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Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef

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Abstract Coral reefs exhibit marked zonation patterns within single reefs and across continental shelves. For sessile organisms these zones are often related to wave exposure. We examined the extent to which wave exposure may shape the distribution patterns of fishes. We documented the distribution of 98 species of wrasses and parrotfishes at 33 sites across the Great Barrier Reef. The greatest difference between labrid assemblages was at the habitat level, with exposed reef flats and crests on mid- and outer reefs possessing a distinct faunal assemblage. These exposed sites were dominated by individuals with high pectoral fin aspect ratios, i.e. fishes believed to be capable of lift-based swimming which often achieve high speeds. Overall, there was a strong correlation between estimated swimming performance, as indicated by fin aspect ratio, and degree of water movement. We propose that swimming performance in fishes limits access to high-energy locations and may be a significant factor influencing habitat use and regional biogeography of reef fishes.

Keywords Biogeography · Habitat use · Ecomorphology · Swimming · Labridae

Introduction

The distribution patterns of animals are often shaped by the interaction between the inherent physiological capacities of animals and the physical attributes of the environment. Habitat use in marine animals can be greatly constrained by their ability to tolerate temperature, salinity, and water motion. One general approach to understanding the interaction between animal performance and the physical environment is to first identify the key mechanical or physiological parameters that underlie performance capacity, and to then explore the impact of performance on patterns of resource use (Motta and Kotrschal 1993; Reilly and Wainwright 1994). In many cases, relatively easily measured morphological parameters can be identified that are strong indicators of behavioral performance (Westneat 1994). Inference of performance from morphology can then be extended from these detailed studies of a few species to other individuals and species that share the same basic functional design. In this way the performance of functional systems can be directly related to ecological parameters such as prey use in fishes (Wainwright 1988) or habitat utilization and foraging mode in bats (Norberg 1994).

Studies that extend the application of ecomorphology to ecology at a community level are rare, although they have been particularly revealing. For example, the importance of jaw morphology and associated feeding performance in structuring patterns of habitat use and behaviour has been shown in sunfishes (Werner et al. 1983; Mittelbach 1984, 1988; Osenberg and Mittelbach 1989; Huckins 1997). Comparable patterns have been described in *Anolis* lizards which display differential habitat use depending on their body size and limb morphology (Losos 1992; Garland and Losos 1994; Beuttell and Losos 1999). In the present study, we examine the potential of ecomorphological analyses to elucidate ecological patterns at larger, biogeographic scales and in communities characterized by high species

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richness. We examine the utility of current understanding of the link between morphology and locomotor performance capabilities of labrid fishes in order to explore ecomorphological relations between morphology, habitat use, and biogeographic distribution patterns for labrid fishes across the Great Barrier Reef. Furthermore, we explore the possible mechanisms that link swimming ability and habitat use.

On the Great Barrier Reef (GBR) the cross-shelf distribution patterns of corals and fishes have been well documented (Done 1982; Williams 1982; Russ 1984), with marked differences between inner-, mid- and outer-shelf reefs. These differences extend along the length of the GBR spanning over 12° of latitude and 2,000 km (Williams 1991). These studies have suggested that, at a reef scale, the greatest determinant of community structure appears to be the position across the continental shelf. However, for mid- and outer-shelf reefs, within-reef variation has been found to exceed differences between shelf locations. For herbivorous fishes, the greatest source of variation in community structure is seen at the habitat or reef-zone scale; shelf position is of secondary importance (Russ 1984). Evidence from recruitment studies suggests that these cross-shelf patterns are maintained by restricted larval distributions and selective settlement and/or recruitment (Williams 1991). However, both Williams (1982) and Russ (1984) suggest that physical factors ultimately determine the cross-shelf patterns, with incident wave action being the main physical factor accounting for differences in fish communities among habitats and reefs.

The mechanism by which wave exposure can determine fish distributions is not discussed, nor does it appear to be immediately apparent. Comparable patterns in corals (Done 1982, 1983) have likewise been related to the degree of wave exposure. In corals, dislodging by wave action during storms is well documented (e.g. Connell 1978), while background levels of wave action may be directly responsible for influencing colony shape, with several examples of “surf-resistant ecomorphs” (Done 1983). But what of reef fishes? Storms may dislodge fishes and increase mortality of juveniles (Lassig 1983), but how can background levels of wave exposure modify fish distributions? Could reef fish distributions be shaped by swimming ability?

Our knowledge of fish locomotion has increased dramatically in recent years, particularly our understanding of those forms using labriform locomotion (*sensu* Webb 1994), i.e. using the pectoral fins as the primary source of propulsion. This locomotion mode is used by the vast majority of reef fish taxa. However, recent studies have revealed considerable complexity and diversity in swimming modes within the Labridae, the namesake of the labriform swimming form. Labrids display perhaps the greatest range of swimming modes found within a single family of fishes. A major axis of this diversity appears to lie in the relative use of drag-based propulsion (i.e. rowing with the pectoral fins) and lift-based propulsive behaviors (i.e. flapping or flying

with the pectoral fins). In drag-based swimming, forward thrust is generated predominantly on the backward stroke; in lift-based locomotion, forward thrust is generated on both the up-stroke and down-stroke components of the swimming cycle. In labrids, fin shape is correlated with propulsive mechanism, with rowing taxa exhibiting a more rounded, low aspect ratio fin, and flying taxa having more elongate, high aspect ratio fins (Westneat 1996; Walker and Westneat 2001). It appears that there may be a performance trade-off between enhanced maneuverability at slow speeds and efficient locomotion at high speeds (Vogel 1994).

Detailed anatomical and functional analyses have provided an understanding of pectoral fin kinematics and the links between fin shape and performance in both labrids (Westneat 1996; Walker and Westneat 1997; Westneat and Walker 1997) and other labroid fishes (Drucker and Jensen 1996a, 1996b, 1997). Additional studies have demonstrated a strong correlation between fin morphology and swimming performance in labrids. This includes measures of both maximum swimming speeds in experimental flumes (Walker and Westneat 2001) and performance under “normal” conditions in the field (Wainwright et al. 1999, 2001), with mean field speeds ranging from 0.8 to 6.8 body lengths per second. Species with higher pectoral fin aspect ratios had significantly higher swimming speeds on the reef. We are therefore 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.

Based on the known mechanical properties of the pectoral fins of labrid fishes, one may hypothesise that the fast swimmers (i.e. those possessing high aspect ratio fins) would be most abundant in high-energy locations where they encounter the greatest water movement. Conversely, one may predict that slower swimmers (with low aspect ratio fins) would be most abundant in sheltered locations. Initial studies of labrids on reefs around Lizard Island have indicated that such patterns do exist at among-habitat scales (Fulton et al. 2001). Given the relationship between morphology and performance, and the diversity of morphologies in the family, labrids represent one of the most promising groups by which to investigate the relationship between swimming abilities and the distribution of fishes on coral reefs. Using labrids as a focal group, this paper examines the extent to which swimming ability and the degree of wave exposure may explain reef fish distribution patterns at a range of spatial scales.

The specific aims are:

1. To determine whether labrid assemblages display distinct cross-shelf and among-habitat distribution patterns across the Great Barrier Reef.
2. To document the range of fin morphologies displayed by labrids in each habitat at each shelf location, using fin morphology as a basis for estimating swimming abilities.

