Reef size and isolation determine the temporal stability of coral reef fish populations

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Abstract. Temporal variance in species abundance, a potential driver of extinction, is linked to mean abundance through Taylor's power law, the empirical observation of a linear log–log relationship with a slope between 1 and 2 for most species. Here we test the idea that the slope of Taylor's power law can vary both among species and spatially as a function of habitat area and isolation. We used the world's most extensive database of coral reef fish communities comprising a 15-year series of fish abundances on 43 reefs of Australia's Great Barrier Reef. Greater temporal variances were observed at small and isolated reefs, and lower variances at large and connected ones. The combination of reef area and isolation was associated with an even greater effect on temporal variances, indicating strong empirical support for the idea that populations on small and isolated reefs will succumb more frequently to local extinction via higher temporal variability, resulting in lower resilience at the community level. Based on these relationships, we constructed a regional predictive map of the dynamic fragility of coral reef fish assemblages on the Great Barrier Reef.

Key words: bootstrapping; conservation; coral reef fish; extinction risk; Great Barrier Reef; island biogeography; randomization test; resilience; stochasticity; Taylor's power law.

Introduction

The ongoing decline and degradation of coral reef ecosystems worldwide (Hoegh-Guldberg et al. 2007, De'ath et al. 2009) underpins the need to quantify the relative impacts of human-induced stressors on these centers of species diversity and endemism, and identify the major drivers of their resistance and resilience (Mumby et al. 2006, Carpenter et al. 2008). Cost-effective allocation of management resources requires tractable methods for prioritizing areas for conservation (Margules and Pressey 2000, Myers et al. 2000). Central to this goal is an ability to rank reefs from those that are most susceptible to disturbance to those that might act as sources for recolonization.

The temporal stability of fish abundances is likely to be an important metric of resilience of coral reef communities to disturbance. In non-reef ecosystems, both theoretical and empirical evidence suggests that sources of demographic and/or environmental stochasticity that cause large fluctuation in population abundance increase the risk of successive bottlenecks (Brook et al. 2008, Melbourne and Hastings 2008) and of total (or effective) abundance falling below a population's

minimum viable size, ultimately leading to its extinction (Caughley 1994, Brook et al. 2006). This risk is expected to increase in coming decades, with major drivers of extinctions displaying synergistic effects under global change (Brook et al. 2008, Melbourne and Hastings 2008).

The temporal stability of assemblages also tends to be positively related to species richness, with lower richness implying fewer but stronger interactions within assemblages (Caughley 1994, McCann 2000). Moreover, species richness generally increases with patch size of habitats and decreases with population isolation (MacArthur and Wilson 1967). Although such relationships are well-established in terrestrial ecosystems (e.g., Lomolino and Weiser 2001), area and isolation effects on community structure and dynamics have only been recently demonstrated for some coral reefs (Sandin et al. 2008). The idea that the temporal stability of fish assemblages on coral reefs varies as a function of reef area and isolation (Graham et al. 2006) has not yet, however, been tested empirically.

We used a 15-year data set of fish abundances obtained from 43 reefs of Australia's Great Barrier Reef (GBR) to test the relationships between reef area and isolation and temporal stability of fish communities. Taylor's power law predicts that the (temporal or spatial) variance of a species' abundance σ^2 increases

with mean abundance μ according to the power law $\sigma^2 = \alpha\mu^\beta$ (Taylor 1961). On a log–log plot, the variance-mean relationship has slope β. This relationship has now been reported for more than 400 species with most slopes falling between 1 and 2, and occasionally >2 (e.g., Taylor et al. 1976). The null expectation for Taylor's power law is $\beta = 2$; however, deviations can result from community-level interactions including direct or indirect competition (Kilpatrick and Ives 2003). Here we test the idea that deviations from Taylor's power law are also a function of reef area and isolation. Specifically, we predicted that fish communities on small, isolated reefs have a higher temporal variance in abundance, potentially indicative of reduced community stability, compared to larger, less-isolated reefs. This prediction is tested on individual fish species and then used to derive regional predictions of fish community resilience to disturbance.

