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A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system

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The Labridae (including wrasses, the Odacidae and the Scaridae) is a species-rich group of perciform fishes whose members are prominent inhabitants of warm-temperate and tropical reefs worldwide. We analyse functionally relevant morphometrics for the feeding apparatus of 130 labrid species found on the Great Barrier Reef and use these data to explore the morphological and mechanical basis of trophic diversity found in this assemblage. Morphological measurements were made that characterize the functional and mechanical properties of the oral jaws that are used in prey capture and handling, the hyoid apparatus that is used in expanding the buccal cavity during suction feeding, and the pharyngeal jaw apparatus that is used in breaking through the defences of shelled prey, winnowing edible matter from sand and other debris, and pulverizing the algae, detritus and rock mixture eaten by scarids (parrotfishes). A Principal Components Analysis on the correlation matrix of a reduced set of ten variables revealed complete separation of scarids from wrasses on the basis of the former having a small mouth with limited jaw protrusion, high mechanical advantage in jaw closing, and a small sternohyoideus muscle and high kinematic transmission in the hyoid four-bar linkage. Some scarids also exhibit a novel four-bar linkage conformation in the oral jaw apparatus. Within wrasses a striking lack of strong associations was found among the mechanical elements of the feeding apparatus. These weak associations resulted in a highly diverse system in which functional properties occur in many different combinations and reflect variation in feeding ecology. Among putatively monophyletic groups of labrids, the cheilines showed the highest functional diversity and scarids were moderately diverse, in spite of their reputation for being trophically monomorphic and specialized. We hypothesize that the functional and ecological diversity of labrids is due in part to a history of decoupled evolution of major components of the feeding system (i.e. oral jaws, hyoid and pharyngeal jaw apparatus) as well as among the muscular and skeletal elements of each component.

ADDITIONAL KEYWORDS: complexity – disparity – feeding – four-bar linkage – Labridae – levers – modularity – pharyngeal jaw apparatus.

INTRODUCTION

The Labridae are a successful group of about 575 species of marine perciform fishes that are most often found in association with reef habitats (Parenti & Randall, 2000). The group is particularly notable for its trophic diversity on coral reefs where wrasses feed on a wide range of invertebrate and fish prey and scarids are among the primary herbivores. The extensive diversity of labrid feeding types includes species that feed on decapod crabs and prawns, polychaete worms, gastropod and bivalve molluscs, other fishes, sea urchins, brittle stars, nemerteans, sipunculans, the mucous of scleractinian corals, ectoparasites of other fishes, amphipods, copepods, isopods and a variety of plankton (Randall, 1967; Westneat, 1995). This extensive ecological diversity may be reflected in biomechanical diversity of the feeding mechanism and labrids therefore hold promise as a model group for

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studying the evolution of feeding mechanics and the characteristics of trophic radiation (Wainwright, 1988; Bellwood & Choat, 1990; Westneat, 1995).

In this study we characterize the diversity of feeding functional morphology of labrid fishes from Australia's Great Barrier Reef. Our overriding aim is to provide a quantitative functional morphological framework for evaluating diversity in the feeding mechanism that could also provide a benchmark for comparison to other fish groups. We measured morphological features from the skull that reflect mechanical properties of the three major components of the feeding mechanism: the oral jaws which are used during capture and manipulation of prey, the hyoid apparatus that powers the expansion of the buccal cavity during suction feeding, and the pharyngeal jaw apparatus which is used to overcome structural defences of prey and in winnowing behaviours. This data set is used to describe and quantify the functional diversity of labrids from the Great Barrier Reef and allows us to address four primary questions. (1) What are the major axes of functional diversity in this assemblage of labrids? (2) Do scarids represent a major mechanical divergence from the functional morphospace of other labrids? (3) Which groups of labrids have the most and least functional diversity? (4) What major associations can be identified between skull mechanics and dietary habits?

MATERIAL AND METHODS

We collected specimens of 130 species of labrid fishes considered by Randall, Allen & Steene (1997) to be part of the Great Barrier Reef fauna. Specimens were collected between February 1998 and June 1999 by SCUBA divers using barrier nets and hand spears, primarily 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. Our sample of 130 species represents about 22% of the 570 species in the worldwide labrid fauna, and about 90% of the Great Barrier Reef fauna (Randall *et al*., 1997). We recognize the Labridae as including the Scaridae and we refer to the non-scarid labrids in our study as 'wrasses'.

In selecting morphological measurements to characterize the form of the skull we explicitly chose variables with known functional implications. In addition to body size, we measured several traits that reflected the mechanical properties of the oral jaws, the hyoid apparatus and the pharyngeal jaw apparatus. These are the principal musculoskeletal systems involved in prey capture, biting, suction feeding by buccal expansion, jaw depression and handling of prey by the pharyngeal jaws (Clements & Bellwood, 1988; Wainwright, 1988; Gobalet, 1989; Bellwood & Choat, 1990; Westneat, 1994; Ferry-Graham *et al*., 2002). Morphological measurements were made on three adult specimens of each species and in a few cases four specimens, for a total of 405 dissected specimens. Within a few hours of capture, while they were still fresh and relaxed, each specimen was weighed and their standard length measured. At this time jaw protrusion was measured as the excursion distance of the anterior symphysis between the two premaxillae as they travelled rostrally when the jaws were protruded manually by depressing the lower jaw. Mouth gape was measured as the horizontal distance between the coronoid processes of the articular bones inside the opened mouth. During measurements of jaw protrusion and mouth gape, the mandible was rotated into a fully depressed position but without forcing it beyond natural extension. After making these measurements each specimen was fixed in 10% buffered formalin for about two weeks before being transferred for storage to 70% ethanol.

Three muscles were carefully removed from each preserved fish and weighed: the adductor mandibulae, the sternohyoideus and the levator posterior (Fig. 1). We used the mass of these muscles as a rough indication of their force-producing capacity, although it is likely that architectural variation and differences in fibre type composition of these muscles also contribute to interspecific variation in peak tension (Powell *et al*., 1984; Wainwright, 1988). If these additional factors do not vary systematically with body size, it can generally be expected that force capacity and power production will scale as the 2/3 power of muscle mass (Schmidt-Nielsen, 1983).

All sections of the adductor mandibulae complex (AM) were removed from one side of the specimen except section Aw (Winterbottom, 1974). The AM (Fig. 1D) originates broadly from the lateral surface of the suspensorium and attaches directly to the articular and by tendons to the maxilla and articular bones. This large muscle complex acts to adduct the jaws and is therefore the muscle that powers biting by the oral jaws (Alfaro, Janovetz & Westneat, 2001; Westneat, 2003). Species with a larger adductor mandibulae, all other features remaining the same, are interpreted as having a stronger bite.

The sternohyoideus muscle (Fig. 1B) originates on the anterior surface of the ventral region of the cleithrum bone and ventrally is continuous with slips of the hypaxial musculature. It attaches to the urohyal bone that connects to the medial hyoid elements by a pair of ligaments. This large muscle acts to retract and depress the hyoid bar and thus the floor of the buccal cavity (Aerts, 1991; De Visser & Barel, 1996, 1998). This complex motion is also the primary cause of buc-

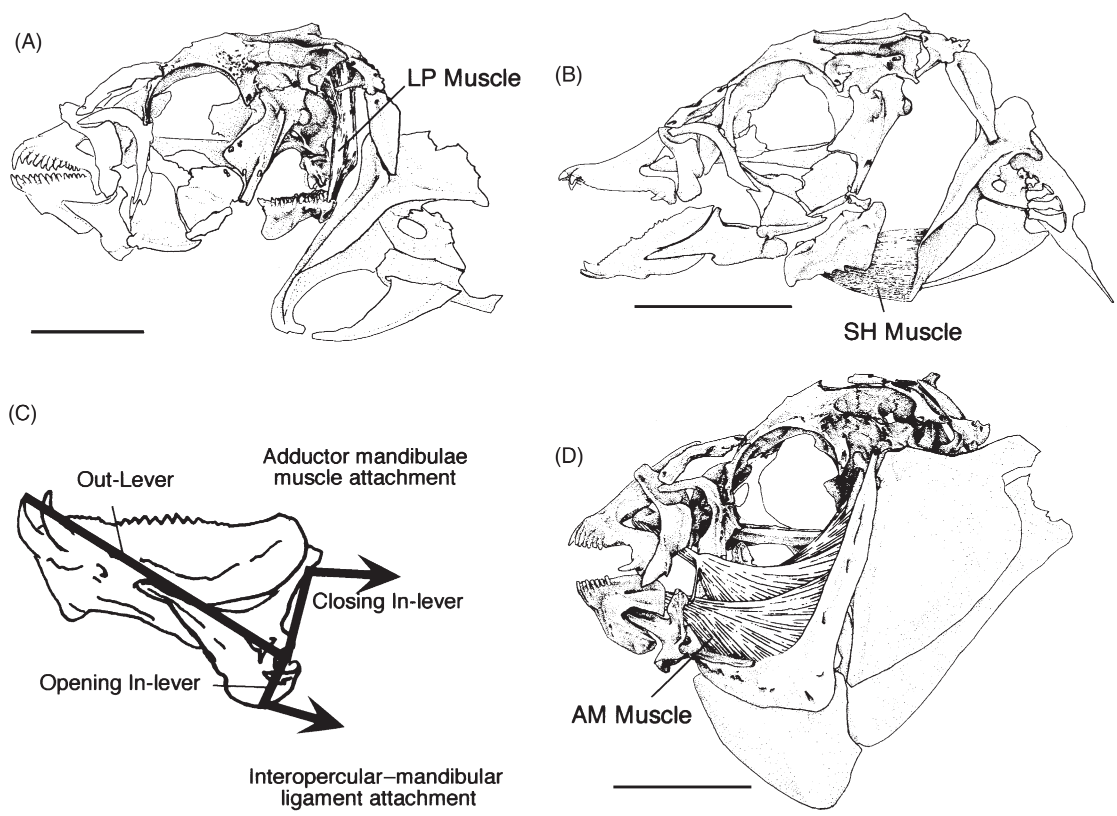


Figure 1. Illustrations of the muscles that were dissected and weighed, and the lever system of jaw opening and closing. (A) Diagram of the levator posterior muscle in *Thalassoma hardwicke*. The operculum and most of the branchial arch elements have been removed to reveal this deep muscle of the pharyngeal jaw apparatus. (B) Diagram of the sternohyoideus muscle in *Bodianus axillaris*. The opercule, sub-, inter- and preopercle bones were removed to reveal this midline muscle that connects the pectoral girdle to the hyoid bar. (C) Levers of the labrid mandible that were measured in this study. See text for detailed description of landmarks. (D) Diagram of the adductor mandibulae muscles in *Stethojulis trilineata*. This complex of muscles attaches the lateral face of the suspensorium to the upper and lower jaws. *Abbreviations*: AM, adductor mandibulae muscle complex; LP, levator posterior muscle; SH, sternohyoideus muscle. Scale bars = 10 mm.

cal expansion in suction-feeding labrids (Westneat, 1990) and the activation pattern of this muscle has been found to be the best predictor of suction pressure in generalized suction-feeding perciform fishes (Lauder, Wainwright & Findeis, 1986; Grubich & Wainwright, 1997). Contraction of the sternohyoideus also acts to depress the mandible by placing tension on the interopercular–mandibular ligament that attaches to the angular bone ventral to the jaw joint (Fig. 1C). Thus, the sternohyoideus is both the major jaw depressor and it plays a central role in buccal expansion during suction feeding.

The paired levator posterior muscle (Fig. 1A) originates on the posterior surface of the neurocranium and inserts on the lateral arms of the fused fifth ceratobranchial bone, the lower pharyngeal jaw (Yamaoka, 1978). This muscle is the primary adductor of the pharyngeal jaws in labrids (Wainwright, 1987; Clements & Bellwood, 1988; Gobalet, 1989) and its relative size has been shown to be a strong constraint on prey use patterns in Caribbean labrids (Wainwright, 1988).

