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ORIGINAL PAPER

Predicting spatial and temporal distribution of Indo-Pacific lionfish (*Pterois volitans*) in Biscayne Bay through habitat suitability modeling

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Abstract Invasive species may exhibit higher levels of growth and reproduction when environmental conditions are most suitable, and thus their effects on native fauna may be intensified. Understanding potential impacts of these species, especially in the nascent stages of a biological invasion, requires critical information concerning spatial and temporal distributions of habitat suitability. Using empirically supported environmental variables (e.g., temperature, salinity, dissolved oxygen, rugosity, and benthic substrate), our models predicted habitat suitability for the 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 five discrete habitat quality classes, whose ranges are supported by statistical deviations from the apparent best conditions described in prior studies. Analysis of the resulting models revealed little fluctuation in spatial extent of the five habitat classes on a monthly basis. Class 5, which represented the area with environmental variables closest to the best conditions for lionfish, occupied approximately one-third of Biscayne Bay, with subsequent habitats declining in area. A key finding from this study was that habitat suitability increased eastward from the coastline, where higher quality habitats were adjacent to the Atlantic Ocean and displayed marine levels of ambient water quality. Corroboration of the models with sightings from the USGS-NAS database appeared to support our findings by nesting 79 % of values within habitat class 5; however, field testing (i.e., lionfish surveys) is necessary to confirm the relationship between habitat classes and lionfish distribution.

Keywords Lionfish · GIS · Habitat suitability modeling · Invasive species · Biscayne Bay

Introduction

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

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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 dependent on current information.

The Indo-Pacific lionfish (*Pterois volitans*) is considered as 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, 2012). 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 geographic information systems (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.

System studied: Biscayne Bay, Florida

Biscayne Bay is a shallow (0.5–3 m) carbonate marine estuary that encompasses an area of roughly 1,110 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 (e.g., 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 –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).

Species studied: 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 and 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 <1 m down to over 300 m (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 Western North 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 <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). All of these values far exceed those found within the native range (Darling et al. 2011).

Thermal tolerance studies on lionfish in both the native Indo-Pacific and invaded Red Sea ranges suggest that the growth optimum occurs between 24 and 27 °C; however, these fish can survive across a large temperature range between 14 and 32.5 °C for acclimated temperatures (Cerino 2010); Kimball et al. (2004) notes that at temperatures below this range, feeding cessation occurs at 12 °C and instantaneous death at 10 °C. Salinity is another key abiotic factor that impacts fish physiology, affecting the ability of fishes to thrive in different habitats. Analysis of the US Geological Survey's 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, experimental evidence shows lionfish can survive prolonged exposure to low-salinity (<8 ppt) for extended periods of time (Jud et al. 2014; Schofield et al. 2014).

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).

Research objectives

The need for accurate habitat suitability information is critical for newly invading species. 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). 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.

Methods

Input data

Seasonal fluctuations in environmental parameters have 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. 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 within Biscayne Bay, which are maintained and monitored via collaboration between Dade County Environmental Resource Management (DERM) and Florida International University (FIU). Additionally, another 34 stations in peripheral areas surrounding the Bay were used to provide the best possible resolution for the study area. The relative

Table 1 Relative location of DERM/FIU water quality stations

Geographic domain	DERM stations	FIU stations	Total stations
Northern Biscayne Bay	26	6	32
West Central Biscayne Bay (Shore)	9	3	12
Intermediate Biscayne Bay	8	6	14
Offshore Central Biscayne Bay	4	8	12
Southern Biscayne Bay	6	2	8
Total	53	25	78

locations of these 78 stations can be seen in Table 1. 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 10 years is necessary to account for inter-annual variations, which may be caused by El Niño and other events, to produce an accurate interpolation of average values for analysis (Esri 1994).

Another key layer 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 obtained through visual surveys and remote sensing (satellite imagery) between 2005 and 2010 into categorical benthic habitat maps. Habitat classification follows the State of Florida System for Classification of Habitats in Estuarine and Marine Environments and the Coastal Marine Ecological Classification System. Both systems use submerged rooted vegetation, 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 remote sensing measurements provided a three-dimensional image of the seafloor to quantify sub-surface rugosity. Although depth in Biscayne Bay is shallow (mean = 1.8 m, maximum = 4 m for unaltered habitats) the availability of microhabitats may allow lionfish to take advantage of local refugia 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).

