

Compensatory immigration depends on adjacent population size and habitat quality but not on landscape connectivity

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Summary

1. Populations experiencing localized mortality can recover in the short term by net movement of individuals from adjacent areas, a process called compensatory immigration or spillover. Little is known about the factors influencing the magnitude of compensatory immigration or its impact on source populations. Such information is important for understanding metapopulation dynamics, the use of protected areas for conservation, management of exploited populations and pest control.

2. Using two small, territorial damselfish species (*Stegastes diencaeus* and *S. adustus*) in their naturally fragmented habitat, we quantified compensatory immigration in response to localized mortality, assessed its impact on adjacent source populations and examined the importance of potential immigrants, habitat quality and landscape connectivity as limiting factors. On seven experimental sites, we repeatedly removed 15% of the initial population size until none remained and immigration ceased.

3. Immigrants replaced 16–72% of original residents in *S. diencaeus* and 0–69% in *S. adustus*. The proportion of the source population that immigrated into depleted areas varied from 9% to 61% in *S. diencaeus* and from 3% to 21% in *S. adustus*. In *S. diencaeus*, compensatory immigration was strongly affected by habitat quality, to a lesser extent by the abundance of potential immigrants and not by landscape connectivity. In *S. adustus*, immigration was strongly affected by the density of potential migrants and not by habitat quality and landscape connectivity. On two control sites, immigration in the absence of creation of vacancies was extremely rare.

4. Immigration occurred in response to localized mortality and was therefore compensatory. It was highly variable, sometimes producing substantial impacts on both depleted and source populations. The magnitude of compensatory immigration was influenced primarily by the availability of immigrants and by the potential improvement in territory quality that they could achieve by immigrating and not by their ability to reach the depleted area.

Key-words: Barbados, Caribbean, coral reef, dusky damselfish, harvesting, longfin damselfish, Pomacentridae, protected area, reserve, source-sink dynamics

Introduction

When populations experience localized mortality, net immigration from adjacent source areas often occurs (Pulliam 1988; McCullough 1996). This compensatory immigration can accelerate the restoration of populations partially or completely eliminated by disturbances of natural (Adams & Warren 2005) or anthropogenic origin (Greathouse, March

& Pringle 2005; Albanese, Angermeier & Peterson 2009) and is critical to metapopulation viability (Pulliam 1988; Hanski 1998). Compensatory immigration can benefit harvesters by increasing local yield (McCullough 1996; Gell & Roberts 2003) but also limits the effectiveness of pest control (Nakata & Satoh 1994; Efford, Warburton & Spencer 2000) and reduces the benefits of protected areas (Woodroffe & Ginsberg 1998; Gundersen *et al.* 2001).

Compensatory immigration varies greatly among studies (Table S1), but there is very little information about the

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factors influencing its magnitude or impact on adjacent source populations. From a theoretical perspective, compensatory immigration should be favoured by optimal habitat selection, especially when associated with competition as suggested by the ideal free and ideal despotic distributions (Fretwell & Lucas 1969) and related models. Conversely, immigration may be constrained by factors affecting the detection of lower density patches and the ability to move towards them. The abundance of potential immigrants could affect compensatory immigration. In some situations, all individuals in a source area might be able to move, and in others, only the ones near the boundary, depending on the size of each area, the distance at which density changes or habitat vacancies can be detected (Nakata & Satoh 1994; Efford, Warburton & Spencer 2000) and the mobility of the species (Rakitin & Kramer 1996; Woodroffe & Ginsberg 1998; Albanese, Angermeier & Peterson 2009). Compensatory immigration may also increase with habitat quality in the depleted area relative to habitat quality in potential source areas because more individuals can be accommodated before density-dependent processes reduce habitat quality to that of the surrounding areas (Fretwell & Lucas 1969; MacCall 1990; Delibes, Ferreras & Gaona 2001). In addition, landscape connectivity (Taylor *et al.* 1993), the degree to which the distribution of habitat patches and the quality of the matrix between them allow organisms to detect available openings and move towards them (Kozakiewicz & Jurasínska 1989; Forcada *et al.* 2008), may increase compensatory immigration by allowing a greater proportion of the source population to move.

Most studies providing evidence for compensatory immigration (Table S1) did not have adequate replication to measure the effect of factors potentially influencing compensatory immigration and lacked spatial or temporal controls to estimate baseline immigration in the absence of localized mortality. Furthermore, most studies carried out a single massive removal and did not continue removal until immigration ceased, a procedure required to assess maximal compensatory immigration. The goals of this study were (i) to quantify compensatory immigration in response to localized mortality, (ii) to assess its impact on populations in adjacent unharvested locations and (iii) to assess the importance of potential immigrants, habitat quality and landscape connectivity as factors influencing the magnitude of

compensatory immigration. We applied a repeated, small, localized removal of two damselfish species in their natural coral reef habitat until immigration ceased, and no individuals remained. We used seven sites, each consisting of a depleted area surrounded by an unharvested source area. Sites varied in the number and density of fish in the source area, habitat quality and landscape connectivity. We also monitored two control sites to estimate immigration in the absence of removal.

