Cichlid jaw mechanics: linking morphology to feeding specialization

C. D. HULSEY*†‡ and F. J. GARCÍA DE LEÓN§¶

**Ecology and Evolutionary Biology, University of Tennessee – Knoxville, 569 Dabney, Hall, Knoxville, TN 37996, USA, ‡Center for Population Biology, University of California – Davis, One Shields Ave, Davis CA 95616, USA, §Laboratorio de Biología Integrativa, Instituto Tecnológico de Cuidad Victoria (ITCV), Cuidad Victoria, Tamaulipas, México, and ¶Centro de Investigaciones Biológicas del Noreste, Program of Conservation and Environmental Planning, La Paz, BCS, México*

Summary

1. The utility of the anterior jaw four-bar linkage model and the trophic consequences of jaw protrusion were investigated in Heroine cichlids by examining the evolutionary relationships among maxillary kinematic transmission (KT), maximum jaw protrusion and dietary specialization on evasive prey.

2. In 31 species of Heroine cichlids, a four-bar linkage model was used to generate kinematic predictions of maxillary KT, the angular amount of maxilla rotation per unit lower jaw rotation, expected during mouth opening. Maxillary KT averaged 0·79 and ranged from 0·58 in *Herichthys tamasopoensis* to 1·06 in *Petenia splendida*.

3. Because the maxilla pushes the toothed premaxilla out during jaw protrusion, we predicted higher maxillary KT should characterize species with greater maximum jaw protrusion. Maximum jaw protrusion ranged from 1·5 to 14·2% of cichlid standard length and was highly correlated with greater maxillary KT.

4. The proportion of fish and crustaceans in the diet of these cichlids was correlated with maximum protrusion, suggesting jaw protrusion may aid in the capture of evasive prey.

5. Phylogenetic independent contrasts indicate changes in anterior jaw mechanics may be necessary for diversification of cichlid jaw protrusion abilities, and the labile evolution of jaw protrusion in Heroine cichlids likely facilitated the repeated specialization on evasive prey during their diversification.

Key-words: Biomechanics, ecomorphology, functional morphology, prey capture, trophic specialization

Introduction

Cichlid diversity in jaw morphology is extensive (Fryer & Iles 1972; Liem 1973), and the variety of feeding modes in these fishes may be unparalleled (Liem 1980; Kaufman, Chapman & Chapman 1997). Yet, how cichlid jaw structure explicitly translates into quantitative differences in mechanics, function and feeding specialization has rarely been assessed. To examine a potential link between cichlid trophic morphology and ecology, we determined if anterior jaw linkage mechanics predict maximum jaw protrusion and if protrusion predicts evasive prey specialization in Heroine cichlids.

Modelling components of the skull as discreet mechanical systems can provide insight into how trophic structure translates into functional and ecological diversity (Westneat 1990; Hulsey & Wainwright 2002; Alfaro, Bolnick & Wainwright 2004; Wainwright *et al.* 2004). Although simple lever systems are integral to the trophic apparatus of all vertebrates, several more complicated levers that function as 'four-bar linkages' may operate during fish feeding. In vertebrates ranging from coelecanths to parrotfish, many ring-like and largely planar musculoskeletal systems with three or more moving components probably function as four-bar linkages (Muller 1987). The hyoid (Muller 1987; Westneat 1990; de Visser & Barel 1996), opercular apparatus (Muller 1987) and anterior jaw system (Westneat 1990, 1994, 1995) can all be modelled as four-bar linkages. However, the anterior jaw four-bar linkage and its evolutionary relationship to feeding abilities have not been examined in any fish group outside the Labridae, including cichlids.

If the four-bar model effectively captures jaw mechanics, changes in the anterior jaw linkage are predicted

†Author to whom correspondence should be addressed: Darrin Hulsey, School of Biology, Georgia Tech, 310 Ferst Drive, Atlanta GA 30332-0230, USA. E-mail: dh251@mail.gatech.edu

to influence cichlid jaw protrusion abilities (Westneat 1990). Mechanically, this linkage predicts how motion input through the lower jaw is transmitted to the maxilla (Westneat 1990; Hulsey & Wainwright 2002). This in turn should influence how the maxilla pushes out the premaxilla during jaw protrusion (Lauder 1982). Therefore, it is predicted that species with linkages exhibiting higher maxillary kinematic transmission (KT), or greater maxillary rotation per unit lower jaw rotation, should possess increased ability to protrude the upper jaw.

However, even if greater maxillary KT were correlated with more extensive jaw protrusion, it would remain unclear what the function of greater jaw protrusion generally is in cichlids. Protrusion may increase the velocity of a cichlid attacking prey (Gibb 1997; Waltzek & Wainwright 2003), adapt feeding movements to the position of escaping prey (Motta 1984; Coughlin & Strickler 1990) or increase the distance from which prey can be sucked into the mouth (Van-Leeuwen & Muller 1984; Ferry-Graham *et al.* 2001; Wainwright *et al.* 2001). Yet, one similar consequence of these functional advantages is that the evolution of greater protrusion may allow predators to capture more 'evasive' prey. Compared with other prey types, fish and crustaceans may generally have enhanced abilities to evasively manoeuvre or rapidly escape a predatory cichlid. By quantifying maximum protrusion and the dietary contribution of fish and crustaceans in many cichlids for which a phylogeny is available, we could test if species

with more protractile jaws generally evolve greater specialization on putatively evasive prey.

