

C.J. Fulton · D.R. Bellwood · P.C. Wainwright

## The relationship between swimming ability and habitat use in wrasses (Labridae)

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**Abstract** Habitat use is described for a local assemblage of wrasses (family Labridae) at the among-habitat and microhabitat scales of two fringing reef sites at Lizard Island, northern Great Barrier Reef. Visual censuses were used to determine the distribution and abundance of species in five reef habitat zones, and their relative positions within the water column over the reef flat. Based on previous theoretical and empirical analysis of labrid locomotion, mean pectoral fin aspect-ratio residuals were used as an estimate of swimming performance to examine the relationship between swimming ability and habitat use. Among-habitat distributions of inferred swimming ability displayed a distinct dichotomy between shallow and deep reef habitat zones, suggesting a relationship with wave energy. High wave energy (shallow) habitats were characterised by labrids with high (above 0.2) pectoral fin aspect-ratio residuals (fish that use lift-based swimming and achieve high sustained swimming speeds). Although low (below -0.2) aspect-ratio residual species were only in abundance in low wave energy (deeper) habitats, they were also present in low numbers (< 7 individuals/100 m<sup>2</sup>) on the high wave energy reef flat. Water-column use within the reef flat indicated that these low aspect-ratio residual species display a restricted use of the water column and may use substratum complexity and boundary layer effects as a refuge from high levels of water movement. Overall, locomotor morphology was a good predictor of among-habitat and microhabitat use for wrasses at this location. We propose that locomotor performance may be a general force in shap-

ing habitat use by wrasses over these two spatial scales. Some deviations from these general patterns are discussed with regard to the role of behaviour as a mediating factor between morphology and ecology.

### Introduction

Biologists have noted for a long time that form is correlated with function, and that this function has implications for the lifestyle of the organism (Borelli 1680/1989; Bock and von Wahlert 1965; Lewontin 1978). Morphology exerts limits on the performance of an animal, which in turn constrains the range of resources, such as food items and space, that an animal can exploit (Wainwright 1994). Whilst this relationship has been found to be useful in terrestrial systems (Losos 1990; Norberg 1994), there are few applications in marine systems (Wainwright 1988). This study therefore examines the extent to which locomotor ability may shape patterns of habitat use in coral reef fishes.

Basic morphology and the requirements for locomotion were linked early on in the study of fishes, with functional explanations residing in the hydrodynamic forces, primarily drag, acting on fishes when they move through their fluid environment (Alexander 1967). Fishes that predominantly use their pectoral fins for swimming (known as labriform locomotion, Webb 1994) have been the focus of several studies examining fin kinematics and morphology in relation to swimming speeds and manoeuvrability (Blake 1979; Lauder and Jayne 1996; Walker and Westneat 1997). These studies have identified two thrust-producing mechanisms within this mode of swimming: drag-based paddling and lift-based flapping. Use of the pectoral fins in drag-based swimming involves the production of thrust on the backward stroke only (Blake 1979), whereas lift-based swimming produces thrust on both the back and forward strokes through a figure-eight sweep similar to flight in hummingbirds (Walker and Westneat 1997).

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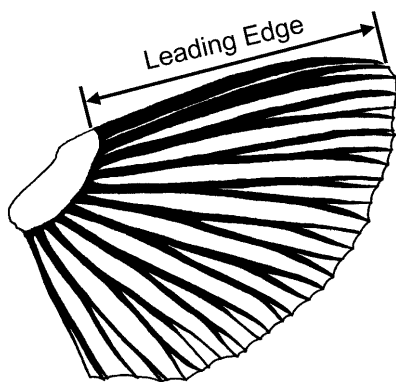
C.J. Fulton (✉) · D.R. Bellwood  
Department of Marine Biology, James Cook University,  
Townsville, Queensland 4811, Australia

E-mail: christopher.fulton@jcu.edu.au  
Fax: +61-7-47251570

P.C. Wainwright  
Section of Evolution and Ecology, University of California,  
One Shields Avenue, Davis, CA 95616, USA

Previously, these extremes in labriform locomotion have only been established among species from different families or genera (Blake 1979; Geerlink 1983; Webb 1994). However, Walker and Westneat (2000) have demonstrated that a range of pectoral fin locomotion modes, on a spectrum between these two extremes, is present within a single family, the Labridae. Furthermore, locomotor mode was found to be correlated with pectoral fin morphology in these fishes (Wainwright et al. 1999; Walker and Westneat 2000), with species that use the flapping mode having higher aspect ratio fins (see Fig. 1) than species that use the paddling mode. Theoretical considerations suggest that high aspect ratio fins are more effective as lift-producing structures and that low aspect ratio fins are best suited to producing drag-based paddling (Vogel 1994; Walker and Westneat 2000). Labrid pectoral fin diversity is considerable, as even species of the same genus (e.g. *Halichoeres*) may have very different fin morphologies (Wainwright et al. 1999).

