

The influence of connectivity on richness and temporal variation of reef fishes

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Abstract To test the effects of connectivity on fish diversity in isolated reef patches we deployed pairs of artificial reefs (AR) at constant distances (12 and 25 m) from a large continuous reef and added series of small ARs to half of them. These small reefs served as stepping-stones to increase fish movement between the large ARs and the continuous reef. Species gain and loss curves were compared to obtain deeper understanding of the underlying mechanisms in relation to the theory of island biogeography. We found that AR without stepping-stones maintained up to 57-fold more individuals than ARs with stepping-stones during mass

recruitment events that were dominated by the family Apogonidae. However, in-between these mass recruitment events the overall impact of the stepping-stones on richness and abundance was small. By contrast, increasing distance from the continuous reef from 12 to 25 m increased fish richness, although this was confounded with time since AR deployment. Increase in richness with distance was predominantly caused by elevated species gain. Our results suggest that fish assemblages respond in distinct ways to two types of isolation: (1) Increased richness with distance from a continuous reef, and (2) increased fluctuation in abundance with decreased connectivity. The latter may be the outcome of accumulation and then abrupt emigrations of fishes from isolated reefs. This study confirms that the spatial setting of reef patches in relation to larger or continuous reefs alters fish assemblages, which may be important for planning AR deployments that maximizes diversity.

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Introduction

Understanding the causes and consequences of spatial heterogeneity for species diversity is one of the major goals of landscape ecology (Turner et al. 2001). The theory of island biogeography postulates that species

richness results from a dynamic equilibrium between the arrival of species and their extinction (MacArthur and Wilson 1967). The theory predicts richness to be highest on large continuous habitats (“mainland”) and decrease with increased isolation due to decreased immigration rates (although rescue effects may also raise extinctions and further lower richness). However, coral patch reefs have been found to contain greater species richness per area than continuous reefs (Ault and Johnson 1998; Chittaro 2002; Nanami and Nishihira 2003a). Moreover, it has been shown that fish diversity can actually increase with small-scale isolation (Shulman 1985; Walsh 1985; Belmaker et al. 2005; Jordan et al. 2005). These effects are likely to be scale-dependent as large and more isolated reefs may not necessarily show similar patterns (Acosta and Robertson 2002; Chittaro 2002; Dorenbosch et al. 2007).

Suggested explanations for increased diversity with isolation at small scales fall into four broad categories: (1) Halos of decreased food resources around continuous reefs. Reef based organisms (e.g. herbivorous fish and sea urchins) may form a halo of decreasing density or impact with increasing distance from the reef (Ogden et al. 1973; Posey and Ambrose 1994; Langlois et al. 2005). A patch reef located in proximity to a large continuous reef (or in proximity to another patch reef) may be within this halo, thereby offering reduced feeding opportunities and consequently reducing overall fish diversity (Jordan et al. 2005). (2) Greater attraction for fish recruits. Isolated reefs may pose a more conspicuous target for fish larvae compared to equivalent sized reefs closer to a continuous reef (Schroeder 1987). (3) Predation. Habitat type and spatial arrangement of habitat units have been shown to alter predation patterns (Nanami and Nishihira 2001; Belmaker et al. 2005; Overholtzer-McLeod 2006; Belmaker et al. 2009b). Predation pressure might decrease with distance from a continuous reef due to a predation halo (Shulman 1985; Sweatman and Robertson 1994; see hypothesis 1 above) or due to other behavioral mechanisms such as hampered predator aggregation on isolated patches (Belmaker et al. 2005). (4) Decreased post-settlement relocation. On coral-reef patches, fish assemblages may assume a metapopulation structure while post-settlement relocation may be enhanced on continuous reefs (Ault and Johnson 1998; Nanami and Nishihira

2002, 2003a). Reduced post-settlement relocation may increase diversity on isolated patches by facilitating metacommunity-based coexistence mechanisms such as colonization-competition tradeoffs (Leibold et al. 2004). In addition, fish may concentrate on isolated patches if following recruitment they are reluctant to leave a secure habitat and traverse stretches of unsuitable habitat with high predation pressure, as predicted by optimal foraging theory (Charnov 1976; Russell et al. 2006). Under the above hypotheses, fish diversity is either altered by connectivity, whereby other habitats are perceived by the organism to be more or less accessible from the examined patch, or by processes that simply covary with distance from other reefs but can be independent of connectivity. No study to date has attempted to tease apart these alternatives.

