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Ecomorphology of locomotion in labrid fishes

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Synopsis

The Labridae is an ecologically diverse group of mostly reef associated marine fishes that swim primarily by oscillating their pectoral fins. To generate locomotor thrust, labrids employ the paired pectoral fins in motions that range from a fore-aft rowing stroke to a dorso-ventral flapping stroke. Species that emphasize one or the other behavior are expected to benefit from alternative fin shapes that maximize performance of their primary swimming behavior. We document the diversity of pectoral fin shape in 143 species of labrids from the Great Barrier Reef and the Caribbean. Pectoral fin aspect ratio ranged among species from 1.12 to 4.48 and showed a distribution with two peaks at about 2.0 and 3.0. Higher aspect ratio fins typically had a relatively long leading edge and were narrower distally. Body mass only explained 3% of the variation in fin aspect ratio in spite of four orders of magnitude range and an expectation that the advantages of high aspect ratio fins and flapping motion are greatest at large body sizes. Aspect ratio was correlated with the angle of attachment of the fin on the body ($r = 0.65$), indicating that the orientation of the pectoral girdle is rotated in high aspect ratio species to enable them to move their fin in a flapping motion. Field measures of routine swimming speed were made in 43 species from the Great Barrier Reef. Multiple regression revealed that fin aspect ratio explained 52% of the variation in size-corrected swimming speed, but the angle of attachment of the pectoral fin only explained an additional 2%. Labrid locomotor diversity appears to be related to a trade-off between efficiency of fast swimming and maneuverability in slow swimming species. Slow swimmers typically swim closer to the reef while fast swimmers dominate the water column and shallow, high-flow habitats. Planktivory was the most common trophic associate with high aspect ratio fins and fast swimming, apparently evolving six times.

Introduction

The Labridae (including wrasses and parrotfishes) is a group of about 550 species of marine fishes that occupy reef and reef associated habitats in tropical and temperate waters throughout the world. They are one of the dominant groups in fish communities on coral reefs, where the parrotfishes have a major effect on benthic assemblages both as herbivores and as the chief bioeroders of reef substrata (Choat 1991, Bellwood 1996), and where wrasses are typically the dominant diurnally active invertebrate predators (Randall 1967, Hobson 1974). Labrids are renowned for their spectacular ecological diversity, which has thus far mostly been recognized as being associated with their feeding biology and reproductive natural history (Randall 1967, Warner & Robertson 1978, Wainwright 1988, Bellwood & Choat 1990, Westneat 1995). However, recent observations have suggested that there may also be considerable variety among labrids in the functional morphology of locomotion (Westneat 1996, Walker & Westneat 2002).

Except during fast starts, labrids propel themselves almost exclusively with their pectoral fins (Walker & Westneat 1997, Webb 1998) and use at least two general fin movement patterns to power their swimming. Like many other groups of animals, labrids appear to generate thrust by using both rowing and flapping movements of their pectoral appendage as well as a variety of intermediate behaviors along this continuum (Walker & Westneat 2002). During a pure rowing stroke an animal generates thrust only on the posteriorly-directed power stroke (Blake 1979), whereas a purely dorso-ventrally flapping appendage generates thrust with both strokes (Daniel 1988, Walker & Westneat 1997, Drucker & Lauder 1999). The persistence of both rowing and flapping propulsion in various lineages has been explored by several authors and is usually attributed to a series of trade-offs between the two mechanisms (Davenport et al. 1984, Fish 1996, Vogel 1994, Walker & Westneat 2000). Rowing generates greater thrust at low speeds, while flapping generates more thrust at high speeds (Vogel 1994). Mechanical efficiency appears to be highest for flapping across all speeds and this advantage becomes greater as speeds increase (Walker & Westneat 2000). However, at very slow speeds rowing may afford greater maneuverability and since thrust is higher for rowing at slow speeds it can be expected to provide greater acceleration (Vogel 1994, Walker & Westneat 2000). Many labrids use locomotor styles that are combinations of rowing and flapping, and can modify the stroke plane angle to power swimming at a wide range of speeds and alternate between cruising and maneuvering (Walker & Westneat 2000).

Performance of pectoral fin locomotion across all styles is influenced by the shape of the pectoral fin. For a flapping fin it can be expected that increased aspect ratio and tapering at the tip will enhance performance by reducing the induced drag from wing tip effects (Vogel 1994). Theoretically, fins used in rowing propulsion are expected to be bilaterally symmetrical and wider at the tip than their base (Blake 1981). This dichotomy between rowing and flapping in the optimal fin shape leads to the prediction that species that prefer to swim at high speeds using a flapping fin motion will tend to have elongate, tapered fins. Species that prefer to swim slowly using a more horizontal stroke plane angle of the fin should have more symmetrical rounded fins. The presence of intermediate morphologies may indicate the effects of phylogenetic constraints or the fact that many fish may adjust their position along the rowing-to-flapping continuum depending on the context of the locomotor behavior.

In this paper we describe pectoral fin morphology for 143 species of labrid fishes of the Great Barrier Reef and the Caribbean and relate this diversity to measures of swimming speed of 43 species swimming undisturbed on the reef. Our aims are to document the diversity of labrid swimming morphology and to extend previous laboratory studies of labrid locomotion to the field setting by relating fin form to swimming on the reef.

Materials and methods

Fin morphology

Analyses of fin morphology were conducted on 933 specimens from 143 labrid species from the Great Barrier Reef region of Australia and the Caribbean. The minimum representation was one specimen per species (10 species) and the maximum was 37. In almost all cases the samples covered common adult body sizes. This collection cumulatively represents about 90% of the labrid species reported for these two regions by Randall et al. (1997) and Randall (1983). Australian fishes were collected between February 1998–June 1999 by scuba divers using barrier nets and hand spears from the area around Lizard Island, in the northern region of the Great Barrier Reef. About two dozen specimens of species not encountered on Lizard Island were obtained from commercial fish collectors who worked the central and northern sections of the Great Barrier Reef. Some of our specimens of *Wetmorella nigropinnata* and *Pseudodax moluccanus* were obtained from collections made in the Solomon Islands in May 1998. Caribbean specimens were collected by hand spear and barrier nets in the vicinity of Lee Stocking Island in the Bahamas during June–July 1999. Fish were placed on ice within an hour of capture and while still fresh the standard length (SL), total length (TL) and body mass were measured prior to dissection and measurement of fin morphology.

Previous research with four species has indicated that labrids using a mostly rowing motion of the pectoral fin move the fin through an anterior–posterior arc, while flapping species move the fin through a more dorso-ventral arc (Walker & Westneat 2002). The major flexion point in the pectoral fin occurs at the point where the fin attaches to the body, at the joints between the bases of the fin rays and the radials (Westneat 1996). We hypothesized that the orientation of the axis of fin motion would be reflected by the orientation of the attachment of the fin to the body, with rowing species having a more vertically oriented attachment and flappers having a more horizontal attachment. We measured the angle of attachment of the fin onto the body by first placing each fish on a sheet of polystyrene with its long axis oriented along a line drawn on the plastic (Figure 1a). The pectoral fin was then elevated to a position approximately perpendicular to the surface of the body and a thread with pins at either end was positioned along the base of the fin to reflect the orientation of the fin base. The fish was then removed and a protractor used to measure the angle of intersection between the thread and the long axis of the fish.