It would be ideal to examine these phylogenetic correlations in a cichlid group exhibiting extensive variation in both diet and jaw protrusion abilities. Although many studies of cichlid trophic diversity have concentrated on African Rift Lake fish (Greenwood 1964; Fryer & Iles 1972), Neotropical cichlids have also undergone substantial trophic diversification (Myers 1966; Stiassny 1991; Winemiller, Kelso-Winemiller & Brenkert 1995). In the Neotropics, the most trophically diverse cichlid group is the Heroines (Hulsey *et al.* 2004). In this group of mostly Central American fish (Martin & Bermingham 1998; Hulsey *et al.* 2004), specialization upon prey as functionally disparate as shrimp and molluscs has evolved multiple times, and greater jaw protrusion may favour the capture of evasive prey such as fish or crustaceans (Eaton 1943; Waltzek & Wainwright 2003). Therefore, the Heroines provide an ideal comparative system to examine phylogenetically independent correlations among these trophic characters.

The evolutionary correlations among maxillary KT, maximum jaw protrusion and specialization on evasive prey were examined in Heroine cichlids. The anterior jaws of 31 cichlid species were first modelled as four-bar linkages, and the maxillary KT estimated. Then, the maximum protrusion each species exhibits was assessed, and the hypothesis that maxillary KT was correlated with greater jaw protrusion was tested using independent contrasts. After determining the contribution of evasive prey to the diet for these cichlids, we determined whether jaw protrusion was correlated, independent of phylogeny, with the inclusion of evasive prey in the diet.

Materials and methods

ANTERIOR JAW KT AND MAXIMUM PROTRUSION

A combination of specimens collected in Central America by the authors from locales reported in Hulsey *et al.* (2004) and museum specimens were used in the quantification of morphology. All species were collected from their native range, preserved in formalin, and then transferred to 70% ethanol. Once preserved, standard length of the fish was measured using callipers. Approximately three specimens of each of the 31 species examined (Table 1) were cleared using trypsin and double-stained using an alcian-blue cartilage stain and alizarin red bone stain (Dinkerhus & Uhler 1977). In cleared and stained specimens, the bones are clearly discernible for morphological measurements and the articulations of the skull are retained. These specimens were used to measure anterior jaw four-bar linkage morphology and maximum protrusion.

The four physical links of the cichlid oral jaw that can be modelled as the anterior jaw four-bar linkage system (Westneat 1990) were first measured (Fig. 1). The morphology underlying this linkage is described in
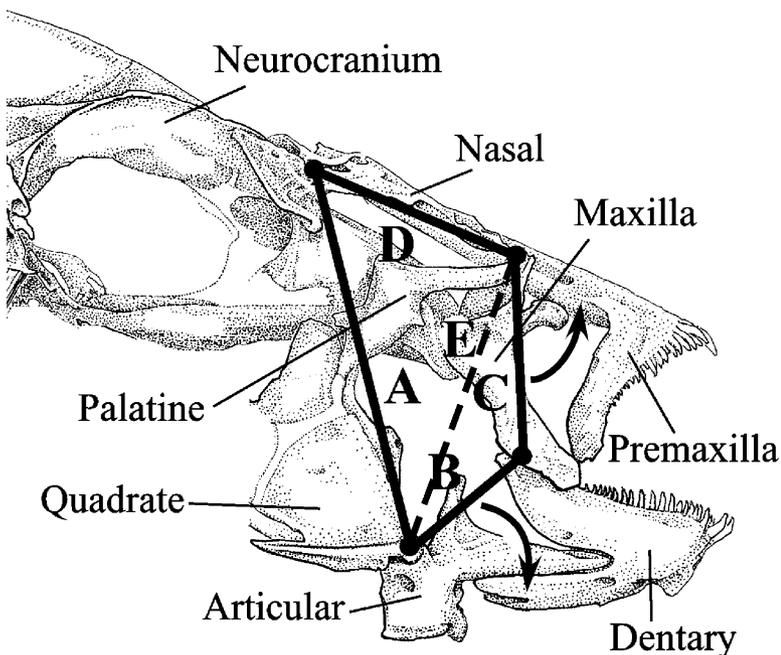

Fig. 1. The anterior jaw of a generalized Heroine shown with the oral jaw half protruded. The bones of the skulls posited to be important in generating maxillary kinematic transmission (KT) and maximum jaw protrusion are diagrammed. The fixed length (A), lower jaw length (B), the maxilla link (C), the coupler link (D) and the diagonal (E) between the nasal/maxilla attachment and the point where the articular rotates on the quadrate are shown. The maxillary (KT) of the linkage was calculated by dividing the maxillary (output) rotation of the linkage by the lower jaw (input) rotation.

