

Patterns of foraging in labrid fishes

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ABSTRACT: Patterns of foraging behaviour are described for a local assemblage of wrasses (Labridae) at the within-habitat scale of 2 fringing reef sites at Lizard Island, northern Great Barrier Reef, to examine the relationship between locomotor abilities and foraging patterns. Focal individual censuses were used to record the distances travelled by individuals over 30 s and 5 min time periods, and their substratum microhabitat preferences during searching and feeding. Size of short-term foraging ranges, estimated by linear start-to-finish distances, appeared to be driven largely by the shape of the foraging path. Two major foraging modes were identified: directed (widely-foraging) and convoluted (restricted). Within each mode, a strong positive relationship was observed between estimated locomotory ability and foraging distances. Four major groups of foraging-microhabitat preferences were apparent: neutral foraging and positive selection towards aggregates, dead coral heads, or live coral. A weak relationship between foraging mode and estimated patch size of preferred microhabitats was observed, with species having a directed foraging mode most frequently selecting more spatially discrete microhabitats.

KEY WORDS: Foraging · Ecomorphology · Habitat use · Selectivity · Labridae · Locomotion · Coral reefs · Patch size

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INTRODUCTION

Foraging behaviour is a key aspect of habitat use by fishes, and constitutes a large component of daily activity. Numerous studies of foraging in fishes have reported patterns of preferences relating to particular habitat types at various scales (Hobson 1975, Cowen 1986, Grossman 1986). Many studies, predominantly theoretical, have attempted to explain foraging-path patterns by relating the distribution and size of preferred habitat patches to patterns of space use during foraging (Siniff & Jessen 1969, Covich 1976). In particular, optimal foraging theory regards the distribution of prey into microhabitat patches and the attendant trade-offs associated with travelling between or remaining within these patches as a major factor affecting the shape of foraging paths (Schoener 1971, Nor-

berg 1977). Theoretical predictions based on the distribution of microhabitats indicate that directed (non-overlapping) paths are best for searching discrete microhabitats in small patches, whereas a convoluted (overlapping) foraging path most efficiently searches locally uniform microhabitats (Siniff & Jessen 1969, Weihs & Webb 1983).

Despite the obvious constraint of locomotory speeds on the distances and areas covered during foraging, locomotor speed has received little attention, although it has been hypothesised that foraging distances will increase with increased locomotion efficiency and speeds within the framework of optimality (Norberg 1977, Pyke 1981). In fishes, Weihs & Webb (1983) suggested that a locomotory mode which produces high sustained swimming speeds would be more efficient for directed searching of discrete microhabitats as opposed to more uniform microhabitats, which are best searched at slow speeds in a convoluted manner. Such a pattern has been reported for terrestrial browsing ruminants

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(Etzenhouser et al. 1998), but similar descriptions for fishes are lacking. Nevertheless, locomotion does appear to shape foraging patterns in fishes by limiting access to various habitats (Klingenberg & Ekau 1996) and microhabitats (Heinimaa & Erkinaro 1999), or by modifying prey capture success (Webb 1994).

Those fishes which primarily use their pectoral fins for swimming (known as labriform locomotion) have been the subject of a series of detailed studies of fin form and kinematics (e.g. Lauder & Jayne 1996, Wainwright et al. 1999, 2002, Walker & Westneat 2000). These studies have identified 2 basic thrust-producing mechanisms: drag-based paddling and lift-based flapping. Furthermore, studies on a single family, the Labridae, have identified a diversity of pectoral fin locomotion modes within this group, on a spectrum between these 2 extremes, with locomotor performance being strongly correlated with the pectoral fin morphology of these fishes (Wainwright et al. 1999, 2002, Walker & Westneat 2000).

Through field observations and flume tank experiments, Wainwright et al. (1999, 2002) and Walker & Westneat (2000) demonstrated that differences in fin morphology (expressed as 'fin aspect-ratio' = [length of leading edge]²/fin area) were strongly correlated with swimming performance in labrids. Field observations indicated that species with high positive aspect-ratio residuals (ARR, a body-size-corrected measure of fin aspect-ratio) displayed average sustained swimming speeds of 4 to 7 body lengths s⁻¹ against much slower average speeds of 1 to 3 body lengths s⁻¹ in species with high negative ARR. Examination of fin kinematics indicated that these extremes were related to a tendency to predominantly use either lift-based (positive residual) or drag-based (negative residual) fin strokes

(Walker & Westneat 2000). These ARR values thus provide a size-independent estimate of swimming ability (from high negative to high positive) within the family Labridae, and provide a unique opportunity to examine the relationship between morphology and ecology in a diverse group of reef fishes. Although ecological implications of swimming mode in shaping within-reef habitat use (Fulton et al. 2001) and cross-shelf biogeography (Bellwood & Wainwright 2001) have already been established, the impact at the within-habitat scale remains unknown.

