2014-05-25

Habitat Suitability and Bioenergetics of an Invasive Marine Fish (Pterois volitans) in Biscayne Bay, Florida

Nicholas Andres Bernal
University of Miami, nbernal@bio.miami.edu

Recommended Citation

Bernal, Nicholas Andres, "Habitat Suitability and Bioenergetics of an Invasive Marine Fish (Pterois volitans) in Biscayne Bay, Florida" (2014). *Open Access Theses*. 493.
https://scholarlyrepository.miami.edu/oa_theses/493

UNIVERSITY OF MIAMI

HABITAT SUITABILITY AND BIOENERGETICS OF AN INVASIVE MARINE FISH (*Pterois volitans*) IN BISCAYNE BAY, FLORIDA

By

Nicholas Andres Bernal

A THESIS

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Master of Science

Coral Gables, Florida

August 2014

UNIVERSITY OF MIAMI

A thesis submitted in partial fulfillment of
the requirements for the degree of
Master of Science

HABITAT SUITABILITY AND BIOENERGETICS OF AN INVASIVE MARINE FISH (*Pterois volitans*) IN BISCAYNE BAY, FLORIDA

Nicholas Andres Bernal

Approved:

Donald L. DeAngelis, Ph.D.
Adjunct Professor
Department of Biology

Daniel J. DiResta, Ph.D.
Senior Lecturer
Department of Biology

John Albert C. Uy, Ph.D.
Associate Professor
Department of Biology

M. Brian Blake, Ph.D.
Dean of the Graduate School

Craig A. Layman, Ph.D.
Associate Professor
Department of Applied Ecology
North Carolina State University

BERNAL, NICHOLAS ANDRES (M.S., Biology)
Habitat Suitability and Bioenergetics of an Invasive Marine Fish (*Pterois volitans*) in Biscayne Bay, Florida. (August 2014)

Abstract of a thesis at the University of Miami.

Thesis supervised by Dr. Donald L. DeAngelis.
No. of pages in text. (72)

As many successful invasive species display varying degrees of plasticity across spatial and temporal habitats, it is often difficult to assess the impacts of a nascent biological invasion on native flora and fauna. Using empirically supported environmental variables (e.g., temperature, salinity, dissolved oxygen, rugosity, and benthic substrate), we created a comprehensive habitat suitability model for invasive lionfish (*Pterois volitans*) in Biscayne Bay, Florida. The use of Geographic Information Systems (GIS) as a platform for the modeling process allowed us to quantify correlations between temporal (seasonal) fluctuations in the above variables and the spatial distribution of discrete habitat classes, whose ranges are supported by statistical deviations from optimal conditions described in prior studies. Building on this theme, we then apply the principles of bioenergetics to better understand how ambient environmental variables across newly invaded habitats impact metabolic function leading to growth and reproduction. Both of these models serve in conjunction to elucidate niche habitats and can led to better understanding of thresholds for prey availability and starvation mortality necessary to sustain individuals across environmental gradients.

ACKNOWLEDGMENTS

I would like to begin by giving a special thanks to academic adviser, Dr. Don DeAngelis, for taking me in as a wayward student and putting the time and effort to help hone my skills. Dr. DeAngelis has shown great faith in me and provided innumerable hours of guidance to share his wealth of experience. His expertise in all facets of ecology has transformed me into a well rounded student. I also thank my committee members, Drs. Al Uy, Craig Layman, and Dan DiResta for taking time out of their busy schedules to help cultivate my breadth of knowledge as a graduate student and for constant feedback on manuscript drafts.

The background research for this project would not have been possible without assistance from Dr. Vanessa McDonough (Biscayne National Park), Judd Patterson (National Park Service), and Omar Abdelrahman (DERM) who generously provided raw data used as model inputs. Dr. Shouraseni Sen Roy (University of Miami) and Chris Hanson (University of Miami) were also essential in furthering my GIS skillset used in this project.

All of this could not have been possible without the support of my wonderful parents, Camilo and Pamela, who taught me to strive for excellence. But most of all, I would like to thank my darling wife, Susanna, who has put up with me throughout this entire journey. The long nights reading and stressing over deadlines would not have been possible without the compassion and love she has given unselfishly and wholeheartedly.

TABLE OF CONTENTS

Chapter 1. INTRODUCTION

Increased transport vectors as a result of rapid globalization have contributed to the estimate of close to 4,300 marine, aquatic, and terrestrial invasive species that are currently established in the US (Corn *et al.* 1999). However, this number represents only a small fraction of the total natural and anthropogenic introductions that have occurred in the US. Although invasion ecology has only recently been established as a field of study, early work by Elton (1958) and his contemporaries had already identified the bottleneck whereby relatively few introduced species can actually establish and negatively impact native ecosystems. This seminal theory is known in familiar form as the "Rule of Tens," which summarizes that approximately ten percent of species transition from casually present to established and, of those established roughly ten percent will become weeds/pests (Booth *et al.* 2003). Despite the fact that only 1% of introductions lead to pest status, invasive species in marine and aquatic ecosystems have had serious impacts on the diversity and abundance of native species (Garton *et al.* 1993, Molnar *et al.* 2008).

To better understand how a biological invasion may impact a native ecosystem, we must determine which factors facilitate the establishment of an invasive species. Modern invasion ecology theory proposes that there are two key general factors underlying successful invasions, one species-based and one ecosystem-based (Kolar and Lodge 2001). The species-based factor includes the suite of unique aspects of individual species that have helped, or will help them colonize and potentially impact novel environments. These traits, which have evolved in their native ranges, often allow successful invaders to act as generalists in their new environments and out-compete native species that are co-evolved to a narrower niche in their particular ecosystem

(Tilman 2004). The invading species may also experience predatory release, as they may not be burdened by coevolved predators and parasites. Additionally, since success relies heavily on being able to maintain a high degree of fitness in variable environments, many invasive species utilize r-selected traits such as fast growth, rapid reproduction, and high dispersal ability (Tilman 2004). Successful invaders display the aforementioned traits and some degree of phenotypic plasticity that ensure stable energy supplies, reproductive cycles, and habitat utilization.

Ecosystem-based mechanisms make up the other aspect that may enable the success of an invasive species within a novel environment. These mechanisms include disruptions and alterations of the natural habitat that may allow an ecosystem to be more vulnerable to invasion (Byers 2002). Disturbance, both natural and anthropogenic, has long been studied as one of the leading pathways to invasion (Elton 1958, Byers 2002). By altering established community structure and dynamics, disturbances have been shown to reduce native species biodiversity by decreasing fitness of specialized individuals co-evolved to specific environmental conditions (Hobbs and Huenneke 1992). Stachowicz *et al.* (1999) examined the role of this loss in biodiversity among populations of sessile marine invertebrates to determine the existence of a positive correlation between biodiversity and resistance of communities to invasion pressure. Loss in biodiversity, often resulting from disturbances, is thus a factor that can facilitate successful invasions in aquatic, marine, or terrestrial environments (Hobbs and Huenneke 1992).

Successful invasion in habitats is more likely when species-based and ecosystem-based mechanisms coincide in time and space. These mechanisms are the filters that determine viability of any species. Understanding the spatial and temporal elements leading from invasion to colonization and subsequent establishment is the key to predicting how, when, and where invasive species may impact native communities. Studies in invasion ecology often use statistical modeling to relate the species characteristics and ecosystem characteristics across time and space to produce quantitative representations of useable habitat for invaders and native species.

These studies of habitat suitability can estimate quantitatively the possible spatial distribution of an invader by identifying areas across a gradient of variable habitats where species have a high probability of occurrence (Williams and Meffe 1998, Sakai *et al.* 2001). Both abiotic (water quality, geoform substrate, etc.) and biotic (benthic substrate, species communities, etc.) factors can be included as layers to create spatial representations; i.e., maps that can predict the potential distribution of a species across space and time. This information places some limits on the physical distribution of a species (Vadas and Orth 2001, Store and Jokimaki 2003). In creating habitat suitability maps, it is also essential to consider how habitat usage and physiological requirements change as an individual moves through different life history stages (Brown *et al.* 2000). This is particularly important in species such as fish, which can undergo rapid morphological change during transition from larvae to adults.

Use of physiological and behavioral models, integrating field and laboratory studies, is also a tool for estimating potential spatial and temporal habitat overlap of invasive and native species, and hence the potential impact of invasive species. Even for a generalist invader, modeling tools require specific data concerning energetics and life history processes to accurately predict distributions. Data from field and laboratory experiments can help determine the fundamental niche (ranges of thermal/salinity tolerance). Modeling bioenergetics can be a useful tool in estimating the effects of environmental parameters on consumption, growth, and reproduction. Since their initial development by Winberg (1960), these models, and subsequent iterations, have been used in a host of studies ranging from estimating the size of prey bases to looking at the impact of stressors on physiological processes.

Chapter 2. PREDICTING SPATIAL AND TEMPORAL DISTRIBUTION OF LIONFISH IN BISCAYNE BAY THROUGH HABITAT SUITABILITY MODELING

Background

Studies of invasion ecology investigate the relationship between species traits and the characteristics of ecosystems to produce quantitative estimates of useable habitat for invaders. For these species, quantifying spatial and temporal distribution is critical to understanding where impacts on native flora and fauna can occur. Habitat suitability modeling (HSM) provides a powerful tool that can identify suitability of patches for a given species across space and time (Rubec *et al.* 1999). The spatial scale of these models is limited only by available data, thus making this tool applicable both at multiple scales.

The need for accurate habitat suitability information is critical for newly invading species, such as the Indo-Pacific lionfish (*Pterois volitans*), the first non-native marine fish to establish self-sustaining populations and spread along the Tropical Western Atlantic (Schofield 2009, 2010). Natural resource managers are concerned about the effects of lionfish on native species and habitats, as it is a generalist predator that could reduce densities of native species and alter trophic structure of marine environments (Albins and Hixon 2008, Morris and Akins 2009, Green *et al.* 2012). Prior research has generated predictive models of lionfish expansion on a regional scale, whereby physiological tolerance and sightings (abundance) data are extrapolated to predict expansion into new areas (Kimball *et al.* 2004, Johnston and Purkis 2011). However, these broad spatial scale models lack the high resolution necessary to accurately investigate species-specific habitation gradients across patches on a smaller scale.

To refine the resolution to the local scale of an important ecosystem, our primary objective was to create a series of temporal high resolution HSMs for lionfish in Biscayne Bay, Florida, using quantitative tools in a GIS platform. Our models relied on statistically transforming known physiological ranges for lionfish to datasets for ambient environmental variables. A combination of physiologically relevant dynamic water quality measures (temperature, salinity, and dissolved oxygen) and static habitat components (benthic cover and rugosity) are used to quantify a species-specific gradient for habitat suitability.

Study System and Species

Study System: Biscayne Bay, Florida

Biscayne Bay is a shallow (0.5 m – 3 m) carbonate marine estuary that encompasses an area of roughly 1110 km^2 in southeastern Florida (Caccia and Boyer 2005). Ecological variability is a common feature of all of the Bay's ecosystems, with differing levels of benthic biota, depth, and ecological disturbance characterizing each of the individual communities (Duever *et al.* 1994). Seasonal fluctuations in surface and aquifer freshwater input to near shore habitats, i.e. mangroves, affects variability of water quality relevant to native flora and fauna (Caccia and Boyer 2005).

There are several driving forces creating ecological variability across Biscayne Bay. Natural seasonality (wet/dry), along with variable inter-annual precipitation, drives nutrient flow across marine and terrestrial ecosystems. Historically, average rainfall values are approximately 130 cm/year, with the wet season (May through November) providing close to 75% of all precipitation; however, analysis of rainfall across the past century reveals the presence of distinct patterns between years (Duever *et al.* 1994). Long-term patterns are often punctuated by severe droughts or sporadic, intense precipitation events, such as those associated with hurricanes. These abiotic processes, which influence key biological phenomena in the Bay, such as juvenile fish recruitment, seagrass growth, and mangrove propagation, may be at risk due to changing freshwater input resulting from habitat alteration and future global climate change (Lindeman *et al.* 1998).

Biscayne Bay supports a variety of habitats ranging from mangrove creeks to seagrass beds and coral reefs. Surveys of these distinct habitats reveal a high degree of biodiversity that exceeds 500 species of fish and 800 species of invertebrates, thus giving rise to a complex food web (Alleman *et al.* 1995). Many of these species have evolved adaptations to cope with the aforementioned ecological variability across benthic habitats (Alleman *et al.* 1995). For example, many native snappers (Family: Lutjanidae) and grunts (Family: Haemulidae) undergo an "ontogenic mangrove-to-reef" migration, whereby the earliest life history stages of these fish occur in the security of mangrove prop roots, followed by a migration to the coral reefs for completion of adult stages (Serafy *et al.* 2003).

Study Species: Indo-Pacific Lionfish (Pterois volitans)

Lionfish forage as opportunistic mid-level ambush predators with feeding preference dominated by juvenile crustaceans, wrasses, and grunts (Albins and Hixon 2008, Morris and Akins 2009, Côté *et al.* 2013). Studies in the invaded range suggest that at ambient temperatures (~26° C) lionfish can consume roughly 9% of their body weight per day in prey items, with successful attack rates between 85% - 88% at dawn and dusk (Green *et al.* 2011). High rates of lionfish predation have been observed to reduce survivorship of newly recruited reef fishes, possibly resulting in the displacement and out-competition of other similar native species (Albins and Hixon 2008, Green *et al.* 2012).

As habitat generalists, lionfish occupy a continuum of depths from shallows less than 1 meter down to over 300 meters (Whitfield *et al.* 2002). Habitat occurrence across the invaded range is highly variable and ranges from coral reefs to tropical lagoons and seagrass beds (Whitfield *et al.* 2002, Barbour *et al.* 2010). Within the invaded Tropical Western Atlantic, notable recruitment success has been seen in disturbed habitats and on artificial structures with high rugosity (Albins and Hixon 2008). Densities of lionfish vary from 21 per hectare off the coast of North Carolina to values greater than 390 per hectare around New Providence, Bahamas, and 450 per hectare in the Exuma Cays, Bahamas (Green and Côté 2009, Morris and Whitfield 2009, Whitfield *et al.* 2007).