Materials and methods

STUDY SITE AND SPECIES

Our study was conducted over three consecutive years (2005–2007), from April/May to August/September in the spur and groove zone of five fringing reefs along the west coast of Barbados (13°10'N, 59°38'W). The spur and groove zone is a naturally fragmented landscape characterized by finger-like, seaward extensions of the main reef with numerous small patches of reef separated by inhospitable matrix characterized by sand and rubble beds (Fig. S1). Seven experimental and two control sites consisted of a rectangular depleted area of about 150 m² [mean ± SD (range) = 148 ± 36 (93–215)] surrounded by a 10-m wide adjacent source area of about 900 m² (918 ± 62 (822–994); Fig. S1). Experimental sites were selected so that the number of damselfish [148 ± 36 (93–215)] and the area covered with reef [63.9 ± 13.4% (45.8–84.3%)] in the depleted area were similar. In contrast, sites varied in the abundance and density of damselfish in the source area, relative habitat quality (RHQ) and landscape connectivity between the depleted and source areas (Table 1) to facilitate the examination of the effects of potentially limiting factors.

Stegastes diencaeus and *S. adustus* are well suited to the experimental studies of compensatory immigration. All individuals defend small, contiguous territories on solid substrate against their own and the other species, with populations approaching saturation. They are highly philopatric with low mobility, yet relocate quickly in response to vacancies (Cheney & Côté 2003). Adult *S. diencaeus* are slightly larger (total length; 8.98 ± 1.95 cm, *n* = 443) and more aggressive than *S. adustus* (K. Turgeon, unpublished data), with territories of about 1.1 m² typically in deeper portions of the spur and groove zone. *S. adustus* (7.16 ± 1.04 cm, *n* = 125) have territories of about 0.8 m² in the reef crest and the upper spur and groove zone, partially overlapping with *S. diencaeus*. Other habitat characteristics in the territory differ somewhat between the species (Waldner & Robertson 1980; Tolimieri 1998; Turgeon 2011), and removed individuals are replaced primarily by conspecifics (Turgeon 2011).

Table 1. Measured factors potentially limiting compensatory immigration on seven sites where the density of two damselfish species (*Stegastes diencaeus* and *S. adustus*) was manipulated. Mean ± 1 standard deviation and the range (in parentheses) are presented for each limiting factor

Measured limiting factors	<i>S. diencaeus</i>	<i>S. adustus</i>
Number of potential immigrants	65 ± 51 (9–155)	83 ± 86 (0–257)
Density of potential immigrants (number m ⁻² of reef)	0.20 ± 0.09 (0.04–0.34)	0.25 ± 0.22 (0.00–0.56)
Absolute habitat quality index (cm)	8.74 ± 0.87 (7.75–10.30)	7.16 ± 0.39 (6.73–7.66)
Relative habitat quality index (cm)	0.10 ± 0.94 (–1.20 to 1.19)	0.12 ± 0.25 (–0.15 to 0.56)
Weighted habitat quality index	0.05 ± 1.05 (–1.12 to 1.205)	0.01 ± 0.87 (–1.03 to 1.53)
Area covered with reef in the source area (m ² ; structural connectivity)	300 ± 135 (52–451)	
WPI (weighted proportional index; structural connectivity)	0.36 ± 0.16 (0.08–0.54)	
WPI _B (functional connectivity)	0.22 ± 0.13 (0.01–0.42)	

DAMSELFISH MAPPING AND REMOVAL

Prior to density manipulation, we caught all residents, individuals > 5 cm total length actively defending a territory in the depleted area, using a modified cast net, measured them to the nearest mm, tagged them (VIE tags; Northwest Marine Technology, Shaw Island, Washington, USA) and mapped their distribution. We also estimated the size to the nearest 0.5 cm and mapped the distribution of all potential migrants in the source area. Because the study initially focused on connectivity and was later expanded to consider the populations in the adjacent source area, measurements in source areas for four experimental sites (HB1, HB2, HB3 and HB4) and one control site (NB1) were taken in 2007, 1 or 2 years following the removal or control observations. We assumed that this interval would have provided sufficient time for the adjacent source populations to return to equilibrium and that there would not have been important changes in the distribution between years. Support for this assumption is provided by the depleted areas which, although more severely reduced than the source areas, recovered up to 80% of their initial population sizes after 1 year (mean = 58%; Turgeon, unpublished observations). Natural variation in abundance and distribution of territories from year to year in these two damselfish species is low, as indicated by measurements of the control sites over the subsequent 3 years (Turgeon, unpublished observations).

After a 2-week observation period, experimental removals occurred as a series of events at 2- to 3-days intervals in the morning during which we removed randomly selected residents and immigrants equal to 15% of the initial population. There were 8–14 removal events per site, depending on the number of immigrants. The day after each removal, we mapped all occupied territories in the depleted area and noted which were occupied by immigrants (untagged). After the last individuals were removed from the depleted area, we continued to check sites at 2- to 3-days intervals and remove any damselfish present until no new immigrants had arrived for 6–7 days. Control sites were observed for comparable periods.

