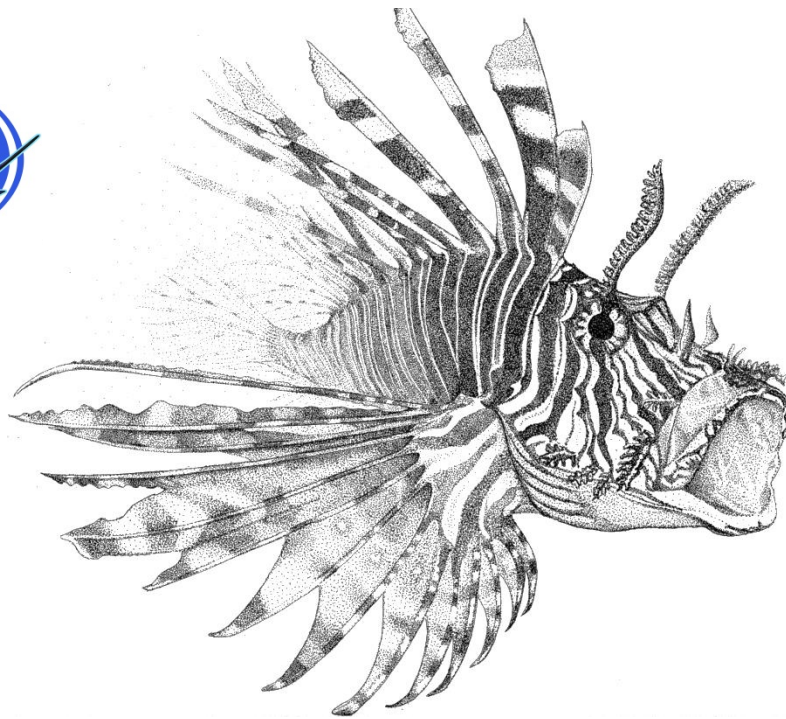


Modeling Lionfish Management Strategies on the West Florida Shelf



UF | IFAS
UNIVERSITY of FLORIDA

Workshop Summary and Results
July 2015
University of Florida

Acknowledgments

We want to thank our sponsors for funding this workshop, which included the Florida Fish and Wildlife Conservation Commission, the Guy Harvey Ocean Foundation, the National Marine Fisheries Service Recruiting, Training, and Research Program, and Florida Sea Grant. We also thank the collaborators from REEF, The Sarasota Lionfish Derby, Keys Marine Lab, the FWC lab in Marathon, Florida, and the staff at Lake Wauberg in Gainesville. Having their collaboration gave the students the chance to interact with the public and share their results, as well as an appreciation of lionfish control efforts in the region. We thank Ed Camp for help with graphic design, and Keys Marine Lab and their fantastic staff for hosting our stay and getting our students in the field and snorkeling on reefs. Our whole team would also like to thank Mendy Allen for her logistical support and guidance with all travel, scheduling, purchasing, and tireless support of all activities. Without her efforts, this workshop would not have been possible.

Workshop Participants

The Students: Samantha Binion (North Carolina State University), Alex Bogdanoff (North Carolina State University), Kristen Dahl (University of South Alabama), Jennifer Granneman (University of South Florida), Holden Harris (Guana Tolomato Matanzas National Estuarine Research Reserve), John Mohan (University of Texas), Merrill Rudd (University of Washington), MaryKate Swenarton (University of North Florida)

Lead Instructors: Dr. Mike Allen (University of Florida), Dr. Rob Ahrens (University of Florida), Dr. David Chagaris (Florida FWC), Dr. James Morris (NOAA National Ocean Service), and Dr. William Patterson (University of South Alabama),

Contributors: Lad Akins (REEF), Leroy Creswell (Florida Sea Grant), Meaghan Faletti and John Hunt (Florida FWC), Stephanie Green (Oregon State University), Elizabeth Mohammed (Caribbean Region Fisheries Mechanism), Sherry Larkin and Diego Valderrama (University of Florida).

Suggested Citation:

Chagaris, D., S. Binion, A. Bodanoff, K. Dahl, J. Granneman, H. Harris, J. Mohan, M. Rudd, M. Swenarton, R. Ahrens, M. Allen, J. Morris, and W. Patterson. 2015. Modeling lionfish management strategies on the West Florida Shelf: workshop summary and results. University of Florida, Gainesville. 31pp.

Table of Contents

Workshop Activities and Objectives	4
Executive Summary	5
Introduction	7
Methods	8
Model description	8
Ecosim scenarios	10
<i>A. Future reef fish management strategies</i>	10
<i>B. Retrospective impacts of fishing</i>	11
Results	12
Lionfish biomass	12
Prey species biomass	12
Fishery species biomass	13
Retrospective impacts of fishing pressure	14
Discussion and Conclusions	15
Data and modeling needs	16
Tables	19
Figures	23
References	30

Workshop Activities and Objectives

The purpose of this workshop was to gain a better understanding of the impacts invasive lionfish (*Pterois volitans/miles*) could have on native reef fish communities in the eastern Gulf of Mexico and to evaluate management policies that mitigate those impacts. Collaborators on the project included scientists from the University of Florida, the University of South Alabama, the National Oceanic and Atmospheric Association (NOAA), Oregon State University, the Florida Fish and Wildlife Conservation Commission (FWC), the Reef Environmental Education Foundation (REEF) the Guy Harvey Ocean Foundation, and Florida Sea Grant. This two-week workshop consisted of one week in Gainesville, Florida (July 7-11, 2015) and one week at the Keys Marine Laboratory in Long Key, Florida (July 13-17, 2015). Eight graduate students from seven universities were selected for participation. The team worked with an Ecopath with Ecosim model to evaluate how reef fish management strategies and lionfish removal efforts would be expected to influence lionfish impacts on the West Florida Shelf ecosystem. The students attended and assisted with the Sarasota Lionfish Derby on July 12, 2015, and they presented their results to the public at the REEF Open House in Key Largo, Florida on July 14, 2015. This white paper summarizes the key findings from the workshop and will be followed by a peer-reviewed journal article, as well as future collaborations.

Executive Summary

Invasion of the South Atlantic, Caribbean and Gulf of Mexico by lionfish (*Pterois volitans/miles*) threatens to alter reef food webs and reduce the abundance of important fish stocks that support fisheries. Efforts to mitigate lionfish impacts have included targeted removal via spearfishing, but it is unclear the degree to which they are effective. Further, no previous studies have explored how changes in management of native reef fish (e.g., reductions in fishing mortality) could potentially influence lionfish biomass and impacts to food webs. In this workshop, we employed an existing trophic dynamic ecosystem model for the West Florida Shelf marine ecosystem (WFS, Chagaris et al. 2015) to explore how lionfish harvest and reef fish management strategies could mitigate impacts of lionfish on reef ecosystems.

Lionfish data inputs to the Ecopath with Ecosim model were obtained from the literature and from recent work in the region. The model included two lionfish age groups (juvenile <6 months and adult). Diet composition of lionfish prey was obtained from published sources and from recently collected data in the Gulf of Mexico. Consumption, growth and maturity parameters for lionfish were obtained from studies of lionfish from the southeast United States. To simulate the lionfish invasion, lionfish were initially set up with low biomass and high fishing mortality rates to keep biomass very low (status quo scenario), and then fishing mortality was reduced to simulate increasing lionfish biomass through time. We projected the model for 30 years after the invasion began in 2010, and we evaluated the relative change in reef fish biomass groups in response to: 1) changes in lionfish harvest rates, and 2) fishing mortality on reef fish stocks.

The simulations suggested that both lionfish removal efforts and reef fish management strategies can partially mitigate impacts of lionfish on reef ecosystems. As lionfish harvest rates increased, relative biomass of reef carnivores, reef omnivores, and shrimp were expected to increase. Similarly, we found evidence of modest increases in biomass of important fishery species (amberjack *Seriola dumerili*, red snapper *Lutjanus campechanus*, red grouper *Epinephelus morio*, and gag grouper *Mycteroperca microlepis*) as lionfish harvest rates increased, with up to 25% biomass improvements for red snapper as lionfish fishing mortality rates increased from zero to 0.6. Vermilion snapper *Rhomboplites aurorubens*, were an important lionfish prey item and were severely affected by the invasion. However, at very high lionfish biomass an increase in vermilion snapper biomass emerged as their predators and competitors declined due to lionfish predation and competition.

The model suggested that fishing mortality rates on reef fish species will influence terminal lionfish biomass and the vulnerability of reef ecosystems to invasion. Scenarios with low reef fish harvest rates (F values of 0.25 current levels) predicted substantially lower future biomass of lionfish (biomass increases of 28 times the 2011 estimated lionfish biomass) compared to current levels of fishing (lionfish biomass increases of 92 times the 2011 biomass values). Thus, the model predicted large lionfish biomass increases under all scenarios over the next 30 years, but management actions such as lionfish harvest and reduced fishing mortality on native predators can at least partially mitigate those increases.