Linkage mechanics were also characterized for the anterior jaw system and the hyoid depression apparatus (Fig. 2). Both systems have been represented by four-bar linkage engineering models (Anker, 1974; Westneat, 1990; Muller, 1996). We measured the four links of each linkage and the diagonal distance at a relaxed resting state with the jaws closed. Four-bar linkages are planar constructs that transmit motion and force from one element, through the four bars of the linkage. Because the linkage is planar and connected in a loop, movement at one joint results in defined compensatory motion at all other joints. The mechanical properties of each linkage were summarized by calculating a kinematic transmission coefficient (KT) as the ratio of output motion for a given unit of input in the system. Analogous to simple levers, low values of KT indicate a ‘force-modified’ linkage system while high KT values indicate a ‘veloc-

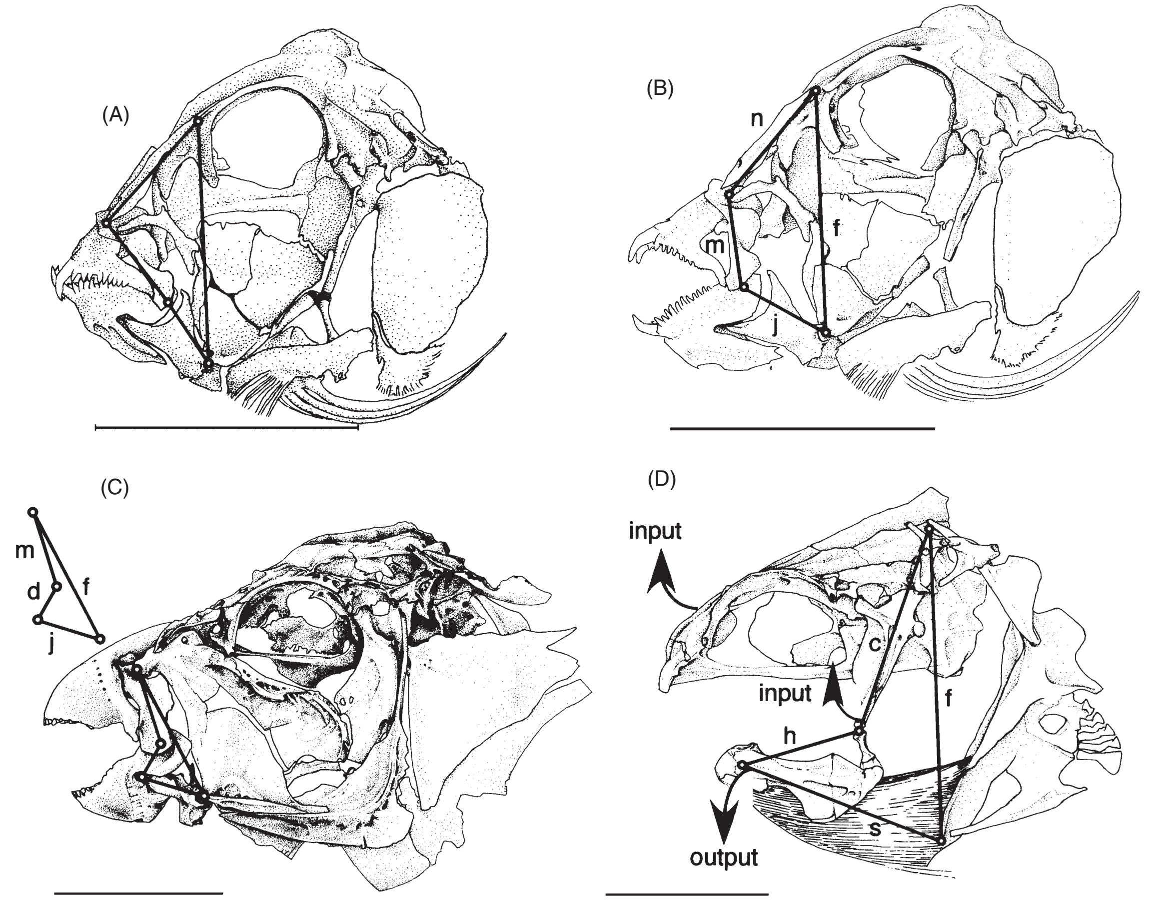


Figure 2. Illustrations of the four-bar linkages that were analysed in this study. (A) and (B): arrangement of the oral jaws four-bar system with the jaws adducted and abducted in *Xyrichtys pavo*. *Abbreviations*: f, fixed link; j, jaw or input link; m, maxillary or output link; n, nasal or coupler link. (C) The modified oral jaw four-bar linkage found in some scarids. This linkage differs from that of wrasses in the presence of an intramandibular joint between the dentary and articular bones. *Chlorurus sordidus* is shown. *Abbreviations*: f, fixed link; j, jaw or input link; d, dentary or coupler link; m, maxillary or output link. (D) The hyoid four-bar linkage of *Cheilinus chlorourus*. *Abbreviations*: f, fixed link; i, input link; h, hyoid or coupler link; s, sternohyoideus or output link. See text for detailed explanations and descriptions of each linkage system. Scale bars = 10 mm.

ity-modified' linkage. Force and velocity transmission are mechanical trade-offs in four-bar linkages (Westneat, 1994; Muller, 1996).

It has previously been demonstrated that the anterior jaws four-bar linkage governs the transfer of lower jaw depression into rotation of the maxilla and protrusion of the premaxillae in four cheiline labrid species (Westneat, 1990). We developed a slight modification of the linkage described by Westneat (1990) for cheilines (in which the fixed link runs from the quadrate–articular joint to a flexion point between the palatine and pterygoids and the coupler link being the palatine bone). In our linkage (Fig. 2A, B) the fixed link is the distance between the quadrate–articular joint and the proximal base of the nasal bone (Fig. 2B, f). The coupler link is the distance from the proximal base of the nasal to the distal end of the nasal at its ligamentous connection to the maxilla (Fig. 2B, n). The output link is the distance from the distal end of the nasal to the confluence between the distal end of the alveolar arm of the premaxilla, the distal arm of the maxilla and the coronoid process of the mandible (Fig. 2B, m). The input link was thus the distance between the latter point and the quadrate–articular joint (Fig. 2B, j). We measured the diagonal distance between the joint connecting the input and output links and the fixed and nasal links. The diagonal was used to determine the position of the linkage at rest. In our rendering, rotation of the mandible was the input motion and maxillary rotation was the output motion. Depression of the mandible and rotation of the maxilla act to protrude the premaxilla. The transmission coefficient was calculated as the ratio between the degrees of maxillary rotation (relative to the position of the fixed link) from a given number of degrees of mandible rotation (opening the mouth). This maxillary KT has been shown to be sensitive to the starting position of the linkage and the angular excursion of the lower jaw in labrids (Hulsey & Wainwright, 2002). An input rotation of 25° was applied to all species, based on our observations from high-speed videos that were recorded of several of these species during prey capture (Westneat, 1990; Ferry-Graham *et al*., 2002). Maxilla rotation, the output, was calculated based on 25° of input from a resting starting position.

Some members of the monophyletic Scaridae (Bellwood, 1994; Streelman *et al*., 2002) were found to possess a novel four-bar linkage of the oral jaws (Fig. 2C). In these fish, the fixed link is the distance between the joint connecting the articular and the quadrate bones and the joint connecting the palatine and maxilla (Fig. 2C, f). The output link is the distance from the maxilla–palatine joint to the joint connecting the maxilla and the dentary bone (distance m). The coupler link is the distance between the maxilla–dentary joint and the intramandibular joint between the dentary and articular bones (distance d). The input link is the distance between the dentary–articular joint and the articular–quadrate joints (distance j). The kinematic transmission coefficient of this system was calculated as the ratio between the degrees of maxillary rotation (relative to the fixed link) produced by 25° of input articular bone rotation.

The hyoid four-bar linkage (Anker, 1974; De Visser & Barel, 1998) has been shown to accurately predict hyoid motion based on an input of cranial rotation in four cheiline labrids (Westneat, 1990). We followed Anker (1974) for the conformation of this linkage system (Fig. 2D). The fixed link was the distance between the attachment of the sternohyoideus muscle to the cleithrum and the attachment of the pectoral girdle to the neurocraniium (distance f). The input link was the distance from the pectoral girdle attachment on the neurocranium to the joint between the interhyal, hyomandibula and symplectic bones (distance c). The coupler link was the distance from the interhyal joint to the connection of the hyoid bar to the basihyal (distance h). The output link was the distance between the hyoid bar connection to the basihyal to the attachment of the sternohyoideus on the cleithrum (distance s). The diagonal was the distance from the joint between the output and fixed links and the joint between the coupler and input links. Shortening of the SH by 10% was required for the model to reflect actual motions in four cheiline species (Westneat, 1990), so we adopted this convention and included SH shortening with cranial rotation in our calculations of the output hyoid depression. Thus, for this linkage system we calculated the transmission coefficient as the ratio of the degrees of angular rotation of the joint between the output and fixed links for 5° of cranial elevation. We selected 5° of cranial elevation based on published values in labrids and our own observations of several of these species (Westneat, 1990; Ferry-Graham *et al*., 2002).

Finally, we measured the opening and closing lever mechanism of the lower jaw (Fig. 1C) and calculated mechanical advantage as in-levers divided by out-levers (Wainwright & Richard, 1995). The in-lever for opening was the distance from the jaw joint to the attachment midpoint of the interopercular mandibular ligament on the angular bone. The in-lever for closing was the attachment midpoint of the adductor mandibulae muscle on the coronoid process of the articular bone. The ratio of in-lever/out-lever for these two motions is the fraction of force exerted at the input location that is transmitted to the anterior tooth row of the jaw. For the scarid taxa that possessed an intramandibular joint (*Scarus*, *Chlorurus* and *Hipposcarus*), these lever systems may not function as they do in other labrids and a single mechanical advantage may not exist. However, we report mechanical advantage of opening and closing in these taxa assuming the intramandibular joint was fused, using the same formula as used with the other labrids. Force transmission trades off directly with velocity transfer, such that levers with a high force transmission must have low velocity transmission (Westneat, 1994; Wainwright & Richard, 1995).

STATISTICAL TREATMENT

Average values per species were calculated for the following 12 variables: body mass, standard length, mouth gape, premaxillary protrusion, adductor mandibulae muscle mass, sternohyoideus muscle mass, levator posterior muscle mass, fifth ceratobranchial bone mass, anterior jaws four-bar linkage KT (maxillary KT), hyoid apparatus four-bar linkage KT (hyoid KT), mouth opening lever ratio and mouth closing lever ratio. For all subsequent analyses the length and mass variables were $\log_{10}$ transformed. Bivariate plots of morphological and mechanical variable against body mass or standard length were used to explore the level of interspecific variation in each trait and the position of individual species in morphospace. We used phylogenetic and taxonomic treatments of labrid subgroups (Bellwood, 1994; Westneat, 1995; Gomon, 1997; Streelman *et al*., 2002) to examine patterns of variation between monophyletic groups of labrids. Several comparisons of trait values between hypothesized natural groups of labrids were conducted using analysis of covariance and body mass as the covariate, although the probability values associated with these tests should be regarded with caution until a well-resolved phylogeny is available.

In order to explore the major axes of diversity in the skull of Great Barrier Reef labrids, a multivariate morphospace of the labrid skull was created using a pair of principal components analyses on a data set of the mean value of each variable per species. An initial analysis was conducted with the data for all labrid species and a second one on a reduced data set that lacked all scarid species, because of their unique jaw morphology. In order to make variables dimensionally similar, the cube root of each mass variable (body mass, AM mass, SH mass, LP mass) was calculated and residuals of all morphological variables were taken from least-squares regressions with cube root of body mass as the size variable. Because the data set was a combination of linear variables and ratios, and therefore variances differed widely among variables, the correlation matrix of the following variables was factored: Maxillary KT, Hyoid KT, mouth opening lever ratio, mouth closing lever ratio, body mass (cube root), adductor mandibulae mass residual, sternohyoideus mass residual, levator posterior mass residual, mouth gape distance residual and premaxillary protrusion distance residual.

Functional diversity of several putatively monophyletic labrid groups was calculated using the factor scores of member species from the principal components analysis on all 130 species. Variance of scores on each PC was calculated for the members of each group, scaled by the proportion of the total variance explained by the component, and summed across all PCs (Foote, 1992, 1997). Five groups were studied. The hypsigenyines (Gomon, 1997) included all species of *Bodianus*, *Choerodon*, *Pseudodax* and *Xyphocheilus* (18 species in total). The cheilines (Westneat, 1995) included all species of *Cheilinus*, *Oxycheilinus*, *Epibulus* and *Wetmorella* (ten species in total). The julidines included all species of *Thalassoma*, *Gomphosus*, *Halichoeres*, *Coris*, *Pseudocoris*, *Hologymnosus*, *Hemigymnus*, *Stethojulis*, *Macropharyngodon*, *Labroides*, *Labropsis*, *Labrichthys*, *Diproctacanthus* and *Pseudojuloides* (57 species in total). The novaculines included all species of *Novaculichthys*, *Xyrichtys* and *Cymolutes* (five species in total). Finally, the scarids (Bellwood, 1994; Streelman *et al*., 2002) included all species of *Scarus*, *Chlorurus*, *Leptoscarus*, *Bolbometopon*, *Cetoscarus*, *Hipposcarus* and *Calotomus* (26 species in total).

We follow Foote (1997) in using group variance to characterize functional diversity. Variance has the valuable property that it does not scale with sample size, making it possible to compare groups of different size. Under a Brownian motion model of character evolution, variance of groups would be expected to increase linearly with the time since the most recent common ancestor in the group (Felsenstein, 1985; Martins, 1994). When relationships among labrids are better resolved it will be possible to estimate the ages of these groups and use this information to compare the rates of functional evolution in different groups. Until then we present these estimates of functional diversity as preliminary observations that are not meant to imply differences in rates of evolution.

RESULTS

Labrids showed considerable diversity in skull morphology and mechanics (Appendix, Figs 3–9). Taxa varied widely in the shape of the skull, with *Choerodon* (Fig. 3A), *Xyrichtys* (Fig. 5C), *Macropharyngodon* (Fig. 6D) and scarids (Figs 2C, 4F) exhibiting the deepest shapes and a trend toward elongation seen in *Cheilio* (Fig. 5A), *Gomphosus* (Fig. 6E) and *Hologymnosus* (Fig. 7D). Skull elongation was typically associated with relatively long jaws. Taxa with relatively large gape also tended to have a long mandible and maxilla (e.g. compare *Oxycheilinus*, Fig. 4B, with *Labropsis*, Fig. 8D). The size of the adductor mandibulae muscle complex was reflected by the size of the fossa formed by the lateral surface of the suspensorium. For example, taxa with a relatively large AM included *Hologymnosus* (Fig. 7D) and *Cymolutes* (Fig. 5D) showed an expanded suspensorium compared to taxa with a small AM such as *Cirrhilabrus* (Fig. 3E) and *Pseudocoris* (Fig. 7C).

