

1 *Short title*

2 Experimental density-dependent immigration

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5 *Full title*

6 Immigration rates during population density reduction in a coral reef fish

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18 **Abstract**

19 Although the importance of density-dependent dispersal has been recognized in theory, few
20 empirical studies have examined how immigration changes over a wide range of densities.
21 In a replicated experiment using a novel approach allowing within-site comparison, we
22 examined changes in immigration rate following the gradual removal of territorial
23 damselfish from a limited area within a much larger patch of continuous habitat. In all sites,
24 immigration occurred at intermediate densities but did not occur before the start of
25 removals and only rarely as density approached zero. In the combined data and in 5 of 7
26 sites, the number of immigrants was a hump-shaped function of density. This is the first
27 experimental evidence for hump-shaped, density-dependent immigration. This pattern may
28 be more widespread than previously recognized because studies over more limited density
29 ranges have identified positive density dependence at low densities and negative density
30 dependence at high densities. Positive density dependence at low density can arise from
31 limits to the number of potential immigrants and from behavioral preferences for settling
32 near conspecifics. Negative density dependence at high density can arise from competition
33 for resources, especially high quality territories. The potential for non-linear effects of local
34 density on immigration needs to be recognized for robust predictions of conservation
35 reserve function, harvest impacts, pest control, and the dynamics of fragmented
36 populations.

37 **Key-words:** Conspecific attraction, density dependence, harvest theory, metapopulation,
38 Pomacentridae, protected area, spillover

39 **Introduction**

40 The connection between density and dispersal has important implications for ecology,
41 evolution, and behavior [1–5]. Over long distances, density-dependent dispersal can
42 influence range expansion and the extinction and colonization of patches [4,6]. When
43 dispersal involves localized movements within populations, density dependence can affect
44 other density-dependent processes such as reproduction, growth, and mortality. In addition,
45 it can affect source-sink dynamics, the function of conservation reserves and reintroduction
46 programs, and the control of pests and invasive species, for example, compensating for
47 localized mortality and increasing movements of animals from protected to harvested areas
48 [7–12].

49 Numerous empirical studies provide evidence for an association between emigration
50 rate and population density [13,14]. However, the broader relationship between local
51 density and dispersal is not well understood, in part because both theoretical and empirical
52 investigations have tended to focus on emigration. The effects of density on the equally
53 important movement and immigration stages of the dispersal process have been largely
54 ignored [5,13,15]. The substantial literature examining the influence of conspecifics on the
55 number of individual marine fish and invertebrate larvae that enter local populations from
56 the plankton [16–18] appears to be an exception. However, this literature has only limited
57 application to questions of density-dependent immigration because the number of
58 individuals arriving (called 'settlement' in this literature) often cannot be distinguished from
59 the number surviving to some early stage ('recruitment'), which itself is often density-
60 dependent [18].

61 Immigration may increase as density increases if Allee effects [19] occur or if
62 conspecific abundance provides an indication of habitat quality [20]. On the other hand,
63 immigration may decrease as density increases because higher densities result in lower *per*
64 *capita* resource availability or lower quality of locations available for settlement [21]. Since
65 the benefits of increasing density are more likely when densities are relatively low and the
66 costs of increasing density are more likely when densities are relatively high, a hump-
67 shaped relationship between immigration and density may be expected when density varies
68 over a broad range [22]. Alternatively, density might have no influence on immigration (*i.e.*
69 density independence) if animals are unable to assess density or resource availability, if
70 populations never approach carrying capacity, if Allee effects are unimportant, or if
71 immigration rate is limited by the availability of potential immigrants.

72 Empirical evidence to indicate whether immigration rate shows a hump-shaped
73 response to density is sparse. Only a few field studies have examined immigration rate over
74 a sufficient number and range of density levels to detect a hump-shaped pattern, if one were
75 present [22–30]. Some studies have presented immigration rate data only after dividing by
76 the number of residents, potentially obscuring lower immigration to sites with fewer
77 residents (discussed below). Finally, almost no studies have used a replicated, experimental
78 design to control for potentially confounding correlates of density and immigration such as
79 habitat quality, functional connectivity, and immigrant availability [22,24,27].

80 In the present study, we examine whether adults of two small, interspecifically
81 territorial coral reef damselfishes show density-related variation in local immigration in
82 response to the experimental manipulation of density from saturation to complete absence

83 of conspecifics. On 7 sites surrounded by suitable, occupied habitat, we repeatedly removed
84 a small, constant proportion of fish, continuing until no fish remained and immigration
85 ceased. Previously, using data from this experiment, we showed that the total number of
86 immigrants arriving over the entire experimental period was influenced by inter-site
87 differences in the availability of potential immigrants in adjacent areas and by the relative
88 habitat quality between the depletion and source areas but not by differences in landscape
89 connectivity [31]. Two control sites had almost no immigration during equivalent
90 observation periods. Here, we examine the number of immigrants arriving after each
91 removal event to ask how immigration rate within sites changes in response to the gradual
92 reduction of density.