In this study, we experimentally increase connectivity between isolated artificial reefs (ARs) and a natural continuous reef by: (1) varying the distance between ARs and the continuous reef, and (2) adding a series of small ARs to half the ARs. These small ARs serve as stepping-stones (*sensu* MacArthur and Wilson 1967) for fish movement and are designed to increase post-settlement relocation between the ARs and the local continuous reef. The ARs with and without stepping-stones should be distinct only if processes related to connectivity are in operation, which correspond to reduced post-settlement relocation of fish or their predators with isolation (hypotheses 3 and 4 above).

To further gauge the causes of the discrepancy between observed patterns and island biogeography theory, we separate richness patterns to the unique contribution of species gained and species lost. This allows us to further tease apart the mechanisms associated with increased diversity on isolated reefs. For example, reduced predation or reduced post-settlement emigration will reduce species loss while increased recruitment will increase species gain. Since accurate time series data is needed for such analyses, the examination of species gain and loss curves has seldom been attempted (but see Gilpin and Diamond 1976; Russell et al. 2006). The relatively long timeframe for which the ARs were assessed in this study (5 years) provides a unique opportunity to assess the causes of reef fish diversity deviation from conventional island-biogeography theory.

Methods

Study site and experimental design

The study was conducted in the northern-most part of the Gulf of Aqaba, Red Sea ($29^{\circ}32'N$, $34^{\circ}58'E$). A large and low (height < 2 m) natural continuous reef runs in a general east–west direction parallel to the shore and ~ 200 m from it at a depth of ca. 25 m (Fig. 1). Four pairs of replicate ARs were deployed at a depth of 22–24 m away from the natural reef on a sandy bottom with no seagrass cover and that was generally devoid of coral-reef associated fish. During the first 3 years the ARs were placed at a distance of 12 m away from the continuous reef (Fig. 1a), while for the final 2 years of this study they were relocated to

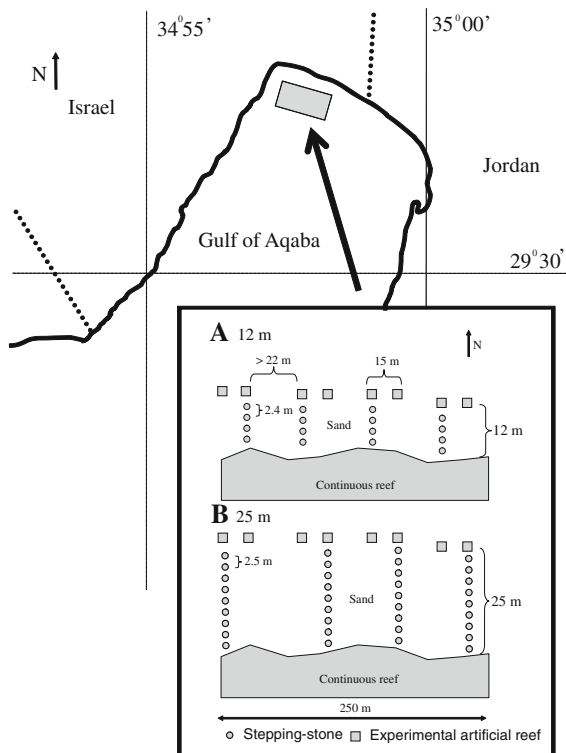


Fig. 1 Map of the northern Gulf of Aqaba, with the area of study site in grey and a schematic representation of the study design enlarged. During the first 3 years of the study the ARs were placed at a distance of 12 m from the continuous reef (a), while during the final 2 years ARs were relocated to a distance of 25 m (b). The locations of the stepping-stones were switched among AR-pairs following relocation. The sizes of ARs and stepping-stones are not to scale

a distance of 25 m (Fig. 1b). For ARs we built 1 m^3 model units made of a metal frame on which a plastic mesh was added in a manner that increased the structural complexity, offering a variety of permanent and transient refuges, while still enabling visual census (Fig. 2; see also Belmaker et al. 2005). To reduce the potential influence of AR-based sea urchin grazing haloes on fish distribution, and to avoid silting, we suspended the reefs 0.8 m above the substrate. This was done by connecting two large (20 l) floatation devices to each AR. The ARs were deployed at a constant distance from a large natural continuous reef in pairs located 15 m apart, with between-pair distance in the range of 22–98 m (inter-pair distances were heterogeneous due to constraints imposed by sea floor structure). While some movement of fish between ARs within a pair was possible, 15 m of open sand was likely enough to reduce most such relocations (Turgeon et al. 2010) especially as visibility within the study area was usually <12 m. Relocations between AR pairs will serve to reduce the total effect of the stepping-stone treatment (see below) making differences among AR pairs conservative.

