

Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape

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Abstract. Functional connectivity, the degree to which the landscape facilitates or impedes movement, depends on how animals perceive costs and benefits associated with habitat features and integrate them into a movement path. There have been few studies on functional connectivity in marine organisms, despite its importance for the effectiveness of Marine Protected Areas. In this study, we asked how open sand and conspecific distribution affected functional connectivity of longfin damselfish (*Stegastes diencaeus*) on fringing reefs in Barbados. We translocated 102 individuals to sites varying in sand gap width and in configuration: Continuous (solid reef between release site and territory); Detour (sand along the direct path between release site and territory, but an alternative, continuous solid U-shaped reef path); and Patch (sand between release site and territory, but an alternative stepping stone path). We visually tracked and mapped every homing path. We found no evidence of a barrier to movement in the Continuous configuration, but sand was a partial barrier in Detour and Patch configurations. The probability of crossing the sand gap dropped below 50% when its width was >1.85 m in Detour and >3.90 m in Patch configuration. Damselfish avoiding large gaps took detours that approximated the route maximizing travel over reef, but they crossed more short sand gaps and fewer conspecific territories, suggesting avoidance of agonistic interactions. This study quantifies for the first time the size and steepness of a barrier to movement in a marine organism, and it provides evidence for effects of both landscape configuration and conspecific distribution on functional connectivity.

Key words: Barbados; coral reef; corridor; fragmentation; gap crossing; longfin damselfish, *Stegastes diencaeus*; marine reserve; Osteichthyes; Pomacentridae; spillover; territory; travel costs.

INTRODUCTION

Functional connectivity (i.e., the degree to which the landscape facilitates or impedes movement among patches [Taylor et al. 1993]) is an organism-based emergent property of the landscape, combining a description of its physical structure with the response of a species to that structure (Tischendorf and Fahrig 2000, Taylor et al. 2007). As a key determinant of metapopulation dynamics, landscape functional connectivity is essential to the persistence of extinction-prone populations (Pulliam 1988, Hanski 1999).

Functional connectivity has strong implications for the site selection of protected areas, because spatially clustered networks of protected areas increase the probabilities of species occurrence and persistence (Cabeza 2003, Lubchenco et al. 2003, Russ et al. 2008). In marine fish and invertebrate populations, demographic connectivity, achieved through long-dis-

tance dispersal of larvae by oceanographic currents, represents the primary opportunity for mixing among fragmented local marine populations (Cowen et al. 2006, Planes et al. 2009). Nevertheless, functional connectivity, which differs from demographic connectivity in being based more on individual behavior and a smaller scale, is also important because it influences the degree to which individuals that have settled in a reserve will be exposed to adjacent fisheries (Zeller and Russ 1998, Kramer and Chapman 1999, Bartholomew et al. 2008).

In heterogeneous landscapes, moving organisms encounter habitat patches differing in food quality and predation risk and may interact positively or negatively with resident conspecifics and congeners. Functional connectivity depends on how they perceive and respond behaviorally to habitat patches and ultimately select a movement path that minimizes costs (Wiens 2002, Bélisle 2005). Functional connectivity is influenced by intrinsic characteristics of the organism such as mobility and perceptual range (Lima and Zollner 1996, McDonald and St. Clair 2004), size (Bakker and Van Vuren 2004), sex (Pither and Taylor 1998), and state (e.g., competitive ability, nutritional and reproductive condi-

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tion [Turcotte and Desrochers 2003]). Extrinsic factors such as the total travel distance (Rothermel and Semlitsch 2002), landscape configuration (i.e., spatial distribution of habitat [Gillies and St. Clair 2008]), and quality of the matrix (Baum et al. 2004, Bender and Fahrig 2005) are also likely to affect functional connectivity.

Translocations and gap-crossing experiments have contributed greatly to our understanding of functional connectivity in terrestrial animals by identifying the minimal width of a barrier to movement (the gap width at which the probability of crossing the barrier drops below some defined probability of crossing) and its steepness (the rate of decrease in the probability of crossing a barrier between the two inflection points). From these studies, we know that for many terrestrial taxa inhabiting highly structured habitats such as forest, open habitat represents a partial barrier (Bélisle and Desrochers 2002, Bakker and Van Vuren 2004, Boschietter and Goedhart 2005, Awade and Metzger 2008), while structured habitats act as corridors that facilitate movement (Baum et al. 2004, Gillies and St. Clair 2008). Social habitat features, such as the distribution of conspecifics, may facilitate movement by indicating high habitat quality or safety (Stamps 1988, Sieving et al. 2004) or impede it through agonistic interactions, but there is little empirical evidence for social effects on functional connectivity. To our knowledge, no study has used an experimental gap-crossing approach comparable to those in terrestrial systems for a marine organism.

Coral reefs are naturally fragmented habitats, composed of solid, often highly structured patches of reef separated by low-complexity substrata such as sand and rubble. Substrata with low structural complexity offer few refuges and are associated with high predation risk (Shulman 1985, Sweatman and Robertson 1994). Large sand gaps are known to impede fish movements between reefs (Ogden and Buckman 1973, Barrett 1995, Chapman and Kramer 2000), although relatively long-distance movements of newly settled juveniles have also been documented (Frederick 1997). However, there is little information about the minimal width or variation in response to width of such barriers. Moreover, on many coral reefs, the territories of the abundant, small, but very aggressive damselfishes might form a social barrier to movement because they can inhibit feeding activity of other species (Foster 1985) and limit access to refuges (Sweatman and Robertson 1994).