Table 1. The number of individuals of species examined for morphology *n*, the average specimen standard length (SL), maximum protrusion (MP) distance, four-bar link measurements as well as their percentage of the fixed length, and estimated maxillary KT for 31 Heroine cichlids

Species	*n*	SL (mm)	MP (mm)	Fixed link (mm)	Nasal link (mm) (% fixed)	Maxilla link (mm) (% fixed)	Lower jaw link (mm) (% fixed)	KT
Archocentrus centrarchus	4	80·5	4·2	10·1	4·6 (0·50)	5·4 (0·54)	4·6 (0·45)	0·83
Archocentrus nigrofasciatus	3	59·4	2·5	6·8	3·7 (0·55)	3·3 (0·48)	2·6 (0·38)	0·78
Archocentrus septemfasciatus	2	66·2	2·3	7·3	4·1 (0·57)	3·2 (0·44)	2·6 (0·35)	0·70
Astatheros alfari	2	86·7	5·5	14·0	7·5 (0·53)	7·3 (0·52)	5·2 (0·37)	0·71
Astatheros macracanthus	3	83·9	3·8	10·3	5·7 (0·56)	6·1 (0·60)	3·8 (0·37)	0·62
Astatheros robertsoni	3	86·7	5·4	11·9	6·6 (0·56)	6·2 (0·52)	4·8 (0·40)	0·78
Caquetaia kraussii	3	75·0	8·5	13·0	4·6 (0·36)	6·7 (0·52)	6·6 (0·51)	0·96
Cichlasoma octofasciatum	4	75·8	3·3	9·7	4·3 (0·44)	5·4 (0·56)	3·7 (0·38)	0·71
Cichlasoma salvini	3	71·8	5·9	9·6	4·3 (0·45)	5·1 (0·53)	4·6 (0·48)	0·90
Cichlasoma trimaculatum	3	74·7	5·1	10·2	4·7 (0·46)	5·4 (0·53)	4·8 (0·47)	0·83
Cichlasoma uropthalmum	3	84·4	5·1	11·5	5·9 (0·51)	6·5 (0·56)	4·3 (0·37)	0·68
Herichthys bartoni	4	81·9	2·4	12·4	6·5 (0·53)	7·6 (0·61)	5·3 (0·42)	0·68
Herichthys cyanoguttatus	3	88·1	4·3	13·6	6·9 (0·51)	7·4 (0·54)	5·4 (0·40)	0·73
Herichthys labridens C	3	77·6	3·9	11·1	5·8 (0·53)	5·5 (0·50)	4·3 (0·39)	0·79
Herichthys labridens ML	3	81·6	3·7	13·1	6·9 (0·53)	6·8 (0·52)	4·7 (0·36)	0·71
Herichthys pantostictus	1	76·8	3·4	12·6	6·5 (0·52)	6·7 (0·53)	5·1 (0·40)	0·76
Herichthys tamasopoensis	3	89·8	1·3	13·0	6·5 (0·50)	7·1 (0·54)	4·1 (0·31)	0·58
Herotilapia multispinosa	2	80·4	2·8	9·0	4·8 (0·53)	5·6 (0·63)	3·2 (0·35)	0·65
Hypsophrys nicaraguensis	2	103·8	3·9	12·4	7·7 (0·62)	5·7 (0·46)	4·3 (0·34)	0·75
Nandopsis managuense	1	116·0	8·0	12·2	4·5 (0·37)	6·8 (0·56)	5·6 (0·46)	0·79
Parachromis dovii	3	59·8	5·9	10·0	4·0 (0·40)	5·9 (0·58)	4·9 (0·49)	0·78
Parachromis loisellei	1	77·5	6·5	7·8	3·5 (0·45)	5·0 (0·64)	4·3 (0·55)	0·84
Paraneetroplus bulleri	3	98·2	3·5	10·1	6·0 (0·59)	5·1 (0·50)	3·8 (0·37)	0·74
Paratheraps fenestratus	3	107·3	4·4	12·7	6·6 (0·52)	7·0 (0·55)	5·0 (0·39)	0·73
Paratheraps guttulatus	3	94·1	4·2	11·5	5·5 (0·48)	5·3 (0·46)	3·9 (0·34)	0·76
Petenia splendida	3	99·7	14·2	17·1	6·7 (0·39)	9·0 (0·53)	10·5 (0·61)	1·06
Thorichthys callolepis	3	84·3	5·1	9·7	5·5 (0·57)	4·6 (0·48)	3·8 (0·39)	0·83
Thorichthys ellioti	3	95·6	5·5	12·8	6·8 (0·53)	6·0 (0·47)	4·7 (0·36)	0·76
Thorichthys helleri	3	82·2	4·4	10·2	5·6 (0·54)	5·6 (0·55)	4·4 (0·43)	0·79
Thorichthys meeki	1	82·0	4·9	9·2	5·5 (0·60)	4·5 (0·49)	3·3 (0·36)	0·73
Vieja maculicauda	3	73·1	3·5	8·4	4·5 (0·53)	4·2 (0·50)	3·0 (0·36)	0·73

more detail elsewhere (Westneat 1990, 1995; Wainwright *et al*. 2004), but the critical elements are described below. The distance from where the nasal attaches to the neurocranium down to the coronoid process was measured as the fixed link (A). As in all four-bar linkages, the fixed link is assumed to be immobile. The lower jaw rotates on this fixed link thereby serving as the input link (B) that transmits motion into the system. The lower jaw link was measured from the base of the coronoid process, the joint where the articular rotates on the quadrate, to the ligamentous attachment of the maxilla on the dentary. In all these cichlids, the articular is fused to the dentary. We then determined the distance between this attachment site of of the maxilla on the dentary and the ligamentous connection of the nasal on the head of the maxilla. This was used as the relevant length of the maxilla (C), the output link in the four-bar linkage. Unlike the original description of the anterior jaw linkage (Westneat 1990) the length of the nasal was measured as the link coupling the maxilla to the neurocranium (D). Westneat (1990) originally described the anterior jaw linkage using the palatine as the coupler link. However, in most Heroine cichlids (C. D. Hulsey, unpublished observation) and in most wrasses (Wainwright *et al*. 2004) the

palatine is immobile. Therefore, the nasal serves to couple the motion of the lower jaw to the motion of the maxilla as these three mobile elements swivel in a ring-like configuration around the fixed link. The links were measured to the nearest 0·1 mm with callipers. Because the fixed link is immobile, is generally highly correlated with SL, and offers a mechanically relevant measure for factoring out size from the linkage (Hulsey & Wainwright 2002), the other links were also presented as a ratio of their fixed link. This ratio allows the size-adjusted estimates of the mobile link lengths to be readily compared.