MEASUREMENT OF LIMITING FACTORS

Population size and density in the adjacent source area

We assumed that all individuals within 10 m of the depleted area were potential migrants based on distances moved during spontaneous extra-territorial exploratory movements called forays (Bartels 1984). Analysis of 630 forays observed during the study showed that 10 m represented the 98th percentile of foray distances, with broad overlap between the species (K. Turgeon, unpublished data). Because area of solid substrate in the adjacent source area varied, we considered both abundance (total number of individuals) and density (number of individuals/m² of reef) in the source area.

Habitat quality

We used mean damselfish body size as a surrogate for habitat quality in each depleted and source area, based on evidence that larger individuals often obtain preferred territories in many fishes, including damselfishes (Lindström 1992; Cheney & Côté 2003; Markert & Arnegard 2007; Turgeon 2011). We considered three indices of habitat quality. Absolute habitat quality of the depleted area (AHQ; mean body size in the depleted area; mm) represents the attractiveness of the depleted area. Relative habitat quality (mean body size in the depleted area minus mean body size in the source area; mm) represents the difference in quality between depleted and source areas.

Weighted habitat quality (WHQ) represents the potential for combined effects of absolute and relative quality. To calculate WHQ, we *z*-standardized AHQ and RHQ for each species and built 10 models where the weight of AHQ and RHQ varied in 10% increments [e.g. Model 1: WHQ = (0 × AHQ) + (1 × RHQ), Model 2: WHQ = (0.1 × AHQ) + (0.9 × RHQ)] and used the one that best predicted compensatory immigration based on AICc scores (Burnham & Anderson 2002). One site (HB1) did not have *S. adustus* in the source area, so the sample size for RHQ and WHQ was 6 rather than 7 for this species. AHQ and RHQ were moderately to strongly correlated (Pearson correlation coefficients; *S. diencaeus*: 0.49, *S. adustus*: 0.72).

Landscape connectivity indices

We used two indices of landscape structural connectivity (i.e. derived from physical attributes of the landscape) and one of functional connectivity (i.e. derived from movements of individuals through a landscape). All indices assume that damselfish are less likely to move over open sand than over solid reef (Turgeon *et al.* 2010). The simplest structural connectivity index was the percentage of the source area covered by solid reef without considering the size of gaps or distance of damselfish from the harvested area. The second structural connectivity index used the components of a proximity index called the weighted proportion index (WPI; with $B_j = 1$; Appendix S1) and used recently by Winfree *et al.* (2005). WPI uses grid cells instead of habitat patches making it suitable for landscapes where discrete habitat patches are not readily defined and assumes that damselfish movement is limited by sand and distance from the harvested area. We developed a functional connectivity index by extending WPI (Appendix S1) to incorporate the size of sand gaps as barriers to movement based on empirical measurements in *S. diencaeus* (Turgeon *et al.* 2010).

DATA ANALYSIS

We expressed compensatory immigration as per cent of original residents replaced by immigrants [(number of immigrants/number of original residents) × 100] for comparison among sites. Because our sample size was limited and there was heteroscedasticity in habitat quality indices, we built separate sets of models for each species to facilitate interpretation and to avoid multi-way interactions with species as a term. We used a two-step approach to evaluate the relationship between the per cent of original residents replaced by immigrants and the limiting factors. First, we used an information theoretic approach based on Akaike's Information Criterion modified for small sample sizes (AICc; Burnham & Anderson 2002) to evaluate which limiting factors or combination of factors best explained the per cent of original residents replaced by immigrants. Candidate models included all single-term predictors (8 models), possible additive effects, excluding additive effects among predictors in limiting factor classes (e.g. among habitat quality indices) to avoid multicollinearity problems (39 models), and plausible two-way interactions (21 models) for a total of 68 candidate models. We did not explore three way interactions because of our small sample size. Each model was fitted using the glm function in R (Generalized linear model; package stats version 2.12.2, R Development Core Team 2011) with an identity link function and a Gaussian error. For each limiting factor or model, we compiled the normalized Akaike weights (w_i ; Burnham & Anderson 2002) which allows ranking the models based on their likelihood and parsimony. The confidence set of candidate models includes all models for which w_i is within 10% of the

maximum weight (Burnham & Anderson 2002). For each species, the per cent of original resident replaced by migrants, population size, density and AHQ index (predictors) were square-root-transformed, and all predictors were *z*-score-transformed prior to analysis.

To examine the effect size and fit of limiting factors (single-order term, additive and interactive effects) on the per cent of original residents replaced by immigrants, we used a Bayesian approach with a Markov Chain Monte Carlo (MCMC) simulation using Metropolis–Hastings sampling (MH adaptive in R; Chivers 2011). The Bayesian approach is appropriate because the Bayesian credible interval (BCI) estimates obtained from MCMC procedures are unbiased and appropriate when the sample size is small as compared to the maximum likelihood estimation method (Ellison 2004; Gelman 2004). Because we did not have any a priori knowledge on parameter distributions, flat priors for regression coefficients were drawn from a normal distribution with a mean of 0 and a standard deviation (SD) of 100. Priors for the error terms were drawn from a gamma distribution with a mean of 0 and SD of 1. Posterior probability distributions are an alternative to hypothesis testing and *P*-values and provide a direct measure of the degree of belief that can be placed on models and on parameter estimates (Ellison 2004; Gelman 2004). To assure accurate MCMC simulations from the prior distributions, an initial ‘burn in’ of 2000 iterations was performed and discarded from analysis. This was followed by 10 000 iterations for each fitted model. After visual inspection for possible autocorrelation and assessing chain convergence (Brooks–Gelman–Rubin diagnostics; Brooks & Gelman 1998), the mean (mean_{pp}) and SD (SD_{pp}) of the posterior prior distributions of each predictor (representing the regression and variance estimates) and the 95% BCI were calculated. The mean_{pp} and SD_{pp} of the parameters were used to assess the effect size of each predictor. We also used a Bayesian approach to examine whether the per cent of original residents replaced by immigrants, the proportion of the source population that immigrated into the harvested area and the proportion of the biomass in the source area that was extracted in response to localized mortality differed between species.