In this study, we used path choice by homing fish following experimental translocation for the first time in a marine system to quantify functional connectivity. Specifically, we asked whether sand formed a barrier to movement of homing longfin damselfish (*Stegastes dienaecus*), and if so, what was the minimal width and steepness of this barrier? In addition, we asked whether the territories of conspecifics and congeners acted as a social barrier to movement. We used the natural variation in the width of sand gaps in two reef

configurations (Detour and Patch) that differ in the extent to which sand formed a barrier to movement, and we used a Continuous configuration (no sand gap) as a control for hidden barriers. Our system offers a unique opportunity to study the effect of structural and social habitat features on movement paths because a highly mobile observer is able to continuously track each translocated individual on a small spatial and temporal scale.

METHODS

Study site and species

We carried out our study between June and August in 2006 and 2007 and in January 2008. We used the spur and groove zone of four fringing reefs along the west coast of Barbados (13°10' N, 59°38' W) at depths of 4–6 m. The spur and groove zone is characterized by finger-like, seaward extensions of the main reef with numerous small patches of reef separated by sand (Lewis 1960; Fig. 1). Longfin damselfish are abundant in this habitat. Both sexes vigorously defend exclusive territories (area, $1.38 \pm 0.57 \text{ m}^2$; mean \pm SD), usually located over rock and eroded dead coral substrata, that provide food in the form of a cropped algal mat and holes used as refuges. Microhabitat distribution is size- and sex-structured (Cheney and Côté 2003; K. Turgeon, *unpublished data*). Males, which grow to larger sizes than females and are usually more aggressive, provide paternal care for eggs and often occupy the edges of the reef where the substratum provides more nest sites (Robertson 1984, Cheney and Côté 2003). Females tend to be found away from the edges. Territory acquisition appears to be vital for survival and reproductive success, and there is no evidence of “floaters” in longfin or other *Stegastes* damselfish populations (Bartels 1984, McDougall and Kramer 2007). Territory locations are very stable in established populations, but territories of experimentally removed individuals are visited by neighbors after as little as three minutes and can be reoccupied within 10–30 minutes (Cheney and Côté 2003, McDougall and Kramer 2007). Thus, absences from a territory may allow increased intrusions and require fighting to regain possession (Sikkel and Kramer 2006). We therefore assumed that this species would be highly motivated to home quickly, although the quality of the territory and the competitive ability of the individual might affect this motivation. We translocated 102 individuals (total length (TL), $9.63 \pm 1.92 \text{ cm}$ (mean \pm SD); range: 5.0–13.0 cm), each only once, all in the adult (dark) color pattern, including both males and females and individuals above and below the threshold of sexual maturity (9.3 cm TL; K. Turgeon, *unpublished data*).

Configurations and site description

We used 23 sites selected to conform to one of three distinct configurations (Fig. 1), with some sites used for more than one translocation because of a limited number of suitable sites (3.38 ± 2.57 translocations