A four-bar linkage has only one degree of freedom during movement if the links are coplanar (Muller 1987). As the bodies of most of the cichlids examined are laterally compressed, this is a reasonable approximation. All angles in the linkage should be defined if the initial angular relationship between the lower jaw and the fixed link, or starting angle, is set. For each individual, a starting angle of 15° was determined by iteratively estimating the diagonal distance (E) from the location where the nasal attaches on the maxilla to the site where the lower jaw link meets the fixed link at the coronoid process (Fig. 1). This diagonal was not measured empirically because of extreme variability obtained when estimating it on cleared and stained

specimens. When the diagonal separating the linkage into two triangles was defined, this allowed all of the angular relationships between the links including the starting angle to be determined exactly from the law of cosines:

$$\text{Cos (angle)} = (A^2 + B^2 - E^2)/(2AB).$$

An input angle of 30° was modelled as the relevant rotation of the lower jaw. Although Heroines probably vary extensively in the amount of lower jaw rotation (Waltzek & Wainwright 2003), 30° was used here. There are also other kinematic outputs of the anterior jaw. However, we examine only maxillary rotation as it should be most relevant for predicting maximum jaw protrusion. After defining the size of the physical links, the starting angle and the input angle, we summarized the mechanical properties of each linkage by the kinematic transmission (KT) (Muller 1987). First, the angular rotation of the output link from the four-bar linkage model was calculated. Then, the output rotation was divided by the input rotation of 30° to determine maxillary KT. With higher predicted maxillary KT, there should be greater amounts of motion transmitted from the lower jaw to the maxilla.

To determine maximum jaw protrusion for each specimen, we first measured the distance from the most posterior point of the eye to the anterior tip of the central tooth on the premaxilla when the jaws were completely closed (Fig. 2). Then, we pulled the jaws open to their maximally protruded state with forceps. The same measurements of distance from the eye to the tip of the premaxillary tooth were then made. These two measurements were subtracted from one another to estimate maximum jaw protrusion for each specimen. The average maxillary KT and maximum protrusion for a given species were used in all comparative analyses.

DIET

We obtained information regarding the percent volumetric contribution of fish and crustaceans to the diet of 31 Heroine cichlids (Table 1). This percentage was used as the contribution of evasive prey (Westneat 1995) to the diet. For 22 of the species, we were able to extract the percentage of evasive prey, the total percentage of fish and crustaceans added together, from published sources. However, for five of these species, only the frequency of occurrence of prey was reported (Chavez-Lomeli, Mattheeuws & Perez-Vega 1988). For these five cichlid species, the percent volumetric contribution of evasive prey was estimated by transforming the frequency of occurrence into an approximation of the volumetric contribution (C. D. Hulsey, unpublished data).

For 10 other species, we quantified the volumetric contribution of evasive prey to the diet in approximately 10 individuals per species (*Astatheros macracanthus* $n = 5$; *Herichthys bartoni* $n = 10$; *H. labridens* C $n = 10$; *H. labridens* ML $n = 6$; *H. tamasopoensis* $n = 10$; *Paraneetroplus bulleri* $n = 10$; *Paratheraps guttulatus* $n = 10$; *Thorichthys callolepis* $n = 9$; *T. ellioi* $n = 10$; *T. helleri* $n = 10$). These gut contents were examined from cichlids collected from the localities reported in Hulsey *et al*. (2004). The volumetric contribution was measured using water displacement, and diet items were identified as fish and crustaceans or other. For analyses, gut contents were simply categorized as the percent contribution of evasive prey (fish + crustaceans) to the total gut volume. For all comparisons of evasive prey to mechanics, arcsin transformations of the percentage of evasive prey were used.

COMPARATIVE ANALYSES

Correlations of maxillary KT, maximum protrusion and evasive prey consumption were examined in a phylogenetic context. Because KT values are size independent (Muller 1987) and approximated a normal distribution, they were not transformed. However, as most structural elements change considerably with size, maximum protrusion was adjusted by standard length. The residuals of a reduced major axis (RMA)
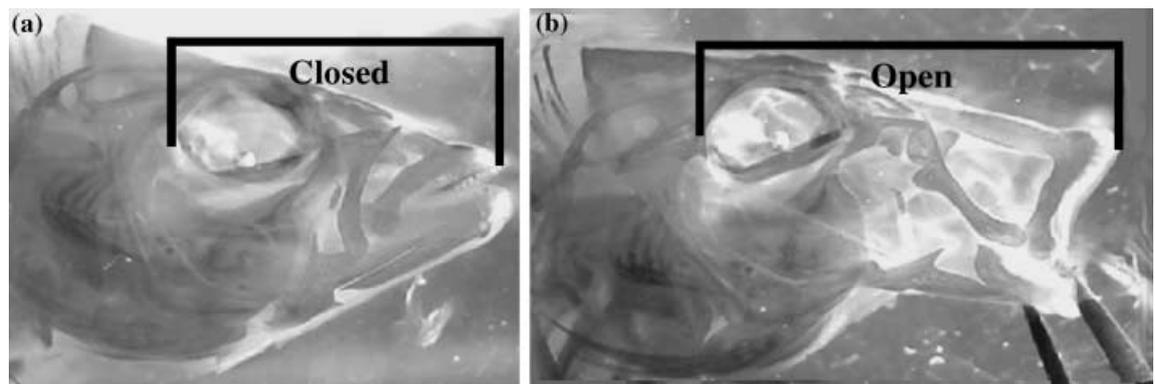
Fig. 2. Cleared and stained *Parachromis dovii* oral jaws shown in (a) unprotruded and (b) protruded state. Prortrusion was estimated using two measures of the linear distance behind the eye to the tip of the anterior tooth on the premaxilla. This linear distance was measured with the jaws forced to be closed (a) and the jaws forced to be fully extended (b) with forceps. Maximum jaw protrusion was the difference in the linear distance when the jaws were closed minus the length when the jaws were fully extended.