Visual censuses of fish assemblages were carried out quarterly (usually in the last 2 weeks of January, April, July and October) for the entire duration of the study (2003–2007; for a total of 20 censuses on each

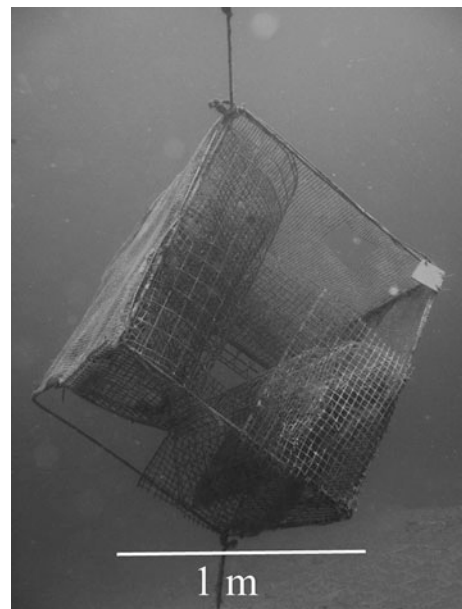


Fig. 2 An experimental AR unit

AR). Surveys were always performed between 6:00 and 8:00. Due to the depth of the ARs (>20 m) we did not consider tidal phases. All surveys were conducted by a single diver (J.B.) with extensive training in under water fish identification, including small and cryptic species (Belmaker et al. 2007, 2008; Belmaker 2009). All fishes that swam within a distance of 0.5 m from the ARs were recorded, i.e., we did not have a minimal size criterion. Only three out of the 67 observed species could not be identified to species level (Supplementary material, Appendix). The survey of each AR was terminated when a new species was not detected for at least 1 min. Fish species that are piscivorous as adults were considered potential predators, while all other species were deemed prey (Supplementary material, Appendix). We acknowledge that this is a simplification of the complex dietary preferences of most fish, but more specific diet categories could not be estimated without detailed gut content analysis.

To experimentally increase connectivity between the ARs and the continuous reef we added to one member of each AR pair 4 small ARs placed at 2.5 m intervals that served as stepping-stones for fish relocation (Fig. 1). Stepping-stones were made of plastic mesh cylinders 30 cm long and 30–45 cm in diameter. As with the larger ARs, these stepping-stone reefs were suspended 0.8 m above the sandy substrate. We switched the presence of stepping-stones between pair members when ARs were relocated from 12 to 25 m away from the continuous reef. Additional five stepping-stones were added at this stage to maintain similar inter stepping stones distances.

Species gain and loss curves

The theory of island biogeography postulates that insular species richness is determined by a dynamic equilibrium between species gained and lost. To separate variation in species gain or loss curves as predictors of species richness heterogeneity we explicitly modeled the number of species gained or lost during a time interval in relation to the distance of the ARs from the natural continuous reef and the presence of stepping-stones. Notice, however, that the observed species gains and losses is modeled and not the true underlying colonization and extinction rates as we do not account for extinction of a species after it colonized

or re-colonization after a species has become extinct. The observed rates approximate the underlying rates over sufficiently small time intervals.

Species gains and losses may depend on species richness either linearly, as predicted by simple non-interactive models, or concavely when interspecific interactions or variation in immigration and extinction are evoked (MacArthur and Wilson 1967; Gilpin and Diamond 1976). Similar to the classical theory of island-biogeography and similar models (Clark and Rosenzweig 1994; Russell et al. 1995, 2006; Belmaker et al. 2009a), we do not explicitly introduce variation among species. However, by allowing non-linear species gain and loss curves we implicitly allow for such variation. Moreover, low interspecific variation is probably a good approximation of fish dynamics on small isolated patches that display stochastic community assembly with little interspecific signal (Sale et al. 1994; Ault and Johnson 1998; Belmaker et al. 2007).

Statistical models

We used linear mixed-effect models (Diaz-Urriarte 2002), implemented in a Bayesian framework, to analyze fish diversity patterns. To determine the best subset of predictors and their interaction during model development, we used the deviance information criterion (DIC, Spiegelhalter et al. 2002). The DIC is conceptually similar to the Akaike Information Criterion (Burnham and Anderson 2002), allowing to choose the best model after penalizing for increased complexity when using Markov Chain Monte Carlo (MCMC) techniques. A difference of more than two in DIC values implies that a particular model is considerably superior over the other.

