

1 Coral life history differences determine the refugium potential of a remote Caribbean reef

2

3 Sarah W. Davies^{12,*,+}, Marie E. Strader^{1*,++}, Johnathan T. Kool³, Carly D. Kenkel^{1,4} and

4 Mikhail V. Matz¹

5

6 1. Department of Integrative Biology, The University of Texas at Austin, 1 University

7 Station C0990, Austin, TX 78712, USA

8

9 2. Department of Marine Sciences, The University of North Carolina at Chapel Hill, 123

10 South Road, Chapel Hill, NC 27599, USA

11

12 3. Geoscience Australia, Cnr Jerrabomberra Ave and Hindmarsh Drive, Symonston,

13 ACT, 2609, Australia

14

15 4. Australian Institute of Marine Science, PMB 3, Townsville MC, Townsville, QLD,

16 4810, Australia

17

18 * These authors contributed equally to this work

19 + Address correspondence regarding experiments to daviessw@gmail.com

20 ++ Address correspondence regarding modeling to stradermarie@gmail.com

21 +++ Address general correspondence to matz@utexas.edu

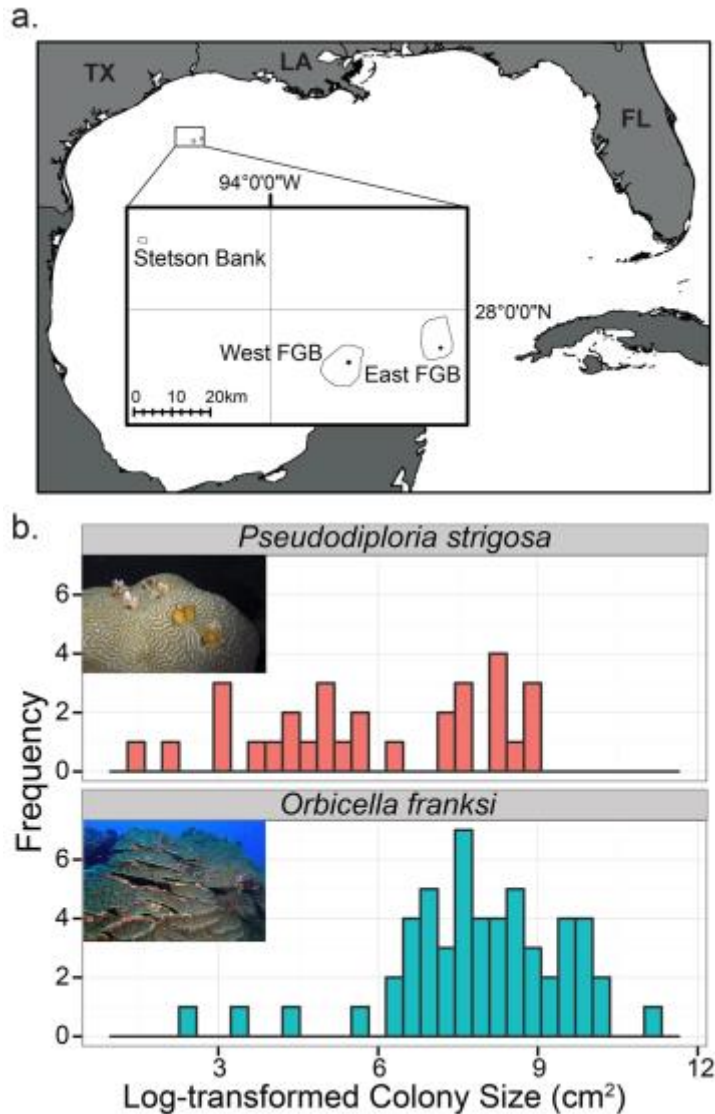
22 **Abstract**

23 Remote populations can influence connectivity and may serve as refugia from climate
24 change. Here, we investigated two reef-building corals (*Pseudodiploria strigosa* and
25 *Orbicella franksi*) from the Flower Garden Banks (FGB) – the most isolated, high-
26 latitude Caribbean reef system that retains high coral cover. We characterized coral size
27 frequency distributions, quantified larval mortality rates and onset of competence,
28 estimated larval production, and created detailed biophysical models incorporating these
29 parameters to evaluate source-sink dynamics from 2009 to 2012. Mortality rates were
30 similar across species but competency differed dramatically: *P. strigosa* was capable of
31 metamorphosis within 2.5 days post fertilization (dpf), while *O. franksi* were not
32 competent until >20dpf and remained competent up to 120dpf. Despite these differences,
33 models demonstrated that larvae of both types were similarly successful in reseeding the
34 FGB. Nevertheless, corals with shorter pelagic larval durations (PLD), such as *P.*
35 *strigosa*, were highly isolated from the rest of the Caribbean, while long PLD corals, such
36 as *O. franksi*, could export larvae to distant northern Caribbean reefs. These results
37 suggest that FGB coral populations are self-sustaining and highlight the potential of long
38 PLD corals, such as endangered *Orbicella*, to act as larval sources for other degraded
39 Caribbean reefs.

40

41 **Introduction**

42 Caribbean reefs have experienced some of the most dramatic coral declines over
43 the last few decades¹, however the Flower Garden Banks (FGB) – a system of two very
44 unusual reefs located 185 km south of the Texas-Louisiana border in the Gulf of Mexico
45 – appear to be the exception. The FGB is populated by only 24 species of reef-building
46 corals² but average coral cover exceeds 56%³, five times that of the general Caribbean
47 average¹. The FGB is one of the northern-most coral reefs in the Caribbean and is highly
48 isolated from other reefs: the nearest neighboring reefs are hundreds of kilometers away
49 along the coast of Tampico, Mexico (645 km) and the Yucatan peninsula (600 km)⁴ (Fig
50 1A). The FGB's isolation, buffering from increased sea surface temperatures due to its
51 high-latitude location, low degradation and high coral cover make it the ideal potential
52 refugium from climate change for Caribbean corals. However, in order to be a good
53 refugium the FGB must meet three requirements: first, FGB coral populations must be
54 self-seeding (i.e., not requiring larval input from elsewhere to sustain populations), and
55 second, coral larvae originating from the FGB must be capable of emigrating and
56 surviving at other Caribbean reefs. Lastly, these reefs must be relatively resilient to
57 recurrent disturbances such as bleaching.



58

59 Figure 1: Size frequency data of *Orbicella franksi* and *Pseudodiploria strigosa* from the
60 Flower Garden Banks (FGB) in 2012. A. Locations of surveys conducted at East FGB
61 (mooring buoy 2) and West FGB (mooring buoy 2) (black dots). B. Size-frequency
62 distributions for *P. strigosa* and *O. franksi* for both the East and West FGB resulting from
63 transects performed in August 2012 with photo insets of each species.
64

65 Corals have bipartite life cycles with dispersive pelagic larvae, and a sedentary
66 adult stage. Connectivity across distant populations is therefore dependent on the
67 successful exchange of these pelagic larvae along ocean currents⁵. Intra and interspecies
68 differences in biological traits can influence the scale of dispersal⁶⁻⁸. Larvae of some

69 species have limited connectivity and only disperse meters from their parents⁹, while
70 other species are highly genetically connected across distant reefs separated by thousands
71 of kilometers^{8,10,11}. The two key life history traits expected to influence connectivity are
72 developmental time required before a larva becomes competent to settle, referred to as
73 pelagic larval duration (PLD), and the larval mortality rate^{12,13}. In addition to life history
74 traits, oceanic currents are strong drivers of larval connectivity and as global climates
75 continue to warm, currents are predicted to dramatically shift, potentially altering the
76 connectivity patterns of many marine species¹⁴⁻¹⁶. In order to fully understand population
77 connectivity of reef-building corals it is essential to understand how ocean currents and
78 life history traits interact to enhance or limit larval dispersal.

79 In this study, we aimed to estimate larval retention and export for the FGB. We
80 used a biophysical model based on regional currents during the weeks following coral
81 mass-spawning events across specific years (2009-2012) that also incorporated
82 experimentally measured larval life history traits for two of the most dominant reef-
83 building corals on the FGB: *Pseudodiploria strigosa* and *Orbicella franksi*. We find that
84 our focal species represent opposite extremes in the timing of competency onset, which,
85 unexpectedly, had little effect on their potential to reseed the FGB. However, only the
86 species with delayed competency, *O. franksi*, had the potential for larval export to other
87 Caribbean reefs.