Thermal tolerance studies on lionfish in both the native Indo-Pacific and invaded Red Sea ranges suggest that the growth optimum occurs between 24°C-27°C; however, these fish can survive across a large temperature range between 14°C to 32.5°C for acclimated temperatures (Cerino 2010). Salinity is another key abiotic factor that impacts fish physiology, affecting the ability of euhaline fish to thrive in different habitats (Schofield 2009). Analysis of the USGS Nonindigenous Aquatic Species (USGS-NAS) database by Johnston and Purkis (2011) found that lionfish sightings generally occur around a mean salinity of 36.11 ppt; however, anecdotal evidence suggests lionfish can survive prolonged exposure to low salinity (<8 ppt) environments for extended periods of time (Jud and Layman 2012).

Currently, the role of lionfish in native food webs remains somewhat of a mystery. Lionfish have been found to prey on small fish and crustaceans from various taxa across a wide range of trophic levels; however, studies using stable isotopes suggest that these diets can be more specialized on the local level (Morris and Akins 2009, Layman and Allgeier 2012). While this generalist diet is known to overlap with that of other mid-level predatory species within the Snapper-Grouper complex, competition within this trophic complex has not yet been established (Albins and Hixon 2008, Côté and Maljkovic 2010, Layman and Allgeier 2012). Additionally, recent assessment of lionfish foraging suggests a high degree of post-recruitment site fidelity, thus potentially limiting the spatial and temporal distribution of lionfish interactions (Jud and Layman 2012, Layman and Allgeier 2012).

Methods

Input Data

The building blocks for HSMs in this study were unique raster layers, which represent datasets extrapolated for GIS analysis. The first three represented dynamic water quality data: temperature, salinity, and dissolved oxygen. These measurements were collected on a monthly basis at 44 stations across Biscayne Bay, which are maintained and monitored via collaboration between the South Florida Water Management District (SFWMD), Dade County Environmental Resource Management (DERM), and Florida International University (FIU). In this study, we isolated only those values collected between 2000 and 2012. Prior surveys of sea surface water quality suggest that a period of at least ten years is necessary to account for inter-annual variation, which may be caused by El Niño and other events, to produce an accurate interpolation of average values for analysis (ESRI 2011).

Another key layer created was a two-dimensional benthic habitat map developed for Biscayne Bay by the National Park Service (NPS) and Florida Department of Environmental Protection (FDEP). These agencies transformed raster images, which were obtained through visual surveys and remote sensing (satellite imagery) between 2005 and 2010, into categorical benthic habitat maps. Habitats classification follows the State of Florida System for Classification of Habitats in Estuarine and Marine Environments (SCHEME) and the newer Coastal Marine Ecological Classification System (CMECS). Both systems utilize submerged rooted vegetation (SRV), which includes seagrasses, oligohaline grasses, and attached and drift macroalgae, as a proxy for benthic biotic habitat (Madley *et al.* 2002).

Light detection and ranging (LIDAR) remote sensing measurements provided a three-dimensional image of the seafloor to quantify sub-surface rugosity. Although average depth in Biscayne Bay is a shallow 1.8 meters, with a maximum of 4 meters for unaltered habitats, the availability of microhabitats may allow lionfish to take advantage of local refuges with favorable conditions during rapid changes in water quality (Roessler *et al.* 1975). Additionally, empirical studies suggest the ability of lionfish to thrive as ambush predators is maximized in areas of high rugosity, where they can use camouflage to remain hidden (Morris and Akins 2009).

Physiological data for lionfish were also incorporated to quantify ranges in the habitat suitability models. These values, discussed further in the next section, were derived from prior laboratory and field studies describing optimal environmental variables for lionfish growth and reproduction. Following model construction, the USGS-NAS database was used as a means to corroborate all outputs. This robust dataset documents historical lionfish sightings across the Tropical Western Atlantic and provides information as to the date, location, and environmental conditions present at the time of a lionfish capture (Schofield 2009). Since data are collected voluntarily, it is difficult to correlate reporting frequency to actual lionfish density reported using scientifically based survey methods (Schofield 2009). To mitigate for the sporadic omission of environmental data, calculation of mean values for environmental conditions used in the models incorporated another lionfish dataset maintained by Biscayne National Park (BNP). Information from this archive is meticulously documented to include all necessary data for creation of model variables.

Model Construction

For this study we used ArcGIS version 10.1, as the core modeling platform (ESRI 2011). The software design and accompanying statistical packages allow for multivariate analysis using mathematical and geospatial statistical methods to model spatial and temporal distributions of study data. To accomplish this task, ArcGIS creates spatial layers, which are mechanisms used to visualize unique datasets (ESRI 2011). Another key feature of ArcGIS is that datasets can be made to interact over space and time through merging or linking of spatial layers (ESRI 2011).

Creating raster layers to represent environmental variables was the first step of model construction. The benthic habitat and rugosity datasets had already been transformed into raster layers; therefore, no modification was needed. Since data for water quality variables (temperature, salinity, and dissolved oxygen)were collected from 44 discrete sampling stations, spatial interpolation was necessary to construct a continuous surface across Biscayne Bay. Kriging is a popular statistical method used to create interpolation surfaces for conversion to a raster layer in this model (Cressie 1990). Related to regression analysis, kriging offers predictions of unobserved locations based on distances from known, measured values of neighbors. The general kriging equation,

$$\hat{Z}(s_0) = \sum_{i=1}^{N} \lambda_i Z(s_i) \qquad (1)$$

is utilized in ArcGIS to “model the statistical correlation as a function of distance” (Cressie 1990, ESRI 2011). Equation 1 describes the prediction location (s_0) as the sum of measured values at a number of locations (s_i; $i = 1$) and the weights of those values (λ_i). The variable N refers to the number of measured values used in the equation. Unlike inverse distance weighting (IDW) and other predictive methods, kriging relies on spatial arrangement of known values, i.e. spatial autocorrelation, to predict new values. A semivariogram model must be used to quantify this arrangement (ESRI 2011).

$$\boldsymbol{Y(S_i, S_j) = \tfrac{1}{2}\, var\, (Z(S_i) - Z(S_j)^2\,),} \qquad (2)$$

The above equation describes how a calculated value, Y, at two points, S_i and S_j, is related to the difference between observed values, Z, at each of those points. This semivariogram described here is equivalent to the square of values between these two points if there is a constant mean; therefore, closer points have lower values for $Z(S_i) – Z(S_j)$ and higher similarity (ESRI 2011). Prior study of water quality in Biscayne Bay reveals temporal trends in empirically collected data resulting from seasonal fluxes in freshwater input (Irlandi *et al.* 2004). To compensate, ordinary kriging was used create monthly raster interpolation surfaces for analysis of seasonal variations (Cressie 1990).

Following the spatial interpolation described above, Jenks Optimization, also known as Goodness of Variance Fit (GVF), was used to create natural breaks during classification of water quality data into five ordinal ranks. This method is widely used in GIS modeling to create statistically relevant classes designed to group values according to a data distribution (Jenks 1967, ESRI 2011). By specifying attributes (variables) and desired number of classes, an algorithm generates initial class boundaries that undergo an iterative process to reduce the total sum of squared deviations towards a threshold level whereby intra-class variation is minimized. Simultaneously, the algorithm balances the above function with increasing variation between classes to a maximum level. For these models, each of the raster (environmental) layers described above was divided into 5 ranks. This process was performed during all 12 monthly iterations, which resulted in different boundaries for ranks that are both spatially and temporally specific. This design resulted in a continuous gradient of lionfish habitat suitability, which is more useful than binary classification systems used in earlier studies.

The biological significance of the five ranks (classes) described above relied on empirical data from prior studies of lionfish physiology. For those variables not well surveyed in lionfish, the model made assumptions based on field observations and studies of similar marine species. Optimal habitat, especially for invasive species, can be viewed as the spatial and temporal zone where growth and reproduction are maximized (Warren *et al.* 2011). For our purposes, this zone encompasses quantifiable values specific to each of the environmental variables modeled (Table 1). By manipulating the Jenks Optimization so that the mean of rank 5 matches optimal growth/reproduction values, we effectively created the best habitat suitability class specific to lionfish.

Subsequent classes represented declining habitat suitability for lionfish in Biscayne Bay. The mean of each descending class (4-1) indicates a lessening degree of quality relative to the optimal (class 5) values. This system quantified spatial and temporal deviation of values from the optimum for all given environmental variables into each habitat class. Optimization of these variables is an independent process, so the datasets (salinity, temperature, dissolved oxygen, rugosity) were individually categorized at each monthly iteration. Theoretically, class 5 should support the highest concentrations of lionfish, with numbers decreasing significantly in each of the following classes.

Final monthly habitat suitability models were created using Spatial Analyst, a suite of GIS tools to manipulate mathematical syntax operations to transform and join multiple raster layers (ESRI 2011). The summation function contained in weighted overlay was used to combine five variable layers into a final monthly output. This function operates by calculating a composite class value at each location (point) within the study area from the mean of original existing values, which may or may not be weighted. For example, let’s consider a hypothetical point with the following habitat class designations: temperature (5), salinity (4), dissolved oxygen (4), rugosity (3), and benthic cover (5). The mean value determined by the raster calculator would be 4.2, which results in a composite class of 4 at that location. All ordinal data classes must exist as integer values; therefore, Spatial Analyst will automatically round non-integer values to the closest whole number (ESRI 2011). With no clear indication of which variables were the most significant in defining habitat suitability for lionfish, each was tested at different weights to determine a best fit scenario for the monthly models. An example of how water quality layers are combined to produce a final output is shown in Figure 1.

Map Corroboration

To test the accuracy of the models, predicted habitat suitability values were compared to lionfish sightings data obtained from the USGS-NAS. While this dataset is far from a complete assessment of lionfish presence/absence, it offers empirical data to cross reference against the models and determine their relative accuracy. Sightings were separated by month and plotted onto the habitat suitability maps, which allowed us to utilize tools from Spatial Analyst to compare to predictive values.

Results

Model Modifications

Following initial analysis and reclassification of raster layers (Figure 1), it was evident that none of the interpolated values for water quality (temperature, salinity, and dissolved oxygen) or rugosity approached optimal physiological ranges for lionfish. This may explain why a majority of lionfish sightings reported have been outside Biscayne Bay in areas of high rugosity with marine-like water quality. Nevertheless, we continued to refer to class 5 as optimal and compensated by adjusting the parameters of the Jenks Optimization that ranked the class of values closest to the optimum range as 5.

Respectively, ranks 4 through 1 decreased in statistically significant amounts to represent declining habitat suitability for lionfish.

Habitat Suitability

At this point it is critical to remember that these models are not designed to predict a binary presence or absence of lionfish at various locales throughout the study area. Rather, we sought to identify trends in spatial and temporal characteristics of environmental conditions where lionfish can maximize growth and reproduction, two aspects essential to the success of invasive species.

Seasonal fluctuations in environmental parameters have long been described as a driving force for habitat suitability of many species in Biscayne Bay (Serafy *et al.* 2003). Understanding the influence of each variable is critical to analyzing the model outputs. Resulting data from spatial interpolations of water quality indicated that salinity undergoes the most significant intra- and inter-monthly variations across Biscayne Bay. The mean monthly range for salinity is 13.3 ppt (~35 ppt to ~22 ppt), which clearly indicates the presence of an important heterogeneous salinity gradient across the Bay. Outputs from interpolation models for dissolved oxygen and temperature revealed more homogeneous intra- and inter-monthly values with mean monthly ranges of 1.6 g/mL and 1.4°C respectively.

Analyses of the model outputs indicated a distinct striation of habitat classes radiating eastward from the shoreline of Biscayne Bay out towards the Atlantic Ocean (Figure 2). A noticeable trend in the data occurred whereby both habitat suitability and class size increased towards the east. The least suitable habitats, class 1, were restricted to the coastal mangroves and seagrass beds of the central and southern Bay within the confines of Biscayne National Park. This was the smallest class by size, comprising roughly 4% of the total 788 km^2 study area. Class 2, with an average area of 14.2%, was distributed along coastal areas and extreme northern and southern regions of Biscayne Bay. Much of the area between mainland Florida and the northern barrier islands, e.g. Miami Beach and Key Biscayne, was occupied by habitat classes 3 and 4 (Figures 2 and 3). These divisions comprised average areas of 23.2% and 26.7% and extended in bands running from the northern boundaries of the Biscayne Bay watershed down the center Bay towards Turkey Point. The final, and most suitable, habitat class also happened to be the largest. Class 5 comprised about one-third of the area in Biscayne Bay, most of which was located in the central region immediately adjoining the Atlantic Ocean known as the Safety Valve. Benthic habitats in this area range from small patch reefs to vast seagrass meadows, faunal plains, and other diverse ecological communities.

Despite high seasonality in ambient water quality characteristics across Biscayne Bay, corresponding data revealed little temporal fluctuation in spatial distribution of the five habitat classes throughout the year. Habitat class 1 varied in area between a high of 4.72% (37.27 km^2) of the total study area in October, to a low of 3.38% (26.66 km^2) in May. Visualization of these slight changes showed the values to be almost indistinguishable when monthly outputs are compared. This trend is also evident for habitat class 4, which fluctuated between a low of 26.08% (205.76 km^2) in November to 27.23% (214.82 km^2) in May, and habitat class 5, with a low of 31.09% (245.26 km^2) in August to a high of 32.65% (257.53 km^2) in May.

Habitat classes 2 and 3 displayed an inverse relationship in their total area over the summer months (May through August). During this time the distribution of class 2 decreased slightly, while class 3 increased (Figures 3). Following little change during the spring, rapid acceleration occurred between July and August where class 2 increased from 95.38 km^2 to 122.78 km^2 and class 3 fell from 194.63 km^2 down to 175.50 km^2. These data indicate a shift towards a decline in summertime habitat suitability across near shore habitats in Biscayne Bay.

Corroboration with Lionfish Data

Between 2004 and 2012 117 lionfish sightings were reported to the USGS-NAS for Biscayne Bay. These values represent a combination of those recorded via scientifically designed sampling efforts by the National Park Service and other government agencies along with randomly reported sightings by civilians. For the latter data points, only those reporting similar criteria to the scientifically backed sets were used. Following the construction of monthly habitat models, these data points were assembled into a layer and projected as independent data points on the monthly model outputs. The spatial distribution of lionfish sightings with respect to habitat class is shown in Table 2.

Lionfish sightings were heavily clustered (79%) in habitat class 5, representing conditions best fitting optimal growth and reproductive ranges from literature values (Table 2). Sightings declined significantly in each subsequent habitat class, with classes 4 and 3 having a combined 20% of the sightings and classes 2 and 1 with less than 1%. Use of the standard deviational ellipse tool in ArcGIS 10.1 allowed for comprehensive analysis of any directional bias present in the lionfish sightings data. This tool functions by determining mean coordinates for a dataset and identifying points within one or more standard deviations from these values (ESRI 2011). Figure 4 shows the original points along with outputs containing one (68% of values) and two (95% of values) standard deviations. The first standard deviation ellipse lies on a northeast to southwest orientation between the northern and southern barrier islands. Sighting values contained within this polygon were clustered in the top habitat classes 4 and 5. A second standard deviation ellipse displays the same directional trend as the prior; however, this polygon extends to envelop most of the northern, central, and southern portions of Biscayne Bay more than 5 km away from the shoreline.

