

A coordinated and sustained international strategy is required to turn the tide on the Atlantic lionfish invasion

Matthew W. Johnston*, Sam J. Purkis

National Coral Reef Institute, Guy Harvey Research Institute, Nova Southeastern University Halmos College of Natural Sciences and Oceanography, 8000 North Ocean Drive, Dania Beach, Florida 33004, USA

ABSTRACT: Atlantic lionfish have caused measurable ecosystem damage in their invaded range. As a matter of urgency, strategies to suppress lionfish have therefore risen to the fore amongst the ocean management community. We use a biophysical model and ocean climate data to demonstrate how Atlantic lionfish larvae are dispersed by currents and how this dispersal, combined with their breeding strategy, negates effective control using methods traditionally executed on a local scale. This study quantitatively emphasizes the high level of larval connectivity that exists between the many nations whose waters now support established lionfish populations. For any given area, our results indicate that the key to suppressing the invasion is to simultaneously choke all upstream linkages that supply external larvae and renourish the local population. On the basis of a case study developed for the Carolinas, USA, an area of high lionfish abundance, the model suggests that such a strategy requires monthly culls that remove 20% of lionfish biomass in the Carolinas and all locations to which the Carolinas are linked hydrographically. Conversely, if culls target only those locales that deliver the majority (95%) of lionfish larvae to the Carolinas, and therefore ignore those locations which contribute the remaining 5% of lionfish larvae, the requisite cull rate exceeds 60% and suppresses lionfish abundance for only 5 yr. The latter finding exposes an intrinsic danger: sparse lionfish left uncontrolled may derail a concerted, yet not comprehensive, effort to control the invader. This study provides a modelling approach to quantitatively target and manage the lionfish population for nations whose waters are now plagued by invasive lionfish.

KEY WORDS: Lionfish · Population control · Lionfish culls · Caribbean · Western Atlantic · *Pterois volitans*

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Two species of the invasive Indo-pacific lionfish *Pterois volitans/miles* (herein referred to simply as 'lionfish') have resided in the western Atlantic and Caribbean for nearly 3 decades. Initially reported offshore Dania Beach, Florida, USA, in 1985 (USGS-NAS 2014), the first lionfishes recorded are thought to be released aquarium pets that succeeded in forming a self-sustaining and reproductive population from as few as 10 founding individuals (Whitfield et

al. 2002, Hamner et al. 2007). After the discovery of lionfish off the South Florida coast in the mid-1980s, lionfish were reported again on several occasions from South Florida in the 1990s, closely followed around 2000 by records from the Carolinas and Bermuda. As lionfish larvae are buoyant and dispersed on ocean currents, it is likely that the Bermuda and Carolinas fish were sourced from larval recruits arriving on the Gulf Stream from breeding populations in South Florida (Schofield 2010, Johnston & Purkis 2011). Next, lionfish were reported in 2004 on

*Corresponding author: johnmatt@nova.edu

the other side of the Gulf Stream from South Florida, in the Bahamas, and subsequently, they spread quickly southwards and eastwards against the mean water flow, pervading the Windward Passage by 2007 (Schofield 2010). This rapid and unexpected trajectory of the invasion is interesting as the Gulf Stream is a strong boundary current that typically serves as an effective barrier to the transport of larval marine organisms between Florida and the Bahamas because the prevailing flow of water in the Bahamas is to the north and west (Carlin et al. 2003, Richards et al. 2007, Freshwater et al. 2009, Kool et al. 2010, Betancur-R et al. 2011). Johnston & Purkis (2015) concluded that the unanticipated Bahamian invasion, proceeding against current gradients, may have been accelerated by lionfish larvae conducted by hurricane-altered water flow. Subsequent to 2007, lionfish rapidly infiltrated the entire Caribbean and Gulf of Mexico. Given that lionfish larvae are pelagically dispersed and adults are non-migratory (Jud & Layman 2012, Akins et al. 2014, Tamburello & Côté 2015), the rapid population expansion of lionfish is likely explained by ocean current patterns in the region.

Lionfish are now the most numerous predatory fish on many coral and artificial reefs spanning the entire tropical western Atlantic, Gulf of Mexico, and Caribbean (referred collectively herein as the 'study domain') (Albins & Hixon 2008, Green et al. 2012). The density of lionfish in some invaded locations far surpasses that of lionfish populations in the Indo-Pacific where they are native (Green et al. 2012). The invasion success of Atlantic lionfish has been meticulously catalogued in the literature, with particular concentration on the ecology of the fish such as their diet (Morris & Akins 2009, Valdez-Moreno et al. 2012), habitat preferences (Albins & Hixon 2008, Morris & Akins 2009, Barbour et al. 2010, Jud & Layman 2012), potential predators (Green & Côté 2009, Mumby et al. 2011, Hackerott et al. 2013), and how lionfish predation has impacted native fauna (Albins & Hixon 2008, Green et al. 2012). Owing in part to a lack of natural predators of Atlantic lionfish (Hackerott et al. 2013), and with the realization that invasive lionfish are now permanent residents, recent work has shifted direction from understanding the ecology of the invader toward exploring options as to how to best control them. The overall aim of lionfish removal programs is to contain the invasion and suppress lionfish abundances or, if feasible, completely eradicate them (Arias-Gonzalez et al. 2011, Barbour et al. 2011, Morris et al. 2011, Green et al. 2014)

Contemporary lionfish control is primarily administered through manual removal (referred to herein as 'culls') of the fish, accomplished during lionfish derby events and recreational spear and hand-net fishing (Barbour et al. 2011). In the Cayman Islands, targeted local culls of lionfish executed over a 205 d span reduced the abundance of lionfish and also shifted the composition of lionfish populations to smaller size classes as a result of culls that targeted mostly large adult fish (Frazer et al. 2012). This demographic shift, albeit likely temporary as lionfish grow quickly, may result in lower predation on native reef fish given that smaller lionfish primarily prey on crustaceans such as shrimps. Bejarano et al. (2014), also studying Cayman Islands lionfish, speculated that targeted lionfish culls are most effective if focused in rugose sites skirting deep water where lionfish are the most abundant. Frazer et al. (2012) suggested that lionfish do not disperse rapidly to fill habitats vacated as a result of removal efforts; however, this should not be surprising given that adults seem non-migratory over distances greater than 2 km (Jud & Layman 2012, Akins et al. 2014, Tamburello & Côté 2015). Conversely, work by Johnston & Purkis (2014a,b) indicated that lionfish are capable of rapid dispersal, though this dispersion is conducted on ocean currents during the pelagic larval duration phase and not by active migration by adult fish. Fish surveys that measured the effectiveness of lionfish culls at the island of Bonaire found that compared to the nearby island of Curacao, which was unfished, lionfish abundance was a factor of 4.2 lower in Bonaire 2 yr after the lionfish management program was initialized (De Leon et al. 2011). Similar to the study by Frazer et al. (2012), lionfish weights and sizes were smaller on Bonaire than Curacao. Both of these studies therefore show that local culls at least have the potential to be effective in controlling lionfish abundance over short timescales.

Barbour et al. (2011) quantified the requisite cull rates to control lionfish using an age-structured population model, concluding that an annual exploitation rate of 35 to 65 % was necessary to cause lionfish overfishing and thus a reduction of lionfish biomass. The authors found that lionfish populations in their model, when left unchecked, subsequently recovered to 90 % of unfished biomass 6 yr after cessation of culls. Importantly, however, the study did not include contributions of larvae from lionfish outside of the model population. Barbour et al. (2011) also acknowledged that, had outside recruits been considered, lionfish abundance might rebound quicker than their study suggests. A similar study by Morris

et al. (2011) used a stage-based matrix population control model to estimate the cull rates required to reduce lionfish abundance. In that study, a 27% monthly cull produced a decrease in lionfish abundance. Barbour et al. (2011) also focused on local controls and did not estimate the influx of larval recruits from outside of their model system. It was also noted by the authors that a substantial reduction of lionfish biomass is likely only in locations where annual cull rates are >50%, and performed on a consistent basis. Arias-Gonzalez et al. (2011) tested the resilience of the lionfish to simulated culls and also the impacts of these culls on Caribbean food-web structure. To do this, they used an Ecopath-with-Ecosim model to alter short-duration (5 yr) lionfish mortality rates, which the authors attributed to fishing pressure. Consistent with the findings of Barbour et al. (2011) and Morris et al. (2011), lionfish biomass quickly rebounded when virtual culls were halted, and frequent lionfish eradications of all age and size classes were necessary to control lionfish abundance.

The lionfish modelling studies of Arias-Gonzalez et al. (2011), Barbour et al. (2011), and Morris et al. (2011) did not consider how hydrographic connectivity within the invasive range of lionfish may alter the dynamics of lionfish abundance. We posit that the quick rebound of lionfish densities as modelled by Barbour et al. (2011) and Arias-Gonzalez et al. (2011) may be exacerbated by constant propagule pressure from unfished upstream populations which those studies did not consider. Johnston & Purkis (2011, 2014a,b) and Betancur-R et al. (2011) demonstrated that invasive lionfish populations are not isolated sub-populations but are instead interconnected, coupled hydrographically. Within the study domain, numerous upstream (source) regions, such as the Florida Keys, supply downstream (sink) locations, such as the Carolinas, with a consistent influx of viable larval lionfish recruits conducted on ocean currents such as the Gulf Stream. Understanding water flow in the study domain, therefore, is of critical importance to understand how regional connectivity via ocean currents may help or hinder control efforts. To fill this knowledge gap, we have herein developed a temporal and spatial model that couples the hydrodynamics of the study domain and the life cycle and breeding strategy of lionfish with the requisite cull rates necessary to control the fish. We speculate that a more widespread and cooperative containment effort, executed between source and sink regions, may yield better suppression of lionfish abundance than the sequestered local control efforts currently being utilized in the field and those scenarios that have

been previously modelled. A comprehensive solution to lionfish control, therefore, may necessitate a unique and multinational collaboration, whereby both source and sink lionfish populations are culled simultaneously to produce the desired outcome of reduced lionfish abundance in downstream localities.