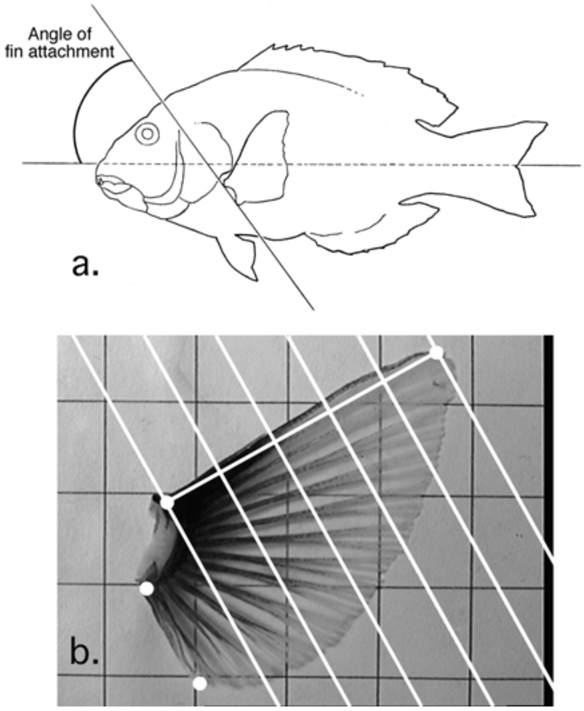


Figure 1. a – Method used to measure the angle of attachment of the pectoral fin against the long axis of the body in labrid fishes. Specimens were oriented with the mid-body axis over a line drawn on a sheet of plastic. The pectoral fin was elevated to 90° from the body and a length of thread was positioned along the axis of fin attachment and pinned into the board below. A protractor was then used to measure the angle of attachment. b – The protocol used to measure the shape of labrid pectoral fins. Points 1–4 were first digitized and a macro was employed that then drew the leading edge of the fin and six equally spaced cords. The intersection of the cords with the leading and trailing edge of the fin were then digitized and a second macro calculated several distances and the projected area of the fin.

The pectoral fin was then excised by cutting it proximal to the base of the fin rays and pinned against a sheet of polystyrene with the fin rays splayed but not stretched. The fin was irrigated with a 100% formalin solution (39% formaldehyde) to fix it in this position. A digital photograph was then taken of each fin against a background grid for scale. Fin shape was analyzed with the aid of macros written for NIH Image. Initially, four points were selected to define the basic outline of the fin (Figure 1b): the base of the leading edge of the fin, the tip of the leading edge, the base of the trailing edge and the tip of the trailing edge. The first macro was then employed to divide the fin into six equally spaced segments demarcated by cords perpendicular to the leading edge of the fin. After digitizing the intersection of each cord with the leading and trailing edge of the fin, the length of each cord was calculated with a second macro. This macro generated several measurements that were used in subsequent analyses. Distances included the length of the leading edge of the fin, the length of the six cords, the length of the trailing edge, and the length of the base of the fin. The total projected area of the fin was also calculated. The aspect ratio (AR) of each fin was calculated as the square of the leading edge length divided by the projected area of the fin. To allow comparisons with aspect ratios of other organisms for which AR is calculated using the span and area of two wings, we multiplied AR values by two. Thus, our AR values include the span and area of both fins, but not the width of the body between the fins.

Swimming speed

To explore the relationship between fin shape and routine swimming speeds on the reef, we estimated swimming speed of 43 labrid species as they moved undisturbed across the reef. Observations were made at Lizard Island, North Direction Island and MacGillivaries Reef (cf. Bellwood & Wainwright 2001), by scuba divers working in 1–10 m depth. Adult and large juvenile fish were observed and timed with a stopwatch as they moved naturally along an approximately straight path and without substantially altering speed. The beginning and end of each trial was marked as the fish passed distinct landmarks on the reef and immediately following each trial the path distance was measured with a tape. Total length of each fish was visually estimated to the nearest 1 cm and path lengths were measured to the nearest 5 cm. Path lengths ranged from 0.45 m up to 13.1 m, with an average of 2.3 m. Swimming speed was estimated for 941 individual fishes, an average of 21.9 observations per species.

Statistical analyses

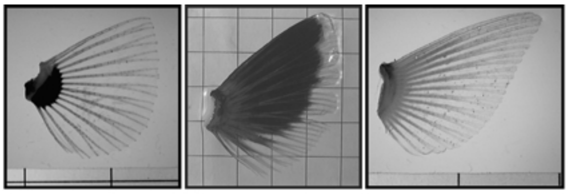
To examine interspecific differences in fin shape the mean AR of all fins analyzed for each species was calculated. Although 10 species were represented by only a single specimen the mean number of individuals per species was 6.2 and in almost all cases our samples covered common adult sizes. The possibility of ontogenetic changes in fin shape was explored by examining the data from all species separately in bivariate plots of fin aspect ratio against body size and calculating least squares regression. A least squares regression of body mass on fin AR was used to test for body size effects. Differences between species with high and low AR fins were explored with a multiple regression run with fin aspect ratio as the dependent variable and Log_{10} of fin projected area and Log_{10} body mass as independent variables. Fin shape diversity was explored in greater detail with a principal components analysis conducted on the correlation matrix of Log_{10} transformed values of the nine linear measurements: the six cords of the fin, the length of the leading edge of the fin, the length of the trailing edge and the length of the fin base.

Values of swimming speed were initially expressed in body lengths sec^{-1} and mean values were calculated for each species. This metric showed strong allometry, so residuals were calculated from a regression of swimming speed on fish TL. A multiple regression was then employed to partition the variance in swimming speed into components attributable to fin AR and attachment angle of the fin. This method allowed us to test for significant effects of each morphological variable, while controlling for, or holding constant, the other independent variables (Pedhazur 1982, Darlington 1990).

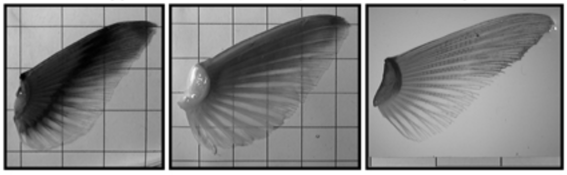
Results

Fin morphology

Pectoral fin shape, as expressed by aspect ratio, varied widely among species (Figure 2, Table 1) from a low of 1.12 in *Pseudocheilinus evanidus* and 1.32 in



Labropsis australis AR = 1.88 *Epibulus insidiator* AR = 2.19 *Thalassoma trilobatum* AR = 3.24



Gomphosus varius AR = 3.66 *Scarus psittacus* AR = 3.24 *Thalassoma quinquivittatum* AR = 3.96

Figure 2. Sample diversity of pectoral fin shape in labrid fishes. Mean AR of the species illustrated range from a low of 1.87 in *Labropsis australis* to a high of 3.93 in *T. quinquevittatum.*

P. octotaenia to a high of 4.48 in *Clepticus parrae*, 4.4 in *Choerodon venustus* and 4.2 in *Stethojulis bandanensis*. A roughly bimodal distribution was observed across species with a smaller hump occurring at an AR of about 2.0 and a larger group of species centered at around 3.0 (Figure 3). AR was variable throughout the range of body masses represented, but a significant effect of body size was found (Figure 4, $r^2 = 0.03$, $F_{1,141} = 5.58$, $p = 0.02$). Although this relationship was significant we chose to not remove size effects in subsequent analyses of fin shape because body mass only accounted for 3% of the variation among species in AR. In contrast to fin shape, fin area showed a regular, slightly allometric relationship with body mass (regression of Log_{10} body mass on fin Area: $r^2 = 0.955$, slope $= 0.618 \pm 0.011$ S.E., $F_{1,141} = 3016$, $p < 0.0001$). A multiple regression with fin AR as the dependent variable and Log fin area and Log body mass as the independent variables revealed no affect of fin area on AR (Log body mass: $F_{1,141} = 4.16$, $p = 0.035$, cumulative $r^2 = 0.028$; Log fin area: $F_{1,141} = 3.23$, $p = 0.109$, cumulative $r^2 = 0.046$). Since AR is calculated as the square of leading edge length divided by fin area, this indicates that variation among species in AR is driven by differences in length of the leading edge rather than projected area of the fin.

Labrid groups differed widely in how conservative fin shape was across species. The genus *Thalassoma* was clustered tightly at the top end of the data set with all eight species falling within the top 28 species

Table 1. Body and pectoral fin characteristics for 143 species of labrid fishes from the Great Barrier Reef and Caribbean. Table entries are means per species. See text for variable descriptions.

