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REPORT

Modeled differences of coral life-history traits influence the refugium potential of a remote Caribbean reef

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Abstract Remote populations can influence connectivity and may serve as refugia from climate change. We investigated two reef-building corals (*Pseudodiploria strigosa* and *Orbicella franksi*) from the Flower Garden Banks (FGB), the most isolated, high-latitude Caribbean reef system, which, until recently, retained high coral cover. We characterized coral size-frequency distributions, quantified larval mortality rates and onset of competence ex situ, estimated larval production, and created detailed biophysical models incorporating these parameters to evaluate the source–sink dynamics at the FGB from 2009 to 2012. Estimated mortality rates were similar between species, but pre-competency differed dramatically; *P. strigosa* was capable of metamorphosis within 2.5 d post-fertilization (dpf) and was competent at least until 8 dpf, while *O. franksi* was not competent until >20 dpf and remained competent up to 120 dpf. To explore the effect of such contrasting life histories on connectivity, we modeled larval dispersal from the FGB assuming pelagic larval durations (PLD) of either 3–20 d, approximating laboratory-measured pre-competency of *P. strigosa*, or 20–120 d, approximating pre-competency observed in *O. franksi*. Surprisingly, both models predicted similar probabilities of local retention at the FGB, either by direct rapid reseeding or via long-term persistence in the Loop Current with larvae returning to the FGB within a month. However, our models predicted that short PLDs would result in complete isolation from the rest of the Caribbean, while long PLDs allowed for larval export to more distant northern Caribbean reefs, highlighting the importance of quantifying larval pre-competency dynamics when parameterizing biophysical models to predict larval connectivity. These simulations suggest that FGB coral populations are likely to be largely self-sustaining and highlight the potential of long-PLD corals, such as endangered *Orbicella*, to act as larval sources for other degraded Caribbean reefs.

Keywords Coral · Connectivity · Biophysical model · Flower Garden Banks · Pelagic larval duration · Pre-competency

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Introduction

Caribbean reefs have experienced some of the most dramatic coral declines over recent decades. However, the Flower Garden Banks (FGB)—a system of two very

unusual reefs located 185 km south of the Texas–Louisiana border in the Gulf of Mexico—appear to be the exception (Jackson et al. 2014). The FGB is populated by only 24 species of reef-building corals (Schmahl et al. 2008), but average coral cover is 55%, which is more than three times greater than the Caribbean average (Jackson et al. 2014). In addition, the FGB is also one of only five Caribbean reefs in the top 95th quantile of coral cover (Jackson et al. 2014). The FGB is one of the northern-most Caribbean coral reefs and is very isolated from other reefs; the nearest neighboring reefs are hundreds of kilometers away along the coast of Tampico, Mexico (645 km), and the Yucatan peninsula (600 km) (Rezak et al. 1990) (Fig. 1a). The FGB's isolation, buffering from increased sea surface temperatures due to its high-latitude location, low degradation and high coral cover make it an ideal potential refugium from climate change for Caribbean corals. However, in order to serve as a refugium the FGB should meet three requirements: first, FGB coral populations should maintain high levels of local retention (i.e., not requiring larval input from elsewhere to sustain populations); second, FGB-originating larvae should be capable of emigrating to and surviving at other Caribbean reefs; and third, these refugia populations must be relatively buffered from recurrent disturbances such as temperature-induced coral bleaching.

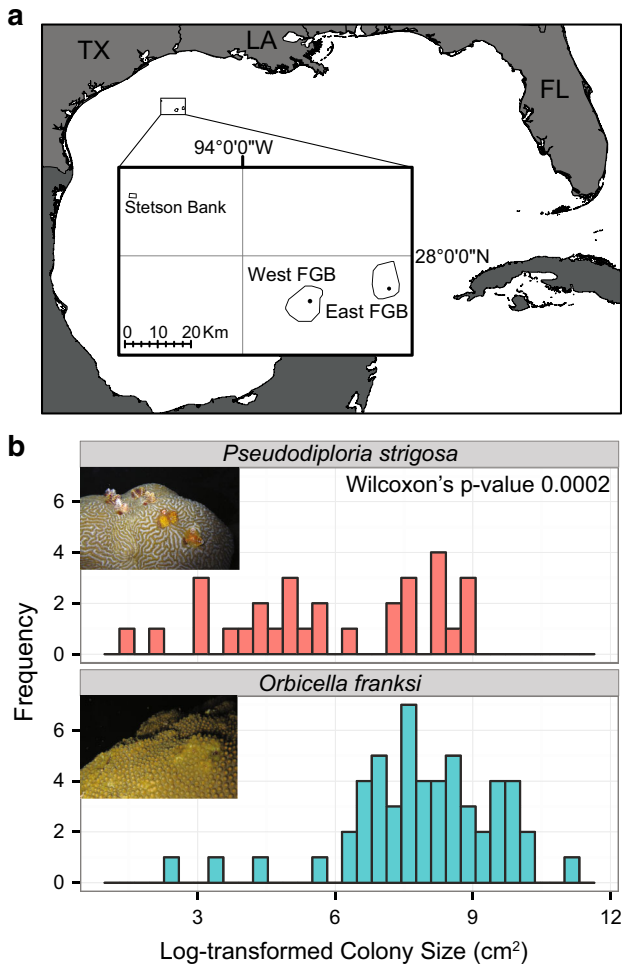

Fig. 1 **a** Locations of surveys conducted at east FGB (mooring buoy 2) and west FGB (mooring buoy 2) (*black dots*). Map was generated in ArcMap 10.2.2 software by ESRI (www.esri.com) using publicly available data from NOAA/National Marine Sanctuary Program and the GSHHG database (Wessel and Smith 1996). **b** Size-frequency distributions for *Pseudodiploria strigosa* and *Orbicella franksi* at east and west FGB from transects in August 2012 with *photograph insets* of each species (Photographs: SW Davies)