The motivation of this study was to determine whether lionfish control at a local level, augmented by control efforts at distant but highly linked locations via larval connectivity pathways (referred to herein as 'links' or 'linkages'), is capable of producing a net reduction of lionfish biomass in a downstream location according to our model. We chose the Carolinas as a focus sub-region upon which to measure the success of synergistic control efforts because dense lionfish populations were reported there by Whitfield et al. (2007, 2014). For the purposes of this study, sub-regions, such as the Carolinas, were deemed as 'precincts' and defined as roughly equal-sized geographical sections that were named according to nearby countries or geographical features following Cowen et al. (2000) and Kool et al. (2010). The Carolinas precinct receives an influx of larval lionfish recruits transported from many upstream locations, such as Cuba, the Florida Keys, the Florida east coast, and Georgia by the Gulf Stream current (Johnston & Purkis 2014a,b). Hence we considered the Carolinas a good example by which to test cull efforts in linked precincts and also anticipate this example to be broadly representative of other linked precincts within the study domain. The purpose of the study was to identify the most critical linkages between precincts and to estimate the percentage of lionfish and the frequency with which the fish must be removed in order to break the links between distant lionfish populations. From this work, it is hoped that a more skillful, coordinated, and sustained lionfish control program between nations linked via ocean currents may be realized, one that may effectively disrupt the connections between distant lionfish populations and reduce lionfish abundance throughout the entire range of the invasion.

MATERIALS AND METHODS

To test the theory that lionfish culls focused in linked precincts may promote a reduction in lionfish abundance as compared with local control alone, we implemented a biophysical model (the 'model') in order to understand water flow that transports larval lionfish between the study precincts and, thus, connectivity between precincts. The model employs a

cellular automaton (CA) and agent-based algorithm which couples lionfish life history characteristics and physical oceanographic conditions to construct a forecast of the spread of Atlantic lionfish. Outputs of the model are date-stamped geographical settlement points of lionfish larvae that can be used to estimate real-world lionfish abundance and also the linkages between distant precincts. The model has been widely engaged and sensitivity-tested to input parameters to study invasive Atlantic lionfish and provides a robust forecast of the spread of the invader that can then be analyzed over space and time (Johnston & Purkis 2014a,b, 2015).

Model logic

The CA model was used to track the temporal and spatial spread of individual lionfish larva as they dispersed through a fixed and regularly spaced two-dimensional (2-D) grid representing the study domain. In a CA model, 4 components define the model system: grid cells, the cell state (containing a lionfish larva or not), neighborhood cells (those cells immediately flanking each grid cell), and a suite of static rules that govern movement of the agent, a lionfish larva, through the model grid. In this employment of the model, each grid cell comprised a set of ocean condition parameters that directed how a lionfish larva moved from cell to cell within the model grid according to the rules. In this study, lionfish larval advection was primarily conducted on ocean currents, with eventual settling dictated by water depth and temperature at the settlement site. The rules were defined considering lionfish life-history traits extracted from the literature (Table 1). A full review of the model logic is provided by Johnston & Purkis (2014b), in Fig. 1, and in the following sections.

The study domain (Fig. 2b) extended from 39° to 11°N latitude and 94° to 69°W longitude and was represented by a fixed 2-D grid with cell dimensions of 10 km × 10 km following Johnston & Purkis (2014b, 2015). Values corresponding to water depth, monthly mean sea surface temperature (SST), and the velocity and direction of ocean current were compiled for each grid cell (Tables 1 & 2). Monthly mean surface water current data for an average year (2006) as simulated by the Hybrid Current Ocean Model (HYCOM) was chosen to condition water flow through the grid (Chassignet et al. 2007, Prasad & Hogan 2007). Ocean current data from HYCOM simulations are commonly used in marine connectivity studies (i.e. Kool et al. 2010, Paris et al. 2013, Johnston & Purkis 2015); how-

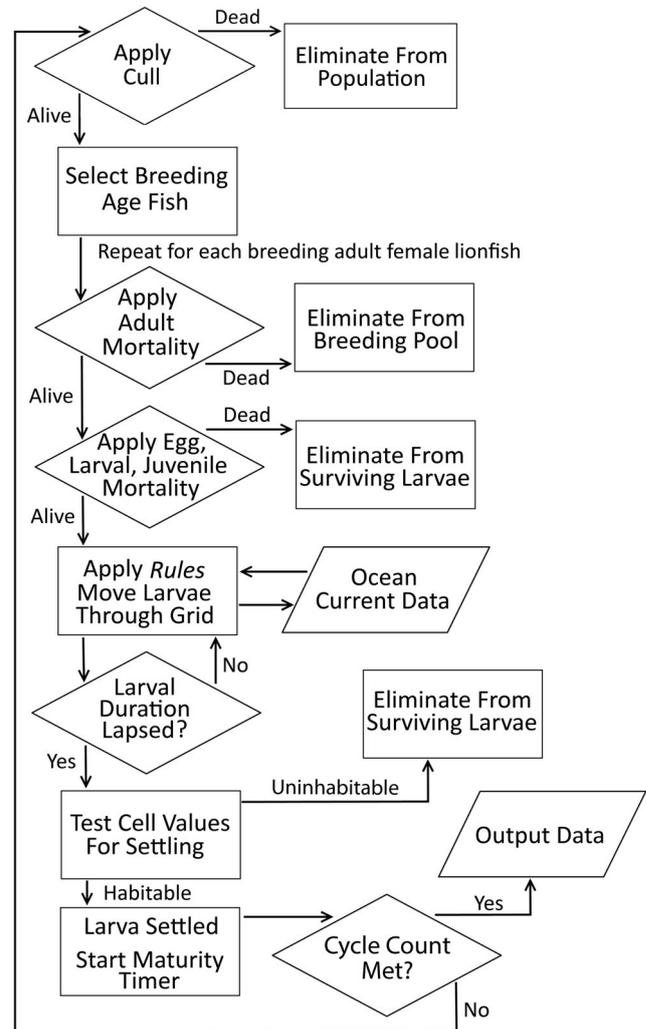


Fig. 1. Flowchart illustrating the process logic of the model

ever, circulation models may not always be accurate, and their blind use without any verification of validity is dangerous. On the other hand, HYCOM simulations have shown to exhibit satisfactory performance over synoptic and seasonal time scales in South Florida (Kourafalou et al. 2009) and also reflect *in situ* observations as measured by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) aboard the OrbView-2 satellite (Chassignet et al. 2005). HYCOM simulations, we therefore deemed, were a useful approximation of global ocean water flow upon which to estimate lionfish population connectivity within the study domain and, so too, linkages between precincts. Johnston & Purkis (2015) demonstrated, by comparing lionfish dispersal during average versus hurricane years using the same model as in this study, that ocean current anomalies forced by hurricanes may have accelerated the spread of lionfish counter to prevailing currents

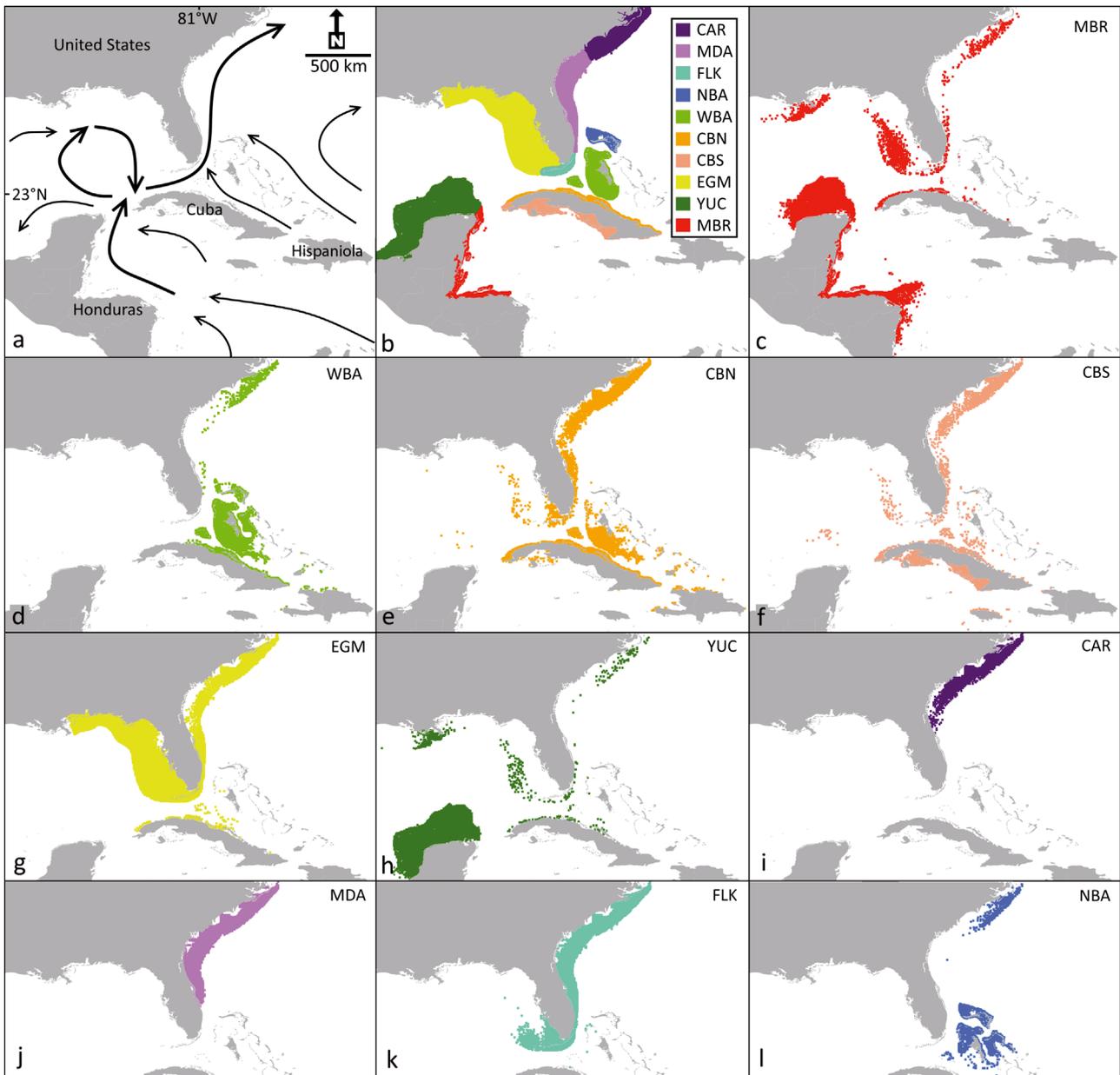


Fig. 2. (a) Circulation pattern of ocean currents in the Caribbean, Gulf of Mexico, and western Atlantic indicated by arrows, (b) precinct definitions, and (c–l) settlement patterns of lionfish larvae spawned from each precinct. Precinct codes are defined in Table 3