93 **Methods**

94 **STUDY SPECIES**

95 Adult and subadult longfin *Stegastes diencaeus* and dusky damselfish *S. adustus* (formerly
96 *S. dorsopunicans*), hereafter ‘damselfish’, of both sexes defend small (about 1 m²)
97 territories on dead coral substrate. These territories provide food (benthic algae), shelter
98 holes, and nest sites for males [31,32], and there are no non-territorial ‘floaters’. Because
99 they are diurnal, active, conspicuous, and occur at high density, they are well suited for
100 studies of immigration. Their fringing reef habitat is a naturally fragmented landscape in
101 which continuous reef and patches of various sizes are separated by a matrix of sand and
102 rubble. Damselfish seldom move far from solid reef substrate, so sand and rubble patches
103 form partial barriers to movement within a reef [33]. Dispersal occurs at two life history
104 stages and spatial scales. After hatching from eggs guarded by males, larvae disperse in the

105 plankton, later settling on the reef as small juveniles. Thus, individuals are unlikely to be
106 closely related to their neighbors, and genetic differentiation is unlikely over relatively
107 large spatial scales [34]. Upon reaching adult size, mortality rate is low, and spontaneous
108 moves are rare [35]. Nevertheless, damselfish relocate quickly in response to vacancies in
109 higher quality habitat [35,36]. This local dispersal or ‘home range relocation’ of adult and
110 subadult individuals, almost certainly from within the same fringing reef and likely from
111 relatively close territories, is the focus of our study. It is similar to the within-patch
112 dispersal of many mammals and birds [30,37,38]. In our study area, adult territories are
113 contiguous on suitable substrate, with their number and spatial extent relatively stable over
114 the annual cycle as well as between years (K. Turgeon, *unpublished data*), as also noted for
115 other territorial damselfishes [39,40]. Stable densities and distributions suggest that these
116 populations are close to saturation on fringing reefs in Barbados.

117 **REMOVAL EXPERIMENT**

118 Our study design mimicked a situation in which localized predation or human exploitation
119 created an attractive sink for immigrants from surrounding source areas that were not
120 subject to the same mortality. To the best of our knowledge, this approach has not been
121 used in previous studies of density-dependent immigration. Although repeated removals
122 may reduce the number of potential immigrants, examining the density-immigration
123 relationship during gradual depletion provides a rare opportunity to examine immigration
124 over a broad range of densities while holding other ecological features constant, as well as
125 providing insight into the impacts of localized harvest and pest removal on dispersal.

126 We conducted the experiment on seven experimental and two control sites in the
127 spur and groove zones of five fringing reefs [experimental: Bachelor Hall (1), Heron Bay
128 (4), Sandy Lane (2); control: North Bellairs (1), South Bellairs (1), S1 Fig.] along the west
129 coast of Barbados ($13^{\circ}10'N$, $59^{\circ}38'W$). Each site consisted of a rectangular depletion area
130 of about 150 m^2 within the much larger spur and groove zone of the fringing reef. We
131 defined a 10-m wide band around the depletion area as a source area for potential
132 immigrants, based on the distances of extraterritorial forays which could serve to detect
133 vacant territories [31,41,42]. We selected experimental sites so that the depletion areas
134 were similar in number of residents, total area, and area of hard substrate (S1 Table). Using
135 natural variation in the shapes of the reefs, we selected source areas to vary in abundance of
136 potential immigrants, quality of the habitat and landscape connectivity [S1 Table; see Fig.
137 S1 in [31] for examples].

138 In the depletion area at each experimental site, we marked all resident damselfish >
139 5 cm (total length) with visible implant elastomer (Northwest Marine Technology, Shaw
140 Island WA, USA) and mapped their territories. Experimental sites were observed at 2 or 3-
141 day intervals for two weeks prior to removal. Then, every 2 or 3 days, we removed a
142 constant number of randomly selected individuals, including both residents and the
143 immigrants that had replaced previously removed residents, equal to about 15% of the
144 original population (i.e., 7 - 10 individuals per event, depending on the number of
145 residents). In one case (site HB1), the sequence was delayed for several days by a
146 hurricane. The day after each removal, we mapped all occupied territories in the depletion
147 area, noting the presence of immigrants (untagged individuals). Approximately 30 hours

148 was considered sufficient to achieve a new equilibrium because about 90% of
149 recolonisations in both species occurred by the end of observations on the second day.
150 Previous studies also found that territory recolonisation in damselfishes often occurs within
151 one day [35,36,43]. Removals continued until no fish remained and immigration had ceased
152 for at least 6 days. (In 2 sites, a single, small individual could not be captured.) Complete
153 trials required approximately five weeks, depending on immigration rate. In the source
154 area, we counted all damselfish > 5 cm once but for logistical reasons were not able to
155 monitor changes in density or position at each removal event. Because of the intensity of
156 data collection, we were able to conduct only one trial at a time. Trials took place between
157 April and September 2005-2007.

158 ETHIC STATEMENT

159 Fish removal was needed to determine if movement occurs when the density is reduced.
160 Prior to the experiment, specimens were marked with an injection of a small amount of
161 inert elastomer under the scales (VIE tag - Northwest Marine Technologies). The tagging
162 procedures required less than 30 s to perform and mortality from this method of tagging is
163 extremely low. To reduce fish stress of these two highly territorial species, we marked them
164 underwater, without anaesthesia, near the site of capture so that they can return to their
165 territories quickly. During the removal experiment, fish were removed using cast nets
166 whenever possible. When cast nets were not successful, we used micro-spearfishing. After
167 capture, fish were immediately euthanized using an overdose of carbon dioxide prepared by
168 dissolving antacid powder (Eno, approx. 5g/L) in sea water. The effects of this localized
169 fish removal on the population and community are similar to the harvest effect produced by

170 fisheries and were expected to have modest effects on competition and predation. Our
171 research complied with the ABS/ASAB Guidelines for the Treatment of Animals in
172 Behavioral Research and Teaching and was approved by the McGill University Animal
173 Care Committee, Animal Use Protocol 5039. Field work did not involve endangered or
174 protected species. No specific permissions were required to harvest these two damselfish
175 species in Barbados.