88

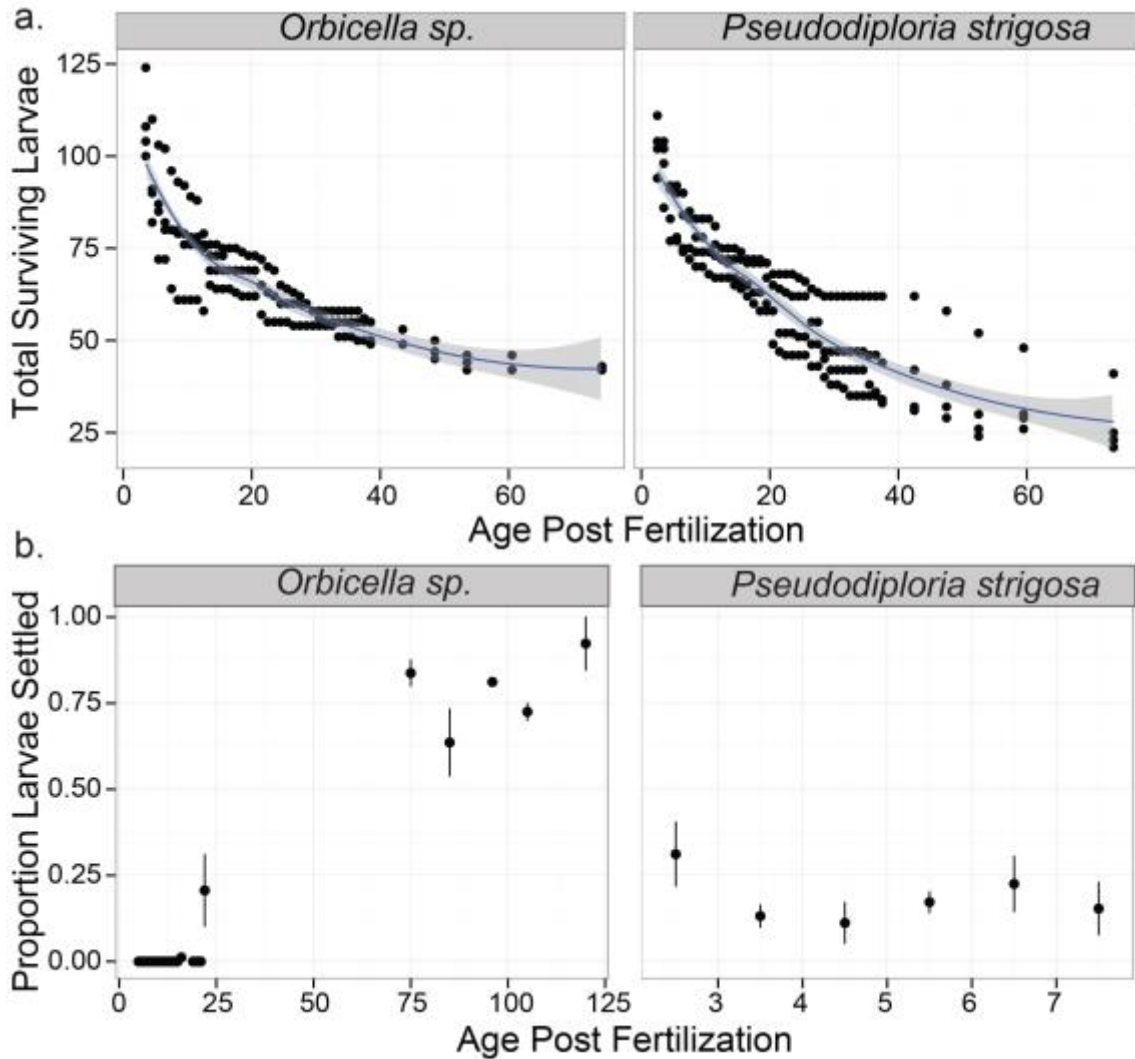
89

90 **Results**

91 *Size-frequencies and larval traits of Psuedodiploria strigosa and Orbicella franksi at*

92 *FGB*

93 Surveys of *O. franksi* and *P. strigosa* revealed similar size frequency ranges
94 across the sampled reefs, however *P. strigosa* colonies were consistently in smaller size
95 classes than *O. franksi* (Fig 1B; Wilcoxon sum rank test, $P=2E-04$). There was very little
96 difference in larval mortality rates between *P. strigosa* and *Orbicella faveolata* (exponent
97 powers of -0.022 and -0.019, respectively, Fig 2A), so mortality rates of both corals were
98 modeled with the exponent power -0.02. The timing of competency onset varied
99 dramatically between *P. strigosa* and *O. franksi*. *P. strigosa* exhibited competence on the
100 very first trial, 2.5 dpf, and maintained competence at least until 8 dpf, at which point no
101 swimming larvae remained in the cultures due to spontaneous metamorphosis (Fig 2B).
102 In contrast, *O. franksi* became competent as late as 21 dpf and remained fully capable of
103 metamorphosis at least until 120 dpf (Fig. 2B). In addition, *O. franksi* were not observed
104 to spontaneously metamorphose even though they were maintained in the same culture
105 conditions as *P. strigosa*. In order to emphasize the contrast in competence onset between
106 *P. strigosa* and *O. franksi* we modeled two non-overlapping competence windows: 3 to
107 20 dpf for the short-PLD model (*P. strigosa* – like) and 20 to 120 dpf for the long-PLD
108 model (*O. franksi* – like).



109

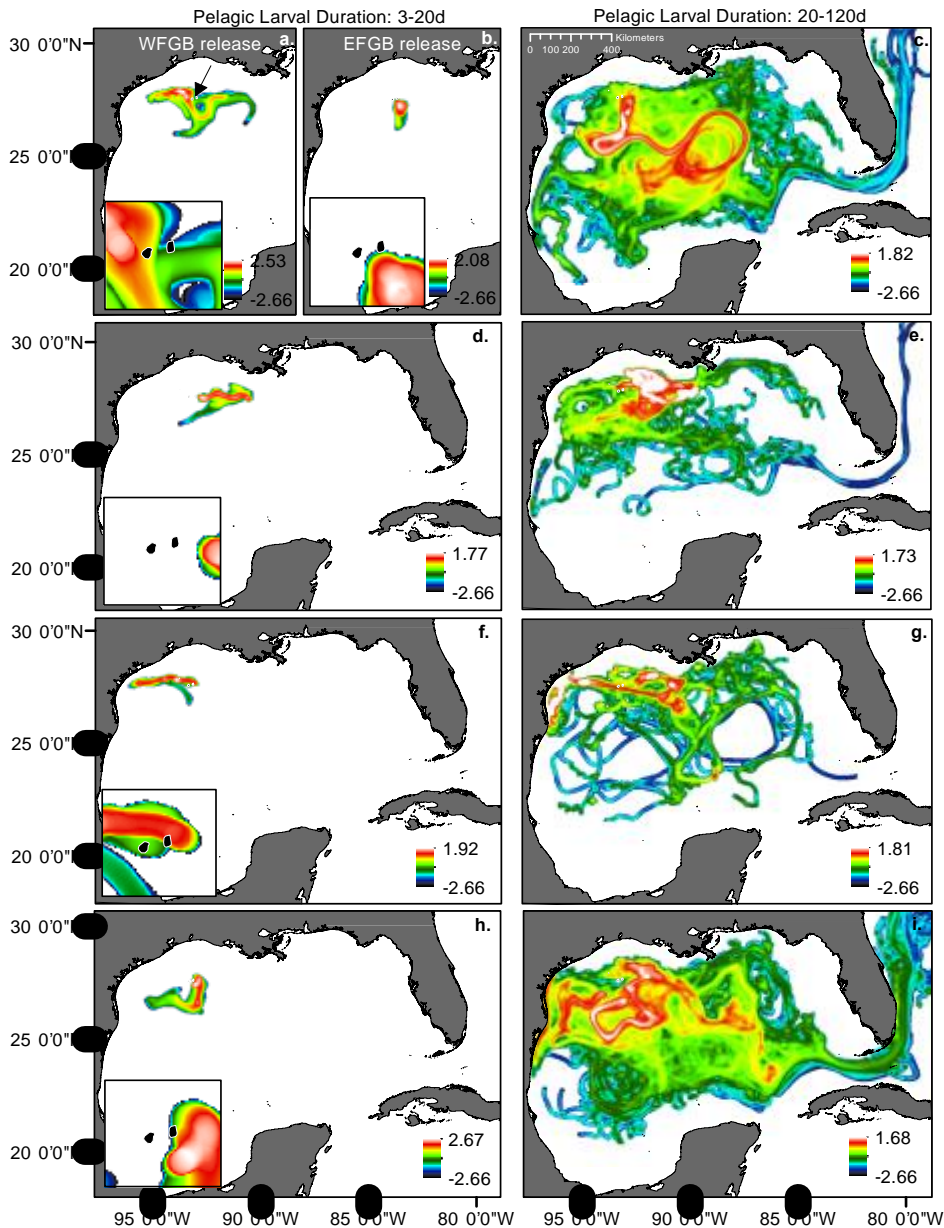
110 Figure 2: Coral larval physiological measurements: A. Mortality estimates for larvae
111 from *Orbicella faveolata* and *P. strigosa* and across four culture replicates. Blue line is
112 loess smoothing, grey shading indicates 95% confidence interval. B. Competency
113 patterns observed for *Orbicella franksi* and *P. strigosa* estimated by the mean proportion
114 of larvae +/- SE settling in response to settlement cue over time. Note the differences in
115 time scale for the two species.