Given the differences in swimming speeds exhibited by labrid species, one may hypothesise that faster-swimming species (using predominantly lift-based locomotion) will have larger foraging ranges and more directed foraging paths than slower species. This study aimed to test this hypothesis by estimating the short-term foraging ranges of labrid species with markedly different locomotory abilities (estimates being based on the pectoral fin ARR). Foraging ranges are described by quantifying short-term foraging distances and the shape of foraging paths. In addition, this study examines the substratum microhabitat selectivity of these labrids during their foraging activities in order to evaluate the relationship between locomotory mode and microhabitat preferences.

MATERIALS AND METHODS

The study was conducted between September 1999 and January 2000 on the reef flat of 2 fringing-reef sites at Lizard Island (14° 40' S, 145° 28' E), northern Great Barrier Reef, Australia. Both sites are located on the north-east aspect of the island, which is indirectly exposed to the prevailing south-east trade winds (Fig. 1). A single observer (C.J.F.) made all behavioural observations within 2 h either side of the morning high tide to minimise observer, tidal and time-of-day effects.

Foraging path and distances. Foraging distances were estimated within the reef flat habitat zone of Site A (Fig. 1) using focal individual censusing. A single individual was followed for 5 min, recording its position every 30 s with sequentially numbered markers. Individuals were followed at a distance (3 to 5 m) selected to minimise observer effects (marked by cessation of feeding or diver avoidance). If the individual was lost or disturbed by the observer, the observation period was aborted. Once an observation period was completed, the linear distances between each sequential 30 s position on the reef, and the distance between the start and finish points (5 min distance) were measured to the nearest 1 cm. This was repeated for 10 individuals of each species. All individu-

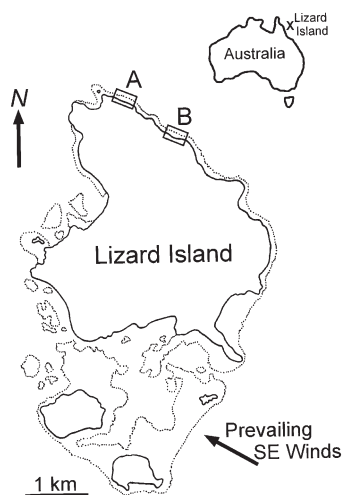


Fig. 1. Location of study sites at Lizard Island, northern Great Barrier Reef

als were of initial colour phase and between 10 and 16 cm in total length (chosen in order to minimise sex or size effects). Nine species, encompassing a wide range of estimated swimming abilities (after Bellwood & Wainwright 2001), were selected for this aspect of the study. It must be noted that this method measures foraging distances only, not home range, and represents a subset of the home range pertaining to a single activity, i.e. foraging (cf. Jennrich & Turner 1969, Dicke & Burrough 1988).

Benthic substratum composition. Censuses of benthic substrata were undertaken at each of the 2 sites (A and B: Fig. 1) following a modification of the point-transect method of Choat & Bellwood (1985). Line transects were placed over the reef flat, perpendicular to the reef crest, at random points along the reef. At 1 m intervals along the 32 m transect, the substratum type was recorded under the tape and at 1 m either side of the transect. A single additional point was then recorded 1 m beyond the end of the line transect to bring the total points recorded to 100. Ten replicate transects were taken at each of the 2 sites. Description of substratum types by functional category (based on growth form or aggregate type) was expanded from those used by Nelson (1993) to 21 categories in total.

Substratum use by foraging labrids. Rapid visual censuses were used to record substratum preferences at each site (A and B). While swimming a non-overlapping path over the reef flat, the activity at time of observation and the nearest substratum type were recorded for each labrid individual observed. This was repeated until a minimum of 10 observations of feeding and/or searching had been obtained for the 17 most abundant reef flat species at each of the 2 sites. Four activities were defined for censusing: 'travelling' whereby the body is orientated parallel and moving relative to the substratum; 'stationary' with the body orientated parallel to the substratum without movement; 'searching', with the head orientated towards the substratum, moving or stationary; 'feeding', whereby the oral jaws are in contact with the substratum. The substratum types recorded were identical to those used in the benthic censuses.

