

Projecting mechanics into morphospace: disparity in the feeding system of labrid fishes

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In no group of organisms has the link between species richness, morphological disparity, disparity in mechanics and functional or ecological diversification been made explicit. As a step towards integrating these measures of diversity, we examine how the mechanics of the anterior-jaw four-bar linkages of 104 species of Great Barrier Reef (GBR) labrid fishes maps into a scale-independent morphospace. As predicted from theory, no relationship exists between overall size and the mechanics of velocity and force transmission in labrid anterior-jaw linkages. Nonetheless, mechanics associated with the anterior jaw appear to have constrained diversification of labrid anterior-jaw morphology. Furthermore, simulations depict a generally nonlinear relationship between the length of individual links and transmission of motion. In addition, no relationship was found between morphological disparity and mechanical disparity among the most species-rich labrid groups from the GBR. It is also established that regions of morphospace equivalent in morphological disparity differ over nearly an order of magnitude in mechanical disparity. These results illustrate that without an explicit interpretation of the consequences of per unit change in morphology, conclusions about diversification drawn only from morphological disparity may be misleading.

Keywords: biomechanics; jaw; functional morphology; ecomorphology; four-bar linkage; wrasse

1. INTRODUCTION

Morphology is widely used as a measure of diversity. However, in no large group of organisms has diversity in morphology, species richness, mechanical consequences of morphology, function and ecology been explicitly connected. Furthermore, we rarely understand either theoretically or empirically what the major factors are influencing the distribution of morphology (Raup 1966; Foote 1997; Schlichting & Pigliucci 1998). We believe that investigating morphological diversity in ecologically important biomechanical systems will allow the links between different measures of diversity to be made explicit and the factors influencing morphological diversity to be explored more rigorously. As a step towards this type of integration, a combination of simulations and empirical morphometrics are used to examine the distribution of species richness, form and mechanical function in the anterior-jaw four-bar linkage morphospace of labrid fishes.

Four-bar linkages are mechanical-lever systems that have been used extensively to describe how skeletal elements transmit both force and motion (reviewed in Muller 1996). These linkages have been used successfully to predict mechanics associated with systems as diverse as the skull levation and jaw-protrusion mechanisms of reptiles and birds (Frazetta 1962; Hoese & Westneat 1996), coral crushing jaws in parrotfish (Muller 1996), the limb joints of mammals (Muller 1996) and feeding mechanisms in fish (Alexander 1967, 1973; Aerts & Verraes 1984; Muller 1987). Moreover, in the subset of the Labridae known as the wrasses, the anterior-jaw four-bar linkage

has been shown to predict accurately the mechanics that are important in jaw protrusion and feeding (Westneat 1990, 1994, 1995). All wrasses, except *Epibulus insidiator* that has a novel six-bar anterior-jaw linkage (Westneat 1991), are thought to possess an anterior-jaw four-bar linkage system (Westneat 1995).

Due to its taxonomic, ecological and morphological diversity, the Labridae (both wrasses and parrotfishes), have been the focus of numerous studies examining the functional morphology of feeding (Liem & Sanderson 1986; Wainwright 1987, 1988; Westneat & Wainwright 1989; Westneat 1990, 1991, 1994, 1995; Sanderson 1991). In this exclusively saltwater group of about 570 species, there are fish that specialize in eating hard-shelled molluscs, plankton, algae, various benthic invertebrates, coral, fish ectoparasites and elusive prey such as shrimp and other fish (Randall 1968; Randall *et al.* 1997). The variety of feeding modes in this group is reflected in the diversity of modifications that occur within the same basic mechanical feeding systems. For example, in 16 species in the cheiline group of labrids, Westneat (1995) found that the anterior-jaw linkage mechanics of fish closely reflected their feeding habits. It was found that species that might need to quickly open and close their mouths because they feed on highly elusive prey had speed-modified anterior-jaw linkages. Alternatively, labrids that had linkages mechanically modified so that they transmitted the most force from the lower jaw to the maxilla as the lower jaw was closed, ate more attached or durable prey items. Thus, the anterior jaw in labrid fishes offers a promising morphological system for examining the relationship between species richness and ecological, mechanical and morphological diversity. However, we currently do not understand what factors limit or promote the diversity of morphology in the anterior jaws of wrasses.

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Understanding the diversity and distribution of structure in multidimensional morphological space, demands knowing which regions of space a group is constrained from exploiting. But to determine what portion of morphological space is unavailable, we must first determine the relevant morphospace into which a group's morphology will be mapped. Delimiting a morphospace can be difficult because of the infinite number of landmarks on organisms that can be used to provide information for a morphospace and designating homologous landmarks is not always easy (Gould 1991). However, when key mechanical systems such as the anterior jaws have been identified, projecting morphology into space becomes simplified. Additionally, the identification of a mechanically relevant morphospace may provide a better means to identify historical or constructional constraints on morphological diversification that generally are inferred only after the observance of a consistent lack of morphospace occupation. With morphology placed in an explicitly mechanical morphospace, we can ask *a priori* and then subsequently test hypotheses about the role of either size or mechanics in constraining the diversification of a group's morphology.

Once a morphospace is defined, measuring disparity or the variance in form among members of a group, is the primary means of formulating quantitative descriptions and tests of morphospace occupation (Foote 1997). Disparity in morphology is widely used as a metric to infer patterns such as ecological 'packing' among species (Findley 1973; Kingston *et al.* 2000), extent of community convergence (Schluter 1986; Winemiller 1991), selectivity during extinction events (Churchill 1996; Roy 1996), the role of speciation and extinction in the diversification of incumbent taxa (Romer 1949; Wagner 1995), as well as rates of ecological diversification (Gould 1970; Eble 2000). The use of morphology to make these inferences is largely due to the recognition that simple tabulation of species number is probably insufficient to represent accurately the patterns and processes of a group's diversification through time and space.

