing patterns and processes across scales. In Hawai‘i, a mid-sized predatory grouper, *roi* (*Cephalopholis argus*) was introduced during the 1950s, and subsequently established and spread throughout the main archipelago. Yet, the seascape factors that drive their distribution, a determination of their impact on the native reef fish assemblage, and methods for assessing and managing *roi* populations, were previously unknown. To address this gap in knowledge, I conducted studies of *roi* in Hawai‘i at three levels of organization: 1) field observations at the population level; 2) field manipulative experiments at the community level; and 3) species distribution modeling at the seascape level. I trace salient factors of *roi* invasiveness and community invasability across the three scales, and relate these to the human social system, as the *roi* introduction effects, and is affected by human communities. I found that with low population mortality rates, introduced *roi* has the potential to be an effective invader. Yet, over a long-term predator removal experiment, *roi* had no effect on the abundance of their prey. Likewise, in the seascape context, populations of *roi* declined in relation to increasing densities of native fish species. In the broadest sense, this introduced species has inspired community-led conservation action in Hawai‘i through *roi* fishing tournaments and thus, *roi* present an opportunity to engage across sectors and strengthen collaborative ocean management.

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CHAPTER I
INTRODUCTION

In an era of global change (Jackson et al. 2001, Mora et al. 2008), species range shifts are predicted to occur more frequently due to changes in climate. Humans provide a direct vector for exotics to establish in new environments through species introductions, thereby creating novel communities of organisms. With accelerating species extinctions (Barnousky et al. 2011) and homogenization of communities and habitats (Vitousek et al. 1997), invasion ecology has emerged as a discipline apace with global change (Elton 1956, Cadotte et al. 2006). The discipline can utilize global change as an instrument through which to understand biodiversity and adaptive capacity (Folke 2006), and in so doing lead the way to a sustainable future. As the planets most pervasive invading species, *Homo sapiens* are also the most inquisitive, and paradoxically are able to both destroy and reveal the secrets of nature. The avoidance of the former action relies on the timing of the latter.

Since Elton's seminal work on invasion ecology from an applied perspective (1958) and further work from basic science approaches (e.g. Baker and Stebbins, 1965) some guiding questions that have driven the field along parallel lines of research are: 1) What biological traits makes a good invader; 2) What determines the invasibility of ecosystems; and 3) How can knowledge of the first two be used to control invasions? The answer to these questions underpin our ability to manage for biodiversity conservation, the sustainability of ecosystem services, and ultimately, human well-being.

It is generally agreed from theory and empirical studies across ecosystems and taxa that weedy species are more likely to be successful invaders and are likely to capitalize on the ecological space provided by disturbance, such as habitat degradation (Sax et al. 2005). The consequence of this advantage is expected to be an increased homogenization of communities with increased habitat disturbance (Cox 2004) and range shifts driven by climate change (Vitousek 1994, Feary et al. 2004).

To the second question, on the invasibility of ecosystems, a paradox is revealed when traced across spatial scales, systems, and study types. An intuitive hypothesis, formulated by Elton (1958) is that species-rich areas are less likely to be invaded compared to the species poor ones, assuming that the former are saturated in regards to niche space, and the latter is vacant in at least one dimension. Thus the prediction is that high diversity correlates with low invasibility.

However, theory, observation, and experimental studies in invasion ecology over the years have led to what is known as the ‘invasion paradox’. A paradox is ‘‘something with seemingly contradictory qualities or phases’’ (Grove 1993) and the meaning here relates to contrasting lines of support for both negative and positive relationships between various measures of ‘success’ of alien species and the aspects of the recipient ecosystems, such as native species diversity (Fridley et al. 2007). The factors that determine the invasability of ecosystems, and the invasiveness of species are thus poorly resolved, because different approaches have revealed different results, depending upon the methodology used and the scale of study.

For example, a variety of observational, experimental, and theoretical studies have documented negative relationships between the number of native species and exotics at fine scales (~ resolution of 10 m^2 or less), and these studies have led to the conclusion that native richness protects ecosystems against invasions (Case 1990, Knops et al. 1999, Levine 2000). In contrast, broad-scale studies (~ resolution of 1 km^2 or more) generally indicate the inverse pattern (Levine and D’Antonio 1999, Shea and Chesson 2002, Byers and Noonburg 2003, Fridley et al. 2004, Davies et al. 2005), resulting in the opposite conclusion - that native species richness can enhance the invasion success of exotics (Davis et al. 2000, Huston 2004).

As there is conflict both between the findings of experimental and observational studies, and between fine-scale and broad-scale observational studies, researchers have sought to explain this paradox (Fridley et al. 2007). Byers and Noonburg (2003) presented a Lotka-Volterra competition model that increased in resource availability (number of unique resources) with increasing spatial scale. Invasion probability was relatively low at fine scales with minimal resources, and the probability of invasion increased with scale in spite of increasing native species richness. Thus, investigating the relationship between native and exotic species, the shift from the negative to positive relationships with increasing spatial extent could be driven by the availability of resources that covary with increase in scale. Further, Levine’s (2000) reasoning from meta-community theory was that, all else being equal, the environmental heterogeneity of large scales would make the diversity-invasibility relationship positive as increased resource types in the environment increases niche opportunities for both natives and exotic invaders alike. Along these lines, a conceptual model of ‘‘niche opportunity’’ was developed to explain the invasion paradox (Shea and Chesson 2002, Davies et al. 2005). This model indicated that, where heterogeneity in resources emerged with increasing scale, shifts in competitive dominance could lead to coexistence of both native and exotic species (Huston and DeAngelis 1994, Tilman 2004). Similarly, fluctuating resources over time would result in the same outcome (Davis et al. 2000).

Further along these lines, Melbourne et al. (2007) proposed an environmental heterogeneity hypothesis of invasions whereby heterogeneity both increases invasion success and decreases impacts to native species in the community. The assumption is that environmental heterogeneity promotes invasion and coexistence mechanisms that are not present in homogeneous environments. Since range expansions and biological invasions are concurrent with homogenization of habitats from altered human land use and pollution, this distinction in invasibility and its impacts is an important one.

Homogeneous environments are less likely to be invaded, but when they are, the event would result in ‘hostile take-over’ by those exotics. In other words, in homogenized land and seascapes, coexistence mechanisms are decreased and the invasion, when it does occur, is more likely to lead to native species extinction, with an associated decrease in biodiversity and the ecosystems services that biodiversity supports (Diaz et al. 2006). Therefore, environmental heterogeneity is an important factor in determining not only the invasability, but also the ecological impact of biological invasions.

If communities are saturated, then they are under local control (Cornel and Lawton 1992), dominated by species interactions such as predation, competition, and mutualism. However, if speciation and dispersal provide fewer species than sites can support, then regional control over communities is dominant, local richness is unsaturated, and those areas are prone to invasion. Thus, Fridley et al. (2007) proposed that: 1) Broad-scale patterns of native and exotic species richness are influenced by abiotic factors such as evolutionary history, disturbance rates, landscape configuration, and environmental heterogeneity; and 2) species interactions are most important in determining native–exotic richness patterns small spatial scales.

Taken together, to resolve the conflict of the invasion paradox, spatial and temporal scales of study, as well as the environmental context in which they are embedded, must be explicit. This paradox underscores the importance of pattern and scale in ecology, where the patterns observed and the underlying processes are sensitive to the extent and resolution of inquiry (Levin 1992). Therefore, insight into the invasion paradox will likely emerge by uncovering scaling rules for linking fine and broad-scale patterns across ecosystems, and by tracing patterns and processes across scales (Fridley et al. 2007).

Panarchy theory posits that small-scale processes aggregate to establish larger scale patterns, and in turn larger scales processes entrain the outcomes of phenomenon operating on the smaller scales (Gunderson and Holling 2002). As such, this theory is a useful heuristic to trace patterns and process across scales of organization. In its broadest sense, panarchy theory is concerned with the dynamic interactions between societies and ecosystems, and the sustainability of those interactions (Gunderson and Holling 2001). As a theory of adaptive change that spans human and natural systems, panarchy is a particularly useful to guide interpretations of studies in invasion ecology. With one foot rooted in the mission-driven science of conservation and restoration ecology, progress in invasion ecology necessarily means engaging with social issues regarding conservation and management. The knowledge generated is meant to guide solutions to environmental problems, and guide adaptive change of coupled human and natural systems into the future.

Connecting panarchy theory to invasion ecology

The dynamics of complex adaptive systems (Levin 1998), such as nature and human societies, can be understood through the conceptual framework of panarchy, which describes system structure and function in discrete spatiotemporal domains, and at hierarchical levels of organization (Holling 2001, Gunderson and Holling 2001). A system is complex if it is made up of diverse constituent parts, and it is adaptive if an autonomous process selects aspects of that system for replication or enhancement (Levin 1998). The human-natural world, and its evolution, can be understood in terms of this metaphor, as a set of complex adaptive systems undergoing change.

Such system dynamics have been described as an adaptive cycle (Holling 1986, Gunderson and Holling 2001) where interactions between living and non-living elements develop, organize, and decay (Figure 1.1). In this cycle, a system proceeds through phases of growth (*r*), conservation (*K*), release (Ω), and reorganization (α) (Holling 1986).

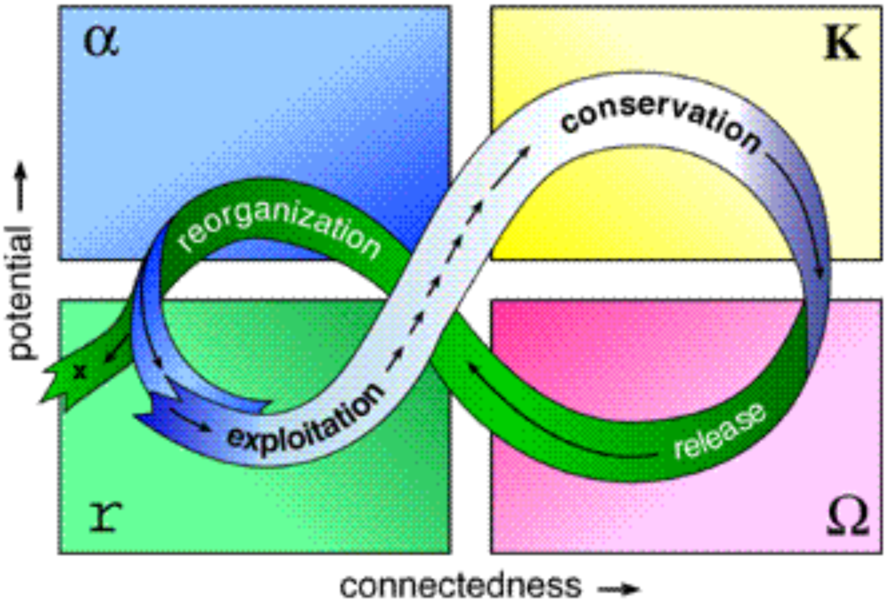

Figure 1.1. The adaptive cycle. A representation of the four ecosystem functions (*r*, *K*, omega, alpha) and the flow of events among them. The cycle reflects changes in two properties: (1) Y axis—the potential that is inherent in the accumulated resources of biomass and nutrients; (2) X axis—the degree of connectedness among controlling variables. Low connectedness is associated with diffuse elements loosely connected to each other whose behavior is dominated by outward relations and affected by outside variability. High connectedness is associated with aggregated elements whose behavior is dominated by inward relations among elements of the aggregates, relations that control or mediate the influence of external variability. The exit from the cycle indicated at the left of the Figure suggests where the potential can leak away or where a change of state into a less productive and organized system is likely. From Panarchy: Understanding Transformations in Human and Natural Systems L.H. Gunderson and C.S. Holling, eds. Copyright © 2001 by Island Press.

A system's trajectory depends on the process of selection among novel combinations that are generated during the reorganization (α) phase. The emergence and maintenance of biodiversity (Lovejoy 2006) in a complex adaptive system can be associated with the back loop of the cycle (release to reorganization) (Gunderson and Holling 2001). Novelty and selection are associated with adaptive capacity – the ability of a system to adapt to change. While the source of novelty may be chaos itself (*sensu* Lorenz 1972) (e.g. an episodic disturbance such as a hurricane creates space for a new combination of species to settle in the rocky intertidal marine ecosystem – reviewed by Underwood 2000), the process of selection could, at least to some extent, be shaped by human actions.

For humans to enhance the resilience of favored ecosystems, such as coral reefs over macro-algal dominated reefs, ecosystem-based management is essential (Levin and Lubchenco 2008). Resilience is the property of an ecosystem to withstand perturbations while still maintaining essentially the same processes and functions (*sensu* Holling 1973), and is associated with the conservation phase (*K*) of the adaptive cycle. Panarchy theory emphasizes interactions of adaptive cycles across scales, and that processes at one scale influence the system dynamics overall (Figure 1.2).

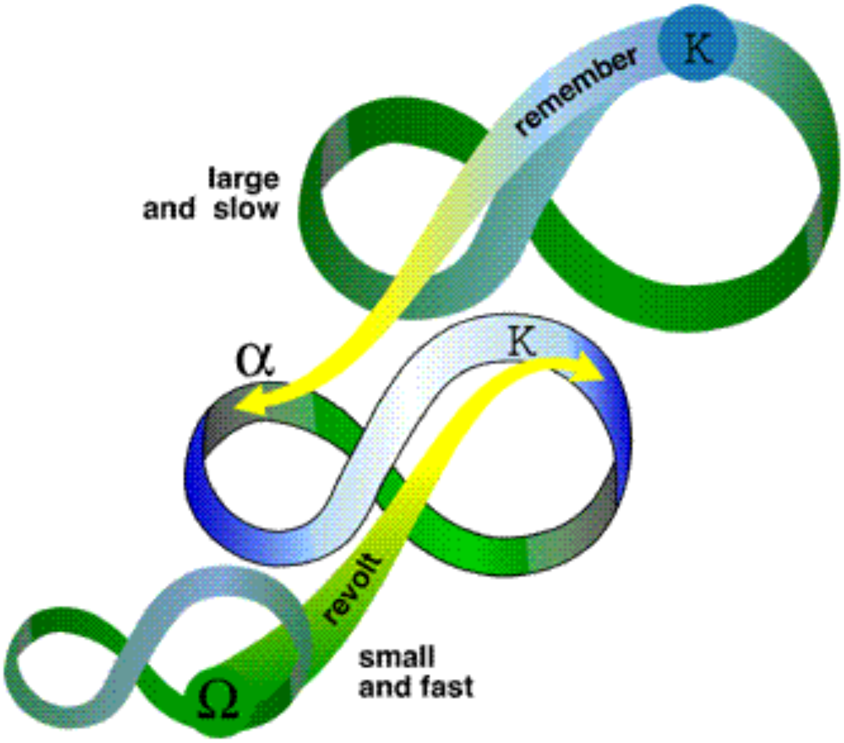

Figure 1.2. A panarchy. Three selected levels of a panarchy are illustrated, to emphasize the two connections that are critical in creating and sustaining adaptive capability. One is the "revolt" connection, which can cause a critical change in one cycle to cascade up to a vulnerable stage in a larger and slower one. The other is the "remember" connection, which facilitates renewal by drawing on the potential that has been accumulated and stored in a larger, slower cycle. The number of levels in a panarchy varies, is usually rather small, and corresponds to levels of scale present in a system. Excerpted from Panarchy: Understanding Transformations in Human and Natural Systems L. H. Gunderson and C. S. Holling, eds. Copyright © 2001 by Island Press.

Drawing from the literature on ecological resilience (Holling 1973, Gunderson and Holling 2001, McClanahan et al. 2007) and its application to complex adaptive systems (Levin 1998), including links to human communities (Berkes et al. 2003, Folke 2006), the third question in invasion ecology posed above is here re-phrased and is the central question that I seek to answer: *How can we use insights from invasion ecology to enhance adaptive capacity in the face of global change?*

Ecosystem impacts of introduced aquatic species

Introduced species can weaken coral reef ecosystem resilience and thus undermine ecosystem services (Vitousek et al. 1997, Ruiz et al. 2007). Invasive predators can reduce biodiversity and abundance of native species via predation or interspecific competition for resources (Balon and Bruten 1986, Faush 1988, Molnar et al. 2008). Marine introductions, though less pervasive than on land, have altered a number of ecosystems globally. In particular, in San Francisco Bay, more than 212 species were introduced, and presently no shallow water habitat therein remains unaltered by introduced species (Cohen and Carlton 1995). In the Great Lakes of North America, sea lampreys (*Petromyzon marinus*) were accidentally introduced, and now parasitize native fish species (Forney 1986). On coral reefs in the Caribbean, the invasive lionfish (*Pterois volitans*) has greatly reduced the recruitment and abundance of native fishes, which in turn can erode coral reef ecosystem resilience (Albins 2013, Albins and Hixon 2013). Together, biological invasions may constitute the largest single threat to the biodiversity of coastal waters (Lowe et al. 2000).

In the future, species invasions are projected to occur more frequently. Certainly, as climates fundamentally change and habitats are degraded, species that can shift in geographic ranges in order to adapt will do so, and the Anthropocene epoch (Crutzen and Stoermer 2000) will bear witness to widespread no-analog communities. This novelty will both provide opportunity for ecologists to discover the mechanisms that underpin coexistence and the evolution of life, as well as challenge human communities to operationalize this knowledge in the form of management for sustainability. Therefore, invasion ecology (Elton 1958), coexistence theory (Chesson 2000), resilience theory (Holling 1978), and social-ecological systems research (Starzomski et al 2004, Berkes and Folke 1998) are inexorably linked and mutually inform one another. When viewed through the panarchy framework (Holling 2001, Gunderson and Holling 2002), these disciplines together illuminate life as a complex adaptive system (Levin 1998), and feature perturbations as a necessity for sustainable development (Berkes et al. 2007). Here I present the case of an introduced marine predatory grouper in an isolated Pacific Island chain as an opportunity for growth in the theory and practice of adaptation to change.

Effects of the introduced grouper *roi* in Hawai‘i:

The Hawaiian archipelago, among the most isolated biogeographic regions in the world, hosts the highest percentage of marine fish endemism in the Pacific (Randall 1987, Allen 2007). Therefore, compared with the rest of the Indo-Pacific region, Hawaii’s shallow-water reef fish assemblages evolved with a small number of benthic predators. In the 1950s, assessments of Hawaii’s fish assemblages determined that an empty ecological niche existed for shallow water game species such as the snappers and groupers. Therefore, it was thought that introducing several mid-size predatory fishes would enhance fish catches (Division of Fish and Game 1956, Maciolek 1984).

Several species (12 grouper, snapper, and emperor fish) including the Peacock Grouper (*Cephalopholis argus,* family Serranidae), known by its Tahitian name *roi*, were selected based on their popularity as food fishes in their native ranges, as well as their ecological characteristic (Oda and Parrish 1982). The Hawai‘i Division of Aquatic Resources (DAR) made three introductions of *roi* between 1956 and 1961, releasing 2,385 *roi* from their native range in French Polynesia. Of these, *roi* and two species of snapper (*Lutjanus kasmira* and *Lutjanus fulvus,* Family Lutjanidae) became established

(Gaither et al. 2012). After a 4-decade lag, these three species increased in abundance, and during the 1990s *roi* became one of the dominant larger bodied predators (with the possible exception of moray eels; Family Muraenidae) on many near-shore reefs throughout the main Hawaiian Islands (Friedlander et al. 2007).

A recent study (Johnston and Purkis 2016) reported results of a biophysical computer model that combined the life history traits of *roi* with prevailing oceanographic conditions in the Hawaiian Islands to hindcast the trajectory of the introduced fish over a 15-year period after initial introduction. The study was able to reproduce the establishment of *roi* (and the failure of the 9 other species to establish) in order to investigate the characteristics that predict invasion success. Their results suggest that low mortality rate, tolerance to water depth, age to maturity, and the quantity of individuals released are the best predictors of the establishment of the introduced fish in the Hawaiian Islands. Indeed, histological research on *roi* reproductive patterns determined a continuous spawning season and relatively early age at maturity (Schemmel et al. 2016), compounded with low natural and fishing mortality (Giddens et al. 2014) and relatively fast growth (Donovan et al. 2013). Together these attributes help explain the 'success' of *roi* in their introduced range due to intrinsic factors, despite the potentially limiting founder population effect (Gaither et al. 2012).

However, local fishers never accepted *roi* as a target species, partially due to high rates of ciguatera poisoning (Bienfang et al. 2011). Without sustained fishing pressure, populations of *roi* continued to increase in abundance by 22% from 1999 to 2005 in west Hawai‘i (DAR, unpublished). *Roi* have also spread throughout the archipelago at a rate of 21 km/year, and have now established populations as far northwest as French Frigate Shoals in the northwestern Hawaiian Islands (NWHI) (Friedlander et al. 2009). Population densities of *roi* are highest in Kona, on the leeward side of Hawai‘i Island. These populations appear to have peaked in abundance in 2004, but have since declined by 50% (Walsh 2011).

The current estimate of population density on the west Hawai‘i coast is 20.2 *roi* ha^{-1} (Giddens et al. 2014), thus dominating the mesopredator guild (Dierking et al. 2009) along with moray eels. In contrast, *roi* in their native range of Moorea likely compete with thirteen other species in the same family, grow at a slower rate (J.H. Choat, unpublished), and display reduced body condition compared to conspecifics in Hawai‘i (Meyer and Dierking 2011). Competitive release has been proposed for the successful proliferation of *roi* populations in Hawai‘i (Meyer and Dierking 2011). Their diet is composed almost exclusively of small fishes (97% diet, mean TL= 7cm), with an annual total consumption estimate of 8.2 million reef fish per year (Dierking 2007). With high relative abundances in the wild, the cumulative effect of *roi* predation on native reef fish is potentially substantial.

A fishery is not feasible for *roi* in Hawai‘i due to their propensity for ciguatera fish poisoning (Dierking 2007). The perceived decline in native fishery species (Friedlander and DeMartini 2002, Williams et al. 2008, Friedlander et al. 2015) has occurred coincident with the spread and increase of *roi* populations. Local fishers attribute the decline in valued food fishes in Hawai‘i to predation by or competition with *roi* (Wood 2010). In turn, this belief has led to local efforts to remove roi from Hawaiian reefs. Multiple *roi* removal initiatives have been organized since 2008 (Wood 2010). “*Roi* Roundup” fishing tournaments are intended to be an environmental conservation movement by the fishing community, with the aim of restoring Hawaii’s native reef fish populations. This social response by the fishing community likely modifies the ecological impact of *roi*, creating a unique social-ecological linkage at the community-level of organization (Ostrom 2009).

The aim of this dissertation is to draw insights from invasion ecology in order to inform sustainability science across disciplinary boundaries. I use panarchy theory as an organizing framework to examine the dynamics of an introduced predatory grouper, *roi* (*Cephalopholis argus*) in Hawai‘i. The point of this heuristic metaphor, is to organize the accumulation of knowledge over discrete studies and extract the salient factors that are consistent or change with scale: population (Chapter II); community (Chapter III); and seascape (Chapter IV). I synthesize these findings and relate them to a 4th level: coupled social-ecological systems (Synthesis/Chapter V). In ascending scales of organization, I address the following central questions:

- What are the natural and fishing mortality rates of *roi* populations in Hawai‘i, and how effective are our methods to assess and control their numbers?

- What are the community-level effects of *roi* on native reef fish populations at the local scale?
- Which environmental and anthropogenic factors predict the distribution and abundance of *roi* and does environmental heterogeneity play a role? Do biotic interactions (density of potential competitors and/or prey) play a role and what is the relationship between *roi* abundance and the densities of native species across the MHI?
- How can the social response (fishers grass-roots invasive species tournaments) to the *roi* introduction be used to reinforce conservation behaviors and environmental stewardship more broadly?

Utilizing this framework, this research aims to contribute to our understanding of global change and adaptive capacity by drawing insights from predatory reef fish invasion ecology from a coupled social-ecological perspective.

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CHAPTER II

Experimental removal of the invasive peacock hind (roi) *Cephalopholis argus,* in Puako, Hawai‘i: methods for assessing and managing marine invasive species

Published as:

Giddens, J., Friedlander, A. M., Conklin, E., Wiggins, C., Stamoulis, K., & Donovan, M. K. (2014). Experimental removal of the invasive peacock hind (roi) Cephalopholis argus, in Puakō, Hawai ‘i: methods for assessing and managing marine invasive species. *Marine Ecology Progress Series*, *511*, 209-221.

ABSTRACT

Invasive species are a growing concern for marine biodiversity, particularly in Hawai‘i with its large proportion of endemic species. This research focused on the feasibility of removing the introduced predatory peacock grouper *Cephalopholis argus*, locally known as *roi*, as a management tool for Hawaiian coral reef ecosystem restoration. The objectives of this study were to investigate the dynamics of *C. argus* on 1.3 hectares (ha) of coral reef at Puako, Hawai‘i, and to (1) compare population density estimate methods in order to accurately evaluate abundance, (2) estimate population mortality and catchability rates, and (3) quantify the re-colonization rates by mapping distribution and movements in response to a depletion experiment. The number of individuals removed during a fish-down experiment provided a direct measure of initial population abundance (20.2 *roi* ha^{-1}). A Leslie depletion model yielded the most accurate assessment of initial density (−15.8% error) compared to belt transects (+ 75.7% error) and tow-board census (−70.2% error). Estimates of total mortality were low (0.12 to 0.14), and fishing mortality ranged from negligible to 8.0% yr^{1} in west Hawai‘i. *Roi* movement was monitored through a mark and re-capture program. Tagged individuals traveled 50 to 150 m from the periphery toward the center of the removal area (1 *roi* every 1 to 2 months). This study engaged the local Hawaiian fishing community in assessing and managing marine invasive fish species, quantified the feasibility of *roi* removal as an ecosystem management tool, and provides evidence for effective *roi* population control through spear-fishing methods at the local (1.3 ha) patch-reef scale.

KEY WORDS: Invasive species · *Cephalopholis argus* · Hawai‘i · Mortality rate · Leslie depletion · Predator removal · Marine introduction · Grouper · Ecosystem restoration

INTRODUCTION

Introduced species are a major anthropogenic stressor that weaken coral reef ecosystem resilience and undermine ecosystem services (Ruiz et al. 1997). Introduced predators can lead to reductions in biodiversity and abundance via predation or competition with native species for resources (Balon & Bruten 1986, Molnar et al. 2008). Although less pervasive than terrestrial introductions, marine introductions have dramatically altered a number of ecosystems around the world. In the Caribbean, the invasive lionfish *Pterois volitans* has had devastating effects on the recruitment and abundance of native fishes, which in turn has led to decreased coral reef ecosystem resilience and function (Albins & Hixon 2013). Because introduced species exacerbate modifications to systems already undergoing multiple environmental and anthropogenic stressors (Hughes et al. 2003, Mora 2008), biological invasions have been identified as one of the largest single threats to the diversity of the world's coastal waters (Lowe et al. 2000).

The Hawaiian Islands are the most isolated archipelago in the world and host one of the highest marine fish endemism rates in the Pacific (Randall 1987, DeMartini & Friedlander 2004, P. Mundy & J. Randall unpubl.). Hawaii's shallow-water reef fish assemblages evolved with a low diversity of benthic predators compared with the rest of the Indo-Pacific region (Hourigan & Reese 1987, Briggs 1999). Assessments of the composition of Hawaii's fish assemblages in the 1950s determined that important shallow-water game fish had declined and families such as snappers and groupers were missing in the Hawaiian fauna. It was thought that the introduction of several mid-size predatory fishes into Hawaiian waters to fill this 'empty niche' would enhance catches in lieu of fisheries regulations (Division of Fish and Game 1956). Because Hawai'i had few near-shore groupers (epinepheline, serranid), the peacock hind *Cephalopholis argus* or *roi* (as it is locally referred to by its Tahitian name) and several other species were selected for introduction based on their ecological characteristics and potential popularity as food fishes in their native ranges.

The Hawai'i Division of Aquatic Resources (HDAR) made 3 introductions of *roi* between 1956 and 1961 from their native range in French Polynesia, with a total of 2385 *roi* released (Randall 1987). After a 4 decade lag, this species increased in abundance during the 1990s and became the dominant predator on many near-shore reefs throughout the main Hawaiian Islands (Friedlander et al. 2007, Dierking et al. 2009). Due to high rates of ciguatera poisoning (Dierking & Campora 2009, Bienfang et al. 2011), many local fishers do not recognize *roi* as a target species. In the absence of sustained fishing pressure, populations of *roi* continued to rise another 22% from 1999 through 2005 (HDAR unpubl. data), spreading 21 km yr^{-1} throughout the Main Hawaiian Islands and as far northwest as French Frigate Shoals in the Northwestern Hawaiian Islands (NWHI; Friedlander et al. 2009). *Roi* populations peaked in 2004 and have declined by 38% since the start of the HDAR fish monitoring program in 1999 (Walsh et al. 2013).