in the Florida Straits and Bahamas. The purpose here, however, was to demonstrate connectivity during an average year and not to precisely replicate the spread of lionfish and effect of culls over an explicit time-frame. Monthly mean surface current data from simulations produced by the HYCOM, therefore, were used in the same manner as in Johnston & Purkis (2014a,b, 2015) to represent ocean circulation. Given this, we anticipate these results can be applied broadly for any particular year. In those marine locations (i.e.

grid cells with ocean water depth > 0 m) lacking HYCOM simulation data, for example the Little and Great Bahama Banks, which are prime lionfish habitat and that demonstrate water flow important to regional connectivity, surface ocean current was extracted from OSCAR (Ocean Surface Current Analysis –Real time) satellite data, also for the year 2006 (Bonjean & Lagerloef 2002). Nearest-neighbor interpolation was used to grid water flow to a resolution of 4 km for both the HYCOM simulation and OSCAR data

Table 1. Model parameters, values, and original sources of data used for inputs in this study.

Parameter name	Value	Justification	Source
Cycles (months)	60	Simulations were created spanning 5 yr, sufficient time to show precinct linkages	
Grid size	10 km	Parameter granularity of the HYCOM ocean current dataset	
SST lower thermal limit	10°C	Documented lower thermal tolerance (upper limit has not been identified in the literature) of lionfish in their introduced range	Kimball et al. (2004)
Depth range	1–300 m	Lionfish are found to water depth of at least 300 m	Albins & Hixon (2011)
Egg duration (PLDE)	3 d	Estimated egg duration of lionfish in the Atlantic	Morris et al. (2011)
Pelagic larval duration (PLD)	28 d	Estimated larval duration of Atlantic lionfish	Ahrenholz & Morris (2010), Morris et al. (2011)
Mortality	0.31 d ⁻¹ (M_e , M_l), 0.165 mo ⁻¹ (M_j), 0.052 mo ⁻¹ (M_a)	Estimated egg (M_e), larval (M_l), juvenile (M_j) and adult (M_a) mortality rates of Atlantic lionfish	Morris et al. (2011)
Female proportion	46 %	Sex ratio of Atlantic lionfish	Morris et al. (2011)
Breeding age	10 mo	Estimated maturation of Atlantic lionfish, given larger size and faster growth in the Atlantic than where they are native	Ahrenholz & Morris (2010)
Larval quantity (q)	200 000	Breeding occurs as often as every 4 d. Estimated monthly quantity of eggs per female, per month, obtained from the literature	Morris et al. (2011)
Founder population per precinct	100		
Monthly breeding cycle	30 d	Larval quantity (q) is based on total quantity per month, and so the cycle was set to 1 mo accordingly	Morris et al. (2011)

Table 2. Physical oceanic parameters, resolution, and original sources of data used for inputs in this study

Parameter name	Resolution	Source and description
Ocean current	10 km	The HYCOM ocean model is a widely used and robust forecast of global ocean currents, based on remotely sensed data and <i>in situ</i> measurements (Chassignet et al. 2007). Monthly mean current values from the HYCOM (GLBa0.08 project) for 2006 were used for this study. In locations where the HYCOM was lacking data, Ocean Surface Current Analysis (OSCAR) monthly mean current values for 2006 were used and interpolated to a resolution of 10 km (Bonjean & Lagerloef 2002)
Sea surface temperature (SST)	4 km	Moderate-resolution Imaging Spectroradiometer (MODIS)-Aqua satellite climatological data (composite monthly mean values) for 2003 to 2012 were used for this study
Ocean depth	4 km	ETOPO1 is a 1 arc-minute global relief model of Earth's surface that integrates land topography and ocean bathymetry (Amante & Eakins 2009) and is the source of water depth data for the model

(neither diluting nor amplifying precision) in order to ensure a tight near-shore fit and also match the resolution of the SST and ocean depth data used (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m533p219_supp.pdf). Though at a lower resolution than the HYCOM simulation data, OSCAR ocean current data are derived from remotely-sensed *in situ*

measurements and proved useful to approximate water flow over shallow bank platforms and near-shore locations where HYCOM simulation data were absent. Finally, model inputs for Atlantic lionfish life-history traits such as fecundity, mortality, and breeding age were sourced from Johnston & Purkis (2014b) (Table 1).

A model simulation commenced by selecting the total count of mature female lionfish in each precinct. A timer was initiated at the start of the simulation to track the total time, in days, that the simulation ran and was incremented by 30 d for each 'cycle', corresponding to one breeding pulse per female lionfish (see Table 1 for all model inputs). For each day spanning the entire duration of a simulation, the timer was queried to select the appropriate time-stamped ocean current and temperature data from a pre-compiled set of oceanic conditions encompassing the entire study area (Table 2). At the onset of each cycle, the estimated adult monthly mortality rate of Atlantic lionfish was imposed upon the entire female breeding population to account for natural mortality (M). For instance, an adult lionfish population of 100 000 individuals incurred a monthly death rate of 5.2% of the population, resulting in 520 lionfish which expired at the start of the cycle. The deceased lionfish were selected at random from the entire model population and removed from the simulation. The remaining viable and breeding adults continued to produce offspring until the end of the simulation or they were selected for death in a subsequent cycle.

Each mature female lionfish bred once per cycle, spawning a finite quantity of larvae, defined as q . To lessen computational demands when running the simulations, only the dispersal of lionfish that survived to adulthood was modelled, defined as S_a . S_a was calculated by sequentially applying the literature-derived lionfish mortality rates (Table 1) for each lionfish life-stage to q over the egg (PLDE), larval (PLD), and juvenile (a) duration periods. The calculation is summarized by the following equation:

$$S_a = M_e^{\text{PLDE}} \cdot M_l^{\text{PLD}} \cdot M_j^a \cdot q \quad (1)$$

Male lionfish outnumber female lionfish (i.e. females are the limiting sex) at a rate of 1:0.85 (46% female [$f = 0.46$]) (Morris et al. 2011), and so only female lionfish were modeled, following Johnston & Purkis (2014b, 2015). To calculate the final quantity of larvae to be modelled, S_a was multiplied by f to arrive at the quantity of female lionfish larvae whose trajectory through the model grid was forecast.

Lionfish larvae followed a Eulerian path from one grid cell to another (i.e. a 'step'). Transition time was calculated by dividing the centroid distance between cells by the velocity of water flow measured in meters per second as forecast by the HYCOM and OSCAR ocean current data. As ontogenetic migration in the water column has not been quantified for lionfish larvae, they moved passively through the model grid on simulated ocean currents. Following previous studies

(i.e. Johnston & Purkis 2014b, 2015), stochastic movement of the larvae was simulated to resolve sub-grid scale processes, such as sporadic and random small-scale (<10 km, the resolution of the model grid) anomalies in ocean current and active ontogenetic vertical/horizontal larval movement, that were not otherwise considered by the model. To include the stochastic component, at each step, a random number generator was used to choose a value between 0.00 and 1.00 from a normal distribution. If the random number generated was >0.95, the larva was moved into a randomly chosen neighboring grid cell rather than the forecasted downstream cell. As the duration of transit through the grid varied for each larva, contingent upon ocean current speed and direction, stochastic larval movement occurred approximately 5% of the time. Using this method, we assumed that the prevailing direction of water flow was able to describe the transport of larvae downstream to a 95% confidence interval. A larval timer kept track of the total duration of larval movement through the grid and was initiated at the onset of each cycle and for each larva. The larval timer was incremented by the total time taken by the larva to travel between grid cells at each step. The timer was queried for each step spanning the pelagic larval duration (PLD) period to retrieve the date-appropriate ocean current and temperature values for the occupied grid cell from the pre-compiled parameter database. Concluding the PLD timeframe, water depth and temperature were fetched from the database for the terminal cell occupied by the lionfish larva. If water depth and the minimum water temperatures fell within the tolerances of lionfish (Table 1), the larva settled in the cell. The juvenile female lionfish remained dormant until maturity, at which time it began contributing offspring to the simulation.

The process of selecting mature female lionfish, computing the viability of offspring to maturity, forecasting the movement of lionfish each larva through the model grid, and evaluating ocean conditions for settlement at the conclusion of the PLD period was repeated for each cycle spanning the 5 yr simulation. The resulting lionfish abundance data were date-stamped and geo-referenced to facilitate their analysis over time and space with a GIS (see also Fig. 1 for a flowchart of the model algorithm).