At present, there is ample evidence that the species richness of a group may not accurately reflect its morphological disparity (Foote 1993*a,b*). However, much less is known about the extent to which morphological disparity can be translated into variation in mechanical properties, and it is the mechanical properties of morphology that influence an organism's functional abilities and ecology. Given the breadth of current knowledge about the ecology and the function of morphological systems in vertebrates, there are remarkably few studies that examine disparity in vertebrate morphology (Gatesy & Middleton 1997; Middleton & Gatesy 2000). Our ignorance of how mechanical disparity maps onto morphological disparity in most groups is also surprising considering the widespread desire to predict the mechanical function and ecology of an organism directly from its morphology (Lauder 1995; Koehl 1996). The need to establish connections between various measures of diversity is even more important when one considers the often incongruent and frequently non-linear associations between morphology, mechanics, function and ecology uncovered when these relationships are examined rigorously (Wainwright *et al.* 1991; Lauder 1996; Aerts *et al.* 2000).

Using the diversity of form and function in the anterior-jaw linkage of 104 species of labrid fishes from the Great Barrier Reef (GBR), a theoretical framework is proposed that could facilitate the comparison of a wide array of vertebrate functional morphology. First, we explore the diversity of morphology and mechanics in the anterior-jaw four-bar linkage. Second, whether size and mechanical constraints influence the range of anterior jaw form in the Labridae is tested. Finally, the link between species richness, morphological disparity and mechanical disparity in anterior jaws is examined so as to determine the extent to which these measures of diversity are concordant.

2. MATERIAL AND METHODS

(a) *Morphometrics*

As in all four-bar linkages, there are four physical units or links in the anterior-jaw four-bar linkage (Westneat 1990). The links move together as the jaws open and close and this motion is coupled and coplanar. Each link has a different mechanical function and corresponds to different anatomical units (figure 1). The fixed link in the system is the suspensorium (A). The other three skeletal elements rotate on the suspensorium during jaw depression and jaw closing. Depression of the lower jaw (B) provides the input motion to this system. Motion of the maxilla (C) is coupled to the movement of the nasal (D) and the nasal is therefore the mechanical equivalent of a coupler link. The maxilla is the output link in the linkage. The kinematic outputs of the anterior-jaw linkage include maxillary rotation, increase in gape and upper jaw protrusion (Westneat 1990, 1994). When the lower jaw is retracted, the anterior jaw undergoes the same kinematic events in reverse.

Measurements of the mechanically informative portions of the anterior jaw made on 304 specimens of 104 GBR wrasse species were used. Three individuals were measured for most species (Appendix A) using dial calipers, and the quantification of links in the anterior-jaw linkage (figure 1) is similar to that presented by Westneat (1990). The lower-jaw link was measured from the base of the coronoid process, at the joint where the articular rotates on the quadrate, to the centre of the attachment of the maxilla on the articular. Then the distance between this attachment point of the ventral shank of the maxilla to the point where the nasal rotates on the maxilla was determined. This was used as the relevant length of the maxilla. The nasal was determined to be a more mechanically reasonable coupler in the four-bar linkage than the palatine (Westneat 1990) in most labrids measured here. Therefore, the nasal was measured as the link connecting the maxilla to the neurocranium. The distance from where the nasal attaches to the neurocranium down to the coronoid process was measured as the fixed link. Detailed morphology of these bones and the morphometrics of these linkages is described in more detail elsewhere (Westneat 1990, 1995).

The four-bar linkage has only one degree of freedom during movement (Muller 1996). Therefore, at any point during jaw rotation, all angles in the linkage are defined if the angular relationship between the lower jaw and the suspensorium is defined. When the jaws are closed and at rest, the angle between the lower jaw and the suspensorium is herein termed the starting angle. This angular relationship is determined by measuring the diagonal distance between the point where the nasal attaches to the suspensorium and where the lower-jaw link meets the maxilla link (figure 1). This diagonal distance (E) was quantified with the jaws in a resting position. Defining the diagonal separating