The linear contrast in species richness between ARs without and with stepping-stones for the i 'th pair, during time the t 'th survey period was modeled as a random draw from a normal distribution with mean Δy and variance σ^2 , such that:

$$\begin{aligned} \Delta y_{i,t} &= y_{\text{no stepping-stones } i,t} - y_{\text{stepping-stones } i,t} \\ &= \beta_0 + \beta_1 * D_t + \pi_t + e_{i,t} \end{aligned} \quad (1)$$

where D is a categorical predictor indicating whether the AR is at a distance of 25 m from the continuous reef, π is the random effect associated with the survey, e is random error and β_0 and β_1 are unknown

parameters. A significant effect of the stepping-stones or distance is associated with parameters β_0 or β_1 , respectively, presenting credible intervals that do not encompass zero. Adding a random effect associated with AR pair or adding an interaction between β_0 and β_1 did not improve model fit ($\Delta\text{DIC} < 2$). π and e were modeled as drawn from a normal distribution such that: $e \sim \text{Normal}(0, \theta_e^2)$ and $\pi \sim \text{Normal}(0, \theta_\pi^2)$. We used uninformative priors, so that $\beta_0/\beta_1 \sim \text{Normal}(0, 1000)$ and $\sigma/\theta_e/\theta_\pi \sim \text{Uniform}(0, 100)$.

When using abundance as the response, we also detected large recruitment events that were clearly not appropriately captured with the above model. We therefore used the following model:

$$\begin{aligned} \Delta y_{i,t} &= y_{\text{no stepping-stones } i,t} - y_{\text{stepping-stones } i,t} \\ &= \beta_0 + \beta_1 * D_t + \beta_2 * \mu + \pi_t + e_{i,t} \end{aligned} \tag{2}$$

which is equivalent to Eq. 1 apart from the addition coefficient β_2 that occurs at probability μ . Credible intervals of β_2 that do not include zero imply large recruitment events occur mostly of ARs without stepping stones. The prior distribution of μ was: $\mu \sim \text{Beta}(1,1)$. This model resulted in much better model fit ($\Delta\text{DIC} = 247$) when compared to Eq. 1.

Similar models were used to simultaneously model the number of species gained or lost during a time interval. The number of species gained was modeled as a random variable drawn from a Poisson distribution such that $\text{Gain}_{i,t} \sim \text{Poisson}(\lambda_{i,t})$, while the number of species lost was drawn from a Binomial distribution $\text{Loss}_{i,t} \sim \text{Binomial}(SR_{i,t}, \delta_{i,t})$, where SR is the species richness at the onset of the time interval. The rate of species gain λ and the per-species probability of loss δ were set as:

$$\begin{aligned} \text{link}(\delta_{i,t}/\lambda_{i,t}) &= \beta_0 + \beta_1 * D_t + \beta_2 * StSt_{i,t} + \beta_3 \\ &\quad * SR_{i,t} + \pi_t + e_{i,t} \end{aligned} \tag{3}$$

where the *link* function is log for λ (species gain) and logit for δ (species loss), SR is species richness, $StSt$ is a categorical predictor indicating whether stepping stones are present or absent and $\beta_0, \beta_1, \beta_2$ and β_3 are unknown parameters. A significant effect of distance or stepping-stones is associated with parameters β_1 or β_2 , respectively, presenting credible intervals that do not encompass zero. We used uninformative priors, so that $\beta_0/\beta_1/\beta_2/\beta_3 \sim \text{Normal}(0, 10)$ and $\sigma/\theta_e/\theta_\pi \sim \text{Uniform}(0, 10)$. The tighter prior distributions

were necessary to reach convergence. Note that, as species richness is a part of the binomial loss function, the parameter β_3 allows for non-linear dependence of species loss on AR richness while for species gain this same parameter represents a linear relationship.

The model parameters were estimated using Gibbs sampling, a MCMC technique, implemented in the computer package WinBUGS (Spiegelhalter et al. 2004). Convergence diagnostics was performed using three chains with dissimilar initial values by examining the Brooks–Gelman–Rubin statistic (Brooks and Gelman 1998). After a burn-in period of 8,000 iterations all parameters demonstrated convergence, and the value of the posterior distributions was estimated from 8,000 additional iterations of the three MCMC simulation chains.

The relationship between average prey and predator abundance on the ARs was examined using Pearson’s correlation. We excluded from this analysis surveys conducted during peak recruitment that may represent anomalous events (total individuals >50). The correlation for ARs with and without stepping-stones were compared by first applying the standard Fisher’s z -transformation (z), modified for small sample size, to the correlation coefficient, r , which can then be compared to $t_{\alpha[\infty]}$ (Sokal and Rohlf 2000). In this analyses predator abundance was square-root transformed and prey abundance $\log_{10}(x + 1)$ transformed, to improve the adherence to the assumption of normality.