Genus	Species	N	Standard length (mm)	Mass (g)	Aspect ratio	Rank♦	Fin angle (°)	Swimming speed ($\text{TL}\cdot\text{s}^{-1}$)✝	TL (mm)
Great Barrier Reef									
Anampses	*caeruleopunctatus*	5	138	120.3	2.84	74	36.2	—	—
Anampses	*geographicus*	5	139	80.8	2.72	54	39.8	2.71	111
Anampses	*meleagrides*	2	68	10.3	2.10	24	58.0	—	—
Anampses	*neoguinaicus**	7	120	51.7	2.79	67	41.2	3.25	103
Bodianus	*anthioides*	4	82	34.5	1.92	15	54.2	—	—
Bodianus	*axillaris*	8	124	54.8	2.40	39	51.3	2.15	119
Bodianus	*diana*	3	131	57.6	2.09	23	59.0	—	—
Bodianus	*loxozonus*	5	157	151.5	2.76	63	55.2	—	—
Bodianus	*mesothorax*	6	108	45.3	2.04	21	51.0	1.65	123
Bodianus	*perditio*	1	118	48.2	2.68	51	55.0	—	—
Bolbometopon	*muricatum*	1	231	480.2	2.82	69	47.8	—	—
Calatomus	*carolinus*	5	207	329.3	2.84	71	41.2	—	—
Calotomus	*spinidens*	1	115	54.0	3.25	107	52.5	—	—
Cetoscarus	*bicolor*	4	204	657.6	2.88	76	40.8	—	—
Cheilinus	*chlorourus*	10	127	95.4	1.93	17	50.1	1.97	108
Cheilinus	*fasciatus*	9	163	209.3	1.96	19	53.0	1.27	244
Cheilinus	*oxycephalus*	8	96	29.7	1.80	8	60.8	—	—
Cheilinus	*trilobatus*	6	159	174.0	1.80	9	52.8	1.73	159
Cheilinus	*undulatus*	4	527	11477.5	2.19	30	45.5	0.74	810
Cheilio	*inermis*	4	97	5.5	2.28	34	55.3	—	—
Chlorurus	*bleekeri*	3	174	289.7	3.58	128	48.0	—	—
Chlorurus	*microrhinos*	5	262	852.2	3.31	111	41.8	—	—
Chlorurus	*sordidus*	14	177	229.2	3.25	106	38.5	3.55	158
Choerodon	*anchorago*	5	168	308.6	2.33	35	52.2	—	—
Choerodon	*cephalotes*	4	206	280.3	1.77	7	58.3	—	—
Choerodon	*cyanodus*	5	232	559.7	3.18	103	58.2	—	—
Choerodon	*fasciatus*	5	152	150.2	2.94	85	48.3	2.20	142
Choerodon	*schoenleinii*	4	184	262.2	1.97	75	60.8	1.76	250
Choerodon	*jordani**	4	99	33.9	2.86	20	57.4	—	—
Choerodon	*venustus*	3	309	1135.0	4.41	142	58.0	—	—
Choerodon	*vitta*	4	151	114.3	1.66	5	56.3	—	—
Cirrhilabrus	*condei*	1	68	7.7	2.91	80	50.0	—	—
Cirrhilabrus	*cyanopleura*	3	62	6.7	2.18	29	48.0	—	—
Cirrhilabrus	*exquisitus*	4	68	7.2	3.41	118	40.8	4.25	80
Cirrhilabrus	*laboutei*	8	75	9.9	3.15	102	41.9	—	—
Cirrhilabrus	*lineatus*	6	83	15.0	2.83	70	38.4	—	—
Cirrhilabrus	*punctatus*	8	74	11.0	3.33	112	47.6	4.13	56
Cirrhilabrus	*scottorum*	9	94	20.6	3.29	109	44.6	—	—
Coris	*aygula*	7	147	220.1	2.77	64	50.6	1.64	350
Coris	*batuensis*	6	117	41.4	2.96	87	50.3	2.35	105
Coris	*dorsomacula*	6	92	15.2	2.92	82	47.0	—	—
Coris	*gaimard*	8	177	168.4	3.11	99	40.0	2.14	172
Coris	*pictoides*	7	93	36.3	2.63	49	56.9	—	—
Cymolutes	*praetextatus*	5	75	7.4	2.92	81	60.5	—	—
Cymolutes	*torquatus*	9	86	9.5	2.11	26	56.1	—	—
Diproctacanthus	*xanthurus*	5	47	2.3	1.90	14	59.7	—	—
Epibulus	*insidiator*	13	150	200.0	2.25	32	45.8	1.45	210
Gomphosus	*varius***	20	155	63.4	3.37	113	38.5	4.40	125
Halichoeres	*biocellatus*	8	87	18.1	2.72	55	55.4	—	—
Halichoeres	*chloropterus*	5	123	59.7	2.45	40	55.3	—	—
Halichoeres	*chrysus*	4	72	8.2	3.07	95	55.5	—	—

Table 1. (*Continued*)

Genus	Species	N	Standard length (mm)	Mass (g)	Aspect ratio	Rank◆	Fin angle (°)	Swimming speed (TL·s^{-1})ϒ	TL (mm)
Halichoeres	*hortulanus*	9	185	178.8	3.54	22	39.5	2.40	172
Halichoeres	*margaritaceus*	7	86	18.0	2.76	124	48.8	—	—
Halichoeres	*marginatus*	3	110	37.6	3.08	61	45.2	3.51	103
Halichoeres	*melanurus*	3	73	9.2	2.21	96	56.2	2.40	88
Halichoeres	*miniatus*	6	63	7.4	2.58	31	55.5	4.59	66
Halichoeres	*nebulosus*	2	69	8.5	2.54	47	55.8	—	—
Halichoeres	*nigrescens*	7	45	2.4	2.27	43	59.3	—	—
Halichoeres	*ornatissimus*	3	69	7.0	2.74	33	55.0	—	—
Halichoeres	*prosopeion*	5	98	23.9	2.73	58	53.3	—	—
Halichoeres	*scapularis*	1	60	3.5	2.39	57	54.2	—	—
Halichoeres	*trimaculatus*	4	107	29.2	3.21	37	49.7	—	—
Halichoeres	*hartzfeldii**	4	84	11.9	2.08	104	45.0	—	—
Hemigymnus	*fasciatus*	6	145	114.0	2.70	52	45.0	2.71	133
Hemigymnus	*melapterus*	16	172	202.8	2.63	50	45.3	2.11	173
Hipposcarus	*longiceps*	2	232	472.6	2.91	79	40.0	—	—
Hologymnosus	*annulatus*	6	144	48.5	3.05	92	32.0	2.15	200
Hologymnosus	*doliatus***	12	192	128.7	3.42	119	30.5	2.01	190
Labrichthys	*unilineatus*	10	111	42.6	1.83	11	53.3	2.88	83
Labroides	*bicolor*	5	91	12.1	2.94	83	52.7	—	—
Labroides	*dimidiatus*	3	59	3.5	3.42	120	54.8	4.29	58
Labroides	*pectoralis*	4	46	2.1	2.40	38	53.7	—	—
Labropsis	*australis*	11	69	10.2	1.87	12	57.0	—	—
Labropsis	*xanthonota**	5	67	6.2	1.88	13	57.3	—	—
Leptojulis	*cyanopleura*	2	59	3.6	4.00	140	52.0	—	—
Macropharyngodon	*choati*	6	70	11.5	2.73	56	58.3	—	—
Macropharyngodon	*kuiteri*	5	63	7.4	3.09	97	50.9	—	—
Macropharyngodon	*meleagris*	7	94	28.5	3.10	98	49.5	3.11	121
Macropharyngodon	*negrosensis*	6	66	8.5	2.79	66	51.1	—	—
Novaculichthys	*taeniourus**	12	158	116.2	2.16	28	44.8	3.03	167
Oxycheilinus	*bimaculatus*	5	66	9.7	1.58	4	61.3	—	—
Oxycheilinus	*digrammus*	21	143	95.8	1.94	18	52.6	1.75	142
Oxycheilinus	*unifasciatus*	5	140	81.8	2.11	25	59.3	2.69	113
Pseudocheilinus	*evanidus*	2	60	6.3	1.12	1	62.4	—	—
Pseudocheilinus	*hexataenia*	4	45	2.1	1.82	10	61.3	—	—
Pseudocheilinus	*octotaenia*	4	70	8.7	1.32	2	66.3	—	—
Pseudocoris	*yamashiroi*	1	66	7.0	3.76	134	30.1	—	—
Pseudodax	*moluccanus*	4	173	165.5	3.53	123	52.0	—	—
Pseudojuloides	*cerasinus*	4	81	9.6	2.58	45	51.8	—	—
Pseudolabrus	*guentheri*	4	99	29.8	2.12	27	61.9	—	—
Pteragogus	*cryptus*	4	55	6.3	1.38	3	57.0	—	—
Pteragogus	*enneacanthus*	1	109	52.6	1.93	16	57.0	—	—
Scarus	*altipinnis*	3	281	609.0	3.86	136	49.5	—	—
Scarus	*chameleon*	6	157	161.4	3.30	110	37.0	—	—
Scarus	*dimidiatus*	1	146	119.0	3.49	122	45.5	—	—
Scarus	*flavipectoralis*	5	176	197.4	3.54	125	37.3	—	—
Scarus	*frenatus*	7	226	474.2	3.05	91	38.9	2.08	221
Scarus	*ghobban*	3	246	572.4	3.28	108	40.0	—	—
Scarus	*globiceps*	5	195	277.8	3.66	129	37.5	—	—
Scarus	*niger*	6	191	328.6	2.97	88	40.5	2.06	256
Scarus	*oviceps*	2	265	780.5	3.57	127	43.5	—	—
Scarus	*psittacus*	8	162	174.9	3.40	115	41.0	—	—
Scarus	*rivulatus*	4	209	415.8	3.22	105	39.7	—	—
Scarus	*schlegeli*	5	203	315.6	3.47	121	40.0	1.62	295
Scarus	*spinus*	3	200	307.9	3.40	117	43.7	—	—

