Hurricanes accelerated the Florida–Bahamas lionfish invasion

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Abstract

In this study, we demonstrate how perturbations to the Florida Current caused by hurricanes are relevant to the spread of invasive lionfish from Florida to the Bahamas. Without such perturbations, this current represents a potential barrier to the transport of planktonic lionfish eggs and larvae across the Straits of Florida. We further show that once lionfish became established in the Bahamas, hurricanes significantly hastened their spread through the island chain. We gain these insights through: (1) an analysis of the direction and velocity of simulated ocean currents during the passage of hurricanes through the Florida Straits and (2) the development of a biophysical model that incorporates the tolerances of lionfish to ocean climate, their reproductive strategy, and duration that the larvae remain viable in the water column. On the basis of this work, we identify 23 occasions between the years 1992 and 2006 in which lionfish were provided the opportunity to breach the Florida Current. We also find that hurricanes during this period increased the rate of spread of lionfish through the Bahamas by more than 45% and magnified its population by at least 15%. Beyond invasive lionfish, we suggest that extreme weather events such as hurricanes likely help to homogenize the gene pool for all Caribbean marine species susceptible to transport.

Keywords: computer simulation, hurricanes, invasive species, lionfish, reef connectivity

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Introduction

Marine invasions are rare. The most successful invaders to date, the predatory Indo-pacific lionfish (*Pterois volitans/miles*), express diverse invasive traits that led to their intense proliferation in the Atlantic (Barbour *et al.*, 2008; Green & Côté, 2009; Albins & Hixon, 2011; Jud *et al.*, 2011; Côté *et al.*, 2013; Cure *et al.*, 2014). Notwithstanding the impacts that have been quantified for Atlantic lionfish (Albins & Hixon, 2008; Morris & Whitfield, 2009; Arias-González *et al.*, 2011), the long-term effects of marine invasive species are unknown because of their novelty. Genetic studies suggest that the Atlantic lionfish population was founded by as few as ten individuals, likely aquarium releases (Whitfield *et al.*, 2002; Hamner *et al.*, 2007). Lionfish were first discovered in South Florida waters in 1985, as reported by the United States Geological Survey Non-indigenous Aquatic Species (USGS-NAS) database (USGS-NAS, 2014). This database is the most comprehensive collection of lionfish records in the Atlantic and therefore serves as a

valuable documentation of this marine invasion (Schofield, 2010). The literature indicates that 'detection lags', where an invasive animal is noticed and reported only after becoming an abundant nuisance, are ubiquitous with invasive species (Lewin, 1987; Crooks & Soulé, 1999; Crooks, 2005). Lionfish were reported from the Bahamas in the year 2004 (USGS NAS, 2014). The USGS-NAS records, however, are not the product of active monitoring and lionfish are known to be cryptic and often not easily observed (Darling *et al.*, 2011). The year 2004 Bahamian lionfish records, therefore, likely reflect a detection lag that trails the pace of the lionfish invasion. As such, locations where lionfish were documented by the USGS-NAS were doubtlessly infested prior to the reported date, which is important when estimating the realized arrival date of lionfish in the Bahamas.

Once established in the Bahamas, lionfish rapidly dispersed south and east against prevailing Bahamian ocean currents, results supported by the 2014 USGS-NAS database and Johnston & Purkis (2011). This pattern of invasion is curious for two reasons. First, adult lionfish are nonmigratory, which likely precludes active movement against prevailing water flow, and second, buoyant lionfish disperse on surface ocean currents and

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their spread should therefore mimic broad-scale circulation patterns (Whitfield *et al.*, 2002; Hare & Whitfield, 2003; Ahrenholz & Morris, 2010; Jud *et al.*, 2011; Morris *et al.*, 2011; Johnston & Purkis, 2013; Luiz *et al.*, 2013). A distinct bio-geographical and genetic connectivity break has been noted between Florida and the Bahamas, caused by the strong northerly flow of the Florida Current (Carlin *et al.*, 2003; Richards *et al.*, 2007; Freshwater *et al.*, 2009; Kool *et al.*, 2010; Betancur-R *et al.*, 2011). Genetic studies suggest, however, that Floridian lionfish are closely related to Bahamian lionfish (Freshwater *et al.*, 2009), indicating connectivity across the Florida Current. Up until now, the mechanism by which lionfish have been able to cross the Florida Current shortly after their introduction to South Florida and disperse against prevailing Bahamian currents has not been satisfactorily addressed. This study posits frequent Atlantic hurricanes to be central to explaining the up-current invasion of lionfish through the Bahamas. For brevity, we will adopt the term 'storms' in the paper as a term to encompass both hurricanes and named tropical storms.

Storms are capable of causing broad disruption to prevailing local ocean current patterns (Wang *et al.*, 2005; Teague *et al.*, 2007). For instance, as Category 3 Hurricane Ivan passed through the northern Gulf of Mexico in 2004, it generated surface current water velocities as fast as 2.14 m/s with maximum near-bottom (a water depth of 52 m) velocities of 1.35 m/s (Wang *et al.*, 2005; Teague *et al.*, 2007). Moreover, ocean current velocities of 1.31 m/s were likewise measured during Ivan at a water depth of 84 m, demonstrating that hurricanes are capable of disturb water flow deep into the water column. Prior to and after Ivan, average current velocities in the northern Gulf measured less than 0.30 m/s (Teague *et al.*, 2007). Importantly, the trajectories of these anomalous currents were aligned with the direction of Ivan's winds. Anomalies in ocean current velocity and direction (hereafter referred to as OCVD), as measured acoustically during Hurricane Ivan, coincide with those forecasted by the Hybrid Current Ocean Model (HYCOM – see Table 1) (Chassignet *et al.*, 2007; Prasad & Hogan, 2007). Previous computer simulations of lionfish dispersal which utilized the HYCOM data (Johnston & Purkis, 2011, 2012, 2014a,b), however, lacked the fidelity to capture hurricane-altered water circulation.