In their native range of French Polynesia, *roi* compete with 13 other species in the same family (Meyer 2008). In their native habitat, they grow at a slower rate (J. H. Choat pers. comm.), have decreased longevity (10 to 15 yr in Moorea vs. 25 to 26 yr in Hawaiʻi) (Donovan et al. 2013), and display reduced body condition compared to conspecifics in Hawaiʻi, suggesting competitive release in the introduced range (Vignon et al. 2009, Meyer & Dierking 2011). In Hawaiʻi, *roi* diets are composed almost exclusively of small fishes (97% diet, mean total length [TL] = 7 cm), with an annual consumption estimate of 8.2 million reef fish yr^{-1} based on data from captive individuals (Dierking 2007). The same authors subsequently noted that Hawaiian *roi* caught in the wild had a stomach vacuity rate of almost 50% (Dierking & Meyer 2009), a finding that is consistent with thousands of *roi* caught at tournaments annually (C. Wiggins pers. obs.). The published diet study did not account for intra-annual variations in prey availability, and therefore, the prey consumed in the wild is probably less than what the laboratory feeding study would predict. Nevertheless, the large-scale consumption potential and high relative abundance indicate that *roi* may play a major role in shaping native reef fish assemblages in Hawaiʻi (Dierking et al. 2009).

A fishery is not feasible for *roi* in Hawaiʻi due to their association with ciguatera fish poisoning (Dierking 2007), although limited commercial harvest takes place. Local fishers attribute the decline in valued food fishes to predation or competition by *roi* (D. Tanaka pers. comm.). This in turn has led to grass-roots efforts to remove *roi* from reefs throughout Hawaiʻi. Multiple *roi* removal initiatives have been organized at the community level since 2008 by fishers to combat the threat they perceive as decimating

Hawaii's native reef fish populations. '*Roi* Roundup' fishing tournaments are intended to be an environmental conservation movement with the aim of restoring Hawaii's native reef fish populations by removing invasive fish, especially *roi*. While research has verified that the predation potential of *roi* can be substantial (Dierking 2007), it is unclear to what degree predation by *roi* (or competition by *roi* with other predators for prey) has detrimental effects and if *roi* removal is feasible as a management tool for restoring native reef fish assemblages.

To address these concerns, this study focused on experimental *in situ roi* removal to assess its feasibility as a management tool and effectiveness as a restoration action. The specific goals were to (1) compare *roi* population density estimation methods in order to accurately evaluate fish abundance, (2) estimate *roi* population mortality and catchability to inform population models, and (3) quantify the re-colonization rates of *roi* by mapping their distribution and movements in response to the depletion experiment.

METHODS

Site description

Two geographic areas were selected for this study. The depth range for both of these areas was between 12 and 18 m (Figure 2.1)

Puako. The coral reef of Puako, West Hawai'i, is dominated by 3000 to 5000 yr old lava flows and carbonate substrate (Hayes et al. 1982). Established in 1985, The Puako Fisheries Management Area (FMA) extends seaward 250 m, or to the edge of the fringing reef, and restricts gill net fishing (HDAR 2011), reducing confounding factors. The treatment site (1.3 ha) is comprised of relatively discrete patch reefs.

Roi removal

Local fishers were contracted to assist with *roi* removal over 11 days during April and May of 2011 at Puako and over 4 days during August 2011 at Ka'upulehu. To the extent possible, fishing effort was kept consistent at each site. SCUBA spear fishers removed *roi* from both treatment sites, recording the number of fishers, hours fished, *roi* total length to the nearest 1 mm, weight to the nearest gram, and location of each fish caught. Dive times ranged from 37 to 56 min, with 1 to 3 dives per day. The effort of *roi* removal was assessed by calculating catch per unit effort (CPUE) of *roi* removal at the treatment sites:

$$CPUE=C/h$$

where C is the catch, h is the number of hours, and total effort was averaged across all divers and dives for each day.

The actual number of *roi* removed during the fish-down experiment at the Puako study site provided a direct measure of the initial population abundance. Because of the high visibility to divers of this large-bodied predator and the high site fidelity within fixed ranges (Meyer 2008), there is high confidence that all *roi* were seen and that > 90% of the population was re- moved. Regular site monitoring and spear-fishing occurred (1 dive-day per month) in order to maintain depleted *roi* populations at the treatment reef.

Population estimates: Leslie depletion model. In a closed population with a constant catch rate, estimates of the initial population size may be obtained by monitoring how the relative abundance decreases with increasing catch. The *roi* population may be considered closed and with a constant catch rate for this analysis based on the low ingress of fish from the adjacent area during the fishing activity (1 *roi* every 1 to 2 months; this study). Only the first 6 days of the 11-day fish-down were used in this analysis, to account for the learned avoidance behavior of groupers to spear-fishers, which might impact catchability rates over time (Côté et al. 2014, present study). Following this approach to estimating local abundance, we constructed a Leslie depletion model (Leslie & Davis 1939). The application of this model assumes that fishing effort in a small area over a number of days would reduce the local population size and that this reduction would be indicated by a significant decline in abundance with accumulated catch. Initial population is estimated by regressing the catch per fisher hour against the cumulative catch:

$$Nt \quad = Nt -1- Kt$$

where Nt is the population at time t, $Nt{-}1$ is the initial population, and Kt is the cumulative catch. CPUE is related to Kt by the slope q, where $CPUE = qNt-1 - qKt$ (Leslie & Davis 1939). A regression of the cumulative catch Ccum against log($CPUE$) is used to estimate *q* and the initial population size, where the intercept is *Nt*−1 (Parkes et al. 1996). To assess catchability, or the gear efficiency for catching *roi*, we conducted a fish-down experiment in two locations and compared the rate of the declining catch per unit effort.

SCUBA divers spent 19:26 hours spear-fishing at the removal site over 11 days and observed a change in *roi* behavior concurrent with targeted fishing effort. Whereas *roi* were initially relatively easy to approach and dispatch, over time, the dwindling number of individuals became very wary of divers and would flee immediately on sight. By changing approach tactics, some of these individuals were dispatched with great effort (1 *roi* per 3 dives). Others were struck but not landed, and two of these fish exhibited an aversion to divers sufficient to make them essentially uncatchable. Although we experimented with time of day, traps, and freediving to dispatch these individuals, none of the alternate methods were successful. This did allow us to differentiate between resident and re-colonizing *roi*, as the new arrivals were easily approached.

Underwater visual survey

Belt-transect survey. Nineteen permanent transects were established at the Puako patch reef treatment site, fixed with GPS location and marked for underwater recognition. Visual fish surveys were conducted along 5 x 25 m belt transects (Friedlander et al. 2007), whereby 2 SCUBA divers swam a fixed bearing in tandem along parallel (~5 m apart) 25 m fixed replicate transects at a constant speed (~15 min per transect). All fishes observed within the transect were identified to the lowest possible taxon, and TL was visually estimated with size bins (0.0 to 4.9 cm TL, 5.0 to 9.9 cm TL, 10.0 to 14.9 cm TL, etc.). Divers were previously trained in visual underwater size and distance-estimation techniques (Kulbicki et al. 2010, Bozec et al. 2011). Each pair of diver observations was averaged to obtain the value of fish abundance for each transect. Live wet mass, W, of all fishes recorded during surveys was calculated from the visually estimated TL using the length–weight relationship $W = a\mathrm{TL}^b$, where *a* is the allometric growth parameter and *b* is a scaling constant. Species-specific length–weight parameters were obtained from published and unpublished sources (Donovan et al. 2013, M. Donovan et al. unpubl.). Fish transect surveys were conducted at Puako during March/April 2011 before any *roi* were removed in order to establish baseline conditions at the treatment site. Follow-up surveys were conducted semi-annually during winter and spring following *roi* removal. At Ka'upulehu, surveys (n = 24) occurred over the course of 17 days during October 2012.

Tow-board survey. To assess *roi* population distributions throughout the wider area, fish censuses focusing solely on *roi* were conducted semi-annually in removal and control areas. This census was conducted using tow-boards following the National Oceanic and Atmospheric Administration Coral Reef Ecosystem Division protocols, and followed isobaths from 10 to 30 m, covering a total area of 0.4 km^2 (Holzwarth et al. 2003). These census rounds took place in April, June, and November 2011 and in June and October 2012. Paired divers were towed from a 50 m tow line, each with a planing board equipped with datasheet, timers, depth gauge, and signaling device for communication with the boat. Divers were towed along a pre-determined course designed to completely cover the area of interest at a constant speed. Maintaining depth ~3 m from the bottom, divers visually estimated and recorded the TL, time, and depth of each *roi* sighting within 5 m of either side of the straight line trajectory. Communication was maintained between diver pairs both above water and during the survey to ensure that *roi* were not double counted.

Mortality estimate model

The equilibrium length of a population is inversely related to the mortality rate experienced by that population (Ricker 1975); therefore, the mean length of a fish population can be used to estimate the mortality rate from basic growth parameters.

Beverton and Holt. Instantaneous total mortality rate *Z* was derived using the length-based Beverton and Holt model (Beverton & Holt 1956):

$$Z = K \times \frac{L_\infty - L}{\bar{L} - L'}$$

where $L\infty$ is mean asymptotic length, *K* is the rate of decline in growth rate with increasing size, *L* is the mean length of the sample, and *L*' is the lower limit of the smallest length class included in the computation. This method assumes equilibrium conditions, an infinite exploitable life-span, and that the dynamics of the population are adequately described by the von Bertalanffy and exponential-mortality models (Beverton & Holt 1956). A range of estimates for Z were calculated by the same equation, based on adding and subtracting one standard error for each von Bertalanffy growth parameter from Donovan et al. (2013) (Table 1 in the present study). The Ault & Ehrhardt (1991) method for estimating instantaneous mortality was developed from a truncated equation for average length to more accurately represent the heterogeneous patterns observed in tropical artisanal fisheries. This method considers the length at first capture as well as the maximum retainable length in the catch and is sensitive to variations in these parameters:

$$\left(\frac{L_\infty - L_{t\infty}}{L_\infty - L_c}\right)^{Z/K} = \frac{Z(L_c - \bar{L}) + K(L_\infty - \bar{L})}{Z(L_\infty - \bar{L}) + K(L_\infty - \bar{L})}$$

where $L\infty$ is asymptotic length, Lt is length at maximum age, Z is total mortality, K is the rate of decline in growth rate with increasing size, L is mean length in the sample, and Lc is the length at first capture (Ault & Ehrhardt 1991).

Minimum and maximum estimates were calculated by the same equation, based on adding and subtracting one standard error for each von Bertalanffy growth parameter from Donovan et al. (2013) (Table 2.1 in the present study).

Linearized catch curve. A catch-curve was constructed to estimate total mortality based on a linear decline of individuals caught from age-based cohorts (Quinn & Deriso 1999). Based on assumptions of a closed population with constant recruitment, instantaneous mortality is modeled following continuous exponential growth where total loss of individuals is equal to total mortality. The log-frequency of catch of each age class is expected to increase until the age class is fully recruited to the fishery and then linearly decline with age. Age-at-length was calculated using an age-length key based on fish collected from the study area from July to November 2011 (Table 2.1 in the present study; Donovan et al. 2013). The probability of each age for a given length interval (2 cm) was used to construct an age-length key by which individuals were then assigned an age by randomly selecting individuals from each length interval (Kimura 1977).

A linear model was fit to the cumulative log frequency of age, and the slope of this line is equal to Z, the instantaneous mortality.

The percentage of annual mortality (A) is calculated as follows:

$$A = 1 - e^{-Z}$$

Alagaraja model. Natural mortality was estimated by the Alagaraja (1984) method, which assumes that 99% of a cohort had died if it were exposed to natural mortality only:

$$M = \frac{-\ln(S)}{T_{\mathrm{m}}}$$

where S is survival (0.05), and Tm is longevity. Natural and the fishing mortality sum to the total mortality; thereby, the mortality due to fishing is calculated from the following relation:

$$Z = F + M$$

where Z is the total mortality, F is fishing mortality, and M is natural mortality.

The population growth parameters were obtained from Donovan et al. (2013), who conducted an age and growth study of West Hawai‘i *roi*.

Movements of *roi*

Roi were tagged to assess the response of surrounding populations to the removal at the treatment reef. Three buffer zones of 250 m were designated with a specific tag-type, color, and anatomical position on captured *roi* to facilitate underwater recognition of place of origin during subsequent underwater monitoring. In total, 67 *roi* from the areas adjacent to the defined removal sites were captured by pole and line (n = 7), in diver-deployed barrier nets (n = 39), and using a modified pole spear with a tag applicator tip (N = 21). All individuals were tagged with a standard Hallprint tagging needle and dart tag (individuals caught with pole and line were measured and weighed) before being released at the capture location. Divers towed a float with a GPS in track mode during tagging and monitoring events. Tagging events were opportunistic from February to October 2011. Movements of tagged *roi* adjacent to and into the cleared area were noted during later monitoring events from June 2011 to July 2012. The geographic coordinates of tagged and re-captured *roi* were obtained by matching the recorded time of capture/re-sight with the logged GPS time- track. The spatial distribution of all tagged, re-sighted, or collected individuals were mapped in ArcGIS10 (ESRI 2011), and distances and directions of movement between tag and recapture locations were measured. Time duration between removal and re-sighting in the treatment zone was used to calculate the immigration rate of surrounding populations after initial removal.

All analyses were conducted in R 2.12.1 (R Development Core Team 2010), with tests considered significant at $p \leq 0.05$.

RESULTS

Initial population abundance was measured by the number of individuals removed from the study site during the fish-down experiment (plus two remaining *roi*). Fishers removed 25 *roi* (totaling 22.5 kg) from the Puako treatment reef during the fish-down effort in late April and early May 2011. The size distribution ranged from 28.8 to 44.3 cm (mean ± SE: 36.8 ± 2.3 cm) (see Table 3). In total, 24 *roi* were removed from the Ka'upulehu treatment reef (totaling 21.7 kg) during 4 days from 15 to 18 August 2011, and the size ranged from 24.4 to 51.8 cm (mean: 36.2 ± 7.3 cm). The measures of initial population abundance provide a direct estimate to evaluate the accuracy of the three fish monitoring methods.

Comparison of three roi population abundance estimate methods

Leslie depletion model

Declines in CPUE during the fish-down effort were modeled using a linear regression to relate CPUE to cumulative catch. Relating the catch per fisher hour to the cumulative catch at Puako produced a regression slope of −0.19. The *x*-intercept along the cumulative catch axis predicted an initial population abundance of 22.7 *roi* (16.9 ha^{-1}) (Fig. 2.2). Since fishing was modeled for only 6 days, natural mortality, recruitment, and immigration are assumed to be negligible. Likewise, for Ka'upulehu, the Leslie depletion experiment predicted an initial population of 11.8 roi ha^{-1}.

Belt transect survey

A total of 19 visual surveys (each 5 × 25 m = 125 m2) were conducted during April and May 2010 to quantify the entire reef fish assemblage at Puako. *Roi* occurred on 44% of transects conducted at the treatment site before removal and accounted for 6.5% of the total fish biomass and 0.4% of the total assemblage numerical density at this location. The mean (±1 SE) population density of *roi* was 35.5 (± 9.3) ind. ha^{-1}, and the mean biomass was 56.0 (± 6.7) kg ha^{-1}. At Ka'upulehu, 24 transects were visually surveyed during October 2012. *Roi* were present on 46% of the transects with an estimated density of 41.6 (± 0.9) ind. ha^{-1} and biomass of 114.7 (± 4.0) kg ha^{-1}.

Tow-board survey

A survey of the size structure and distribution of the adjacent *roi* population (0.4 km^2 area encompassing both treatment and adjacent patch reef sites) was conducted before and after targeted removal. Overall, *roi* populations decreased in density by 59.8% (from 9.2 to 3.7 ind. ha^{-1}), though they maintained a similar size range, 18 months after *roi* removal (Fig. 2.3, Table 2.2). The final tow-board survey occurred one month following a community volunteer removal event in which 21 volunteer spear fishers captured 353 *roi* in two days within ~12 ha adjacent to the Puako study site. Tow-board surveys of *roi* before and after the community volunteer removal event documented a sharp decrease in population density, from 7.3 to 3.7 *roi* ha^{-1} (Fig. 2.2).

The three methods for estimating *roi* population density yielded vastly different results (Table 2.3). The Leslie depletion model yielded the most accurate estimate of 16.9 *roi* ha^{-1} compared to the actual number of *roi* removed (20.2 ha^{-1}) during the fish-down experiment. The tow-board survey method underestimated *roi* density by 70.2%, and the belt transect method overestimated *roi* by 75.7%.

Roi population mortality

Roi population mortality was assessed by a variety of methods using growth parameters specific to North Kona *roi* populations (Table 2.1 in the present study; Donovan et al. 2013). Total mortality *(Z)* estimates varied by method. The age-structured catch curve (Fig. 2.4) yielded an estimate (±1 SE) of $Z = 0.14$ (± 0.03). The Ault and Erhardt method yielded a similar estimate of $Z = 0.14$ (± 0.02). The Beverton and Holt equation yielded a slightly lower estimate of $Z = 0.12$ (± 0.08).

Natural mortality *(M)* was calculated using Alagaraja's method, which yielded $M = 0.17$. The annual fishing mortality rate was calculated using the Ault and Erhardt method (0.0 to 7.8%) and the Beverton and Holt method (0.0 to 5.8%; Table 2.4) with Alagaraja's estimate of natural mortality.

Comparisons of catchability at 2 locations

CPUE in relation to cumulative catch was compared at Puako and Ka'upulehu (Fig. 2.2). The original *roi* density (mean ± SE) at Ka'upulehu (41.6 ± 0.01) was higher than at Puako (35.5 ± 9.2) and the catchability, or *q*, declined more steeply at Puako ($q = -0.19$) compared to Ka'upulehu ($q = -0.03$) ($F1, 6 = 15.22$, $p < 0.01$), implying that catchability depends on the initial population density.

Roi movements

In total, 67 *roi* were externally tagged in three zones stratified by distance (250 m) surrounding the treatment reef (Fig. 2.5). Six *roi* were re-captured and five were re-sighted in 18 months of monitoring. Distances traveled by *roi* averaged (±1 SD) 94.1 (± 38.4) m and generally occurred from the periphery of the removal reef toward the center, with an immigration rate of 1 *roi* every 1 to 2 months.

DISCUSSION

This study evaluated several methods for assessing the population density and mortality rate of a marine invasive fish (*roi*) species as well as the feasibility of *roi* removal as a management and restoration tool.

The 25 *roi* removed from the Puako treatment site, plus the two remaining, represent the initial population abundance and is the reference point with which to compare three population estimate methods. In contrast to stock assessment comparisons in which the initial population number is not known, this depletion experiment provided a unique opportunity to directly compare the accuracy of estimate methods to the lower bound of the initial *roi* density at the removal reef.

The Leslie depletion model yielded the most accurate population density estimate, with an error of only 15.8%. This method assumes a closed population, which was reasonable for the six day period of the experiments. It was also assumed that the catchability coefficient *(q)* was constant, given that the same spear-fishers (i.e. same skill level) participated in the fish-down events.

One source of error in the depletion experiment may be that, as a result of the removals, some individuals may have become overly cryptic and were thus not counted during the removal exercise. If there were more individuals, or if individuals emigrated out of the study area during removal activity, that would lessen the disparity between the depletion model and actual vs. alternate population estimates. It is unlikely that emigration was of a sufficient magnitude to confound fish-down results. The treatment reef was separated from adjacent areas by distinct sand channels, and the continued presence of wary wounded *roi* on the treatment reef might indicate that site attachment of individuals (Meyer 2008) is substantially stronger than the emigration from removal areas. Further, only the first six days of the fish-down effort were used in the depletion model, thus reducing this possible source of error. The similarity of the depletion model estimate with the actual numbers of *roi* removed during the fish-down experiment corroborates the models predicting initial population numbers by using catch and effort data.

The belt-transect method yielded the highest estimate of population abundance by far. Non-instantaneous surveys potentially over-count mobile species, as transects swum in ~15 min allows observers to record mobile fishes that are initially occupying a larger area than the transect dimensions. However, since *roi* are among the slower-moving of the mobile predators, the relative bias due to mobility would be less pronounced in this species (Ward-Paige et al. 2010). Other sources of error in the belt transect method may be specific to the behavioral patterns of *roi*. The mean home range of the species was estimated to be 1236 m^2 (Meyer 2008), which would encompass multiple transects, increasing the probability of counting the same individual more than once during the ~1 week survey period, as the density of transects along patches of reef was quite high (~15 ha^{-1}). Fixed-area visual survey methods may accurately determine abundances of new recruits and other cryptic species with small home ranges; however, population density estimates for large-bodied, territorial predators such as *roi* should consider the possible over-counting bias introduced with the fixed-area visual survey method for a small area heavily surveyed within a short (<1 week) time frame (present study).

In contrast, the tow-board survey method underestimated *roi* population density at Puako by more than half compared to the actual number of *roi* removed from the patch reef during the fish-down experiment. *Roi* behavior may be alerted by engine noise, the oscillation of the tow line in the water, and/or the presence of two highly visible divers towed behind a boat, and wary *roi* may seek shelter without being observed within 5 m to either side of the diver. This behavior of a semi-cryptic species in a complex habitat likely explains the drastic difference between tow-board surveys and belt-transect methods in which divers survey close to the reef and can identify sheltered *roi* that might otherwise remain out of view during tow-board surveys of the same area. More time is spent in a smaller area during belt-transect surveys, maximizing the chance of observing benthic-associated individuals (Stamoulis & Friedlander 2013). The use of tow-boards for assessing abundances of fish species such as *roi* that are accustomed to the threat signaled by boats and divers should account for the bias introduced by this conspicuous method. While the consistent use of either the belt-transect or tow-board method could provide a relative measure of *roi* density, caution should be used when expanding the density estimates obtained by either for use in management planning. Belt-transect results might grossly overestimate the threat posed by *roi* populations, and conversely, tow-board surveys might underestimate the threat. Both methods could be calibrated by comparison to estimates obtained using the Leslie depletion model (present study).

Mortality and catchability

Total mortality *(Z)* estimates for North Kona *roi* populations differed among stock assessment methods. The Beverton & Holt (1956) model is best applied to long-lived, slow-growing species such as *roi*, which explains the better fit compared to the Ault & Ehrhardt (1991) method that is applicable to short-lived tropical species. Previous work suggests that *roi* growth does not conform well to the von Bertalanffy growth function (VBGF), and therefore, models based on VBGF parameters should be interpreted cautiously (Donovan et al. 2013). Alternative methods, such as the re-parametized VBGF (Francis 1988, Trip et al. 2008) and the double model (Porch et al. 2002), performed better for *roi* in West Hawai‘i. Although ages were calculated from site-specific growth parameters (Donovan et al. 2013), calculated age becomes less accurate as fish samples approach the mean asymptotic length (Quinn & Deriso 1999), introducing error when including the larger fish in assessment calculations.

The natural mortality rate *(M)* estimated from the Alagaraja (1984) method (0.17) is low compared to *M* of 0.40 estimated from the native range of *roi* (Froese & Pauly 2011). However, most similar-sized groupers, besides *Epinehelus guttatus* (0.68), exhibit a lower *M* ranging from 0.18 to 0.30 (Polovina & Ralston 1987). The low *M* obtained in this study is reasonable for Hawai‘i *roi* because of their low vulnerability to predation, food fishing, and parasites (Meyer & Dierking 2011).

Likewise, the calculated fishing mortality *(F)* estimate of ~0.0 to 8.0% yr^{-1} is low, though realistic for *roi* in Hawai‘i given their avoidance as a food fish due to associations with ciguatera poisoning (Dierking & Campora 2009). However, despite the risks of ciguatera, *roi* are targeted in reported commercial landings. A total of 1472 kg were reported from 2004 to 2009, which comprised ~1% of all state inshore commercial landings (HDAR 2010). This catch may be partly from *roi* round-up tournaments (J. Giddens pers. obs.), and recreational catch is likely much higher than commercial catch for many reef species (J. Kittinger et al. unpubl.). Catch peaked in 2010 at 1920 kg, and North Kona contributed 1% of the total landings statewide (HDAR 2010). This relatively low commercial fishing pressure explains the low *F* for this population of *roi*.
Because catchability depends in part on the initial density (present study), efficacy of removal will vary by site. Fishing pressure may be high in localized areas where *roi* are

targeted in focused efforts during community *roi*-roundup events and during individual fisher efforts haphazardly throughout the year. Given the low natural mortality of *roi*, it is still unclear what broad-scale effect volunteer removal has on populations of *roi*. A statewide *roi* population and fisheries assessment will elucidate the larger impacts of removal efforts. Likewise, this manipulative field experiment opens the opportunity to test the ecological effects of the introduced predatory grouper in Hawaiʻi (J. Giddens et al. unpubl.).

***Roi* distribution and movements**

The removal experiment suggests that it is possible to fish down and maintain depleted (< 90%) populations with a sustained low level of targeted fishing effort. The slow immigration rate of 1 *roi* every 1 to 2 months indicates that 2-monthly, 1 day fishing efforts are sufficient to maintain a locally depleted population. Fish assemblage surveys every six months following removal show no *roi* at the treatment reef 2.5 yr following removal, as any new individuals were dispatched through routine maintenance dives throughout the study period. Given the low ingress of *roi* after 2 yearrs of tagging and monitoring, it is not likely that the additional community *roi* removal at an adjacent reef could have substantially impacted the immigration rate (Fig. 2.1).

These results suggest that long-term *roi* eradication is feasible for communities in Hawaiʻi. However, based on recurring SCUBA diving costs (compressed air, tank rental), fisher hours, and boat time, it was costly (~\$400 ha^{-1}) to remove *roi* via the SCUBA-spear fishing method. Alternatively, volunteer-based *roi* round-up events have the potential to impact a larger reef area over a shorter period of time. For example, the community-wide *roi* removal event with 21 volunteer spear fishers dispatched 353 *roi* in 2 days in the ~12 ha adjacent to the Puako study site. Note that these events might decrease catchability over a larger area, making it more difficult for SCUBA spear-fisher removal, as was observed for lionfish that learned to avoid fishers after culling events in the Caribbean (Côté et al. 2014). Tow-board surveys documented a sharp decrease in *roi* population density (from 7.3 to 3.7 *roi* ha^{-1}) following the volunteer fishing effort. A community *roi* tournament costs approximately \$300 with food, one NGO (non–governmental organization) staff member, and supplies (C. Wiggins pers. obs.).

Competitive *roi* tournaments are also expensive to conduct (costing approximately $2800 for insurance, trophies, T-shirts, food, and entertainment; D. Tanaka pers. comm.), although the community-driven events fulfill social as well as ecological objectives. These events are community exchanges which likely reinforce the social institutions that lead to successful co-management of common resources (Basurto & Ostrom 2009, Kittinger 2013) and ease the fishing pressure on native species.

Experiments on lionfish removal at replicate patch reefs in the Caribbean documented that even partial culling, while requiring substantially less resources than complete eradication, could halt the erosion of native reef fish biomass (Green et al. 2013). *Roi* tournaments should prioritize accurate catch data collection to determine the broad-scale and site-specific effects of focused *roi* removal in Hawai‘i and should be designed to complement targeted removal efforts to maximize efficiency.

The long-term effects of *roi* removal on the native reef fish assemblage are still unclear. This removal experiment presents the opportunity to assess the assemblage-level effects of *roi* in Hawai‘i. Further, *roi* population dynamics can be examined in relation to the recipient ecosystem regime to identify characteristics that may have contributed to the successful invasion of *roi* over the past several decades. Defining the relative contributions of bottom-up vs. top-down control of *roi* populations might elucidate a threshold-specific target for management (Kelly et al. unpubl.).

For example, mesopredator release (Prugh et al. 2009) due to overfishing of top predators can lead to declining prey and local extinctions (Stallings 2009, Albins & Hixon 2013). Predation rates in the NWHI are high compared to the Main Hawaiian Islands, where *roi* dominate the piscivore guild (Friedlander & DeMartini 2002). *Roi* may be fulfilling a niche that is only opened by overfishing of the native predators. By comparison, in the Caribbean, larger predators such as sharks and groupers (Maljkovi et al. 2008) might be able to prey upon invasive lionfish or suppress foraging success through behaviorally mediated indirect effects, presenting a top-down biocontrol on lionfish populations (Côté et al. 2013). Similarly, in Hawai‘i, awareness could be brought to the preservation of top predators and their role in suppressing *roi* populations.
In addition, the availability of prey may control *roi* populations. As generalist predators, roi may feed preferentially on those species most common on the reef (Dierking et al.

