Similar regional effects among local habitats on the structure of tropical reef fish and coral communities

Scott C. Burgess*†, Kate Osborne and M. Julian Caley

ABSTRACT

Aim We examined data on corals and reef fishes to determine how particular local habitat types contribute to variation in community structure across regions covering gradients in species richness and how consistent this was over time.

Location Great Barrier Reef (GBR), Australia.

Methods We compared large-scale (1300 km), long-term (11 years) data on fishes and corals that were collected annually at fixed sites in three habitats (inshore, mid-shelf and outer-shelf reefs) and six regions (latitudinal sectors) along a gradient of regional species richness in both communities. We used canonical approaches to partition variation in community structure (sites × species abundance data matrices) into components associated with habitat, region and time and Procrustes analyses to assess the degree of concordance between coral and fish community structure.

Results Remarkably similar patterns emerged for both fish and coral communities occupying the same sites. Reefs that had similar coral communities also had similar fish communities. The fraction of the community data that could be explained by regional effects, independent of pure habitat effects, was similar in both fish (33%) and coral (36.9%) communities. Pure habitat effects were slightly greater in the fish (31.3%) than in the coral (20.1%) community. Time explained relatively little variation (fish = 7.9%, corals = 9.6%) compared with these two spatial factors.

Conclusions Our results indicate either that fish and coral communities were structured in similar ways by processes associated with region, habitat and time, or that the variation in fish community structure tracked variation associated with the coral communities at these sites and thereby reflects an indirect link between the environment and the structure of fish communities mediated by corals. Irrespective of the causes of such commonality, we demonstrate that community structure, not just species richness, can be related to both habitat differences and regional setting simultaneously.

Keywords Australia, community structure, coral, Great Barrier Reef, habitat, local–regional, long-term study, reef fish.
causes variation in the number and type of species that accumulate in a region, may be evident in the diversity of local communities drawn from different regional species pools (Ricklefs, 1987; Schluter & Ricklefs, 1993; Leibold et al., 2004). Overlaid on these processes (which operate at small and large spatial scales and evolutionary time-scales) are smaller-scale temporal processes (years to decades) such as disturbance and succession that can also influence local demography and the assembly of communities (Sousa, 1984; Connell et al., 1997). The challenge, then, is to understand the relative contributions of these many spatial and temporal processes and their interactions to the assembly of biological communities at local and regional scales.

Inferences about the assembly of biological communities are commonly drawn from a range of metrics that vary in complexity, including species richness, species abundance distributions (SADs) and compositional patterns (McGill et al., 2007). In terms of species richness, previous studies of coral communities have demonstrated linear relationships between local and regional species richness (Cornell & Karlson, 1996; Karlson & Cornell, 1998; Karlson et al., 2004) – a pattern consistent with many observations of terrestrial systems (Ricklefs, 1987; Ricklefs & Schluter, 1993; Caley & Schluter, 1997; Srivastava, 1999). However, what such relationships do not reveal is if two sites with the same species richness necessarily share SADs or species compositions (Connolly et al., 2005). Similarly, comparatively little is known about how regional species richness relates to the abundance and composition of communities (hereafter community structure) among habitats and the degree to which such relationships may vary through time. Gradients in regional species richness, environmental differences among habitats and temporal processes may all lead to different patterns of species abundances and composition at local scales (Stirling & Wilsey, 2001; Connolly et al., 2005). Therefore, including compositional information, in addition to abundance, in a multivariate framework should provide further clues as to the processes structuring communities and identify if, and if so which, particular sites or habitats contain species (or life-history traits) that are consistently common or rare across different regions, habitats or over time.