Our study postulates that anomalous ocean surface currents, forced by storm–force winds, transported larval lionfish from Florida to the Bahamas prior to the year 2000. We offer quantitative evidence that, once lionfish established in the Bahamas, storm-induced currents accelerated expansion of the invasive population throughout the Bahamas spanning the years 2000–2007. On the basis of this work, we are able to identify opportunities in which lionfish could have conceivably breached the Florida Current. We also estimate the effect of hurricanes on the progress of the lionfish invasion-front through the Bahamas.

Materials and methods

To test the hypothesis that strong eastward-flowing water during storms transport lionfish from South Florida to the Bahamas, we first scrutinized the HYCOM daily surface OCVD data for the 2004–2005 hurricane seasons. The HYCOM dataset was selected for study as it is a widely employed and robust coupled ocean-atmosphere prediction model that we deem a useful global approximation of ocean currents upon which to estimate the transport of larval fish (Chassignet *et al.*, 2007). From this examination of daily HYCOM surface OCVD data, it was possible to detect water direction and velocity anomalies in the Florida Current that may facilitate cross-stream transport of lionfish larvae. We focused our inquiry on a 40 000 km^2 expanse of the Florida Straits incorporating South Florida and the northwestern Bahamas (25.5 N to 27.5 N and −80.5 W to −78.5 W) (Fig. 1). For this area, we next implemented a biophysical computer model, which is an evolution of that previously employed by Johnston & Purkis (2011, 2012, 2014a,b) to simulate the spread of lionfish through the Bahamas. The simulations were founded on a small virtual breeding population in the north central Bahamas that we deemed to be established by larval lion-

Table 1 Physical Oceanic Parameters Used in the Model. Oceanic parameters, resolution, and original sources of data used for inputs in this study

Parameter name	Resolution	Source and description
Ocean current	10 km	Monthly mean current values from the HYCOM (GLBa0.08 project) for the year 2006, and daily data were harvested for the years 2004–2005 storm seasons. Ocean Surface Current Analysis (OSCAR) monthly mean current values for the year 2006 were used and interpolated to a resolution of 10 km where HYCOM data was incomplete (Bonjean & Lagerloef, 2002)
Sea surface temperature (SST)	4 km	Moderate-resolution Imaging Spectroradiometer (MODIS)-Aqua satellite climatological data (composite monthly mean values) for the years 2003 to 2012
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)
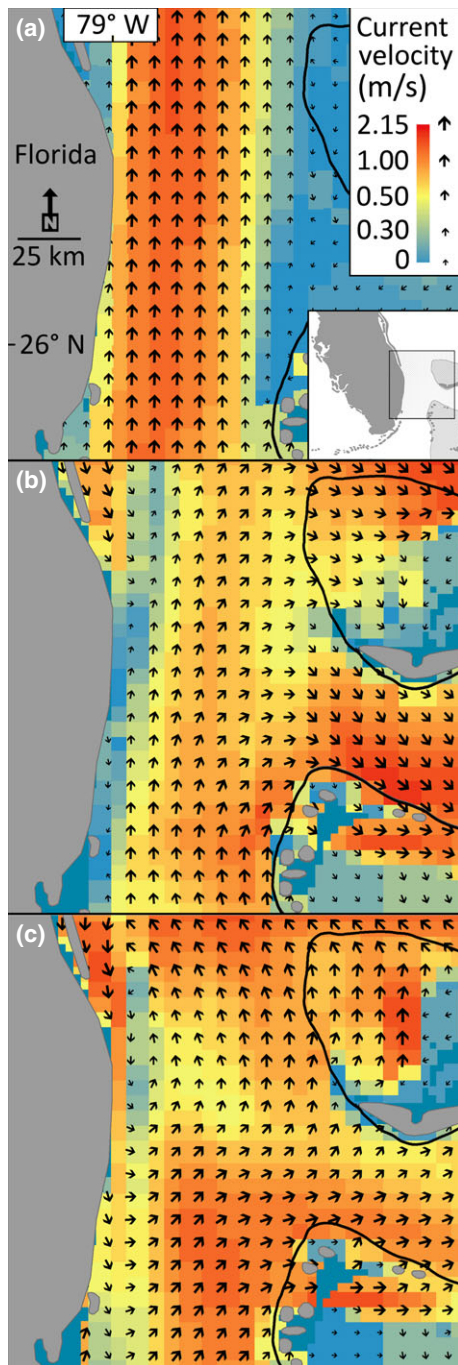
Fig. 1 Water flow in the Florida Straits in hurricane vs. nonhurricane times. Water flow in the Florida Straits denoted by arrows for water flow direction and red (fast) to blue (slow) scale for water velocity. Water flow during an average year (a), during hurricanes Jeanne (b), and Wilma (c).

fish transported from South Florida prior to the year 2000. The simulations captured monthly mean surface OCVD for an average year (Fig. 1a, Fig. S1) with daily OCVD data for the July–November hurricane seasons of the years 2004

and 2005, when a total of ten storm systems crossed the Florida Straits (Fig. 2b, c).

Analysis of Hurricane-altered ocean currents in the Florida Straits

A fixed 2-D grid represented the study area with a cell size of 10 km × 10 km. Each grid cell contained values corresponding to physical oceanographic conditions, such as water depth, sea surface temperature, and direction and velocity of water flow (Table 1, 2). First, the daily HYCOM OCVD data for the Florida Straits was queried to isolate grid cells that contained water flowing to the north, northeast, east, and southeast. The resultant grid cells were then tallied for each direction and each day spanning the years 2004 and 2005 hurricane seasons. Next, the total counts registered were calculated as a percentage of the total quantity of grid cells containing OCVD data in the Florida Straits (2539 grid cells) and plotted, with date on the *x*-axis and percentage of total on the *y*-axis (Fig. 2b, c). Daily average flow velocities were also computed for each direction and included in the graph, with the date on the *x*-axis and mean velocity on the *y*-axis. Ocean currents flowing south, southwest, west, and northwest were not inspected as they do not conduct lionfish spread from Florida to the Bahamas. Anomalies in water flow direction and speed are conspicuous in the daily HYCOM data during the passage of hurricanes and are highlighted on the plots (Fig. 2b, c). The strengths of storms are denoted with small (<Category 3 – weak) to large dots (Category 5 – strong) (Fig. 2a–c). This diagram is useful to demonstrate alterations in water flow direction and velocity when strong vs. weak hurricanes impact the Florida Straits.