Many marine organisms, including corals, have bipartite life cycles with dispersive pelagic larvae and a sedentary adult stage. Connectivity across distant populations is therefore dependent on the successful exchange of these pelagic larvae along ocean currents (Jones et al. 2009). Intra- and inter-specific differences in biological traits can influence the scale of dispersal (Kinlan and Gaines 2003; Shanks et al. 2003; Davies et al. 2015). Larvae of some species have limited connectivity and only disperse meters from their parents, while other species are highly genetically connected across distant reefs separated by thousands of kilometers (Gaines et al. 2007; Jones et al. 2009; Van Oppen et al. 2011; Davies et al. 2015). The key life-history trait expected to influence connectivity is pelagic larval duration (PLD), which is the total time a larva spends in the water column before settlement. PLD can be affected by larval pre-competency period, which is the development time required before a larva becomes competent, larval mortality rate, the availability of suitable settlement substrate and post-settlement survival (Cowen 2002, 2007; Graham et al. 2008; Figueiredo et al. 2013; Humanes et al. 2016). In addition to life-history traits, currents are strong drivers of larval connectivity. As global climates continue to warm, currents are predicted to dramatically shift, potentially altering connectivity patterns of many marine species (Munday et al. 2009; Kendall et al. 2015; Wilson et al. 2016). Oceanic warming can also alter larval traits, typically by increasing the timing of development and the onset of competency (Heyward and Negri 2010). To understand coral larval dispersal dynamics, it is essential to disentangle how currents and life-history traits interact to enhance or limit dispersal. These types of biophysical data can in turn inform genetic studies of effective gene flow to generate a more accurate representation of population connectivity in the sea.

In this study, we aimed to estimate larval retention and export for the FGB using biophysical model simulations that were based on regional currents during the weeks following annual coral broadcast-spawning events across specific years (2009–2012). Our models also incorporated experimentally measured larval life-history traits for two of

the most dominant reef-building corals on the FGB: *Pseudodiploria strigosa* and *Orbicella franksi*.

Materials and methods

Study species

Pseudodiploria strigosa was used for both larval mortality and pre-competency trials, but for logistical reasons related to spawn-time variation across years, two species of the *Orbicella* species complex were used to measure larval traits: *Orbicella faveolata* for mortality and *O. franksi* for competency.

Size-frequency transects

Coral size-frequency distributions can be key indicators for assessing inter-annual variation in recruitment (Ebert et al. 1993; Meesters et al. 2001), which is an interesting comparison to the predictions of larval dispersal potential made with biophysical models. On 8 and 9 August 2012, divers completed a total of eight size-frequency transects targeting *O. franksi* and *P. strigosa* following protocols established by the Florida Reef Resiliency Program (Wagner et al. 2010) (http://frrp.org). Four transects were completed at west (WFGB, (27°52.526N, 93°48.836W, 24 m) and east (EFGB, 27°54.516N, 93°35.831W, 21 m) FGB (Fig. 1). In brief, communities were surveyed using 10-m^2 belt transects placed randomly at each site. The diameter, height and percentage live tissue of all corals ≥4 cm diameter were recorded. Due to limited dive times at these depths (19–27 m), the smallest corals quantified here likely represent 1–2 yr of growth and our data therefore lack information on very recent recruitment events. It is possible that younger recruits were present, but smaller size classes were not measured since recruits are difficult to identify to species and are highly cryptic. Colony sizes were log-transformed to visualize size-frequency differences between coral species, and size-frequency distributions were compared using a Wilcoxon rank sum test in *R*.

Larval rearing

Samples were collected under the FGB National Marine Sanctuary permit #FGBNMS-2009-005-A3. On the evening of 18 August 2011 (8 d after the full moon, 2115 hrs Central Daylight Time, CDT), divers collected gamete bundles directly from ≥3 individuals of the broadcast-spawning Caribbean coral species (*P. strigosa* and *O. franksi)* at the EFGB using spawning nets. Numbers of spawning individuals collected were limited by dive time and spawning synchrony between the targeted species, but care was taken to ensure at least three individuals were cross-fertilized. Gamete bundles were allowed to cross-fertilize in 3 L of 1-μm filtered seawater (FSW) for one hour in sterile 6-L plastic containers. Excess sperm was removed by rinsing through 150-μm nylon mesh. Larvae were reared in 1-μm FSW in three replicate plastic culture vessels stocked at a density of 2 larvae mL^{-1} in a temperature-controlled room set at 28 °C, a typical summer mean temperature on the reef at the Flower Garden Banks National Marine Sanctuary (FGBNMS). Water changes were completed daily until the larvae reached 7 d post-fertilization (dpf), after which very few larvae died and water was changed every 3 d. Larvae were transferred to the University of Texas at Austin on 21 August 2011 and used in all pre-competency trials.

On the evening of 8 August 2012 (2330 hrs CDT), divers collected gamete bundles from four spawning *O. faveolata* colonies and the next evening at 2115 hrs CDT, divers successfully collected from eight spawning *P. strigosa.* Cultures of both species were fertilized and maintained as described for 2011, but four culture replicates were maintained instead of three. Larvae were transferred to the University of Texas at Austin on 10 August 2012 and were used in mortality trials. All research in 2012 was completed under the permit #FGBNMS-2012-002.

Mortality trials

Laboratory-estimated mortality trials began on 11 August 2012 for *O. faveolata* and *P. strigosa* using methods similar to Graham et al. (2016). Four replicate trials ($N = \sim 100$ larvae per trial, one trial per culture replicate) per species were conducted. Each trial started with at least 100 larvae maintained in a culture container with 0.5 L of FSW. For the first 38 d, surviving swimming larvae were counted daily and transferred into new culture containers with FSW. From 39 to 74 dpf, larvae were quantified every 5 d.

Pre-competency trials

For pre-competency trials each well in six-well plates received 10 mL of FSW and a drop of a uniform slurry of finely ground crustose coralline algae freshly collected at the FGB, which has previously been shown to elicit settlement in both species (Davies et al. 2014). Twenty larvae of *O. franksi* or *P. strigosa* were then added to each well ($N = 3$ replicates per species, one per culture replicate), and proportions of metamorphosed larvae (visual presence of mesenteries attached to the plate) were quantified after 24 h using a stereomicroscope MZ-FL-III (Leica, Bannockburn, IL, USA). Trials began 2.5 dpf and were repeated daily until all larvae remaining in vessels had

spontaneously metamorphosed or cultures reached an age of 22 dpf. Trials were then arrested and larvae were maintained until they were 75 dpf, and trials were conducted approximately every 7 d until larvae reached ~120 dpf.