3. To establish whether fish assemblages differ significantly between habitats in terms of the range of fin morphologies, to evaluate the extent to which this correlates with habitat-specific patterns of water movement, and to test the predictions based on the functional properties of labrid pectoral fins.

Overall, does fin morphology and estimated swimming ability provide a useful predictor of labrid distribution patterns?

Materials and methods

Fish censuses

Fish censuses were conducted between November 1998 and February 1999 in the northern sector of the Great Barrier Reef. Three reefs were censused in each of three cross-shelf locations (Fig. 1). Three inner reefs were selected 8 to 21 km from the mainland: Turtle Group North, Turtle Group South, and Nymph Island. Midshelf reefs 22–36 km from the mainland were MacGillivray Reef, and unnamed reefs 14–149 and 14–150. These reefs were selected because of their similar size, location, and condition: all had suffered relatively little in the 1997–1998 *Acanthaster* outbreaks. Outer-shelf reefs 46–55 km from the mainland were Yonge, Day, and Hicks Reefs. In this region, the outer-shelf reefs form an almost complete barrier along the continental margin.

Four habitats were censused. The *slope* was the steeply inclined region of reef between 8 and 14 m (12 m target depth) on the seaward side of the reef, immediately below the crest. The *crest* was the region that marked the transition between the shallow upper regions of the reef and the steeply inclined reef slope (depth 1–4 m; 0–1 m above mean spring low, MSL). *Reef flat* censuses were 8–15 m behind the crest, usually in the region of the wave break; depth was 0–1 m above MSL. The *backreef* region lay at the rear of

the reef flat where the reef begins to fall away. Back censuses covered a depth range from 1–5 m and marked the shallowest region of the backreef area.

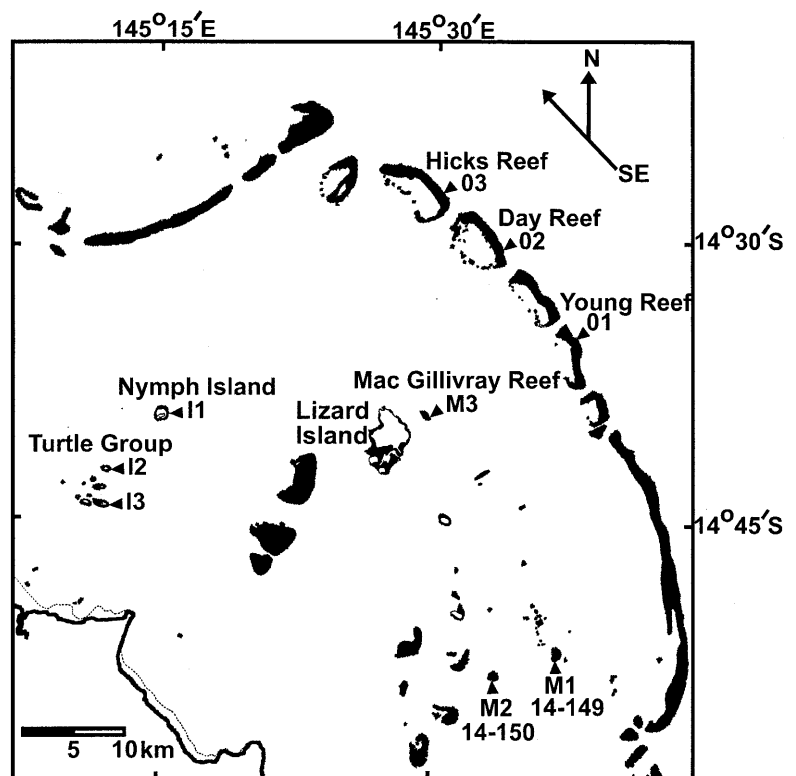
On inner shelf reefs, the physical distinction between habitats broke down, with the seaward edge of the reef gradually rising from a shallow sloping sand base at 6 m to a reef flat. There was no clear crest. The complete seaward slope was therefore censused as the slope/crest.

Each census consisted of two simultaneous (1 and 5 m wide) 20-min timed swims parallel to the reef crest (modified after Bellwood 1996 and Ackerman and Bellwood 2000). Prior to censusing, a 5-m tape was laid to help in the estimation of the transect width. All labrids greater than 10 cm total length (TL) in a 5-m-wide transect (and in the water column to the surface) were recorded over a 20-min swim (the labrids are taken to include parrotfishes, i.e. Labridae and Scaridae). Individual fishes were identified and placed into 5-cm size categories. Care was taken not to re-census fish that were “pushed” along the reef during the census. The beginning and end of each census was marked by a surface marker buoy. A simultaneous 1-m-wide transect covering the same ground censused all individuals below 10 cm, paying particular attention to cryptic and juvenile individuals. Fish were placed in size categories 2.5–4.9 or 5.0–9.9 cm. Few specimens were seen below 2.5 cm; most were recent recruits and are not considered in the analyses. All observations were made by the senior author or M. Marnane.

Four 20-min censuses were conducted in each habitat on each reef. Adjacent censuses were separated by at least 20 m. Where possible, censuses in each habitat were carried out on the same section of reef (i.e. on outer reefs the slope and crest sites were parallel to each other). Outer reef sites were located 1–2 km along the reef away from the reef channel. For smaller reefs, the censuses almost covered the whole reef perimeter.

At the end of each dive, the buoys at the beginning and end of each census were marked using a differential GPS (Garmin 12XL GPS with a Communications Systems International ABX-3 beacon receiver) and the distance between marks estimated. Trials of the apparatus (using tapes) indicated that estimated distances were accurate to within 5 m. The differential GPS enabled the data to be expressed in densities per unit area rather than numbers per unit

Fig. 1 Cross-shelf census sites in the northern section of the GBR, showing inner-shelf reefs (*I1*, *I2*, *I3*), mid-shelf reefs (*M1*, *M2*, *M3*), and outer-shelf reefs (*O1*, *O2*, *O3*) along the margin of the continental shelf. Mainland is shown at *bottom left*. Prevailing wind is from the southeast



effort. Each census was approximately 235 m long (mean 234.5 ± 55.5 SE; range 110–400, $n = 132$). Over the range of census lengths encountered, no relationship was found between total fish numbers (individuals > 10 cm) and census length ($r^2 = 0.02$; $t = 1.6$, $p = 0.11$).

The advantage of the above method was that it reduced observer effects when compared to tape transects (labrids include both diver-positive and -negative species). The timed swims also permitted rapid coverage of large areas, enabling rare species to be detected along with diver-negative species. The split censuses (> 10 and < 10 cm) reduced problems of diver overload (recording too many species/size categories) and enhanced the likelihood of detecting small or cryptic species. The GPS readings resulted in values per unit area and, unlike other timed swimming methods, allowed for the effects of currents, etc. on swimming efficiency.

Data analysis

Data were standardized to individuals per 100 m² to accommodate differences in transect width (1 or 5 m) and transect length. Individuals in the smallest size class (2.5–4.9 cm) were only included in species where the adult TL was less than 160 mm TL. Principal components analyses (PCA; in SPSS) were used to investigate differences between sites. These analyses were based on the mean number of individuals per 100 m² at each of 33 sites (three to four habitats, three reefs, three shelf locations; mean of four transects per site). The analyses were based on the covariance matrix of $\log_{10}(x + 1)$ transformed data. To provide an objective description of site groupings, a Ward's method cluster analysis was performed on squared Euclidean distances drawn from the PCA output of the log abundance data, with significance tests of the cluster analysis following Sandland and Young (1979a, 1979b). This method represents a more conservative approach to the identification of clusters than simply relying on hierarchical clustering methods (e.g. Williams and Hero 1998).