Linkages between precincts

To understand the complex linkages between precincts within the study domain, it was necessary to

Table 3. Precinct names and code definitions and the top 3 linkages per precinct used for the study

Precinct	Precinct code	Primary link	Secondary link	Tertiary link	Percentage of total
Carolinas	CAR	MDA	FLK	CBN	95.8
Florida Keys	FLK	EGM	YUC	CBN	99.5
Mid-Atlantic	MDA	FLK	EGM	CBN	94.4
Cuba North	CBN	WBA	CBS	MBR	98.1
Cuba South	CBS	CBN	EGM	MBR	99.6
Western Bahamas	WBA	CBN	NBA	CBS	99.7
Northern Bahamas	NBA	WBA	CBN	CBS	100
Meso-american Barrier Reef	MBR	YUC			100
Yucatan	YUC	MBR	CBS	CBN	99.9
Eastern Gulf of Mexico	EGM	FLK	MBR	YUC	97.8

use the model to simulate the distribution and settling pattern of larvae spawned by founding populations in each precinct. To do this, and following Cowen et al. (2000), Kool et al. (2010), and Johnston & Purkis (2014a,b), the study area was partitioned into 19 precincts of roughly equal geographical size. From the initial count of 19 precincts, the number selected for modeling was pruned to 10 (Table 3,

Fig. 2b), determined by those that indicated high linkages to the Carolinas (see Fig. 7b in Johnston & Purkis 2014a).

For the purposes of our analysis, each of the 10 study precincts performed as both an exporter and an importer for each lionfish larva modelled. A precinct was classified as an exporter if a lionfish larva was spawned from the breeding population within the precinct boundaries but then settled in a distant location outside of the precinct. Conversely,

when a larva settled within the confines of a precinct, but was produced from a population outside of the precinct, the precinct was categorized as an importer for that larva. To examine the exporter/importer relationships between precincts, we used the same random founder locations as Johnston & Purkis (2014b) for each of the 10 study precincts (Table 3, Fig. 2b) and performed 10 model runs. Each founder location comprised an initial breeding female lionfish population of 10 (i.e. 100 founder individuals per precinct), a quantity we deemed sufficient to illustrate broad-scale linkages within the study domain. Simulations were then conducted over a timespan of 5 yr. It should be noted that the precise quantities of lionfish modelled in our simulation do not represent actual wild lionfish populations as only the offspring of 100 female fish were modelled per precinct. Rather, the abundances reported should be viewed as a representation of the relative quantities produced by lionfish populations residing in each of the study precincts. During each model run, the exporter precinct was tracked for each larva as it transitioned through the model grid, and the eventual recruitment location of the larva within an importer precinct was recorded. From these data, a transition matrix was created that plots exporter population locations against the settling points of larvae in order to illustrate medium-duration (5 yr) mesoscale connectivity between the 10 precincts in the study domain (Fig. 3). Next, the mean counts of lionfish produced from each exporter precinct were computed over the 10 model runs, binned by importer precinct. From this calculation, it was possible to determine not only the quantity of lionfish that established in an importer precinct but also the exporter precincts that contributed the greatest quantity of lionfish to that precinct. Finally, for each importer precinct, the exporter precincts

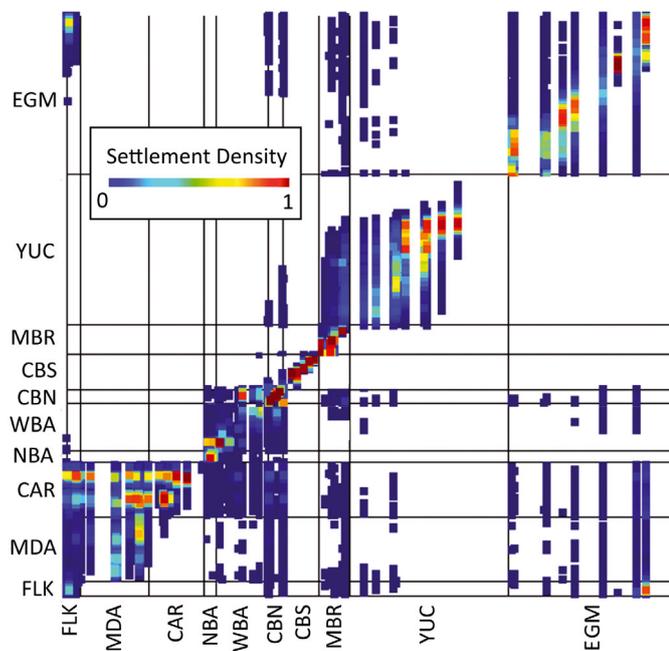


Fig. 3. Transition matrix for the study domain delineated by precincts. Exporter locations (i.e. 'sources') are located on the x-axis, and resulting settling locations in importer precincts (i.e. 'sinks') are indicated on the y-axis. Quantities of settled larvae per location are indicated using a red-to-blue (i.e. high to low) color scheme, standardized from 1 to 0. Vertical banding indicates spread beyond the source location. Groups of squares lying on a bottom-left to top-right diagonal indicate short larval dispersal from the source population

that contributed $\geq 95\%$ of the total quantity of lionfish recruits to the importer precinct were identified and classified as ‘major exporters’ of lionfish larvae to that importer precinct. In all cases, each precinct had ≤ 3 major exporters (Table 3), and therefore, each exporter precinct was categorized (per importer precinct) as a primary, secondary, or tertiary linkage, determined by the quantity of larvae that they contributed (Fig. 4). Settling locations of lionfish from one sample simulation per precinct were then mapped in a GIS (Fig. 2c-1). This analysis is useful to demonstrate the linkages between the 10 precincts selected for this study.

The simulations can also help to demonstrate overall trends as to whether a precinct exports, imports, or retains the majority of its lionfish larvae according to the model. To do this, each precinct was examined individually, and the total quantity of lionfish larvae either imported into or exported from were binned according to the origination of the larvae, categorized as (1) self-recruitment, if the larva originated from and also recruited to the same precinct, (2) exported, if the larva was spawned in the precinct and was exported to a distant precinct, or (3) imported, if the lionfish larva recruited to the precinct but was spawned from a distant precinct (Fig. 5). This evaluation quantifies the precincts that contain the greatest abundance of lionfish at the conclusion of the simulation as well as whether precincts retain their larvae or have the potential to seed downstream precincts with larval lionfish recruits.

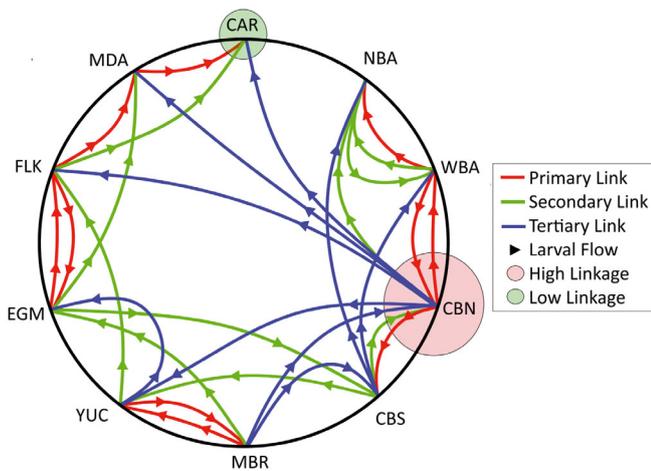


Fig. 4. Primary, secondary, and tertiary linkages between the 10 studied precincts. Precincts are arranged roughly geographically from southernmost (MBR) to northernmost (CAR). Primary linkages are indicated in red, secondary in green, and tertiary in blue. Arrows illustrate the direction of larval flow. The precincts sharing the most (CBN) and least linkages (CAR) are circled

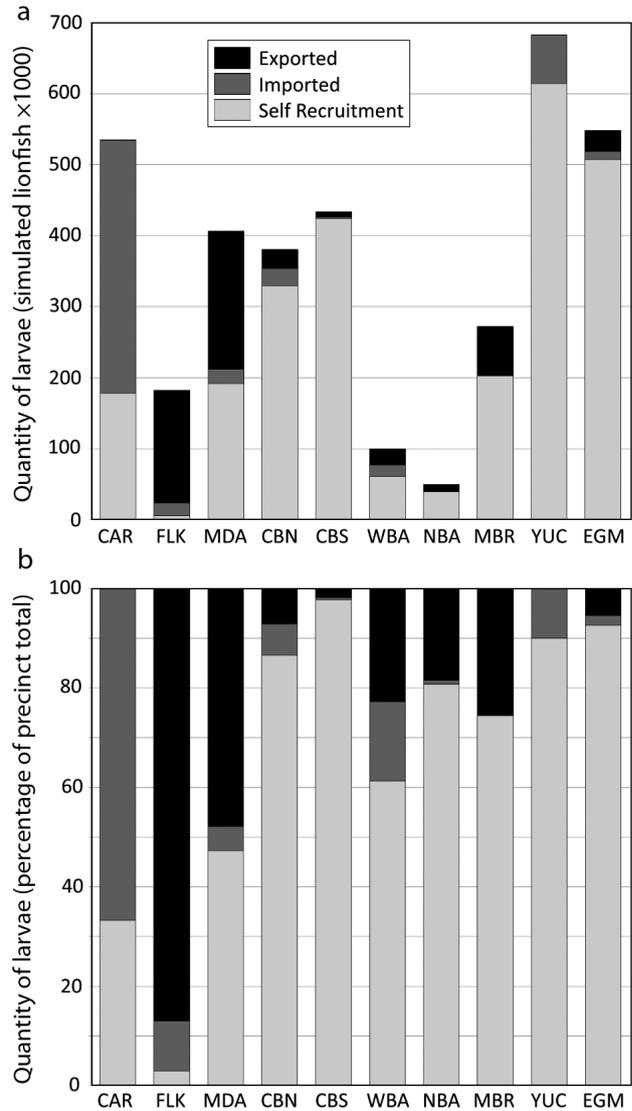


Fig. 5. Precinct exports, imports, and self-recruitment. The (a) quantity and (b) percentage of total female lionfish larvae which either self-recruit to (light grey), are imported to (dark grey) or are exported from (black) each precinct

Simulating the effects of lionfish culls

A suite of simulations was executed next using the same conditioning parameters as when modelling precinct linkages and in 4 guises (Table 4). The simulations tested whether monthly or yearly local Carolina culls, performed in conjunction with culls imposed on the major exporters of lionfish larvae to the Carolinas, or, alternately, basin-wide, were able to reduce lionfish abundance in the Carolinas precinct.

