

Interactions Between the Pharyngeal Jaw Apparatus, Feeding Behaviour, and Ontogeny in the Cichlid Fish, *Haplochromis piceatus*: A Study of Morphological Constraints in Evolutionary Ecology

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ABSTRACT I found evidence of a morphological constraint on the food choice of young stages of a cichlid fish. The constraint is not a developmental one because it is not imposed by developmental changes. I found no evidence of developmental constraints. In gradual transitions developmental constraints may be rare, in contrast to their regular occurrence in sudden transitions. I suggest that flexible muscle activation and reserve capacity (structural capacity in excess of functional demand) provide organisms with mechanisms that buffer against the effects of form changes and as such facilitate ontogenetic and evolutionary changes.

A mathematical model for piercing prey in the pharyngeal jaws is applied to a juvenile cichlid fish. The maximum possible biting forces and the best biting directions were calculated. Piercing forces were measured that were generated when natural prey were pierced. The results were compared with the feeding behaviour in the laboratory and in the field and with results from an adult. The model predicts great flexibility of the pharyngeal jaw apparatus. Furthermore, the model predicts that a shift in biting point, prey size, or predator size leads to changes in muscle recruitment. The *m.transversus ventralis* is predicted to play an important role in pharyngeal biting.

The model explains why large fish can easily pierce *Chaoborus* larvae and pupae, whereas a fish of 2.5 cm is just able to pierce larvae (symmorphosis) and is unable to pierce pupae. The inability of small fish to pierce pupae is due to a morphological constraint. This constraint is imposed by the size of the cross-sectional areas of the muscles that generate the biting force. © 1993 Wiley-Liss, Inc.

It is an important question to what extent morphological transformations change the relationship between organism and environment. What is, for example, the role of morphological transformations in the causation of the niche shifts that occur during the ontogeny of almost every animal? To examine this question, morphological constraints (constraints imposed by the bauplan) must be followed through ontogeny. When it is shown that the feeding behaviour throughout a particular ontogenetic stage is constrained because of the morphology, this does not necessarily mean that the constraint is a developmental one (Galis, '90). It can be that the relation between form and function is optimal given the size of the animal, but that the morphological constraint is one imposed by the size of the organism. A developmental constraint is, for example, the inability of metamorphosing anurans to swim or jump well (Wassersug and Sperry, '77). Juveniles can swim well and adults can jump well. The rapid change from one stage to another seems to constrain

the performance during the metamorphosis stage in between (see also de Jongh, '68).

In this study I tried to investigate the importance of morphological parameters for the feeding behaviour of *Haplochromis piceatus* Greenwood and Gee.

The diet (realized trophic niche) of *H. piceatus* is known from stomach content analyses (Witte and Witte-Maas, '87; Witte, '87; Galis, '90). It feeds on cladocerans, copepods, insect larvae, insect pupae, and algae. Through ontogeny the average size of the food items increases. The only absolute difference in the composition of prey in the diet is the absence of insect pupae in the diet of fish smaller than 4 cm standard length (SL). The dietary changes are not likely to be caused by different spatial distributions of the fish, because comparisons were made of fish caught at the same time and place. Behavioural experiments in aquaria showed that

the profitability (measured as energy gain per unit time and per unit body weight) of eating *Chaoborus* larvae is equal for individuals differing no less than thirty times in body volume (Galís and de Jong, '88). Apparently the congruence between form and function, in terms of the consumption of *Chaoborus* larvae, is as good for adults as for any other stage within this size range. Behavioural experiments showed that fish of 2.7 cm SL did eat *Chaoborus* pupae, but in contrast to larger fish they needed more handling time for pupae than for larvae (Galís, '90). Apparently, there is a difference between the potential and the realized niche, because in nature fish smaller than 4 cm SL do not eat pupae (Fig. 1). Fish smaller than 2.7 cm SL did not feed on pupae, neither in nature nor in behavioural experiments where they were hungry and no other food was offered. This suggests that the ability of these small fish for eating *Chaoborus* pupae is limited if not non-existent. Fish between 1.9 and 2.7 cm SL did eat *Chaoborus* larvae. The difference in strength between the cuticula of larvae and pupae may be relevant for piercing the prey. Therefore, in this study the hypothesis is tested that fish between 1.9 and 2.7 cm SL can pierce the larvae of *Chaoborus* with their pharyngeal jaw apparatus but have problems or are unable to pierce its pupae.

In a previous study a mathematical model is presented that calculates, in static equilibrium, the total muscle force that is necessary to generate a specified (peak) pharyngeal biting force at the mo-

ment of piercing prey in a specified biting direction (Galís, '92). Because without further specifications there exist several solutions (the system is under-terminated), the solution was chosen that minimizes the total muscular force necessary to generate the biting force. The rationale is that natural selection favours the minimization of effort necessary to generate biting forces (Seireg and Arvikar, '73; Alexander, '81). The model predicts the best biting direction for a given position and size of prey; it predicts the maximum biting (piercing) force of the fish (calculating the maximum possible force of each muscle on the basis of the cross-sectional area) and identifies the muscles that should contribute (and how much) in piercing. Simulations were carried out for an adult specimen of 5 cm SL (Galís, '92). The predicted best biting directions were compared with directions of the teeth on the lower jaw. The predictions of the maximum biting force were tested with a force gauge to which a lower pharyngeal jaw was attached. The force gauge registered the peak force exerted at piercing of a *Chaoborus* larva or pupa by the teeth of a lower pharyngeal jaw. These tests confirmed the hypothesis that adult *H. piceatus* (> 5 cm) are able to pierce *Chaoborus* larvae and pupae with their pharyngeal jaw apparatus. In the present study, results are presented of simulations of the model for parameters of a juvenile specimen of 2.5 cm SL. The predictions of the maximum biting forces have again been tested with experimentally determined piercing forces and the predicted

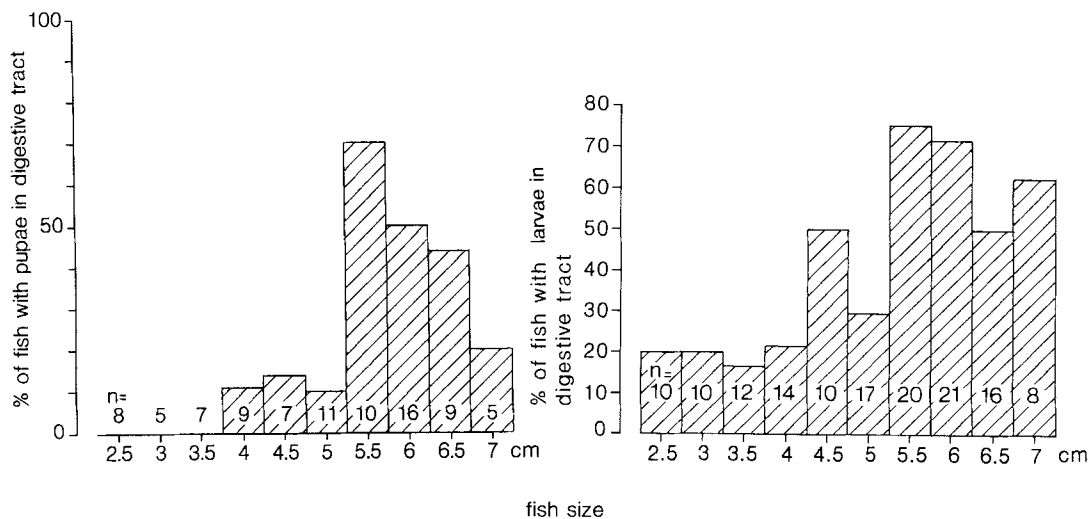


Fig. 1. Frequency distributions of stomach contents. The left graph shows that small specimens of *H. piceatus* (below 4 cm SL) do not feed on *Chaoborus* pupae whereas they do feed

on the softer *Chaoborus* larvae (right graph), including the fourth instar larvae that have the same size as pupae. (Modified from Galís, '90.)

best biting directions are compared with directions of the teeth on the lower jaw. The results of the juvenile specimen are compared with those of the adult (Galis, '92) and with data on the feeding behaviour (Galis, '90).

In this way I test the hypothesis that small *H. piceatus* have insufficient piercing capability for feeding on *Chaoborus* pupae and are therefore constrained in their feeding behaviour by their morphology.