Discussion

Model Limitations

Although our models perform well relative to the available sightings data, there are inherent limitations difficult to account for. Each dataset was formatted specifically to the needs of its creators; therefore, the use of different units, datums, projections, and other features created some discrepancies during modeling. For example, the base layer upon which the entire model rests was created in the NAD83 (2011) datum. All subsequent layers and data had to be transformed into this datum for proper convergence, thus resulting in placement errors for certain features. Fortunately, algorithms internal to ArcGIS mitigated most errors to only a few meters, reducing any significant effects on data outputs (ESRI 2011).

Issues with data availability also provided model limitations. Since benthic habitat and rugosity layers were provided by BNP, there was higher resolution for areas contained within park boundaries. Data from the National Oceanic and Atmospheric Administration (NOAA) and FDEP were used to create layers for the remainder of Biscayne Bay; however, these datasets lacked the resolution of those provided by BNP. Corroboration of our models with actual lionfish sightings brought about other issues of data availability. While this database is maintained by USGS, inputs originate from hundreds of different sources, ranging from academic institutions to private individuals and consultants. Although all of the data used were verifiable and complete, without a specified scientific sampling regimen it can be difficult to standardize for model validation.

Spatial interpolation is accepted as an accurate means to predict data for unobserved locations; however, predictive methods always contain some level of uncertainty in modeling real world processes. Continuously shifting currents, tides, and hydrological features make predictions of water quality highly spatially and temporally dependent. To account for directional biases resulting from these phenomena we utilized tools to predict anisotropy This attempts to smooth the hourly changes to longer term average change.

Every model must make assumptions that simplify real world processes to best elucidate some phenomenon. For our models, minor deficiencies resulting from the available data and methods that we chose do not diminish the accuracy and importance of model outputs. Slight deviations have little impact on the artificially constructed habitat suitability classes other than shifting them by a few meters. Overall, the model was successful in fulfilling its purpose: to define a gradient of habitat suitability for lionfish across Biscayne Bay.

Habitat Suitability Evaluation

Although these models do not consider every available aspect of the environment, inclusion of key water quality variables and benthic habitat features have yielded accurate predictions of suitability for fish in marine, freshwater, and estuarine habitats (Rubec *et al.* 1999). Additionally, the use of GIS provides a well-supported framework for necessary spatial and temporal interpolations to generate dynamic models encompassing the study area.

While lionfish have been sighted in low-salinity estuarine systems, their physiology has evolved to have highest fitness in stable marine conditions, such as those found in native habitats across the Indo-Pacific (Whitfield *et al.* 2002). This being the case, we expect growth, reproduction, and dispersal to be maximized in class 5 for reasons described above. All 12 iterations of the model describe habitat class 5 with the most stable, least fluctuating water quality parameters throughout the year. Mean values for temperature (25.9°C - 26.5°C), salinity (33 ppt - 36 ppt), and dissolved oxygen (6.5 g/mL - 7.2 g/mL) in class 5 indicate a strong affinity to marine conditions (Caccia and Boyer 2005).

Figure 2 shows that habitats occupying this optimal class designation border the Atlantic Ocean, which may explain ambient stability and marine water quality variables. Additionally, these habitats tend to be farther from the mainland, with an average minimum distance of 5 km. This is significant because freshwater fluxes during the rainy season can severely alter water quality across near shore benthic habitats. Runoff from natural and anthropogenic sources has been observed to drop salinity levels in these habitats down below 20 ppt, which seems to account for declining spatial and temporal habitat suitability along the coastline (Irlandi *et al.* 2004). As depth increases farther from shore, from an average of 1.8 m to over 4 m in class 5, water quality tends to fluctuate less. This is especially true for temperature; shallow areas of Biscayne Bay are more susceptible to rapid temperature changes from extreme heat or cold than deeper ones.

The most startling prediction from our models is the spatial distribution of optimal habitat for lionfish across the Bay. With almost a third of the total area identified as class 5, the implications are daunting. Our models suggest that vast expanses of Biscayne Bay could support viable populations of lionfish throughout the year near a physiological optimum. Even in sub-optimal near shore habitats defined by the model, lionfish populations may be sustained for most of the year. Limitations on the potential range of lionfish appear to be slight, as evidenced by sightings of permanent populations in areas of low salinity and temperatures (Jud and Layman 2012, Kimball *et al.* 2004). The currently occupied Biscayne Bay habitats may ultimately provide a refugia for population expansion into other parts of the Bay where lionfish have not yet been sighted. Proximity to the Atlantic Ocean and Gulfstream may also disperse lionfish, which drift as larvae for up to a month, to other areas outside of South Florida (Whitfield *et al.* 2002).

Although further scientific testing is necessary to verify how accurate our models are at predicting lionfish habitat suitability, corroboration with existing sightings data from the USGS-NAS database is very promising. Close to 79% of sightings occur within habitat class 5, with statistical analysis further indicating clustering along a NE/SW bias adjacent to the Atlantic Ocean. These findings indicate class 5 as a good match for optimal habitat, especially given the strong assumption that lionfish preferentially inhabit stable areas with marine water quality. Declining sightings in lower habitat classes may indicate a rapid drop off in lionfish productivity. Unfortunately, without a uniform sampling methodology for these collections, these findings may be an artifact of errors due to unequal sampling. Bioenergetics modeling is planned to attempt to quantify the degree of viability for lionfish populations in each of the five habitat classes.

Conclusions

The onset of a biological invasion is a critical stage where understanding the spatial and temporal context of potential impacts for rapidly establishing invasive species on native ecosystems is of utmost importance. To assess these factors requires critical information about the predicted distribution of individuals across habitats within the range. For the lionfish invasion in Biscayne Bay, the use of HSMs presented in this manuscript may prove to be useful and straightforward for ecosystem managers.

Although our findings suggest little flux in lionfish habitat suitability throughout the year, changes in area of classes 2 and 3 (Figure 3) during summer months may be significant in determining lionfish distribution. During increased freshwater inputs into Biscayne Bay in the wet season (May – October), near shore habitats routinely experience hypo-saline conditions that facilitate fish migrations (Serafy *et al.* 2003). As lionfish are year-long spawners, these salinity gradients may disrupt larval settlement into near shore habitats. Datasets from NOAA, which maintain comprehensive monthly survey data of mangroves, seagrass beds, and other near shore habitats, have yet to identify a single lionfish between 1990 and present in Biscayne Bay. These findings appear to support our model restricting habitat suitability within 5 km of the shoreline.

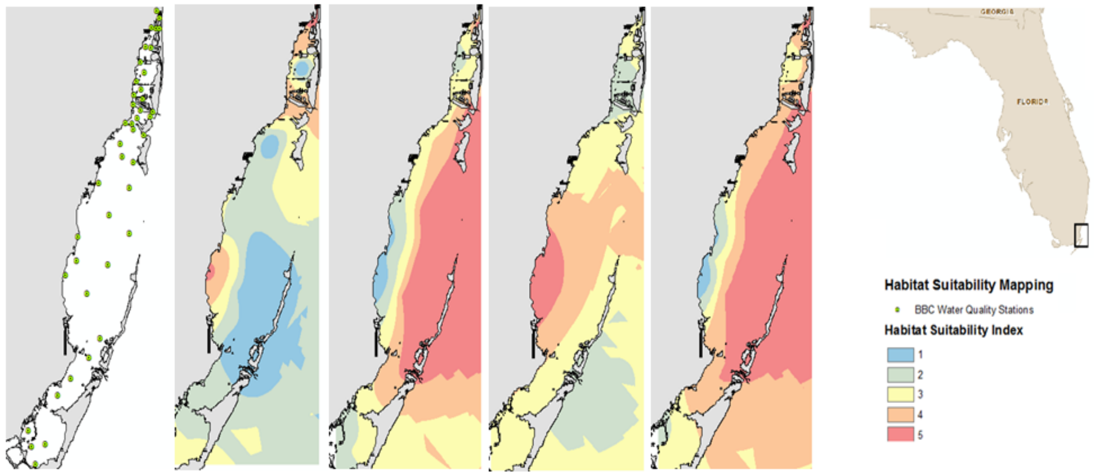
In theory, this modeling technique is easily replicable for other species, provided similar or higher quality environmental and species-specific data are available. Alterations or improvements to the models are dependent on the needs of the end users, who might range from environmental managers to scientists. Ideally, studies of smaller areas could yield model resolutions down to a daily time step. If the range being modeled has more complete and uniform input data, then accuracy could be increased as slight errors and discrepancies following data combination are diminished. Manipulation of variables and inclusion of other dynamic features, such as a three-dimensional hydrology, could also improve model functionality.

Table 2.1 Optimal values for lionfish suitability.

Environmental Variable	**Value(s)**	**Source(s)**
Temperature	29.8°C (consumption) 26.5°C (mean value)	Cerino (2010) Johnston and Purkis (2011) Kimball *et al.* (2004)
Salinity	36 ppt (mean value)	Johnston and Purkis (2011) Whitfield *et al.* (2002)
Dissolved Oxygen (DO)	7 g/mL	Claireaux and Lagardere (1999)
Rugosity	2 units	Wedding *et al.* (2008) Green *et al.* (2012)

Table 2.2 Lionfish sightings from USGS-NAS database by habitat class.

Habitat Class	Lionfish Sightings	Percentage by Class
1	0	0%
2	1	1%
3	7	6%
4	17	14%
5	92	79%



WQ Stations Temperature Salinity Dissolved Oxygen Habitat Suitability

Figure 2.1 Progression of map layers for water quality variables and study area. Panel 1, furthest to the left, shows the locations of 44 water quality stations across Biscayne Bay where raw data were collected for this project. Panels 2-4 each show a series of hypothetical final outputs for spatial interpolation (kriging) of individual water quality variables. The kriging process relies on averaging 12 years (2000-2012) of continuous data at each of these locations to compensate for inter-annual variation and accurately quantify the seasonality of these variables in Biscayne Bay. Panel 5 represents the final habitat suitability map, which combines classifications from the three previous layers via Map Algebra operations as described in the methods.

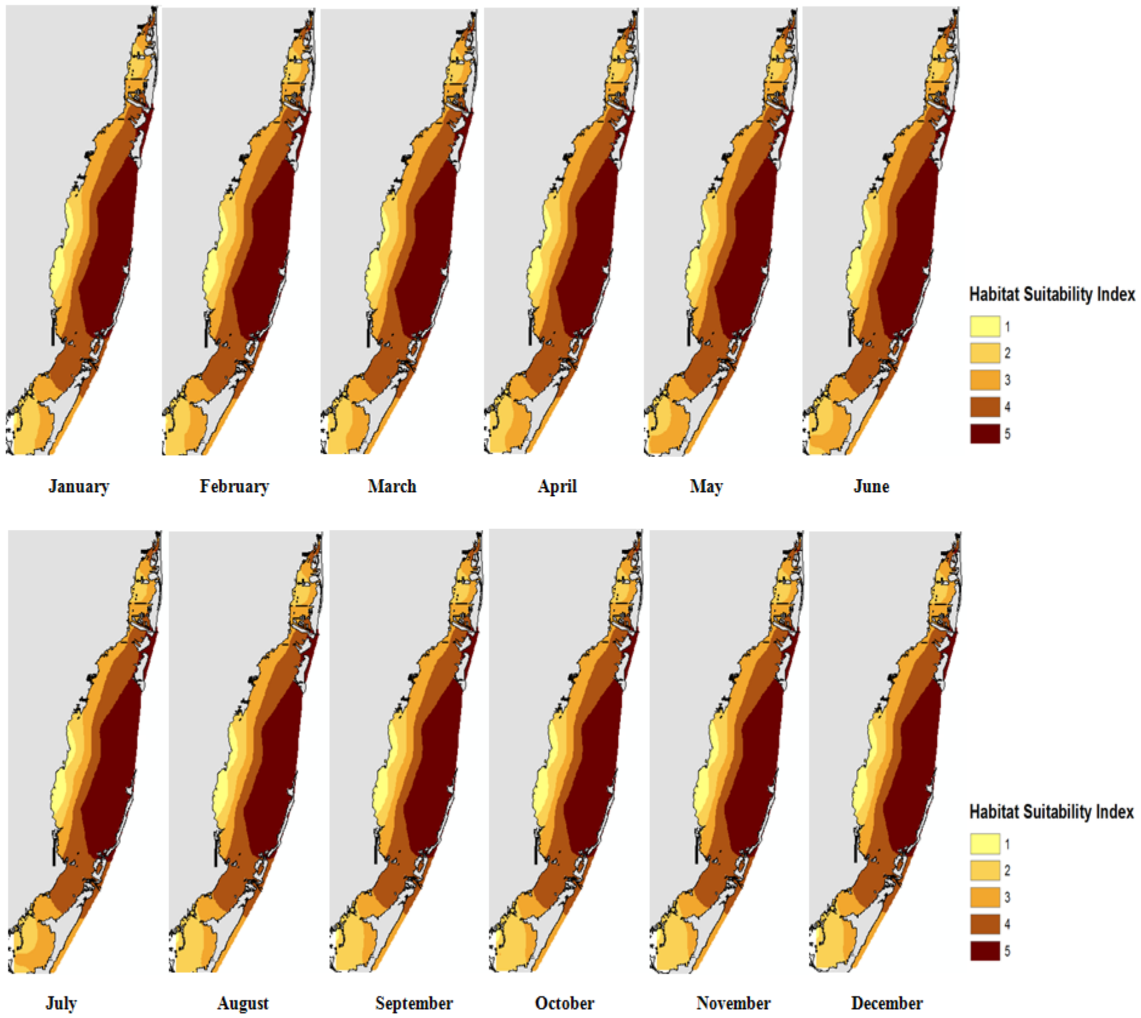


Figure 2.2 Optimal habitat (class 5) is the most prolific, occupying about one-third of the study area. Habitats close to the coastline tend to be of lesser quality for lionfish, with a noticeable increase in size and suitability radiating eastward from shore. Noticeable differences in area of both class 2 and 3 are evident in these summer months.

