Assembly rules and functional groups at global biogeographical scales

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Summary

1. The taxonomic and functional composition of reef fish assemblages are quantified in three biogeographical regions: Great Barrier Reef, French Polynesia and Caribbean. Assemblages are described in three habitats of differing wave exposure. Functional abilities are estimated based on published analyses linking fin morphology and swimming performance.

2. Two questions were addressed: (1) To what extent are labrid assemblages similar among habitats and regions? (2) To what extent are functional characteristics of fish assemblages shaped by differences in biodiversity, evolutionary history and species composition?

3. All three regions display highly congruent patterns of habitat use, in terms of assemblage structure and functional characteristics, despite a five-fold difference in species richness, limited or no species overlap, and a 3·2-Myear history of isolation. Exposed reef crest assemblages were dominated by fishes with fins reflecting lift-based high-speed locomotion. In contrast to abundance-based patterns, species presence/absence data were uninformative.

4. The relationship between swimming ability and habitat use reveals underlying assembly rules at a functional level, emphasizing the utility of functional attributes as a metric for comparing system-level properties in taxonomically distinct faunas.

Key-words: Biodiversity, coral reef fishes, Labridae, swimming performance

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Introduction

The impact of the global loss of biodiversity is increasingly attributed to the loss of functional rather than taxonomic groups (Chapin *et al.* 2000; Tilman 2000; Duffy *et al.* 2001). As such, there is an urgent need to understand the processes shaping the functional characteristics of assemblages. Furthermore, it is critically important to identify appropriate functional measures when one is interested in comparing ecosystem function or any specific system-level processes.

Functional analyses measure ecologically relevant attributes of taxa, quantifying performance and/or resource use. These analyses provide a description of biotas based on ecological rather than taxonomic characteristics (Steneck & Dethier 1994). Such a functional or ecomorphological approach specifically addresses the relationship between form, performance and ecology, using abilities rather than taxonomic status to evaluate ecological patterns (Arnold 1983;

Wainwright & Reilly 1994). This method has been successfully applied to analyses of distribution patterns, particularly in terms of habitat selection, in numerous taxa including bats (Norberg 1994), freshwater sunfishes (Werner *et al.* 1983; Mittelbach 1984, 1988; Osenberg & Mittelbach 1989; Huckins 1997) and *Anolis* lizards (Losos 1992; Garland & Losos 1994; Beuttell & Losos 1999). Although most examples are drawn from low-diversity systems, this approach has been applied with comparable success to more diverse systems, including benthic marine algae (Steneck 1997). In most cases, the comparisons have been restricted to local or regional biogeographical scales. We expand this approach to examine functional characteristics of assemblages at a global scale, in a system characterized by taxonomic and functional diversity: coral reefs. Furthermore, we examine the utility of analyses based on species presence *vs* abundance in explaining patterns of habitat use in reef fishes. We hypothesize that reef fish assemblages display common functional characteristics over global biogeographical scales.

The Labridae (wrasses and parrotfishes) was selected as the model taxon. It is one of the most

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diverse and abundant groups of fishes on coral reefs. Functional studies have identified a range of swimming abilities in these fishes related to the relative use of two thrust-producing behaviours: rowing with an anterior–posterior fin motion and flapping the fins along the dorso-ventral axis. Use of the pectoral fins in rowing involves the production of thrust on the backward stroke only, whereas the flapping behaviour produces thrust on both the dorsal and ventral strokes of the swimming cycle (Walker & Westneat 1997, 2002; Drucker & Lauder 1999). In labrids, fin shape is strongly correlated with the propulsive mechanism, with rowing taxa exhibiting a more rounded, low-aspect ratio fin, and flapping taxa having more elongate, high-aspect ratio fins (Walker & Westneat 2000, 2002). It appears that there is a performance trade-off between enhanced manoeuvrability at slow speeds using low-aspect ratio fins and efficient locomotion at high speeds using high-aspect ratio fins (Vogel 1994; Fish 1996; Walker & Westneat 2000).