Table 1. (*Continued*)

Genus	Species	N	Standard length (mm)	Mass (g)	Aspect ratio	Rank♦	Fin angle (°)	Swimming speed (TL·s^{-1})ϒ	TL (mm)
Stethojulis	*bandanensis***	14	81	14.8	4.15	141	23.2	4.52	94
Stethojulis	*interrupta*	1	66	4.1	2.70	53	33.2	—	—
Stethojulis	*strigiventer*	5	66	7.3	3.06	93	26.1	—	—
Stethojulis	*trilineata*	7	105	34.3	3.76	133	22.4	4.98	106
Thalassoma	*amblycephalum*	14	80	11.8	3.68	130	43.3	6.76	61
Thalassoma	*hardwicke***	10	115	48.5	3.79	135	29.9	3.87	122
Thalassoma	*jansenii***	31	119	49.0	3.91	138	33.2	4.00	119
Thalassoma	*lunare*	37	117	42.9	3.54	126	38.3	3.11	121
Thalassoma	*lutescens*	5	117	37.2	3.40	116	41.2	5.21	93
Thalassoma	*quinquevittatum*	9	103	42.8	3.93	139	33.0	5.66	104
Thalassoma	*trilobatum*	7	120	50.0	3.69	131	36.5		
Wetmorella	*nigropinnata*	3	44	2.0	1.66	6	57.0		
Xyrichtys	*aneitensis*	3	125	52.3	2.76	62	53.3		
Xyrichtys	*pavo*	3	178	237.3	2.75	60	42.3		
Caribbean:									
Bodianus	*rufus*	6	237	416.2	2.38	36	50.0		
Clepticus	*parrae***	25	99	41.6	4.48	143	33.2		
Cryptotomus	*roseus*	5	44	2.0	3.04	90	51.5		
Halichoeres	*bivittatus*	5	99	22.3	2.74	59	52.4		
Halichoeres	*garnoti*	7	132	47.4	3.02	89	47.3		
Halichoeres	*maculipinna*	9	106	25.8	2.78	65	46.7		
Halichoeres	*pictus*	6	87	10.9	3.88	137	39.3		
Halichoeres	*poeyi*	9	72	8.1	2.80	68	52.3		
Halichoeres	*radiatus*	4	99	27.6	3.14	101	49.5		
Lachnolaimus	*maximus*	3	382	2216.7	2.62	48	35.0		
Scarus	*guacamaia*	1	172	202.0	2.56	44	47.5		
Scarus	*iserti*	15	117	85.1	2.96	86	46.0		
Scarus	*taeniopterus*	16	145	166.6	2.84	72	44.7		
Scarus	*vetula*	5	268	786.8	3.38	114	38.6		
Sparisoma	*atomarium*	8	55	4.9	2.48	41	50.4		
Sparisoma	*aurofrenatum**	11	178	226.6	3.06	94	41.8		
Sparisoma	*chrysopterum*	14	145	170.3	2.84	73	46.2		
Sparisoma	*radians*	7	68	10.1	2.50	42	47.3		
Sparisoma	*rubripinne*	4	287	825.0	2.58	46	39.5		
Sparisoma	*viride***	8	277	836.6	2.90	78	37.5		
Thalassoma	*bifasciatum*	7	81	9.9	3.72	132	42.0		
Xyrichtys	*martinicensis*	4	83	11.3	3.12	100	42.6		
Xyrichtys	*novacula*	9	96	18.2	2.88	77	54.2		
Xyrichtys	*splendens***	11	84	12.8	2.94	84	39.3		

* = scaling of fin aspect ratio $p < 0.05$.

** = scaling of fin aspect ratio $p < 0.01$.

♦ = 'Rank' indicates the rank of aspect ratio values for those species in the total list, with '1' being the lowest AR.

☨ = Swimming speed and TL represent the mean values from field observations of swimming fishes.

in the data set (Figure 4, Table 1). The cheilines, including *Cheilinus*, *Oxycheilinus*, *Wetmorella*, and *Epibulus*, consistently fell out in the bottom quartile of the list, as did their relatives *Pseudocheilinus* and *Pteragogus*. In marked contrast, *Choerodon* species varied throughout the full range of the list, with *C. venustus* having the second highest AR fin in the entire data set and *C. vitta* having the fifth lowest AR. Similarly, the 21 species of *Halichoeres* were distributed widely in the list. Parrotfishes (i.e., *Bolbometapon*, *Calotomus*, *Cetoscarus*, *Chlorurus*, *Hipposcarus*, *Leptoscarus*, *Sparisoma*, *Scarus*) varied widely throughout the upper three-quarters of the list.

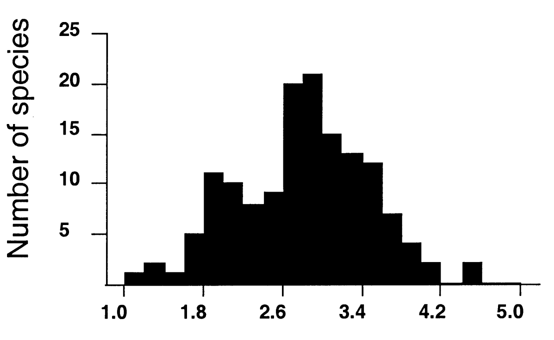


Figure 3. Frequency histogram of the mean pectoral fin aspect ratio of 143 species of labrid fishes.

The principal components analysis of nine distances from the fins yielded two components that accounted for 97.7% of the variance in the data set (Table 2). All variables except the length of the distal-most cord (Figure 1b) loaded on PC1 with correlations above 0.94, indicating that PC1 could be interpreted as an overall size factor. PC2 accounted for 7.2% of the variation and was characterized by a negative loading of cords 1–3, especially the first cord at −0.69, and positive loading of all other variables, led by the leading edge at 0.28. Regression of fin aspect ratio on PC2 scores showed a strong relationship (Figure 5, $r^2 = 0.62$, $F_{1,140} = 224.3$, $p < 0.0001$).

