

## DO FLATFISH FEED LIKE OTHER FISHES? A COMPARATIVE STUDY OF PERCOMORPH PREY-CAPTURE KINEMATICS

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### Summary

The kinematics of prey capture in two bilaterally asymmetrical pleuronectiform flatfish species (*Pleuronichthys verticalis* and *Xystreureys liolepis*) and two symmetrical percomorph species (*Lepomis macrochirus*, a centrarchid, and *Cheilinus digrammus*, a labrid) were compared to test the hypothesis that flatfish have distinct prey-capture kinematics from those quantified for other percomorph fishes. Size-matched individuals of both flatfish species were video-taped feeding using a high-speed video system. Cephalic displacement and timing variables were quantified and compared with data from similarly sized *L. macrochirus* and *C. digrammus* previously collected by other researchers using similar experimental methodology. Nested multivariate analyses of variance indicated that there was no significant difference in prey-capture kinematics between flatfish and non-flatfish taxa, but that prey-capture kinematics did differ among the four taxa. Multiple nested analyses of variance revealed that the

taxa differed in 7 of 11 kinematic variables. *Post-hoc* tests and comparisons with other fish taxa suggest that individuals of *P. verticalis* possess an unusual combination of prey-capture kinematics including large hyoid depression, large neurocranial rotation, large upper jaw protrusion and small gape. Previous research has suggested that this combination of traits is associated with suction-based prey capture. Correspondingly, the ram-suction index calculated for *P. verticalis* is more negative (indicating a greater use of suction) than that calculated for the other taxa. When homologous kinematic variables are compared across these four taxa, flatfish do not appear to have similar prey-capture kinematics. However, both flatfish species are distinct from the two symmetrical percomorph species in their asymmetrical jaw movements.

Key words: prey capture, feeding behavior, kinematics, flatfish, asymmetry, Pleuronectiformes, Percomorpha.

### Introduction

Flatfishes (Pleuronectiformes) are a successful group of marine temperate shallow-water fishes with approximately 520 extant species (Nelson, 1976). A potential contributing factor to their success is a novel adaptation to a benthic existence; all mature flatfish have both eyes on one side of their head. This adaptation allows flatfish to lie on the bottom on their eyeless (or blind) side and search the surrounding environment for potential prey items with the two eyes located on the eyed (or ocular) side of the body. This modification, in combination with cryptic coloration, presumably also allows these fishes to remain undetected by potential predators.

Although the position of both eyes on one side of the head has allowed flatfish to adapt to a benthic existence, this modification has also necessitated morphological changes in the head and jaws. All flatfish have some degree of cephalic bilateral morphological asymmetry (Hensley and Ahlstrom, 1984; Yazdani, 1969). Thus, all flatfish share a morphological feature unique among the vertebrates – bilateral morphological asymmetry of the feeding apparatus. Bilateral asymmetry of

the head and jaws has the potential to affect the feeding behavior of these fishes, and this raises the question: do flatfish feed like other fishes? In order to answer this question, the feeding behavior of flatfishes is compared with that of related symmetrical fishes to determine whether flatfish species share specific features of prey-capture behavior.

### *Relationships among percomorph taxa*

Systematists have yet to determine how closely related flatfish are to other fishes in the clade Percomorpha. Early researchers (Norman, 1930; Regan, 1910) proposed that flatfishes have evolved from the Serranidae (the grouper family, suborder Percoidei, order Perciformes). Recent research has supported the general hypothesis that a group of percoid fishes may have been the ancestors of modern flatfish, but a specific group has not been identified (Carroll, 1988; Chapleau, 1993; Lauder and Liem, 1983). However, flatfish are believed to be a monophyletic group within the Percomorpha. Since flatfish are all descended from a common ancestor

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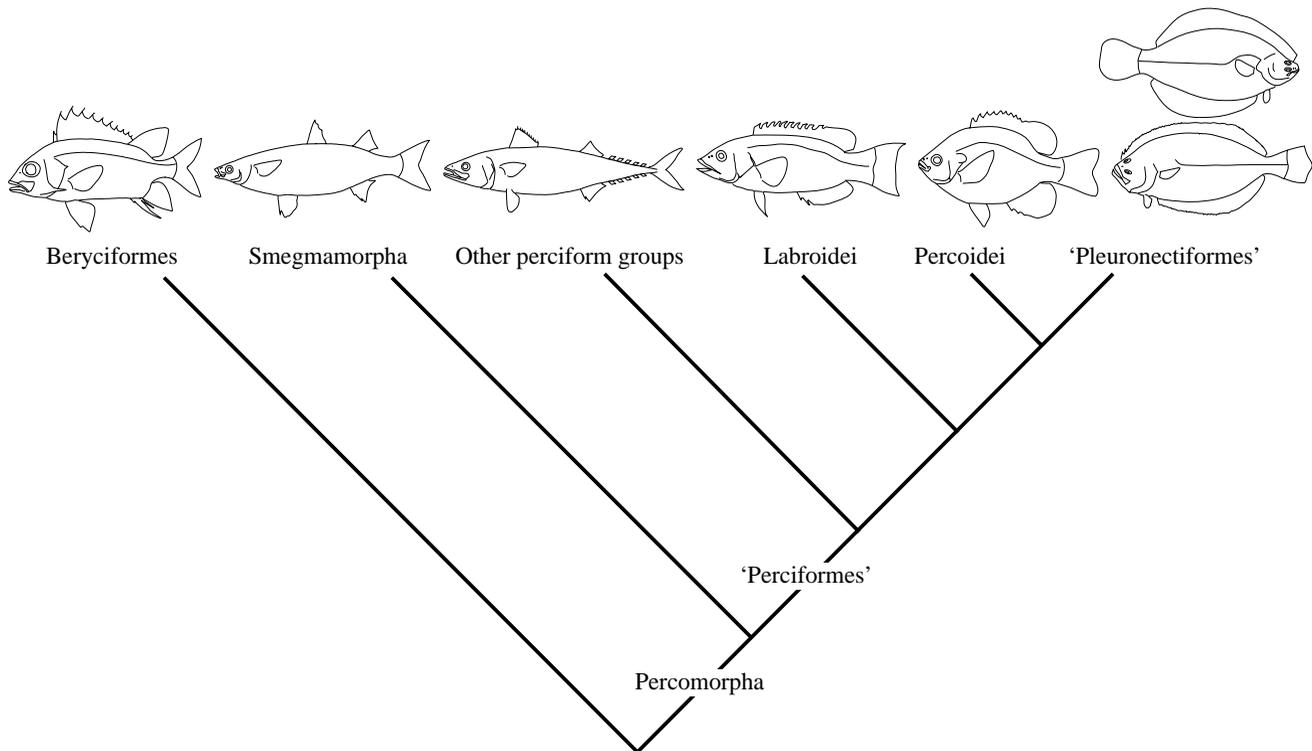


Fig. 1. Simplified cladogram modified from several sources (Johnson and Patterson, 1993; Lauder and Liem, 1983) depicting the current proposed relationship among flatfishes (Pleuronectiformes), sunfishes (Percoidei) and wrasses (Labroidei). Line drawings of representative species (modified after Nelson, 1976) from each group are located over the group name. Two line drawings are given for the Pleuronectiformes to illustrate that *Pleuronichthys verticalis* (upper) is a right-eyed flatfish, that *Xystreureys liolepis* (lower) is a left-eyed flatfish, and that these two species are currently classified in two different families within the Pleuronectiformes.

(Chapleau, 1993), this provides an additional reason to predict that all flatfish might share certain aspects of their feeding behavior.

Fig. 1 depicts a highly simplified cladogram showing the current hypothesized relationships among selected percomorph taxa. A recent revision of the Percomorpha by Johnson and Patterson (1993) suggests that, because flatfish share many morphological traits with other perciform taxa, they should be considered a monophyletic, derived group within the order Perciformes. However, the order Perciformes lacks a single shared derived characteristic to support its monophyly (Johnson and Patterson, 1993; Lauder and Liem, 1983), and relationships between the families within the order are also ambiguous. It is believed that the closest living relatives of the flatfishes are members of the suborder Percoidei (a group which includes Serranidae, the groupers, and Centrarchidae, the sunfishes). More distantly related are the Labroidei (e.g. Labridae, the wrasses) and other perciform groups. Thus, *Lepomis macrochirus*, a centrarchid, and *Cheilinus digrammus*, a labrid, represent two bilaterally symmetrical percomorph taxa and provide a relevant taxonomic comparison with the flatfishes.

#### *Diet and feeding behavior*

Flatfish might be predicted to share a unique feeding behavior because of their bilateral morphological asymmetry

and shared ancestry. However, other factors are known to be correlated with certain aspects of feeding behavior. For example, diet and feeding mode have been shown in several studies to be good predictors of functional parameters measured during prey capture.

Lauder (1983) showed that, despite being closely related, species within a single genus (*Lepomis*) show significant variation in the morphology of feeding structures and the physiology of feeding behavior (as measured by differences in muscle activity patterns during prey processing). In this genus, functional changes in feeding behavior are associated with well-defined dietary shifts. Thus, changes in the morphology and physiology of feeding apparently allow closely related species to exploit different prey types. Lauder (1983) did not, however, quantify the prey-capture kinematics of these species.

In addition, convergence in feeding mode has been described for unrelated percomorph species. Norton and Brainerd (1993) found that taxonomically diverse species of perciform fish (in two families, Centrarchidae and Cichlidae) shared similar feeding behavior when the behavior was defined by the amount of suction generated by the fish during prey capture. They attributed this result to similarities among taxa in the type of prey consumed, the feeding mode (overtaking the prey *versus* capturing it by suction) and the habitat occupied. In this case, the selective pressures of the

environment appear to override any 'constraints' of phylogeny to create taxonomically divergent species with functionally convergent prey-capture modes. Norton and Brainerd (1993) suggest that the proximate mechanism for generating these similarities in prey-capture behavior is convergence in cephalic morphology (e.g. all fish taxa with dorso-ventrally deep heads and small mouths were good suction feeders). However, in their study, there was no analysis of the cephalic kinematic movements of the predator during prey capture, so the kinematic basis of prey capture for these species is still unknown.

### Goals

There are two alternative hypotheses for the present study. Flatfish may share kinematic features of prey capture because of their bilateral morphological asymmetry and shared ancestry. Alternatively, diet and habitat may strongly influence prey-capture behavior and create divergent prey-capture kinematics within the flatfish clade. Therefore, the goals of the present study are (1) to determine the similarities and differences in the morphology of the feeding structures of flatfish and other percomorph fishes, (2) to assess the utility of diet as a predictor of prey-capture kinematics, and (3) to determine whether flatfish have prey-capture kinematics which are distinct from those found in other percomorphs. In order to accomplish these goals, the present study examines cephalic morphology and prey capture in two bilaterally asymmetrical pleuronectiform flatfish species (*Pleuronichthys verticalis* and *Xystreuryx liolepis*) and two symmetrical percomorph species (*Lepomis macrochirus*, a centrarchid, and *Cheilinus digrammus*, a labrid). More specifically, the present study (1) compares statistically the cephalic morphology of the four species, (2) describes briefly the diets of the four species as reported in the literature, and (3) compares statistically the

kinematics of prey capture among the four taxa to determine whether flatfishes are more similar to one another in their feeding behavior than they are to the symmetrical percomorph fishes.

### Materials and methods

#### Collection of morphological data

Anatomical drawings of the head and jaws of *L. macrochirus* (Rafinesque), *X. liolepis* (Jordan and Gilbert) and *P. verticalis* (Jordan and Gilbert) were made using preserved specimens, a Zeiss microscope with a *camera lucida* attachment, a graphics tablet and a Macintosh computer. Specimens were killed and chemically preserved by immersion in buffered formalin for several days and transferred to a 70% ethanol solution. Specimens were then cleared and stained in order to examine the cephalic bones and cartilage. Drawings were made from cleared and stained individuals using the *camera lucida* and the graphics tablet. The anatomical drawing of the head and jaws of *C. digrammus* (Lacepède) was modified from Westneat (1990). The published drawing was scanned into a computer graphics program and the style of the drawing was modified to facilitate comparisons with the other taxa.