116

117 *Short PLD results in occasionally abundant but highly variable reseeded*

118 Short PLD occasionally lead to a very high probability of reseeded, but only on
119 specific days in years when currents are favorable. In 2009, only larvae released from
120 WFGB on August 10 and 11 could reseed either bank (probabilities of reseeded: 4.3E-03
121 and 1.3E-04, respectively), and the probability of reseeded on August 10 when released

122 from WFGB was larger than any other release date in our analysis (Fig 3A,B, Table 1,
123 Supplemental Fig S1). In 2010 and 2012 no short-PLD larvae were found within the
124 boundaries of the FGB (Fig. 3D,H). In 2011, short-PLD larvae released from EFGB
125 could reseed the FGB (simulation for WFGB for that year was not generated), but the
126 probability was lower ($5.4E-04$) than on August 10 2009 (Fig. 3F, Table 1). The mean
127 probability for short PLD larvae to reseed the FGB in 2009-2012 was $5.8E-04$. The total
128 reproductive output for *P. strigosa* at WFGB and EFGB was estimated at $4.7E+09$ and
129 $9.2E+09$ eggs, respectively (Supplemental Table 1). Therefore, the mean potential
130 reseed events for short PLD larvae released in mass-spawn nights across all
131 simulations run for 2009-2012 was $2.9E+06$ (Fig. 4A). Notably, none of the simulated
132 spawning events for the short PLD larvae resulted in any export to other reef systems
133 besides the FGB.



134

135 Figure 3: Surface heatmaps of particle dispersal from the Flower Garden Banks (FGB,
136 arrow). Images show the density of particles for a 12-km radius around a 1-km cell
137 integrated over pelagic larval durations (PLDs) of 3-20 days (A, B, D, F, H) and 20-120
138 days (C, E, G, I). Particle density is displayed on a \log_{10} scale. Release dates are August
139 11, 2009 (A, B, C), August 31, 2010 (D, E), August 19, 2011 (F, G) and August 8, 2012
140 (H, I). (A) Represents particles released from WFGFB, (B-I) represent larvae released
141 from EFGB. For short PLDs (3-20 days, A, B, D, F, H), insets show variation in
142 particle's reseeded area of FGB (black area) between years.

143

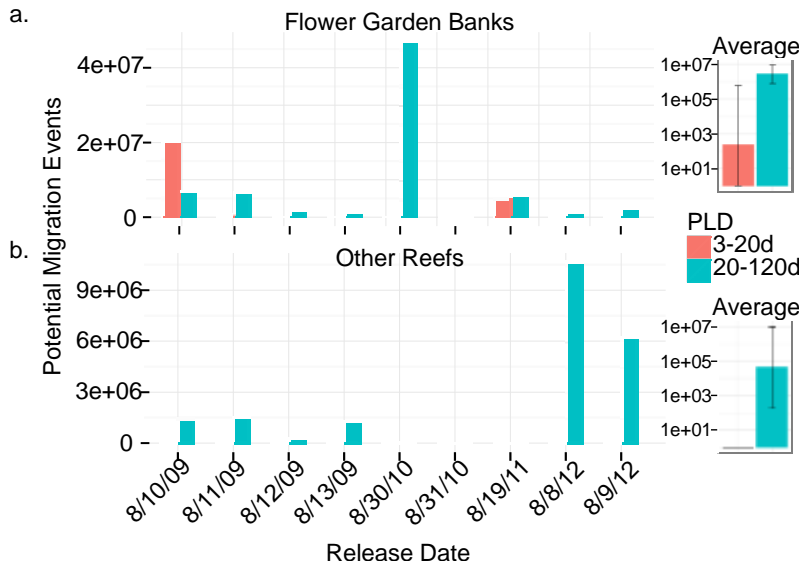
144

145 Table 1: Probability of larval reseeding to FGB and probability of larval export to other
 146 reefs. Proportion calculated as number of particles within area/total particles for set PLD
 147 (short: 3-20 days; long: 20-120 days).

Date	Bank	PLD	Reproductive Output (# eggs)	P(reseeding)	P(export)	Total larvae reseeded	Total larvae exported
10-Aug-09	West	short	4.73E+09	4.3 E-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

149 *Long PLD results in low but consistent reseeded*

150 Simulations demonstrated that long-PLD larvae (competency from 20 to 120 dpf)
151 had similar average probabilities of reseeded ($3.3E-04$) as short-PLD larvae ($5.8E-04$),
152 but the long-PLD larvae reseeded more consistently over the years (Table 1, Fig 3). On
153 August 11 2009, the major spawning night for that year, the probabilities of long-PLD
154 reseeded when released from WFGB or EFGB were $2.7E-04$ and $1.7E-04$, respectively
155 (Fig. 3C, Table 1). On peripheral spawning nights in 2009 (August 10, 12 and 13),
156 simulations showed similar probabilities of reseeded (Table 1). The highest probability
157 of long PLD larval reseeded, $3eE-03$, was observed for the August 30, 2010 simulation
158 for the EFGB (Table 1, Supplemental Fig 3). Interestingly, larvae with longer PLDs had a
159 dramatically higher probability of reseeded their home reef than larvae with short PLDs
160 when released on August 30, 2010 (Table 1, Supplemental Fig 3). In 2011 and 2012, the
161 probability of long PLD larvae reseeded the FGB ranged from $1.7E-06$ to $1.2E-04$ (Fig.
162 3G,I, Table 1). Total *Orbicella franksi* reproductive output was calculated as $1.02E+10$
163 and $2.26E+10$ eggs, for WFGB and EFGB respectively (Supplemental Table 1). At the
164 FGB, *O. franksi* has much higher overall coral cover (26.90% at WFGB and 27.56% at
165 EFGB) than *P. strigosa* (9.60% at WFGB and 8.20% at EFGB)¹⁷. These differences in
166 percent cover account for the ~3-5x greater reproductive output calculated for *Orbicella*
167 *sp.* when compared to *P. strigosa*. Therefore, for a mass spawn night, the average number
168 of potential reseeded events of *Orbicella* larvae to the FGB between 2009 and 2012 was
169 $8.3E+06$ (Fig 4).



170

171 Figure 4: Larval particles with potential to colonize coral reef environments. Output from
172 West and East FGB is summed. (A) Flower Garden Banks (reseeding) (B) Other reefs as
173 defined in [UNEP-WCMC, WorldFish Centre, WRI, TNC]. PLD = pelagic larval
174 duration. Insets show harmonic mean number of particles for each PLD +/- SD.
175

176 *Long PLD enables larval export beyond the FGB*

177 No export events were observed for short PLD larvae, but larvae with PLDs of
178 20-120 days remained in the water column long enough to be exported to reefs outside of
179 the FGB. For 2009 simulations, the probability of larval export to other reefs ranged from
180 1.1E-06 to 5.7E-05, similar to the probability of reseeding back to the FGB. After
181 accounting for total *O. franksi* reproductive output, this resulted in 1.1E+04 - 1.3E+06
182 potential larval export events in 2009, depending on the day and bank of release (Table 1,
183 Fig. 4B). In 2009, long PLD larvae were observed in Broward and Palm Beach, the
184 Florida Keys (Dry Tortugas up to Elliott Key), Bay of Campeche reefs (Bajos del Norte,
185 Bajo Madagascar, Alacranes, Arenas, Triangulos, Lobos, Bajo Madaga) (reefs defined in
186 Sanvicente-Añorve et al 2014 and Millennium Coral Reef Mapping Project 2005) and
187 Northern Cuba (west of Cayo Coco). This larval export varied greatly from year to year:

188 in 2010 only a single larva in the simulation (released from WFGB on August 30)
189 dispersed to a reef other than FGB (Little Bahama Banks), resulting in an export
190 probability of 3.1E-06, and no larvae were exported to other reefs in 2011. In 2012
191 simulations suggested export to other reefs at even higher rates than those observed in the
192 2009 simulation: probability of larval export ranged from 5.5E-05 to 1.20E-04. After
193 considering reproductive output, between 5.6E+05 and 9.4E+06 possible larvae were
194 exported in 2012 (Table 1, Fig 4B). The destinations of exported larvae in 2012 were
195 Broward and Palm Beach, the middle to upper Florida Keys (Islamorada up to Elliott
196 Key), Bay of Campeche reefs (Bajos del Norte, Alacranes, Arenas) and the Bahamas
197 (Cay Sal Banks and Little Bahama Banks).