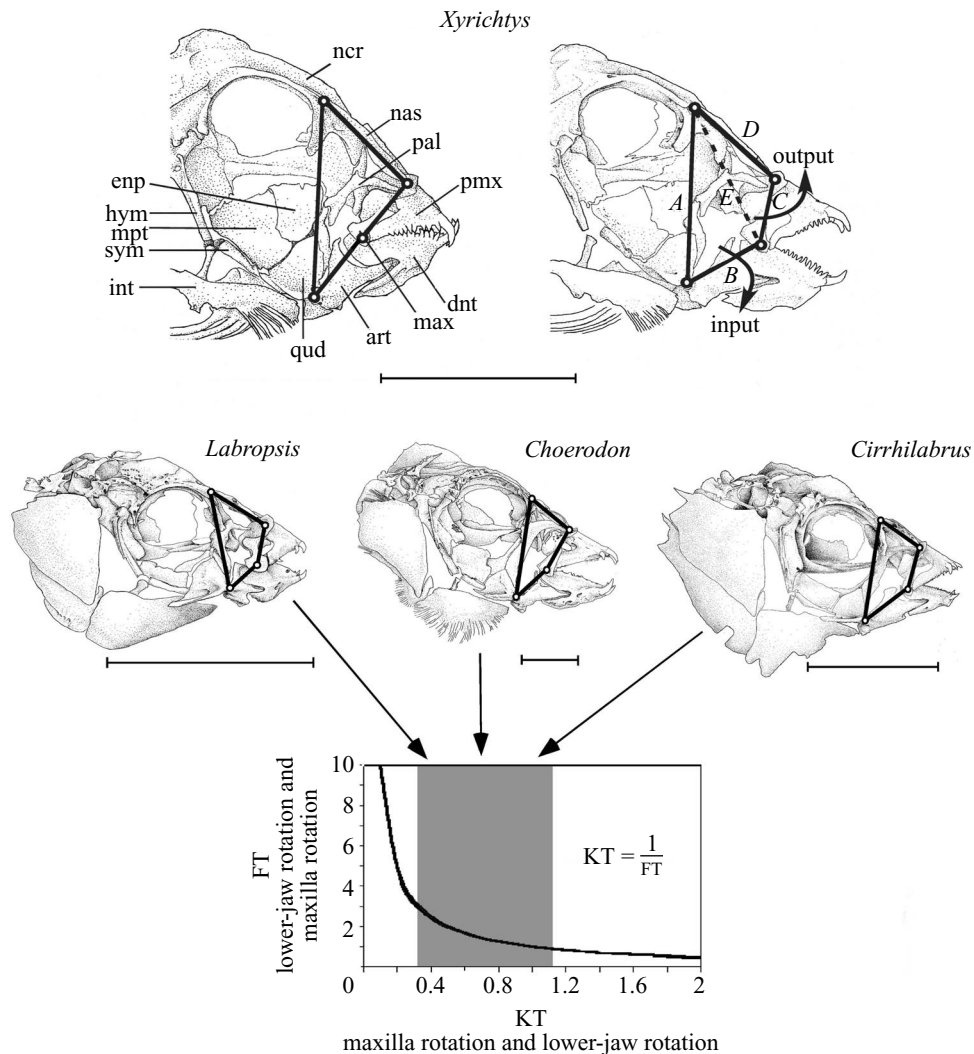


Figure 1. Anterior-jaw four-bar linkage. The configuration of the elements of the four-bar linkage are pictured in both the resting and mouth open position in *Xyrichtys*. The fixed link (*A*) was measured as the distance between the attachment of the nasal on the suspensorium and the quadrate-articular joint. The input link (*B*) was quantified as the distance between the quadrate-articular joint and the centre of attachment of the maxilla on the lower jaw. The size of the output link (*C*) is the length of the maxilla. The length of the nasal (*D*) was quantified as the coupler link. Finally, the diagonal distance between the nasal attachment on the suspensorium and the maxilla attachment on the lower jaw (*E*) is measured. As the lower jaw is depressed, the maxilla rotates resulting in premaxillary protrusion and increase in gape. The relevant anatomy of the four-bar anterior-jaw linkages for the labrid groups *Labropsis*, *Choerodon* and *Cirrhilabrus* are also shown during the middle of the jaw opening. The scale bar under each anatomical drawing is 1 cm in length. The range of empirically derived anterior-jaw linkage morphology is condensed into KT (kinematic transmission) values ranging from 0.36 to 1.07. This area is demarcated in grey on a plot of KT versus FT. Values of KT are determined when the angle of maxillary rotation is divided by the angular arc of lower-jaw depression. The line depicting KT plotted against FT (force transmission) demonstrates the nonlinear but reciprocal relationship between these variables. Abbreviations: qud, quadrate; art, articular; max, maxilla; dnt, dentary; pmx, premaxilla; pal, palatine; nas, nasal; ncr, neurocranium; enp, endopterygoid; hym, hyomandibula; mpt, metapterygoid; sym, symplectic; int, interpercle.

the linkage into two triangles allows all of the angular relationships between the links, including the starting angle (θ) to be determined exactly from the law of cosines as follows:

$$\cos \theta = \frac{A^2 + B^2 - E^2}{2AB}.$$

Finally, the input angle is the angular rotation of the input link. In the anterior-jaw linkages, the input angle is the angular depression of the lower jaw. Although there are other kinematic outputs of the anterior jaw, in this study we only examine rotation of the maxilla.

(b) Kinematic transmission and morphology

Bones in the anterior-jaw linkage, like other levers such as screwdrivers and wheelbarrows, do not create but just transmit the motion and force imparted to them from muscles. For most skeletal-lever systems, a useful measure of mechanics is what proportion of motion or force transferred into the system is transferred out of the system. Therefore, after defining the size of the physical links, the starting angle, and the input angle, the mechanical properties of each linkage were summarized by calculating a kinematic transmission coefficient (KT) for each linkage (Barel *et al.* 1977). The KT was calculated as the ratio of angular output motion of the linkage to its angular input motion

(Westneat 1994). In the anterior jaws, KT is equivalent to the maxilla rotation divided by the lower-jaw rotation and reflects how motion is amplified through the linkage. Like most lever systems, the anterior-jaw four-bar linkage has an inherent trade-off between the transmission of force and velocity. To illustrate this with an example closer to personal experience, one could think of a screwdriver rotating on the fulcrum provided by the top of a can of paint. The large in-lever above the paint can one holds and the small out-lever at the end of the screwdriver on the other side of the fulcrum allow the efficient transmission of force. However, as the lid of the paint can is forced open it does not move very quickly (low KT). KT can then be thought of as the inverse of the mechanical advantage, force transmission (FT), or how force is amplified through the linkage (figure 1). Therefore, representing all linkages with the single value of KT simultaneously describes the FT of the linkage. Higher KT anterior-jaw linkages transmit a greater amount of motion from the lower jaw to the maxilla than linkages with low KT. However, this amplification of motion results in these linkages not effectively transmitting force from the lower jaw to the maxilla as the jaw is closed during biting.

Calculations of KT for theoretical linkages were all performed using a program written in LISPSTAT (<http://www.stat.umn.edu/~luke/xls/xlsinfo/xlsinfo.html>). The KTs for empirically measured linkages were determined from the starting angle derived from the anterior-jaw morphometrics and 30° of lower-jaw rotation. The KTs for these actual linkages were calculated using macros written in EXCEL. To determine if there was a clear relationship between morphological variation and jaw mechanics, a principle components analysis (PCA) was performed using SYSTAT 9 on the linkages of the 104 species of labrids. For the PCA, we analysed separately the morphometrics derived for the 304 individuals measured, as well as the average species values of lengths of the suspensorium, lower jaw, maxilla and the nasal so that each of the 104 species was only represented once. *Cheilinus undulatus* was excluded from the analysis because the large size of its links made this species an extreme outlier. Due to the large amount of variation described by the first two PC axes, only the scores of each species on the first two PC axes were regressed against the KT for each species.

(c) Anterior-jaw linkage morphospace

A three-dimensional morphospace was constructed for use as a framework for simulations and to visualize the distribution of empirically measured linkages. This morphospace had three axes: lower-jaw length, maxilla length, and nasal length. As the mechanics of the linkages are scale independent, we divided the length of each of the other links by the length of the fixed link. This standardized each empirical linkage to a linkage with a suspensorium of 1.0. This standardization allowed the linkages to all be mapped into the same three-dimensional morphospace and simultaneously preserved all mechanical properties of the linkage.

Next, a mechanical barrier to the construction of functional linkages was demarcated. If the lengths of the other three links do not sum to greater than the length of the fixed link, there can be no motion in a linkage (Muller 1996). If such morphologies existed, some labrid anterior jaws would not function as a four-bar linkage. Thus, in the morphospace we constructed, connection of the four units of the linkage is equivalent to links on all three axes summing to at least 1.0. To explore the relationship of the empirically measured four-bar linkages to this mechanical barrier, the ratio values of the input link, output link

and coupler link were summed and the distribution of these values determined.