Analyses. The distances travelled by each individual were rescaled to body lengths to account for any size effects within the narrow size range observed (10 to 16 cm total length). A $\log_{10}(x + 1)$ transformation was performed to satisfy requirements for normality and homoscedascity. One-way ANOVA, with species as the fixed factor, was performed on the foraging distance data for 30 s distances (the first 30 s interval from each observation period) and 5 min (start-finish) distances. A tortuosity ratio, providing an estimation of the foraging-path pattern (specifically the degree of convolution), was calculated for each observation pe-

riod, following Secor (1994):

$$\frac{\text{total distance travelled (sum 30s distances)}}{\text{start-finish (5 min) distance}}$$

Ratio values for each species were then compared using a 1-way ANOVA, with species as the fixed factor, after log-transformation to satisfy ANOVA assumptions. A Student-Newman-Keuls post hoc test was performed on the mean ratio values to reveal possible groupings among species.

The analysis of foraging substratum preference included only 2 of the 4 defined activities—searching and feeding—as these were considered to be the best indicators of foraging use of the microhabitats. Following the protocols described by Manly et al. (1993), the universe of available substratum types was defined as all benthic structures used by the individuals observed. This universe included 3 of the 4 larger functional categories (dead/live, coral/non-coral) fused from the 13 substratum categories used during censusing. Categories were fused to ensure that expected values were greater than 5, as required for chi-square analysis (Manly et al. 1993). A chi-square goodness-of-fit analysis was used to compare the observed use (searching and feeding) of the substratum types by each species to expected values calculated using the censused availability of substratum types on the reef flat at each site.

Selection indices were then calculated following the (Sampling Design I Protocol A) procedure described by Manly et al. (1993) to make a post hoc examination of category selectivity. Values >1.0 (including 95% CI) indicate positive selection, values <1.0 indicate negative selection, and values ~ 1.0 indicate neutral selection (Manly et al. 1993). Bonferroni inequality ($\alpha/2k$; where: $\alpha = 0.05$, and $k =$ number of categories) was used in the calculation of confidence intervals to reduce any significance errors from multiple comparisons within each species.

To obtain an indication of effective patch sizes, the spatial distribution of the substratum categories (indicating contiguous vs smaller, discrete microhabitats) was estimated using the number of sequentially censused points of the same habitat category on each transect. For each of the 4 habitat categories, 1 estimate of patch size was randomly taken from each transect from each of the 2 sites. These patch sizes were then compared using a 2-way ANOVA, with site and substratum category as fixed factors, and post hoc analyses by Tukey's HSD test. While a 1 m distance is large in relation to some organisms, and increases the chance of jumping from one microhabitat patch to another (over-estimating continuous patch size), this measure estimates the size of substratum patches at a scale appropriate to foraging distances in labrids.

RESULTS

Foraging path and distances

Whilst foraging distances were found to be significantly different between species, both over 30 s distances ($F = 138.76$, $df = 8, 81$, $p < 0.001$), and 5 min start-to-finish distances ($F = 75.69$, $df = 8, 81$, $p < 0.001$), no clear relationship was initially apparent between distance travelled and swimming ability. When species are ranked from slowest to fastest, *Cheilinus chlorurus*, *Hemigymnus melapterus* and *Gomphosus varius* display a significantly greater foraging distance than species of similar estimated swimming ability (adjacent to each other in Fig. 2).

Tortuosity ratios were also significantly different among species ($F = 20.20$, $df = 8, 81$, $p < 0.001$), with 3 post hoc groupings indicated (Fig. 3). One major grouping ($p = 0.750$) contained the 3 species *Gomphosus varius*, *Hemigymnus melapterus* and *Cheilinus chlorurus*, which all displayed low ratio values (< 4.0) indicating they have a directed foraging path (start-to-finish distance close to total distance travelled). The other 6 species were contained within 2 overlapping groups, 1 of which was of borderline ($p = 0.055$) significance (Fig. 3). These species displayed high ratio values (> 5.0), which indicates high tortuosity (convoluted) foraging paths with a start-finish distance much shorter than the total distance travelled (Fig. 3).

The degree of tortuosity of the foraging path appears to be independent of swimming ability, with negative and positive fin aspect-ratio residual (ARR) species contained within each group (Fig. 3). However, within the 2 major groupings, there appeared to be a strong positive relationship between linear distance travelled