To understand the relative roles of regional diversity, habitat and temporal processes in structuring abundances and composition patterns within biological communities, variation in community structure can be partitioned among a common set of habitats in multiple regions hosting different levels of diversity (Schluter & Ricklefs, 1993; Legendre et al., 2005). The proportion of variation explained by each of these factors should provide indications of the relative importance of various processes that could be structuring particular communities. For example, the proportion of variation in community structure among habitats that is independent of regional setting estimates the degree to which local processes determine community structure. Similarly, the proportion of variation in community structure among regions, after partitioning out pure habitat effects, estimates the degree of regional control of community structure (Borcard et al., 1992; Legendre et al., 2005). To separate these effects and their interactions from local processes operating on ecological time-scales, variation in community structure over time can also be partitioned from spatial effects associated with habitat and region (Legendre & Legendre, 1998). Such temporal effects may act independently, or in conjunction with, effects of habitat and region, but they remain poorly understood because of a general lack of time-series data available for ecological sampling at sufficiently large spatial scales.

The degree to which habitat, regional diversity and time are associated with variation in community structure may also vary as a function of the life-history characteristics of the constituent species in communities. Few studies have examined communities of very different trophic or taxonomic level from the same environment, though Connolly et al. (2005) reported that the frequency distributions of corals and Labrid fish species abundances across the Indo-Pacific (covering a gradient in species richness) both approximated a log-normal distribution, which did not vary across habitats at different depths. A log-normal distribution, where few species have very low or very high abundance, can result from stochastic variation in the environment and population growth rates (Connolly et al., 2005). Therefore, the similarity between corals and fishes was used in this case to argue against niche-based explanations of community structure. Similarly, the most common fish and coral families across the Indo-Pacific contribute a similar proportion to local species richness across a gradient in regional richness, suggesting that similar or linked mechanisms control the composition of both fish and coral communities over these large scales (Bellwood & Hughes, 2001). Though large-scale patterns in species richness are beginning to be revealed, it is still not known if different communities show similar abundance and compositional patterns across regions, habitats or time, and if these factors affect different communities in a comparable manner.

Here we use canonical methods to partition variation due to habitat, region and time in fish and coral community structure on Australia’s Great Barrier Reef (GBR). We then assess the degree of concordance between these two communities across these same three factors. The spatial (1300 km of coastline) and temporal (11 years) scales at which these communities have been monitored enabled us to include gradients in species richness, habitats common to all regions and shorter-term ecological dynamics; a combination of which is rare in most studies of community structure. By including both fish and coral communities in these analyses, we were able to explore potential commonality between these patterns of community structure in groups of species with very different life histories, but which occupy the same patches of habitat. While it is known that both fish and coral species richness vary across these habitats, we ask how much variation in community structure among habitats is consistent across different regions encompassing gradients in species richness, and conversely how much the regional setting mediates the degree to which these habitats explain variation in this structure. In addition, given the potential for extensive temporal variation in the abundances of these species (Caley et al., 1996), we also partitioned the effect of time.
METHODS

Study system and communities

The habitat types studied vary with respect to local physical parameters including water clarity, turbidity, wave exposure and nutrient inputs across the continental shelf (Fabricius & De’ath, 2001). The sampling covered gradients in regional species richness of <40% for fishes (Russell, 1983) and c. 33% for corals (Veron, 1993) from the southern to the northern GBR. Variation in the ambient physical environment also varies among latitudinal regions, but less systematically than among shelf habitats (Fabricius & De’ath, 2001). Corals are sessile and compete for a comparatively small set of limiting resources, mostly space and light, whereas fishes can use a broader range of trophic and habitat resources, which can include corals, and, being mobile, have greater control over what they can access and use as juveniles and adults (e.g. Wilson et al., 2008). In addition, dispersal potential differs markedly between corals (hours to days; Babcock & Heyward, 1986) and fishes (weeks to months; Brothers et al., 1983), the latter being potentially more demographically open to immigration from local and regional sources (Caley et al., 1996).

Sampling design and survey methods

Survey data from the long-term monitoring programme (LTMP) at the Australian Institute of Marine Science (Sweatman et al., 2008) were used in these analyses. Data used here were taken from annual surveys (1994–2004) on fixed sites on 46 reefs of the GBR. Survey reefs were chosen according to their latitude (= region) and position across the continental shelf (= habitat). A total of six regions were sampled, covering a distance of approximately 1300 km along the continental shelf (Fig. 1). Three shelf positions were sampled (inner, mid- and outer shelf) in the four northernmost regions, but the geography of the southern GBR regions provides only mid- and outer-shelf reefs in the Swains region, and only outer-shelf reefs in the Capricorn Bunkers region (Fig. 1). We refer to each habitat × region combination as a locality. In most cases, three reefs were sampled within each locality, but this number varied slightly between two and four, particularly in the southern regions. At each reef sampled, three sites were positioned on the perimeter of its north-eastern flank. At each site, five permanently marked transects, 50 m long and running along the 6–9 m depth contour, were sampled.