Biophysical model

The Conn4D biophysical dispersal model (Kool and Nichol 2015) was used to estimate dispersal patterns for each species independently. Conn4D uses oceanographic current information in conjunction with an advection diffusion scheme and individual-based behavior to simulate larval trajectories. The model employs a Lagrangian-based dispersal algorithm that uses dynamically interpolated velocity values in conjunction with fourth-order Runge–Kutta integration to calculate advection and a Weiner process to account for diffusion (Dimou and Adams 1993). Horizontal and vertical coefficients of diffusivity were based on open-ocean values from Ledwell et al. (1993, 1998), although dispersal is likely to be insensitive to changes in diffusivity parameters (Treml et al. 2015). Oceanographic data were obtained from the HYbrid isopycnal Coordinate Model (HYCOM) Gulf of Mexico 31.0 experiment (Chassignet et al. 2007). We parameterized the models to reflect the exponential decrease in larval laboratory-estimated mortality measured for both genera. Due to negligible differences in estimated mortality rates across genera (*P. strigosa* vs *O. faveolata*), average larval mortality rates were used as reasonable approximations for both long- and short-PLD larvae in all simulations. Simulations did not encompass a full 4D model since larvae were assumed to stay in surface waters as passive drifters, which has been previously assumed in other models of coral dispersal (i.e., Wood et al. 2016). Therefore, particle depth was kept constant at 5 m. Dates of particle release were as follows: 10, 11, 12, 13 August 2009, 30, 31 August 2010, 11 August 2011 and 8, 9 August 2012. These dates reflect observed spawning at FGB, 8 d after the full moon in late July/August (Emma Hickerson, Research and Permits Coordinator at the FGBNMS, personal communication). FGB coral spawning is highly predictable (Vize et al. 2005), but the night of the mass spawn can be flanked by nights with smaller gamete output. Therefore, for some years simulations were run on flanking days (2009, 2010, 2012). Simulated particles were released from either WFGB (27.83°N, 93.83°W) or EFGB (28.00°N, 93.58°W). For each simulation, 1000 particles were released and allowed to drift for 120 d. Output files were split into two non-overlapping time windows of 3–20 d for the simulated 'short-PLD' and 20–120 d for the simulated 'long-PLD' datasets. We chose these non-overlapping competency windows to model two distinct life-history strategies, long and short PLDs. This was an intentional simplification for model clarity; in the real world, we acknowledge that there will always be individual variation in PLD within each species, which would result in less strict competency thresholds.

Analysis

Output data were visualized in ArcGIS 10.2. Input data were transformed from decimal degrees to a projected coordinate system NAD 1983 UTM Zone 16 N using the 'project (data management)' tool, and visualized within the Gulf of Mexico. Particle location in the Gulf of Mexico was summarized as a density surface by calculating the number of particles on or within a 12-km radius of a given pixel location, and raster output was set to a 1-km cell size. Density surface rasters were $\log_{10}$-transformed using the 'raster calculator.' Total particle number within the FGBNMS boundary and within the boundary of other reefs (as defined by UNEP-WCMC et al. 2010) for each PLD was calculated using the 'select by location' tool. This gives the total number of times any particle intersects the specified boundary, not the total number of particles with a final destination within the boundary. In some cases, a particle stays within the specified boundary for several days, which influences its probability of settling within the specified reef boundary as it represents the amount of time a larva is exposed to suitable habitat. For each simulation, particle numbers within each boundary during a specified PLD was divided by the total number of particles for that simulation, giving a probability of particle existence within each specified boundary. This probability of particle presence within the FGB and in other reefs was multiplied by the total reproductive output of each species from each bank to give a value representing the potential migration events. Total reproductive output for East and West FGB was estimated by multiplying fecundity data (number of eggs m^{-2}) from parameters measured in Szmant (1986) for *P. strigosa* (35,200 eggs m^{-2}) and in Szmant et al. (1997) for *O. franksi* (27,000 eggs m^{-2}) by area of coral cover of each species at each bank (Schmahl et al. 2008; Johnston et al. 2014) (Electronic supplementary material, ESM, Table S1).

Results

Size-frequencies and larval traits of *P. strigosa* and *O. franksi* at FGB

Orbicella franksi and *P. strigosa* surveys revealed similar size-frequency ranges across sampled reefs; however, *P. strigosa* colonies were consistently in smaller size classes than *O. franksi* (Wilcoxon sum rank test, $P = 0.0002$;

Fig. 1b). Very little difference in laboratory-estimated larval mortality rates between *P. strigosa* and *O. faveolata* (exponent powers of −0.022 and −0.019, respectively; Fig. 2a) were observed, so both species mortality rates were modeled with the exponent power −0.02 and this rate was also considered to be a good estimate for *O. franksi*. Pre-competency onset timing differed dramatically between *P. strigosa* and *O. franksi*. *Pseudodiploria strigosa* exhibited competence on the first measured trial, 2.5 dpf, and maintained competence at least until 8 dpf, at which point no swimming larvae remained in cultures due to spontaneous metamorphosis (Fig. 2b). In contrast, *O. franksi* became competent at 22 dpf and remained fully capable of metamorphosis at least until 120 dpf (Fig. 2b). In addition, *O. franksi* were not observed to spontaneously metamorphose even though they were maintained in identical culture conditions as *P. strigosa.* To emphasize the contrast in competence onset between *P. strigosa* and *O. franksi,* we simulated two non-overlapping competence windows: 3–20 dpf for the short-PLD model (*P. strigosa*-like) and 20–120 dpf for the long-PLD model (*O. franksi*-like).