Model construction

Our 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. For this study we used ArcGIS version 10.1, as the core modeling platform (Esri 1994). 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 that are used to visualize unique datasets. Another key feature of ArcGIS is that datasets can be made to interact over space and time through merging or linking of spatial layers.

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, dissolved oxygen) were collected from 44 discrete sampling stations, spatial interpolation was necessary to construct a continuous surface across Biscayne Bay. Kriging was 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 1994). 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 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 1994).

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

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 1994). Prior study of water quality in Biscayne Bay revealed 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, was used to create natural breaks during classification of water quality data into five habitat classes. 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 1994). 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 five classes. This process was performed for all 12 monthly iterations, resulting 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 relies on empirical data from prior studies of lionfish physiology and bioenergetics. While tolerance data from these studies is currently limited, there is accurate estimation for temperature, dissolved oxygen, salinity, and rugosity (Cerino 2010; Schofield et al. 2014; Jud et al. 2011; Kimball et al. 2004). In this study the best habitat suitability coincides with the spatial and temporal zone where growth and reproduction are maximized (Warren et al. 2011). For our purposes, these classes are quantifiable from values specific to each of the environmental variables included (Table 2). By manipulating the Jenks Optimization so that the mean of rank 5 matches these values, we effectively created the best habitat suitability class specific to lionfish during a given time.

Table 2 Empirical data used to support lionfish suitability

Environmental variable	Value(s)	Citation
Temperature	29.8 °C (max consumption) 12 °C (feeding cessation) 10 °C (instantaneous death)	Cerino (2010), Johnston and Purkis (2011), Kimball et al. (2004)
Salinity	35 ppt (mean ocean salinity)	Johnston and Purkis (2011); Whitfield et al. (2002)
	5 ppt (lowest threshold for lionfish)	Jud et al. (2014), Schofield et al. (2014)
Dissolved oxygen (DO)	7 mg/L (max respiration)	Shul'man and Love (1999)
Rugosity	2 units	Wedding et al. (2008), Green et al. (2012)

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 best conditions available (class 5). This system quantified spatial and temporal deviation of values from class 5 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 1994). 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 examplefor 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, resulting 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 1994). 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 Fig. 1.

Baseline comparison using preliminary data

Following model construction, the USGS-NAS database was used to compare sightings against model 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). While this dataset is not a complete assessment of lionfish presence/absence, it offers empirical data to cross reference against the models.

Between 2004 and 2012, 117 lionfish sightings were reported to the USGS-NAS for Biscayne Bay. Major contributors to this dataset are scientific institutions such as the National Oceanic and Atmospheric Administration (NOAA), Reef Environmental Education Foundation, and the NPS. Some of the data included in this database was collected voluntarily by self-reporting citizen scientists; however, all entries were scrutinized prior to inclusion in in this study and had to include accurate location, depth, and ambient water quality parameters before being accepted.

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. Sightings were separated by month and plotted onto the habitat suitability maps, which allowed us to use tools from Spatial Analyst to compare to predictive values. 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