regression between standard length and maximum protrusion were used in all correlations. Although we could not accurately estimate intraspecific variation because of our limited within-species sampling, we assumed the variation in specimen standard length and protrusion was equal for the RMA regression.

Correlations among species values may not be statistically independent owing to shared evolutionary history (Felsenstein 1985). Therefore, we examined phylogenetically independent contrast correlations between the trophic variables. For the phylogenetic backbone of these analyses, we used the phylogeny in Hulsey *et al*. (2004) based on sequences of the cytochrome *b* gene. For the independent contrasts, the phylogenetic topology with branch lengths was first imported into the program Tree Edit 1·0 (Rambaut & Charleston 2002). The raw branch lengths in the topology were then smoothed using non-parametric rate smoothing (Sanderson 1997) because there was substantial heterogeneity in the branch lengths owing to non-clock-like molecular evolution (Hulsey *et al*. 2004). Then, for the species in the original phylogeny that were not examined here and for all but one individual per species that was examined (GenBank accession numbers available from the author), the sequences were pruned from the topology. The branch lengths and topology for the species remaining in the tree were then exported into CAIC (Purvis & Rambaut 1995). Using the crunch algorithm, which assumes both variables are continuous, the correlations among independent contrasts of anterior jaw KT and maximum protrusion residuals as well as the correlation between maximum protrusion residuals and percent contribution of evasive prey were examined.

Results

ANTERIOR JAW KT AND MAXIMUM PROTRUSION

The relative length of the morphological elements of the four-bar linkage varied considerably among species (Table 1). The KT in the Heroines species examined was lowest in *Herichthys tamasopoensis* (0·58) and highest in *Petenia splendida* (1·06). The mean anterior jaw KT was 0·79. The variation in jaw protrusion was also extensive. *Petenia splendida* displayed the greatest jaw protrusion of any species examined, 14·2% of its standard length. The average protrusion distance for the Heroine cichlids examined was 5·9% of their standard length. *Herichthys tamasopoensis* had the least amount of protrusion ability at 1·5% of its standard length.

DIET

The amount of evasive prey included in the diet was highly labile across the Heroine phylogeny (Table 1). Both fish and crustaceans constituted over 50% of the gut volume in several cichlid species. Several species
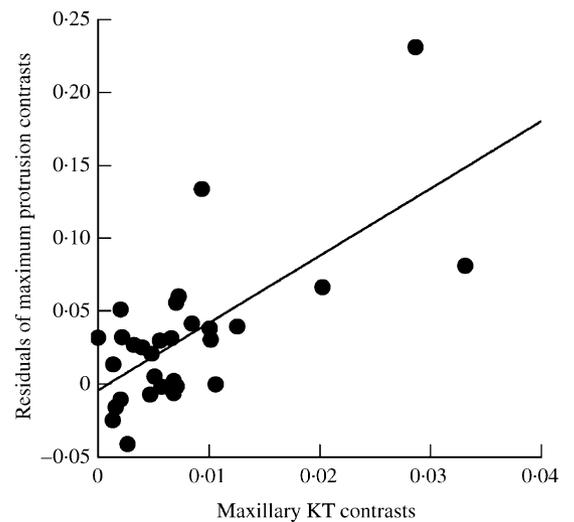

Fig. 3. Because the maxilla helps to push the premaxilla anteriorly during jaw protrusion, higher maxillary KT should be correlated with greater jaw protrusion. The relationship between maxillary KT contrasts and maximum jaw protrusion contrasts in the Heroines cichlids was significant ($r = 0.45$, and $P = 0.012$).

included little or no evasive prey in the diet, and *Petenia splendida* had the diet composed of the greatest percentage of evasive prey, 96%.

COMPARATIVE ANALYSES

After phylogenetic correction, higher maxillary KT was correlated with greater maximum protrusion residuals (df = 30, slope = 1·4, $r = 0.45$ and $P = 0.012$; Fig. 3). Likewise, the independent contrasts of protrusion residuals were significantly correlated with contrasts of percentage evasive prey in the diet (df = 30, slope = 0·2, $r = 0.37$ and $P = 0.036$).