Simulations were also used to examine the KT expected from possible anterior-jaw morphologies. The simulations allowed us to identify regions of morphospace where the relationship between linkage morphology and KT was nonlinear. This also provided an opportunity to identify regions of space that are mechanically untenable for labrids to occupy. In the simulated morphospace, we varied the lower jaw, maxilla and nasal by 0.05 units of the fixed link. Lower-jaw values used in the simulations ranged from 0.2 to 0.8 of the size of the fixed link. The values used for the nasal and maxilla ranged from 0.3 to 0.9 of the length of the fixed link. These values circumscribe the region of anterior-jaw linkage values that were empirically found in the 104 labrid fishes examined. Starting angles of 0, 10, 20, 30 and 40°, and input angles of 10, 20, 30 and 40° were also used because these values probably encompass relevant values for the anterior jaw when in use during feeding (Westneat 1990). Therefore, if the starting and input angles caused KT values for particular linkages to vary, this variation would be incorporated into our analysis. With these simulations we explored 2197 different morphologies. When accounting for variation in starting angle and input angle, 35 152 possible configurations of the anterior-jaw linkage were examined. The values obtained from the simulations indicate that the effects of starting angle and input angle on KT were probably minor. This confirms the finding of Westneat (1994) that input angle had little effect on anterior-jaw linkage KT during actual feeding sequences of several GBR labrid species included in our analysis. Therefore, we focus our analysis on the three mobile links in the anterior jaws. The simulations were used to produce contour plots of the relationship between morphological variables and their relationship to KT for the three possible combinations of two mobile links (i.e. lower jaw versus maxilla). Contour plots were produced using the default NEXPO smoothing option in SYSTAT 9 to integrate all simulated starting angles, input angles and all length values simulated for the third mobile link (i.e. nasal values for the other two links above).

(d) Morphological and mechanical disparity

To calculate the mechanical disparity for the different regions of the three-dimensional morphospace, we delineated cubes of the theoretical morphospace that at least one labrid species occupied. Each cube contained exactly the same amount of morphospace. For the lower jaw, maxilla and nasal axes of these cubes, a region that was one-tenth the length of the suspensorium formed the length of each axis in the morphologically equivalent cubes. Cubes overlapped only at their edges. Using 30° of input to the lower jaw and a starting angle of 20° between the lower jaw and the suspensorium, the angular rotation of the maxilla for the eight vertices of each cube was calculated. This input to the linkage is representative of angular rotation measured for lower-jaw kinematics in labrids (Westneat 1990) and the value of starting angle is close to the average found for labrids measured here. As each value was derived from 30° of input, the angular rotation of the maxilla is equivalent to KT values in which only the output changes. The eight values of angular rotation of the maxilla were then used to compute a measure of the variance or mechanical disparity in maxillary rotation for each morphologically equivalent cube of morphospace. The number of species that fell into the region that each cube bounded was determined. Finally, the number of species that

Table 1. Principal components analysis and anterior-jaw morphology.

(The first two axes of the PCA explained 98.7% of the variance in the anterior-jaw morphology. Almost all of the variation in the suspensorium was explained by PC1. The nasal and the lower jaw loaded most heavily for PC2 but in opposite directions.)

variable	PC1	PC2
suspensorium	0.994	0.000
nasal	0.967	0.242
maxilla	0.987	-0.006
lower jaw	0.968	-0.235
eigenvalue	3.834	0.114
cumulative percentage of variance	95.85	98.69

fell into regions of cube morphospace with similar mechanical variance was tabulated.

We also wanted to determine if morphological disparity of smaller monophyletic groups in the Labridae was a good predictor of mechanical (KT) disparity. The relationship between the variance in the links with size removed (the nasal, maxilla and lower-jaw link divided by the fixed link) and the variance in KT for the ten largest, assumed to be monophyletic, groups (genera) of labrids were examined. The variance of each of the three size-independent links was summed from the GBR species examined in each of these groups and then regressed against the variance in species KT for each group. The ten groups included were *Anampses*, *Bodianus*, *Cheilinus*, *Choerodon*, *Cirrhilabrus*, *Coris*, *Halichoeres*, *Macropharyngodon*, *Stethojulis* and *Thalassoma*.

3. RESULTS

(a) Morphometrics

The lower-jaw link was generally found to be smaller than the other links and ranged from 0.21 of the fixed link in *Xyrichtys aneitensis* to 0.58 in *Wetmorella nigropinnata*. The average size of the lower-jaw link was 0.39 ± 0.058 of the fixed link. The maxilla of these labrids averaged 0.55 ± 0.063 and spanned values from 0.39 (*X. aneitensis*) to 0.71 (*Xiphochelilus typus*) of the fixed link. The ratios of the nasal to the suspensorium are the most variable and extend from 0.30 in *X. typus* to 0.88 in *Chelio inermis*. The average size of the nasal was smaller than the maxilla at 0.51 ± 0.086 of the fixed link.

(b) Kinematic transmission and morphology

Kinematic transmission ranged from a low of 0.36 to a high of 1.07 (figure 1; Appendix A). The mean KT value was 0.70 ± 0.16 for the 104 species examined. The PCA of all 304 individuals (not shown) and the PCA of the 104 species averages gave virtually identical results (table 1). The first PC axis (PC1) explained a large majority of the variance (95.9%) in linkage morphology. All four morphological variables loaded most heavily for this axis with the suspensorial link loading greater than 99%. Of the four variables examined on the second PC axis (PC2), the lower jaw and nasal loaded most heavily for PC2. PC2 only explained 2.8% of the variance in the labrid linkage morphology. Interestingly, the lower jaw (-0.235) and nasal (0.242) loaded in opposing directions. The