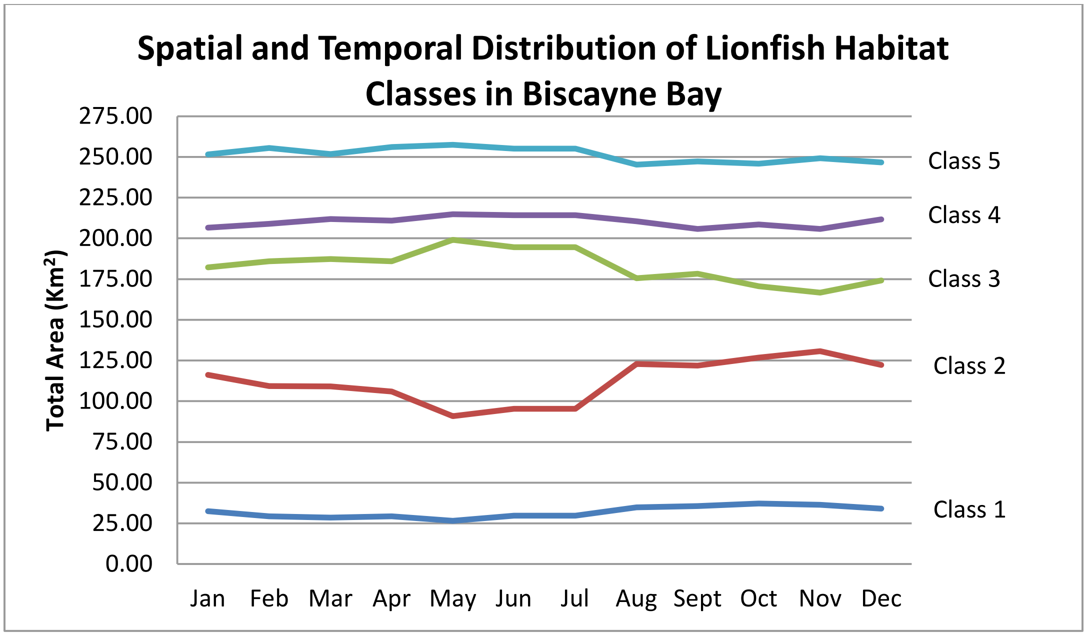


Figure 2.3 Change in area of habitat classes over time. Classes 1, 4, and 5 change very slightly throughout the year, while classes 2 and 3 exhibit and inverse relationship, with class 2 decreasing over the summer and class 3 increasing in area during the same time.

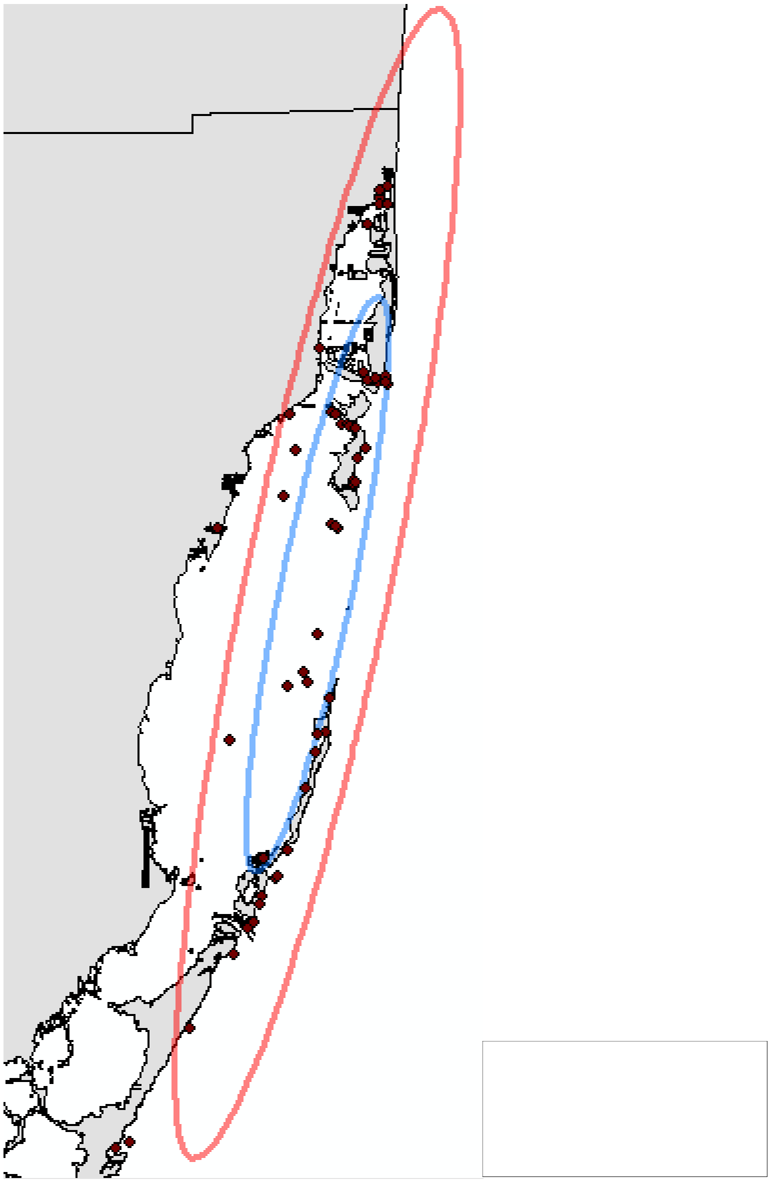


Figure 2.4 Statistical analysis of reported lionfish sightings. Raw data as reported to the USGS-NAS database between 2004 and 2012 is depicted as diamond points. SD 1 represents an ellipse containing points within one standard deviation from the center (mean). Clustering of sightings along the border of Biscayne Bay and the Atlantic Ocean is evident from this figure. SD 2 expands the ellipse to include two standard deviations, or 95% of values, which continues along a similar trend as SD 1.

Chapter 3. DEFINING THE ROLE OF STRESSORS ON BIOENERGETICS OF INDO-PACIFIC LIONFISH

Background

A major impact following the lionfish (*P. volitans*) invasion of a given area is a clear reduction in recruitment of native fish species to benthic habitats (Albins and Hixon 2008). Prior studies on feeding ecology suggest that these cumulative effects may result from rapid consumption of a wide range of prey items (Morris & Akins 2009, Morris and Whitfield 2009). In the case of Biscayne Bay, analysis of over 500 lionfish stomachs revealed consumption of 916 prey species comprising 406 fish species (12 families), 509 crustaceans, and 1 gastropod (Harold *et al.* unpublished data). This generalist diet may have significant overlap with diets of native fishes, such as those from the Snapper-Grouper complex, occupying a similar niche (Morris *et al.* 2009).

Whether an invading species, such as the lionfish, can significantly alter the community that it invades depends, first of all, on the ability of the species to survive in the novel environment, and secondly on its ability to increase in numbers to a sufficient degree to exert competitive or predatory pressure on native species. Anecdotal evidence suggests that lionfish can tolerate a wide breadth of environmental conditions (Jud & Layman 2012). But quantification in terms of its fitness across this range of conditions has yet to be determined. The question we are asking here is whether lionfish is likely to survive and possibly to flourish in Biscayne Bay. Subsequent work will attempt to predict the effects of a substantial population of lionfish on the existing community in Biscayne Bay

Seasonal and spatial variation in ambient water quality for lionfish throughout the 1100 km^2 Biscayne Bay watershed has been analyzed in Chapter 1. A prediction from the statistical models in that paper regards the spatial distribution of optimal habitat for lionfish across the Bay. Almost 1/3 of the total area was identified as very good habitat. The models seem to suggest that large expanses of Biscayne Bay could support viable populations of lionfish throughout the year by maintaining environmental variables very close to the physiological optimum. Even in sub-optimal near shore habitats defined by the model, lionfish populations may be sustained for most of the year. Limitations on the potential range of lionfish in coastal southern Florida appear to be slight, as evidenced by sightings of permanent populations in areas of low salinity and temperatures (Jud and Layman 2012; Kimball *et al.* 2004).

However, these results are mostly based on somewhat patchy occurrence data, rather than rigorous studies, and do not necessarily indicate the long-term success of the lionfish population. To better determine the range of viability of the lionfish across Biscayne Bay, it is necessary to determine, on a physiological level, how the lionfish cope with the range of conditions, including conditions that can be considered stressors on the fish.

To better comprehend the underlying factors that allow or prevent spatial and temporal impacts of a biological invasion, energy requirements must first be identified. Bioenergetics is a field of applied modeling that is particularly relevant to such a task. By quantifying energy allocation and use for individuals, this methodology allows for accurate estimations of maintenance, growth, and reproduction (Hartman and Kitchell 2008). These models have been used for decades to unravel the impacts of particular fish populations on aquatic communities on many different scales (Kitchell *et al.* 1977, Rice *et al.* 1983, Stewart *et al.* 1983, Hewett & Johnson 1987). Our goal here is to extend an existing bioenergetics model (Cerino 2010). In particular, we add aspects to the model that allow us to better assess the effect of environmental factors of temperature and salinity, as well as food intake, on the growth and survival of individuals. We examine the model under a range of conditions typical of regions of Biscayne Bay.

Methods: Models

Winberg (1956) outlined the basic tenets of fish bioenergetics through the following equation:

$$Consumption = Growth + R + S + F + U \tag{1}$$

where all processes requiring energy are summed to equal *Consumption*, representing biomass consumption. Somatic and gonadal (reproductive) growth are represented by *Growth,* and metabolism, as a factor of respiration, is represented by *R*. Specific dynamic action (*S*), egestion (*F*) and excretion (*U*) comprise the remaining model parameters. These latter three are constant fractions of consumption in this equation, while consumption and respiration are weight- and temperature-dependent functions.

Cerino (2010) modified this basic model "to determine the effect of temperature and body size on the consumption and respiration rates of lionfish across the range of thermal tolerance." Laboratory and field data collected from populations in the western North Atlantic Ocean were used to calibrate the model. Data suggest maximum consumption rates for lionfish occur at 29.8°C, which was extrapolated to estimate feeding rates for wild populations. Building upon this foundation, we develop here a more comprehensive model for lionfish bioenergetics that includes allocations to reversible and irreversible biomass, reproduction, and thresholds for mortality. The model specifically addresses environmental conditions in Biscayne Bay, Florida, where salinity is variable. Additionally, this model will incorporate data on feeding ecology to infer impacts on the trophic structure of benthic habitats in Biscayne Bay.

Bioenergetics:

Following Cerino (2010) we start with a general equation for energy balance that equates consumed energy with its allocation to several uses in the fish (Winberg 1956), but is modified to express growth as a function of consumption minus losses;

$$Growth = Consumption - R - S - F - U \;. \tag{2}$$

Here $Consumption$ is the instantaneous rate of consumption;

$$Consumption = p * C_{max} f_{Temp,c} \tag{3}$$

where C_{max} is the maximum possible rate of consumption per unit biomass of the fish, $f_{Temp,c}$ is a function of temperature that decreases $Consumption$ when the ambient temperature is not at the optimum for the fish, and p represents the fraction of the maximum biomass of prey that the fish was able to capture and ingest. The term R represents respiration;

$$R = RA * W^{RB} f_{Temp,r} ACT \;. \tag{4}$$

The set of factors $RA*W^{RB}*f_{Temp,r}$ represents the per unit biomass respiration at rest, modified by temperature. The variable W is fish wet weight, RA and RB are constant parameters, and the factor ACT is a multiplier that accounts for the level of activity above resting. The term F is the fraction of consumed energy per unit biomass that is egested;

$$F = FA * Consumption\,; \tag{5}$$

U is the fraction of energy consumed per unit biomass excreted;

$$U = UA * Consumption\,; \tag{6}$$

and S is the specific dynamic action, or energy used in digesting food;

$$S = SDA * (Consumption - F),$$

where *FA*, *UA*, and *SDA* are constants. We follow Cerino (2010) further to use a functional form for C_{max};

$$C_{max} = CA * W^{CB} \tag{7}$$

where *CA* and *CB* are constants, and functional forms for $f_{Temp,c}$ and $f_{Temp,r}$, which are given by

$$f_{Temp,c} = V^{x} e^{x(1-V)} \tag{8}$$

where

$$V = \frac{CTM - Temp}{CTM - CTO}$$

$$Z = log(CQ) * (CTM - CTO)$$

$$Y = log(CQ) * (CTM - CTO + 2.)$$

$$X = Z^{2}\left(1 + \left(1 + \left(\frac{40}{Y}\right)^{1/2}\right)^{2}\right)\frac{1}{400.}$$

$$f_{Temp,r} = V^{x} e^{x(1-V)} \tag{9}$$

Where now

$$V = \frac{RTM - Temp}{RTM - RTO}$$

$$Z = log(RQ) * (RTM - RTO)$$

$$Y = log(RQ)*(RTM - RTO + 2.)$$

$$X = Z^2\left(1+\left(1+\left(\frac{40}{Y}\right)^{1/2}\right)^2\right)\frac{1}{400.}$$

The parameter values used by Cerino in the above equations are given in Table 1.

The purpose of our bioenergetics modeling is to determine viability of the lionfish under various environmental conditions; in particular, different temperatures, salinities, and levels of food intake. Two further extensions of the model beyond that of Cerino (2010) are needed to do this. First, the fish mortality must be expressed in terms of lack of ability to balance the energy equation over a period of time, leading to starvation. In order to model possible starvation of fish, it is convenient to divide the biomass of fish into irreversible, W_{irrev}, and reversible, W_{rev}, components, following Persson *et al.* (2004);

$$W_{irrev}(t+1) = W_{irrev}(t) + Growth * FWV \qquad (10)$$

$$W_{rev}(t+1) = W_{rev}(t) + Growth * (1 - FWV) \qquad (11)$$

where FWY is the partition fraction,

$$FWY = \frac{W_{rev}}{W_{irrev}}\frac{1}{(1+q_J)q_J} \qquad \text{(if } W_{irrev} < W_{irrev,f}\text{)}$$

$$FWY = \frac{W_{rev}}{W_{irrev}}\frac{1}{(1+q_A)q_A} \qquad \text{(otherwise)}$$

$W_{irrev,f}$ = size at maturation

where total biomass is

$$W = W_{irrev} + W_{rev}$$

and where q_J, q_A, and $W_{irrev,f}$ are constants. However, for lionfish we do not use $W_{irrev,f}$, but assume that the fish mature at 500 days. The values q_J and q_A are given are for perch, which we will use in our model for the time being, until better values for lionfish are available. After maturation, some fraction of the reversible weight, W_{rev}, can be called on for reproduction.