Results

COMPENSATORY IMMIGRATION AND EFFECTS ON ADJACENT SOURCE POPULATION

Removal of residents was followed by substantial, though variable, immigration by *S. diencaeus* on all sites and by *S. adustus* on two of the seven sites. Even with repeated removal, however, the number of immigrants never exceeded the number of original residents. On the seven experimental sites, there was no immigration during the 2-week period before removal. By the end of the removal treatment, the total number of *S. diencaeus* immigrants varied from 5 to 26 immigrants ($\text{mean} \pm \text{SD} = 15 \pm 8$), resulting in the replacement of 15.6% to 72.2% of original residents (Fig. 1a). The total number of *S. adustus* immigrants ranged from 0 to 20 (6 ± 8), resulting in the replacement of 0% to 69% of original residents (Fig. 1a). There was no strong support for a difference between species in the per cent of original residents replaced ($\text{Mean}_{\text{pp}} \pm \text{SD}_{\text{pp}} = 25.0 \pm 13.4$, $\text{BCI} = -13.0$ to 51.2 , $n = 14$). The contribution of immigrants to the total harvest [(number of immigrants/total number removed) \times 100] ranged from 13.5% to 41.9% in *S. diencaeus* and from

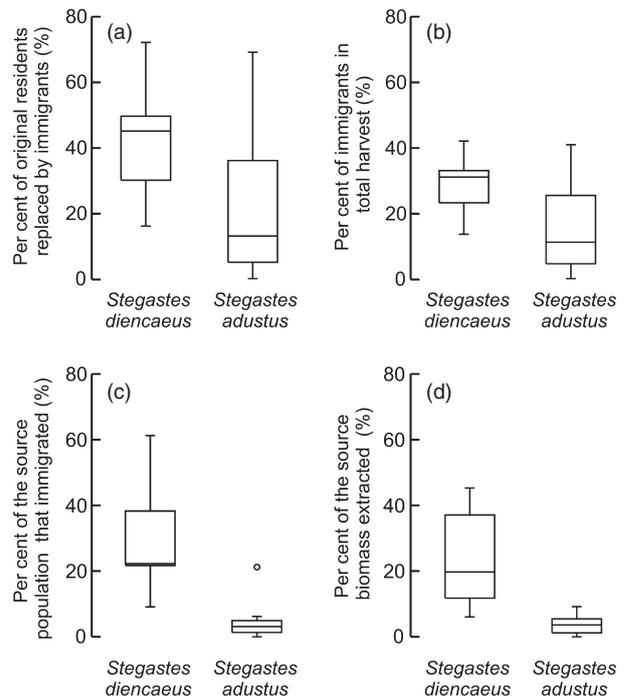


Fig. 1. (a) Per cent of original residents replaced by immigrants, (b) per cent immigrants in total harvest, (c) per cent of the source population that immigrated to the depleted area and (d) per cent of source biomass extracted following compensatory immigration for *Stegastes diencaeus* and *S. adustus*. Horizontal line shows the median, the box represents the 25th and 75th percentiles, the top whisker ranges from the 75th to the 90th percentile and the bottom whisker ranges from the 25th to the 10th percentile.

0% to 40.8% in *S. adustus* (Fig. 1b). There was no strong support for a difference between species in the contribution of immigrants to total harvest (24.7 ± 13.0 , $\text{BCI} = -0.70$ to 50.2 , $n = 14$). Without removal, there was almost no immigration. On the two control sites, we observed immigration of only one *S. diencaeus* and no *S. adustus* immigrants. Two *S. diencaeus* disappeared on control site NB1, and two *S. diencaeus* and one *S. adustus* disappeared on SB1.

Compensatory immigration to the depleted areas had a large impact on the adjacent source populations of *S. diencaeus* and a smaller one on *S. adustus*. The source populations ranged from 0.28 to 5.74 times the size of depleted populations in *S. diencaeus* (1.88 ± 1.84) and from 0.00 to 8.57 times in *S. adustus* (3.79 ± 2.69). In *S. diencaeus*, 9% to 61% of the adjacent source population migrated into the depleted area (Fig. 1c) and in *S. adustus* 3–21% (Fig. 1c). This represented 6% to 45% ($24 \pm 16\%$) of the total biomass in *S. diencaeus* and 2–9% ($4 \pm 3\%$) of the total biomass in *S. adustus* (Fig. 1d). There was strong support for a difference between species in the proportion of the source population that immigrated ($\text{Mean}_{\text{pp}} \pm \text{SD}_{\text{pp}} = 37.3 \pm 10.4$, $\text{BCI} = 16.7$ – 57.8 , $n = 14$) and in the proportion of the total biomass that was extracted from the adjacent source area via compensatory immigration ($\text{Mean}_{\text{pp}} \pm \text{SD}_{\text{pp}} = 30.8 \pm 7.7$, $\text{BCI} = 15.7$ – 45.9 , $n = 14$).