Morphological measurements were made on four or five individuals of each of the four taxa. Individuals used in this analysis were not the same individuals used for the kinematic analysis; these specimens were obtained from research laboratory or museum collections. Morphological variables were measured from preserved specimens of each species in the same size range as those used in the kinematic study (Fig. 2): four individual *C. digrammus* of standard length (SL) 9.5–11.4 cm, four individuals of *L. macrochirus* of SL 14.6–15.9 cm, four *X. liolepis* of SL 15.2–16.5 cm and five *P.*

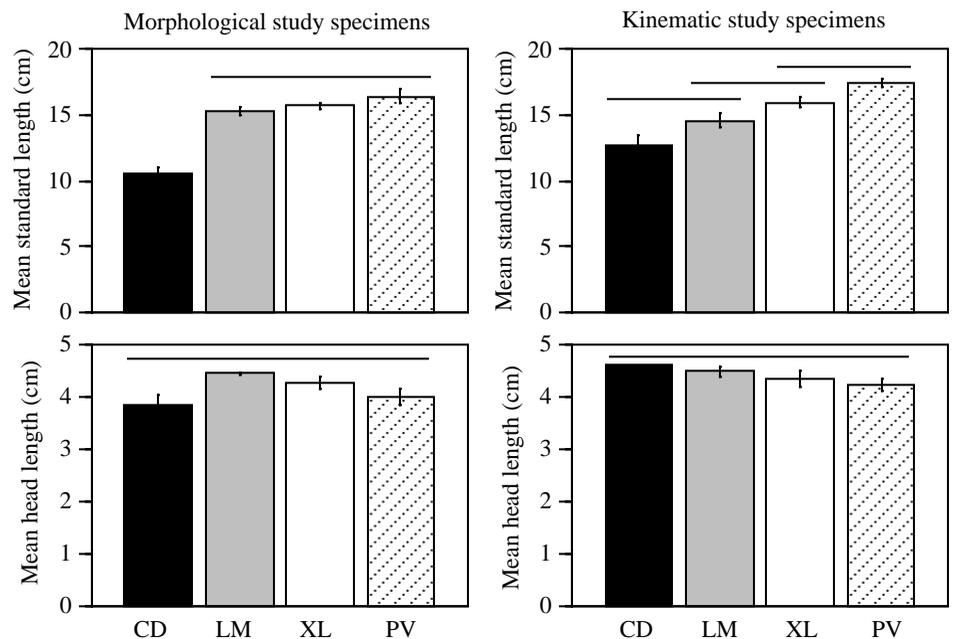


Fig. 2. Mean ( $\pm$  S.E.M.,  $N=4-5$ ) standard length and head length measurements for morphological and kinematic specimens from all taxa. The results of Tukey–Kramer *post-hoc* tests are indicated by the lines above the bars. Taxa unified by a line were not statistically different from one another for a given variable. CD, *Cheilinus digrammus*; LM, *Lepomis macrochirus*; XL, *Xystreuryx liolepis*; PV, *Pleuronichthys verticalis*.

*verticalis* of *SL* 15.3–17.8 cm. A one-way analysis of variance (ANOVA) indicated that there was a significant difference among taxa in terms of standard length (d.f.=3,13;  $P < 0.001$ ), but there was no significant difference in terms of head length (d.f.=3,13;  $P > 0.05$ ). Head length has recently been proposed as a better criterion for size matching than standard length (Wainwright and Richard, 1995). Therefore, for the purposes of the present study, the specimens were well size-matched.

Morphological variables were measured using calipers either directly from the preserved specimens or from X-ray images of the cephalic region of the specimens. X-ray images were obtained using a Hewlett-Packard Faxitron 43855A X-ray machine at 30 kV intensity and 40–50 s exposure. The following variables were measured directly from the preserved specimens: standard length (*SL*), head length from the anterior tip of the upper jaw to the posterior margin of the operculum, length of the mandible from the anterior tip to the posterior margin, distance from the anterior tip of the upper jaw to the connection of the upper jaw to the lower jaw (*via* the lip ligament), and distance from the anterior tip of the lower jaw to the connection of the lower jaw to the upper jaw (*via* the lip ligament). Four additional morphological variables were measured from the X-ray images: the length of the neurocranium from the base of the skull to the anterior tip of the vomer, the depth of the neurocranium at its deepest point (from the ventral surface of the skull to the superoccipital crest), the length of the ascending process of the premaxilla, and the dorso-ventral length of the hyoid apparatus (the length of the hyoid from the dorsal tip of the epihyal to the ventral tip of the hypohyal as measured from a lateral view). Variables associated with the opercular series were not measured because kinematic variables describing medial-lateral opercular movements were not measured for all taxa (see below).

Because flatfish demonstrate cephalic morphological asymmetry, four of the morphological variables described above were measured for the two flatfish species from the ocular and blind sides of the head (i.e. paired morphological variables). These variables were: head length, mandible length, distance from the tip of the upper jaw to the connection with the lower jaw, and distance from the tip of the lower jaw to the connection with the upper jaw. The length of the ascending process of the premaxilla was not considered to be a paired variable because it was impossible to quantify asymmetry in this structure using the X-ray images.

#### *Collection of diet and kinematic data*

Diet data given in the present study were collected from published accounts of the food habits of all four species (see Results). The kinematic data were collected from four sources (Gibb, 1995, 1996; Gillis and Lauder, 1995; Westneat, 1990). All four species were filmed or video-taped in George V. Lauder's laboratory at the University of California, Irvine. A brief description of the methodology used to record and quantify prey capture in each study is given below.

Standard lengths of the flatfish were measured from the video tapes of feeding events. Lengths reported by Gillis and

Lauder (1995) and Westneat (1990) were used for the other two species. Head length was measured as the distance from the anterior tip of the mandible to the distal edge of the opercular series near the pectoral fin for all species. This variable was measured digitally from the video tapes of feeding events for the flatfish and for *L. macrochirus*. For *C. digrammus*, this variable was measured from a single high-speed film frame of one individual (reproduced in Westneat, 1990). This image was scanned into a computer, scale was determined using a reference grid in the image, and head length of the fish was measured from the image using a digitizing program.

Data for the kinematics of prey capture in the labrid *Cheilinus digrammus* were obtained from M. Westneat (personal communication; details of this study can be found in Westneat, 1990). *C. digrammus* data were obtained from three individuals (*SL* 11.8–13.7 cm, head length of one representative individual was 4.6 cm) feeding on shrimp pieces presented to the fish using forceps. Three prey-capture events were filmed for each individual at 200 fields  $s^{-1}$  using a Redlake LOCAM intermittent high-speed cine camera. Fish were filmed from a lateral view using one camera. Film images were projected onto a digitizing pad and kinematic variables were quantified using digitizing software. Westneat (1990) defined the same point in time across all nine prey-capture events using a predefined value of lower jaw depression. These data were re-analyzed in the present study using the beginning of mouth opening as the same point in time (time 0) for all prey-capture events so that the timing of kinematic events was calculated relative to the gape cycle.

Gillis and Lauder (1995) provided data for the prey-capture kinematics of *Lepomis macrochirus*. Four individual *L. macrochirus* (*SL* 13.9–15.9 cm, head length 4.3–4.7 cm) were video-taped at 200 fields  $s^{-1}$  using a NAC high-speed video system, and five sequences were collected for each individual. Fish were presented with earthworm pieces (3–4 cm long) dropped into the water through a plastic tube and were video-taped simultaneously from the lateral and ventral views. Video sequences were downloaded to a computer, and kinematic variables were measured using a custom-designed digitizing program. All timing variables were measured relative to the onset of mouth opening (time 0).

Details of the methods used for video-taping *Pleuronichthys verticalis* are given in Gibb (1995). Four individuals of this species (*SL* 15.9–18.3 cm, head length 3.9–4.4 cm) were filmed using a NAC high-speed video system at 200 fields  $s^{-1}$ . Small earthworm pieces (approximately 2 cm long) were placed on the tank bottom using forceps. Three views (ocular side, blind side and gular region of the fish) were recorded for each individual because flatfish possess the potential for kinematic bilateral asymmetry during prey capture (Gibb, 1995, 1996). Thus, four sequences per individual simultaneously recorded lateral and ventral views of the tank (anatomically the gular region and blind side of the fish), and four sequences per individual simultaneously recorded ventral and dorsal views of the tank (anatomically the ocular and blind sides). Video

images were downloaded to a computer and digitized using a custom-designed digitizing program. Kinematic variables were measured for both the ocular and the blind sides of the head, and timing variables were measured relative to mouth opening (time 0). Several sequences measured for *P. verticalis* were re-analyzed in the present study to ensure that all data were collected using comparable methods.

Data for *Xystreurus liolepis* (SL 14.9–18.2 cm, head length 3.9–4.6 cm) were measured using the same methods as used for *P. verticalis* with two exceptions: fish were video-taped feeding at 250 fields  $s^{-1}$  (instead of 200 fields  $s^{-1}$ ) and five fish were video-taped (instead of four). Further details are given in Gibb (1996).

A one-way ANOVA revealed that for the kinematic specimens there was a significant difference in standard length among taxa (d.f.=3,12;  $P < 0.001$ ). However, as with the morphological specimens, there was no significant difference in head length among the taxa (d.f.=3,10;  $P > 0.05$ ). Therefore, all taxa were considered to be size-matched in the present study (Fig. 2).

#### Kinematic variables

The following 11 kinematic variables were measured for all taxa. Three variables associated with jaw displacement were calculated: maximum gape (cm), the maximum distance between the anterior tips of the upper jaw (premaxilla) and lower jaw (mandible); maximum lower jaw depression (degrees), the maximum ventral rotation of the mandible relative to the body; and maximum upper jaw protrusion (cm), the maximum anterior displacement of the premaxilla. Three timing variables describing these movements were calculated as the interval between the beginning of mouth opening and the maximum value of the specific kinematic parameter: time to maximum gape (ms), time to maximum lower jaw depression (ms) and time to maximum protrusion of the upper jaw (ms). One additional timing variable, gape cycle time (ms), was calculated as the total amount of time the mouth was open during prey capture.

Two displacement variables describing movements of the neurocranium and hyoid were measured. Cranial rotation (degrees; often termed 'cranial elevation' in previous studies) was measured as the maximum angular rotation of the neurocranium dorsally relative to the body. Maximum hyoid depression (cm) was determined by the most ventral position of the hyoid. Two timing variables describing these movements were calculated as the interval between the beginning of mouth opening and the maximum value of the specific kinematic parameter: time to maximum cranial rotation (ms) and time to maximum hyoid depression (ms).

Variables associated with medial-lateral movements of the opercula were measured for *L. macrochirus*, *P. verticalis* and *X. liolepis* but not for *C. digrammus* (because only a lateral view was recorded). Two variables quantified timing and displacement of the opercular series during prey capture. Maximum opercular expansion (cm) occurred when the opercula were maximally laterally displaced. The time to

maximum opercular expansion (ms) was calculated as the interval between the beginning of mouth opening and the maximum lateral expansion of the opercular series.

Of the 13 variables described above, four involved unpaired structures, the neurocranium and the hyoid. For these structures, kinematic timing and displacement variables were quantified for the flatfish species from the blind-side view only. However, all other variables involved movements of paired structures with the potential for functional asymmetry. Therefore, nine variables were calculated for the flatfish for both the blind and the ocular sides of the head (paired kinematic variables).

Raw values for kinematic variables for each prey-capture event were used for all individuals. Ratios (e.g. displacement variable/head length) were not used to attempt to correct for size effects for two reasons: (1) the fish were not significantly different in head size (Fig. 2), and (2) ratios create numerous statistical problems for data analysis (Atchley and Anderson, 1978; Atchley *et al.* 1976; Packard and Boardman, 1987).

#### Statistical analyses

In general, statistical tests were performed on two combinations of the morphological variables described above. All morphological variables measured (with the exception of standard length and head length) were used for this analysis. One combination (hereafter termed the blind-side morphological variables) included the four variables measured from the blind side of the flatfishes, the three variables measured for symmetrical cephalic structures from the flatfishes, and all variables measured for *C. digrammus* and *L. macrochirus*. The second combination of variables (ocular-side morphological variables) included the four variables measured from the ocular side of the flatfishes, the three variables measured for symmetrical cephalic structures from the flatfishes, and all variables for *C. digrammus* and *L. macrochirus*.