Detailed anatomical and functional analyses have provided an understanding of pectoral fin kinematics and the basis of these links between fin shape and performance (Walker & Westneat 1997, 2002; Westneat & Walker 1997). Additional studies have demonstrated a strong correlation between fin morphology and swimming performance in labrids in both experimental flumes (Walker & Westneat 2000) and under 'normal' conditions on the reef (Wainwright, Bellwood & Westneat, 2002) (Fig. 1). Furthermore, field studies have established consistent links between fin morphology and ecology in terms of foraging behaviour (Fulton & Bellwood 2002a) and habitat use, in both adults
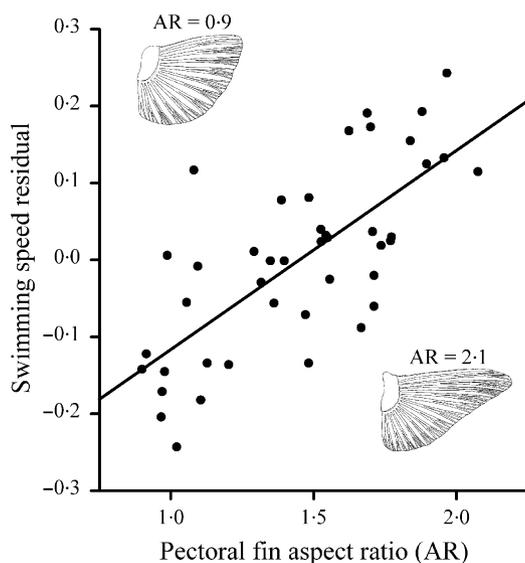
(Bellwood & Wainwright 2001; Fulton, Bellwood & Wainwright 2001) and juveniles (Fulton & Bellwood 2002b). We are thus able to construct a function plot for fin morphology, i.e. one can predict, with reasonable confidence, the swimming performance of labrid fishes with specific fin morphologies. The present study will take advantage of these ecomorphological correlates to examine patterns of habitat use in reef fishes. Our aim is to determine if, and to what extent, assembly rules shape the functional characteristics of reef fish assemblages across global biogeographical scales.

Materials and methods

GEOGRAPHICAL VARIATION IN FISH ASSEMBLAGES

Censuses were taken of fishes on reefs exposed to oceanic swells at two locations in each of three regions: (1) the northern Great Barrier Reef, with 139 labrid species (Yonge and Hicks reefs, between November 1998 and February 1999); (2) French Polynesia, with 70 species (Moorea and Tahiti, in September 2000); (3) Caribbean, with 28 species (around Lee Stocking Island, Bahamas, and Bonaire, June–July 1999). Species numbers refer to the total labrid fauna documented in each region (after Bellwood & Wainwright 2001; Randall 1985, 1996, respectively); censused species richness values were 98, 55 and 25, respectively. At each location, censuses were taken of three habitats: the slope, crest and back-reef. The slope was the steeply inclined region of reef between 8 and 14 m on the seaward side of the reef, immediately below the crest. The crest marked the transition between the shallow upper regions of the reef and the steeply inclined reef slope (depth 1–4 m). The back reef region lay in protected water at the rear of the reef (depth 1–5 m). Each census consisted of two simultaneous (1 and 5 m wide) 20-min. timed swims parallel to the reef crest. All labrids >10 cm total length (TL) in the 5-m wide transect and <10 cm in the 1-m transect were recorded (modified after Bellwood & Wainwright 2001). An evaluation of the utility and limitations of this method is provided in Ackerman & Bellwood (2000). Labrids include parrot-fishes, i.e. Labridae and Scaridae, but excluded the water column planktivore *Clepticus*. Four censuses were conducted in each habitat at each location. Data were standardized to individuals per 20 min to accommodate differences in transect width (1 or 5 m). Principal components analyses (PCAs) were used to investigate differences in among-habitat variation in labrid assemblages in each of the regions (covariance matrix of the mean number of individuals per 20 min).