The biophysical model and simulations

Four scenarios were modeled, and simulations (each comprised of 10 model runs) with different conditioning parameters were conducted for each. *Scenario one:* HYCOM mean-monthly OCVD data were used as model inputs, exclusive of all daily storm data (compiled for the year 2006 which is a year without hurricanes in the Florida Straits – see the Implementation of the Model section for a full discussion of the OCVD data used). This scenario serves as a baseline against which results from model runs that consider storm-induced circulation patterns can be numerically compared. *Scenario two*: HYCOM mean-monthly OCVD data, inclusive of the year 2004 daily HYCOM storm season data, were used as model inputs, quantifying the impact of the year 2004 storm season alone. *Scenario three*: HYCOM mean-monthly OCVD data, inclusive of the year 2005 daily HYCOM storm season data, were used as model inputs, quantifying the impact of the year 2005 storm season alone. *Scenario four*: HYCOM mean-monthly OCVD data were coupled with HYCOM daily OCVD data for the 2004 and 2005 storm seasons to parameterize the simulation. The purpose of this fourth
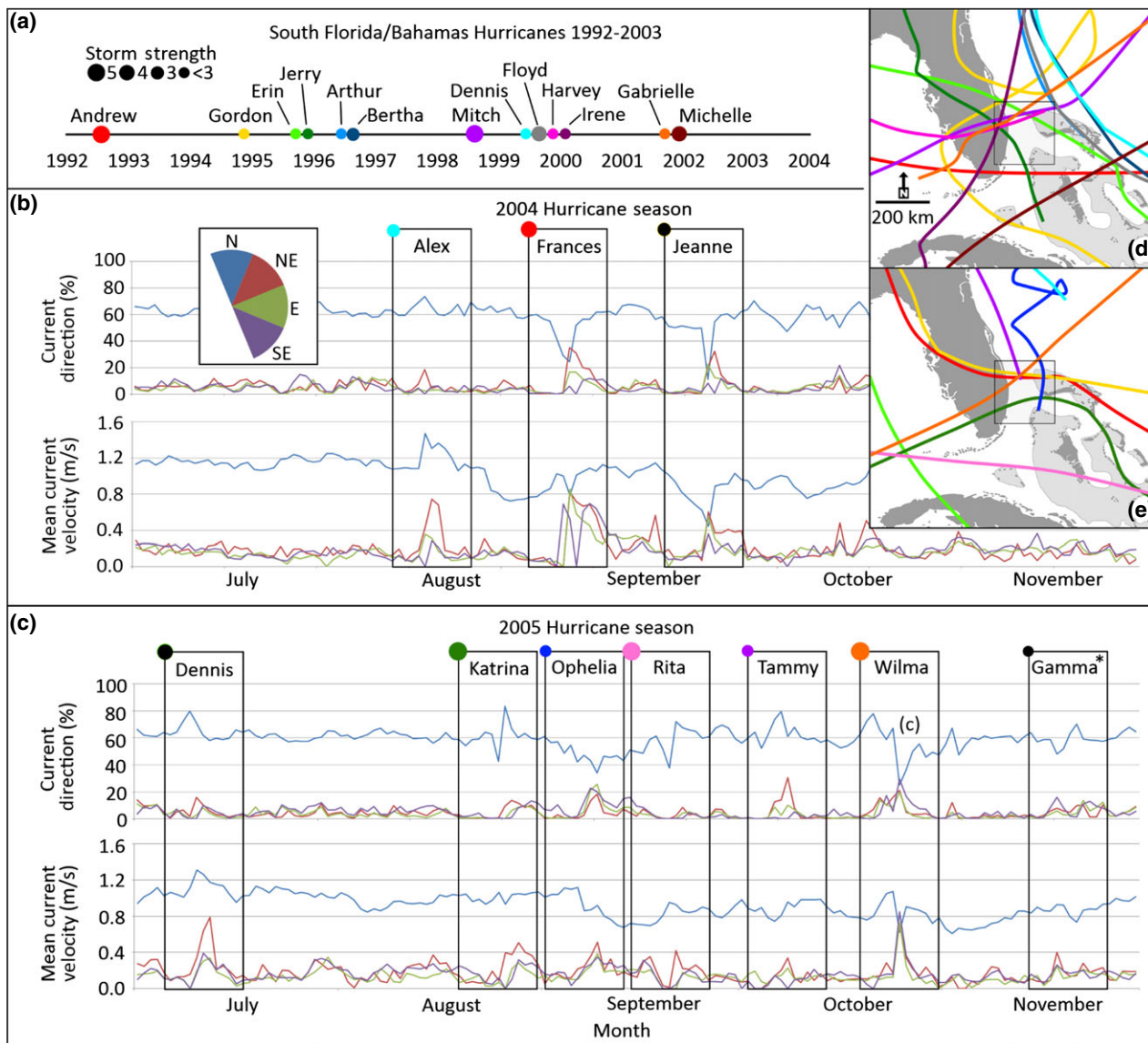
Fig. 2 Storms and water flow in the Florida Straits for the 1992 through 2005 storm seasons. Hurricane activity affecting the Florida Straits (d) spanning the years 1992 to 2004 (a, d). Daily analysis of hurricane data in the Florida Straits for the years 2004 (b) and 2005 (c) hurricane seasons. Color of the plot lines indicates the direction of water flow. The path of hurricanes during the 2004 and 2005 seasons (e). Storms impacting the Florida Straits are indicated via black boxes (b, c). Each box spans 12 days. Graduated dots (a–c) indicate the intensity of storms and are color-coded, matching the storm path as indicated in (d) and (e). An * denotes a tropical storm.

scenario was to evaluate whether consecutive storm seasons may further increase the distribution of lionfish larvae and amplify the size and density of reproductive populations when compared to a single storm season.

