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A Model for Biting in the Pharyngeal Jaws of a Cichlid Fish: *Haplochromis piceatus*

FRIETSON GALIS

University of Leiden, Division of Ecological Morphology and Division of Animal Ecology, P.O. Box 9516, 2300 *RA Leiden, The Netherlands*

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A mathematical model for piercing of prey in the pharyngeal jaws of a cichlid fish is presented to explain prey choice. The model allows simulation of static (pharyngeal) biting forces for various biting point locations and prey sizes. The maximum possible biting forces and the best biting directions were calculated using optimization techniques. The optimization criterion used was the minimization of the total muscular force that is necessary to generate the biting force. The system parameters for the model were obtained from a reconstruction of serial sections and from dissections of an adult *Haplochromis piceatus*.

Experiments were carried out to determine the piercing forces that are generated when natural prey (*Chaoborus* sp. larvae and pupae) are pierced with a lower pharyngeal jaw. These results were compared with data on the feeding behaviour.

The model predicts that at each specific biting point, biting forces can be generated in a range of directions. It predicts that a shift in biting point and or in prey size leads to changes in muscle recruitment. The results of the model clarify a number of morphological features: the twist of the fibres of the m.retractor dorsalis and the presence and position of the two m.m.levatores interni and the m.transversus ventralis. The predictions of the model explain in mechanistic terms an important aspect of the prey choice of *H. piceatus* in the field and in aquarium experiments.

1. Introduction

The pharyngeal jaw apparatus (PJA) of cichlids is a complex musculo-skeletal system formed from modified gill arch elements and within which the food is masticated and transported.

Systematists are interested in the PJA, because most of the characters used in diagnosing the Labroidei are elements of the PJA (e.g. Kaufman & Liem, 1982; Stiassny & Jensen, 1987) and because the great inter- and intra-specific anatomical differentiation of the PJA reflects a great versatility in food-processing functions which has enabled the enormous radiation of cichlids and other Labroidei (Liem & Greenwood, 1981; Kaufman & Liem, 1982; Stiassny & Jensen, 1987; Wainwright, 1988).

Functional morphologists have been concerned with the PJA mainly in two ways. Some have compared the form of the PJA in different trophic groups, discussing the relation between form differences and plausible functional differences, while others have compared electromyographic recordings with cineradiographic data.

Molluscivores have attracted attention in comparison with insectivores, or piscivores because of the much increased size of most elements of the PJA (e.g. Witte

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& Barel, 1976, 1989, 1990; Hoogerhoud & Barel, 1978; Liem & Kaufman, 1984; Meyer, 1987; Wainwright *et al.*, 1989, 1990; Wainwright, 1988).

An important conclusion from such functional morphological comparisons is that small alterations of the structures may lead to profound differences in function.

The occurrence of striking polymorphisms in *Cichlasoma minckleyi*, *C. citrinellum*, *C. managuense* and *Astatochromis alluaudi* has led to studies of the phenotypic plasticity involved in these form differences (Greenwood, 1965; Hoogerhoud, 1986; Meyer, 1987, 1990; Witte *et al.*, 1990).

Comparisons of electromyographic and cinematographic data show considerable intraspecific variation both in muscle action patterns and in movements of the jaws (e.g. Liem, 1973, 1978, 1979; Aerts *et al.*, 1986). Although the ability of fish to alter muscle electrical activity patterns according to the size, position and nature of prey has been demonstrated several times (Ballintijn *et al.*, 1972; Elshoud-Oldenhave & Osse, 1976; Liem, 1978, 1979, 1980; Lauder, 1981, 1983; Sibbing, 1982; Wainwright & Lauder, 1986; Wainwright, 1989) and is viewed as functional, there is still a widespread emphasis and enthusiasm for the stereotypy of muscle action patterns caused by preprogrammed muscle action patterns (e.g. Liem, 1986; Wainwright, 1989; Wainwright *et al.*, 1990; but see Aerts, 1990). However, as intraspecific and intra-individual variation in electromyograms is very large, (e.g. Shaffer & Lauder, 1985; Wainwright, 1986; Wainwright & Lauder, 1986; Sanderson, 1988), this contradicts the importance of stereotypy in muscle action patterns. In addition, mainly large muscles that are easily accessible have been incorporated in the studies and modulation may have been overlooked in cases where smaller, but also relevant muscles were excluded. The schematic representation *per se* of electromyographic data may add to a false impression of stereotypy.

A quantitative biomechanical model is necessary to identify which muscles need to contribute (and how much) to perform a certain action. Moreover in a general sense, such a model is essential to investigate whether a morphological feature provides a performance advantage (Alexander, 1988; Wainwright & Lauder, 1990). Previous work on the pharyngeal jaw apparatus of labroids has only formulated verbal biomechanical models, while only mathematical models can provide such quantitatively testable predictions. The only exception is a model for crushing with the PJA of Caribbean wrasses (Labridae) of Wainwright (1988). However, only one muscle (the m.levator posterior) is involved in this model.

Adult *H. piceatus* specimens feed both on *Chaoborus* larvae and pupae (Witte & Witte-Maas, 1987; Galis, 1990). Small *H. piceatus* specimens [<4 cm standard length (S.L.)] have never been found with *Chaoborus* pupae in their digestive tract, whereas they do eat fourth instar larvae. Since the difference in strength between the cuticula of larvae and pupae seems to be most relevant to the piercing of prey, the piercing of prey was chosen as the function to be analysed in this study. *Chaoborus* larvae in the stomach of *H. piceatus* merely have transversal slits which allow entrance of digestive fluids. These transversal slits are the result of piercing, possibly followed by lateral movements. My hypothesis is that the lack of pupae in the diet of small fish is caused by an inability of the fish to pierce pupae with the PJA.

This study presents a mathematical model that calculates in static equilibrium the individual muscle forces that are necessary to generate a specified (peak) biting force,

at the moment of piercing prey in a specified biting direction. I chose to select the solution of the model that minimizes the total muscle force necessary to generate the biting force, because there are more potentially contributing muscles and reaction forces than required by the model for a unique solution. The rationale is that natural selection favours the minimization of effort necessary to generate biting forces (Seireg & Arvikar, 1973; Alexander, 1981). The model predicts the best biting direction (minimum requirement of muscle force) for a given prey position and size; it predicts the maximum biting force (on the basis of the cross-sectional area of the individual muscles) of the fish and identifies the muscles that should contribute (and by how much) to the piercing. The predicted best biting directions were compared with directions of the teeth on the lower jaw and the predictions of the maximum biting forces were tested with experimentally determined piercing forces. The results were compared with the above mentioned data on the food selection of *H. piceatus*. In this way the prediction of the ability of *H. piceatus* to pierce specific prey items provides an insight into morphological constraints for the feeding behaviour. With this objective in mind, this study was followed by a comparison of an adult with a juvenile (Galis, in press), to identify size and developmental constraints.

2. Material and Techniques

2.1. FISHES

Haplochromis piceatus specimens were caught in the Mwanza Gulf of Lake Victoria (Tanzania) between 1 February 1979 and 29 July 1980, and 2 September 1983 and 28 February 1984. Wild-caught specimens were used for dissection, except for the determination of tooth direction and the dry weight conversion factor (see below) where freshly-killed specimens were used of the F5-generation. Wild-caught specimens were preserved in 70% ethanol after being fixed in 4% formalin.

2.2. RECONSTRUCTION

For a description of the reconstruction techniques see Anker (1974). For a description of an adult specimen (5 cm S.L., 3 ml volume) of *H. piceatus* from serial sections see Galis (1990). The reconstruction (Fig. 1) was extended to the centres of the attachment areas of the m.geniohyoideus, three points of the hyoid (H1, articulation of hyoid and central axis; H2, rostro-ventral contact point of left and right hyoid; H3, articulation of hyoid and interhyal) and a third reference point (R3, the most ventral point on the neurocranium at the place of attachment of the ligament of Baudelot). Errors of measurement due to the reconstruction technique were estimated to be maximally 5% (with the help of reference grooves in the block in which the fish head was embedded, Anker personal communication and see Anker, 1974).

2.3. CROSS-SECTIONAL AREA OF THE MUSCLES

The cross-sectional area of the muscles was calculated by dividing the volume by the average length of the muscle fibres. For a description of the determination of dry

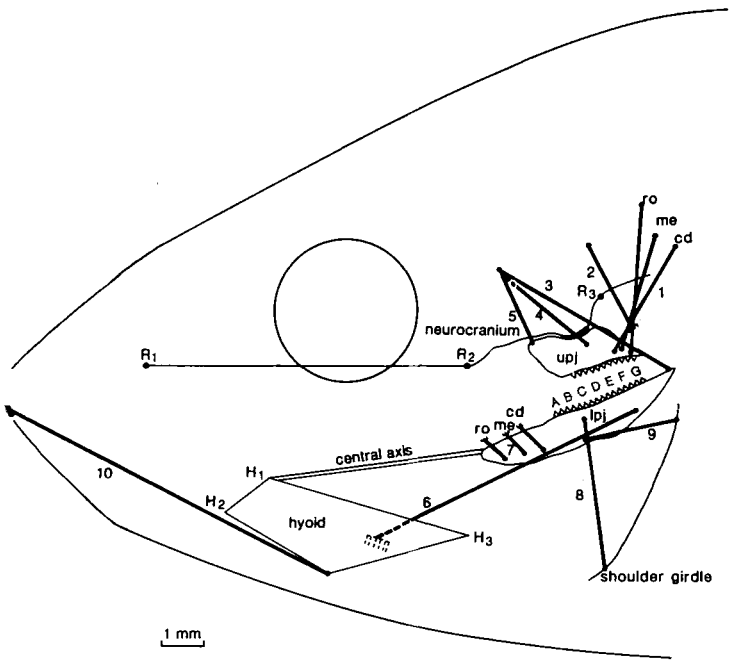

FIG. 1. Projection of muscles and bony elements in the medial plane based on reconstructed points. R1, R2 and R3 are reference points marking the ventral side of the neurocranium: R1 at the point of attachment of the palatine-vomerine notch ligament, R2 at the place of the opening through which the arteria carotica passes and R3 at the point of attachment of the ligament of Baudelot. H1 to 3 are points on the hyoid: H1, tansition of hyoid and central axis; H2, contact point of left and right hyoid; H3, transition of hyoid and interhyal. Numbers mark the lines of action of the following muscles: (1) m.retr.dl. (no, rostral part; me, middle part, cd, caudal part); (2) m.lev.post.; (3) m.lev.ex.4; (4) m.lev.int.lat.; (5) m.lev.int.med.; (6) m.ph.hy.; (7) m.trans.vl. (ro, rostral part; cd, caudal part); (8) m.ph.cleith.ex.; (9) m.ph.cleith.int.; (10) m.geniohy. A–G denote chosen seven prey positions. Note that the m.pharyngohyoideus (6) runs from the LPJ to the urohyal and the m.levator posterior from the neurocranium to epibranchial 4. The rostro-dorsal side of the m.transversus ventralis (7) attaches to ceratobranchial 4.

weight and length see Galis (1990). To calculate fresh weight, dry weight values were multiplied by 7·08. This factor was determined by comparison of the weight of fresh m.sternohyoid tissue and its dry weight after fixation in formalin and ethanol. The specific gravity of the muscles was assumed to be 1·06 when calculating their volume (Alexander, 1958).