Results

Mass recruitment events, encompassing as much as a 57-fold increase in density, were recorded exclusively on reefs without stepping-stones (Fig. 3). The direct influence of stepping-stone absence on these recruitment events is strengthened by the fact that they appeared only on ARs without stepping-stones, even though the location of the stepping-stones was switched between ARs within a pair when moved from a distance of 12–25 m. Nevertheless, during regular surveys, ARs without stepping-stones did not have more individuals or species than reefs with stepping stones, and the difference between them was independence of distance from the natural continuous reef (Fig. 3). Although mass recruitment events were striking, they were short lived and ARs with and

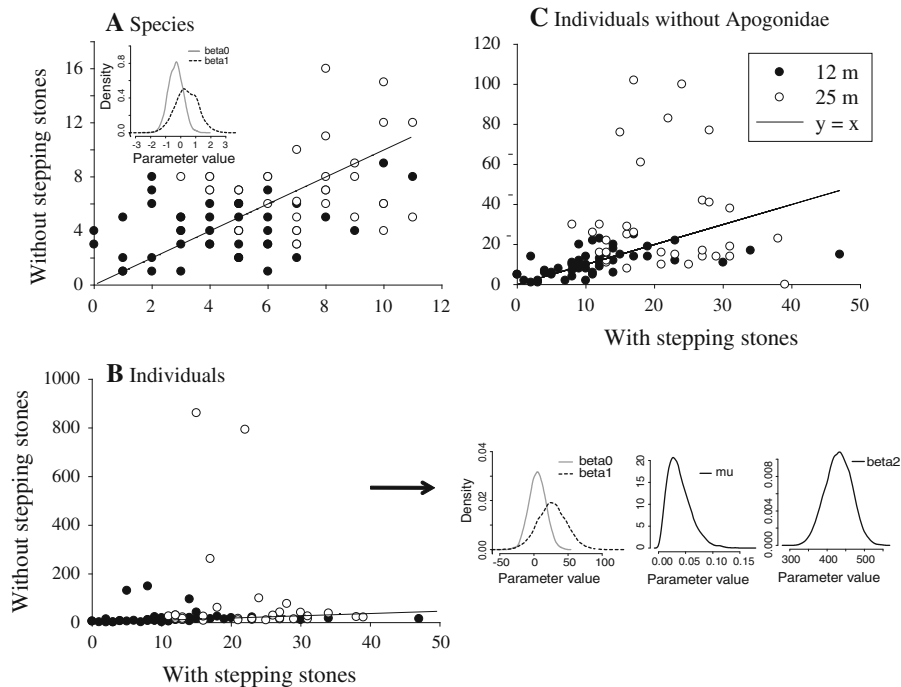


Fig. 3 The number of **a** species; **b** individuals; and **c** Individuals excluding the Apogonidae family, on the ARs without stepping-stones plotted against their paired ARs with the stepping-stones. Each point represents a single survey and no distinction is made between spatial and temporal replication. The four pairs of ARs were either located 12 m away from the continuous reef (*full dots*) or 25 m away (*empty dots*). Points above the solid $y = x$ line indicate higher values for ARs without stepping-stones. Posterior distributions of the parameters associated with the statistical models are shown as *insets*.

without stepping-stones usually displayed similar densities by the following survey (3 months interval). Although several different fish species were found to recruit together, recruitment events were dominated by members of the family Apogonidae (compare Fig. 3b and c).

To further examine richness patterns in relations to island-biogeography theory, we broke down total richness changes to the species gain and loss curves. We found that increasing the distance from 12 to 25 m from the continuous reef resulted in increased species gained (Fig. 4a; 95% credible intervals for β_1 gain that do not include zero: $0.15 < \beta_1 < 0.83$) and to a lesser extent reduction in species lost (95% credible intervals for β_1 loss that include zero: $-1.23 < \beta_1 < 0.09$; $\Delta\text{DIC} < 2$). In contrast, the presence of stepping-stones had little effect on species gained or loss (Fig. 4b; 95% credible intervals for β_2 that

In both (a) and (b) the posterior distribution of β_0 and β_1 overlap zero and $\Delta\text{DIC} < 2$, indicating little difference between ARs with and without stepping stones and that this difference is independent of distance from the continuous reef. In contrast, for β_2 in (B) credible intervals did not encompass zero and $\Delta\text{DIC} = 247$ (compared to a model without β_2), indicating that large recruitment events, occurring at probability μ , are predominantly associated with ARs without stepping-stones

include zero. β_2 gain: $-0.19 < \beta_2 < 0.25$; β_2 loss: $-0.10 < \beta_2 < 0.52$; in both cases $\Delta\text{DIC} < 2$). Finally, species gain was independent of species richness (95% credible intervals for β_3 gain that include zero: $-0.09 < \beta_3 < 0.20$; $\Delta\text{DIC} < 2$) while species loss was curvilinearly dependent on richness, as evident by an effect of species richness beyond that incorporated into the binomial loss function (95% credible intervals for β_3 loss: $0.01 < \beta_3 < 0.17$).