Our EwE model revealed complex trophic interactions that have implications for management of reef fish stocks and mitigation of the impacts caused by invasive lionfish. The effects of lionfish predation were strongest on lionfish prey, including but not limited to reef carnivores, reef omnivores, shrimp, and vermilion snapper. The EwE model served as a valuable tool to simultaneously evaluate these policies, and showed that lionfish impacts on the system could be at least partially mitigated by a combination of reef fish management and directed lionfish removal efforts. Future work in this area should include field collections to reduce data gaps, and spatial modeling efforts to explore habitat-specific invasion dynamics and the localized effects of lionfish control efforts.

Introduction

The introduction of non-native species has increased with growing global connectivity (Molnar et al. 2008). Non-native species that proliferate in recipient ecosystems are referred to as invasive species, which can inflict a range of ecological effects through direct predation on native biota or competition for food and space. For example, fish invasions have been shown to interrupt reciprocal prey subsidies thus restructure stream and forest food webs (Baxter et al. 2004), and have led to large-scale degradation of critical habitats in marine systems (Kimbrow et al. 2009). Degraded or disturbed ecosystems themselves are more susceptible to invasive species than pristine systems (Stachowicz et al. 1999, Altman and Whitlatch 2007), and one of the more prevalent forms of anthropogenic disturbance on marine ecosystems around the globe is overfishing (Albins and Hixon 2013). Overfishing has the potential to alter food webs and compromise systems' resiliency in the face of other stressors (Frank et al. 2005, Mumby et al. 2006, Daskalov et al. 2007). Lower abundance of predatory fishes via fishing causes lower natural mortality for invasive species, as well as less competition for resources in their invaded range (Albins and Hixon 2013).

Invasive species mitigation is typically labor intensive and expensive, often with limited success (Engeman and Vice 2001). In the United States alone, the cost of damage and control for non-native vertebrates is an estimated \$47 billion each year (Fall et al. 2011). Therefore, developing and evaluating strategies to mitigate the ecological impacts of non-native species in their invaded range is a management priority. Removal efforts and biocontrol are commonly implemented to mitigate the impacts of non-native species, but effects of other management strategies that influence food webs and impacts are not fully considered. Thus, in systems with high complexity and connectivity there is a need to apply integrated, ecosystem-based management that simultaneously evaluates multiple policy options as means to control invasions and mitigate impacts (e.g., direct harvest of invasive species combined with reduced fishing on native predators).

Trophic dynamic models provide a tool to explore a range of management actions, identify data gaps to prioritize future data collection, and reduce uncertainty in estimates of ecological impacts stemming from non-native species. Our research utilized the ecological modelling software Ecopath with Ecosim (EwE), to explore expected changes to ecosystem structure and function resulting from invasive lionfish and to provide recommendations for their control. These tools have recently been used to evaluate the expected impacts of invasive species

in freshwater, marine, and terrestrial systems (e.g., Pine et al. 2007, Arias-González et al. 2011, Langseth et al. 2012). The models can provide strategic advice for developing policy options that meet conservation and utilization goals, and policy choices can be assessed by a variety of system metrics, including biodiversity, benefits to protected species, and economic value of fisheries. In our application, we employed an existing trophic dynamic ecosystem model to estimate impacts of an invasive lionfish (*Pterois volitans/miles*) on the West Florida Shelf marine ecosystem (WFS, Chagaris et al. 2015), and explored potential mitigation of those impacts via different fishery management actions.

Lionfish are native to the Indo-Pacific but recently have become established in the temperate and tropical western Atlantic (Whitfield et al. 2002). Since invading the Gulf of Mexico (GoM) in 2010, lionfish populations have grown exponentially (Dahl and Patterson 2014, Switzer et al. 2015) and their ecological impacts on economically important species, native species diversity, and protected species have the potential to be severe. In response, management agencies are encouraging recreational and commercial fishermen to harvest lionfish in an effort to reduce their population and mitigate ecosystem impacts. While these efforts may be having success at localized scales, they have not thwarted the invasion throughout the larger region. Other possible lionfish control options, such as induced top-down control through management of native predators, have yet to be explored. Our objectives were to: (1) estimate the impacts that lionfish are having on the native reef fish community of the WFS, (2) assess the efficacy of direct lionfish harvest to mitigate those impacts, and (3) evaluate how management strategies for commercially-important reef fish (e.g., groupers and snappers) could be used to control lionfish and reduce impacts to other species/functional groups.

Methods

Model description

We modified the reef-fish based EwE model developed by Chagaris et al. (2015) to include lionfish and estimate their impacts in the WFS ecosystem. The model included 43 fish groups, with commercially important grouper and snapper species modeled as multiple age classes. In total, the model describes 70 biomass pools including fishes, mammals, birds, invertebrates, primary producers, detritus groups, and fishing fleets. The spatial domain extends from the Florida Panhandle south to, but excluding, the Florida Keys, and from shore to the 250-

m isobath, covering an area of approximately 170,000 km² (Figure 1). Additional details on model specifications and input parameterization are described in Chagaris et al. (2015).

Lionfish were added to the model as two age stanzas (0-6 and 6+ months) to capture ontogenetic shifts in diet (Morris and Akins 2009, Munoz et al. 2011, Dahl and Patterson 2014) and vulnerability to removal by spearfishing. Lionfish biomass density estimates from non-reef and natural hard-bottom reef habitats were derived from the SEAMAP trawls on the WFS (Switzer et al. 2015) and an ROV survey of natural reefs in the northern GoM (Dahl and Patterson 2014) (Table 1). Although lionfish density on artificial reefs can be two orders of magnitude higher than on natural reefs (Dahl and Patterson 2014), we only used natural reef estimates because the total footprint of artificial reefs was estimated to be very small (< 0.01% of modeled area). A rugosity grid from the USGS (Robbins et al. 2010, <http://pubs.usgs.gov/ds/477/>) was used to identify “reef” habitat, defined as any area with rugosity greater than 3.5 (Figure 1). Based on this approach, 93% of the shelf was classified as non-reef habitat (i.e. accessible by the SEAMAP trawl) and 7% as reef (surveyed by the ROV study), and habitat-specific lionfish density estimates (B ; mt/km²) were averaged and weighted accordingly for the Ecopath base year 2011. Biomass accumulation rate (BA) was calculated as $(B_{2012}-B_{2011})/B_{2012}$ in order to capture the change in biomass that occurred during the Ecopath base year (i.e., from 2011 to 2012).

Consumption (Q) estimates for lionfish were derived from a bioenergetics study that estimated daily consumption rates (g/g/day) as a function of body mass and temperature under laboratory conditions (Cerino 2015). Using the size structure from the SEAMAP trawl survey, we estimated a population-wide annual consumption rate (Q/B) at optimal temperature of 29.8° C (Table 2) and adjusted it downward to about 60% optimum feeding to account for actual bottom temperatures on the WFS (based model output from a HYCOM oceanographic model of the system). Instantaneous natural mortality of lionfish was estimated with the Lorenzen (1996) function based on body mass. Consumption and mortality parameters were calculated using known size distributions of lionfish from the SEAMAP survey (Switzer et al. 2015). Consumption and mortality were then averaged over the size bins 50-150 mm for juveniles and >150mm for adults, weighted by the biomass in each size bin (Table 2). Growth and maturity parameters (Von-Bertalanffy K , W_{mat}/W_{∞}) were taken from growth studies of lionfish from the southeast United States (Barbour et al. 2011). Preliminary estimates suggest these parameters are comparable on the WFS (Dahl and Patterson unpublished data).

The diet composition of juvenile and adult lionfish was averaged across multiple sources (Table 3 and Table 4) and weighted by the number of stomachs in the study, proximity to WFS, data type (e.g. measurements in volume or mass held more influence than numerical or occurrence studies), and habitat type (reef vs. non-reef). Cannibalism on juvenile lionfish was included in the adult lionfish's diet composition as it has been documented in multiple systems, including the northern Gulf of Mexico using DNA barcoding analysis (Valdez-Moreno et al. 2012, Côté et al. 2013, Dahl and Patterson, unpublished data).

There are several approaches to simulating species invasions with EwE (Langseth et al. 2012). In our model, the lionfish invasion was modeled with Ecopath base lionfish biomass at low levels and an artificial fishery that is set to zero in Ecosim to initiate the invasion. In Ecopath, landings were entered such that fishing mortality (F) was equal to M based on the Lorenzen equation. Thus, production rate (P/B), or total mortality (Z) in Ecopath was set at twice the M in order to maintain natural mortality after fishing was released. This method was chosen because it initializes the model with a realistic starting biomass of lionfish that does not create mass balance issues in Ecopath, allows one to estimate the vulnerability exchange rates, and is relatively simple to implement.