Modeled simulations suggest short PLDs may result in occasionally abundant but highly variable levels of local retention at the FGB

Model-simulated short PLDs occasionally led to a very high probability of local retention of larval particles, but only on specific days in years when currents were favorable. In 2009, only larvae released from WFGB on 10 and 11 August could reseed either bank (probabilities of reseeding: 4.3E−03 and 1.3E−04, respectively), and the reseeding probability on 10 August when released from WFGB was greater than any other release date in our analysis (Fig. 3a, b; Table 1; ESM Fig. S1). In 2010 and 2012, no model-simulated short-PLD larvae were retained within the FGB boundaries (Fig. 3d, h). In 2011, short-PLD larvae released from EFGB could potentially reseed the FGB (simulation for WFGB was not generated for that year), but the probability was lower (5.4E−04) than on 10 August 2009 (Fig. 3f; Table 1). The mean probability for short-PLD larvae to reseed the FGB in 2009–2012 was 5.8E−04. Based on published fecundity estimates and percent coral cover at FGB for *P. strigosa* (Szmant 1986; Johnston et al. 2014), the realistic total

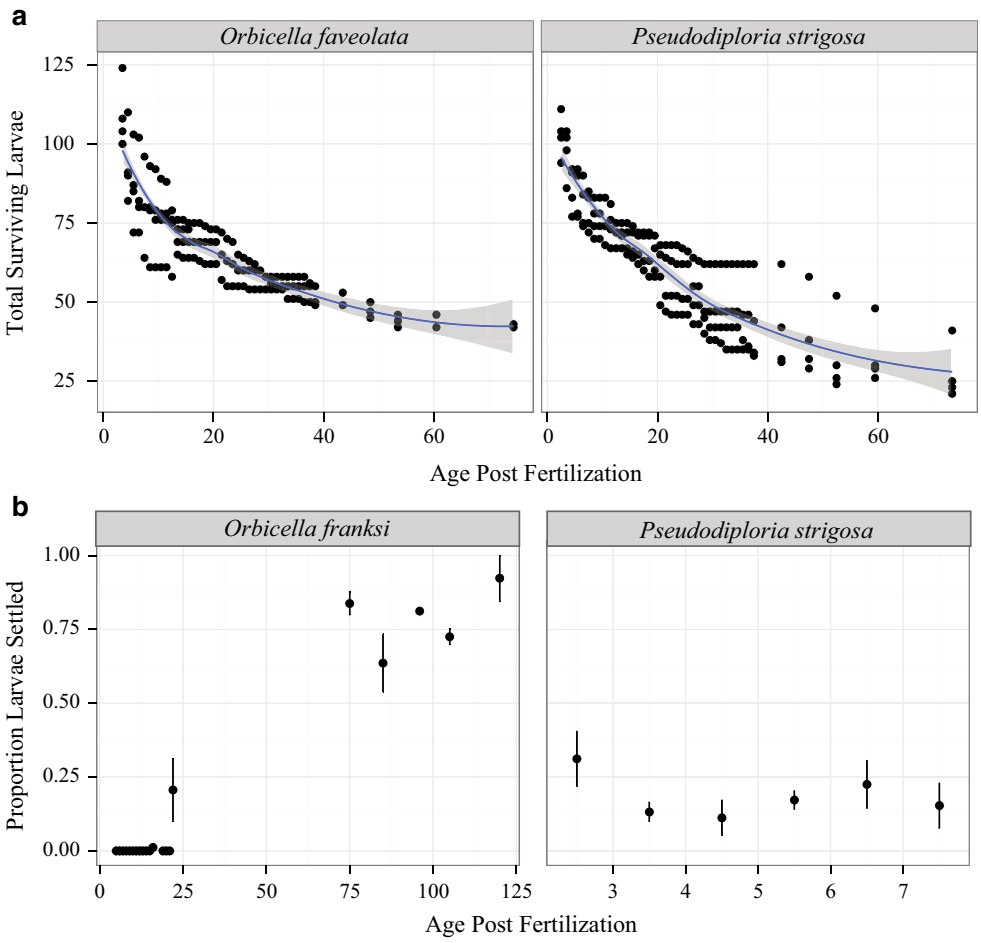

Fig. 2 **a** Mortality estimates for larvae of *Orbicella faveolata* and *Pseudodiploria strigosa* and across four culture replicates. *Blue line* is loess smoothing, *gray shading* indicates 95% confidence interval. **b** Pre-competency patterns for *O. franksi* and *P. strigosa* estimated by the mean proportion of larvae (±SE) settling in response to settlement cue over time. Note the differences in time scale for the two species