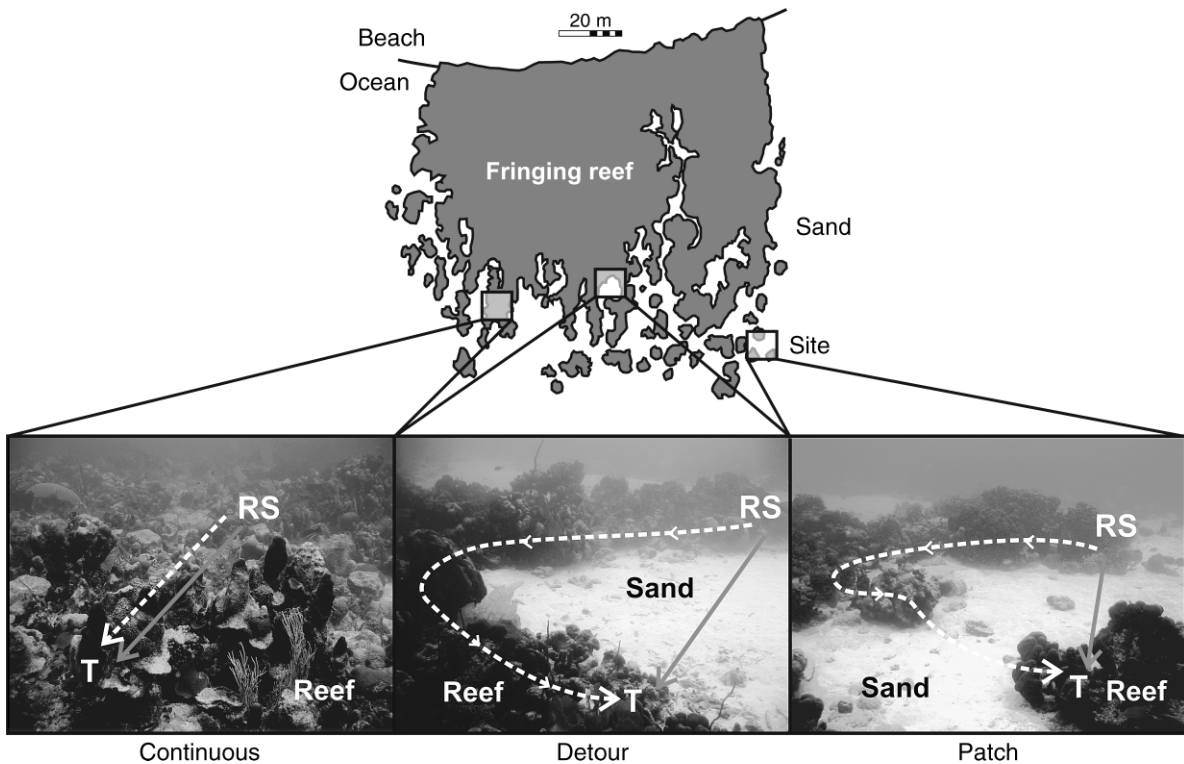


FIG. 1. Illustration of the natural fragmentation of a fringing reef used to generate the three configurations used in this study: Continuous, Detour, and Patch. "T" indicates the territory location, and "RS" indicates the release site location for translocations. The solid lines represent the direct linear homing path that could be used to minimize energetic costs and agonistic interactions, and the dotted lines represent the shortest detour that could be used to maximize the use of reef along the pathway.

per site (mean \pm SD); range: 1–11 translocations). In the Continuous configuration, the shortest path between the release site and the territory passed over solid substratum. In the Detour configuration, the shortest path crossed a sand gap, but continuous reef was available along a roughly U-shaped alternative route. In the Patch configuration, the shortest path crossed a sand gap and all alternative routes also required movements across at least one sand gap. Detour sites were selected so that the shortest distance over reef was at least 1.5 times longer than the linear path, therefore incurring at least small energetic and time costs for individuals that chose the alternative. We chose a large range of sand gap widths (4.57 ± 2.31 m; range: 1.00–10.60 m), linear distances imposed between release site and territory (7.05 ± 2.93 m; 2.15–16.50 m) and distances along the shortest alternative route that maximized the use of reef (8.54 ± 2.91 m; 3.45–17.20 m). These distances are similar to spontaneous "forays" (Bartels 1984) beyond the territorial borders (3.20 ± 2.19 m; 0.44–23.3 m, $N = 602$ "forays"; K. Turgeon, unpublished data). Prior to translocations, each site was drawn on a Plexiglas slate with a 1×1 m grid. We used the measured distance between distinctive reference points on the reef to export and georeference the raster map in a GIS program (MAPINFO Professional 6.5, Pitney Bowes Business Insight, Troy, New York, USA). On each site, we

mapped all conspecific and congeneric (*S. adustus*, *S. planifrons*) territories by observing each individual for 10 minutes and mapping territory boundaries in relation to fixed reference points. We estimated the size of conspecifics and congeners (to the nearest centimeter, TL) and, whenever possible, the sex, based on courtship behavior or the presence of a nest.

Translocation

Using SCUBA, each focal individual was caught using a modified cast net, sexed by examination of the urogenital pore (Thresher 1984), measured to the nearest 0.5 cm (TL), and carried to the release site in the net. After release, one diver started a timer and followed the individual at a distance of 3–4 m, drawing its path on the slate. Damselfish are highly tolerant of divers and we were familiar with and careful not to elicit predator avoidance behavior; even a distance of 2 m has been indicated as large enough to not alter their behavior (Levin et al. 2000). A second diver noted the time of every attack or aggressive display by conspecifics and congeners as well as the size of the aggressor. Each translocation required 20–40 minutes. Fish were considered not to have homed if they remained in a shelter for more than 25 minutes or started to defend a new territory near the release site. We observed no predation attempts during our experiment. If homing was success-

ful, we measured the linear distance between the center of the focal individual's territory and the release site, the width of the imposed sand gap, and the length of the homing path, with a measuring tape. All translocations were carried out between 09:00 and 17:00 hours, because longfin damselfish are strictly diurnal, resting in holes on the reef at night.

Path mapping and description of predictors

We georeferenced each hand-drawn homing path onto the respective site map. From these paths, we extracted the following predictors using the GIS software: the linear distance from the release site to the territory, the width of the imposed sand gap along the line between the release point and territory, the distance of the shortest route that maximized the use of reef in Detour and Patch configurations, damselfish density (number of individual territories per linear meter) along the homing path, along the shortest detour that maximized the use of reef, and along the linear distance. We used the field measurements to check these values. We also used the software to estimate the percentage of sand along the homing path, the linear distance, and the shortest detour that maximized the use of reef as well as the number of sand gaps along the homing path in the Patch configuration. For Detour and Patch configurations, we calculated the configuration ratio, which is the distance along the shortest detour that maximized the use of reef divided by the size of the imposed sand gap. This dimensionless value represents the relative increase in distance travelled for a translocated individual avoiding a sand gap (2.27 ± 1.34 ; range: 1.5–7.9).

Model construction and assessment

We used the information theoretic approach for model selection and assessment of performance. To select the best subset of models among the entire set of candidate models, we used the Akaike's Information Criterion modified for small sample sizes (AICc). For each candidate model, we compiled the normalized Akaike weights (w_i) to address model selection uncertainty (Burnham and Anderson 2002, Johnson and Omland 2004). The confidence set of candidate models includes all models for which w_i is within 10% of the maximum weight (Burnham and Anderson 2002). We used the conventional model averaging when more than one candidate model had substantial support as explanations of the response variables (Burnham and Anderson 2002). To determine the reliability of predictor estimates, we calculated the weighted unconditional standard error with its associated confidence intervals (95% CI).