Through field observations and flow tank experiments, Wainwright et al. (1999) and Walker and Westneat (2000) demonstrated that these differences in fin morphology are strongly correlated with swimming performance. In the field, species with highly positive aspect-ratio residuals (body-size-corrected measures of fin aspect ratio) displayed average sustained swimming speeds of 4–7 body lengths  $s^{-1}$  (for individuals 9–11 cm total length), compared to slower average speeds of 1–3 body lengths  $s^{-1}$  in species with highly negative aspect-ratio residuals. Examination of fin kinematics indicated that these extremes were related to a tendency to use either lift-based (positive residual) or drag-based (negative residual) fin strokes (Westneat and Walker 1997). Thus, aspect-ratio residuals provide an indicator of swimming ability with which to compare the swimming abilities of species within the family Labridae without the confounding effects of size. Such detailed information regarding the functional abilities of labrids provides a unique opportunity to examine the role of



**Fig. 1** Diagram of a pectoral fin demonstrating the measurements used to calculate pectoral fin aspect ratio: aspect ratio = (length of leading edge)<sup>2</sup>/total fin area. Species with a high aspect ratio have a longer fin (leading edge) for a given fin area

morphology in shaping patterns of habitat use in a family of reef fishes. This study will use this information to examine the relationship between locomotion and habitat use at two spatial scales: among habitat zones, and microhabitat use (water-column utilisation).

Differential use of reef habitat zones has been well documented for reef fishes at the within-reef scale (Williams 1982; Russ 1984; Green 1996). Several factors have been identified that may shape these among-zone distribution patterns, including taxon-specific microhabitat selection during settlement (Sale et al. 1984), the influence of resident adults on settlement (Sweetman 1985), differential mortality between habitats (Robertson 1988; Connell and Jones 1991), migrations (Robertson 1988; Green 1996), and interspecific competition (Robertson and Gaines 1986).

Wave energy has also been considered as a physical factor driving among-zone distribution patterns, primarily in sessile organisms. Rocky and sandy shore organisms and their changing zonation patterns and functional adaptations in response to wave energy are classic examples (Riedl 1971; Denny 1994). Zonation of corals on reefs has also been described in terms of wave energy (Bradbury and Young 1981; Done 1983). Functional explanations for such patterns have been based on the influence of wave action on the supply of nutrients and removal of wastes (Riedl 1971; Jokiel 1978), and adaptations to mechanical stress, such as the surf-resistant morphologies exhibited by ubiquitous coral species when under conditions of high wave exposure (Done 1983). Comparable studies examining highly mobile marine organisms, such as fishes, are lacking, and although reef fish assemblages have been found to change across gradients of wave energy (Bradbury and Young 1981; Williams 1982; Russ 1984), no functional explanation has been proposed.

Despite the scarcity of studies in marine systems, the relationship between water flow and habitat use has been well documented in freshwater stream fish communities (e.g. Chipps et al. 1994; Lonzarich and Quinn 1995). Patterns of water-column use have been identified within these communities, with species either located in mid-water or closely associated with the substratum (Bain et al. 1988; Wood and Bain 1995). It has been suggested that this is a result of differences in the ability of species to hold their position while swimming under conditions of high water flow (Sagnes et al. 1997; Heinimaa and Erkinaro 1999). As the two swimming modes of labrids, drag-based and lift-based, are believed to differ in their efficiency for sustained high swimming speeds (Vogel 1994; Walker and Westneat 1997), a similar situation may exist in labrids. Water-column use by the slower-swimming (drag-based) species may be expected to be more restricted in reef habitats of high water movement than that of the faster-swimming (lift-based) labrids.

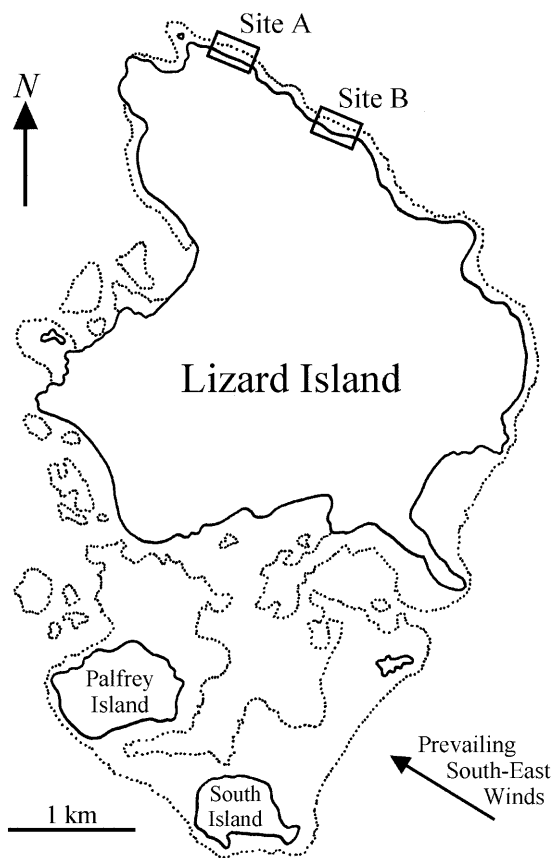
The specific aims of this study, therefore, were to (1) describe the distribution of labrids among five habitat zones of two semi-exposed reefs; (2) determine if labrids

display differential patterns of water-column use; and (3) evaluate the relationship between these aspects of habitat use and the inferred swimming abilities of each species.