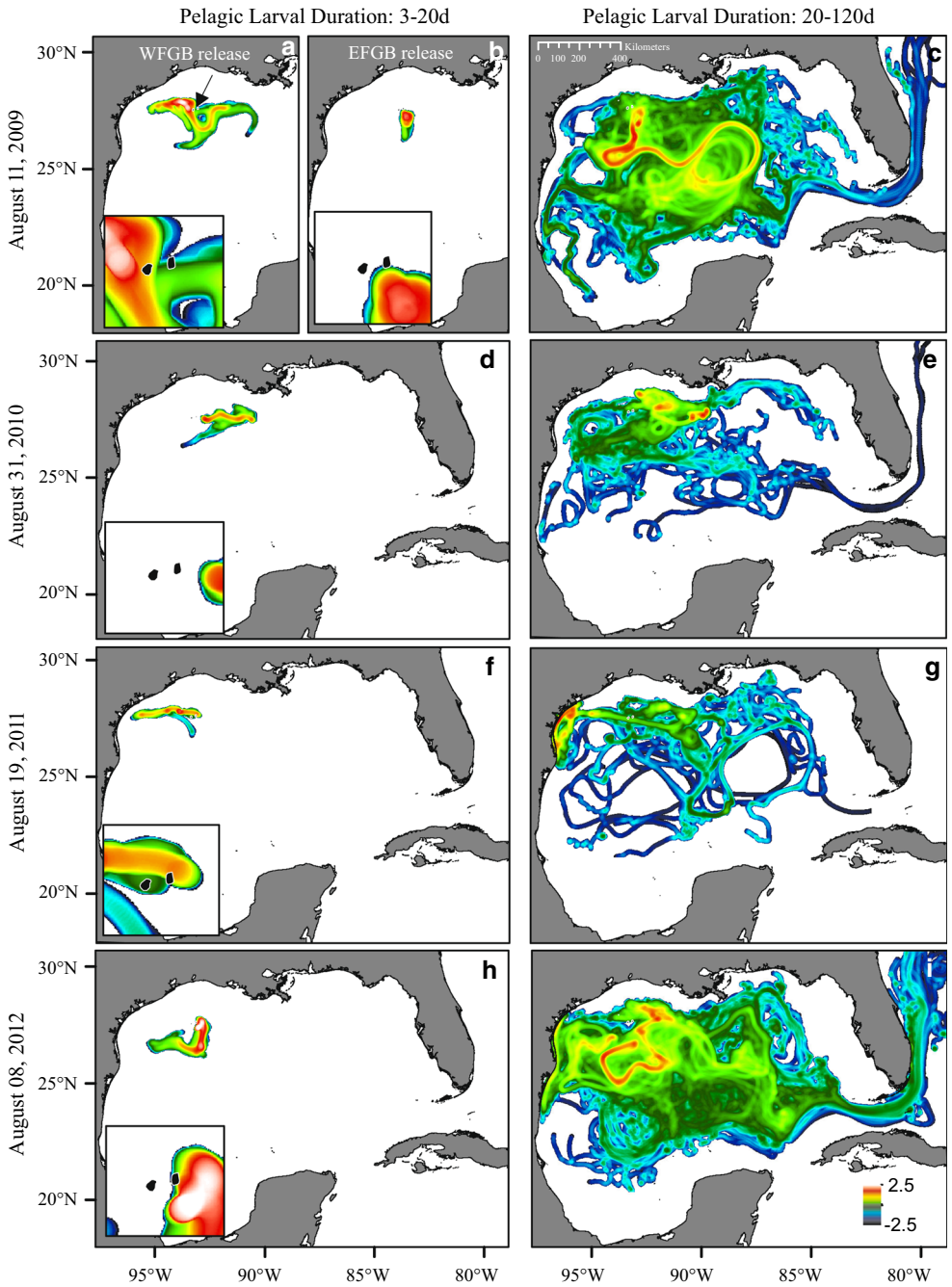

Fig. 3 Surface heatmaps of particle dispersal from the Flower Garden Banks (FGB, *arrow*). Images show the density of particles for a 12-km radius around a 1-km cell integrated over pelagic larval durations (PLDs) of 3–20 d (**a**, **b**, **d**, **f**, **h**) and 20–120 d (**c**, **e**, **g**, **i**). Particle density is displayed on a $\log_{10}$ scale. Release dates are 11 August 2009 (**a**, **b**, **c**), 31 August 2010 (**d**, **e**), 19 August 2011 (**f**, **g**) and 8 August 2012 (**h**, **i**). **a** Represents particles released from WFGB, and **b**–**i** represent larvae released from EFGB. For short PLDs (3–20 d; **a**, **b**, **d**, **f**, **h**), *insets* show variation in particle's reseeding area of FGB (*black area*) between years. Maps were generated in ArcMap 10.2.2 software by ESRI (www.esri.com) using publicly available data from NOAA/National Marine Sanctuary Program and the GSHHG database (Wessel and Smith 1996)

reproductive output for the short-PLD species at WFGB and EFGB is 4.7E+09 and 9.2E+09 eggs, respectively (ESM Table S1). Therefore, the mean number of potential reseeding events for short-PLD larvae released in broadcast-spawning nights across all simulations for 2009–2012 was 2.9E+06 (Fig. 4a). Notably, no simulated spawning events for the short-PLD larvae resulted in any export to other reef systems besides the FGB.

Table 1 Probability of larval reseeding to Flower Garden Banks and probability of larval export to other reefs

Date	Bank	PLD	Reproductive output (# eggs)	P (reseeding)	P (export)	Total larvae reseeded	Total larvae exported
10 Aug 09	West	Short	4.73E+09	4.3E−03	0	2.0E+07	0
		Long	1.02E+10	7.2E−05	4.1E−05	7.3E+5	4.2E+5
	East	Short	9.15E+09	0	0	0	0
		Long	2.36E+10	2.7E−04	4.4E−05	6.4E+6	1.0E+6
11 Aug 09	West	Short	4.73E+09	1.3E−04	0	6.1E+5	0
		Long	1.02E+10	2.7E−04	2.0E−05	2.8E+6	2.0E +5
	East	Short	9.15E+09	0	0	0	0
		Long	2.36E+10	1.7E−04	5.7E−05	4.0E+6	1.3E+6
12 Aug 09	West	Short	4.73E+09	0	0	0	0
		Long	1.02E+10	4.3E−05	1.1E−06	4.4E+5	1.1E+4
	East	Short	9.15E+09	0	0	0	0
		Long	2.36E+10	7.0E−05	1.3E−05	1.7E+6	3.1E+5
13 Aug 09	West	Short	4.73E+09	0	0	0	0
		Long	1.02E+10	9.6E−05	0	9.8E+5	0
	East	Short	9.15E+09	0	0	0	0
		Long	2.36E+10	2.0E−05	5.6E−05	4.7E+5	1.3E+6
30 Aug 10	East	Short	9.15E+09	0	0	0	0
		Long	2.36E+10	2.0E−03	3.1E−06	4.7E+7	7.3E+4
31 Aug 10	East	Short	9.15E+09	0	0	0	0
		Long	2.36E+10	3.0E−05	0	7.1E+5	0
19 Aug 11	East	Short	9.15E+09	5.4E−04	0	4.9E+6	0
		Long	2.36E+10	2.5E−04	0	5.9E+6	0
8 Aug 12	West	Short	4.73E+09	0	0	0	0
		Long	1.02E+10	1.2E−04	1.2E−04	1.2E+6	1.2E+6
	East	Short	9.15E+09	0	0	0	0
		Long	2.36E+10	1.7E−06	4.0E−04	4.0E+4	9.4E+6
9 Aug 12	West	Short	4.73E+09	0	0	0	0
		Long	1.02E+10	2.0E−04	5.5E−05	2.0E+6	5.6E+5
	East	Short	9.15E+09	0	0	0	0
		Long	2.36E+10	2.0E−05	2.4E−04	4.7E+5	5.7E+6

Proportion calculated as number of particles within area/total particles for set pelagic larval duration (PLD): short 3–20 d; long 20–120 d