We used Generalized Linear Mixed Models (GLMMs, lmer library in R with the restricted maximum likelihood method) to produce candidate models that examined the effects of predictor variables on response variables, to account for spatial and individual effects in the data and to infer statistical

support. Non-normally distributed predictors and response variables were log-transformed and every predictor was z -standardized prior to analysis. For each candidate model, we examined the Tolerance value (1/Variance Inflation Factor) which is a measure of the amount of variation unique to each retained predictor and is used to detect multicollinearity problems.

We investigated three questions. First, we evaluated the percentage deviation of homing paths from alternative paths (linear path or shortest path along the reef that maximized the use of reef) and compared the deviations of homing paths on Detour and Patch configurations with those on Continuous configuration. We calculated the deviation from the linear path for damselfish that crossed the sand gap and from the linear and shortest path for those that did not cross the sand gap. We used a treatment contrast (Continuous configuration as a priori contrast) and a Gaussian error structure with an identity link function in our GLMM. We controlled for spatial independence by using site, nested within reef as random factors.

Our second question was whether the probability of crossing a sand gap was a function of structural (width of the sand gap, configuration ratio), social (damselfish density along the alternative path maximizing the use of reef), and intrinsic characteristics predictor (size and sex). We allowed an interaction between sand gap width and configuration ratio because we predicted that larger configuration ratios would increase the probability of gap crossing. We built separate models for Detour and Patch configurations because the variances of two predictors (damselfish density, configuration ratio) were very different among configurations. We built an a posteriori model to test whether configuration affected the probability of crossing a sand gap by using sand gap width, configuration, and the interaction between these two predictors to test for a difference in barrier steepness among configurations. We used a binomial error structure with a Logit link function and controlled for spatial independence by using site, nested within reef.

Our third question was whether microhabitat characteristics (i.e., proportion of sand and density of conspecifics and congeners) along the homing path differed from those along the shortest route maximizing the use of reef in Detour and Patch configurations for damselfish that did not cross the sand gap. We used a binomial error structure with a Logit link function and we controlled for individual effect and for spatial independence among sites and reefs by nesting individual within site, within reef.

RESULTS

When released, most individuals hid in a hole or under a ledge for a short period of time and then initiated the homing. Homing sometimes began following an attack by a nearby territory holder. Homing individuals usually adopted a paler color on their heads, erected their dorsal fins, and alternated between pauses and bouts of rapid

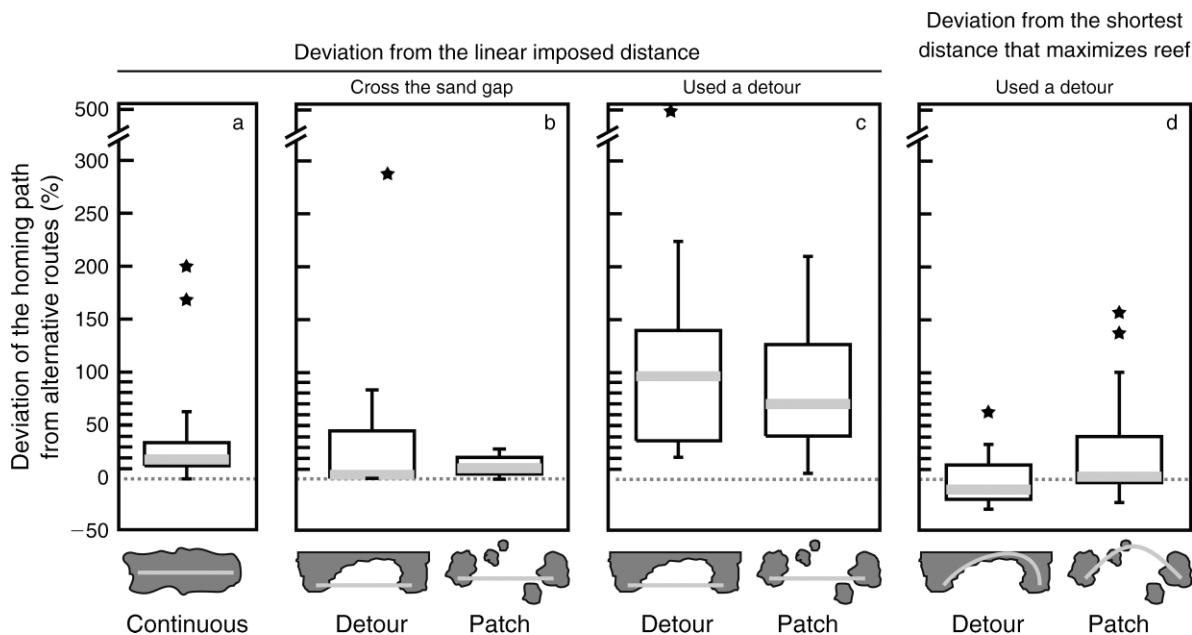


FIG. 2. Deviation (%), calculated as the percentage of deviation in distance of the homing paths used for returning to a territory from alternative routes (linear path and shortest route that maximizes reef). (a) On Continuous configuration, deviations are calculated from the linear path from the release site to the territory. In Detour and Patch configurations, deviations are calculated separately for fish that crossed the sand gap and for those that used a detour along the reef. (b) For fish that crossed the sand gap, we calculated the deviation from the linear path. (c) For damselfish that did not cross the sand gap and used a detour, we calculated the deviation from the linear path and (d) from the route that maximized the use of reef. In the box plots, the 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. Stars indicate outliers.

swimming. Rather than immediately chasing or biting, conspecific and congeneric territory holders often performed a rapid charge without making contact. Of the 102 translocated damselfish among the three configurations, 18% did not home (6% on Continuous, 3% on Detour, and 9% on Patch configurations). Fish that did not home were smaller and released farther from their territories (K. Turgeon et al., *unpublished analyses*). The following analyses include only fish that successfully homed.