MORPHOLOGICAL PARAMETERS

The relationship between pectoral fin aspect ratio and swimming capabilities is inferred based on previous studies of swimming in labrids (Walker & Westneat 1997,
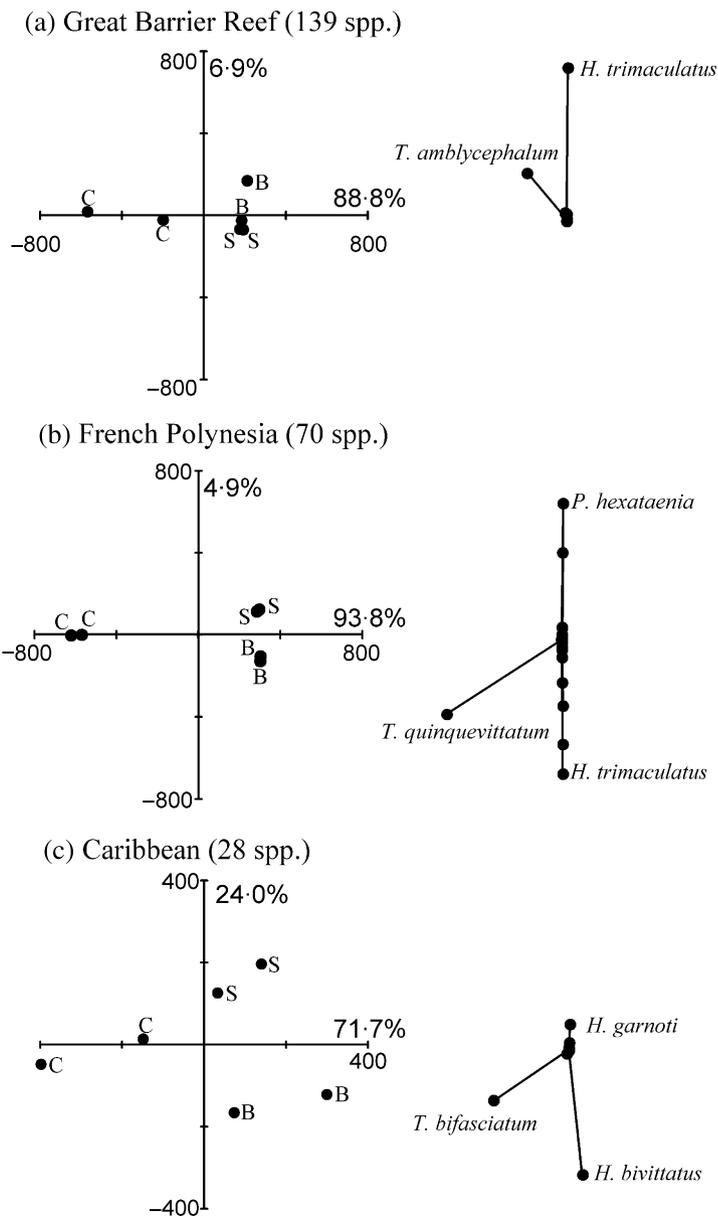

Fig. 1. Fin morphology and routine field swimming speeds in labrid fishes (modified after Wainwright *et al.* 2002). Illustrated fins show variation in shape from an aspect ratio of approx. 0·9–2·1. The correlation $r = 0.72$, covering a nine-fold difference in swimming speeds from 0·74 to 6·76 body lengths s^{-1}, with the vertical axis corrected for body size effects.

(a) Great Barrier Reef (139 spp.)

(b) French Polynesia (70 spp.)

(c) Caribbean (28 spp.)

Fig. 2. Patterns of habitat use by labrid assemblages in three biogeographical regions characterized by markedly different species richness. Each figure shows PC1 and PC2, and the percentage variation explained by each axis. In each location the crest sites (C) are clearly separated from the slope (S) and back (B) sites. Each region is analysed separately, with two locations per region. To the right are species vector plots from the PCA. Each point indicates the location of one species, however, only the two or three species with the highest loadings are labelled; note the presence of a single *Thalassoma* species driving PC1 (the unit circles have been adjusted for comparison).

2000, 2002; Westneat & Walker 1997; Wainwright *et al*. 2002). These studies establish a biomechanical link between fin shape, fin function and swimming performance in labrid fishes. Aspect ratios of the species observed were taken from Wainwright *et al*. (2002) supplemented by additional values for 32 species (P. C. Wainwright, unpublished data). Differences in mean aspect ratios among habitats and regions were examined by calculating the mean aspect ratio for (a) all *individuals* and (b) all *species* in each habitat in each region (each habitat based on eight transects,

locations pooled). Expected mean aspect ratios for assemblages in each region were calculated based on bootstrapped values (200 iterations) of all individuals or species censused in the region (± estimated 95% confidence intervals).

Results

The fish assemblages in the three biogeographical regions (Great Barrier Reef, French Polynesia and Caribbean) display highly congruent patterns of habitat segregation (Fig. 2). In each region, the crest is clearly separated from the other two habitats and is characterized by large numbers of *Thalassoma*. The separation of sites on PC1 explains a huge proportion of the variation (71–93%) and is driven primarily by a single *Thalassoma* species (i.e. this species accounts for most of the variation among sites). The *Thalassoma* species differs in each region, with *T. amblycephalum* (Bleeker) on the Great Barrier Reef, *T. quinquevittatum* (Lay & Bennett) in French Polynesia and *T. bifasciatum* (Bloch) in the Caribbean.