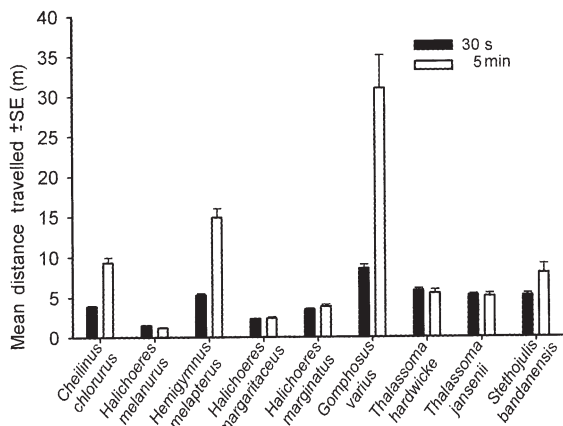


Fig. 2. Distances travelled over reef flat by 9 species of labrids after 30 s and 5 min time periods. Species are ranked from left to right by estimated swimming ability, slowest to fastest, following Bellwood & Wainwright (2001) (n = 10)

Table 1. Pearson's correlation coefficients (r) for the relationship between swimming ability (as denoted by aspect-ratio residual) and distance travelled over 30 s and 5 min time periods for 9 species of labrids combined, and divided into 2 foraging modes ('Directed', 'Convoluted')

Foraging Group	30 s		5 min	
	r	p	r	p
All	0.44	<0.01	0.015	0.885
Directed	0.874	<0.001	0.757	<0.001
Convoluted	0.889	<0.001	0.765	<0.001

and fin ARR (Fig. 4). Correlations between swimming ability (ARR) and distance travelled over 30 s and 5 min periods were increased markedly by separating the 9 species into the 2 main foraging groupings directed and convoluted (Table 1). However, it should be noted that the high correlation coefficient of the direct foraging group is based on 3 species only.

Benthic substratum composition

Non-living substrata comprised 50 and 54% of the substratum at Sites A and B, respectively, with coral matrix being the largest single component (averaging 20 and 23%, respectively), and branching coral the dominant type of living substratum (averaging 14 and 15%) (Fig. 5). The 13 substratum types were grouped within the 4 larger categories of dead aggregates, dead coral, live coral and live other for further analyses (Fig. 5). Patch size, as estimated by sequential records

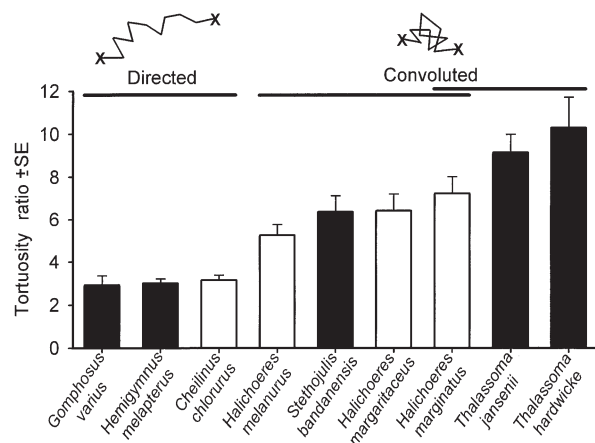


Fig. 3. Tortuosity ratio (total distance travelled [sum 30 s distances]: linear distance between start and finish points) for 9 species of labrids. Diagrammatic representation of foraging paths is indicated above the major SNK post-hoc groupings. Open (filled) bars indicate species with low (high) aspect-ratio residual (ARR) fins, tending towards drag-based, slow locomotion, (lift-based, fast locomotion) (n = 10)

on the transect line, was significantly different between substratum categories, with no significant site or interaction effects (Table 2). The substratum category of dead aggregates had an average sequential record of 2.15 and 2.36 m for Sites A and B respectively), and was grouped separately from the other 3 substratum categories, which displayed significantly lower values (Table 3). Whilst it is recognised that this estimation of patch size may be limited by the scale at which it was conducted (1 m intervals), the broad indications are that those substratum categories which display low abundance are also more spatially discrete, with smaller effective patch sizes at a 1 m scale.

Substratum use by foraging labrids

Searching and feeding activities were observed for a total of 901 individuals belonging to 17 labrid species. No selection was recorded for the live other category, except 1 individual of *Thalassoma janseni*. Although zero use of a substratum category is a valid expression of selectivity, this category was removed from further analyses to allow examination of preferences within those 3 substratum categories used by the labrids censused. Of the 17 species examined, 15 displayed a neutral or negative selection towards live coral at either 1 or both sites (Table 4). In addition to this general trend, there appeared to be 4 broad selection groups (Table 4): (1) *Labrichthys unilineatus* and *Labropsis australis* were major exceptions to the general labrid trend, displaying a strong positive selection towards live coral at both sites; (2) neutral selection for all 3 of the used categories was found in *Thalassoma hardwicke*, *T. janseni*, *Halichoeres hortulanus*, *H. margaritaceus*, *H. melanurus* and *Coris gaimard*; (3) positive selection towards intact dead coral was made by *Gomphosus varius*, *Hemigymnus melapterus*, *H. fasciatus*, *H. marginatus* and *Anampses neoguinaicus* at 1 or both sites; (4) *Stethojulis bandanensis*, *Novaculichthys taeniourus*, *Macropharyngodon meleagris* and *Halichoeres trimaculatus* tended to positively select the substratum category dead aggregates.