The average abundance of predatory fish was not significantly different between reefs with and without stepping-stones (12 m away: $F_{1,4} = 0.01$, $P = 0.84$; 25 m away: $F_{1,4} = 0.49$, $P = 0.49$). Although the correlation between predator and prey abundance was higher on ARs with stepping-stones (Pearson's correlation; $r = 0.79$, $n = 8$, $P < 0.05$) than on reefs without stepping-stones (Pearson's correlation; $r = 0.35$, $n = 8$, $P = 0.39$), this difference was not

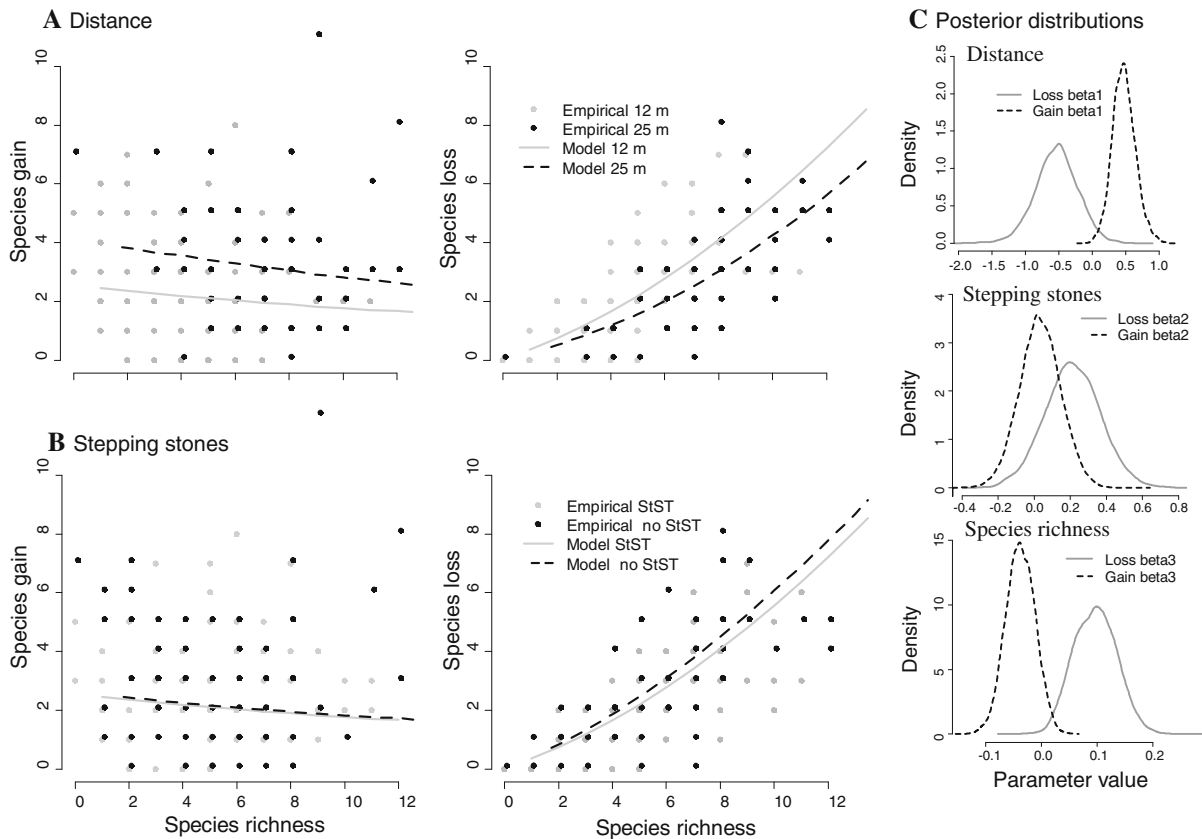


Fig. 4 Species gain and loss in relation to species richness, displaying the effect of **a** distance from the continuous reef; **b** the presence of stepping stones (*StSt*); and **c** the posterior distributions of the parameters associated with distance, *StSt*

and species richness (β_1 , β_2 and β_3 , respectively). Dots represent empirical relationships and lines are the mean predictions from the statistical models

significant ($P > 0.05$). The average number of predatory fish on the ARs increased after relocation from 12 to 25 m (paired *t* tests; $t_{ratio} = 3.1$, $df = 7$, $P < 0.05$).

Discussion

By manipulating both distance from a natural continuous reef and connectivity directly, through the addition of stepping-stones, we were able to address the underlying causes of increased diversity in isolated small patch reefs. We found that fish richness increased with distance from the continuous reef. In contrast, the presence of stepping-stones did not have an effect on either richness or abundance during periodic surveys. However, extreme recruitment events, both when the ARs were at 12 m and

when at 25 m away from the continuous reef, occurred exclusively on reefs without stepping-stones (Fig. 3b). The presence of stepping-stones should not alter anything but post-recruitment relocation. Therefore, providing corridors for fish movement via stepping-stones can modify total fish abundance, even at distances as small as 12–25 m, indicating that small-scale isolation can pose a significant barrier to the dispersal of some coral-reef fish (see also Turgeon et al. 2010).