Long PLD results in low but consistent reseeding

Simulations suggested that long-PLD larvae (pre-competency from 20 to 120 dpf) had similar average probabilities of reseeding (3.3E−04) as short-PLD larvae (5.8E−04), but long-PLD larvae reseeded more consistently over the years (Table 1; Fig. 3). On 11 August 2009, the major spawning night for that year, probabilities of long-PLD larvae reseeding when released from WFGB or EFGB were 2.7E−04 and 1.7E−04, respectively (Fig. 3c; Table 1). On peripheral spawning nights in 2009 (10, 12 and 13 August), simulations showed similar probabilities of reseeding (Table 1, ESM Fig. S2). The highest probability of long-PLD larval reseeding, 2E–03, was observed for the 30 August, 2010 simulation for the EFGB (Table 1; ESM Fig. S3). Interestingly, simulated larvae with longer PLDs had a dramatically higher probability of reseeding their home reef than larvae with short PLDs when released on 30 August 2010 (Table 1; ESM Fig. S3). In 2011 and 2012, the probability of long-PLD larvae reseeding the FGB ranged from 1.7E−06 to 1.2E−04 (Fig. 3g, i; Table 1). Based on previous estimates of *O. franksi* coral cover and reproductive output (Szmant et al. 1997; Johnston et al. 2014), a long-PLD coral species could produce 1.02E+10 and 2.26E+10 eggs at WFGB and EFGB, respectively (ESM Table S1). At the FGB, *O. franksi* has much higher overall coral cover (26.90% at WFGB and 27.56% at EFGB) than *P. strigosa* (9.60% at WFGB and 8.20% at EFGB) (Johnston et al. 2014). These differences in percentage cover account for the ~3–5 times greater total

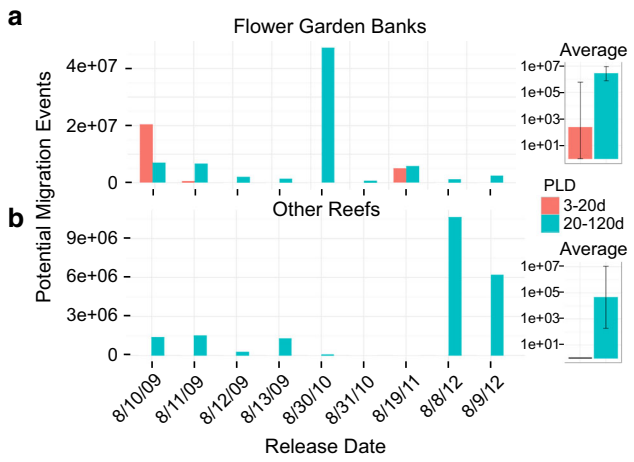

Fig. 4 Larval particles with potential to colonize coral reef environments, summed output from West and East FGB. **a** Flower Garden Banks (reseeding). **b** Other reefs as defined in UNEP-WCMC et al. (2010). *PLD* pelagic larval duration. *Insets* show harmonic mean number of particles for each PLD (±SD)

reproductive output calculated for long-PLD versus short-PLD species. Therefore, for the main mass spawn night, the average number of potential reseeding events to the FGB for a long-PLD coral between 2009 and 2012 was 8.3E+06 (Fig. 4).

Long PLD enables larval export beyond the FGB

No export events were observed for short-PLD larvae, but larvae with PLDs of 20–120 d remained in the water column long enough to be exported to reefs outside the FGB. In simulations of 2009, the probability of larval export to other reefs ranged from 1.1E−06 to 5.7E−05, similar to the probability of reseeding back to the FGB. After accounting for total *O. franksi* reproductive output, this resulted in 1.1E+04 to 1.3E+06 potential larval export events in 2009, depending on the day and location of release (Table 1; Fig. 4b). In 2009, long-PLD larvae were exported to Broward and Palm Beach, the Florida Keys (Dry Tortugas up to Elliott Key), Bay of Campeche reefs (Bajos del Norte, Bajo Madagascar, Alacranes, Arenas, Triangulos, Lobos, Bajo Madaga) (reefs defined in Sanvicente-Añorve et al. 2014; UNEP-WCMC et al. 2010) and northern Cuba (west of Cayo Coco) (ESM Fig. S2). Simulated larval export varied greatly from year to year; in 2010 only a single larval particle (released from WFGB on 30 August) dispersed to a reef other than FGB (Little Bahama Banks) (ESM Fig. S3), resulting in an export probability of 3.1E−06, and no larvae were exported to other reefs in 2011. In 2012, simulations suggest export to other reefs at even higher rates than those observed in 2009; probability of larval export ranged from 5.5E−05 to 1.20E−04. After considering reproductive output, between 5.6E+05 and 9.4E+06 possible larvae were exported in 2012 (Table 1; Fig. 4b, ESM Fig. S4). The 2012 export destinations were Broward and Palm Beach, the middle to upper Florida Keys (Islamorada up to Elliott Key), Bay of Campeche reefs (Bajos del Norte, Alacranes, Arenas) and the Bahamas (Cay Sal Banks and Little Bahama Banks) (ESM Fig. S4). Overall, across these four years, average potential larval export is 2.4E+0.6, which is approximately one-third of the potential larval reseeding events (Fig. 4). We did not include a comparison with probability of larval loss due to mortality, since it is invariably 4–5 orders of magnitude larger than the probability of either reseeding or export.

Discussion

Contrasting pre-competency dynamics among coral species

Most broadcast-spawning coral larvae become competent on completion of larval development, typically 4–6 dpf, after which competence declines (Harrison and Wallace 1990; Baird 2001; Miller and Mundy 2003; Figueiredo et al. 2013). Both *P. strigosa* and *O. franksi* deviate from this general pattern, but in opposing directions. *Pseudodiploria strigosa* becomes competent by 2.5 dpf, while *O. franksi* cultured in identical conditions and offered identical settlement cues did not exhibit competence until 22 dpf. In addition, once *O. franksi* acquired competence, no decline in competence was detected, even up to 120 dpf. Previously, we have observed similar pre-competency onset ranges for the same populations of FGB corals—3–4 dpf for *P. strigosa* and 14–22 dpf for *O. franksi* (Davies et al. 2014)—suggesting that the pre-competency differences between these species are consistent across years, at least for FGB populations. In comparing these two pre-competency extremes, previous research has also found very early pre-competency periods (2–3 d) in other coral species, including *Pectinia lactuca* and *Platygyra sinensis* from Singapore (Tay et al. 2011), and *P. daedalea* on the Great Barrier Reef (Miller and Mundy 2003). Long pre-competency periods have also been detected in corals, although rarely, with a 12-d pre-competency period observed in *Acanthastrea lordhowensis* (Wilson and Harrison 1998). Although there are no published data on *O. franksi* competence from other regions, larvae of its congener, *O. faveolata*, from Belize typically became competent at 6 dpf (Ritson-Williams et al. 2014). Similarly, *O. faveolata* larvae from the Florida Keys began gaining competence at 6 dpf and exhibited 100% competence by 24 dpf (Vermeij et al. 2006).