METHODS

Study reefs

The GBR consists of more than 2900 reefs extending over 2300 km between 9° S and 24° S latitude and covering approximately 350 000 km^2 (Appendix E). Between 1992 and 2006, reef communities of the GBR have been monitored yearly by the Australian Institute of Marine Science's (AIMS) Long Term Monitoring Program (LTMP; Sweatman et al. 2005). As part of the LTMP, fish communities have been surveyed on 48 reefs in six sectors (Cooktown/Lizard Island, Cairns, Townsville, Whitsunday, Swains [see Plate 1], and Capricorn Bunkers) spanning much of the GBR (Appendix E). In each sector (with the exception of the Swains and Capricorn-Bunker sectors), at least three reefs were sampled in each of three shelf positions (i.e., inner, mid, and outer).

Survey methods and fish data collection

At each reef, three sites in a single habitat (the first stretch of continuous reef on the northeast flank of the reef, excluding vertical drop-offs) and separated by >250 m were selected for sampling. Within each site, five permanently marked 50 m long transects were deployed roughly parallel to the reef crest, each separated by 10–40 m along the 6–9 m depth contour. Within these transects, abundances of 251 species representing 10 families (Appendix A) were estimated each year. Small site-attached species such as damselfishes (Pomacentridae) were counted in a 1 m wide strip and a 5 m wide transect was used for larger, mobile species (see Halford and Thompson 1996 for detailed methods). Only adult fish (>1 year old) were recorded, these being distinguished from juveniles by their size and coloration. Over this period, sites were sampled by different divers. All divers completed annual calibration exercises to ensure consistency (i.e., there were no systematic biases) using proven methods (Halford and Thompson 1996).

Because data were missing for five of the 48 reefs, only data from 43 reefs were considered here. This data-culling ensured that the same number of yearly samples was considered for each reef. For each fish species, a mean yearly estimate of abundance recorded at each reef (N) was calculated as the total number of individuals recorded at each reef (5 transects $\times$ 3 sites) divided by the number of years sampled (15). Temporal variance of abundance observed for each reef and for each fish species (σ^2) was calculated as the variance among the 15 yearly estimates of abundance.

Reef area and isolation

Reef area and isolation were estimated for the study reefs, as well as for all reefs of the GBR, from a shapefile (computed from a Landsat TM image) where each reef was represented by a minimum convex polygon and using geographic information system packages in R (packages PBSmappping and spatstat; R Development Core Team 2008). Reef area (in km^2) was defined as the total area of underwater reef from datum to 30 m depth. Reef isolation was primarily defined according to area-based (i.e., buffer) measures, which are more appropriate to describe habitat connectivity in fragmented landscapes than simple distance-based (i.e., nearest-neighbor) measures (Moilanen and Nieminen 2002). Nonetheless, we also compared these results with a distance-based measure, i.e. the shortest distance to the nearest reef or land mass. Area-based isolation (in km^2) was estimated as the total non-reef and non-land areas within increasing radii from each of the surveyed reefs, excluding the area of the focal reef. We used 10, 30, 70, and 150 km as radial distances because larval dispersal distances for a variety of reef fishes are thought to be typically on the order of 0 to 100 km (Kinlan and Gaines 2003, Cowen et al. 2006). The indices of reef isolation estimated using increasing radii were correlated (Spearman's $\rho > 0.23$; $P < 0.001$); however, we used the 70-km radius to quantify reef isolation because it contributed most to the first axis of a principal component analysis of reef isolation indices and gave the most even distribution of reefs along an isolation gradient (Appendix B, Appendix F).

Analysis

Among the 251 fish species observed on the GBR, we selected those that matched the criteria proposed by Gaston and McArdle (1994) to ensure an appropriate analysis of variance–mean relationships. These criteria were that (1) the samples (i.e., yearly counts on each reef) on which the variance was based should number more than 15, (2) there should be more than five variance–mean pairs (i.e., reefs), and (3) the range of abundances should be as large as possible, ideally encompassing at least two orders of magnitude. A total of 18 species from six families (Appendix C) matched these criteria and were analyzed here. Potential effects of reef area and isolation on species abundances were

investigated using a multivariate analysis of variance (MANOVA) using a Bray-Curtis distance matrix and 1000 permutations (Legendre and Anderson 1999).