MATERIAL AND TECHNIQUES

H. piceatus specimens were caught in the Mwanza Gulf of Lake Victoria (Tanzania) between 1-2-'79 and 29-7-'80, and 2-9-'83 and 28-2-'84. The specimens were preserved in 70% ethanol after being fixed in 4% formalin.

Reconstruction

For a description of the reconstruction techniques, see Anker ('74). For a description of the reconstruction from serial sections of a juvenile

specimen (2.5 cm SL) and an adult specimen (5 cm SL) of *H. piceatus* see Galis ('90). The reconstructions (Fig. 2) were extended to the centers 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; and 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 are estimated to be maximally 5% [with the help of reference grooves made before staining and sectioning in the block in which the fish head was embedded; see Anker, '74].

Cross sectional area of the muscles

The cross sectional area of the muscles was calculated by dividing the volume (based on dry weight) by the average length of the muscle fibers for minimally 6 and maximally 17 specimens. For a description of the determination of dry weight and

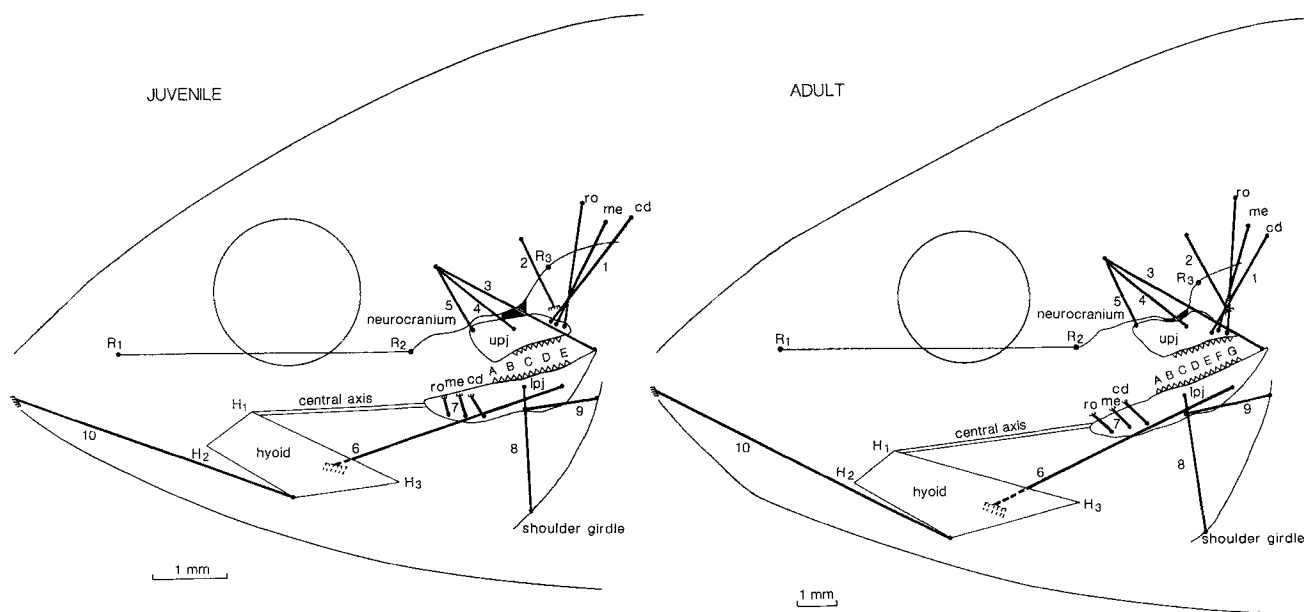


Fig. 2. Projection of muscles and bony elements in the medial plane based on reconstructed points of a juvenile (left, 2.5 cm SL) and an adult specimen (5 cm SL). R1, R2, and R3 are reference points marking the ventral side of the neurocranium: R1 at the point of attachment of the palatine-vomerine notch 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, transition 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. (ro, 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.; and 10) m.geniohy. A to G denote seven chosen 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. The most prominent differences between juvenile and adult are the differences in length of the lpj, the hyoid and m. geniohyoideus (nr.10) and the position of the m.retractor dorsalis (nr.1). (Modified from Galis, '92.)

length see Galis ('90). Dry weight was multiplied by 7.08 to give fresh weights. See Galis ('92) for the determination of this conversion factor. The specific gravity of the muscles was assumed to be 1.06 (Alexander, '58) when calculating their volume.

Maximum muscle force

For the maximum isometric muscle stress production, an intermediate value of 2.5 N/mm² was taken from those available in the literature (Weis-Fogh and Alexander, '77; Altringham and Johnston, '82; Johnston and Salomonski, '84).

Computer simulations

Simulations were carried out for three prey thicknesses and five prey positions for the juvenile specimen (Fig. 2). The simulations of the adult specimen are described in Galis ('92). Five instead of seven prey positions were selected (A to E and A to G, Fig. 2), because the lower pharyngeal jaw is relatively shorter in the juvenile than in the adult specimen (compared to the length of the reference line R1–R2).

The biting force in the simulations is 0.23 N. This value was chosen to enable comparison of the results with those of the adult specimen (Galis, '92). However, because the relation is linear all values can be multiplied and divided by the same values to get information on other biting forces.

The three selected prey thicknesses are 0.125, 0.25, and 0.5 mm; 0.125 mm is approximately the size of large cladocerans and copepods. The other two values are approximately the size of *Chaoborus* larvae (0.25 mm) and *Chaoborus* pupae (0.5 mm) when they are compressed at the moment of piercing as estimated by eye at the moment the peak force was recorded. The largest prey thickness used in the calculations for the adult specimen (1 mm) to simulate piled prey was excluded, because the smaller specimens never eat more than one larva at a time and thus piling between the pharyngeal jaws cannot occur.

Tooth direction

A specimen with a standard length of 2.55 cm was deep frozen in liquid nitrogen and sectioned parallel to the medial plane. The cut surface was photographed and the directions of the teeth were measured from the medial plane.

Piercing force

The force necessary to pierce a fourth instar larva or pupa of *Chaoborus* sp. was measured with an Aikoh CPU digital force gauge 7502B. A dry lower

pharyngeal jaw of a specimen of 2.5 cm S.L. was glued (with Collall glue) to a movable piston. A petridish 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 ca. 0.23 mm/s 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 first positioned between the pharyngeal jaws, before the jaws move again to pierce the food. Higher speeds would probably damage the teeth. With this technique it is not possible to measure the biting forces necessary to pierce cladocerans and copepods because their small size makes it impossible to touch them with the piston without directly pressing the platform and registering higher values than necessary for piercing.

Terminology

The terminology follows Barel et al. ('75) and Anker ('78) for anatomical terms and Feynman et al. ('63) for physical terms.

Anatomy and kinematic assumptions

For a more detailed description of the anatomy and kinematic assumptions see Galis ('92). The upper pharyngeal jaws are paired. The strong interconnections between the third and fourth pharyngobranchials provide that the pharyngobranchials 3,4 function as a single mechanical unit (Barel et al., '75; Liem, '78). The upper pharyngeal jaw can slide forward and backward along the neurocranium. Cineradiographic data show that the mobility of the upper pharyngeal jaws can be largely independent of the lower pharyngeal jaw (Liem, '73, '78; Aerts et al., '86). The transmittance of force of the m. transversus ventralis (nr. 7, attached to the lower jaw and to ceratobranchial 4) via the ceratobranchial 4 and epibranchial 4 to the upper pharyngeal 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 (nr. 10). 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, '73).

The lower pharyngeal jaw of cichlids is composed of the united fifth ceratobranchials functioning as a single unit (Nelson, '69). It does not articulate

with the shoulder girdle (unlike the lower pharyngeal jaw in Labridae and some pomacentrids, Liem and Greenwood, '81; Kaufman and Liem, '82; Stiasny and Jensen, '87) and is suspended from the neurocranium by a muscular sling, composed of the m. levator externus 4 (nr. 3, Fig. 3F) and parts of the m. obliquus posterior (Liem, '73; Aerts, '82). The m. levator posterior does not form part of the muscular sling as in labrids and durophagous cichlids and embiotocids (Liem and Greenwood, '81; Liem and Sanderson, '86), because it does not insert on the lower pharyngeal jaw. 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 model

This section is modified from Galis ('92). A static approach was chosen for reasons explained in Galis ('92). Static equilibrium implies that in x, y, and z directions the sums of all forces and of all torques (moments) equal zero: $\Sigma F_x = 0$; $\Sigma F_y = 0$; $\Sigma F_z = 0$; $\Sigma T_x = 0$; $\Sigma T_y = 0$; $\Sigma T_z = 0$. The model can be reduced to a two dimensional one because the biting force is modeled 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 4). This reduces the number of equations to three: two for the sums of the forces in x and y directions and one for the sum of the torques with respect to a rotation centre: $\Sigma F_x = 0$; $\Sigma F_y = 0$; $\Sigma T = 0$. The forces of the ten muscles (Fig. 3F,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 Introduction). Another possible optimization criterion that we did not explore is the maximization of the biting force (Koolstra et al., '88; van Eijden et al., '90). It is likely that the results would be somewhat different if this optimization criterion had been applied. The linear optimization problem was solved with the SIMPLEX method for linear programming (Dantzig, '63). 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 biting directions at each prey position and prey

thickness (Fig. 3). For each prey position and prey thickness the biting direction was chosen which requires the lowest total muscle force.