LIMITING FACTORS

Compensatory immigration was limited by habitat quality and possibly by the abundance of potential migrants in *S. diencaeus* and only by density of potential migrants in *S. adustus*. Below, we consider the direction and magnitude of the effects of each limiting factor.

Potential migrants

The per cent of original residents replaced by immigrants increased with both population size and density of conspecifics in the source area for both species. The effect size of population size was similar for both species, but the effect size of density was twice as large for *S. adustus*. The evidence for an effect of population size and density was much stronger for *S. adustus* than for *S. diencaeus* as shown by the 95% BCI (Tables 2 and 3, Fig. 2a,b). In *S. adustus*, density in the source area had extremely high support ($w_i = 0.931$) and was at least 13 times more likely than population size to explain the per cent of original residents replaced by immigrants (Table 3).

Habitat quality

In general, the per cent of original residents replaced by immigrants increased with increasing values of all three habitat quality indices for both species, but the support was much stronger for *S. diencaeus* than for *S. adustus* in which one site with high habitat quality but low immigration exerted a strong effect on the relationship (Tables 2, 3, Fig. 2c,d,e). For *S. diencaeus*, none of the indices included zero within their 95% BCI (Table 2), but WHQ had the highest support and was 42 times more likely than AHQ and 180 times more likely than RHQ to predict per cent of original residents replaced by immigrants, as indicated by w_i values. The weighting that provided the highest AICc scores for WHQ was $0.4 \times \text{RHQ} + 0.6 \times \text{AHQ}$. In *S. adustus*, the three habitat quality indexes performed quite poorly, and all included zero within their 95% BCI (Table 3, Fig. 2c,d,e). The weighting that provided the best WHQ consisted of $0.1 \times \text{RHQ} + 0.9 \times \text{AHQ}$. Site HB4 strongly influenced the relationship (Fig 2c,d,e, Table S2). Without this point, the per cent of original residents replaced by immigrants increased more strongly with increasing habitat quality

Table 2. Effect size of z-scored predictors on the per cent of original residents replaced by immigrants for *S. diencaeus*. The table shows all models with univariate predictors and one model with an additive effect. Other models with additive and interactive effects did not have support based on AICc scores. For each predictor, the mean and SD from posterior prior and the 95% Bayesian credible interval (BCI) are presented. We also present the AICc and w_i (Akaike weight) from maximum likelihood estimation with the use of a glm in R. Predictors in bold do not include zero within their 95% BCI

Predictors	Mean	SD	95% BCI	AICc	w_i
Models with univariate predictors					
Population size in the source area (PSSA)	0.755	0.446	-0.177 to 1.641	27.337	0.003
Density in the source area	0.435	0.591	-0.736 to 1.651	31.378	< 0.001
Absolute habitat quality index (AHQ_D)	0.883	0.328	0.260 to 1.600	23.370	0.023
Relative habitat quality index (RHQ_D)	0.796	0.399	0.002 to 1.611	26.297	0.005
Weighted habitat quality index (WHQ_D)	0.958	0.201	0.543 to 1.395	15.910	0.955
Reef cover in the source area	0.684	0.485	-0.432 to 1.609	27.824	0.002
Structural connectivity index (WPI)	0.500	0.562	-0.698 to 1.675	30.604	< 0.001
Functional connectivity index (WPI _B)	0.283	0.668	-1.278 to 1.255	29.400	< 0.001
Model with additive effects					
PSSA + WHQ_D				22.005	0.050
PSSA	0.314	0.166	0.011 to 0.692		
WHQ_D	0.781	0.174	0.398 to 1.080		

Table 3. Effect size of z-scored predictors on the per cent of original residents replaced by immigrants for *S. adustus*. The table shows all models with univariate predictors. No model with additive and interactive effects had support based on AICc scores. For each predictor, the mean and SD from posterior prior and the 95% Bayesian credible interval (BCI) are presented. We also present the AICc and w_i (Akaike weight) from maximum likelihood estimation with the use of a glm in R. Predictors in bold do not include zero within their 95% BCI

Predictors	Mean	SD	95% BCI	AICc	w_i
Population size in the source area (PSSA)	0.846	0.377	0.061 to 1.616	24.160	0.069
Density in the source area	0.932	0.217	0.484 to 1.375	18.938	0.931
Absolute habitat quality index (AHQ _A)	0.192	0.528	-0.813 to 1.329	32.374	< 0.001
Relative habitat quality index (RHQ _A)	-0.320	0.757	-1.958 to 1.227	33.540	< 0.001
Weighted habitat quality index (WHQ _A)	0.093	0.769	-1.471 to 1.641	33.809	< 0.001
Reef cover in the source area	0.341	0.567	-0.804 to 1.454	32.036	< 0.001
Structural connectivity index (WPI)	0.262	0.680	-0.985 to 1.629	32.430	< 0.001
Functional connectivity index (WPI _B)	0.411	0.570	-0.685 to 1.616	32.154	< 0.001