Scenario 1 measured the effects of annual virtual culls executed at varied rates for the major exporters of lionfish recruits to the Carolinas in addition to local

Table 4. Four scenarios were modelled at varying cull rates and frequencies. The culls were either basin-wide or only in those precincts which were major exporters of larvae to the Carolinas, in addition to local Carolina culls

Scenario	Frequency	Rate (%)	Target precincts (in addition to the Carolinas)
1	Yearly	50, 90	Major exporters
2	Monthly	10, 60	Major exporters
3	Monthly	10, 20	All
4	Yearly	90	All

culls in the Carolinas. This simulation was also useful to evaluate if remnant lionfish in those precincts that contributed the remaining 5% of larvae to the Carolinas, which were not culled, were capable of sustaining the invasive population according to our simulation. We imposed a moderate 50% annual cull rate

over a period of 5 yr, such as may be realized during annual lionfish derbies. To emulate the lionfish culls, a culling routine was initiated during the model simulation at Months 12, 24, 36, and 48 that randomly selected 50% of settled lionfish of all age classes (juveniles and adults) for elimination from the model. Next, an analogous but more intense 90% annual cull rate was simulated. The total quantities of lionfish that settled in each of the major exporter precincts to the Carolinas, in addition to the Carolinas, were summed per cycle (i.e. 1 mo) and plotted for each cull rate (Fig. 6a,b).

In Scenario 2, similar simulations were performed as in Scenario 1 but with monthly culls (beginning at Month 12) in place of annual in order to determine whether consistent removals reduced lionfish abundance swifter than sporadic efforts. Simulations were created varying the monthly cull rate from 10% to 60% and similarly plotted (Fig. 6c,d).

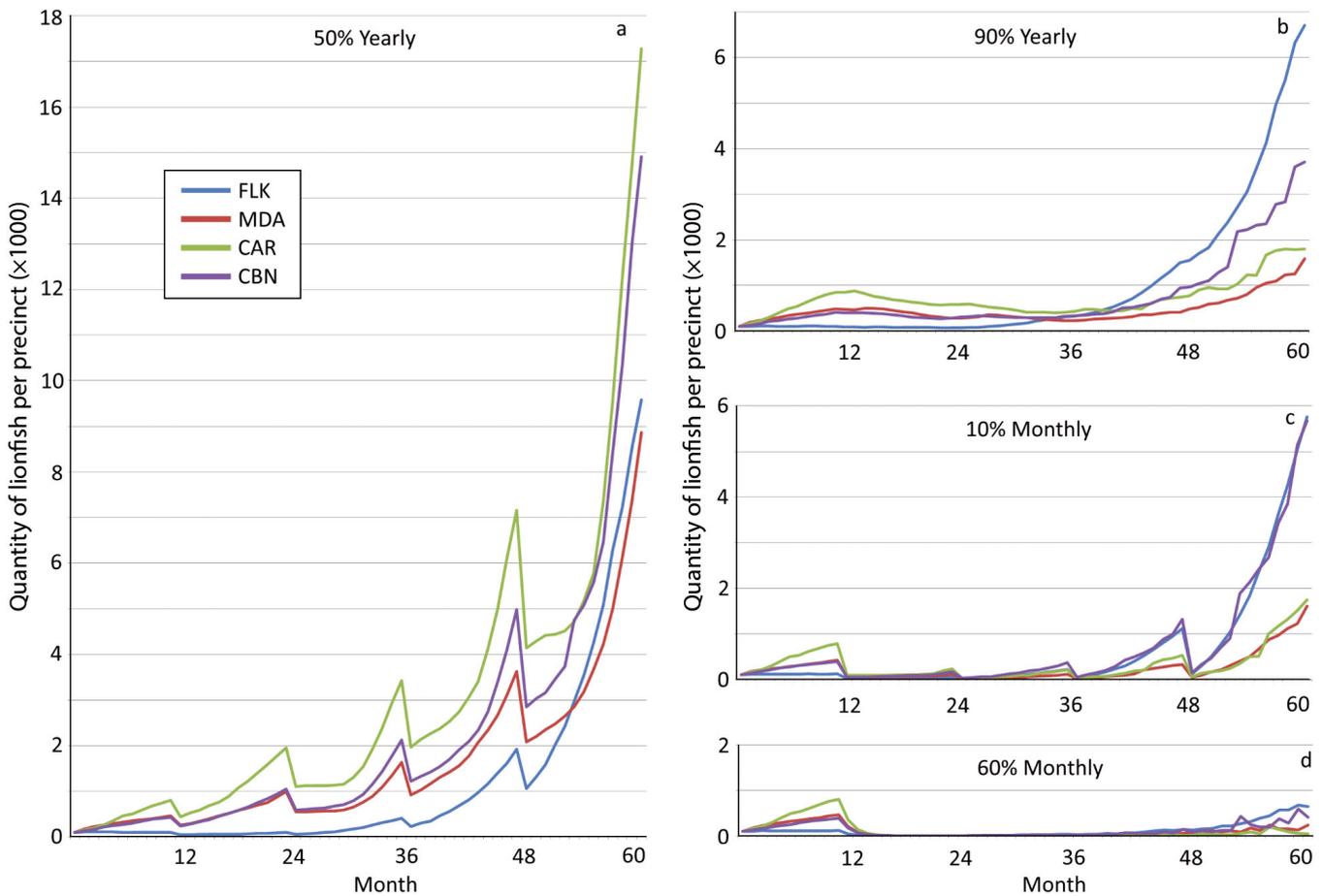


Fig. 6. Five-year plot of lionfish populations which incur yearly or monthly culls in precincts highly linked to the Carolinas (CAR). Monthly lionfish abundance plots for simulations that are culled at (a) 50% and (b) 90% annual cull rates and (c) 10% and (d) 60% monthly cull rates for those populations showing the top 3 linkages to CAR. The x-axis in each plot indicates the date in months, and the y-axis represents lionfish abundance

Simulations created for Scenario 3 levied monthly culls basin-wide, i.e. all 10 study precincts that showed linkages to the Carolinas and that produced 100% of the lionfish larvae in our simulation. This simulation was done to test the concept that basin-wide control may be more effective at curbing lionfish populations than culls executed only in those precincts that were the major exporters of larvae to the Carolinas. The culls were first modelled at a low (10%) monthly exploitation rate given the reality that wholesale lionfish culls and also cooperation amongst nations to perform these culls may be a difficult task (Boom 2012). The same simulations were then executed at an increased 20% monthly lionfish cull in order to quantify if a stronger effort may achieve greater success, should this cull level be deemed attainable (Fig. 7).

Finally, simulations in Scenario 4 imposed basin-wide, but infrequent, annual culls performed at a high-intensity 90% exploitation rate. This final simulation tested if comprehensive annual lionfish culls that removed the majority of lionfish in all habitats and depths were more effective than low-effort, but consistent, monthly culls which removed lionfish in the same capacity.

RESULTS

Connectivity between precincts

When examining the diffusion pattern of lionfish spawned from random populations in each precinct (Figs. 2 & 3), it is clear that the study domain is a dynamic and highly connected environment, as seen by the wide dispersal of lionfish larvae from precincts such as the Meso-american Barrier Reef, Cuba North, and Cuba South. This is especially relevant given that lionfish are capable of producing reproductive populations from few founding individuals (Whitfield et al. 2002, Hamner et al. 2007). If such a minimal quantity of lionfish indeed propagated the entire invasive population in the Atlantic, it follows that even weak linkages between precincts should be regarded with caution. Founder lionfish in each precinct (i.e. 100 founder lionfish per precinct) produced the same quantity of larvae over the 5 yr model run. Given this, and from observing the simulations, it is evident that the majority (but not all) lionfish offspring from some precincts (i.e. the Western Bahamas, Florida Keys, and the Northern Bahamas) were swept into inhabitable water by the conclusion of the PLD period and were not able to settle accord-

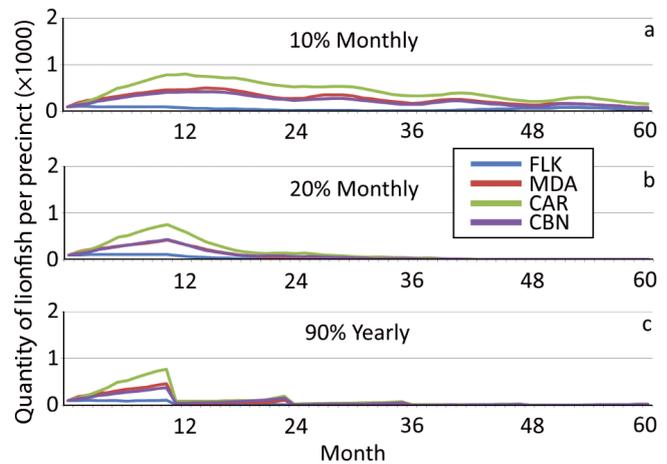


Fig. 7. Five-year plot of lionfish populations which incur monthly culls in all precincts linked to the Carolinas (CAR). Monthly lionfish abundance plots for simulations that are culled at low-intensity 10% and 20% rates in all 10 study precincts which are linked to CAR. The x-axis in each plot indicates the date in months, and the y-axis represents lionfish abundance

ing to the criteria stipulated in the model's logic. This can be seen by the low total quantities of those lionfish larvae that were spawned from and that recruited to, or were exported from, the Northern Bahamas, Western Bahamas, and Florida Keys precincts (Fig. 5a). According to the simulation, many precincts retained a high percentage of their lionfish larvae (i.e. the Western Bahamas, Cuba North, Cuba South, Eastern Gulf of Mexico, and the Yucatan), and some exported a large proportion of their lionfish larvae (i.e. the Florida Keys, Mid-Atlantic, and Meso-american Barrier Reef) (Fig. 5b). One precinct, the Carolinas, imported the majority of its lionfish larvae from upstream locations, though all but 2 other locations—the Northern Bahamas and the Meso-american Barrier Reef precincts—imported a portion of their resident populations from at least 1 of the 10 study precincts (Figs. 2 & 5).