2009). Little is presently known about the recruitment patterns and the juvenile survival rates of *roi* in Hawai‘i. Further research in these areas relating to the greater ecosystem regime would inform our general understanding of predatory fish invasion biology and elucidate efficient measures for *roi* population control.

For the public, the perceived decline in native reef fish may be disproportionally attributed to *roi*, compared to other anthropogenic sources such as run-off, eutrophication (Hamnett et al. 2006), and overfishing (Williams et al. 2008). *Roi* may be considered a ‘scapegoat’ in this regard. Nevertheless, stakeholder participation in invasive species management could be an avenue by which to raise awareness of near-shore reef environmental issues and to engage citizens in addressing these concerns. The momentum around *roi* removal might catalyze collective action towards sustainable resource use and strengthen the community attributes, such as social cohesion and knowledge sharing, that characterize resilient social-ecological systems (Basurto & Ostrom 2009, Ostrom 2009). There is a potential for the ‘scapegoat’ to become a catalyst for sustainability.

Our findings suggest that it is feasible to control *roi* populations at the local (<1.3 ha) patch reef scale. However, because the near-shore environment of Hawai‘i is characterized largely by contiguous reef habitats, there is difficulty in directly scaling up this experiment ecologically and economically. Removal efforts should be conducted over a broad spatial scale to determine any additional challenges to sustained *roi* depletion over contiguous habitats, such as increased immigration rates from deep or adjacent reefs. A combination of the controlled fish-down method coupled with community-driven volunteer events may be the most cost-effective method for removing *roi* and, at the same time, raising fisher participation in community-based ecosystem management. Collaboration at the local and state level will be needed to efficiently reduce and maintain depleted *roi* populations for fisheries management and ecosystem restoration.

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FIGURES

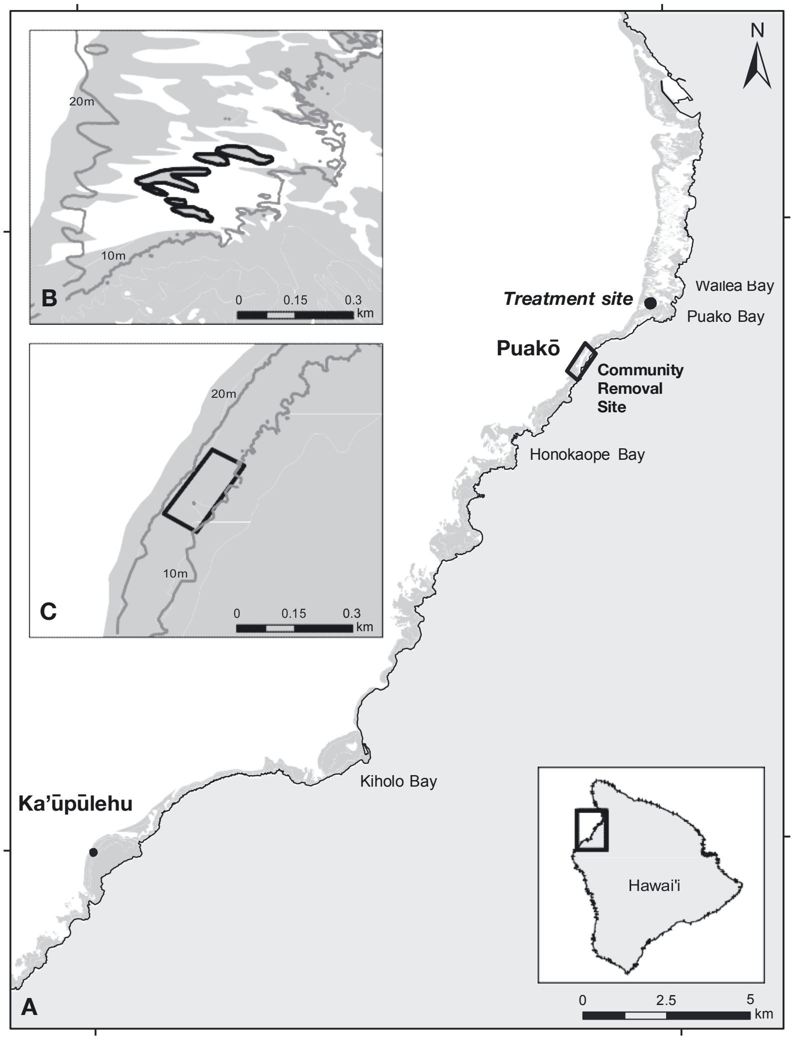


Fig. 2.1. (A) West Hawai‘i, showing study sites and the community removal site (outlined in bold), with details of the (B) Puako and (C) Ka’upulehu experimental *roi* removal areas. Hard bottom reef habitat (dark grey) and depth contours from 0 to 30 m are shown

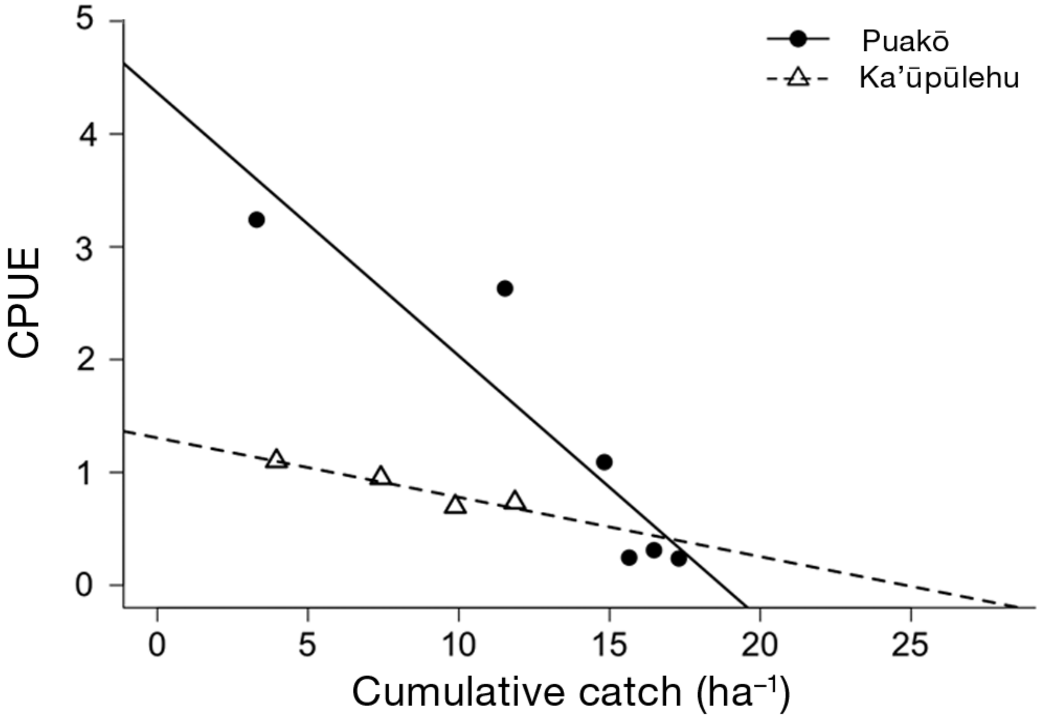


Fig. 2.2. Leslie depletion model for 25 *roi* removed from a 1.3 ha patch reef in Puako, West Hawai‘i (solid line) over 11 d from March to April 2011, and for 24 *roi* removed from Ka’upulehu, West Hawai‘i (dashed line) over 4 d in August 2011

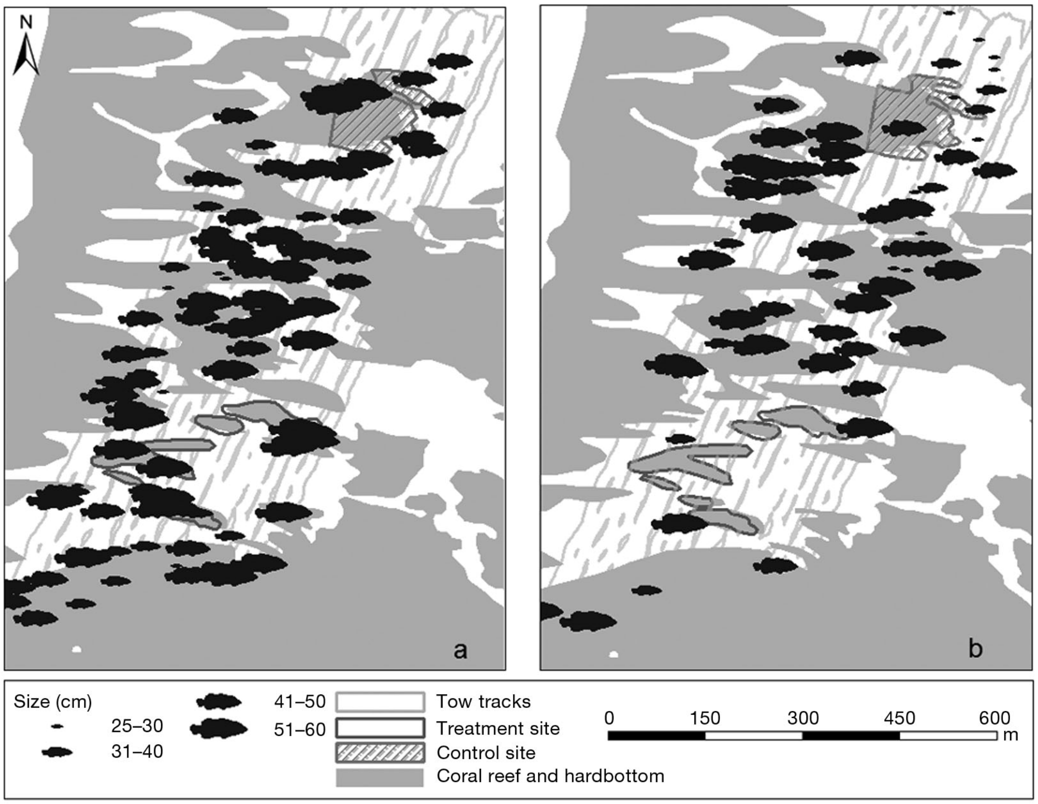


Fig. 2.3. *Roi* distributions for (a) tow-board Census 1 before removal at the treatment site and for (b) Census 5 after removal at the treatment site in Puako, West Hawai‘i

Fig. 2.4. Age-structured catch curve of North Kona *roi* collected from July to November 2011 (n = 203). The log-frequency of catch of each age class is expected to increase until the age class is fully recruited to the fishery and then linearly decline with age. The slope of this line is equal to *Z*, the total mortality. Only fish ≥5 yr old (fully recruited to the fishery) were included in this analysis

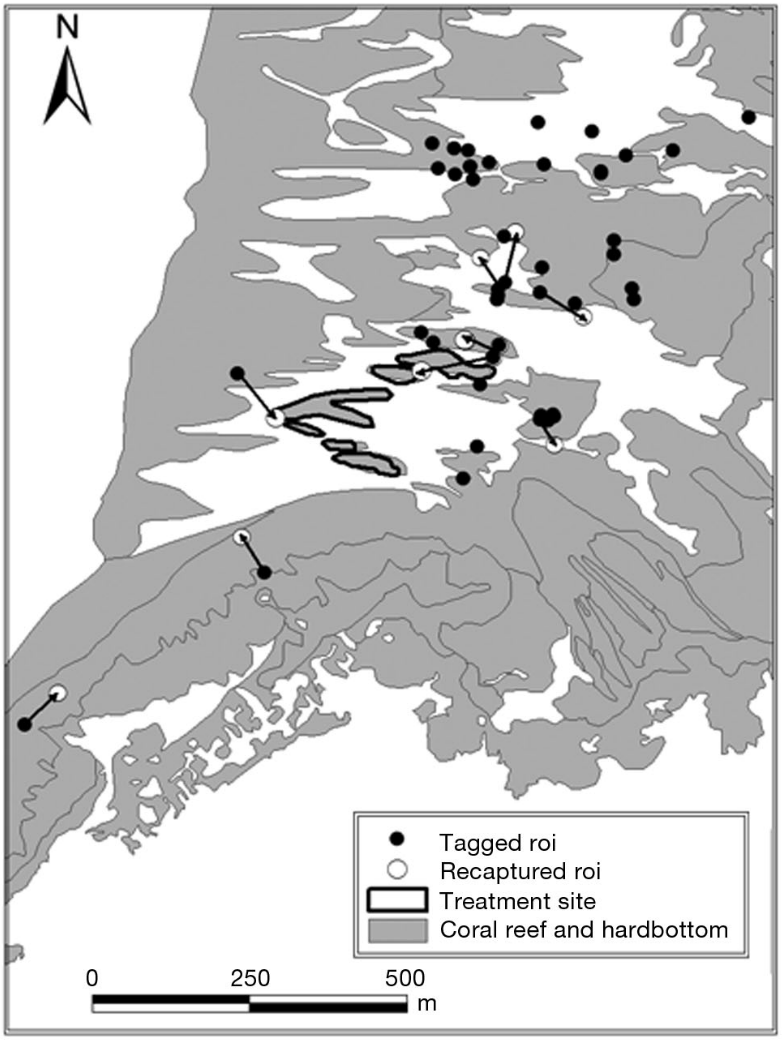
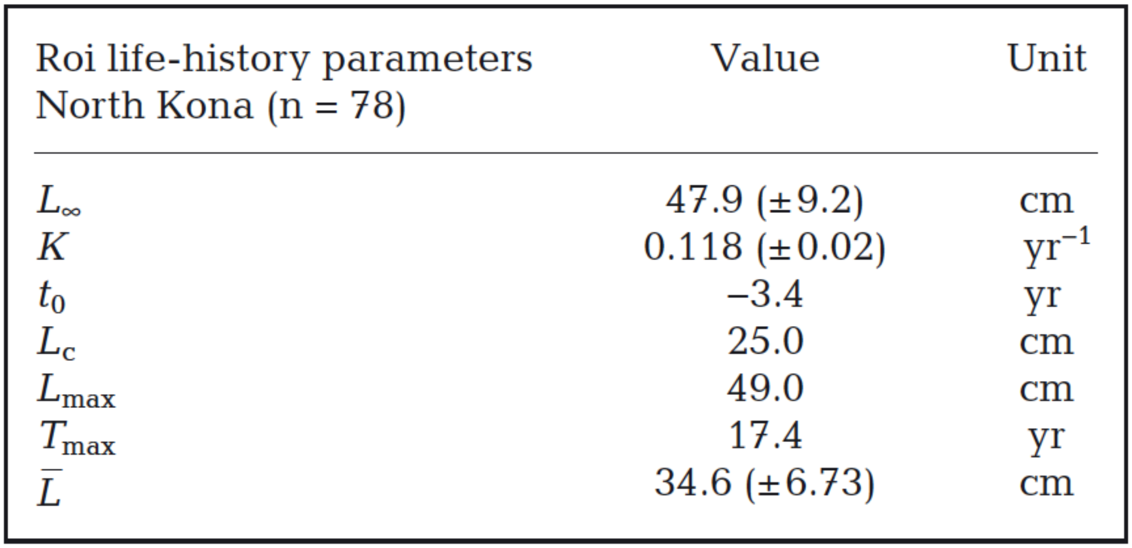


Fig. 2.5. *Roi* tag and recapture locations in 250 m zones surrounding the treatment reef in Puako, West Hawai'i. Arrows indicate direction and distance traveled by *roi* from the original tag location

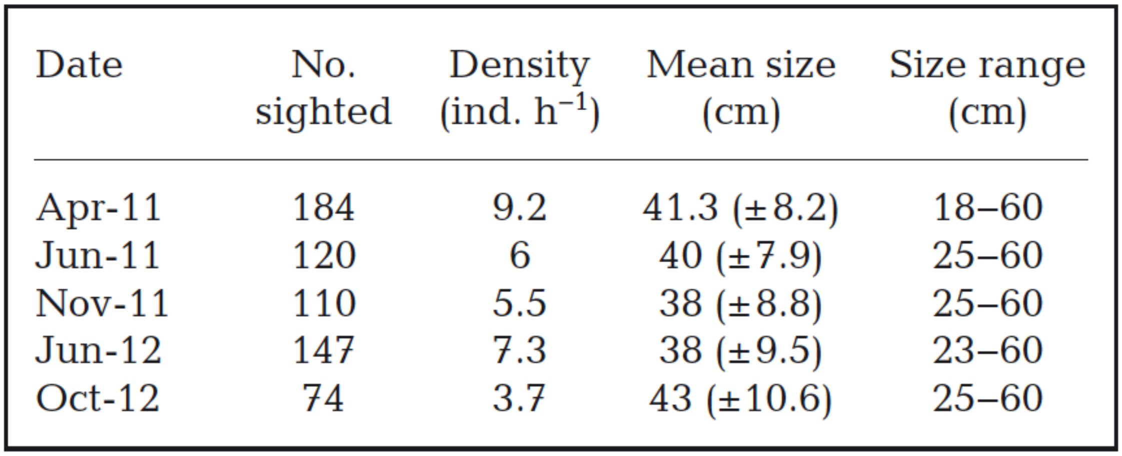
TABLES

Table 2.1. North Kona *roi* life-history parameters adapted from Donovan et al. (2013), where $L\infty$ is the mean asymptotic length, K is the rate of decline in growth rate with increasing size, $t0$ is the theoretical age at which length is 0 cm, Lc is the minimum size of individuals fully recruited to the fishery, Lmax is the maximum size, Tmax is the mean of the oldest 20% of individuals, and L is the mean length. Values are mean ± maximum and minimum estimates



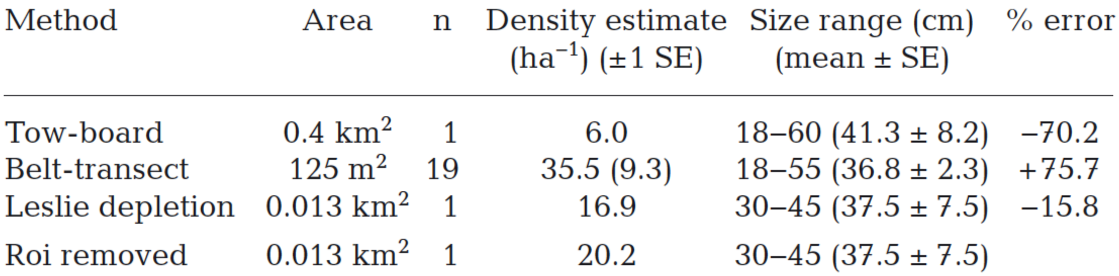
Roi life-history parameters North Kona (n = 78)	Value	Unit
L_∞	47.9 (±9.2)	cm
K	0.118 (±0.02)	yr^{-1}
t_0	−3.4	yr
L_c	25.0	cm
$L_{\max}$	49.0	cm
$T_{\max}$	17.4	yr
$\bar{L}$	34.6 (±6.73)	cm

Table 2.2. Results of 5 tow-board population census rounds before (April 2011) and after the targeted fish-down event. The census is designed to cover the entire study area; therefore, the *roi* counts are summed. Numbers presented are totals (n = 1) for each survey. Note that the final census round (October 2012) follows a community-wide volunteer removal event in the ~12 ha adjacent to the study site



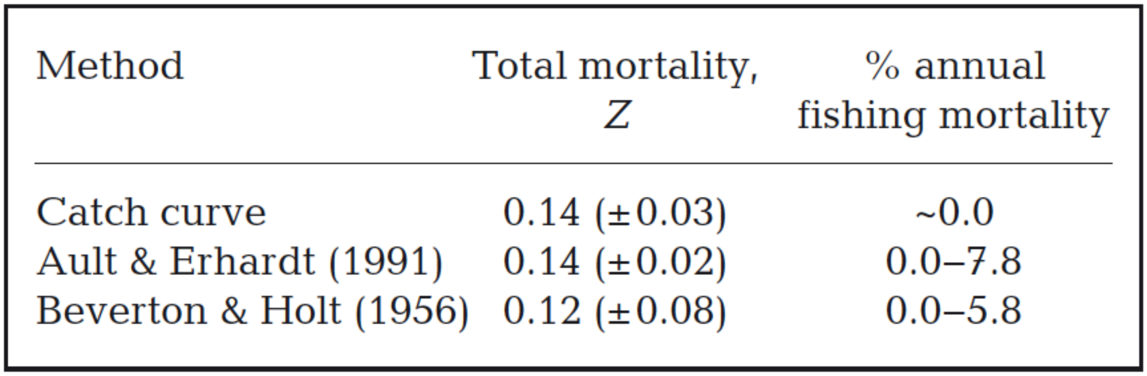
Date	No. sighted	Density (ind. h^{-1})	Mean size (cm)	Size range (cm)
Apr-11	184	9.2	41.3 (±8.2)	18–60
Jun-11	120	6	40 (±7.9)	25–60
Nov-11	110	5.5	38 (±8.8)	25–60
Jun-12	147	7.3	38 (±9.5)	23–60
Oct-12	74	3.7	43 (±10.6)	25–60

Table 2.3. Comparison of Puako *roi* population density assessment methods and actual *roi* removed



Method	Area	n	Density estimate (ha^{-1}) (±1 SE)	Size range (cm) (mean ± SE)	% error
Tow-board	0.4 km^2	1	6.0	18–60 (41.3 ± 8.2)	−70.2
Belt-transect	125 m^2	19	35.5 (9.3)	18–55 (36.8 ± 2.3)	+75.7
Leslie depletion	0.013 km^2	1	16.9	30–45 (37.5 ± 7.5)	−15.8
Roi removed	0.013 km^2	1	20.2	30–45 (37.5 ± 7.5)	

Table 2.4. Mortality estimates based on intermediate and high estimates for *L*∞ and *K* from Donovan et al. (2013)



Method	Total mortality, Z	% annual fishing mortality
Catch curve	0.14 (±0.03)	~0.0
Ault & Erhardt (1991)	0.14 (±0.02)	0.0–7.8
Beverton & Holt (1956)	0.12 (±0.08)	0.0–5.8

CHAPTER III

Experimental test for assemblage-level effects of the introduced Peacock hind (*Cephalopholis argus*) on Hawaiian reef fishes

Submitted to Biological Invasions

as:

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ABSTRACT

The peacock hind *Cephalopholis argus* (family Serranidae), locally known as '*roi*', was introduced from French Polynesia to Hawaii in the mid-20th century as a food fish. However, because of its association with ciguatera fish poisoning, it is rarely fished for food. Previous research indicates that *roi* could have a negative impact on native reef fish assemblages because of their high densities and prey consumption rates. However, it is unclear whether *roi* add to the cumulative mortality of prey (Predation Hypothesis), or whether predation is instead compensatory (Doomed Surplus Hypothesis). This study experimentally assessed the effects of *roi* on reef fish populations through a long-term (5.5 year) predator removal experiment. A Before-After-Control-Impact study design was used to assess changes in fish assemblages following the removal of *roi* on 1.3 ha of patch reef. Increases in the density of prey-sized fish (<15 cm TL) were observed 18 months after *roi* removal. However, those effects did not translate into sustained increases in prey. While increases in potential competitors, wrasses (family Labridae), particularly the piscivorous ringtail wrasse *Oxycheilinus unifasciatus*, were observed on *roi*-free reefs, the fish assemblage did not diverge substantially in composition. Native reef fish appeared to resist the potential negative impacts of predation by *roi*, possibly through a refuge in size for some fish families. Management to protect intact fish assemblage size-structure could serve to bolster native resistance to invading species. In considering the threats facing coral reefs, and the possible solutions, *roi* removal alone will not likely replenish native fishery resources.

Key words: Introduced species, predator removal experiment, mesopredator, doomed surplus, biotic resistance, Hawai'i

INTRODUCTION

Multiple stressors threaten the resilience of coral reefs (Nyström et al. 2000; Jackson et al. 2001; Hughes et al. 2011), and of those, introduced species are a human-mediated pressure that is preventable with proper foresight and knowledge (Elton 1958; Vitousek et al. 1997). The diversity-invasibility hypothesis (Elton 1958; Levine and D'Antonio 1999), postulates that more diverse communities are less likely to become invaded because the ecological niche space is fully utilized (the "species packing" concept of MacArthur 1955, 1970). Such "priority effects" (Connell and Slatyer 1977; Shulman 2015) decreases the likelihood of an invasion since species that are already established outcompete those that enter an area in low numbers (Case 1990, 1991). A corollary to this is that there is an inherent vulnerability of islands because they are generally lower in species number than mainland geographies, with niche-space available for colonization (Herbold and Moyle 1986; Crawely 1987; Elton 1958).

In the past, a number of species were introduced to the Hawaiian Islands to bolster the nearshore fishery (Oda and Parrish 1981). Due to its geographic isolation, Hawaiian shallow-water reef fish assemblages evolved with a comparatively small proportion of benthic predators (Randall 1987; Hourigan and Reese 1987; Heemstra and Randall 1993; Allen 2006). Because game species, such as snappers and groupers, were considered depauperate in the 1950s and 60s, the Hawaii Division of Aquatic Resources (HDAR) undertook a species introduction program to fill a perceived "empty ecological niche" (Oda and Parrish 1981). While the introduction of three (out of 12) of the mid-sized predators was 'successful' in terms of establishment (Gaither et al. 2012), the intention of augmenting the fishery was not met. These species became a nuisance, rather than a boon to fishers (Randall 1987).

The peacock hind (*Cephalopholis argus*, Family Serranidae), locally known by its Tahitian name *roi*, was introduced from French Polynesia in three phases between 1956 and 1961 (Oda and Parrish 1981). A total of 2,385 *roi* were released in multiple locations in Hawaii. After an initial lag period, *roi* increased in abundance during the turn of the century and became the numerically dominant predator on many near-shore Hawaiian reefs (Friedlander et al. 2007; Dierking et al. 2009), with the possible exception of moray eels (Muraenidae). High propagule pressure (Johnston and Purkis 2016), early age at maturity (Schemmel et al. 2016), and relatively fast growth rates (Donovan et al. 2012), compounded with low natural and fishing mortality (Giddens et al. 2014) together help explain the 'success' of *roi* in their introduced range, despite the potentially limiting founder population effect (Gaither et al. 2012). Furthermore, enemy release is a likely factor in the successful proliferation of *roi* in Hawaii (Meyer and Dierking 2011; Gaither et al. 2013). *Roi* in their native range co-occur with thirteen other species in the same family, grow at a slower rate, and display reduced body condition compared to conspecifics in Hawaii (Meyer and Dierking 2011). An understanding of the impacts of *roi* on the native reef fish assemblage is needed to assess the outcome of this species introduction.

The role of predation: The diversity-invasibility hypothesis (Elton 1958; Levine and D'Antonio 1999), maintains that sites with higher biodiversity are more resistant to invasion. However, when invaders are superior competitors or use different resources than native species or are voracious predators, then the effect of diversity is likely to be weak (Tilman 2004). In these instances, the impact of an exotic species on native ecosystems is more likely determined by how the predator and prey interact, and it is this interaction that determines the availability of resources for a newcomer (Olyarnik et al. 2009). Previous research on *roi* in Hawaii suggests that the predation can be substantial, with consumption of up to 142 reef fish per year per individual (Dierking 2007). In contrast, results from a long-term (>15-year) coral reef ecosystem-monitoring program in west Hawaii found no correlation between *roi* and native reef fish abundance (Walsh 2010), suggesting that *roi* do not affect abundances of prey species. Given this discordance, it is not clear whether predation by *roi* (or competition by *roi* with other predators for prey or territory) is having a detrimental effect on native reef fish assemblages. Predators can potentially have a large and potentially cascading effect on the ecosystem (Paine 1966; Hixon 1991, 2015). Alternatively, a predator may merely consume the 'doomed surplus' of the prey population (Errington 1946), (i.e., those individuals that would have suffered mortality due to limiting resources). These hypotheses (the 'doomed surplus' vs. the predation hypotheses) then represent the two extremes explaining the role of predation in structuring reef fish communities.

Field manipulative experiments can help to elucidate the nature of predator effects on the ecosystem (Doherty and Sale 1986; Hixon 1991, 2015, Hixon and Carr 1997; Albins 2015). For example, the invasive Red Lionfish (*Pterios volitans*) in the Caribbean dramatically decreased prey species abundance and diversity over short time scales (<2 month) (Albins and Hixon 2008; Green et al. 2012; Albins 2013; Benkwitt 2013), yet these changes may not shift adult fish biomass over longer timescales. A recent experiment (14 months) found no difference in adult fish biomass, though the diversity and abundance of small-sized fishes (<10 cm TL) were reduced within a few seasons after lionfish removal (Albins 2015). Explicitly distinguishing the time-scale of field manipulations is important in order to decipher the short vs. long-term response of a community after a disturbance (Levin 1992).