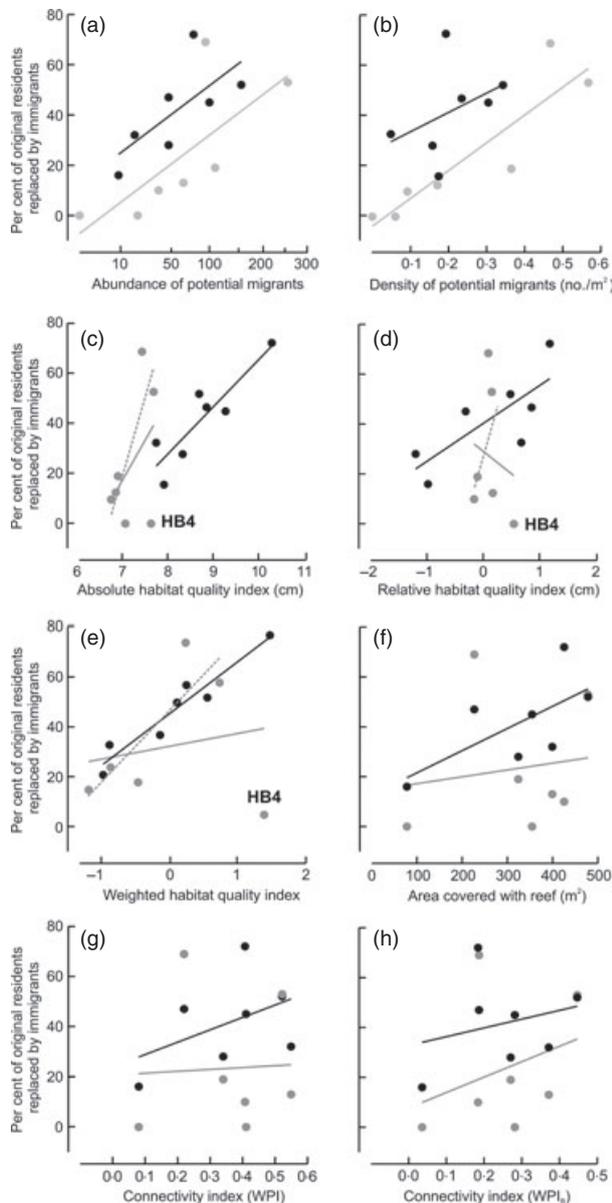


Fig. 2. Per cent of original residents replaced by migrants in relation to (a) the abundance of potential migrants in the source area, (b) density of potential migrants (number m^{-2} of reef), (c) the absolute habitat quality index (AHQ; cm), (d) the relative habitat quality (RHQ; cm), (e) the weighted habitat quality index (WHQ), (f) the area of the source area covered with reef, (g) WPI the structural connectivity index and (h) WPI_6 , the functional connectivity index. *S. diencaeus* relationships are in black and *S. adustus* relationships are in grey. Lines represent the best fit linear regressions. Dotted grey lines represent the best linear fit in *S. adustus* without the effect of site HB4.

(Fig. 1c,d,e), but the predictors were still not supported based on AICc scores, and their 95% BCI overlapped with zero (Table S2).

Landscape connectivity

Although the per cent of original residents replaced by immigrants tended to increase with all three connectivity indexes

in both species, the support for an effect was extremely weak based on AICc scores and w_i , and all three indices included zero within their 95% BCI (Tables 2, 3, Fig. 2f,g,h). WPI_6 did not strongly outperform simpler structural connectivity indices such as the effect of the area covered with reef in the source area and WPI (Tables 2, 3).

Relationships among predictors

In *S. diencaeus*, the model including the additive effect of the WHQ_D and population size in the source area had some support based on AICc scores and the 95% BCI of both variables (Table 2). In *S. adustus*, no additive effect had support. There was no support for an interaction among predictors in either species.

Discussion

IMMIGRATION PARTIALLY COMPENSATES FOR LOCALIZED MORTALITY

By repeatedly harvesting small proportions of damselfish populations until all individuals had been removed and immigration ceased, we have provided one of the first replicated quantifications of the magnitude of compensatory immigration in response to localized mortality. Immigration, averaging 42% and 23% of the original populations in *S. diencaeus* and *S. adustus*, respectively, shows that individuals from adjacent areas can substantially compensate for localized mortality, even in species considered to have very low mobility (Sale 1971) and therefore not expected to show strong compensatory immigration following localized mortality (Halpern, Lester & Kellner 2009). The near absence of immigration in control sites and prior to removal in depleted areas indicates that immigration depends on vacancies and is therefore a compensatory process.