Assumptions

- 1) The movements of the lower and upper jaw are independent (see Galis, '92).
- 2) The lower jaw pushes against the prey and thereby pushes the upper jaw against the neurocranium. The upper jaw must exert a force on the prey that is equal in size, in line, and opposite in direction.
- 3) The position of the upper jaw is held constant.
- 4) 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).
- 5) The friction coefficient for the gliding of the upper jaw along the neurocranium is zero.
- 6) Only biting directions that run through the dental area of pharyngobranchial 3,4 of the upper jaw are considered feasible.
- 7) The position of the lower jaw is determined by the size and position (A to E, Fig. 3E) 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. 3D). The point of attachment of the m. transversus ventralis (Fig. 3F, 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).
- 8) 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 on Anatomy and kinematic assumptions).
- 9) The force of the m. geniohyoideus is transmitted to the lower pharyngeal jaw via the hyoid and the central axis (see Anatomy and kinematic assumptions). The force of the m. geniohyoideus (nr. 10 in Figs. 2, 3F) 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.
- 10) The force of the m. levator posterior (nr. 2 in Fig. 2) is calculated by projecting the line of action of this muscle on the line of action of the m. levator externus 4.
- 11) The position of the ceratobranchials 4 is constant throughout the piercing (see Galis, '92). The muscular force for the stabilization of ceratobranchials 4 is excluded from the analysis.
- 12) Acceleration and elasticity (see van Leeuwen, '92) at prey piercing

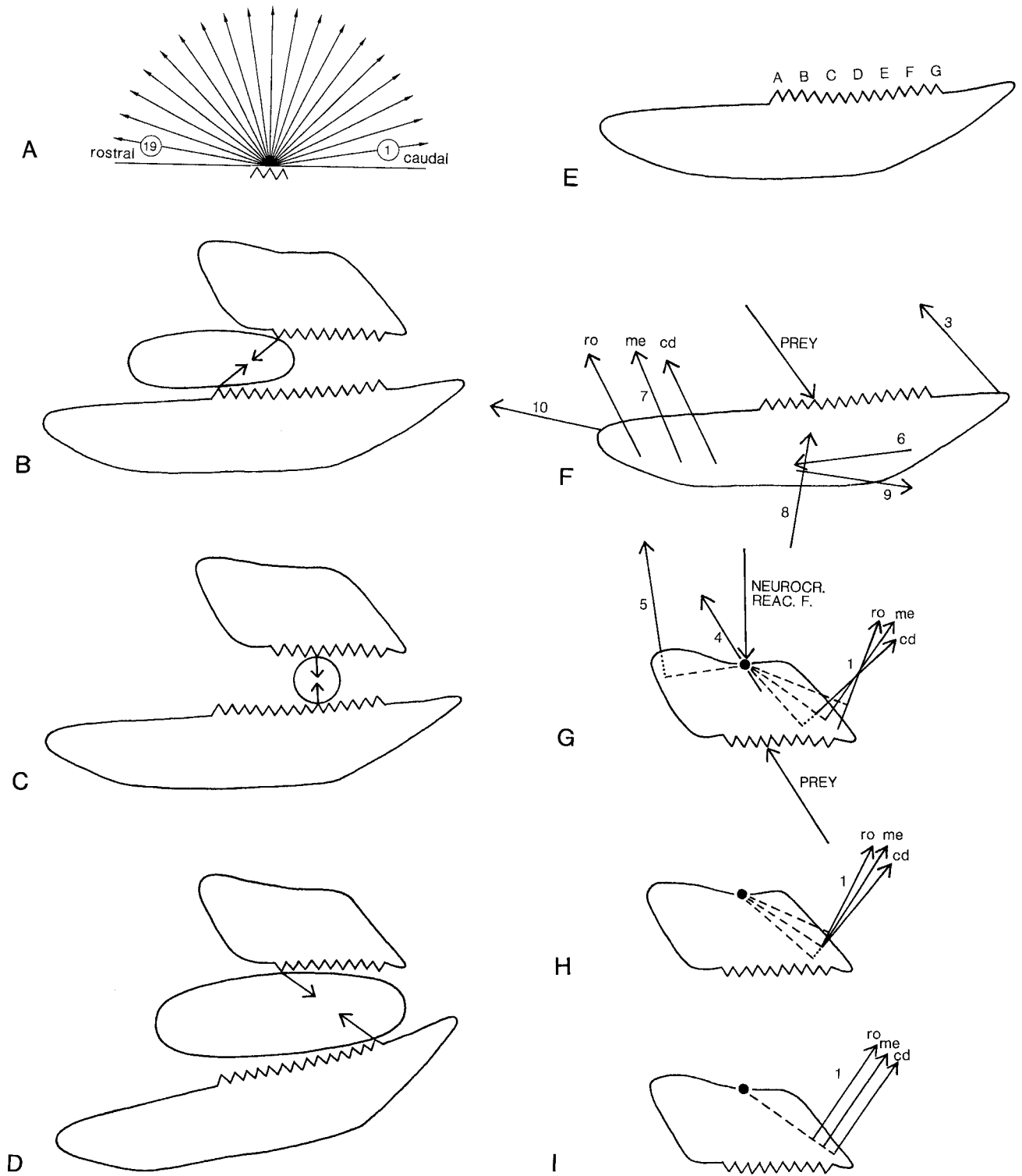


Figure 3.

are unimportant because of the slow speed of the piercing. For a more detailed list of the assumptions see Galis ('92).

RESULTS

Simulations of the model (juvenile specimen)

Lower pharyngeal jaw

The effect of rostral and caudal lines of action of the m. transversus ventralis. The m. transversus ventralis (nr. 7) was divided into three lines of action because the projections on the medial plane of the areas of attachment are large (Fig. 2). The recruitment of the rostral line of action is sometimes an improvement compared to the middle line of action. The decrease in the muscular force that is exerted on the lower pharyngeal jaw using the rostral line of action rather than the middle line of action (to generate the biting force) is 1.5 to 16.4%. The recruitment of the caudal line of action is under no conditions an improvement compared to the medial or rostral line of action. Probably this line of action will be used only when the force of the rostral and medial lines of action is insufficient.

Predictions of muscle activity patterns. The m. levator externus 4 (nr. 3, Fig. 2 and 2F), m. transversus ventralis (medial line of action, nr. 7 me) and m. pharyngocleithralis internus (nr. 9) are predicted to contribute to the biting force at all prey thicknesses in the rostral prey positions (Table 1, prey thickness 0.125 and 0.25 and prey positions B and C; prey thickness 0.5 and prey position A).

The m. pharyngocleithralis internus usually does not directly contribute to the biting force because of its position, but counteracts an excess of forward directed force (generated by the other muscles). It is the only muscle that can pull the lower pharyngeal jaw backward. The m.m. levator externus 4, transversus ventralis, and geniohyoideus (nr. 10) are active at positions D and E at all prey thicknesses. The rostral line of action of the m. transversus ventralis (nr. 7 ro) is active instead of the medial one at positions B, C, and D and a prey thickness of 0.5 mm. The same recruitment of lines of actions occurs at a prey thickness of 0.25 mm at prey position D to E (Table 1 and Fig. 4). At a prey thickness of 0.125 mm this combination of lines of action is not active at all. The m.m. pharyngohyoideus (nr. 6), levator externus 4 and geniohyoideus are active at the most caudal position E and the largest prey thickness (0.5 mm).