Table 2. Results of 2-way ANOVA comparing patch size (defined as number of continuous points on transect line) of the 4 substratum categories defined in Fig. 5. Site and substratum category are fixed factors

Source of variation	df	SS	MS	F	p
Substratum	3	14.684	4.895	62.891	<0.001
Site	1	0.002	0.002	0.026	0.873
Substratum × Site	3	0.306	0.102	1.311	0.277
Error	72	5.603	0.078		

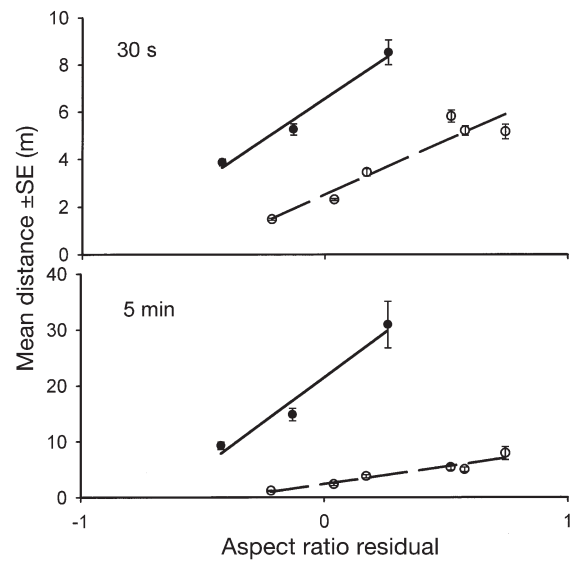


Fig. 4. Relationship between distance travelled and fin aspect-ratio residual (proxy for swimming ability/speeds), for both 30 s and 5 min time periods. Standard errors are based on n = 10. Continuous and dashed trend lines indicate the 2 major foraging modes: directed and convoluted, respectively (identified by analysis of tortuosity ratios: Fig. 3)

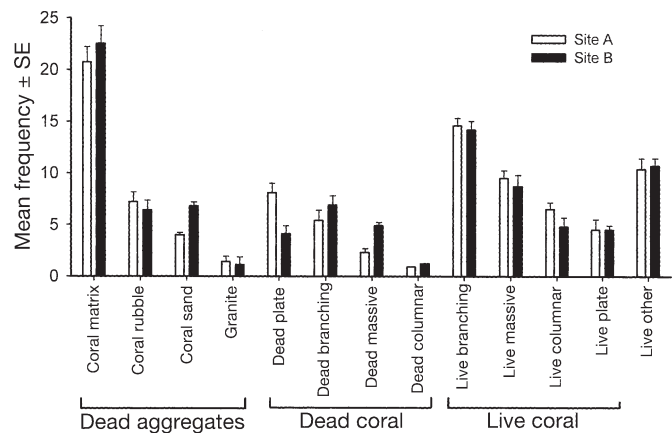


Fig. 5. Percentage cover of substratum categories on the reef flat at 2 fringing reef sites of Lizard Island. Brackets indicate the larger functional groups used for analyses, (n = 10)

Table 3. Patch size of substratum categories as estimated by average number (±SD) of sequential points at 1 m intervals on transect lines (n = 10), at 2 reef flat sites. Post hoc groupings are also indicated

Substratum category	Site A	Site B	Tukey's HSD
Dead aggregates	2.15 ± 0.25	2.36 ± 0.61	A
Live coral	1.61 ± 0.14	1.48 ± 0.17	B
Dead coral	1.27 ± 0.26	1.26 ± 0.16	C
Live other	1.17 ± 0.13	1.15 ± 0.15	C

Table 4. Selectivity of microhabitats during the foraging activities of labrids on the reef-flat habitat zone of 2 fringing reef sites (A and B), based on chi-square goodness-of-fit test (df = 2) and the foraging index of Manly et al. (1993), where +: positive, -: negative, ∙: neutral. ns: not significant; *, **, ***: significant at p < 0.05, <0.01, <0.001, respectively; blanks: no observations recorded