Discussion

In Heroine cichlids, anterior jaw morphology, four-bar linkage mechanics, jaw protrusion and this group's repeated specialization on evasive prey appear to have been coupled during evolution. The nasal, maxilla and lower jaw links all changed substantially during Heroine diversification, and this morphological divergence clearly has mechanical consequences (Westneat 1990). Heroine KT ranged from 0·58 to 1·06, and this variation in linkage mechanics was probably important in Heroine trophic diversification as maxillary rotation is critical in determining the extent to which the jaws can be maximally protruded (Westneat & Wainwright 1989; Westneat 1990).

Higher Heroine maxillary KT was significantly correlated with the evolution of greater jaw protrusion (Fig. 3). Examination of the two Heroine species with the most extreme values for both trophic characters makes the relationship of KT to maximum jaw protrusion readily apparent. *Herichthys tamasopoensis* exhibited the least and *Petenia splendida* had the greatest maxillary KT predicted from the anterior jaw linkage

model. Accordingly, for the Heroines examined, maximum jaw protrusion ranged from a low of 1·5% of standard length in *H. tamasopoensis* to a high of 14·2% of standard length in *P. splendida*. The maxillary KT diversity recovered suggests that an approximate doubling of maxillary rotation per unit lower jaw rotation has facilitated the substantial variation in Heroine jaw protrusion. Although modifications of the *adductor arcus palatini* muscle (Ferry-Graham *et al.* 2001), cranial elevation (Ferry-Graham *et al.* 2001; Waltzek & Wainwright 2003) and other linkages such as the hyoid (Westneat & Wainwright 1989; Westneat 1991; de Visser & Barel 1998) could also influence jaw protrusibility,

the anterior jaw linkage was likely critical in the evolution of both more protractile jaws and the utilization of evasive prey in Heroine cichlids.

Jaw protrusion is evolutionarily correlated with feeding on fish and crustaceans in Heroines (Fig. 4). At one extreme, *Petenia splendida*, with its extensive ability to protrude its jaws, exhibits a diet composed of 96% fish (Chavez-Lomeli, Mattheeuws & Perez-Vega 1988). Alternatively, Heroines with much less jaw protrusion rarely feed on evasive prey (Table 1). Most of these species forcefully scrape algae, tear plant material or pull sessile invertebrates off the substrate. These trophic habits proabably demand structural modifications of the oral jaw that trade-off with the capabilities conferred by highly protrusible jaws (Westneat 1994; Wainwright *et al.* 2004). Cichlid species possessing jaws modified for force production are unlikely to make effective use of extensively protrusible jaws when capturing prey.

However, jaw protrusion in many cichlids probably aids in prey capture through increasing attack velocity, enhancing the accuracy of predatory attacks or augmenting the efficiency of a suction feeding strikes (Waltzek & Wainwright 2003). If it could be shown that live cichlids preferentially use their maximum protrusion abilities to capture more evasive prey, it would further corroborate our results. Suggestively, *P. splendida* does exhibit more jaw protrusion when feeding on *Poecilia reticulata*, a fish, as compared with feeding on *Artemia* sp., a slow swimming brine shrimp (Wainwright *et al.* 2001). However, this experimental comparison points out a potential weakness of our analyses. Because we would have classified both of these prey types as evasive, there is an obvious need to refine the classification of prey types according to more quantitative estimates of escape abilities. Furthermore, not all cichlids with extensive jaw protrusion specialize on what we categorized as evasive prey (Table 1). For example, *Astatheros robertsoni* and *Thorichthys meeki* display substantial jaw protrusion but consume mostly detritus, molluscs and insects (Chavez-Lomeli, Mattheeuws & Perez-Vega 1988). In these species, the jaws protrude subterminally, and protrusion may have other important functions such as allowing these species to exploit benthic prey while maintaining their body in a horizontal position. Nevertheless, the phylogenetically independent correlation between maximum protrusion and consumption of fish and crustaceans for approximately 30% of the extant Heroine species (Hulsey *et al.* 2004) suggests more protractile jaws have probably generally evolved in this group to enhance the ability to capture evasive prey.

The evolution of more protrusible jaws is one of the major axes along which trophic diversification in bony fishes has occurred (Schaeffer & Rosen 1961; Lauder 1982). However, in order to understand why the evolution of jaw protrusion is such a major theme in the evolution of cichlids and other fishes, we must understand the mechanical attributes that make variation in
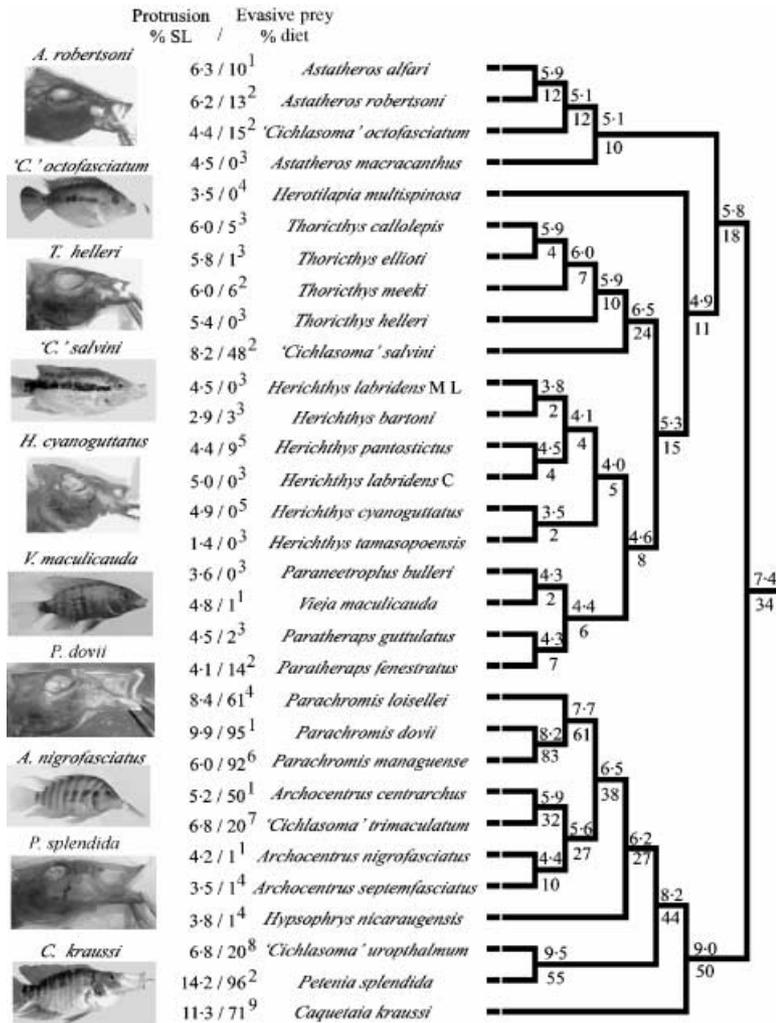