2.4. MAXIMUM MUSCLE FORCE

For the maximum isometric muscle stress production, an intermediate value of 2·5 N mm^{-2} was taken from those available in the literature (Weis-Fogh & Alexander, 1977; Altringham & Johnston, 1982; Johnston & Salomonski, 1984).

2.5. COMPUTER SIMULATIONS

Simulations were carried out for 19 biting directions [Fig. 2(a)], three prey thicknesses (0·25, 0·5 and 1 mm) and for seven prey positions or biting points [Fig. 2(e): A–G]. The selected prey thicknesses are 0·25 mm and 0·5 mm, approximately those

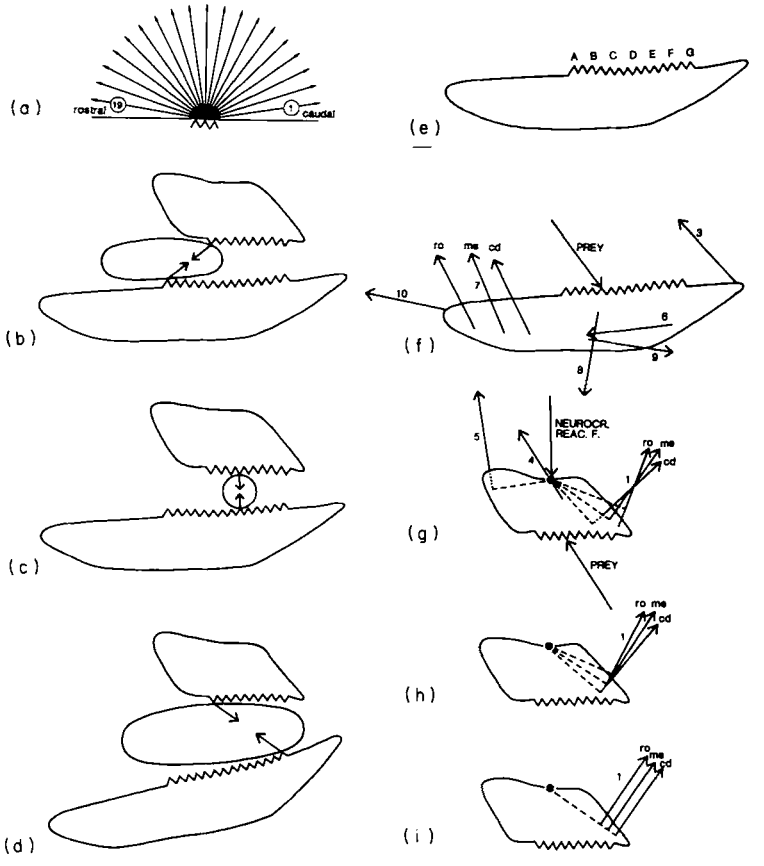

FIG. 2. Simulation scheme. (a) Indicates the 19 choices of biting directions. (b), (c) and (d) are examples indicating forces that are exerted on the prey. The shape of the prey is arbitrarily chosen. (d) Shows the downward rotation of the lower pharyngeal jaw to accommodate a large prey item. (e) Indicates the seven chosen biting points. (f) and (g) show a free-body diagram of the lower pharyngeal jaw and the upper pharyngeal jaw and the forces that are exerted on them. The length of the arrows is arbitrarily chosen. Numbers refer to the lines of action of the muscles: (1) m.retr.dl. (ro, me and cd indicate resp. rostral medial and caudal part); (3) m.lev.ex.4; (4) m.lev.int.lat.; (5) m.lev.int.med.; (6) m.ph.hy.; (7) m.trans.vl.; (8) m.ph.cleith.ex.; (9) m.ph.cleith.int.; (10) m.geniohy. The solid dot in (g), (h) and (i) indicates the rotation centre. The broken lines in (g) indicate the lever arms of the lines of action showing that on the rostral side the m.levator internus lateralis (nr. 4) has the smallest lever arm (negligible) and largest horizontal projection and on the caudal side this is the case for the caudal part of the m.retractor dorsalis. (h) Shows three theoretical lines of action of the m.retractor dorsalis which have lever arms of the same size (broken lines). (i) Shows theoretical parallel lines of action of the m.retractor dorsalis, of which the rostral line of action has the smallest lever arm and horizontal projection and the caudal one the largest lever arm and horizontal projection.

of *Chaoborus* (sp.) larvae and pupae, respectively, when they are compressed at the moment of piercing and 1 mm which coincides with prey piled on top of each other.

2.6. TOOTH DIRECTION

A fresh aquarium specimen with a standard length of 6 cm, was deep frozen in liquid nitrogen and sectioned parallel to the medial plane. The cutting surface was photographed and the directions of the teeth were measured from the medial plane.

2.7. PIERCING FORCE

The force, necessary to pierce a *Chaoborus* larva or pupa, was measured with an Aikoh CPU digital force gauge 7502B. A dry lower pharyngeal jaw was glued (with collall glue) to a movable piston. A Petri dish was placed on a small stationary platform with a live fourth instar *Chaoborus* larva or pupa in a drop of water at its centre. The piston was lowered at a speed of 0·23 mm sec^{-1} such that the larva or pupa was pierced and the peak force was recorded. A low speed was chosen to simulate the likely situation in which food is positioned between the pharyngeal jaws, before the jaws move again to pierce the food. Higher speeds would probably damage the teeth. After determination of the required piercing forces with the force gauge, the results of the computer simulations were converted to values corresponding to a biting force of 0·23 N which is the average force needed to pierce a pupa (see Table 6).

3. Terminology

The terminology follows Barel *et al.* (1975) and Anker (1978) for anatomical terms and Feynman *et al.* (1963) for physical terms.

4. Anatomy and Kinematic Assumptions

4.1. UPPER PHARYNGEAL JAW

The upper pharyngeal jaws are paired. Each consists of a pharyngobranchial 3,4 (of the third and fourth gill arch) that is movably connected with pharyngobranchial 2. Pharyngobranchials 3,4 bear an articulation facet that together with one on the pharyngeal apophysis of the neurocranial base form a synovial joint (i.e. facets separated by fluid). The upper pharyngeal jaw can slide forward and backward along the neurocranium. The position of the upper (and lower) pharyngeal jaw in the reconstructed situation (Fig. 1) is the most rostral one possible. Movement in a dorso-lateral direction is possible, because the articulation cartilage of the neurocranium extends in this direction. The strong interconnections between the third and fourth pharyngobranchials provide that the pharyngobranchials 3,4 function as a single mechanical unit (Barel *et al.*, 1975; Liem, 1978). The transverse muscles of the upper pharyngeal jaw are excluded from this study because they probably do not

contribute to the biting force (in the medial plane, see sections) that is modelled. The remaining muscles that insert on the upper pharyngeal jaw, the m.levator internus medialis [Fig. 2(g): nr. 5], m.levator internus lateralis (nr. 4) and m.retractor dorsalis (nr. 1), have their origin on the neurocranium (Fig. 1). These muscles are all parallel-fibred and their length at the moment of analysis is close to their rest length.

Cineradiographic data show that the mobility of the upper jaws can be independent of the lower paryngeal jaw (Liem, 1973, 1978; Aerts *et al.*, 1986). The transmittance of force of the m.transversus ventralis (attached to the lower jaw and to ceratobranchial 4) via the ceratobranchial 4 and epibranchial 4 to the upper jaw is probably negligible. I expect that the force of the m.transversus ventralis on the ceratobranchial 4 is counteracted by the m.levator posterior (running from the neurocranium to epibranchial 4) as well as by the m.geniohyoideus. The m.geniohyoideus pulls rostrally on the ceratobranchial 4 via the central axis and the hyoid. The m.sternohyoideus (not reconstructed) which pulls caudally on the ceratobranchial 4 via the urohyal is not active in the electromyograms of the insectivorous *H. burtoni* during the power phase (Liem, 1973).