There is a relationship between the ratio of irreversible to reversible biomass and starvation mortality. For perch (Persson *et al.* 2004) this is given by

$$\begin{aligned} \text{Starvation mortality rate} &= \mu_s(W_{irrev}, W_{rev}) = s\left(\frac{q_s W_{irrev}}{W_{rev}} - 1\right) \quad \text{if } W_{rev} < q_s W_{irrev} \qquad (12) \\ &= 0 \ \ \text{(otherwise)} \end{aligned}$$

where q_s is a constant (see Table 1 for perch).

The second extension that is necessary in the lionfish model of Cerino (2010) is to include the effects of salinity. Just as there is a function f_{Temp} that quantifies the effect of temperature on the consumption and respiration rates, there should exist a function $f_{Salinity}$ that quantifies the effect of different levels of salinity on these rates. Because of the current absence of data for a salinity function for lionfish, we will hypothesize specific relationships using information from similar species to lionfish (see next section).

We are making assumptions, in the absence of hard data at this point, concerning reproduction. Our basic assumption is that energy for reproduction is diverted from reversible growth. We assume that the fraction of energy diverted begins at 500 days (~1.5 years), which coincides with onset of reproductive maturity, and asymptotes at a large fraction of the reversible growth. A general expression for this transition is

$$Re\,production = \frac{Re\,prod_1 e^{k_{reprod}(t - t_{reprod})}}{1 + Re\,prod_2 e^{k_{reprod}(t - t_{reprod})}} \qquad (13)$$

Here $Reprod_1$ and $Reprod_2$ are constants whose ratio, $Reprod_1/\,Reprod_2$, is the ultimate fraction that is diverted to reproduction as the fish ages, k_{reprod} is the sharpness at which the fish transitions to allocation to gonadal growth, and t_{reprod} is the age at which the diversion reaches the half-point. As in Cerino (2010), these constants represent a loss rate of 1% reversible lionfish body weight as a result of each spawn. This correlates to 0.25% of reversible weight lost per day, which is multiplied by the *Growth* term to yield reversible weight. In the model, reproduction can shut down if reversible weight, W_{rev}, falls below the ratio with irreversible weight, W_{irrev}, specified in Equation (12).

Effects of salinity stress:

Our model uses the same balanced bioenergetics equation as presented in the section above, which serves as a template for additional parameters, such as the effect of temperature. We want to include salinity as a third factor, besides consumption and temperature, affecting growth. It is convenient to think of both temperature and salinity as potential stressors, when either of them deviates from the values that are optimal for the species. That is, we assume that stress on individuals results from environmental conditions deviating from optimal levels. The Cerino (2010) model describes consumption as a function of temperature, whose correlation has been well established in many marine species (Palomares and Pauly 1989). Our model also includes stress caused by changes in salinity gradients, which is common in many coastal estuaries and lagoons.

Salinity has been described as a dominant environmental stressor driving bioenergetics of native fish populations in Biscayne Bay (Serafy *et al.* 2003). Since lionfish typically display high site fidelity, long term exposure to various salinity levels must be accounted for in our model (Jud & Layman 2012). By quantifying the impacts of this stressor on lionfish, we can determine the energetic costs of osmoregulation and how these changes ultimately result in altered growth and consumption parameters under different salinity levels (Rao 1968, Nordlie *et al.* 1991).

To perform this task we must first describe how salinity mediated stress will impact the variables in the bioenergetics equation (2). One possible hypothesis for modeling the effects of salinity is that it is possible to treat salinity in a similar manner as a pollutant in studies of fish ecotoxicology, whereby the effects of a compound on an individual or population are predicted over a period of time (Truhaut 1977). Changes in energy expended to combat this stressor equate to the innate cost of osmoregulation relative to its concentration (salinity gradient). A general function for the level of stress on a model process:

$$s = \frac{1}{c_T} \max(0, c_0 - c_v) \tag{14}$$

is derived from the Dynamic Energy Budget (DEB) theory, which allows for "analysis and interpretation of toxicants effects on life history traits such as growth, reproduction, and survival" (Jager and Zimmer 2012). Assuming that sufficiently low salinity is a stressor, then stress (*s*) increases in a linear fashion once salinity has fallen below the "no-effect concentration" (c_0 here, for consistency with Jager and Zimmer 2012), with c_v representing the deviation of the salinity from c_0 and c_T controlling the strength of the effect of increasing deviation. This information can be visualized in Figure 1.

We assume here that salinity stress affects only has a direct effect on the respiration, *R*; that is, respiration becomes *R* (1 + *s*). Values from these adjustments can be directly incorporated into models to quantify changes in consumption under different salinities to maintain observed growth and respiration rates. Additionally, graphical analysis will yield a series of curves describing tolerable ranges for growth and respiration across a salinity gradient similar to that found in Biscayne Bay. Little specific data on salinity tolerance for lionfish, or the stress effects of deviations from the optimal value, are available to us at present. There are relevant data, however, from Jud *et al.* (2014) showing healthy survival of lionfish over long time periods at 5 ppt. For simplicity we can tentatively assume that the mean levels of open ocean salinity are optimal for the lionfish and that salinity remains optimal down to 5 ppt. Data for species that are believed to be physiologically similar to lionfish to estimate the effect of salinity are reviewed in the Appendix..

Modeling growth:

We can simulate the growth of an individual fish from the post-larval stage by solving the differential equation, where relative growth rate, *Growth*, or growth rate per unit biomass, is;

$$\frac{dW}{dt} = Growth * W = (Consumption - R - S - F - U) * W \quad , \tag{15}$$

where R is now replaced by $R(1 + s)$. This integration occurs over the life span of the individual (with t being equated to age) and will produce results concerning survival and reproduction under given conditions. The conditions that will be studied are the following: effects of prey availability, p, temperature, *Temp*, and salinity stress, s.

Using equation (15), these conditions will be manipulated in a series of simulations designed to model average and extreme conditions found in Biscayne Bay. Integration will occur on daily time steps for up to 15 years, which is the average lifespan of lionfish in the wild (Morris and Whitfield 2009). Feeding rates will be adjusted based on field observations (Albins and Hixon 2008, Green *et al.* 2011). The effects of a temperature continuum on lionfish respiration and consumption have been examined by Cerino (2010) through laboratory experiments. Our model will incorporate resulting data from this study that matches observed values/gradients for the study area. Salinity tolerance has not been well studied in lionfish, other than observation of populations persisting at low levels (<10 ppt) (Jud and Layman 2012), and more recent work showing long-term survival at 5 ppt (Jud *et al*. 2014). Since hypersaline conditions are not present in the study area, our models will focus on determining the effects of salinity gradients ranging from marine levels (30-40 ppt) down to hyposaline conditions (0-10 ppt).

Estimation of proportion, p, of maximum rate of ingestion:

The value of *p*, that is, the rate of ingestion of prey by a lionfish as a proportion of its maximum possible rate of ingestion, is the crucial factor in determining whether or not the lionfish can survive in an environment and what its reproductive output will be. In principle, the ingestion rate of prey can be calculated if both the stomach contents and rate of decomposition of the prey in the lionfish stomachs are known. In that case, one could write an equation;

$$\frac{dSc(t)}{dt} = pC_{\max} - \alpha Sc(t) \tag{16}$$

where *Sc(t)* is the stomach contents and α is the rate of prey decomposition. Then, at steady state,

$$p = \frac{\alpha Sc^{*}}{C_{\max}} \tag{17}$$

where *Sc** is the steady state equilibrium stomach content biomass.

Since Morris and Akins (2009), as well as a few others, have compiled extensive databases for lionfish gut content, input data to calculate *Sc* should be relatively straightforward. This approach will work well, as the majority of stomachs of lionfish contain amounts of prey biomass that are close to the mean over the whole population. This situation should hold true as prey are relatively small compared with the predator, with a mean 14.5% of the total length, and are consumed at a relatively high rate (0.089g prey/lionfish g). In this case, *Sc** can be taken to be the mean biomass per stomach.

At present, there are no direct empirical measures of lionfish prey turnover rates (α) in the literature. To estimate the value of α, we could in principle use laboratory data on known consumption rates, along with stomach contants data to calculate α. Such models have been well studied in freshwater fish and describe evacuation rates as exponential functions which are relatively common across varying taxa (Elliott and Persson 1978, Bromley 1994). Understanding the relationship between said rates and two factors, temperature and prey size, is critical in calculating decomposition rates. We will not pursue calculating evacuation rates here, but leave it for future study.

Methods: Simulations

Using parameters and equations outlined in the prior section, we aim to combine all of these features into a complete simulation of lionfish bioenergetics following Equation 15. This process can be achieved using Matlab 8.2, which is a “multi-paradigm numerical computing environment and fourth-generation programming language” (MATLAB 2013). The base script will allow for complex interactions between mathematical representations calculating each variable in the bioenergetics equation over time. Additionally, programming will incorporate constants for parameter values as defined in previous work by Cerino (2010) and others. This experimental design permits manipulation of any parameter or variable across the entire script and can allow for quantification of impacts on model outputs (consumption, growth, etc.).

The role of both consumption and respiration as temperature-dependent functions in marine fish has long been established, and subsequently confirmed in lionfish by Cerino (2010). To test if our model assumptions are in line with prior studies, we will examine how individuals respond to exposure at temperatures ranging from 10°C to 40°C. Although the range of temperatures observed in Biscayne Bay is much smaller, examining how the model reacts for individuals exposed to both extreme heat (>35°C) or cold (<15°C) can provide insight as to its validity.

With many unknown values and theoretical estimates in the model, it is essential that simulations reflect biologically relevant phenomena. Investigating how lionfish cope with different stressors, apart from temperature, is one of the main objectives of this model. Given the energetic requirements posed by high fecundity and rapid growth rates, it is logical to assume that alteration of the *Consumption* term below a threshold may pose a significant stress to lionfish. Most variation in *Consumption* is likely to come from variations in the parameter p, which represents the fraction of the maximum biomass of prey that the fish is able to capture and ingest. In reality, p is stochastic, as consumption occurs as discrete events, which are partly random. However, for simulation purposes we will assume p is constant during any given simulation, though, because p can vary greatly, as prey availability differs in different situations, including across and within benthic habitats, we will consider the whole range of possible values of *p* in different simulations.

To establish values for *p* that will support lionfish and prevent starvation, which is governed by the amount of energy that is available from *Consumption* to meet metabolic demands, we will utilize Equation (15) as described in the prior section. Empirical data on lionfish diet preference and consumption rates will be used to define the parameters when possible. Once simulations with a range of values for *p* are performed, we can calculate a threshold below which lionfish will trend towards starvation.

Another environmental stressor that can impact survivorship of lionfish is salinity in certain ranges. Similar to other metabolic processes, osmoregulation has the ability to put high energy demands in fish. This parameter, which is incorporated into the model as the stress effect *s*, has a direct impact on the *Respiration* term. Jud *et al.* (2014) found that lionfish can persist at low salinities down to 5ppt with no difference in mortality, behavior, or growth for over one month when compared to subjects at 35ppt for the same time period. With few data available to determine how salinities <5ppt impact lionfish bioenergetics, we will make assumtions in the model to determine trajectories for growth, respiration, and consumption under these stressful conditions.

Results

Varying the Prey Availability, p:

To begin testing the model, we examined how variation in *p* affects biological processes, which are defined by the overall bioenergetics model; consumption, growth, and respiration. As mentioned previously, altering the variable *p* between model runs can simulate how much prey biomass lionfish are able to capture and consume across different habitats. This is critical in understanding what threshold conditions are necessary to sustain lionfish and what factors may ultimately lead to starvation.

Beginning the simulation with a 2 gram lionfish, divided equally between reversible weight, we varied *p* in discrete increments of 0.1 between 0 (no consumption) and 1 (max consumption). This simulation assumed an environment of 25°C and 30 ppt, which coincides with conditions found for Biscayne Bay in Chapter 1. The plots (Figures 2a, b) represent model outputs for total weight and consumption vs. time. Growth rates are plotted against time in Figure 2c. One of the first findings following initial model runs was that *p* values below 0.3 result in negative values for some of the bioenergetics equations. This outcome can be interpreted as death of the individual. Plots for those values are not shown.

As expected, larger values of *p* facilitate increased rates of growth, consumption, and weight (total, reversible, and irreversible). The highest values of growth, and subsequently weight gain, occur from time 0 days until 500 days (roughly 1.5 years), at which reproduction begins in lionfish and energy is diverted away from growth to gonadal output. While growth rates slow as the organisms get larger, they never quite reach an asymptotic state. Consumption and weight continue to increase in a linear fashion across all values of *p* above 0.5, which seems to indicate an indeterminate growth plan that is common across many taxa of marine fish.

One of the most interesting findings from this portion of the study can be seen in Figure 2d, which represents a plot of final reversible/irreversible weight vs. *p*. Although both values increase along with *p* in proportion, the absolute gap between these values also increases rapidly. The model is designed so that irreversible weight always maintains a higher proportion of biomass than reversible weight. Therefore, the disparity between these absolute biomass values is low initially. Overall respiration and maximum consumption (C_{max}) decline as weight increases over time. These measures are identical for all values of p as they are calculated per unit biomass.

Varying the Temperature, TEMP:

In this section we varied temperature between simulations, which remains constant throughout the time period of each simulation, to determine how growth of individuals, in terms of the same variables simulated in the section above, responds to differences in temperature. The relationship between temperature and elements of the bioenergetics equations, such as consumption and growth, has been surveyed in lionfish; therefore, resulting data from our model will be compared to empirical values in the discussion section. Following prior model runs, values for other key variables, in this case salinity and p, were set at 30 ppt and 0.5 respectively. These values coincide with both empirical evidence and assumptions made about ambient conditions in Biscayne Bay.

The manipulation began with a wide range of values from 0°C and 40°C that were plotted as increments of 5°C for consumption, total weight, and growth rate (Figures 3a, b, c). The plot of 30 °C shows the highest rates for all graphs, with subsequent plots declining in value. Initial findings reveal that at temperatures below 10°C and in excess of 30°C the individuals' trend towards negative growth and consumption, resulting in failure of the individual lionfish to survive for those ranges. For clarity, these lines have been removed from the plots.

The model predicts rapid growth and weight gain until age 500 days, which is the age of onset of reproduction. After this time growth rates start to level off towards approximate asymptote at all temperatures (Figure 3c). Total weight and consumption continue to increase throughout the model run; however, these rates slow following reproductive maturity (Figures 3a, b). Both reversible and irreversible weight increase over the model duration as shown in Figure 3d. The gap between the two widens over time as irreversible weight accumulates faster with an increase in temperature; however, despite a growing disparity the ratio between reversible to irreversible weight does not change, because of the effects of *FWY* in altering allocation.