## Materials and methods

### Study sites

The study was conducted between September 1999 and January 2000 at Lizard Island (14°40'S, 145°28'E), a continental island in the northern section of the Great Barrier Reef, Australia. Two fringing reef sites were used, Site A and Site B, which are obliquely exposed to the prevailing south-east trade winds (Fig. 2). These sites were chosen based on their similar aspect and habitat zone characteristics: a wide, shallow reef flat, narrow crest, and almost vertical slope that descends to a base of coral sand and small coral



**Fig. 2** Map of Lizard Island indicating the location of the two study sites

bommies (Choat and Bellwood 1985). According to position on the reef profile, depth, and degree of wave exposure, the reef was divided into five habitat zones: inner flat, outer flat, crest, slope, and base (Table 1).

### Among-habitat distribution and abundance

Among-habitat distributions of labrid species were determined by visual censuses using a modification of the tape transect method. An observational SCUBA diver recorded the size and abundance of all wrasses encountered within a 5-m-wide strip (estimated by comparison with a tape at the beginning of the transect), while being guided by a second SCUBA diver. The second diver swam parallel to the first whilst deploying a 50-m length of cord to measure distance. This procedure minimised disturbance of the transect prior to censusing. Censusing of each replicate was divided into two components following Bellwood and Alcalá (1988): a 50×5-m transect for individuals > 10 cm total length (TL), then a 50×2.5-m transect for individuals < 10 cm TL. This was repeated three times within each of the five habitat zones, at each of the two sites. All censusing was conducted within 2 h either side of the morning high tide to minimise any tidal or time-of-day effects.

All observations of individuals < 10 cm TL were doubled to correct for the different areas censused for < 10 cm TL (125 m<sup>2</sup>) and > 10 cm TL (250 m<sup>2</sup>) individuals. After initial data exploration to check the assumptions of normality and homoscedasticity, violations were corrected using  $\log_{10}(x+1)$  transformations. To reduce dimensionality of the abundance data for 43 species, a principal component analysis was conducted on the covariance matrix of the transformed data of species abundance within each habitat zone, at each of the two sites. Differences in the assemblage of species among habitat zones were tested using the method of Sandland and Young (1979a, b). Habitat-specific mean aspect-ratio residuals (sum of the product of each individual and its corresponding aspect-ratio residual, divided by the total number of individuals in each habitat zone) were compared using a one-way analysis of variance (ANOVA) and Tukey's HSD post-hoc test. Graphical presentations displaying aspect-ratio residuals utilised values from Wainwright et al. (1999) and Bellwood and Wainwright (2001), where further details of these morphological measures are given.

### Water-column use

Censusing of water-column use was conducted within the reef flat habitat zone at each of the two sites. Following a non-overlapping path over the reef flat, a focal individual census technique was used to record the species, total length, and vertical height above the substratum each time a labrid individual was encountered. Lengths were estimated to the nearest centimetre, distances to the nearest 5 cm. This was repeated until a minimum of 40 observations were recorded from individuals > 10 cm TL for the majority of species found on the reef flat, at each of the two sites. All censusing was conducted within 2 h either side of the morning high tide to minimise any tidal or time-of-day effects.

After initial data exploration to check the assumptions of normality and homoscedasticity, violations were corrected using

**Table 1** Defining characteristics of each reef habitat zone

Habitat zone <sup>a</sup>	Position	Depth range (m)	Wave exposure
Inner flat	Reef flat adjacent to shoreline	1–3	Moderate
Outer flat	Between inner flat and crest	1–3	Moderate-high
Crest	Seaward edge of reef flat	1–3	Moderate-high
Slope	Steep descent between flat and base	3–8	Low-moderate
Base	Flat, sandy area at bottom of slope	7–10	Nil-low

<sup>a</sup> Sources: Done 1983; Choat and Bellwood 1985; Nelson 1992; Green 1996

$\log_{10}(x + 1)$  transformations. A two-way ANOVA was performed on the transformed height from substratum data with site and species as fixed factors. A least-squares regression analysis was performed on the log-log transformed data to examine the relationship between height and fin aspect-ratio residuals.