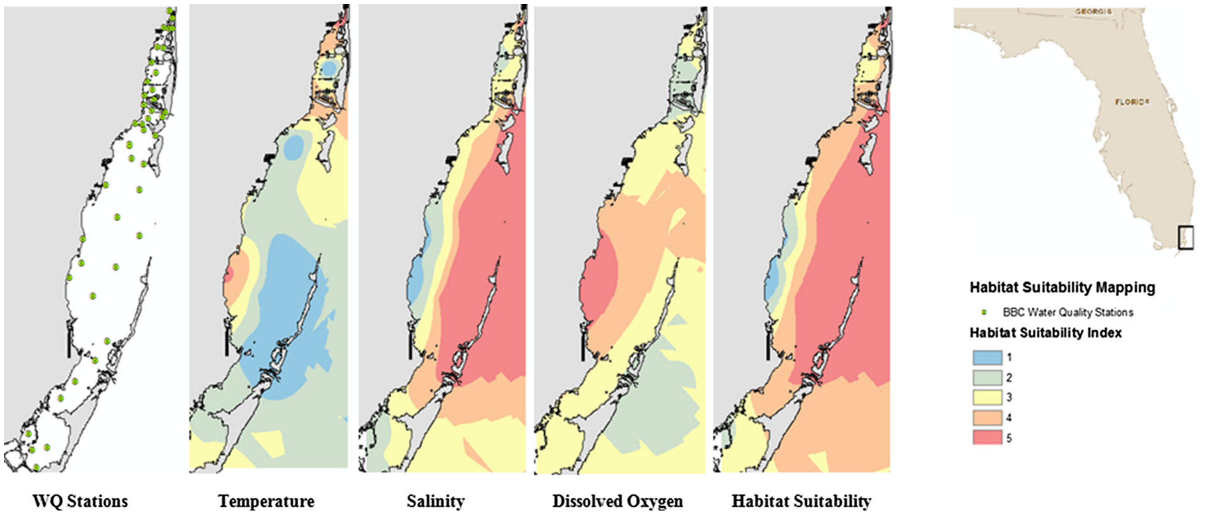

Fig. 1 Progression of map layers for water quality variables and study area. *Panel 1*, furthest to the *left*, shows the locations of 44 water quality stations within Biscayne Bay. *Panels 2–4* each show a series of hypothetical final outputs for spatial interpolation (kriging) of individual water quality 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