Varying Salinity, s:

Here we tested how long term exposure to low salinities (<5ppt) impacts lionfish bioenergetics as seen in variables for consumption and weight, based on our assumed salinity effects on respiration (Figure 1). While osmoregulation is assumed to cause high stress on respiration, and subsequently increase energy demand in hyposaline environments, none of these variables have been quantified as of yet. Our model plots salinity as increments of 1 ppt between 5 ppt and 0 ppt for time vs. total weight, reversible weight, irreversible weight, consumption, and growth. Although studies suggest that long term exposure to conditions below 5ppt are lethal, this model is designed under the assumption that the effects are on respiration and thus only indirectly on possible mortality. This assumption allows for us to track long term impacts throughout the average life span of a lionfish.

Based on model outputs, salinity has only a slight impact on the above variables until reproductive maturity occurs (Figures 4 a, b, c, d). After this point, which is built into the model at 500 days, the gap between each salinity value becomes wider, taking into consideration that salinity stress effects increase at some rate as ambient levels trend towards zero. As expected, growth, weight (total, irreversible, and reversible), and consumption each decline as salinity is lowered, although they each increase slightly over time. When zero salinity is plotted, the model predicts a trajectory just barely above the x-axis for these three variables.

The most significant influence of low salinity can be seen in its' effects on individual respiration. Figure 5 plots how respiration per unit biomass vs. total weight changes at each of the six salinity levels measured. As predicted by the model and shown in Figure 1, values below c_0 (5 ppt) will decrease in a linear fashion. These trajectories begin to level off around 150 grams that continues across all weights until a terminal size is predicted by the model.

Discussion

Lionfish have evolved to tolerate and thrive in a wide range of environmental conditions, which has allowed them to successfully invade and rapidly proliferate across numerous habitats in the invaded range. Lionfish energy demands are governed by factors such as high fecundity, venom defense, and rapid growth, but are moderataed by its slow swimming speed (Fishelson 1973). In this model, we coalesce knowledge from prior bioenergetics studies of lionfish and augment elements from well-studied fish species to create a model based on the model of Cerino (2010), but more complex in structure to allow defining the effects of temperature, salinity, and prey consumption on the survival of individuals. While some of these additions are not species-specific to lionfish, the assumptions made about unknown variables are biologically reasonable and designed to provide a framework for further empirical research. In this section we discuss our expansion of the lionfish bioenergetics model and what future data needs to be incorporated for improving the model.

One of the most significant findings from this model is determining a threshold for p, which is the rate of ingestion of prey by a lionfish as a proportion of its maximum possible rate of ingestion. In the Cerino (2010) model, p is assumed to be 0.6 for all trials to "fit field measurements for growth." This assumption disregards natural variability in lionfish feeding rates, which can differ between life stages and habitats. Our model extends the model of Cerino (2010) to allow for variation in p to determine when starvation will occur. (This does not, however, take into account the possibility that lionfish might be able to switch to a lower metabolic rate under low food intake rates. We have no information concerning that possibility.)

Assuming favorable ambient conditions (30°C and 30 ppt) the model calculates a minimum value for this variable as 0.3. Below this point consumption rates do not support respiration levels, which results in negative values for the bioenergetics equations. Biologically, this signals a "negative growth" pattern that ultimately leads to starvation of the animal as seen in Equation 12. Empirical evidence suggests that lionfish feeding cessation occurs at 16°C and lethal salinity effects are present below 5 ppt

(Kimball *et al.* 2004, Jud *et al.* 2014). Manipulating these factors independently reveals that alone they have little effect on the threshold of *p*. However, the additive effects of both sub-optimal conditions results in the minimum *p* value rising from 0.3 to 0.4, which falls in line with studies from other marine species showing an increase energy demand resulting from homeostatic pathways, such as osmoregulation, in stressful environments (Jager and Zimmer 2012).

Although we have provided some minimum threshold of *p* necessary to support lionfish, much more information is needed to better understand the correlation between *p* and consumption, growth, reproduction, and respiration in the wild. Much of the data used for lionfish bioenergetics originate from laboratory studies where fish are fed *ad libitum*; therefore the next logical step would be to determine lower values *p* either from field or laboratory studies and integrate those findings into the model. One might assume that seasonal changes and prey availability across habitats may play a major role in defining *p* and subsequently determining where and when lionfish have the essential energy supply to prevent starvation. This information can be plugged into habitat suitability analyses, such as the model described in Chapter 1, to further refine our understanding of what habitats and microhabitats may be available for lionfish to use throughout the year.

As a whole, mortality has not been well surveyed for lionfish. There are three classes of mortality that can be incorporated into a population model: natural, predation, and starvation. The life span is estimated between 10-15 years in captivity, but to date there is little information on how long lionfish can live in the wild; this lack of data is common for a nascent invasion. Predation mortality is assumed to be low, or negligible, for adults and juveniles, as only a few instances of predation by native species (snappers, groupers, eels, etc.) are on record (Morris and Whitfield 2009). There is even less work investigating starvation mortality, which we have made a clear objective to incorporate into this model to provide a gateway in further defining the realized niche of lionfish.

Throughout the life of most fish there exists a delicate balance of growth that is partitioned between reversible (fat, muscle, gonadal) and irreversible (bones, scales, organs) weight (Persson *et al.* 2004). During the life history of an animal there is variable allotment of energy towards both; however, a certain quantity of reversible weight must always be available as a proportion of total weight, or else the animal could trend towards starvation and eventual mortality. Our model incorporates respiration (homeostasis) and consumption as the underlying elements that define when starvation can occur. This improvement upon prior models allows for increased sensitivity in determining realistic conditions that may exclude lionfish from certain environments.

Validating our model assumptions for some of the variables in determining starvation is a critical next step. Recent research has provided good data for consumption rates and respiration, but questions still remain concerning the intricacies of lionfish reproduction. As a highly fecund species that is capable of spawning every four days, lionfish can be assumed to require a significant amount of energy to maintain such an evolutionary plan. The model assumes that energy is diverted from reversible weight to reproduction beginning about 1.5 years, which is in line with field data (Morris and Whitfield 2009). What remains unknown is how readily lionfish can slow or terminate reproduction in stressful environments. Other species, such as brown trout and Australasian snapper, can alter reproductive rates within hours of stress onset via a depression of gonadal steroids (Pankhurst and Van Der Kraak 1997). Future empirical study can validate if this is the case for lionfish, which would refine the model and our overall understanding of lionfish bioenergetics.

Environmental variability lies at the core of our model, as this overarching and often stochastic factor dictates the rate at which variables comprising the bioenergetics equations operate. Of the numerous characteristics that define marine environments, temperature and salinity may be the most influential. The former has long been known to regulate internal processes, and for this reason has received serious attention in lionfish studies. Cerino (2010) describes 30°C as the optimal temperature for consumption based on both field and laboratory studies. This was independently validated by testing a range of temperatures between 10°C and 40°C. As expected, weight (total, reversible, and irreversible) also increases the most over time when conditions are at 30°C.

For growth, there is a much wider range that fosters maximum rates. Plotting model outputs shows little difference for values between 25°C and 30°C throughout most of the life of a lionfish, with convergence occurring after 10 years of age (Figure 8). In the sub-tropics and tropics, these temperatures are readily supported, thus offering lionfish optimal conditions for growth year round (Kimball *et al.* 2004, Johnston and Purkis 2011). The implications of these findings further support evidence that long term impacts of the lionfish invasion on native prey species will be severe. These rates are much faster than assumed for the native competitors in the Snapper-Grouper complex; therefore, a significant shift in local food webs may occur as lionfish overtake the trophic position of these native mid-level predators (Manooch 1987).

Although the role of temperature is well defined, that of salinity is still not well known. Following the assumption that negative effects increase linearly towards zero ppt, the model was outfit to effect respiration rates once salinity becomes lower than a threshold concentration of 5 ppt. The correlation between respiration and other factors in the bioenergetics model assures that stress effects will be well represented in quantifying consumption, growth, and weight. This strategy follows the work of Jager and Zimmer (2012), who use similar justification for measuring the impact of environmental toxins, and was chosen due to the lack of data concerning lionfish salinity tolerance.

The threshold concentration comes from recent work by Jud *et al.* (2014) that supports a minimum threshold of 5 ppt for long term exposure, citing that no difference was found between lionfish held at this concentration vs. marine levels (35 ppt) for one month. It may even be possible that lionfish can tolerate temporary exposure to salinities below 5 ppt, which can occur in estuarine and mangrove systems (Jud *et al.* 2014, Serafy *et al.* 2003). Model output seen in Figure 5 clearly shows an asymptote for all salinity values around 150 grams. This finding seems to coincide with prior empirical evidence that salinity effects are strongest during developmental stages for marine fish, which in turn provides some support that larger lionfish may tolerate low salinity concentrations much better as they age (Truhaut 1977).

Although new evidence seems to suggest that environmental factors may play a lesser role in limiting the range of lionfish, there still exists a monumental gap in data availability. As more information becomes available, the model can be reconfigured to become a closer embodiment of reality. Inclusion of salinity as a natural stressor and limiting factor of bioenergetics processes is an improvement over prior models; however, this work only scratches the surface. With little empirical data to validate this portion of the model, our main goal is to provide a framework so that future research can be incorporated to refine the model. Hopefully, similar techniques can be used to assess impact of other stressors (oxygen, turbidity, pollutants, etc.) as separate and additive entities. Until the role of such stressors on lionfish bioenergetics can be more accurately defined, it will be difficult to assess habitat suitability on a local scale across the native range.

The importance of understanding bioenergetics for an invasive species cannot be overstated, especially in the nascent stages of a biological invasion. Determining how critical factors such as consumption and respiration are affected by ambient conditions (temperature, salinity, prey availability, etc.) can allow us to quantify growth and reproductive capacity across multiple habitats. By focusing on the most productive habitats, environmental managers may be able to selectively control populations of invasive species and minimize long term impacts on native flora and fauna. For lionfish, research has shown that regular culling has the potential to be effective in minimizing impacts and diverting those that do occur away from vulnerable native species (Frazer *et al.* 2012).

If this is truly the case, then the model we present here has the potential to provide assistance in determining very detailed spatial and temporal understanding of where these animals can thrive. Building upon the model developed by Cerino (2010), our bioenergetics model serves to further the understanding of these complex processes by updating pertinent information as it has become available. Additionally, we incorporate quantitative measures of stress to determine how key variables are affected under adverse conditions that may lead to mortality via starvation. There still remain many assumptions made in the model yet to be quantified with empirical evidence; however, we are confident that future research in the field will continue to upgrade the model as we have done.

Table 3.1 Parameter values used in bioenergetics model

Parameter	Value	Description
RA	0.0085	intercept at RTO ($g \cdot g^{-1} \cdot d^{-1}$)
RB	-0.28	slope of allometric respiration function
FA	0.2	egestion/consumption
UA	0.06	excretion/consumption
SDA	0.2	specific dynamic action
CA	0.603	intercept at CTO
CB	-0.465	coefficient of mass dependence
CTM	34.5	maximum temperature (°C) for consumption
CTO	29.8	optimum temperature (°C) for consumption
CQ	3.2	Q_{10} value for consumption
RTO	32	optimum temperature (°C) for respiration
RTM	34.5	maximum temperature (°C) for consumption
RQ	2.08	Q_{10} value for respiration
q_J	0.74	maximum juvenile energy balance
q_A	1.37	maximum adult energy balance
q_S	0.2	starvation mortality threshold (perch)
ACT	1.8	activity multiplier
Reprod	0.005	weight diverted for reproduction

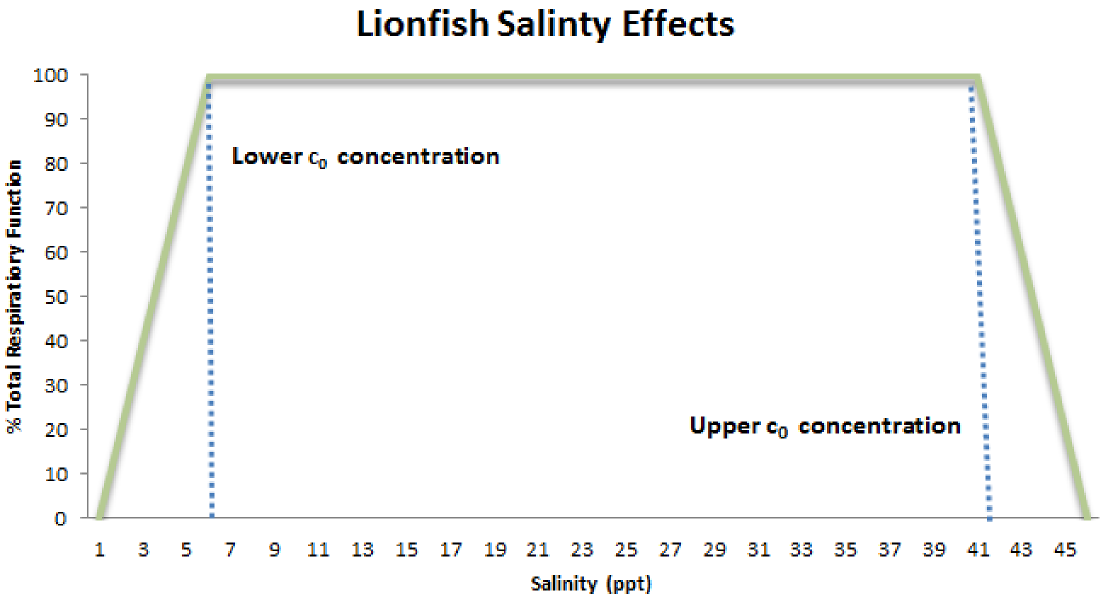


Figure 3.1 Visualization of Equation 14. Describes the lower and upper threshold concentrations for salinity beyond which the organism experiences an impact in respiration rate. The premise of our model rests on extrapolating fish toxicology effects from Persson *et al.* (2004) and applying them in a similar fashion to salinity. Based on findings from Jud *et al.* (2014) that salinity effects are not apparent until concentrations fall below 5 ppt, Figure 1 theoretically demonstrates the linear relationship between salinities below this threshold (c_0) and decline in respiration.