In order to determine the ecological effects of *roi* in Hawaii, we conducted a long-term (five and a half year) predator removal experiment and measured the effects of *roi* removal on the species composition and size structure of the fish assemblage. *Roi* preferentially prey upon juvenile and recruit fishes (Dierking 2007); therefore, the two size groups potentially affected by roi informed our three main predictions: 1) the density of small (<15 cm TL) prey-sized fish would increase following *roi* removal; 2) a time-lagged difference in the density of fish > 15 cm TL would occur as prey fish released from predation at the juvenile stage survived to adulthood; and 3) other mesopredators that potentially compete with *roi* for prey would increase following *roi* removal.

METHODS

A Before-After-Control-Impact (BACI) (Smith 2002) approach was used to assess changes in reef fish assemblages associated with *roi* removal. The experimental removal and adjacent control sites consisted of a series of patch reefs with high *roi* densities (The Nature Conservancy unpublished data) in Puako, west Hawaii Island (Figure 3.1). The removal site was selected in part because it is a series of patch reefs surrounded by sand, thus facilitating removal efforts and slowing immigration. Though there were no similar sized isolated patch reefs in the area, we chose a control site that was surrounded by three sides with sand. An important consideration was that the control site was far enough from the removal site to be outside of the typical home-range) (A. Meyer pers. comm.). The habitat of both the removal and control sites consisted of finger coral (*porites compressa*) reef in the depth-range of 6 to 15 m. We initiated baseline monitoring and community outreach in 2010. In May 2011 local fishers assisted with *roi* removal from the treatment reef via spearfishing. We removed and maintained depleted populations of *roi* from 1.3 ha of reef, and followed the response of the fish assemblage for four and a half years after *roi* removal.

Fish assemblage and benthic monitoring: Thirty-five (20 *roi*-removal and 15 reference) permanent transects were established at randomly selected sites with similar habitat and *roi* population densities. Visual fish surveys were conducted along each transect by two scuba divers swimming side-by-side and identifying, counting, and sizing all fish within parallel 5 x 25 m belts. Divers swam each transect at a constant speed (*c.* 10-15 minutes per transect depending on complexity of the habitat) and all fish observed within the transect were identified to the lowest possible taxon, with sizes estimated to the nearest cm. Surveyors were previously trained and calibrated in visual underwater size estimation techniques based on practice with various lengths of fish models that were later collected and measured. To establish baseline condition, the removal and reference reefs were surveyed twice (November 2010 and March/April 2011), prior to initiating *roi* removal. Following removal, surveys were conducted semi-annually, (Summer; March-June and Winter; October-November) for the duration of the experiment.

Analysis: Live wet mass (biomass), W, of all fishes recorded during surveys was calculated from the visually estimated total length (TL) using the relationship $W=a\mathrm{TL}^b$ where a is the allometric growth parameter and b is a scaling constant. Species-specific length–weight parameters were obtained from published and unpublished sources (Donovan et al. 2012; Froese and Pauly 2011). In order to limit the effects of extreme observations, the response variables (fish biomass and abundance) were restricted to their species-specific 95% quantile range. Response variables for parallel transects were averaged to obtain a single value per site.

Linear Models: We tested for changes in the fish assemblage due to *roi* removal via a Before-After-Control-Impact (BACI) experimental design, where a significant interaction between ‘site’ (removal and reference) and ‘time period’ (before and after) indicates a significant treatment effect (Osenberg and Schmitt 1996; Pinheiro and Bates

2000). We used a linear mixed-effects model (LMM) framework to account for the hierarchical structure of the data set (Zuur et al. 2009). First, the permanent transects were grouped by 'site' (removal vs. reference reef), so that in the LMM 'transect ID' was treated as a random effect, nested within 'site' as a fixed effect. Second, to account for our repeated measures of permanent transects through time, 'survey date' was treated as a random effect, nested within 'time period' as a fixed effect.

Prey-sized fishes were grouped for analysis, and included all fishes < 15 cm TL, based on previous gut content analysis (Dierking at al. 2009) and field observations. The response of prey-sized fishes to *roi* removal was measured as abundance (number per m^2), which is a more sensitive metric compared to biomass for small fishes. In contrast, reef fish biomass (g/m^2) was used to capture the overall fish assemblage response. Potential competitors of *roi* include other reef mesopredators, therefore, the biomass (g/m^{-2}) of those species with a trophic level rank of 4.0 and above (www.fishbase.org) were grouped for analysis to test for changes in potential competitor densities following *roi* removal.

To meet the parametric assumptions of a normal distribution, response variables (biomass and abundance per m^{-2}) were $\log_{10}+1$ transformed and 4th root transformed, respectively. Mixed models were developed with the lme4 package in R, version 3.1.1 (R package lme4: Bates et al. 2014; R Core Development Team 2013). A maximum likelihood estimate was used to fit the models and approximate F-tests were used for hypothesis testing with the 'Anova' function in the package *lmerTest* version 2.0-32 (Kuznetsova et al. 2015). Model fits were assessed by visual inspection of the residuals. In order to examine any species-level shifts in the fish assemblage after roi removal, general linear models were constructed for the community as a whole, and for each species present (134 in total). Multivariate analyses were conducted using the statistical package *mvabund* version 3.11.9 in R (Wang et al. 2012), which is a model-based approach to test shifts in assemblage composition. The procedure constructs a linear model both to test for shifts in the assemblage as a whole, and for each constituent species. The species-specific *P*-values are adjusted to control the family wise error rate by resampling through a Holm's step-down multiple testing process (Westfall and Young 1993; Wang et al. 2012). Thus the species-specific effects were assessed in a hypothesis-testing framework. Raw count data (numbers per species) were modeled as a negative binomial distribution (to account for over-dispersion in the counts) in order to estimate the species-specific treatment effects of *roi* removal. The non-independence of the repeated measures design was accounted for by permuting the likelihood ratio test within time periods (survey round).

RESULTS

One hundred and thirty-four fish species from 28 families were observed during the surveys. Fish biomass and abundance generally peaked during the winter and declined during the summer, showing a seasonal pattern at all study sites from 2010 to 2015 (Figure 3.2 for small (<15 cm TL) fish abundance and Figure 3.3 for total fish biomass, respectively).

Small (<15 cm TL) prey-sized fish abundance: Eighteen months post *roi*-removal (winter), the increase in small (<15 cm TL) prey density was significantly greater at the *roi* removal compared to the reference reef ($F_{2,44} = 8.42$, $P=0.001$, Figure 3.2). However, by month-24 (summer) differences were no longer significant by location. Results of the overall linear mixed effects model (LMM) did not show a significant effect of the site-by-period interaction for the removal relative to reference locations ($F_{1,349}= 0.2$, $P=0.64$, Appendix Table SI 3.1) indicating no effect four and a half years post-removal. The model was subsequently re-fit with additive fixed effects (period + location+ season) and a random treatment-by-date interaction. The full hierarchical model with random effects explained 38.5% of the variability in the data ($R^2 =0.385$), while the fixed effects-only model accounted for just 8.9% indicating the random factors accounted for much of the variability in the model. The removal site maintained higher overall small fish abundance ($F_{1,25}= 15.7$, $P<0.001$) (Figure 3.2, Table 3.1), but the higher fish density observed was not due to *roi* removal.

Total fish biomass: We observed no effect of *roi* removal on total fish biomass ($F_{1,351}= 0.08$, $P=0.76$, Appendix SI 3.1) so, the model was re-fit with additive fixed effects (period + location + season) and a random treatment-by-date interaction. Although the treatment-by-date random term was not a significant predictor of total fish biomass, the magnitude and direction of the correlation parameter (-0.53) suggests that with higher overall fish density, the treatment effect of removing *roi* decreased. The model explained 37% of the variability in the data. The treatment site was significantly higher in total fish biomass ($F_{1,27}$=7.75, *P*<0.01) (Table 3.1), but the higher biomass at the treatment site was not due to *roi* removal.

Both the control and the treatment sites oscillated within an upper and a lower bound. They diverged in low-density years, and converged in high-density years, so that the years with higher overall fish biomass experienced a smaller treatment effect. Because the convergence in fish biomass occurred yearly, the removal of *roi* did not impact overall fish biomass over the long-term (four and half years after *roi* removal).

Native Piscivores: Potential competitors of roi include other reef mesopredators. We found a significant increase in wrasse (Labridae) biomass at the *roi* removal site ($F_{1,351}$ = 4.17, *P*=0.04, Table 3.2, Figure 3.4). This increase was driven primarily by the piscivorous ringtail wrasse *Oxycheilinus unifasciatus* (Figure 3.5).

Species-level multivariate analysis: The total species-level assemblage did not shift significantly in response to *roi* removal ($F_{1,120}$ = 34.48, *P*=0.48; Table 3.3). A null model was constructed with time alone as a predictor, in order to assess any treatment effects. The time-only model showed a significant difference in the assemblage composition ($F_{1,122}$ = 163.5, *P*=0.04; Table 3.3). These results indicate that many small shifts in assemblage composition may in sum make up a significant difference over time, but none can be attributed to a single species, and that these changes cannot be attributed to *roi* removal.

DISCUSSION

The results of our long-term (five and a half year) field experiment reveal seasonal and fleeting effects of *roi* removal on the density of small (<15 cm TL) prey-sized fish. However, removal of *roi* did not translate into sustained increases in prey, nor to increases in total fish biomass. Rather, both sites experienced seasonal and yearly fluctuations, and did not diverge in terms of total fish biomass over time. Thus, we found no indication that juvenile fish released from *roi* predation, experienced increased survivorship into adulthood. Instead, the seasonal predator effect on small size classes indicates that *roi* consume the “doomed surplus” (Errington 1946) of the prey populations. This pattern is consistent with predation as a compensatory process, rather than an additive source of prey mortality in our system (Errington 1946).

The effect of roi removal on the fish assemblage was negatively correlated to survey date across years, indicating that the higher the overall prey fish density, the smaller the effect of *roi* removal. The proportion of prey consumed per capita was reduced at high prey densities, thereby allowing the prey population to swamp any predator effects with sufficiently high densities. Thus the proportion of the prey population consumed declined even if predator consumption rates remained steady (apparent density-dependence, Sale and Tolimieri 2000; Hixon and Webster 2002; Tolimieri 2015).

Increases in a potential competitor of *roi*, the wrasses, were observed at the removal site, indicating that prey released in the absence of *roi* could have been consumed by these potentially competing mesopredators. Further, although not measured here, transient predators such as sharks (Order Carcharhiniformes) and jacks (Family Carangidae) could have potentially aggregated at the *roi* removal reef and consumed the excess prey. Because predator aggregative responses can be heterogeneous over time (Hassell 1966; Oaten and Murdoch 1975; Murdoch et al. 1992), our sampling frequencies may not have coincided with transient predator visitations. A further methodological consideration is that benthic predators, particularly eels are underestimated in belt transect visual fish surveys (reviewed by Usseglio 2015). Further studies are needed to assess cryptic as well as transient predator responses in open reef systems.

There are a few reasons why the effect of *roi* on prey fish in Hawaii could be minimal. First, the predation intensity may not be as intense as was previously reported (Dierking 2007). Introduced *roi* in Hawaii consume many small fish, as demonstrated by laboratory feeding experiments (Dierking 2007). However, laboratory studies risk over-estimating a predator's consumption rate as foraging in the wild is fundamentally different from feeding *ad libidum* in the lab (MacKenzie et al. 1990). When fed in captivity, the search time of a predator is essentially negligible (Abrams 1982) therefore laboratory methods could overestimate predator consumption rates (MacKenzie et al. 1990). Indeed, observations of *roi* caught off of the west Hawaii coast noted a 44.9% stomach vacuity rate (prevalence of empty stomachs) in the 285 *roi* caught (Dierking and

Meyer 2009). The reported consumption rates of *roi* in captivity, likely represent an upper limit, rather than an expected mean in the wild.

Secondly, *roi* are generalist predators (Shpigel and Fishelson 1989; Parrish 1987) with a wide dietary breadth. A study assessing prey selectivity of *roi* in Hawaii reported that half of the fish families present on the reef in 2003 were also represented in the diet (Dierking et al. 2009). However, selectivity for certain prey families was found, and these were attributed, in part, to the increased availability during recruitment pulses of settlers to the reef. Thus, as a trophic generalist, *roi* could consume by chance encounter the more common species on the reef (O'Brien 1974). By consuming the most abundant prey fish, *roi* could act as a source of density-dependent mortality for native fish in Hawaii, which is important for prey fish population regulation (Murdoch 1994; Hixon et al. 2002).

In contrast, predators with selective feeding habits might extirpate rare species, if those were the preferred prey. Similarly, if predators reached sufficiently high densities, they could reduce abundance and diversity of the prey community even by consuming species in equal proportion (equivalent predation *sensu* Van Valen 1974) (Hixon 1986). Lionfish in the Caribbean are capable of extirpating rare species (Albins 2013), and dramatically decreased prey species abundance and diversity (Albins and Hixon 2008; Green et al. 2012; Côté et al. 2013), but this has not been observed with *roi* in Hawaii.

Thirdly, the availability of refuge space and other prey defenses may reduce the impact of *roi* on native Hawaiian reef fish. The same dietary composition study showed avoidance for certain species (the apogonids) that hid in small reef crevices that are inaccessible to *roi* (Dierking et al. 2009). Further, other cryptic families such as Blennidae, Scorpaenidae, and Gobidea were disproportionally absent in the diet, and this was attributed to their crypsis and close proximity to shelter in the reef (Dierking et al. 2009). The 'novel predator archetype' (Cox and Lima 2006) and poorly defended prey ('prey naiveté'; Diamond and Case 1986; Carthey and Banks 2014) have been invoked in explaining the lionfish's success in the invaded range. In contrast, *roi* in Hawaii appear to be naturalized, and even engage in multi-species hunting with native eels (J. Giddens, pers. obs). Many native Hawaiian fish species currently maintain connectivity with parent populations at other locations across the Pacific where predatory groupers are abundant (Eble et a. 2011a, 2011b, Bowen et al. 2013; Bowen 2016). Therefore, the novel predator archetype and prey naiveté may not be pertinent hypotheses for explaining the success of *roi* in Hawaii, both because of the evolutionary history of reef fish in the tropical Pacific, and their time (more than half a century) since introduction.

Nevertheless, *roi* are a dominant mesopredator (along with moray eels, Family Muraenidae**)** in their introduced range (Dierking et al. 2009). Predators can depress prey populations whether they are generalist or specialists, if predator densities are sufficiently high (Hixon 1986). With high relative abundances, the cumulative effect of *roi* predation is potentially substantial if native fish lack the ability to repel invaders, i.e., biotic resistance (*sensu* Levine 2000). Some prey fish species (e.g. parrotfishes, larger surgeonfishes, trumpetfish and filefish) can reach a size refuge as adults when they are no longer vulnerable to the gape-limited size selection of *roi*. These adults could continually contribute offspring to the next generation regardless of *roi* densities. Adult stages could therefore serve as an ontogenetic refuge from predation and as a source of high reproductive output, replenishing fish populations despite predation by *roi* on some portion of the juveniles of that species. Together, the predation intensity of *roi* could be effectively negligible over multi-year timescales because of the availability of shelter for prey and the size refuge reached in adulthood by some fish families.

CONCLUSIONS

While introduced reef fish predators represent a possible threat to coral reef ecosystems, our results indicate that *roi* in Hawaii do not additively diminish native reef fish populations in a patch reef system over multi-year timescales. Both the *roi*-removal and the control reefs experienced fluctuations in reef fish abundance and biomass, independent of *roi* density. Because *roi* at Puako exhibit higher densities than most locations in Hawaii (The Nature Conservancy unpublished data), we expect these results to be generally applicable to Hawaiian reef systems where *roi* are present. The native reef fish assemblage appears to maintain biotic resistance to potential negative consumptive effects of *roi*, for example through evasion and through a refuge in size for some fish families. However, if the apparent balance between predator and prey populations were to be disturbed due to other pressures such as overfishing or habitat degradation, then the ability of the native fish assemblage to resist invasion may be impaired. As intact ecosystem processes likely foster coexistence mechanisms and thus bolster native reef fish resistance to invading species, management should address multiple angles to increase ecosystem resilience as a whole, and maintain the adaptive capacity of these diverse systems into the future. In considering the many threats facing Hawaiian reefs, and the many possible solutions, *roi* removal alone will not likely replenish native fishery resources.

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FIGURES

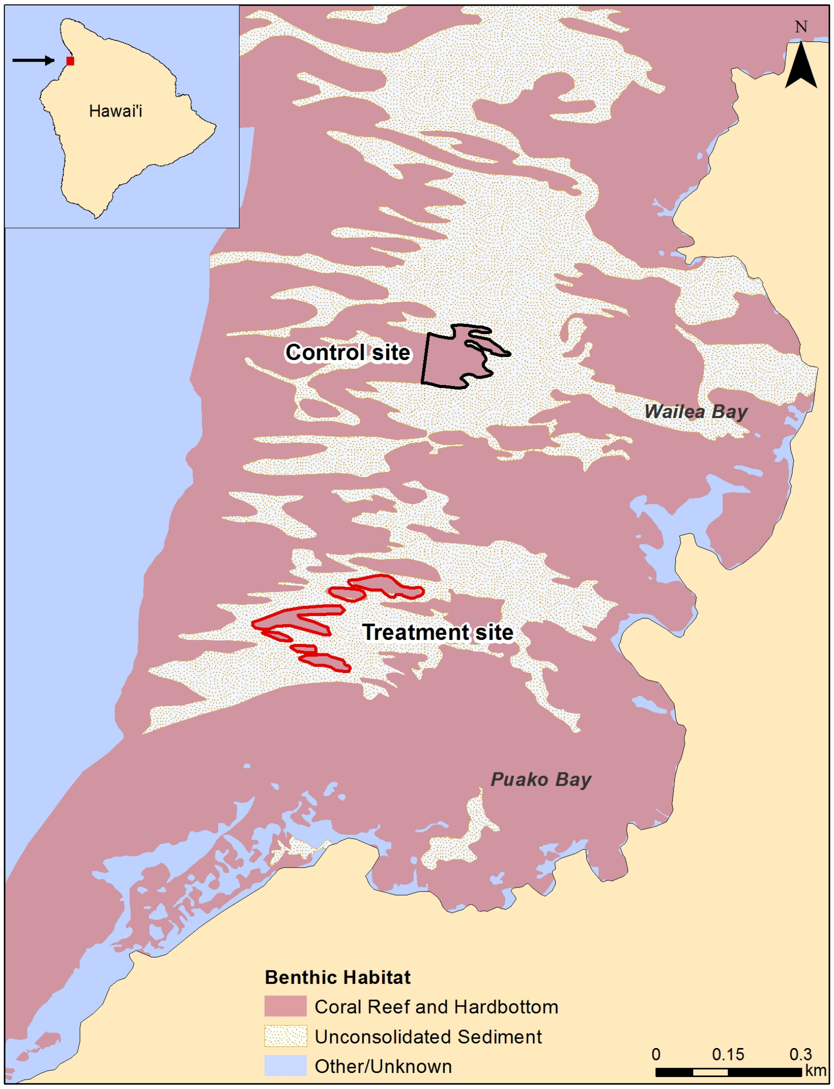

Fig 3.1 Map of *roi* removal study sites, in Puako, west Hawaiʻi with substrate type (hard-bottom vs. unconsolidated sediment) shown

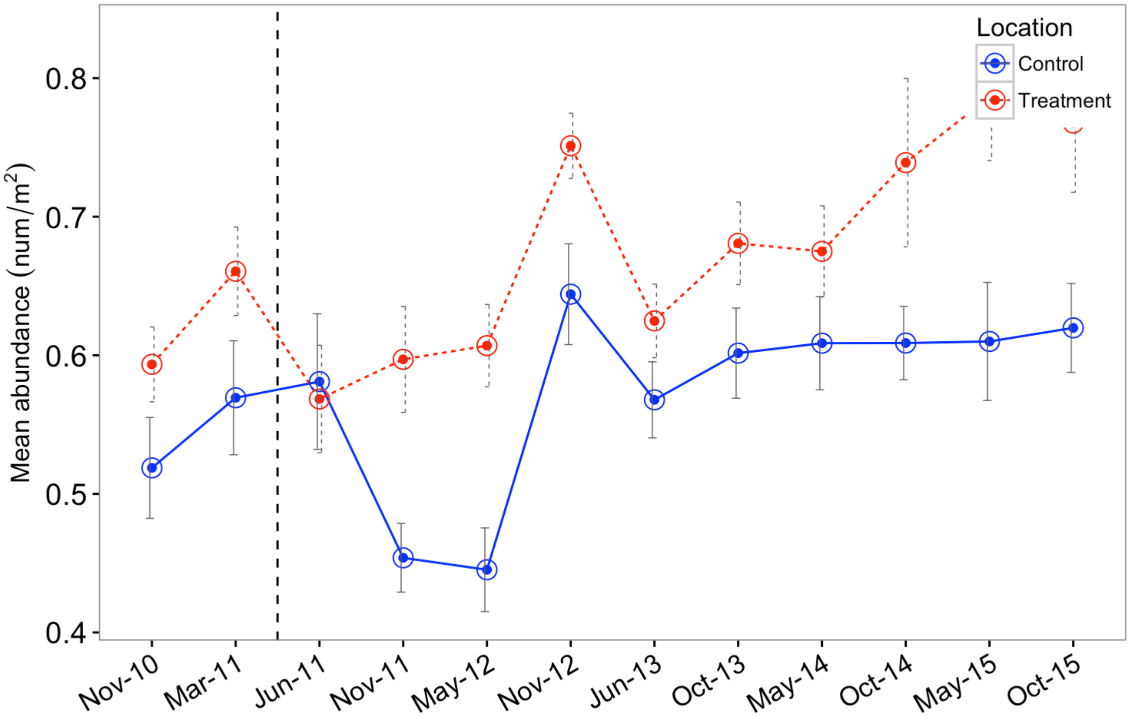

Fig 3.2 Trend line for small (≤15cm) prey species during 5.5-year *roi* removal experiment at the Puako, west Hawai‘i study site. Fish-down event is marked by the dashed line. Error bars are standard error of the mean

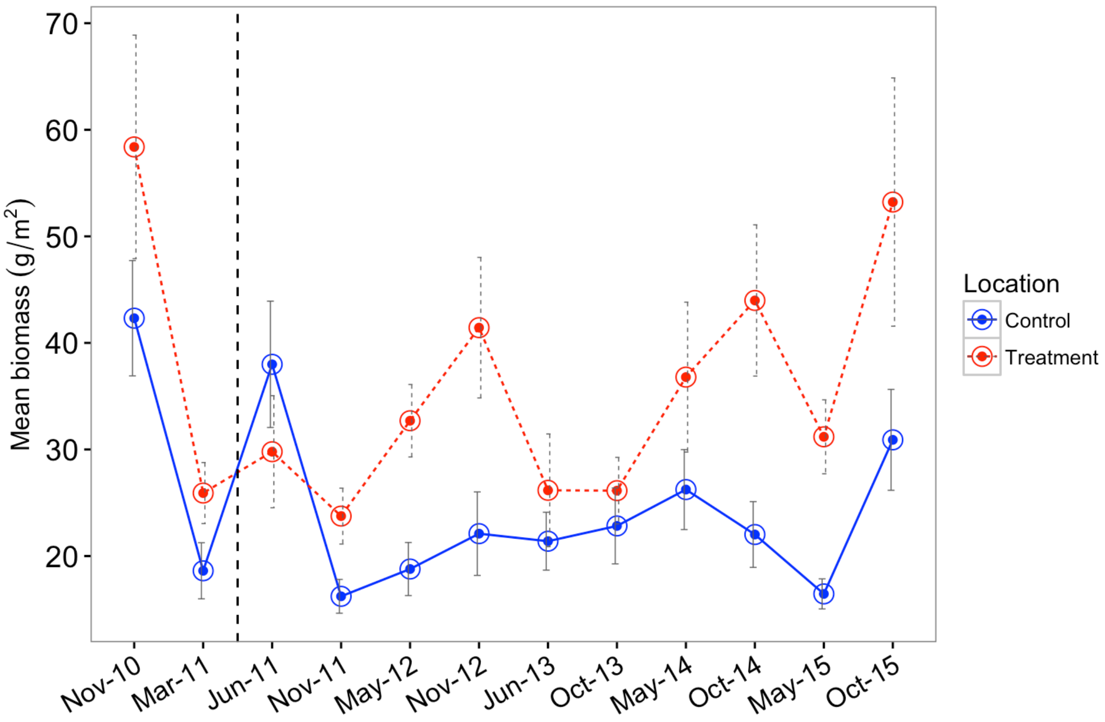

Fig 3.3 Trend line for total fish biomass (excluding *roi*) during 5.5-year roi removal experiment at the Puako, west Hawai‘i study site. Fish-down event is marked by the dashed line. Error bars are standard error of the mean

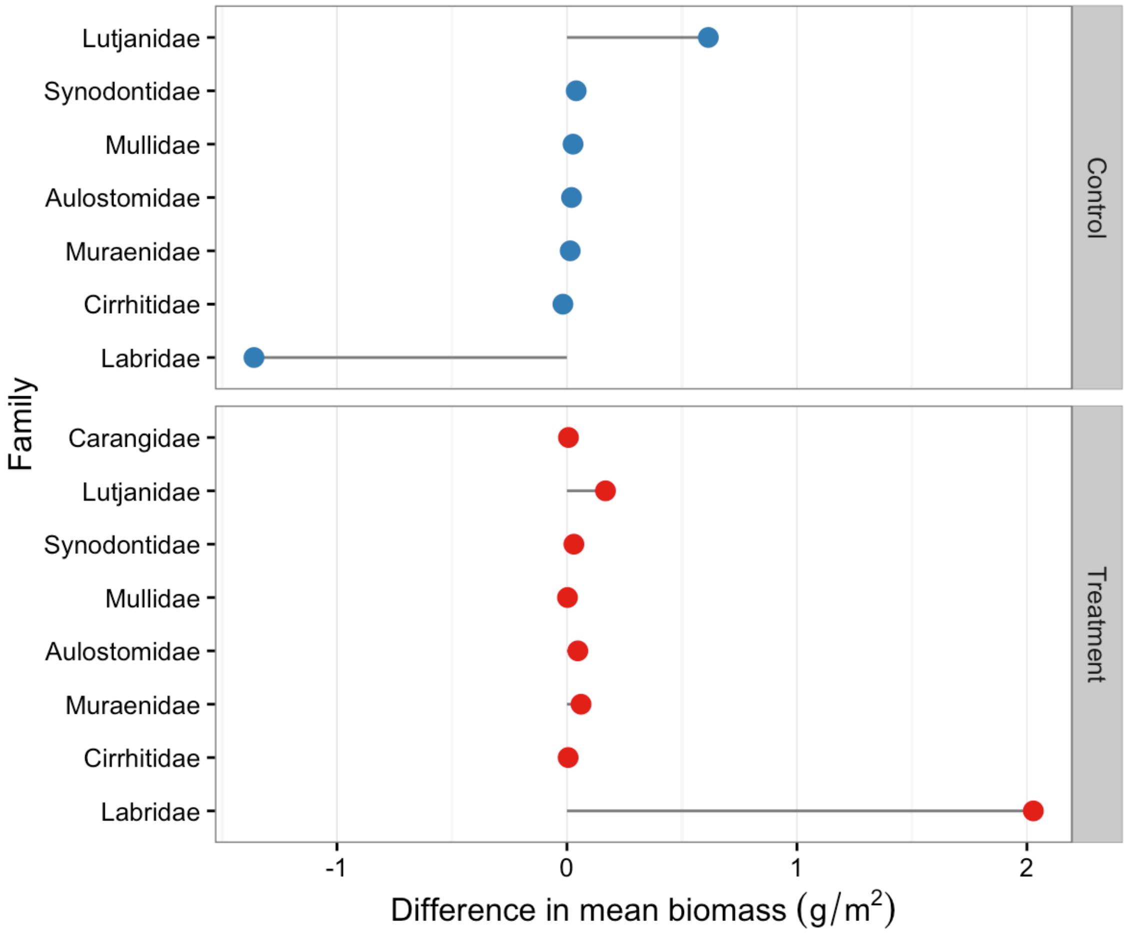

Fig 3.4 Fish family-specific differences at the Puako, west Hawai‘i study site for piscivore biomass (trophic level rank > 4.0) 4.5 years after *roi* removal. Grey lines highlight the direction and magnitude of change (zero being no change in biomass)