**Results**

Among-habitat distribution and abundance

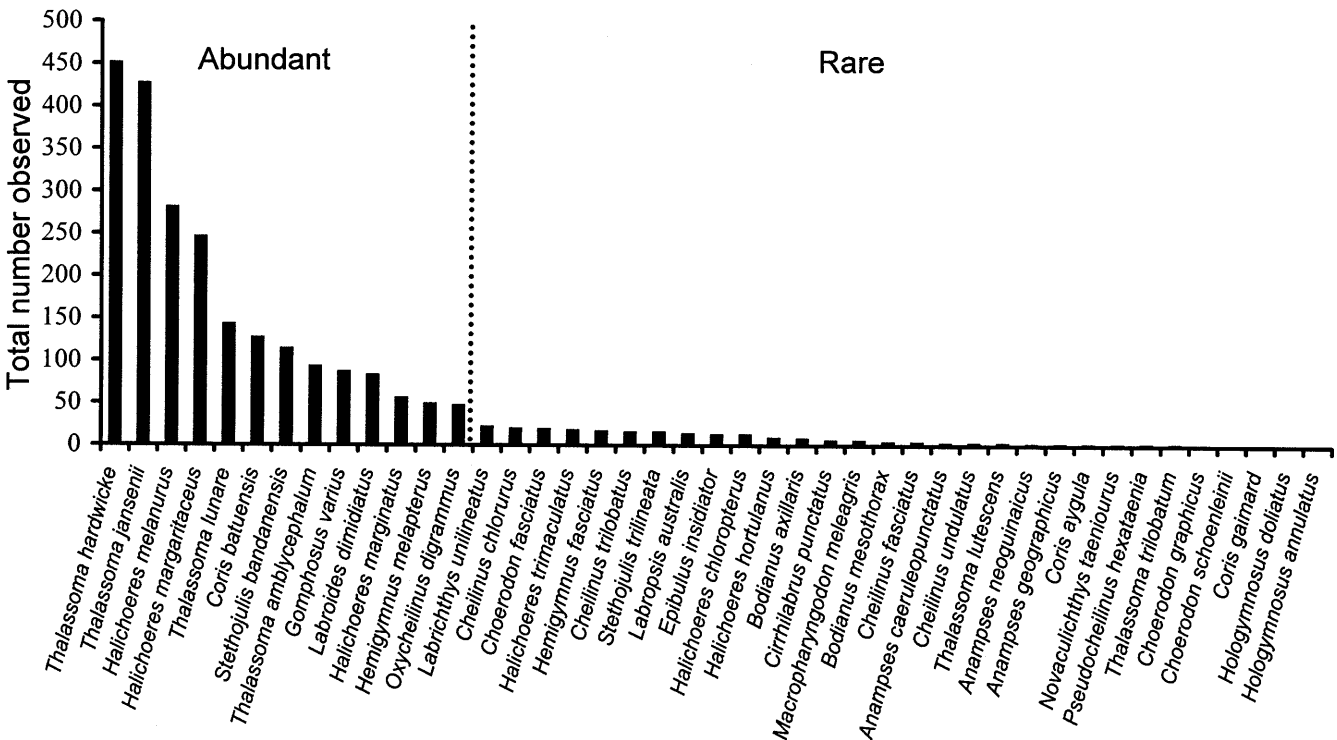
Forty-three labrid species (2,435 individuals) were censused from the two fringing reef sites. The ranked total abundance of species exhibited a negative exponential curve (Fig. 3), with 13 (30%) species categorised as abundant and 30 (70%) rarely observed (fewer than ten individuals observed). Most of the abundant species exhibited a limited distribution with regard to depth, with the majority being abundant in either the shallow or deeper habitat zones (Fig. 4). A few species had a more even distribution among the five habitat zones, for example, *Halichoeres melanurus*, *Labroides dimidiatus*, *Hemigymnus melapterus*, and *Oxycheilinus digrammus* (Fig. 4).

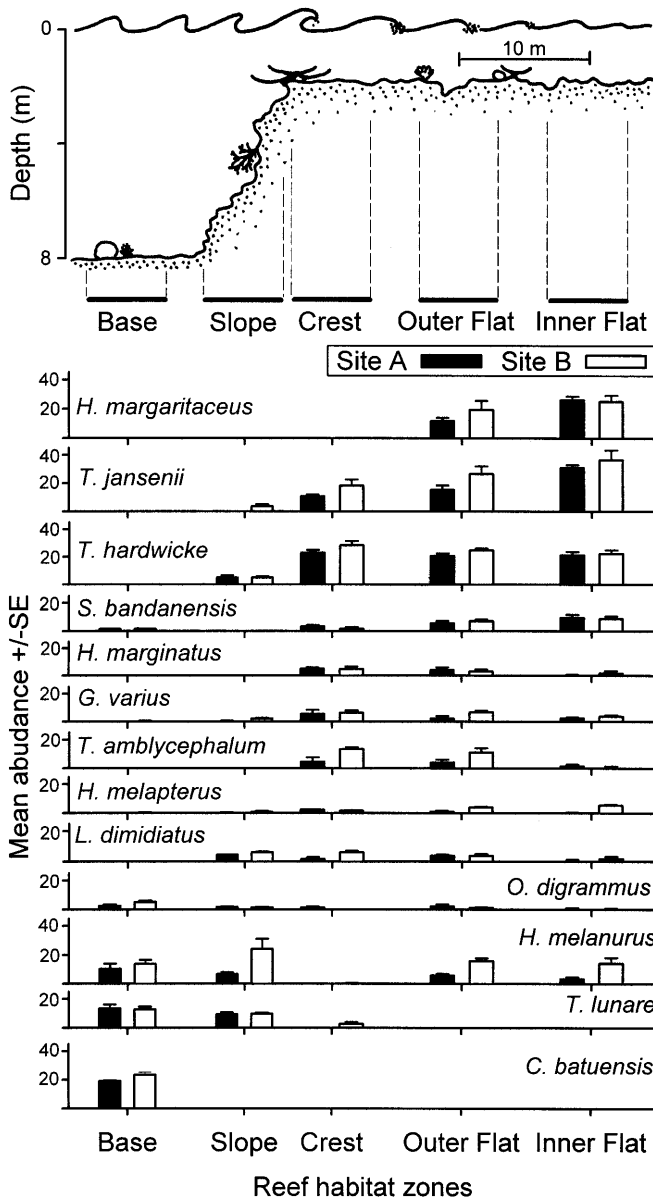
Principle component analysis supported this general observation. The first principal component, which explains 58.8% of the variation in species distributions, revealed a major division between the shallow habitats