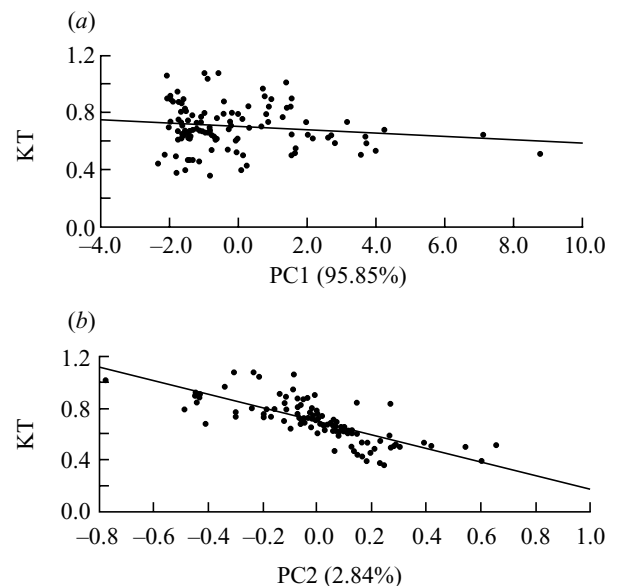


Figure 2. Regression of KT (kinematic transmission) and the PC (principal components) loadings derived from anterior-jaw morphometrics of 104 labrid species. There was no statistical relationship between PC1 loadings and KT ((a) $R^2 = 0.018$; $p < 0.183$), indicating that there might not be a relationship between size of the anterior jaws and KT. There was a significant relationship between PC2 loadings and KT ((b) $R^2 = 0.544$; $p < 0.001$).

regression of KT scores versus PC1 scores (figure 2) produced no significant relationship ($R^2 = 0.018$; $p < 0.183$). However, PC2 had a highly significant relationship with KT ($R^2 = 0.544$; $p < 0.001$).

(c) Anterior-jaw linkage morphospace

Examining the empirically measured linkages in morphospace indicated several interesting aspects of anterior-jaw diversification in this group (figure 3). First, no links are longer than their respective fixed link. Second, there do not appear to be large holes in the anterior-jaw distribution in morphospace and this region is densely occupied. Also, if one adds the sizes of the input link, output link and coupler link, the average summed size relative to the fixed link (1.0) is only 1.46 ± 0.015 . The smallest relative linkage size was found in *X. aneitensis* with a combined total of 1.14 times the size of the fixed link. This indicates that all four-bar linkages had sufficient size to produce viable anterior-jaw linkage mechanics. *Chelio inermis* had the largest links (1.92) relative to the fixed link. In general, the labrids are located fairly close to the hard mechanical limit set by the mechanical constraint that the three movable links must add to a length greater than the fixed link.

The simulations show that combinations of links generally have nonlinear relationships to KT when links change in length. The simulations also demonstrate that we should expect larger lower-jaw links to produce higher KT values in general. Additionally, they indicate that longer maxillae in the anterior jaw result in fairly unambiguous decreases in KT. The relationship of length of the nasal link to KT ranges from having almost no effect when lower-jaw size is small to having fairly unpredictable effects on linkages that have long lower-jaw links. Additionally, the plot of the length of the lower jaw versus

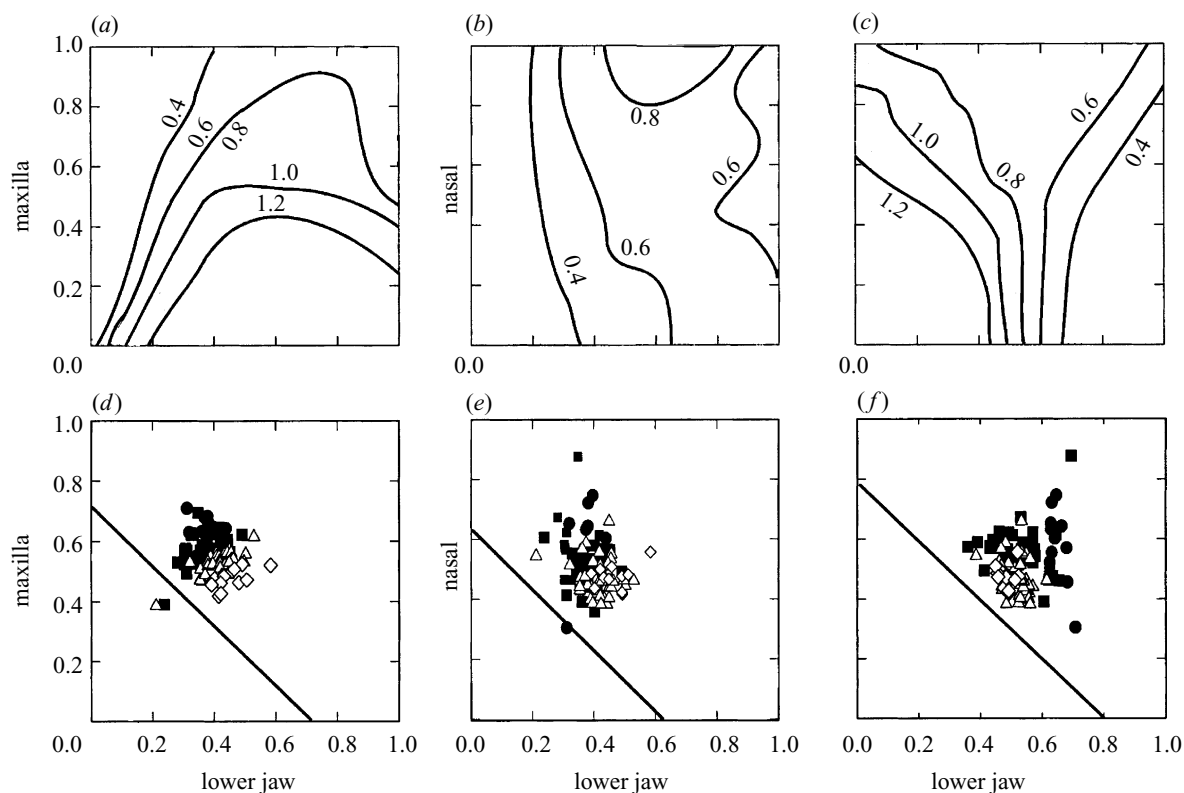


Figure 3. Simulated and empirical values of anterior-jaw KT. The contour plots (a)–(c) depict the relationships expected between two links from simulations of all possible linkage configurations and 20° input. Other input angles gave qualitatively similar results. Many regions of morphospace produce linkages that are outside the range empirically measured in the labrids. (d)–(f) Actual morphospace occupation of two links of all 104 species standardized by their fixed links. The KT values represented are divided into four classes: filled circle, 0.3–0.5; filled square, 0.5–0.7; open triangle, 0.7–0.9; and open diamond, 0.9–1.1. To provide insight into the proximity of all labrid anterior jaws to their mechanical limit, we show where the anterior jaws of all species lie in relation to a single linkage in which mobile links only add to the length of the fixed link. The diagonal lines represent the minimum possible values of lower jaw and maxilla size for the shortest empirically measured labrid nasal (*Xiphocheilus typus*) in (d), of lower jaw and nasal size for the shortest empirically measured labrid maxilla (*Xyrichtys aneitensis*) in (e), and of maxilla and nasal size for the shortest empirically measured lower jaw (*X. aneitensis*) in (f). The need for a functioning linkage to compensate for one link being small in order for the four-bar linkage to function may best be illustrated by *X. typus*, which has the longest maxilla link. The few points that lie on or below the lines have long third mobile links that presumably allow linkages to continue to function as a four-bar linkage. No labrid nasal + maxilla + lower-jaw links were found to be shorter than their fixed link, but linkages nevertheless do appear to lie close to the mechanical barrier of minimum length for functioning four-bar linkages.