Species	Chi-square		Dead other		Dead coral		Live coral	
	A	B	A	B	A	B	A	B
<i>Thalassoma hardwicke</i>	ns	ns	∙	∙	∙	∙	∙	∙
<i>Thalassoma janseni</i>	ns	ns	∙	∙	∙	∙	–	–
<i>Halichoeres hortulanus</i>	ns	**	∙	∙	∙	∙	–	–
<i>Coris gaimard</i>	*	ns	∙	∙	∙	∙	–	–
<i>Halichoeres melanurus</i>	ns	ns	∙	∙	∙	∙	∙	–
<i>Halichoeres margaritaceus</i>	ns	ns	∙	+	∙	∙	∙	–
<i>Stethojulis bandanensis</i>	***	***	+	+	∙	∙	–	–
<i>Novaculichthys taeniourus</i>	***	***	+	+	∙	∙	–	–
<i>Macropharyngodon meleagris</i>	***	***	+	+	∙	∙	–	–
<i>Halichoeres trimaculatus</i>	***	**	+	+	∙	∙	–	–
<i>Gomphosus varius</i>	***	**	∙	–	+	∙	–	–
<i>Hemigymnus melapterus</i>	***	ns	∙	∙	+	∙	–	–
<i>Hemigymnus fasciatus</i>	**	***	∙	∙	+	+	–	–
<i>Halichoeres marginatus</i>	***	**	∙	∙	+	+	–	–
<i>Anampses neoguinaiicus</i>	**	***	∙	∙	∙	+	–	–
<i>Labrichthys unilineatus</i>	***	***			∙		+	+
<i>Labropsis australis</i>	***	***					+	+

These selection groupings appear to have some phylogenetic independence, with several species of *Halichoeres* spread among the different groups. Similarly, no apparent relationship with swimming ability exists. Neutral foragers exhibited a range of ARR from –0.219 to +0.576; dead coral foragers from –0.131 to +0.261, and aggregate foragers from –0.349 to +0.742. Almost total overlap in ARRs was evident between these 3 selection groups. Coral foragers were the exception, with both species possessing a negative aspect-ratio residual of similar magnitude (–0.457 and –0.382, respectively).

Table 5. Comparison of substratum preferences, shape of foraging path and swimming ability, for 9 species of labrids. Swimming ability is represented by the sign of their fin aspect-ratio residual (ARR) which indicates a tendency for either lift-based (+) or drag-based (–) locomotion following Bellwood & Wainwright (2001); na: not available

Species	Preferred substratum		Foraging Path	ARR
	Category	Patch size		
<i>Cheilinus chlorurus</i>	na	na	Directed	–
<i>Hemigymnus melapterus</i>	Dead coral	Small	Directed	+
<i>Gomphosus varius</i>	Dead coral	Small	Directed	+
<i>Halichoeres marginatus</i>	Dead coral	Small	Convolute	+
<i>Halichoeres melanurus</i>	Neutral	Large	Convolute	–
<i>Halichoeres margaritaceus</i>	Neutral	Large	Convolute	–
<i>Stethojulis bandanensis</i>	Aggregate	Large	Convolute	+
<i>Thalassoma hardwicke</i>	Neutral	Large	Convolute	+
<i>Thalassoma janseni</i>	Neutral	Large	Convolute	+

DISCUSSION

The diversity of morphological forms within the family Labridae is reflected in their patterns of foraging on coral reefs. No simple relationship exists between the size of short-term foraging ranges and fin morphology for the 9 species censused. Rather, the significant differences between species appear to be driven by the shape, or tortuosity, of the foraging path, which separates these species into 3 or more probably 2 major groupings: convolute and directed foraging modes. Theoretical and empirical studies on many vertebrate groups have identified a similar dichotomy in foraging paths based on morphological and ecological characters: wide-ranging foragers and localised foragers (Schoener 1971, Covich 1976, Huey & Pianka 1981, Webb 1984).

Highly convolute foraging paths, which have many directional changes within a small area, were found in species with both positive ARR fins (lift-based, fast swimmers) and negative ARR fins (drag-based, slower swimmers). Similarly, directed foraging paths were found among species exhibiting both swimming modes. Once separated into these foraging-path groups, however, estimated swimming ability was strongly positively correlated with the distances travelled. This trend agrees with the intuitive prediction that foraging distances will increase with increasing swimming speed within a given time period, and is consistent with the observations of Wainwright et al. (1999, 2002) who found a strong positive relationship between short-duration (<10 s) swimming speed over linear distances and ARRs.