Statistical tests performed on the morphological data included principal components analysis (PCA), multivariate analysis of variance (MANOVA), multiple nested analyses of variance (nested ANOVAs) and Tukey–Kramer *post-hoc* tests. PCAs were performed using Statview (version 4.5) for the Macintosh and MANOVAs, ANOVAs and *post-hoc* tests were performed using SuperANOVA (version 1.11) and SAS (version 6.10) for the Macintosh.

PCAs were used to examine the morphological variables using both the ocular- and blind-side variable sets to provide a multivariate summation of the variation in the data. PCAs were also used to determine whether the taxa were separated by any of the principal components and to calculate the principal component scores to be used in the MANOVAs. Subsequently, MANOVAs were used to test the null hypothesis that there was no significant morphological difference among taxa. However, in the overall data set, the number of morphological variables measured exceeded the minimum number of observations (four individuals), so the entire data set could not be used. Therefore, one-way

MANOVAs (testing the effect of taxon) were performed on the first three principal component factors from the PCAs of the ocular- and blind-side morphological variables.

Multiple one-way ANOVAs were performed on the morphological data to determine which variables were contributing to differences among taxa. A sequential Bonferroni correction (Rice, 1989) was used to adjust the significance level of these results to take into account the multiple simultaneous tests being performed (four symmetrical variables plus three blind-side variables plus three ocular-side variables, giving a total of 10 ANOVAs). After the ANOVAs had been performed, Tukey–Kramer *post-hoc* tests were performed on the variables which differed among taxa to determine which species were significantly different from one another.

Kinematic variables were analyzed in a very similar manner to the morphological variables; again the data were divided into two combinations. One combination (blind-side kinematic variables) included the nine variables measured from the blind side of the flatfishes, the four variables measured for unpaired structures from the flatfishes and all variables measured for *C. digrammus* and *L. macrochirus*. The second combination of variables (ocular-side kinematic variables) included the nine variables measured from the ocular side of the flatfishes, the four variables measured for unpaired structures from the flatfishes and all variables for *C. digrammus* and *L. macrochirus*.

In general, the same suite of statistical tests and the same statistical programs were used to examine the kinematic data as were used to examine the morphological data. As above, PCAs were used to examine the kinematic variables using both the ocular- and blind-side variable sets and PCA scores were used for MANOVAs. Two-level nested MANOVAs were used to test the null hypothesis that there was no significant difference in prey-capture kinematics between flatfish and non-flatfish taxa. For this analysis, taxon was nested in flatfish *versus* non-flatfish taxa, and individual was nested within taxon. Since the minimum number of observations was three (three feeding events for each *C. digrammus* individual), MANOVAs were performed on the first two principal component factors from the PCAs of the ocular- and blind-side kinematic variables.

Multiple nested ANOVAs (with individual nested within taxon) were performed on the kinematic variables to determine which variables contributed to differences among taxa. A sequential Bonferroni correction (four unpaired variables plus seven blind-side variables plus seven ocular-side variables, giving a total of 18 ANOVAs) was made to account for simultaneous statistical tests. Tukey–Kramer *post-hoc* tests were performed on the kinematic variables which showed a significant effect of taxon to determine which species were significantly different from one another.

#### *Ram–suction index*

The ram–suction index (RSI) was calculated from the video images of prey capture. This index (Norton and Brainerd,

1993) quantifies the relative contributions of movement by the predator towards the prey and movement of the prey towards the predator. The index is described as a ratio:

$$RSI = (D_{\text{predator}} - D_{\text{prey}}) / (D_{\text{predator}} + D_{\text{prey}}).$$

In this equation,  $D_{\text{predator}}$  is the distance traveled by the predator during the feeding event and  $D_{\text{prey}}$  is the distance traveled by the prey. Using this index, a prey-capture event in which the prey is sucked into the mouth of an unmoving predator has an RSI of  $-1$ . A prey capture event where the predator overtakes a stationary prey item has an RSI of  $+1$ .

The RSI was calculated for all individuals and all prey-capture events for *L. macrochirus*, *X. liolepis* and *P. verticalis* using the anterior tip of the premaxilla on the fish and the distal tip of the prey item as landmarks. The RSI was not calculated for *C. digrammus* because individuals were fed pieces of prey held with forceps; this method of presenting prey does not allow any prey movement during the capture event.

## Results

### *Diet and habitat*

Results describing the diet and habitat of the four taxa have been taken from the literature. *Cheilinus digrammus* is a tropical coral reef species which feeds on small fishes and elusive decapod crustaceans (Randall *et al.* 1990; Westneat, 1994). *Lepomis macrochirus* is found in temperate lakes of North America and its diet consists primarily of zooplankton (e.g. Keast, 1978; Werner, 1977). The two flatfish species are found in temperate marine waters off the coast of California. *Xystreurys liolepis* feeds primarily on decapods and other elusive crustaceans (Allen, 1982; Kramer, 1991), and the diet of *P. verticalis* is composed mainly of benthic soft-bodied invertebrates, particularly tube-dwelling polychaetes (Allen, 1982; Kramer, 1991).

### *Morphological description*

Morphological drawings of *C. digrammus* illustrate the shallow neurocranium and small supraoccipital crest of this species (Fig. 3A). The anterior jaws are large and the premaxilla and the mandible have caniform teeth. There are large incisors in the anterior region of both the upper and the lower jaw. The neurocranium of *L. macrochirus* is deep and has a large supraoccipital crest (Fig. 3B). The premaxilla and the mandible are smaller than those of *C. digrammus*. There are numerous small caniform teeth on both the upper and the lower jaw of this species, but there are no large incisors.

The neurocranium of *X. liolepis* is shallow and the supraoccipital crest is small (Fig. 3C). The mandible, maxilla and premaxilla are large, and there are numerous small caniform teeth present on the upper and lower jaws. With the obvious exception of asymmetry in the neurocranium, most of the bones of the head exhibit little bilateral asymmetry in *X. liolepis* (Fig. 3C). However, some morphological asymmetry is present in the bones of the jaws. The maxilla is consistently longer (although it is a similar shape) on the ocular side of the

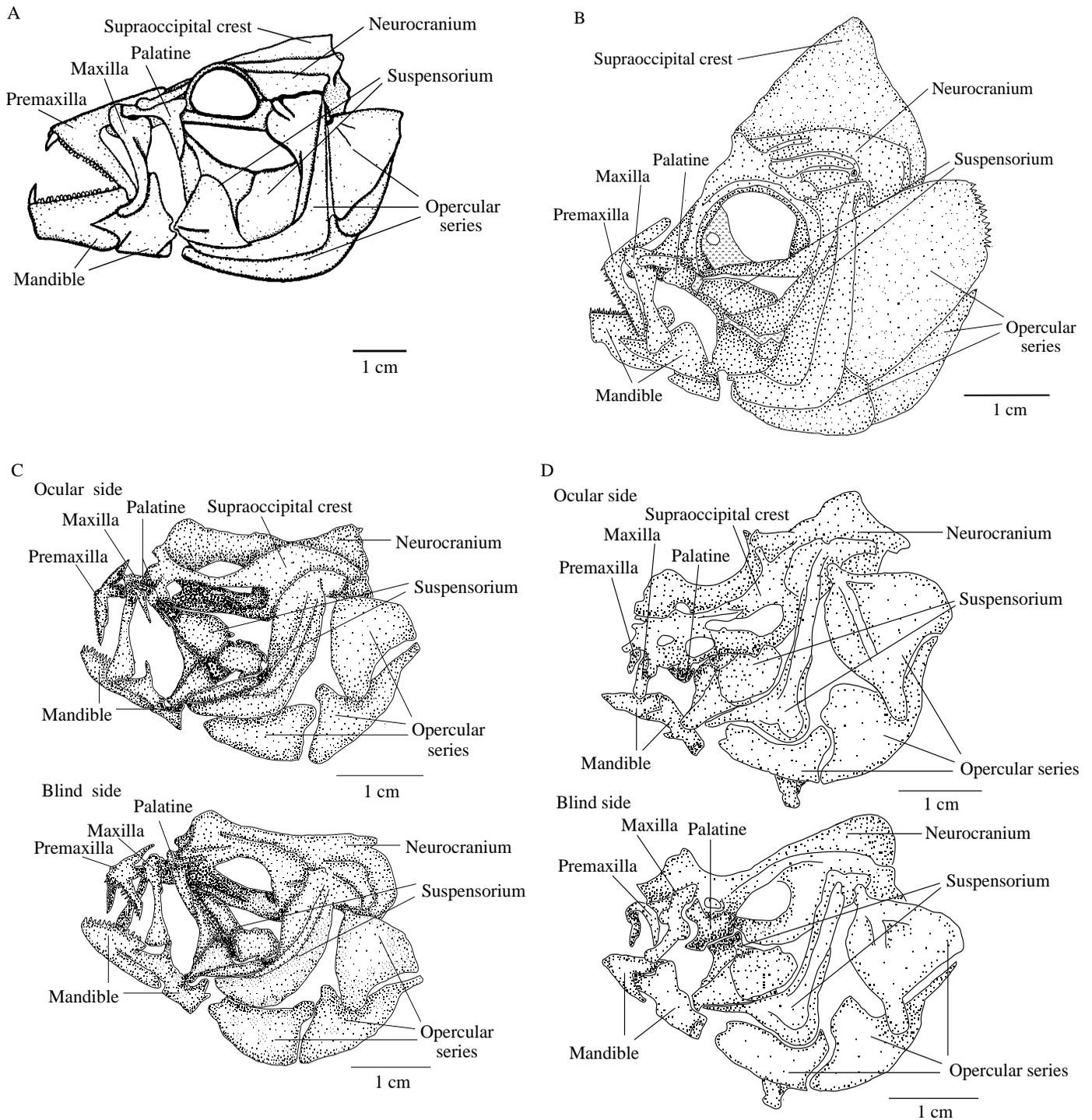


Fig. 3. Line drawings of the neurocranium and jaws of four species of fish: (A) *Cheilinus digrammus*, (B) *Lepomis macrochirus*, (C) *Xystreurus liolepis* and (D) *Pleuronichthys verticalis*. A is modified from Westneat (1990) and B and C are modified from Gibb (1995, 1996). In these illustrations, bones are stippled with individual dots and cartilaginous structures are stippled with clusters of dots. Note that for *X. liolepis* the blind side of the head has been reversed to facilitate comparisons with the ocular side, and for *P. verticalis* the ocular side of the head has been reversed to facilitate comparisons with the blind side.

head than on the blind side of the head, and the palatine bone is smaller and has a different shape on the ocular side of the head. The neurocranium and jaws of *P. verticalis* are more asymmetrical in morphology than those of *X. liolepis*

(Fig. 3D). The bones of the suspensorium, palatine and anterior jaws are larger on the blind side than on the ocular side of the head. The bones of the upper jaw are small and point towards the blind side of the head. Small conical teeth are present only

Table 1. Values of paired morphological variables for all taxa

Variable	CD	LM	XL		PV	
			Ocular-side	Blind-side	Ocular-side	Blind-side
Head length (cm)	3.83±0.20	4.43±0.03	4.26±0.12	4.25±0.12	4.06±0.15	3.99±0.16
Mandible length (cm)	1.57±0.07	1.89±0.03	2.07±0.08	2.10±0.06	1.44±0.08	1.57±0.07
Distance from tip of upper jaw to lip ligament (cm)	0.95±0.04	1.06±0.05	1.38±0.06	1.34±0.05	0.56±0.02	0.63±0.04
Distance from tip of lower jaw to lip ligament (cm)	0.91±0.06	1.05±0.07	1.30±0.05	1.27±0.06	0.57±0.04	0.61±0.04
N	4	4	4		5	

CD, *C. digrammus*; LM, *L. macrochirus*; XL, *X. liolepis*; PV, *P. verticalis*.  
 Values are means ± S.E.M.

Table 2. Values of unpaired morphological variables for all taxa

Variable	CD	LM	XL	PV
Standard length (cm)	10.5±0.43	15.3±0.29	15.7±0.28	16.4±0.56
Neurocranium length (cm)	2.96±0.04	3.38±0.03	3.17±0.09	3.03±0.12
Neurocranium depth (cm)	1.17±0.06	2.57±0.07	1.12±0.03	1.39±0.07
Hyoid depth (cm)	1.9±0.07	0.63±0.04	0.80±0.04	1.17±0.05
Length of ascending process of premaxilla (cm)	1.3±0.05	0.84±0.08	0.70±0.01	0.63±0.04
N	4	4	4	5

CD, *C. digrammus*; LM, *L. macrochirus*; XL, *X. liolepis*; PV, *P. verticalis*.  
 Values are means ± S.E.M.

on the blind side of both the upper and the lower jaw, and point inwards towards the center of the mouth (teeth are not visible in Fig. 3D because of this orientation).