that of the maxilla indicates that as jaw length increases and maxilla length decreases there is a large increase in KT. The graph of the relationship between the maxilla and the nasal also indicates that for linkages with both short nasals and short maxillae that $KT > 1.2$. Empirically, several labrids rest near the edge of these regions.

(d) Morphological and mechanical disparity

In the regions or cubes of equivalent morphological variation, we identified nearly an order of magnitude range in variance in maxillary rotation (figure 4). The variance in maxillary rotation ranges from 3.3 to 32.2° . The variance in maxillary rotation for 25 cubes of equivalent morphospace was calculated. Cubes containing 23 species of labrids were excluded from the analysis because at least one of the vertices of these cubes produced no value of KT. This resulted from the fact that many of the empirical linkages were extremely close to regions of morphospace that are mechanically infeasible due to the limit on how short the total length of linkages can be. The mean variance of morphologically equivalent cubes is $15.1 \pm 5.7^\circ$ of

maxillary rotation. Members of the group *Halichoeres* as well as *Gomphosus varius* and *Bodianus perditio* were located in the cubes with the highest KT variance. The regions of lowest variance contained several *Anampses*, *Coris* and *Choerodon* species as well as *X. typus*.

The variance in the morphology of the three non-fixed links ranged from 0.003 11 in *Cheilinus* to 0.008 91 in *Stethojulis*, and KT variance ranged from 0.0055 in *Anampses* to 0.0280 in *Stethojulis*. There was no significant relationship between morphological disparity and mechanical (KT) disparity among the ten most species-rich groups of labrid fishes ($R^2 = 0.18$; $p < 0.221$). When *Stethojulis*, the largest outlier group, was removed (figure 5), we obtained similar non-significant results ($R^2 = 0.076$; $p < 0.472$).

4. DISCUSSION

The GBR wrasses exhibited extensive diversity of both anterior-jaw morphology and anterior-jaw mechanics. Although factors associated with size appear to have had

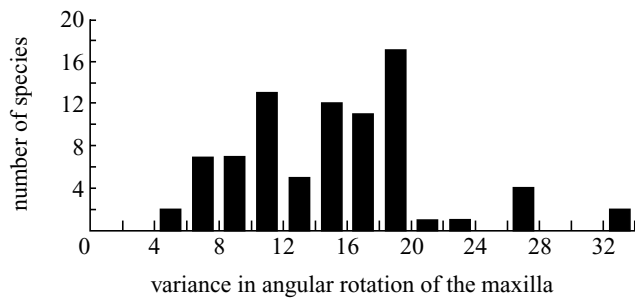


Figure 4. The relationship between the number of labrid species and variance in the rotation of the maxilla for cubes of equivalent morphospace is depicted. The variance in maxillary rotation was calculated from the eight values of angular rotation determined for the eight vertices of each of the morphospace cubes. All morphospace cubes were equivalent in the volume of morphology they encompassed. The variance in maxillary rotation ranged over nearly an order of magnitude.

little effect on the functional diversification of anterior jaws in this group, several mechanical constraints on morphological diversification remain viable hypotheses. Additionally, it is found that not only is there no direct mapping between species richness and morphological disparity, but also in the anterior-jaw morphospace and among putatively monophyletic genera, there is no congruence between morphological disparity and mechanical disparity.

(a) Kinematic transmission and morphology

The KT inferred from the anterior-jaw linkage for many labrids provides an intriguing insight into the potential functional and ecological demands placed on fish that specialize on particular prey types. At present, the feeding habits of most GBR labrids are poorly known. Therefore, we will only discuss two broad categories of feeding mode that contain some of the species with the most speed-modified (high KT) and most force-modified (low KT) linkages.

Although speed-modified lever systems are generally expected to be found in species that eat elusive prey, such as fish or shrimp (Westneat 1995), we also found high KT linkages in species that are thought to be plankton specialists. However, the KT of lineages specialized to eat plankton were highly variable. Species such as *Leptojulius cyanopleura*, *Pseudocoris yamashiroi* and *Thalassoma amblycephalum* had intermediate KT values, whereas the largely planktivorous group *Cirrhilabrus* (Randall *et al.* 1997) consistently had some of the highest KT values identified. The variability in the KT of the anterior jaw in this feeding guild could simply indicate that specializing on plankton does not strongly constrain anterior-jaw mechanics.

Additionally, as has been shown previously (Westneat 1994), it was found that groups such as *Coris* and *Choerodon* that generally eat attached prey, such as molluscs, had more force-modified linkages, or lower KT, than groups that specialize on more elusive prey. However, some of the lowest KT values were found in *Labroides*, *Labropsis*, *Diproctocanthus* and *Labrichthys*. These groups contain many cleaner as well as corallivorous species (McIlwain & Jones 1997). The removal of parasites that are attached to other fish and feeding on coral may be feeding modes

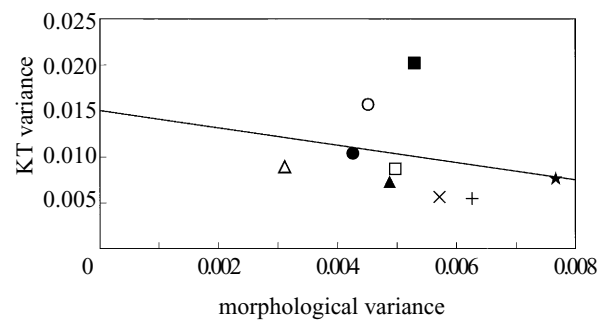


Figure 5. Regression of species KT (kinematic transmission) coefficient variance versus the summed morphological variance in the nasal/fixed, maxilla/fixed and lower jaw/fixed links in the ten most species-rich groups of labrids on the Great Barrier Reef. These groups are *Anampses* (plus sign), *Bodianus* (multiplication symbol), *Cheilinus* (open triangle), *Choerodon* (star), *Cirrhilabrus* (open circle), *Coris* (open square), *Halichoeres* (filled triangle), *Macropharyngodon* (filled circle), *Stethojulis* (not shown), and *Thalassoma* (filled square). No significant relationship was found ($R^2 = 0.18$; $p < 0.221$) even when the outlier *Stethojulis* was excluded ($R^2 = 0.076$; $p < 0.472$).

that one might consider as requiring forceful bites and the anterior-jaw mechanics corroborates this idea.