The most sensitive parameters in Ecosim models are the vulnerability parameters (v_{ij}), which define the maximum predation mortality rate ($M2_{ij}$) caused by predator j on prey i , relative to Ecopath base rates that can be exerted on a prey item at high predator biomasses. For our base scenario, we specified vulnerability settings that would cause a maximum predation mortality by lionfish on each of their prey items equal to 50% of each prey items' natural mortality rate (e.g., lionfish predator maximum effectiveness = 50%). Under this configuration, when lionfish reach carrying capacity the maximum instantaneous predation mortality rate on a prey item with $M = 0.8 \text{ y}^{-1}$ would be 0.4 y^{-1} . Sensitivity analyses were conducted to evaluate how the lack of cannibalism or different assumptions about lionfish predator effectiveness (25% or 100% of M) could affect estimates of lionfish productivity and their prey.

Ecosim scenarios

A. Future reef fish management strategies

We explored multiple Ecosim scenarios to investigate how reef fish management strategies and lionfish removal efforts might be expected to influence lionfish and their impacts on reef ecosystems. All scenarios were run for 30 years beginning in 2011. In the first scenario, we established the status quo state, which is a modeled state of the WFS in which the lionfish

invasion did not occur. Because groups are increasing and decreasing in the status quo simulation (due to bioaccumulation and fishing), this scenario was used as a reference to quantify the impacts of the lionfish invasion scenarios. During the status quo simulation, lionfish fishing mortality remained at Ecopath base and the vulnerabilities of their prey were set to 1 in order to suppress the invasion.

Next, a series of scenarios was simulated to evaluate how the combined effects of direct lionfish harvest and current reef fish harvest could mitigate lionfish impacts on the ecosystem. Changes in top predator biomass was achieved by manipulating fishing effort exerted by fleets that target upper trophic level reef fish including recreational private boat, recreational charter boat, recreational head boats, commercial vertical long-line, and commercial bottom long-line fleets. In these scenarios, fishing effort was set to 25, 100, and 200% of current fishing levels to simulate a range of exploitation rates on reef fish and predict lionfish impacts under each scenario. Under each of these settings, we evaluated the impacts of the lionfish invasion on the reef community over a range of lionfish harvest levels. Harvest levels (F) were run in 10% increments as a proportion of natural mortality (M), between 0 to 100% (e.g. $F = 0.1 y^{-1}$ to $F = M = 0.66 y^{-1}$). Lionfish harvest was only applied to the adult lionfish stanza, as the juvenile size class were considered invulnerable to the current, primary method of harvest (i.e., spearfishing).

As a metric of comparison, we refer to the change in biomass (ΔB) expressed as the relative difference between the biomass in the terminal year of each lionfish scenario (2041) and the biomass in the terminal year of the status quo scenario (i.e., very low lionfish biomass). The ΔB for each group was estimated as:

$$\Delta B = (B_{invasion} - B_{status\ quo}) / B_{status\ quo} \quad (1)$$

such that biomass increases from status quo will be expressed as positive and biomass declines from status quo will be negative. Thus, the ΔB values represented a proportional biomass increase or decrease for each group after the invasion.

B. Retrospective impacts of fishing

We explored whether the WFS ecosystem may have been more vulnerable to the lionfish invasion in 2011 because of depleted native reef fish stocks resulting from historically high fishing mortality. To do so, we manipulated the fishing effort of all fleets ten years prior to the lionfish invasion. For the simulated time period 2000 to 2041, effort for all fleets was set to 0.25, 1, and 2 times current efforts to simulate the lionfish invasion under low, moderate (status quo), and high exploitation levels. For the pre-invasion years 2000 to 2010, lionfish were

subjected to a fishing effort high enough to keep their biomass negligible. Starting in year 2011, the lionfish invasion was simulated by removing fishing effort on lionfish. We then compared species biomass over time relative to the initial year to compare impacts of the lionfish invasion under alternative hypothetical exploitation states for the WFS ecosystem.

Results

Lionfish biomass

In all the scenarios tested, changing the levels of lionfish and reef fish harvest resulted in large changes in lionfish biomass (relative to Ecopath base biomass). Relative lionfish biomass was highest with no lionfish harvest in all cases, and decreased as lionfish harvest increased. Adult and juvenile lionfish biomass were predicted to be about 100 times higher than the status quo (suppressed biomass) scenario under no lionfish harvest and current levels of fishing mortality for reef fish (Figure 2b). Relative adult lionfish biomass decreased at a faster rate than relative juvenile lionfish biomass as lionfish harvest rates increased (Figure 2). At the highest lionfish harvest rates tested ($F = M = 0.66 \text{ y}^{-1}$), relative lionfish biomass still increased between 30- and 70-fold (for the lower and higher reef fish harvest rates, respectively), compared to the status quo scenario. Lionfish biomass increased in all three reef fish harvest scenarios (lower, current, and higher), with largest biomass under the scenario with highest reef fish harvest (double current reef fish F) combined with no lionfish harvest (rel B = 117; Figure 2c). Lionfish biomass was lowest under the scenario with lower reef fish harvest ($F = 0.25 \times \text{current}$) and high lionfish harvest ($F = M = 0.66 \text{ y}^{-1}$) (rel B = 34.4; Figure 2a, b). This indicates that lionfish biomass was influenced by both reef fish fishing mortality and by lionfish control efforts.

Prey species biomass

The common prey species of lionfish exhibited varying degrees of response to the lionfish invasion under different levels of reef fish harvest rates and lionfish removals. Due to direct predation by lionfish, biomass of reef omnivores and shrimp decreased when lionfish harvest rates were lower (Figure 3). The relative biomass change for reef omnivores and shrimp was similar across scenarios of reef fish harvest, indicating these functional groups are more greatly impacted by the lionfish invasion than by reef fish management. In contrast, the relative biomass of reef carnivores was more severely impacted by lower levels of reef fish harvest, and remained closer to the status quo at higher levels of reef fish harvest (Figure 3). As lionfish harvest rates increased, relative biomass of reef carnivores, reef omnivores, and shrimp were

expected to increase. Reef carnivores appeared to be influenced more by top-down effects from native reef fishes than from lionfish, as illustrated by increasing biomass with increasing fishing mortality on native predators (Figure 3).

Vermilion snapper displayed contrasting patterns of biomass change compared to the other common prey species of lionfish. At lower reef fish harvest levels, vermilion snapper biomass was higher and, because they are targeted in the reef fish fishery their decline was more pronounced as reef fish harvest rates increased (Figure 3). However, as lionfish harvest rates increased, biomass of vermilion snapper declined, which was an opposite pattern to other prey items. Patterns of vermilion snapper biomass over time contrasted with other prey items under scenarios of varying lionfish harvest rates and the response was more dynamic (Figure 4). For example, when lionfish were at moderate biomass (under $F = M = 0.66 \text{ y}^{-1}$) vermilion snapper relative biomass fell to around 50% of initial biomass after 10 years and remained there for the duration of the simulation. When lionfish were at high biomass ($F = 0$), vermilion snapper declined more rapidly during the first 10 years but then began a gradual increase for the remainder of the simulation. This delayed response occurred because other competitors and predators of vermilion snapper started to be affected by the lionfish invasion after prey resources were foraged down, and those indirect effects become more important than the direct effects of lionfish. Thus, vermilion snapper biomass was influenced by complex interactions of directed harvest on this species as well as depletion of prey and changes in competition that occurred if lionfish biomass was reduced via fishing.

Fishery species biomass

Four species of commercially and recreationally important WFS reef fish (greater amberjack, red snapper, red grouper, and gag grouper) responded marginally to an increasing harvest on lionfish and strongly to direct harvest rates (as expected). Under current reef fish harvest levels, increasing fishing mortality on lionfish yielded increases in a relative biomass of greater amberjack, red snapper, red grouper and gag grouper by 17%, 25%, 13%, and 5% respectively (Figure 5b). These relatively small changes in commercially-important reef fish biomass with increases in lionfish harvest held true across fish harvest rates (Figure 5a-c). Because these commercially-important reef species are primary targets of the commercial and recreational fishing fleets, their biomass exhibited strong declines with increases in fishing mortality regardless of lionfish harvest rates. Reducing reef fish harvest to 25% of current fishing effort resulted in relative biomass gains for all commercially important species examined (Figure

5a). Overall, lionfish harvest was predicted to show only modest improvements in commercially important reef fish biomass (less than 25% biomass increases in all cases).