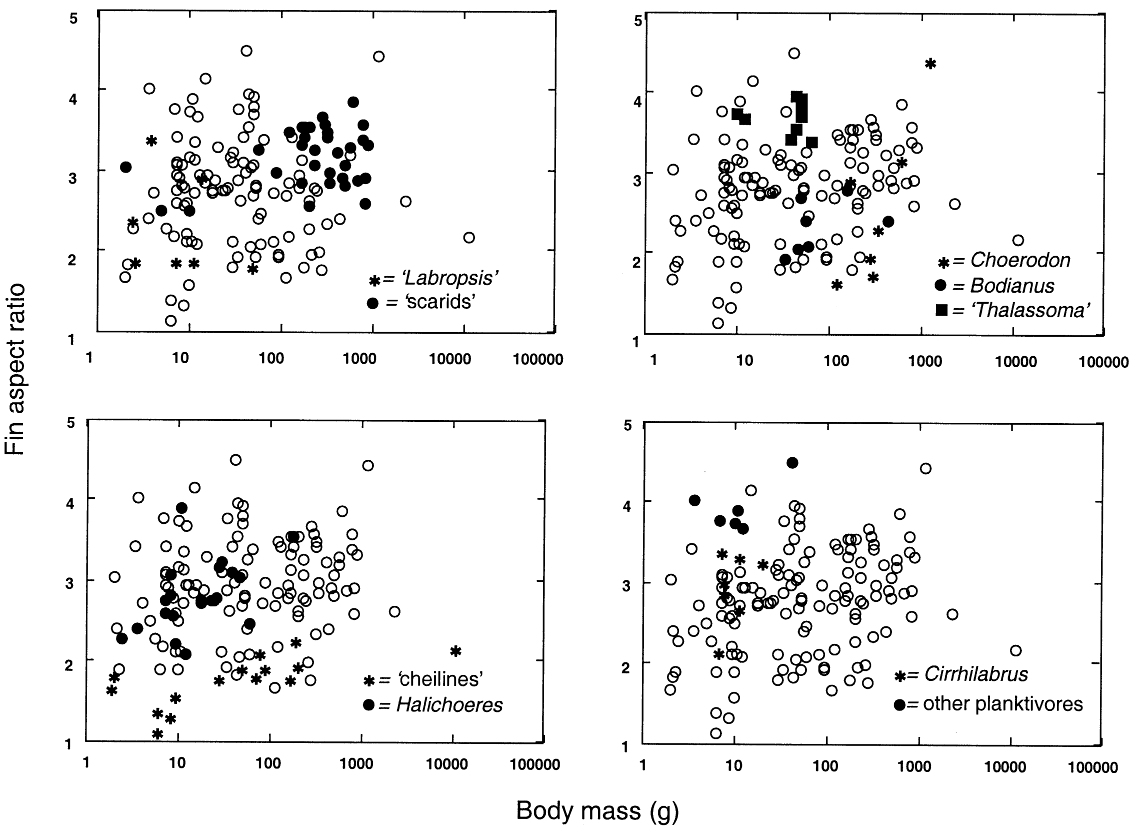


Figure 4. Plots of average pectoral fin AR against body mass for 143 species of labrid fishes. The effect of body mass is significant but explains only 3% of the variation in aspect ratio. Aspect ratios for members of several labrid groups are highlighted by different symbols. '*Labropsis*' group includes all species of *Labropsis*, *Labrichthys*, and *Labroides*. 'Scarids' includes all species of the Scaridae plus *Pseudodax*. '*Thalassoma*' includes all species of *Thalassoma* plus *Gomphosus*. 'Cheilines' includes all species of *Cheilinus*, *Oxycheilinus*, *Wetmorella*, *Epibulus*, *Pseudocheilinus*, and *Pteragogus*. 'Other planktivores' includes *T. bifasciatum*, *T. amblycephalum*, *P. yamashiroi*, *Leptojulis cyanopleura*, and *C. parrae*.

Table 2. Loadings from a principal components analysis performed on the correlation matrix of nine distances that characterize the shape of the pectoral fin in 143 species of labrid fishes. The six cords are evenly spaced spans of the fin perpendicular to the leading edge (Figure 1b) with Cord 1 being the most distal. Values in column headings are percent variance explained by each principal component.

Variable	PC1 (90.6%)	PC2 (7.2%)	PC3 (1.2%)	PC4 (0.6%)
Cord 1	0.72	−0.69	0.08	−0.08
Cord 2	0.97	−0.20	−0.08	0.11
Cord 3	0.99	−0.03	−0.06	0.07
Cord 4	0.99	0.05	−0.01	0.04
Cord 5	0.99	0.08	0.03	0.02
Cord 6	0.99	0.07	0.05	0.05
Leading edge	0.95	0.28	0.12	−0.09
Fin base	0.97	0.17	0.14	−0.02
Shortest fin ray	0.96	0.10	−0.23	−0.13

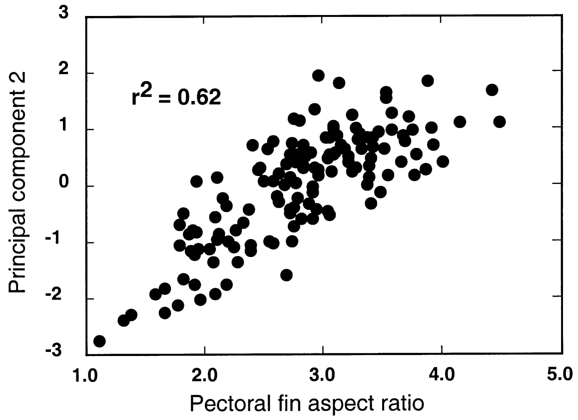


Figure 5. Plot of principal component 2 scores against fin aspect ratio for 143 species of labrid fishes. The strong relationship (r = 0.79) indicates that the major shape axis of the fin data set is associated largely with variation in aspect ratio.

Although our sample sizes were often not large enough to be considered robust tests of the hypothesis, eight species showed significant scaling of aspect ratio with standard length ($p < 0.01$, Table 1, Figure 6): *C. parrae*, *Gomphosus varius*, *Hologymnosus doliatus*, *Sparisoma viride*, *Stethojulis bandanensis*, *Thalassoma jansenii*, *T. hardwicke*, and *Xyrichtys splendens*. An additional seven species met a less conservative $p < 0.05$ criterion for significant scaling of AR. In all species, except *X. splendens*, AR increased with body size. Aspect ratio decreased with body size in *X. splendens*, and a trend toward this was seen in *X. novacula* ($p = 0.08$). Most species that displayed increasing AR during ontogeny were among those with the highest average AR.

The angle of orientation of the base of the pectoral fin on the long axis of the body ranged from about 22° to about 67° (Figure 7). Based on the skeletal system of the fin (Westneat 1996), this variable appears to accurately reflect the orientation of the major axis of bending at the base of the pectoral fin, and thus the lower the angle of attachment the more dorso-ventral the swing of the moving fin. The correlation between angle of attachment of the pectoral fin and fin aspect ratio was 0.65, indicating a strong trend for species with high aspect ratio fins to swing the fin dorso-ventrally, as is seen in the flapping behavior (Walker & Westneat 2000). Some exceptions to this trend were notable. For example, *C. venustus* had the second highest aspect ratio in our study but the angle of fin attachment, 58°, suggests that the fin moves primarily in an antero-posterior axis.