*Statistical analyses of morphological data*

Statistical analyses of the cephalic morphology confirmed observations made of the cleared and stained skulls. Mean values of each morphological variable for each taxon are given in Tables 1 and 2. In the multivariate analysis, principal

component 1 (PC1), principal component 2 (PC2) and principle component 3 (PC3) together accounted for 94 % of the variation in the data (Table 3). Five out of the seven morphological variables loaded highly (0.6 or higher) on PC1: mandible length, distance from tip of upper jaw to lip ligament, distance from tip of lower jaw to lip ligament, neurocranium length and hyoid depth (which had a high negative loading). The length of the ascending process of the premaxilla loaded very highly on PC2, although hyoid depth and distance from

Table 3. Principal component loadings of morphological variables analyzed for *Cheilinus digrammus*, *Lepomis macrochirus*, *Xystreurus liolepis* and *Pleuronichthys verticalis*

	Component loadings					
	Ocular-side variables			Blind-side variables		
	PC1	PC2	PC3	PC1	PC2	PC3
Proportion of variance explained:	52.2%	27.3%	14.9%	52.8%	26.2%	15.4%
Mandible length (cm)	0.94	0.22	-0.11	0.94	0.18	-0.21
Distance from tip of upper jaw to lip ligament (cm)	0.83	0.49	-0.17	0.83	0.51	-0.14
Distance from tip of lower jaw to lip ligament (cm)	0.81	0.56	-0.09	0.78	0.60	-0.04
Neurocranium length (cm)	0.78	-0.29	0.38	0.79	-0.23	0.40
Neurocranium depth (cm)	0.47	-0.53	0.65	0.47	-0.50	0.68
Hyoid depth (cm)	-0.74	0.61	0.23	-0.78	0.57	0.19
Length of ascending process of premaxilla (cm)	-0.19	0.76	0.62	-0.26	0.75	0.60

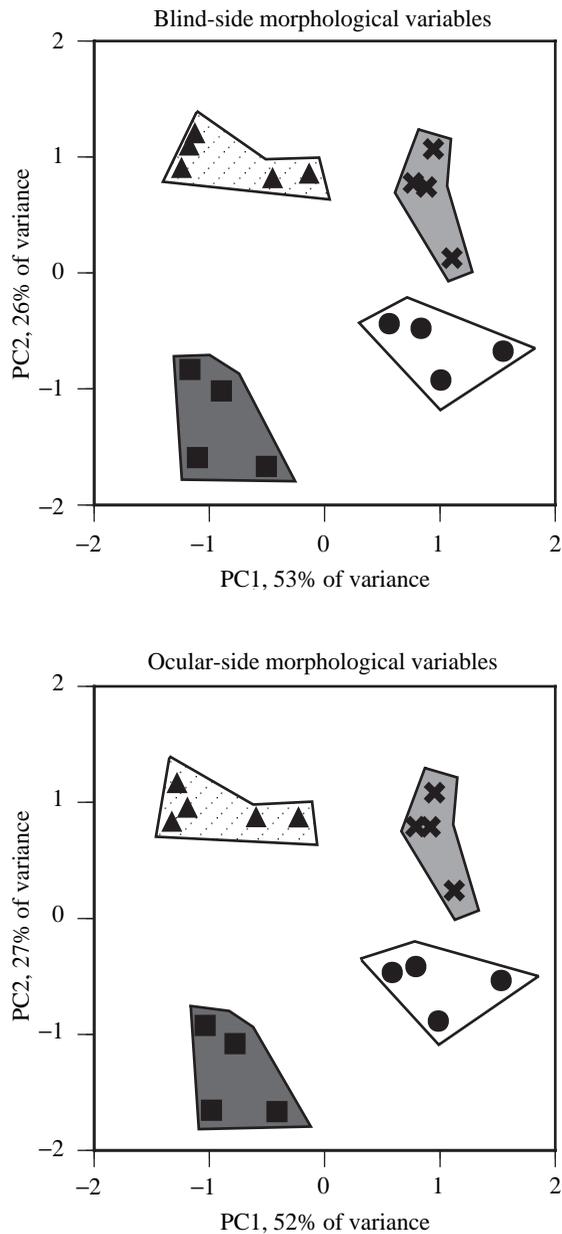


Fig. 4. Principal components analysis of the cephalic morphology for all four taxa based on two sets of seven variables: blind-side variables and ocular-side variables. Each symbol represents one specimen: ■, *C. digrammus*; ×, *L. macrochirus*; ●, *X. liolepis*; ▲, *P. verticalis*. Factor loadings for morphological variables are given in Table 3.

tip of lower jaw to lip ligament had component loadings close to 0.6 (Table 3). For PC3, neurocranium depth and length of the ascending process of the premaxilla both had component loadings of 0.6 or higher (Table 3). Plotting the individual factor scores for each morphological specimen revealed that PC1 and PC2 separate the taxa out into four distinct groupings with no overlap between any of the taxa. Individuals with negative scores on PC1 apparently have small mouths and large hyoids, while individuals with positive scores have large mouths and small hyoids (Fig. 4; Table 3). However, PC2 and PC3 do not have such clear interpretations. In general,

Table 4. *F*-statistics of multiple one-way ANOVAs performed on the morphological variables measured for all taxa

Morphological variable	Among taxa d.f.=3,13
Unpaired variables	
Neurocranium length (cm)	4.3*
Neurocranium depth (cm)	121.8*
Hyoid depth (cm)	124.9*
Length of ascending process of premaxilla (cm)	41.2*
Ocular-side variables from flatfish	
Mandible length (cm)	17.4*
Distance from tip of upper jaw to lip ligament (cm)	56.1*
Distance from tip of lower jaw to lip ligament (cm)	43.1*
Blind-side variables from flatfish	
Mandible length (cm)	18.7*
Distance from tip of upper jaw to lip ligament (cm)	41.1*
Distance from tip of lower jaw to lip ligament (cm)	31.7*

\*Significant difference at  $P < 0.05$ , using the sequential Bonferroni method described by Rice (1989).

however, taxa were separated from one another by PC1, PC2 (Fig. 4) and PC3.

MANOVAs on the first three principal components for the blind- and ocular-side morphological variables indicate that there was a significant morphological difference among the taxa (blind-side variables,  $F$ -value 72.3; ocular-side variables,  $F$ -value 76.7; in both cases, Wilks' Lambda  $P < 0.001$ ). Multiple one-way ANOVAs revealed that all of the morphological variables were significantly different among the taxa (Table 4), although neurocranium length had a very low  $F$ -value relative to the other variables (which confirms that the taxa were well size-matched). *Post-hoc* tests indicate that *C. digrammus* have a long ascending process of the premaxilla and a deep hyoid and *L. macrochirus* have a very deep neurocranium (Fig. 5). *X. liolepis* has a large distance between the jaw tips and the lip ligaments, and *P. verticalis* has a short distance between the jaw tips and lip ligaments (Fig. 6). The lower jaw is longer in *L. macrochirus* and *X. liolepis* than it is in *P. verticalis* and *C. digrammus* (Fig. 6). Thus, no clear pattern of morphological similarity exists among the taxa (i.e. no taxon is consistently similar to any other), which confirms the results of the PCA (Fig. 4).

#### Statistical analyses of kinematic data

Mean values of each kinematic variable for each taxon are given in Tables 5 and 6. Principal components analysis revealed that the taxa were best separated by principal component 1 (PC1). This component accounted for approximately 39% of the variation in the data (Table 7) and eight out of the 11 kinematic variables had high component loadings (approximately 0.6 or greater) on PC1. These variables can be subdivided into two groups which loaded either highly negatively or highly positively on PC1. Maximum hyoid depression, time to maximum hyoid

Fig. 5. Mean ( $\pm$  S.E.M.,  $N=9-20$ ) values of unpaired morphological variables which were significantly different among taxa. The results of Tukey–Kramer *post-hoc* tests are indicated by the lines above the bars. Taxa unified by a line were not statistically different from one another for a given variable; a dashed line indicates that the taxon below the dashes is not included in that statistical grouping. CD, *C. digrammus*; LM, *L. macrochirus*; XL, *X. liolepis*; PV, *P. verticalis*.

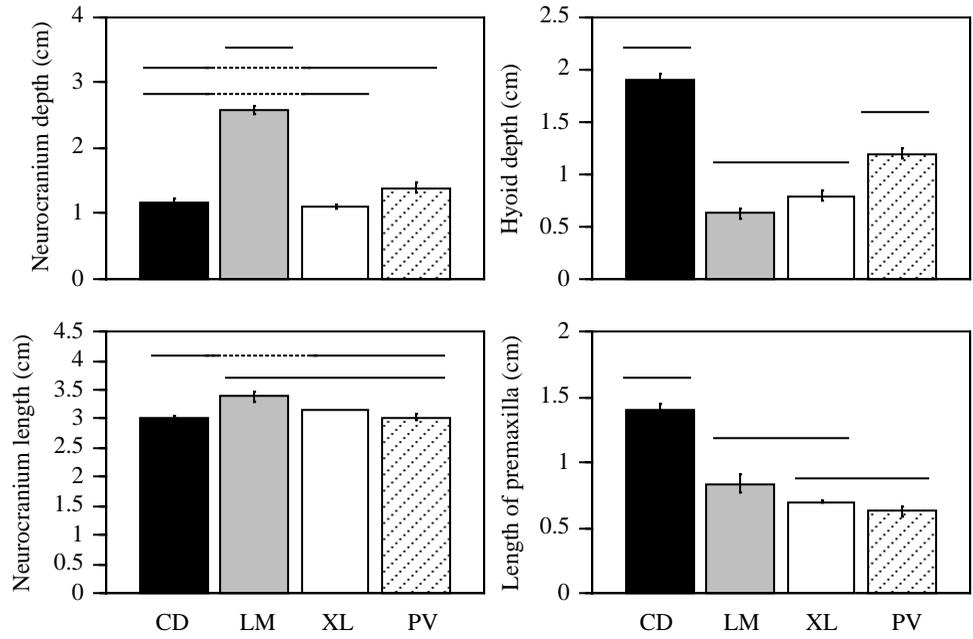
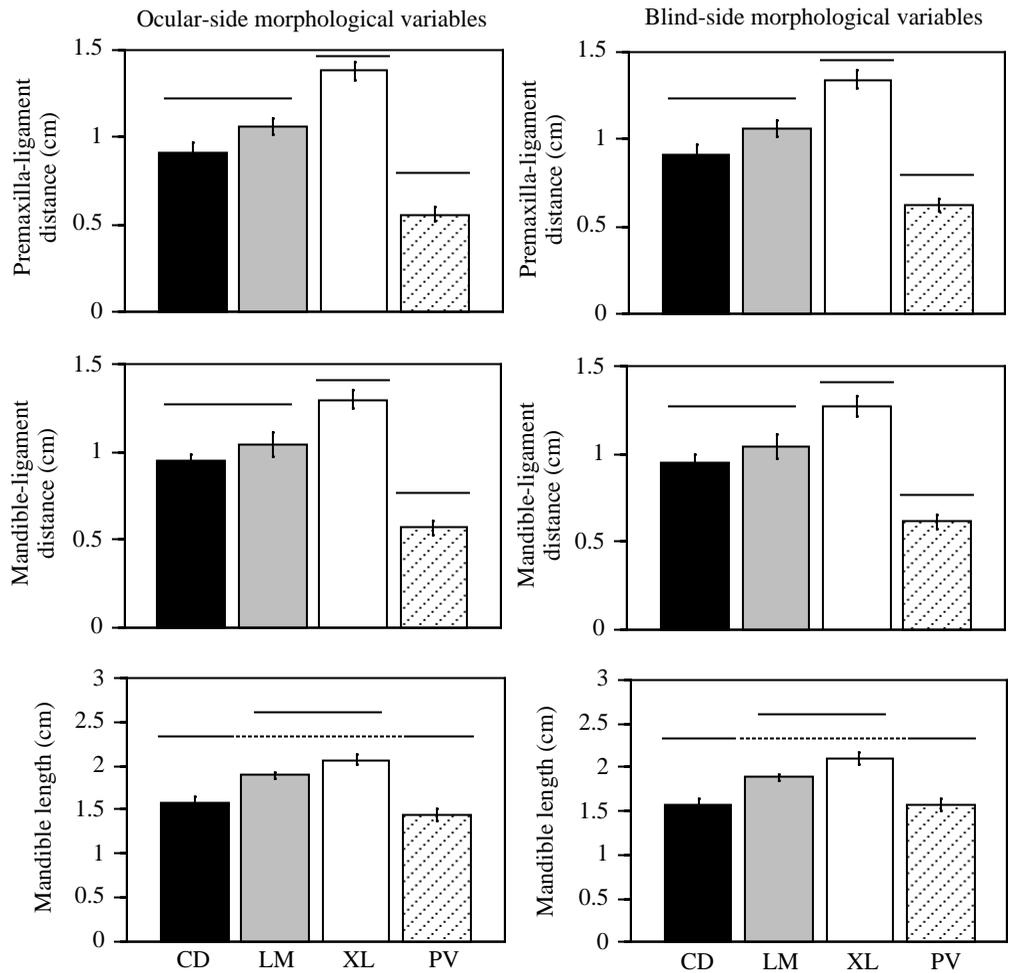