Open sand area as a barrier

On Continuous sites, damselfish homed in a nearly linear path with a median deviation from the imposed linear distance of only 19% (Fig. 2a). This deviation was independent of the total imposed distance and corresponded to an additional median distance of ~ 1.50 m. On Detour and Patch configurations, almost one-third (Detour 28%, Patch 29%) of the damselfish crossed the imposed sand gap and also homed in a nearly linear path (median increase: Detour 4%, Patch 11%; Fig. 2b). Their deviations were comparable to those observed on Continuous configuration (Table 1, Fig. 2a, b). On Detour and Patch configurations, the homing path of damselfish that did not cross the sand gap and used a detour was longer than the linear imposed distance (median increase: Detour 97%, Patch 71%; Fig. 2c) and deviations from the linear imposed distance were larger than the deviations observed on Continuous configura-

tion (Table 1, Fig. 2a, c). Homing paths were similar to the shortest route maximizing reef in Patch (3% longer; Fig. 2d) but differed slightly in the Detour configuration (10% shorter; Fig. 2d), because damselfish sometimes “cut corners” to use a shorter path than the shortest route maximizing reef (Table 1, Fig. 2a, d).

To explain the probability of crossing the sand gap, we retained three candidate models in the Detour and two in the Patch configuration (based on the AICc scores) and performed model averaging. The width of the sand gap was the most influential predictor, explaining 26% of the Percent of Deviance in Detour and 34% in Patch configurations (Appendix A). Sand gaps greater than 1.85 m reduced the probability of crossing a sand gap below 50% in Detour configuration. This value was 3.90 m in Patch configuration (Fig. 3). The steepness of the barrier (i.e., the rate at which the probability of crossing a sand gap decreased) was sharp in both configurations. Each additional 0.5 m decreased the probability of crossing by 25% (Fig. 3). We found no support for an interaction between sand gap width and the configuration in the a posteriori model, but both predictors were supported (GLMM, $N = 55$, sand gap estimate = -2.41 ± 0.71 (estimate \pm SE) Configuration estimate = 3.02 ± 1.17 ; both predictors did not include zero in the 95% CI). Thus, the configuration affected the probability of crossing a sand gap at a given width but did not affect the steepness of the barrier. On Patch

TABLE 1. Generalized linear mixed models used to compare the deviation of the homing path of longfin damselfish (*Stegastes diencaeus*) from alternative paths (linear or shortest path that maximizes the use of reef) on Detour and Patch configurations with those on Continuous configurations.

Predictor	Estimate \pm SE	95% CI
a) Deviation from the linear path for damselfish that crossed the sand gap ($n = 47$)		
(Constant)	0.05 \pm 0.26	-0.45 to 0.55
Config.: Detour vs. Continuous	0.21 \pm 0.48	-0.72 to 1.13
Config.: Patch vs. Continuous	-0.41 \pm 0.35	-1.11 to 0.29
b) Deviation from the linear path for damselfish that used a detour ($n = 70$)		
(Constant)	-0.47 \pm 0.16	-0.78 to -0.16
Config.: Detour vs. Continuous	1.01 \pm 0.26	0.51 to 1.51
Config.: Patch vs. Continuous	0.66 \pm 0.26	0.15 to 1.17
c) Deviation from the shortest path on the reef for damselfish that used a detour ($n = 70$)		
(Constant)	0.26 \pm 0.17	-0.07 to 0.59
Config.: Detour vs. Continuous	-0.78 \pm 0.27	-1.31 to -0.26
Config.: Patch vs. Continuous	-0.15 \pm 0.27	-0.68 to 0.38

Notes: The study area was on fringing reefs in Barbados. Deviations were from the shortest path on the reef that maximized the use of reef for damselfish that used a detour along the reef instead of crossing the sand gap. All models include a constant. For the configuration predictor, we used a treatment contrast with Continuous configuration as the contrast. Predictors in boldface type do not contain zero within the 95% confidence intervals.