Our analysis implemented a hybrid cellular automaton and agent-based model to forecast the diffusion, settling capacity, and resulting adult populations of lionfish in the Bahamas. The simulation data provided date-stamped geographic points of settlement of lionfish larvae, which mature to adulthood, and can then be summarized over space and time within a GIS framework. The diffusion and settlement of lionfish larvae throughout the grid was governed by a simple set of rules which were built upon lionfish biological traits and tolerances to water depth and temperature (Kimball *et al.*, 2004; Albins & Hixon, 2011). The mechanics of the model have been reviewed in detail (Johnston & Purkis, 2011, 2012, 2013, 2014a,b) and therefore only a brief overview is provided.

Model overview

The first step toward creating a simulation was to identify the quantities and grid cell locations of breeding lionfish composing the entire simulated population. At the onset of a

simulation (as opposed to a subsequent simulation cycle), the founder population was selected and a temporal timer was started to track the total simulation time. For the duration of the simulation, the timer recorded the date and was incremented by 30 days for each successive cycle (representing one lionfish breeding pulse). The timer was queried throughout the simulation run to retrieve time-stamped OCVD data from a database of values. Next, the estimated monthly adult mortality rate was applied to the entire population to reflect adult die-off (mortality) per month. For example, if an adult lionfish population comprises 1000 individuals, 1000 was multiplied by the monthly mortality rate of 0.052^{-mo} to arrive at 52 lionfish that died during the simulated month. The dead lionfish were removed from the simulation by selecting 52 fish at random, with the remaining fish eligible to contribute larvae in the next iteration of the simulation.

Each mature female lionfish in the population was assumed to breed once per 30-day cycle, producing a defined quantity of larvae, demarcated as q (see Table 2 for all parameter input values and their justification). The survival rate to adulthood (S_a) was calculated for every lionfish larva produced, but only the dispersal of those larvae that survive to maturity was simulated to reduce computational overhead. To calculate S_a, we started with a 100% larval survival rate and then, using lionfish mortality rates for each life stage (M_e, M_l, M_j), decremented the rate each day during the egg (d_e) and larval (d) duration periods. Next, juvenile mortality was imposed per month spanning the juvenile-to-adult transition (a). Finally, the survival rate calculated thus far was multiplied by the quantity of eggs produced per cycle by a single lionfish (q), quantifying S_a. The calculation is summarized by the equation:

$$S_a = (M_e^{d_e})(M_l^{d-d_e})(M_j^{a})(q) \qquad (1)$$

The proportion of male to female lionfish (f) used was 1 : 0.85 (46% female). To determine the number of female lionfish (S_p, assuming a companion male lionfish as males are more plentiful than females) which remained viable to breeding age, we multiplied the number of surviving adults by the ratio of females using the equation:

$$S_p = (S_a \times f) \qquad (2)$$

S_p represented the quantity of female larvae whose movement through the grid was projected in the simulation.

Lionfish larvae moved passively through the model grid on simulated surface water currents forecast by the HYCOM circulation model (see Table 1 for more about the HYCOM),

Table 2 Parameter Inputs Used in the Model. Parameter description, values, justification, and original sources of parameter data used for the model inputs

Parameter name	Value	Justification	Source
Founder location	24.817°N −79.683°W	Western Bahamas location adjacent to South Florida	
Cycles (months)	96	Simulations were created spanning the years 2000 – 2007, the estimated time frame in which lionfish settled the Bahamas and populations expanded	
Grid size	10 km	Parameter granularity of the interpolated HYCOM ocean current dataset	
SST lower thermal limit	10 °C	Documented lower thermal tolerance of invasive lionfish	Kimball *et al.* (2004)
Depth range	1–300 m	Estimated depth range of invasive lionfish	Albins & Hixon (2011)
Egg duration (d_e)	3 days	Estimated egg duration of lionfish in the Atlantic	Morris *et al.* (2011)
Larval duration (d)	28 days	Estimated larval duration of Atlantic lionfish	Morris *et al.* (2011)
Mortality (M_e, M_l, M_j, M_a)	0.31 day^{-1} (M_e, M_l), 0.165 m^{-1} (M_j), 0.052 m^{-1} (M_a)	Estimated mortality rates of Atlantic lionfish	Morris *et al.* (2011)
Female proportion	46%	Sex ratio of Atlantic lionfish	Morris *et al.* (2011)
Breeding age	10 months	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 days. Estimated monthly quantity of eggs per female, per month	Morris *et al.* (2011)
Founder population	150	Small founder population located in the western Bahamas	
Monthly breeding cycle	30 days	Larval quantity (q) is based on total quantity per month, and so the cycle has been set to one month accordingly	Morris *et al.* (2009)

and so time-stamped water velocity and direction were compiled for each cell in the fixed 2-D grid to allow spatial and temporal forecasts of their movements. The larva transition time, in days, from one grid cell to the next was computed by multiplying the distance between cells (using the geographic coordinates of the cell center) by the water velocity measured in m/s. A stochastic component was included to resolve sub-grid scale processes, such as active larval movement, which were not captured by the model. To integrate these stochastic movements, larvae moved into a randomly chosen neighboring grid cell 5% of the time during each cell-to-cell transition instead of moving into the predicted downstream cell. A larval timer, which kept track of the date, was initiated at the onset of larval movement and was used to track the total time that the individual larva transitioned through the grid. The larval timer was also used to fetch the date-appropriate parameter values from the database for the cell that was occupied by the larvae at any particular moment in time. If the larval timer date fell within the year 2004–2005 storm seasons, and the simulation was flagged to utilize daily storm data, cell values for OCVD data were selected from the daily HYCOM dataset for the storm date. If the date fell outside of the year 2004–2005 storm seasons, values were selected from the year 2006 HYCOM monthly mean dataset, a year that was unaffected by Atlantic storms.

Once the larval timer indicated that the larval duration period has lapsed, the final cell occupied by the larva was selected as a potential settling location. Next, ocean depth and sea surface temperature were retrieved for the cell to evaluate for suitable conditions (see Table 2) in which lionfish larvae were able to settle. If habitable conditions existed in the cell, that is, water depth shallower than the lionfish depth limit and the yearly minimum and maximum temperatures fell within lionfish tolerances, the cell was marked colonized with an individual lionfish. The lionfish lay dormant until the breeding age was reached, at which time the female lionfish began breeding on the next 30-day simulation cycle.