Hard and soft corals (scleractinia and octocorallia, respectively) were sampled using a video recorder in an underwater housing. The percentage cover of hard and soft corals was estimated from the video footage using a point-sampling technique (Adbo et al., 2004). Corals were identified to the highest possible level of taxonomic resolution. For hard corals, most could be identified to genus and some to species. For soft corals, most could be identified to family or genus. The growth form of the coral was also recorded. Corals were then grouped into 36 categories mainly based on genus and growth form, but in a few cases also family. These categories (listed in Table 1) were used in all subsequent analyses to investigate the structure of these coral communities. This pooling into categories was necessary for two reasons linked to the long-term nature of the monitoring programme. First, the ability to reliably identify all corals within a particular species group varies with species, image quality and observer. Second, over the history of the LTMP, the level of classification used has changed slightly because observers have had slightly different levels of taxonomic expertise. The 36 categories used here represent the most reliable classification of coral taxa identifiable from these video images. Similarity between coral and fish community patterns reported here should be interpreted in terms of coral community structure defined by these categories. Previous studies on the effects of grouping on analyses of community structure, however, indicate that the patterns of spatial variability in community structure tend to be preserved (Somerfield & Clarke, 1995; Chapman, 1998; Anderson et al., 2005), especially at larger spatial scales like those used in this study and with grouping at the level of genus (Somerfield & Clarke, 1995; Anderson et al., 2005).

Fishes were counted using visual census following the protocols of Halford & Thompson (1996). Relatively large and mobile
fish species were surveyed along a 50 m × 5 m corridor. Smaller and more site-attached species from the family Pomacentridae (Damselﬁshes) were counted on a return pass along the same transects but using a 50 m × 1 m corridor. Only fish considered > 1 year old, based on their size and coloration, were counted. All fish species (249 in total) were identiﬁed to and analysed as individual species.

**Data analysis**

**Summary of spatial and temporal patterns in fish and coral community structure**

Non-metric multidimensional scaling (nMDS) solutions, using Bray–Curtis dissimilarity indices, were used to visualize spatial and temporal patterns in the fish and coral community datasets. nMDS was performed for each year separately, as well as on spatially and temporally averaged datasets in both communities. Both fish and coral community datasets (sites × species matrices) were converted to relative abundances (i.e. row standardi- zed) prior to analyses. Only abundant fish species \((n > 10)\) were included to minimize zero values, resulting in c. 200 species of ﬁshes (depending on the subset of data). Two dimensions were chosen in the nMDS and in all ordinations stress values were less than 0.2. To identify species that were principally responsible for determining the reef dissimilarities, species scores were calculated as weighted averages of the reef scores. The weighted averages were ‘expanded’ so that their biased weighted variance was equal to the biased weighted variance of the corresponding reefs (Legendre & Legendre, 1998).
Variance partitioning

Partial redundancy analysis (pRDA) was used to estimate the proportion of variance in the fish and coral community datasets that related to habitat, region, time and their interactions (Borcard et al., 1992; Legendre & Legendre, 1998; Legendre et al., 2005). pRDA is the extension of partial linear regression to cases with multivariate responses, where the variation in the community matrix is attributed to one set of factors, once the effect of other factors has been taken into account. It is essentially a principal components analysis (PCA) ‘constrained’ by explanatory factors (region, habitat and time in our case). The percentage variation explained by each factor is equal to the (constrained) eigenvalues for the respective canonical axis divided by the sum of all (unconstrained) eigenvalues in the community (response) matrix (Legendre & Legendre, 1998).