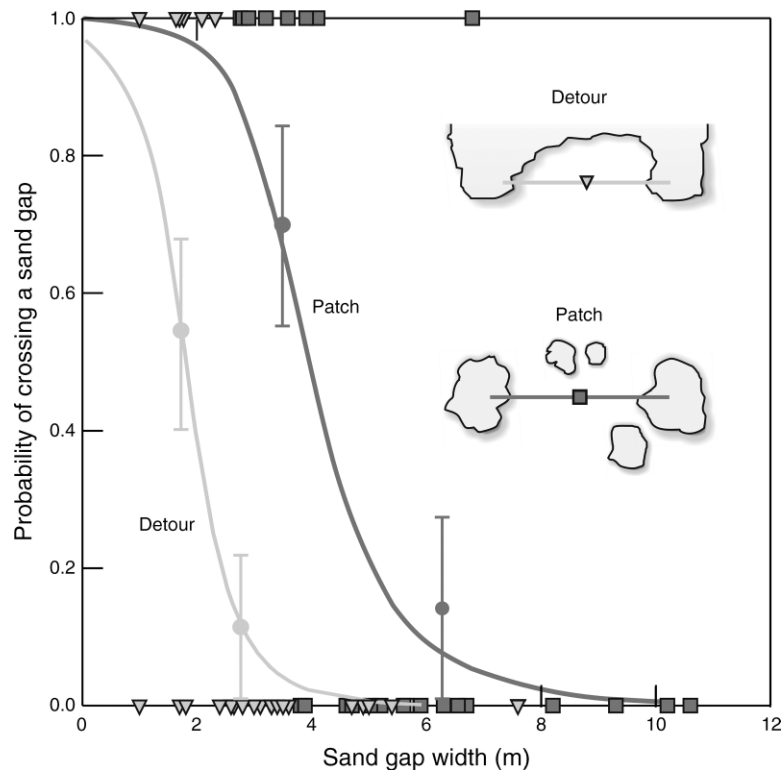


FIG. 3. Probability of crossing an imposed sand gap in Detour and Patch configurations as a function of the width of the sand gap. The probability of crossing was evaluated with a Generalized Linear Model (GLM), with Reef and Sites as random factors. The lines represent the best-fitting Logit regressions for each configuration. The triangles and squares represent the sand gap widths tested. We evaluated the fit and uncertainty of the Logit curve by using empirical probabilities (represented by small circles, calculated for two specified ranges of sand gaps, and corresponding to the proportion of sand gaps crossed over all sand gaps in the specified range). The closer the circles are to the line, the better the fit. A measure of uncertainty (binomial SE, error bars) is presented for each empirical probability.

TABLE 2. Generalized Linear Mixed Models (GLMM) used to explain the difference between the homing path and the shortest alternative route that minimizes the use of sand in (a) and (b).

Predictors	Estimate \pm SE	95% CI
a) Percentage of sand		
(Constant)	4.68 \pm 2.91	-1.02 to 10.4
Percentage of sand	5.42 \pm 2.42	0.68 to 10.2
Config.: Patch vs. Detour	-5.32 \pm 2.95	-11.09 to 0.45
Percentage of sand \times Config.: Patch vs. Detour	-3.96 \pm 2.51	-8.89 to 0.97
b) Damsel fish density		
(Constant)	-0.23 \pm 0.94	-2.07 to 1.61
Damsel fish density	0.67 \pm 2.45	-4.13 to 5.47
Config.: Detour vs. Continuous	5.10 \pm 1.84	1.48 to 8.71
Config.: Patch vs. Continuous	1.61 \pm 1.26	-0.86 to 4.07
Density \times Config.: Detour vs. Continuous	-8.72 \pm 3.52	-15.6 to -1.82
Density \times Config.: Patch vs. Continuous	-5.51 \pm 3.67	-12.7 to 1.69

Notes: Panel (a) includes the percentage of sand along the paths for Detour and Patch configurations, and panel (b) includes damselfish density along paths for the three configurations. Parameter estimates, standard errors (SE), and the 95% confidence intervals (CI) of each parameter are presented. All models include a constant. For the configuration predictor, we used a treatment contrast; Detour configuration was the contrast with the percentage of sand predictor, and Continuous was the contrast for the damselfish density predictor. Predictors in boldface type do not contain zero within the 95% confidence intervals.

configurations, damselfish crossed 1–6 gaps (median width = 2.55 m, 1.13–3.28 m). Even though they crossed larger imposed sand gaps in Patch than in Detour configuration, most damselfish crossed the smallest sand gap available when there was a choice.

Other predictors had some support for effects on the probability of crossing a sand gap, but their estimates included zero within the 95% CI (Appendix A). The configuration ratio had support in the Detour configuration model when interacting with sand gap width, as predicted (Appendix A). When the configuration ratio was large, the probability of crossing the sand gap increased slightly. Damselfish density along the alternative route that maximized the use of reef was suggested to affect the likelihood of crossing a sand gap in both configurations (Appendix A). The probability of crossing a sand gap was higher when damselfish density was high along the alternative route. Damselfish body size and sex were not good predictors of the probability of crossing a sand gap.

Microhabitat used on detours

The paths used by damselfish had more sand than the alternative route that maximized the use of reef, independently of the configuration (Detour 50% more, Patch 10% more; Table 2, Fig. 4a). Trials in which the path was greater than the alternative route that maximized the use of reef were associated with more attacks on Continuous and Patch but not Detour configurations (Appendix B). The number of attacks received was not related to damselfish density along the homing path in any configuration (Appendix B).

The paths used by damselfish had a lower damselfish density than the alternative route on Detour and Patch configurations, but this pattern has statistical support only on Detour configuration (Table 2). Damselfish used a path that had 37% fewer conspecifics/m than the

alternative route that maximized use of the reef on Detour and 25% fewer damselfish/m on Patch configuration (Table 2, Fig. 4b). On Continuous configurations, the trend was in the opposite direction (6% more damselfish/m along the used path; Table 2, Fig. 4b).

DISCUSSION

By following the return of damselfish translocated to reef configurations of different patterns and sand gap widths, we have been able to quantify for the first time the size and the steepness of a barrier to movement in a marine organism. We have provided evidence that sand is a barrier, that the probability of crossing this barrier drops sharply as its width increases (steepness), and that the width but not the steepness of the drop depends on the configuration of reef around the barrier. Nevertheless, the selected path crossed more sand than the path that offered maximal use of reef, and at the same time, in the Detour configuration, crossed fewer conspecific territories.