Striking variation among labrid taxa was seen in oral jaw dentition, often showing clear associations with what is known about feeding in labrids (summarized in Randall *et al*., 1997; Westneat, 1999). Scarids (Fig. 4F) and *Pseudodax* (Fig. 3F), both herbivores, have flattened tooth surfaces. Many of the predators, such as *Oxycheilinus* (Fig. 4B), *Pseudocheilinus* (Fig. 3C), *Pteragogus* (Fig. 3D), of relatively large, elusive prey have large, sharp raptorial teeth. Relatively stout raptorial teeth were also seen in crustacean predators and durophagous taxa such as *Choerodon fasciatus* (Fig. 3A), *Cheilinus oxychephalus* (Fig. 4A), *Halichoeres marginatus* (Fig. 6A), *Coris gaimard* (Fig. 7B), *Novaculichthys* (Fig. 5B), *Xyrichtys* (Fig. 5C) and *Cymolutes* (Fig. 5D). Planktivores, e.g. *Cirrhilabrus* (Fig. 3E) and *Pseudocoris* (Fig. 7C), have reduced dentition. Taxa that feed on small benthic microcrustacea tend to have small teeth (*Hemigymnus* and *Stethojulis*, Fig. 9; *Pseudojuloides*, Fig. 4E) or anteriorly orientated teeth (*Anampses*, Fig. 6C). The ectoparasite-feeding ‘cleaner wrasses’, *Labroides* (Fig. 8A, C), have small raptorial teeth. The coral mucous feeders, *Diproctacanthus*, *Labrichthys* and *Labropsis* (Fig. 8B, D) have short, stout raptorial teeth that may be used in wounding coral to induce mucous secretion.

The monotypic taxa *Epibulus* (Fig. 4C, D) and *Gomphosus* (Fig. 6E) are two particularly extreme, unique

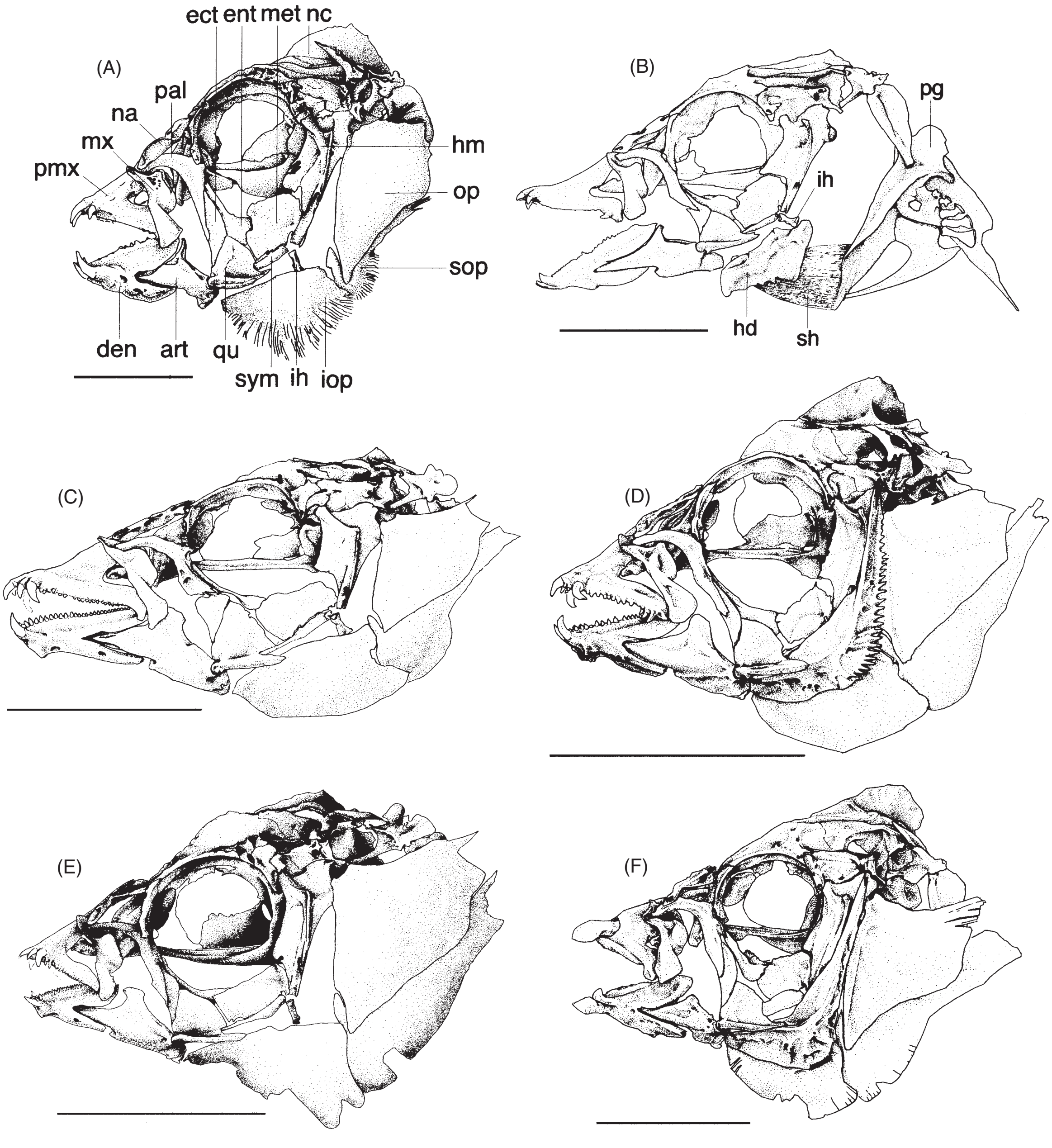


Figure 3. Representative labrids illustrating diversity of the trophic apparatus. (A) *Choerodon fasciatus*; (B) *Bodianus axillaris*; (C) *Pseudocheilinus octotaenia*; (D) *Pteragogus cryptus*; (E) *Cirrhilabrus lineatus*; (F) *Pseudodax moluccanus*. Bone name abbreviations: art, articular; ect, ectopterygoid; ent, entopterygoid; den, dentary; hd, hyoid bar; hm, hyomandibula; ih, interhyal; iop, interopercle; met, metapterygoid; mx, maxilla; na, nasal; nc, neurocranium; op, opercle; pal, palatine; pg, pectoral girdle; pmx, premaxilla; qu, quadrate; sop, subopercle; sym, symplectic. Scale bars = 10 mm.

forms. *Epibulus* has novel joints in the suspensorium that permit extreme lower jaw protrusion (Westneat & Wainwright, 1989), a very long mandible and high maxillary KT. The longest jaws found belonged to *Gomphosus varius*, a species that was not otherwise mechanically extreme.

Species body mass ranged from 2.3 g in the diminutive *Pseudocheilinus hexataenia* to 28 880 g in the giant *Cheilinus undulatus* with a mean of 436 g and a median of 55.5 g. Gape ranged from 1.7 mm in *Labroides pectoralis* to 80.5 mm in *Cheilinus undulatus*. Mass of the levator posterior muscle ranged from 0.001 g in *Labroides dimidiatus* to 118 g in *Cheilinus undulatus*. After removing body-size effects (i.e. calculating residuals from plot against log of cube root of body mass), gape ranged 3.4-fold among species, pre-

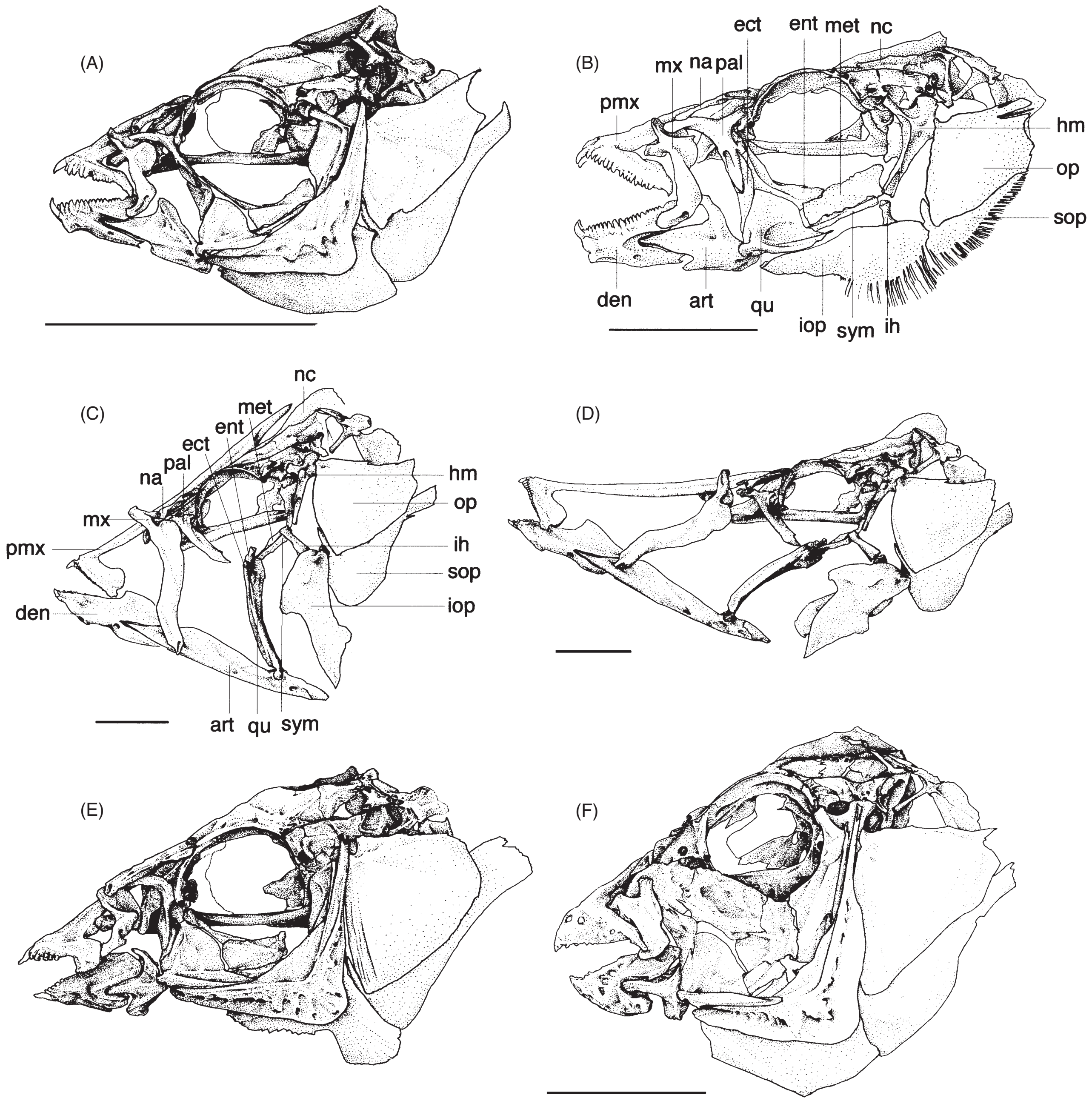


Figure 4. Representative Great Barrier Reef labrids illustrating diversity of the trophic apparatus. (A) *Cheilinus oxycephalus*; (B) *Oxycheilinus digrammus* with preopercle removed; (C) & (D) *Epibulus insidiator* with the jaws retracted in (C) and extended in (D); (E) *Pseudojuloides cerasinus*; (F) *Cetoscarus bicolor*. Abbreviations as in Fig. 3. Scale bars = 10 mm.

maxillary protrusion distance ranged 40-fold, adductor mandibulae mass ranged 17.5-fold, sternohyoideus mass ranged 12.8-fold, and levator posterior mass ranged 477-fold.

The mechanical transmission properties of the mandible and four-bar systems of the oral jaws and the hyoid apparatus also varied considerably among species. The jaw-closing lever ratio ranged from 0.13 in *Cirrhilabrus condei* to 1.04 in *Scarus rivulatus*, the jaw-opening lever ratio ranged from 0.08 in *Gomphosus varius* to 0.39 in *Scarus rivulatus*, and the oral maxillary KT ranged from 0.45 in *Xyphocheilus typus* to 1.52 in *Cirrhilabrus exquisitus*. The hyoid KT ranged from 0.07 in *Anampses neoguinaicus* to 4.7 in

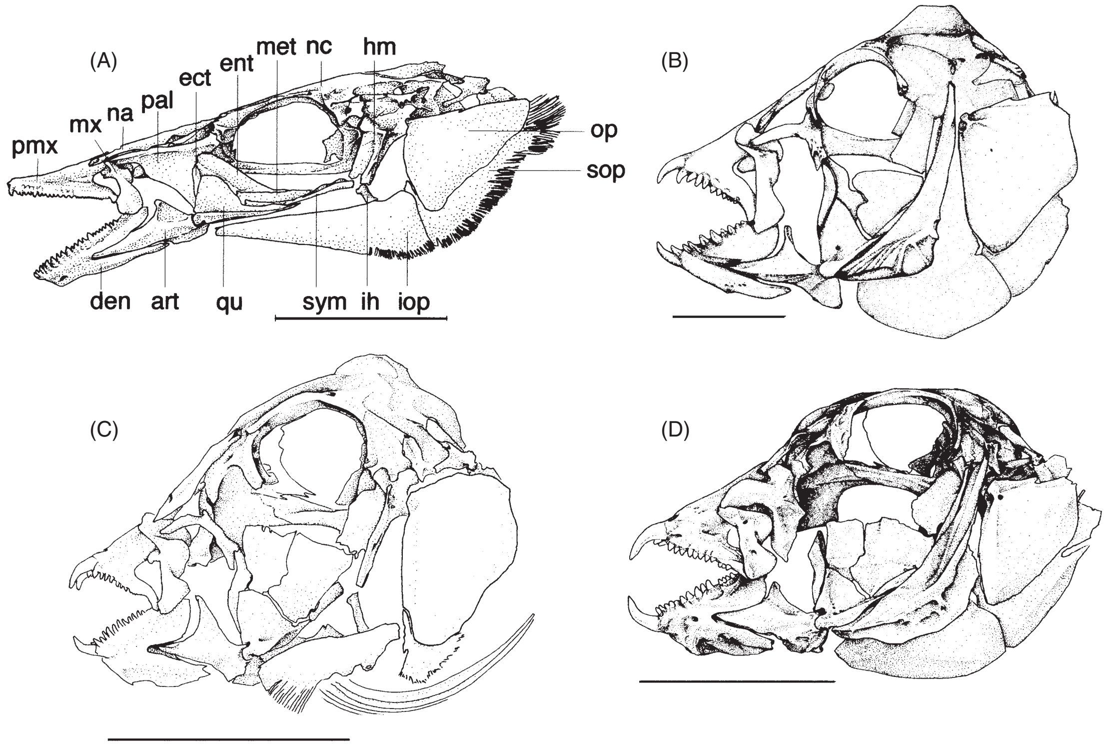


Figure 5. Representative Great Barrier Reef labrids illustrating diversity of the trophic apparatus. (A) *Cheilio inermis* with preopercle bone removed; (B) *Novaculichthys taeniourus*; (C) *Xyrichtys pavo*; (D) *Cymolutes praetextatus*. Abbreviations as in Fig. 3. Scale bars = 10 mm.