Fig. 6. Mean ( $\pm$  S.E.M.,  $N=9-20$ ) values of paired morphological variables which were significantly different among taxa. The results of Tukey–Kramer *post-hoc* tests are indicated by the lines above the bars. Taxa unified by a line were not statistically different from one another for a given variable; a dashed line indicates that the taxon below the dashes is not included in that statistical grouping. CD, *C. digrammus*; LM, *L. macrochirus*; XL, *X. liolepis*; PV, *P. verticalis*.



depression, maximum cranial rotation and maximum upper jaw protrusion all loaded with high positive values. In contrast, maximum gape, time to maximum gape, time to lower jaw

depression and gape cycle time all loaded with high negative values.

Plotting the factor scores for all individuals of each species

Table 5. Values of paired kinematic variables which were measured from the ocular and blind side for the flatfish taxa and from one side of the head for the other taxa

Variable	CD	LM	XL		PV	
			Ocular-side	Blind-side	Ocular-side	Blind-side
Maximum gape (cm)	1.56±0.06	1.16±0.05	0.99±0.06	1.02±0.06	0.50±0.03	0.73±0.04
Time to maximum gape (ms)	36.7±0.8	42.5±3.0	32.6±3.7	32.5±4.4	20.7±3.7	22.1±2.8
Gape cycle time (ms)	61.1±2.2	65.5±4.2	75.9±8.7	79.7±9.0	38.5±3.4	44.3±5.1
Maximum upper jaw protrusion (cm)	0.53±0.05	0.46±0.02	0.72±0.04	0.63±0.05	0.92±0.03	1.04±0.05
Time to maximum upper jaw protrusion (ms)	40.0±0.8	41.2±2.8	38.0±4.7	36.3±4.8	39.3±3.7	43.6±6.9
Maximum lower jaw depression (degrees)	37.3±1.3	39.5±2.1	34.7±2.3	33.1±1.9	33.9±1.1	33.6±0.8
Time to maximum lower jaw depression (ms)	32.8±0.9	42.3±3.0	33.0±4.1	31.8±4.5	20.3±2.1	20.7±2.0
Maximum opercular expansion (cm)	–	0.38±0.02	0.63±0.03	0.63±0.04	0.52±0.11*	0.64±0.13*
Time to maximum opercular expansion (ms)	–	89.5±12.1	99.6±7.9	96.1±8.8	66.9±13.7*	126.5±32.0*
<i>N</i>	9	20	20		*16, in all other cases, <i>N</i> =14	

CD, *C. digrammus*; LM, *L. macrochirus*; XL, *X. liolepis*; PV, *P. verticalis*.  
Values are means ± S.E.M.

Table 6. Values of unpaired kinematic variables measured for all taxa

Variable	CD	LM	XL	PV
Maximum hyoid depression (cm)	0.47±0.05	0.38±0.02	0.59±0.02	0.89±0.07
Time to maximum hyoid depression (ms)	45.6±1.9	51.0±3.0	69.8±8.1	103.4±10.0
Maximum cranial rotation (degrees)	8.8±0.5	9.0±0.5	12.5±0.6	27.6±1.4
Time to maximum cranial rotation (ms)	37.8±1.9	47.8±4.0	55.0±6.5	40.6±2.5
<i>N</i>	9	20	20	16

CD, *C. digrammus*; LM, *L. macrochirus*; XL, *X. liolepis*; PV, *P. verticalis*.  
Values are means ± S.E.M.

Table 7. Principal component loadings of kinematic variables analyzed for *Cheilinus digrammus*, *Lepomis macrochirus*, *Xystreurus liolepis* and *Pleuronichthys verticalis*

Variable	Component loadings			
	Ocular-side variables		Blind-side variables	
	PC1	PC2	PC1	PC2
Proportion of variance explained:	39 %	21 %	38 %	19 %
Maximum gape (cm)	–0.79	–0.13	–0.67	–0.16
Time to maximum gape (ms)	–0.76	0.53	–0.74	0.53
Gape cycle time (ms)	–0.62	0.37	–0.58	0.40
Maximum upper jaw protrusion (cm)	0.61	0.52	0.78	0.32
Time to maximum upper jaw protrusion (ms)	–0.35	0.76	–0.29	0.74
Maximum lower jaw depression (degrees)	–0.20	0.02	–0.19	–0.23
Time to maximum lower depression (ms)	–0.69	0.53	–0.70	0.58
Maximum hyoid depression (cm)	0.78	0.34	0.78	0.32
Time to maximum hyoid depression (ms)	0.64	0.55	0.64	0.45
Maximum cranial rotation (degrees)	0.82	0.32	0.81	0.41
Time to maximum cranial rotation (ms)	–0.06	0.43	–0.05	0.30

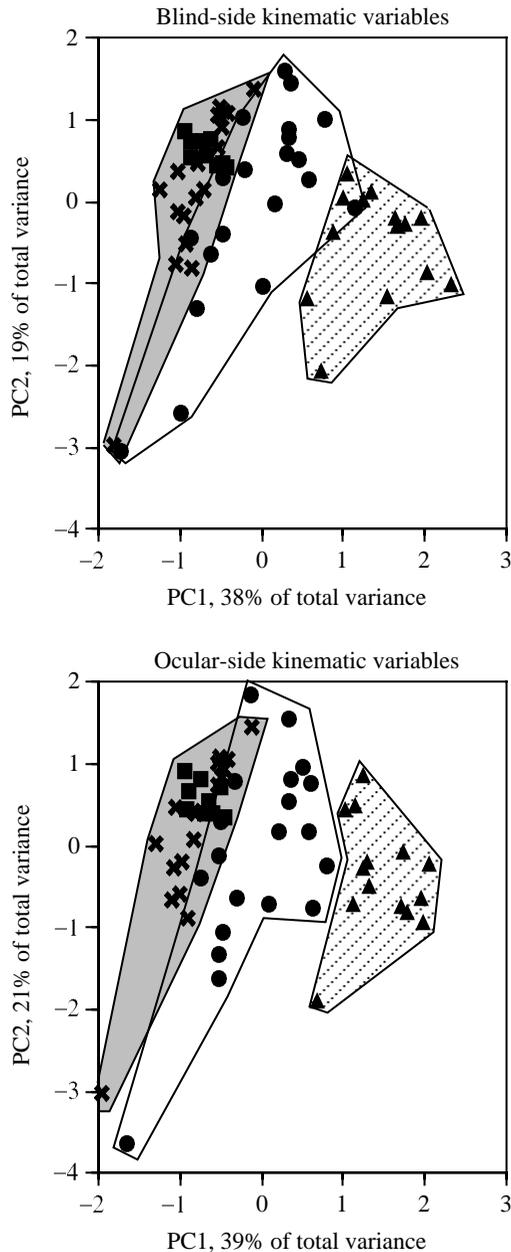


Fig. 7. Principal components analysis of the kinematics of prey capture for all four taxa based on two sets of 11 variables: blind-side variables and ocular-side variables. Each symbol represents one prey-capture event for one individual: ■, *C. digrammus*; ×, *L. macrochirus*; ●, *X. liolepis*; ▲, *P. verticalis*. Factor loadings for the kinematic variables are given in Table 7. Note that the taxa are divided into three groups by the first principal component (PC1).

illustrates that *C. digrammus* and *L. macrochirus* cannot be distinguished from one another using either PC1 or PC2 (Fig. 7); all feeding events for *C. digrammus* are nested within those for *L. macrochirus*. There is some overlap between these two symmetrical perciform species and *X. liolepis* on PC1. Similarly, there is a little overlap between *X. liolepis* and *P. verticalis* on PC1, but *P. verticalis* is completely distinct from *C. digrammus* and *L. macrochirus*.

When the information from the component loadings (Table 7) and the plot of the principal component scores for each feeding event (Fig. 7) are combined, it is evident that feeding events in which fish produced a high degree of cranial rotation, a large amount of premaxillary protrusion, extreme depression of the hyoid and took a long time to reach maximum hyoid depression had high positive scores on PC1. Most *P. verticalis* strikes had high positive scores for PC1. In contrast, in feeding events with high negative scores, the fish produced a large gape, had a long gape cycle time and a long time to maximum gape and to maximum lower jaw depression. Pre-capture events for both *C. digrammus* and *L. macrochirus* had negative scores on PC1. *Xystreureys liolepis* prey-capture events achieved PC1 scores of approximately 0, which suggests that this species was intermediate in these eight kinematic parameters.

PC2 accounted for approximately 20% of the variation in the PCA (Table 7), but it did not separate the taxa into distinct groups (Fig. 7). Only time to maximum upper jaw protrusion loaded very highly in this component (Table 7). PC2 appears to summarize individual variation in prey-capture events. Events with a very long time to maximum protrusion of the premaxilla have high positive values on PC2 (Fig. 7). The range of scores on PC2 was quite high for all species except *C. digrammus*.

In order to be sure that results of this analysis would not be different if the opercular variables were included, PCA was conducted on the 13 variables (including opercular displacement and timing) common to the studies of *L. macrochirus*, *X. liolepis* and *P. verticalis*. PCAs performed on both the 13 ocular- and blind-side variables yielded remarkably similar results to the PCAs performed on the smaller data set which excluded opercular data. The opercular variables had low loadings on PC1 (less than 0.40) and the taxa still separated into three groupings, with *L. macrochirus* having the most negative scores on PC1, *P. verticalis* the most positive and *X. liolepis* having intermediate scores.

The two-level nested MANOVAs performed on the first two principal components (from the 11 variables common to all studies) showed that there was no significant difference in prey-capture kinematics between flatfish and non-flatfish taxa (d.f.=2,1) when either the blind- or the ocular-side variables were considered for the flatfish species (blind-side variables,  $F$ -value 1.1; ocular-side variables,  $F$ -value 2.3; in both cases, Wilks' Lambda  $P > 0.05$ ). In contrast, the MANOVA indicated that there was a significant effect of taxon (d.f.=4,22) on the kinematic data (blind-side variables,  $F$ -value 7.9; ocular-side variables,  $F$ -value 8.2; in both cases, Wilks' Lambda  $P < 0.001$ ). Similarly, there was significant individual variation (d.f.=24,92) in the kinematic data (blind-side variables,  $F$ -value 2.7; ocular-side variables,  $F$ -value 3.9; in both cases, Wilks' Lambda  $P < 0.001$ ).