198

199 **Discussion**

200 *Corals from the FGB exhibit unusual competency dynamics*

201 Larvae of most broadcast-spawning scleractinian corals become competent upon
202 completion of larval development, typically 4-6 dpf, after which competence declines¹⁸⁻
203 ²⁰. Both FGB coral species studied here, *Pseudodiploria strigosa* and *Orbicella franksi*,
204 deviate from this pattern, but in opposing directions. *P. strigosa* becomes competent by
205 2.5 dpf, while *O. franksi* cultured in identical conditions, did not exhibit competence until
206 20 dpf. In addition, once competence was acquired in *O. franksi*, no decline in
207 competence was detected, even up to 120 dpf. Davies et al (2014) observed similar
208 competency onset ranges: 3-4 dpf for *Pseudodiploria* (formerly *Diploria*) *strigosa* and
209 14-20 dpf for *O. franksi*, indicating that competency patterns reported here are consistent
210 across years for populations of these species at the FGB. While two-day pre-competency

211 periods have been observed in *Pectinia lactuca* and *Platygyra sinensis* from Singapore²¹
212 and *Platygyra daedlia* on the Great Barrier Reef¹⁸ no other study has ever reported delay
213 of competency by as much as 20 dpf, as was observed here in FGB *O. franksi*. Although
214 there is no published data on competence in *O. franksi* from other regions, larvae of a
215 congener, *Orbicella faveolata*, from Belize became competent at a typical 6 dpf²².
216 Similarly, *O. faveolata* larvae from the Florida Keys began gaining competence at 6 dpf
217 and exhibited 100% competence by 24 dpf²³. It is therefore possible that unusual
218 competence dynamics of FGB corals may be specific to the FGB populations – the
219 possibility of which requires clarifications in future studies.

220

221 *PLD and reseeding potential*

222 Along the lines of Darwin's hypothesis about the loss of flight ability in insects and birds
223 following colonization of remote islands²⁴, one might predict that corals at an isolated
224 reef such as the FGB would be selected for short PLDs to facilitate reseeding. However,
225 we find that both short-PLD and long-PLD models result in similar average FGB
226 reseeding probabilities (Fig. 4), suggesting that FGB reseeding might not necessarily
227 require the loss of long-distance dispersal potential. The possibility that the optimal PLD
228 for the FGB reseeding could be bimodal has been suggested by an earlier study tracking
229 drifters released from the FGB during two annual coral spawning events in 1997 &
230 1998²⁵. There, it was demonstrated that while there was a high likelihood of drifters'
231 returning to the FGB within the first 30 days, they were also entrained in Loop Current
232 eddies and could recirculate back to the FGB after several months. The two coral species
233 modeled here appear to take advantage of these two alternative reseeding strategies, but

234 whether their unusual PLDs are a result of local selection at the FGB remains to be
235 determined, especially considering that these species are rarely observed to recruit²⁶.

236 A large body of research links short PLD to high reseeded and low connectivity,
237 while long PLD is linked to lower reseeded values and higher connectivity^{7,27,28}. Given
238 that our long-PLD species had a late onset of competency and was able to both reseed
239 and disperse, our results support the alternative view that this paradigm may be too
240 simplistic within the real seascape²⁹. Still, our study agrees with previous genetic³⁰ and
241 oceanographic modeling work performed in the region^{25,30} in that we find that species
242 with early onset of competency and short PLDs are capable of reseeded, but are indeed
243 highly isolated from neighboring reefs.

244

245 *Dispersal is highly variable among larval cohorts*

246 Larval release timing significantly affected dispersal probabilities (Fig. 3). In
247 2010 the probability of FGB reseeded was far greater for long PLD larvae than for short
248 PLD larvae and only one long PLD larva was exported to another reef. In contrast, in
249 2011 simulations, similar probabilities of reseeded were observed for both short and
250 long PLD larvae, with no larval export to other reefs regardless of PLD. Finally, in 2009
251 and 2012 long PLD larvae had high probabilities of export while short PLD larvae
252 exhibited the highest probability of reseeded in 2009 and no chance of reseeded in
253 2012.

254 Spatial variation in the pattern of larval release also interacts with temporal
255 variation, resulting in dramatically different dispersal patterns, even over relatively small
256 geographic distances³¹. The east and west FGB are only 18 kilometers apart, but in 2009,

257 EFGB short PLD larvae dispersed further east and had no chance of reseeding across all
258 four days while WFGB short PLD larvae drifted west but were more likely to be
259 maintained in the vicinity of FGB or circulate back (Fig. 3AB, Supplemental Fig S1).
260 The opposite pattern was observed in 2012 where only EFGB larvae reseeded while
261 WFGB larvae drifted west and were never able to return to FGB. However, in spite of
262 this variance, recurrence of high-probability reseeding events indicates that FGB coral
263 populations are likely to be demographically self-sustaining.

264

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

266 Surface currents in the GOM tend to be dominated by the Loop Current (LC),
267 which is a continuation of the Caribbean current that intrudes the GOM through the
268 Yucatan Channel³². The position and degree of LC intrusion into the GOM is variable in
269 season and across years³³ and can vary from flowing directly into the Florida current to
270 intruding the GOM as far as 29.1°N
271 (<http://oceancurrents.rsmas.miami.edu/caribbean/loop-current.html>). The degree of LC
272 intrusion into the GOM influences the likelihood of large warm water eddies being cast
273 off and flowing westward into the GOM. These eddies can be large enough that a full
274 rotation can be up to 30 days³⁴. Large scale eddy formation from the LC is irregular³³, but
275 is more prevalent in the summer months³⁵ when broadcast-spawning corals release their
276 gametes. Lugo-Fernández *et al.* (2001) suggest that as much as 43% of larvae released
277 from FGB are likely to get caught up in these offshore eddies. The results of our
278 simulations support this assertion: we find that larval transport in the GOM is highly
279 affected by LC eddy circulation. For example, in 2009, high numbers of larvae became

280 entrained in a large eddy that was detached from the LC on Sept 2³⁶. The density of
281 larvae released from the FGB in other years appeared to be less affected by these large-
282 scale eddies. However, in nearly all of our simulations with long PLD larvae (20-120
283 days), surviving particles were eventually able to enter the LC, likely through eddy
284 entrainment, and be dispersed by either the Florida Current (moving towards the Florida
285 Keys and Miami or the Bahamas) or westward through the Yucatan Current and
286 potentially into the Campeche shelf reefs.

287 Interestingly, larvae from the FGB were never observed to enter the Western
288 Caribbean directly, presumably due to the LC acting as a dispersal barrier (Fig 3).
289 Connectivity between the FGB and the Western Caribbean must therefore be facilitated
290 by stepping-stones, which likely include Florida, Bahamas and potentially Cuba.
291 Although our modeling data suggest that some FGB larvae can disperse to reefs in the
292 southern GOM, other research has shown that these reefs on the Campeche banks are
293 likely sink populations due to the constraint of the LC on dispersal into the Western
294 Caribbean³⁷. Johnson *et al.* (2013) modeled red snapper larval dispersal from the southern
295 GOM and reported very high probabilities of reseeded (67-73%) with 0.33% of larvae
296 arriving at other reefs, including the FGB, but no larvae dispersed outside the GOM.
297 Thus, the FGB might be an important stepping-stone between the southern GOM and
298 other reefs in the Northern Caribbean.

299

300 *FGB as a refugium*

301 The ability of FGB to act as a refugium is contingent on the population's ability to
302 withstand stress and the frequency of disturbances. In other potential coral refugia sites in

303 the southern hemisphere, bleaching events have been reported^{39,40}. However, despite the
304 occurrence of these events at other high latitude sites, the FGB continues to be resilient to
305 these disturbances and remains one of the healthiest reefs in the Caribbean³. Our data
306 show that for species with long PLDs, the FGB can act as a source of larvae for distant
307 reefs in the southern GOM, Florida, the northern and western Bahamas and Northern
308 Cuba, highlighting the potential of the comparatively remote and pristine FGB to act as a
309 refugium. Our simulations predict the possibility for large export events across the
310 Florida reef tract, which are orders of magnitude higher than previously predicted²⁵. This
311 result demonstrates that highly detailed models including specific times and locations of
312 larval release as well as important life history traits, such as larval competency
313 parameters, can drastically change predictions of larval transport between sites and
314 overall source/sink dynamics.

315 Characterizing potential refugia populations is critical for reef management and
316 the design of reserve networks, as individuals migrating from these sites could modulate
317 characteristics of future populations^{29,41}. Both the FGB and the Florida Keys are
318 maintained as United States national marine sanctuaries, however, anthropogenic
319 influences and coral cover of endangered groups, including *Orbicella*, is dramatically
320 different between these ecosystems (Galindo *et al.* 2006; Palandro *et al.* 2008, Emma
321 Hickerson, personal communication). Fishing and tourism strongly affect Florida reef
322 ecosystems and hard coral cover has significantly declined over the last 30 years⁴³. Our
323 data demonstrate the potential for larvae released from the FGB to contribute to *Orbicella*
324 *franksi* populations in the Florida Keys. Continued protection of highly fecund colonies

325 from the pristine FGB reefs may be important for maintaining larval supply and genetic
326 diversity along degraded Florida reefs.