Swimming observations

Labrid species varied by about an order of magnitude in swimming speed, as measured in body lengths s^{-1}. Average swimming speed showed a significant allometry, decreasing with fish size. The correlation between AR and fin angle in the overall data set was −0.65, but in the taxa included in the swimming analysis this correlation was −0.77. The correlation of swimming speed residual with AR was 0.72 and with attachment angle of the fin it was −0.59 (Figure 8). This pattern of correlation among the three variables was reflected in the multiple regression model run for the data on 43 species, with the residual of swimming speed on TL as the dependent variable and AR and the angle of fin attachment as independent variables. The analysis revealed a significant effect of AR on swimming speed, but no independent effect of the angle of attachment of the fin on the body (fin aspect ratio: $F_{1,141} = 6.54$, $p = 0.002$, cumulative $r^2 = 0.522$; angle of fin attachment: $F_{1,141} = 2.72$, $p = 0.181$, cumulative $r^2 = 0.543$). Fin AR accounted for 52% of the variation in residual swimming speed, but angle of fin attachment only increased the r^2 of the model by an additional 2%. Thus, AR and fin angle were redundant in terms of their predictive power for swimming speed, with neither variable providing substantial independent information about swimming speed.

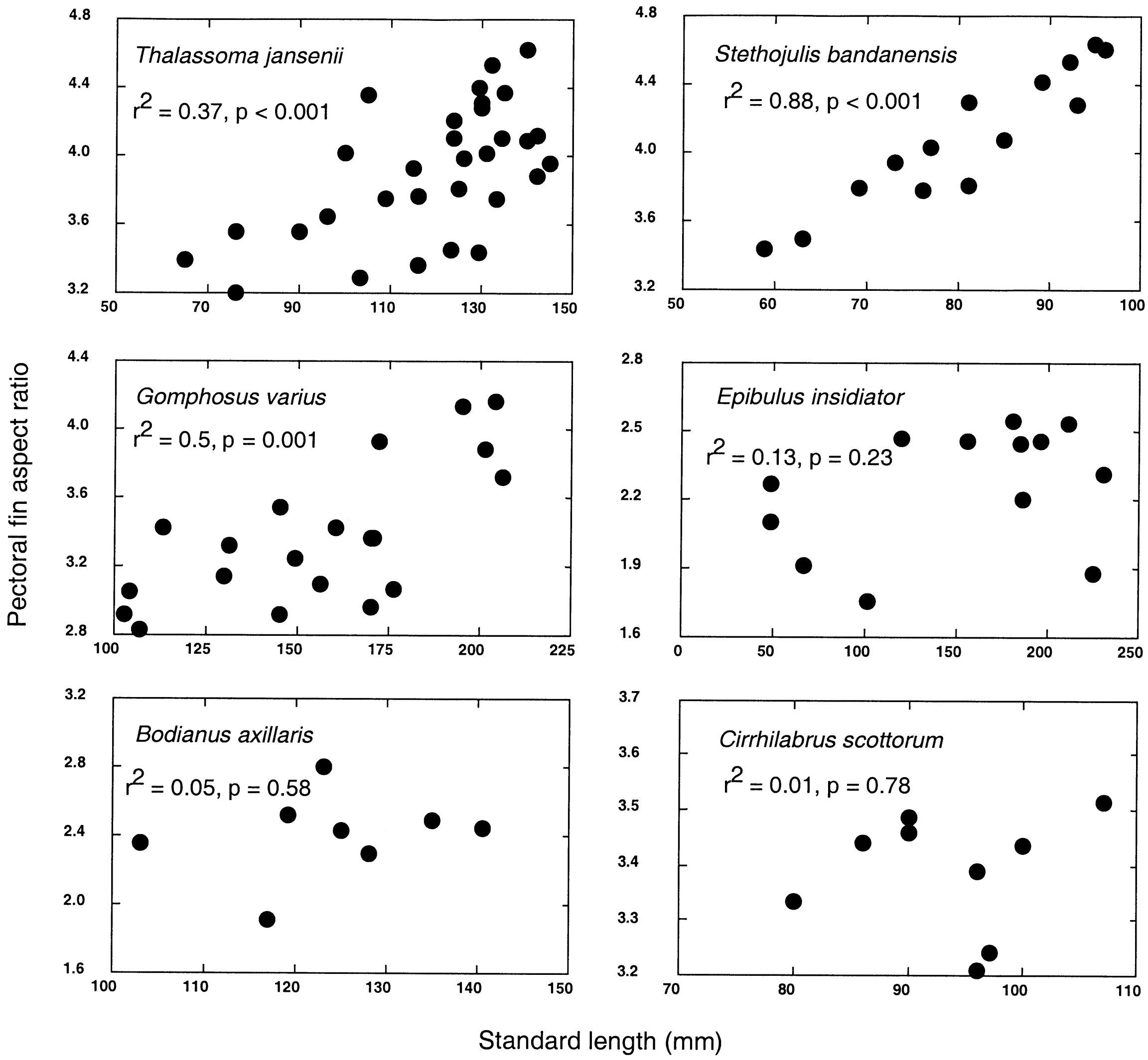


Figure 6. Plots of pectoral fin aspect ratio against fish standard length in ontogentic series from six species of wrasses from the Great Barrier Reef. Significant scaling of aspect ratio was found in eight of 143 species. In all but one of the eight, aspect ratio increased with body size.

Discussion

Labrid fishes have evolved along an axis of locomotor diversity characterized by a transition from rowing behavior at one extreme and flapping behavior at the other extreme. This is an axis of diversification that is seen in a number of groups, including marine mammals (Fish 1992, 1996), turtles (Davenport et al. 1984, Wyneken 1997), swimming birds (Baudinette & Gill 1985), batoid elasmobranchs (Rosenberger 2001) and numerous non-vertebrate metazoan taxa (see Walker & Westneat 2000). Labrids show a wide range of pectoral fin shapes and a variable orientation of the fin on the body. The previously unrecognized variation in the labrid locomotor system described here can be added to the already well-documented range of labrid feeding mechanics and reproductive systems. Although still relatively unexplored, it appears that locomotion may represent another major axis of ecomorphological variation within the Labridae with important implications for habitat use and other aspects of ecology (Bellwood & Wainwright 2001, Fulton et al. 2001, Fulton & Bellwood 2002).

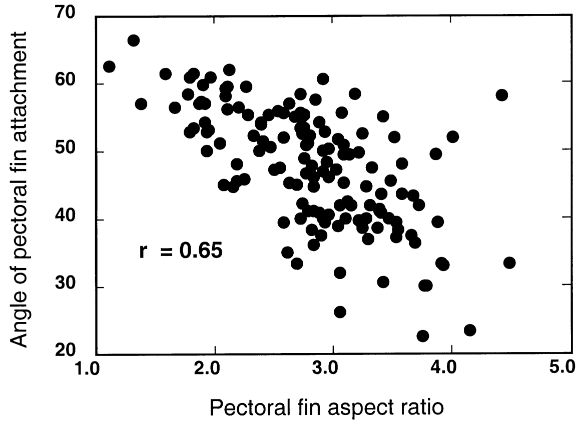


Figure 7. Plot of angle of attachment of the pectoral fin against fin aspect ratio in 143 species of labrid fishes. Species with high aspect ratio fins tend to have a shallow angle of attachment of the fin on the body, indicating a dorsol–ventral axis of fin motion, or flapping locomotion.

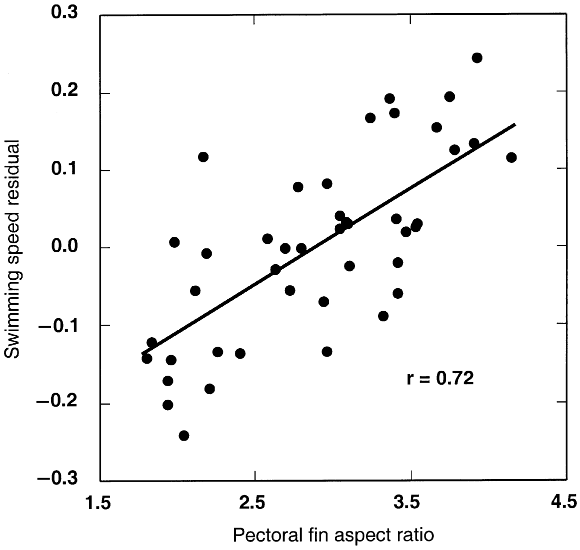


Figure 8. The residual of swimming speed on total length plotted against fin aspect ratio for 43 species of labrids from the Great Barrier Reef. Species with higher aspect ratio fins tended to have faster size-specific swimming speed.