In coral reef fish, there is some evidence of compensatory immigration from research on recolonization of reefs (Gundermann & Popper 1975; Brock, Lewis & Wass 1979; Syms & Jones 2000; Lowry & Suthers 2004), on territoriality and interspecific competition in damselfishes (Sale 1976; Hixon 1980; Hourigan 1986; Meadows 2001) and on emigration from marine reserves (Amargós *et al.* 2010). In six of these studies that provided enough information, compensatory immigration ranged from 40% to 286% (mean 103% over a period of 20–120 days; Table S1.1). Although most were performed in a patch reef environment where open sand would be expected to limit fish movement and involved only a single large removal event, compensatory immigration was often higher than in the present study. This difference might be related to the larger size of the fishes and their territories or to higher RHQ of the depleted areas in the other studies. The magnitude of compensatory immigration is also variable in other taxa. Immigration varied from 17% to 550% in freshwater fishes (mean 108% over a period of 30–365 days; Table S1.2), from 24% to 130% in reptiles and amphibians

(47% over a period of 55–365 days; Table S1.3), from 25% to 373% in birds (106% over a period of 9–90 days; Table S1.4) and from 2% to 1085% in mammals (153% over a period of 15–1825 days; Table S1.5). Only three studies in birds and four in mammals used a repeated, small harvest strategy rather than a massive single harvest (Table S1). Repeated harvest including immigrants, until immigration ceases, seems likely to maximize compensatory immigration.

COMPENSATORY IMMIGRATION AFFECTS ADJACENT SOURCE POPULATIONS

By estimating the size of the population that could immigrate into the depleted area, we have provided one of the first documentations of the effect of compensatory immigration on adjacent source populations. Of these potential migrants, an average of 35% and a maximum of 61% of the *S. diencaeus* emigrated, indicating a potentially very large effect of localized mortality on adjacent source populations. The effect on *S. adustus* was considerably smaller, averaging only 5%. Defining the potential source population is a logistical challenge. It is possible that we underestimated the number of potential immigrants because damselfish fish initially outside the source area could eventually enter the source and then the depleted area by a domino-like effect or a ‘vacuum’ effect, involving a series of territory relocations (e.g. Stickel 1946; Nakata & Satoh 1994; Whiteman & Côté 2004). On the other hand, we may have overestimated potential immigrants because the great majority of the documented forays were much < 10 m. Some fish within the defined source area, especially the slightly smaller *S. adustus*, may have been unable to detect vacant territories.

Previous studies have generally not measured the impact of localized mortality on adjacent source populations, even when they had the appropriate data. We found only six studies, all on mammals, which provided the information required to estimate the effect of compensatory immigration on sources or protected populations (Stickel 1946; Nakata & Satoh 1994; Efford, Warburton & Spencer 2000; Gundersen *et al.* 2001; Loveridge *et al.* 2007; Rosatte *et al.* 2007). In these studies, the proportion of the source population that emigrated varied from 2% to 55%, which is comparable to our results, despite considerable variation.

FACTORS INFLUENCING THE MAGNITUDE OF COMPENSATORY IMMIGRATION

The cessation of immigration to vacant territories clearly showed that some factors other than the existing vacancies limit damselfish immigration. This study provides some of the first evidence that the availability of potential immigrants and habitat quality affects compensatory immigration. Surprisingly, functional connectivity had little influence.

Potential migrants

Adjacent source populations influenced compensatory immigration in both species, but the statistical support was stronger for *S. adustus* than for *S. diencaeus*. In *S. adustus*, both total abundance and density had positive effects, but density predicted compensatory immigration better than total abundance did. In *S. diencaeus*, abundance was a strong predictor when controlling for habitat quality, but neither abundance nor density had an effect as a single predictor. The lower support for an effect of adjacent populations in *S. diencaeus* might be related to lower variation in abundance and density in this species. At a given level of habitat quality, density should be important as a reflection of resource limitation that might favour home range relocation (Fretwell & Lucas 1969; Rosenzweig 1981), but abundance determines the actual number of possible migrants. In our system, however, the interpretation of density effects is complicated by interspecific territoriality, which implies that heterospecific density could also influence tendency to relocate.

Numerous studies have recognized the importance of source population size as a potential influence on population recovery but have not directly measured it (Nakata & Satoh 1994; Sheldon & Meffe 1995; Efford, Warburton & Spencer 2000; Albanese, Angermeier & Peterson 2009). To the best of our knowledge, the only replicated study of the influence of adjacent population size is Rosatte *et al.*'s (2007) investigation of raccoon (*Procyon lotor*) populations in which there was very little immigration and no variation among sites following substantial reductions. Thus, our study provides the first evidence of a role for this widely expected limiting factor.

Habitat quality

Higher habitat quality in the depleted area resulted in higher compensatory immigration in *S. diencaeus* but had less, if any, effect on *S. adustus*. In *S. diencaeus*, all three indices of habitat quality correlated positively with compensatory immigration. However, the WHQ index, which combined the 60% absolute and 40% RHQ, was a much better predictor than either absolute or relative quality alone. The absolute and RHQ indices were moderately correlated in *S. diencaeus*, suggesting that compensatory immigration is facilitated by both the ‘pull’ of an attractive destination and the ‘push’ of a poor quality current location. In *S. adustus*, the weak effect of habitat quality might have been a consequence of smaller sample size (one site had no potential immigrants), the extreme and inconsistent pattern in site HB4 or the important role of adjacent density and population size.