327

328 *Outlook for future research*

329 The largest remaining knowledge gap in the modeling of coral larval dispersal is how to
330 translate the probability of larvae arriving to a certain location (such as the results of our
331 modeling) into the actual recruitment rate. Throughout this paper we followed other
332 authors in implicitly assuming (i) that recruitment probability is directly proportional to
333 the larval arrival probability, (ii) that this proportion is the same for different coral
334 species, and (iii) that this proportion is independent of the environmental conditions at the
335 target location. One indication that these assumptions might be unrealistic is the size-
336 frequency distribution of adult corals observed at the FGB (Fig. 1B): *P. strigosa* shows a
337 significantly higher proportion of smaller colonies than *O. franksi*, which, since the
338 growth rates of the two species are similar⁴⁴, suggests higher recent recruitment of
339 *P. strigosa*. However, our model predicts that short-PLD larvae of *P. strigosa* should be
340 on average less likely to arrive to FGB than the long-PLD larvae of *O. franksi* (Fig. 4A).
341 One explanation for this apparent discrepancy is that *P. strigosa* larvae might be more
342 efficient at recruiting, or suffer less post-settlement mortality than *O. franksi*. It is also
343 conceivable that the recruitment probability might scale non-linearly with numbers of
344 arriving larvae such that recruitment effectively occurs only when very high numbers of
345 larvae arrive, which would be more likely for the short-PLD *P. strigosa* (Fig. 4A).
346 Finally, the strength of ecological barriers to larval dispersal (i.e., due to environmental
347 differences rather than physical separation of the habitats) remains entirely unknown. It is

348 possible that larvae produced in one type of habitat would not be physiologically and/or
349 genetically predisposed to survive in a different type of habitat, the situation termed
350 “phenotype-environment mismatch”⁴⁵. This mismatch could be particularly relevant for
351 FGB-originating larvae, since the FGB is a very unusual reef compared to the rest of the
352 Caribbean. More research is needed to investigate these possibilities and develop more
353 realistic models.

354

355 **Methods**

356 *Study species*

357 *Pseudodiploria strigosa* was used both for larval mortality and competency trials, but for
358 logistical reasons two different species of the *Orbicella* species complex were used to
359 measure larval traits: *Orbicella faveolata* for mortality and *O. franksi* for competency.
360 Due to negligible differences in mortality rates across genera (*P. strigosa* versus *O.*
361 *faveolata*) we assumed that their average larval mortality rates would be a good
362 approximation for both *Pseudodiploria* and the *Orbicella* species complex.

363

364 *Size-frequency transects*

365 On August 8 and 9, 2012 divers completed a total of eight size frequency
366 transects targeting *Orbicella franksi* and *Pseudodiploria strigosa* following protocols
367 established by the Florida Reef Resiliency Program⁴⁶ (<http://frp.org>). Four transects were
368 completed at both the WFGB (27° 52.526 N, -93° 48.836 W) and EFGB (27° 54.516 N, -
369 93° 35.831 W) (Fig 1). In brief, communities were surveyed using 10-m² belt transects,
370 randomly placed at each site. The diameter, height and percent live tissue of all corals ≥ 4

371 cm in diameter were recorded. Colony sizes were log-transformed to visualize size-
372 frequency differences between the two corals and these size-frequency distributions were
373 compared using a Wilcoxon rank sum test in R.

374

375 *Larval rearing*

376 Samples were collected under the FGBNMS permit # FGBNMS-2009-005-A3.
377 On the evening of August 18, 2011 (eight days after the full moon, 2115CDT), gamete
378 bundles from ≥ 3 individuals of each broadcast-spawning Caribbean coral species (*P.*
379 *strigosa* and *O. franksi*) were collected from the east FGB. Gamete bundles were brought
380 to the surface and allowed to cross-fertilize in 3L of 1 μm filtered seawater (FSW) for
381 one hour in sterile 6L plastic containers. Excess sperm were removed by rinsing through
382 150 μm nylon mesh. Larvae were reared in 1 μm FSW in three replicate plastic culture
383 vessels stocked at a density of 2 larvae per ml in a temperature controlled room (28°C).
384 Larvae were transferred to the laboratory at the University of Texas at Austin on August
385 21, 2011 and used in all competency trials.

386 On the evening of August 8, 2012 (2330CDT) divers collected gamete bundles
387 from four spawning *O. faveolata* colonies and the next evening (August 9, 2012 at
388 2115CDT) divers collected from eight spawning *P. strigosa*. Cultures for both species
389 were fertilized and maintained as described in 2011. Larvae were transferred to the
390 University of Texas at Austin on August 10, 2012 and these larvae were used in mortality
391 trials. All research in 2012 was completed under the Flower Garden Banks National
392 Marine Sanctuary permit #FGBNMS-2012-002.

393

394 *Mortality trials*

395 Mortality trials began on August 11, 2012 for *O. faveolata* and *P. strigosa*. Four
396 mortality trials per species were conducted. Each trial started with 100 larvae housed in a
397 bowl with 0.5 L of FSW. For the first 38 days the surviving swimming larvae were
398 counted daily and transferred into new bowls. After that the larvae were counted every
399 five days until 74 days post fertilization (dpf).

400

401 *Competency trials*

402 For competency trials each well in a six-well plate received 10 ml of FSW and a
403 drop of a uniform slurry of finely ground crustose coralline algae collected at the FGB,
404 which has previously been shown to elicit settlement in both species⁴⁷. Twenty larvae of
405 *O. franksi* or *P. strigosa* were then added to each well (n = 3 replicates per species) and
406 the proportions of metamorphosed larvae (visual presence of septa) were quantified after
407 24 h using a stereomicroscope MZ-FL-III (Leica, Bannockburn, IL, USA). Trials began
408 2.5 dpf and were repeated until all larvae that remained in vessels had spontaneously
409 metamorphosed.

410

411 *Biophysical model*

412 We used the Conn4D biophysical dispersal model⁴⁸ to estimate dispersal patterns
413 for each species independently. Conn4D uses oceanographic current information in
414 conjunction with an advection diffusion scheme and individual-based behaviour to
415 simulate larval trajectories. Oceanographic data was derived from the HYbrid isopycnal
416 Coordinate Model (HYCOM)⁴⁹. We parameterized the models to reflect the exponential

417 decrease in larval mortality measured for both genera. Simulations did not encompass a
418 full 4D model since coral larvae were assumed to stay in surface waters as passive
419 drifters. Therefore, the depth of particles was kept at a constant 5 meters. Dates of
420 particle release were as follows: August 10th, 11th, 12th and 13th 2009, August 30th and
421 31st 2010, August 11th 2011 and August 8th and 9th 2012. These dates were the dates of
422 observed spawning at FGB, eight days after the full moon in late July/August (Emma
423 Hickerson, personal communication). Coral spawning at the FGB is highly predictable⁵⁰,
424 however the night of the mass spawn can be flanked by nights that have smaller outputs
425 of gametes. Therefore for some years we ran simulations on these flanking days.
426 Simulated particles were released from either West (27.83° N 93.83° W) or East (28.00°
427 N 93.58° W) FGB. For each simulation, 1000 particles were released and allowed to
428 drift for 120 days. Output from each simulation was recorded as a text file with latitude,
429 longitude, depth, time, distance and duration traveled for each particle, as in⁴⁸. Output
430 files were split into two non-overlapping time windows of 3-20 days for the “short PLD”
431 and 20-120 days for the “long PLD” datasets.

432

433 *Analysis*

434 Simulated particle dispersal was visualized in ArcGIS 10.2. Input data was transformed
435 using the ‘Project (Data Management)’ tool from Decimal Degrees to a Projected
436 Coordinate system NAD 1983 UTM Zone 16N and visualized within the Gulf of Mexico.
437 The location of the particles in the Gulf of Mexico was summarized as a density surface
438 by calculating the number of particles on or around a 12-km radius and raster output was
439 set to a 1-km cell size. Density surface rasters were log₁₀ transformed using the ‘raster

440 calculator'. The number of total particles within the boundary of the FGBNMS and
441 within the boundary of other reefs (as defined by UNEP-WCMC, WorldFish
442 Centre, WRI, TNC) for each PLD was calculated using the 'select by location' tool. This
443 gives the total number of times any particle intersects the specified boundary, not the
444 total number of particles with a final destination within the boundary. In some cases, a
445 particle stays within the specified boundary for several days, which influences its
446 probability of being a migrant within the specified reef boundary. For each simulation,
447 the number of particles within each boundary during a specified PLD was divided by the
448 total number of particles for that simulation, giving a probability of particle existence
449 within each specified boundary. This probability of particle presence within the FGB and
450 in other reefs was multiplied by the total reproductive output of each species from each
451 bank to give a value representing the potential migration events. Total reproductive
452 output for East and West FGB was estimated by multiplying fecundity data (number of
453 eggs/m²) from parameters measured in Szmant (1986) for *Pseudodiploria strigosa*
454 (35,200 eggs/m²) and in Smant *et al.* (1997) for *O. franksi* (27,000 eggs/m²) by area of
455 coral cover of each species at each bank^{2,17} (Supplemental Table 1).