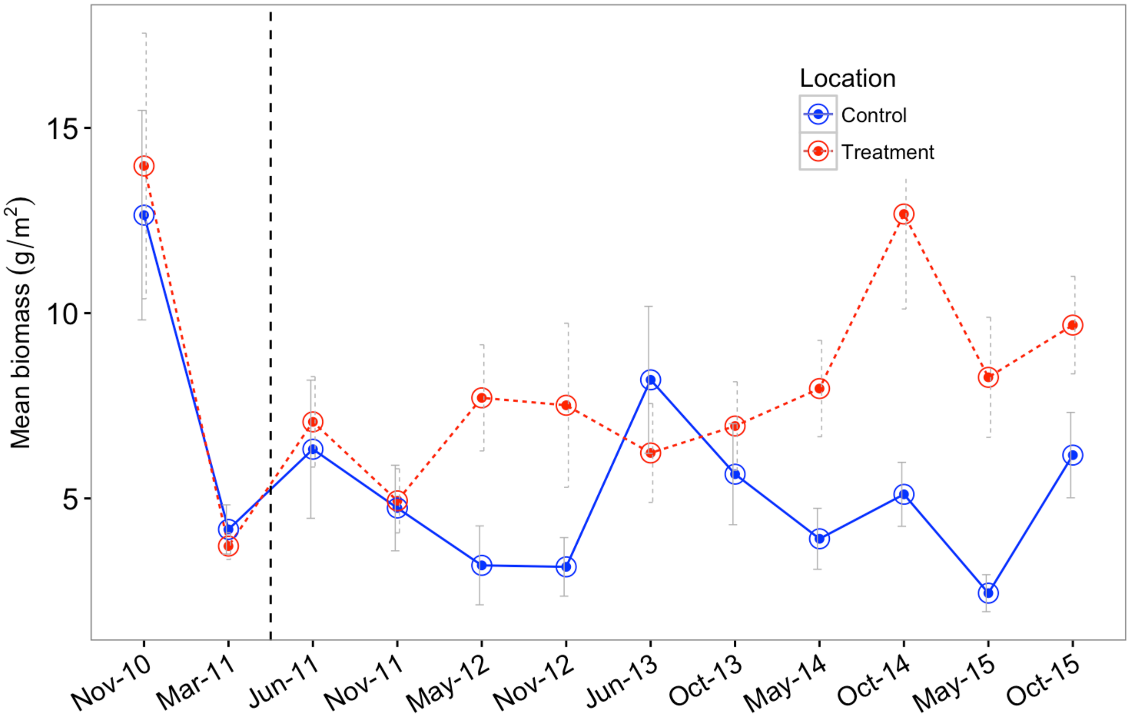

Fig 3.5 Trend line for Labrid biomass during 5.5-year *roi* removal experiment at the Puako, west Hawai‘i study site. Fish-down event is marked by the dashed line. Error bars are standard error of the mean

TABLES

Table 3.1 Model-fitted estimates of the fixed effects (Season + Location + Period) for (log+1 transformed) total fish biomass and for small (<15cm) fish abundance, significant p-values are in **bold**

	Predictor	Coef *B*	SE(*B*)	*df*	*F*	*p*
All fish						
	Intercept	3.13	0.18			**<0.001**
	Site	0.30	0.11	27	7.75	**<0.01**
	Period	-0.16	0.17	9.0	0.93	0.36
	Season	0.18	0.13	8.9	1.95	0.195
Small fish						
	Intercept	0.84	0.02			**<0.001**
	Site	0.03	0.01	25.8	15.7	**<0.001**
	Period	0.01	0.02	9.0	0.60	0.45
	Season	0.01	0.01	8.9	0.45	0.51

Table 3.2 Model-fitted estimates of the fixed effects (Season + Location + Period) for piscivores and Labrid (log+1 transformed) biomass, significant *p*-values are in indicated in **bold**

	Predictor	Coef *B*	SE(*B*)	*df*	*F*	*p*
Piscivores						
	Site	0.26	0.06	62	5.15	0.28
	Period	0.05	0.11	9.4	0.11	0.19
	Season	0.08	0.06	9.1	1.96	0.12
	Site*Period	-0.16	0.12	350	1.16	0.19
Labridae						
	Site	-0.01	0.18	58.8	2.41	0.12
	Period	-0.40	0.21	9.13	1.39	0.26
	Season	0.19	0.13	8.96	1.99	0.19
	Site*Period	0.38	0.18	351	4.17	**0.04**

Table 3.3 Hypothesis test for multivariate changes in fish species composition after *roi* removal (negative binomial model for crossed site-by-time interaction), significant *p*-values are indicated in **bold**

	Res.Df	Df.diff	Dev	Pr(>Dev)
Multivariate test:				
Site X Time	121	1	34.48	0.48
Time	122	2	163.5	**0.04**
Univariate Tests:				
All species not significant	120	1	11.849	0.64 <>1.0

SUPPLEMENTARY INFORMATION

SI Table 3.1 Table of non-significant interaction terms

	Predictor	Coef *B*	SE(*B*)	*df*	*F*	*p*
All fish						
	Site	0.27	0.19	7.67	7.67	<0.01
	Period	-0.19	0.19	9.09	1.01	0.33
	Site*Period	0.04	0.13	351	0.08	**0.76**
Small fish						
	Site	0.03	0.01	47.4	11.5	<0.001
	Period	0.01	0.02	9.0	0.53	0.48
	Site*Period	0.01	0.01	349	0.20	**0.64**

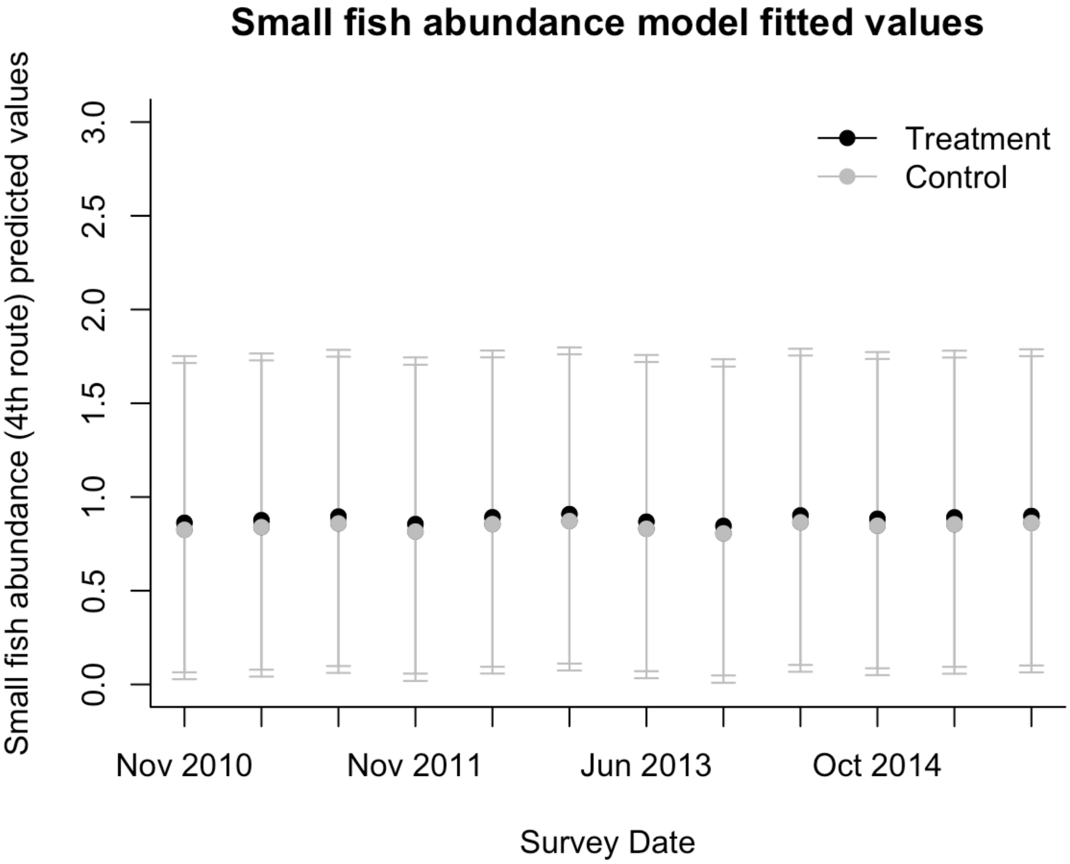

Fig SI 3.1 Model fitted values (4^{th} route transformed small fish abundance) for control and treatment sites by survey date

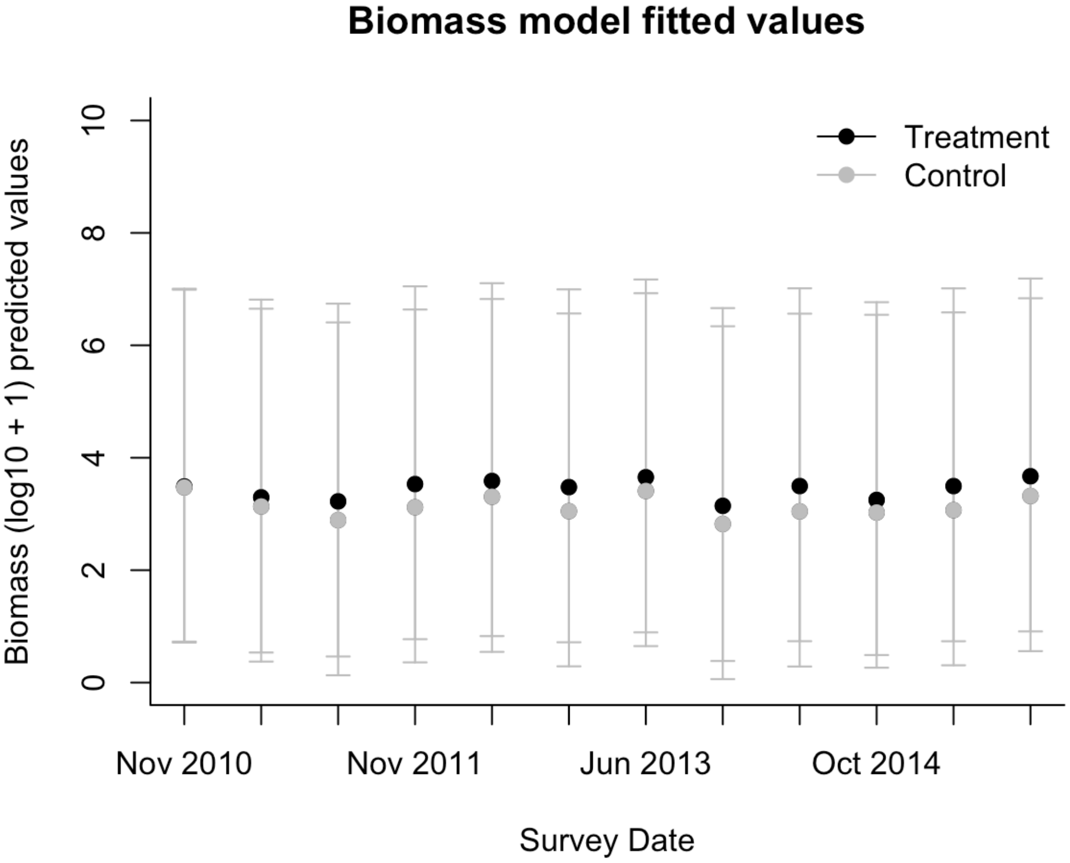

Fig SI 3.2 Model-fitted values (log+1 total fish biomass) for control and treatment sites by survey date

CHAPTER IV

Ecosystem vulnerability or resistance to invasion: potential environmental, anthropogenic, and biotic drivers of an exotic predatory fish distribution in Hawai‘i

To be submitted as:

Giddens, J., Friedlander, A. Stamoulis K., Donovan, M. Delevaux, J

Key words: boosted regression tree; *Cephalopholis argus*; introduced species; marine fish invasion; biotic resistance; species distribution; environmental heterogeneity

ABSTRACT

Global change is accelerating species range shifts. Whether ecosystems will be resistant or vulnerable to species invasions is an imperative question to answer, ultimately, for the sustainability of human well-being. In marine systems, at the seascape level, environmental heterogeneity has been proposed as an important component of ecosystem invasibility, with increased diversity and complexity leading to increased ecological opportunity, and therefore a greater likelihood of successful invasions. In Hawai‘i, a mid-sized predatory grouper, *roi* (*Cephalopholis argus*; Family Serranidae) was introduced during the 1950's, and subsequently established and spread throughout the Main Hawaiian Islands (MHI), yet their distributions, and the environmental, anthropogenic, and biotic community drivers of abundance were unknown. We used a machine learning technique (Boosted Regression Trees) to assess the importance of 22 environmental and anthropogenic predictor variables at the seascape level, as well as 2 community-level factors (density of potential competitors and prey) from a database > 4,000 sites compiled from various sources across the MHI. Seascape-level environmental predictors were the most important factors in explaining *roi* distributions (depth, habitat complexity, and coral cover). Measures of increased ecological opportunity, defined as a diversity of accessible resources as a result of environmental heterogeneity and habitat complexity, were also important predictors of *roi* densities. Anthropogenic factors were important, but ranked last in percent deviance explained by the final model. Biotic interactions were also important, explaining ~ 10 % and ~ 19 % of the deviance by piscivores and prey, respectively. A negative relationship between *roi* and native fishes at intermediate densities was found, and could be indicative of intraspecific competition in *roi* and/or biotic resistance by native species. However, this apparent resistance manifests itself only at sufficient densities of native fishes. Therefore, maintaining intact coral reef fish assemblages with high standing stocks of native species are likely important for ecosystems to resist the potential negative impacts of exotic species.

INTRODUCTION

Human activity has re-shaped earth's ecosystems through habitat modification, global climate change, and through species introductions (Vitousek et al. 1997; Halpern et al. 2006). The response of ecosystems to these mounting anthropogenic pressures is an uncontrolled experiment unfolding (Chapin et al. 2000; Scheffer & Carpenter 2003). Increased knowledge of the salient factors that facilitate or deter species invasions would enable foresight into the potential re-assortments of communities due to species range shifts with global change or introductions of non-natives that are transported by human vectors (Elton 1958; Lockwood et al, 2003). Our ability to manage for biodiversity conservation and the flow of ecosystem services relies on this fundamental understanding of invasion susceptibility vs. resistance (Hannah et al. 2002; Carpenter et al. 2009).

Previous research has focused on the traits of successful invaders (Kolar & Lodge, 2001), yet properties of the ecosystem also influence the outcome of invasions (Vitousek 1986). Species interactions take place within the context of environments and scales of resource availability, therefore studies of traits alone can lead to conflicting conclusions about the drivers of 'successful' establishment, growth, and spread of invading species (Allen et al. 1999; 2006).

The outcomes of species range shifts or introductions could be mediated by environmental heterogeneity or habitat complexity (Levin 1992; Tilman & Kareiva 1997). A classic hypothesis is that environments with spatial and temporal heterogeneity are more open to invasion because of the increased ecological opportunity provided by a variable habitat (Davies et al. 2005; Melbourne et al. 2007). Heterogeneity can be defined as the variety of structural elements (spatial), or variability in physical parameters (temporal) (Stoner & Lewis 1985; Kovalenko et al. 2012). Habitat complexity here refers to spatial structure, as the texture of the landscape (*sensu* Holling 1992). Both types of environmental heterogeneity lead to increased microhabitat availability, which can provide colonizing species with resources such as food, or enemy-free space. This diversity of accessible resources that is underutilized by existing taxa is referred to as ecological opportunity (Losos 2010; Yoder et al. 2010; Kovalenko et al. 2012).

At the community-level, biotic resistance through species interactions (e.g. interspecific competition) has been well studies in terrestrial plant communities, and is thought to play a role in deterring or absorbing impacts of species invasions (Elton 1958; Levine & D'Antonio 1999; Levine et al. 2004). Under this hypothesis, the characteristics of the community determine resistance or vulnerability to invasions at the local scale (Cornel & Lawton 1992). However, less is known about the relative importance of human, environmental, and biotic community drivers of introduced species distributions in their exotic range, especially in the marine environment (but see Côté et al. 2013; Hixon et al. 2016).

In Hawai'i, a mid-sized predatory grouper, the Peacock Hind locally known by its Tahitian name, *roi* (*Cephalopholis argus*, family Serranidae) was introduced during the 1950's, and subsequently established throughout the main archipelago (Randall 1987). This species, (along with 11 others from the lutjanid, serranid and lethrinid families) was intentionally introduced to augment the nearshore fishery by filling a perceived empty ecological niche for benthic predators (HDAR 1950). *Roi* (and two snapper species) established as a results of these introductions, yet are avoided as food fishes because of the high incidence of ciguatera associated with these species (Dierking & Campora 2009). Instead, the perceived declines in native fishery species are popularly attributed to predation by *roi*, which in turn has led to grass-roots initiatives to cull *roi* through spearfishing tournaments (Giddens et al. in prep).

While previous studies identified species traits and historical events that facilitated the successful establishment and spread of *roi* in Hawai'i (Johnston & Purkis, 2016), the environmental, anthropogenic, and biotic drivers of their present distribution across the Main Hawaiian Islands (MHI) was unknown. To address this gap, we used a machine learning technique (Boosted Regression Trees) (Elith et al. 2008) to assess the importance of 23 environmental and anthropogenic predictor variables at the seascape level, as well as community-level factors (density of potential competitors and prey) from a database of > 4,000 sites compiled from various sources across the MHI. Our questions were: 1) Which environmental and anthropogenic factors determine the distributions of *roi* and does ecological opportunity provided by habitat complexity and environmental heterogeneity play a role; and 2) Do biotic interactions (density of competitors or density of prey) play a role and what is the relationship between *roi* and native species densities across the MHI? By investigating these questions, our aim was to gain an understanding of the seascape factors that facilitate or deter species invasions on coral reefs.

METHODS

To examine *roi* population distributions across the MHI in relationship to biotic environmental (prey and piscivore biomass, benthic habitat composition), abiotic environmental, and human factors, existing data from underwater visual surveys of fish assemblages were compiled from current partnerships with federal and non-federal monitoring programs (Friedlander et al. in review; Costa et al. 2016). These data come from 20 different datasets contributed by 9 different collaborators since 2000. In total, the database consists fish data with 20,986 observations from 4,782 sites (Figure 4.1; Table SI 4.1).

Each dataset was checked for errors and completeness, transformed into a consistent format, and standardized to account for overall differences in survey dimensions and methods. To standardize data among methods, calibration factors were calculated using an automated software program that utilizes general linear models and Monte Carlo simulations (Nadon 2014). Sites where surveys were conducted at more than one time were averaged.

Statistical modeling

Boosted Regression Tree (BRTs) models can be used to estimate relationships between reef fish variables (SI 4.1) and the biophysical predictor datasets (SI 4.2) (Elith et al. 2008). The estimated relationships can then be used to produce maps of spatial distribution, and determine the variable's importance in predicting *roi* distributions (Elith & Lethwick 2009). Statistical modeling and spatial prediction were performed in R (R Core Team 2014) using the *dismo* (Hijmans et al. 2016) and *raster* (Hijmans & van Etten 2014) packages.

BRTs are useful for modeling nonlinear relationships without assuming a particular probability distribution. Tree-based approaches to model-fitting estimate relationships between the response and predictor variables by using a series of binary splits on the predictor variables. These splits partition the data into groups of response homogeneity (Breiman et al. 1984; De'ath & Fabricius 2000) and can handle the non-linear relationships and interactions of ecological data (De'ath & Fabricius 2000). BRT models employ a machine learning technique, where multiple trees are fit sequentially and then combined to generate an ensemble model (Schapire 2003; De'ath 2007; Elith et al. 2008). Each iteration of the tree-fitting process uses a random subset of 'training' data (a portion of the data set used to assess the model performance). This introduction of stochasticity to the model fitting process results in a reduction of total model variance and an increase in predictive performance (De'ath 2007; Elith et al. 2008).

Roi biomass was modeled using a Gaussian (normal) distribution after fourth root transformation to improve the normality of the distribution. Survey data for the MHI were randomly divided into model training (70%) and test (30%) subsets, where the test dataset was withheld from model fitting and used to evaluate model performance. Models were fit for a range of parameter value combinations (learning rate, bag fraction, and tree complexity, see Elith et al. 2008), and for each parameter value combination, the optimal number of boosting iterations (trees) was determined using 10-fold cross-validation (described in detail in Elith et al. 2008). To select the optimal model, predictive deviance was computed by averaging the unexplained variation in the response variable (by comparing the test and training datasets at each iteration) and the number of trees that minimized predictive deviance was selected. A final BRT model was fit to the training dataset using the optimal number of trees and fitting parameter combinations identified through the model tuning process. For model simplification, the change in predictive deviance was computed relative to the initial model by sequentially dropping the least important predictor, and re-fitting the model (Elith et al. 2008). A final model was fit using the simplified set of predictor variables. For the final model, predictive performance was evaluated by calculating the predictive deviance through 10-fold cross-validation of the training and test subsets. The mean predictive deviance across the 10 iterations was used to calculate a cross-validation estimate of the percent deviance explained (PDE) (Elith et al. 2008). To compare how well the model performs when predicting data that was independent of model fitting, the "Test PDE" was determined by calculating the percent deviance explained by the model when evaluated using the model test dataset. Both test and cross-validation PDE indicate overall model fit, and higher values for these metrics indicate greater confidence in predictions across space, and assessment of relationships between response and predictor variables.

Prediction across space

To calculate spatially explicit predictions and prediction uncertainties, bootstrapping can be used to generate a suite of fitted BRT models. Training data were repeatedly sampled with replacement to create 25 bootstrap samples. A BRT model was fit to each bootstrap sample and used to make a prediction to a spatially explicit gridded map using the values of the predictor variables at each grid cell. The set of 25 spatial predictions were used to calculate the prediction mean and coefficient of variation (Elith et al. 2008).

Predictor variable importance and partial dependence

In order to predict the ecological drivers behind the spatial distributions of *roi*, the BRT model outputs provided a summary of the relative importance of the predictor variables used in model fitting, based on how often a variable is used for splitting (Elith et al. 2008). Further, partial dependence plots were generated for each biophysical and community predictor variable to visualize the individual effect of the predictor variable on *roi* distributions (De'ath 2007; Elith et al. 2008).

Predictor dataset

We tested among four categories of environmental variables at the seascape (among-island) scale, which were: habitat composition, geography, topography, and oceanography (SI 4.1 and Table 4.1), following Stamoulis et al. (2016). Population density was used as a proxy for human influence (Williams et al. 2008). Wave power was considered an inverse proxy for human influence, as sites with higher wave power are less accessible to humans (Stamoulis et al. 2016). Environmental heterogeneity was measured by two factors that quantify the diversity of structural elements (Kovalenko et al. 2012), and they include the Shannon Diversity Index, which accounts for the richness and evenness of habitat-forming species in an area (Shannon & Weaver 1949), and the Proximity Index, which quantifies the spatial context of a habitat patch, including the diversity of habitat forming species, in relation to its neighbors (Gustafson & Parker

1994) (detailed descriptions of both metrics in Table 4.2). Habitat complexity variables (texture of the landscape, *sensu* Holling 1992) included measures of topographic complexity and spatial configuration from habitat variables.

Measures of habitat composition were generated from benthic habitat maps for the MHI (Battista et al., 2007). These were simplified into five benthic cover classes, including crustose coralline algae (CCA), coral, macroalgae, turf algae, and soft bottom habitat. Geographic variables included projected latitude and longitude, distance to shore, and proximity to human population (SI Table 4.2 and Table 4.1). Seafloor topography variables were derived from a gridded synthesis of multibeam sonar and LiDAR (Light Detection and Ranging) bathymetry at 5 m resolution. From this information, depth and a suite of seafloor complexity datasets were derived. The mean and standard deviation of the 5 m resolution datasets were computed within a 60 x 60 m grid (SI Table 4.2 and Table 4.1). Metrics were derived for several neighborhood sizes (60 m, 120 m, and 240 m radii) to account for varying home-range sizes of fishes in Hawai‘i. Oceanographic variables were based off of a 10-year (2000-2009) hindcast model at 500 m resolution (Stopa et al. 2013) representing wave states around the MHI. Details of these landscape scale predictors are described in Stamoulis et al. (2016).

Biotic variables at the community scale consisted of *roi* biomass, and the biomass of prey-sized fished (all fishes <15 cm TL) and potential competitor biomass (piscivores of trophic level > 4, Froese & Pauly 2011). Biomass was estimated from fish count data using the allometric length–weight conversion: $W=aTL^b$, where parameters a and b are species-specific fitting parameters, TL is total length (cm), and W is weight (g). Fitting parameters were obtained from a comprehensive assessment of Hawai‘i reef fish length-weight relationships (Donovan et al. in prep), and from published sources (Froese & Pauly 2011).

Three BRT models were run to assess the relative importance, and the relationships of these environmental, human, and biotic community factors in determining *roi* distributions across the MHI. These were: 1) *Roi* biomass as a function of environmental and anthropogenic variables to determine rank order of importance, and whether environmental heterogeneity plays a role in predicting *roi* densities; 2) Model 1 plus prey to examine the importance of prey (all fishes < 15 cm TL) as a predictor variable, as well as the shape of the relationship between *roi* and prey densities; 3) Model 1 plus potential competitors to examine the importance of competitors as a predictor variable, as well as the shape of the relationship between *roi* and competitor densities. Potential competitors are defined as all piscivorous fishes (trophic level ≥ 4). Models 1-3 were compared in terms of the amount of deviance explained, to determine the predictive performance of environmental variables only, compared to when piscivorous or prey fishes are included in the model.

We hypothesized that measures of seafloor structural complexity and diversity are primary predictors of *roi* abundance because of the increased ecological opportunity created by microhabitat availability in heterogeneous environments. Further, we hypothesized that these complexity and diversity measures explain more variability in *roi* distributions compared to measures of human impacts (human population density) or biotic factors (density of piscivorous or prey-sized fishes) because the larger scale environmental drivers entrain smaller scale community interactions and human impacts (Gunderson & Holling 2001). Furthermore, we hypothesized that *roi* and native species have a positive relationship, responding synchronously to increased ecological opportunity provided by habitat complexity and diversity. However, if biotic resistance by native species affected *roi* population densities, then we would see a negative relationship between *roi* and native species abundance across the MHI archipelago.

RESULTS

Environmental and anthropogenic variables:

Environmental variables were most important in predicting *roi* densities (Figure 4.2). Foremost was depth, which accounted for 11.9% of the variance explained, and showed a positive relationship where more *roi* were found with increasing depth (Figure 4.3). Coral cover was the second most important variable, with a positive relationship that accounting for 10.2% of the variance explained by the model. Habitat structural complexity (slope of slope) was also positively correlated with roi densities, accounting for 8.5% of the variability. Latitude had a generally negative relationship, with less *roi* found farther north, accounting for 8.1% of the deviance (Figure 4.2). *Roi* were found in areas with very low and very high wave power, but in low densities at intermediate values of this variable. (Wave power also interacted with depth, as there is less wave motion at deeper depths.) Slope of slope at the 240 m scale had a generally positive, but more variable relationship than at the 5 m scale (Figure SI. 4.1).

Finally, distance to human populations played only a modest role in explaining the distribution of *roi* (13.1 % of relative contribution). The final model accounted for 53.6% PDE for the training data set, 21.2% for the test data set, and 27.3 in cross validation (Table 4.2).

Biotic (prey and potential competitor) variables:

Prey: A second BRT (model 2) was fit with environmental and human variables from model 1 described above, with the addition of prey biomass (all fishes < 15 cm TL) to investigate the relationship between *roi* and prey biomass across the MHI, while accounting for the effect of the seascape drivers identified in model 1. By investigating this relationship, we aimed to gain a better understanding of the role that biotic interactions (relative predator-prey densities) played in determining the community's vulnerability or resistance to invasion.

The five most important predictor variables for determining *roi* abundances, including the biotic interactions of prey species were habitat complexity (slope of slope) (25%), (depth) (23%), prey biomass (19%), latitude (18%), and wave power (15%), respectively (Figure 4.4). The overall model explained 44.2 % PDE for the training data set, 29.1% for the test data set, and 26.0% in cross validation. These measures indicate slightly less confidence in predictions compared to the environment only model, but with 5 instead of 20 predictor variables, indicating more explanatory power for each individual predictor in the simplified model (model 2, accounting for prey biomass).

The relationship between *roi* and prey was non-linear and saturating (Figure 4.5). There was an initial positive relationship, where increases in prey corresponded with increases in *roi* densities. At a threshold of prey biomass (~ 40 g/m^{-2}) *roi* densities peaked, and then responded negatively to increases in prey biomass up to a limit. At ~ 50 g/m^{-2} of prey biomass, *roi* densities remained constant at about 0.6 g/m^{-2}.

Potential competitors: A third BRT (model 3) was fit with environmental and human variables from model 1 described above, with the addition of piscivorous fish biomass (fish of trophic level ≥ 4) to investigate the relationship between *roi* and potential competitor biomass across the MHI, while accounting for the effect of the seascape drivers identified in model 1. By investigating this relationship, we aimed to gain better understanding of the role that biotic interactions (interspecific competition) played in determining the community's vulnerability or resistance to invasion.