Best biting direction. The biting direction which requires the smallest muscle force for the muscles of the lower pharyngeal jaw usually points forward (numbers higher than 10 in Fig. 2A; Table 2, Fig. 4). This is because the lines of action of the m. levator externus 4 (nr. 10), the m. transversus ventralis (nr. 7), the m. pharyngohyoideus (nr. 6), and the m. geniohyoideus (nr. 10, via the central axis) are all directed forward (Fig. 2, 3F). The only other muscle that is included in the best biting direction is the m. pharyngocleithralis internus (nr. 9). When a forward directed biting force is not possible (rostral prey positions, Fig. 3B), the best biting direction for the lower pharyngeal jaw is the least backward one (Fig. 4D). The best biting direction for the lower pharyngeal jaw changes with increasing prey thickness towards a less forward direction (lower number in Fig. 3A). This is mainly because at a larger prey thickness the lower pharyngeal jaw is rotated downwards to a larger extent (see section on Model, assumption 9 in Galis, '92, illustrated in Fig. 3D), with the effect that all 19 biting directions are rotated to a more forward direction (relative to the position of the fish). The best biting direction for the lower pharyngeal jaw changes with a more backward prey position towards a more forward direction (Table 2).

Upper pharyngeal jaw

The effect of crossed lines of action of the m. retractor dorsalis. The muscle fibers of the m. retractor dorsalis (nr. 1) are twisted (Figs. 3G, 5). Simulations of the adult specimen (Galis, '92) showed that crossed lines of action of this muscle lower the muscular force that is exerted during biting, compared

Fig. 3. Simulation scheme. (A) indicates the nineteen 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 five chosen prey positions. (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 rostral, middle, and caudal part, respectively); 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.; and 10) m.geniohy. The solid dot in (G) (H) and (I) indicates the rotation centre. The broken lines indicate the lever arms of the lines of action showing in (G) 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.

TABLE 1. Muscle recruitment and the contributions of the individual muscles and the neurocranial reaction force in the medial plane to a biting force of 0.23N only in the best direction (see arrows in Figs. 3A and 6, in N and in percentages of the muscular force of the lower and upper pharyngeal jaws)¹

Prey positions	A		B		C		D		E	
	N	%	N	%	N	%	N	%	N	%
Prey thickness 0.125 mm										
Best direction nr.	—		11		16		18		19	
Lower jaw										
m.lev.ex.4(nr.3)	—		0.12	23.5	0.15	61.6	0.15	59.6	0.20	81.0
m.ph.hy.(nr.6)	—		0	0	0	0	0	0	0	0
m.trans.vl.me(nr.7)	—		0.21	39.8	0.07	30.9	0.03	12.9	0.01	2.8
m.trans.vl.ro.	—		0	0	0	0	0	0	0	0
m.ph.cleith.int.(nr.9)	—		0.19	36.7	0.02	7.5	0	0	0	0
m.geniohy.(nr.10)	—		0	0	0	0	0.07	27.5	0.04	16.1
Upper jaw										
m.retr.dl.ro(nr.1)	—		0.04	55.7	0	0	0	0	0	0
m.retr.dl.me.	—		0	0	0.02	11.8	0	0	0	0
m.retr.dl.cd.	—		0	0	0.18	88.2	0.26	80.8	0.28	66.4
m.lev.int.lat.(nr.4)	—		0.04	44.3	0	0	0	0	0	0
m.lev.int.med.(nr.5)	—		0	0	0	0	0.06	19.2	0.14	33.6
neur.react.force	—		0.30	0	0.29	0	0.34	0	0.44	0
Prey thickness 0.25 mm										
Best direction nr.	—		10		14		16		17	
Lower jaw										
m.lev.ex.4(nr.3)	—		0.10	19.9	0.15	49.0	0.16	69.4	0.15	64.9
m.ph.hy(nr.6)	—		0	0	0	0	0	0	0	0
m.trans.vl.me(nr.7)	—		0.21	41.1	0.11	36.3	0	0	0	0
m.trans.vl.ro.	—		0	0	0	0	0.05	19.6	0.02	8.7
m.ph.cleith.int.(nr.9)	—		0.19	39.0	0.05	14.7	0	0	0	0
m.geniohy.(nr.10)	—		0	0	0	0	0.03	11.0	0.01	26.4
Upper jaw										
m.retr.dl.ro(nr.1)	—		0.04	55.5	0	0	0	0	0	0
m.retr.dl.me.	—		0	0	0.12	53.7	0	0	0	0
m.retr.dl.cd.	—		0	0	0.10	46.3	0.23	92.0	0.26	78.3
m.lev.int.lat.(nr.4)	—		0.03	44.5	0	0	0	0	0	0
m.lev.int.med.(nr.5)	—		0	0	0	0	0.02	8.0	0.07	21.7
neur.react.force	—		0.30	0	0.32	0	0.31	0	0.36	0
Prey thickness 0.5 mm										
Best direction	6		8		11		12		13	
Lower jaw										
m.lev.ex.4(nr.3)	0.02	4.8	0.73	15.8	0.13	36.6	0.16	67.5	0.18	75.0
m.ph.hy.(nr.6)	0	0	0	0	0	0	0	0	0.02	6.7
m.trns.vl.me(nr.7)	0.20	41.1	0	0	0	0	0	0	0	0
m.trans.vl.ro.	0	0	0.18	38.9	0.13	36.3	0.07	30.5	0	0
m.ph.cleith.int.(nr.9)	0.26	54.1	0.21	45.2	0.10	27.1	0	0	0	0
m.geniohy.(nr.10)	0	0	0	0	0	0	0.01	1.9	0.04	18.3
Upper jaw										
m.retr.dl.ro(nr.1)	0	0	0	0	0	0	0	0	0	0
m.retr.dl.me.	0	0	0	0	0.07	56.6	0	0	0	0
m.retr.dl.cd.	0	0	0	0	0.05	43.3	0.26	78.3	0.23	92.0
m.lev.int.lat.(nr.4)	0.14	55.6	0.04	66.7	0	0	0	0	0	0
m.lev.int.med.(nr.5)	0.11	44.3	0.02	33.3	0	0	0.07	21.7	0.02	8.0
neur.react.force	0.42	0	0.28	0	0.30	0	0.36	0	0.25	0

¹It can be seen that changes in prey thickness and prey position leads to different combinations of active muscles.

to a single line of action (nr. 1 me), or compared to lines of action that are parallel (Fig. 3I). When the lines of action are parallel, the caudal line of action (nr. 1 cd) has the largest lever arm (Fig. 3I). The caudal line of action is always selected rather than the central line, but the difference in total

muscular force is negligible. When the lines of action cross each other the rostral line of action has the largest lever arm and the smallest horizontal projection (perpendicular to the neurocranial reaction force of the skull), whereas the caudal line of action has the smallest lever arm and the largest