The $\log(\hat{\sigma}^2)$–$\log(\hat{N})$ regression was calculated for each species separately using all 43 reefs. Interspecific differences in the estimate of the regression slope ($\hat{\beta}$) were investigated using general linear mixed-effect models (GLMM) including the taxon (genus nested within family) as a random effect accounting for the non-independence of species due to shared evolution (e.g., Bradshaw and Brook 2010), and maximum adult total length (L_∞, in cm; Froese and Pauly 2009) and total abundance across all reefs and years (N_t) as fixed effects. Models were compared using Akaike's information criterion corrected for small sample sizes (AIC_c) that provides an index of Kullback-Leibler information loss and was used to assign relative strengths of evidence to the competing models (Burnham and Anderson 2002). The percent deviance in $\hat{\beta}$ that is explained by the model (D) provided an index of a model's goodness-of-fit. Partial residuals as a function of L_∞ were plotted to visualize relationships.

Reefs were then ranked according to reef area and a sliding window was used to select 12 reefs of increasing area with a step of 1 for a total of 31 groups of reefs. For each group of reefs, the $\log(\hat{\sigma}^2)$–$\log(\hat{N})$ regression was computed for each species. The mean and standard deviation of $\hat{\beta}$ observed for a given group of reefs were then calculated across the 18 species. The same analysis was done for reef isolation.

To provide statistical evidence for the relationship between Taylor's power law slopes and reef area (or isolation), we constructed a randomization test where the sliding window procedure was reiterated 1000 times after randomly permuting the area (or isolation) estimates associated with the 43 reefs. The resulting variation in Taylor's power law slopes (δ) described the relationships with area and isolation expected under a null model, against which the observed relationships can be compared. To test for potential biases in these observed relationships arising from measurement error, we constructed a bootstrapping procedure based on a resampling-with-replacement design. We randomly resampled transects within a site 1000 times for each reef and recalculated the slopes of the power-law relationship using the sliding window procedure. Resampling was done at the transect level because variation in fish abundances among transects within the same site was most likely to reflect any measurement error, whereas variation among sites within a reef largely arises from factors such as wave or current exposure. The variation in the resulting slopes (δ') with area (or isolation) described the observed relationships while encompassing a possible measurement error (i.e., variance of the δ' distribution). Where the distributions of δ and δ' differ, this indicates evidence for a relationship between Taylor's power law slopes and reef area (or isolation) that is not affected by the effects of assumed measure-

ment error. The R code used for the randomization and bootstrapping procedures is available upon request by emailing the authors.

To examine interactive effects of reef area and isolation on $\hat{\beta}$, reefs were evenly divided among three size classes of reef area and three classes of isolation. The classes of reef area and isolation were then combined to produce a 3×3 matrix, each matrix cell being the combination of one class of area and one class of isolation, and consisting of four or five reefs. For each species, the $\log(\hat{\sigma}^2)$–$\log(\hat{N})$ regression was recalculated using reefs corresponding to each cell of the matrix successively, and $\bar{\beta}$ (mean $\hat{\beta}$) was calculated from the 18 species-specific values of $\hat{\beta}$.

All reefs of the GBR (i.e., over 2900 reefs) were then assigned one class of area and one class of isolation using the classification defined above for the sampled reefs. Mean expected $\hat{\beta}$, as defined in the aforementioned 3×3 matrix, was assigned to each reef of the GBR and mapped.

RESULTS

The $\log(\hat{\sigma}^2)$–$\log(\hat{N})$ regression consistently gave values of $\hat{\beta} < 2$ for all species ($1.16 < \hat{\beta} < 1.84$; Fig. 1). The highest-ranked GLMM explained 83.3% of deviance in $\hat{\beta}$ from a combination of family, genus and L_∞ (Table 1); L_∞ alone explained ~35% in the deviance in $\hat{\beta}$ and was negatively correlated with $\hat{\beta}$ (Appendix G). The permutation MANOVA indicated an effect of reef area on species abundances ($P < 0.001$, $R^2 = 0.18$; see Appendix C for coefficients), but no evidence for an effect of reef isolation as per area ($P = 0.410$, $R^2 = 0.02$) or distance ($P = 0.564$, $R^2 = 0.01$).

According to the sliding window procedure, mean $\hat{\beta}$ across species decreased with reef area [$\delta' \sim \mathcal{N}(-0.015, 1 \times 10^{-5})$; $P < 0.001$] and increased with reef isolation [($\delta' \sim \mathcal{N}(0.052, 9 \times 10^{-5})$; $P < 0.001$; Fig. 2; also see Appendix H]. The mean $\hat{\beta}$ also increased when reef isolation was estimated using distance [$\delta' \sim \mathcal{N}(-0.58, 1.51)$; $P < 0.001$; Appendix I] instead of area.