of inner flat, outer flat, and crest, and the deeper habitat zones of base and slope, at each of the two sites (Fig. 5). Very little separation was evident between the same habitat zones at each site on either of the two components. Furthermore, analysis following Sandland and Young (1979a, b) identified a significant division between shallow (flats and crest) and deep (base and slope) habitat zones ( $P=0.02$ ). Habitat-specific aspect-ratio residuals (denoted by the bubble sizes on the scatterplot of Fig. 5) indicate that individuals found within the shallow habitat zones have, on average, much higher aspect-ratio residuals than individuals found in deeper habitat zones. This is supported by ANOVA analysis (Table 2), and Tukey’s HSD post hoc test, which identified two groups based on mean aspect-ratio residuals per habitat: base and slope ( $P=0.96$ ), and inner flat, outer flat, and crest ( $P=0.09$ ).

Similarly, individual species that tend to be most abundant in the shallower habitats tend to have higher, positive aspect-ratio residuals than those species that are abundant in deeper habitats (Fig. 6). In particular, *Thalassoma hardwicke*, *T. janseni*, *T. amblycephalum*, *L. dimidiatus*, *Gomphosus varius*, *Stethojulis bandanensis*, and *Halichoeres marginatus* all possess high positive aspect-ratio residuals and characterise the crest and flat habitats (Fig. 6). Those species that are abundant in the deeper habitats of slope and base, *Cheilinus fasciatus*, *T. lunare*, *Coris batuensis*, and *H. melanurus*, possess much lower aspect-ratio residuals (Fig. 6). Note that the majority of species with negative aspect-ratio residuals are clustered in the centre of the species vector plot, suggesting they occur either rarely or in all habitats with equal abundance (Fig. 6).

**Fig. 3** Total abundance of all labrid species censused on the north-eastern fringing reef of Lizard Island. Measures of abundance correspond to a cut-off of ten individuals observed in total

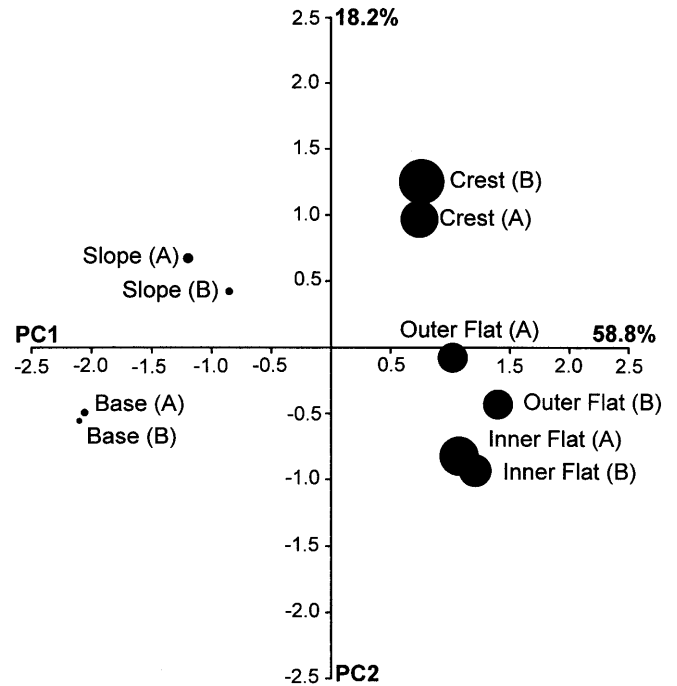




**Fig. 4** Among-habitat distribution and abundance of abundant labrids (more than ten total individuals observed) at two obliquely exposed sites at Lizard Island. Full species names given in Fig. 3, abundances are individuals per 250 m<sup>2</sup>

**Water-column use**

Water-column use was censused for 24 labrid species (2,559 individuals) in the reef flat zone at each of the two sites and was found to be significantly different between species, with no significant site effect or site-species interaction (Table 3). All species used the bottom half of the water column (Fig. 7A). Mean height from the substratum, pooled at the level of site, increased markedly with an increase in aspect-ratio residual for the 24 species censused (log-log linear regression,  $r^2=0.49$ ,  $P<0.001$ ; Fig. 7B). One major exception to this general trend was *S. bandanensis*, whose mean height in the