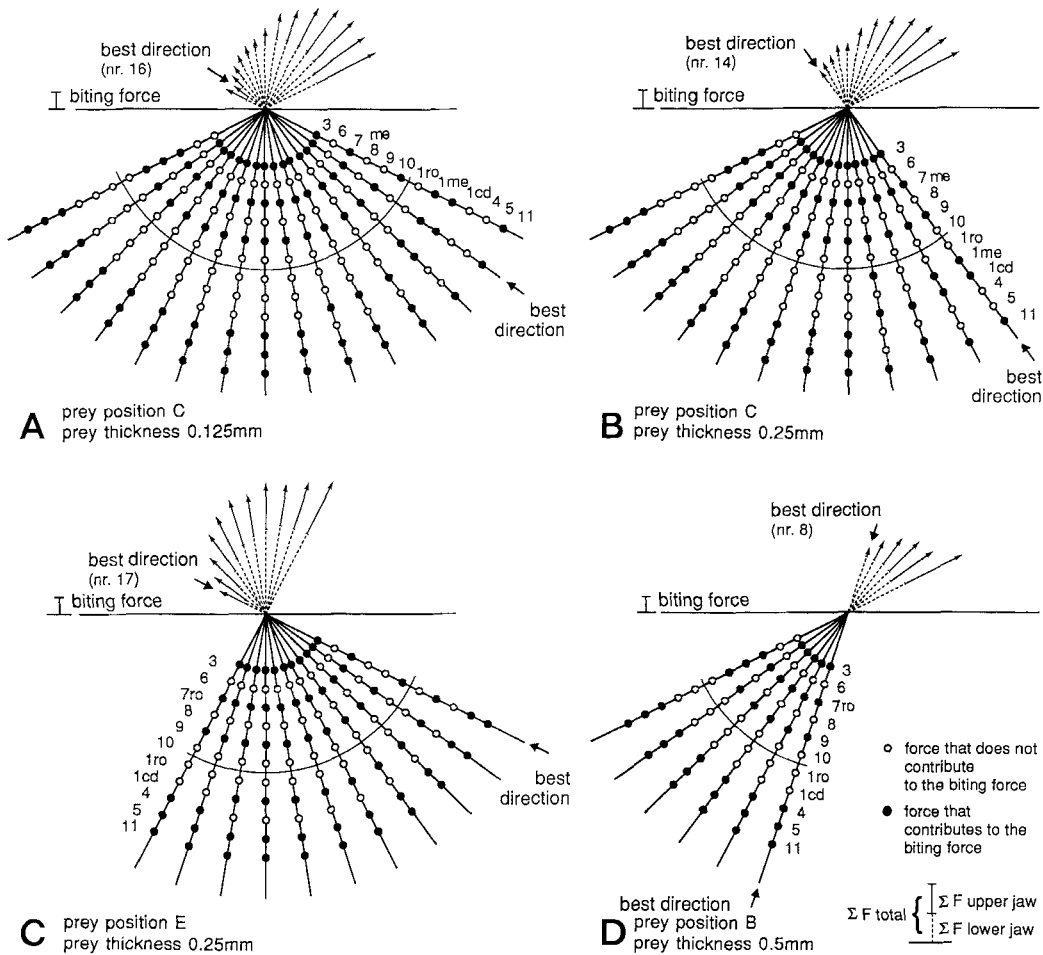


Fig. 4. Force diagrams indicating 1) the contributing forces and 2) the feasible biting directions indicated by the arrows (of which the lines of action intersect the tooth surface of the upper jaw). The directions of the arrows refer to the directions indicated in Figure 3A. The length of the arrows 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 (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); m. pharyngocleithralis externus (nr.8); m. pharyngocleithralis internus (nr.9); m. geniohyoideus (nr.10); m. retractor dorsalis (nr.1; ro, rostral part; me, middle part; cd, caudal part); m. levator internus lateralis (nr.4); m. levator internus medialis (nr.5); and the neurocranial reaction force. Diagrams A to D are examples of four prey positions and thicknesses.

horizontal projection (Fig. 3G). The decrease in the muscular force due to the crossed lines of action is almost as large as that in the adult (Galis, '92). Again the effect of the crossed lines of action is largest at the most caudal prey position (E; the decrease in the muscle force that is exerted on the upper jaw at this prey position, compared to parallel lines of action, is 47.2%, 53.1%, and 58.0%, at prey thicknesses 0.125, 0.25, and 0.5 mm, respectively). If the fibers are less twisted, such that the three lines of action insert at the same point on the lower pharyngeal jaw (Fig. 3H), the decrease in the muscu-

lar force compared to parallel lines of action would still be considerable amounting to 31.6, 35.5, and 38.9%, respectively of the muscle force on the upper pharyngeal jaw.

Predictions of the muscle activity patterns. The lines of action of the caudal part of the m. retractor dorsalis (nr. 1 cd, Figs. 2, 3G), the m. levator internus medialis (nr. 5) and the neurocranial reaction force (Fig. 3G) are predicted to contribute to the best biting force at the caudal positions D and E at all prey thicknesses (Table 1). At prey position C, the middle and caudal part of the m. re-

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 in Fig. 3A. [The best biting direction changes with a more backward prey position towards a more forward direction (higher number).]

Prey positions	Best biting direction (nr.)				
	A	B	C	D	E
Prey thickness 0.125mm					
Lower jaw	—	11	17	18	19
Upper jaw	—	10	11	11	11
Both jaws	—	11	16	18	19
Prey thickness 0.25 mm					
Lower jaw	—	10	14	16	17
Upper jaw	—	10	10	16	17
Both jaws	—	10	14	16	17
Prey thickness 0.50 mm					
Lower jaw	6	8	11	12	13
Upper jaw	6	8	11	12	13
Both jaws	6	8	11	12	13

tractor dorsalis (nr. 1 me) are active at all prey thicknesses. The rostral line of action of the m. retractor dorsalis (nr. 1 ro) and the m. levator internus lateralis (nr. 4) are active at prey position B, at a prey thickness of 0.125 and 0.25 mm. The m.m. levatores interni are active at prey positions A and B at a prey thickness of 0.5 mm. The neurocranial reaction force is always selected in the simulations. It contributes to the biting force, but not to the total muscular force. The component of the biting force that is perpendicular to the neurocranial reaction force of the skull (for simplicity called the horizontal component or projection) needs to be counteracted by muscular force. When this horizontal force component is directed forward, one or more of the lines of action of the m. retractor dorsalis must be active to counteract it and when it is directed backward the m. levator internus medialis or lateralis must be active. The caudal line of action of the m. retractor dorsalis (nr. 1 cd) and the

m. levator internus lateralis (nr. 4) have the best horizontal projections (Fig. 3G). The torque of the neurocranial reaction force is zero and, therefore, cannot counteract the torque of the biting force. When the torque of the biting force is clockwise directed (seen from the left as in Fig. 2) (in forward biting directions), one of the lines of action of the m. retractor dorsalis needs to be selected to counteract it. When the torque is anti-clockwise directed (in backward biting directions), the m. levator internus medialis needs to be selected. The rostral line of action of the m. retractor dorsalis and the m. levator internus medialis have the largest lever arms (Fig. 3G). The line of action of the m. levator internus lateralis runs approximately through the rotation centre and the lever arm is therefore negligible. When the biting force runs through the rotation centre, its torque is zero. When this is the case and the biting direction is also in line with the neurocranial reaction force, no muscular force is necessary.

When muscular force is necessary to counteract the torque and horizontal component of the biting force, there is always one line of action selected with a large lever arm and a small horizontal force component plus one with a small lever arm and a large horizontal force component.

Best biting direction. A vertical biting direction (approximately as in nr. 10, Fig. 3A) at a central prey position (C) approaches most closely to the situation where no muscular force is necessary, a biting force in line with the neurocranial reaction force (Fig. 4a,b, solid parts of arrows and Table 2). A backward or vertical biting direction is the most effective for the rostral prey positions (A and B). A forward biting direction is the most effective for the caudal positions (D and E). This is because the lever arm is smallest for rostral prey positions at backward biting directions and for caudal positions at

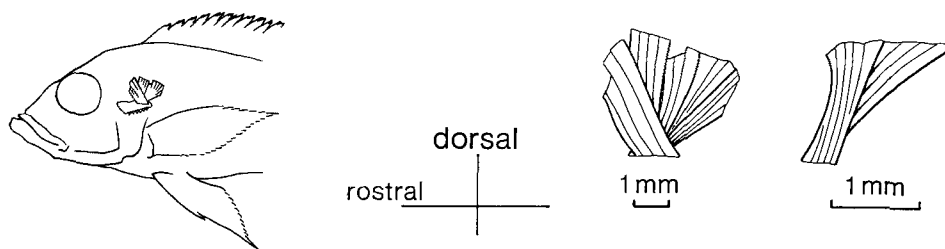


Fig. 5. The position of the m. retractor dorsalis in the fish is indicated in the left figure. The figures to the right show the fiber direction of the m. retractor dorsalis of an adult (left,

6 cm SL) and a juvenile specimen (2.5 cm SL), illustrating clearly how the fibers run in different directions. (Modified from Galis, '92.)

forward biting directions, whereas the biting force in all instances has a small horizontal projection in the vertical direction (the horizontal component of the biting force cannot be compensated by the neurocranial reaction force). There is no clear relation between the best direction and prey thickness.

Best biting direction for the entire pharyngeal jaw apparatus

Summation of the muscle forces of the lower and upper jaw leads to a backward directed or vertical biting force that is best for rostral prey positions because forward directed forces are not possible (Table 2, Fig. 6). The best biting direction is more forward the more the prey position is caudal. In central and caudal prey positions the best biting direction is always directed forward.

Prey position and prey thickness

The rostral prey positions A and B are least suitable for biting at all prey thicknesses (Fig. 6). The muscle force required for biting at position C is the smallest at the smallest prey thickness of 0.125 mm and slowly increases with increasing prey thickness. The situation is the reverse for the most caudal position E, where the required muscle force decreases with increasing prey thickness. In between, at position D, the least force is required at the intermediate prey thickness of 0.25 mm. Considering that

the largest prey items, *Chaoborus* pupae, are not eaten in nature, the central prey positions C and D are the best for biting of realistically sized prey items. The teeth at positions A, B, and E may be more important for transporting prey and holding the prey within the pharyngeal jaws.