176 DATA ANALYSIS

177 *Scaling immigration rate*

178 We carried out separate analyses of immigration rate using per site scaling (total number of
179 immigrants arriving on the site following each removal event), per new vacancy scaling
180 (number of immigrants/number of damselfish removed at each event), and *per capita*
181 scaling (number of immigrants/number of damselfish present following each removal
182 event). Per site scaling provides the most direct measure of immigrant movement and is
183 equivalent to per unit area scaling. We included per new vacancy scaling because territory
184 availability was the limiting resource and relating immigration to vacancies was therefore
185 likely to illuminate the processes involved [e.g., [25]]. Because 92% of all immigrants ($n =$
186 122) settled on territories from which the owner had been removed during the immediately
187 preceding event rather than during previous removal events, we scaled to the number of
188 new vacancies rather than total vacancies. Even though removal of a constant number of
189 damselfish at each event means that per site and per new vacancy scaling would produce
190 similar patterns over most of the density range, important variation could occur at low
191 densities where the total number of remaining damselfish was less than the number to be

192 removed. *Per capita* scaling was included for completeness because demographic rates,
193 including emigration and immigration, are normally scaled to the population size in
194 analyses of density dependence [44]. However, it is important to recognize that relating
195 immigrants per damselfish to number of damselfish is an example of spurious correlation
196 (Y/X vs. X) that can produce a negative correlation even if immigration rate per site does
197 not change with density [45]. This is referred to as ‘apparent’ or ‘pseudo-density
198 dependence’ [18]. For per site scaling, we included data on immigration before the start of
199 removal as well as data after the number of residents had been reduced to zero. Per vacancy
200 scaling could not include data before any fish had been removed and *per capita* scaling
201 could not include data after density had been reduced to zero, because the values were
202 undefined.

203 *Statistical analyses*

204 To assess density dependence of immigration, we used curve-fitting analyses to compare
205 the fit of 6 alternative functions for each site and then examined the generality of the
206 pattern with Generalized Additive Mixed effect Models (GAMM) on the combined dataset.
207 Both analyses examined the relationship between the total number of damselfish still
208 present on each site after each removal event, including both residents and earlier
209 immigrants (independent variable), and the number of immigrants arriving at the site
210 between that removal and the subsequent count (dependent variable). For the independent
211 variable, number of damselfish was equivalent to density because area was constant within
212 sites. For the dependent variable, we scaled the number of immigrants in three ways to
213 facilitate interpretation as described above. We combined both species for this analysis

214 because territories were defended interspecifically, because there was too much variation in
215 relative numbers of the two species between sites and between removal events for separate
216 analyses by species, and because a preliminary analysis did not indicate an effect of species
217 on the response to density (K. Turgeon, *unpublished analysis*).

218 For each site, we compared the fit of six alternative functions corresponding to
219 density independence, linear negative or positive density dependence, exponential negative
220 or positive density dependence, saturating positive density dependence, and two functions
221 that can model a hump-shaped combination of negative and positive density dependence
222 (Table 1). Including alternative functions (linear and exponential for monotonic functions,
223 polynomial and Ricker for hump-shaped relationships) allowed greater flexibility in the fit.
224 The saturating positive density-dependent function addressed the potential for immigration
225 to be constant and then drop at lower density as the source became depleted. Parameters for
226 each function were estimated with maximum likelihood approach with the mle2 function
227 (normal probability distribution) available on the bbmle package version 1.0.4.1 [46]. To
228 compare the support of each function to explain observed immigration, we used the
229 Information Theoretic Approach [47]. We used Akaike's Information Criterion modified for
230 small sample sizes (AICc) to assess the fit of each function to observed data. Lower AICc
231 values indicated a better fit. We calculated the difference between AICc for each model i
232 and the lowest observed AICc (ΔAICc) and compiled normalized Akaike weights (w_i) the
233 probability that function i is the best function, given the data and set of candidate functions
234 [48]. For each site, we also computed the “evidence ratio” to compare the relative

235 likelihood of any two functions (w_i/w_j ; [48]). To determine the best function overall, we
236 calculated the mean Akaike weights (mean w_i) for each function.

237 **Table 1.** Alternative functions fit to the data relating immigration (I_t) to the number of
238 damselfish remaining on the site (D_t) following each removal event, where a and b are
239 estimated parameters. For per site scaling, I_t equaled the total number of immigrants arriving
240 on the site between the removal and the subsequent count. For per new vacancy scaling, I_t
241 equaled the total number of immigrants arriving on the site between the removal and
242 subsequent count divided by the number of damselfish removed. For *per capita* scaling, I_t
243 equaled the total number of immigrants arriving on the site between the removal and the
244 subsequent count divided by the number of damselfish remaining immediately after the
245 removal.

Function	Pattern
$I_t = b$	1) Density independent
$I_t = aD_t + b$	2) Linear negative or positive density dependence
$I_t = ae^{-bD_t}$	3) Exponential negative or positive density dependence
$I_t = a(1 - e^{-bD_t})$	4) Saturating positive density dependence
$I_t = -aD_t^2 + bD_t$	5) Quadratic polynomial (hump-shaped)
$I_t = aD_t e^{-bD_t}$	6) Ricker (hump-shaped)

246 For the combined analysis, we used Generalized Additive Mixed effects Models
247 (GAMMs) because they combine the utilities of linear mixed models [49] and Generalized
248 Additive Models (GAM; [50] so that random factors, fixed factors and nonlinear predictor
249 variables can all be estimated in the same model. Rather than fitting curves as in the site
250 analysis, GAMMs model nonlinear relationships between density and immigration as a
251 smoothing function. Because of the potential temporal autocorrelation between successive
252 removal events and the risk of violating the assumption of residual independence in
253 interpreting *p*-values, we used an autoregressive correlation structure (corAR1) in the
254 GAMM. Site identity was used as a random factor, and the autocorrelation in error structure
255 was accounted for by nesting the removal event sequence within site. To make sites more
256 comparable, the independent variable was changed from number of damselfish at each
257 removal event to the proportion of the initial number. GAMMs for all three scales were fit
258 using the mgcv package v. 1.7-28 in R [51,52].