Piscivorous fish biomass was a relevant predictor of *roi* distributions, ranking 5th out of 10 in importance (accounting for 10.5% of deviance in the model), after environmental predictor variables (Figure 4.6). The top predictors in the piscivore model were similar in variable importance compared to models 1 and 2 (e.g. coral cover, depth, and topographic complexity). Yet an additional complexity at a broader spatial scale (slope of slope and bathymetric position index at 240 m neighborhood radius) was identified as important in predicting *roi* densities in the piscivore model (Figure 4.6). Piscivores had a similar relationship to *roi* compared to prey species; that is a non-linear saturating relationship (Figure 4.7). Both *roi* and piscivore biomass increased together with a positive relationship at low population density. At a peak of ~ 25 g/m^2 for piscivores, *roi* density decreased, and finally plateaued at 0.55 g/m^2. With increasing piscivore densities, *roi* densities remained stable.

DISCUSSION

To better understand the properties that make ecosystems vulnerable or resistant to invasion, we examined the relative influence of habitat, anthropogenic, and biotic variables in determining the invasion success of an introduced marine predatory grouper across the MHI. Measures of model performance (percent deviance explained) for our three BRTs indicated a well-performing model (Elith 2008). From these predictive models, we characterized the relationship of introduced *roi* population densities to the recipient ecosystem biophysical drivers of fish abundance, and here present the first assessment of *roi* distributions and their drivers at the seascape (among-island) scale.

Roi distributions:

Roi were found primarily in deep, coral rich, and topographically complex habitats. Coral cover was one of the most important drivers for *roi* abundance, whereas it was not a primary driver for other fish assemblage metrics (biomass, richness) in Hawaiʻi (Stamoulis et al. 2016). Instead, the principal drivers for resource fishes (those species caught for food), total fish biomass, endemic fish biomass, and species richness generally correlated with measures of structural complexity and human impacts (human population density and wave power as a proxy for inaccessible locations) (Stamoulis et al. 2016). *Roi* were found in higher densities in the southern and leeward parts of the archipelago, which may be an entrained response to the higher coral cover found in those areas (Costa & Kendall 2016). Higher coral cover and reduced wave action on the deeper fore-reef slopes, could also explain why *roi* densities increased with depth. In sum, high coral cover emerged as the prime habitat for *roi*, which distinguishes habitat affinities of this introduced predator from the general predictors of reef fish assemblage metrics that are well documented in the literature (refuge from humans and high topographic complexity) (Friedlander et al. 2007; Pittman et al. 2009; Williams et al. 2015; Stamoulis et al. 2016).

Relationship to biophysical drivers of fish abundance:

Roi had a generally linear and positive response to depth and coral cover. Positive relationships were also observed with measures of topographic complexity and environmental heterogeneity (diversity of elements), as expected under the environmental heterogeneity hypothesis (Melbourne et al. 2007), which postulates that a greater diversity and abundance of species is found in more complex and heterogeneous environments. These findings correspond with the literature and have been documented in empirical research (Friedlander et al. 1998; 2003; Graham & Nash 2013; Stamoulis et al. 2016). The physical diversity and complexity of habitat structures in Hawaiian coral reefs present open ecological opportunities for *roi* to establish.

Roi had a bimodal response to wave power as they were found in abundance in areas with low and high, but not at intermediate levels of wave energy. To explain their peak in abundance at low and high wave energy sites, the former could be an entrained response due to their habitat affinity with high coral cover, which is found in low wave energy sites. The latter could be indicative of a response to human impacts. Areas of low fishing pressure generally correspond to areas that are inaccessible to humans, such as high wave power (and deeper) sites. Thus, wave power has been used as an inverse proxy for human impacts in previous studies (Williams et al, 2008; Stamoulis et al. 2016). Here, this measure could signal a de facto refuge from humans in areas with higher wave power. Fish biomass, especially for resource species, was strongly correlated with high wave energy areas across the MHI, as opposed to leeward sites that are easily accessible to humans on a year-round basis (Stamoulis et al. 2016). The relationship of increased *roi* densities with higher wave energy could be a response to a direct lack of human fishing pressure, or indirectly through an increase in food availability at these sites.

Roi and human population density also had a bimodal relationship, with high *roi* densities in areas with no humans, that dropped dramatically, but not incrementally with increasing human population densities. This signal could be heavily influenced by the effect of increased overall fish biomass in no-take marine protected areas (no humans) (Friedlander et al. 2007). After the initial decrease in *roi* densities, the relationship was only slightly negative with increasing human population, as *roi* are generally not targeted for food due to risk of ciguatera (Dierking & Campora 2009). They are targeted in culling tournaments and opportunistically across the state (Giddens et al. in prep), which could contribute to their decrease in densities with increasing human population.

Seascape variable importance and the role of environmental heterogeneity in determining invasion success at the seascape level:

Measures of habitat composition, geography, and topography were strongly correlated with *roi* densities. Proxies for refuge from human pressure, such as wave power and depth were strong correlates, but second to environmental drivers. These findings are consistent with studies in the MHI (Stamoulis et al. 2016) and across the Pacific Ocean (Williams et al. 2015; Heenan et al. 2016) for drivers of reef fish abundance and distributions in relation to human and environmental variables at the seascape (archipelagic and between archipelago-scale). Measures of environmental heterogeneity (Shannon Diversity Index and Proximity Index) were less important in determining *roi* distributions across Hawaiian reefs, compared to measures of structural complexity. Environmental heterogeneity can facilitate establishment, but the structural complexity provided by physical texture was a more prominent driver in this marine system (Friedlander & Parish 1998).

Role of biotic interactions (prey and potential competitors) in determining invasion success at the community-level:

Roi correlations with prey and piscivore groups were characterized by non-linear and saturating relationships. At intermediate densities, a negative relationship revealed decreasing *roi* biomass while native fish biomass increased. This pattern could indicate either intra- or interspecific competition as limiting *roi* population growth. Given that native species densities increased while *roi* decreased, biotic resistance by native species could serve to limit *roi* populations (Elton 1958; Tillman 1999). The priority effect (Shulman et al. 1993; Almany 2003), whereby the prior establishment of species deters newcomers and determines the species assemblage through competition or predation, could function to increase ecosystem resistance to invasions.

Alternatively, the pattern of decreasing *roi* densities at intermediate biomass levels could be indicative of self-limiting population growth as a result of intraspecific competition. Direct demographic density dependence occurs when there is positive population growth rate at low densities and a negative population growth rate at high densities, and can be measured through changes in the per capita gain rates and/or loss rates of a population (Murdoch 1994; Hixon et al. 2002). This regulated growth was observed in invasive lionfish in the Caribbean through a field manipulative experiment, which measured demographic rates (growth, recruitment, immigration, and loss) in a gradient of experimental plots from naturally occurring to increased lionfish densities (Benkwitt 2013). Lionfish exhibited direct density dependence in individual growth rates, however, there was no evidence for density dependence in recruitment, immigration, or loss (mortality plus emigration). The likely mechanism was intraspecific exploitative competition indicating that lionfish numbers could be limited by prey availability (Benkwitt 2013).

In comparison, space may be the limiting resource causing intraspecific competition and ultimately regulating populations of *roi* in Hawai‘i. Unlike transient native piscivores such as jacks, *roi* form harems and hold home ranges. Also, unlike other serranids, *roi* do not undertake spawning migrations (Shpigel & Fishelson 1991). Instead they remain in their home ranges year round where males defend their territory and the females within their social group against conspecifics. Thus, the dominant male secures the opportunity to mate with females within his home range (Donaldson 1995). Female home ranges are nested within the male's range, with the dominant female holding the largest territory (up to 100 m^2 in the Red Sea) (Shpigel & Fishelson 1991). An earlier study in Hawai'i (Meyer 2008) documented a mean home range of 1236 m^2 for *roi*, which generally included several shelter sites (mean of 598 m^2) in areas of high reef complexity where *roi* spent the majority of time (Meyer 2008). Defending these home ranges, and the status within the social hierarchy that territory confers, may ultimately limit *roi* population densities in Hawai'i.

While our results show a negative relationship between *roi* and native reef fish at intermediate densities, our study is based on correlation analysis, and therefore cannot distinguish the causative mechanism behind the pattern, only that there is one. Field manipulative experiments are needed to distinguish the role of inter vs. intraspecific competition in limiting *roi* densities, by measuring demographic rates at a range of *roi* population densities with appropriate controls (Hixon 1991; Benkwitt et al. 2013).

In both Hawai'i and the Caribbean, if biotic resistance were to play a role in limiting predatory fish invasions, there would need to be sufficient densities of native predators and competitors to suppress populations of non-native species. The diversity-invasibility hypothesis (Elton 19958; Tilman 1999) states that areas with high native species richness and/or biomass are less likely to be invaded by an exotic species because of decreased ecological opportunity where a reef is saturated at the community level. Our results are consistent with this hypothesis, as the observed negative relationship appears only at sufficiently high native fish densities.

Scale-dependence

Our study shows a non-linear relationship between *roi* and native fish biomass, such that the correlation of the introduced predator with native species had a different sign depending on the densities of species. A positive relationship of native and introduced species alike may reflect a biotic response to increasing resource availability and ecological opportunity provided by environmental heterogeneity and habitat complexity, and/or a refuge from human pressures (Menge et al. 1985; Friedlander et al.

2003).

Previous studies on the impacts of exotic species in invaded ecosystems have shown contrasting results (Allen et al. 1999). Likewise, previous studies testing the diversity/biomass-invasibility hypothesis have been contradictory, and have shown positive, negative, or neutral relationships between diversity and invasibility in various systems and at various spatial and temporal scales (Sax & Brown 2000). Together our results indicate that studies to determine the effect of an introduced species on the native fish assemblage could have different results depending on the initial densities of species, as well as the environmental context. As our correlational results show a non-linear relationship to environmental and human drivers of *roi* distribution and abundance, we do not expect that the impacts of this introduced species will be consistent in different seascape contexts.

To understand the general factors that determine predatory fish invasion success, including traits of the predator, prey, and recipient ecosystem, a comparison between Caribbean and Hawaiian fish introductions would be a fruitful area of further research (Cote et al. 2012; Hixon et al. 2016). Lionfish and *roi* share similar traits that could be associated with invasiveness; they are trophic generalists (Shpigel & Fishelson 1991; Albins & Hixon 2008; Harms-Tuohy et al. 2016), with early age at maturity (Morris 2009, Schemmel et al. 2016) and continuous reproduction (Morris et al. 2011, Schemmel et al. 2016), and they have a tolerance for a wide range of environmental conditions (e.g. depth) (Cote et al. 2013; Johnston & Purkis 2016). Other factors are distinct between the two regions. For example, prey *naïveté* and the novel predator archetype (Cox & Lima 2006; Sih et al. 2010) are proposed species traits of the prey and predator, respectively, that facilitated the lionfish invasion of Caribbean reefs (Albins 2015; 2016; Anton et al. 2016). These are unlikely explanations for the 'success' of *roi* in Hawai'i, first because of the substantial time since introduction (> 60 yrs), and also because native fish maintain connectivity with parent populations in other areas of the Pacific where serranids are present (Eble et al. 2011a; 2011b; Bowen et al. 2013; Bowen 2016).

One factor common to both locations is that potential competitors and predator biomass has been severely decreased compared to historical levels (Jackson et al. 2014; Pandolfi et al. 2005), compared to remote areas (Jackson et al. 2014, Friedlander &

DeMartini 2002, Willams et al. 2010; Williams et al. 2015), and compared to what can be expected given the environmental conditions and socioeconomic capacity of the area (Cinner et al. 2016).

Altered ecosystems are more vulnerable to invasions and are prone to regime shifts following disturbances such as coral bleaching events or storms (Vitousek 1990; Scheffer et al. 2001; Hughes et al. 2003). Disturbances can trigger ecosystem shifts from coral to maco-algal dominated states, with the associated loss of ecosystem goods and services (Folke et al. 2004). Without intact ecosystem structure, invasions can have more dramatic effects (Hobbs & Huenneke 1992). For example, in Hawaiʻi, invasive algae (Stimson et al. 2001; Vermeij et al. 2009) required intensive human resource efforts to control the spread and impact to coral reef ecosystems (Conklin & Smith 2005). Managing ecosystems prone to regime shifts requires action before the critical bifurcation point is reached (Scheffer et al. 2012). Effort to restore a system that has undergone change to an alternate stable state (Mumby et al. 2007) will be more costly or impossible (Selkoe et al. 2015). Therefore, to maintain invasion resistance of coral reef ecosystems in an era of global change, it is imperative to maintain high standing stocks of native species to preserve intact structure and resilience of ecosystem functions.

Conclusions:

Our results show that environmental variables are of principal importance in predicting the distribution and abundance of introduced *roi* in Hawaiʻi. Studies on the impacts of invasive species at the local level (e.g. patch reef-scale) may result in different conclusions depending on their environment and the densities of native species at the site. Therefore, the environmental context at the seascape level (environmental heterogeneity and habitat) in relation to the densities of species at the community level, may explain the contrasting results of previous studies.

Biotic resistance could play a role in limiting *roi* populations, possibly through the priority effect of established native species. Alternatively, intraspecific competition by *roi* defending territories against other *roi* could explain the negative relationship between native species and *roi* at intermediate densities. If territory space limits *roi* densities, but not native species at intermediate densities, we would expect to see the negative relationship noted above. Experiments are needed to decipher between the relative roles of inter- and intraspecific competition if either or both are indeed important. Regardless of the exact mechanism, what is clear is that intact ecosystems are more resilient to invasion, and management should strive to maintain high standing stocks of native species to bolster resistance to disturbance, such as invasive species.

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FIGURES

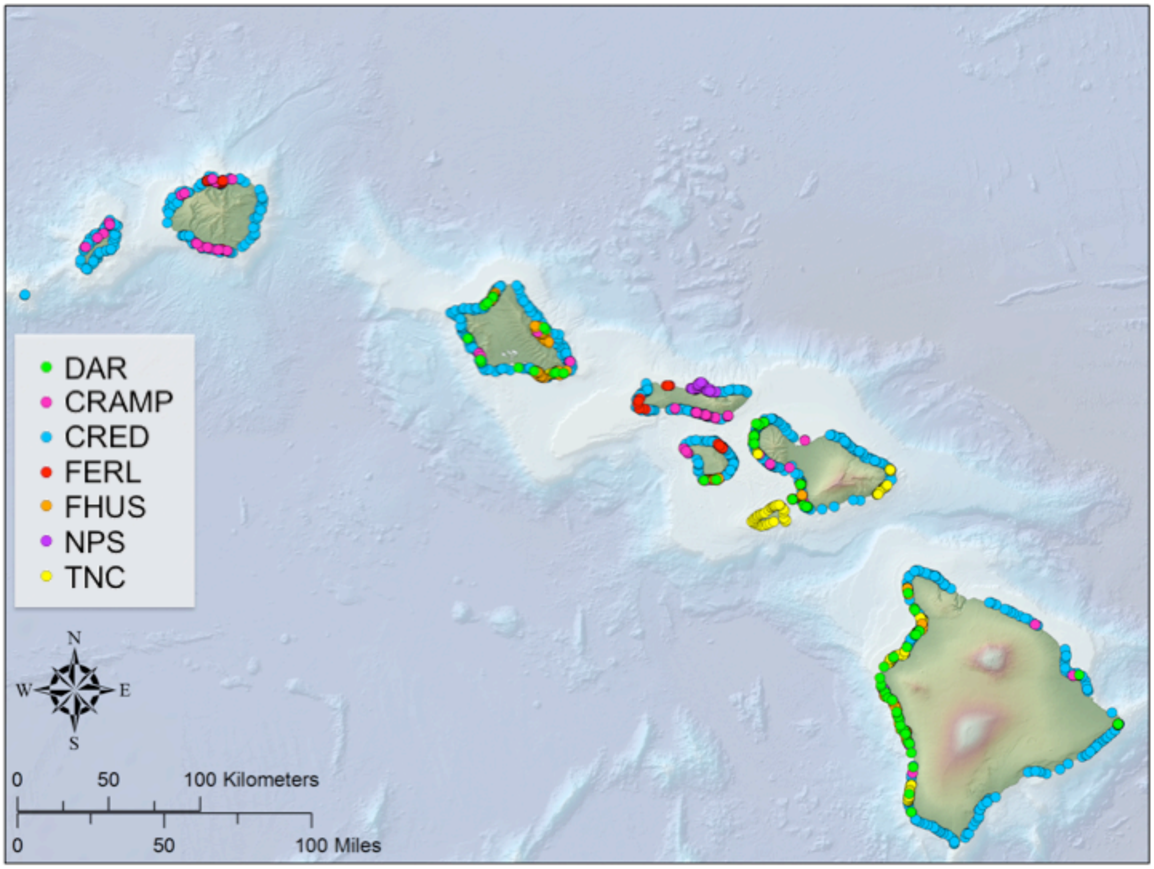
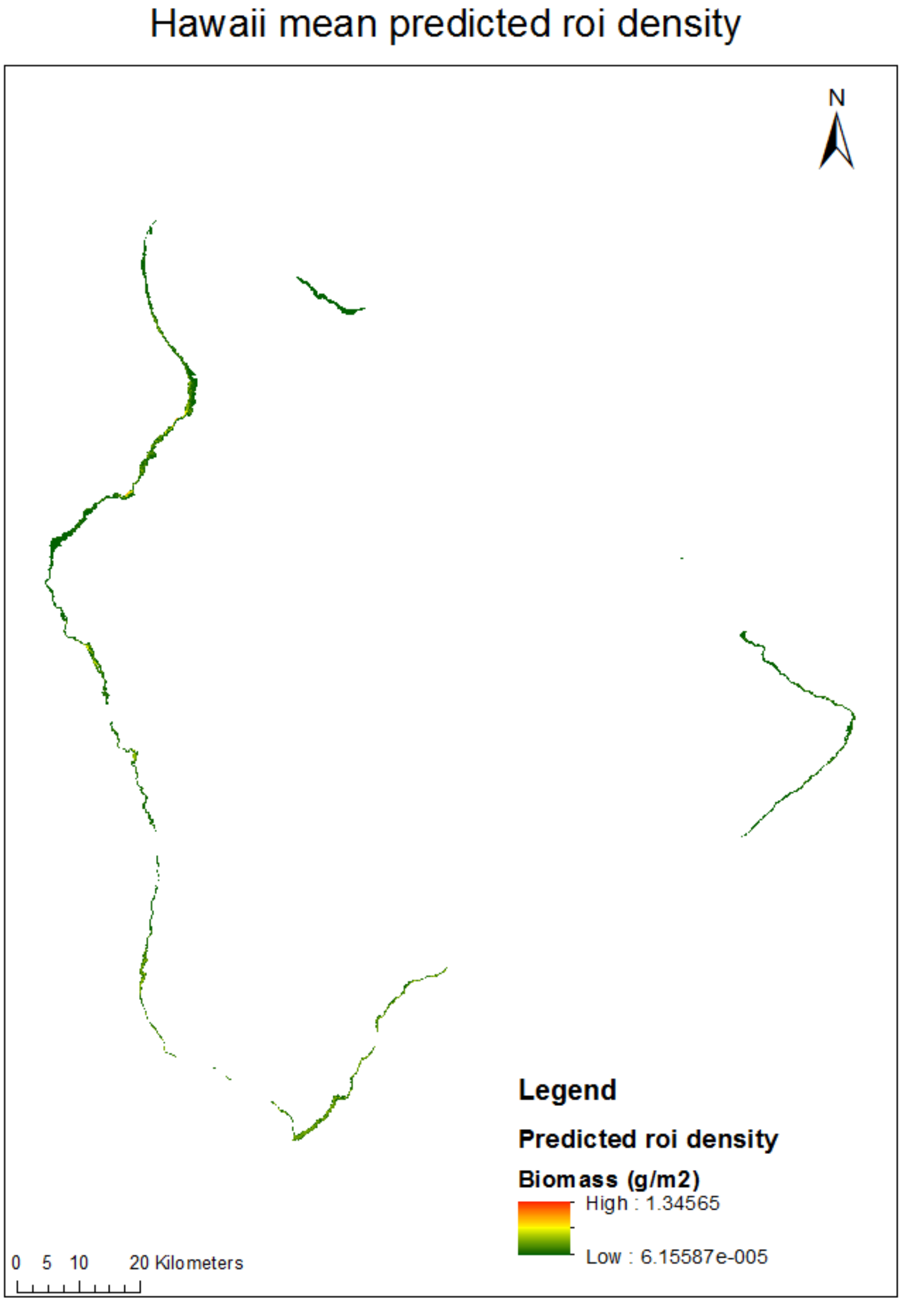
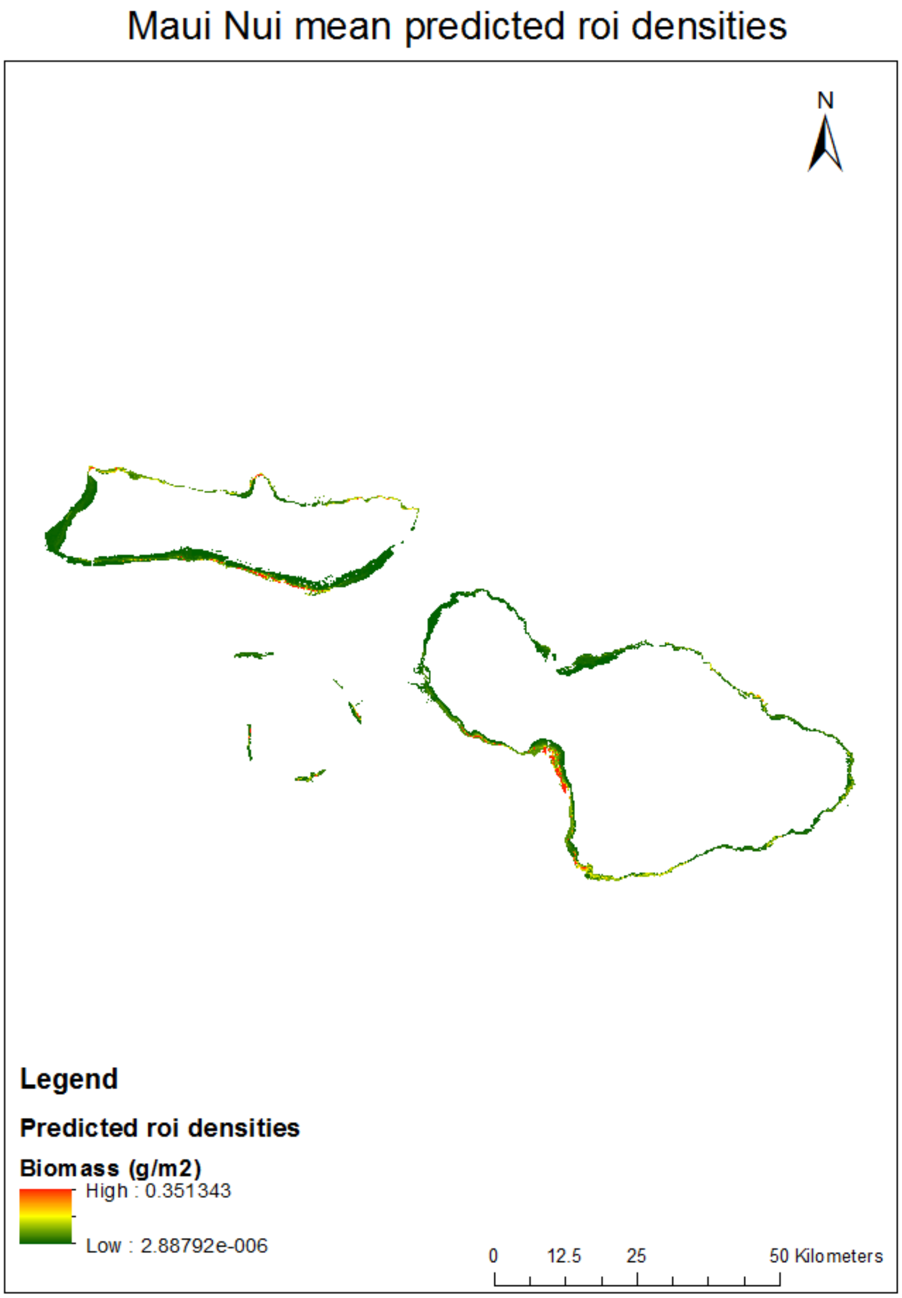


Figure 4.1. Map of compiled reef fish survey datasets for the Main Hawaiian Islands. Acronyms: FERL - Fisheries Ecology Research Lab, University of Hawaiʻi; TNC - The Nature Conservancy Hawaiʻi Marine Program; NPS - National Park Service; FHUS - Fish Habitat Utilization Study, NOAA Biogeography Program; CRED - Coral Reef Ecosystem Division, NOAA Pacific Islands Fishery Science Center; DAR - Division of Aquatic Resources, State of Hawaiʻi; CRAMP - Coral Reef Assessment and Monitoring Program, University of Hawaiʻi. Map by Joey Lecky. Modified from Donovan et al. in review

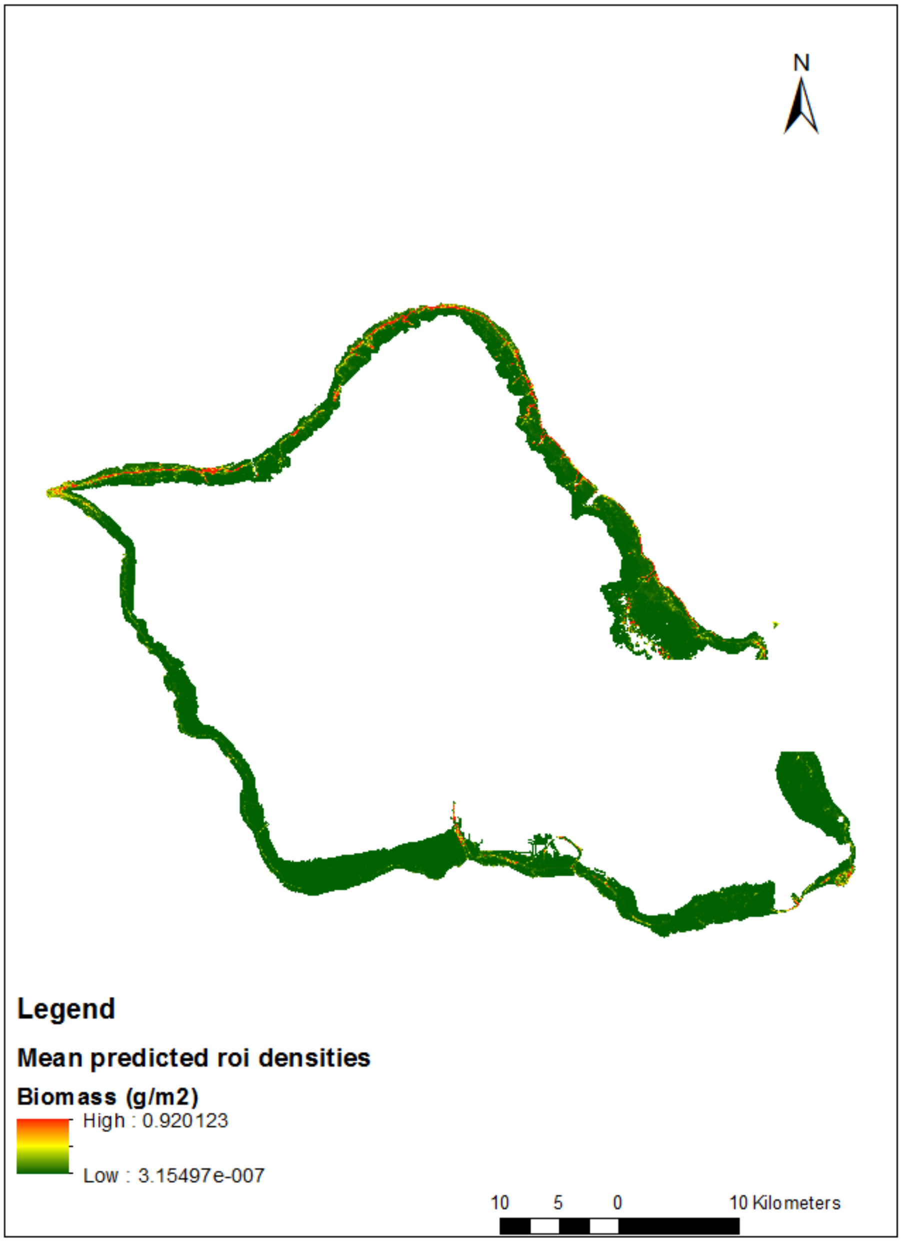

Hawaii mean predicted roi density
N
Legend
Predicted roi density
Biomass (g/m2)
High : 1.34565
Low : 6.15587e-005
0 5 10 20 Kilometers

a)

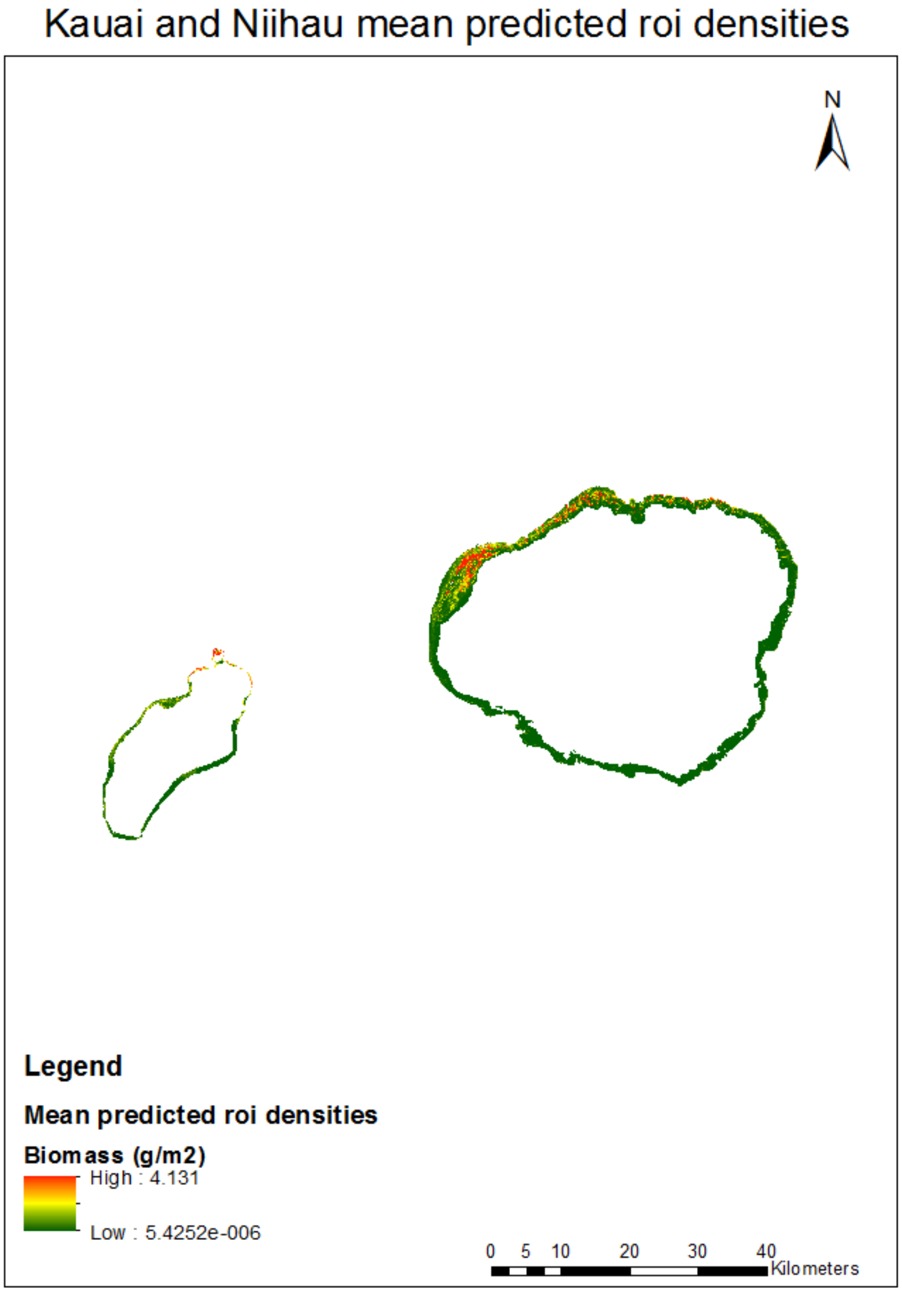

Maui Nui mean predicted roi densities
N
Legend
Predicted roi densities
Biomass (g/m2)
High : 0.351343
Low : 2.88792e-006
0
12.5
25
50 Kilometers

b)

Oahu mean predicted roi densities



c)



d)

Figure 4.2 Predicted *roi* densities for a) Hawaii Island; b) Maui Nui; c) Oahu; and d) Kauai and Niihau based on boosted regression tree modeled relationships between *roi* biomass and environmental predictor variables.