Projections of lionfish biomass over a 30-year simulation were examined for three different scenarios: worst case, expected, and best case (Figure 6). All scenarios displayed exponential increases in lionfish biomass from the start of the invasion on the WFS in 2011, and reached stable lionfish biomass levels by approximately 2021. Under the worst case scenario, which included high reef fish harvest (2x current levels), no lionfish cannibalism, no lionfish harvest, and high lionfish predator effectiveness (max M_2 by lionfish equal to M of prey), relative lionfish biomass stabilized at 262 times the base biomass estimates from 2010. In contrast, under the best-case scenario, which included low reef fish harvest (25% of current levels), lionfish cannibalism on their juveniles, high lionfish harvest ($F=1.0 \text{ y}^{-1}$, $M=0.66 \text{ y}^{-1}$), and low lionfish predator effectiveness (max M_2 is 25% of prey M), relative lionfish biomass stabilized at 28 times current biomass levels (Figure 6). The expected scenario, which includes current reef fish harvest, lionfish cannibalism on their juveniles, realistic lionfish harvest rates of 3% annual biomass, and medium lionfish predator effectiveness (max M_2 equal to 50% of prey M), lionfish reached an equilibrium biomass of 92x current levels (Figure 6). This would imply that lionfish biomass in the region is expected to increase dramatically under all scenarios, but management actions such as lionfish harvest and reef fish fishing mortality can at least partially mitigate those increases.

Retrospective impacts of fishing pressure

To test whether the WFS ecosystem could have been more resistant to a lionfish invasion if it had experienced lower historical fishing pressure, we adjusted fishing pressure to allow all predator biomasses to rebuild for 10 years prior to the invasion (Figure 7). When fishing fleet effort was set to the status quo level, lionfish biomass increased 182x relative to pre-invasion biomass. Higher and lower rates of fishing fleet effort resulted in relative lionfish biomass increasing or decreasing by 16%, respectively (Figure 7). If fishing pressure on the WFS had been lower prior to 2010, the lionfish invasion would still have occurred, but equilibrium biomass may have been considerably lower than is currently predicted. Thus, high fishing mortality on reef fish likely makes the system more vulnerable to lionfish invasion.

Discussion and Conclusions

Our EwE model revealed complex trophic interactions that have implications for management of reef fish stocks and mitigation of the impacts of the lionfish invasion. The effects of lionfish predation were strongest on lionfish prey, including but not limited to reef carnivores, reef omnivores, shrimp, and vermilion snapper. Increasing lionfish removal efforts improved abundance of most mid-level consumers in the food web, indicating that removal efforts can at least partially mitigate lionfish impacts. Slight increases in lionfish harvest resulted in increases in biomass of adult shrimp, reef carnivores and omnivores. Harvest of lionfish, even at relatively low levels, translated into increases (large ones in some cases) of the biomass of the rest of the community.

We also demonstrated how reducing fishing mortality on recreationally and commercially important reef species would be predicted to result in lower lionfish biomasses. This top-down effect by native predators was observed despite the assumption that lionfish are not preyed upon by other species, thus implying that competition for food with native species is strong. Furthermore, our findings suggest that rebuilding native predator populations may be a viable management option to reduce lionfish biomass and impacts, and that targeted fishery harvest policies on the WFS could potentially decrease lionfish abundances and mitigate impacts of lionfish in the system.

The trophic dynamic model allowed us to propose new hypotheses about complex interactions in the ecosystem. For most taxa that were preyed on by lionfish (e.g. shrimp, reef omnivores), or competed with lionfish (e.g. snappers), increasing lionfish harvest rates resulted in biomass increases. Interestingly, increasing lionfish harvest rates caused decreases in the biomass of vermilion snapper, even though vermilion snapper are an important lionfish prey item. Due to a release of species that prey on vermilion snapper predators and competitors, the model predicted that the net overall impact of lionfish harvesting to be negative on vermilion snapper biomass. Further, because vermilion snapper are also harvested in various fisheries, their abundance was controlled by directed fishing mortality. The observation that increasing lionfish harvest rates may negatively impact other mesopredators in the system, is a counterintuitive finding that has important implications for invasive lionfish management and highlights the need for trophic dynamics models as tool for managing resources in complex ecosystems.

Our model showed that slight increases in lionfish harvest could lead to declines in future lionfish biomass. Recruitment overfishing of lionfish was expected to occur at annual exploitation estimates around 0.3 to 0.6 y^{-1} (Barbour et al. 2011), and our model showed that lionfish population declines could occur at fishing mortality rates in this range. Here, we only simulated harvest impacts on adult lionfish as the juvenile group was structured to be invulnerable to spearfishing. However, harvesting juvenile lionfish through the use of traps or fish aggregation devices (FADs) might also enhance mitigation efforts.

The model showed that disturbance due to fishing in the WFS system likely caused the region to be more vulnerable to invasion. It is possible that historical and current levels of exploitation on the WFS made the system less resistant to the lionfish invasion than if exploitation had been lower. These results are in accordance with our findings that higher fishing mortality for commercially valuable reef species allow lionfish populations to thrive due to complex dynamics, including competition for prey and habitat availability. Similarly, Stachowicz et al. (2002) found that exploited marine fish communities are more vulnerable to disturbances such as non-native species invasions. In the tradeoff between utilization and conservation of marine resources, it is important to consider how exploitation affects the state of the current fish community, as well as the potential for future changes.

A multi-prong approach that includes management of reef fish biomass together with lionfish removal efforts probably offers the most promise to minimize lionfish impacts. The EwE model served as a valuable tool to simultaneously evaluate these policies, and showed lionfish impacts on the system could be at least partially mitigated by a combination of reef fish management and directed lionfish removal efforts. In turn, our results suggest fisheries management policies aimed at increasing reef fish biomass and diversity could lessen the susceptibility of the system to additional invaders. As global connectivity and the exotic animal trade continue to increase, lowering overall reef fishing pressure may prove to be our best defense against subsequent introductions of non-native fishes.

Data and modeling needs

This model was constructed using the best available data available on lionfish from the WFS; however, because lionfish have only recently invaded the WFS, there are still several aspects of lionfish trophic interactions in the system that are poorly understood. For instance, lionfish have been found in the diets of large-bodied groupers in the Caribbean (Maljkovic et al. 2008), but uncertainty remains as to whether groupers or other piscivores actively prey upon

either juvenile or adult lionfish (Bernadsky and Goulet 1991; Diller et al. 2014). Because of these uncertainties, predation mortality on lionfish was not incorporated into our model. Future model scenarios should explore the effects of predation mortality on lionfish by native predators. Results from DNA barcoding of lionfish prey items have indicated cannibalism exists within red lionfish (Valdez-Moreno et al. 2012; Cote et al. 2013; Dahl and Patterson unpublished data), thus we included model runs with cannibalism in this study. However, most examinations of lionfish diets (over 20 published studies) have not found lionfish present in the gut of larger conspecifics. If the bulk of lionfish cannibalism results from depredation on newly-settled juveniles, then perhaps the lack of observations of cannibalism among conventional diet studies is understandable. Continued collection of diet data, including the use of novel techniques like DNA barcoding of unidentified prey, will be important for reducing uncertainty in future model predictions. Furthermore, DNA barcoding may be a useful technique to identify potential depredation of newly-settled lionfish by native GoM reef fishes.

Lionfish densities on the WFS are exponentially increasing and carrying capacity is difficult to estimate at this point in the invasion. The densities of lionfish on the WFS have been estimated to a depth of 100 m (Dahl and Patterson 2014; Switzer et al. 2015), but lionfish are known to exist to depths of 300 m (Schofield et al. 2010). If lionfish exist at depths below 100 m on the WFS, this may substantially alter our estimates of WFS lionfish biomass and spawning potential. Additionally, lionfish density estimates from artificial reefs were excluded from the model. Lionfish density on these reefs can be two orders of magnitude higher than natural reefs (Dahl and Patterson 2014). Artificial reefs on the WFS can serve as oases for a wide variety of marine species, but are estimated to constitute less than 0.01% of the total WFS area, thus that habitat was not considered in this exercise.

This study included empirical lionfish diet data primarily from the northern GoM (Dahl and Patterson 2014, Dahl, unpublished data) which was supplemented with diet data from around the Caribbean and western Atlantic. We have assumed these diet data are representative of the entire modeled region, but recognize that lionfish diet from the mid and southern WFS has not been studied. Future adjustments to the diet matrix could also consider behavioral and morphological aspects to identify fish as potential prey items for lionfish (Green and Cote 2014).