The logic of selecting breeding lionfish, calculating survival of each spawned larva to adulthood, forecasting larval advection through the grid, and settlement was repeated for every viable (alive) female lionfish for the extent of the simulation. The resulting data provided data-stamped geographic points of settlement of lionfish that were then summarized over space and time in a GIS (see Fig. 3 for a flowchart which graphically illustrates the process).

Implementation of the model

Following previous employments of the model, we first compiled monthly mean HYCOM OCVD data for a proxy year, a method that has precedence in the literature (Johnston & Purkis, 2014a,b). To completely isolate the effects of storm-driven water on the diffusion of lionfish larvae, the year 2006, a storm-free year, was chosen to represent dates outside of the years 2004–2005 storm seasons. These data were then coupled with daily HYCOM OCVD data for the 2004 and 2005 hurricane seasons (7/04–11/04 and 7/05–11/05). The 2004–2005 seasons were chosen because they parallel the time frame in

which lionfish dispersal in the Bahamas was profuse (USGS-NAS, 2014). Though robust, the HYCOM dataset does lack near shore and shallow-bank resolution such as those shallow waters bathing the Great and Little Bahama Banks. Likewise, in locations where the HYCOM was lacking data, we obtained monthly mean OCVD data for the year 2006 from the Ocean Surface Current Analysis (OSCAR) database (Bonjean & Lagerloef, 2002). Near-shore fit for both the HYCOM and OSCAR data was performed via nearest-neighbor interpolation, providing 100% OCVD data coverage for the entire study area for storm and nonstorm years. A small population of 150 reproductive female lionfish in the northwest Bahamas acted as a founder population for running the model (see Table 2 for model inputs). The precise number of founder lionfish used in the simulations is not important to the overall trends and patterns produced by the model. It should be borne in mind that our model aimed in particular to track the dispersal of a fledgling founding population of lionfish through the Bahamas, and for this reason, it would be illogical to set magnitude of the starting population higher than a few hundred breeding pairs. For each scenario (no hurricanes, year 2004 hurricanes, year 2005 hurricanes, years 2004–2005 hurricanes combined), 10 simulations were produced spanning the years of study 2000–2007. For every 30 days of model time, an average cumulative lionfish population size was calculated. Next, the quantity and percentage of population difference from the nonhurricane simulation were independently plotted for the three hurricane scenarios, with the year on the x-axis and population change on the y-axis (Fig. 4). The plot conveys the response of lionfish population size to hurricane-altered currents. To test the population changes observed for statistical significance, given the expectation that storms do increase the numbers of lionfish (and thus rejecting the null hypothesis, H_0, that storms do not increase the size of lionfish populations), we performed a one-tailed t-test. The t-test was conducted between the mean lionfish population size obtained from the 10 sample simulations for scenario one and the mean counts of the 10 simulation runs for each of scenarios two, three, and four. Finally, USGS-NAS lionfish records through the year 2007 were mapped in a GIS to contrast the simulation results with actual lionfish reports (Fig. 5a). For the nonhurricane (simulation one) and years 2004–2005 combined simulations (simulation four), the mean numbers of lionfish per grid cell and for three time-steps (<2004, <2006, <2008) were also plotted (Fig. 5b, c). The resulting GIS map depicts lionfish settling locations in the Bahamas for years with and without hurricanes, as documented by our computer simulations.

Results

Storm-altered water flow between Florida and the Bahamas

Analysis of the daily 2004–2005 HYCOM storm season data revealed fluctuations in water direction and speed in the Florida Straits, from northerly dominated flow, which blocks cross-Florida Current
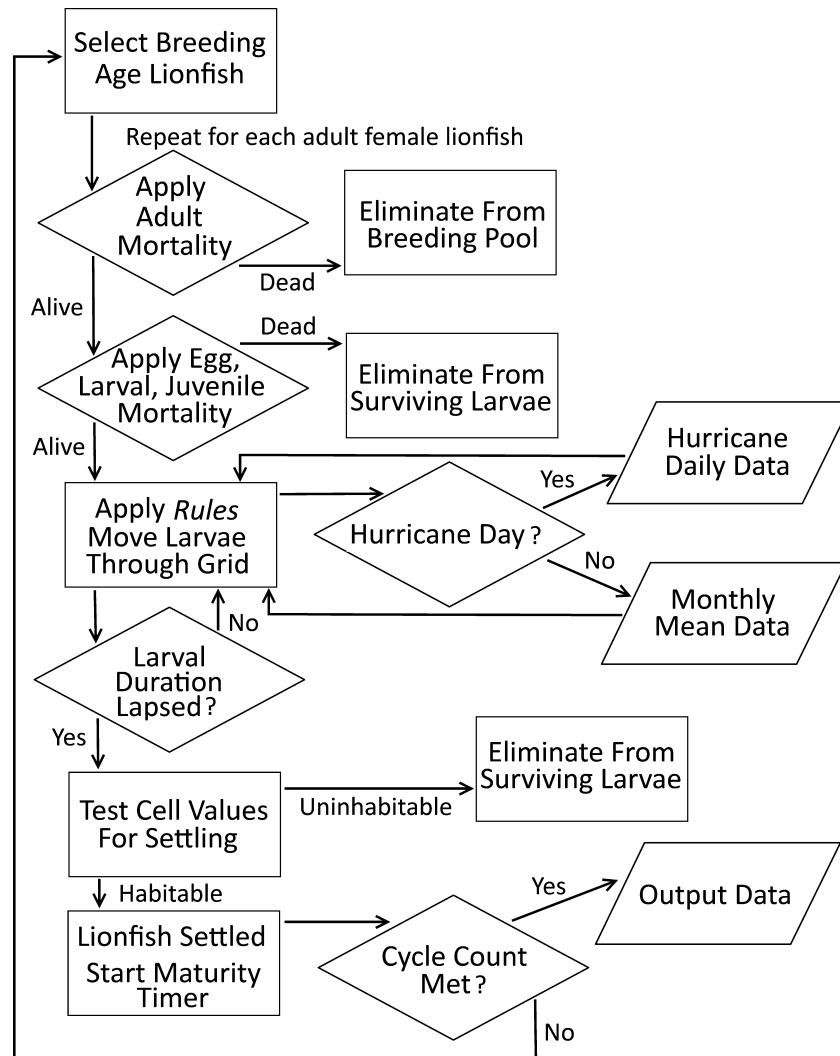
Fig. 3 Model Flowchart. Flowchart illustrating the process logic of the model.

transport of lionfish larvae, punctuated by easterly flow when the eye of a storm passes through the Florida Straits (Figs 1, 2). Category 3 or stronger hurricanes, such as Wilma, Jeanne, and Frances affected greater variances in the direction and velocity of surface water flow in the HYCOM data than weak storms, such as Ophelia, Tammy, and Gamma (Fig. 2b, c, e).