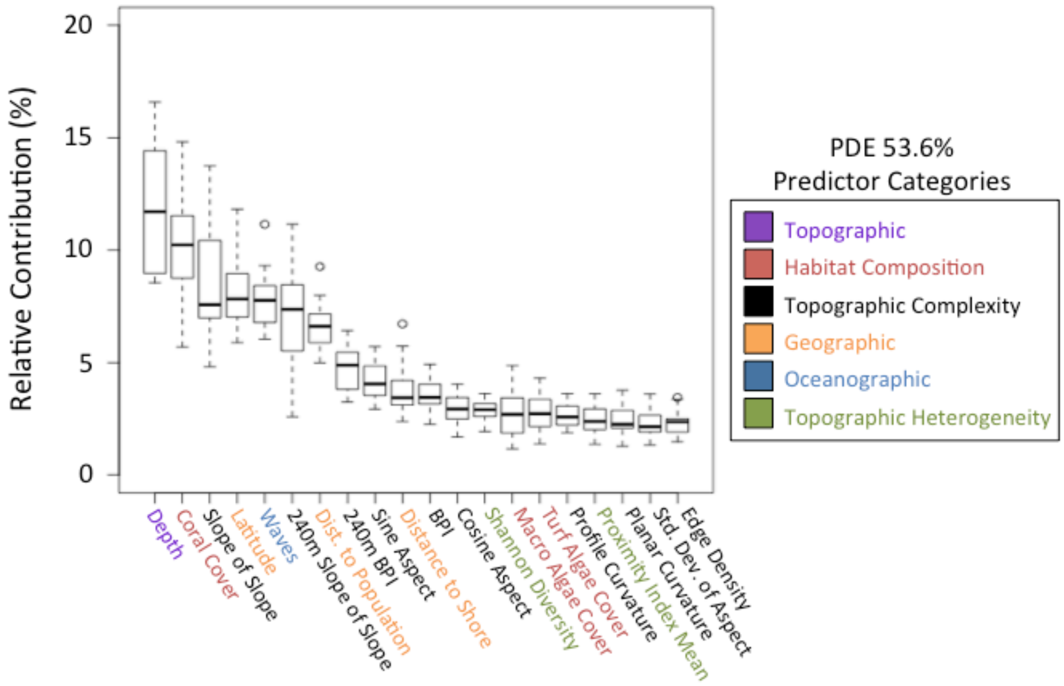


Figure 4.3. Model 1 (human and environment) Boxplot of environmental and anthropogenic variable importance (mean ± SE) in explaining *roi* densities across MHI. Abbreviations are shown in Table 4.1. Open circles represent outlier observations. Color illustrates the predictor categories

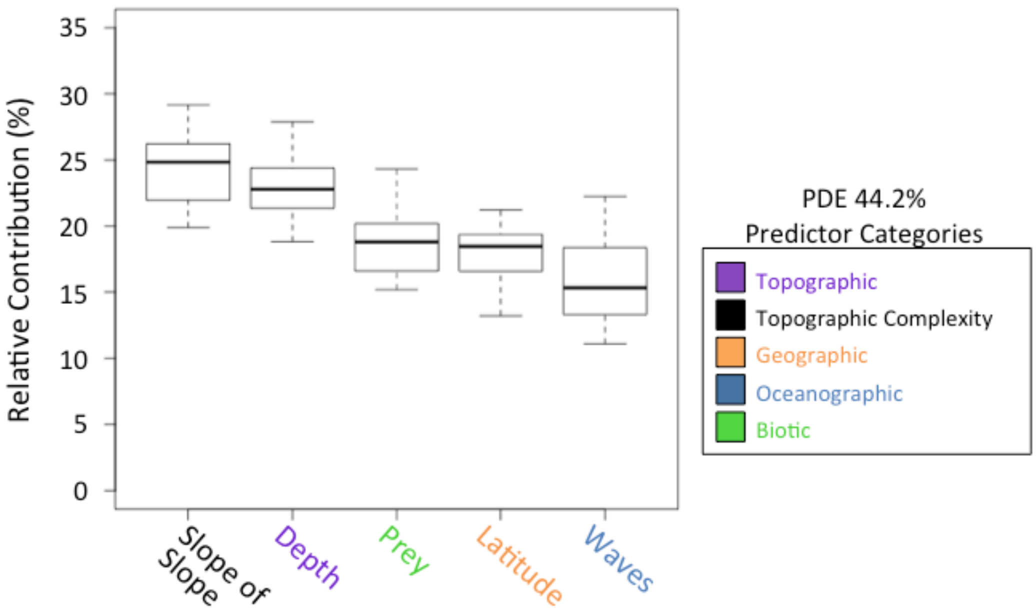


Figure 4.4. Boxplot of anthropogenic, and biotic (prey) predictor variables (mean ± SE) that determine *roi* distributions in the MHI. Abbreviations are shown in Table 4.1. Color illustrates the predictor categories

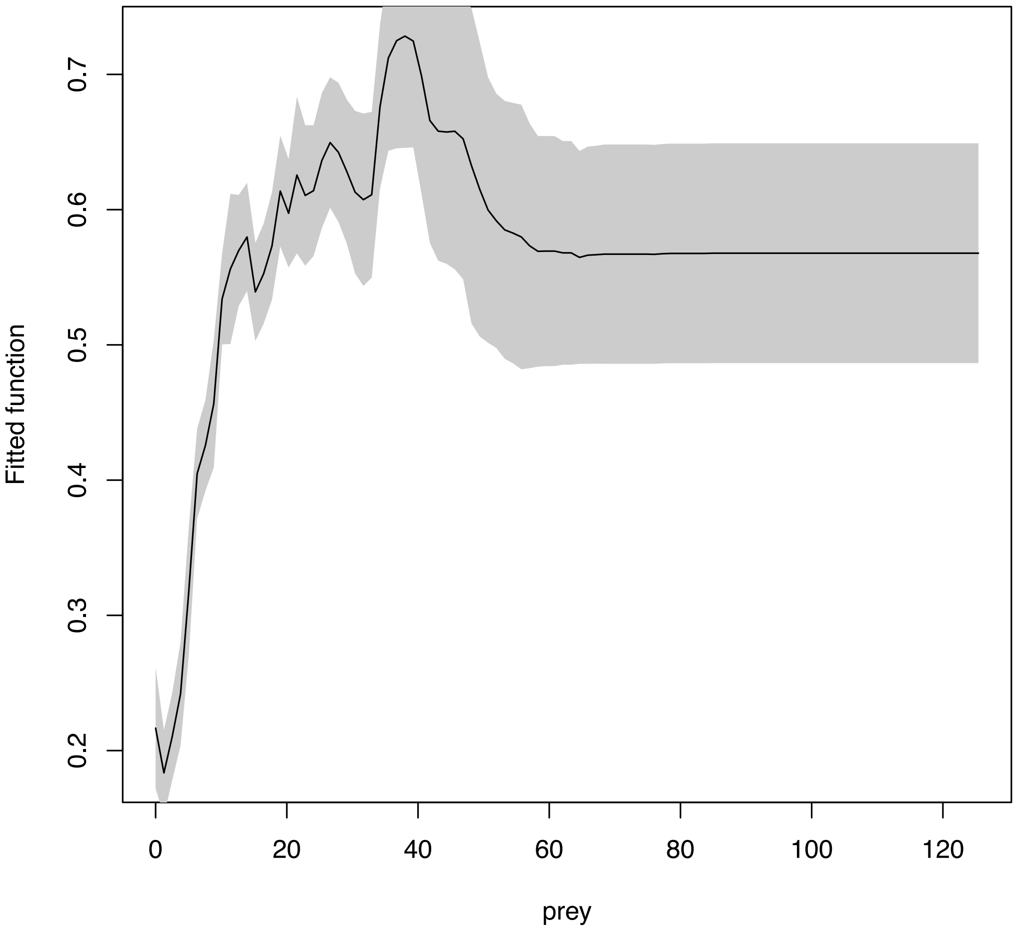


Figure 4.5. Model 2 (with prey) partial dependence plot of *roi* with prey. Y-axis is fitted values for *roi* biomass (g m^2). Grey shaded area shows the 95% confidence interval of the model predictions

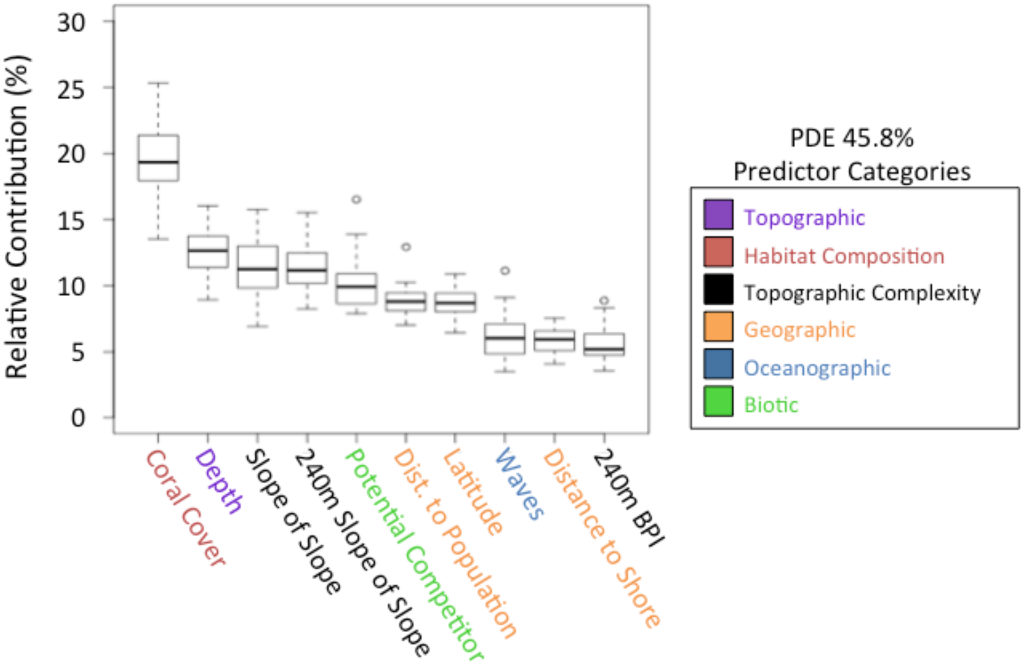


Figure 4.6. Model 3 Boxplot of anthropogenic, and biotic (potential competitor) predictor variables (mean ± SE) that determine *roi* distributions in the MHI. Abbreviations are shown in Table 4.1. Open circles represent outlier observations. Color illustrates the predictor categories

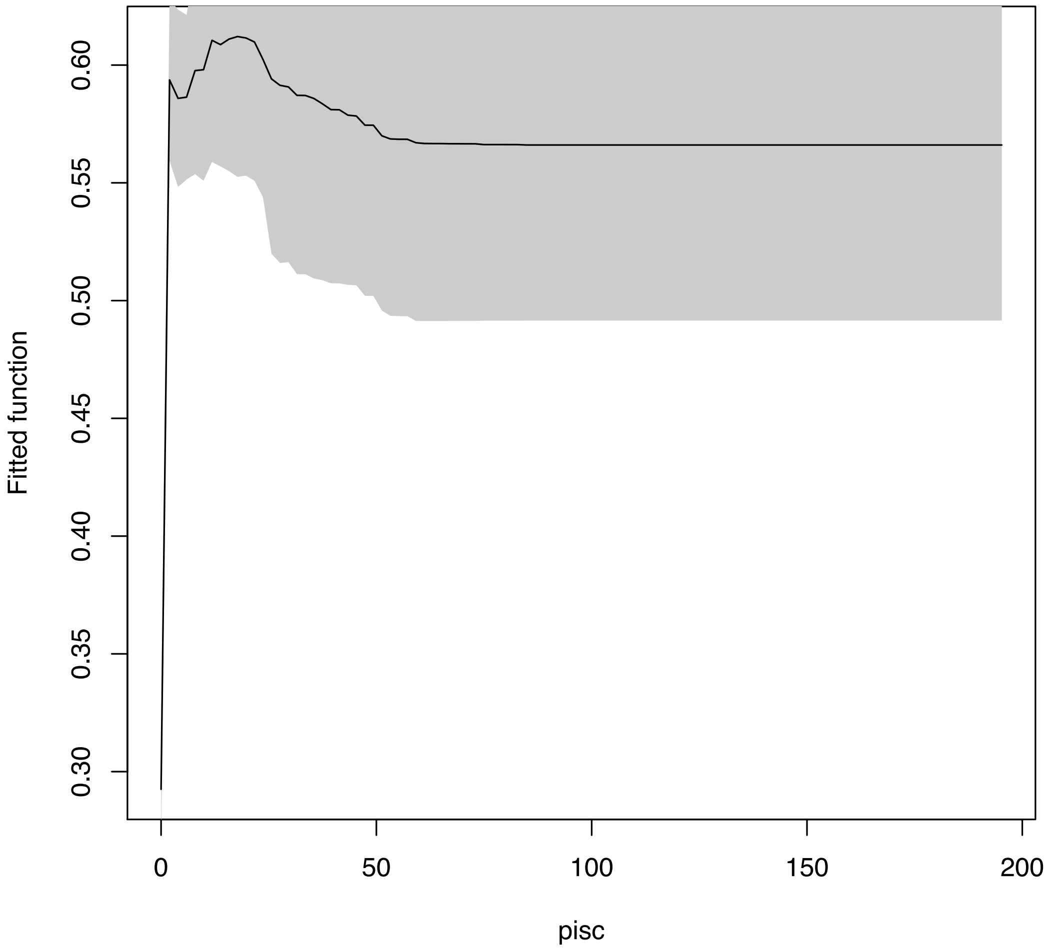


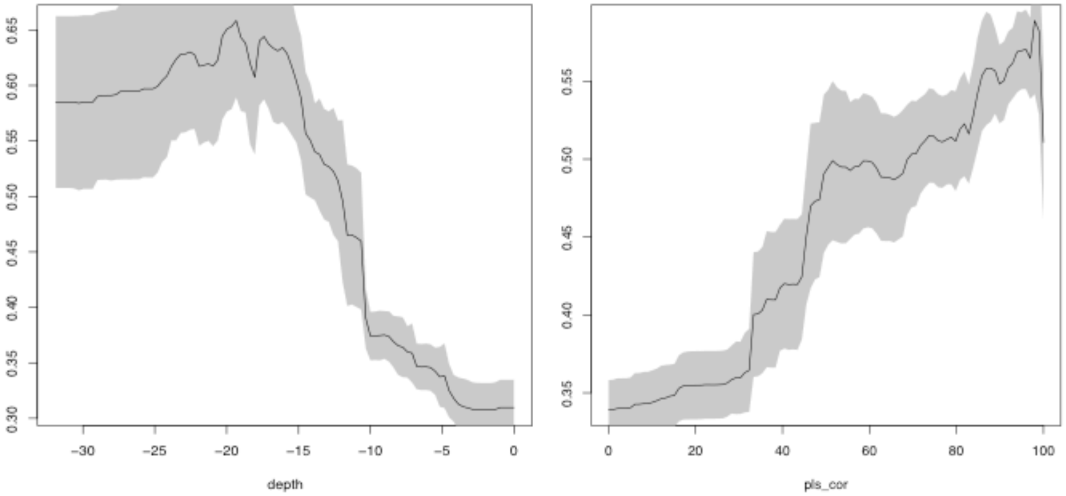
Figure 4.7. Model 3 (with potential competitors) partial dependence plot of *roi* with piscivores. Y-axis is fitted values for *roi* biomass (g m^2), grey shaded area shows the 95% confidence interval of the model predictions

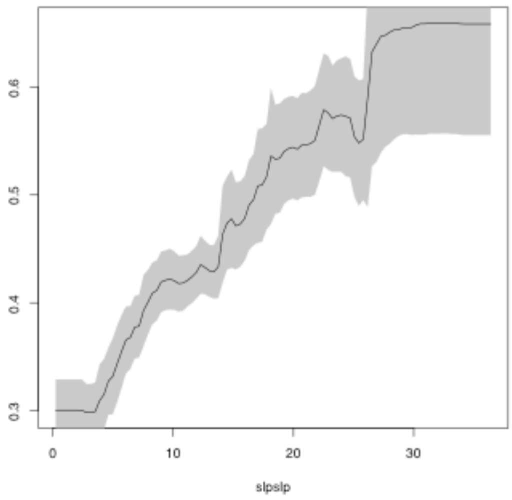
TABLES

Table 4.1. Table1. Simplified predictor data set with descriptions for BRT modeling of *roi* distributions in the MHI. [1.] Indicates community scale, all others are at the seascape scale. B=Biotic, C=Complexity, H=Heterogeneity

Name	**Abbrv**	**Units**	**Category**	**Measure**	**Description**
Prey biomass	prey	g/m^2	Biotic	B[1]	Biomass of prey (<15 cm TL)
Piscivore biomass	pisc	g/m^2	Biotic	B[1]	Biomass of piscivores (trophic level >4)
Sum human population within 15km	dist2pop	Number of people	Geographic	NA	Sum of human population in a 15 km neighborhood
Distance to shore	dist2shore	Meters	Geographic	NA	Straight line distance to the shoreline
Latitude	lat	Meters	Geographic	NA	Latitude at model grid cell centroid
Edge density of coral	ed_cor	m/hectare	Habitat composition	C	Seascape configuration - amount of edge present
CCA cover	pls_cca	Percent	Habitat composition	C	Seascape composition
Coral cover	pls_cor	Percent	Habitat composition	C	Seascape composition
Macro algae cover	pls_mac	Percent	Habitat composition	C	Seascape composition
Soft bottom cover	pls_sof	Percent	Habitat composition	C	Seascape composition
Turf cover	pls_tur	Percent	Habitat composition	C	Seascape composition
Proximity index mean	pro_mn	Untless	Habitat composition	H	Seascape composition
Shannon diversity index	shdi	Untless	Habitat composition	H	Richness and evenness of habitat-forming species
Wave power	wav_Pmn	Kilowatts/ meter	Oceanographic	NA	Wave height x wave period
Aspect standard deviation	asp_sd	Degree	Topographic	C	Max rate of change in depth
Bathymetry	depth	Meters	Topographic	NA	Seafloor depth
Bathymetric position index	bpi	Meters	Topographic	C	Location relative to surrounding area
Bathymetric position index at the 240 m scale	bpi_240	Meters	Topographic	C	Location relative to surrounding area
Cosine aspect	cosasp	Untless	Topographic	C	Max rate of change in depth
Planar curvature	plcurv	Radians	Topographic	C	Seafloor curvature - converge or diverge over the curve
Profile curvature	prcurv	Radians	Topographic	C	Seafloor curvature - accelerate or decelerate over the curve
Sine aspect	sinasp	Untless	Topographic	C	Max rate of change in depth
Slope of slope	slpslp	Degree	Topographic	C	Max rate of change in seafloor slope
Slope of slope at the 240 m scale	slpslp_240	Degree	Topographic	C	Max rate of change in seafloor slope