Scarus dimidiatus. These transmission properties indicate, for example, that 13% of adductor muscle force is transmitted to the toothed tip of the dentary in *Cirrhilabrus condei*, whereas 104% of the adductor force is transmitted to the dentary tip in *Scarus rivulatus*. Mandibular depression of 25° would result in 11.3° of maxillary rotation in *Xyphocheilus typus* and 38° of maxillary rotation in *Cirrhilabrus exquisitus*.

Interspecific scaling relationships indicated a combination of isometric features and some strong allometry (Table 1). Both the mass of the sternohyoideus muscle and gape scaled isometrically. Jaw protrusion scaled with negative allometry, although when the wrasses were considered separately protrusion scaled with positive allometry (slope = 0.41; isometry would be 0.33). All other morphological variables scaled with positive allometry, led by mass of the levator posterior muscle that showed particularly strong allometry (slope = 1.44, isometry = 1.0).

Scarid jaw mechanisms

Parrotfish adductor muscle and levator posterior sizes did not differ significantly from wrasses (ANCOVA; $P < 0.35$, $P < 0.75$, respectively), but a lower scaling exponent of the sternohyoideus in parrotfish (ANCOVA interaction term; $P < 0.001$) resulted in the parrotfishes in our sample all falling below the wrasses in the space formed by SH mass and body mass. Parrotfish tended to show extreme values of KT in the hyoid four-bar system and all parrotfish had higher jaw-closing lever ratios than any wrasse (Fig. 10). A plot of the scores on the first two principal components for the total assemblage of 130 species revealed complete separation of parrotfishes and wrasses (Fig. 11). This separation was achieved primarily along PC1. PC1 was most highly, but negatively, correlated with the jaw-closing and –opening lever ratios and positively correlated with mass residual of the sternohyoideus muscle, gape distance residual and jaw protrusion (Table 2). This axis reflects the tendency for scarids to have high jaw lever ratios, little jaw protrusion, a relatively small gape, small sternohyoideus muscle and large body size. The second PC was positively correlated with hyoid KT, adductor mandibulae mass, levator posterior mass, gape distance and body mass. This axis provided separation primarily among wrasses: taxa such as *Pseudocoris*, members of the *Labropsis–Labroides* group, *Anampses* and *Cirrhilabrus* showed low scores on PC2, whereas *Pseudocheilinus*, some *Choerodon*, *Pteragogus* and *Oxycheilinus* were

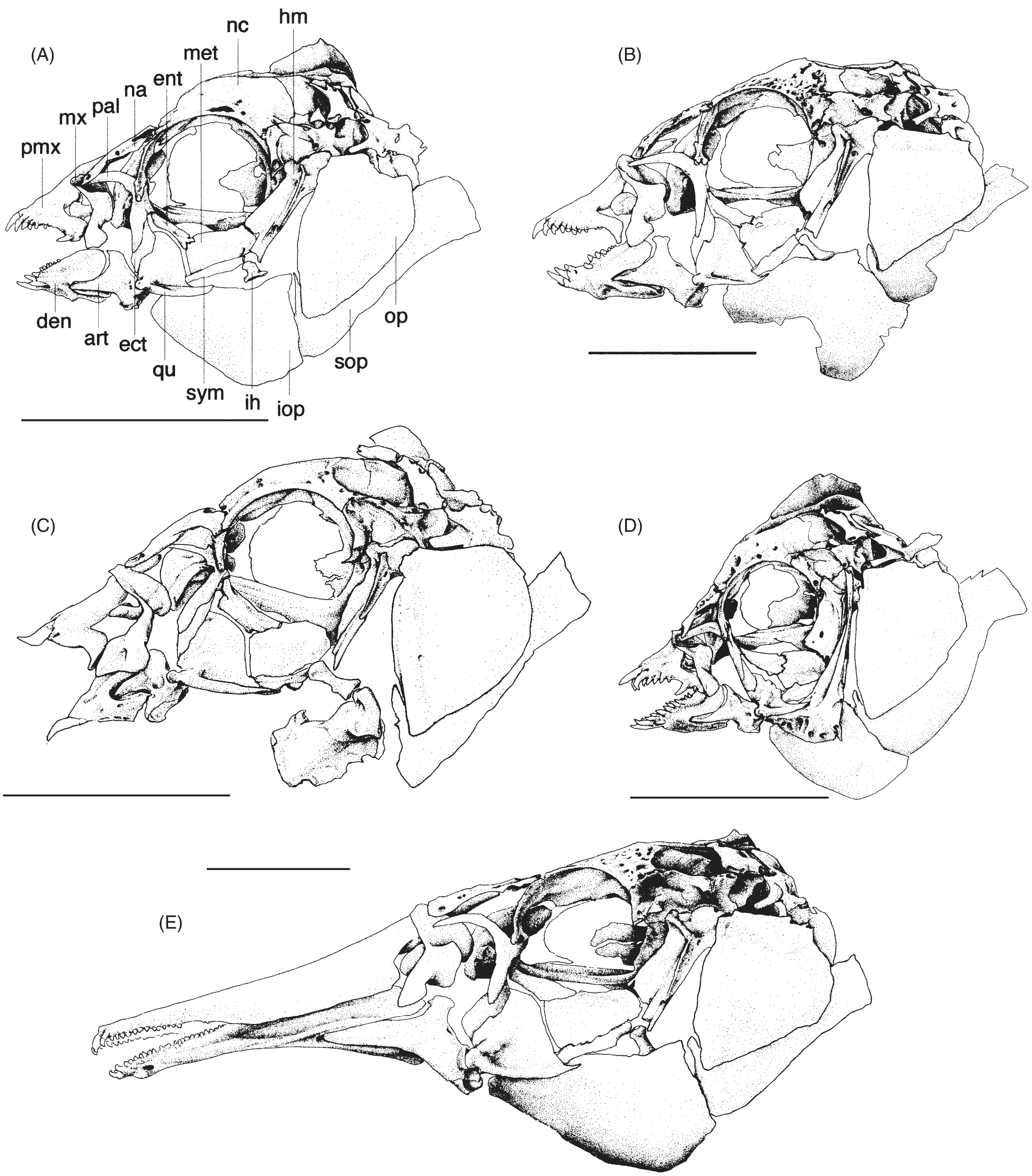


Figure 6. Representative Great Barrier Reef labrids illustrating diversity of the trophic apparatus. (A) *Halichoeres marginatus* with preoporcle removed; (B) *Thalassoma quinquevittatum* with preopercle removed; (C) *Anampses twistii* with preopercle removed; (D) *Macropharyngodon choati*; E. *Gomphosus varius*. Abbreviations as in Fig. 3. Scale bars = 10 mm.

among those with the highest scores. A discriminant analysis using the first two PCs accurately categorized all species as wrasse or parrotfish (discriminant function Wilk's lambda = 0.138, d.f. = 2, $P < 0.0001$).

MORPHOMETRICS OF WRASSES

With the wrasses separated from scarids, 13 of 45 correlations between variables were significant after Bonferroni correction (Table 3). Even in some cases

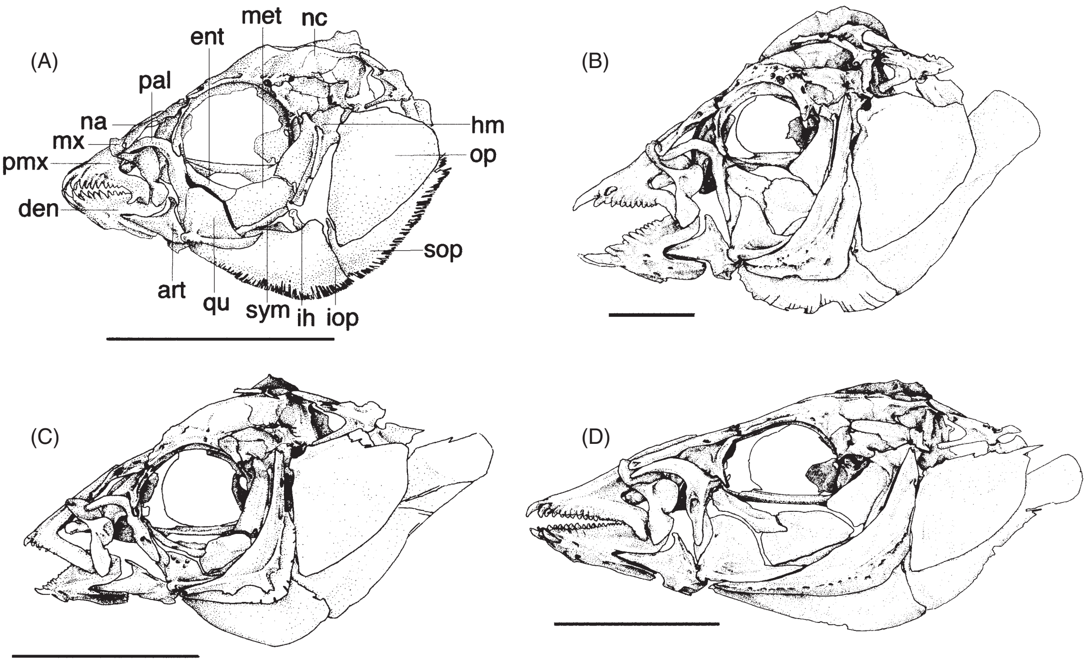


Figure 7. Representative Great Barrier Reef labrids illustrating diversity of the trophic apparatus. (A) *Coris pictoides* with preopercle removed; (B) *Coris gaimard*; (C) *Pseudocoris yamashiroi*; (D) *Hologymnosus annulatus*. Abbreviations as in Fig. 3. Scale bars = 10 mm.

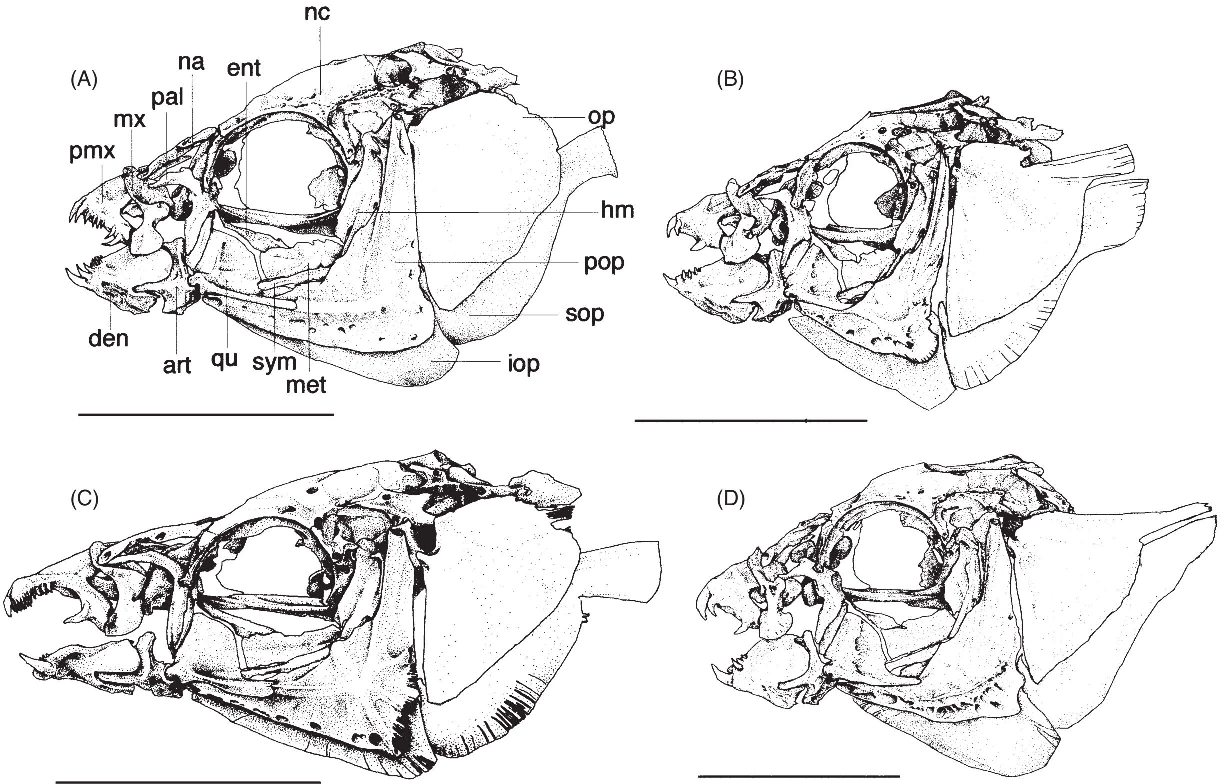


Figure 8. Representative cleaner wrasses and their relatives. (A) *Diproctacanthus xanthurus*; (B) *Labrichthys unilineatus*; (C) *Labroides bicolor*; (D) *Labropsis xanthonota*. Abbreviations as in Fig. 3. Scale bars = 10 mm.