When classes of reef area (small, area < 3.82 km^2; medium-sized, $3.82 \leq$ area < 8.46 km^2; large, area ≥ 8.46 km^2) and reef isolation (connected, isolation $\leq 4.67 \times 10^3$ km^2; partially isolated, $4.67 \times 10^3 <$ isolation $\leq 5.86 \times 10^3$ km^2; isolated, isolation $> 5.86 \times 10^3$ km^2) were combined, the highest $\hat{\beta}$ were observed for the reefs that were both small and isolated, and the lowest for both large and connected reefs (Fig. 3A).

Mapping mean expected $\hat{\beta}$ over the entire reef complex showed that the temporal variance of fish abundances was generally lower than expected in the north (Cooktown/Lizard Island sector), and higher than expected in the southern reefs of the Swains sector (Fig. 3B). Indeed, reef area varied with longitude and latitude ($wAIC_c = 0.73$; $D = 6.8\%$; Appendix D) and was generally greater on northwestern reefs, whereas reef isolation varied with longitude, latitude and their
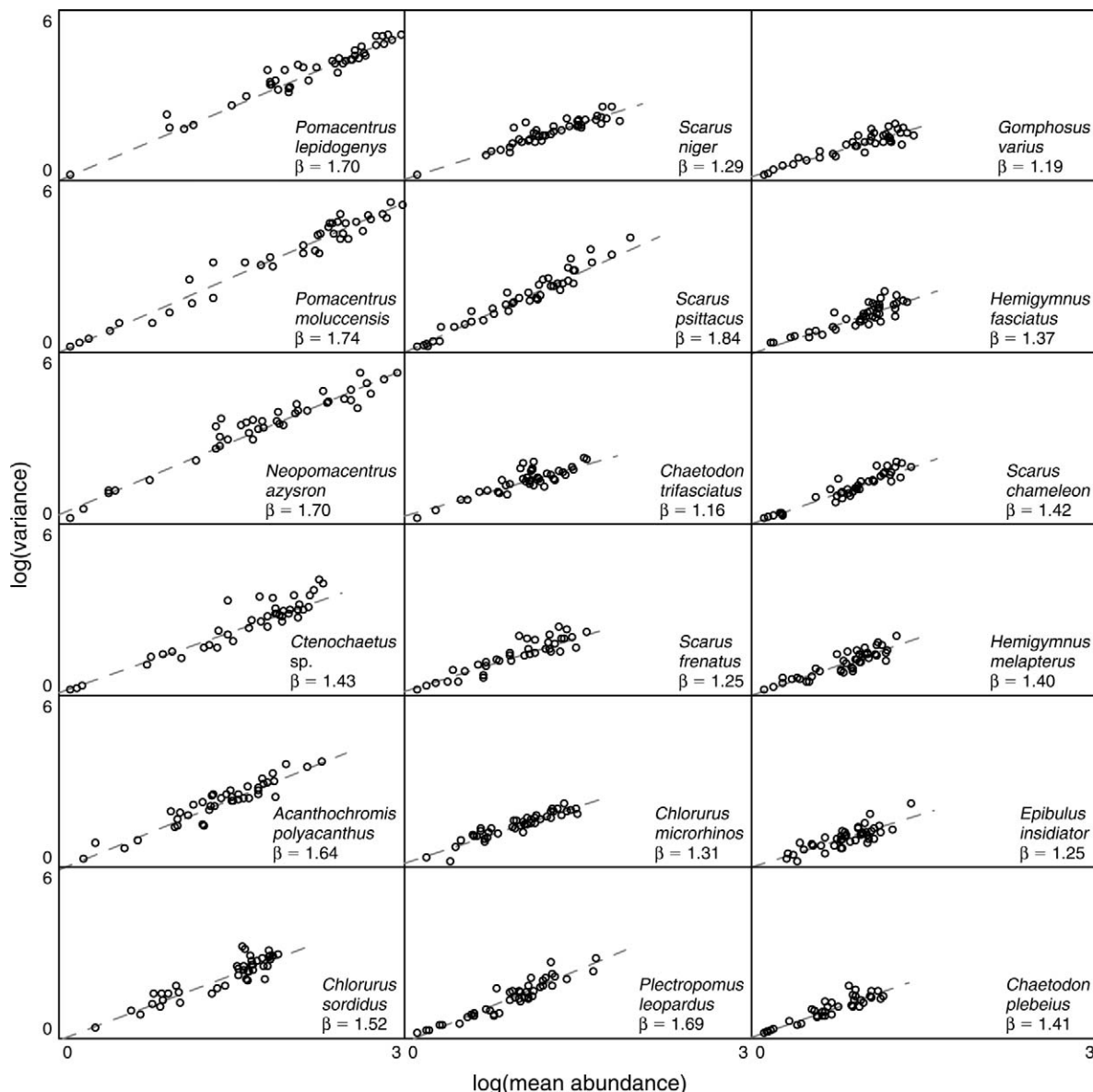
FIG. 1. Linear regression of the log temporal variance of abundance as a function of the mean abundance for the 18 individual fish species considered (see Appendix C for fish codes). The dotted line indicates the regression line with a slope of β.