In the daily HYCOM storm season data, water flow in the Florida Straits fluctuated to the greatest extent when the eyes of strong storms crossed just north of the center of the Straits. When storms follow this path, south-wall winds (i.e., those flanking the south rim of the storm eye) concentrate eastward-flowing water, originating in South Florida, to the Bahamas (Figs 1, 2b, c, e). When dissecting the data for storms passing from east-to-west which originated in the western

Atlantic (such as Frances, Jeanne, Katrina, and Rita), the proportion of north-flowing currents and water velocities dropped by 33% during Katrina and 70% during Frances and Jeanne. In the daily storm season data, these decreases were followed 2-to-10 days later (but averaging two-to-five) by increases in both velocity and northward flow to prestorm levels or greater (a 33% increase during Katrina) during the passage of the east wall. Accordingly, eastward-flowing currents and also water velocity both opposed this trend, first with a marked increase, followed by a gradual drop-off. The opposite was seen for storms that tracked west-to-east, such as Wilma. Wilma instigated the greatest disruption of water flow in the Florida Straits of all storms in the considered time period, with a maximum eastward velocity of 1.61 m/s and mean of 0.59 m/s, according to the HYCOM data.
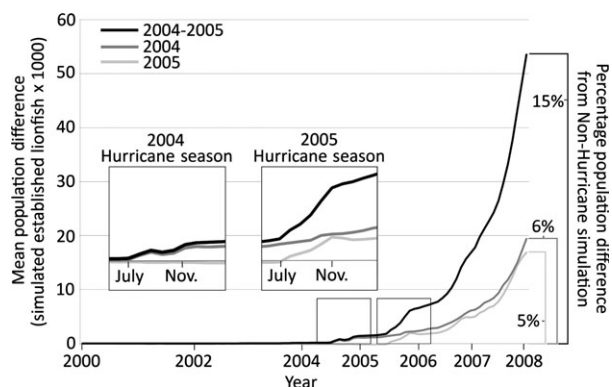
Fig. 4 Analysis of the difference in population sizes in hurricane years vs. nonhurricane years. The *x*-axis indicates the date in years, and the left *y*-axis indicates the average population difference for hurricane simulations from the nonhurricane simulation. The percentage difference of the total is shown on *y*-axis on the right of the graph. The inset sub-figures present detailed plots for the hurricane seasons of the years 2004 and 2005.

Effects of storms on lionfish population size and invasion progress

Simulations built for scenario one (nonhurricane) revealed an average adult Bahamian lionfish population of $3.2 \times 10^5 \pm 2.0 \times 10^4$ total number of individuals at the conclusion of 2007. The average difference in population size from scenario one for the three storm simulations were 1.9×10^4 (a 6% increase in lionfish population) for scenario two (the year 2004 alone), 1.6×10^4 (a 5% increase in Bahamian lionfish) for scenario three (the year 2005 alone), and 5.4×10^4 (15% more Bahamian lionfish) for scenario four (the years 2004–2005 combined) (Fig. 4). Significance testing found t-values of 0.039 (scenario one-to-two), 0.030 (scenario one-to-three), and 5.1×10^{-6} (scenario one-to-four), all values below a 0.05 significance level. As such, we reject H_0 and suggest that lionfish population sizes were amplified when storms are incorporated in the simulation runs. Projecting five years subsequent to the end of the simulation (through the year 2012), and excluding additional storm seasons, the population difference between nonstorm and storm simulations was 9.0×10^6 lionfish.

When plotted in a GIS, USGS-NAS lionfish records through the year 2007 are distributed south and east in the Bahamas, with the farthest lionfish record 1050 km from South Florida (Fig. 5a). Lionfish populations in the nonstorm simulation do progress to the southeast, but only reach the edge of the Windward Passage by the end of the year 2007, a dispersal distance of 900 km from South Florida (Fig. 5b). When the year 2004–2005 storm seasons
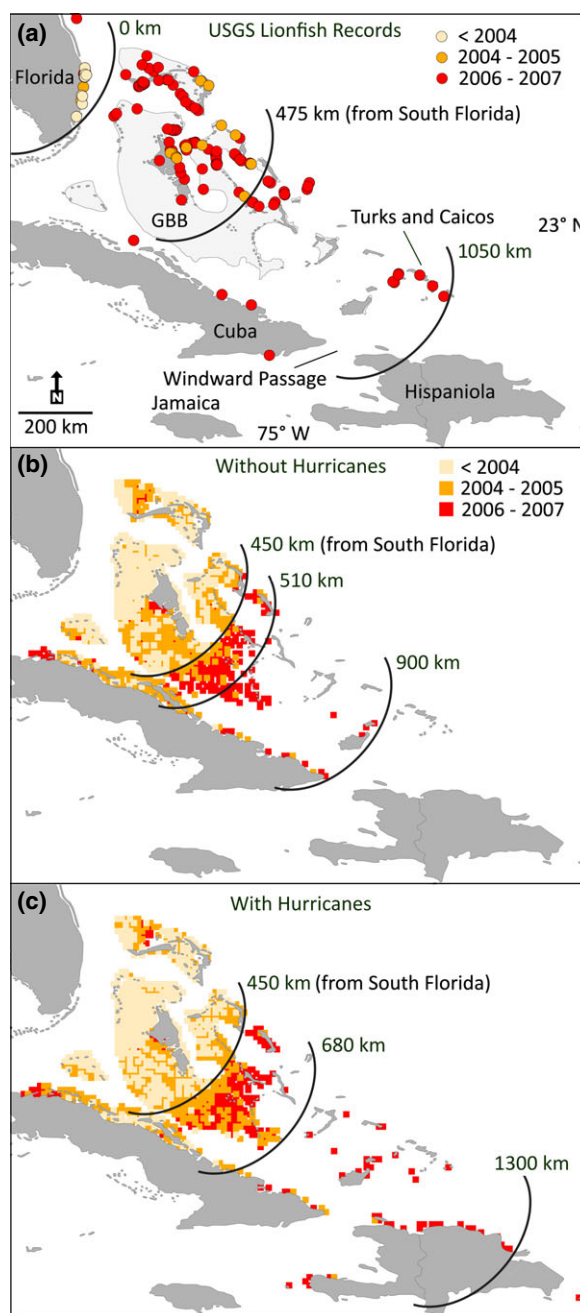
Fig. 5 United States Geological Survey Non-indigenous Aquatic Species lionfish records and the population progression according to the simulations. USGS-NAS lionfish records through the year 2007 (a). Yellow dots indicate records prior to 2004, orange dots signify the years 2004 and 2005, and red dots illustrate the years 2006 and 2007. The 'French curve' highlights the moving lionfish invasion-front in km from South Florida. Settled lionfish populations are indicated via square symbols for the nonhurricane (b) and hurricane (c) simulations.