Table 1. Scaling of five morphological measurements of the labrid feeding apparatus

Variable	Slope	SE	y-intercept	SE	R^2
Gape distance	0.34	0.013	0.25	0.026	0.836
Jaw protrusion	0.26	0.027	0.09	0.052	0.416
AM mass	1.26	0.027	–2.97	0.051	0.946
SH mass	0.95	0.026	–2.27	0.050	0.911
LP mass	1.44	0.061	–3.78	0.118	0.813

Least-squares regressions were fitted to the relationship between $\log_{10}$ transformed values of each variable and $\log_{10}$ body mass.

where characters reflected mechanical systems that were linked, there was often no correlation. For example, maxillary KT was not correlated with adductor mandibulae mass residual (Fig. 12A), jaw-closing mechanical advantage was not correlated with gape residual (Fig. 12C), and maxillary KT was not correlated with gape residual (Fig. 12E). However, there was a negative association between maxillary KT and jaw-opening lever ratio (Fig. 12B) indicating that species with velocity and displacement enhanced transmission of lower jaw depression to upper jaw rotation also tended to have similar modifications in the jaw depression mechanism. Mass residuals of all three muscles and gape were correlated, indicating that species with large mouths tend to have large feeding muscles. Species with relatively large mouths also tended

Table 2. Principal Components Analysis on trophic characters of 130 species of labrid fishes from the Great Barrier Reef. Table entries are correlations between the ten variables and each principal component

Variable	PC1 (33.9%)	PC2 (20.1%)	PC3 (14%)	PC4 (10.4%)
Closing ratio	–0.86	0.41	0.02	0.17
Opening ratio	–0.83	–0.09	0.23	–0.07
Maxillary KT	0.18	–0.11	–0.67	0.6
Hyoid KT	–0.45	0.71	–0.19	0.29
Gape distance[1]	0.66	0.56	0.05	0.04
Jaw protrusion[1]	0.65	0.01	0.41	0.43
AM mass[2]	0.09	0.58	–0.21	–0.54
SH mass[2]	0.79	0.26	0.4	–0.02
LP mass[2]	0.29	0.67	–0.34	–0.09
Body mass	–0.43	0.50	0.59	0.26

[1] residual from log–log regression with cube root of body mass.
[2] residual from log–log regression of cube root muscle mass vs. cube root body mass.

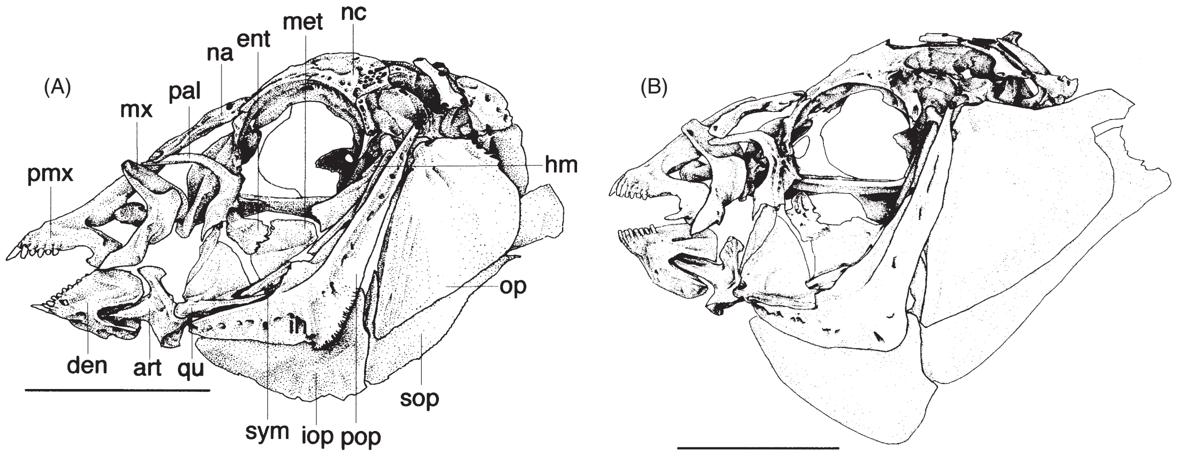


Figure 9. Illustrations of the skull of (A) *Hemigymnus melapterus* and (B) *Stethojulis trilineata*. Abbreviations as in Fig. 3. Scale bars = 10 mm.

Table 3. Correlation matrix for ten trophic variables measured on 105 species of wrasses from the Great Barrier Reef

Variable	Close ratio	Open ratio	Maxillary KT	Hyoid KT	Gape	Protrusion	AM	SH	LP
Open ratio	0.14								
Maxillary KT	–0.16	–0.31							
Hyoid KT	–0.03	–0.51*	0.19						
Gape[1]	0.01	–0.36*	0.10	0.63*					
Protrusion[1]	–0.09	–0.19	0.21	0.09	0.26				
AM[2]	0.21	–0.20	–0.02	0.16	0.47*	–0.08			
SH[2]	0.02	–0.16	–0.08	0.25	0.52*	0.38*	0.45*		
LP[2]	0.14	–0.54*	0.07	0.39*	0.43*	0.06	0.37*	0.37*	
Body mass[3]	0.47*	–0.07	–0.30	0.06	0.01	0.01	0.01	0.01	0.01

[1] residual from log–log regression with cube root of body mass.

[2] residual from log–log regression of cube root muscle mass vs. cube root body mass.

[3] body mass expressed as log of cube root body mass.

*significant correlation after Bonferroni correction at $P < 0.05$.

to have a velocity-modified hyoid four-bar system (Fig. 12F).

The wrasse-only PCA generated four PCs with eigenvalues greater than one that accounted for 71.2% of the variation in the morphological data set (Table 4; Fig. 13). PC1 accounted for 31% of the original variance and was not correlated with body mass, but had high correlations with the mass residuals of the three muscles, gape, hyoid KT, and a negative correlation with the jaw-opening lever ratio. Species with high scores on this axis thus tended to have relatively large mouths, large feeding muscles and velocity-modified transmission in the hyoid and lower jaw depression systems. Among the species with the highest PC1 score were the three species of *Pseudocheilinus*, *Pteragogus*, several cheilines, species of *Bodianus* and *Choerodon*. Taxa with the lowest scores on this axis included all members of the *Labropsis*/*Labroides* group, species of *Anampses*, and *Stethojulis*. PC2 loaded most heavily on the jaw-closing lever ratio, body size and negatively on the oral maxillary KT. Species with high scores on this axis tended to be large and have force-modified oral jaws. The species with the highest score on the second PC included *Cheilinus undulatus,* other cheilines, *Thalassoma jansenii*, *T. hardwicke*, *Xyrichtys aneitensis* and several species of *Choerodon*. Species scoring lowest on PC2 included members of *Cirrhilabrus, Pseudocoris* and *Pseudocheilinus evanidus*. The centre of the space demarked by PC1 and PC2 included several species of *Halichoeres*, *Hologymnosus*, some *Thalassoma*, *Macropharyngodon*, *Coris* and *Novaculichthys*.

The third PC was negatively correlated with the jaw-opening lever ratio, the sternohyoideus residual and jaw protrusion, but positively correlated with body mass and hyoid KT (Table 4; Fig. 13B). The highest score on this axis was achieved by *Pseudodax moluccanus* and the lowest scores were found for *Labropsis*, *Hemigymnus* and *Stethojulis*. PC4 was most highly correlated with jaw protrusion and body mass, and was negatively correlated with adductor muscle mass. The highest score on this axis was achieved by *Epibulus insidiator*, *Cheilinus undulatus* and *Hemigymnus*, while the lowest scores were seen in species of *Labroides*, *Cymolutes* and *Xyrichtys*.

With only ten species, the cheilines showed the highest functional diversity of the five groups compared (Fig. 14). Novaculines and the hypsigenyines were the least diverse. Scarids were notable for having moderate diversity in spite of the trophic constancy typically thought to characterize the group.

DISCUSSION

The feeding apparatus of Great Barrier Reef labrid fishes is a diverse musculoskeletal system with marked variation in the major feeding muscles and the skeletal linkage systems used for biting and manipulating prey, suction feeding, and processing in the pharyngeal jaws. This assemblage of fishes represents a model of biomechanical diversity, offering an opportunity to explore general principles of the mechanical basis of trophic radiation.

PARROTFISHES

One labrid lineage, the Scaridae, has invaded a novel region of morphospace, radiating along an axis that is largely orthogonal to the major axis of diversity in wrasses (Fig. 11). The parrotfish feeding apparatus can be distinguished from that of other labrids. It is based on a combination of a relatively small mouth, limited upper jaw protrusion, and particularly by a small sternohyoideus muscle and high mechanical

Table 4. Principal Components Analysis on wrasses of the Great Barrier Reef. Entries are correlations between the first four principal components and the ten variables describing feeding structures

Variable	PC1 (30.7%)	PC2 (17.6%)	PC3 (11.8%)	PC4 (11%)
Closing ratio	0.03	0.76	0.19	0.13
Opening ratio	–0.68	0.24	–0.47	–0.08
Maxillary KT	0.23	–0.63	0.27	0.06
Hyoid KT	0.71	–0.09	0.35	0.05
Gape distance[1]	0.83	0.04	–0.14	–0.01
Jaw protrusion[1]	0.34	–0.27	–0.38	0.75
AM mass[2]	0.57	0.36	–0.25	–0.47
SH mass[2]	0.65	0.17	–0.60	0.09
LP mass[2]	0.72	0.12	0.19	–0.20
Body mass	0.01	0.69	0.34	0.49

[1] = residual from Log–Log regression with cube root of body mass.
[2] = residual from Log–Log regression of cube root muscle mass vs. cube root body mass.

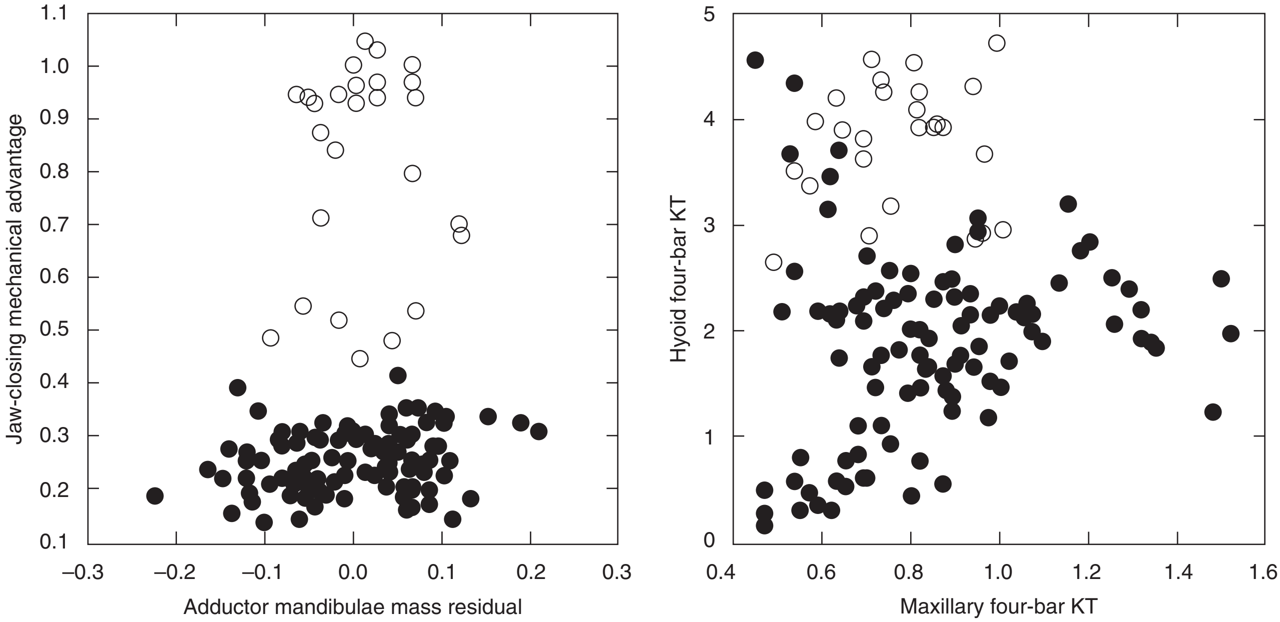


Figure 10. Scatterplots of trophic characters of Great Barrier Reef labrid fishes. Points represent means of each species. Closed circles represent wrasses and open circles represent scarid species. Note that all scarids have higher mechanical advantage in the jaw-closing system than all wrasses but that parrotfish show high interspecific variation. Scarids are restricted to the upper left quadrant of the plot of hyoid and jaw transmission coefficient.

advantage in the jaw-closing and -opening systems. This lineage includes forms with a novel oral jaw four-bar linkage mechanism that involves motion at the intramandibular joint between the articular and dentary bones. Interestingly, although parrotfishes are well known for feeding by scraping and gouging rocky reef surfaces and for their modified pharyngeal jaw apparatus that is used to grind food, neither the size of the adductor mandibulae nor the levator posterior muscles could be distinguished from other labrids. However, all parrotfish had higher jaw-closing lever ratios than any wrasse (Fig. 10A) and a small sternohyoideus muscle. Thus, the modifications that characterize the parrotfish feeding apparatus feature a force-modified jaw-closing lever system and the accompanying loss of kinematic and velocity transmission. The reduction in sternohyoideus muscle size reflects a loss of reliance on suction feeding for prey capture in this group, a feature that distinguishes them from other labrids (Alfaro & Westneat, 1999). It may be that by

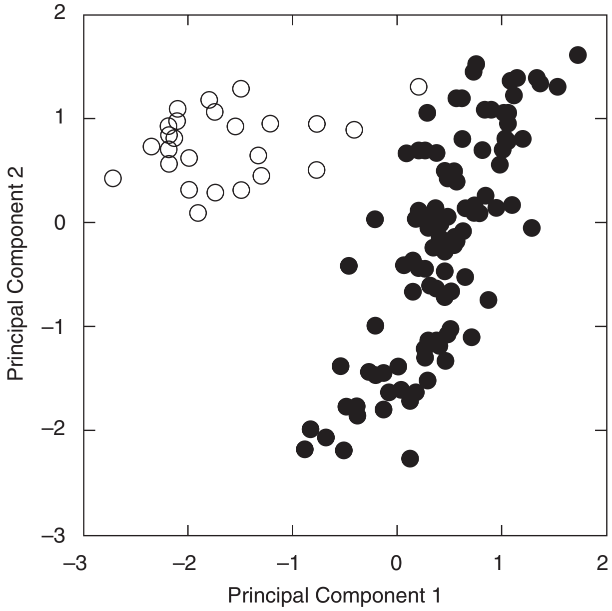


Figure 11. Scatterplot of the dispersion of labrids in the space of the first two principal components of an analysis of trophic characters of the skull. Open symbols represent scarid species and closed symbols represent wrasse species. Note that scarids occupy a region of morphospace completely separate from wrasses. See Table 2 for factor loadings and text for discussion.

specializing on a grazing style of feeding, parrotfishes have lost the need to maintain even a moderate kinematic transmission system in their mandible as would be effective in the capture of more elusive prey, permitting the acquisition of particularly efficient force transmission.