TABLE 1. Summary of general linear mixed-effect model comparisons using Akaike's information criterion corrected for small sample sizes (AIC_c).

Model	k	LL	ΔAIC_c	$wAIC_c$	D
fam(gen) + L_∞ + N_t	6	20.57	0.00	0.79	85.73
fam(gen) + L_∞	5	19.16	2.60	0.21	83.31
fam(gen)	4	12.04	16.60	0.00	63.19
fam(gen) + N_t	5	12.04	16.83	0.00	63.21

Notes: The response variable is the species-specific slope of Taylor's power law for reef fishes and modeled as a function of the taxon [genus nested within family, fam(gen)] as a random effect, maximum adult total length (L_∞, in cm) and total abundance observed on the Great Barrier Reef across all reefs and years (N_t) as fixed effects. Shown are the number of parameters (k), model maximum log-likelihood (LL), change in AIC_c (ΔAIC_c), AIC_c weight ($wAIC_c$) and the percentage of deviance explained (D). D is a measure of the structural goodness-of-fit of the model. Model sequences are ordered by increasing AIC_c.
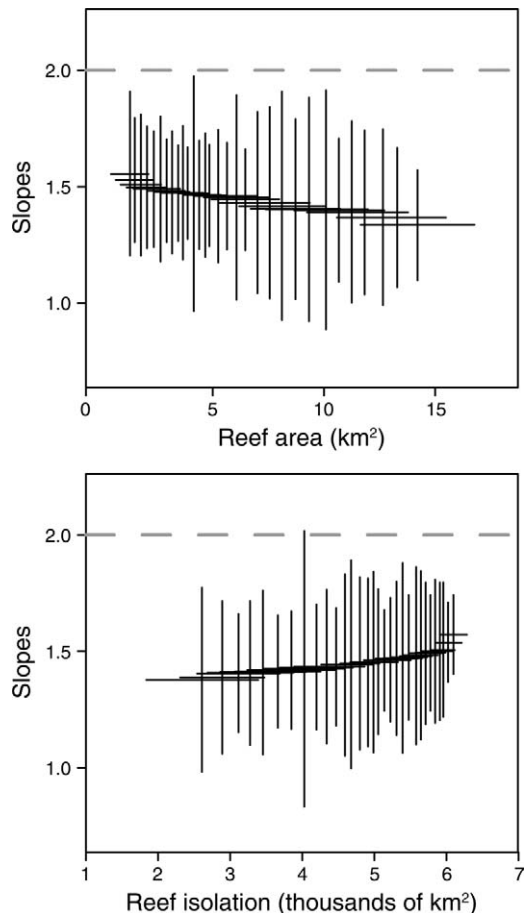
FIG. 2. Range of species-specific slopes of Taylor's power law regression as a function of reef area (top panel) and reef isolation (bottom panel). Horizontal error bars depict the standard deviation of reef area (or reef isolation) within each group of 12 reefs, selected using a sliding window of increasing reef area (or reef isolation). Vertical error bars show the standard deviation of regression slopes across the 18 study species. Bars cross each other at the mean values.

interaction (wAIC$_c$ > 0.99, D = 34.4%) and was greater on southeastern reefs.