259 **Results**

260 Immigration occurred almost exclusively at intermediate densities. It never occurred during
261 the pre-removal period when densities were maximal, but started after the first removal in
262 three sites (SL1, SL2, BH1) and after the second removal in three others (HB3, HB2 and
263 HB4) but only after the sixth removal in HB1 (Fig. 1). After the first occurrence of
264 immigration in each site, immigration followed most subsequent removals until density
265 became very low. In 6 sites, there was no immigration after density was reduced to 0 or to a
266 single uncapturable individual. In 1 site (HB4), 2 individuals arrived after density was

267 reduced to zero the first time. However, most sites did have 1 - 4 immigrants when density
268 was first reduced to 1 or 2 individuals.

269 For per site scaling (*i.e.* the total number of immigrants arriving after each removal
270 event), the curve-fitting analysis of individual sites indicated that the best function was
271 hump-shaped density dependence in 5 sites (Ricker function in 3, polynomial in 2) and
272 density independence in 2 sites (Table 2, Fig. 1). In comparison to density independence,
273 the evidence ratio for density dependence was high (> 56) for 3 sites and moderate (2.6 –
274 3.0) in the other two. On average, the hump-shaped Ricker function provided the best fit as
275 indicated by the mean w_i (Table 2), with a moderate evidence ratio compared to density
276 independence (2.3). The fitted functions indicated that, on average, immigration per site
277 continued to rise until density was less than half the starting density (peaks occurred
278 between 6% – 50% of the starting population, mean = 29%, Fig. 1). For the combined
279 dataset analysis, the GAMM supported a hump-shaped pattern (significance of the
280 smoothing term; $p = 0.014$; Fig. 1). As density decreased, mean immigration rose to a broad
281 peak between about 10 and 40% of the starting population, dropping to a very low level
282 only when density approached zero. These patterns were strongly influenced by but not
283 completely dependent on the very low immigration at zero density; when zero density data
284 were excluded from the analysis, the hump-shaped pattern remained very strong in the
285 GAMM analysis of the combined data and was most likely in 3 individual sites, but density
286 independence became slightly more likely than hump-shaped density dependence in 2 sites
287 for which a hump-shaped function fit best with zero density included (K. Turgeon,
288 unpublished analyses).

289 Table 2. AICc scores (AICc) and Akaike weights (w_i) for each of the six empirical functions predicting the observed number of
 290 immigrants arriving on the site following a removal event in relation to population size of damselfish following that removal
 291 event (site scaling) on seven experimental sites. The mean Akaike weight (Mean w_i) for each function is given at the bottom of
 292 each column. For each site and the mean of all sites, the function with the highest support is indicated by bold w_i . Sites are
 293 ordered as in Fig. 1. See Figure 1 for site abbreviations and Table 1 for the functions.

Site	Density-independent		Linear		Negative exponential		Saturation		Quadratic polynomial		Ricker	
	AICc	w_i	AICc	w_i	AICc	w_i	AICc	w_i	AICc	w_i	AICc	w_i
HB1	32.68	0.000	34.20	0.000	32.96	0.001	37.18	0.000	39.48	0.000	28.20	1.000
HB3	54.76	0.001	54.37	0.001	55.35	0.001	57.87	0.000	60.53	0.000	41.29	0.996
BH1	37.53	0.232	41.24	0.036	41.40	0.053	40.22	0.060	41.16	0.038	35.52	0.702
SL2	52.23	0.011	55.90	0.002	55.90	0.002	51.82	0.014	44.16	0.647	45.54	0.324
SL1	72.48	0.152	75.54	0.033	75.58	0.032	74.06	0.069	70.54	0.400	70.82	0.337

294 Table 2. Continued and concluded

Site	Density-independent		Linear		Negative exponential		Saturation		Quadratic polynomial		Ricker	
	AICc	w _i	AICc	w _i	AICc	w _i	AICc	w _i	AICc	w _i	AICc	w _i
HB2	35.22	0.487	37.38	0.165	37.94	0.125	40.02	0.044	41.14	0.025	37.52	0.154
HB4	49.64	0.623	53.57	0.096	53.57	0.096	53.69	0.090	53.05	0.124	58.55	0.008
Mean w _i		0.215		0.048		0.041		0.040		0.176		0.503

295 For per new vacancy scaling, the best function for individual sites was hump-shaped
296 (Ricker function) in all 5 sites that showed a hump-shaped response in per site scaling and
297 density-independent in the other 2 sites (S2 Table, S2 Fig. black dots and lines). Compared
298 to density independence, the evidence ratio for density dependence was high in 3 sites ($>$
299 10.9) but low at the other 2 (1.3 – 1.5). On average, the Ricker function provided the best
300 fit (Mean w_i ; S2 Table) but was only slightly more likely than density independence
301 (evidence ratio = 1.6). The proportion of new vacancies occupied by immigrants following
302 individual removal events ranged from 0 to 1 but was almost always less than 0.3 (median
303 = 0.25, 95% CI = 0.20 – 0.31, N = 77; S2 Fig. black dots). For the combined dataset
304 analysis, the GAMM supported a hump-shaped relationship between the number of
305 immigrants per new vacancy and the proportion of the initial abundance (significance of the
306 smoothing term; $p = 0.016$; S2 Fig.).