SUPPLEMENTARY INFORMATION

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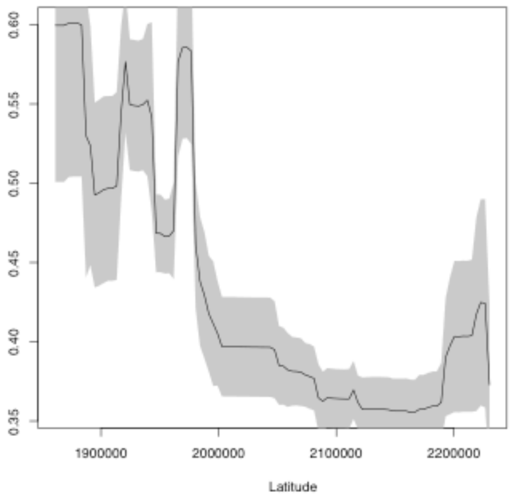
slpslp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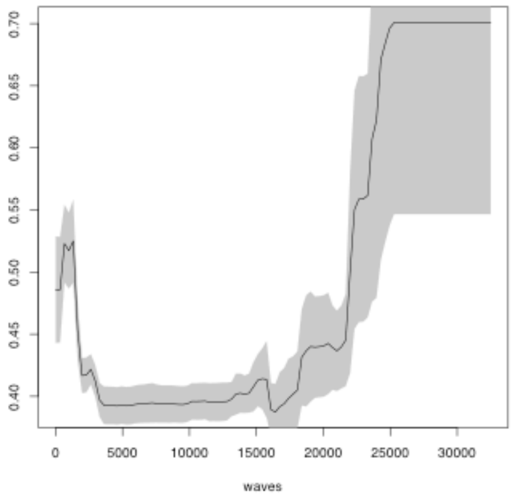
Latitude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10000
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20000
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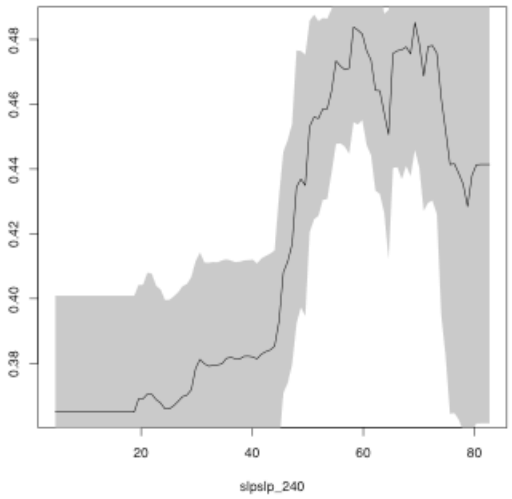
waves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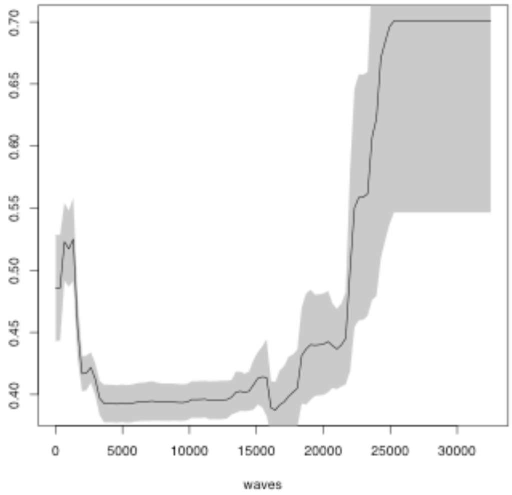
40
60
80
slpslp_240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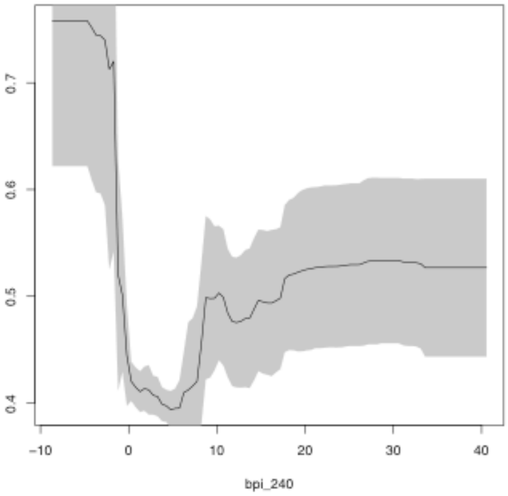
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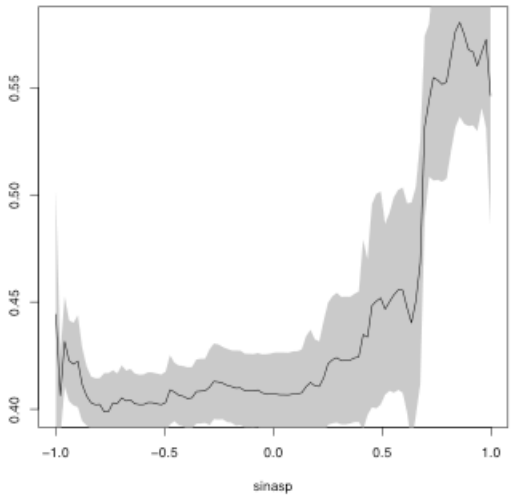
bpi_240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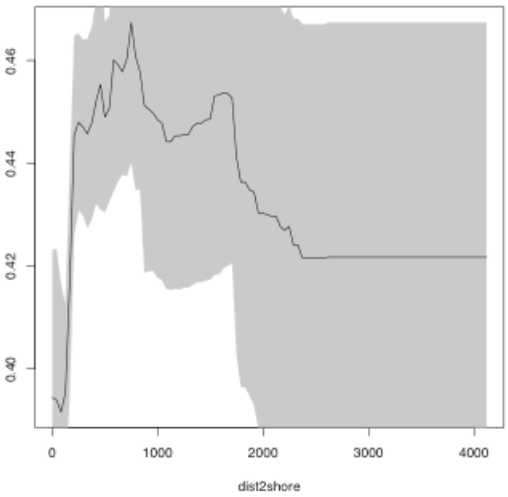
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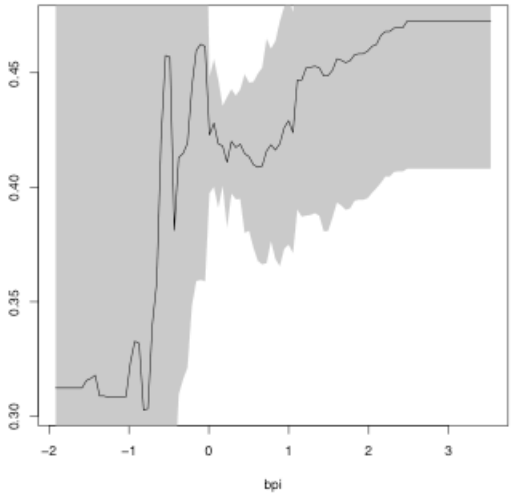
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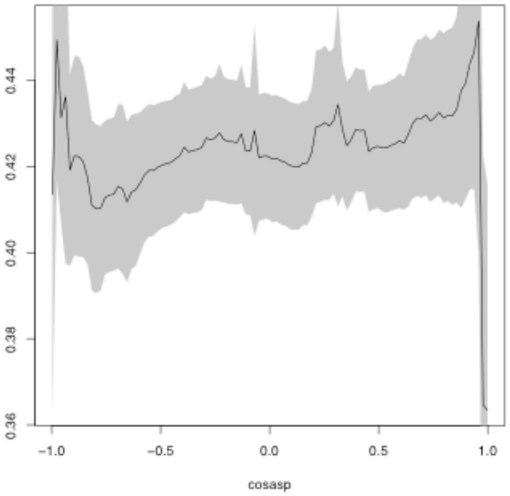
3
bpi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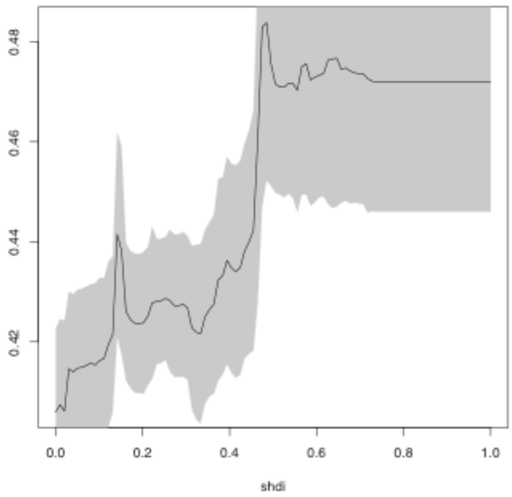
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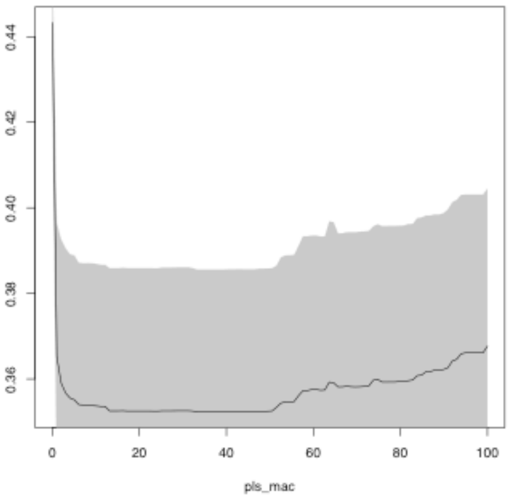
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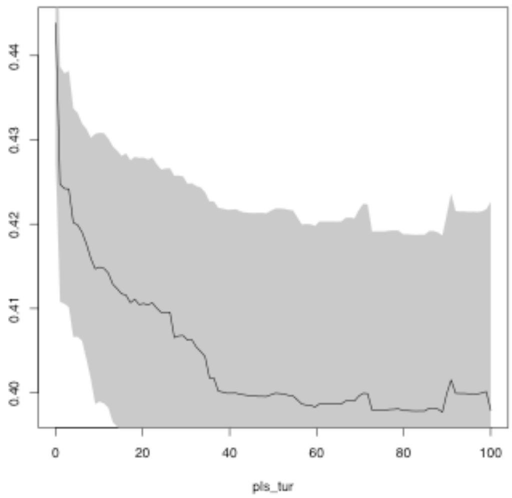
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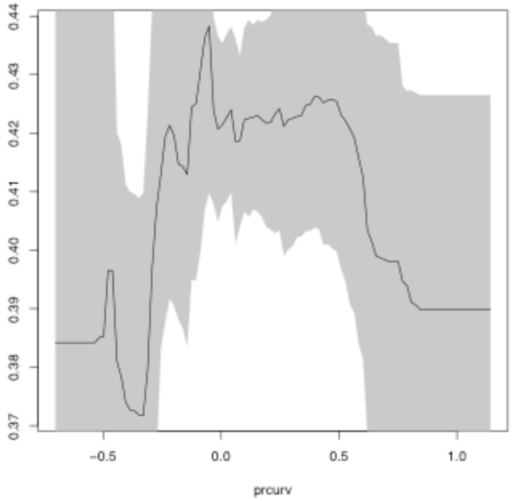
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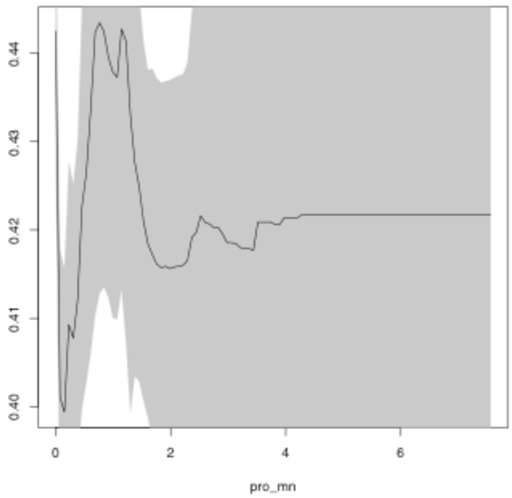
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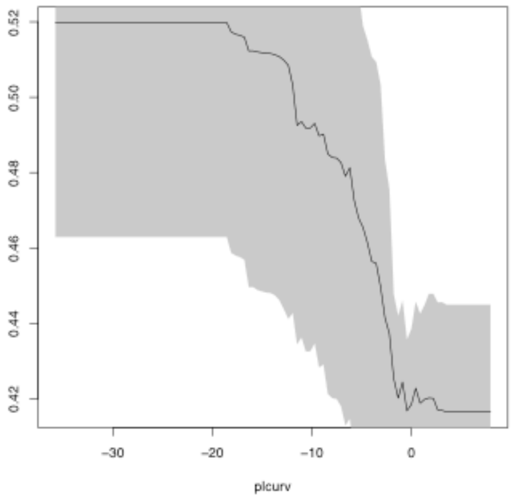
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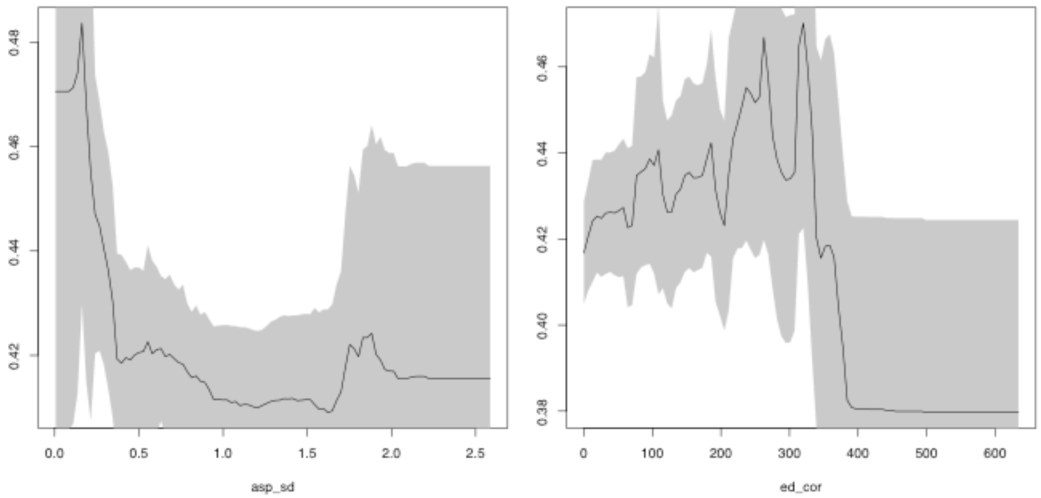

Figure SI 4.1 Model 1 (human and environment) Partial Dependence plots. Abbreviations are as in Table 1. Y-axes are fitted values for roi biomass (g/m^2)

Table SI. 4.1. List of compiled reef fish survey datasets including source, geographic coverage, number of transects, and years

Program	Geographic coverage	# Transect	Year range
FERL	Kāne‘ohe Bay, Oahu	180	2012-2013
FERL	Pūpūkea, O‘ahu	80	2010
FERL	Lana‘i	74	2012
FERL & TNC	Ka‘ūpūlehu-Kiholo, Hawai‘i	299	2012
FERL & NPS	Hanalei, Kaua‘i	120	1992-2012
FHUS (NOAA Biogeography)	Hanauma Bay, Pūpūkea, Honolua, Kealakekua	1,006	2002-2008
NOAA CRED	NWHI and MHI	6,585	2000-2013
NWHI RAMP	NWHI	120	2005
DAR - Kona	West Hawai‘i	8,138	1999-2012
DAR - Oahu	O‘ahu	462	2007-2012
DAR - Maui	Maui	1,640	2000-2012
CRAMP	O‘ahu, Maui, Kaua‘i	380	1998-2012
NPS	Kalaupapa, Moloka‘i and Hawai‘i	501	2004-2012
TNC	Maui, Hawai‘i, O‘ahu	452	2008-2012
TNC	Kaho‘olawe	42	2009
FERL	Mo‘omomi, Moloka‘i	6	2000
FERL	La‘au, Moloka‘i	18	2005
FERL	Lāwa‘i, Kaua‘i	17	2007
FERL	Hā‘ena, Kaua‘i	55	2013-2014
DAR & CRED	Kahekili, Maui	811	2008-2013

Acronyms: FERL - Fisheries Ecology Research Lab, University of Hawai‘i; TNC - The Nature Conservancy Hawai‘i Marine Program; NPS - National Park Service; FHUS - Fish Habitat Utilization Study, NOAA Biogeography Program; CRED - Coral Reef Ecosystem Division, NOAA Pacific Islands Fishery Science Center; DAR - Division of Aquatic Resources, State of Hawai‘i; CRAMP - Coral Reef Assessment and Monitoring Program, University of Hawai‘i

Table SI 4.2. Table of environmental predictor variables and descriptions

Metric	**Class**	**Type**	**Description**	**Analytical tool**
Surface aspect	Bathymetry	Aspect	Slope direction	DEM Surface Tools (Jenness 2013)
Depth (mean)	Bathymetry	Depth	Average depth	ArcGIS Spatial Analyst tools (ESRI 2011)
Bathymetric position index (60m, 120m, 240m)	Bathymetry	Seascape context	Relative topographic position of a point based its elevation and the mean elevation within a neighborhood	Benthic Terrain Modeler tool (Wright et al. 2012)
Cosine aspect	Bathymetry	Aspect	Cosine of slope direction (derived from transforming the mean aspect into “northness”)	ArcGIS Spatial Analyst tools (cosine function) (ESRI 2011)
Planar curvature (mean & sd)	Bathymetry	Structure	Second derivative of slope	DEM Surface Tools (Jenness 2013)
Profile curvature (mean)	Bathymetry	Structure	Second derivative of slope	DEM Surface Tools (Jenness 2013)
Rugosity (240m)	Bathymetry	Structure	Surface area to planar area ratio	DEM Surface Tools (Jenness 2013)
Sine aspect	Bathymetry	Aspect	Sine of slope direction (derived from transforming the mean aspect into “eastness”)	ArcGIS Spatial Analyst tools (sine function) (ESRI 2011)
Slope (60m, 240m)	Bathymetry	Slope	Maximum rate of change from a cell to its neighbors	ArcGIS Spatial Analyst tools (ESRI 2011)
Slope of slope	Bathymetry	Structure	Second derivative of slope	ArcGIS Spatial Analyst tools (ESRI 2011)
Percent of landscape	Habitat composition	Class Area-Edge	Percent of 60m "landscape" made up of each cover type	Exhaustive sampling using a 60m radius moving window analysis in Fragstats v4.2
Edge density	Habitat composition	Class Area-Edge	Edge length of each cover type divided by total landscape area	Exhaustive sampling using a 60m radius moving window analysis in Fragstats v4.2
Patch shape index (mean)	Habitat composition	Class Shape	A measure of cover type patch shape complexity	Exhaustive sampling using a 60m radius moving window analysis in Fragstats v4.2
Fractal dimension (mean)	Habitat composition	Landscape Shape	Mean patch complexity at the landscape level	Exhaustive sampling using a 60m radius moving window analysis in Fragstats v4.2
Contiguity index (mean)	Habitat compositi	Landscape Shape	Mean spatial connectedness of patches	Exhaustive sampling using a 60m radius

	on			moving window analysis in Fragstats v4.2
Contiguity index (sd)	Habitat composition	Landscape Shape	Variation in patch spatial connectedness, large contiguous patches result in larger values	Exhaustive sampling using a 60m radius moving window analysis in Fragstats v4.2
Proximity index distribution (mean)	Habitat composition	Landscape Aggregation	Measure of patch isolation	Exhaustive sampling using a 60m radius moving window analysis in Fragstats v4.2
Shannons diversity index	Habitat composition	Landscape Diversity	Diversity of benthic cover types in the landscape	Exhaustive sampling using a 60m radius moving window analysis in Fragstats v4.2
Proximity to human population	Human impacts	Human impacts	Sum human population within 15km radius (Williams et al. 2008)	ArcGIS Spatial Analyst tools (ESRI 2011)
Wave power (mean)	Wave exposure	Wave power	Wave height x wave period (Holthuijsen, 2010) from 500 m resolution SWAN model,Booij *et al.*, 1999.	Matlab
Wave power (sd)	Wave exposure	Wave power	Variation in wave power (Holthuijsen, 2010) from 500 m resolution SWAN model,Booij *et al.*, 1999.	Matlab
Distance to shore	Land based/ human impacts	Distance to shore	Distance to nearest land	ArcGIS Spatial Analyst Euclidean Distance tool (ESRI 2011)
Latitude	Geographic location	north/south	Angular distance north or south on the earths surface	Marine Geospatial Ecology Tools (MGET, http://mgel.env.duke.edu/mget)
Longitude	Geographic location	east/west	Angular distance east or west on the earths surface	Marine Geospatial Ecology Tools (MGET, http://mgel.env.duke.edu/mget)

CHAPTER V

SUMMARY

The purpose of this dissertation was to evaluate the impact of introduced *roi* (*Cephalpholus argus*) on the native reef communities of Hawaiʻi. Because a determination of the invasiveness of species and the invasability of ecosystems is sensitive to the extent and resolution of inquiry, this ʻinvasion paradox' can best be understood by tracing patterns and processes across scales. Therefore, I conducted studies of *roi* in Hawaiʻi at three levels of organization: 1) field observations at the population level; 2) field manipulative experiments at the community level; and 3) species distribution modeling at the seascape level. I traced salient factors of *roi* invasiveness and community invasability across the three scales, and related these to the human social system, as the *roi* introduction effects, and is affected by human communities.

Chapter 2 (population): *What are the natural and fishing mortality rates of roi populations in Hawaiʻi, and how effective are our methods to assess and control their numbers?*

- This research focused on the feasibility of removing *roi* as a management tool for Hawaiian coral reef ecosystem restoration. Estimates of total mortality were low (0.12 to 0.14), and fishing mortality ranged from negligible to 8.0% yr−1 in west Hawaiʻi. *Roi* movement was monitored through a mark and re-capture program. Tagged individuals traveled 50 to 150 m from the periphery toward the center of the removal area (1 *roi* every 1 to 2 mo). This study provided evidence for effective roi population control through spearfishing methods at the local (1.3 ha) patch-reef scale.

Chapter 3 (community): *What are the community-level effects of roi on native reef fish populations at the local scale?*

- This study experimentally assessed the effects of roi on reef fish populations through a long-term (5.5 yr) predator removal experiment. Increases in the density of small (<15 cm TL) prey-sized fish were observed 18 months after roi removal. However, those effects did not translate into sustained increases in prey over time. While increases in potential competitors, including wrasses (Family Labridae), especially the piscivore ringtail wrasse *Oxycheilinus unifasciatus*, were observed on roi-free reefs, the fish assemblage did not diverge substantially in composition. Native reef fish appear to resist the potential negative impacts of predation by roi. Some fish families reach a refuge in size from predation by roi. Management to protect intact fish assemblage size-structure could serve to bolster reef fish resistance to invading species. In considering the many threats facing Hawaiian reefs, and the many possible solutions, roi removal alone will not likely replenish native fishery resources.

Chapter 4 (seascape): *Which environmental and anthropogenic factors predict the distributions of roi and does environmental heterogeneity play a role? Do biotic interactions (density of potential competitors or density of prey) play a role in the distribution of roi, and what is the relationship between roi abundance and the densities of native species across the MHI?*

- Seascape-level environmental predictors were the most important factors in determining *roi* distributions (depth, habitat complexity, and coral cover). Measures of increased ecological opportunity, defined as a diversity of accessible resources as a result of environmental heterogeneity and habitat complexity, were important predictors of *roi* densities. Anthropogenic factors were important, but ranked last in percent deviance explained by the final model. Biotic interactions were also important predictors, explaining ~ 10 % and ~ 19 % of the deviance by piscivores and prey, respectively. A negative relationship between *roi* and native fishes at intermediate densities was found, and could indicate biotic resistance by native species. Alternatively, intraspecific competition by *roi* defending territories against other *roi* could explain the negative

> relationship observed at intermediate densities. If territory space limits *roi* densities, but not native species at intermediate densities, we would expect to see the negative relationship noted above. Experiments are needed to decipher between the relative roles of inter- and intraspecific competition if either or both are indeed important.

We return to the final question posed in the Dissertation Introduction. Most broadly, I asked: *How can we use insights from invasion ecology to enhance adaptive capacity in the face of global change?* Given that the impacts of the *roi* introduction in Hawaii depend upon the scale of study, the overall outcome lies in how we as an ocean community choose to respond. The social response (fishers grass-roots introduced species tournaments) to the roi introduction could be leveraged to reinforce conservation behaviors and environmental stewardship more broadly, and thus enhance social-ecological adaptive capacity in an ever-changing world.

SYNTHESIS: **Social and ecological dimensions of roi in Hawai‘i; an approach for leveraging community participation in science and management**

While it is widely recognized that human activities substantially impact the health of coral reefs through pollution, habitat modification, and species introductions (Knowlton 2001; Jackson et al 2001), there is also considerable evidence for the ability of human communities to successfully self-organize to address environmental problems and maintain flows of benefits from ecosystems (Ostrom 2009). Community-based management (CBM) is recognized as a viable solution to environmental degradation from local threats such as land-based pollution, overfishing, and invasive species, particularly in island ecosystems with long histories of community management (Johannes 1992, Cinner et al. 2009). Research on historical human-environmental relationships (Kittinger et al. 2011, McClenachan and Kittinger 2012), cultural knowledge systems and practices (Johannes 1992, Poepoe et al. 2007, Friedlander et al. 2013) and comparative studies of community attributes (Basurto 2008, Cinner 2009b) show that under certain scenarios, human behavior patterns and resource use intensity levels can constitute sustainable interactions with ecosystems rather than causing degradation and decline (McClenachan and Kittinger 2012). In order to understand and support ‘successful’ ecosystem-based co-management initiatives, there is a need to identify the key social and ecological factors associated with sustainable resource use (Ostrom 2009).

To address this gap, studies of ecosystem change have begun to incorporate research that considers the effects of human dimensions. This area of research is characterized as ‘social-ecological systems’ (SES) research, because it focuses on the linkage between human and environmental systems and the sustainability of these interactions. Within the past few decades, SES frameworks have been advanced in a general form (Turner et al. 2003, Redman et al. 2004, Ostrom 2009) and for coral reef SES in particular (Basurto 2008, Kittinger et al. 2012, Cinner and Kittinger 2015). This SES perspective, because of its focus on adaptability to change, is an instructive lens through which to view the dynamics of a marine invasive species, and their management in Hawaiʻi.

The *roi* introduction to Hawaiʻi is novel from a Social-Ecological Systems (SES) standpoint because of the unique sociocultural legacies that have developed in the Hawaiian Islands. Often, traditional resource management of islands systems reflects a reciprocal relationship between the environment and human society (Johannes 1992). Social-ecological reciprocity is linked by environmental feedbacks to social systems (e.g., social perceptions and institutions), as well as societal feedbacks (e.g., actions and policies from human institutions) to ecosystems. The sociocultural traditions for reef resource management that have developed in Hawaiʻi may be driven by the island-specific awareness of resource limitation (Kittinger 2012). However, in large-scale and globalized systems, the relationship between environmental resource limitation and the reciprocal institutional response from society may become decoupled (Cinner et al. 2009).

Studies from the fields of environmental psychology (Lewicka 2011) and sociology (Giddens 1984, Bandura 1991) have shown that conservation action is linked to the sense of human agency, the sense that individuals are co-creators and not objects of their reality. Social cognitive theory (Bandura 1989) states that agency and self-efficacy (people's beliefs in their abilities to produce effects) is what makes individuals feel responsible to the larger social-ecological system. This theory predicts that if humans do not perceive that they make a difference, if they do not detect reciprocity (feedbacks) between levels of the social system (i.e. government and institutions), then they are less likely to feel political responsibility. Likewise, if people do not detect reciprocity between human action and environmental feedbacks, they are less likely to engage in conservation activities.

Ocean stewardship behavior (and by extension, fisheries rule compliance) can be built through social-network learning. A recent study of Hawaiʻi long-line fishers showed that individual fishing behaviors (e.g. employing methods to avoid by-catch) were linked with the social-network in which the fisher was associated, not with other factors such as ethnicity, indicating that fishing behavior can be shaped through social learning (Barnes-Mauthe et al. 2013). Social norms can evolve rapidly through learning (Ehrlich and Levin 2005) and the social cohesion reinforced at invasive species tournaments might represent such an opportunity for the cultural evolution of sustainable resource management.

Hawaiʻi invasive species tournament participants might form a social network that collaboratively manages the common pool fisheries resource in an ecological dimension by shifting targets away from heavily exploited species, and in a social dimension by raising awareness to modify individual-based fishing behavior to ocean stewardship behavior. Roi fishers could represent a shift in the conventional SES framework, from a top-down to bottom-up process regulating fishing control rules (Tissot et al. 2009, Friedlander et al. 2013, Ayers and Kittinger 2015). This bottom-up approach to fisheries management would reverse the conventional social-systems framework whereby fishers participate in setting the conditions and control rules for successful CBM, demonstrating individual agency and efficacy, in a tightly linked reciprocal relationship among social and ecological sub-systems. Fishing tournaments present an opportunity for social learning, and adaptive co-management could function as a selective agent, reinforcing conservation ethic and norms. It is imperative to connect scientists, managers, and fishers to achieve this goal, and one step in this direction is to support fisher's environmental stewardship (invasive species tournament) initiatives through a fisheries assessment.

In this synthesis, I frame my dissertation in the context of linked social-ecological systems research. The dissertation's ecological results presented herein, can be arranged into a social-ecological systems framework, thus identifying the linkages that occur between systems, and the pertinent questions arising from the interaction (Figure 5.1).

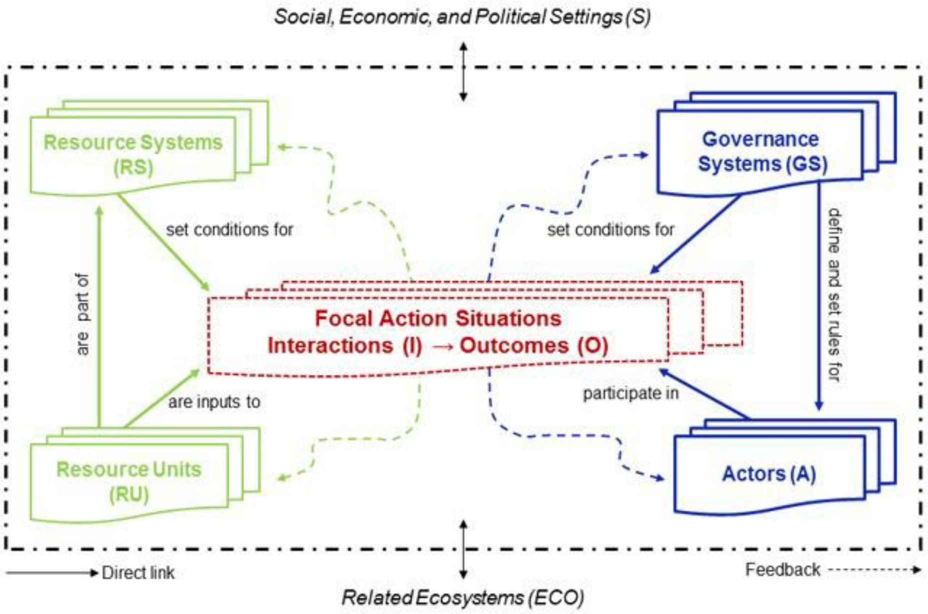

Figure 5.1. Social-Ecological Systems Framework revised from McGinnis and Ostrom (2013). In my study, the Focal Action Situation is invasive species management. On the ecological side (in green) the resource unit is the introduced *roi* in relation to native reef fish populations, which I examine in Chapter II. The resource systems are the coral reef biophysical regimes across the archipelago, which I examine in Chapter IV. On the social side (in blue) are the actors (fishers) who are participating in management and resource use. I discuss the linkages and feedbacks between these activities in my dissertation synthesis (Chapter V).

Supporting fishers who organize to control *roi* populations: a fisheries assessment

Engaging with introduced species tournaments to collect and share fisheries data, can serve to build the relationships between scientists, managers, and fishers. This dissertation is meant to develop knowledge, and through the process develop relationships, thereby laying the groundwork for social-ecological research of introduced species management. This synthesis ties the ecological research on an introduced marine predatory grouper in Hawaiʻi, to the wider goals of supporting coral reef ecosystem and fisheries management, and fostering resilient social-ecological systems into the future.

Returning to the panarchy metaphor and the adaptive cycle (Figure 1.1 and 1.2), I argue that the novel element of invasive species disturbance (release), and the social norms that are evolving through tournament events as a response to the introductions (*r* phase), is an opportunity for collaborative management to encourage and select for ocean stewardship behavior (*K* phase). Therefore, the social response to ecosystem change is an opportunity to organize sustainable behaviors, and enhance social-ecological adaptive capacity.

Summary and synthesis across the studies:

We found that with low population mortality rates, introduced *roi* has the potential to be an effective invader. Yet, over a long-term predator removal experiment, *roi* had no effect on the abundance of their prey. An increase in a potentially competing piscivore was found, but no overall shift in the reef fish community assemblage resulted from experimental *roi* removals. Therefore, predation by *roi* is likely to be a compensatory rather than an additive process, as *roi* apparently consume the ‘doomed surplus’ of native prey-sized fishes. This result indicates that larger processes such as recruitment pulses, possibly swamp predator consumptive effects at the local scale. Likewise, in the seascape context, *roi* distributions were driven by environmental variables such as habitat complexity. At intermediate densities, populations of *roi* declined in relation to increasing densities of native fish species. This pattern points to some biotic limiting factor that limits *roi* populations, and larger scale experiments are needed to explain the causative mechanism. At the level of the coupled human-natural system, *roi* tournaments have engaged community member across the state, not only with the intention of culling *roi* populations, but also to raise awareness about ocean conservation issues more broadly. Tournaments shift fishing targets from exploited species directly to the invader. They also have potential indirect effects, operating at the scale of distal drivers, where socially learned attitudes and perceptions shape human behavior towards sustainable interactions with the sea. In sum, a potentially effective invader minimally impacted the native reef fish assemblage, and showed signs of population limitation at the seascape scale. In the broadest sense, this introduced species has inspired community-based management of ocean resources in Hawaiʻi. Thus, the introduction of *roi* presents an opportunity to engage across sectors and strengthen collaborative ocean management for a sustainable and thriving future.

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