4.2. LOWER PHARYNGEAL JAW

The lower pharyngeal jaw of cichlids is composed of the united fifth ceratobranchials functioning as a single unit (Nelson, 1967). It does not articulate with the shoulder girdle (unlike the lower pharyngeal jaw in Labridae and some Pomacentrids, Liem & Greenwood, 1981; Kaufman & Liem, 1982; Stiassny & Jensen, 1987) and is suspended from the neurocranium by a muscular sling, composed of the m.levator externus 4 [Fig. 2(f): nr. 3] and parts of the m.obliquus posterior (Liem, 1973; Aerts, 1982). The m.levator posterior does not form part of the muscular sling like in labrids and durophagous cichlids and embiotocids (Liem & Greenwood, 1981; Liem, 1986), because it does not insert on the lower pharyngeal jaw. Although the lower pharyngeal jaw is connected with the branchial basket, there is still independent mobility (Liem, 1978; Anker, 1989). The mobility is possible because of a ligamentous connection, involving the central ligament (Anker, 1989). The central axis is anchored by ligaments to the hyoid (Fig. 1: H1; see Anker, 1989 for anatomical details). Movements of the hyoid will be transmitted to the central axis, which via the central axis will elicit movements of the lower pharyngeal jaw. The m.geniohyoideus (nr. 10) runs from the dentary to the hyoid. With the exception of the m.geniohyoideus and the m.levator posterior, the muscles that in this analysis are considered to operate the lower pharyngeal jaw are directly attached to it: the m.levator externus 4 which runs from the neurocranial base to the lower pharyngeal jaw (m.adductor branchialis 5 was considered together with m.levator externus 4, because it is inextricably connected with the tendon of the latter muscle in *H. piceatus*). The m.transversus ventralis (nr. 7) which runs from the ceratobranchial 4 to the lower pharyngeal jaw; the m.m.pharyngocleithralis internus (nr. 9) and externus (nr. 8) which run from the shoulder girdle to the lower pharyngeal jaw; the m.pharyngohyoideus which runs from the lower pharyngeal jaw to the urohyal; the m.levator posterior which runs

from the neurocranium to epibranchial 4, and is connected to the myosept of m.levator externus 4. The muscles are all parallel-fibred and their length at the moment of analysis is close to their rest length, with the exception of the m.geniohyoideus. With the model we explored, whether at high biting forces, the force of the m.levator posterior needs to support the force of the m.levator externus 4 (the force of the m.levator posterior can be transmitted to the ventral horn of the lower pharyngeal element via the epibranchial 4 and connective tissue of the levator externus 4, Anker, 1978).

5. The Model

A static approach was chosen because this avoids complex mathematics while maintaining the essentials for analysing peak muscular forces in mastication. This is reasonable because the forces generated by the muscles during power phases are much higher than the forces due to accelerations of the jaw elements (Weijs, 1980; Otten, 1983). Static equilibrium implies that in x, y and z directions the sum of all forces and that of all torques (moments) equal zero: $\sum F_x=0$; $\sum F_y=0$; $\sum F_z=0$; $\sum T_x=0$; $\sum T_y=0$; $\sum T_z=0$. The model can be reduced to a two-dimensional one because the biting force is modelled in the medial plane and because of the bilateral symmetry around the medial plane of the fish, provided that a correction is made for the angle of the lines of action of the muscles in the third dimension (see conversion factors, Table 2). This reduces the number of equations to three: two for the sum of the forces in x and y directions and one for ther sum of the torques with respect to a rotation centre: $\sum F_x=0$; $\sum F_y=0$; $\sum T=0$. The forces of the ten muscles [Fig. 2 (f) and (g)] are the unknowns. The angles of the lines of actions of the muscles with the x and y axes are known, so the lever arms can be calculated if the centres of rotation are known. There is no unique solution because there are, both for the upper and lower jaw, more unknowns than equations. In the analysis, the solution was searched for that minimizes the total muscular force that is necessary to generate a specified biting force (see section 1). Another possible optimization criterium that we did not explore is the maximization of the biting force (Koolstra *et al.*, 1988; Van Eyden *et al.*, 1990). It is likely that the results would be somewhat different if this optimization criterium had been applied. The linear optimization problem was solved with the SIMPLEX method for linear programming (Dantzig, 1963). This algorithm searches for the minimum or maximum of a linear function that is subjected to linear constraints. The minimum total biting force was calculated for 19 different directions at each prey position and prey thickness (Fig. 2). For each prey position and prey thickness the biting direction was chosen which requires the lowest total muscle force.

5.1. ASSUMPTIONS

(1) The movements of the lower and upper jaw are independent (see section 4). This implies different sets of equations for both jaws. (2) The lines of action

of the muscles are assumed to run through the centres of the attachment areas (Galis, 1990). (3) The lower jaw pushes against the prey and thereby pushes the upper jaw against the neurocranium. The lower jaw must exert a force on the prey that is equal in size, in line and opposite in direction. (4) The position of the upper jaw is held constant. We chose the position found in the reconstructed situation (Fig. 1) because it coincides with the upper jaw position during the power phase of the insectivorous cichlid *H. burtoni*, as determined with cineradiography by Liem (1973). (5) The rotation centre of the upper jaw is kept constant in the middle of the articulation facet with the neurocranium (the point of contact of the upper jaw and the neurocranium). In reality the position of the rotation centre probably varies and may have a somewhat more dorsal position. However, a small change in position (and in direction of the neurocranial reaction force) makes the calculation considerably more complicated and has little influence on the results. (6) The friction co-efficient for the gliding of the upper jaw along the neurocranium is zero. (7) Only biting directions that run through the dental area of pharyngobranchial 3,4 of the upper jaw are considered feasible. The small dental area of pharyngobranchial 2 is not considered because it does not articulate with the skull. (8) The position of the lower jaw is determined by the size and position [Fig. 2(e): A–G] of the prey. The lower pharyngeal jaw is rotated around the tip of the horns until the shortest distance from the contact point to the dental plane of the upper jaw is equal to the prey thickness [Fig. 2(d)]. The point of attachment of the m.transversus ventralis [Fig. 2(f): nr. 7] on ceratobranchial 4 is rotated to the same extent (because the ceratobranchials 4 are similarly rotated). The length of this muscle is not influenced by the rotation. The lengths of the other muscles are hardly influenced by the rotation with the exception of the m.pharyngocleithralis externus (nr. 8). The m.pharyngocleithralis externus cannot contribute much to the biting force because of its position [Fig. 1 and Fig. 2(f)]. (9) The rotation centre of the lower jaw, when biting, is the point of contact with the prey (the lower pharyngeal jaw is suspended in a muscular sling, see section 4). When the prey is damaged such that it does not move anymore, the prey may provide stability to the pharyngeal jaws. When the prey stabilizes the position of the pharyngeal jaws relative to each other, the rotation centre of the lower pharyngeal jaw is the same as that of the upper one. This situation was not explored in the analysis. (10) The force of the m.geniohyoideus is transmitted to the lower jaw via the hyoid and the central axis (see section 4). The force of the m.geniohyoideus [Fig. 1: nr. 10 and Fig. 2(f)] is determined by calculating the projection of the line of action on the central axis. The validity of this approach is debatable, however, because a three-dimensional biomechanical model of this force transmission is lacking. (11) The force of the m.levator posterior (Fig. 1: nr. 2) is calculated by projecting the line of action of this muscle on the line of action of the m.levator externus 4. (12) The position of the ceratobranchials 4 is constant throughout the piercing (see section 4). The muscular force for the stabilization of ceratobranchials 4 is excluded from the analysis. (13) Acceleration and elasticity (see van Leeuwen, 1992) at prey piercing are unimportant because of the slow speed of the piercing.

6. Results

6.1. SIMULATIONS

6.1.1. *Simulations with a single line of action for the m.retractor dorsalis*

The results of these simulations, show that at prey position C, there is a markedly lower sum of the muscular forces than at other prey positions [prey thickness 0·5 mm, Fig. 3, see also Fig. 2(b)]. That from prey position A–B and D–G, the effectivity of biting should be so much lower is surprising. It suggests that one more of the assumptions is an oversimplification. The results in Table 1 demonstrate that when the m.retractor dorsalis [Fig. 2(g): nr. 1 me] is active, either the m.levator internus

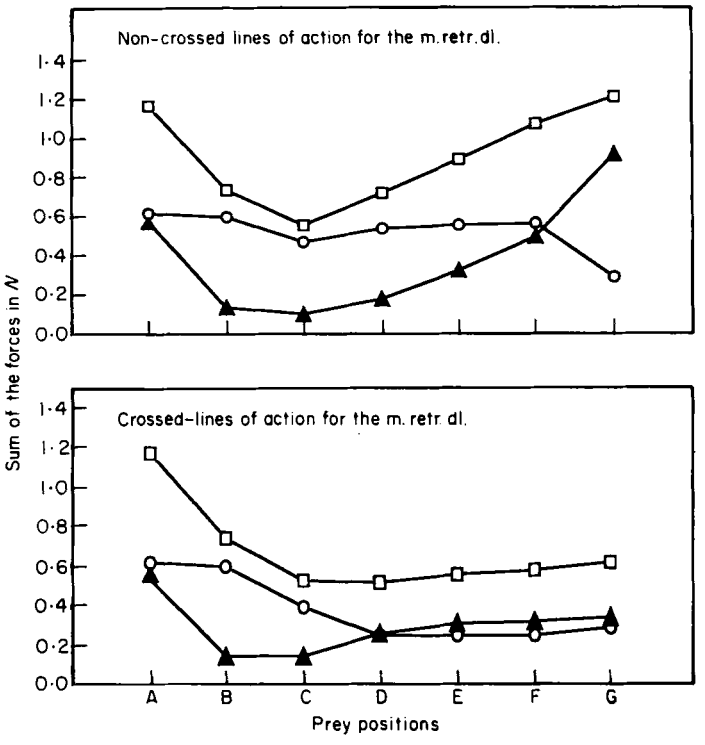

FIG. 3. The total muscle force necessary to generate a biting force of 0·23 N, the muscle force exerted on the lower pharyngeal jaw and on the upper pharyngeal jaw are given at prey positions A–G for simulations with a non-crossed lines of action for the m.retractor dorsalis [upper graph; nr. 1 ro and cd in Fig. 2(i)]. The results of the simulations with a single line of action (nr. 1 me) are virtually the same. The lower graph shows the results for crossed lines of action for the m.retractor dorsalis [nr. 1 ro and cd in Fig. 2(g)]. Prey thickness 0·5 mm. At the prey positions C, D, E and F, the different size of the muscular forces acting on the upper pharyngeal jaw leads to a different biting direction that requires the lowest total muscle force for generating the biting force (the best biting direction). Therefore, at these prey positions the value of the sum of the muscle forces on the upper pharyngeal jaw are different in the upper and lower graph. In this figure it is demonstrated that the total muscle force is considerably lower for crossed lines of action of the m.retractor forsalis at the caudal prey poitions. (□), $\sum F$(lpj+upj); (○), $\sum F$(lpj); (▲), $\sum F$(upj).