Fin parameters

A positive association between pectoral fin aspect ratio and swimming capabilities was assumed to extend throughout the Labridae based on previous studies (Westneat 1996; Walker and Westneat 1997, 2001; Westneat and Walker 1997; Wainwright et al. 1999). Pectoral fin aspect ratio (length of leading edge squared divided by fin area) was measured following Fulton et al. (2001). For each species, a mean aspect ratio was calculated based on three adult specimens. Most specimens were collected from the Great Barrier Reef, in the region of Lizard Island, with a few additional specimens obtained from commercial aquarium collectors. Details of changes in fin morphology will be provided elsewhere (Wainwright et al. 2001). To allow for variation in fish size, the mean aspect ratio for each species was plotted against mean body size (standard length) and residual values calculated from the regression line for all species. Mean aspect ratio residuals were obtained for 114 species; these values are provided in the Appendix. This represents 82% of the 139 labrid species recorded from the GBR and 100% of the 98 species recorded in the censuses (lists provided in Appendix). In mean aspect ratio residuals, positive values indicate higher aspect ratios than expected at a given size and negative values indicate a smaller aspect ratio than expected. Based on kinematic data from several labrids, high positive values are associated with a lift-based (flying) swimming mode and faster swimming speeds; low negative values are associated with slower speeds and a drag-based (rowing) swimming mode (Westneat and Walker 1997; Walker and Westneat 2001). Average field swimming speeds of 41 labrid species measured on the Great Barrier Reef were strongly correlated with pectoral fin aspect ratio residuals (Wainwright et al. 1999). Thus, labrid species with higher aspect ratio fins are known to have faster "typical" swimming speeds on the reef.

Differences in mean aspect ratios among habitats and shelf locations were examined using 2-way ANOVA for all species and all

individuals. For species, the mean aspect ratio residual (ARR) is calculated as the mean ARR of all species recorded in a census. Mean individual ARR's are based on the mean estimated ARR of all individuals recorded in a census (i.e. species values were adjusted in proportion to the relative abundance of the species in the census). Homogeneity of variance and normality of the data were examined using residual plots and Levene's test; both were within acceptable limits.

Results

The Labridae display distinct cross-shelf trends in the composition of fish assemblages (Fig. 2). This is marked by replacement of species, with a few species restricted largely to inner- (e.g. *Halichoeres nebulosus*) or outer- (e.g. *Cirrhilabrus exquisitus*) shelf reefs. However, the greatest change is in the relative abundance of wide-spread species, which display much greater densities in particular shelf positions, e.g. *Hemigymnus melapterus* and *Stethojulis strigiventer* on inner-shelf reefs or *Thalassoma lutescens* on outer-shelf reefs (note that Fig. 2 is restricted to abundant taxa on slopes only).

Despite these differences between shelf locations, the greatest source of variation was at a habitat level (Fig. 3). Cluster analysis reveals a significant division between crest/flat assemblages on mid-/outer-shelf reefs and all other sites ($p < 0.008$). Within this mid/outer crest/flat group, flat and crest sites cluster regardless of their shelf location. Only one reef crest site departed from this general pattern. At this site (M1), recent damage by *Acanthaster* had left the crest with large open areas of algal-covered rock. These areas were occupied by *Thalassoma janseni*, a common reef-flat species.

These patterns of site association are most clearly seen in the PCA (Fig. 4). In this analysis the first two components accounted for 39.2 and 16.1% of the variance, respectively, which is relatively high given the large number of variables considered (98 spp.). The first component appears to be driven largely by cross-shelf and habitat-related differences, while the second component reflects depth and possibly relative species evenness (species with low scores on PC 2 tend to be locally abundant). The taxa responsible for the ordinations are shown by the species vector loadings on PC 1 and 2 (Fig. 5). In this figure only those species that lie more than 0.1 units from the centroid are included (with the exception of *Oxycheilinus digrammus* and *Stethojulis strigiventer*). The remaining 75 species with low scores were either rare or uncommon but widespread. In a minority of species a few individuals were recorded from almost all locations (e.g. *Epibulus insidiator*, *Chlorurus microrhinos*). In both instances these species contribute little to the separation of fish assemblages (the scores of all species are given in the Appendix).

The strongest feature to arise from the ordination and cluster analysis is that the sites are separated based on the degree of exposure first, then on shelf location. The only location where sites were clustered based

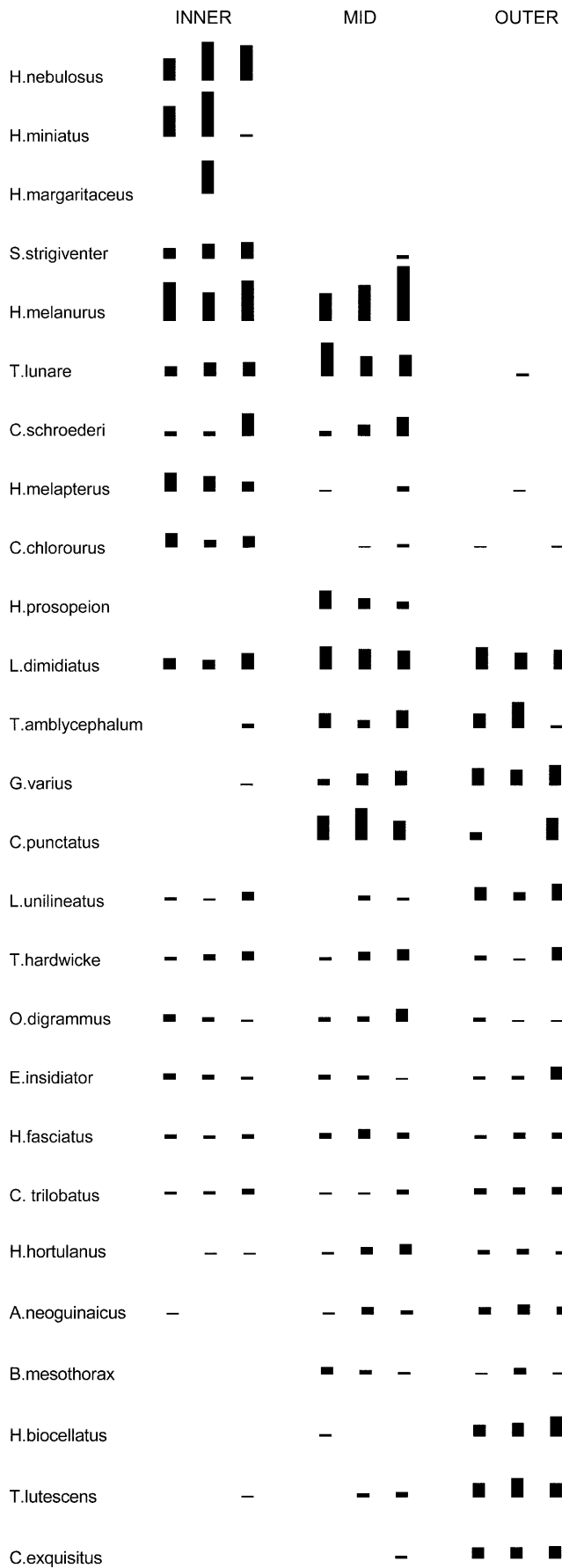


Fig. 2 Distribution patterns of labrids across the continental shelf. Abundant wrasse taxa from reef slope sites only. *Vertical bars* give relative mean log abundance of individuals from four transects at each replicate reef. The figure presents only a small subset of the labrids censused on reef slope sites. Full species names are given in the Appendix

on shelf location was on inner-shelf reefs. At the other locations, habitat was more important than shelf location: slopes and backs clustered together at both mid- and outer-shelf locations, while outer- and mid-shelf crests and flats clustered together.