Fig. 4. The phylogenetic relationships among the Heroines examined as well as the evolution of maximum protrusion and evasive prey use. Several fish species representing the diversity in Heroine jaw protrusion are depicted. Maximum jaw protrusion as a percentage of SL and the percentage of evasive prey in the diet are given to the left of individual species names. The sources of the diet data for each species are given as a superscript to the percentage (1 = Winemiller, Kelso-Winemiller & Brenkert 1995; 2 = Chavez-Lomeli, Mattheeuws & Perez-Vega 1988; 3 = this study; 4 = Bussing 1993; 5 = Darnell 1962; 6 = Gestring & Shafland 1997; 7 = Yanez-Arancibia 1978; 8 = Martinez-Palacios & Ross 1988; 9 = Winemiller 1989). Ancestral reconstructions from squared changes parsimony that can be used to generate independent contrasts are depicted above (reconstructed maximum jaw protrusion as a percentage of SL) and below (reconstructed percentage of evasive prey in the diet) nodes. Greater maximum jaw protrusion was evolutionarily correlated with the percentage of evasive prey in the diet ($P = 0.036$) using independent contrasts.

jaw protrusion feasible as well as the ecological consequences of jaw protrusion that make this variation favourable. Testing how jaw mechanics, jaw function and their ecological consequences are linked may ultimately provide mechanistic connections among all of the phenotypic elements of cichlid trophic diversity.

Acknowledgements

References

Alfaro, M.E., Bolnick, D.I. & Wainwright, P.C. (2004) Evolutionary dynamics of complex biomechanical systems: an example using the four-bar mechanism. *Evolution* **58**, 495–203.

Bussing, W.A. (1993) Fish communities and environmental characteristics of a tropical rain forest river in Costa Rica. *Revista de Biología Tropical* **41**, 79–809.

Chavez-Lomeli, M.O., Mattheeuws, A.E. & Perez-Vega, M.H. (1988) Biología de los peces del río San Pedro en vista de determinar su potencial para la piscicultura. *Instituciónes Nacional Investigacíon Recursos Biología* **1**, 1–222.

Coughlin, D.J. & Strickler, J.R. (1990) Zooplankton capture by a coral reef fish: an adaptive response to evasive prey. *Environmental Biology of Fishes* **29**, 35–42.

Darnell, R.M. (1962) Fishes of the Rio Tamesi and related coastal lagoons in East-Central Mexico. *Publications of the Institute of Marine Science University of Texas* **8**, 299–365.

Dinkerhus, G. & Uhler, L.H. (1977) Enzyme clearing of Alcian bluestained whole vertebrates for demonstration of cartilage. *Staining Technologies* **52**, 229–232.

Eaton, T.H. (1943) An adaptive series of protractile jaws in cichlid fishes. *Journal of Morphology* **72**, 183–190.

Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist* **125**, 1–15.

Ferry-Graham, L.A., Wainwright, P.C. & Hulsey, C.D. & Bellwood, D.R. (2001) Evolution and mechanics of long jaws in butterflyfishes (family Chaetodontidae). *Journal of Morphology* **248**, 120–143.

Fryer, G. & Iles, T.D. (1972) *The Cichlid Fishes of the Great Lakes of Africa*. Oliver and Boyd, Edinburgh.

Gestring, K. & Shafland, P. (1997) Selected life history attributes of the exotic jaguar guapote (*Cichlasoma managuense*) in Florida. *Florida Scientist* **60**, 137–142.

Gibb, A.C. (1997) Do flatfish feed like other fishes? A comparative study of percomorph prey-capture kinematics. *Journal of Experimental Biology* **200**, 2841–2859.

Greenwood, P.H. (1964) Explosive speciation in African lakes. *Proceedings of the Royal Institute Great Britain* **40**, 256–269.

Hulsey, C.D. & Wainwright, P.C. (2002) Projecting mechanics into morphospace: disparity in the feeding system of labrid fishes. *Proceedings of the Royal Society B* **269**, 317–326.