TABLE 1

Predicted muscle recruitment for a prey thickness of 0·5 mm. Simulation series with one line of action for the m.retractor dorsalis. Numbers refer to biting directions, such that nr. 1 is the most backward directed and nr. 19 is the most forward directed [see Fig. 2(a)]. This table should be read as follows: at prey position A and in biting directions 1–7 the neurocranial reaction force is selected with the m.levator internus lateralis and medialis etc. It can be seen that the m.retractor dorsalis is never selected without one of the m.m.levatores interni

Biting force generated by the neurocranial reaction force and:	m.lev.int.med.+ m.lev.int.lat. at biting directions nr.	m.retr.dl.+ m.lev.int.lat. at biting directions nr.	m.retr.dl.+ m.lev.int.med. at biting directions nr.
Prey position A	1–7	8–14	15–19
B	1–8	9–13	14–19
C	1–8	9–13	11–19
D	1–9	—	10–19
E	1–8	—	9–19
F	1–7	—	8–19
G	1–6	—	7–19

lateralis (nr. 4) or medialis (nr. 5) must also be active. The m.retractor dorsalis, which has an anti-clockwise torque (seen from the left as in Fig. 1) is incorporated when the torque of the biting force of the lower pharyngeal jaw switches from anti-clockwise to clockwise. It is also incorporated when the horizontal component of the biting force (the component that is parallel to the neurocranium and that is perpendicular to the neurocranial reaction force) switches from a backward direction to a forward one. The m.retractor dorsalis can, only under very restricted conditions, exactly counteract both the clockwise torque and the forward directed horizontal component of the force. As the lever arm of the m.levator internus medialis is large and the horizontal projection of the force is small, this muscle must be active when there remains an excess of torque after compensation of the forward directed horizontal force. The m.levator internus lateralis is included when there is an excess of backward directed horizontal force after compensation of the torque, because its lever arm is negligible and its horizontal projection is large. This combination on the rostral part of the upper pharyngeal jaw of a muscle with a large lever arm and small horizontal projection and a muscle with a small lever arm and a large horizontal projection is effective. The combination is also effective when the torque of the biting force is anti-clockwise and the horizontal component of the biting force is backwards directed. There is always a combination of forces of the m.m.levatores interni that exactly counteracts horizontal force and torque.

6.1.2. *The effect of crossed lines of action for the m.retractor dorsalis*

The effectiveness of the m.retractor dorsalis for biting would be improved were it to consist of two lines of action, one with a large lever arm and small horizontal projection of the force and one with a small lever arm and large horizontal projection of the force. Naturally, one line of action is an oversimplification for a muscle with

such extensive areas of attachment. In order to fulfil the just mentioned demands, the muscle fibres of the m.retractor dorsalis should run either in a V-shape, or they should cross each other. The fibre direction cannot be deduced from the reconstruction. Observation of anatomical preparations shows that the muscle fibres indeed cross (Fig. 4)!

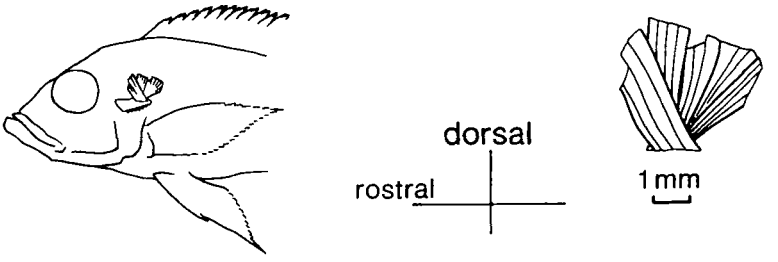

FIG. 4. The position of the m.retractor dorsalis in the fish is indicated in the left figure. The figure to the right shows the fibre direction of the m.restractor dorsalis of an adult specimen (6 cm S.L.), illustrating clearly how the fibres run in different directions.

Inclusion of the crossed lines of action [Fig. 2(g): nr. 1 ro and cd; belonging to parts of the muscle with equal cross-sectional areas] has a drastic effect on the total muscular force (necessary to generate the biting force), at the backward positions of the prey (Fig. 3). At prey position G, the total muscular force is reduced by 49% from 1·21–0·62 N, because the muscular force that is exerted on the upper jaw is reduced from 0·92–0·34 N. At the rather central prey position D the reduction in the total muscle force is still 22% (from 0·72–0·51 N). At the prey positions C, D, E and F the different size of the muscular forces acting on the upper pharyngeal jaw leads to a different biting direction that requires the lowest total muscle force for generating the biting force (the best biting direction; Fig. 3).

If the lines of action (nr. 1 ro and cd) would have a V-shape [Fig. 2(h)] this already substantially reduces the total muscle force: at position G there is a decrease by 32% from 1·21–0·82 N. If the lines of action would be parallel as in Fig. 2(i) there is hardly any reduction (±1%) and the caudal part is always selected, because it has the largest lever arm. In this case it would be difficult to explain the extension of the m.retractor dorsalis in rostral direction, that results in a more vertical position of this muscle in adults of *H. piceatus* than in juveniles (Galis, 1990). A large rostral extension and twisted muscle fibres are found in the m.retractor dorsalis of the piscivorous *H. squamipinnis* and the molluscivorous *H. mylodon* (Hoogerhoud & Barel, 1978: fig. 3) and *A. alluaudi* (Smits, personal communication). The muscle fibres are less twisted in the insectivorous *H. iris* (Smits, personal communication). With the crossed lines of action, the rostral extension can be explained as an addition of a component with a large lever arm and small horizontal projection.

To be consistent, the effect of several lines of action was also determined for the m.tansversus ventralis, another muscle with large attachment areas [Figs 1 and 2(f)]. The effect of this division is much smaller, as will be discussed below. Such a division of lines of action was not carried out for the m.pharyngocleithralis externus, because

this muscle is never selected in the simulations. This muscle probably plays a role in lowering of the lower pharyngeal jaw (Liem, 1973).

6.2. LOWER PHARYNGEAL JAW

6.2.1. *Predictions of muscle activity patterns*

At most prey positions, mm.levator externus 4 [Fig. 2(f): nr. 3] transversus ventralis (nr. 7) and pharyngo-cleithralis internus (nr. 9) are predicted to be the best combinations over a large range of directions [Fig. 5(a), (b), (c), (d) and (e)]. The m.pharyngocleithralis internus functions only to counteract an excess of force in rostral direction. In more forward biting directions [higher number, Fig. 2(a)], where this function is not necessary, the m.m.geniohyoideus (nr. 10, via the central axis), levator externus 4 and transversus ventralis are active [Fig. 5(b), (c), (d) and (f)]. In even more forward biting directions at caudal prey positions, the m.transversus ventralis is not active and either the m.pharyngohyoideus (nr. 6) is active together with the m.m.geniohyoideus and levator externus 4 [prey thickness 0·5 mm and 1 mm, Fig. 5(d) and (f)] or the m.pharyngocleithralis internus (prey thickness 0·25 mm and caudal prey positions, Fig. 5(b)]. At prey position G and prey thickness 0·5 mm [Fig. 4(d)], the m.pharyngocleithralis internus is active instead of the m.geniohyoideus in the most forward biting directions. In the situation where the lower jaw is downward rotated to the largest extent [position G at prey thickness 1mm, Fig. 5(f)], mm.levator externus 4, pharyngocleithralis internus and geniohyoideus are active and in more backward directions, the m.m.pharyngohyoideus, levator externus 4 and geniohyoideus are active. The position and direction of the line of action of the caudal part of the m.transversus ventralis (nr. 7 cd) is nowhere an improvement compared to the middle part, but activity of the more rostral line of action (nr. 7 ro) is an improvement in the best biting directions of position B to E at prey thickness 1 mm. Although this muscle also has large attachment areas (Galis, 1990) the improvement is not so drastic as the improvement for the m.retractor dorsalis in the caudal prey positions and reduces the muscle force that is exerted on the lower jaw by 7–11%. Contrary to the m.retractor dorsalis, the muscle fibres of the m.transversus ventralis run more or less parallel. The m.levator posterior is never active, because the maximum force of the m.levator externus 4 is always sufficient (see below).

6.2.2. *Best biting direction*

Most muscles that contribute to the biting force act in a forward (rostro-dorsad) direction on the lower pharyngeal jaw: mm.levator externus 4, transversus ventralis, geniohyoideus and pharyngohyoideus [Fig. 2(g)]. Therefore, the best biting direction (lowest sum of the muscle forces) for the lower pharyngeal jaw is usually pointing in a forward direction (broken lines in Fig. 5 and Table 2). Only the m.pharyngocleithralis internus is directed backward. The best biting direction is only backward when there are no forward biting directions feasible [prey positions A and B, Fig. 5(e) and Table 2]. The best biting direction for the lower pharyngeal jaw changes