Fish assemblages in the three regions also share similar habitat-related functional characteristics, despite a five-fold difference in labrid species richness (Fig. 3a). The mean aspect ratios of the individuals in each habitat display a highly congruent pattern among regions (Fig. 3a). In each region, the crest has the highest mean aspect ratio, considerably higher than expected,
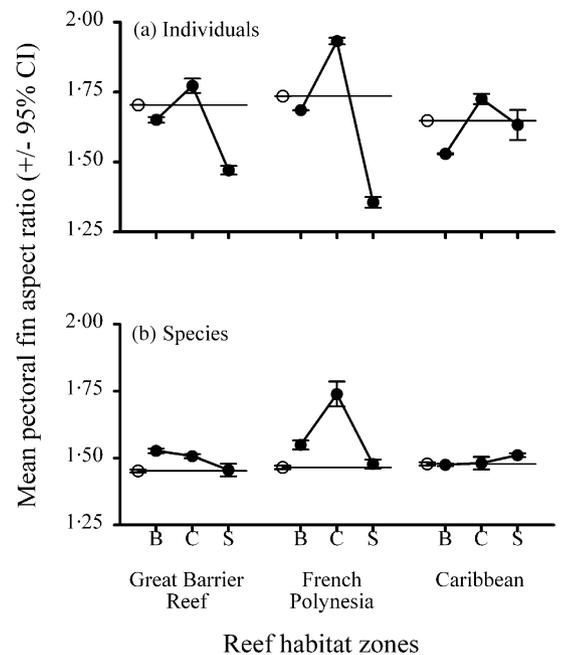

Fig. 3. Mean fin aspect ratios of assemblages among habitats based on (a) all individuals within each habitat and (b) species present within each habitat (no allowance for species abundances). Expected values for each region (open circles) are bootstrap estimates (200 iterations) of the mean fin aspect ratios of assemblages (±95% CI, *n* = 200) based on all individuals or species recorded from each region. The individual CIs are less than a line thickness.

with the three regions having broadly comparable values (all >1·7). With the exception of the Caribbean slopes, the assemblages all depart significantly from a random allocation from the available pool of individuals (crests invariably higher, backs and slopes lower). In the Caribbean, the slope values are unusually high and variable, reflecting a significant input from the ubiquitous *T. bifasciatum* and a depauperate fauna with few low-aspect ratio species.

If the assemblages are described solely on the aspect ratios of the species present (not taking the number of individuals into consideration) all habitats become broadly comparable (Fig. 3b). Clearly individuals and not species drive the functional characteristics of assemblages.

Discussion

Habitat-related differences in fish assemblages are among the best documented small-scale patterns recorded for coral reef fishes (e.g. Bouchon-Navaro & Harmelin-Vivien 1981; Russ 1984). Locomotor performance may play a major role in shaping the distribution patterns of wrasses on the Great Barrier Reef, at a range of spatial scales (Bellwood & Wainwright 2001; Fulton, Bellwood & Wainwright 2001). We show here that such functional attributes may underlie patterns of habitat use at a global biogeographical scale.

Highly congruent patterns of habitat occupation were found from the Great Barrier Reef, to French Polynesia and in the Caribbean. In each region, exposed reef crests were occupied by large numbers of one species in the genus *Thalassoma*. Estimates of the functional abilities of individuals in these assemblages provided a means of describing common patterns of habitat use across wide biogeographical scales. In functional terms, patterns of habitat use were retained irrespective of regional species richness or species composition. However, in contrast to previous work that describes assembly rules in reef fishes at global scales (Bellwood & Hughes 2001), taxonomic patterns were found to be relatively uninformative. Congruent patterns were seen only when species abundances were taken into consideration. Assembly rules based on functional abilities manifest at an individual rather than a species level.