The vulnerability parameters in EwE control the degree to which predators will influence prey populations and the strength of the density-dependent interactions in the system. The vulnerabilities of lionfish prey are currently unknown and were specified in order to simulate

maximum predation mortality rates relative to natural mortality (i.e. 25, 50, and 100% of M for each prey item). The vulnerability parameters will substantially alter the influence of lionfish predation on other components of the food web, and thus, these parameters should be explored experimentally. One option for estimating vulnerabilities empirically would be to evaluate predation mortality by lionfish across a gradient of prey densities, prey types, and habitat complexity (e.g., Green et al. 2014).

Expanding the model to the spatially explicit component, Ecospace, would allow us to explore the localized impacts of the lionfish invasion. In Ecospace, biomasses are modeled dynamically across a defined area based on habitat associations and food availability (Walters et al. 1999; Pauly et al. 2000). Because lionfish densities vary across habitat types and depths, the Ecospace model would allow us to develop more realistic predictions of lionfish invasion impacts across smaller spatial scales. In the current model, lionfish harvest is averaged across the WFS; yet, there is evidence that high fishing effort on lionfish may lead to localized depletion (Cote et al. 2014). Thus, an Ecospace model would additionally allow us to examine the effects of localized depletions on lionfish invasion dynamics on the WFS. Expansion of this tool to be spatially explicit would improve the strategic planning utility of the model for management that could better optimize the tradeoff between resource utility and ecological conservation.

Tables

Table 1. Biomass density estimates (mt/km²) from the SEAMAP trawl survey on the WFS and ROV survey in the Northern Gulf of Mexico on natural and artificial reefs. For the NGoM study, biomass was estimated from numbers using year-specific mean body weight.

year	SEAMAP trawl density	NGoM ROV Natural Reef	NGoM Artificial Reef
2010	8.01227E-07		
2011	0.00015	0.01828	2.16421
2012	0.00044	0.25294	15.79714
2013	0.00643	0.96308	31.15802
2014	0.01493	1.41240	82.15318
Percent Habitat	0.93	0.07	
2011 Biomass	0.00142		
BA	0.66	0.93	
Average BA	0.80		

Table 2. Derivation of consumption (Q, g/g/day) and natural mortality (M) input parameters.

Daily consumption was calculated using the bioenergetics equation ($Q \text{ (g/g/day)} = 0.603wt^{-0.465}$) at optimal temp of 29.7 C) of Cerino et al. (2012). Mortality was based on the Lorenzen (1996) equation for body weight ($M = 3.69wt^{-0.305}$). Input values were calculated as the average over the size classes 50-150 mm for juveniles and >150 mm for adults, weighted by the biomass in each length bin (mm TL) from the SEAMAP trawl survey.

length bin	length mid	SEAMAP total n	body Wt (g)	biomass g	Q	M y^{-1}
(50,75]	62.5	8	4	36	0.301	2.339
(75,100]	87.5	13	12	153	0.191	1.739
(100,125]	112.5	24	24	585	0.137	1.393
(125,150]	137.5	50	43	2175	0.104	1.168
(150,175]	162.5	97	70	6836	0.083	1.008
(175,200]	187.5	124	107	13214	0.069	0.888
(200,225]	212.5	112	153	17134	0.058	0.796
(225,250]	237.5	93	211	19619	0.050	0.721
(250,275]	262.5	98	282	27605	0.044	0.660
(275,300]	287.5	90	366	32972	0.039	0.610
(300,325]	312.5	55	466	25638	0.035	0.566
(325,350]	337.5	26	582	15137	0.031	0.529
(350,375]	362.5	12	716	8589	0.028	0.497
(375,400]	387.5	2	868	1736	0.026	0.469
(400,425]	412.5	4	1040	4158	0.024	0.443
juvenile					25.664	1.256
adult					14.056	0.662

Table 3. Diet composition of juvenile lionfish from six different studies used to generate an average diet composition for the model.

ref	Munoz et al. (2011)	Valdez-Moreno et al. (2012)	Faletti and Ellis (2013)	Layman and Allgeier (2012)	Dahl and Patterson (2014)	FWC	Avg
nstomachs	183	157	32	122	247	52	
location	W Atl	Caribbean	GoM	Bahamas	NGoM	WFS	
units	number	number	number	volume	mass	volume	
Prey Group	Percent Diet						
other snapper			0.02				0.00
triggerfish/hogfish						0.00	0.00
Black sea bass					0.01		0.00
reef carnivores	0.55	0.67	0.21	0.41	0.04		0.19
reef omnivores	0.26	0.32	0.02	0.51	0.25		0.25
large coastal carnivores					0.00		0.00
small coastal carnivores	0.03	0.01			0.07		0.04
Sardine-Herring-Scad	0.08				0.06		0.04
Adult Shrimps			0.31	0.02	0.13	0.62	0.15
Lobsters					0.01	0.01	0.00
Large Crabs				0.02	0.01		0.01
Stomatopods				0.01	0.02	0.01	0.01
Echinoderms/Large gastropods	0.01				0.00		0.00
Small mobile epifauna				0.03	0.02	0.03	0.02
Other Mesozooplankton					0.00		0.00
CarnivZooplank					0.00		0.00
UI crustacean	0.07		0.02			0.00	0.01
UI decapod					0.00		0.00
UI fish			0.42		0.38	0.33	0.25
UI invert					0.02		0.01

Table 4. Diet composition of adult lionfish from three different studies used to generate an average diet composition for the model.

ref	Cote et al. (2013)	Morris and Akins (2009)	Dahl and Patterson (2014)	
nstomachs	130	699	977	
location	Caribbean	Caribbean	NGoM	
units	number	volume	mass	
Prey Group	Percent Diet			Avg
Vermillion snapper			0.03	0.02
other snapper		0.00		0.00
Black sea bass			0.05	0.03
reef carnivores	0.62	0.18	0.13	0.15
reef omnivores	0.32	0.15	0.20	0.19
large coastal carnivores			0.00	0.00
small coastal carnivores	0.06	0.00	0.07	0.05
coastal omnivores		0.00		0.00
Sardine-Herring-Scad complex			0.04	0.03
Anchovies and silversides		0.01		0.00
Squid			0.01	0.01
Adult Shrimps		0.22	0.02	0.08
Lobsters			0.00	0.00
Large Crabs			0.01	0.01
Octopods		0.00	0.00	0.00
Stomatopods		0.00	0.00	0.00
Echinoderms/Large gastropods		0.00	0.00	0.00
Small mobile epifauna		0.00	0.00	0.00
UI crab		0.01		0.00
UI crustacean		0.00		0.00
UI decapod			0.00	0.00
UI fish		0.42	0.43	0.41
UI invert			0.01	0.00