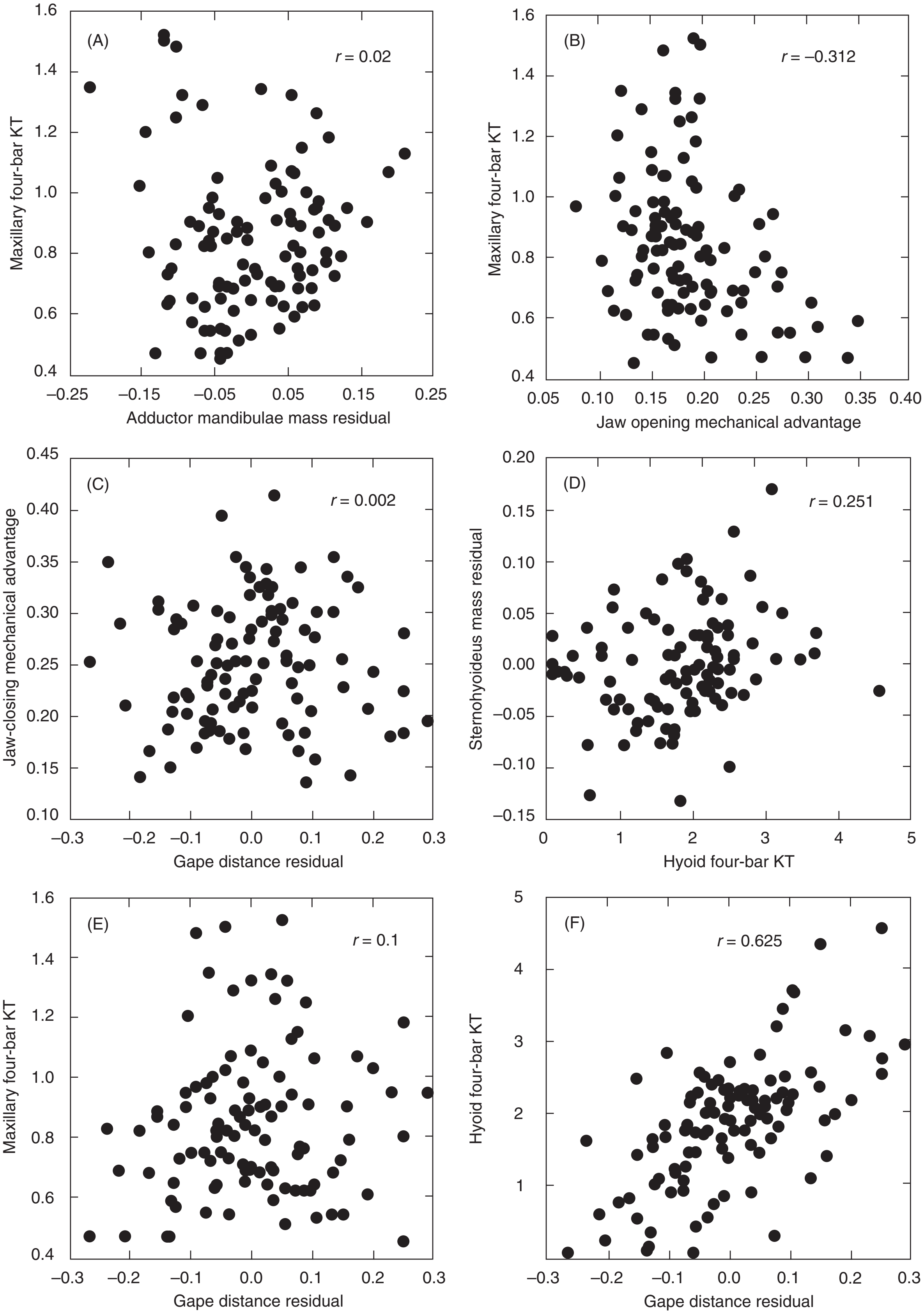
WRASSES

Wrasses showed extensive diversity in feeding-related structures and the different components of the skull showed drastically different levels of diversity. For example, jaw protrusion distance ranged 40-fold among species, when considering residuals from plots against log of cube root of body mass, as compared to a 3.4-fold range for gape. Similarly, the variance in jaw protrusion residual was about three times that of variance in gape residual (0.041 vs. 0.013). The sternohyoideus and adductor mandibulae muscles contributed strongly to wrasse diversity, varying 12.8- and 17.5-fold among species and having variances of 0.004 and 0.007, respectively. However, these muscles fell far short of the extraordinarily variable levator posterior, a muscle that ranged in size 477-fold among species and that had a variance in the residuals of 0.04, nearly six times the variance of the adductor mandibulae and ten times that of the sternohyoideus. This muscle was shown to strongly reflect a prey hardness gradient of prey use in Caribbean labrids (Wainwright, 1988). The mass of this muscle is closely related to its force-producing capacity, and because it is the primary adductor of the pharyngeal jaw apparatus, it closely reflects biting strength and the ability to crack the protective coverings of shelled prey.

The linkage mechanics of the jaw and hyoid system also showed high variability. For the mechanical advantage of the mandible, ranges of 0.13–0.4 for the closing system and 0.08–0.35 for the opening system are considerably wider than previously reported for smaller groups of labrids (Westneat, 1994; Wainwright & Richard, 1995; Wainwright & Bellwood, 2002). Similarly, the range in maxillary KT of 0.45–1.52 and in the hyoid KT of 0.16–4.55 were both more than twice the range previously reported in cheiline labrids and their relatives (Westneat, 1995).

To what extent does the morphological variation of wrasses that is described in Figure 13 map onto variation in patterns of prey use? A detailed analysis of this question is the focus of an ongoing study, but some preliminary patterns are clear from published accounts of wrasse feeding habits. Planktivory has apparently evolved several times in labrids (Randall, 1967; Hobson & Chess, 1978; Wainwright, Bellwood & Westneat, 2002) and several instances of this feeding habit are seen in the GBR fauna. Members of the genus *Cirrhilabrus* are believed to be planktivores as is *Thalassoma amblycephalum*, *Pseudocoris yamashiroi* and *Leptojulis cyanopleura* (Randall *et al*., 1997). *Pseudocoris* and six *Cirrhilabrus* species have the lowest PC2 scores from the wrasse-only PCA. Nine of the 19 lowest scores on PC2 belong to planktivores. These species have among the highest maxillary KT values, moderate to small mouths and substantial jaw protrusion.

Species with high PC2 scores appear to mostly be durophagous (*Choerodon anchorago*, *Cheilinus fasciatus*, *Cheilinus trilobatus* and *Choerodon fasciatus*) (Westneat, 1994). These species are large and have high jaw-closing mechanical advantage, high jaw-opening mechanical advantage and large levator posterior muscles. Species with the highest PC1 scores (*Oxycheilinus* spp., *Pteragogus* spp., *Pseudocheilinus octotaenia*) tend to have a large mouth, large feeding muscles, moderately high maxillary KT and appear mostly to be predators of relatively large, elusive prey (Westneat, 1994). Species that scored lowest on PC1 tend to have a small mouth, small muscles, low jaw protrusion, low maxillary KT and high jaw-opening mechanical advantage. This combination implies that relatively weak muscles are used to move small jaws with poor kinematic transmission. These species are mostly predators of small crustaceans that live in sand or algal turfs (e.g. *Anampses* spp.), ectoparasites


(A)
r = 0.02
Maxillary four-bar KT
1.6
1.4
1.2
1.0
0.8
0.6
0.4
–0.25
–0.15
–0.05
0.05
0.15
0.25
Adductor mandibulae mass residual
(B)
r = –0.312
Maxillary four-bar KT
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
Jaw opening mechanical advantage
(C)
r = 0.002
Jaw-closing mechanical advantage
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
–0.3
–0.2
–0.1
0.0
0.1
0.2
0.3
Gape distance residual
(D)
r = 0.251
Sternohyoideus mass residual
0.20
0.15
0.10
0.05
0.00
–0.05
–0.10
–0.15
0
1
2
3
4
5
Hyoid four-bar KT
(E)
r = 0.1
Maxillary four-bar KT
1.6
1.4
1.2
1.0
0.8
0.6
0.4
–0.3
–0.2
–0.1
0.0
0.1
0.2
0.3
Gape distance residual
(F)
r = 0.625
Hyoid four-bar KT
5
4
3
2
1
–0.3
–0.2
–0.1
0.0
0.1
0.2
0.3
Gape distance residual

of other fishes (*Labroides*), or coral mucous feeders (*Labroides* spp., *Labrichthys*) (Randall *et al*., 1997). Like the planktivores, species in this latter group have a small mouth and small muscles, but they differ in having poor kinematic and velocity transmission of the jaws and low jaw protrusion.

THE LABRID RADIATION

A striking feature of the labrid radiation is the large level of independence of trophic characters (Table 3). The weak correlation matrix for the feeding variables (Table 3) indicates both functional diversity and that labrids have been able to enhance diversity by capitalizing on many different combinations of functional traits. For example, among the wrasses adductor mandibulae mass residual and maxillary KT are not correlated (Fig. 12A). The diversity that is permitted by the lack of association between these traits maps onto distinct ecomorphs. Having a relatively large adductor mandibulae muscle and force-modified oral jaw four-bar linkage characterizes several durophagous taxa (e.g. *Choerodon fasciatus*, *Cheilinus fasciatus*) in which it is possible that selection has favoured a strong oral jaw bite for removing relatively immobile prey from their holdfasts. A large adductor muscle with a velocity-modified oral jaw four-bar linkage characterizes predators of large elusive prey (e.g. *Pseudocheilinus*, *Pteragogus*, *Oxycheilinus*). In this case, the large adductor muscle may provide high power during the explosive expansion and compression that characterizes the kinematics of suction feeding on elusive prey (Ferry-Graham *et al*., 2001, 2002). A small adductor muscle and high maxillary KT characterizes planktivores (e.g. *Cirrhilabrus*, *Pseudocoris*), while a small muscle and low maxillary KT typifies predators of very small benthic crustaceans (e.g. *Anampses*, *Stethojulis*, *Labroides*). An interesting hypothesis to test in the future is that a history of correlated evolution among these mechanical traits has nevertheless led to a pattern among living species in which the variables are uncorrelated.

Cheilines showed higher functional diversity than the other major groups of labrids (Fig. 14). Members of this group range widely in properties of the feeding mechanism and in their feeding ecology (Westneat, 1995). Adult body size varies enormously from the 3.8-g *Wetmorella nigropinnata* up to the 28 880-g *Cheilinus undulatus*. This group includes the labrid with the highest jaw protrusion, (*Epibulus insidiator*), the labrids with the highest gape residual (*Oxycheilinus bimaculatus* and *O. unifasciatus*), the labrids with the 2nd largest adductor mandibulae muscle (*Oxycheilinus digrammus*) and the 2nd smallest adductor mandibulae (*Epibulus insidiator*). Cheilines are also among the labrids with the largest (*Cheilinus fasciatus*) and among the smallest (*Epibulus* and *Cheilinus undulatus*) levator posterior muscle. The diversity of feeding habits in this group maps onto this functional diversity. Among the cheilines are predators of elusive prey such as fishes and prawns (*Oxycheilinus digrammus*, *O. unifasciatus* and *Epibulus*), predators of amphipods (*Wetmorella nigropinnata*), decapods (*Cheilinus chlorourus*) and molluscs (*Cheilinus fasciatus*) (Westneat, 1994). With the notable exceptions of herbivory and detritivory that are seen in scarids, cheilines utilize a large part of the range of prey seen throughout labrids. The next step needed in interpreting the high functional diversity in this group would be to scale the variation to the age of the clade, as could be estimated from DNA sequence data (Martins, 1994; Cuervo & Moller, 1999). Cheilines may represent a particularly explosive functional radiation within the Labridae or they may show comparable rates of morphological evolution to other groups and be a very old lineage.

The extensive ecological diversity seen in cheilines appears to differ substantially from that seen in scarids. Although scarids showed lower functional diversity than cheilines, they were more diverse than the hypsigenyines or novaculines and near equally diverse as the much more species-rich julidines. While scarids show some variability in the food they eat, it is unlikely that they show the dietary diversity of the julidines or hypsigenyines. The morphological diversity in scarids may relate strongly to the mechanisms they use to extract algae and detritus from the reef. Scarids vary in how deeply their grazing penetrates into rock surfaces (Bellwood & Choat, 1990) and may differ somewhat in the make-up of their diet (Choat, Clements & Robbins, 2002). Functional diversity of GBR scarids is moderately high (Fig. 14), reflecting in large part the very high variance in jaw-closing ratio seen in this group. Those taxa identified by Bellwood & Choat (1990) as scrapers (all *Scarus* spp. and *Hipposcarus longiceps*) have smaller adductor mandibulae muscles and higher jaw-closing lever ratios than those species that are excavators (*Chlorurus*, *Cetoscarus*, *Bolbometopon*).