Maximum biting force

The maximum possible biting force (based on the cross-sectional area of the muscles) in the best direction can be achieved at the central position C at all three prey thicknesses, with the highest value at a prey thickness of 0.25 mm and the lowest at 0.5 mm (Fig. 6). The most rostral and most caudal prey positions are the worst in this respect. The muscle that limits the biting force most involves the lower jaw on five occasions and the upper jaw on eight (Table 3). However, when only prey are considered that belong to the natural diet, the largest prey thickness (0.5 mm) must be discounted and then the lower jaw is involved only on two occasions and the upper jaw only on six.

Comparison with the adult specimen

When making comparisons with adults, it has to be noticed that for a given size of prey the lower jaw needs to be rotated further downward in the juvenile specimen than in the adult specimen. The pattern of the selection of the muscles generally

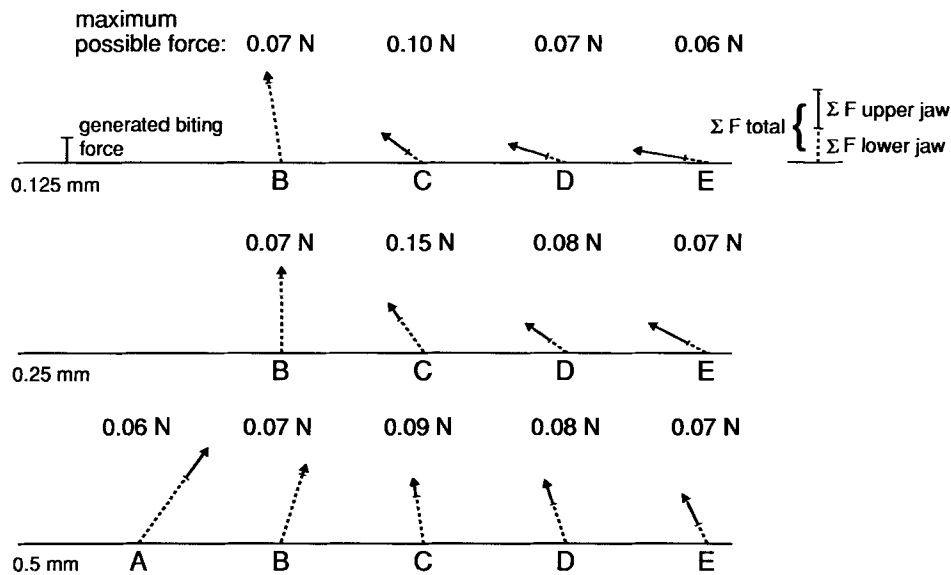


Fig. 6. The best biting direction as indicated by the arrows (the direction for which the sum of the forces is minimal (see Fig. 4) for prey thicknesses 0.125 mm., 0.25 mm, and 0.5 mm at all prey positions (A to E, see Fig. 3E). The directions of the arrows refer to the directions indicated in Figure 3A. The length of the arrows indicates the muscular force that is exerted on

the lower pharyngeal jaw (broken part of the arrow) and on the 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.

TABLE 3. The most limiting muscle for the maximum possible biting force is given for prey position A to E and prey thicknesses 0.125 mm, 0.25 mm, and 0.5 mm. The most limiting muscle belongs less often to the lower pharyngeal jaw than to the upper pharyngeal jaw.

Prey thickness	Most limiting muscles belonging to lower (L) or upper (U) jaw					
	0.125 mm		0.25 mm		0.5 mm	
Prey position A	—		—		m.ph.cl.in.	(l)
B	m.ph.cl.in.	(l)	m.ph.cl.in.	(l)	m.ph.cl.in.	(l)
C	m.retr.dl.cd.	(u)	m.retr.dl.cd.	(u)	m.trans.vl.	(l)
D	m.retr.dl.cd.	(u)	m.retr.dl.cd.	(u)	m.retr.dl.cd.	(u)
E	m.retr.dl.cd.	(u)	m.retr.dl.cd.	(u)	m.retr.dl.cd.	(u)

agrees with that of the adult specimen, both for the lower jaw and the upper jaw (Galís, '92). In the juvenile specimen the middle line of action of the m. retractor dorsalis (nr. 1 me, Fig. 3G) is sometimes better than the rostral or caudal one (nr. 1 ro and cd), whereas that is never the case in the adult. As in the adult, there is always one line of action selected with a large lever arm and a small horizontal force component plus one with a small lever arm and a large horizontal force component. The twist in the fibers of the m. retractor dorsalis (Figs. 3G, 5) is almost as important in the juvenile specimen as in the adult specimen. The m. retractor dorsalis is relatively larger in the adult and extends more in the rostral direction (Fig. 5). The general trend is the same in the juvenile and the adult with regard to the best biting direction. In the adult and the juvenile the central prey positions are the best for biting of realistically sized prey items. The relation between prey thickness and sum of the muscular forces is only the same in the adults and the juvenile for the most caudal positions in that the sum decreases with increasing prey thickness. However, this relation holds true for all prey positions in the adult specimen whereas this is not the case in the juvenile (see Fig. 6). The maximum biting force is also highest in the centre of the tooth surface for both juvenile and adult. The

adult is capable of generating much higher biting forces, because of the much larger size of its muscles (Table 4).

Direct and indirect tests of the model

Quantitative importance of muscles

The relative contribution of muscles to biting force changes with prey position, prey thickness, and biting direction (Table 1). The muscles that generate the largest part of the biting force at the prey positions C and D at realistic prey thicknesses (0.125 mm and 0.25 mm) are the m. retractor dorsalis for the upper jaw and the m. levator externus 4 and m. transversus ventralis for the lower jaw. The results of Table 4 reveal that these muscles, which must generate the most force, are the strongest muscles (the large m. geniohyoideus excepted, which generates little force; the m. geniohyoideus is not directly attached to the lower pharyngeal jaw, Fig. 2, and its contribution to the biting of the pharyngeal jaw is only one of its many functions, van Dobben, '35; Osse, '69; Anker, '74; Aerts et al., '87; Liem, '91).

Tooth direction

The direction of the teeth (Fig. 7) coincides well with the best biting directions at the different prey positions (Fig. 6).

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 plane¹

Muscles	Max. force (N)		Conversion factor		Max. force in medial plane (N)	
	juvenile	adult	juvenile	adult	juvenile	adult
m.retr.dl.	0.23	0.88	1.00	1.00	0.23	0.88
m.lev.ex.4	0.10	0.36	0.98	0.98	0.10	0.35
m.lev.int.lat.	0.04	0.14	0.86	0.87	0.03	0.12
m.lev.int.med.	0.06	0.22	0.59	0.61	0.04	0.13
m.ph.hy.	0.05	0.11	0.98	0.99	0.05	0.11
m.trans.vl.	0.12	0.36	0.56	0.71	0.07	0.26
m.ph.cleith.int.	0.06	0.30	0.58	0.77	0.03	0.23
m.geniohv.	0.31	0.91	0.91	0.82	0.28	0.75

¹This 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 three-dimensional projection (see Model). 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.

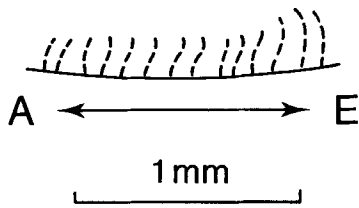


Fig. 7. Longitudinal section through the medial plane showing the size and direction of teeth (from base to tip) on the lower pharyngeal jaw of a specimen of 2.55 cm SL. A and E denote prey positions (see Fig. 3E). These results correspond well with the results shown in Figure 6.

The required forces for piercing of *Chaoborus* larvae and pupae and the capability of the pharyngeal jaw apparatus to pierce *Chaoborus* larvae and pupae

The force necessary for piercing *Chaoborus* pupae with the teeth of the lower jaw is on average higher than that for *Chaoborus* larvae (Table 5). This result is expected, because the cuticula of the pupae are stronger than those of the larvae. The observed variation in the piercing forces is not surprising considering the age differences of the pierced larvae and pupae and the different size and shape of the teeth (depending on the position on the pharyngeal jaw).