The percentage variation explained by habitat represents the fraction of the community data that could be explained by habitat effects independent of any regional effects. Similarly, the percentage variation explained by region represents the fraction of the community data that could be explained by regional effects independent of any habitat effects. The interaction term estimates the fraction of the variation in the community data that was shared by both habitat and regional effects. Therefore, following Schluter & Ricklefs (1993), the total influence of region includes the variation explained by region plus its interaction with habitat. The percentage variation explained by time, and the interactions with spatial factors, estimates the degree to which community structure changed in response to short-term processes such as disturbance. It should also be noted that all estimates of relative variance include sampling error, but this is minimized though sampling permanently marked transects and using consistent methodologies. Using partial redundancy analysis, where the terms are fitted sequentially and measures of variation are based on different degrees of freedom, does not allow for direct comparison of the magnitudes of relative proportions of variation explained by the spatial model terms within each community (Legendre & Legendre, 1998). It does, however, allow comparisons among communities in the magnitude of relative proportions of variation explained by a particular spatial term and comparison of spatial versus temporal variation. Prior to pRDA, the percentage cover of benthic taxa was arcsine square-root transformed. Abundances of each fish species were transformed using the Hellinger metric, which standardizes the data to a measure of relative abundance (i.e. row standardized), downscaling the influence of very abundant species.

Significance tests

To assess the significance of spatial and spatio-temporal differences in the structure of fish and coral communities, eigenvalues from each canonical axis in the pRDA were tested for significance using permutation tests within a multivariate analyses of variance framework (Legendre & Legendre, 1998; Anderson & ter Braak, 2003). The null hypothesis tested was that there is no difference in community structure between the factors of interest. The spatially structured, repeated-measures sampling design necessitated a multilevel analysis. The error term for the spatial effects of habitat and habitat interactions was the among-reef variation. The error term for the effect of year and year by spatial interactions was the model residuals. Restrictions of the permutations for each term in the model were determined by the exchangeability of observations under the appropriate null hypothesis for the term dependent on the multilevel sampling design (Anderson & ter Braak, 2003). Empirical distributions of the F-statistic were estimated by permuting all observations on reefs for tests of spatial effects averaged over sampling years, such as habitat, region and their interactions. Permutations were generated under a reduced model such that residuals were permuted having accounted for the preceding terms in the model (Legendre & Legendre, 1998). For time-dependent effects, observations within reefs were permuted under the reduced model. Permutations within reefs were restricted to cycle through years to give appropriate tests for temporally autocorrelated observations. Inferential tests for terms in the models were based on 1000 permutations. Due to the structural imbalance in the sampling design, terms were fitted sequentially such that the effects were tested conditional only on the preceding effects in the model. Potential effects on the order of entry of factors into the model were examined. Order of entry did not affect the results presented here in any material way, and therefore is not considered further.

Concordance between fish and coral communities

Given that similar components of variance due to habitat, region and time were evident between fish and coral communities (see Results), we were interested in assessing how much of this similarity could be attributed to the similarity of paired communities of fishes and corals on the same reefs. To this end, Procrustes analysis was used on the nMDS ordination solutions described above. Procrustes analysis is similar to the Mantel test, though it has the advantage of assessing concordance between direct observations and their ordination solutions (rather than transforming data into distance matrices, as is done in the Mantel test). Procrustes analysis was used to scale and rotate the nMDS ordinations of fish and coral communities to find the optimal superimposition that minimized the sums of squared differences. The sum of the squared residuals between the final configurations (m²) was then used as a measure of association, such that the greater the similarity between the configurations, the lower the m² value (Jackson & Harvey, 1993; Peres-Neto & Jackson, 2001). Residuals are presented as a proportion of the maximum value (standardized residuals). To estimate the significance of the Procrustean fit (m²), a permutation procedure (protest) was used (Jackson, 1995; Peres-Neto & Jackson, 2001). This procedure repeatedly randomizes the configuration of one matrix, by randomly permuting the observations within rows in relation to each other which maintains its within-matrix covariance structure, and recalculate the m² value. The percentage of m² values equal to or less than the observed m² value is the
significance level of the test. We used 1000 permutations. The null hypothesis was a random association between fish and coral communities. To visualize the concordance between fish and coral community structure at each reef, nMDS ordinations are presented in their optimal superimposition (i.e. after the Procrustes rotation of the fish ordination). All analyses were performed in R 2.4.1 (R Development Core Team, 2006).