(b) Anterior-jaw linkage morphospace

Theoretically, the four-bar linkage system of the anterior jaw should transmit motion and force in the same manner independent of fish size. As long as the anterior-jaw links scale isometrically, and no other factors that might be size dependent influence its diversification, this theoretical prediction should hold. Thus, placing labrid anterior jaws in a three-dimensional, size-independent morphospace should not be problematic. However, simply accepting theoretical predictions could result in misleading simplifications because mechanical systems frequently change in morphology and ecological function as organisms grow in size (Wainwright & Richard 1995; Wainwright & Shaw 1999) or in groups of organisms that vary along body-size axes (Lauder 1995; Schmidt-Nielsen 1995; Koehl 1996). However, our results show that diversification in the mechanical function of labrid anterior jaws appears to be independent of size.

Although PC1 explained *ca.* 96% of the variation in morphology in the linkages, it explains very little of the mechanical variation in anterior jaws in this group. If PC1 is interpreted as size, then it would appear that the variation in the length of the suspensorium could be explained largely as variation due to change in body size. Variation in size is an important component of the ecological disparity of labrids and several groups included here, such as *Coris* or *Choerodon*, have diversified along a size axis (Randall *et al.* 1997). However, it is interesting that groups within the Labridae that vary greatly in size do not generally have extensive mechanical variation in their anterior jaws.

The small overall variation in morphology described by PC2 heavily influences the KT or jaw mechanics of these species. This variation in anterior-jaw shape may be necessary for wrasses to use the wide range of functionally unique prey items that they exploit, such as fishes, coral

and ectoparasite picking. The PCA corroborates the simulation studies for the suggestion that, in general, longer lower-jaw links and shorter maxillae result in higher KT linkages. However, the simulations did not suggest there would be a negative relationship between the lower jaw link and the nasal link that would greatly influence KT. Nevertheless, the unforeseen negative relationship between these two links on PC2 appears to be responsible for much of the variation in labrid jaw mechanics.

(c) *Limits to anterior-jaw form*

The distribution of the morphology and mechanics of anterior jaws in morphospace indicates that several mechanical limits may influence the distribution of anterior jaws in morphospace. For example, the individual links must all have some length or there would be only three links in the system. No motion can be transferred through a linkage system that only contains three links (Westneat 1994; Muller 1996). Another factor that may constrain the minimum size of the links is the need for the bones in the linkage to be a certain size to provide effective attachment and rotation points for muscles, ligaments and other bones (Middleton & Gatesy 2000). So, it is possible that some of the smaller-sized links are actually approaching this limit and that these mechanical considerations also limit the morphological diversity of these linkages.

The range of KT values (0.36–1.07) examined here may also represent both upper and lower limits to acceptable mechanical transfer of force and motion in the anterior jaws of labrids. The simulations indicate that many theoretically possible anterior-jaw morphologies not explored by the Labridae would result in the production of KT that may not be viable for the feeding demands made of actual labrid jaws. In fact, from the simulations, it appears that combinations of large lower-jaw links and short maxilla produce KT values well above any values recorded for labrids found on the GBR. Additionally, linkages containing both small nasal links and small maxilla links produce linkage mechanics that are higher than those found in any wrasse anterior-jaw link measured.

Finally, we could not reject the hypothesis that labrid anterior-jaw diversification is mechanically constrained due to the necessity of all of the linkages adding up to the fixed link. This functionally necessary length of the nasal + maxilla + lower jaw mechanically limits how relatively small the links in anterior jaws can evolve to be and still produce viable four-bar linkages. No linkages are shorter than this limit. However, it appears that the actual linkages are very close morphologically to this limit. Therefore, it may be that this hard mechanical limit greatly influences how anterior jaws are diversifying in this clade.

(d) *Disparity*

One of the clearest results from this analysis was that there is a nonlinear relationship between KT and the relative size of different skeletal elements in the anterior-jaw four-bar linkage (figure 3). The nonlinear relationship of KT and linkage morphology could conceivably be offset by the input of force and motion from muscles, examining more complicated outputs of this lever system, such as increase in mouth gape, or the connections of these mechanical outputs to those of other lever systems and mor-

phology. However, we think incorporating the mechanics of these more complicated or separate functional components into this type of analysis would probably only make the relationship between mechanics and morphology more nonlinear. The nonlinear relationship of morphology to mechanics is also apparent in the lack of congruence among species diversity, morphological disparity and mechanical disparity in anterior jaws. If mechanics mapped one-to-one onto morphology, each cube of morphospace should have the same amount of variance in maxillary rotation. In contrast to being similar, the variance in maxillary rotation in the equivalent cubes of morphospace varied over nearly an order of magnitude (figure 4). This variation may be dependent in part on the size of the cubes, but would probably only become greater as the cubes were made smaller. One advantage of using this type of morphospace is that the scale on which species differ in morphospace could be used as the scale in which one looked for variation in mechanical variance. Finally, it would be interesting to know if this discordance between morphospace occupation and mechanics exists in many biomechanical systems.

There was also no relationship detected between the morphological variance of putatively monophyletic groups and KT variance. This result was obtained despite examining structural variance in the three traits that have a direct effect on KT. The nonlinearity of KT production undoubtedly was the cause of this lack of congruence. This indicates that even when morphology is known to have direct mechanical consequences, assuming a linear relationship between it and ecological function can be inappropriate. Furthermore, because the mechanics of these linkages are strongly indicative of the feeding ecology in wrasses (Westneat 1995), the variation in mechanics probably reflects elements of ecological diversity that neither species richness nor morphological diversity would accurately represent. This incongruity between morphological disparity and mechanical disparity should provide a cautionary note to studies that make conclusions on the basis of comparisons of disparity in morphology. Without an explicit interpretation of the consequences of per unit change in morphology, conclusions drawn from morphological measures may be equally or perhaps more misleading than simple measures of species richness.