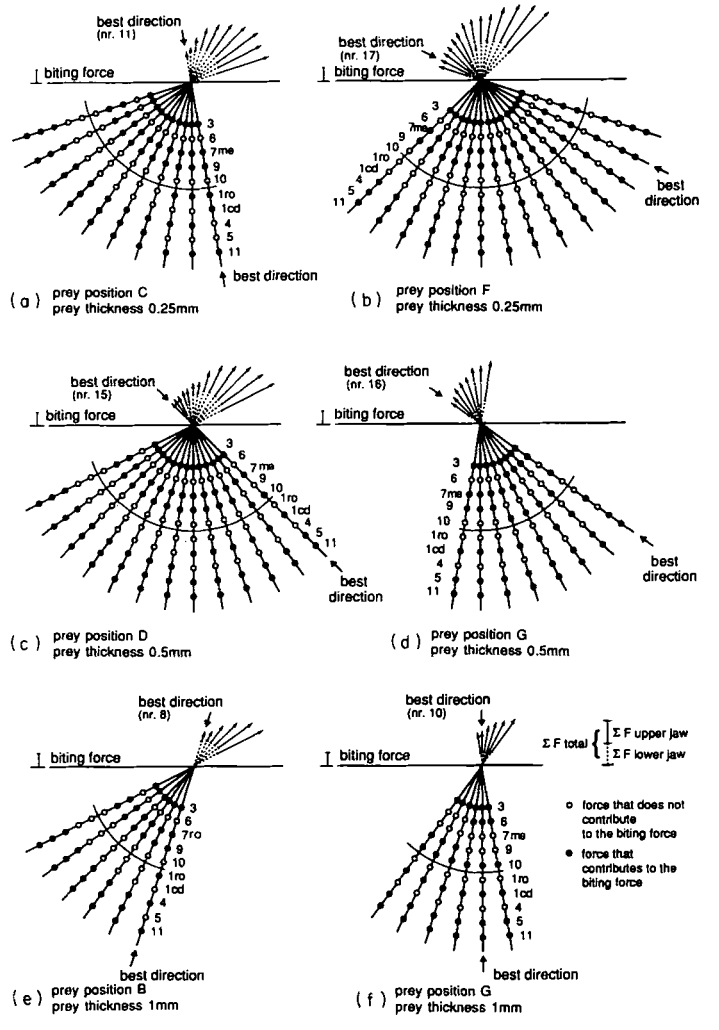

FIG. 5. Force diagrams indicating (1) the contributing forces and (2) the feasible biting directions as indicated by arrows (of which the lines of action intersect the tooth surface of the upper jaw). The directions of the arrows refer to the directions indicated in Fig. 2(a). The length of the arrows indicates the muscular force that is exerted on the lower jaw (broken part of the arrow) and upper jaw (solid part) and the total muscular force necessary to generate the biting force (entire arrow). The best direction is the one of which the total muscular force is minimal. The size of the biting force (vertical bar) can be freely chosen because of the linear relationship between the forces. The solid points indicate active muscles, the open points indicate inactive muscles. The abbreviations refer from top to bottom to: m.levator externus 4 (nr. 3); m.pharyngohyoideus (nr. 6); m.transversus ventralis (nr. 7; ro, rostral part; me, middle part; cd, caudal part); m.pharyngocleithralis internus (nr. 9); m.geniohyoideus (nr. 10); m.retractor dorsalis (nr. 1; ro, rostral part; cd, caudal part); m.levator internus lateralis (nr. 4); m.levator internus medalis (nr. 5); the neurocranial reaction force. Diagrams (a)–(f) are examples of four prey positions and thicknesses.

TABLE 2

The best biting directions for the lower pharyngeal jaw, the upper pharyngeal jaw and for both jaws combined, indicated with a number as indicated in Fig. 2. The best biting direction changes with a more backward prey position towards a more forward direction (prey position G and prey thickness 1 mm excepted)

	Best biting direction (nr.)						
Prey positions	A	B	C	D	E	F	G
Prey thickness 0·25 mm							
Lower jaw	—	8	11	16	17	17	15
Upper jaw	—	8	10	10	10	17	19
Both jaws	—	8	11	14	14	17	17
Prey thickness 0·5 mm							
Lower jaw	3	9	12	15	15	14	14
Upper jaw	5	9	9	10	15	16	16
Both jaws	5	9	12	15	15	16	16
Prey thickness 1 mm							
Lower jaw	3	8	10	11	11	11	9
Upper jaw	6	8	8	10	11	12	11
Both jaws	6	8	8	11	11	12	10

with increasing prey thickness towards a less forward direction [lower number in Fig. 2(a)]. This is mainly because at a larger prey thickness the lower pharyngeal jaw is rotated downward to a larger extent [see section 5, assumption 9, illustrated in Fig. (8)], with the effect that all 19 biting directions are rotated more forward relative to the position of the fish.

6.3. UPPER PHARYNGEAL JAW

6.3.1. *Predictions of muscle activity patterns*

The optimization criterion that determines the best muscle action pattern is the minimization of the total muscular force necessary to generate the biting force. As the neurocranial reaction force [Fig. 2(h)] does not contribute to the muscular force, this force is always selected in the simulations and maximally used.

The neurocranial reaction force has no torque because its line of action passes through the rotation centre [Fig. 2(h)]. There is a single situation where no muscular force is necessary and the neurocranial force is the only one necessary to counteract the biting force of the lower jaw on the prey. This is when the biting force is in line with and opposite to the neurocranial reaction force (the biting force has no horizontal component and no torque).

In the most backward biting directions both m.m.levatores interni (nr. 4 and 5) are active to counteract the anti-clockwise torque and the horizontal component of the biting force, at all prey positions and sizes. In more forward directions, m.m.levator internus medialis (nr. 5) and retractor dorsalis caudalis (nr. 1 cd) are active in the central and caudal prey positions [D–G at prey thickness 0·25 mm and 0·5 mm,

Fig. 5(b), (c) and (d) and positions C–G at prey thickness 1 mm, Fig. 5(f)], while m.m.retractor dorsalis rostralis and levator internus lateralis are active in the remaining, more rostral positions [Fig. 5(a) and (e)]. In the most forward directions, the rostral and caudal lines of action of the m.retractor dorsalis (nr. 1 ro and cd) are selected, for prey thickness 0·5 mm and 1 mm (non-feasible directions) and for prey thickness 0·25 mm at position A–C [Fig. 5(a)]. At a prey thickness of 0·25 mm (where the lower pharyngeal jaw is least rotated downwards) and at the caudal prey positions D–G, the switch to both the rostral and caudal line of action of the m.retractor dorsalis does not occur. At the rostral positions B and C, the switch to the rostral component of the m.m.retractor dorsalis and levator internus lateralis is followed by another switch in the most forward directions, to the m.levator internus medialis and the caudal part of the m.retractor dorsalis.

Thus, the neurocranial reaction force is always combined with one line of action that has a large lever arm and small horizontal force component and one that has a small lever arm and a large horizontal force component.

6.3.2. *Best biting directions*

A vertical biting direction with respect to the tooth surface [Fig. 2(a): nr. 10] combined with a central prey position requires very low muscle forces for the upper jaw [Fig. 5(a)]. This is true for all three prey thicknesses (Fig. 6, solid lines). A forward biting direction is the best for all prey sizes at caudal prey positions and a

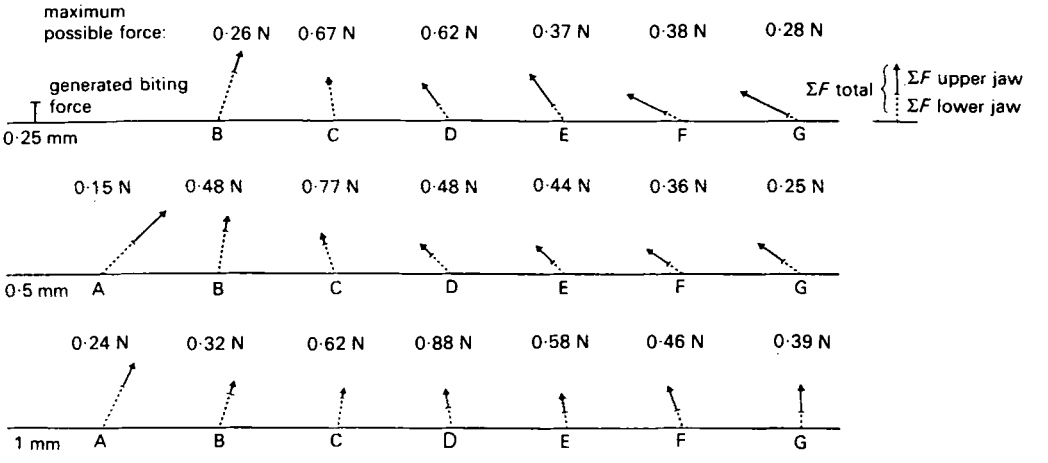

FIG. 6. The best biting direction as indicated by arrows (the direction for which the total muscular force necessary to generate the biting force is minimal, see Fig. 5, for prey thicknesses 0·25 mm, 0·5 mm and 1 mm at all prey positions (A–G). The directions of the arrows refer to the directions indicated in Fig. 2(a). The length of the arrows indicates the muscular force that is exerted on the lower pharyngeal jaw (broken part of the arrow) and upper pharyngeal jaw (solid part) and the total muscular force (entire arrow). The maximum possible biting forces, based on cross-sectional area of the muscles, are indicated above the arrows. The size of the biting force can be freely chosen because of the linear relationship between the forces.

backward biting direction is the best at rostral prey positions (Table 2); this is to be expected in view of the small size of the torque. At rostral and caudal prey positions a considerable horizontal component of the biting force has to be counteracted, which results in higher total muscular forces than at the central prey positions (Fig. 6, solid lines).

6.4. BEST BITING DIRECTIONS FOR THE ENTIRE PHARYNGEAL JAW APPARATUS

Summation of the muscle forces on the lower and upper pharyngeal jaw in feasible directions (of which the lines of action intersect the tooth surface of the upper pharyngeal jaw) leads to best biting directions that point backward at rostral prey positions and point forward at the remaining prey positions (Fig. 6 and Table 2). A single exception exists: a vertical direction for the most caudal prey position G at a prey thickness of 1 mm. However, the two best biting directions are the most forward biting directions among the set which are feasible [see the two shortest arrows in Fig. 5(f)].

6.5. PREY POSITION

The best prey position for biting is in the centre of the dental area, that is positions C and D for prey thicknesses 0·25 and positions C, D and E for prey thickness 0·5 mm and 1 mm (Fig. 6). Although *Chaoborus* larvae and pupae are extremely agile, which limits the potential for positioning of the prey, it seems unlikely that the fish will exert much force at the most rostral and caudal positions. Transport of the prey and holding the prey within the jaws seem to be more likely functions of the teeth at these positions. Another possibility is that the fish does bite the prey with the rostral teeth when the lower pharyngeal jaw (and all the prey positions) is in a more backward position. For a prey thickness of 0·5 mm, the translation of the lower pharyngeal jaw in a backward direction such that the prey position B is moved to the original prey position C, makes biting at position B more effective compared to the original position B. Even so 4% more muscle force is necessary than in the original prey position C. Translation of prey position A to the original prey position C leads to a total muscle force that is also lower, but 8% higher than at the original position C. A backward translation of prey position G similar in size as the translation from position A to B is disadvantageous because the total muscle force increases by 50% and by 3600% if the upper jaw is also translated in a similar way. A rostral translation of prey position G to the original prey position F is not possible because the position of the lower pharyngeal jaw is the most rostral one possible (see section 4).