Similarly, the relationship between estimated swimming ability (fin morphology) and substratum preferences is complex, with considerable within-taxon diversity. Four broadly discernible groups of substratum preferences were apparent: live coral (2 spp.), dead coral heads (4 spp.), aggregate substrates (4 spp.), and species which exhibited neutral selection for most substratum types (6 spp.). The only major trend was for neutral to negative selection towards live coral for all species except the 2 coral foragers. Such general preferences for dead substra-

tum types agrees with previous studies of labrid foraging (Hobson 1974), whilst the coral-foraging species *Labrichthys unilineatus* and *Labropsis australis* have previously been described as coral feeders in the literature (McIlwain & Jones 1997, Randall et al. 1997). Species within each of these broad-preference groups displayed a diversity of fin morphologies and swimming modes, with the exception of the coral foragers, which both possessed a very low fin aspect-ratio for their size.

Foraging-path patterns have been suggested as an important factor in understanding the spatial exploitation of microhabitats, as they provide a greater insight into how locomotion interacts with spatial distributions by examining the actual use of space (Schoener 1971). Such studies have identified the shape of foraging paths as being a response to the distribution of food items. Spatially discrete food items (or small patches) are most efficiently exploited through searching the greatest non-overlapping distance—a directed foraging pattern (Siniff & Jessen 1969, Weihs & Webb 1983)—whereas locally abundant food distributed in relatively larger patches is effectively utilised by searching in localised areas through high turning rates (Schoener 1971, Huey & Pianka 1981), i.e. following a convoluted, and seemingly random path. In the labrids examined, patterns of substratum preferences within the 2 foraging strategies were consistent with these expectations. Except for 1 species, *Halichoeres marginatus*, those species with highly convoluted foraging paths displayed neutral selection for all substratum types, or positive selection towards large aggregate substratum patches (Table 5). Such apparently random foraging agrees with the expectations of a convoluted (highly-overlapping) foraging path (Siniff & Jessen 1969, Weihs & Webb 1983), as it represents preference for substratum microhabitats in large to very large (all available habitats) patches. Similarly, species with a directed foraging path tended to display positive selection towards intact dead coral heads which may be considered a discrete microhabitat as they displayed a much smaller continuous record than the aggregate substratum microhabitat, or all substratum categories taken together (Table 5). Again, this agrees with expectations for a foraging path which is largely non-overlapping (Siniff & Jessen 1969, Weihs & Webb 1983).

One important consideration in studies of selectivity is the potential differences in perception between the observer and the study species. Larkum et al. (1988) demonstrated that nitrogen fixation, which is nutritionally important to algal grazers, is vastly different within patches that seem uniform to the observer. With regard to the benthic invertebrate feeding wrasses (Hobson 1974), these foraging patterns may reflect the

patterns of distribution of the preferred prey themselves, not just the habitats in which prey occur. This will depend on the sensory cues to which the fishes respond during foraging, i.e. whether they detect likely habitat patches, or detect the food items themselves (Schoener 1971). Until these sensory cues are understood, variation in preferred prey type among species will be inextricably associated with foraging patterns.

Scale is an equally important consideration. The categorisation of the spatial distribution of microhabitats into discrete and uniform was based on estimations of patch size at the 1 m scale. A clear relationship between foraging and locomotion mode may not be apparent at this spatial scale, but may be observed at another scale of habitat use, such as between reef habitat zones which differ markedly in their physical and biological characteristics (Done 1983). Moermond (1979) and Losos (1990) considered large-scale habitat types to be more important than microhabitats in determining the foraging pattern of lizards, with differences in locomotion strategies correlating more strongly with different habitat zones than with microhabitats.

In conclusion, labrids exhibit a diversity of foraging-path patterns and microhabitat preferences during foraging. In foraging paths, there exists a major dichotomy between directed and convoluted path shapes. This dichotomy has no apparent relationship to locomotor morphology in the labrid species observed, but appears to be driven largely by the spatial distribution of preferred substratum habitats. Within each of the foraging groups, however, there is a strong positive relationship between swimming ability and foraging distances. This pattern highlights the utility of performance measures when examining foraging patterns and the value of comparing abilities with a range of ecological attributes. Such a quantitative examination of foraging patterns in reef fishes also provides an indication of the scale at which coral reef habitats are utilized by fishes, and will help to establish appropriately sized protected reef areas for management and conservation.