**Fig. 5** Ordination plot of habitat zones on principal components 1 (PC1) and 2 (PC2), after analysis of the mean abundance of labrids across five habitat zones at the two fringing reef sites. Bubble diameters are scaled to indicate the mean aspect-ratio residual of all individuals in each habitat zone

**Table 2** Results of one-way ANOVA on mean aspect-ratio residual per habitat for five reef habitat zones at two locations, with habitat as the fixed factor

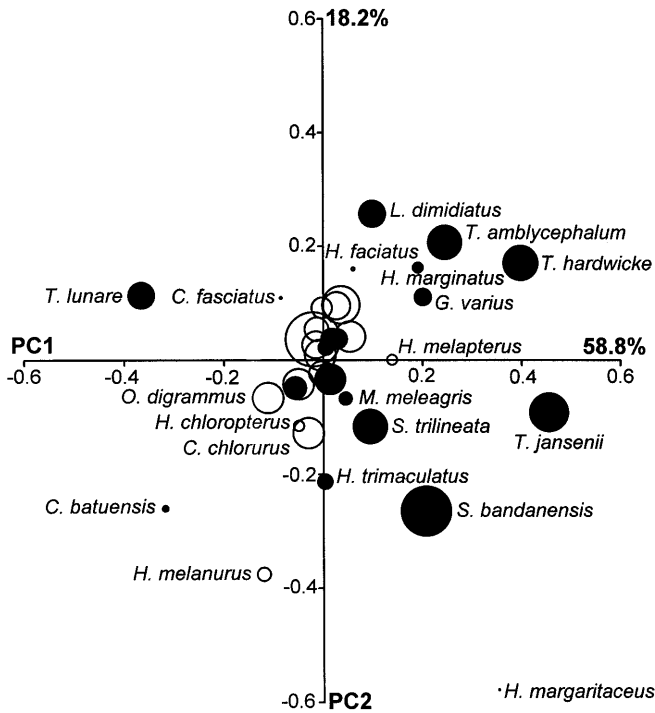
Source of variation	df	SS	MS	F	P value
Habitat zone	4	0.19	$4.70 \times 10^{-2}$	45.88	< 0.001
Error	5	$5.12 \times 10^{-3}$	$1.03 \times 10^{-3}$		
Total	9	0.20			

water column was similar to species with a much lower aspect-ratio residual (Fig. 7B).

The genus *Thalassoma* appears to contribute considerably to the observed pattern, with three of the five species that use the water column extensively being in this genus (Fig. 7B). However, *L. dimidiatus* and *H. hortulanus* also contributed to this pattern of increased water-column use with high positive aspect-ratio residuals (Fig. 7B).

**Discussion**

Distinctive patterns in the distribution and abundance of labrids among reef habitat zones revealed a strong division between depths, with most species being present in abundance in either the shallow (inner/outer flat, crest) or deeper (slope, base) habitat zones. This depth-related dichotomy of distributions agrees with that



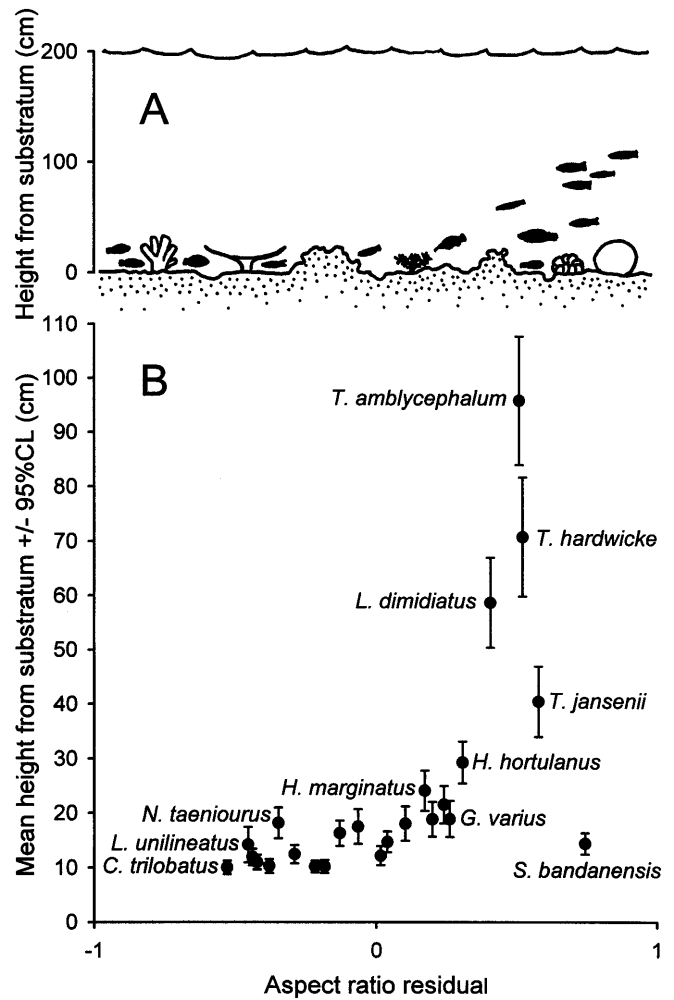
**Fig. 6** Species vector plot on principal components 1 (*PC1*) and 2 (*PC2*), indicating the contribution of each species towards the segregation of habitat zones (Fig. 5). *Bubble* diameters are scaled to the mean aspect-ratio residual of each species. *Open circles* represent negative aspect-ratio residuals (tending towards a drag-based swimming mode); *solid circles* represent positive aspect-ratio residuals (tending towards a lift-based swimming mode). Full species names given in Fig. 3