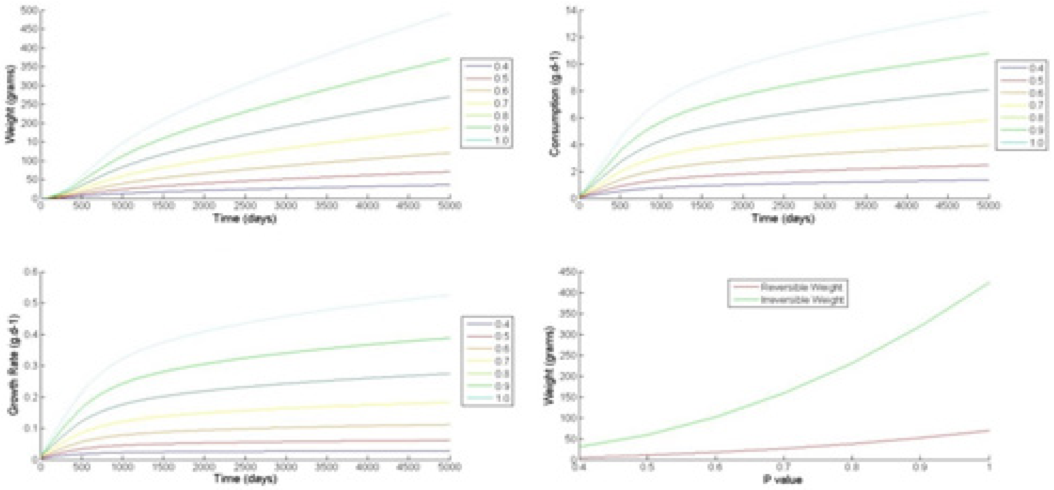
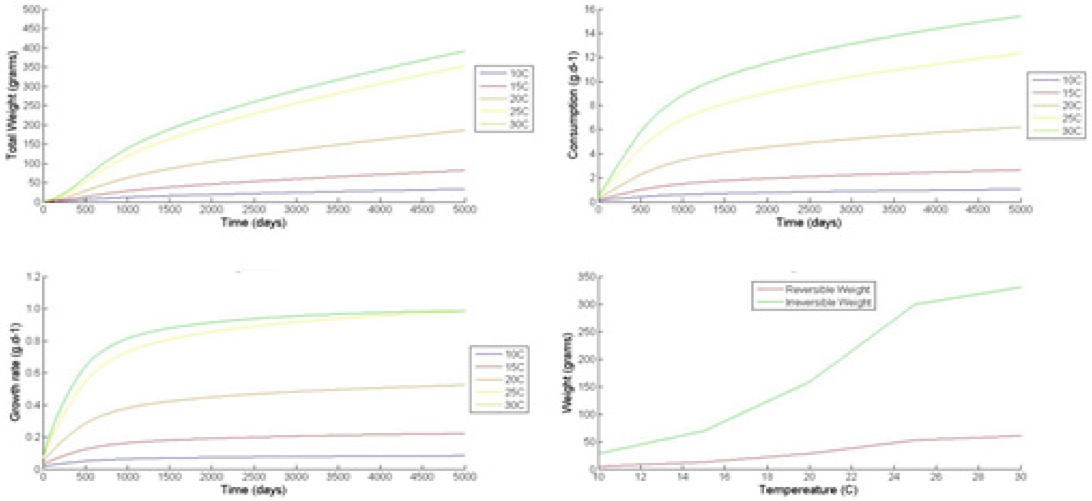


Figure 3.2 Effects of varying *p* on total weight vs. time (a), consumption vs. time (b), growth vs. time (c), and weight vs. *p* value (d). As expected, higher values of *p* yield higher consumption rates, which are manifested in more growth and weight gain for the individual. Values for *p* below 0.4 result in death of the organism and are not plotted on these figures. Although Cerino (2010) used *p* of 0.6 as a constant for determining these rates, the graphs above reveal that weight, consumption, and growth rates can surpass these levels. This may be possible in environments with high prey density. Figure 2d shows an exponential increase of final irreversible weight after 500 days at increasing *p* values, whereas reversible rate increases at a much slower, though exponential, rate due to costs of respiration and reproduction.



Figures 3.3 Effects of varying *Temp* on total weight vs. time (a), consumption vs. time (b), growth vs. time (c), and weight vs. *Temp* value (d). Values for *Temp* below 10°C and above 30°C are not shown as they result in death of the organism. This is in line with prior thermal tolerance studies conducted by Kimball *et al.* (2004). There is little to no difference between total weight (Figure 3a) and growth rate (Figure 3c) for values between 25°C and 30°C, which coincide with ambient conditions found in Biscayne Bay. Figure 2b shows maximum consumption around 30°C and coincides with findings from Cerino (2010). The plot of final reversible vs. irreversible weight (Figure 3d) shows a similar difference between reversible and irreversible weight as that seen in Figure 2d.

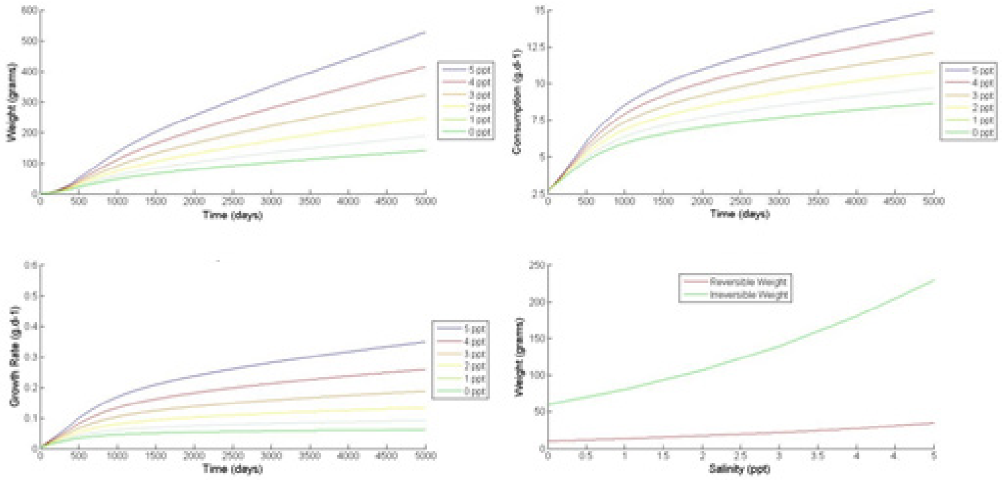


Figure 3.4 Effects of varying *Salinity* on weight vs. time (a), consumption vs. time (b), growth vs. time (c), and weight vs. *Salinity* value (d). Due to the lack of knowledge on empirical effects of low salinity, this portion of the model follows assumptions made in constructing Figure 1. Empirical evidence from Jud *et al.* (2014) suggests that long term survival below 5 ppt is not likely; however, for this model we have excluded mortality to investigate potential lifelong effects of this stress on an organism. Figures 4a, b, and c each show the same correlation; as *Salinity* decreases, so does total weight, consumption, and growth. The plot of final reversible vs. irreversible weight (Figure 4d) shows a similar differences between reversible and irreversible weight as that seen in Figure 2d.

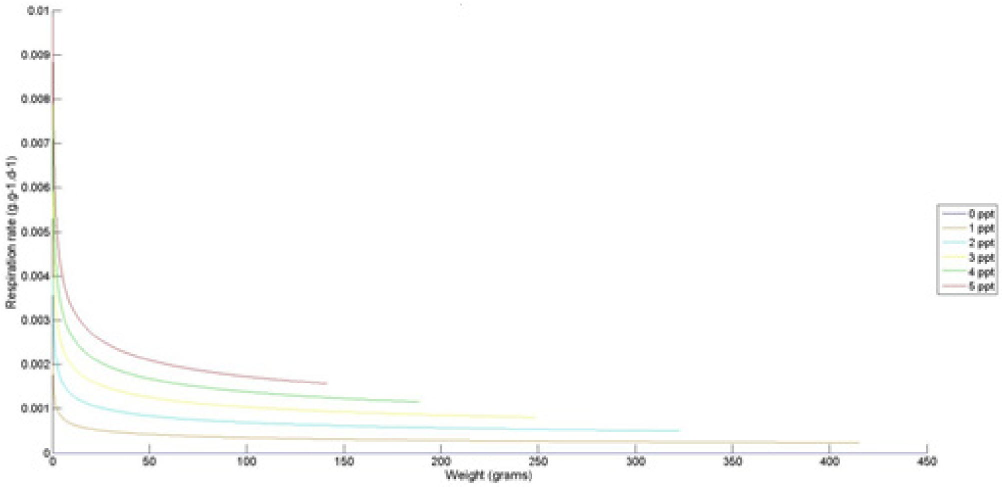


Figure 3.5 Effects of *Salinity* on *Respiration* vs. total weight. As described by the model, decreases in *Salinity* result in a direct linear decrease in *Respiration*. Naturally, the rate is expected to decrease per gram as the organism grows. Values at all salinity levels reach an asymptote when the organism reaches about 150g.

References

Ahrenholz DW, Morris JA (2010) Larval duration of the lionfish, *Pterois volitans* along the Bahamian Archipelago. *Environmental Biology of Fishes, 88,* 305-309

Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Marine Ecology Progress Series, 367*, 233-238

Alleman RW, Bellmund SA, Black DW, Formati SE, Gove CA, Gulick LA (1995) An Update of the surface water improvement and management plan for Biscayne Bay. Technical Supporting Documents and Appendices. (Ed: Mulliken, J. D. and J. A. VanArman). Planning Department. South Florida Water Management District. West Palm Beach, Florida

Barbour AB, Montgomery ML, Adamson AA, Diaz-Ferguson E, Silliman BR (2010) Mangrove use by the invasive lionfish *Pterois volitans*. *Marine Ecology Progress Series, 401*, 291–294

Booth BD, Murphy SD, Swanton CJ (2003) *Weed ecology in natural and agricultural systems*. Cambridge, MA: CABI Publishing

Browder JA, Alleman R, Markley S, Ortner P, Pitts PA (2005) Biscayne Bay conceptual ecological model. *Wetlands*, *25*(4), 854-869

Brown JM, McPeek MA, May ML (2000) A phylogenetic perspective on habitat shifts and diversity in the North American *Enallagma* damselflies. *Systems Biology*, 49, 697–712

Byers JE (2002) Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos, 97(3),* 449–458

Caccia VG, Boyer JN (2005) Spatial patterning of water quality in Biscayne Bay, Florida as a function of land use and water management. *Marine Pollution Bulletin, 50,* 1416–1429

Cerino C (2010) Bioenergetics and trophic impacts of invasive Indo-Pacific lionfish: MSc thesis. Greenville: East Carolina University. 72 p

Claireaux G, Lagardere JP (1999) Influence of temperature oxygen and salinity on the metabolism of the European sea bass. *Journal of Sea Research, 42*, 157-168

Corn ML, Buck EH, Rawson J, Fischer E (1999) Harmful non-native species: issues for Congress. Washington, DC: Congressional Research Service, Library of Congress

Côté IM, Maljkovic A (2010) Predation rates of Indo-Pacific lionfish on Bahamian coral reefs. *Marine Ecology Progress Series, 404*, 219-225

Côté IM, Green SJ, Morris JA Jr, Akins JL, Steinke D (2013) Diet richness of invasive Indo-Pacific lionfish revealed by DNA barcoding. *Marine Ecology Progress Series, 472*, 249-256

Cressie NA (1990) The Origins of Kriging. *Mathematical Geology, 22*, 239–252

Duever MJ, Meeder JF, Meeder LC, McCollom JM (1994) The climate of south Florida and its role in shaping the Everglades ecosystem. Pages 225-248. In Davis, S.M. and J.C. Ogden Eds. *Everglades: The Ecosystem and its Restoration*. St. Lucie Press, Delray Beach, Florida. 826 pp

Elton CS (1958) *The ecology of invasions by animals and plants*. Methuen, London.

ESRI (2011) ArcGIS desktop: release 10.1 Redlands, CA: Environmental Systems Research Institute

Florida Department of Environmental Protection (2011) Site-specific information in support of establishing numeric nutrient criteria in Biscayne Bay technical report. Tallahassee, Florida

Frazer TK, Jacoby CA, Edwards MA, Barry SC, Manfrino CM (2012) Coping with the lionfish invasion: can targeted removals yield beneficial effects? *Reviews in Fisheries Science*, *20*(4), 185-191

Garton W, Berg D J, Stoeckmann AM, Hagg WR (1993) Biology of recent invertebrate invading species in the Great Lakes: The spiny water flea, *Bythotrephes cederstoemi*, and the zebra mussel, *Dreissena polymorpha*. *Indiana Academy of Science,* 63–84

Green SJ and Côté IM (2009) Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs, 28*, 107

Green SJ, Akins JL, Côté IM (2011) Foraging behaviour and prey consumption in the Indo-Pacific lionfish on Bahamian coral reefs. *Marine Ecology Progress Series, 433*, 159–167

Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive atlantic coral reef fish declines. *PLoS ONE, 7(3)*, e32596

Hartman KJ, Kitchell JF (2008) Bioenergetics modeling: progress since the 1992 symposium. *Transactions of the American Fisheries Society*, *137*(1), 216-223

Hewett SW, Johnson BL (1987) A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute

Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology, 6*, 324-337

Irlandi EA, Orlando BA, Biber PD (2004) Drift algae–epiphyte–seagrass interactions in a subtropical *Thalassia testudinum* meadow. *Marine Ecology Progress Series, 279*, 81–91

Jager T, Zimmer EI (2012) Simplified dynamic energy budget model for analyzing ecotoxicity data. *Ecological Modelling*, *225*, 74-81

Jenks GF (1967) The data model concept in statistical mapping. *International Yearbook of Cartography, 7*, 186-190

Johnston MW, Purkis SJ (2011) Spatial analysis of the invasion of lionfish in the western Atlantic and Caribbean. *Marine Pollution Bulletin, 62(6)*, 1218-1226

Jud ZR, Layman CA, Lee JA, Arrington DA (2011) Recent invasion of a Florida estuarine/riverine system by the lionfish *Pterois volitans*. *Aquatic Biology, 13*, 21-26

Jud ZR, Layman CA (2012) Site fidelity and movement patterns in the invasive lionfish, *Pterois spp*. *Journal of Experimental Marine Biology and Ecology, 414-415*, 69-74

Jud ZR, Nichols PK, Layman CA (2014) Broad salinity tolerance in the invasive lionfish *Pterois spp*. may facilitate estuarine colonization. *Environmental Biology of Fishes*, 1-9

Kimball M, Miller J, Whitfield P, Hare J (2004) Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. *Marine Ecology Progress Series, 283*, 269-278

Kitchell JF, Stewart DJ, Weininger D (1977) Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Board of Canada*, *34*(10), 1910-1921