◄

Figure 12. Representative scatterplots of trophic characteristics of the skull in wrasse species. Note that there is no association between variables in plots (A), (C) and (E) (also see Table 3), indicating that wrasses have evolved to adopt an extensive range of trait combinations during their evolutionary history. This widespread independence of trophic features is seen as an important component of the mechanical diversity of the labrid skull.

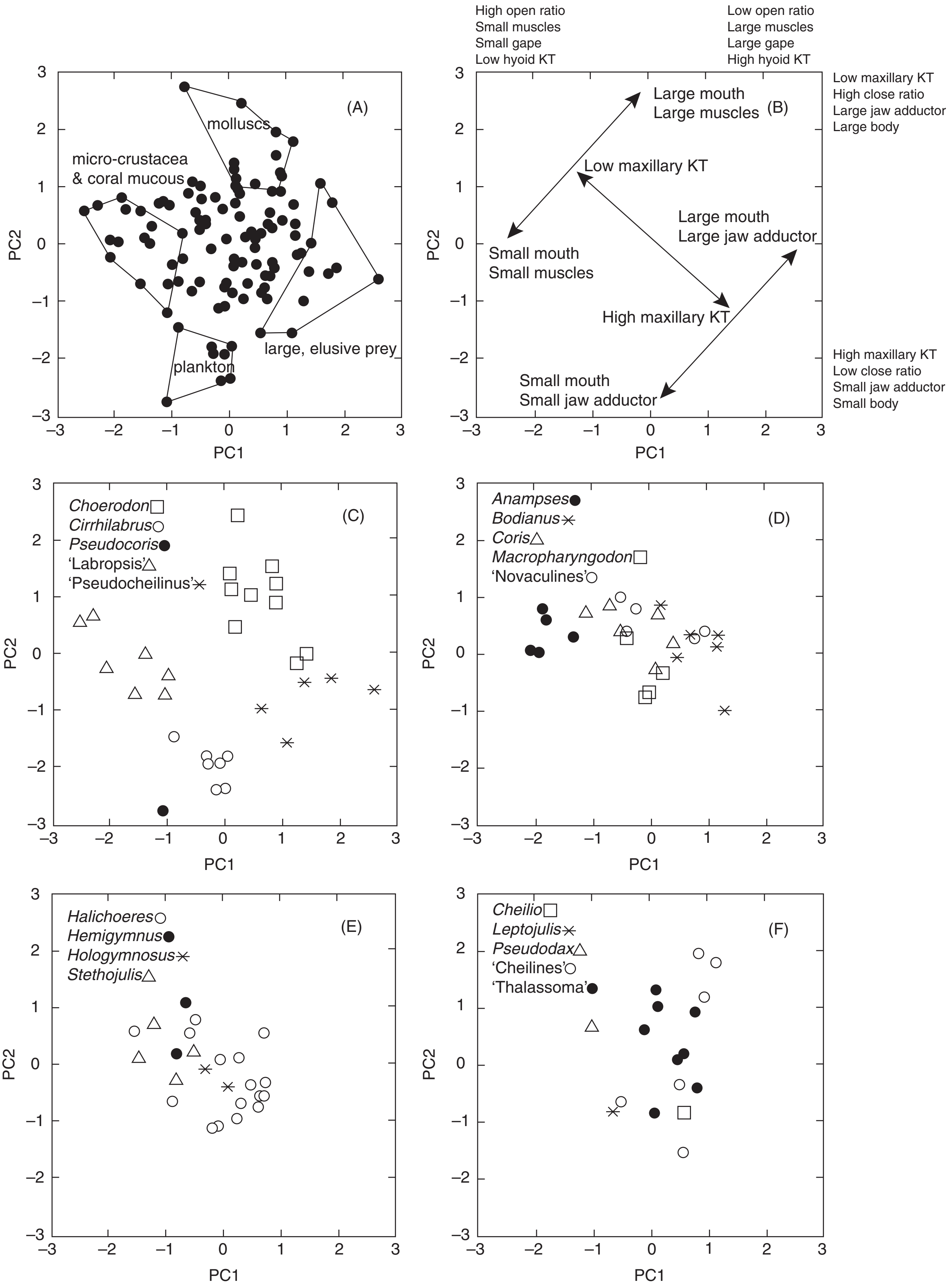

(A)
molluscs
micro-crustacea & coral mucous
plankton
large, elusive prey
(B)
High open ratio
Small muscles
Small gape
Low hyoid KT
Low open ratio
Large muscles
Large gape
High hyoid KT
Low maxillary KT
High close ratio
Large jaw adductor
Large body
High maxillary KT
Low close ratio
Small jaw adductor
Small body
Large mouth
Large muscles
Low maxillary KT
Small mouth
Small muscles
Large mouth
Large jaw adductor
High maxillary KT
Small mouth
Small jaw adductor
(C)
Choerodon□
Cirrhilabrus○
Pseudocoris●
'Labropsis'△
'Pseudocheilinus'✳
(D)
Anampses●
Bodianus✳
Coris△
Macropharyngodon□
'Novaculines'○
(E)
Halichoeres○
Hemigymnus●
Hologymnosus✳
Stethojulis△
(F)
Cheilio□
Leptojulis✳
Pseudodax△
'Cheilines'○
'Thalassoma'●
PC1
PC2
−3
−2
−1
0
1
2
3

Figure 13. Plots of the first two principal components from an analysis conducted only on wrasse species. (A) shows the position of all wrasse species in this space with groups of species with shared trophic habits enclosed in polygons; (B) indicates the axes of mechanical diversity that are found within this space; (C)–(F) show the positions of members of various groups of wrasses. For italicized taxa all Great Barrier Reef members of the genus are shown. 'Cheilines' = all species of *Cheilinus*, *Oxycheilinus*, *Epibulus* and *Wetmorella*; 'Labropsis' = all species of *Labropsis*, *Labroides*, *Diproctacanthus* and *Labrichthys*; 'Novaculines' = All species or *Novaculichthys*, *Cymolutes* and *Xyrichtys*; 'Pseudocheilines' = all species of *Pseudocheilinus* and *Pteragogus*; 'Thalassoma' = all species of *Thalassoma* and *Gomphosus*.

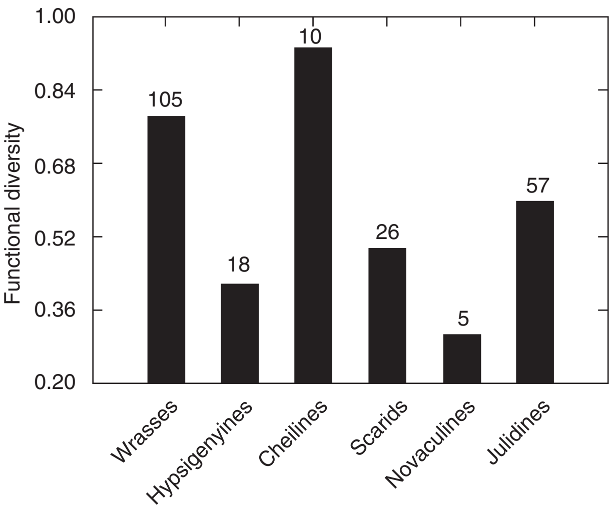


Figure 14. Bar graph of functional disparity in Great Barrier Reef members of five putatively monophyletic groups of labrids. Diversity for each group was calculated as the summed variance of all ten principal components scaled for the percent of variance explained by each principal component. Numbers above each bar are the number of species included in each group.

CONCLUSIONS

The Labridae are ecologically variable and show extensive diversity in the mechanical properties of their feeding apparatus. Labrids achieved this diversity by evolving feeding systems that combine many different functional attributes, rather than exhibiting a strongly correlated suite of characters. Thus, oral jaw linkage systems with high kinematic transmission are found in combination with small, intermediate and large adductor mandibulae muscles. Mouth size and mechanical advantage of the adductor mandibulae muscle also occur in many combinations. In spite of this tendency for independence of trophic features, major axes of diversity do exist. The strongest axis completely separates the feeding systems of scarids from those of wrasses on the basis of the former having a small mouth with limited jaw protrusion, a small sternohyoideus muscle and very high mechanical advantage of the adductor muscle attaching to the mandible. Within wrasses the major axis of diversity contrasted species with big mouths, large feeding muscles and high mechanical advantage of the mouth opening muscles, against species with a small mouth, small muscles and a speed-modified mouth-opening system. The second axis of wrasse diversity contrasted species that were large and had high mechanical advantage of the jaw adductor muscle and the oral jaw linkage system, with species that had high kinematic transmission of the oral jaws, speed-modified jaw opening and small body size.

Diversity was not spread evenly among labrid groups. Cheilines were the most functionally diverse group of labrids, greatly exceeding the variation seen in the more species-rich julidines and hypsigenyines. The moderate diversity of scarids was surprising in light of the tendency to view this group as showing very little trophic variation. The data presented in this paper will provide a benchmark against which to compare the functional diversity in the feeding systems of other major teleost radiations.

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APPENDIX

Morphological and mechanical characteristics of the body and feeding apparatus in 130 species of labrid fishes from the Great Barrier Reef. Values represent means for three or more typical sized adult fish for each species. Please see text for explanations of variables.

Genus and species	Standard length (mm)	Body mass (g)	Gape distance (mm)	Protrusion distance (mm)	Adductor mandibulae mass (g)	Sterno-hyoideus mass (g)	Levator posterior mass (g)	Jaw-closing lever ratio	Jaw-opening lever ratio	Max. KT	Hyoid KT
Wrasses:											
Anampses caeruleopunctatus	157.3	153.7	7.87	5.23	0.212	0.769	0.0310	0.15	0.30	0.47	0.16
Anampses geographicus	143.5	91.3	5.60	7.00	0.224	0.478	0.0381	0.21	0.21	0.47	0.25
Anampses melanurus	75.5	11.9	3.05	2.20	0.015	0.053	0.0013	0.19	0.34	0.47	0.10
Anampses meleagrides	105.0	27.6	4.00	2.55	0.043	0.158	0.0130	0.29	0.31	0.57	1.01
Anampses neoguinaicus	146.0	81.6	4.83	5.60	0.200	0.431	0.0267	0.25	0.26	0.47	0.07
Bodianus anthioides	120.8	63.6	8.05	2.35	0.231	0.275	0.2891	0.28	0.19	0.70	2.70
Bodianus axillaris	118.0	48.8	6.67	4.10	0.208	0.221	0.1899	0.27	0.16	1.07	2.14
Bodianus diana	131.3	57.6	9.30	6.57	0.277	0.434	0.0666	0.17	0.15	1.15	3.22
Bodianus loxozonus	122.8	54.4	8.80	5.43	0.263	0.354	0.3664	0.25	0.14	0.74	2.19
Bodianus mesothorax	127.7	61.5	7.90	3.93	0.272	0.330	0.5372	0.27	0.16	0.93	2.33
Bodianus perdito	118.0	48.2	9.10	4.90	0.221	0.394	0.0981	0.20	0.11	0.62	2.14
Cheilinus chlorourus	154.0	137.3	11.77	6.33	0.942	1.373	0.6760	0.32	0.16	0.87	1.58
Cheilinus fasciatus	198.3	298.1	19.27	8.23	2.058	2.245	5.2517	0.35	0.18	0.68	1.11
Cheilinus oxycephalus	100.5	36.5	7.00	4.00	0.110	0.182	0.0670	0.30	0.17	1.34	1.91
Cheilinus trilobatus	195.3	267.4	17.33	8.93	2.343	3.378	2.1740	0.34	0.18	0.77	1.81
Cheilinus undulatus	867.7	28850.0	79.53	40.40	174.543	327.567	117.7000	0.39	0.25	0.75	2.56
Cheilio inermis	299.7	325.3	22.43	5.50	3.436	1.511	0.6062	0.14	0.10	0.79	1.39
Choerodon anchorago	190.3	362.6	16.63	5.83	2.716	2.187	2.7830	0.41	0.20	0.59	2.18
Choerodon cephalotes	213.3	300.0	20.40	9.50	0.858	2.028	0.6490	0.30	0.15	0.54	2.55
Choerodon cyanodus	262.7	755.7	27.63	12.30	5.166	6.779	2.0944	0.28	0.17	0.64	3.69
Choerodon fasciatus	152.3	151.1	12.08	4.10	0.934	0.854	0.5311	0.34	0.21	0.79	2.33
Choerodon graphicus	154.3	184.4	14.53	7.83	1.001	1.133	0.4708	0.28	0.17	0.62	3.46
Choerodon jordani	117.0	49.3	11.17	4.53	0.122	0.269	0.2180	0.21	0.13	0.61	3.14
Choerodon schoenleinii	190.3	283.2	15.27	7.90	1.111	1.550	1.1114	0.32	0.16	0.68	2.22
Choerodon sugillatum	112.7	40.2	9.57	4.80	0.076	0.344	0.0619	0.23	0.15	0.54	4.33
Choerodon venustus	308.7	1135.0	32.77	17.53	7.087	9.353	5.0731	0.30	0.17	0.53	3.67
Choerodon vitta	156.7	126.6	12.13	12.17	0.411	0.849	0.0539	0.26	0.17	0.51	2.19
Cirrhilabrus condei	68.0	7.7	4.30	2.40	0.007	0.027	0.0008	0.13	0.18	1.25	2.52
Cirrhilabrus cyanopleura	66.3	7.2	3.37	2.70	0.007	0.036	0.0012	0.21	0.20	1.32	2.19