**Table 3** Results of two-way ANOVA on mean height in the water column of adult individuals (> 10 cm TL) from 24 species of labrid. Site and species are fixed factors

Source of variation	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P</i> value
Site	1	9.58×10 <sup>-3</sup>	9.58×10 <sup>-3</sup>	0.07	0.786
Species	23	155.73	6.77	52.11	<0.001
Site×species	23	1.63	7.06×10 <sup>-2</sup>	0.54	0.962
Error	2,511	326.25	0.13		
Total	2,559	483.80			

found by Green (1996), who demonstrated that these patterns were maintained not only over several locations, but also over a temporal scale of many years. This depth scale also relates to a gradient in wave energy, with deeper habitats having a much lower incident wave energy than shallow habitat zones under the same degree of exposure (Roberts et al. 1975; Done 1983).

Using a quantitative proxy for swimming ability (pectoral fin morphology), we found that individuals in shallow habitat zones tend to have a much higher fin aspect ratio for their size than individuals in deeper habitat zones. Bellwood and Wainwright (2001) described a similar pattern across the Great Barrier Reef, both within and among reefs. Overall, species that tend predominantly to use a lift-based mechanism of pectoral



**Fig. 7A, B** Height above the substratum of labrid individuals > 10 cm total length (TL). **A** Schematic diagram indicating positions relative to average water depth. **B** Mean height above the substratum for 24 species of labrid on the reef flat at two fringing reef sites. Data are pooled at the level of site (*n* > 80 for each species). Only species that illustrate extremes of the trend are labelled, with full species names given in Fig. 3

locomotion, which produces high sustained swimming speeds, occur in greater abundance in areas of high water movement than species that tend to use the much slower drag-based mechanism.

The few studies that have examined the relationship between fish distributions and water flow have reported a similar segregation of species between habitats of high and low water movement (Bradbury and Young 1981; Bain et al. 1988), but the mechanisms remain unclear. One possible mechanism producing this pattern may be wave energy constraining habitat use by species, based on their swimming abilities. Given that drag-based locomotion is an inefficient mode of pectoral locomotion under conditions of high water velocity (Vogel 1994), it is possible that these species are avoiding high wave energy habitats due to the disproportionately high energetic demands of successfully procuring food, or competing with other species under these conditions (cf.

Webb 1994). Habitats with high wave energy may require species to swim at high speeds; at speed, lift-based locomotion is believed to be the most efficient swimming mode (Vogel 1994; Walker and Westneat 2000). Increasing efficiency would imply that these species are better able to exploit reef habitats with increased water movement.

A number of pre- and post-settlement processes may also contribute to the origins and/or maintenance of these patterns. Evidence suggests that microhabitat selection at settlement may be important for some labrid species (Eckert 1985; Green 1996), and distributions of new recruits (individuals that have become visible to censusing) have been found to coincide with adult distributions for some labrid species (Williams 1991; Green 1996). However, other labrids display post-recruitment migrations between habitat zones (Green 1996). The impact of swimming ability on these migrations remains to be determined. Interspecific competition (Robertson and Gaines 1986), availability of shelter holes (Roberts and Ormond 1987), and the structure and composition of the substratum (Luckhurst and Luckhurst 1978) have also been proposed as important factors in determining among-habitat distributions. However, Green (1996) examined the possibility of associations between species and habitat complexity and composition at Lizard Island and found no significant correlation.

Species that predominantly use drag-based swimming (negative aspect-ratio residuals) are not entirely absent from habitats with high wave energy (they just occur there in low abundance). This suggests that if water movement is important, it is not the sole factor, and other processes must be operating to allow these species to occur in high wave energy areas. One such modifying factor could be the behavioural use of microhabitats that provide a refuge from high water movement, as reported in fast-flowing currents (Chipps et al. 1994; Gerstner 1998). This would allow species to occupy areas of higher water movement than expected from their functional abilities.

Water-column use was found to differ significantly between labrid species, with a relationship between water-column use and pectoral fin morphology being evident. Species that predominantly use a lift-based swimming mode tended to have a higher position in the water column than those species that use drag-based swimming. Species of the genus *Thalassoma* contributed substantially to this pattern, suggesting phylogenetic considerations may be important. However, some phylogenetic independence is maintained by the fact that *Labroides dimidiatus*, *Halichoeres hortulanus*, and *H. marginatus* also use the water column extensively.