When the major exporters of lionfish larvae were identified for each precinct, we found that 2 precincts, Cuba North and Cuba South, exported lionfish larvae to 8 of the 10 locations modeled (Fig. 2, Table 3). Cuba North was the leading exporter, being a primary export link to 2 precincts, the Western Bahamas and Cuba South, a secondary link to 1, the Northern Bahamas, and a tertiary link to 4, the Yucatan, Florida Keys, Mid-Atlantic, and the Carolinas. In contrast, the Carolinas was a major exporter to zero of the 10 study precincts and instead imported >65% of its lionfish larvae in the simulations (Fig. 5).

Effects of virtual culls on lionfish abundance in the Carolinas

Yearly lionfish culls that were executed for Scenario 1 (Table 4), at rates of both 50% and 90%, did not lessen lionfish abundance in any of the 4 precincts (i.e. the Carolina, Mid-Atlantic, Florida Keys, and Cuba North precincts) at the end of 5 yr (Fig. 6). Conversely, lionfish populations in all 4 highly linked precincts proceeded to build at a fast pace after each annual cull. Monthly culls, i.e. Scenario 2, curbed lionfish populations at a swifter rate than yearly culls; however, only a 60% monthly cull rate was capable of reducing lionfish abundance in the Carolinas to a quantity below that of the initial population of 100 females at the conclusion of the 5 yr simulation (Fig. 6).

When the scope of monthly lionfish culls was expanded to include virtual culls conducted basin-wide (i.e. all 10 precincts considered in the study), a dramatic reduction in lionfish abundance was witnessed in the Carolinas, Mid-Atlantic, Florida Keys, and Cuba North precincts (Fig. 7) for both monthly and yearly culls at the end of 5 yr (Scenarios 3 and 4). A 10%, monthly, and basin-wide cull reduced lionfish biomass to that below the initial founder quantity of 100 females in the Mid-Atlantic and Florida Keys precincts; however, this was not true in the Carolinas or Cuba North. When the monthly basin-wide cull rate was increased to 20%, however, lionfish in the Florida Keys, Cuba North, and Carolinas precincts were extirpated, and lionfish abundance in the Mid-Atlantic precinct comprised only 4% of the initial founder population. Annual culls imposed at an intense exploitation rate of 90% (Scenario 4) saw lionfish eliminated from the Florida Keys precinct; however, remnant lionfish persisted in the remaining 3 precincts with abundances ranging from 8% to 23% of the initial population.

DISCUSSION

This paper delivers 4 relevant findings that are essential to understand and consider when developing a strategy to suppress, or ideally, locally eliminate, invasive Atlantic lionfish: (1) Sporadic yearly lionfish culls that leave remnant populations are not effective at curbing lionfish biomass over a temporal span of >5 yr, given the constraints of our study. This result suggests that the typical recreational lionfish 'derby' approach to culls, which are typically infrequent events that do not cull the entire population,

is not a long-term solution to control lionfish. (2) Monthly lionfish culls are more effective than yearly, though we found these successes only spanned 5 yr. (3) Culling lionfish residing in Cuban waters, in particular, may provide far-reaching remunerations to all nations within the study domain. (4) Basin-wide and low-intensity 20% monthly lionfish culls appear able to swiftly reduce lionfish biomass, and therefore, we find this cull scenario to be the most effective at controlling lionfish abundance. Given these results, we suggest that international collaboration is paramount if a successful reduction in lionfish is to be attained for all nations harbouring invasive lionfish populations within the study domain.

The simulations first give insight into the complex linkages that exist between precincts within the study domain. When examining the linkages between the 10 study precincts, a clear south-to-north flow of larvae was apparent, commencing in the southernmost precinct, the Meso-american Barrier Reef, and terminating in the northernmost precinct, the Carolinas (Fig. 2). Winter water temperatures north of Cape Hatteras, North Carolina, USA, fall below the lower thermal tolerance of invasive lionfish and most other tropical fauna as noted by Briggs (1974); therefore, the Carolinas precinct is likely the northernmost survival limit of lionfish larvae flowing north from the greater Caribbean (Whitfield et al. 2014). It is curious to note that 2 studies of lionfish densities reported extremely high abundances of lionfish from the waters offshore North Carolina (Whitfield et al. 2007, 2014). Our simulation indicated that the Carolinas was the only precinct modelled that received imports from all 10 study precincts (Fig. 2). As the resident Carolina lionfish population and the study by Whitfield et al. (2007) pre-date established lionfish populations upstream of this location (i.e. those population in Cuba, the Florida Keys, etc.), the high densities reported by the authors may be attributed to early colonization of lionfish in the Carolinas around the year 2000 (Schofield 2010) and a subsequent mature lionfish population near ecosystem carrying-capacity limits. The densities noted by Whitfield et al. (2014), however, were discovered after lionfish were already abundant in upstream locations and may reflect the vast quantities of larval lionfish arriving in the Carolinas from upstream precincts as found by this study. Though not a major exporter to any of the 10 precincts considered in this study, it should be noted that the Carolinas do likely export lionfish to regions outside of the study domain. This can be seen by lionfish populations in Bermuda, likely sourced from the Carolinas,

and also lionfish reported along the northeastern seaboard of the United States where populations are ephemeral owing to winter water temperatures that fall below the 10°C thermal tolerance of the fish (Kimball et al. 2004).

Though regions to the south of the Meso-american Barrier Reef precinct were not considered here, it is probable that the overall flow of lionfish larvae is directed from south to north following prevailing ocean currents in the region as modelled by Johnston & Purkis (2014b) (Fig. 2a). As such, the Meso-american Barrier Reef, a precinct that imported lionfish only from the Yucatan in this study, is expectedly linked to those regions to the south that were not incorporated into our simulation. When measuring the impacts of distant recruits on lionfish abundance in the Carolinas alone, and given the constraints of this study, those locations midway between the Meso-american Barrier Reef and Carolinas precincts were the most prominent exporters of lionfish larvae to the Carolinas. Importantly, Cuba North and Cuba South exported lionfish to 8 of the 10 precincts according to the simulations (Fig. 2, Table 3). It follows, therefore, that should a comprehensive lionfish cull program be initiated within the study domain, a primary location to implement the program would be in Cuba in order to deliver the greatest reduction of lionfish recruits over a wide spatial expanse.

While manual culls accomplished by spear-fishing typically target adult lionfish, predominantly when consumption of the fish is the primary motive, other lionfish control models suggest that culls should target juvenile lionfish in conjunction with mature fish (Arias-Gonzalez et al. 2011, Morris et al. 2011). The culling routine used in this study selected both juvenile and adult lionfish at random for removal, following the recommendation of Morris et al. (2011), who found that eliminating both juvenile and adult lionfish was the most effective at decreasing lionfish abundance.

The study simulations evidenced that when eradicating 90% of lionfish, annually, from the Carolinas and the major exporters of lionfish larvae to the Carolinas (i.e. Mid-Atlantic, Florida Keys, and Cuba North—Scenario 1), lionfish abundance in all 4 precincts swiftly rebounded after each cull (Fig. 6). As such, we find that sporadic local lionfish controls that are not complete, such as those executed during annual culls that do not target deep and distant lionfish, are not effective at controlling lionfish populations over the long term, in agreement with Morris et al. (2011) and Arias-Gonzalez et al. (2011). The population rebound found here differs from that shown by Arias-Gonzalez

et al. (2011) (i.e. their Fig. 6); in their study, lionfish biomass remained low when intense rates of fishing-related mortality were imposed on the population. The disparity logically results from the constant influx of lionfish larvae from distant and uncontrolled lionfish populations in our model as these arrivals were not considered in their modelling study. At the end of the simulation produced for Scenario 1, the Carolinas lionfish abundance was a factor of 19-fold greater than that of the initial founding population of 100 individual breeding females (Fig. 6). Contrasting monthly culls of 10% and 60% enacted on the same precincts (Scenario 2), a cull rate of 60% was required to reduce lionfish abundance in the Carolinas to that below the original founder population at the end of 5 yr. Still, this high rate of exploitation was unable to reduce lionfish abundance in the Mid-Atlantic, Florida Keys, and Cuba North precincts to fewer than the 100 founding individuals. Instead, lionfish abundance in the remaining 3 precincts had increased in magnitude at the end of the 5 yr simulation. Given this, it is likely that beyond 5 yr, even monthly culls at a rate of 60% would be insufficient to reduce lionfish abundance in the Carolinas.

In stark contrast, consistent monthly and low-intensity culls of 10% of the population imposed basin-wide (Scenario 3) realized a marked reduction in lionfish populations in all 4 precincts. When this low cull rate was doubled from 10% to 20%, lionfish populations effectively dropped to zero in the Carolinas precinct and also in the precincts that were major exporters of larvae to the Carolinas. Given a similar but nearly complete 90% annual eradication of lionfish (Scenario 4), lionfish numbers were also reduced to that below the initial founder population in all 4 precincts (Fig. 7c). Remnant populations persisted in 3 of the precincts, however, which is concerning given that the entire invasive population is thought to stem from perhaps as few as 10 individuals (Whitfield et al. 2002, Hamner et al. 2007). Contrasting monthly and yearly basin-wide culls, we find that consistent and low-effort monthly culls are more effective at reducing lionfish abundance than high-intensity annual culls.