Sand gaps as a barrier to movement

When there was solid reef between the release site and the territory, the homing path of translocated damselfish was nearly linear over distances of 4.0–16.5 m. This suggests that there are no major barriers to movement on solid reef, and that deviations observed in other configurations were a response to the sand gaps. When small sand gaps separated the release site and the territory, homing paths remained nearly linear. However, for larger sand gaps, damselfish consistently avoided the gap and took a longer detour. This shows that open sand is a powerful barrier to damselfish movement. Unfortunately, many studies of gap crossing failed to provide such controls, creating ambiguity regarding the influence of a specific barrier type (Bakker and Van Vuren 2004, Bosschietter and Goedhart 2005). Detour distances of 1.5–5.9 times longer than the direct path over sand suggest

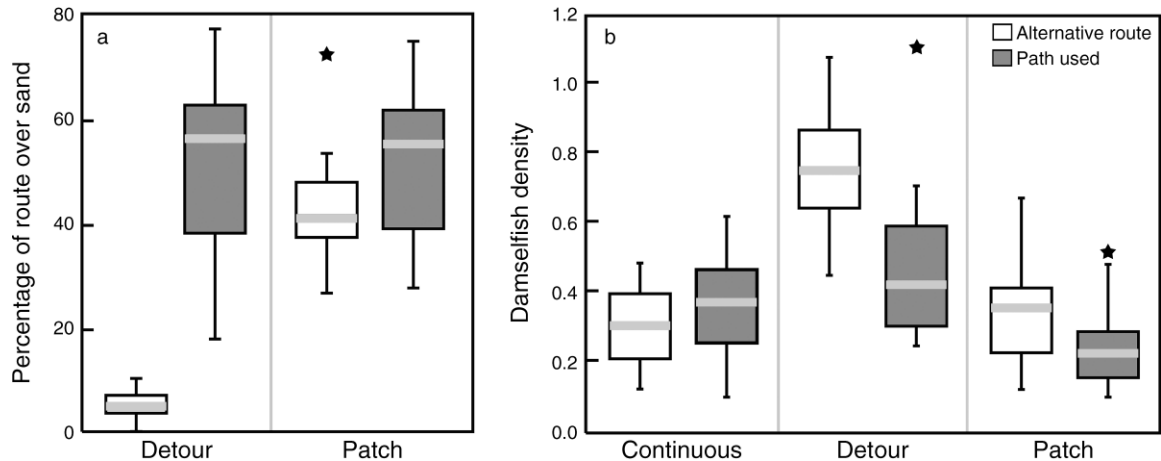


FIG. 4. Differences between the path used by homing damselfish (gray box plots) and the alternative path that maximized the use of reef (white box plots) for (a) percentage of the route over sand and (b) damselfish density along paths in the three configurations. For Detour and Patch configurations, only fish that did not cross the imposed sand gap and used a detour are included. For Continuous configuration, there was no sand along either the linear or observed paths. Box plots are as in Fig. 2.

that damselfish perceive the cost per unit distance of crossing wide gaps as at least 5.9 times higher than that of moving over reef. The higher cost is likely to be due to increased risk of predation. Tethering experiments using small coral reef fishes have provided evidence that predation risk is higher over sand, particularly within 2 m of the reef edge, as a result of a low shelter availability coupled with a higher encounter rate with predatory fishes (Shulman 1985, Sweatman and Robertson 1994). Contrary to findings in birds and mammals (Bélisle and Desrochers 2002, Bakker and Van Vuren 2004), we did not find clear evidence for a trade-off between the relative increase in the distance required for a detour and the probability of crossing a gap. In addition to the possible high cost of moving over wide sand gaps, damselfish may lack sufficient prior information about the landscape or a sufficient perceptual range ability (Lima and Zollner 1996) to make such decisions.

Although it is widely accepted that large sand gaps and other habitats with low structural complexity often impede movements of reef fishes and other marine organisms, the evidence is indirect and incomplete. The presence of “grazing halos” (i.e., zones of almost bare sand up to 10 m from reefs in seagrass beds [Hay 1984, Sweatman and Robertson 1994]) suggests that herbivorous reef fishes forage mainly within this distance. Telemetric studies have observed avoidance of sandy substratum in some reef fish species (Meyer and Holland 2005, Afonso et al. 2008) but not others (Meyer et al. 2000, Chateau and Wantiez 2009). Mark–recapture studies indicated that coral reef fish rarely moved between reefs separated by >20 m, although translocated fish of several species returned home across these same gaps (Chapman and Kramer 2000). Studies on recolonization of depopulated patch reefs surrounded by sand suggest that gaps of 100–130 m provide a partial