6.6. PREY THICKNESS

With increasing prey thickness, the total muscular force necessary to generate a specified biting force decreases at all prey positions (Fig. 6). The effect is least in the central positions that are most suitable for biting. The position of the jaws at the two smallest prey thicknesses (0·25 and 0·5 mm) approaches the situation when one

larva or pupa is eaten. In aquaria several pupae and or larvae are eaten at the same time and stored in the buccal cavity (Galis & de Jong, 1988; Galis, 1990). It is unclear whether prey mastication between the jaws happens one by one in a single layer, or whether several prey are piled on top of each other (prey thickness 1 mm in the simulations). Experiments with cineradiography were thus far not successful in providing the answer to this question. Piling of larvae or pupae is predicted by the model to reduce the muscular force required for biting.

6.7. MAXIMUM BITING FORCE

The maximum possible biting force (based on cross-sectional area of the muscles) is largest at the prey positions that require the least amount of muscle force for biting (prey positions C and D, see Fig. 6). The muscle that most limits the maximum biting force involves the lower pharyngeal jaw on nine occasions, and the upper pharyngeal jaw on 11 (Table 3). This suggests that at least for biting, the capabilities of the upper and lower jaw are matched.

TABLE 3

The most limiting muscle for the maximum possible biting force is given for prey position A–G and prey thicknesses 0·25 mm, 0·5 mm and 1 mm. The most limiting muscle belongs almost as often to the lower pharyngeal jaw as to the upper pharyngeal jaw. This suggests that at least for biting, the capacities of both pharyngeal jaws are matched

		Limiting muscles, belonging to lower (l) or upper (u) jaw		
Prey thickness		0·25 mm	0·5 mm	1 mm
Prey position	A	—	m.lev.int.lat. (u)	m.lev.int.lat. (u)
	B	m.trans.vl. (l)	m.lev.int.lat. (u)	m.trans.vl.ro. (l)
	C	m.trans vl. (l)	m.trans.vl. (l)	m.trans.vl.ro. (l)
	D	m.lev.ext.4 (l)	m.retr.dl.cd. (u)	m.trans.vl.ro. (l)
	E	m.lev.int.med. (u)	m.retr.dl.cd. (u)	m.retr.dl.cd. (u)
	F	m.lev.int.med. (u)	m.ph.hy. (l)	m.retr.dl.cd. (u)
	G	m.lev.int.med. (u)	m.ph.hy. (l)	m.retr.dl.cd. (u)

6.8. DIRECT AND INDIRECT TESTS OF THE MODEL

6.8.1. *Quantitative importance of muscles*

The relative contribution of muscles to the biting force changes with prey position, prey thickness and biting direction and is indicated (see Table 5). Comparison of these results that are predicted by the model with the maximum force that can be produced by the muscles reveals that the strongest muscles, the m.retractor dorsalis, m.levator externis 4 and m.transversus ventralis (Table 4), generate for the major part the biting force in the best biting directions at the central prey positions (positions C and D for prey thicknesses 0·25 and positions C, D and E for prey thickness 0·5 mm and 1 mm, Fig. 6). The m.geniohyoideus only contributes much at prey position D

TABLE 4

Maximum possible force based on cross-sectional area for each muscle (on one side) and the factor for converting muscle forces to forces in the x, y plane. This conversion factor is the cosinus of the angle between the line of action and its projection on the medial plane for all muscles except for the m.geniohyoideus, where it is the projection on the central axis (see section 5). The conversion factor is rather high for most muscles and low for the m.levator internus medialis, the m.transversus ventralis and the m.pharyngocleithralis internus

Muscles	Max. force (N)	Conversion factor	Max. force in medial plane (N)
m.retr.dl.	0·88	1·00	0·88
m.lev.ex.4	0·36	0·98	0·35
m.lev.int.lat.	0·14	0·87	0·12
m.lev.int.med.	0·22	0·61	0·13
m.ph.hy.	0·11	0·99	0·11
m.trans.vl.	0·36	0·71	0·26
m.ph.cleith.int.	0·30	0·77	0·23
m.geniohy.	0·91	0·82	0·75

and E at a prey thickness of 0·5 mm (and at the less favourable prey positions F and G at a prey thickness of 0·25 mm). It is also a strong muscle but it is not directly attached to the lower pharyngeal jaw (Fig. 1) and its contribution to the biting of the pharyngeal jaws is only one of its many functions (van Dobben, 1935; Osse, 1969; Anker, 1974).

6.8.2. *Tooth direction*

The directions of the teeth (Fig. 7) coincide well with the best biting directions at the different prey positions (Fig. 6). The directions of the teeth may also function to keep the prey within the dental area of the jaws. This is not investigated in this paper.

6.8.3. *Forces necessary for piercing of prey*

The force that is necessary to pierce a *Chaoborus* larva is on average lower than that for a pupa (Table 6). Intuitively, this result can be expected because the strength of the cuticula of the pupa is larger than that of a larva. *Haplochromis piceatus* feeds in nature both on *Chaoborus* larvae and pupae (Witte & Witte-Maas, 1987; Galis, 1990). The variability in the experimentally determined piercing forces is not surprising owing to the variability in the age of the fourth instar larvae and pupae. Older larvae and pupae are stronger and, therefore, more difficult to pierce. Another source of variation is the position of the prey relative to the lower jaw. The prey wriggles a lot and standardization of the prey position in the experiments is therefore not possible. Tooth size and shape vary with position on the pharyngeal jaws (Witte & Witte-Maas, 1987) and therefore the position of the prey on the lower pharyngeal jaw must also have influenced the size of the piercing forces in the experiments.

TABLE 5

Muscle recruitment and the contributions of the individual muscles and the neurocranial reaction force in the medial plane to a biting force of 0·23 *N only in the best direction (see arrows in Fig.* 6) *(in N and in percentages of the muscular force of the lower and upper pharyngeal jaw). Simulations with crossed lines of action for the m.retractor dorsalis. It can be seen that changes in the prey thickness and position lead to different combinations of active muscles*

Prey positions		A N	A %	B N	B %	C N	C %	D N	D %	E N	E %	F N	F %	G N	G %
Prey thickness 0·25 mm															
Best direction nr.				8		11		14		14		17		17	
Lower jaw	m.lev.ex.4	—	—	0·10	19·4	0·15	36·5	0·15	65·2	0·17	73·7	0·12	46·7	0·13	51·4
	m.ph.hy.	—	—	0	0	0	0	0	0	0	0	0	0	0	0
	m.trans.vl.	—	—	0·20	38·8	0·15	36·5	0·08	32·6	0·06	25·6	0·01	4·1	0	0
	m.trans.vl.ro.	—	—	0	0	0	0	0	0	0	0	0	0	0	0
	m.ph.cleith.int.	—	—	0·22	41·8	0·11	27·7	0	0	0	0	0	0	0·01	0·2
	m.geniohy.	—	—	0	0	0	0	0·01	2·3	0·01	0·7	0·12	49·2	0·12	48·4
Upper jaw	m.retr.dl.ro.	—	—	0	0	0·03	71·3	0	0	0	0	0	0	0	0
	m.retr.dl.cd.	—	—	0	0	0·01	28·7	0·18	75·2	0·19	58·2	0·29	68·2	0·31	68·2
	m.lev.int.lat.	—	—	0·18	83·1	0	0	0	0	0	0	0	0	0	0
	m.lev.int.med.	—	—	0·04	16·9	0	0	0·06	24·8	0·14	41·9	0·14	31·8	0·18	37·9
	neur.react.force	—	—	0·39	0	0·26	0	0·28	0	0·46	0	0·44	0	0·49	0

Prey thickness 0·5 mm														
Best direction nr.		5		9		12		15		15		16		16	
Lower jaw	m.lev.ex.4	0·04	7·2	0·10	21·6	0·13	42·3	0·13	52·8	0·14	58·6	0·12	47·4	0·11	39·0
	m.ph.hy.	0	0	0	0	0	0	0	0	0·01	0·9	0·11	44·4	0·16	57·5
	m.trans.vl.	0·20	40·3	0·20	41·8	0·13	40·8	0·04	16·1	0	0	0	0	0	0
	m.trans.vl.ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	m.ph.cleith.int.	0·26	52·5	0·17	36·7	0·05	16·9	0	0	0	0	0	0	0·01	3·5
	m.geniohy.	0	0	0	0	0	0	0·08	31·1	0·10	40·5	0·02	8·2	0	0
Upper jaw	m.retr.dl.ro.	0	0	0·03	26·6	0·05	36·6	0	0	0	0	0	0	0	0
	m.retr.dl.cd.	0	0	0	0	0·09	63·8	0·23	96·9	0·25	88·1	0·29	92·8	0·30	92·3
	m.lev.int.lat.	0·31	70·9	0·09	73·4	0	0	0	0	0	0	0	0	0	0
	m.lev.int.med.	0·13	40·3	0	0	0	0	0·01	3·1	0·03	11·9	0·02	7·2	0·02	7·7
	neur.react.force	0·53	0	0·33	0	0·32	0	0·31	0	0·33	0	0·30	0	0·32	0
Prey thickness 1 mm															
Best direction nr.		6		8		10		11		11		12		10	
Lower jaw	m.lev.ex.4	0·04	9·0	0·10	25·3	0·11	30·6	0·14	53·1	0·15	66·8	0·14	57·3	0·14	58·2
	m.ph.hy.	0	0	0	0	0	0	0	0	0	0	0·06	25·7	0·08	30·6
	m.trans.vl.	0·21	42·8	0	0	0	0	0	0	0	0	0	0	0	0
	m.tranns.vl.ro.	0	0	0·16	39·9	0·13	36·4	0·10	38·74	0·06	27·0	0	0	0	0
	m.ph.cleith.int.	0·23	48·2	0·14	34·7	0·12	33·0	0·02	8·2	0	0	0	0	0	0
	m.geniohy.	0	0	0	0	0	0	0	0	0·01	6·2	0·04	16·9	0·03	11·2
Upper jaw	m.retr.dl.ro	0	0	0·04	37·1	0·01	46·6	0·04	20·4	0	0	0	0	0	0
	m.retr.dl.cd.	0	0	0	0	0	0	0·14	79·6	0·19	96·9	0·23	88·2	0·27	91·6
	m.lev.int.lat.	0·19	79·3	0·07	62·9	0·01	53·4	0	0	0	0	0	0	0	0
	m.lev.int.med.	0·05	20·7	0	0	0	0	0	0	0·01	3·0	0·03	11·8	0·02	8·4
	neur.react.force	0·41	0	0·32	0	0·25	0	0·32	0	0·31	0	0·34	0	0·32	0