RESULTS

Spatial and temporal patterns in fish and coral community structure

nMDS ordinations of both fish and coral communities revealed a gradient in the structure of these communities across habitat types (Fig. 2). Generally, outer-shelf reefs were more similar to mid-shelf reefs than they were to inner-shelf reefs. However, some reefs within a particular habitat type were just as dissimilar to each other as they were to reefs in another habitat type. These within-habitat type differences related to regional sectors so that reefs within each locality were generally more similar to each other than to reefs in other localities. This pattern was consistent for ordinations of both fish and coral communities.

Variance partitioning

Habitat, region and time all contributed significantly to the structure of the fish and coral communities studied here (Table 2). The proportion of total variation attributed to each factor was also qualitatively similar for the fish and coral com-

Figure 2 Non-metric multidimensional scaling (nMDS) ordination of (a) coral and (b) fish community structure (relative abundances) at each reef using a time-averaged dataset. Solid lines group similar habitat types (inshore, mid-shelf or offshore). Each reef is coded according to its locality using a combination of a code for region (CL – Cooktown-Lizard Island, CA – Cairns, TO – Townsville, WH – Whitsundays, SW – Swains, CB – Capricorn-Bunkers) and for shelf position (I = inner, see Fig. 1). The nMDS ordination of the fish community (b) is presented in its optimal configuration after Procrustes rotation ($r^2 = 0.67, P < 0.001$; see ‘Concordance between fish and coral communities’ in Methods for further details) to visualize the concordance between spatial patterns of fish and coral community structure. Panels (c) and (d) show the weighted species scores for influential coral taxa (see Table 1 for classifications) and fish species, respectively.
munities. The proportion of variation attributable to spatial factors was much larger than that attributable to temporal effects in both communities (i.e. fishes = 85.5% [space] vs. 7.9% [time]; corals = 82% [space] vs. 9.6% [time], Table 2). The proportion of total variation attributable to regional effects was similar for both communities (fishes = 33%, corals = 36.9%). This regional component was made up of a component attributable to the unique influence of region (fishes = 19.9%, corals = 20.3%) plus a component attributable to the shared influence of habitat and regional setting (interaction between habitat and region: fishes = 13.1%, corals = 16.3%).

The proportion of variation among habitats that was consistent across different regions covering gradients in species richness was slightly greater in the fish communities than in the coral communities (fishes = 31.3%, corals = 20.1%), whereas the interaction of habitat with region contributed slightly less in the fish community. Within-habitat variation (i.e. among reefs within localities) also contributed a similar amount in both communities (fishes = 21.2%, corals = 26.1%). There were also significant temporal effects with habitat, region and their interaction, though these made a small contribution towards the total variation.

Spatial patterns of variance partitioning in fish and coral community structure were driven by contrasting patterns of relative abundance of constituent species. Figures 3 and 4 summarize general trends for some of the more abundant species. Some species of coral (e.g. tabulate Acropora spp.) and fish (e.g. Scaurus globiceps) showed increasing relative abundance from inshore to offshore habitats and with increasing latitude. Other species of both coral (e.g. branching Porites spp.) and fish (e.g. Pomacentrus moluccensis) showed decreasing relative abundance from inshore to offshore habitats which was fairly consistent across regional sectors. The remaining taxa (e.g. soft corals and Neopomacentrus azysron) had relative abundance patterns across habitats that differed among regional sectors (Figs 3 & 4).