Comparison of the experimentally determined piercing forces with the maximum biting forces predicted with the model (which were calculated before the experiments were carried out) shows that the pharyngeal jaw apparatus of the juvenile is able to pierce most of the larvae (prey thickness of appr. 0.25 mm) because the maximum possible force that can be exerted at position C is 0.15 N (compare 0.4–0.18 N in Table 5 with the maximum possible forces in Fig. 6). However, the fish will not be able to pierce *Chaoborus* pupae (a prey thickness of appr. 0.5 mm) because this requires a minimum biting force of 0.11 N and the predicted maximum biting force is 0.9 N. The values of the maximum biting forces depend on the optimization criterion (the minimization of the sum of the muscular forces).

If the optimization criterion had been the maximization of the biting force (see Koolstra et al., '88; van Eijden et al., '90), the results would have been somewhat higher in some situations. However at the prey thickness of the pupae (0.5 mm) a biting force of 0.11 N or higher is not possible, because simulations with a specified biting force of 0.11 N subject to the constraints of the maximum possible forces of the individual muscles (Table 4) do not yield a solution.

Comparison with the adult specimen

The results concerning the quantitative importance of the muscles and the tooth direction correspond well with those of the adult specimen (Galis, '92). The forces necessary for piercing *Chaoborus* larvae and pupae are on average lower for the juvenile than for the adult. This must be due to the finer points of the juvenile teeth. Although the adult fish must thus exert more force to pierce its prey, its maximum possible biting force is (due to the larger cross section of its muscles) so much higher, that according to the model both larvae and pupae can be pierced easily.

Comparison with the feeding behaviour

The results of the model and of the experiments with the force gauge show that the hypothesis that fish between 1.9 and 2.7 cm SL can pierce larvae but have problems or are unable to pierce *Chaoborus* pupae is confirmed for a specimen of 2.5 cm. This hypothesis is based on the fact that fish of this size class eat *Chaoborus* larvae and do not eat pupae in experiments (Galis and de Jong, '88; Galis, '90). In nature fish between 2.3 and 4 cm eat larvae and do not eat pupae (*H. piceatus* smaller than 2.3 cm cannot be identified in the field; Witte, personal communication).

Morphological constraint on the feeding behaviour

The absence of pupae in the diet of fish smaller than 2.7 cm is thus due to a morphological constraint.

TABLE 5. Forces necessary for piercing *Chaoborus* larvae and pupae. Measured with a lower jaw glued on a force gauge.¹

	Range of piercing forces in N		Average piercing force in N		<i>n</i>	
	juvenile	adult	juvenile	adult	juvenile	adult
<i>Chaoborus</i> larvae	0.04–0.18	0.07–0.23	0.09	0.13	20	20
<i>Chaoborus</i> pupae	0.11–0.20	0.15–0.31	0.15	0.23	20	20

¹The lower values of the piercing forces for the juvenile in comparison to the adult must be due to the finer points on the teeth of the juvenile. The forces necessary for piercing *Chaoborus* pupae with the juvenile pharyngeal jaw are higher than the maximum predicted biting forces (Fig. 6, prey thickness 0.5 mm).

Furthermore, it is most likely that the difference in potential and realized niche of fish between 2.7 and 4 cm is partly due to a limited piercing ability. Fish of 2.5 cm cannot pierce pupae at all. Considering the almost isometric changes of most parameters (Galís, '90) and the large variation in the experimentally determined piercing forces (Table 5), it is to be expected that the ontogenetic phase of total inability to pierce is followed by a phase in which piercing of pupae is not fully effective. For individuals of this size range the morphological constraint is not an absolute one as is the case for smaller individuals but one that lowers the efficiency.

Conclusions and discussion

Validity of the model

The applicability of the model is supported by the correspondence between 1) the muscles predicted by the model to exert most of the force (Table 1) and the calculated potential strength of the muscles (Table 4), 2) the predicted best biting directions (Fig. 6) and actual tooth direction (Fig. 7), 3) the overlap between the predicted range of possible biting forces ($<$ maximum biting force, Fig. 6) and the experimentally determined forces that were required to pierce *Chaoborus* larvae (Table 5), and 4) the lack of overlap between the predicted possible biting forces (Fig. 6) and the experimentally determined forces that were required to pierce *Chaoborus* pupae (Table 5). As mentioned before, *Chaoborus* larvae occur in the natural diet of juveniles, whereas pupae are not only absent in the natural diet of juveniles smaller than 4 cm even though available (Fig. 1) but are also not eaten in experiments by hungry juveniles smaller than 2.7 cm even in the absence of other prey (Galís, '90). For the adult, the model predicts a range of possible biting forces that includes all the experimentally determined forces that were required to pierce *Chaoborus* larvae and pupae (Galís, '92). This agrees well with the occurrence of both prey types in the natural diet of adults (Galís, '90). For the adult, there appears to be a reserve capacity regarding the piercing of *Chaoborus* larvae and pupae, whereas for the juvenile the capacity of the pharyngeal jaws is only just large enough for the larvae (symmorphosis, Weibel et al., '91), this means that the reserve capacity is not of the same size throughout ontogeny.

Muscle recruitment

The results of this study confirm earlier findings (Galís, '92) that a change in position or size of the prey must lead to changes in muscle recruitment

during biting in the pharyngeal jaws, i.e. different combinations of muscles are recruited. Furthermore the size of the predator also influences muscle recruitment (Fig. 8). I agree with Aerts ('90) that the importance of muscle modulation (variations in muscle activity patterns; Liem, '78) seems to be underestimated in the literature. Muscle modulation may have gone unnoticed in experimental studies because relevant muscles were excluded from the analysis (Galís, '92). It seems possible that part of the high variation that is found in electromyographical data in prey capture studies (e.g., Shaffer and Lauder, '85; Wainwright, '86; Wainwright and Lauder, '86; Sanderson, '88) may be due to modulation of the muscles in response to changes in position of prey or to changes in prey thickness. In some instances the use of immobile prey (Liem, '73; Wainwright, '91) or the long training on experimental prey prior to the experiments (see Wainwright, '86) may have emphasized the impression of stereotypy.

The importance of the m. transversus ventralis

The results of this study and the previous one on an adult fish show that the absence of the m. transversus ventralis in electromyographical studies may be a particularly serious flaw. For many situations pharyngeal biting is impossible without this muscle, because the contraction of the m. geniohyoideus instead of the m. transversus ventralis implies a much larger force contribution per se and requires an extra contribution of the m. pharyngocleithralis internus (to counteract the excess of anteriorly directed force) that exceeds by far the capacities of the latter muscle.

The m. retractor dorsalis

The m. retractor dorsalis is supposed to have only one line of action in electromyographical studies. The assumption of crossed lines of action for this muscle in the simulations with the model, not only lowers the muscular force necessary for biting in the adult (Galís, '92) and in the juvenile, but in doing so offers a functional explanation for the conspicuous twist of the fibers of this muscle. The combination of a line of action with a large lever arm and a small horizontal projection and one with a small lever arm and a large horizontal projection is essential for counteracting both the torque and the horizontal force of the biting force of the lower jaw while keeping the total muscular force low (Galís, '92). The assumption of more than one line of action also explains the extension of this muscle rostro-dorsally in large fish as an addition of a