456 References

- 457 1. Gardner, T. a, Côté, I. M., Gill, J. a, Grant, A. & Watkinson, A. R. Long-term
458 region-wide declines in Caribbean corals. *Science* **301**, 958–60 (2003).
- 459 2. Schmahl, G. P., Hickerson, E. L. & Precht, W. F. in *Coral Reefs of the USA* (eds.
460 Riegl, B. M. & Dodge, R. E.) 221–261 (Springer Netherlands, 2008).
461 doi:10.1007/978-1-4020-6847-8_6
- 462 3. Zimmer, B., Duncan, L., Aronson, R. B., Deslarzes, K. J. P. & Dies, D. R. *Long-*
463 *term monitoring at the East and West Flower Garden Banks, 2004-2008. Volume*
464 *I: Technical Report.* (US Dept of the Interior, Bureau of Ocean Energy
465 Management, Regulation, and Enforcement, Gulf of Mexico OCS Region, 2010).
- 466 4. Rezak, R., Gittings, S. R. & Bright, T. J. Biotic assemblages and ecological
467 controls on reefs and banks of the Northwest Gulf of Mexico. *Am. Zool.* **30**, 23–35
468 (1990).
- 469 5. Sale, P. F. in *Population and Community Biology* 197–210 (1991).
- 470 6. Kinlan, B. P. & Gaines, S. D. Propagule Dispersal in Marine and Terrestrial
471 Environments : a Community Perspective. *Ecology* **84**, 2007–2020 (2003).
- 472 7. Shanks, A. L., Grantham, B. a. & Carr, M. H. Propagule Dispersal Distance and
473 the Size and Spacing of Marine Reserves. *Ecol. Appl.* **13**, 159–169 (2003).
- 474 8. Davies, S., Trembl, E., Kenkel, C. & Matz, M. Exploring the role of Micronesian
475 islands in the maintenance of coral genetic diversity in the Pacific Ocean. *Mol.*
476 *Ecol.* **24**, 70–82 (2015).
- 477 9. Jones, G., Srinivasan, M. & Almany, G. Population Connectivity and Conservation
478 of Marine Biodiversity. *Oceanography* **20**, 100–111 (2007).
- 479 10. Gaines, S. D., Gaylord, B., Gerber, L. R., Hastings, A. & Kinlan, B. P. The
480 Ecological Consequences of Dispersal in the Sea. *Mar. Popul. Connect.* **20**, 90–99
481 (2007).
- 482 11. Van Oppen, M. J. H., Peplow, L. M., Kininmonth, S. & Berkelmans, R. Historical
483 and contemporary factors shape the population genetic structure of the broadcast
484 spawning coral, *Acropora millepora*, on the Great Barrier Reef. *Mol. Ecol.* **20**,
485 4899–4914 (2011).
- 486 12. Cowen, R. K. in *Ecology of Coral Reef Fishes: Recent Advances* 149–170

- 487 (Academic press, 2002).
- 488 13. Cowen, R. K. Population Connectivity in Marine Systems. *Oceanography* **20**, 14–
489 21 (2007).
- 490 14. Munday, P. L. *et al.* Climate change and coral reef connectivity. *Coral Reefs* **28**,
491 379–395 (2009).
- 492 15. Kendall, M. S., Poti, M. & Karnauskas, K. B. Climate change and larval-transport
493 in the ocean: Fractional effects from physical and physiological factors. *Glob.*
494 *Chang. Biol.* 1532–1547 (2015). doi:10.1111/gcb.13159
- 495 16. Wilson, L. J. *et al.* Climate-driven changes to ocean circulation and their inferred
496 impacts on marine dispersal patterns. *Glob. Ecol. Biogeogr.* 1–17 (2016).
497 doi:10.1111/geb.12456
- 498 17. Johnston, M. A., Nuttall, M. F., Eckert, R. J. & Embesi, J. A. *Long-Term*
499 *Monitoring at the East and West Flower Garden Banks, 2013 Annual Report.*
500 (2014).
- 501 18. Miller, K. & Mundy, C. Rapid settlement in broadcast spawning corals:
502 implications for larval dispersal. *Coral Reefs* **22**, 99–106 (2003).
- 503 19. Harrison, P. & Wallace, C. in *Coral reef ecosystems* 133–207 (Elsevier, 1990).
- 504 20. Baird, A. H. The ecology of coral larvae: settlement patterns, habitat selection and
505 the length of the larval phase. (James Cook University, 2001).
- 506 21. Tay, Y. C., Guest, J. R., Chou, L. M. & Todd, P. A. Vertical distribution and
507 settlement competencies in broadcast spawning coral larvae: Implications for
508 dispersal models. *J. Exp. Mar. Bio. Ecol.* **409**, 324–330 (2011).
- 509 22. Ritson-Williams, R., Arnold, S. N., Paul, V. J. & Steneck, R. S. Larval settlement
510 preferences of *Acropora palmata* and *Montastraea faveolata* in response to diverse
511 red algae. *Coral Reefs* **33**, 59–66 (2014).
- 512 23. Vermeij, M., Fogarty, N. & Miller, M. Pelagic conditions affect larval behavior,
513 survival, and settlement patterns in the Caribbean coral *Montastraea faveolata*.
514 *Mar. Ecol. Prog. Ser.* **310**, 119–128 (2006).
- 515 24. Darwin, C. *On the origin of species by means of natural selection, or the*
516 *preservation of favoured races in the struggle for life. A facsimile of the first*
517 *edition with an introduction by Ernst Mayr.* (Harvard University Press., 1859).

- 518 25. Lugo-Fernández, A., Deslarzes, K. J. P., Price, J. M., Boland, G. S. & Morin, M.
519 V. Inferring probable dispersal of Flower Garden Banks coral larvae (Gulf of
520 Mexico) using observed and simulated drifter trajectories. *Cont. Shelf Res.* **21**, 47–
521 67 (2001).
- 522 26. Davies, S. W., Matz, M. V. & Vize, P. D. Ecological complexity of coral
523 recruitment processes: effects of invertebrate herbivores on coral recruitment and
524 growth depends upon substratum properties and coral species. *PLoS One* **8**,
525 e72830 (2013).
- 526 27. Sponaugle, S. *et al.* Predicting Self-Recruitment in Marine Populations :
527 Biophysical Correlates and Mechanisms. *Bull. Mar. Sci.* **70**, 341–375 (2002).
- 528 28. Foster, N. L. *et al.* Connectivity of Caribbean coral populations: complementary
529 insights from empirical and modelled gene flow. *Mol. Ecol.* **21**, 1143–57 (2012).
- 530 29. Cowen, R. K. & Sponaugle, S. Larval dispersal and marine population
531 connectivity. *Ann. Rev. Mar. Sci.* **1**, 443–466 (2009).
- 532 30. Galindo, H. M., Olson, D. B. & Palumbi, S. R. Seascape Genetics: A Coupled
533 Oceanographic-Genetic Model Predicts Population Structure of Caribbean Corals.
534 *Curr. Biol.* **16**, 1622–1626 (2006).
- 535 31. Kough, A. S. & Paris, C. B. The influence of spawning periodicity on population
536 connectivity. *Coral Reefs* **34**, 753–757 (2015).
- 537 32. Oey, L., Ezer, T. & Lee, H. Loop Current, rings and related circulation in the Gulf
538 of Mexico: A review of numerical models and future challenges. *Circ. Gulf Mex.*
539 *Obs. Model.* **161**, 31–56 (2005).
- 540 33. Alvera-Azcárate, A., Barth, A. & Weisberg, R. H. The Surface Circulation of the
541 Caribbean Sea and the Gulf of Mexico as Inferred from Satellite Altimetry. *J.*
542 *Phys. Oceanogr.* **39**, 640–657 (2009).
- 543 34. Berger, T. J. Louisiana-Texas Shelf Physical oceanography Program Eddy
544 Circulation Study. **I**, 1992–1995 (1997).
- 545 35. Chang, Y. L. & Oey, L. Y. Why does the Loop Current tend to shed more eddies
546 in summer and winter? *Geophys. Res. Lett.* **39**, 1–7 (2012).
- 547 36. Taylor, P., Lindo-atichati, D., Bringas, F. & Goni, G. International Journal of
548 Remote Loop Current excursions and ring detachments during 1993 – 2009. 37–41