Table 2 Nonparametric multivariate analysis of variance (based on eigenvalues from each canonical axis in the partial redundancy analysis (pRDA) of spatial and temporal variation in (a) reef fish relative abundance and (b) percentage cover of 36 coral taxonomic categories.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>Variation (%)</th>
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<tr>
<td>(a) Reef fishes</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td>Habitat</td>
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<td>35.34</td>
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<td>31.3*</td>
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<td>8.98</td>
<td>5.98</td>
<td>19.9***</td>
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<td>4.22</td>
<td>2.81</td>
<td>13.1***</td>
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<td>21.2</td>
<td>85.5*</td>
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<tr>
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<td>0.25</td>
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<td>0.14</td>
<td>2.51</td>
<td>1.1</td>
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<td>Year × region</td>
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<td>0.17</td>
<td>3.07</td>
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<td>Year × habitat × region</td>
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<td>(b) Corals</td>
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<td></td>
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<td>664.46</td>
<td>12.68</td>
<td>20.1*</td>
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SS, sums of squares; MS, mean squares.
The percentage variation explained by each factor is the (constrained) eigenvalues for the respective canonical axis divided by the sum of all (unconstrained) eigenvalues in the community (response) matrix. Inferential tests were based on 1000 permutations of residuals under a reduced model and are represented by asterisks.
***P < 0.001. Subtotals give the summed percentage of total variation due to ‘shelf habitat,’ ‘regional setting,’ ‘spatial factors,’ and ‘temporal factors across local habitat and region.'
Concordance between fish and coral communities

Procrustes analyses indicated that in every year of sampling, and for the time-averaged sample, there were non-random similarities between fish and coral community structure (Table 3). These results indicate that similarities between communities in the proportion of variation attributed to habitat, region, time and their interactions, was related to the similarity of the structure of coral communities on particular reefs with the structure of the fish communities on the same reefs. Analysis of the residuals from the Procrustes procedure on time-averaged datasets indicated that the concordance between fish and coral communities was greatest in localities in northern regions (Cairns inner and mid-shelf, Cooktown Lizard outer-shelf) and least in southern regions (Capricorn Bunkers outer shelf, Townsville inner shelf and Whitsunday mid-shelf) (Figs 5 & 6). There was no consistent pattern in the degree of concordance across habitats: in the Townsville region, similarity increased (decreasing residuals) from inshore to offshore habitat, while the reverse was true in the Whitsunday and Cairns regions.

Discussion

Our exploration of macroecological patterns of these fish and coral communities revealed strongly consistent patterns in the partitioning of their structure into habitat, region and time effects and their interactions. Generally, spatial patterns in the community structure of corals were correlated with those of the fish communities. Our results demonstrate that not only are the numbers of species in local coral reef communities regionally enriched (Cornell & Karlson, 1996; Karlson et al., 2004), but there is also a large regional effect reflected in local community structure across habitat types and a comparatively small temporal component, at least over little more than a decade. The results reported here extend previous studies on coral reefs that have found similar patterns between fish and coral richness (Bellwood & Hughes, 2001; Karlson et al., 2004), SADs (Connolly et al., 2005) and compositional patterns (Bellwood & Hughes, 2001).

Variation in community structure associated with different habitats across the continental shelf of the Great Barrier Reef.
could occur through spatial niche separation and/or spatially limited dispersal (Leibold et al., 2004; Legendre et al., 2005). Studies of fish (Williams, 1982) and hard (Done, 1982) and soft (Dinesen, 1983) corals have previously nominated differences in wave energy, sediment loads and water clarity as possible environmental drivers of niche separation among species, and consequently differences in community structure across these habitat types. The strikingly similar patterns reported here between fish and coral community structure could arise at least in part if the relative importance of these cross-shelf niche-based processes were similar and function in similar ways for these two communities despite clear differences in the biology of their component species. In addition, spatial variation in patterns of larval dispersal may also account for some of the spatial effects reported here. Regional-scale modelling of larval reef fish dispersal on the northern GBR suggests that cross-shelf mixing is much less than along-shelf mixing, so that dispersing larvae are likely to have a much greater probability of settling on a reef in the same shelf zone (i.e. inner-, mid- or outer-shelf positions) than in another (James et al., 2002). Theory suggests that the homogenizing influences of dispersal within a shelf zone could then generate differences among shelf habitats, independent of, or in conjunction with, other environmental drivers (Leibold et al., 2004; Legendre et al., 2005). Such an effect could also explain the similarity of pattern reported here since the only means of large-scale movement among reefs in the large majority of species in both communities is via larval dispersal.