The presence of more individuals on ARs without stepping-stones during mass recruitment suggests that reduced connectivity may increase abundance by hampering effective post-settlement relocation and forcing fish to temporarily remain on isolated ARs. However, as ARs with and without stepping-stones eventually reached similar abundance levels, it appears that connectivity influences the time it takes

to emigrate without altering the underlying AR's carrying capacity. This is in line with the proposition that on patch reefs fish post-settlement relocation is reduced and assemblages may assume a temporal metapopulation structure (Ault and Johnson 1998; see also Nanami and Nishihira 2003b). Similar evidence for higher temporal variability in abundance with increased isolation was recently obtained at much larger spatial scales (Mellin et al. 2010). The absence of large recruitment events on ARs with stepping-stones further suggests that post-recruitment relocation between the ARs and the continuous reef might buffer fish assemblages against fluctuations caused by environmental variability or unpredictable recruitment. This supports previous studies that suggest that predictability of fish abundance by environmental variables is higher (Ault and Johnson 1998; Nanami and Nishihira 2002, 2003b).

Although we found significant differences in fish abundance between ARs with and without stepping-stones the overall effect was small during most years. Nearly all differences found during seasons of extremely high recruitment disappeared by the following censuses. In addition, most of the difference could be attributed to a single fish family—Apogonidae (compare Fig. 3b and c). Strong fluctuations in the abundance of Apogonidae in isolated, but not continuous, habitats have also been observed in other studies (Nanami and Nishihira 2002, 2003a, b). Therefore, this group appears to be particularly responsive to connectivity. Many members of the Apogonidae family, characterized by small size and cryptic lifestyle, are particularly attracted to complex habitats where they roost during the day (Mellin and Ponton 2009). As these species may disperse to feed over the open habitats at night, ARs positioned on a sandy or seagrass bottoms may be more attractive than ARs over coral reefs (Mellin and Ponton 2009). Nevertheless, this cannot explain the difference in Apogonidae abundance between ARs with and without stepping-stones as both were found on similar substrate and at similar distances. Thus, the observed difference must originate from a direct response to connectivity. The presence of Apogonidae reduces predation pressure on other species via positive indirect effects (Webster and Almany 2002). Consequently, the higher overall fish diversity frequently found on isolated habitats might, to some degree, be an indirect consequence of the

higher abundance of Apogonidae leading to lower predation on other species.

While most studies concentrate on examining variation in species richness, we were able to use the long duration for which the ARs were observed to separate total richness to the number of species gained and lost. This allows us to directly examine the variation in species gain and loss in relation to connectivity and island-biogeography theory. Under the simplest island-biogeography scenario, invoking no biological interactions among species who share similar dispersal and extinction probabilities, both species gain and loss curves are linearly related to richness. Species interactions and interspecific variation in colonization and extinction rates are expected to make these curves curvilinear (MacArthur and Wilson 1967; Gilpin and Diamond 1976), reducing the temporal variance in species richness (Diamond and Gilpin 1980). Surprisingly, we found the number of species gained to be almost invariant to species richness (Fig. 4a, b). As species gain should decrease with species richness as the pool of potential colonizers is exhausted, this suggests that the number of potential colonizers is so large that the dependence on richness cannot be statistically detected. The absence of curvilinearity in the species gain curve also downplays the importance of biological interactions and variation among species for AR colonization. In contrast, we find species loss to be curvilinearly related to richness. This means that either interspecific interactions enhance extinction probabilities as richness increases or that species differ in their extinction probabilities. One likely reason for differences in extinction probabilities is variation in the predisposition of species to traverse exposed habitat (Chapman and Kramer 2000), and thus emigrate out of the ARs.

Increased richness with distance from the continuous reef was associated with increased species gain and to a lesser extent decreased species loss (credible intervals for the latter overlapped 0; Fig. 4a). However, distance was confounded with time because all ARs were relocated to 25 m after 3 years. It is therefore conceivable that succession has elevated diversity on these ARs independent of distance. Nevertheless, we found little evidence of structural modification of the ARs through time as most epifauna consisted of algae and mollusks that displayed high seasonal turnover accompanied by little buildup. If distance is indeed the main factor associated with

increased richness, and not deployment time (age), our results are consistent with elevated post-recruitment relocation to distant reefs, for example due to increased resources associated with being distant from the grazing halo of reef-based organisms (Langlois et al. 2005). Although direct recruitment might have been elevated in distant reefs, we feel this to be unlikely as ARs at both distances contained predominantly adult fish (outside of mass recruitment events).