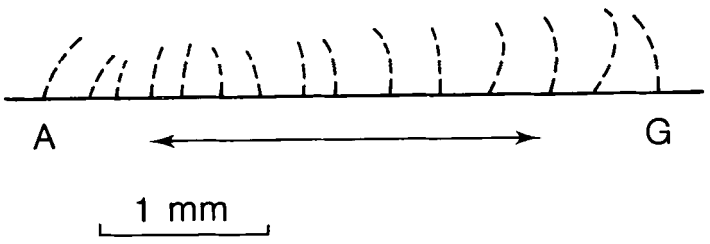

FIG. 7. Longitudinal section through the medial plane showing the size and direction of teeth (from base to tip) on the lower pharyngeal jaw. A and G denote prey positions [see Fig. 2(b)]. These results correspond well with the results shown in Fig. 6.

TABLE 6

Force necessary for piercing Chaoborus *larvae and pupae. Measured with a lower jaw glued on a force gauge*

	Range of piercing forces	Average piercing force	*n*
Chaoborus larvae	0·07 N–0·23 N	0·13 N	20
Chaoborus pupae	0·15 N–0·31 N	0·23 N	20

6.8.4. *Ability of the fish to pierce prey*

The maximum biting forces predicted by the model (before the experiments were carried out) show that the fish is able to pierce both prey types (Fig. 6 and Table 6).

6.8.5. *Comparison with electromyographical data of* Haplochromis burtoni

We compared the predictions of the model with electromyographical data of the insectivorous *H. burtoni* when feeding on frozen (immobile!) *Gammarus* sp. (Liem, 1973). At the end of phase 1a, which most likely coincides with the piercing, the following muscles are active: m.levator externus 4 (very strong), m.retractor dorsalis and m.levator posterior (weakly) and possibly m.pharyngocleithralis internus (weakly) and m.geniohyoideus. The m.levatores interni and m.transversus ventralis are not included in the analysis. As far as conclusions are possible on the basis of only one phase of the electromyogram and one generalized diagram, the results are in agreement with our predictions.

7. Conclusions and Discussion

The good agreement between the results of the simulations and the direct and indirect tests show that this model can be applied with some confidence. The model clarifies a number of features hitherto not understood, such as the complicated twisted nature of the fibres of the m.retractor dorsalis. This twist has not received attention before. The twist enables subdivision of the muscle into a part with a large lever arm and a small horizontal projection and one with a small lever arm and a large horizontal projection. The resulting increase in biting effectivity is much higher than without the twist. The

model thus provides a functional explanation for the more vertical angle of this muscle in some species and ontogenetic stages (see Galis, 1990). For the same reason, the model clarifies the presence of two, instead of one, m.m.levatores interni and the position of both these muscles. For the lower pharyngeal jaw, it shows that the recruitment of the force of the m.m.levator externus 4, the transversus ventralis, the pharyngocleithralis internus and the m.geniohyoideus are often necessary for the pharyngeal bite of *H. piceatus*. The recruitment of the m.pharyngohyoideus is necessary in some biting directions. The m.transversus ventralis has thus far not been included in functional morphological analyses of the pharyngeal jaw apparatus and the m.pharyngocleithralis internus has often not been included in analyses of biting. Our results support the view that the PJA is a highly flexible system (Liem, 1973; Liem & Osse, 1975; Greenwood, 1984) which is supposed to be of great importance for the impressive adaptive radiation of the cichlids. The results of the model show that the pharyngeal jaw apparatus can generate biting forces in a wide range of directions at specific biting points and at different positions of the lower jaw (Figs 5 and 6). This flexibility provides robustness for the model, since adjustments to small changes in biting direction, jaw position and/or prey position can be made by the fish with small force modulations and sometimes by changes in the muscle recruitment. Flexibility of the PJA in combination with peripheral sensory feedback is essential when dealing with agile prey like *Chaoborus* larvae and pupae.

7.1. MUSCLE MODULATION

The results of this study and that of Aerts (1990) suggest that the current emphasis of the stereotypy of muscle modulation and preprogammed motor patterns is exaggerated for cichlids and possibly also for other fish. In the central part of the dental area, that is most suitable for biting, a small shift in biting point (e.g. from prey position C to D) has to lead to a shift in muscle recruitment. The shift from the m.transversus ventralis to the m.pharyngohyoideus could not be noticed in electromyograms, because the m.transversus ventralis has until now been excluded from the analyses. Furthermore, when the m.pharyngocleithralis internus is excluded, like in the study of Liem (1978), the shift from the m.pharyngocleithralis internus to the m.geniohyoideus cannot be found. The activity of the m.m.levatores interni is difficult to measure because of their small size and medial position and is therefore excluded from electromyogram studies. This also leads to missed shifts in muscle recruitment. Finally, if the electromyographic activity of the m.retractor dorsalis is measured at only one point, more modulation is missed if our hypothesis of the different lines of action is true. Part of the extreme variability that is found in electromyographical data may therefore be explained by functional muscle activity modulation. The predictions on muscle recruitment must be tested with electromyography. In conclusion, a quantitative biomechanical model is a necessary tool for the design of experiments, because intuition alone does not lead to the selection of the relevant features.

IMPLICATIONS FOR OTHER SPECIES

The model can easily be adapted for other cichlids. An important difference between insectivores (*H. piceatus*) on the one hand and molluscivorous cichlids (and

embiotocids) on the other, is the insertion of the m.levator posterior. Part of this muscle continues past the epibranchial 4 and inserts on the lower pharyngeal jaw in the latter fish (Liem, 1986). One part still inserts on the epibranchial 4 and probably counteracts the ventrad directed force of the m.transversus ventralis on the ceratobranchial 4. The consequence of the insertion on the lower pharyngeal jaw is an extra available muscle for the generation of biting force by the lower jaw. The m.levator posterior runs in a considerably more vertical direction than the other muscles of the lower pharyngeal jaw (Fig. 1). The best biting directions will therefore be more vertical and inclusion of the m.pharyngocleithralis internus (for compensation of forward directed forces) will be necessary less often. The best biting direction based on tooth directions in molluscivores will also be vertical because the main direction of the molariform teeth is not forward (like most teeth of *H. piceatus*) but vertical. The inclusion of the m.levator posterior is therefore, advantageous for crushing molluscs not only because of its extra force when attached to the lower jaw but also because of its vertical position. Extension of this model to three-dimensional movements will be useful in analysing the more complicated movements of the pharyngeal jaws in molluscivores (Smits, in preparation).

Further evidence for the validity of the model comes from a parallel study on a juvenile specimen (Galis, in press). As in the present study, the prey-piercing capability of the PJA that is predicted on the basis of the natural diet and feeding experiments is confirmed by the comparison of calculated maximum biting forces with measured piercing forces. This shows that the biomechanical model provides an insight into the role of morphology in explaining patterns of resource use by revealing constraints and possibilities of the feeding behaviour.

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REFERENCES

AERTS, P. (1982). Development of the musculus levator externus IV and the musculus obliquus posterior in *Haplochromis elegans* Trewavas, 1933 (Teleostei: Cichlidae): a discussion on the shift hypothesis. *J. Morph.* **173,** 225–235.

AERTS, P. (1990). Variability of the fast suction feeding process in *Astatotilapia elegans* (Teleostei: Cichlidae): a hypothesis of peripheral feedback control. *J. Zool., Lond.* **220,** 653–678.

AERTS, P., DE VREE, F. & VANDEWALLE, P. (1986). Pharyngeal jaw movements in *Oreochromis niloticus* (Teleostei:- Cichlidae): preliminary results of a cineradiographic analysis. *Annls. Soc. R. zool. Belg.* **116,** 75–82.

ALEXANDER, R. MCN. (1958). The densities of Cyprinidae. *J. exp. Biol.* **36,** 333–340.

ALEXANDER, R. MCN. (1981). Mechanics of skeleton and tendons. In: *Handbook of Physiology. Section I: The Nervous System.* Vol. II: *Motor control* (Brooks, V. B., ed.) Bethesda, MO: American Physiological Society.

ALEXANDER, R. MCN. (1988). The scope and aims of functional and ecological morphology. *Neth. J. Zool.* **38,** 3–22.

ALTRINGHAM, J. D. & JOHNSTON, I. A. (1982). The pCa-tension and force-velocity characteristics of skinned fibres isolated from fish fast and slow muscles. *J. Physiol. Lond.* **333,** 421–449.

ANKER, G. C. (1974). Morphology and kinetics of the head of the stickleback *Gasterasteus aculeatus*. *Trans. zool. Soc. Lond.*, **32**, 311–416.

ANKER, G. C. (1978). The morphology of the head-muscles of a generalized *Haplochromis* species: *H. elegans* Trewavas 1933 (Pisces, Cichlidae). *Neth. J. Zool.* **28**, 234–271.

ANKER, G. C. (1989). The morphology of joints and ligaments in the head of a generalized *Haplochromis* species: *H. elegans* Trewavas 1923 (Teleostei, Cichlidae). *Neth. J. Zool.* **39**, 1–40.

BALLINTIJN, C. M., BERG, A. VAN DEN & EGBERINK, B. P. (1972). An electromyographic study of the adductor complex of a free swimming carp (*Cyprinus carpio*) during feeding. *J. exp. Biol.* **57**, 261–283.