Fin morphology and swimming speed

The central result of this study is that the major axis of variation in labrid pectoral fin shape can be characterized by differences in AR. The labrids in our study varied by almost four orders of magnitude in body size, but this range was only weakly associated with changes in fin shape. Body mass only explained 3% of the variation in fin aspect ratio and no other systematic changes in shape with size were found. However, the strong relationship between fin aspect ratio and the second principal component (correlation = 0.79) indicates that the major shape axis involves this mechanically important trait. The variation among species in AR was driven by differences among species in length of the leading edge, as fin area did not affect AR, independent of body size effects.

Individual pectoral fins are asymmetrical structures, with the leading edge always being at least a little longer than the trailing edge (Figure 2). The principal components analysis indicated that differences among taxa in fin shape were caused by inverse changes in length of the leading edge and the two most distal cords (Table 2, Figure 1b). Higher aspect ratio fins typically had an elongate leading edge that narrowed considerably at the tip. The relative length of the trailing edge of the fin did not contribute to this shape axis. A weak but significant correlation between fin aspect ratio and PC3 scores (r = 0.33) indicated an orthogonal axis in which fins with high scores tended to have a long leading edge and base, with a relatively short trailing edge.

AR was strongly correlated with the orientation of the fin where it attached to the body. Higher AR fins tended to attach at a shallower angle to the long axis of the body, indicating a more dorsal–ventral axis of fin motion than in species with lower AR fins (Figure 7). This angle of attachment is a measure of the orientation of the joint between fin ray bases and the radial elements upon which the rays rotate (Westneat 1996). The angle probably incorporates morphological change in the orientation of the radials as well as the degree of rotation of the entire pectoral girdle relative to the long axis of the body. Further study of the mechanical design of the musculoskeletal system of the pectoral girdle and fin will clarify internal changes that may affect stroke kinematics during swimming.

These differences among species in fin shape and angle of attachment of the fin on the body can be expected to have consequences for locomotor mechanics. Labrids are known to exhibit a range of pectoral fin locomotor mechanisms ranging from underwater flight, in which the fins move dorsally–ventrally, to rowing, in which the fins move in an anterior–posterior axis (Walker & Westneat 2002). Although details of locomotor mechanics have been reported for only a few labrid species (Walker & Westneat 1997, Westneat & Walker 1997) our data are consistent with this being a major axis of labrid locomotor diversity.

One interesting implication of the nature of variation in fin form in labrids (Figure 3) is that many species may exhibit intermediate propulsions systems that employ elements of both flapping and rowing behaviors.

Studies of the mechanics of locomotion indicate substantial differences in thrust and efficiency profiles at either end of the row-flap continuum of pectoral fin swimming. Calculations of thrust production (Vogel 1994) indicate that at very low speeds rowing generates considerably more thrust than flapping, but as speed increases the thrust produced by rowing falls precipitously while flapping produces relatively high thrust across a broad range of speeds. Mechanical efficiency, or the ratio of useful work to total work may be higher in labriform swimmers using flapping appendages across all speeds (Walker & Westneat 2000). Thus, across most swimming speeds both thrust and mechanical efficiency are considerably greater for flapping appendages. A single fin shape and stroke motion will not be optimal for both cruising thrust and rapid maneuvering force. The range of intermediate styles for fin stroke kinematics and fin shape found in the Labridae may enable these animals to sacrifice some efficiency in cruising locomotion in order to also be capable of rapid, high-thrust forces during maneuvers.

Fin shape and natural swimming speed on the reef

We present data that links the fin shape of labrid fishes to their routine swimming speeds on the reef. Theoretical studies discussed above suggest that flapping species are likely to have higher critical swimming speeds and lower costs of transport than similar rowing species (Walker & Westneat 2000). In support of this idea, a recent comparison of swimming performance in four labrid species (Walker & Westneat 2002) found that two flapping species had higher critical swimming speeds than two rowing species. Our data from 43 species moving about the reef reflect routine swimming behavior, rather than maximal swimming performance. Beyond the laboratory based observations on maximal performance, we find a significant relationship between fin shape and this routine swimming speed, indicating that the relationships between fin stroke mechanics and fin shape influence the swimming speeds used by fishes at a wide range of motivational levels.

The multiple regression identified fin AR as a highly significant predictor of residual swimming speed but once AR was accounted for, the angle of attachment of the fin did not add significantly to this model. This result indicates that substantial accuracy ($r = 0.72$) can be achieved in estimating routine rates of size-corrected locomotion by labrids based simply on AR of the pectoral fin. However, we emphasize that this result should not be taken as evidence that the angle of attachment of the fin does not have a causal link to swimming speed. Angle of attachment of the pectoral fin was correlated with swimming speed ($r = -0.56$), but because fin AR and angle of attachment were strongly correlated, most of the effect of attachment angle was captured in the relationship between swimming speed and AR. This analysis should be seen as an interpretation of the utility of fin aspect ratio as an ecomorphological predictor of swimming speed in labrids, not as a test of the causal role of either variable in underlying swimming speed (Darlington 1990, James & McCulloch 1990).

High AR fins and flapping fin motion appear to have clear advantages for fish moving at all but the slowest speeds, but many species in our analysis had low aspect ratio fins and appear to use a rowing fin motion. What are the advantages of this swimming mechanism that are lost in trade-offs by the fast-swimming, flapping species with high aspect ratio fins? The drag-based rowing mechanism appears to provide greater acceleration and thrust at low speeds (Vogel 1994) and several authors have suggested that the drag-based rowing mechanism may enhance maneuverability in these taxa (Blake 1981, Vogel 1994, Fish 1996, Walker & Westneat 2000). Our recent analyses of habitat use in labrid fishes (Bellwood & Wainwright 2001, Fulton et al. 2001) indicate that species with low aspect ratio fins are more abundant in deeper and calmer habitats and tend to occur in closer association with the structure of the reef. In contrast, taxa with high aspect ratio fins dominate in shallow water habitats characterized by high water movement, and are relatively abundant in the water column above the reef.

Body size effects

Several species exhibited considerable allometry of fin shape (Figure 6), although the majority of species showed no significant changes in AR with body size. All of the species that showed increasing aspect ratio with size were taxa characterized by high AR fins, including two species of *Thalassoma*, *Gomphosus*, *Clepticus*, *Hologymnosus* and *Sparisoma viride*. This pattern may relate to the observation from theoretical treatments of lift-based propulsion that low Reynolds numbers cause a very low lift to drag ratio, such that the advantage of flapping over rowing increases with mass of the swimming body (Thom & Swart 1940, but see Daniel 1988). Although our samples for most taxa were insufficient to be considered robust tests for the presence of allometry it is clear that diversity exists in this phenomenon, even among fairly closely related taxa. For example, a sample of 37 *T. lunare* showed no indication of fin shape scaling, while other *Thalassoma* species did (Table 1). Interestingly, of all *Thalassoma* examined *T. lunare* is the only one to be recorded in highest numbers in sheltered locations (Bellwood & Wainwright 2001). In contrast to *Thalassoma*, the two Caribbean species of *Xyrichtys* displayed significantly decreasing aspect ratio with increasing body size. It is not known whether the species of *Xyrichtys* undergo ontogenetic habitat shifts but we note that these species live in sandy habitats adjacent to reefs and frequently swim into the sand both to escape threats and to rest overnight. It may be that this behavior abrades their fins, causing a lowering of AR with time. A study of habitat use by Great Barrier Reef labrids revealed no significant movement among reef zones during ontogeny, but documented marked ontogenetic changes in water column use within habitats. This was particularly marked in species with high AR fins (Fulton & Bellwood 2002).