- 549 (2013).
- 550 37. Sanvicente-Añorve, L., Zavala-Hidalgo, J., Allende-Arandía, M. & Hermoso-
551 Salazar, M. Connectivity patterns among coral reef systems in the southern Gulf of
552 Mexico. *Mar. Ecol. Prog. Ser.* **498**, 27–41 (2014).
- 553 38. Johnson, D. R., Perry, H. M. & Lyczkowski-Shultz, J. Connections between
554 Campeche Bank and Red Snapper Populations in the Gulf of Mexico via Modeled
555 Larval Transport. *Trans. Am. Fish. Soc.* **142**, 50–58 (2013).
- 556 39. Harrison, P. L., Dalton, S. J. & Carroll, A. G. Extensive coral bleaching on the
557 world's southernmost coral reef at Lord Howe Island, Australia. *Coral Reefs* **30**,
558 775 (2011).
- 559 40. Thomson, D. P., Bearham, D. & Graham, F. High latitude, deeper water coral
560 bleaching at Rottneest Island, Western Australia. *Coral Reefs* **30**, 1107 (2011).
- 561 41. Palumbi, S. R. Population genetics, demographic connectivity, and the design of
562 marine reserves. *Ecol. Appl.* **13**, 146–158 (2003).
- 563 42. Palandro, D. A. *et al.* Quantification of two decades of shallow-water coral reef
564 habitat decline in the Florida Keys National Marine Sanctuary using Landsat data
565 (1984-2002). *Remote Sens. Environ.* **112**, 3388–3399 (2008).
- 566 43. Donahue, S. *et al.* *The State of Coral Reef Ecosystems of the Florida Keys. The*
567 *state of coral reef ecosystems of the United States and Pacific Freely Associated*
568 *States: 2008.* (eds Waddell JE, Clarke AM) (2005). at
569 <<http://ccma.nos.noaa.gov/ecosystems/coralreef/coral2008/pdf/FloridaKeys.pdf>>
- 570 44. Muslic, A. *et al.* *Linear Extension Rates of Massive Corals from the Dry Tortugas*
571 *National Park (DRTO), Florida.* (2013).
- 572 45. Marshall, D. J., Monro, K., Bode, M., Keough, M. J. & Swearer, S. Phenotype-
573 environment mismatches reduce connectivity in the sea. *Ecol. Lett.* **13**, 128–40
574 (2010).
- 575 46. Wagner, D. E., Kramer, P. & Woesik, R. Van. Species composition, habitat, and
576 water quality influence coral bleaching in southern Florida. *Mar. Ecol. Prog. Ser.*
577 **408**, 65–78 (2010).
- 578 47. Davies, S. W., Meyer, E., Guermond, S. M. & Matz, M. V. A cross-ocean
579 comparison of responses to settlement cues in reef-building corals. *PeerJ* 1–20

- 580 (2014). doi:10.7717/peerj.333
- 581 48. Kool, J. T. & Nichol, S. L. Four-dimensional connectivity modelling with
582 application to Australia's north and northwest marine environments. *Environ.*
583 *Model. Softw.* **65**, 67–78 (2015).
- 584 49. Chassignet, E. P. *et al.* The HYCOM (HYbrid Coordinate Ocean Model) data
585 assimilative system. *J. Mar. Syst.* **65**, 60–83 (2007).
- 586 50. Vize, P. D., Embesi, J. a., Nickell, M., Brown, D. P. & Hagman, D. K. Tight
587 temporal consistency of coral mass spawning at the Flower Garden Banks, Gulf of
588 Mexico, from 1997-2003. *Gulf Mex. Sci.* **23**, 107–114 (2005).
- 589 51. Szmant, A. M. Reproductive ecology of Caribbean reef corals. *Coral Reefs* **5**, 43–
590 53 (1986).
- 591 52. Szmant, A. M., Weil, E., Miller, M. W. & Colon, D. E. Hybridization within the
592 species complex of the scleractinian coral *Montastraea annularis*. *Mar. Biol.* **129**,
593 561–572 (1997).
- 594

595 **Author Contributions**

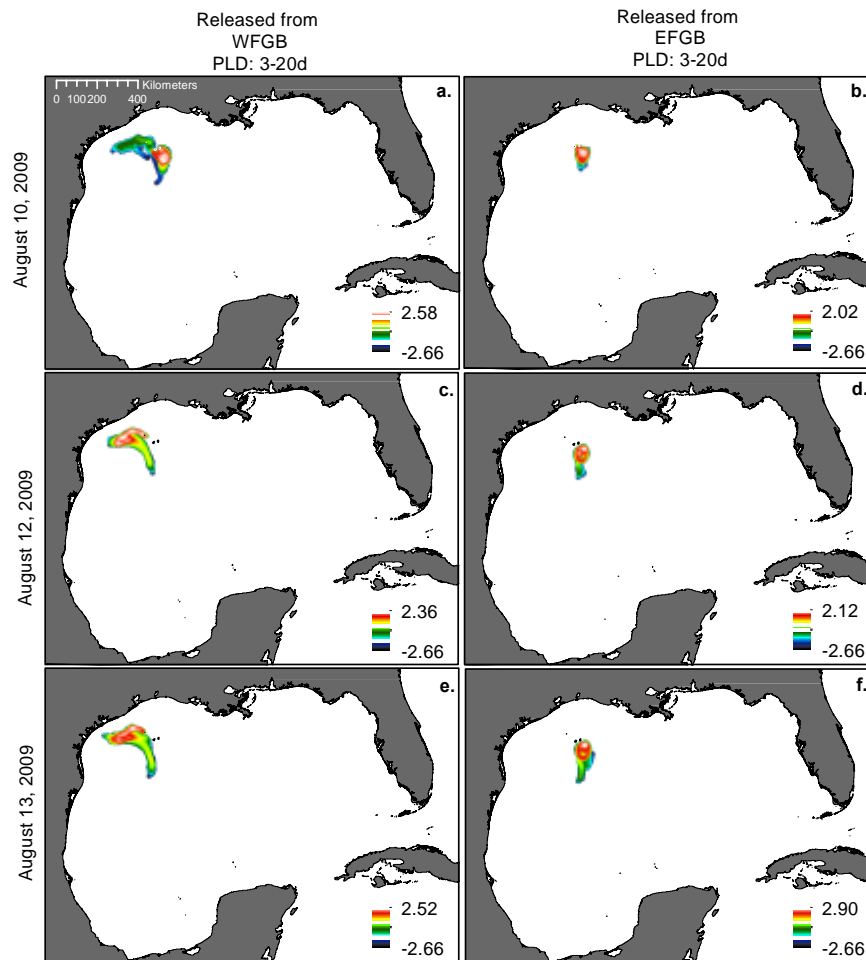
596 SWD and JTK conceived the study. Data was collected by SWD and CDK. Data was

597 analyzed by SWD and MES. All authors wrote and reviewed the manuscript.

598 Acknowledgements

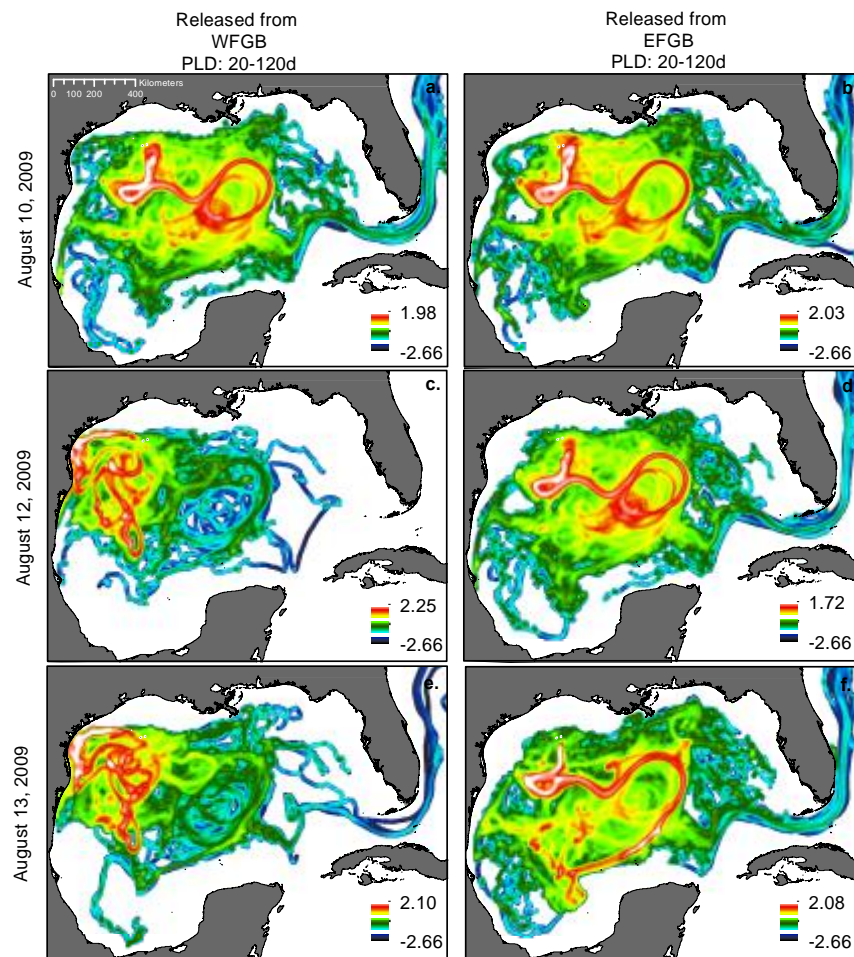
599 We are grateful to the staff and volunteers at the Flower Garden Banks National Marine
600 Sanctuary (FGBNMS) for providing boat time, field assistance and permits across several
601 coral spawning field seasons. Thanks to Eli Meyer for assistance in the field. We
602 acknowledge Thanapat Pongwarin and Sarah Guermond for their assistance in the
603 laboratory measuring life history traits. In addition, we acknowledge ARCCoE for the
604 opportunity to initiate this collaborative study. This research was funded in part by the
605 PADI Foundation Grant to S.W.D. Computing resources were provided by Australia's
606 National Computational Infrastructure (NCI). JK publishes with the permission of the
607 Chief Executive Officer of Geoscience Australia.