COMPARISON OF JUVENILE-AND ADULT MUSCLE RECRUITMENT

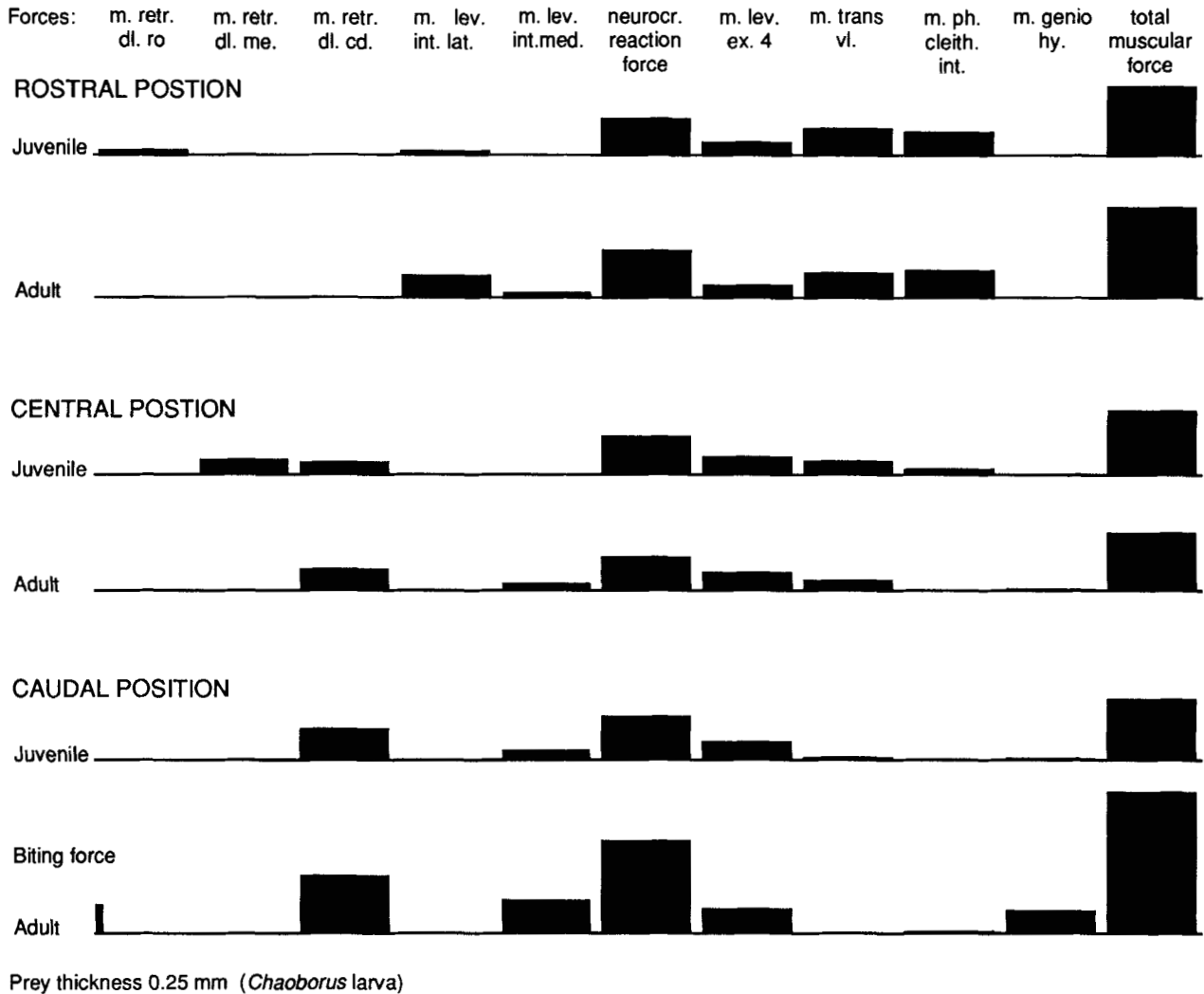


Fig. 8. Comparison of predicted juvenile (2.5 cm, SL) and adult (5 cm, SL) muscle recruitment for piercing of a *Chaoborus* larva at a rostral, central and caudal prey position. Contributions of individual muscles and of the neurocranial reaction

force are indicated. Note that total muscular force does not include the neurocranial reaction force. The net biting force that is exerted on the prey is indicated in the left lower corner (see also Fig. 4).

component with a large lever arm and small horizontal projection. (Fig. 5). The m.m. levatores interni form a similar combination of lines of action on the rostral side of the upper pharyngeal jaw, one with a large lever arm and a small horizontal projection and one with a small lever arm and a large horizontal projection.

Versatility of the pharyngeal jaw apparatus of cichlids

The results support the view that the pharyngeal jaw apparatus of cichlids is a highly flexible system. According to Liem and coauthors (Liem,

'73, '79, '80; Liem and Osse, '75; Liem and Sanderson, '86), the flexibility of the highly integrated pharyngeal jaw apparatus is the main factor that has enabled the diversity of feeding habits of cichlids. They attribute much of the flexibility to the suspension of the lower pharyngeal jaw in a muscular sling and to the variability of muscle activity patterns (modulatory multiplicity) that Liem found in piscivores (Liem, '78) and insect pickers (Liem, '79). The results of this study and a previous one (Galís, '92) emphasize the importance of the flexibility of muscle activity patterns during biting and further suggest that the complicated structure of the

m. retractor dorsalis may play a role in allowing flexibility.

Morphological constraints

The model explains the absence of *Chaoborus* pupae in the diet of small *H. piceatus* (Galís, '90) as a result of morphological constraints. These constraints are mainly due to differences in size of the cross-sectional areas of the muscles between juveniles and adults. In these parallel fibered muscles, the cross-sectional area is directly correlated with the maximum possible force that can be exerted. Predictions of the model for the adult on the basis of measurements on the juvenile instead of on the adult change very little as long as the values of the cross-sectional areas are taken from the adult. This is because of the almost isometric increase of most parameters (Galís, '90 and Fig. 1). Therefore the morphological constraint is one imposed by the size of the organism. It is not a developmental constraint because it is not one imposed by developmental changes. Yamaoka ('78) and Wainwright ('87, '88) also found evidence that the size of the musculature is indicative of pharyngeal jaw crushing strength in the Labridae. Wainwright ('88) showed that ontogenetic stages of labrids switched from soft-bodied to hard-shelled prey at 3–5 N crushing strength, even though this crushing strength occurred at a different body size in each species. It seems that, as in *H. piceatus*, the absence in the diet of hard prey in certain ontogenetic stages is due to limitations of the crushing capacity of the pharyngeal jaw apparatus.

Developmental constraints

Each developmental stage has to be viable and adaptive (Bonner, '88; Wake and Roth, '89; Liem, '91; Galís, '90). During rapid transitions, when many form-function relations change in a rapid and more or less synchronous way, it is more likely that one or more form-function relations will be temporarily suboptimal than during gradual transitions. Indeed metamorphosing animals are usually more vulnerable to predation than they are during other stages of their life (Arnold and Wassersug, '78, Stearns, '82). Metamorphosing anurans are not well adapted to either the juvenile or the adult habitat (de Jongh, '68; Wassersug and Sperry, '77). Other examples of vulnerabilities during drastic changes are, e.g., the period of first feeding in fish larvae (Blaxter, '88), the transition from cutaneous to gill respiration in fish larvae (De Silva and Tytler, '73), and the myelination of neurons in mammals (Davison and Dobbing, '66; Oppenheim, '81). Apparently

developmental constraints play a role in sudden transitions (see also Galís, '93). Thus far no such developmental constraints have been found during more gradual transitions. This study shows that the gradual increase in the thickness of the muscles (and thus of their force generating capability) combined with the flexibility of the muscle activity patterns presumably causes a gradual increase in the capability of the pharyngeal jaw apparatus for biting. The results of Heidweiller et al. ('92a,b) on drinking in chickens during development link up nicely with these results. They found that both the acquisition of novel motor action patterns and the flexibility of the motor activity patterns are necessary to maintain drinking ability throughout ontogeny.

Thus, the scanty evidence suggests that during gradual transitions flexibility of muscle activity patterns provides organisms with a mechanism that buffers the effects of form changes and enables them to avoid developmental constraints that temporarily hamper performance.

The results show that the reserve capacity (structural capacity in excess of functional demand) of the pharyngeal jaws for piercing prey is not constant during ontogeny. The above-mentioned vulnerability of animals during sudden transitions also suggests a lower reserve capacity at such times than at other times, even a barely sufficient reserve capacity. Ontogenetic transitions may require extra reserve capacity before and after transitions that is larger than strictly necessary at those times. This extra reserve capacity creates freedom not only for ontogenetic changes but also for evolutionary changes. Both phenotypic plasticity, such as flexible muscle activation, and reserve capacity may thus facilitate ontogenetic and evolutionary changes.

This study makes predictions for the ability of juvenile *H. piceatus* to pierce *Chaoborus* larvae and the inability to pierce *Chaoborus* pupae based on the comparison of predicted maximum biting forces of the pharyngeal jaw apparatus with (afterwards) measured piercing forces. This was similarly done for an adult specimen in a previous study (Galís, '92a). The results explained experimental and field data on the feeding behaviour of *H. piceatus* during ontogeny (Galís and de Jong, '88). These results combined with the allometric data from an ontogenetic series (Galís, '90) show how a biomechanical model helps elucidate the morphological basis of feeding abilities and of feeding constraints through ontogeny. As such it provides an insight into the relationships between form and function during ontogeny and into the role of the morphology in constraining and determining patterns of resource use.

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