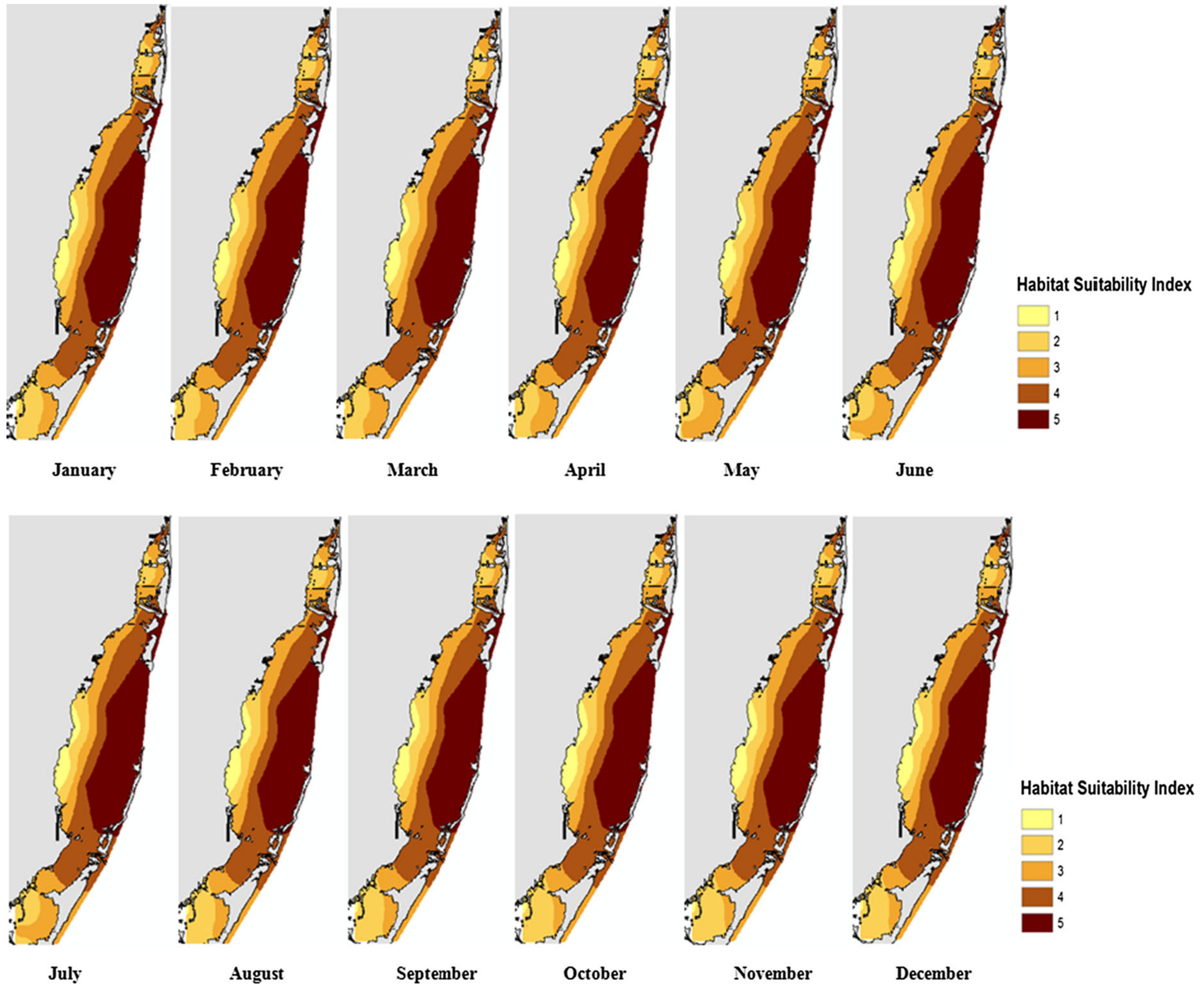

Fig. 2 Throughout most of the year, optimal habitat (class 5) is the prolific and occupies about one-third of the study area. Habitats close to the coastline tend to be of lesser quality for lionfish, with a noticeable increase in size and suitability radiating eastward from shore. Noticeable differences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

determining the mean coordinates for a dataset and identifying points within one or more standard deviations from these values (Esri 1994).

Results

Habitat suitability

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 was ~13 ppt (22–35 ppt), which indicated the presence of a 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 mg/L (7.1–5.5 mg/L) and ~1.4 °C (26.5–25.1 °C) respectively.

Analyses of the model outputs indicated a distinct striation of habitat classes radiating eastward from the shoreline of Biscayne Bay towards the Atlantic Ocean (Fig. 2). 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

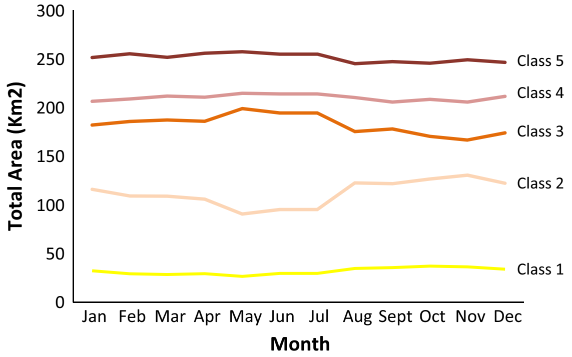

Fig. 3 Change in area of habitat classes over time. Classes 1, 4, and 5 change very slightly throughout the year, while classes 2 and 3 exhibit and inverse relationship, with class 2 decreasing over the summer and class 3 increasing in area during the same time

Table 3 Lionfish sightings from USGS-NAS database by habitat class

Habitat class	Lionfish sightings	Percentage by class	Lionfish/ (km^2)
1	0	0	0
2	1	1	0.0089
3	7	6	0.038
4	17	14	0.0808
5	92	79	0.3659

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 barrier islands was occupied by habitat classes 3 and 4 (Figs. 2, 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 its southern boundary. 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. 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 was 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 (Fig. 3). Following little change during the spring, rapid acceleration occurred between July and August where class 2 increased from 95.38 to 122.78 km^2 and class 3 fell from 194.63 down to 175.50 km^2. These data indicated a shift towards a decline in summertime habitat suitability across near-shore habitats in Biscayne Bay.