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology, 16*, 199-204

Layman CA, Allgeier JE (2012) Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in The Bahamas. *Marine Ecology Progress Series, 448*, 131-141

Madley KA, Sargent B, Sargent FJ (2002) Development of a system for classification of habitats in estuarine and marine environments (SCHEME) for Florida Unpublished report to the U.S. Environmental Protection Agency, Gulf of Mexico Program (Grant Assistance Agreement MX-97408100) Florida Marine Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, Florida. 43 pp

Manooch III CS (1987) Age and growth of snappers and groupers. *Tropical snappers and groupers: biology and fisheries management. Ocean Resouce. Marine Policy Series. Westview Press, Inc., Boulder and London*, 329-373

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment, 6(9)*, 485-492

Morris JA Jr, Whitfield PE (2009) Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA Technical Memorandum *NOS NCCOS 99 (57)*

Morris Jr JA, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environmental Biology of Fishes*, *86*(3), 389-398

Morris Jr JA, Whitfield PE (2009) Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment

Morris JA, Sullivan CV, Govoni JJ (2011) Oogenesis and spawn formation in the invasive lionfish, *Pterois miles* and *Pterois volitans*. *Scientia Marina, 75*, 147-154

Nordlie FG, Walsh SJ, Haney DC, Nordlie TF (1991) The influence of ambient salinity on routine metabolism in the teleost *Cyprinodon variegatus*. *Journal of Fish Biology*, *38*(1), 115-122

Pankhurst NW, Van Der Kraak G (1997) Effects of stress on reproduction and growth of fish. *Fish Stress and Health in Aquaculture*, 73-93

Palomares ML, Pauly D (1989) A multiple regression model for prediction the food consumption of marine fish populations. *Marine and Freshwater Research*, *40*(3), 259-273

Persson L, Claessen D, De Roos AM, Byström P, Sjögren S, Svanbäck R, Wahlström E, Westman E *(*2004*)* Cannibalism in a size-structured population−energy extraction and control. *Ecological Monographs*, *74,* 135–157

Prakash S, Balamurugan J, Kumar TA, Balasubramanian T (2012) Invasion and abundance of reef-inhabiting fishes in the Vellar estuary, southeast coast of India, especially the lionfish *Pterois volitans*. *Current Science(Bangalore)*, *103*(8), 941-944

Railsback SF, Rose KA (1999) Bioenergetics modeling of stream trout growth: temperature and food consumption effects. *Transactions of the American Fisheries Society*, *128*(2), 241-256

Rao GMM (1968) Oxygen consumption of rainbow trout (*Salmo gairdneri*) in relation to activity and salinity. *Canadian Journal of Zoology*, *46*(4), 781-786

Rice JA, Breck JE, Bartell SM, Kitchell JF (1983) Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. *Environmental Biology of Fishes*, *9*(3-4), 263-275

Robles MD, Armentano T, DiResta D, Lara MR, Jones DL, Butler MJ (2005) Condition of the natural resources of Biscayne National Park. A State of the Parks Technical Report. NatureServe, Arlington, Virginia

Roessler M, Beardsley GL, Rehrer R, Garcia J (1975) Effects of thermal effluents on the fishes and benthic invertebrates of Biscayne Bay-Card Sound, Florida. Technical Report, University of Miami, Florida

Rubec PJ, Bexley JCW, Norris H, Coyne MS, Monaco ME, Smith GS, Ault JS (1999) Suitability modeling to delineate habitat essential to sustainable fisheries. *Fish Habitat: Essential Fish Habitat and Restoration. American Fisheries Society Symposium, 22,* 108-133

Sakai AK, Allendorf FW, Holt JS (2001) The population biology of invasive species. *Annual Review of Ecological Systems*, 3322, 305–32

Schofield PJ (2009) Geographic extent and chronology of the invasion of non-native lionfish *Pterois volitans* and *P. miles*) in the Western North Atlantic and Caribbean Sea. *Aquatic Invasions, 4*, 473-47

Schofield PJ (2010) Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus 1758] and *P. miles* [Bennett 1828]) in the Western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. *Aquatic Invasions, 5*, 117-122

Serafy JE, Faunce CH, Lorenz JJ (2003) Mangrove shoreline fishes of Biscayne Bay, Florida. *Bulletin Marine Science, 72*, 161–180

Stachowicz JJ, Whitlatch R, Osman R (1999) Species diversity and invasion resistance in a marine ecosystem. *Science, 286(5444),* 1577-1579

Stewart DJ, Weininger D, Rottiers DV, Edsall TA (1983) An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. *Canadian Journal of Fisheries and Aquatic Sciences*, *40*(6), 681-698

Store R, Jokimaki J (2003) A GIS-based Multi-Scale Approach to Habitat Suitability Modeling. *Ecological Modeling, 169*, 1–15

Tilman D (2004) "Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly". *Proceedings of the National Academy of Sciences, 101(30),* 10854–10861

Truhaut R (1977) Ecotoxicology: objectives, principles and perspectives. *Ecotoxicology and Environmental Safety*, *1*(2), 151-173

Vadas RL, Orth DJ (2001) Formulation of habitat suitability models for stream-fish guilds: do the standard methods work? *Transactions of the American Fisheries Society*, 130, 217-235

Warren II RJ, Bahn V, Kramer TD, Tang Y, Bradford MA (2011) Performance and reproduction of an exotic invader across temperate forest gradients. *Ecosphere, 2(20)*, art14

Wedding LM, Friedlander AM, McGranaghan M, Yost RS, Monaco ME (2008) Using bathymetric lidar to define nearshore benthic habitat complexity: Implications for management of reef fish assemblages in Hawaii. *Remote Sensing of Environment, 112*, 4159–4165

Whitfield PE, Gardner T, Vives SP, Gilligan MR, Courtenay Jr WR, Ray GC, Hare JA (2002) Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. *Marine Ecology Progress Series, 235*, 289-297

Whitfield PE, Hare JA, David AW, Harter SL, Muñoz RC, Addison CM (2007) Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the Western North Atlantic. *Biological Invasions, 9*, 53–64

Williams JD, Meffe GK (1998) "Nonindigenous Species". Status and Trends of the Nation's Biological Resources. Reston, Virginia: United States Department of the Interior, Geological Survey 1

Winberg, G. G., (1960). Rate of metabolism and food requirements of fish. *Fisheries Research Board of Canada Translation Series 194,* 1-202

Appendix: SYNTHESIS OF INFORMATION ON EFFECTS OF SALINITY ON FISH GROWTH THROUGH COSTS OF OSMOREGULATION

While the correlation between temperature and bioenergetics of marine fish has been well established for the past half century, the effects of varying salinity in these processes has only been sparsely surveyed within existing literature. This element of water quality plays a role in nearly every aquatic ecosystem from marine to estuarine; therefore, defining energetic costs of osmoregulation is a critical aspect to understanding growth and reproduction of species under variable conditions.

Estimates for the metabolic expenditures resulting from osmoregulation vary by taxa across teleost fishes. A review of literature values by Boeuf and Payan (2001) reveals that many studies estimate between 20 to 50% of total energy budgets are used by fishes for maintenance of osmoregulation; however, newer studies put the value much lower at around 10%. However, Bushnell and Brill (1992) estimate that in highly active and migratory species, such as tunas and dolphin fish, the figure can be closer to between 54 – 68% of non-swimming metabolic output. Either way, numerous sources across the literature confirm the importance of maintaining a balance between internal and environmental salinity for optimal physiological function.

Seminal experiments conducted by Holliday (1969) have laid the foundation for study of salinity mediated effects in the developmental stages of teleost fish. His findings confirm that these early stages of life history can be particularly sensitive to changes in salinity gradients. Unlike juvenile and adult fishes, which display directed mobility and acclimation controls, eggs are highly susceptible to environmental impacts during fertilization and embryonic development (Tandler *et al.* 1995). Much work has been done on flatfish species, especially flounders, to show how different gradients of salinity alter fertilization success (Hart and Purser 1995, Nissling *et al.* 2002). Once again, the optimal salinity for these processes is taxa specific with many flounder species around 25-25 psu, red tilapia at 18 psu, and striped bass around 5 psu (Hart and Purser 1995, Watanabe *et al.* 1990, Peterson *et al.* 1996).

Following fertilization, "fish are dependent on both internal (nervous, endocrinological and neuroendocrinological) and external (ecological) factors, which control or synchronize many activities or functions, including growth capacity" (Boeuf and Payan 2001). Unlike growth in many other animals, fish growth is continuous throughout the organism's lifetime; this makes environmental factors much more influential over a longer time span. To facilitate efficient regulation of blood salinity levels, teleost fish develop a complex series of chemoreceptor and sensor cells (i.e. prolactin) directly connected to the central nervous system (Grau *et al.* 1994). These complex interactions of neuronal and hormonal networks work in unison to regulate "drinking" of salt water in a constant effort to replace water lost due to an osmotic imbalance between internal and external environments (Boeuf and Payan 2001). While all of these processes are essential for the survival of marine fish, they do not come without an energetic cost, which can ultimately play a major role in growth disparities between different environments.

In a comprehensive review conducted by Boeuf and Payan (2001), a vast majority of study species revealed a clear and significant influence of salinity on growth; however, it was also noted that all of these studies indicate temperature as a critical co-factor. For Atlantic halibut (*Hippoglossus hippoglossus)* reared in captivity, Imsland *et al.* (2007) found that highest growth rate and food conversion occurs at 15 ppt, which is significantly lower than native habitat salinities of 32 ppt. This finding is supported by further research suggesting that marine fish species tend to display bell-shaped growth curves, with growth rates being highest at intermediate salinities from 12-19 ppt (Lambert *et al.* 1994; Gaumet *et al*. 1995). These salinity profiles match coastal and estuarine environments, where juveniles from many species of marine fish display very high growth rates. Studies from marine species, such as Atlantic Cod (*Gadus morhua*), may provide an explanation for this phenomenon as a means to achieve the highest food conversion efficiency (Gaumet *et al*. 1995). Regardless of intake, which varies across species, maximizing calories is a critical process for marine fish to grow.

Consumption is yet another aspect dependent on abiotic environmental factors. Winberg (1960) describes this variable as the key driving force behind in fish bioenergetics that regulates growth and maintenance processes. I have done a cursory literature search, which has revealed many studies relating changes in temperature to varying consumption rates across taxa, but few regarding the role of salinity. Buckel *et al.* (1995) concluded in short-term experiments (7 days) that salinity “had no effect on growth or consumption rate” for juvenile bluefish (*Pomatomus saltatrix*). Additionally, a comprehensive study examining relative food consumption estimates across 38 marine and freshwater species also found salinity to have no effect for species well adapted to these environments (Palomares and Pauly 1998). These findings seem to contradict the high energetic cost of osmoregulation found in many fishes, as such high costs would seem to imply that consumption should increase as salinity deviates from the species’ optimum in order to compensate for the costs.

An explanation for this phenomenon may be found in research conducted by Perez-Pinzon and Lutz (1991) into osmoregulation of juvenile common snook (*Centropomus undecimalis*). Here, no differences in activity related costs of osmoregulation were found across varying salinities, suggesting that marine fish may be able to increase efficiency as dictated by activity. These conclusions support a hypothesis that at rest many species may possess sufficient energy reserves to cope with changing salinity gradients and may help to explain why consumption does not change across salinities despite increased metabolic rates from osmoregulation.

Appendix References

Boeuf G, Payan P (2001) How should salinity influence fish growth?. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, *130*(4), 411-423.

Buckel JA, Steinberg ND, Conover DO (1995) Effects of temperature, salinity, and fish size on growth and consumption of juvenile bluefish. *Journal of Fish Biology*, *47*(4), 696-706.

Bushnell PG, Brill RW (1992) Oxygen transport and cardiovascular responses in skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) exposed to acute hypoxia. *Journal of Comparative Physiology B*, *162*(2), 131-143.

Gaumet F, Boeuf G, Severe A, Le Roux A, Mayer-Gostan N (1995) Effects of salinity on the ionic balance and growth of juvenile turbot. *Journal of Fish Biology*, *47*(5), 865-876.

Grau EG, Richman III NH, Borski RJ 1994 Osmoreception and a simple endocrine reflex of the prolactin cell of the tilapia *Oreochromis mossambicus*. *Prospectives in Comparative Endocrinology*, 251–256.

Hart PR, Purser GJ (1995) Effects of salinity and temperature on eggs and yolk sac larvae of the greenback flounder (*Rhombosolea tapirina*). *Aquaculture*, *136*(3), 221-230.

Holliday FGT (1969) The effects of salinity on the eggs and larvae of teleosts. *Fish Physiology*, *1*, 293-311.

Imsland AK, Björnsson BT, Gunnarsson S, Foss A, Stefansson SO (2007) Temperature and salinity effects on plasma insulin-like growth factor-I concentrations and growth in juvenile turbot (*Scophthalmus maximus*). *Aquaculture*, *271*(1), 546-552.

Lambert Y, Dutil JD, Munro J (1994) Effects of intermediate and low salinity conditions on growth rate and food conversion of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, *51*(7), 1569-1576.

Nissling A, Westin L, Hjerne O (2002) Reproductive success in relation to salinity for three flatfish species, dab (*Limanda limanda*), plaice (*Pleuronectes platessa*), and flounder (*Pleuronectes flesus*), in the brackish water Baltic Sea. *ICES Journal of Marine Science: Journal du Conseil*, *59*(1), 93-108.

Palomares MLD, Pauly D (1998) Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine and Freshwater Tesearch*, *49*(5), 447-453.

Pérez-Pinzón MA, Lutz PL (1991) Activity related cost of osmoregulation in the juvenile snook (*Centropomus undecimalis*). *Bulletin of Marine Science*, *48*(1), 58-66.

Peterson RH, Martin-Robichaud DJ, Berge O (1996) Influence of temperature and salinity on length and yolk utilization of striped bass larvae. *Aquaculture International*, *4*(2), 89-103.

Tandler A, Anav FA, Choshniak I (1995) The effect of salinity on growth rate, survival and swimbladder inflation in gilthead seabream (*Sparus aurata*) larvae. *Aquaculture*, *135*(4), 343-353.

Watanabe WO, Clark JH, Dunham JB, Wicklund RI, Olla BL (1990) Culture of Florida red tilapia in marine cages: the effect of stocking density and dietary protein on growth. *Aquaculture*, *90*(2), 123-134.

Winberg GG (1960) Rate of metabolism and food requirements of fish. *Fisheries Research Board of Canada Translation Series 194,* 1-202.