These patterns are reflected in the distribution of species with respect to their estimated swimming abilities. If the mean aspect ratio residuals of the species (as a size-independent estimate of aspect ratios) are given on the vector plot (Fig. 6), one can see a strong trend, with the exposed sites being characterized by species with high aspect ratios, i.e. faster swimmers. All of these species are in the genus *Thalassoma*: *T. amblycephalum*, *T. janseni*, and *T. quinquevittatum*. Although exposed sites have large numbers of these high aspect ratio species, this analysis cannot determine if exposed sites had significantly more fish with high aspect ratios than did

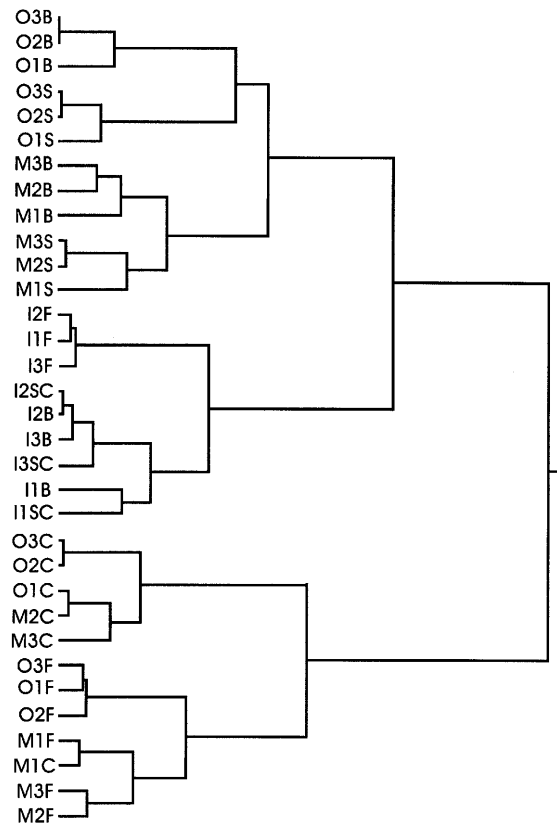


Fig. 3 Cluster analysis of habitats using Ward's method based on squared Euclidean distances drawn from principal components analysis of $\log(n + 1)$ mean abundance data for all species. *O* Outer reef; *M* mid-shelf reef; *I* inner-shelf reef; *B* reef back; *F* reef flat; *C* reef crest; *S* reef slope; *numbers* refer to replicate reefs (see Fig. 1)

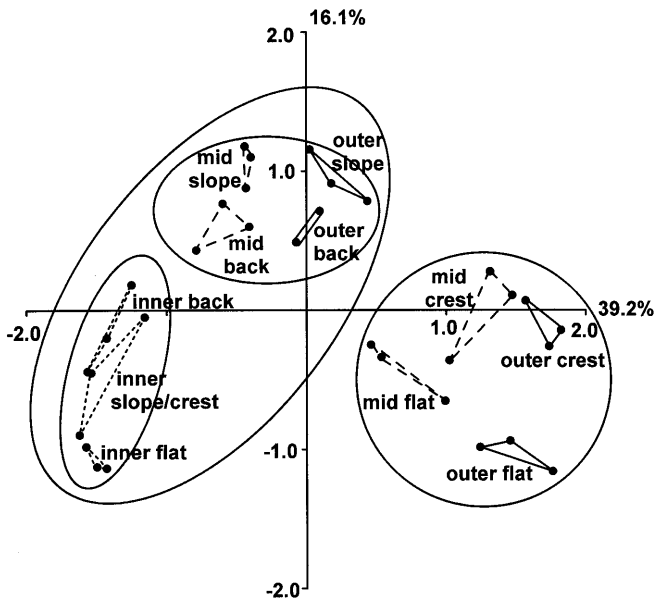


Fig. 4 Relationships between labrid assemblages at 33 sites across the GBR. Principal components analyses, PC 1 and 2, showing relationships between sites. Sites were located in four habitats (slope, crest, flat, back) at three replicate reefs (inner, mid, outer) in each shelf location. Each site is based on 4x20-min transects. Sites are grouped following the four primary clusters identified in cluster analysis (Fig. 3)

sheltered sites. If, however, the mean aspect ratio residuals are calculated for all species in each habitat and for all individuals in each habitat, a distinct pattern emerges. For both the species and individuals present, there are significant differences between shelf positions and habitats but with a significant shelf \times habitat interaction factor (Table 1). However, the patterns differ for the two analyses. For species, the mean aspect ratio residuals are high on outer flats, low on inner backs, and broadly comparable at all other locations (Fig. 6a). At an individual level (i.e. based on the mean of all individuals rather than species in the assemblages), the pattern is much stronger, with much higher mean aspect ratio residuals on mid- and outer-shelf flats and crests (Fig. 6b). This pattern reflects the fact that the high aspect ratio species of *Thalassoma* are particularly abundant on the more exposed reef locations (Figs. 5 and 7). All inner-reef habitats and mid/outer slopes and backs are characterized by labrid assemblages with relatively low mean aspect ratios.

If the data are re-examined looking at high aspect vs. low aspect ratio species separately (i.e. positive and negative aspect ratio residuals, respectively), the overall contribution of individuals with the two swimming modes can be evaluated. Among-habitat patterns are driven to a large extent by the relatively high abundance of high aspect ratio individuals on mid/outer flats and crests (Fig. 7). There is a corresponding but much smaller decrease in the abundance of low aspect ratio individuals at these sites.