BAREL, C. D. N., WITTE, F. & OIJEN, M. J. P. VAN (1975). The shape of the skeletal elements in the head of a generalized *Haplochromis* species: *H. elegans* Trewavas 1933 (pisces, Cichlidae). *Neth. J. Zool.* **26**, 163–265.

DANTZIG, G. B. (1963). *Linear Programming and Extensions*. Princeton, N.J.: Princeton University Press.

DOBBEN, W. H. VAN (1935). Ueber den kiefermechanismus der knochenfische. *Arch. neerl. Zool.* **2**, 1–72.

EIJDEN, T. M. G. J. VAN, BRUGMAN, P. & OOSTING, J. (1990). Coactivation of jaw muscles: recruitment order and level as a function of bite force direction and magnitude. *J. Biomechanics* **23**, 475–485.

ELSHOUD-OLDENHAVE, M. J. W. & OSSE, J. (1976). Functional morphology of the feeding system in the ruff-*Gymnocephalus cernua* (L.1758) (Teleostei, Percidae). *J. Morph.* **150**, 399–422.

FEYNMAN, R. P., LEIGHTON, R. B. & SANDS, M. (1963). *The Feynman Lectures on Physics*. Reading, MA: Addison-Wesley.

GALIS, F. (1990). Ecological and morphological aspects of changes in food uptake through the ontogeny of *Haplochromis piceatus*. In: *Behavioural Mechanisms of Food Selection* (Hughes, R. N., ed.) NATO ASI Series, Vol. G **20**. Berlin: Springer-Verlag.

GALIS, F. (in press). Morphological constraints on behaviour through ontogeny. The importance of developmental constraints. In: *Behavioural Ecology of Fisches* (Huntingford, F. & Torricelli, P., eds) Chur, Switzerland: Academic Publishers.

GALIS, F. & DE JONG, P.W. (1988). Optimal forgaging and ontogeny; food selection by *Haplochromis piceatus*. *Oceologia* (*Berlin*) **75**, 175–184.

GREENWOOD, P. H. (1965). Environmental effects on the pharyngeal mill of a cichlid fish, *Astatoreochromis alluaudi* and their taxonomic implications. *Proc. Linn. Soc. Lond.* **176**, 1–10.

GREENWOOD, P. H. (1984). African cichlids and evolutionary theories. In: *Evolution of Fish Species Flocks* (Echelle, A. A. & Kornfield, I., eds) pp. 141–154. Orono, ME: University of Maine at Orono Press.

HOOGERHOUD, R. J. C. (1986). Taxonomic and ecological aspects of morphological plasticity in molluscivorous haplochromines (Pisces, Cichlidae). *Ann. Mus. Roy. Afr. Centre Sci. Zool.* **251**, 131–134.

HOOGERHOUD, R. J. C. & BAREL, C. D. N. (1978). Integrated morphological adaptations in piscivorous and mollusc-crushing *Haplochromis* species. In: *Proceedings of the Zodiac Symposium on Adaptation* (Osse, J. W. M., ed.) pp. 52–56. Wagenngen: Pudoc.

JOHNSTON, I. A. & SALOMONSKI, J. (1984). Power output and force-velocity relationship of red and white muscle fibres from the Pacific blue marlin (*Makaira nigricans*). *J. exp. Biol.* **111**, 171–177.

KAUFMAN, L. S. & LIEM, K. F. (1982). Fishes of the suborder labroidei (Pisces: Perciformes): phylogeny, ecology, and evolutionary significance. *Breviora* **472**, 1–19.

KOOLSTRA, J. H., EIJDEN, T. M. G. J. VAN, WEIJS, W. A. & NAEIJE, M. (1988). A three-dimensional mathematical model of the human masticatory system predicting maximum possible bite forces. *J. Biomechanics* **21**, 563–576.

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 bases of trophic specialization in sunfishes (Teleostei, Centrarchidae). *J. Morph.* **178**, 1–21.

LEEUWEN, J. L. VAN (1992). Muscle function in locomotion. In: *Mechanics of Animal Locomotion* (Alexander, R. McN., ed.) pp. 191–250. *Advances in Comparative and Environmental Physiology* Vol. II.Heidleberg: Springer Verlag.

LIEM, K. F. (1973). Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Syst. Zool.* **22**, 425–441.

LIEM, K. F. (1978). Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. *J. Morph.* **158**, 323–360.

LIEM, K. F. (1979). Modulatory multiplicity in the feeding mechanism of cichlids, as exemplified by the invertebrate pickers of Lake Tanganyika. *J. Zool. Lond.* **189**, 93–125.

LIEM, K. F. (1980). Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am. Zool.* **20**, 295–314.

LIEM, K. F. (1986). The pharyngeal jaw apparatus of the Embiotocidae (Teleostei): a functional and evolutionary perspective. *Copeia* **1986**(2), 311–323.

LIEM, K. F. & GREENWOOD, P. H. (1981). A functional approach to the phylogeny of the pharyngognath teleosts. *Am. Zool.* **21**, 83–101.

LIEM, K. F. & KAUFMAN, L. S. (1984). Intraspecific macroevolution: functional biology of the polymorphic cichlid species *Cichlasoma minckleyi*. In: *Evolution of Fish Species Flocks* (Echelle, A. A. & Kornfield, I., eds) Orono, ME: University of Maine at Orono Press.

LIEM, K. F. & OSSE, J. W. M. (1975). Biological versatility, evolution and food resource exploitation in African cichlid fishes. *Am. Zool.* **15**, 427–454.

MEYER, A. (1987). Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, cichlidae) and their implications for speciation in cichlid fishes. *Evolution* **41**, 1357–1369.

MEYER, A. (1990). Morphometrics and allometry in the trophically polymorphic cichlid fish, *Cichlasoma citrinellum*: alternative adaptations and ontogenetic changes in shape. *J. Zool., Lond.* **221**, 237–260.

NELSON, G. J. (1969). Gill arches and the phylogeny of fishes, with notes of the classification of vertebrates. *Bull. Am. Mus. Nat. Hist.* **141**, 475–552

OSSE, W. M. (1969). Functional morphology of the head of the perch (*Perca fluriatilish*): an electromyographic study. *Neth. J. Zool.* **19**, 289–392.

OTTEN, E. (1983). The jaw mechanism during growth of a generalized *Haplochromis* species: *H. elegans* Trewavas 1933 (Pisces, Cichlidae). *Neth. J. Zool.* **33**, 44–98.

SANDERSON, S. L. (1988). Variation in neuromuscular activity during prey capture by trophic specialists and generalists (Pisces: Labridae). *Br. Behav. Evol.* **32**, 257–268.

SEIREG, A. & ARVIKAR, R. J. (1973). A mathematical model for evaluation of forces in lower extremities of the musculo-skeletal system. *J. Biomech.* **6**, 313–326.

SHAFFER, H. B. & LAUDER, G. V. (1985). Aquatic prey capture in Ambystomatid Salamanders: patterns of variation in muscle activity. *J. Morph.* **183**, 273–284.

SIBBING, F. A. (1982). Pharyngeal mastication and food transport in the carp (*Cyprinus carpio* L.): a cineradiographic and electromyographic study. *J. Morph.* **172**, 223–258.

STIASSNY, M. L. J. & JENSEN, J. S. (1987). Labroid intrarelationships revisited: morphological complexity, key innovations, and the study of comparative diversity. *Bull. Mus. Comp. Zool.* **151**, 269–319.

WAINWRIGHT, P. C. (1986). Motor correlates of learning behaviour: feeding on novel prey by pumpkinseed sunfish (Lepomis gibbosus). *J. exp. Biol.* **126**, 237–247.

WAINWRIGHT P. C. (1988). Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. *Ecology* **69**, 635–645.

WAINWRIGHT P. C. (1989). Prey processing in haemulid fishes: patterns of variations in pharyngeal jaw muscle activity. *J. exp. Biol.* **141**, 359–375.

WAINWRIGHT, P. C. & LAUDER, G. V. (1986). Feeding biology of sunfishes: patterns of variation in the feeding mechanism. *Zool. J. Linn. Soc.* **88**, 217–228.

WAINWRIGHT, P. C. & LAUDER, G. V. (1990). The evolution of feeding biology in sunfishes (Centrarchidae). In: *Systematics, Historical Ecology and North American Freshwater Fishes* (Mayden, R. L., ed.) Stanford, CT: Stanford Press.

WAINWRIGHT, P. C., OSENBERG, C. W. & MITTELBACH, G. G. (1990). Trophic polymorphism in the pumpkinseed sunfish (Lepomis gibbosus): effects of environment on ontogeny. *Funct. Ecol.* **5**, 40–55.

WAINWRIGHT, P. C., SANFORD, C. J., REILLY, S. M. & LAUDER, G. V. (1989). Evolution of motor patterns: aquatic feeding in lower vertebrates. *Br. Behav. Evol.* **34**, 329–341.

WEIS-FOGH, T. & ALEXANDER, R. MCN. (1977). The sustained power output from striated muscle. In: *Scale Effects in Animal Locomotion* (Pedley, T. J., ed.) pp. 511–525. London: Academic Press.

WEIJS, W. A. (1980). Biomechanical models and the analysis of form: a study of the mammalian masticatory apparatus. *Am. Zool.* **20**, 707–719.

WITTE, F. & BAREL, C. D. N. (1976). The comparative functional morphology of the pharyngeal jaw apparatus of piscivorous and intrapharyngeal mollusc-crushing *Haplochromis* species. *Rev. Trav. Inst. Peches marit.* **40**, 793–796.

WITTE, F. & WITTE-MAAS, E. L. M. (1987). Implications for taxonomy and functional morphology of intraspecific variation in haplochromine cichlids of Lake Victoria. In: *From form to fishery. An ecological and taxonomical contribution to morphology and fishery of Lake Victoria cichlids.* Thesis, Rijksuniversiteit Leiden, The Netherlands.

WITTE, F. *et al.* (1990). Phenotypic plasticity of anatomical structures and its ecomorphological significance. *Neth. J. Zool.* **40**, 278–298.