Increased species gain with distance, in particular, seems at odds with the theory of island biogeography (MacArthur and Wilson 1967), empirically verified in numerous systems (Rosenzweig 1995). We suggest that at scales of 10 s of meters, the decrease in immigration rates with distance might have been overridden by the increased tendency of fish to move to, and remain on, ARs following the higher resources present around them. This hypothesis can also explain the scale-dependence of this pattern, where at larger scales the expanse of open habitat separating the patch from the continuous reef becomes a larger obstacle for fish movement resulting in a decrease in richness with isolation.

As predatory fish may themselves be reluctant to traverse a great expanse of shelter-free habitat, isolation may decrease predation pressure in small isolated reefs, thereby increasing fish abundance and richness (Shulman 1985; Sweatman and Robertson 1994; Belmaker et al. 2005). However, predator abundance was similar in ARs with and without stepping-stones. Moreover, the number of predators did not decrease (it actually increased) when distance from the continuous reef was increased, although fish abundance and richness were elevated. This combines with the evidence for elevated species gain as a major driver, to suggest reduced predation is not the main cause of higher richness and abundance in distant reefs. Nevertheless, the interaction between transient and resident predators may have strong implications for prey mortality (Hixon and Carr 1997) and transients may be more prevalent on connected reefs (Overholtzer-McLeod 2006). As the presence of transient predators, such as the members of the family Carangidae, cannot be accurately estimated from our censuses we cannot entirely dismiss the role of predation in shaping diversity patterns. It is also noteworthy that the correlation between predator and prey abundance was higher on ARs with stepping-stones (although not significantly

so, possibly due to low power). This may indicate that the ability of predators to respond to changes in prey density may be hampered in distance or less connected reefs.

Separating richness to gain and loss curves allowed us to demonstrate that neither is strongly affected by connectivity, as manipulated by the presence of the stepping-stones. The small overall effect of the stepping-stones compared to the distance from the natural reef in shaping patterns of fish richness and abundance suggests that altered connectivity, and thus post-recruitment relocation, is not the main factor causing elevated richness on isolated patches. However, both elevated diversity (Shulman 1985; Walsh 1985; Belmaker et al. 2005; Jordan et al. 2005) and decreased predictability (Ault and Johnson 1998; Nanami and Nishihira 2002, 2003b) have been associated with decreased connectivity. As richness and abundance are often regulated by different mechanisms (Mellin et al. 2007), fish assemblages might respond to two distinct ways to isolation: (1) Increased diversity with distance from a continuous reef, and (2) Increased fluctuation in abundance, and hence predictability, with decreased connectivity. Increased fluctuation in abundance may be the joint outcome of stochastic and unpredictable predation, evident here by the lower correlation between predators and prey on ARs without stepping stones (see also Belmaker et al. 2005), and behavioral reluctance to traverse open unsheltered habitats (Chapman and Kramer 2000). Behavioral reluctance to emigrate out of isolated patches might escalate fluctuations in abundance in the presence of threshold behaviors, where individuals that are reluctant to emigrate at low densities do so at high densities. Although more detailed behavioral observations are needed to ascertain this hypothesis, we believe such behavior thresholds underlie the accumulation of individuals and their abrupt disappearance from ARs without stepping-stones.

From an applied perspective, ARs are frequently used to mitigate anthropogenic habitat and diversity losses. The results suggest that, at the scale of 10 s of m, AR configurations that constitute of isolated and distant reefs will achieve higher overall fish diversity when compared with similar sized, tighter spaced ARs closer to continuous reefs. Our study combine with others at small scales (Ault and Johnson 1998; Overholtzer-McLeod 2004; Jordan et al. 2005;

Overholtzer-McLeod 2006), larger scales (Dorenbosch et al. 2007; Fernandez et al. 2008; Grober-Dunsmore et al. 2008; Mellin et al. 2010), and those examining inter-habitat relationships (such as mangroves, seagrass and coral reefs; Mumby et al. 2004; Grober-Dunsmore et al. 2007; Mumby and Hastings 2008) to demonstrate that habitat configuration and connectivity can profoundly influence fish diversity.

In this study, we adapted the patch-mosaic paradigm of landscape ecology (sensu McGarigal and Cushman 2005) to explore how the processes of colonization and extinction shape diversity patterns on spatially distinct ARs. However, natural reefs are likely also comprised of continuous multi-dimensional gradients that do not easily succumb to categorization into suitable and unsuitable habitats. Understanding how connectivity influences diversity in complex landscapes while accounting for variability in perception distances and behavior remains a major future challenge.

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