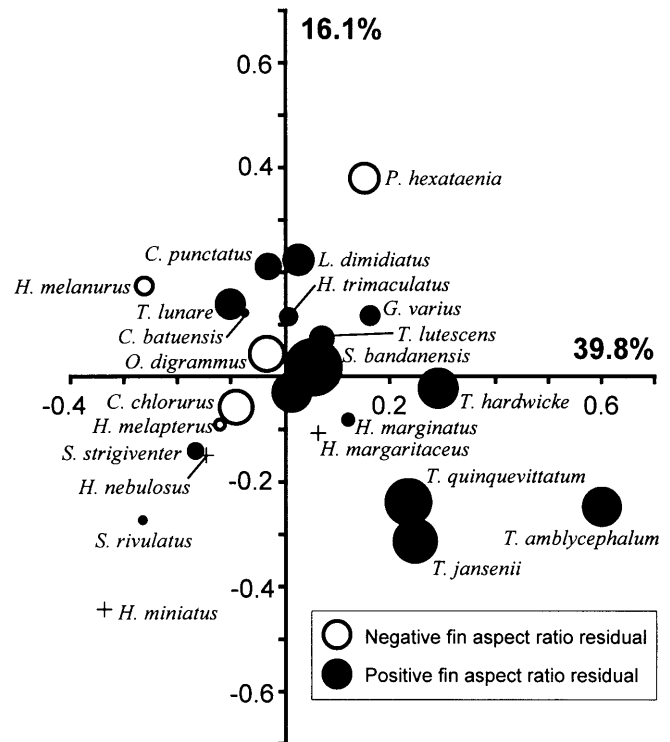


Fig. 5 Relationship between estimated swimming ability and contribution to labrid assemblages across the GBR. Species vectors for PC 1 and 2. Only species with values above 0.1 from the centroid are included (except for *O. digrammus* and *S. strigiventer*). Comparison of species vectors here with Fig. 4 emphasizes the importance of *Thalassoma* species (*T. janseni*, *T. amblycephalum*, and *T. quinquevittatum*) in uniting exposed mid- and outer-shelf sites. Each species is marked by a circle or cross. Diameter of circle is proportional to mean aspect ratio residual for that species. Solid circles species with pectoral fins with positive aspect ratio residuals (these swim by lift-based locomotion and often achieve high speeds); open circles species with negative aspect ratio residuals (these have drag-based locomotion and are usually slow swimmers); cross species with values less than 0.1. Mean aspect ratio residuals for all species are given in the Appendix

Discussion

Distribution patterns and wave exposure

Cross-shelf and cross-reef habitat-related differences in fish assemblages are among the best documented small-scale biogeographic patterns recorded for coral reef fishes. Cross-shelf patterns have been described for a range of families at several locations on the GBR (Williams 1991), while faunal changes across reef profiles have been recorded in numerous locations from the Red Sea to Moorea (e.g. Bouchon-Navaro 1981; Bouchon-Navaro and Harmelin-Vivien 1981). Although local distributions may be correlated with benthic features (Bouchon-Navaro and Bouchon 1989), broader scale patterns are more often attributed to physical features, particularly the degree of wave exposure (Williams 1982; Russ 1984).

The interactions between topology, currents, and wave-induced water movement result in complex pat-

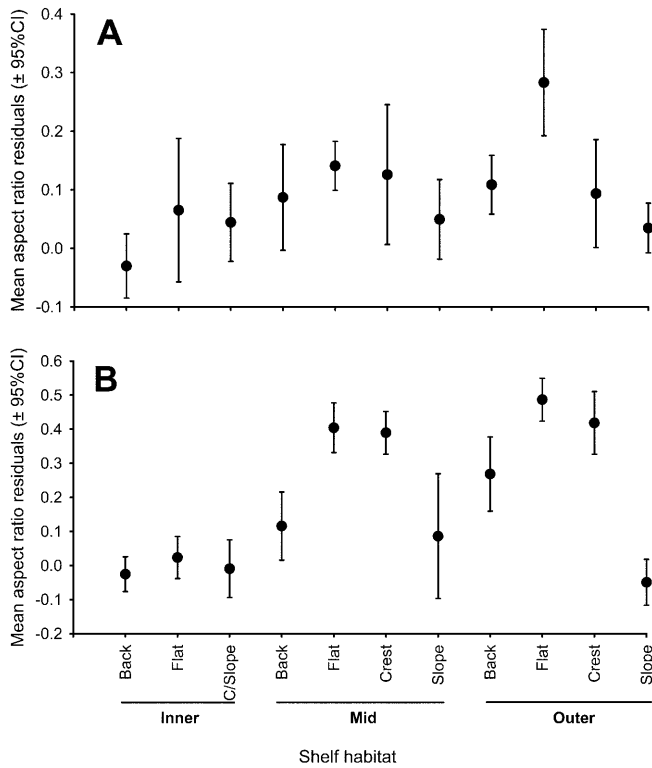


Fig. 6 Mean aspect ratio residuals of labrid assemblages among habitats and reefs across the GBR ($n = 3$ reefs per habitat). **A** Means of all species censused; **B** means of all individuals censused

Table 1 Effect of shelf location and habitat on mean aspect ratio residuals of labrid assemblages based on both species and individuals (2-way ANOVA; data as in Fig. 7; mid- and outer reefs only)

	MS	df	F	<i>p</i>
Species				
Shelf	0.02	1.88	11.0	0.001
Habitat	0.12	3.88	64.9	<0.001
Shelf × habitat	0.04	3.88	20.0	<0.001
Individuals				
Shelf	0.02	1.88	5.5	0.021
Habitat	0.94	3.88	209.7	<0.001
Shelf × habitat	0.09	3.88	20.1	<0.001

terns of water movement around reefs. Nevertheless, a number of field studies permit some tentative conclusions to be drawn with regards to water movement at various locations on reefs. The outer reef flat near the wave break has the greatest water movement, driven largely by wave activity (Roberts et al. 1975; Kench 1998). Here, the breaking waves and shallow depth will concentrate the effects of wave motion and wave disruption (Roberts et al. 1975). On reefs exposed to oceanic swells (the equivalent of GBR outer reef sites), modal current speeds on the outer flat are in the region of 20–25 cm s^{-1} , but half-second current samples commonly exceed 40 cm s^{-1} and may reach 140 cm s^{-1} (Kench 1998). The crest, lying immediately seaward of

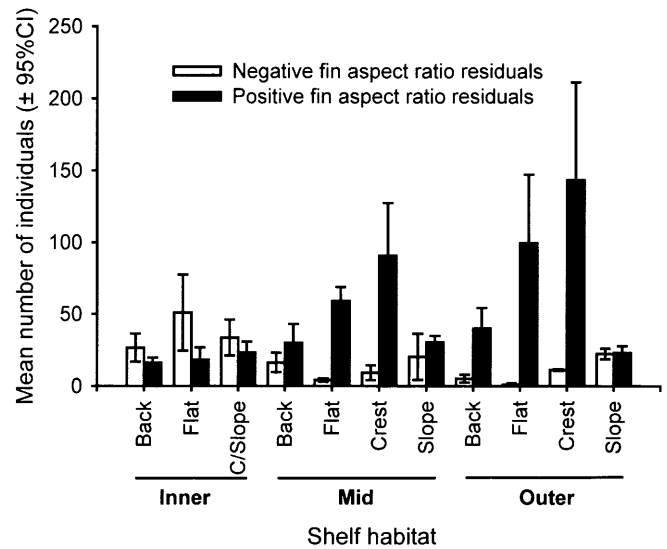


Fig. 7 Mean number of individuals with low aspect ratio residuals vs. high aspect ratio residuals in labrid assemblages across the GBR. Individuals are divided into high vs. low categories based on mean aspect ratio residual for the species. Mean aspect ratio residuals > 0 indicate that these species have a larger aspect ratio than would be expected for a fish of a given size. For each value $n = 3$ reefs

the wave break, is slightly deeper than the flat and the waves are relatively intact. Here, water movement, although still predominantly wave induced, is likely to be slightly less than on the reef flat, since the intact waves and greater depth will limit the effects of wave motion when compared to the flat (Roberts et al. 1975). These sites contrast greatly with back and slope sites where water movement is greatly reduced. A large proportion of energy is dissipated as the water passes over the reef flat. By the time water reaches the backreef area, approximately 50–80% of the energy is lost (Young 1989; Hardy and Young 1996; Kench 1998). Currents here are in the region of 15 cm s^{-1} and short-term wave motion rarely rises above 30 cm s^{-1} (Kench 1998). Down the reef slope, wave-induced water movement also decreases rapidly. Although longshore currents are likely to increase in importance with increasing depth, at 12 m the total force and velocity of water movement is probably at the lowest levels seen on the fore reef, with less than 20% of the energy or velocity recorded in the upper layers (cf. Dietrich 1963; Roberts et al. 1975).