A series of nested ANOVAs confirmed the trends evident in the PCA; seven of the 11 variables were significantly different among the taxa. Those variables include three unpaired variables (Tables 6, 8), maximum cranial rotation, maximum

Table 8. F-statistics for multiple nested ANOVAs performed on the kinematic variables measured for all taxa

Variable	Among taxa d.f.=3,12	Among individuals within taxa d.f.=12,47
Unpaired variables		
Maximum hyoid depression (cm)	12.3*	3.4*
Time to maximum hyoid depression (ms)	5.1*	5.7*
Maximum cranial rotation (degrees)	39.3*	4.5*
Time to maximum cranial rotation (ms)	1.4	1.6
Ocular-side variables from flatfish		
Maximum gape (cm)	17.8*	4.7*
Time to maximum gape (ms)	4.7*	1.6
Gape cycle time (ms)	2.2	4.7*
Maximum upper jaw protrusion (cm)	13.3*	2.9*
Time to maximum upper jaw protrusion (ms)	0.1	2.0*
Maximum lower jaw depression (degrees)	1.0	2.6*
Time to maximum lower jaw depression (ms)	5.8*	1.3
Blind-side variables from flatfish		
Maximum gape (cm)	9.5*	5.1*
Time to maximum gape (ms)	4.7*	1.1
Gape cycle time (ms)	1.7	5.8*
Maximum upper jaw protrusion (cm)	22.1*	1.6
Time to maximum upper jaw protrusion (ms)	0.4	1.0
Maximum lower jaw depression (degrees)	1.2	4.0*
Time to maximum lower jaw depression (ms)	6.2*	1.0

\*Significant at  $P < 0.05$ , using the sequential Bonferroni method described by Rice (1989).

hyoid depression and time to maximum hyoid depression, and four paired variables (Tables 5, 8), maximum upper jaw protrusion, time to maximum lower jaw depression, maximum gape and time to maximum gape. It is interesting to note that the same paired variables were significantly different when either the blind-side or the ocular-side variables were considered for the flatfish species (Table 8).

Tukey–Kramer *post-hoc* tests indicated that, in general, *P. verticalis* had the most distinct prey-capture kinematics when the four taxa were compared. *Post-hoc* tests revealed that *P. verticalis* has the largest cranial rotation, hyoid depression, time to maximum hyoid depression (Fig. 8) and upper jaw protrusion (Figs 8, 9). This species has a shorter time to maximum gape and time to maximum lower jaw depression, as well as a smaller maximum gape (Fig. 9) when either the blind-side or the ocular-side variables are considered.

The PCA suggested that gape cycle time also contributed to

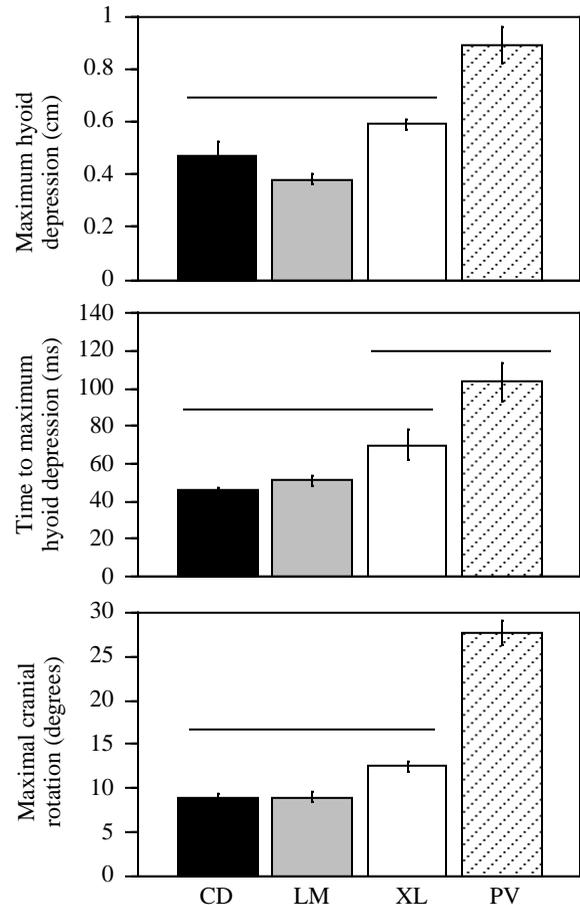


Fig. 8. Mean ( $\pm$  S.E.M.,  $N=9-20$ ) values of unpaired kinematic variables which were significantly different among taxa. The results of Tukey–Kramer *post-hoc* tests are indicated by the lines above the bars. Taxa unified by a line were not statistically different from one another for a given variable. CD, *C. digrammus*; LM, *L. macrochirus*; XL, *X. loiepis*; PV, *P. verticalis*.

differences among taxa (Table 7; Fig. 7), although the nested ANOVA did not indicate that this parameter varied significantly among taxa. Fig. 10 illustrates the non-significant trend that individuals of *P. verticalis* tended to have the shortest gape cycle time of all four taxa.

The RSI calculated for *L. macrochirus* was  $-0.10 \pm 0.07$ , for *X. loiepis* it was  $0.32 \pm 0.10$  and for *P. verticalis* it was  $-0.39 \pm 0.06$  (means  $\pm$  S.E.M.). This index suggests that *X. loiepis* have a large ram (movement of the predator) component to their strike, *P. verticalis* have a large suction (movement of the prey) component to their strike, and *L. macrochirus* have almost equal parts ram and suction.

## Discussion

### Morphological differences among taxa

Descriptive and quantitative analyses of the morphology of the four taxa suggest that each species has a distinct combination of cephalic characteristics. There is no clear

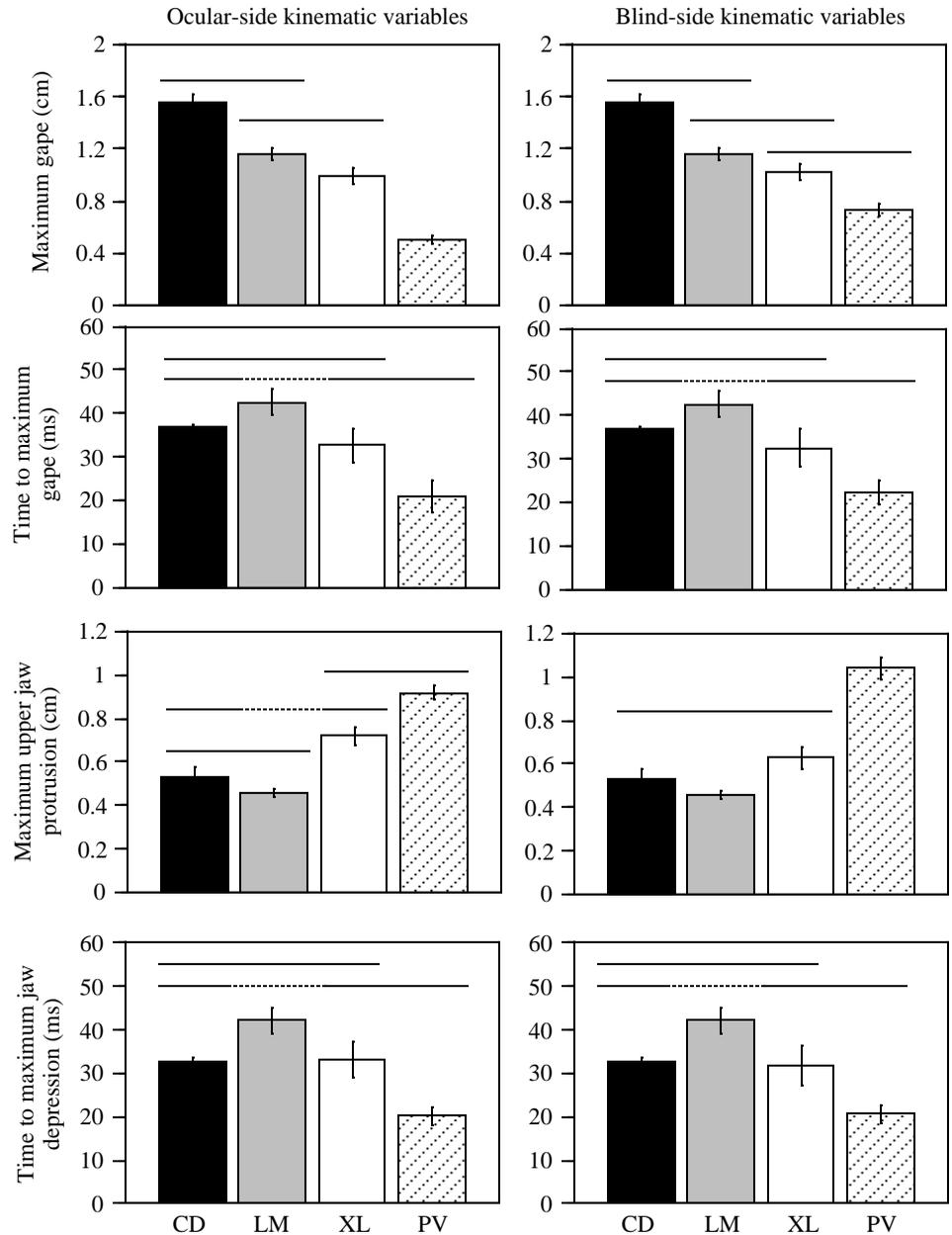


Fig. 9. Mean ( $\pm$  S.E.M.,  $N=9-20$ ) values of paired kinematic variables which were significantly different among taxa. The results of Tukey–Kramer *post-hoc* tests are indicated by the lines above the bars. Taxa unified by a line were not statistically different from one another for a given variable; a dashed line indicates that the taxon below the dashes is not included in that statistical grouping. CD, *C. digrammus*; LM, *L. macrochirus*; XL, *X. liolepis*; PV, *P. verticalis*.

pattern of similarity among the taxa, nor does any one species stand out as distinct. In addition, the results of the comparison of cephalic morphology suggest that differences among the taxa do not serve as predictors of differences in feeding kinematics. For example, *C. digrammus* has the longest ascending process of the premaxilla (Fig. 5), but one of the smallest maximum upper jaw protrusions (Fig. 9). Conversely, *P. verticalis* has a short ascending process (Fig. 5), but the largest maximum upper jaw protrusion (Fig. 9). Clearly, the length of the ascending process of the premaxilla is not a good predictor of the amount of upper jaw protrusion that will be produced.

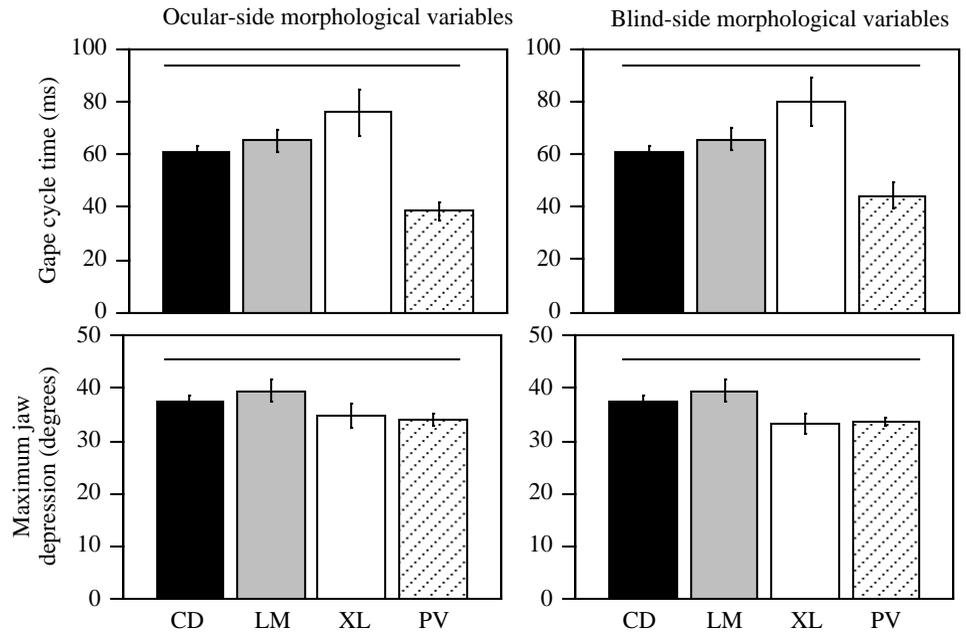
Other variables demonstrate a similar pattern. The hyoid depth of *P. verticalis* is significantly smaller than that of *C. digrammus* (Fig. 5), but *P. verticalis* has a significantly larger

maximum hyoid depression (Fig. 8). *X. liolepis* appears to have the largest potential gape as quantified by all morphological variables describing the jaws (Fig. 6), but it has one of the smallest maximum gapes in the study (Fig. 9). In a very few cases, morphology does appear to predict function; *P. verticalis* has the smallest jaws (Fig. 6) and the smallest maximum gape (Fig. 9). However, there is clearly no consistent form–function relationship between the morphological and kinematic data.