Comparisons between traditional morphospaces are often difficult to make because the number of potential morphological measurements that can be produced is virtually infinite and because the comparisons in space frequently depend on measurements made on homologous points (Gould 1991). Nevertheless, simply revelling in the multidimensionality and idiosyncratic nature of the morphology found in different types of organism will not provide a common framework in which to examine morphological or functional disparity. It may seem obvious that the infusion of biomechanics into the study of morphospace could provide extensive insight into why organisms are distributed as they are in morphospace. However, studies that explicitly examine biomechanically relevant morphospace are rare. However, it is becoming increasingly evident that simple biomechanical models can be used to explain a huge amount of the ecologically relevant mechanical variation in the morphology of organisms. If understanding the differential filling of morphospace is

vital to comprehending life on Earth (Vermeij 1987), then explicitly biomechanical morphospaces could provide the framework to compare and mechanically understand the structural variety of systems as seemingly disparate as the limb joints of mammals and the jaws of fish.

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APPENDIX A: NUMBER OF INDIVIDUALS QUANTIFIED AND SPECIES' KINEMATIC TRANSMISSION

If there were more than or less than three individuals measured for each species, the number of individual anterior jaws quantified is indicated using a superscript after the species name.

Anampses caeruleopunctatus (0.43), *Anampses geographicus*⁴ (0.50), *Anampses meleagrides*² (0.39), *Anampses melanurus* (0.37), *Anampses neoguinaicus* (0.52), *Bodianus anthioides*⁴ (0.69), *Bodianus axillaris* (0.79), *Bodianus diana* (0.79), *Bodianus loxozonus*⁴ (0.70), *Bodianus mesothorax* (0.76), *Bodianus perditio*¹ (0.90), *Cheilinus chlorourus* (0.90), *Cheilinus fasciatus* (0.70), *Cheilio inermis* (0.51), *Cheilinus oxycephalus*² (0.80), *Cheilinus trilobatus* (0.74), *Cheilinus undulatus* (0.66), *Chlorurus sordidus*² (0.63), *Choerodon anchorago* (0.59), *Choerodon cephalotoes* (0.54), *Choerodon cyanodus* (0.65), *Choerodon fasciatus* (0.74), *Choerodon graphicus* (0.62), *Choerodon jordani* (0.50), *Choerodon schoenleinii* (0.64), *Choerodon sugillatum* (0.54), *Choerodon venustus* (0.52), *Choerodon vitta* (0.51), *Cirrhilabrus condei*¹ (0.95), *Cirrhilabrus cyanoptera* (0.89), *Cirrhilabrus exquisitus* (0.87), *Cirrhilabrus laboutei* (0.81), *Cirrhilabrus lineatus* (0.73), *Cirrhilabrus punctatus*² (0.83), *Cirrhilabrus scottorum* (1.04), *Coris aurilineata* (0.67), *Coris aygula*² (0.55), *Coris batuensis* (0.71), *Coris dorsomaculata* (0.80), *Coris gaimard* (0.77), *Coris pictoides* (0.67), *Cymolutes praetextatus*² (0.76), *Cymolutes torquatus*⁴ (1.08), *Diproctacanthus xanthurus*⁵ (0.70), *Gomphosus varius* (1.01), *Halichoeres biocellatus* (0.77), *Halichoeres chloropterus* (0.73), *Halichoeres chrysus* (0.65), *Halichoeres hartzfeldii* (0.68), *Halichoeres hortulanus*⁴ (0.85), *Halichoeres margaritaceus* (0.68), *Halichoeres marginatus*² (0.76), *Halichoeres melanurus*² (0.64), *Halichoeres melasmapomus*² (0.88), *Halichoeres miniatus* (0.73), *Halichoeres nebulosus*² (0.62), *Halichoeres nigrescens* (0.90), *Halichoeres ornatissimus* (0.75), *Halichoeres prosopion* (0.67), *Halichoeres scapularis* (0.80), *Halichoeres trimaculatus* (0.79), *Hemigymnus fasciatus* (0.84), *Hemigymnus melapterus* (0.59), *Hologymnosus annulatus*⁴ (0.72), *Hologymnosus doliatus*¹ (0.36), *Labrichthys unilineatus* (0.61), *Labroides bicolor* (0.47), *Labroides dimidiatus* (0.50), *Labroides pectoralis*² (0.44), *Labropsis australis* (0.45), *Labropsis xanthonota* (0.49), *Leptojulius cyanopleura* (0.74), *Macropharyngodon choati* (0.78),

Macropharyngodon kuiteri (0.87), *Macropharyngodon meleagris*⁴ (0.63), *Macropharyngodon negrosensis* (0.71), *Novaculichthys taeniorus* (0.74), *Oxycheilinus bimaculatus* (0.53), *Oxycheilinus digrammus* (0.50), *Oxycheilinus unifasciatus* (0.65), *Pseudocheilinus evanidus* (0.63), *Pseudocheilinus hexataenia* (1.06), *Pseudocheilinus octotaenia* (0.66), *Pseudocoris yamashiroi* (0.61), *Pseudodax moluccanus*¹ (0.89), *Pseudojuloides cerasinus*⁴ (0.73), *Pseudolabrus guentheri* (0.68), *Pteragogus cryptus* (0.74), *Pteragogus emneacanthus*² (0.60), *Stethojulis bandanensis* (0.66), *Stethojulis interrupta*¹ (0.67), *Stethojulis strigiventor*² (0.47), *Stethojulis trilineata* (0.88), *Thalassoma amblycephalum* (0.67), *Thalassoma hardwicke* (0.92), *Thalassoma janseni* (0.97), *Thalassoma lunare* (0.84), *Thalassoma lutescens*² (0.61), *Thalassoma quiquevittatum* (0.70), *Thalassoma trilobatum*² (0.65), *Wetmorella nigropinnata* (0.92), *Xyrichtys aneitensis*² (0.83), *Xyrichtys pavo* (0.63), *Xiphocheilus typus* (0.40).

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