Along the northern GBR, the outer reefs form an almost complete barrier and will filter out a large portion of the incident wave energy. With a restricted area for wave propagation, the mid and inner reefs are exposed to considerably less wave activity. Average wave heights in the northern GBR region (based on the Bureau of Meteorology estimates for 1999) are 2.0 m outside the reef and 1.3 m inside the barrier reef (representing a wave-energy loss of approximately 57%, cf. Dietrich 1963). These values provide a crude estimate of relative water movement in the various reef locations. They also permit tentative comparisons to be made

between the mean aspect ratios of individuals in labrid assemblages and water movement in these locations (Fig. 8). This comparison reveals a clear trend for increased mean fin aspect ratios in labrid assemblages in exposed locations.

Distribution patterns, habitat use, and swimming performance

The distribution of labrids across the GBR is consistent with the suggestion that wave action and/or water movement is a significant factor in shaping labrid assemblages. The correlation between two factors (estimated water movement and fin morphology), which are logically linked through biomechanical properties and realized swimming performance, suggests that this may be a causal relationship rather than an indirect correlation based on topography, coral cover, food availability, etc. The clearest pattern is seen on mid- and outer-shelf reefs, where flat and crest sites are characterized by large populations of species with high aspect ratio fins and relatively few individuals with low aspect ratio fins (negative aspect ratio residuals). This pattern breaks down on inner-shelf reefs. It is possible that on inner-shelf reefs, wave energy is too low to segregate assemblages among habitats. This lack of faunal separation is reflected in the lack of a physical distinction between the reef crest and slope at these sites.

The question remains as to why individuals with high aspect ratio fins should be so abundant at high exposure sites and individuals with low aspect ratio fins abundant in sheltered locations. Are the slow swimming, low as-

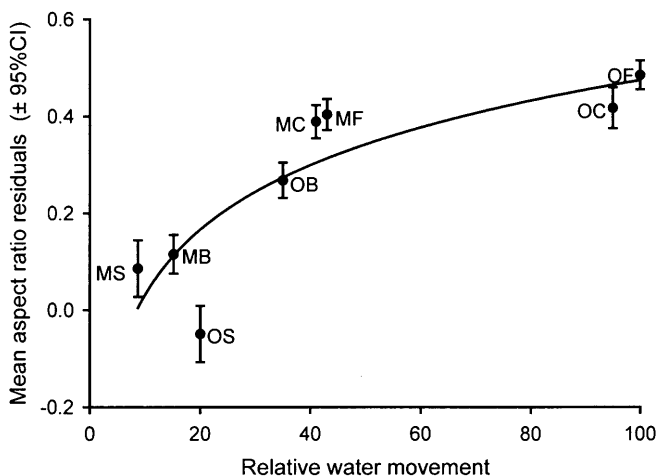


Fig. 8 Relationship between mean aspect ratio residuals for individuals in labrid assemblages across the GBR (from Fig. 7) and estimated water movement at each site. Estimated water movement as a percentage of energy recorded near the wave break on the outer flat of outer barrier reefs: mid 43% outer; crest 95% flat; slope 20% flat; back 35% flat; references given in text). The trend is indicated by regression $y = -0.324 + 0.172 \ln x$ ($r^2 = 0.77$). (Based on mid- and outer reefs only). For definition of abbreviations see Fig. 3

pect ratio forms physically or biologically excluded from these high exposure locations? Or does the converse apply, with high aspect ratio individuals being excluded from sheltered locations? The evidence suggests that the former scenario is most likely as sheltered sites include many species and individuals with high aspect ratios. Some species, such as *Thalassoma hardwicke* and *T. janseni*, are present across the whole GBR, while others such as *Stethojulis strigiventer* are recorded in greatest numbers from sheltered sites. Indeed, *S. strigiventer* is a common inhabitant of calm coastal reefs throughout the Indo-Pacific (cf. Myers 1989).

The evidence also suggests that low aspect ratio-based locomotion may be disadvantageous in high wave exposure locations. In these locations high aspect ratio individuals are well represented. Low aspect ratio species did occur in exposed locations but only in very low numbers. These species were not necessarily absent, just under-represented, even though the observations were undertaken in periods of exceptionally calm weather (for logistical reasons). The observed patterns are therefore likely to underestimate the impact of wave action as it is during these calm periods that movement into exposed locations is likely to be highest.

So why were low aspect ratio species under-represented in these high exposure locations? Competitive exclusion is possible, and it has been shown to determine distribution patterns and habitat use in reef fishes (Robertson 1996). Although no interspecific aggression in labrids was observed during the censuses, such territoriality and intraspecific aggression has been recorded in a number of crest-dwelling herbivorous labrids and acanthurids (Choat and Bellwood 1985; Robertson and Gaines 1986). Removal experiments would be required to resolve this issue.

Although the correlation between wave exposure and swimming ability (as indicated by the aspect ratios) suggests that the relationship is based on a physical interaction, there is no direct evidence. It may be noteworthy, however, that the few low aspect ratio individuals recorded from exposed locations were often closely associated with the substratum, hiding in holes or under corals, in contrast to the abundant high aspect ratio individuals which were frequently recorded in open areas and in the water column. A similar pattern has been described in labrids at Lizard Island by Fulton et al. (2001). The close associations between low aspect ratio individuals and the substratum may enable these fishes to utilize eddies and other hydrological features associated with topographic irregularities at a microhabitat scale as a possible means of maintaining position during periods of strong water movement. A comparable mechanism has been proposed for freshwater fishes in fast-flowing streams (Sagnes et al. 1997) and in lutjanid schools in reef channels (Potts 1970).

These observations bring to the fore the related question of juvenile distributions. In some species, aspect ratio increases with body size. Mechanical models indicate that the energetic advantage of the lift-based

propulsion system over drag-based locomotion is reduced, or even reversed, at small body sizes (Walker and Westneat 2001). Thus, the locomotor abilities of juvenile high aspect ratio species may be more similar to those of low aspect ratio taxa. One may therefore expect to see an ontogenetic habitat shift as in fresh-water fishes (Sagnes et al. 1997) and some scarids (Bellwood and Choat 1989) or a shift in behavior and microhabitat use. In labrids, the latter appears to apply, with most species with high aspect ratios settling into adult habitats, but they appear to use microhabitat features as a means of avoiding excessive water movement during the juvenile period. This settlement of juveniles into “adult” habitats suggests that the distribution patterns are not simply a result of prevailing exposure regimes, but that the patterns are a result of selective recruitment and that the match between ability and location may be an adaptive response to these locations. The relative contribution of evolutionary adaptation vs. phenotypic plasticity is unknown.