DISCUSSION

For 18 fish species of the Great Barrier Reef, smaller reef area and greater reef isolation were associated with greater temporal variance in abundance, which also differed among species and was the highest for small-bodied species. These patterns suggest a hierarchy of drivers of the temporal stability of fish assemblages, whereby life-history characteristics of species such as body size interplay with extrinsic influences such as the size and spatial arrangements of reefs. Within fish communities, small-bodied species probably dominate abundances and exhibit higher temporal variation because small body size is often associated with reduced longevity, early maturity and high mortality (e.g., Depczynski and Bellwood 2006). This combination of

life history traits results in population size being highly sensitive to fluctuations in recruitment (Robertson 1998). At small, isolated reefs, fish communities are more susceptible to stochastic processes associated with low-probability immigration from larger source populations (Moilanen and Nieminen 2002, Hanski et al. 2004). Indeed, theory predicts that for most coral reef fish species, a 30-day larval period and dispersal over
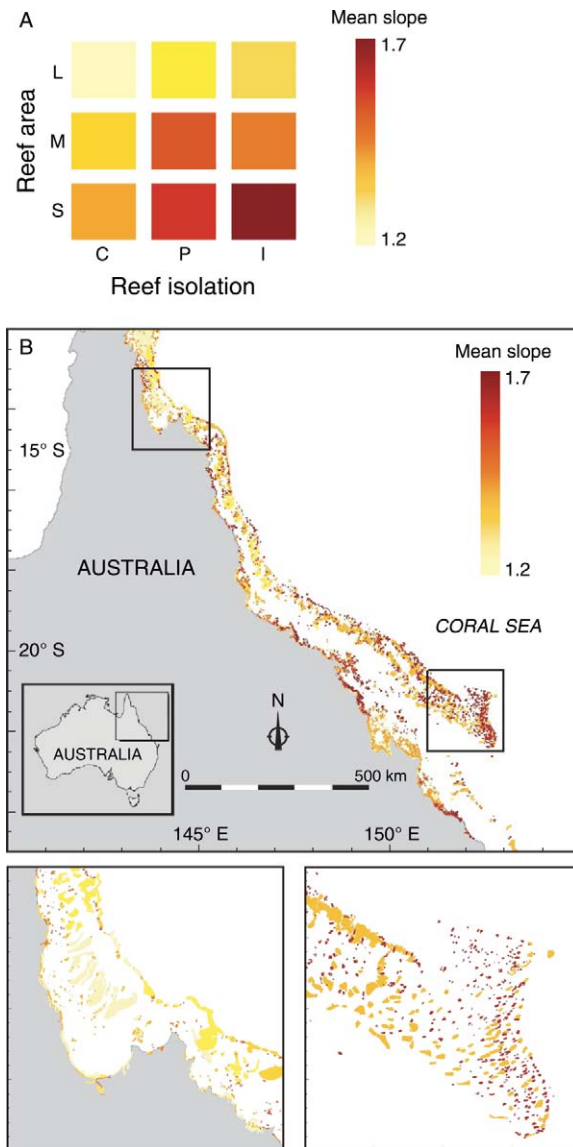

FIG. 3. (A) Cross-factor effects of reef area and reef isolation on the mean of the species-specific slopes of the regression the log-transformed temporal variance of abundance against the log-transformed mean abundance. Reefs are grouped by area (S, small; M, medium-sized; L, large) and isolation (C, connected; P, partially isolated; I, isolated). (B) Map of mean predicted values of the slope of Taylor's power law relationship for reef fish communities of the Great Barrier Reef. Top and bottom insets correspond to Cooktown/Lizard Island and Swains latitudinal sectors, respectively.

PLATE 1.   Bait fish in the Swains sector, Great Barrier Reef, Australia. Photo credit: Australian Institute of Marine Science.

>100 km should result in <10% of larvae surviving (Cowen et al. 2006). If so, pulses of immigration to isolated reefs should occur less often and be more variable in size than on better connected reefs. Small reefs might also be subject to greater fluctuations in abundance because smaller areas support fewer species (e.g., Rosenzweig 1999), among which strong interactions are assumed to elicit high temporal variation in an individual species' population dynamics (e.g., McCann 2000). By contrast, population dynamics on larger and more connected reefs are probably affected by a greater number of species interlinked by relatively weaker interactions, including competition and predation, such that temporal variation in abundances is dampened (Kilpatrick and Ives 2003).