Figures

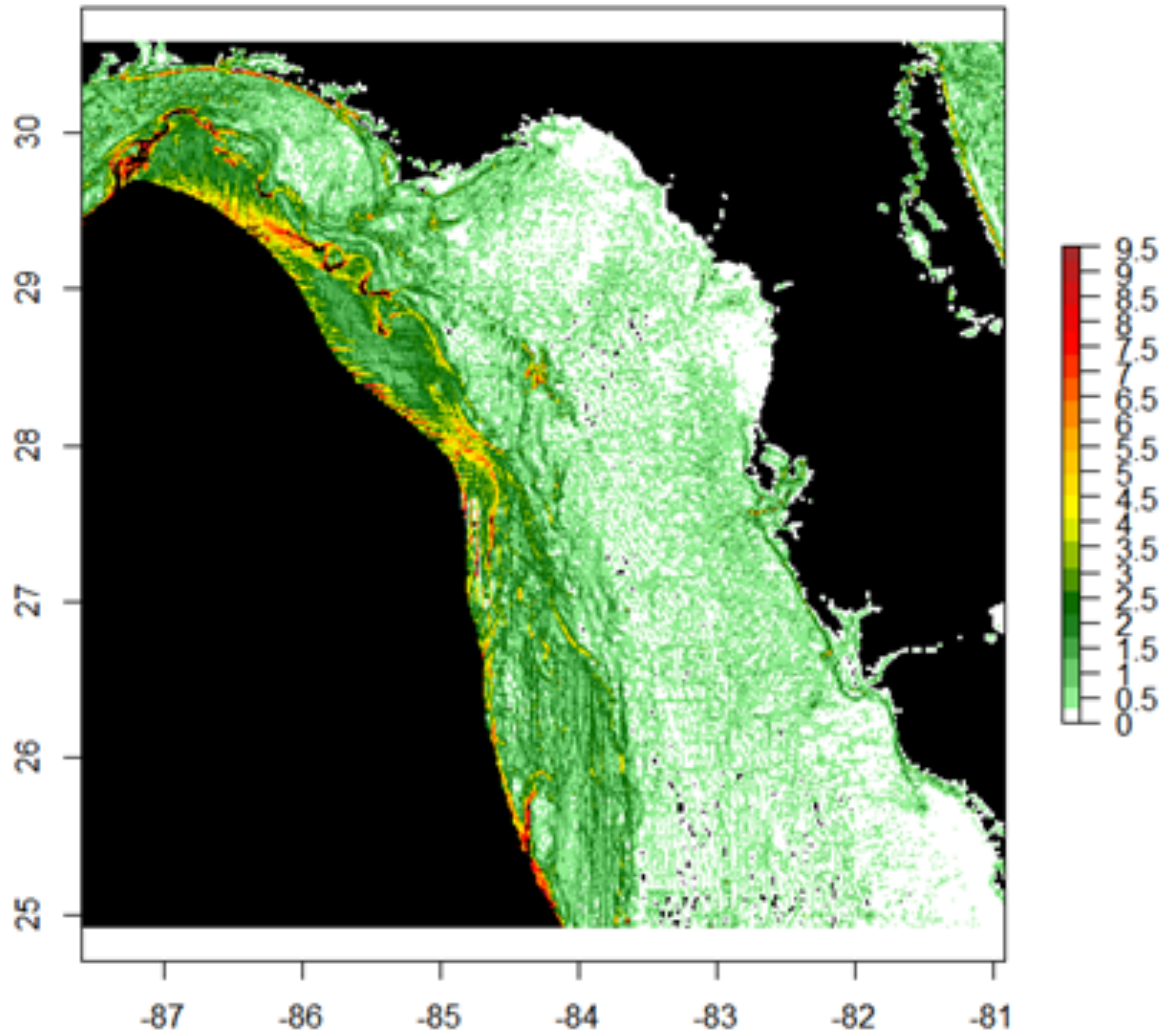


Figure 1. Rugosity map of the West Florida Shelf produced by the USGS (Robbins et al. 2010, <http://pubs.usgs.gov/ds/477/>). Rugosity reflects the change in elevation between neighboring 8 cells, is expressed as m/1000m. Warmer colors indicate areas of higher elevation (> 3.5) which were classified as reef habitat.

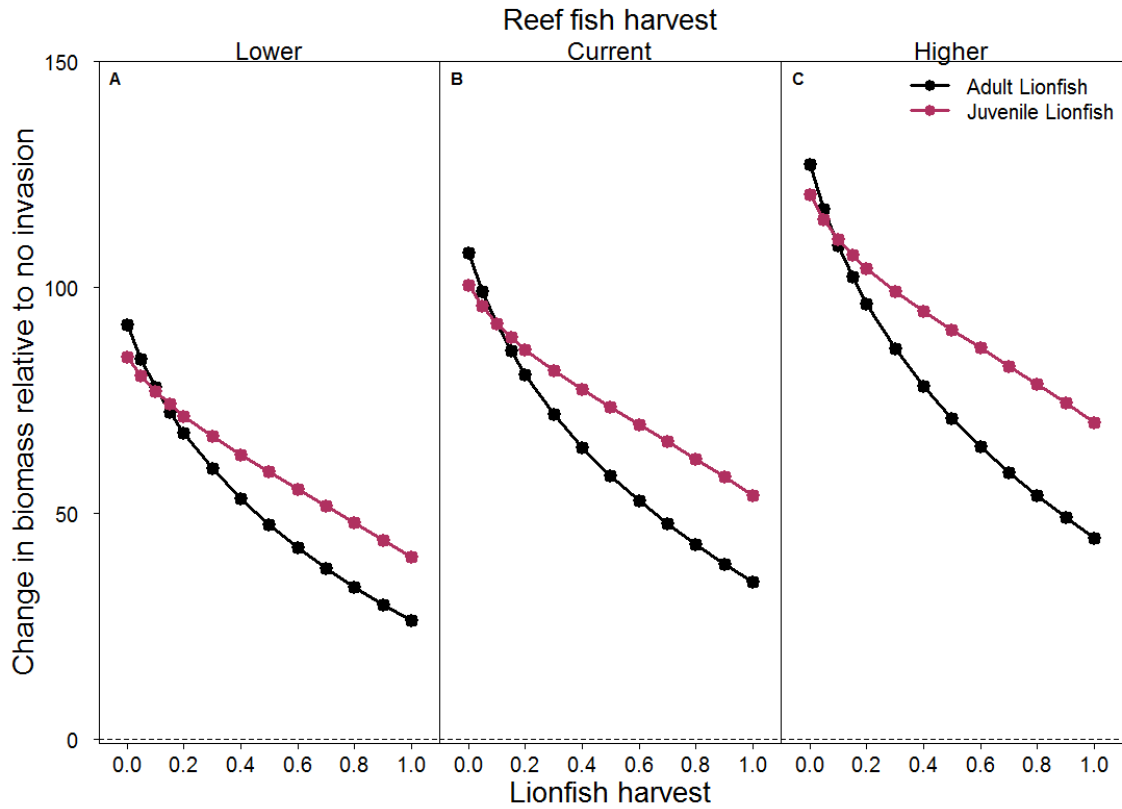


Figure 2. The proportional change in biomass of lionfish relative to the status quo scenario of no lionfish invasion in the terminal year of the simulation (Equation 1) for juvenile and adult lionfish, respectively. The invasion was simulated for 30 years under three levels of reef fish harvest, including current reef fish fleet effort (B), lower (25% of current effort, A) and higher (200% of current effort, C) and across varying degrees of lionfish harvest. Fishing mortality on lionfish is represented as a proportion of natural mortality ($M = 0.66 \text{ y}^{-1}$). The dotted line indicates where the biomass would be the same with and without the lionfish invasion.

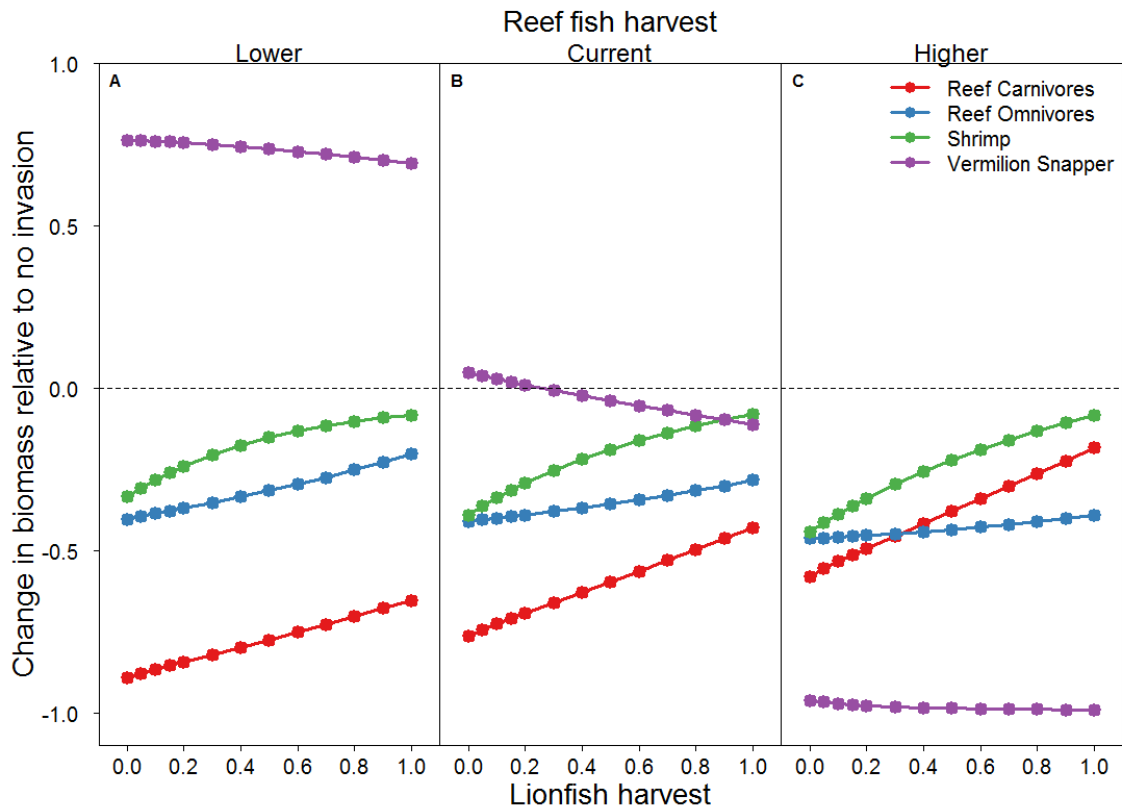


Figure 3. The proportional change in biomass of common lionfish prey species relative to the status quo scenario of no invasion in the terminal year of the simulation Change in biomass relative to the status quo (Equation 1) for common lionfish prey species including vermilion snapper, reef carnivores, reef omnivores, and shrimp at the end of each 30-year simulation. Prey species responses to the invasion were evaluated simulated under three levels of reef fish harvest, including current efforts (B), lower (25% of current effort, A) and higher (200% of current effort, C) and across varying degrees of lionfish harvest. Fishing mortality on lionfish is represented as a proportion of natural mortality ($M = 0.66 \text{ y}^{-1}$). The dotted line indicates where the biomass would be the same with and without the lionfish invasion.