Freshwater stream fishes have been found to differ in their water-column use, with a segregation of species according to depth (Bain et al. 1988; Wood and Bain 1995). An assemblage of seagrass fishes was also found to exhibit differences in water-column use, although this was largely categorical and between different fish families (Motta et al. 1995). Such patterns have been ex-

plained in terms of body morphology and the ability of each species to hold station (Grossman et al. 1998), due to the presence of a water velocity gradient with depth. Water velocity decreases with proximity to the substratum, with a sharp reduction in velocity in the boundary layer immediately adjacent to the substratum due to local frictional effects (Vogel 1994; Wood and Bain 1995). Such a gradient of water movement may also apply to reef flat systems on coral reefs (Young 1989; Hardy and Young 1996). This gradient has prompted suggestions that species whose morphology is not suited to high water velocities may be restricted to the boundary layer, or that they persist by using other benthic structures as a refuge from water flows (Lonzarich and Quinn 1995; Gerstner 1998).

The relationship between fin morphology and water-column use by labrids may occur through a similar mechanism. By interpreting water-column position in terms of proximity to the substratum it becomes apparent that species using predominantly drag-based locomotion appear to be largely restricted to a position that is close to the substratum (within 20 cm), whereas species tending towards lift-based locomotion occupy distances of up to 1 m from the substratum. This suggests that drag-based species may in fact be using substratum topography (Fig. 7A) and the boundary layer to avoid the high levels of water movement that are characteristic of shallow habitat zones on coral reefs (Roberts et al. 1975; Done 1983). When considering refuges, predation also suggests itself as a likely factor in producing such patterns of microhabitat use. Predation risk may interact with swimming ability to restrict the distance to which fishes may stray from protective refuges, based on their ability to return to those refuges when under threat (Mittelbach 1986). This distance may be determined largely by swimming speeds (Milinski 1986), although it should be noted that escape responses are considered to consist largely of whole-body and caudal locomotion rather than pectoral fin swimming (Domenici and Blake 1997).

Deviations from the general trend suggest that the potential for microhabitat use provided by their morphology may not always be realised by each species. *Stethojulis bandanensis* is a striking example, with a very high fin aspect-ratio residual, but a restricted water-column use similar to species with much lower aspect-ratio residuals. This poses the question, why do labrids move into the water column at all? Only two of the species studied have food resources known to be located in the water column, the planktivorous *Thalassoma amblycephalum*, and the cleaner-wrasse *L. dimidiatus* (Randall et al. 1997), with the majority of labrids being considered benthic foragers (Hiatt and Strasburg 1960; Hobson 1974; Randall et al. 1997). Foraging probably does influence water-column use in some species but may not be the only factor driving water-column use within the family.

Although competition is thought to be important in the segregation of species in microhabitat use (Werner

and Hall 1977; Robertson and Gaines 1986), there have been few observations of competitive interactions in the water column among labrids, beyond possible aggressive interactions concerning reproductive territories (Thresher 1984). Reproductive activities may indeed be the explanation for such water-column use; however, no reproductive behaviours such as pair spawning or mid-water aggressive interactions were observed during the census period.

Microhabitat availability has been shown to determine larger-scale patterns of distribution and abundance in reef fishes, most effectively in those species that are highly site attached, such as the coral-dwelling gobies (Munday et al. 1997), or those that have particular dietary requirements, such as corallivorous chaetodontids (Bell and Galzin 1984). Behavioural use of microhabitats may also determine large-scale distribution patterns. If species are using microhabitats as refuges from water movement, this would have implications for interpreting larger-scale distribution patterns based on functional abilities. Behavioural use of microhabitats has the potential to explain deviations in distribution patterns from those expected by functional ability, as found in the among-habitat distribution of labrids. Occupation of the reef flat by slow-swimming, drag-based species is probably facilitated by their ability to avoid high wave energy by remaining close to the substratum and using holes and crevices as physical refuges.

In conclusion, the among-habitat distribution patterns of labrids show a clear dichotomy marked by depth and fin morphology. This relationship appears to be a result of wave energy interacting with swimming ability to constrain habitat use, possibly mediated through differences in efficiency of movement at high speeds. Similarly, differences in water-column use were related to fin morphology and swimming ability, with suggestions that species predominantly using drag-based pectoral locomotion are avoiding high water movement through proximity to the substratum. Not all species used the potential for extensive habitat use that their morphology may otherwise suggest (e.g. *S. bandanensis*). Why some labrids use the water column remains unclear.

Ultimately, ecomorphology provides a means of gaining a functional insight into ecological patterns, but the actual patterns are not always a simple extrapolation of morphological differences. Caution must be applied when attempting to suggest patterns of ecology based on morphological differences alone. The results presented here indicate that acceptance of intuitive predictions of ecological patterns, without any validation by field observations, may be misleading. Behaviour is a major modifying factor, altering actual patterns beyond those expected by interpretations of morphology and performance interacting with the physical attributes of habitats. Insights into possible modifying factors were found in this study through the examination of habitat use over more than one scale. Morphology and performance may explain patterns of distribution and abundance but this link depends on the species and spatial scale concerned.

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