Associations between fin shape and ecology

The Labridae is a large group that displays marked diversity in feeding habits and habitat use. Phylogenetic relationships have been worked out for several labrid subgroups (Westneat 1993, Bellwood 1994, Gomon 1997, Bernardi et al. 2000) but lack of a phylogeny for the entire group makes it difficult to interpret labrid swimming functional morphology and ecology in a fully-informed phylogenetic framework. However, we offer some informal interpretations of ecomorphological patterns in anticipation of ongoing systematic research.

Many of the taxa that have been proposed to represent basal labrid lineages (Gomon 1997), *Lachnolaimus*, *Choerodon*, and *Bodianus*, are characterized mostly by intermediate pectoral fin AR (Figure 4, Table 1). Assuming that intermediate fin morphology is therefore the primitive condition within the Labridae, we infer at least two independent origins of particularly low AR fins. The first case is in the cheiline and pseudocheiline wrasses and their relatives. As described by Russell & Randall (1980) and Westneat (1993) this includes from our study *Pteragogus*, *Pseudocheilinus*, *Oxycheilinus*, *Wetmorella*, *Epibulus* and *Cheilinus*. These Indo-Pacific taxa represent most of the labrid species in our data set with the lowest aspect ratio fins and highest fin attachment angles. These taxa tend to occupy microhabitats that are very close to the reef substrate (Fulton et al. 2001) and are characterized by low levels of water motion (Bellwood & Wainwright 2001). For example, *Pseudocheilinus* rarely venture more than a few centimeters from reef structures. An interesting exception to the low AR pattern within this group is seen in the comparatively high AR fins of *Cirrhilabrus*, a group that is discussed below.

A second trend toward very low aspect ratio fins is seen in members of the coral mucous and ectoparasite-feeding group that includes *Diproctacanthus*, *Labrichthys*, *Labropsis* and *Labroides* (Figure 4). The former three genera are all primarily coral feeders and have among the lowest AR fins in our data set, but *Labroides* was notable in its diversity. Species of *Labroides* are thought to feed mostly on ectoparasites of other fishes and often spend considerable amounts of time swimming well up in the water column (Fulton et al. 2001). *Labroides* may represent a change to more active swimming behavior within this otherwise slow swimming group.

Several groups appear to show independent trends toward high aspect ratio fins, flapping fin motion and faster swimming behavior. The variation of trophic biology, habitat use and morphological modifications associated with high AR fins with a shallow angle of attachment on the body underlies at least two common features of these groups. First, it appears that all groups capitalize on the increased mechanical efficiency associated with flapping fin motion as compared to a rowing action. Mechanical models suggest that thrust and efficiency are considerably enhanced for flapping fin motions at high speeds (Vogel 1994, Walker & Westneat 2000). Thus, for species that cover relatively long distances in their daily activities, the energetic benefits of a more efficient swimming mode may be considerable. Second, many of these groups may take advantage of the increased speeds that are attained using flapping fin motion. This effect may be particularly acute in species of *Thalassoma* that swim about the reef at high speeds and are therefore able to overcome the water motion characterized by the most exposed reef habitats (McGee 1994, Bellwood & Wainwright 2001). Thus, whether it is because of the challenges of rapid water motion, feeding in midwater habitats away from cover, or the need to move a large body over large distances, flapping fin motion and higher aspect ratio fins appear to permit these taxa to swim faster with greater efficiency than would be experienced with a rowing fin motion and low aspect ratio fins.

The most frequent association of feeding biology and fin form occurred between planktivory and higher AR fins (Figure 4). All plankton-feeding specialists in our data set had relatively high AR pectoral fins. Six of the 14 species with the highest aspect ratio fins are zooplanktivores, including *Clepticus, Halichoeres pictus* and *T. bifasciatum* from the Caribbean (Randall 1967, Wainwright 1988), *Leptojulis cyanopleura*, *Pseudocoris yamashiroi*, and *T. amblycephalum* from the GBR. Species of *Cirrhilabrus*, members of the cheiline/pseudocheiline complex (Westneat 1993) are mostly planktivorous (Randall et al. 1997) and show a distinct trend toward higher aspect ratio fins and faster swimming than seen in their close relatives. Taken together, these taxa may represent six independent examples of this association.

Why might enhanced swimming performance be so commonly associated with planktivory? Coral reef planktivores are characterized by feeding in the water column, often well above the reef (Hobson & Chess 1978, Fulton et al. 2001). These taxa use the reef as a refuge and retreat to it when predators approach (Hobson & Chess 1978). Some benefit for these taxa may be gained from the absolutely higher swimming speeds afforded by high AR fins, but we suspect that the major advantage to these fish is in the cost of locomotion. We suggest that these taxa may swim considerable distances because of their foraging mode and that the greater efficiency achieved by the flapping fin motion and high AR fins underlies the repeated evolution of this association between locomotor form and ecology.

Other groups that show a distinct trend toward high AR fins and fast swimming are unrelated to planktivory. For example, *Thalassoma* and *Gomphosus* may represent a natural group and are especially well represented among those species with the highest AR fins. Species in these genera are fast swimmers and are the dominant members of labrid communities in high-energy habitats of the Great Barrier Reef (Bellwood & Wainwright 2001). Over 85% of labrids in the wave swept ‘reef flat’ of the outer Great Barrier Reef are members of *Thalassoma* (Bellwood & Wainwright 2001). In this group enhanced swimming performance may permit animals to successfully negotiate particularly high flow environments. The presence of high AR fins and fast swimming may be preadaptations in this group that facilitated the zooplantivorous feeding found in *T. amblycephalum* and *T. bifasciatum*.

Stethojulis is another group of fast swimming species with high AR fins. However, the role of fast, lift-based swimming in this group remains unclear. These species are microcrustacean predators that forage low over the reef but do not specialize on high energy habitats (Bellwood & Wainwright 2001, Fulton & Bellwood, 2001). Both *Thalassoma* and *Stethojulis* display internal modifications for enhanced swimming performance as our cursory observations indicate that they have larger pectoral fin musculature than taxa with low AR fins.

Most parrotfishes had high AR fins, although this group was also notable for its fin shape diversity. Parrotfish are typically larger than wrasses and many species cover considerable distances in their daily herbivorous grazing forays (Bellwood 1995a, b). These behavioral tendencies to swim long distances coupled with the differential increase in efficiency of flapping fin motion at larger body sizes suggest that many parrotfishes achieve less costly locomotion through these modifications from the basal labrid condition.

Two groups were notable for the variety of fin shape found among their member species. The eight species of *Choerodon* ranged from among the lowest aspect ratio to among the highest aspect ratio fins. Our impression is that this group represents both marked diversity in swimming ability and fin shape diversity that may not be related to swimming. For example, the pectoral fin of *C. venustus* (AR = 4.42) tapers markedly at the tip, but the fin is quite flimsy and may not be able to withstand the forces experience were it used in flapping motions. In contrast, *C. fasciatus* (AR = 2.94) does appear to utilize a flapping fin motion. Aspect ratio in 21 species of *Halichoeres* ranged from 2.08 in *H. zeylonicus* to 3.88 in *H. pictus*. The latter species is unusual in this genus in being a specialized zooplanktivore that spends much of its time swimming well above the reef.

Finally, we note that pectoral fin propulsion and the rowing-flapping axis of behavioral variation may be common among fishes inhabiting coral reefs. Other major reef fish groups that primarily use pectoral fin locomotion, or have numerous members that do, include the Pomacentridae, Acanthuridae, Siganidae, and Pomacanthidae. Less is known about locomotor diversity in these groups but it is clear that pectoral locomotion will feature prominently in future research on the ecology of locomotion in reef fishes. Resolved phylogenetic hypotheses and laboratory measures of swimming performance will permit repeated tests of the possible adaptive explanations for the origins and diversification of pectoral locomotion in these groups.

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