The advantages conferred by high aspect ratio-based locomotion remain to be determined. During heavy seas, poor swimmers may be dislodged from the exposed portion of the reef, but shelter is often relatively close, and what of the remaining time? Even small fishes are capable of maintaining relatively high speeds ($20\text{--}60\text{ cm s}^{-1}$) for short periods (Stobutzki and Bellwood 1994). The key may lie in the duration of the swimming activity. It appears that high aspect ratio fins and flight have evolved several times in labrids with a range of ecological correlates, although they all may be based on one principle: locomotor efficiency. High aspect ratio-based flight may be the most expensive locomotor mode per unit time, but it is arguably the most efficient way of moving at speed for prolonged periods. It has been proposed that flapping appendages generate more thrust at higher speeds, while rowing appendages generate more thrust at slower speeds (Vogel 1994). Furthermore, flapping appendages appear to be more efficient at higher speeds, and drag based systems more efficient at low speeds (Walker and Westneat 2001). Having greater efficiency at higher swimming speeds may be an advantage for fishes that occupy exposed locations characterized by greater water motion. However, the use of the lift-based system of flight may have broader adaptive advantages within labrids. High aspect ratio fins, and probably the flapping-fin motion of lift-based locomotion, appear to have evolved separately in several labrid groups including planktivores (*Cirrhilabrus*, *Leptojulid*, *Pseudocoris*, *Clepticus*, etc.) and in a range of benthic feeders (*Thalassoma*, *Gomphosus*, *Stethojulis*, and scarids). Existing phylogenies (Bellwood 1994; Gomon 1997) suggest that both *Clepticus* and scarids are relatively derived taxa in lineages in which the basal taxa have low aspect ratios (a detailed analysis of the evolution of locomotion in labrids is in preparation by Westneat et al.). While the diet of the various high aspect ratio taxa ranges from plankton to benthic invertebrates and algae, all feeding modes involve considerable movement, be it

holding station against water currents (*Cirrhilabrus*) or waves (*Thalassoma*) or covering large areas when foraging (*Gomphosus*, *Scarus*). In each case, efficient movement at speed may be the common factor that characterizes these foraging modes.

These observations bring to the fore the question of phylogenetic independence. High-energy locations are characterized by large numbers of *Thalassoma* (and to a lesser extent *Gomphosus* and *Halichoeres*). If these three taxa form a single lineage, then this suggests that there may have been only a single “invasion” of high-energy locations by wrasses. Just as the parrotfishes mark the sole labrid lineage to exploit algal/detrital resources in the tropics (cf. Bellwood 1994), a single *Thalassoma*–*Gomphosus*–*Halichoeres* lineage may be the sole occupant of high-energy locations. One lineage may thus have a disproportionately large role in shaping habitat utilization patterns by labrids on coral reefs. Although labrids with high aspect ratio fins have been successful in other reef environments, the relative dearth of labrids with low aspect ratio fins in high-energy locations suggests the possibility that evolutionary modifications of locomotor biomechanics and physiology could represent a major innovation in a *Thalassoma*–*Gomphosus*–*Halichoeres* lineage which permitted it to become so successful in high-energy reef habitats. However, such a pattern would also indicate a strong phylogenetic constraint on this relationship. This highlights the need for a critical appraisal of the patterns discussed here using phylogenetically independent contrasts (Felsenstein 1985) or other methods for removing phylogenetic effects from comparative data sets (e.g. Cheverud et al. 1985; Martins and Hansen 1997). However, such analyses must await the development of reasonably well-resolved species-level trees of labrid relationships.

Locomotor performance, ecomorphology, and biogeography

Biogeography has several phases, from the description of patterns based on presence/absence data, through documentation of relative abundances, examination of mechanisms maintaining patterns, and finally to an understanding of the factors responsible for the origins of these patterns. While distribution patterns in reef fishes appear to be maintained by differential settlement or recruitment, the underlying factors responsible for the origins of these patterns are less clear. This study provides one line of evidence which may provide an explanation for the distribution patterns of fishes based on locomotor performance.

The data also highlight the relative utility of presence/absence vs. relative abundance data in biogeographic studies. The former measure proved to be relatively insensitive compared to patterns examined based on relative abundances. In high-energy locations, low aspect ratio species were not absent, but they were only recorded in very low numbers. Exclusion or avoidance is

manifest at the individual not the species level. The results have identified a strong correlation between swimming ability and distribution patterns and provided a framework for investigating the nature of this relationship. A number of previous studies have demonstrated the strong relationship between the distribution of sedentary or relatively immobile benthic taxa and water movement (Denny 1994). The results of the present study suggest that such considerations may extend to more mobile members of aquatic communities. Ecomorphological studies, therefore, may not only enable us to understand the abilities of a species at a small scale, but also help explain larger-scale phenomena including habitat use, local assemblage structure, and regional biogeography.

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Appendix

The additional Table 2 shows mean aspect ratio residuals and species vector scores for labrid fishes from the Great Barrier Reef region.

Table 2 Wrasses and parrotfishes (Labridae) from the Great Barrier Reef region. *C* Species recorded from the Coral Sea; *D* usually found in deep water (>25 m); *S* recorded from the southern GBR; *O* usually recorded in off-reef habitats (sand, rubble, seagrass); *R* based on occasional sightings; *P* published record. Figures in right-hand column are mean aspect ratio residuals (the regression equation is $y=0.001x+1.23$, $r^2=0.06$) followed by species vector scores for PC 1 and 2 (cf. Fig. 5)

Wrasses	Mean aspect ratio residuals and species vector scores
<i>Anampses caeruleopunctatus</i>	0.016; 0.001, 0.006
<i>A. femininus</i> ^a S	
<i>A. geographicus</i>	-0.044; -0.021, 0.000
<i>A. meleagrides</i>	-0.267; 0.005, -0.006
<i>A. melanurus</i> ^a RC	
<i>A. neoguinaicus</i>	0.015; 0.025, 0.099
<i>A. twistii</i> ^a R	
<i>Bodianus anthioides</i>	-0.372; 0.000, 0.002
<i>B. axillaris</i>	-0.185; 0.013, 0.043
<i>B. bimaculatus</i> ^a RDC	
<i>B. diana</i>	-0.352; -0.001, 0.004
<i>B. loxozonus</i>	-0.047; 0.002, 0.009
<i>B. mesothorax</i>	-0.374; 0.001, 0.036
<i>B. perditio</i> ^a RS	-0.041
<i>Cheilinus chlorurus</i>	-0.425; -0.090, -0.058
<i>C. fasciatus</i>	-0.458; -0.019, 0.026
<i>C. oxycephalus</i>	-0.454; -0.006, 0.033
<i>C. trilobatus</i>	-0.532; 0.041, 0.024

Table 2 (Contd.)