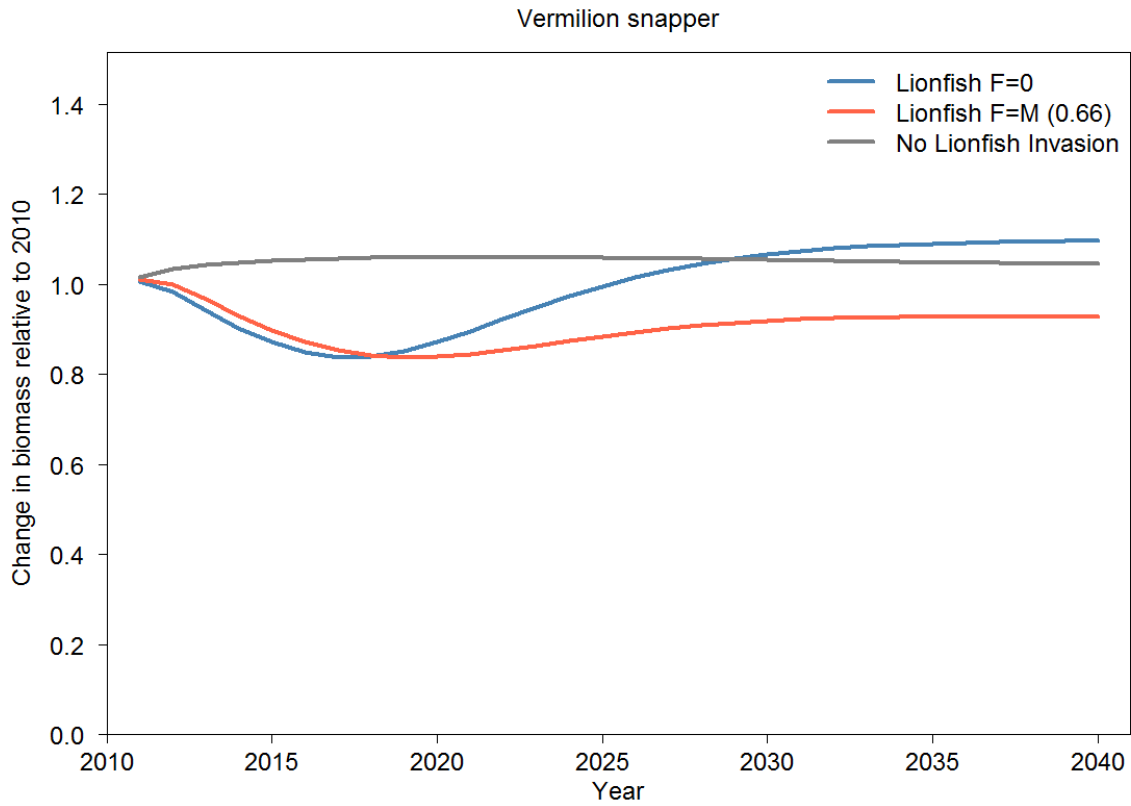


Figure 4. Patterns of vermilion snapper relative biomass over time (the ratio of vermilion snapper biomass compared to 2010), under high and low simulated lionfish harvest scenarios, and thus low and high lionfish biomass, respectively, as well as the status quo scenario of no lionfish invasion.

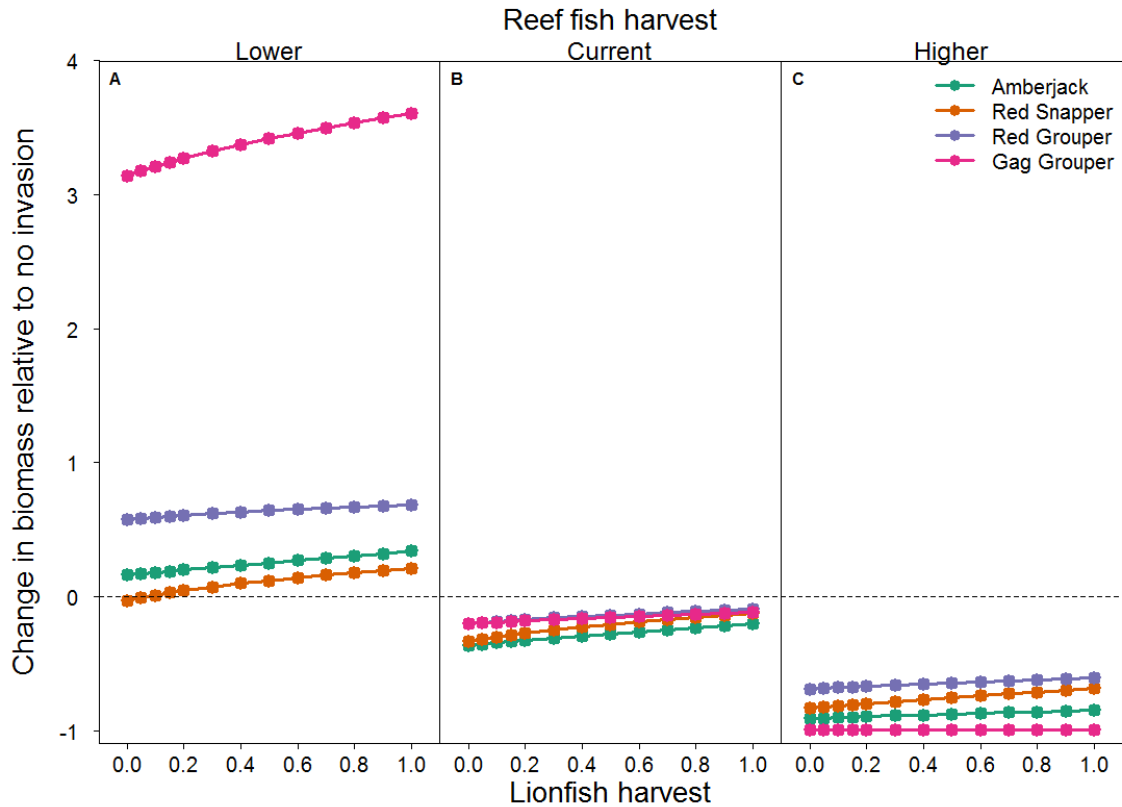


Figure 5. The proportional change in biomass of commercially important species on the WFS relative to the status quo scenario of no invasion in the terminal year of the simulation Change in biomass relative to the status quo (Equation 1) for commercially important species on the WFS including amberjack, red snapper, red grouper, and gag grouper at the end of each 30-year simulation. Species responses to the invasion were evaluated under three levels of reef fish harvest, including current effort (B), lower (25% of current effort, A) and higher (200% of current effort, C) and across varying degrees of lionfish harvest. Fishing mortality on lionfish is represented as a proportion of natural mortality ($M = 0.66 \text{ y}^{-1}$). The dotted line indicates where the biomass would be the same with and without the lionfish invasion.