307 For *per capita* scaling, the best-fitting function was density-dependent for all 7 sites
308 (S3 Table, S2 Fig. grey lines and dots). The best function was hump-shaped (Ricker) for
309 the 5 sites that showed hump-shaped relationships with per site and per new vacancy
310 scaling, negative exponential for 1 site that had been density independent with per site and
311 per new vacancy scaling and tied between hump-shaped (Ricker) and negative exponential
312 for the other. The evidence ratio for density dependence (Ricker and negative exponential)
313 compared to density independence was very high (> 100) for 5 sites and moderate and high
314 for the other 2 (2.1, 6.7). On average, the best fit was hump-shaped (Ricker; Mean w_i ; S3
315 Table) with high evidence ratios in comparison to density independence (16.8) and the
316 negative exponential (6.1). For the combined dataset analysis, the GAMM supported a

317 negative relationship between the number of immigrants *per capita* and the proportion of
318 the initial abundance (significance of the smoothing term; $p < 0.001$; S2 Fig.).

319 **Discussion**

320 Patterns of damselfish immigration in response to repeated small removals provided
321 evidence that immigration rate was non-linearly density-dependent with a maximum at
322 intermediate density. This relationship was supported by the GAMM analysis of the
323 combined data, by the presence of immigration at intermediate densities in contrast to the
324 near absence of immigration at the lowest and highest densities at all sites, and by support
325 for a hump-shaped relationship in 5 of 7 individual sites as well as the Akaike weights
326 averaged over all 7 sites. The statistical patterns for individual sites were similar with both
327 site and per new vacancy scaling. This was expected because the number of fish removed at
328 each event was constant for each site over most of the trial. However, although per new
329 vacancy scaling did not allow inclusion of the starting density before the first removal, it
330 did provide additional support by correcting for the limited number of new vacancies
331 generated by removal events at the lowest densities when the number of remaining
332 individuals was less than the prescribed number of individuals to be removed.

333 There was less support for density independence than for hump-shaped density
334 dependence. Density independence, the null hypothesis, was the best fitting model in 2
335 sites, and a good second alternative to hump-shaped functions in two others and in the
336 mean Akaike weights. Note that support for density independence was based not on
337 constant immigration over densities but on variable immigration that was not fit better by
338 any alternative pattern. Because there was only a single trial at each site, we cannot be sure

339 that there are true differences in the pattern of density dependence among sites. We found
340 no consistent relationships between site characteristics and strength of support for a hump-
341 shaped function (K. Turgeon, unpublished analyses). Although other studies have identified
342 spatial variation in immigration rates [24,29], we are not aware of any studies that have
343 examined differences among sites in the patterns of density dependence. Variable patterns
344 in territory availability arising from random selection of damselfish to be removed could
345 explain some of the variation in the fit of alternative functions. For example, removal
346 events in which more of the vacated territories were of high quality, closer to abundant
347 potential source populations, or adjacent to each other early in the sequence would have
348 been likely to favor higher immigration at high densities, thereby reducing support for a
349 hump-shaped pattern. Conversely, a high proportion of poor-quality territories made
350 available in the middle part of the sequence would reduce immigration where high
351 immigration was expected. Whether due to differences in factors influencing density
352 dependence or to the stochastic effects of removal patterns or both, among-site variation in
353 the pattern of density dependence highlights the importance of replication in such dispersal
354 studies, despite the logistical challenges of achieving it.

355 The support for negative density dependence with *per capita* scaling was likely a
356 mathematical artifact. In the two sites in which the density independent function provided
357 the best fit with per site scaling, there was a good fit to the negative exponential with *per*
358 *capita* scaling. Because a negative statistical trend is the expected result of relating Y/X to
359 X when Y shows no relationship to X, this is probably a spurious correlation, sometimes
360 referred to as pseudo-density dependence [18,45]. Apparently, the hump-shaped pattern

361 was sufficiently strong that it still provided the best fit with *per capita* scaling in the other 5
362 sites and in the average for all sites (S3 Table). However, the stronger negative trend
363 resulting from *per capita* scaling is apparent in all sites (S2 Fig.), resulted in increased
364 support for the negative exponential in 2 sites and the average for all sites (S3 Table), and is
365 reflected in the GAMM on the combined data, which indicated a simple negative
366 relationship. This pattern also may have been affected by limitations of the GAMM for
367 modeling the extremely sharp changes. [18], reviewing cases of larval fish recruitment to
368 coral reefs, noted that diverse patterns of positive, negative or neutral density dependence
369 with site scaling all became negative with *per capita* scaling. [30] also found that positively
370 density-dependent immigration of red-backed shrikes to their population became negative
371 with *per capita* scaling. Unlike other demographic variables, the numerator and
372 denominator of *per capita* immigration are derived from different populations,
373 necessitating that patterns be interpreted with caution.

374 Our study provides the first experimental evidence for a hump-shaped relationship
375 between immigration rate and local density. Only three observational studies have also
376 found hump-shaped relationships. Spiny lobsters (*Panulirus argus*) immigrating into
377 marine reserves when disturbed by sport fishing showed a hump-shaped relationship
378 between density in the reserves and immigration per site [28]. Hump-shaped relationships
379 in larval settlement, probably not confounded by post-settlement mortality, have also been
380 reported in barnacles *Semibalanus balanoides* [23] and humbug damselfish *Dascyllus*
381 *trimaculatus* [24].