Comparison with lionfish data

Lionfish sightings were heavily clustered (79 %) in habitat class 5 (Table 3). 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 <1 %. 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 and data limitations

Although our models performed well relative to our hypotheses, there are inherent limitations in both the model and data used. Each dataset was formatted specifically to the needs of its creators; therefore, the

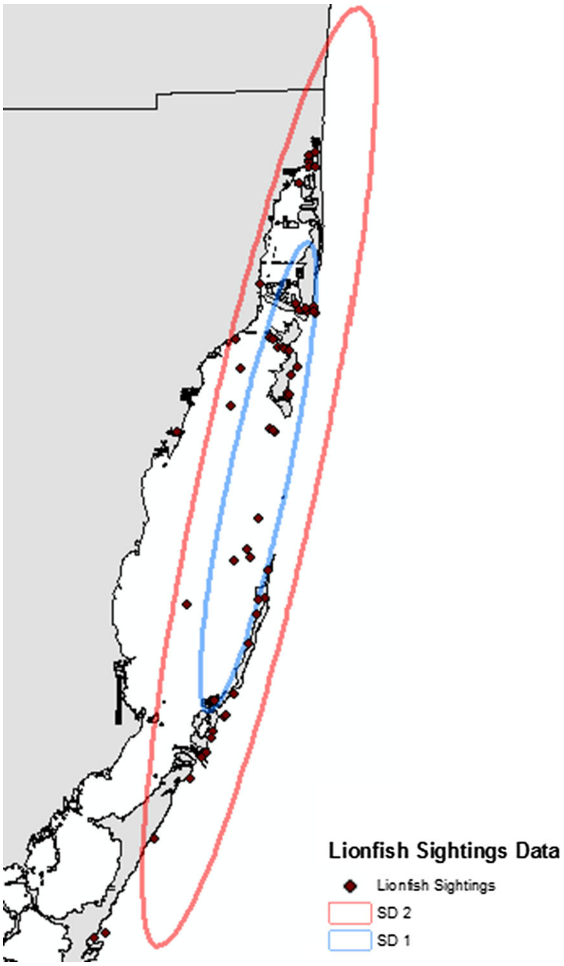

Fig. 4 Statistical analysis of reported lionfish sightings. Raw data as reported to the USGS-NAS database between 2004 and 2012 is depicted as *diamond points*. *SD 1* represents an ellipse containing points within one standard deviation from the center (mean). Clustering of sightings along the border 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

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. Fortunately, algorithms internal to ArcGIS mitigated most errors to only a few meters, reducing any significant effects on data outputs (Esri 1994).

Issues with data availability also provided model limitations. Since benthic habitat and rugosity layers were provided by NPS, there was higher resolution for areas contained within park boundaries. Data from NOAA and FDEP were used to create layers for the remainder of Biscayne Bay. Comparison 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 (Rykiel 1996). 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 used tools to predict anisotropy. This attempts to smooth the hourly changes to longer-term average change.

Lionfish have been present in Biscayne Bay for about 20 years. This has provided some time for lionfish to become established, but it by no means guarantees that the lionfish population has had time to reach equilibrium with its suitable habitats. Thus the presence data may be biased towards areas that were more easily reached by lionfish. Habitat predictions of our model may change in the future if the lionfish population is still in a process of establishing its range across the bay. This being the case, it is best to consider the utility of our model as a hypothesis for future distribution of lionfish across Biscayne Bay as they fill their ecological niche over time (Rykiel 1996).

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 native habitats across the Indo-Pacific are marine (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 (25.9–26.5 °C), salinity (33–36 ppt), and dissolved oxygen (6.5–7.2 mg/L) in class 5 indicate a strong affinity to marine conditions (Caccia and Boyer 2005).

Habitats contained in class 5 border the Atlantic Ocean, which may explain ambient stability and marine water quality variables (Fig. 2). Additionally, these habitats tended to be farther from the mainland, with an average minimum distance of 5 km. This was 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 reduce salinity levels in these habitats to <20 ppt, which may 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 apparently very good 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). Habitats in Biscayne Bay that are currently occupied may ultimately provide refugia for population expansion into other parts of the Bay where lionfish have not yet been sighted. Proximity to the Atlantic Ocean and Gulf-stream may also disperse lionfish, which drift as larvae for up to a month to other areas outside of South Florida (Ahrenholz and Morris 2010; Johnston and Purkis 2014; Whitfield et al. 2002).

Although further scientific testing is necessary to verify how accurate our models are at predicting lionfish habitat suitability, comparison with existing sightings data from the USGS-NAS database is 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. Fewer sightings in lower habitat classes may indicate a 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 or the declining size of each habitat class following 5. 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. Assessment of 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 paper may 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 (Fig. 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.

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