Why did the effect of habitat interact with region in these coral and fish communities? At least three sources of these differences are possible in both communities. First, differences between regions in the numbers and types of taxa present could lead to different community structures in the absence of any habitat differences (Schluter & Ricklefs, 1993). Second, large-scale climatic variables that differ among regions may influence a species’ probability of colonizing similar habitats in different regions. For example, inshore habitats along the entire coast, while similar in their position across the continental shelf, experience different magnitudes of terrestrial input (e.g. freshwater, sediment and nutrients related to patterns of rainfall), which

Figure 4 Patterns of relative abundance (temporally averaged at each reef) for three abundant fish species (Scarus globiceps, Pomacentrus moluccensis and Neopomacentrus azysron) across shelf habitats (x-axis) and regional sectors (arranged north to south down the page). Dark bars represent the median, the box represents 50% of the data, and the whiskers represent the minimum and maximum values.
potentially adds another level of environmental variability within this habitat zone (Fabricius & De’ath, 2001). Third, the distance between habitats increases from the northern regions to the southern regions as the continental shelf widens (Fig. 1), so that shelf habitats potentially become more isolated (James et al., 2002) and, through spatially limited dispersal, may lead to differences in the degree to which one region exhibits community variation across shelf habitats compared with another (Leibold et al., 2004). It might be expected, however, that corals have less potential than fishes for ecologically significant levels of connectivity among shelf habitats due to their shorter pelagic larval durations. So the effects of spatially limited dispersal should be greater for corals than fishes and may explain why the interaction between habitat and region contributed slightly less in the fish communities.

It is also possible that the dynamics of each community are not independent of each other. The commonality of community patterns reported here could reflect a reliance of reef fishes on live corals for food and shelter. If so, environmental gradients and disturbances influencing these corals could influence the structure of these fish communities (Jones et al., 2004; Wilson et al., 2006, 2008; Graham et al., 2007; Munday et al., 2008). Even though a low proportion of reef fish species on the GBR are obligate live-coral-dwellers and coral-feeders (Munday et al., 2008), declines in abundances of reef fish species in response to coral loss often occur in species that do not directly use live corals for food and shelter (Wilson et al., 2006), suggesting that the reliance of fishes on corals may involve indirect pathways. Because of the observational nature of this study, it is not

Table 3 Concordance between non-metric multidimensional-scaling (nMDS) ordinations of fish and coral community structure for each year and for all years combined (time-averaged). Stress values are in percentage.

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of reefs</th>
<th>nMDS stress</th>
<th>Benthic</th>
<th>Fish</th>
<th>( m^2 )</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>29</td>
<td>16.13</td>
<td>12.77</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>1995</td>
<td>44</td>
<td>16.26</td>
<td>13.93</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>1996</td>
<td>45</td>
<td>15.60</td>
<td>14.58</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>1997</td>
<td>43</td>
<td>15.15</td>
<td>13.74</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>46</td>
<td>14.25</td>
<td>16.38</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>1999</td>
<td>45</td>
<td>13.95</td>
<td>15.22</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>46</td>
<td>14.48</td>
<td>15.45</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>2001</td>
<td>45</td>
<td>14.23</td>
<td>16.40</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>2002</td>
<td>45</td>
<td>13.09</td>
<td>16.31</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>2003</td>
<td>46</td>
<td>15.24</td>
<td>15.79</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>2004</td>
<td>45</td>
<td>13.97</td>
<td>17.04</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Time-averaged</td>
<td>46</td>
<td>13.12</td>
<td>15.58</td>
<td>0.46</td>
<td>&lt;0.001</td>
<td></td>
</tr>
</tbody>
</table>

Concordance is based on Procrustes rotation analysis (see Methods for details) where \( m^2 \) is a measure of association between fish and coral nMDS ordinations (lower values indicate a greater similarity between ordinations). P-values indicate the significance level of the observed \( m^2 \) value. All P-values are less than 0.05 indicating non-random similarities in pattern between fish and coral communities.