#### Kinematic differences among taxa

The results of the present study suggest that there is no stereotypical pattern of prey capture among flatfish. The flatfish taxa are not more similar to one another in prey-capture kinematics than they are to symmetrical percomorph fishes.

Fig. 10. Mean ( $\pm$  S.E.M.,  $N=9-20$ ) values of gape cycle time and maximum lower jaw depression. Taxa unified by a line were not statistically different from one another for a given variable. Although there were no significant differences among taxa, there is a clear trend for *P. verticalis* to have a very short gape cycle time relative to those of the other three taxa. In contrast, lower jaw depression shows no such trend. CD, *C. digrammus*; LM, *L. macrochirus*; XL, *X. liolepis*; PV, *P. verticalis*.



Instead, the data indicate that, although the prey capture kinematics of *L. macrochirus* and *C. digrammus* are very similar to one another (Fig. 7), the kinematic patterns of prey capture in *X. liolepis* are also similar to those of the symmetrical perciform fishes (Figs 8, 9). In contrast, *P. verticalis* has several features of prey capture which make it distinct from the other three taxa (Figs 8, 9).

During prey capture, *P. verticalis* has large values of three displacement variables: cranial rotation, hyoid depression and upper jaw protrusion (Tables 5, 6; Figs 8, 9). Since the individuals used in the study of *P. verticalis* are some of the largest individuals (in standard length) used in this comparison (Fig. 2), this raises the possibility that these fish produced the largest movements simply because they were bigger. There are three lines of evidence that the variables measured for *P. verticalis* are not simply larger as a result of size effects. First, the head size of *P. verticalis* individuals was not significantly different from those of the other fish used in the study (Fig. 2), and head length should be a better predictor of the magnitude of cephalic movements than standard length. Second, one of the kinematic variables which differed among taxa is not size-dependent because it quantifies an angle: cranial rotation. Lastly, at least one variable, maximum gape, shows the opposite effect to what would be predicted if these differences were caused by differences in standard length among taxa; maximum gape was smaller on both the ocular and the blind sides for *P. verticalis* than it was for the other taxa (Table 5; Fig. 9).

Given that the unusual features of *P. verticalis* do not appear to be a consequence of body size, what are the possible functional interpretations of these kinematic patterns? The large cranial rotation, hyoid depression, upper jaw protrusion and small gape produced by *P. verticalis* during prey capture suggest that individuals of this species may rely on the

production of suction to capture prey items. Previous research has indicated that fish which have a large buccal volume and a small gape are the most efficient suction feeders (for a complete discussion of this principle, see Norton and Brainerd, 1993). Therefore, the unusual kinematics of prey capture in *P. verticalis* suggest that this species is a suction feeder.

In addition, research on the prey-capture behavior of *P. verticalis* (Gibb, 1995) has shown that this species has extreme opercular compression during the preparatory phase of feeding (i.e. the phase that occurs before the mouth opens). Compression of the opercular series and the suspensorium during the preparatory phase reduces the volume of water inside the orobranchial and opercular cavities (Lauder, 1985; Liem, 1978). After this compression, *P. verticalis* rotate the neurocranium dorsally and depress the 'floor' of the mouth via the hyoid apparatus in order to enlarge the volume of the orobranchial cavity rapidly. These movements combine to create negative pressure (i.e. reduced pressure relative to ambient pressure) inside the orobranchial cavity. The jaws are then extended towards the prey item (as the lower jaw is depressed and the premaxilla protruded) and a very small gape is produced. Water is drawn into the small hole created by mouth opening, producing suction, which pulls the prey item into the mouth.

This explanation of the function of the unusual kinematics of *P. verticalis* is supported by the ram-suction index calculated for this species ( $-0.39$ ). The negative value suggests that *P. verticalis* utilize a large suction component during prey capture. In contrast, the other flatfish species examined in this study has a large ram component to its prey-capture behavior.

There were also timing differences between *P. verticalis* and the other taxa. In general, *P. verticalis* had the fastest prey-capture kinematics; this species had the shortest time to maximum gape (Fig. 9) and tended to have the shortest gape

cycle time (Fig. 10). It is possible that the rapid movements of the upper and the lower jaws facilitate the production of suction during prey capture. Also, since *P. verticalis* feeds on tube-dwelling polychaetes, it may be necessary for individuals of this species to produce a rapid strike in order to capture the polychaete before it can retreat into its protective tube. Finally, the gape cycle of *P. verticalis* could simply be a byproduct of a small maximum gape (i.e. it takes less time to open the jaws to a maximum gape of 0.75 cm than it does to a maximum gape of 1.0 cm). At this point, none of these possibilities can be eliminated.

One timing variable, however, demonstrated the opposite trend; *P. verticalis* had one of the longest times to maximum hyoid depression of the four taxa (Fig. 8). It is not clear what function this prolonged movement serves. The initial movement of the hyoid is quite rapid – it moves more than 0.6 cm ventrally in 20 s during mouth opening (see Fig. 5 in Gibb, 1995). This rapid movement should create a substantial change in buccal volume, which would produce reduced pressure in the buccal cavity. However, subsequent movement of the hyoid occurs over a considerably longer period (0.3 cm in 70–80 s; Gibb, 1995) than the initial movement. Slow and prolonged hyoid depression could allow continued expansion of the buccal cavity to accommodate the posterior movement of water as the anterior jaws retract. Alternatively, hyoid depression may be involved in transporting the prey item further into the buccal cavity after it has been captured.

#### Comparisons with other taxa

The prey-capture kinematics of *P. verticalis* appears to be unusual when compared with the four other taxa examined in this study. However, it is not clear from a four-species comparison how unusual individuals of *P. verticalis* are when compared with other fish taxa. Table 9 summarizes kinematic data taken from the literature for 13 actinopterygian taxa in nine families (Lauder, 1979, 1980, 1981; Elshoud-Oldenhave, 1979; Richard and Wainwright, 1995; Westneat, 1990, 1994; Lauder and Liem, 1981) and one sarcopterygian taxon (Bemis and Lauder, 1986). These studies were chosen because they represent a broad range of fish taxa and the experimental methodology used in these studies is similar to that used for the four taxa examined in the present study. A recent study of flatfish feeding has described prey capture in two other species of flatfish, *Pleuronectes platessa* and *Limanda limanda* (Bels and Davenport, 1996). Unfortunately, their study did not measure the displacement of kinematic variables and it was conducted at much colder (approximately 10 °C colder) temperatures than the studies used here. Because of these differences these recent flatfish data are not comparable with the present data and are not included here.

In Table 9, kinematic variables that quantify linear measurements are reported for individuals of a size range similar to those used in the present study (including *Lebiasina boruca*, *Micropterus salmoides*, *Luciocephalus pulcher* and most of the labrids) and variables that quantify angles are

included for all studies regardless of size range (as scaling effects do not confound these measurements). Therefore, these data can be used to help investigate whether the feeding kinematics of *P. verticalis* are unusual when compared with a broad range of fish taxa.

*P. verticalis* do appear to have a high degree of cranial rotation during prey capture. The majority of the taxa described have cranial rotations in the range 5–15°. However, two taxa (*Amia* and *Micropterus*) have a similar amount of cranial rotation to *P. verticalis*, and *Luciocephalus pulcher* have an even greater amount (40°). *P. verticalis* have the smallest maximum gape reported for individuals in this size range. The gape cycle time of *P. verticalis* is short when compared with those of most other taxa, although the labrid *C. trilobatus* also has a very short gape cycle. *P. verticalis* have greater hyoid depression compared with all labrids, but it is not large when compared with several other taxa that have twice this value (e.g. *Micropterus salmoides* and *Luciocephalus pulcher*), and an identical pattern is present for premaxillary protrusion. *P. verticalis* have the longest times to maximum hyoid depression of any of the taxa reported in Table 9.

In summary, *P. verticalis* appears to have an exceptionally small maximum gape, a short gape cycle time and a long time to maximum hyoid depression. In addition, the combination of this very small gape with large premaxillary protrusion, hyoid depression and cranial rotation is unusual. The other taxa that show large values for these three kinematic variables also have a very large gape (2–3 cm). Thus, the particular combination of kinematic variables found in *P. verticalis* may be unusual and suggests a modification of feeding kinematics for suction feeding.

#### Similarities between taxa

The statistical comparison of the prey-capture kinematics of the four species in the present study revealed another surprising result: for all variables, the prey-capture events of individuals of *C. digrammus* and *L. macrochirus* were statistically indistinguishable (Figs 7–9). Individuals of these two species had very similar values for the displacement and timing of all aspects of prey capture examined (Tables 5, 6; Figs 8, 9). This is surprising for three reasons. First, there are distinct differences in diet between the two species. The wrasse, *C. digrammus*, feeds on fishes and elusive crustaceans, while the bluegill, *L. macrochirus*, feeds on zooplankton. These prey items are very different in size (with zooplankton being very small) and are believed to be different in terms of elusiveness (with fish thought to be quite elusive). Second, these two species are quite different in cephalic morphology (Figs 3A,B, 4), and differences of this nature have traditionally been interpreted as adaptations of the skull and jaws for feeding. Finally, *C. digrammus* and *L. macrochirus* are not believed to be closely related (Fig. 1). In a two-species comparison, the *a priori* prediction for these two species would be that they would have very different prey-capture kinematics. Interestingly, a difference would be predicted if diet and habitat, comparative morphology or phylogeny were used to generate the prediction.

Table 9. A comparison of kinematic data for actinopterygian fish taxa and one sarcopterygian taxon (Lepidosiren)

Source	Family	Species	Standard length (cm)	Maximum cranial rotation (degrees)	Time to maximum cranial rotation (ms)	Maximum lower jaw depression (degrees)	Time to maximum lower jaw depression (ms)	Maximum gape (cm)	Time to maximum gape (ms)	Gape cycle time (ms)	Maximum upper jaw protrusion (cm)	Time to maximum upper jaw protrusion (ms)	Maximum hyoid depression (cm)	Time to maximum hyoid depression (ms)
Bemis and Lauder (1986)	Lepidosirenidae	<i>Lepidosiren paradoxa</i> <sup>2</sup>	15–20	6	NA	NR	NA	NA	NA	NA	NA	NA	NA	NA
Lauder (1980)	Lepisosteidae	<i>Lepisosteus oculatus</i> <sup>2</sup>	NR	12	NA	30	NA	NA	NA	NA	NA	NA	NA	NA
Lauder (1980)	Amiidae	<i>Amia calva</i> <sup>2</sup>	NR	23	NA	30	NA	NA	NA	NA	NA	NA	NA	NA
Lauder (1979)	Erythrinidae	<i>Hoplias malabaricus</i> <sup>2</sup>	NR	13	NA	59	NA	NA	NA	NA	NA	NA	NA	NA
Lauder (1981)	Lebiasinidae	<i>Lebiasina boruca</i> <sup>2,4</sup>	13.2–14	15	45	NR	NR	3	25	55	NR	NR	1.5	35
Lauder (1981)	Salmonidae	<i>Oncorhynchus mykiss</i> <sup>2,5</sup>	NR	8	NA	22	NA	NA	NA	NA	NA	NA	NA	NA
Elshoud-Oldenhave (1979)	Percidae	<i>Stizostedion lucioperca</i> <sup>2,4</sup>	20–50	10	NA	30	NA	NA	NA	NA	NA	NA	NA	NA
Richard and Wainwright (1995)	Centrarchidae	<i>Micropterus salmoides</i> <sup>3</sup>	13.0	26	35	62	35	2.2	35	65	2.3	30	2.5	30
Westneat (1990)	Labridae	<i>Cheilius chlorurus</i> <sup>2</sup>	11.8–13.7	7	40	40	40	1.3	40	80	0.5	40	0.3	50
Westneat (1994)	Labridae	<i>Cheilius fasciatus</i> <sup>1</sup>	14.8–15.4	5	35	32	30	1.2	35	65	0.5	35	0.2	45
Westneat (1994)	Labridae	<i>Cheilius trilobatus</i> <sup>1</sup>	11.0–13.7	6	25	31	25	1.2	25	45	0.5	25	0.3	35
Westneat (1994)	Labridae	<i>Oxycheilinus bimaculatus</i> <sup>1</sup>	5.8–7.3	9	NA	22	20	NA	NA	NA	NA	NA	NA	NA
Westneat (1994)	Labridae	<i>Oxycheilinus unifasciatus</i> <sup>1</sup>	9.5–12.1	13	20	28	20	1.5	20	50	0.6	20	0.5	30
Lauder and Liem (1981)	Luciocephalidae	<i>Luciocephalus pulcher</i> <sup>2</sup>	11	40	30	NR	NR	2	25	70	1.5	15	2	35
Westneat (1990)	Labridae	<i>Cheilinus digrammus</i> <sup>6</sup>	11.8–13.7	9	38	37	33	1.6	37	61	0.5	40	0.5	46
Gillis and Lauder (1995)	Centrarchidae	<i>Lepomis macrochirus</i> <sup>6</sup>	13.9–15.9	9	48	40	42	1.2	43	66	0.5	41	0.4	51
Gibb (1996)	Paralichthyidae	<i>Xystreurus liolepis</i> <sup>6,7</sup>	14.9–18.2	13	55	35/33	33/32	1.0/1.0	33/33	76/80	0.7/0.6	38/36	0.6	70
Gibb (1995)	Pleuronectidae	<i>Pleuronichthys verticalis</i> <sup>6,7</sup>	15.9–18.3	28	41	34/34	20/21	0.5/0.7	21/22	39/44	0.9/1.0	40/44	0.9	103

NA, comparisons not applicable because animals used were not in a comparable size range or size is unknown; NR, variables not measured or not reported by the author.