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LITERATURE CITED

- Bellwood DR, Wainwright PC (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs* 20:139–150
Choat JH, Bellwood DR (1985) Interactions amongst herbivo-

- rous fishes on a coral reef: influence of spatial variation. *Mar Biol* 89:221–234
- Covich AP (1976) Analyzing shapes of foraging areas: some ecological and economic theories. *Annu Rev Ecol Syst* 7: 235–257
- Cowen RK (1986) Site-specific differences in the feeding ecology of the California sheephead, *Semicossyphus pulcher* (Labridae). *Environ Biol Fish* 16:193–203
- Dicke M, Burrough PA (1988) Using fractal dimensions for characterizing tortuosity of animal trails. *Physiol Entomol* 13:393–398
- Done TJ (1983) Coral zonation: its nature and significance. In: Barnes DJ (ed) *Perspectives on coral reefs*. Brian Clouston Publisher, Manuka, Australia, p 107–147
- Etzenhouser MJ, Owens MK, Spalinger DE, Murden SB (1998) Foraging behaviour of browsing ruminants in a heterogeneous landscape. *Landscape Ecol* 13:55–64
- Fulton CJ, Bellwood DR, Wainwright PC (2001) The relationship between swimming ability and habitat use in wrasses (Labridae). *Mar Biol* 139:25–33
- Grossman GD (1986) Food resource partitioning in a rocky intertidal fish assemblage. *J Zool (Lond)* 1:317–355
- Heinimaa S, Erkinaro J (1999) Fast-flowing areas affect the feeding activity of migrating Atlantic salmon smolts in tributaries of a subarctic river. *J Fish Biol* 54:688–690
- Hobson ES (1974) Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish Bull (Wash DC)* 72: 915–1031
- Hobson ES (1975) Feeding patterns among tropical reef fishes. *Am Sci* 63:382–392
- Huey RB, Pianka ER (1981) Ecological consequences of foraging mode. *Ecology* 62:991–999
- Jennrich RI, Turner FB (1969) Measurement of non-circular home range. *J Theor Biol* 22:227–237
- Klingenberg CP, Ekau W (1996) A combined morphometric and phylogenetic analysis of an ecomorphological trend: pelagization in Antarctic fishes (Perciformes: Nototheniidae). *Biol J Linn Soc* 59:143–177
- Larkum AWD, Kennedy IR, Muller WJ (1988) Nitrogen fixation on a coral reef. *Mar Biol* 98:143–155
- Lauder GV, Jayne BC (1996) Pectoral fin locomotion in fishes: testing drag-based models using three-dimensional kinematics. *Am Zool* 36:236–238
- Losos JB (1990) Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecol Monogr* 60:369–388
- Manly BFJ, McDonald LL, Thomas DL (1993) *Resource selection by animals: statistical design and analysis for field studies*. Chapman & Hall, Melbourne
- McIlwain JL, Jones GP (1997) Prey selection by an obligate coral-feeding wrasse and its response to small-scale disturbance. *Mar Ecol Prog Ser* 155:189–198
- Moermond TC (1979) The influence of habitat structure on *Anolis* foraging behaviour. *Behaviour* 70:147–167
- Nelson VM (1993) Patterns of cover, diversity and spatial arrangement of benthos at Lizard Island, Great Barrier Reef. In: Richmond RH (ed) *Proc 7th Int Coral Reef Symp* 2:827–832 University of Guam Press, Mangilao, Guam
- Norberg RA (1977) An ecological theory on foraging time and energetics and choice of optimal food searching method. *J Anim Ecol* 46:511–529
- Pyke GH (1981) Optimal travel speeds of animals. *Am Nat* 118:475–487
- Randall JE, Allen GR, Steene RC (1997) *Fishes of the Great Barrier Reef and Coral Sea*, 2nd edn. Crawford House Publishing, Bathurst
- Schoener TW (1971) Theory of feeding strategies. *Annu Rev Ecol Syst* 11:369–404
- Secor SM (1994) Ecological significance of movements and activity range for the sidewinder, *Crotalus cerastes*. *Copeia* 1994(3):631–645
- Siniff DB, Jessen CR (1969) A simulation model of animal movement patterns. *Adv Ecol Res* 6:185–219
- Wainwright PC, Bellwood DR, Westneat MW (1999) Pectoral fin diversity and evolution in labrid fishes. *Amer Zool* 39:55A
- Wainwright PC, Bellwood DR, Westneat MW (2002) Ecomorphology of locomotion in labrid fishes. *Environ Biol Fish* (in press)
- Walker JA, Westneat MW (2000) Mechanical performance of aquatic rowing and flying. *Proc R Soc Lond Ser B Biol Sci* 267:1875–1881
- Webb PW (1984) Body form, locomotion and foraging in aquatic vertebrates. *Amer Zool* 24:107–120
- Webb PW (1994) The biology of fish swimming. In: Maddock L, Bone Q, Rayner JMV (eds) *Mechanics and physiology of animal swimming*. Cambridge University Press, Cambridge, p 45–62
- Weihls D, Webb PW (1983) Optimization of locomotion. In: Webb PW, Weihls D (eds) *Fish biomechanics*. Praeger, New York, p 16–32

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