Despite the extensive theoretical literature on animal distribution in relation to habitat quality based on the ideal free distribution (Fretwell & Lucas 1969) and its derivatives (Rosenzweig 1981; MacCall 1990), there is almost no empirical support for the prediction that immigration in response to localized mortality would be higher in better habitats. Peterson & Bayley (1993) removed fish from stream sites selected to represent local variation, but found that recolonization

was not related to any of these characteristics. Other studies not involving removal, however, do provide evidence for an effect of habitat quality on immigration in natural systems (e.g. Lin & Batzli 2001; Bélanger & Rodríguez 2002).

Connectivity

Neither index of structural complexity nor the index of functional connectivity predicted compensatory immigration in either species. Although connectivity varied among sites and immigration showed an upward trend with all three indices, no index had strong support either as a single predictor or after accounting for source population size and habitat quality. We had expected functional connectivity, which we estimated for the first time using the probability of crossing barriers, to have stronger predictive power than indices of structural connectivity. A previous study had demonstrated that even small sand gaps represented significant partial barriers to movement in *S. diencaeus* (Turgeon *et al.* 2010). Although it is possible that our index still failed to capture relevant functional connectivity, we suggest that functional connectivity may not strongly influence territory relocation at scales of metres and days in damselfish even though it is relevant at smaller spatial and temporal scales. Damselfish can use circuitous routes to overcome sand barriers (Turgeon *et al.* 2010), and most damselfish may have been able to find a path to vacant territory when allowed several days to do so.

Landscape connectivity and proximity among patches should facilitate movement and population recovery following disturbance (Crooks & Sanjayan 2006; Hilty, Lidicker & Merenlender 2006). This idea is well supported by numerous empirical studies showing that habitat patches closer to source populations or linked by corridors or 'stepping stones' had a higher recolonization or immigration rate than more isolated patches or those in the presence of a partial barrier (e.g. coral reef fishes: Brock, Lewis & Wass 1979; Frederick 1997; freshwater fish: Albanese, Angermeier & Peterson 2009; Sheldon & Meffe 1995; small mammals: Henderson, Merriam & Wegner 1985; Kozakiewicz & Jurasinska 1989). Gap-crossing studies and translocation experiments also show that distance and quality of the matrix affect movement among habitat patches (e.g. Bélisle & Desrochers 2002; Stevens *et al.* 2004; Turgeon *et al.* 2010). Nevertheless, several indices of structural connectivity (Winfree *et al.* 2005; Magle, Theobald & Crooks 2009; Prugh 2009) as well as our index of functional connectivity have not shown strong capacity to predict immigration and colonization in a variety of systems. Thus, the role of connectivity in compensatory immigration remains an important open question.

Additive and interactive effects of multiple limiting factors

Studies of factors limiting compensatory immigration could be confounded by interactions among factors. For example, habitat quality in the depleted area and population size in the source areas might only have an effect above a minimal level of landscape connectivity. With seven sites varying in three

potentially limiting factors, this study is the first to look at potential additive and interactive effects to explain variation in compensatory immigration in response to localized mortality. An additive effect of habitat quality and population size influenced compensatory immigration in *S. diencaeus*. The greater increase in immigration with increasing habitat quality than with increasing source population size suggested that habitat quality had a greater impact on compensatory immigration in this species. Some well-replicated studies on insects suggest that habitat quality and structural connectivity can covary and interact to explain immigration and/or emigration from habitat patches in some (Haynes *et al.* 2006; Matter *et al.* 2009), but not all cases (Moilanen & Hanski 1998). Examining the interactions among factors increases the requirement for adequate replication and variation among sites. As a result of these logistical challenges, very few studies have been able to examine the effect of multiple limiting factors on immigration, and none have examined immigration in response to localized mortality.

CONCLUSIONS AND IMPLICATIONS

This study has implications for the management of exploited and endangered animal populations. Significant compensatory immigration increased yield of depleted areas by up to 40%, providing evidence that protected areas can benefit nearby harvesters in the short term, despite the doubts about the usefulness of protected areas as a management tool (Roberts *et al.* 2001; Gell & Roberts 2003; Hilborn *et al.* 2004). However, compensatory immigration also substantially reduced adjacent populations, indicating a potentially serious vulnerability of protected populations to nearby harvest. Such effects could reduce metapopulation viability, especially in species such as large carnivores that have low reproduction rates and high mobility (Woodroffe & Ginsberg 1998). In addition, variation of about 55% to 70% in the magnitude of compensatory immigration among seven sites reveals the importance of replication in such studies, despite the logistical challenges. The combined effects of habitat quality and the size of the source population imply that protected areas will have difficulty achieving high densities of threatened populations in the face of nearby harvest if they are situated in poorer quality habitats, unless they are also very large relative to mobility of the species concerned. To strengthen the potential to use protected areas as a conservation and management tool, it is increasingly important to understand the processes underlying compensatory immigration.

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Supporting Information

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

Figure S1. Schematic representation of the study design illustrating the naturally fragmented nature of fringing reefs and the size of the depleted and source areas.

Table S1. Summary of studies providing evidence for compensatory immigration in vertebrates.

Table S2. Effect size and support of habitat quality indices to explain the per cent of original residents replaced by immigrants for *S. adustus* without the inclusion of site HB4.

Appendix S1. Equations and description of the parameters used to calculate the weighted proportional index (WPI; structural connectivity) and WPI_B (functional connectivity).

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