Cirrhilabrus exquisitus	66.3	6.6	3.63	2.57	0.005	0.020	0.0008	0.19	0.19	1.52	1.99
Cirrhilabrus laboutei	74.3	9.1	3.47	2.80	0.011	0.030	0.0009	0.21	0.14	1.29	2.40
Cirrhilabrus lineatus	90.0	19.0	4.50	2.97	0.018	0.094	0.0025	0.22	0.20	1.50	2.50
Cirrhilabrus punctatus	76.5	12.0	3.30	3.05	0.009	0.049	0.0008	0.22	0.12	1.20	2.85
Cirrhilabrus scottorum	97.7	25.4	4.50	2.67	0.032	0.080	0.0051	0.25	0.16	1.48	1.23
Coris aurilineata	81.7	12.2	4.13	2.37	0.032	0.067	0.0110	0.32	0.24	0.69	2.09
Coris aygula	226.5	325.8	13.43	9.25	0.755	1.257	2.3580	0.25	0.17	0.64	1.72
Coris batuensis	128.0	55.2	6.13	2.20	0.167	0.221	0.1002	0.31	0.17	0.75	0.91
Coris dorsomacula	100.7	20.3	4.97	3.03	0.050	0.092	0.0291	0.25	0.17	0.84	1.92
Coris gaimard	211.7	228.4	9.63	6.60	0.660	0.841	0.7542	0.31	0.19	0.87	0.55
Coris pictoides	71.0	7.1	3.73	1.70	0.018	0.044	0.0057	0.27	0.21	0.69	2.32
Cymolutes praetextatus	93.7	10.5	4.57	1.27	0.088	0.056	0.0050	0.31	0.18	1.13	2.46
Cymolutes torquatus	85.8	9.3	5.48	1.53	0.063	0.028	0.0038	0.32	0.17	1.07	1.97
Diproctacanthus xanthurus	56.8	4.5	2.36	1.38	0.012	0.026	0.0001	0.20	0.28	0.75	0.92
Epibulus insidiator	227.5	472.6	16.40	48.60	0.821	3.025	0.3140	0.23	0.23	1.02	1.70
Gomphosus varius	189.7	104.3	8.00	12.40	0.676	0.630	0.1410	0.17	0.08	0.97	1.17
Halichoeres biocellatus	97.3	24.6	5.43	2.33	0.044	0.121	0.0380	0.17	0.11	0.69	2.31
Halichoeres chloropterus	127.7	63.0	5.87	4.10	0.204	0.250	0.1080	0.29	0.18	0.73	1.10
Halichoeres chrysus	79.3	10.9	3.70	0.73	0.010	0.031	0.0070	0.18	0.17	0.73	1.75
Halichoeres hortulanus	196.5	214.3	8.93	6.45	0.815	1.002	1.1900	0.30	0.19	0.88	1.42
Halichoeres margaritaceus	97.7	26.1	5.47	2.77	0.061	0.162	0.0291	0.22	0.20	0.71	1.65
Halichoeres marginatus	128.5	52.0	4.35	2.95	0.074	0.185	0.0183	0.35	0.22	0.83	1.64
Halichoeres melanurus	79.5	11.4	3.50	2.60	0.017	0.043	0.0093	0.19	0.17	0.93	2.16
Halichoeres melasmapomus	57.5	4.2	2.85	2.00	0.006	0.013	0.0130	0.29	0.15	0.90	2.30
Halichoeres miniatus	80.3	12.9	4.07	2.37	0.047	0.080	0.0120	0.25	0.20	0.80	2.02
Halichoeres nebulosus	69.0	8.5	4.15	1.15	0.028	0.064	0.0090	0.25	0.18	0.63	2.10
Halichoeres nigrescens	52.0	3.3	2.80	1.90	0.007	0.015	0.0010	0.29	0.20	0.90	2.81
Halichoeres ornatissimus	68.8	7.0	2.97	1.77	0.010	0.039	0.0057	0.19	0.17	0.85	2.28
Halichoeres prosopeion	94.8	21.4	4.98	3.05	0.034	0.077	0.0220	0.18	0.16	0.98	1.52
Halichoeres scapularis	63.3	5.6	3.90	2.17	0.012	0.022	0.0080	0.25	0.18	0.91	2.03
Halichoeres trimaculatus	112.7	33.7	5.97	3.17	0.079	0.218	0.0610	0.21	0.15	0.87	2.46
Halichoeres hartzfeldii	91.7	14.8	5.47	2.63	0.029	0.076	0.0197	0.18	0.15	0.76	2.29
Hemigymnus fasciatus	132.7	84.8	7.83	9.90	0.122	0.574	0.0401	0.27	0.19	0.63	0.08
Hemigymnus melapterus	173.3	177.7	11.23	13.13	0.556	1.401	0.1290	0.30	0.24	0.54	0.56
Hologymnosus annulatus	196.8	139.8	8.95	4.55	0.791	0.945	0.0749	0.21	0.12	1.00	2.23
Hologymnosus doliatus	210.3	123.5	8.93	4.53	0.541	0.635	0.0620	0.23	0.15	0.98	1.77

APPENDIX *Continued*

Genus and species	Standard length (mm)	Body mass (g)	Gape distance (mm)	Protrusion distance (mm)	Adductor mandibulae mass (g)	Sterno-hyoideus mass (g)	Levator posterior mass (g)	Jaw-closing lever ratio	Jaw-opening lever ratio	Max. KT	Hyoid KT
Labrichthys unilineatus	132.3	63.4	4.93	2.13	0.154	0.145	0.0017	0.29	0.23	0.69	0.59
Labroides bicolor	97.0	14.8	3.73	1.47	0.022	0.039	0.0002	0.18	0.28	0.55	1.06
Labroides dimidiatus	66.0	4.4	2.03	1.23	0.005	0.010	0.0002	0.22	0.24	0.65	1.55
Labroides pectoralis	55.0	3.2	1.67	1.00	0.008	0.013	0.0004	0.17	0.21	0.68	0.81
Labropsis australis	82.7	18.9	3.73	1.00	0.063	0.095	0.0007	0.20	0.35	0.59	0.35
Labropsis xanthonota	68.7	6.6	2.77	1.63	0.015	0.019	0.0003	0.23	0.27	0.55	1.26
Leptojulis cyanopleura	65.3	4.5	2.60	1.07	0.006	0.014	0.0002	0.25	0.16	0.82	2.01
Macropharyngodon choati	81.7	17.2	4.90	1.90	0.024	0.087	0.0382	0.24	0.14	0.82	1.75
Macropharyngodon kutieri	71.0	9.6	3.03	1.80	0.010	0.045	0.0214	0.22	0.16	0.90	1.67
Macropharyngodon meleagris	118.3	47.6	5.35	2.48	0.090	0.253	0.1545	0.28	0.18	0.84	1.64
Macropharyngodon negrosensis	71.7	10.7	3.17	1.27	0.015	0.055	0.0350	0.20	0.17	0.95	1.83
Novaculichthys taeniourus	188.7	169.8	13.40	6.13	1.079	0.815	0.1381	0.30	0.23	1.00	1.44
Oxycheilinus bimaculatus	73.7	12.3	8.47	2.53	0.045	0.083	0.0208	0.20	0.18	0.95	2.95
Oxycheilinus digrammus	149.3	97.5	13.50	7.80	0.981	1.138	0.1213	0.33	0.12	0.90	1.91
Oxycheilinus unifasciatus	149.7	100.0	17.17	8.40	0.726	1.394	0.0814	0.28	0.14	0.80	2.54
Pseudocheilinus evanidus	59.0	6.0	4.00	2.23	0.015	0.024	0.0049	0.16	0.12	1.06	2.27
Pseudocheilinus hexataenia	41.0	2.3	2.37	1.57	0.006	0.009	0.0008	0.28	0.19	1.26	2.07
Pseudocheilinus octotaenia	74.0	9.9	6.57	3.53	0.048	0.147	0.0510	0.18	0.14	0.95	3.07
Pseudocoris yamashiroi	80.7	11.0	3.47	3.13	0.005	0.023	0.0013	0.18	0.12	1.35	1.84
Pseudodax moluccanus	179.8	183.7	8.70	3.15	0.424	0.567	0.2710	0.31	0.18	0.89	2.48
Pseudojuloides cerasinus	80.8	9.6	2.50	1.83	0.012	0.051	0.0027	0.14	0.20	0.82	0.75
Pseudolabrus guentheri	104.3	36.4	9.10	3.40	0.213	0.287	0.0700	0.26	0.18	0.72	2.38
Pteragogus cryptus	54.0	6.6	4.93	2.03	0.015	0.042	0.0181	0.24	0.19	1.03	2.18
Pteragogus enneacanthus	97.5	31.8	9.85	4.30	0.137	0.236	0.0750	0.22	0.19	1.18	2.76
Stethojulis bandanensis	89.7	19.6	4.97	4.27	0.026	0.082	0.0037	0.34	0.30	0.65	0.86
Stethojulis interrupta	68.5	6.3	3.43	2.20	0.008	0.038	0.0011	0.30	0.27	0.70	0.90
Stethojulis strigiventer	75.5	11.3	4.80	2.30	0.014	0.048	0.0020	0.22	0.22	0.62	0.28
Stethojulis trilineata	121.0	45.5	6.23	3.87	0.049	0.244	0.0082	0.27	0.26	0.80	0.43
Thalassoma amblycephalum	89.3	14.1	4.63	3.37	0.021	0.070	0.0028	0.25	0.19	1.05	2.33
Thalassoma hardwicke	148.3	85.7	8.63	6.27	0.440	0.537	0.1220	0.35	0.15	0.89	0.74
Thalassoma jansenii	138.7	70.8	8.43	5.80	0.486	0.552	0.1580	0.33	0.13	0.89	1.37

Thalassoma lunare	154.0	79.0	7.77	5.23	0.378	0.350	0.1130	0.30	0.16	0.82	1.46
Thalassoma lutescens	116.3	30.7	5.13	4.00	0.116	0.198	0.2180	0.24	0.14	0.72	1.47
Thalassoma quinquevittatum	134.0	55.8	7.80	5.87	0.200	0.642	0.0651	0.22	0.15	1.09	1.91
Thalassoma trilobatum	191.3	203.8	13.43	6.67	0.840	1.590	0.2810	0.32	0.20	0.64	2.18
Wetmorella nigropinnata	46.2	3.8	3.03	1.17	0.008	0.014	0.0030	0.18	0.18	1.32	1.92
Xyphocheilus typus	108.7	42.1	12.00	2.87	0.089	0.187	0.0530	0.18	0.13	0.45	4.55
Xyrichtys aneitensis	126.7	51.0	7.37	2.10	0.302	0.162	0.0302	0.33	0.25	0.91	1.75
Xyrichtys pavo	177.7	237.3	12.87	5.23	1.621	0.861	0.1590	0.23	0.27	0.94	1.66
Scaridae:											
*Bolobometopon muricat*um	473.8	5920.1	28.15	3.55	55.984	14.356	31.1810	0.52	0.21	0.57	3.37
Calotomus carolinus	230.0	467.4	18.47	1.20	1.277	1.182	1.7592	0.48	0.15	0.71	2.90
Calotomus spinidens	68.5	11.2	5.15	1.10	0.023	0.057	0.0679	0.45	0.14	0.87	3.92
Cetoscarus bicolor	359.0	1956.2	21.48	1.94	19.284	5.698	8.3376	0.48	0.20	0.54	3.50
Chlorurus bleekeri	173.7	207.0	10.13	1.90	1.961	0.390	0.5962	0.70	0.31	0.64	3.89
Chlorurus frontalis	295.7	930.0	15.40	4.60	9.302	1.755	2.3061	0.80	0.26	0.64	4.20
Chlorurus microrhinos	259.7	698.0	13.10	3.33	6.743	0.753	2.4333	0.54	0.28	0.49	2.64
Chlorurus sordidus	190.0	283.7	12.23	2.98	3.072	0.558	0.7340	0.68	0.29	0.58	3.97
Hipposcarus longiceps	223.4	432.3	14.38	5.58	1.684	1.342	1.3360	0.71	0.21	0.82	3.91
Leptoscarus vaigiensis	222.7	306.3	16.67	2.37	0.976	1.410	1.095	0.55	0.18	0.75	3.16
Scarus altipinnis	262.5	763.5	13.28	4.65	4.123	1.436	1.5935	0.95	0.34	0.82	4.24
Scarus chameleon	179.7	231.6	11.33	4.33	0.844	0.390	0.5690	0.84	0.28	0.95	2.87
Scarus dimidiatus	164.5	183.5	8.05	2.90	1.284	0.439	0.3111	1.00	0.36	0.99	4.73
Scarus flavipectoralis	200.7	279.1	11.20	4.53	0.978	0.477	0.6013	0.93	0.27	1.01	2.95
Scarus forsteni	211.0	289.0	9.70	2.60	1.645	0.410	0.7898	1.03	0.29	0.94	4.32
Scarus frenatus	239.7	509.5	10.37	4.23	3.310	1.147	0.8967	0.97	0.38	0.74	4.25
Scarus ghobban	258.7	612.0	14.27	4.57	2.672	1.141	1.3002	0.87	0.37	0.85	3.92
Scarus globiceps	203.7	316.3	9.00	1.37	1.537	0.452	0.4500	1.00	0.34	0.69	3.82
Scarus niger	241.3	584.0	10.93	4.47	3.452	1.404	1.2550	0.96	0.34	0.71	4.57
Scarus oviceps	234.3	551.5	10.90	5.08	4.739	1.190	0.8261	0.97	0.34	0.80	4.53
Scarus psittacus	201.0	287.8	10.27	4.53	0.933	0.365	0.5807	0.94	0.32	0.96	2.92
Scarus quoyi	185.3	262.3	11.03	3.77	1.258	0.724	0.4410	0.93	0.28	0.81	4.09
Scarus rivulatus	222.7	418.8	10.60	5.07	2.389	1.041	1.0830	1.04	0.39	0.86	3.94
Scarus rubroviolaceus	321.0	1242.8	15.60	3.98	9.328	2.319	3.7540	0.94	0.31	0.73	4.35
Scarus schlegeli	223.0	415.1	11.23	3.77	1.348	0.668	0.8970	0.94	0.31	0.97	3.67
Scarus spinus	199.7	307.9	8.73	4.13	2.337	0.514	0.4294	0.94	0.34	0.69	3.61