382 A positive relationship between density and immigration similar to the one we
383 found between low and intermediate densities has been reported in several previous studies.
384 In studies covering a broad density range, density and immigration per site or per vacancy
385 were positively associated in three studies of birds [25,26,30] and in two studies of larval
386 crabs and fishes [22,27]. Studies with a more limited range of densities (often simply
387 presence/absence) also provide evidence for a positive effect of conspecifics in birds
388 (where it is referred to as 'conspecific attraction' and often studied using models and song
389 playback rather than established conspecifics, reviewed by [53], in marine invertebrate
390 larvae (where it is referred to as 'gregarious settlement' reviewed by [16], and in *Dascyllus*
391 damselfish larvae [54–56].

392 Removal experiments on a variety of territorial species suggest that a negative
393 relationship between density and immigration like that we found between intermediate and
394 high densities should be common, but there is relatively little support for this relationship in
395 studies covering a broad density range. Studies designed to test for the presence of a surplus
396 breeding population in territorial birds have often found rapid, complete or partial
397 replacement of removed territory holders [reviewed by [57]]. Similar patterns have been
398 found in some mammals [*e.g.*, [10]], reptiles [*e.g.*, [58]], fishes, including territorial
399 damselfishes (*e.g.*, [59,60]), and insects (*e.g.*, [61]). This suggests that immigration might
400 be proportional to the reduction in density, but direct evidence over a range of densities is
401 limited. An experiment using small juvenile humbug damselfish showed a nonlinear
402 negative relationship [24], although *per capita* scaling makes interpretation difficult. An
403 observational study on song sparrows *Melospiza melodia* immigrating to small islands

404 reported a negative relationship in males but no relationship in females [29]. Two studies of
405 larval fish recruitment covering a broad range of densities found a negative effect of adult
406 density, but the study designs were unable to rule out post-settlement mortality as a factor
407 [62,63]. Among studies with a limited density range, we are aware of only one showing a
408 negative effect of density on larval fish settlement [64]. Thus, the negative trend we
409 observed over most of the density range is only the third example of such a pattern over a
410 broad density range. However, taken together, the literature suggests that both positive and
411 negative trends may occur, suggesting that hump-shaped relationships may be observed
412 more commonly if a sufficiently broad range of densities is studied.

413 The extremely low rate of immigration at very low densities in our study could be a
414 consequence of vacant habitat avoidance (the inverse of conspecific attraction), reduced
415 availability of potential immigrants, or both. If conspecific attraction exerts a powerful
416 influence on habitat selection, individuals might avoid otherwise suitable habitat lacking
417 conspecifics. Conspecific attraction can be favored by selection if the presence or
418 abundance of other individuals indicates higher habitat quality (habitat cueing) or if higher
419 density increases fitness (Allee effect) through improved predator avoidance, increased
420 access to mates, or other benefits [20,65]. Previous studies that found positive correlations
421 between density and immigration per site in nesting birds, spiny lobsters, as well as the
422 settlement and recruitment of marine larvae have attributed the patterns to this phenomenon
423 [22,25,26,28,66]. Allee effects might occur in damselfish because individuals with
424 neighbors are more able to resist intrusions by competing herbivorous parrotfish and
425 surgeonfish [60,67,68]. In addition, isolated damselfish have increased costs of mating and

426 decreased choice because of the risks of longer excursions from their territory, especially if
427 they have to travel over open sand [41,69].

428 An alternative explanation for very low immigration at the lowest densities is
429 depletion of the supply of potential immigrants. Successive removals in the depletion area
430 could reduce the pool of potential immigrants both by lowering the number of fish in the
431 surrounding source areas and by providing more choice of territories for those individuals
432 remaining. If immigrants moving to the depletion area were themselves quickly replaced by
433 others from more distant areas, immigrant depletion effect would be minor, but if
434 individuals were rarely replaced, the consequences could be substantial. Although we were
435 not able to census the potential source populations after each removal during the
436 experiment, we observed that many damselfish remained within 10-m of the borders of the
437 depletion area even after we had removed the last individual. It is possible that these
438 individuals remaining in the source areas were not part of the pool of potential immigrants
439 because their territory quality was already high enough that it could not be improved by
440 relocation. If depletion of potential immigrants had a predominant influence on
441 immigration rate, we would have expected a gradual reduction in immigration rate, with
442 immigration stopping at a range of densities depending on the supply. The observed pattern
443 of a gradual increase in immigration rate with a consistent, abrupt drop to zero only when
444 density was nearly zero suggests that other processes such as avoidance of vacant habitat
445 were involved. Uncertainty about the origin of immigrants is widespread in field studies of
446 density-dependent immigration as is uncertainty about settlement location in studies of density-
447 density-dependent emigration. This uncertainty creates a risk that studies of density-

448 dependent dispersal may be confounded by correlations between source and settlement
449 densities as result of natural spatial and temporal variation and as a result of unrecognized
450 effects of experimental density manipulations on adjacent populations. Thus, improved
451 insights in future dispersal studies may be gained by monitoring both source and settlement
452 populations, despite the substantial logistical challenges of doing so.