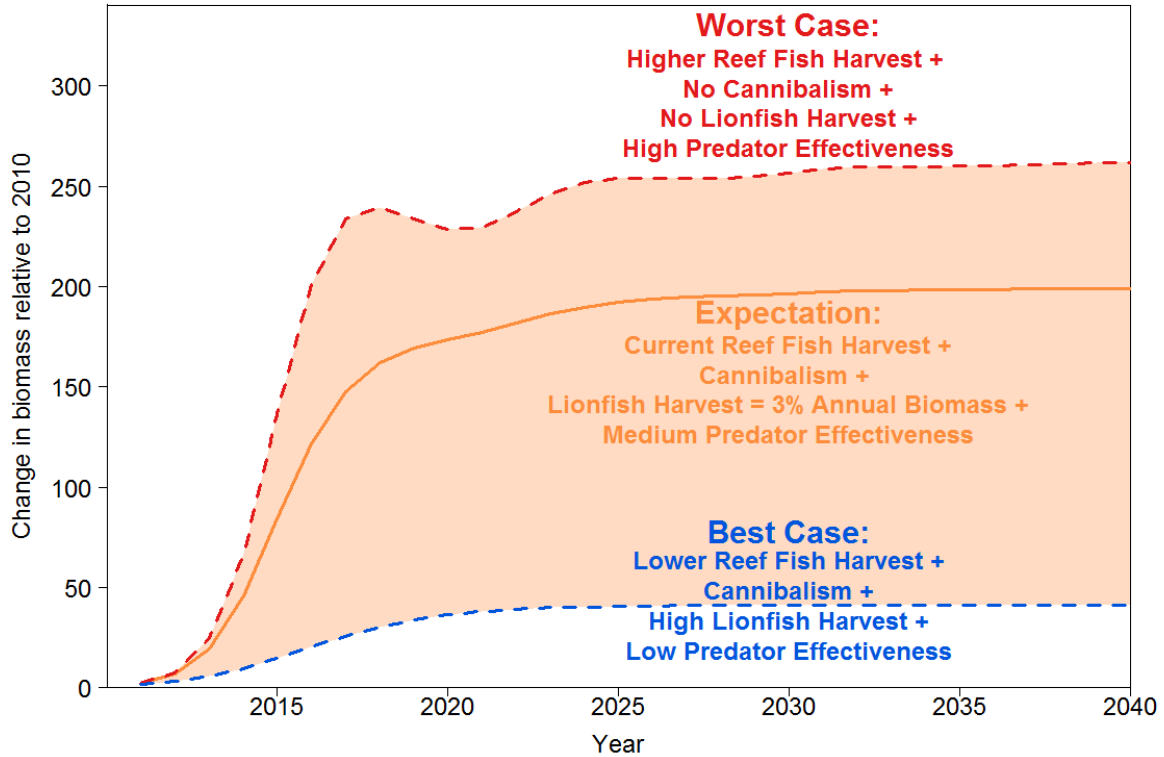


Figure 6. Simulated 30-year change in adult lionfish biomass relative to the base biomass in 2010 under three scenarios: the expected scenario (current reef fish harvest, adult lionfish cannibalism on juveniles, lionfish harvest at 0.05 of natural mortality, and 0.5 vulnerability of lionfish prey species to predation), the worst case scenario (200% the current reef fish harvest, no adult lionfish cannibalism on juveniles, no lionfish harvest, 1.0 vulnerability of lionfish prey species to predation), and the best case scenario (25% current reef fish harvest, adult lionfish cannibalism on juveniles, lionfish harvest levels at natural mortality, and 0.25 vulnerability of lionfish prey species to predation).

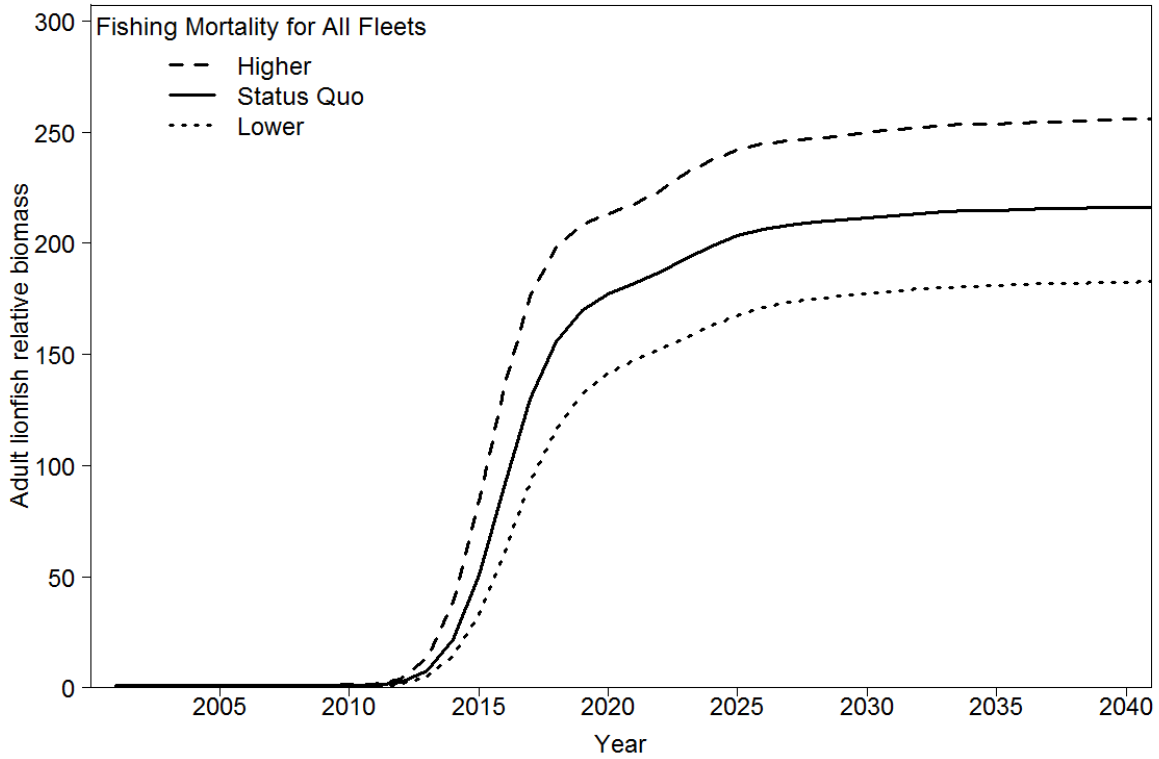


Figure 7. Retrospective simulations to compare susceptibility of the ecosystem to lionfish invasion under different fishing effort scenarios. The lines show relative biomass compared to base levels in 2000, each representing a different level of fishing pressure on native species. All fishing fleets were set to either status quo (100% current), higher (200% current), or lower (25% current) levels of effort, to simulate the effect of various levels of pre-invasion biomass of native species on future lionfish biomass.

References

- Albins, ME, and M. A. Hixon. 2013. Worst case scenario: potential long term effects of invasive lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environmental Biology of Fishes* 96:1151-1157.
- Arias-González JE, González-Gándara C, Luis Cabrera J, Christensen V (2011) Predicted impact of the invasive lionfish *Pterois volitans* on the food web of a Caribbean coral reef. *Environ Res* 111:917–925
- Barbour, A B, Allen MS, Frazer TK, Sherman KD. 2011. Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. *PLoS ONE* 6(5):e19666.
- Baxter C V, Fausch KD, Murakami M, Chapman PL (2004) Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology* 85:2656–2663
- Chagaris DD, Mahmoudi B, Walters CJ, Allen MS (2015) Simulating the trophic impacts of fishery policy options on the West Florida Shelf using Ecopath with Ecosim. *Mar Coast Fish* 7:44–58
- Daskalov GM, Grishin AN, Rodionov S, Mihneva V (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proc Natl Acad Sci U S A* 104:10518–23
- Engeman RM, Vice DS (2001) Objectives and integrated approaches for the control of brown tree snakes. *Integr Pest Manag Rev* 6:59–76
- Frank KT, Petrie B, Choi JS, Leggett WC (2005) Trophic cascades in a formerly cod-dominated ecosystem. *Science* (80-) 308:1621–1623.
- Green, S. J. and I. M. Cote. 2014. Trait-based diet selection: prey behaviour and morphology predict vulnerability to predation in reef fish communities. *Journal of Animal Ecology* 83:1453-1460.
- Jackson JB, Kirby MX, Berger WH, Bjorndal K a, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes J a, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* (80-) 293:629–37
- Kimbrow DL, Grosholz ED, Baukus AJ, Nesbitt NJ, Travis NM, Attoe S, Coleman-Hulbert C (2009) Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. *Oecologia* 160:563–575
- Langseth BJ, Rogers M, Zhang H (2012) Modeling species invasions in Ecopath with Ecosim: An evaluation using Laurentian Great Lakes models. *Ecol Modell* 247:251–261
- Logan J, Haas H, Deegan L, Gaines E (2006) Turnover rates of nitrogen stable isotopes in the salt marsh mummichog, *Fundulus heteroclitus*, following a laboratory diet switch. *Oecologia* 147:391–395

- Mumby PJ, Dahlgren CP, Harborne AR, Kappel C V, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* (80-) 311:98–101
- Pauly, D., V. Christensen, and C. Walters. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science* 57(3):697-706.
- Pine WE, Kwak TJ, Rice JA (2007) Modeling management scenarios and the effects of an introduced apex predator on a coastal riverine fish community. *Trans Am Fish Soc* 136:105–120
- Robbins, L., Knorr, P., and M. Hansen. 2010. Cartographic production for the FLaSH Map Study: generation of rugosity grids, 2008. USGS Data Series. 477.
- Salomon AK, Gaichas SK, Shears NT, Smith JE, Madin EMP, Gaines SD (2009) Key features and context-dependence of fishery-induced trophic cascades. *Conserv Biol* 24:382–394
- Stachowicz, JJ, Fried H, Osman RW, Whitlatch RB (2002) Biodiversity, invasion resistance, and marine ecosystem function: Reconciling pattern and process. *Ecology* 83(9):2575-2590.
- Walters, C., D. Pauly, and V. Christensen. 1999. Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2(6):539-554.