were included in the model, the lionfish invasion-front progresses southeast through the Bahamas more rapidly than if storms were omitted, extending

1300 km from South Florida spanning the same time frame (Fig. 5c).

Discussion

Storms open a gateway between Florida and the Bahamas

The minimum straight-line distance between South Florida and the Bahamas is 87 km, and water flowing eastward from Florida at 1 m/s will traverse this span in 24 h. Storms drive ocean surface and sub-surface water (as witnessed during Ivan to depths of at least 84 m) approximately in the direction of their winds which, in the Northern Hemisphere, is counter-clockwise. For example, south-wall winds, which extend from the southern edge of the storm to the eye (the rotational axis of the storm), blow eastward, and in doing so, direct water generally to the east. The maximum current velocity produced by Wilma, as forecast by the HYCOM data, was slower than the fastest water flow (2.14 m/s) measured during Hurricane Ivan (another Category 3 storm), suggesting that actual water flow velocity realized during hurricanes may be even greater than those velocities predicted by the HYCOM. The flux of lionfish across the Florida Straits forecasted by our model can therefore be considered conservative. In accordance with our simulation, storms passing closest to the Florida Straits, such as Wilma, open transport windows for buoyant larvae spanning 2-to-10 days (Fig. 2c, e), which is ample time for lionfish larvae drifting in surface or near-surface waters to traverse the Florida Current barrier in less than 24 h.

Spanning the years 1992–2003, thirteen storms passed through the Florida Straits and plausibly opened transport windows for lionfish larvae (Fig. 2a). Of these thirteen storms, the eyes of storms Erin, Mitch, Harvey, Irene, Gabrielle, and Michelle passed north of the center of the Florida Straits, and presumably produced and shifted high-velocity water eastward (Fig. 2d). Notably, the storms Mitch in the year 1998, and Dennis, Floyd, Harvey, and Irene in 1999 impacted the Florida Straits and the year 1999 storms followed in rapid succession, perhaps amplifying the rate of dispersion over a single storm season. Given that the fastest easterly flow in the daily HYCOM data occurred during the passage of such storms, and that detection lags suggest that cryptic lionfish may occupy a location well before their eventual reporting date, we speculate that lionfish breached the Florida–Bahamas barrier sometime during the year 1998 or 1999 hurricane seasons.

Storms increase lionfish population size and speed the invasion-front through the Bahamas

Lionfish numbers for all simulations exhibited an expanding population with exponential growth, as was forecast by Johnston & Purkis (2011) and also reflected in the USGS-NAS lionfish records. When the 2004 and 2005 storm seasons were analyzed collectively, the increase in lionfish populations in scenario four (15%) was more than the combined increases for the year 2004 (6%) and year 2005 (5%) seasons singularly (Fig. 4). This 4% net increase in lionfish populations can be attributed to a compounding effect, whereas those additional lionfish produced during the 2004 storm season were capable to breed and contribute larval recruits during the course of the year 2005 storm season. The increase observed implies that consecutive storm seasons further amplified reproductive populations when compared to a single storm season in the model.

The lionfish invasion-front progressed southeast through the Bahamas more rapidly when the 2004–2005 storm seasons were included than if storms were omitted, extending 1300 km from South Florida (Fig. 5c). This distance represents a 45% increase in dispersal due to storm-altered water flow. In the 2004–2005 storm simulation, lionfish populations traversed the Windward Passage, settled the Turks and Caicos and bridged northern Hispaniola. The USGS-NAS reports lionfish from southern Cuba and also the Turks and Caicos (but not Hispaniola) by the conclusion of 2007, in agreement with our computer model. Lionfish populations were not forecast by the simulation in any of these three locations when hurricanes were absent (Fig. 5b).

In light of these results, we deem that simulation four, which includes the movement of water wrought by storms for the years 2004 and 2005 (Fig. 5c) more accurately reflects the realized infiltration of lionfish through the Bahamas as compared to the simulation that ignores storms (Fig. 5b). Our data further suggest that lionfish observations from Hispaniola exhibited a detection lag and that the invader bridged the Windward Passage prior to 2007, facilitated by storm-forced ocean circulation.