453 While competition for a variety of resources could explain the negative relationship
454 between density and immigration that we observed over most of the density range,
455 competition for space seems the most likely in our system. In territorial species, space itself
456 can become limiting when all suitable habitat is occupied and territories cannot be
457 compressed below a minimal size [57,70–72]. Immigration then depends on the re-
458 occupation of the territory of a resident that dies, emigrates, or is physically displaced
459 [32,72,73]. In our study, the very low rate of immigration in control sites and the lack of
460 immigration during pre-removal observations on experimental sites follow this pattern. If
461 neighbors of individuals removed at high densities expand their territories into the
462 unoccupied space before it can be discovered by potential immigrants [74], then
463 opportunities for immigration may be limited until densities are low enough that such
464 expansion provides no additional benefit. Mutual defense in which individuals from several
465 territories simultaneously attack a potential immigrant [75] could reduce the probability of
466 both detecting and occupying a vacancy at high densities [76]. In addition, if vacant
467 territories are more likely to be occupied by nearby individuals [77], then removals early in
468 the removal sequence would be more likely to be taken by residents than by immigrants, as
469 operationally defined in our experiment.

470 Dispersal of post-settlement fish from protected areas to locations where harvesting
471 is allowed, often called ‘spillover’ in the marine fisheries and conservation literature,
472 reduces the protective effect of reserves. It therefore decreases the number of eggs and
473 larvae exported but at the same time provides resources for harvesters outside the reserve
474 [78]. Similar processes have been proposed for terrestrial systems [79]. While spillover can
475 occur through density-independent processes, it has been widely recognized that density-
476 dependent emigration from reserves could enhance spillover [11,80,81]. However, little
477 attention has been given to the potential density-dependence of immigrants settling in
478 harvested areas. Decreasing immigration with decreasing density at low density raises the
479 possibility that excessive harvest outside a reserve might inhibit movement from the
480 reserve. Indeed, conspecific attraction could even induce movement from harvested areas
481 into reserves [11].

482 In conclusion, this study provides evidence that density can strongly affect
483 immigration in complex ways, with both positive and negative correlations occurring at the
484 same site at different levels of density. While some of the possible mechanisms involved
485 may be limited to very local scales (*e.g.*, depletion of potential immigrants) or be restricted
486 to territorial species (*e.g.*, territorial expansion, mutual defense), others are likely to operate
487 at much larger scales and affect populations with other social systems and dispersal patterns
488 (*e.g.*, resource competition, conspecific attraction, and vacant habitat avoidance). For
489 theoretical explorations of metapopulation dynamics, reserve design and dispersal
490 evolution, our results reinforce recent calls for more recognition of density dependence at
491 all stages of the dispersal process [15], as pioneered by [82]. In addition, our results suggest

492 that simple formulations of dispersal probability as either a difference from or proportion of
493 carrying capacity [83] may be inadequate. It is important that empirical studies of dispersal
494 recognize the potential for density dependence in immigration as well as emigration, cover
495 a broad enough density range to detect such complex patterns, and carefully consider the
496 scaling of immigration rates. Localized harvest and pest control programs offer
497 opportunities to undertake such studies through gradual removal. Despite a long history of
498 using removal experiments to address a variety of questions ranging from habitat
499 preference and social organization to population regulation, interspecific competition, and
500 assemblage structure [57,58,61,84–86] and even emigration [87], ours appears to be the
501 first to use this method to examine immigration over a wide range of densities in the field.

502 **Acknowledgements**

503 We are indebted to S. Rouleau, A. Ménard, É. Castonguay, J. Grégoire, A. E. Hall, S.
504 Theleme, A. Robillard, V. Duclos, K. Gotanda and B. Spelke for their help in the field.
505 Thanks to T. Avgar, J. Grant, M. Hixon, R. McLaughlin and R. Warner for valuable
506 comments on previous versions of this manuscript. We also want to thank Bellairs
507 Research Institute and High Tide Watersports for their logistical assistance and support
508 during the field work.

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Figure caption

Figure 1. Relationship between the number of immigrants arriving on a site after a removal event and the number of damselfish remaining following each removal event (site scaling) for each individual site and for all sites combined (upper left panel). Individual sites are ordered by strength of support for a hump-shaped (Ricker or polynomial) function and identified by abbreviations (Bachelor Hall Reef: BH1; Heron Bay Reef: HB1, HB2, HB3, HB4; Sandy Lane Reef: SL1, SL2). Lines represent the best fitting empirical function based on maximum likelihood estimates (MLE) of parameter values. For all sites combined, the abscissa indicates the proportion of the initial number of fish on the site before removal. Each point represents the mean \pm 1 SE of all points falling within bins of 0.1, with density = 0 shown separately. Sample sizes per bin vary depending on replacement rates. The short inside tick marks on the abscissa represent observed proportion values. The black line in the upper left panel represents the significant smoothing term function from a GAMM model and the dashed lines represent the Bayesian credible interval as calculated by the mgcv package v. 1.7-28 in R.