Hulsey, C.D., Garcia de Leon, F.J., Sanchez-Johnson, Y., Hendrickson, D.A. & Near, T.J. (2004) Temporal diversification of Mesoamerican cichlid fishes across a major biogeographic boundary. *Molecular Phylogentics and Evolution* **31**, 754–764.

Kaufman, L.S., Chapman, L.J. & Chapman, C.A. (1997) Evolution in fast forward: haplochromine fishes of the Lake Victoria Region. *Endeavour* **21**, 23–30.

Lauder, G.V. (1982) Patterns of evolution in the feeding mechanism of actinopterygian fishes. *American Zoologist* **22**, 275–285.

Liem, K.F. (1973) Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Systematic Zoology* **22**, 425–441.

Liem, K.F. (1980) Adaptive significance of intra- and interspecific differences in the the feeding reperoires of cichlid fishes. *American Zoologist* **20**, 295–314.

Martin, A.P. & Bermingham, E. (1998) Systematics and evolution of Lower Central American cichlids inferred from analysis of cytochrome *b* gene sequences. *Molecular Phylogenetics and Evolution* **9**, 192–203.

Martinez-Palacios, C.A. & Ross, L.G. (1988) The feeding ecology of the Central American cichlid *Cichlasoma uropthalmus* (Gunther). *Journal of Fish Biology* **33**, 665–670.

Motta, P.J. (1984) Mechanics and functions of jaw protrusion in teleost fishes: a review. *Copeia* **1984**, 1–18.

Muller, M. (1987) Optimization principles applied to the mechanism of neurocranium levation and mouth bottom depression in bony fishes (Halecostomi). *Journal of Theoretical Biology* **126**, 343–368.

Myers, G.S. (1966) Derivation of the freshwater fish fauna of Central America. *Copeia* **1966**, 766–773.

Purvis, A. & Rambaut, A. (1995) Comparative analysis by independent contrasts (CAIC): an apple macintosh application for analysing comparative data. *Bioinformatics* **11**, 247–251.

Rambaut, A. & Charleston, M. (2002) TreeEdit. phylogenetic tree editor v. 1.0 alpha 10. http://evolve.zoo.ox.ac.uk/software/TreeEdit/main.html.

Sanderson, M.J. (1997) A nonparametric approach to estimating divergence times in the absence of rate constancy. *Molecular Biology and Evolution* **14**, 1218–1231.

Schaeffer, B. & Rosen, D.E. (1961) Major adaptive levels in the evolution of the Actinopterygian feeding mechanism. *American Zoologist* **1**, 187–204.

Stiassny, M.L.J. (1991) Phylogenetic relationships of the family Cichlidae: an overview. *Cichlid Fishes: Behavior, Ecology, and Evolution* (ed. M.H.A. Keenleyside), pp. 1–18. Chapman & Hall, London.

Van-Leeuwen, J.L. & Muller, M. (1984) Optimum sucking techniques for predatory fish. *Transactions of the Zoological Society of London* **37**, 137–170.

de Visser, J. & Barel, C.D.N. (1998) The expansion apparatus in fish heads, a 3-D kinetic deduction. *Netherlands Journal of Zoology* **48**, 361–395.

Wainwright, P.C., Ferry-Graham, L.A., Waltzek, T.B., Carroll, A.M., Hulsey, C.D. & Grubich, J.R. (2001) Evaluating the use of ram and suction during prey capture by cichlid fishes. *Journal of Experimental Biology* **204**, 3039–3051.

Wainwright, P.C., Bellwood, D.R., Westneat, M.W., Grubich, J.R. & Hoey, A.S. (2004) A functional morphospace for the skull of the labrid fishes: patterns of diversity in a complex biomechanical system. *Biological Journal of the Linnean Society* **82**, 1–25.

Waltzek, T.B. & Wainwright, P.C. (2003) Functional morphology of extreme jaw protrusion in Neotropical cichlids. *Journal of Morphology* **257**, 96–106.

Westneat, M.W. (1990) Feeding mechanics of teleost fishes (Labridae: Perciformes): a test of four-bar linkage models. *Journal of Morphology* **205**, 269–296.

Westneat, M.W. (1991) Linkage biomechanics and evolution of the unique feeding mechanism of *Epibulus insidiator* (Labridae: Teleostei). *Journal of Experimental Biology* **159**, 165–184.

Westneat, M.W. (1994) Transmission of force and velocity in the feeding mechanisms of labrid fishes (Teleostei, Perciformes). *Zoomorphology* **114**, 103–118.

Westneat, M.W. (1995) Feeding, function, and phylogeny: analysis of historical biomechanics in labrid fishes using comparative methods. *Systematic Biology* **44**, 361–383.

Westneat, M.W. & Wainwright, P.C. (1989) The feeding mechanism of the sling-jaw wrasse *Epibulus insidiator* (Labridae; Teleostei): evolution of a novel functional system. *Journal of Morphology* **202**, 129–150.

Winemiller, K.O. (1989) Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan Ilanos. *Environmental Biology of Fishes* **26**, 177–200.

Winemiller, K.O., Kelso-Winemiller, L.C. & Brenkert, A.L. (1995) Ecological diversification and convergence in fluvial cichlid fishes. *Environmental Biology of Fishes* **44**, 235–261.

Yanez-Arancibia, A. (1978) Taxonomía, ecología, y estructura de las comunidades de peces en lagunas costeras con bocas efimeras del Pacifico de Mexico. *Publicaciones Especiales Centro de Ciencias Del Mar Y Limnología* **2**, 1–306.