Critically, as witnessed here, uncultured precincts from which the Carolinas imported just 5% of lionfish larvae were able to effectively negate 60% monthly culls executed in the Carolinas and its major exporters at the end of 5 yr according to our simulation (Scenario 1). Similarly, those lionfish remaining after a nearly complete 90% annual cull, conducted basin-wide (Scenario 2), were able to continue propagating the lionfish invasion according to our simula-

tion. Only Scenario 3, where comprehensive, basin-wide monthly culls were imposed at low-intensity rates of 20%, accomplished a significant reduction in lionfish abundance in the Carolinas and its major exporters according to our simulation. The difference seen by this study when culling lionfish numbers in the precincts that are major exporters of larvae to the Carolinas versus all precincts from which the Carolinas imports larvae exposes an intrinsic danger; even sparse and uncontrolled lionfish populations, such as those in deep water beyond the reach of recreational divers, may derail a concerted, yet not comprehensive, cull effort to control invasive lionfish.

The environmental and economic losses instigated by invasive species in the United States alone cost USD 120 billion annually (Pimentel et al. 2005), though costs due to lionfish have not yet been quantified. Lionfish have been shown to reduce the recruitment of native prey fishes by 65% over a period of 2 yr in the Bahamas (Green et al. 2012) and biomass of all teleosts on artificial reefs introduced with lionfish over a 5 wk span by 79% (Albins & Hixon 2008). These studies signify that the economic damage done to ecosystems in the study domain perhaps surpasses the expensive and laborious efforts which must be undertaken to control the invader. Still, lionfish control costs must be well-considered against economic losses when planning for a broad-scale application of lionfish culls. To date, the per-unit effort cost to remove lionfish has not been enumerated and is an area of research that needs study.

Local lionfish removal programs are increasing in frequency and scope in many nations within the study domain and have proven moderately successful at reducing local lionfish populations (Barbour et al. 2011). Most of these programs, however, are conducted using spears or hand-nets and are limited to recreational dive limit depths (~30 m), therefore leaving deep lionfish uncontrolled (Barbour et al. 2011). These untargeted deep lionfish populations are concerning, given that Bejarano et al. (2014) found that deep-reef terraces may serve as potential refugia for the fish. Additionally, locations that are distant to human populations are not often fished and perhaps may serve as reservoirs for burgeoning lionfish populations. Lionfish show low vulnerability to a hook and line fishery, though some success has been seen by reef-trap fisheries which often haul large quantities of lionfish as by-catch (Morris & Whitfield 2009). Indeed, these trap-fisheries are capable of targeting lionfish at depth; however, for these reef-traps to be useful, they would necessitate a design that substantially reduces the bycatch of native fauna. Such a

device has yet to be developed but is an area of study apt for evaluation.

When simulating lionfish populations via a stage-based control model, Morris et al. (2011) found that a cull rate of 27% was sufficient to control the invader in the short term and within the confines of their study, though they did not consider outside recruits in their model. Our study echoes the findings of Morris et al. (2011), forecasting that a similar 20% monthly cull rate, though performed at a broad spatial scale, would be obligatory to reduce lionfish abundance in the Carolinas. Our study also found that a 20% basin-wide cull rate appears to be a critical chokehold level at which lionfish culls may be successful to control lionfish populations in the Carolinas as well as those precincts directly linked to the Carolinas. Still, a 20% decrease in lionfish numbers in all Atlantic habitats that contain lionfish is a lofty goal given that lionfish show extreme habitat plasticity, the costs of invasive species controls are extraordinarily high, and to date, cooperation between nations to achieve such a goal has not been realized (Pimentel et al. 2005, Morris & Akins 2009, Barbour et al. 2010, Albins & Hixon 2011, Boom 2012, Jud & Layman 2012). If a concerted and international effort is to be conceived to reduce lionfish biomass, we suggest a 20% monthly cull of lionfish basin-wide to be the critical cull level necessary to substantially reduce the abundance of lionfish. Given the acknowledged difficulties in implementing such an international lionfish management plan, a more approachable and realistic goal would be for high-risk locations to use a study, such as this one, to identify the top linkages to their specific location and then to partner with those upstream nations to develop a comprehensive lionfish removal plan beneficial to both parties.

Lionfish population connectivity as seen by our Eulerian model is reflective of broad-scale patterns generated by Lagrangian models that used similar ocean current models (i.e. HYCOM and MICOM) to simulate connectivity patterns of other marine organisms within the study domain (Cowen et al. 2000, Paris et al. 2005, Kool et al. 2010). For example, Kool et al. (2010) and Cowen et al. (2000) (the latter authors engaging a model that incorporated active larval movement) also found that populations of reef organisms in Northern Cuba were weakly linked to populations in the Florida Keys and strongly linked to those in the Bahamas. These authors found that the Meso-american Barrier Reef was moderately linked to the Florida Keys and Northern Cuba, mirroring our results (see Fig. 5 in Cowen et al. 2000,

Fig. 4 in Kool et al. 2010, Figs. 2 & 3 here). A connectivity break between Florida and the Bahamas, noted by Cowen et al. (2000), was prominent in our simulation (Figs. 1 & 2d,k,l), and Paris et al. (2005) also found high self-recruitment (of several snapper species) in Cuba with weak larval flow to the Florida Keys, similar to our results. Unfortunately, the domains of these 3 comparative studies did not extend northward past the Florida Keys, and so the Carolinas, our focal region, was not represented in their results. Given the similar regional connectivity witnessed between Cowen et al. (2000), Paris et al. (2005), Kool et al. (2010), and our study, however, we anticipate our findings to be a reasonable approximation of connectivity though the entire study domain given an average year when weighed against other existing Lagrangian studies. It follows that should we have implemented a similar Lagrangian model, instead of a Eulerian model, the cull rates and frequency we quantify here to contain the invasion—the overall aim of this study—would likely have remained unchanged. Still, we acknowledge that an interpolation in time and space within the advection process (i.e. interpolation of the monthly ocean current data and also particle trajectories between cell centers) was not done here and that Lagrangian models more accurately describe larval flow on ocean currents over discrete timeframes than the model employed for this analysis. Finally, it is worth noting that the HYCOM simulations significantly lacked ocean current forecasts for shallow waters that are prime lionfish habitat and that are also important to larval connectivity, i.e. in areas such as the Bahama Banks and near-shore shallow locations. Should we have excluded ocean current data for these shallow waters and solely relied on the HYCOM simulation data, forecasting the potential settlement of lionfish within and the advection of lionfish larvae across these areas would not have been possible. Instead, we compiled a merged HYCOM/OSCAR dataset that captured high-resolution HYCOM simulation data and also lower-resolution, but still critical, remotely sensed OSCAR data in shallow areas where HYCOM lacked fidelity (Fig. S1). We reason this combined flow field provided the best approximation of ocean currents within the study domain given presently available water flow data.

Our study results are subject to estimation errors owing largely to a paucity of life-history data for Atlantic lionfish which were used to parameterize the model. Natural mortality (M) has not been quantified for any larval tropical scorpaenid and is an element

to which lionfish, and most marine fish, population models are the most sensitive (Barbour et al. 2011, Morris et al. 2011, Johnston & Purkis 2014b). The mortality rates used in this study comprise the ranges reported for many marine fish with pelagic larval phases and are consistent with those used in similar lionfish modelling studies (Barbour et al. 2011, Morris et al. 2011, Johnston & Purkis 2014a, 2014b, 2015). Given that lionfish are chemically protected and are largely immune to predation by native fishes (Hackert et al. 2013), natural mortality of invasive lionfish may be lower than the value we used for this study. As a result, we may have produced an underestimation of the rate of lionfish culls that are necessary to control the invasive population. Still, the conditioning parameters used have been sensitivity tested (Johnston & Purkis 2014a, 2014b), and the distribution patterns of lionfish larvae produced by the model have been shown robust to alterations of M . All lionfish life history traits that parameterize the model were sourced from the literature and from past lionfish modelling studies, and therefore, our methodology is consistent with best modelling practices to date and current knowledge of Atlantic lionfish behaviour.

This study used monthly mean, instead of high-resolution daily, ocean current and SST data to parameterize the model, and therefore, the temporal variability of those values was likely dampened. Given this, a conservative measure of lionfish dispersal may have been produced by the simulations, and this potential underestimation should be considered when interpreting our results. Going forward, the model would benefit from the integration of 3-dimensional water flow and also increased resolution of ocean current forecast data as they become available. Further, considering ontogenetic movement of larvae and also the inclusion of 'sensory zones' surrounding potential settlement sites (i.e. simulating horizontal movements of late-stage larvae towards reef cues) would strengthen the model outputs. Unfortunately, lionfish larval movement has not been documented in the literature, and so we presumed lionfish larvae are concentrated in surface waters, similar to other reef fish larvae that are pelagically dispersed (Paris & Cowen 2004).

Our simulations reveal that the abundance of invasive Atlantic lionfish cannot be reduced in a focus region without coordinated, frequent, sustained, and comprehensive lionfish culls in nations to which that location is hydrographically connected. The linkages that we identify between the 10 study precincts are a useful guide when planning a control strategy for

lionfish within the study area. Finally, the Cuba North and Cuba South precincts are key exporters of lionfish larvae to the majority of precincts in our study, and we suggest these sites are critical locations that should be preferentially targeted by lionfish control efforts.

Acknowledgements. We thank the National Coral Reef Institute for their unwavering support of this research effort. Funding for this study was provided by the Guy Harvey Research Institute. This is NCRI publication 175.