It is important to note that the *O. franksi* pre-competency dynamics observed here were quantified ex situ and, despite notable consistency across years in the late pre-competency onset in our lab, we cannot guarantee that if culture conditions were different or some other settlement cues were offered, *O. franksi* would not have exhibited earlier pre-competency onset. In addition, given that larval mortality was also measured ex situ and the parameters of the model were based on mortality rates of a sister species, we suggest caution when interpreting these results. The use of the sister-species mortality curve in our model is a reasonable approximation given the lack of published mortality data for *O. franksi*; however, it remains to be seen how the variation in larval mortality is structured on phylogenetic and ecological scales. Mortality in a sister species from the same location may be a better approximation than mortality of the same species from an ecologically different location. In any case, realized *O. franksi* mortality will almost certainly be lower than laboratory-estimated mortality and these deviations prevent us from claiming that we have constructed explicit models for specific coral species and populations. Nevertheless, our study is valuable as a theoretical insight into how connectivity and reseeding could vary for two contrasting PLD patterns, both of which appear to be realistic in the absence of contradicting evidence.

PLD and reseeding potential

One might predict that corals at an isolated reef such as the FGB would be selected for short PLDs to facilitate reseeding. However, we found that both short-PLD and long-PLD simulations resulted in similar average FGB reseeding probabilities (Fig. 4), suggesting that FGB reseeding might not necessarily require the loss of long-distance dispersal potential. It is therefore possible that the optimal PLD for reseeding FGB could be bimodal, as has been suggested in an earlier study tracking drifters released from the FGB during two annual coral spawning events in 1997 and 1998 (Lugo-Fernández et al. 2001). That study demonstrated that while there was a high likelihood of drifters returning to the FGB within the first 30 d, they were also entrained in Loop Current eddies and could recirculate back to the FGB after several months.

A large body of research links short PLD to high local retention and low connectivity, while long PLD has been linked to lower local retention and higher connectivity (Sponaugle et al. 2002; Shanks et al. 2003; Foster et al. 2012), although this is not always the case (Cowen et al. 2003). Given that the long-PLD species modeled here had a late onset of pre-competency and could both reseed and disperse in modeled simulations, our results suggest that this paradigm may be too simplistic within the real seascape (Cowen and Sponaugle 2009). Nevertheless, our study concurs with previous genetic (Galindo et al. 2006) and oceanographic modeling for the region (Lugo-Fernández et al. 2001; Galindo et al. 2006) in that species with early onset of pre-competency and short PLDs are potentially capable of reseeding, but are indeed highly isolated from other reefs. Overall our results demonstrate the importance of quantifying larval pre-competency dynamics for a wider range of species to better parameterize biophysical models to predict larval connectivity.

Simulated dispersal is highly variable among larval cohorts

Larval release timing significantly affected dispersal probabilities (Fig. 3). In 2010, the probability of FGB larvae being locally retained was far greater for long-PLD larvae than for short-PLD larvae and only one long-PLD larva was exported to another reef. In contrast, in 2011 simulations, similar probabilities of local retention were observed for both short- and long-PLD larvae, with no larval export to other reefs regardless of PLD. Finally, in 2009 and 2012 long-PLD larvae had high probabilities of export, while short-PLD larvae exhibited the highest probability of local retention in 2009 but no chance of retention in 2012.

Spatial variation in the pattern of larval release also interacts with temporal variation, resulting in dramatically different simulated dispersal patterns, even over relatively small geographic distances (Kough and Paris 2015). EFGB and WFGB are only 18 km apart, but in 2009, EFGB short-PLD larvae dispersed further east and had no chance of reseeding across all four spawning nights while WFGB short-PLD larvae drifted west but were more likely to be maintained in the vicinity of FGB or circulate back (Fig. 3a, b; ESM Fig. S1). The opposite pattern was observed in 2012 simulations where only EFGB larvae reseeded, while WFGB larvae drifted west and were never able to return to FGB. Despite this variance, recurrence of high-probability modeled reseeding events suggests that FGB coral populations are likely to be demographically self-sustaining. These results highlight how dramatic inter-annual variation in dispersal potential can be within this region during the years we modeled. It is not possible for four years to be fully representative of the inter-annual variability in the region, so the extent of this variability remains to be fully explored with future modeling.

Long PLD is essential for larval export from the FGB to other reefs

Gulf of Mexico (GOM) surface currents tend to be dominated by the Loop Current (LC), which is a continuation of

the Caribbean Current that intrudes the GOM through the Yucatan Channel (Oey et al. 2005). The position and degree of LC intrusion into the GOM is variable in season and across years (Alvera-Azcárate et al. 2009) and can vary from flowing directly into the Florida Current to intruding the GOM as far as 29.1°N (http://oceancurrents.rsmas.miami.edu/caribbean/loop-current.html). The degree of LC intrusion into the GOM influences the likelihood of large warm-water eddies being cast off and flowing westward into the GOM. These eddies can be large enough that a full rotation can be up to 30 d (Berger et al. 1997). Large-scale eddy formation from the LC is irregular (Alvera-Azcárate et al. 2009), but is more prevalent in the summer (Chang and Oey 2012) when broadcast-spawning corals release their gametes. Lugo-Fernández et al. (2001) suggested that as much as 43% of FGB larvae are likely to get caught up in these offshore eddies. Our simulations support their suggestion; simulated larval transport in the GOM is highly affected by LC eddy circulation. For example, in 2009, high numbers of simulated larvae were entrained in a large eddy that was detached from the LC on 2 September (Taylor et al. 2013) (Fig. 3). The density of larvae released from the FGB in other years appeared to be less affected by these large-scale eddies. However, in nearly all simulations with long-PLD larvae (20–120 d), surviving particles were eventually able to enter the LC and be dispersed by either the Florida Current (moving toward the Florida Keys and Miami or the Bahamas) or westward through the Yucatan Current and potentially onto the Campeche shelf reefs (Fig. 3). In addition, we were not able to quantify *O. franksi* competency after 120 dpf, so longer competency and longer-range export may be possible for this species.