Figure 5 Standardized residuals following Procrustes rotation on time-averaged nMDS ordinations showing the degree of association between fish and coral community structure across shelf positions (x-axis) and regional sectors (arranged north to south down the page). Residuals are the differences, at each reef, between the fish and coral nMDS ordinations after the optimal Procrustes rotation was found (see Methods for details). Standardized residuals are the residuals as a proportion of the maximum residual (which occurred at reef 19–131, Fig. 6). Lower residuals indicate where reefs with similar coral communities had similar fish communities.
possible to say whether the patterns observed here represent an indirect link between the environment and fish expressed through corals as intermediaries, or a manifestation of some other environmental variable directly affecting the partitioning of variation in community structure in these two communities in a similar way. It is interesting to note, though, that across the Indo-Pacific similar species abundance and resource use distributions have been reported for corals and Labrid reef fishes (Connolly et al., 2005), as well as a similar representation of common families of fishes and corals across regional species richness gradients (Bellwood & Hughes, 2001). Irrespective of the source(s) of this common partitioning, more research is required on the importance of benthic communities in reef fish demography for determining the distribution and abundance of fishes within and among multiple regions (Wilson et al., 2008).

Compared with spatial factors, the inclusion of time in our analyses contributed comparatively little to improving the amount of variation in community structure that could be explained. Although studies have shown that temporal sequences of disturbance and recovery of local communities on reefs can be dramatic and important to their local ecologies (Connell et al., 1997), our results indicate that such temporal dynamics are less important to the overall structuring of reef communities than are larger-scale spatial processes. This is despite frequent disturbances from multiple agents to GBR communities. The most notable being cyclones affecting 20–25% of the sampled reefs in the 1996–97 and 1999–2000 sampling seasons, bleaching occurring on 15% of the sampled reefs in 1997–98 and 2002–03 sampling seasons, outbreaks of crown-of-thorns starfish predation, peaking at 31% of the sampled reefs in the 1999–2000 sampling season, and increased prevalence of coral disease incidences since 1998–99 (Dolman et al., unpublished data). Therefore, the impacts of disturbances and recovery from them at local scales appear to be bounded to some extent by habitat effects and regional setting. It is important to realize, though, that the full spectrum of disturbance and recovery dynamics of these communities may not have been captured during these 11 years of monitoring. Recovery of coral and fish communities to pre-impact conditions can take longer than a decade in the absence of subsequent disturbances (Connell et al., 1997; Halford et al., 2004; Sweatman et al., 2008) and the recovery of fish communities may lag that of coral communities since many fish species depend on corals for shelter and/or food (Graham et al., 2007; Wilson et al., 2008).

In summary, our exploration of macroecological patterns in these fish and coral communities indicates that either both communities were structured in similar ways by processes associated with region, habitat and time, or that there is an indirect link between the environment and the structure of fish communities mediated by corals. The consistency of the patterns reported here, and previously for local–regional species richness relationships (e.g. Caley and Schluter, 1997), makes a compelling argument for the need to better understand factors affecting the structure of biological communities, and not just species richness, across a diversity of scales. Understanding the causes of these patterns and their consistency would be particularly useful in the spatial management of a diverse range of biological communities facing increased degradation and loss world-wide.

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REFERENCES


**BIOSKETCHES**

**Scott Burgess** is currently doing a PhD in the School of Biological Sciences at the University of Queensland, Australia. His research interest is in spatial ecology, particularly the roles of dispersal and connectivity in determining marine population and community dynamics.

**Kate Osborne** is currently a coral reef ecologist in the Reef Monitoring Project at the Australian Institute of Marine Science. Her research interests are coral reef health and patterns of disturbance and recovery of coral reefs.

**Julian Caley** is currently a principal research scientist at the Australian Institute of Marine Science with research interests in population and community ecology, macroecology, and evolutionary biology. His research explores ecological and evolutionary processes that generate and maintain biodiversity.

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