A number of factors are likely to influence our perception of population stability and its relationship to extrinsic forcings. Even though the area- and distance-based estimates of reef isolation gave similar results here, area-based measures are expected to perform better than distance based ones in fragmented landscapes (Moilanen and Nieminen 2002). The measurement error that was incorporated here in the among-transect variance within each site did not invalidate the observed patterns. However, measurement error can scale with mean abundance and produce slopes <2; such analytical artifacts need to be guarded against. We advocate the consideration of measurement error in further applications of Taylor's power law where possible, and propose the bootstrapping procedure used

here combined with a randomization test to evaluate the contribution of measurement error to the patterns observed. Demographic stochasticity is another potential cause for unexpected slopes of Taylor's power law (Kilpatrick and Ives 2003) and its spatial variability is, therefore, the most likely source of the patterns observed here.

Our results have important implications for predicting the resilience of reef ecosystems to natural and anthropogenic disturbances. Highly variable dynamics raise extinction risk by increasing the frequency with which small populations fall below minimum viable sizes (Brook et al. 2008, Melbourne and Hastings 2008). For coral reefs in particular, fish assemblages associated with small and isolated reefs have been slower to recover from habitat loss caused by major disturbances (Graham et al. 2006; but see Halford and Caley 2009) than fish assemblages on larger, more connected continental reefs (Halford et al. 2004). Small and isolated reefs might thus be more susceptible to climate change-driven degradation than continental reef systems where larval replenishment from less-impacted reefs is more likely (Graham et al. 2006). Our results therefore support the idea that small and isolated reefs are more susceptible to local species extinctions because of the inherent tendency for their resident populations to be more variable, and slower to recover from disturbance because of low and variable immigration. However, additional research on abundance and rarity patterns of constituent species

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will be required before relationships of temporal variance with reef resilience can be better understood.

Several other knowledge gaps also need to be addressed. Even though it is predicted by theory, the relationship between temporal abundance patterns, total population size and extinction risk still needs to be evaluated empirically for coral reef fishes. Additionally, further research is required to quantify how the relationship between mean abundance and its temporal variance differs among trophic guilds or functional groups to determine whether particular taxa are more susceptible to disturbance and, by proxy, local extinction. Our investigations of the effects of reef area and isolation on temporal variance of abundances for fishes should also be also tested using other reef taxa with less capacity to disperse, such as corals.

Being able to predict population size stability accurately from simple habitat traits such as area and isolation, which can be measured remotely, would represent an important and novel tool for cost-effective allocation of conservation resources in the face of global change. If small and isolated habitat patches are indeed more susceptible to stochastic processes, their resident populations are more likely to become locally extinct more often than on larger, well-connected habitats. If so, and where ecological triage (Walker 1992) is necessary, our results support the idea that conservation resources would be better allocated to the protection of large, connected habitats or some combination of habitats that optimize area and connectivity in a given landscape. We strongly encourage conservation efforts that account for spatial gradients in habitat area and connectivity. In coral reefs, complementary studies have revealed that mean fish abundance can be predicted from other habitat characteristics (Mellin et al. 2010), suggesting that a combination of area, isolation and habitat suitability models will provide the most efficient and effective ecological tools for informing the prioritization process for future conservation.

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APPENDIX A

Species observed by underwater visual census on the Great Barrier Reef, Australia (*Ecological Archives* E091-219-A1).

APPENDIX B

Results of the principal component analysis of reef isolation indices estimated using 10, 30, 70, 150 km kernels (*Ecological Archives* E091-219-A2).

APPENDIX C

Species observed on the Great Barrier Reef and selected for the species-specific analysis (*Ecological Archives* E091-219-A3).

APPENDIX D

Summary of generalized linear models (GLM) of reef area and isolation as a function of longitude and latitude (*Ecological Archives* E091-219-A4).

APPENDIX E

Position of the reefs monitored yearly since 1993 on the Great Barrier Reef (*Ecological Archives* E091-219-A5).

APPENDIX F

Histograms of reef distribution according to reef isolation based on kernels of 10, 30, 70, 150 km (*Ecological Archives* E091-219-A6).

APPENDIX G

Partial residuals of the slope of Taylor's power law as a function of maximum adult total length (*Ecological Archives* E091-219-A7).

APPENDIX H

Frequency of the rate of variation in the mean slope of Taylor's power law: expected values under a null model and empirical values encompassing measurement error, as a function of reef area and reef isolation (*Ecological Archives* E091-219-A8).

APPENDIX I

Results obtained using the shortest distance to nearest neighbor as a measure of reef isolation (reef isolation by distance, km) (*Ecological Archives* E091-219-A9).

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