<sup>1</sup>Mean values rounded to the nearest millimeter, millisecond or degree; s.e.m. for these variables given in the original paper.

<sup>2</sup>Variable measured from a graph in the original paper.

<sup>3</sup>Values calculated using scaling regressions for kinematic variables given in the original paper.

<sup>4</sup>Values obtained from sequences in which this species was feeding on live fish.

<sup>5</sup>Formerly known as *Salmo gairdneri*.

<sup>6</sup>Data used in the present study; s.e.m. for these variables given in Tables 5 and 6.

<sup>7</sup>Data for flatfish paired kinematic variables given as ocular-side value/blind-side value.

Comparisons of the data used in this study with data collected for other labrid species suggest that all labrid species studied to date are quite similar to *L. macrochirus* in maximum gape, hyoid depression and upper jaw protrusion (Table 9). However, there is some variation among the labrids in maximum cranial rotation, lower jaw depression and all timing variables. Thus, *L. macrochirus* does not appear to be identical in prey-capture kinematics to all labrids, although it probably could not be statistically distinguished from this family of fishes on the basis of its prey-capture kinematics.

In contrast, *M. salmoides* (the largemouth bass, another centrarchid species) appears to be quite different from both *L. macrochirus* and all the labrids in several variables. *M. salmoides* has a much larger cranial rotation, lower jaw depression, gape, hyoid depression and premaxillary protrusion than do *L. macrochirus* and the labrids. In fact, *M. salmoides* appears to produce very large values for all displacement variables when compared with all other similarly sized fish taxa studied to date.

There is no clear explanation for why *L. macrochirus* has prey-capture kinematics more like the wrasses than like the other centrarchid for which feeding kinematics are well described (*M. salmoides*). Perhaps *L. macrochirus* and the labrids both use some type of unspecialized (and possibly primitive) feeding behavior which is common among many fishes. However, if this is true, *M. salmoides* clearly does not use this behavior. More research comparing the prey-capture kinematics of labrids and centrarchids will be necessary to understand this surprising result.

#### *Functional asymmetry during prey capture*

Thus far, the present analysis has considered only kinematic parameters which could be compared across all taxa. Analysis of these homologous variables does not support the hypothesis that flatfish are more similar to one another in prey-capture behavior than they are to labrid or percoid fishes. However, this analysis does not take into account those kinematic variables that were measured only for flatfish: variables which describe specific functional asymmetries that occur during prey capture.

Previous research has found that both *P. verticalis* and *X. liolepis* exhibit some functional asymmetry during prey capture. *X. liolepis* display only a moderate degree of functional asymmetry; the ventral portion of the maxilla (see Fig. 3C) moves farther anteriorly on the ocular side than on the blind side during mouth opening (Gibb, 1996). The asymmetrical movement of the maxilla eliminates the 'V' created by mouth opening on the ocular side and probably blocks one potential escape route of the prey item.

*P. verticalis* demonstrate more extreme functional asymmetry. Individuals of this species bend their jaws out of the midline down towards the blind side, and they produce a larger gape on the blind side than on the ocular side of the head during prey capture (Gibb, 1995). Presumably, this bending of the jaws towards the substratum allows individuals of this species to direct suction towards the prey item. Thus, these two species of flatfish are similar to one another in that prey capture

in both has certain asymmetrical features. However, they do not have the same functional asymmetries.

#### *Do flatfish feed like other percomorph fishes?*

There is clearly no stereotypical kinematic pattern of flatfish feeding. *X. liolepis* is more similar in its prey-capture kinematics to *C. digrammus* and *L. macrochirus* than it is to *P. verticalis*. Thus, flatfish do not appear to have shared derived kinematic features of prey capture. Although the two flatfish species in the present study can be collected off the coast of Southern California, USA, in the same bottom trawls, they may be exploiting different ecological niches. *X. liolepis* appears to be a generalist predator with ram-dominated prey-capture kinematics. *P. verticalis*, in contrast, possesses the prey-capture kinematics of a highly specialized suction feeder. These results correspond well with the details known of their natural history.

The only feature of prey-capture kinematics shared between the two flatfish taxa was the presence of some type of functional asymmetry during prey capture. This would appear to support the recent phylogenetic proposal that flatfish are highly specialized perciform fishes. However, since all flatfish possess some morphological asymmetry of the head and jaws, they all have the potential for asymmetry in prey-capture kinematics.

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#### References

- ALLEN, M. J. (1982). *Functional Structure of Soft-Bottom Fish Communities of the Southern California Shelf*. La Jolla: University of California, San Diego. 577pp.
- ATCHLEY, W. R. AND ANDERSON, D. (1978). Ratios and the statistical analysis of biological data. *Syst. Zool.* **27**, 71–78.
- ATCHLEY, W. R., GASKINS, C. T. AND ANDERSON, D. (1976). Statistical properties of ratios. I. Empirical results. *Syst. Zool.* **25**, 137–148.
- BELS, V. L. AND DAVENPORT, J. (1996). A comparison of food capture and ingestion in juveniles of two flatfish species, *Pleuronectes platessa* and *Limanda limanda* (Teleostei: Pleuronectiformes). *J. Fish Biol.* **49**, 390–401.
- BEMIS, W. E. AND LAUDER, G. V. (1986). Morphology and function

- of the feeding apparatus of the lungfish, *Lepidosiren paradoxa* (Dipnoi). *J. Morph.* **187**, 81–108.
- CARROLL, R. L. (1988). *Vertebrate Paleontology and Evolution*. New York: W. H. Freeman & Co. 590pp.
- CHAPLEAU, F. (1993). Pleuronectiform relationships: a cladistic reassessment. *Bull. mar. Sci.* **51**, 516–539.
- ELSHOUD-OLDENHAVE, M. J. W. (1979). Prey capture in the pike-perch, *Stizostedion lucioperca* (Teleostei, Percidae): a structural and functional analysis. *Zoomorph.* **93**, 1–32.
- GIBB, A. C. (1995). Kinematics of prey capture in a flatfish, *Pleuronichthys verticalis*. *J. exp. Biol.* **198**, 1173–1183.
- GIBB, A. C. (1996). The kinematics of prey capture in *Xystreureys liolepis*: do all flatfish feed asymmetrically? *J. exp. Biol.* **199**, 2269–2283.
- GILLIS, G. B. AND LAUDER, G. V. (1995). Kinematics of feeding in bluegill sunfish: is there a general distinction between aquatic capture and transport behaviors? *J. exp. Biol.* **198**, 709–720.
- HENSLEY, D. A. AND AHLSTROM, E. H. (1984). Pleuronectiformes: Relationships. In *Ontogeny and Systematics of Fishes, Special Publication 1, American Society of Ichthyologists and Herpetologists* (ed. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr and S. L. Richardson), pp. 670–687. Lawrence, KS: Allen Press.
- JOHNSON, G. D. AND PATTERSON, C. (1993). Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bull. mar. Sci.* **51**, 554–626.
- KEAST, A. (1978). Trophic and spatial interrelationships in the fish species of an Ontario temperate lake. *Env. Biol. Fish.* **3**, 7–31.
- KRAMER, S. H. (1991). The shallow-water flatfishes of San Diego county. *Calif. COFI Rep.* **32**, 128–142.
- LAUDER, G. V. (1979). Feeding mechanics in primitive teleosts and in the halecomorph fish *Amia calva*. *J. Zool., Lond.* **187**, 543–578.
- LAUDER, G. V. (1980). Evolution of the feeding mechanisms in primitive actinopterygian fishes: A functional anatomical analysis of *Polypterus*, *Lepisosteus* and *Amia*. *J. Morph.* **163**, 282–317.
- LAUDER, G. V. (1981). Intraspecific functional repertoires in the feeding mechanism of the characoid fishes *Lebiasina*, *Hoplias* and *Chalceus*. *Copeia* **1981**, 154–168.
- LAUDER, G. V. (1983). Functional and morphological basis of trophic specialization in sunfishes (Teleostei, Centrarchidae). *J. Morph.* **178**, 1–21.
- LAUDER, G. V. (1985). Aquatic feeding in lower vertebrates. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 210–229. Cambridge: Harvard University Press.
- LAUDER, G. V. AND LIEM, K. F. (1981). Prey capture by *Luciocephalus pulcher*: implications for models of jaw protrusion in teleost fishes. *Env. Biol. Fish.* **6**, 257–268.
- LAUDER, G. V. AND LIEM, K. F. (1983). The evolution and interrelationships of the actinopterygian fishes. *Bull. Mus. comp. Zool.* **150**, 95–197.
- LIEM, K. F. (1978). Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. I. Piscivores. *J. Morph.* **158**, 323–359.
- NELSON, J. S. (1976). *Fishes of the World*. New York: John Wiley & Sons. 416pp.
- NORMAN, J. R. (1930). *A Systematic Monograph of the Flatfishes (Heterosomata)*, vol. 1, *Psettodidae, Bothidae, Pleuronectidae*. London: British Museum of Natural History. 459pp.
- NORTON, S. F. AND BRAINERD, E. L. (1993). Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. exp. Biol.* **176**, 11–29.
- PACKARD, G. C. AND BOARDMAN, T. J. (1987). The misuse of ratios to scale physiological data that vary allometrically with body size. In *New Directions in Ecological Physiology* (ed. M. E. Feder, A. F. Bennett, W. W. Burggren and R. B. Huey), pp. 216–239. Cambridge: Cambridge University Press.
- RANDALL, J. E., ALLEN, G. R. AND STEENE, R. C. (1990). *Fishes of the Great Barrier Reef and Coral Sea*. Honolulu: University of Hawaii Press. 507pp.
- REGAN, C. T. (1910). The origin and evolution of the teleostean fishes of the order Heterosomata. *Ann. Mag. nat. Hist.* **6**, 484–496.
- RICE, W. R. (1989). Analyzing tables of statistical tests. *Evolution* **43**, 223–225.
- RICHARD, B. A. AND WAINWRIGHT, P. C. (1995). Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): kinematics of prey capture. *J. exp. Biol.* **198**, 419–433.
- WAINWRIGHT, P. C. AND RICHARD, B. A. (1995). Scaling the feeding mechanism of the largemouth bass (*Micropterus salmoides*): motor pattern. *J. exp. Biol.* **198**, 1161–1171.
- WERNER, E. E. (1977). Species packing and niche complementarity in three sunfishes. *Am. Nat.* **111**, 553–578.
- WESTNEAT, M. W. (1990). Feeding mechanics of teleost fishes (Labridae; Perciformes): a test of four-bar linkage models. *J. Morph.* **205**, 269–295.
- WESTNEAT, M. W. (1994). Transmission of force and velocity in the feeding mechanisms of labrid fishes (Teleostei, Perciformes). *Zoomorph.* **114**, 103–118.
- YAZDANI, G. M. (1969). Adaptations in the jaws of flatfish (Pleuronectiformes). *J. Zool., Lond.* **159**, 181–222.