LITERATURE CITED

- Ahrenholz DW, Morris JA (2010) Larval duration of the lionfish, *Pterois volitans* along the Bahamian Archipelago. *Environ Biol Fishes* 88:305–309
- Akins JL, Morris JA, Green SJ (2014) In situ tagging technique for fishes provides insight into growth and movement of invasive lionfish. *Ecol Evol* 4:3768–3777
- Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish *Pterois volitans* reduce recruitment of Atlantic coral-reef fishes. *Mar Ecol Prog Ser* 367:233–238
- Albins MA, Hixon MA (2011) Worst case scenario: potential long-term effects of invasive predatory lionfish (*Pterois volitans*) on Atlantic and Caribbean coral-reef communities. *Environ Biol Fish* 96:1151–1157
- Amante C, Eakins BW (2009) ETOPO1 1 Arc-Minute Global Relief Model: procedures, data sources and analysis. NOAA Tech Memo NESDIS NGDC 24:19
- Arias-González JE, González-Gándara C, Luis Cabrera J, Christensen V (2011) Predicted impact of the invasive lionfish *Pterois volitans* on the food web of a Caribbean coral reef. *Environ Res* 111:917–925
- Barbour AB, Montgomery ML, Adamson AL, Díaz-Ferguson E, Silliman BR (2010) Mangrove use by the invasive lionfish *Pterois volitans*. *Mar Ecol Prog Ser* 401:291–294
- Barbour AB, Allen MS, Frazer TK, Sherman KD (2011) Evaluating the potential efficacy of invasive lionfish (*Pterois volitans*) removals. *PLoS ONE* 6:e19666
- Bejarano S, Lohr K, Hamilton S, Manfrino C (2014) Relationships of invasive lionfish with topographic complexity, groupers, and native prey fishes in Little Cayman. *Mar Biol* 162:1–14
- Betancur-R R, Hines A, Acero AP, Orti G, Wilbur AE, Freshwater DW (2011) Reconstructing the lionfish invasion: insights into Greater Caribbean biogeography. *J Biogeogr* 38:1281–1293
- Bonjean F, Lagerloef GSE (2002) Diagnostic model and analysis of the surface currents in the tropical Pacific Ocean. *J Phys Oceanogr* 32:2938–2954
- Boom BM (2012) Biodiversity without borders. *Science and Diplomacy*, September 2012, available at www.sciencediplomacy.org/article/2012/biodiversity-without-borders (accessed 11 January 2015)
- Briggs JC (1974) *Marine zoogeography*. McGraw Hill, New York, NY
- Carlin JL, Robertson DR, Bowen BW (2003) Ancient divergences and recent connections in two tropical Atlantic reef fishes *Epinephelus adscensionis* and *Rypticus saponaceous* (Percoidei: Serranidae). *Mar Biol* 143:1057–1069
- Chassignet EP, Hurlburt HE, Smedstad OM, Barron CN and others (2005) Assessment of data assimilative ocean models in the Gulf of Mexico using ocean color. In: Sturges W, Lugo-Fernandez A (eds) *Circulation in the Gulf of Mexico: observations and models*. Am Geophys Union, Washington, DC, p 87–100
- Chassignet EP, Hurlburt HE, Smedstad OM, Halliwell GR and others (2007) The HYCOM (hybrid coordinate ocean model) data assimilative system. *J Mar Syst* 65:60–83
- Cowen RK, Lwiza KM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? *Science* 287:857–859
- De Leon R, Vane K, Vermeij M, Bertuol P, Simal F (2011) Overfishing works: a comparison of the effectiveness of lionfish control efforts between Bonaire and Curaçao. *Proc 64th Gulf and Caribbean Fisheries Institute*, October 31 to November 5, 2011
- Frazer TK, Jacoby CA, Edwards MA, Barry SC, Manfrino CM (2012) Coping with the lionfish invasion: Can targeted removals yield beneficial effects? *Rev Fish Sci* 20:185–191
- Freshwater DW, Hines A, Parham S, Wilbur A and others (2009) Mitochondrial control region sequence analyses indicate dispersal from the US East Coast as the source of the invasive Indo-Pacific lionfish *Pterois volitans* in the Bahamas. *Mar Biol* 156:1213–1221
- Green SJ, Côté IM (2009) Record densities of Indo-Pacific lionfish on Bahamian coral reefs. *Coral Reefs* 28:107
- Green SJ, Akins JL, Maljkovi A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. *PLoS ONE* 7:e32596
- Green SJ, Dulvy NK, Brooks AL, Akins JL, Cooper AB, Miller S, Côté IM (2014) Linking removal targets to the ecological effects of invaders: a predictive model and field test. *Ecol Appl* 24:1311–1322
- Hackerott S, Valdivia A, Green SJ, Côté IM and others (2013) Native predators do not influence invasion success of Pacific lionfish on Caribbean Reefs. *PLoS ONE* 8:e68259
- Hamner RM, Freshwater DW, Whitfield PE (2007) Mitochondrial cytochrome b analysis reveals two invasive lionfish species with strong founder effects in the western Atlantic. *J Fish Biol* 71:214–222
- Johnston MW, Purkis SJ (2011) Spatial analysis of the invasion of lionfish in the western Atlantic and Caribbean. *Mar Pollut Bull* 62:1218–1226
- Johnston MW, Purkis SJ (2014a) Lionfish in the eastern Pacific: a cellular automaton approach to assessing invasion risk. *Biol Invas* 16:2681–2695
- Johnston MW, Purkis SJ (2014b) Are lionfish set for a Mediterranean invasion? Modelling explains why this is unlikely to occur. *Mar Pollut Bull* 88:138–147
- Johnston MW, Purkis SJ (2015) Hurricanes accelerated the Florida-Bahamas lionfish invasion. *Glob Chang Biol* 21:2249–2260
- Jud ZR, Layman CA (2012) Site fidelity and movement patterns of invasive lionfish, *Pterois* spp., in a Florida estuary. *J Exp Mar Biol Ecol* 414–415:69–74
- Kimball ME, Miller JM, Whitfield PE, Hare JA (2004) Thermal tolerance and potential distribution of invasive lionfish (*Pterois volitans/miles* complex) on the east coast of the United States. *Mar Ecol Prog Ser* 283:269–278
- Kool JT, Paris CB, Andréfouët S, Cowen RK (2010) Complex migration and the development of genetic structure in subdivided populations: an example from Caribbean coral reef ecosystems. *Ecography* 33:597–606

- Kourafalou VH, Peng G, Kang H, Hogan PJ, Smedstad OM, Weisberg RH (2009) Evaluation of global ocean data assimilation experiment products on South Florida nested simulations with the Hybrid Coordinate Ocean Model. *Ocean Dyn* 59:47–66
- Morris JA Jr, Akins JL (2009) Feeding ecology of invasive lionfish (*Pterois volitans*) in the Bahamian archipelago. *Environ Biol Fishes* 86:389–398
- Morris JA Jr, Whitfield PE (2009) Biology, ecology, control and management of the invasive Indo-Pacific lionfish: an updated integrated assessment. NOAA Tech Memo NOS NCCOS 99
- Morris JA Jr, Shertzer KW, Rice JA (2011) A stage-based matrix population model of invasive lionfish with implications for control. *Biol Invasions* 13:7–12
- Mumby PJ, Harborne AR, Brumbaugh DR (2011) Grouper as a natural biocontrol of invasive lionfish. *PLoS ONE* 6: e21510
- Paris CB, Cowen RK (2004) Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnol Oceanogr* 49:1964–1979
- Paris CB, Cowen RK, Claro R, Lindeman KC (2005) Larval transport pathways from Cuban snapper (Lutjanidae) spawning aggregations based on biophysical modeling. *Mar Ecol Prog Ser* 296:93–106
- Paris CB, Helgers J, Van Sebille E, Srinivasan A (2013) Connectivity Modeling System: a probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. *Environ Model Softw* 42:47–54
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol Econ* 52: 273–288
- Prasad TG, Hogan PJ (2007) Upper-ocean response to Hurricane Ivan in a 1/25° nested Gulf of Mexico HYCOM. *J Geophys Res C* 112:C04013. doi:10.1029/2006JC003695
- Richards VP, Thomas JD, Stanhope MJ, Shivji MS (2007) Genetic connectivity in the Florida reef system: comparative phylogeography of commensal invertebrates with contrasting reproductive strategies. *Mol Ecol* 16:139–157
- 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. *Aquat Invasions* 5: S117–S122
- Tamburello N, Côté IM (2015) Movement ecology of Indo-Pacific lionfish on Caribbean coral reefs and its implications for invasion dynamics. *Biol Invasions* 17: 1639–1653
- USGS-NAS (2014) United States Geological Survey-Non-indigenous Aquatic Species database (USGS-NAS). <http://nas.er.usgs.gov> (accessed 4 November 2014)
- Valdez-Moreno M, Quintal-Lizama C, Gómez-Lozano R, del Carmen García-Rivas M (2012) Monitoring an alien invasion: DNA barcoding and the identification of lionfish and their prey on coral reefs of the Mexican Caribbean. *PLoS ONE* 7:e36636
- Whitfield PE, Gardner T, Vives SP, Gilligan MR, Courtenay WR Jr, Ray GC, Hare JA (2002) Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. *Mar Ecol Prog Ser* 235:289–297
- Whitfield PE, Hare JA, David AW, Harter SL, Munoz RC, Addison CM (2007) Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the Western North Atlantic. *Biol Invasions* 9:53–64
- Whitfield PE, Muñoz RC, Buckel CA, Degan BP, Freshwater DW, Hare JA (2014) Native fish community structure and Indo-Pacific lionfish *Pterois volitans* densities along a depth-temperature gradient in Onslow Bay, North Carolina, USA. *Mar Ecol Prog Ser* 509:241–254

Editorial responsibility: Alejandro Gallego, Aberdeen, UK

Submitted: January 22, 2015; Accepted: June 19, 2015
 Proofs received from author(s): July 31, 2015