barrier (Brock et al. 1979, Ogden and Ebersole 1981). In a study of movements of newly settled juvenile reef fish from several families among units in experimental arrays of artificial reefs, there appeared to be a trend for movement to drop sharply at distances between 5 and 20 m (Frederick 1997: Fig. 2), but the distance effect was not examined, perhaps because it was confounded with species differences (which did affect movement) and because the author’s primary interest was in the unexpected amount of movement. In a study of density-dependent predation on newly settled juvenile reef fishes, on the other hand, a gap of 5 m was enough to prevent nearly all movement by both juvenile and adult coral reef fish (Overholtzer-McLeod 2006). Invertebrates show similar patterns: the predation rate of blue crabs (*Callinectes sapidus*) on juvenile oysters is higher when there is a vegetated corridor linking marshes and reefs instead of a sandy bottom (Micheli and Peterson 1999). Defaunated drift algae located within seagrass beds had a greater abundance of amphipods compared to drift algae located on sand, providing a corridor to amphipod movement (Brooks and Bell 2001). These previous studies have provided evidence that sand may impede movement and could represent a partial barrier for marine organisms. However, they did not examine a sufficient range of barrier widths to be able to quantify the size and steepness of the barrier. By testing a wide range of gap widths, our study shows that sand gaps are significant barriers to movement, even for homing individuals, at least when alternative paths are available. The size of gaps that inhibit movement under these conditions are much smaller than most of the upper limits to movement indicated by previous studies.

Our study is most comparable to previous studies of small, forest passerines crossing open gaps between forest patches. Data are available to compare 10 species

from five studies to our results (Desrochers and Hannon 1997, St. Clair et al. 1998, Bosschietter and Goedhart 2005, Creegan and Osborne 2005, Awade and Metzger 2008; Appendix C). These species range in mass from 6 to 21 g, similar to the mean mass of 19 g for damselfish in this study. However, the widths at which the probability of crossing the gap drops below 50% are much larger (14–133 m; median = 49 m; Appendix C). This may be related to higher mobility of the passerines, which have average breeding territory diameters of 20–247 m, as compared to 1.3 m in the damselfish (Appendix C). However, the barrier width is unrelated to territory size among the passerines (GLM; $R^2 = 0.13$).

In addition to the narrow width of barriers to damselfish movement, we also found that the barrier was very steep. The estimated probability of crossing dropped from 75% to 25% in only 0.3 m (Detour configuration) or 1.2 m (Patch configuration). Equivalent values for the data set from forest birds ranged from 18 to 126 m (Appendix C). The steepness of the barrier appears to be related to its size among forest birds (GLM; $R^2 = 0.61$, $P = 0.004$), as well as in the data set including both birds and damselfish, although there is considerable variation (GLM; $R^2 = 0.72$, $P < 0.001$). Steepness of barriers is of interest as it influences the proportion of a population that moves over different distributions of gaps. If a gradual barrier is the result of intraspecific variation in the probability of crossing, intermediate barriers may generate selection in metapopulations.

Microhabitat selected when using a detour

Damselfish faced with large sand gaps in Patch and Detour configurations detoured along alternative routes that came close to the shortest distance that allowed them to maximize the use of reef. However, the microhabitat of their paths deviated from the expected alternative in crossing more sand but fewer conspecific territories. This suggests that detouring fish reduced the risk of attacks from conspecifics by “cutting corners” as they skirted the larger gap. It seems less likely that moving across short sand gaps was simply a way of reducing the travel distance because there was not a significant difference between the actual distance travelled and the distance along the alternative route maximizing reef.

Although the presence of conspecifics has been suggested as a potential influence on movement paths (Bakker and Van Vuren 2004, Bêlisle 2005), to our knowledge our study provides the first support for this proposal. While conspecifics or congeners may indicate resource quality (Stamps 1988) or safety (Sieving et al. 2004, Schmidt et al. 2008), crossing conspecific territories may also result in agonistic interactions that reduce vigilance and increase vulnerability to predation (Brick 1998). Minimizing the length of detours requires skirting the edge of the reef where the damselfish encountered are more likely to be large aggressive males, as compared

to farther from the edge (Cheney and Côté 2003; K. Turgeon, *unpublished data*). The increased threat posed by large males along the edge in Detour and Patch and the potential higher familiarity with neighbors on Continuous configuration (Levin et al. 2000) may explain why damselfish avoided conspecific territories along the edge in Detour and Patch but not on Continuous configurations.

Implications for conservation

In coral reef fishes, identifying the size at which a sand gap (or any other habitat feature) acts as a barrier to movement and how steep the barrier is has strong implications for the design of effective Marine Protected Areas. Boundaries between fished areas and reserves that are located on sufficiently large sand gaps will increase the protective effect of reserves and therefore the size and reproductive output of fish within their boundaries. On the other hand, when reserves are intended to provide postsettlement individuals to a fishery, it is important that boundaries cross continuous reef (Bartholomew et al. 2008) or small gaps between adjacent patches so that fish can emigrate toward adjacent fished areas (Kramer and Chapman 1999).

The empirical evidence we provide for a negative impact of dominant and aggressive individuals on conspecific movement along the edge could have strong implications for landscape restoration, especially when establishing corridors. The distribution of dominant individuals on fragmented configurations could block dispersal even after structural connectivity has been restored (Hilty et al. 2006).

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APPENDIX A

Generalized Linear Mixed Models used to explain the probability of crossing an imposed sand gap in Detour and Patch configurations in relation to environmental and social habitat predictors (*Ecological Archives* E091-235-A1).

APPENDIX B

Generalized Linear Mixed Models used to explain the number of agonistic interactions experienced during homing in relation to the deviation of the homing path and to the density of damselfish along the homing path (*Ecological Archives* E091-235-A2).

APPENDIX C

Summary table of the size and steepness of a barrier to movement for 11 species distributed among six studies in relation to species mass and territory diameter (*Ecological Archives* E091-235-A3).