Interestingly, in our simulations, FGB larvae never entered the Western Caribbean directly, presumably due to the LC acting as a strong barrier (Fig. 3). Connectivity between the FGB and the Western Caribbean might be facilitated by stepping-stones, which could include Florida, Bahamas and potentially Cuba. Although our modeling data suggest that some FGB larvae can disperse to reefs in the southern GOM, other research has shown that reefs on the Campeche banks are likely sink populations due to the constraint of the LC on dispersal into the Western Caribbean (Sanvicente-Añorve et al. 2014). Johnson et al. (2013) modeled red snapper larval dispersal from the southern GOM and reported very high probabilities of reseeding (67–73%) with 0.33% of larvae arriving at other reefs, including the FGB, but no larvae dispersed outside the GOM. Thus, it would be interesting to test whether the FGB is an important stepping-stone for coral larvae connecting the southern GOM and other reefs in the northern Caribbean.

FGB as a refugium

The ability of FGB to act as a refugium is contingent on the population's ability to withstand stress and the frequency of disturbances. Bleaching events have been reported in other potential coral refugia sites in the southern hemisphere (Harrison et al. 2011; Thomson et al. 2011). However, until the recent bleaching and mortality events of 2016 (http://flowergarden.noaa.gov/newsevents/2016bleachingarticle.html), the FGB was buffered from these disturbances and was one of the healthiest reefs in the Caribbean (Zimmer et al. 2010; Jackson et al. 2014). Our simulations indicate that for species with long PLDs, the FGB could potentially act as a larval source for distant reefs in the southern GOM, Florida, the northern and western Bahamas and northern Cuba, highlighting the potential of the comparatively remote and pristine FGB to act as a refugium. Our simulations predict the possibility of large export events across the Florida reef tract, which are orders of magnitude higher than previously estimated (Lugo-Fernández et al. 2001). This result demonstrates that highly detailed models including specific times and locations of larval release as well as important life-history traits, such as larval pre-competency parameters, can drastically change predictions of larval transport between sites and overall source/sink dynamics.

Characterizing potential refugia is critical for reef management and the design of reserve networks, as emigration from these sites could be crucial for corals' long-term persistence in the region (Palumbi 2003; Cowen and Sponaugle 2009). Both the FGB and the Florida Keys are maintained as US National Marine Sanctuaries, but anthropogenic influences and coral cover of endangered groups, including *Orbicella,* are dramatically different between these ecosystems (Galindo et al. 2006; Palandro et al. 2008; Emma Hickerson, Research & Permits Coordinator at the FGBNMS, personal communication). Fishing and tourism strongly affect Florida reef ecosystems, and hard coral cover has significantly declined over the last 30 yr (Donahue et al. 2005). Our simulations demonstrate the potential for FGB larvae to contribute to *O. franksi* populations in the Florida Keys. Continued protection of highly fecund colonies from the FGB may be important for maintaining larval supply and genetic diversity along degraded Florida reefs. In this regard, it is alarming that widespread and unexplained mortality of reef organisms at FGB occurred in June 2016, followed by a strong coral bleaching event in August of the same year (http://flowergarden.noaa.gov/newsevents/2016bleachingarticle.html).

Outlook for future research

The largest remaining knowledge gap in the modeling of coral larval dispersal is how to translate the probability of larvae arriving to a certain location (such as the results of our simulations) into realized recruitment rates. We implicitly assumed that (1) recruitment probability (including post-settlement survival) is directly proportional to the larval arrival probability, (2) this proportion is the same across species, and (3) this proportion is independent of the environmental conditions at the target location. One indication that these assumptions might be unrealistic is the size-frequency distribution of FGB adult corals (Fig. 1b); *P. strigosa* had a significantly higher proportion of smaller colonies than *O. franksi*, which, given that these species exhibit similar growth rates (Muslic et al. 2013), suggests higher recent (over the last 1–5 yr) recruitment of *P. strigosa*. However, our simulations predict that short-PLD larvae (*P. strigosa*-like) should be less likely to arrive to FGB on average than the long-PLD larvae (*O. franksi*-like, Fig. 4a). Therefore, there is the possibility that *P. strigosa* and *O. franksi* larvae might not behave equivalently to our short- and long-PLD models. One explanation for this discrepancy is that *P. strigosa* larvae might be more efficient at settling once they arrive at a location, or suffer less post-settlement mortality than *O. franksi*, which would lead to overall higher recruitment rates. It is also conceivable that the recruitment probability might scale non-linearly with numbers of arriving larvae such that recruitment effectively occurs only when very large numbers of larvae arrive, which would be more likely for the short-PLD coral, *P. strigosa* (Fig. 4a). In addition, it is likely that we have overestimated dispersal capabilities since we quantified particle density within specific boundaries while ignoring the fact that some larvae may settle early and then stop dispersing. In terms of model limitations, a previous study performed a comprehensive sensitivity analysis of connectivity parameters (Treml et al. 2015) that is widely applicable across models, including the one presented here. It is possible that increasing model precision through increasing the number of particles released and increasing release sites may fine-tune our model, but these modifications would be unlikely to change overall results. Finally, the strength of ecological barriers to coral connectivity (i.e., due to environmental factors affecting post-settlement survival of immigrants rather than physical separation of the habitats) remains entirely unknown. It is possible that larvae produced in one habitat would not be physiologically and/or genetically predisposed to survive as recruits in a different habitat, the situation termed 'phenotype–environment mismatch' (Marshall et al. 2010). This mismatch could be particularly relevant for FGB-originating larvae, since the FGB is deep compared to the rest of the Caribbean and vertical connectivity may be different in shallow and deep reefs (Serrano et al. 2014). More research is needed to investigate these possibilities to develop more realistic biophysical models. In particular, research focused on assessing the population genetics of these two species across the Caribbean to directly test our biophysical model would be of specific interest.

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