Wrasses	Mean aspect ratio residuals and species vector scores
<i>C. undulatus</i>	-0.796; 0.004, 0.002
<i>Cheilio inermis</i>	-0.215; -0.003, -0.003
<i>Choerodon anchorago</i>	-0.279; -0.019, -0.011
<i>C. cephalotes</i> ^a O	-0.605
<i>C. cyanodus</i>	0.071; -0.029, -0.036
<i>C. fasciatus</i>	0.049; -0.006, 0.028
<i>C. graphicus</i>	-0.010, -0.012
<i>C. jordani</i> ^a O	
<i>C. schoenleinii</i>	-0.474; -0.010, -0.008
<i>C. venustus</i> ^a SD	0.590
<i>C. vitta</i> ^a O	
<i>Cirrhilabrus condei</i> ^a R	
<i>C. exquisitus</i>	0.389; 0.004, 0.055
<i>C. laboutei</i> ^a	0.252
<i>C. lineatus</i> ^a	0.078
<i>C. punctatus</i>	0.342; -0.029, 0.211
<i>C. scottorum</i> ^a	0.295
<i>C. 'cyanopleura</i> ^a P	-0.220
<i>Coris aurilineata</i> ^a S	
<i>C. aygula</i>	-0.029; 0.002, 0.004
<i>C. batuensis</i>	0.104; -0.073, 0.122
<i>C. dorsomacula</i>	0.114; -0.002, 0.008
<i>C. gaimard</i>	0.013; -0.003, 0.017
<i>C. pictoides</i> ^a S	-0.034
<i>Cymolutes praetextatus</i> ^a O	
<i>C. torquatus</i> ^a O	-0.282
<i>Diproctacanthus xanthurus</i> ^a P	-0.343
<i>Epibulus insidiator</i> ^a	-0.292; -0.013, 0.035
<i>Gomphosus varius</i>	-0.261; 0.163, 0.117
<i>Halichoeres biocellatus</i>	0.021; 0.005, 0.081
<i>H. chloropterus</i>	-0.160; -0.030, 0.011
<i>H. chrysus</i> ^a C	0.215; 0.00, 0.00
<i>H. hortulanus</i>	0.306; 0.030, 0.067
<i>H. margaritaceus</i>	0.039; 0.065, -0.107
<i>H. marginatus</i>	0.172; 0.121, -0.082
<i>H. melanurus</i>	-0.219; -0.262, 0.174
<i>H. melasmapomus</i> ^a RC	
<i>H. miniatus</i>	-0.020; -0.337, -0.443
<i>H. nebulosus</i>	-0.048; -0.146, -0.149
<i>H. nigrescens</i>	-0.001, -0.000
<i>H. ornatissimus</i>	0.050; 0.000, 0.003
<i>H. prosopion</i>	0.013; -0.010, 0.059
<i>H. scapularis</i> R	-0.111; -0.000, -0.000
<i>H. trimaculatus</i>	0.240; 0.009, 0.114
<i>H. zeylonicus</i> ^a R	
<i>Hemigymmus fasciatus</i>	-0.066; 0.009, 0.050
<i>H. melapterus</i>	-0.131; -0.120, -0.091
<i>Hologymnosus annulatus</i>	0.115; -0.000, 0.004
<i>H. doliatus</i>	0.239; -0.001, 0.000
<i>H. longipes</i> ^a P	
<i>Labrichthys unilineatus</i>	-0.457; 0.031, 0.070
<i>Labroides bicolor</i>	0.124; 0.016, 0.016
<i>L. dimidiatus</i>	0.405; 0.028, 0.223
<i>L. pectoralis</i>	-0.091; 0.003, -0.001
<i>Labropsis australis</i>	-0.382; -0.006, 0.009
<i>L. xanthonota</i>	-0.376; 0.000, 0.011
<i>Leptojulis cyanopleura</i> ^a R	0.693
<i>Macropharyngodon choati</i>	0.043; -0.001, 0.004
<i>M. kuiteri</i> ^a O	0.234; 0.00, 0.00
<i>M. meleagris</i>	0.199; 0.026, -0.014
<i>M. negrosensis</i>	0.079; 0.007, 0.004
<i>Novaculichthys taeniourus</i>	-0.349; 0.003, 0.004
<i>Oxycheilinus bimaculatus</i> ^a D	-0.524
<i>O. digrammus</i>	-0.441; -0.032, 0.044
<i>O. unifasciatus</i>	-0.352; 0.011, 0.004
<i>Pseudocheilinus evanidus</i>	-0.748; 0.002, 0.019
<i>P. hexataenia</i>	-0.376; 0.153, 0.379

Table 2 (Contd.)

Wrasses	Mean aspect ratio residuals and species vector scores
<i>P. octotaenia</i>	-0.660; 0.00, 0.00
<i>Pseudolabrus guentheri</i> ^a S	
<i>Pseudocoris yamashiroi</i> ^a C	-0.567
<i>Pseudojuloides cerasinus</i> ^a D	-0.044
<i>Pseudodax moluccanus</i>	0.315; 0.000, 0.000
<i>Pteragogus cryptus</i>	-0.609; -0.008, -0.005
<i>P. enneacanthus</i> ^a R	-0.405
<i>Siethojulis bandanensis</i>	0.742; 0.056, 0.018
<i>S. interrupta</i>	0.036; 0.005, -0.007
<i>S. strigiventer</i>	0.214; -0.166, -0.141
<i>S. trilineata</i>	0.515; 0.015, -0.029
<i>Suezichthys gracilis</i> ^a SR	
<i>Thalassoma amblycephalum</i>	0.507; 0.601, -0.248
<i>T. hardwicke</i>	0.519; 0.292, -0.022
<i>T. janseni</i>	0.576; 0.248, -0.313
<i>T. lunare</i>	0.394; -0.100, 0.139
<i>T. lutescens</i>	0.321; 0.072, 0.073
<i>T. purpureum</i>	0.001, -0.002
<i>T. quinquevittatum</i>	0.605; 0.235, -0.239
<i>T. trilobatum</i>	0.462; 0.009, -0.012
<i>Wetmorella albofasciata</i> ^a PD	
<i>W. nigropinnata</i> ^a R	-0.457
<i>Xyrichtys aneitensis</i> ^a O	-0.009
<i>X. pavo</i> ^a O	-0.081
<i>X. pentadactylus</i> ^a RO	
Parrotfishes	
<i>Bolbometopon muricatum</i>	-0.111; 0.031, -0.028
<i>Calotomus carolinus</i>	-0.070; -0.000, 0.001
<i>C. spinidens</i> ^a RO	0.251
<i>Cetoscarus bicolor</i>	-0.047; 0.008, 0.015
<i>Chlorurus bleekeri</i>	0.340; -0.002, 0.010
<i>C. frontalis</i> ^a R	
<i>C. japonensis</i>	0.002, -0.002
<i>C. microrhinos</i>	0.096; -0.006, 0.057
<i>C. sordidus</i>	0.170; 0.009, 0.075
<i>Hipposcarus longiceps</i>	-0.066; -0.000, 0.018
<i>Leptoscarus vaigiensis</i> ^a RO	
<i>Scarus altipinnis</i>	0.271; -0.014, 0.051
<i>S. chameleon</i>	0.223; 0.002, 0.045
<i>S. dimidiatus</i>	0.330; -0.000, 0.004
<i>S. flavipectoralis</i>	0.319; -0.011, 0.027
<i>S. forsteni</i>	0.144; 0.001, 0.010
<i>S. frenatus</i>	-0.012; 0.051, 0.044
<i>S. ghobban</i>	0.031; -0.047, -0.032
<i>S. globiceps</i>	0.356; 0.013, 0.011
<i>S. longipinnis</i> ^a R	
<i>S. niger</i>	0.013; -0.005, 0.131
<i>S. oviceps</i>	0.224; 0.016, 0.026
<i>S. psittacus</i>	0.264; 0.013, 0.020
<i>S. quoyi</i> R	-0.000, 0.001
<i>S. rivulatus</i>	0.117; -0.265, -0.273
<i>S. rubroviolaceus</i>	0.015, -0.008
<i>S. schlegeli</i>	0.252; -0.030, 0.119
<i>S. spinus</i>	0.219; 0.013, 0.034
<i>S. xanthopleura</i> ^a RC	

^aSpecies not seen in censuses

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