Indo-Pacific fish species have wide geographical ranges and as a consequence the Great Barrier Reef and French Polynesia share many species, the latter being a subset of the former with only half the species richness (only four species from French Polynesia were not found on the Great Barrier Reef). The species shared include *Thalassoma amblycephalum* and *T. quinquevittatum*. It may be expected that habitat-specific assemblages would be similar. What is striking is that although functional patterns are maintained (the crest has large numbers of individuals with high-aspect ratio fins), the species composition differs. In French Polynesia *T. quinquevittatum* dominates the crest, on

the Great Barrier Reef, *T. amblycephalum*. Furthermore, although both are in the genus *Thalassoma*, their ecology is quite different: *T. amblycephalum* is a small (5–12 cm), schooling, predominantly planktivorous species, while *T. quinqevittatum* is a larger (9–16 cm), solitary, benthic omnivore. Patterns of inferred swimming ability of assemblages are maintained regardless of changes in the taxonomic or trophic status of the dominant species.

This predictability is highlighted by the Caribbean assemblages which display the same functional patterns as the Indo-Pacific locations despite sharing no labrid species, having only 28 species (a fifth of the Great Barrier Reef), only one *Thalassoma* species, and a history of isolation from the Pacific spanning over 3·2 Myear. This isolation may have had significant implications. The Caribbean has a history of faunal loss (Jackson *et al.* 1996; Bellwood 1997; Budd & Johnson 1999) and the depauperate labrid assemblage lacks many of the low-aspect ratio groups found in the Indo-Pacific. These taxa form a significant part of Indo-Pacific reef slope communities (Bellwood & Wainwright 2001) and their absence may be partly responsible for the relatively high Caribbean slope values, and the lack of variation among habitats when compared with the two Indo-Pacific sites.

The extent and nature of the similarity among regions emphasizes the importance of phylogeny in shaping reef fish assemblages around the globe. There is little evidence of phylogenetic independence, with *Thalassoma* playing a dominant role in all three regions. For reef fishes, the world's oceans are not necessarily phylogenetically independent as they all share a common history (Bellwood & Wainwright 2002). Nevertheless, the value of functional analyses remains. Fin morphology may tell us little about trophic ecology, but at every spatial scale examined from microhabitats (Fulton *et al.* 2001) to reefs around the globe, fin morphology provides a reliable indicator of habitat use.

The results implicate a significant and universal constraint on fish distributions – wave exposure. In all three regions, despite differences in species number and composition, the mean aspect ratios of individuals on the crest were broadly comparable. It is in this habitat that swimming performance is likely to be a significant constraint. In sheltered locations both high- and low-aspect ratio taxa persist, but here other factors are likely to be operating. The exceptional success of the genus *Thalassoma* on reef crests represents a significant departure from the more generalized pattern of labrid ecology. The acquisition of a high-aspect ratio fin, however, is not unique to this group (it has arisen in several lineages) but it may have been a key innovation that permitted the successful colonization and domination of shallow high-energy locations (Bellwood & Wainwright 2001).

The loss of *Thalassoma* would have a profound effect on labrid assemblages, as it is invariably the

numerically dominant taxon in exposed locations. It is interesting to note that this genus is absent or present in extremely low numbers in temperate waters, which often have diverse labrid faunas. The consequences for labrid occupation of high-energy locations remain unclear, but they will invariably differ from their tropical counterparts. Whether functionally analogous taxa are represented or if the high-energy regions are unoccupied remains to be determined.

It has long been recognized that communities display assembly rules based on ecological attributes (Stephenson & Stephenson 1949; Cody & Diamond 1975), with taxonomically and geographically distinct communities sharing a similar ecological structure. From their inception assembly rules have been largely based on patterns of resource use (Fox 1999; but see Bellwood & Hughes 2001). In terrestrial systems, resource use is often identified based on functional attributes relating to trophic status, with an emphasis on biological interactions. Physical conditions are also important but have received less attention (Strange & Foin 1999). In marine systems, the strong relationship between the distribution of sedentary benthic taxa and water movement is well documented (Stephenson & Stephenson 1949; Denny 1994). It appears that such physical forcing factors may also shape the distribution patterns of highly mobile taxa, including fishes, and may account for the apparent assembly rules in the functional composition of labrid assemblages on coral reefs.

In biogeography one can describe patterns based on presence/absence data, relative abundances or assemblage structures. In each case the patterns may be based on either taxonomic or functional groups. These two metrics may not be interchangeable. The relationship between swimming ability and habitat use was found to transcend biogeographical and taxonomic boundaries. Functional characteristics of reef fish assemblages and habitat-associated assembly rules apply irrespective of species richness or taxonomic composition. However, these habitat-associated functional attributes manifest only at an individual level. The results emphasize the utility of functional attributes as a metric for comparing system-level properties in taxonomically distinct faunas.

Acknowledgements

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