608 **Supplemental Figures and Tables**



609
610
611
612
613
614
615

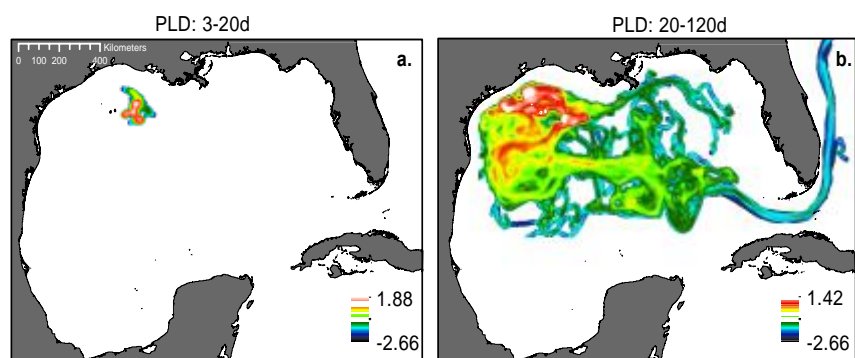
Supplementary Figure 1: Surface heatmaps of larval particle dispersal from West (A, C, E) and East (B, D, F) Flower Garden Banks, TX in 2009. Images show the density of larval particles for a 12-km radius around a 1-km cell, integrated over 3-20 days after release. Particle density displayed on a \log_{10} scale. (A-B) particles were released on August 10, 2009. (C-D) particles were released on August 12, 2009. (E-F) particles were released on August 13, 2009.



616
617
618
619
620
621
622
623

Supplementary Figure 2: Surface heatmaps of larval particle dispersal from West (A, C, E) and East (B, D, F) Flower Garden Banks, TX in 2009. Images show the density of larval particles for a 12-km radius around a 1-km cell, integrated over 20-120 days after release. Particle density displayed on a \log_{10} scale. (A-B) particles were released on August 10, 2009. (C-D) particles were released on August 12, 2009. (E-F) particles were released on August 13, 2009.

624



625

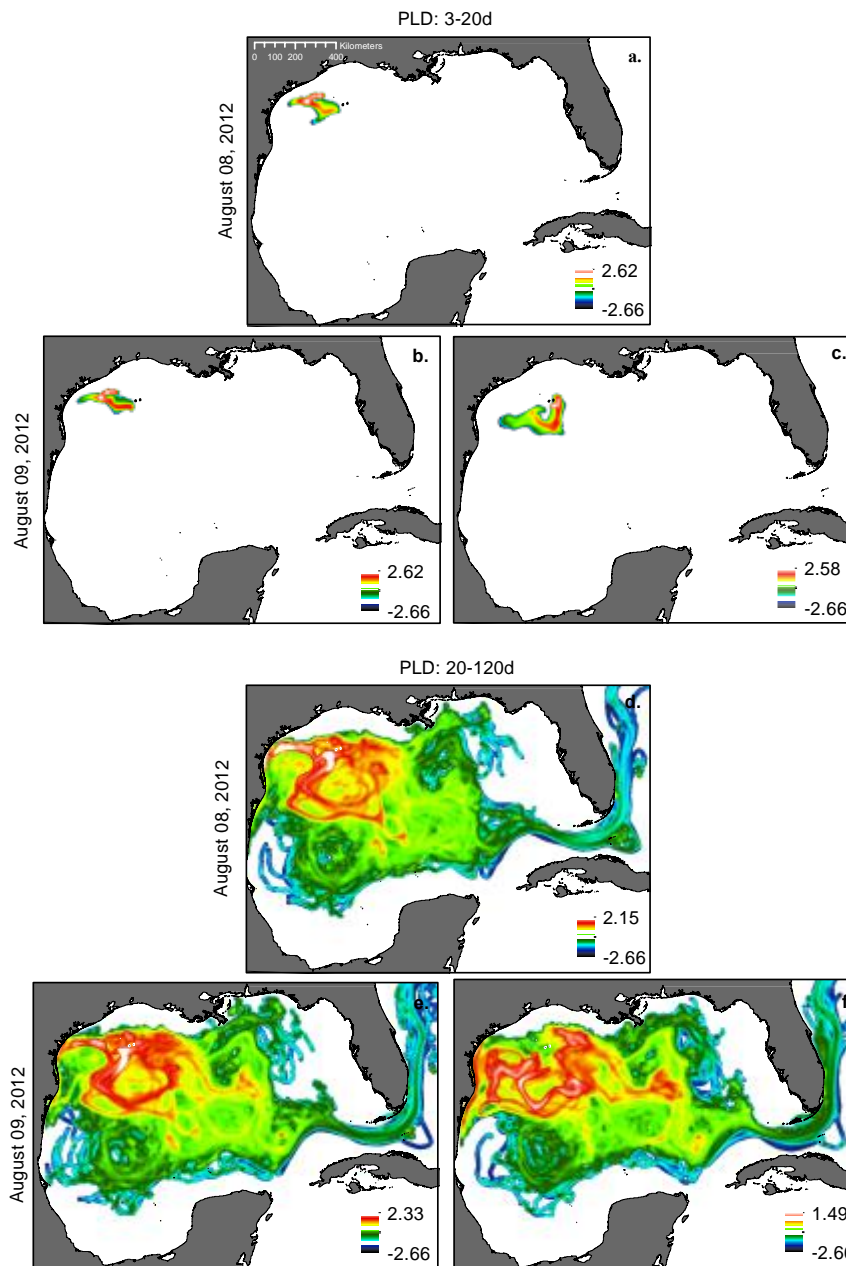
626

627

628

629

Supplementary Figure 3: Surface heatmaps of larval particle dispersal from East Flower Garden Banks on August 30, 2010. Images show the density of larval particles for a 12-km radius around a 1-km cell, integrated over 3-20 days (A) and 20-120 days (B) after release. Particle density displayed on a log₁₀ scale.



630
631
632
633
634

Supplementary Figure 4: Surface heatmap of larval particle dispersal from West (A, C, D, E) and East (C, E) Flower Garden Banks, TX in 2012. Images show the density of larval particles for a 12-km radius around a 1-km cell, integrated over 3-20 days (A, B, C) and 20-120 days (D, E, F) on August 8 (A-C) and August 9 (D-E) 2012.

635 Supplemental Table 1: Reproductive output estimated for both *Pseudodiploria strigosa*
636 and *Orbicella franksi* for both the East and West Flower Garden Banks. Total area of
637 WFGB reef cap <150ft deep is 1.4E+6 m² and total area of EFGB reef cap <150ft deep is
638 3.17E+6 m² ¹⁷. Eggs per polyp were estimated at 270/cm² (90 per polyp x 3 polyps/cm²)
639 for *Orbicella franksi* and 352/cm² (8 eggs/gonad x 22 gonads/polyp x 2 polyps/cm²) for
640 *Pseudodiploria strigosa*.

	% Cover	Area (m ²)	Eggs/m ²	Total eggs
WFGB				
<i>P. strigosa</i>	9.60	1.34E+05	3.52E+04	4.73E+09
<i>O. franksi</i>	26.90	3.77E+05	2.70E+04	1.02E+10
EFGB				
<i>P. strigosa</i>	8.2	2.60E+05	3.52E+04	9.15E+09
<i>O. franksi</i>	27.56	8.74E+05	2.70E+04	2.36E+10

641