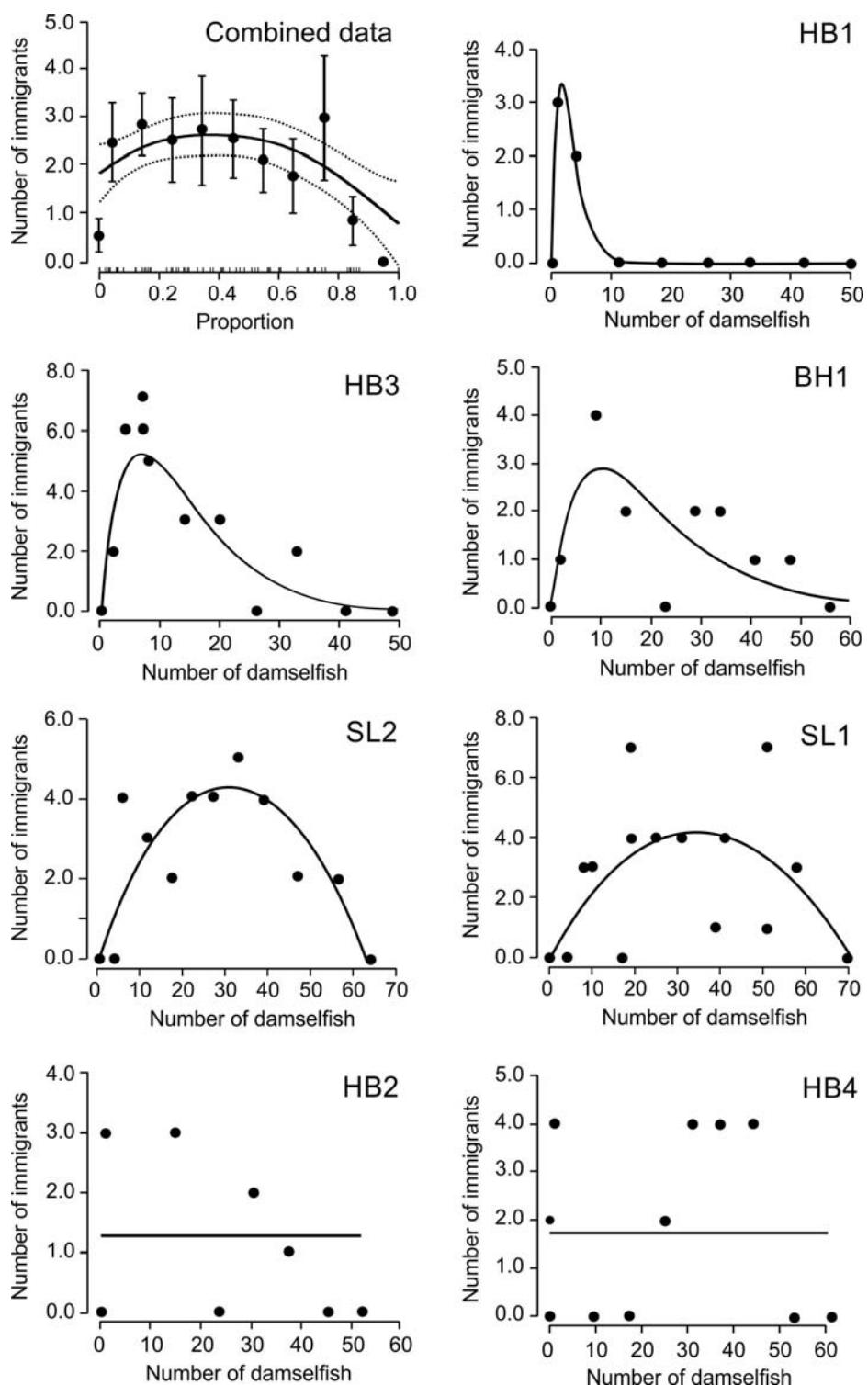


Figure 1.

Supporting Information captions

S1 Figure: Location of experimental and control sites

Location and names of fringing reefs along the west coast of Barbados, West Indies. Reefs are shown as dark green and the area covered by the Barbados Marine Reserve as light blue. On the left, two reefs illustrate the positions of reef zones, with the spur and groove zone used in this study shown in light green.

S1 Table: Habitat variables of the seven sites

Habitat variables of seven sites in which the density of two damselfish species (*Stegastes diencaeus* and *S. adustus*) was manipulated. See Figure 1 for site abbreviations.

S2 Table: Model support (AICc scores) for per new vacancy scaling

Per new vacancy scaling. AICc scores (AICc) and Akaike weights (w_i) for each of the six empirical functions predicting observed immigration rate per new vacancy (number of immigrants/number of damselfish removed in a removal event) in relation to population size following each removal event (not including saturation because new vacancies = 0) on seven experimental sites. Sites are ordered as in Figure 1. The mean Akaike weight (Mean w_i) for each function is given at the bottom of each column. For each site and the mean of all sites, the function with the highest support is indicated by bold w_i . See Figure 1 for site abbreviations and Table 1 for the functions.

S3 Table: Model support (AICc scores) for *per capita* scaling

Per capita scaling. AICc scores (AICc) and Akaike weights (w_i) for each of the six empirical functions predicting observed *per capita* immigration rate (number of immigrants/number of remaining damselfish) in relation to population size following each removal event (excluding population size = 0) on seven experimental sites. The mean Akaike weight (Mean w_i) for

each function is given at the bottom of each column. For each site and the mean of all sites, the function with the highest support is indicated by bold w_i . Sites are ordered as in Figure 1. See Figure 1 for site abbreviations and Table 1 for the functions.

S2 Figure: Relationships between immigration and the number of damselfish for new vacancy and *per capita* scaling

Relationships between immigration (per new vacancy scaling: black dots and lines, left ordinate; *per capita* scaling: grey dots and lines, right ordinate) and the number of damselfish remaining following each removal event for each individual site and for all sites combined (upper left panel). Individual sites are ordered by strength of support for a hump-shaped (Ricker) function and abbreviated as in Fig. 1. Lines represent the best fitting empirical function based on maximum likelihood estimates (MLE) of parameter values. For all sites combined, the abscissa indicates the proportion of the initial number of fish on the site before removal. Each point represents the mean ± 1 SE of all points falling within bins of 0.1, with density = 0 shown separately. Sample sizes per bin vary depending on replacement rates. The short inside tick marks on the abscissa represent observed proportion values. The solid lines in the upper left panel represent the significant smoothing term functions from GAMM models and the dashed lines represent the Bayesian credible intervals.