Computer simulations that mimic biophysical systems often produce inaccurate results due to data omission, parameter limitations such as data resolution, or flaws in the model logic. To abate potential errors, the life-history traits expressed by Atlantic lionfish and used in the study were harvested from the literature (Morris et al., 2011; Johnston & Purkis, 2014a), although these traits are naturally variable and cannot be treated as explicit. The values we used were our best estimates

of the traits exhibited by Atlantic lionfish. The model we implemented has been previously used to study lionfish and *Chromileptes altivelis* in the Atlantic (Johnston & Purkis, 2011, 2012, 2014a,b) and has been thoroughly tested against variations in parameter input values and proven sensitive to alterations in mortality rate in the same manner as most fish population models. However, this sensitivity does not adversely affect the dispersal patterns of the species being modeled (Johnston & Purkis, 2013, 2014a,b). As such, the conclusion that storms increase the dispersal of lionfish would not have changed had we chosen to use different parameter values within the variability ranges as documented for Atlantic lionfish.

It should be noted that other relatively sedentary adult fish (for example damselfish) and invertebrates such as conch are found on both sides of the Florida Current, indicating that larval exchanges are predicted across the Straits over time. For lionfish, the Florida–Bahama crossover was swift and ensued less than 20 years after their introduction to South Florida, sooner than would be anticipated given the Florida–Bahamas connectivity break documented in the literature (Carlin *et al.*, 2003; Richards *et al.*, 2007; Freshwater *et al.*, 2009; Kool *et al.*, 2010; Betancur-R *et al.*, 2011). We suggest this rapid transposition may be attributed to storm-forced ocean currents. Further, many Caribbean species spawn during the summer months and perhaps may be harnessing the dispersive features of frequent Caribbean storms to better spread around the region. Our results propose that perhaps native Caribbean marine organisms with similar reproductive strategies as to the lionfish may take advantage of storm-altered water flow to enhance distribution of their offspring. Moreover, extreme weather events, such as hurricanes and tropical storms, likely help to homogenize the gene pool in the Caribbean for all marine species susceptible to transport.

We did not incorporate ontogenic migration in our model as these data are noticeably lacking for lionfish. The paucity of migration data, however, is not synonymous with an absence of vertical or horizontal lionfish larval movement. Indeed, many marine fish with planktonic larval stages are capable of ontogenic migrations within the upper 60 m of the water column (though concentrated usually in the upper 20 m) which aid them in traversing strong currents, such as the Florida straits, and in population retention (Paris & Cowen, 2004). These movements may also serve to protect larvae from the dangerous surface conditions produced by high wind and churning waves during passing storms, although floating lionfish egg sacs may still be venerable to disassociation and subject to greater mortality rates. Still, measurements of OCVD data during

storms confirm that current anomalies can extend at least 84 m deep into the water column and are not limited to surface currents (Wang *et al.*, 2005; Teague *et al.*, 2007). It follows that should planktonic lionfish move deeper within the top 60 m of the water column during storms, they would be similarly swept by storm-altered currents as to those lionfish larvae floating in surface waters. Given this, the conclusion that storms accelerated the Florida–Bahamas dispersal of lionfish would likely remain the same had ontogenic vertical or horizontal migration been integrated into the model.

Implications for the spread of Floridian invasive species

Atlantic storms transported non-native *Schistocerca gregaria* (African locusts) to the Windward Islands (Richardson & Nemeth, 1991), accelerated the invasion of *Pittosporum undulatum* (cheesewood tree) in Jamaica (Bellingham *et al.*, 2005), and carried *Phakopsora pachyrhizi* (Asian soybean rust) to Louisiana during hurricane Ivan (Stokstad, 2004). However, marine invasive fishes are not documented in the literature as storm distributed. South Florida coastal waters are a hot spot for non-native marine introductions (Semmens *et al.*, 2004), and the USGS-NAS database records 33 non-native marine fish and one crustacean from within the studied Florida Straits. Accounts of *Chromileptes altivelis* (panther grouper), *Penaeus monodon* (Asian tiger shrimp), and *Platax orbicularis* (orbicular batfish) are recorded in the USGS-NAS database and, in common with lionfish, all three species reproduce via pelagic, current-distributed larvae (Motoh, 1981; Sugama *et al.*, 2003; Leis *et al.*, 2013). These three invaders have been recorded in low numbers in South Florida. On the basis of our computer simulations, however, it is conceivable that hurricane-driven ocean circulation could introduce them to the Bahamas if reproductive populations expand. Still, establishment of non-natives introduced to the Bahamas via the Straits is not guaranteed, and it is likely that their success pivots on invasive traits of the inductees that may serve to facilitate their inhabitation. Given this caveat, Bahamian waters provide a much broader marine ecosystem when compared to degraded South Florida habitats where the non-natives have been recorded (Wilkinson, 2008). As such, a favorable environment in the Bahamas may allow species introduced by storms from South Florida to easily establish Bahamian populations.

The recent (2011) discovery of invasive Asian tiger shrimp in South Florida is particularly concerning. Widespread and frequent records suggest that reproductive populations are already established in the Gulf of Mexico and the Atlantic and may indicate that the shrimp exhibits invasive traits empowering their

success in their introduced range (USGS-NAS, 2014). Thankfully, these shrimp are not yet reported from the Bahamas. The Bahamian absence may be attributed to a lack of hurricanes, which we demonstrate are capable of transport pelagic larvae across the Florida Current, impacting the Florida Straits in the years since the shrimp's arrival in South Florida (given a likely detection lag, most likely a few years before 2011). As an aggressive predator of benthic invertebrates, Asian tiger shrimp prey on and compete for resources with commercially important native species such as the pink shrimp (*Farfantepenaeus duorarum*) (Marte, 1980). Should storm-forced currents spread *Penaeus monodon* to the Bahamas, and also fuel their progress through the Islands, as observed with lionfish, then the consequences to native Bahamian prey could be considerable. Finally, the literature suggests that warming oceans, resulting from anthropogenic climate change, may increase the intensity of Atlantic hurricanes (Webster *et al.*, 2005; Anthes *et al.*, 2006). It is disconcerting that more intense storms may become a common transport mechanism between Florida and the Bahamas for non-native species residing in the Florida Straits. Going forward, the community should be aware that lionfish will likely not be the last invasive marine species to benefit from altered water circulation instigated by hurricanes.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Monthly-mean water flow in the Florida Straits for the year 2006. Monthly-mean analysis of ocean current direction (a) and velocity (b) in the Florida Straits for the year 2006. The color of the plot lines indicates the direction of water flow.