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Feeding mechanics in primitive teleosts and in the halecomorph fish *Amia calva*

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(With 18 figures in the text)

The mechanics of feeding in *Salmo gairdneri* and *Hoplias malabaricus*, two generalized predaceous teleosts, was studied using high-speed movies (200 frames per second). In *Hoplias*, the feeding mechanism is characterized by an extreme anterior swing of the maxilla and rapid depression of the hyoid occurring synchronously with mandibular depression and neurocranial elevation. A similar feeding sequence is observed in *Salmo* although the movements of the head are neither as extreme nor as rapid.

The anterior swing of the maxilla, usually attributed to mandibular depression, increased when the ligamentous connection of the maxilla to the mandible was severed. A mechanical model of the jaw was constructed to elucidate the functional interrelationships of the neurocranium, maxilla and mandible.

Films of the "holostean" *Amia calva* feeding show that the feeding mechanism is of a fundamentally different nature than that of primitive teleost fishes. Extreme anterior swinging of the maxilla occurs synchronously with jaw opening but branchiostegal expansion and hyoid depression only reach a maximum well after the jaws have begun to close. The existence of a highly efficient levator operculi—opercular series—mandible coupling is hypothesized on the basis of the rapid initial jaw opening.

This pattern of feeding movements in *Amia* has necessitated a revision of current theories on the nature and significance of the "holostean" feeding mechanism and sheds new light on the adaptive significance of certain characters in fossil actinopterygians.

Contents

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Introduction

Modern teleost fishes, a highly successful group, are represented today by more species than the combined number of all other Recent vertebrates (Myers, 1958). This success is due at least in part to the morphologically complex and highly kinetic teleost jaw which evolved from the generalized predaceous pholidophorid feeding mechanism in the Triassic.

Throughout the course of this evolution, the fundamentally predaceous feeding mechanism seems to have represented the main line of evolutionary advancement, with specialized forms adapted to feeding on specific food items radiating from the generalized predaceous stock. Within the Teleostei, then, a study of the generalized predaceous forms at each level of adaptation can give major insights into the evolutionary significance of morphological innovations in jaw structure.

In particular, a detailed analysis of the feeding mechanisms of generalized fishes at the basal teleostean level can be used as a link between extinct fishes of the holostean grade and morphologically advanced teleostean fishes. Surprisingly, very little data exist on the jaw mechanics of primitive teleosts although a rather large body of data has been accumulated on the advanced teleostean groups (e.g. Alexander, 1967; Eaton, 1935; Liem, 1967, 1970, 1973; Osse, 1969). Those studies that do exist on primitive teleosts (Tchernavin, 1948; 1953, Alexander, 1966, 1969; Vrba, 1968) are based primarily on the manipulation of dead specimens with occasional still photographs to supplement the analysis. No detailed comparison of feeding in basal teleostean fishes has yet been done.

The objectives of this study, then, are (1) to examine the feeding mechanism of two members of basal teleostean superorders: *Hoplias malabaricus* (Ostariophysi) and *Salmo gairdneri* (Protacanthopterygii), (2) to examine the feeding mechanism of the holostean *Amia calva*, (3) to compare the mechanics of feeding in these three fishes with reference to phylogenetic position, morphologic differences, and convergent evolution, and finally (4) to discuss the evolution of the actinopterygian feeding mechanism with particular reference to increased morphological and functional versatility at the holostean level of advancement.

Materials and methods

High-speed cinematography was used to examine the jaw movements of *Salmo gairdneri*, *Hoplias malabaricus*, and *Amia calva* during feeding. Filming was conducted with an Eclair GV-16 Super camera at 200 frames per second and 1/1200 second shutter speed. An f9.5–95 mm Angenieux Zoom lens and Kodak 16 mm 4X reversal film were used in conjunction with the Eclair camera, and positive prints were made from the important feeding and coughing sequences. Dial calipers, rulers, and a protractor were used to measure the positions of the various jaw elements from the prints.

Surgical modification of the jaw in specimens of *Salmo* and *Hoplias* was performed with the aid of Tricaine Methanesulfonate, a standard anaesthetic for cold-blooded animals.

Specimens of *Hoplias*, *Salmo* and *Amia* were dissected as an aid in interpreting the high-speed film sequences. The following specimens were examined: *Hoplias malabaricus*: Museum of Comparative Zoology (MCZ) 46009, MCZ 48541 (cleared with trypsin and stained following the procedure of Taylor, 1967), and 2 uncatalogued specimens; *Salmo gairdneri*: 5 uncatalogued specimens; *Amia calva*: 2 uncatalogued specimens.

Results

The concept of a mechanical unit (Gans, 1969) will be used to divide the primitive fish jaw into six components. These mechanical units consist of one or more bony elements and may be joined together by muscle and/or connective tissue to form mechanical couplings (*sensu* Liem, 1967, 1970).

The six mechanical units are: (1) the premaxilla and neurocranium, (2) the suspensorium, (3) the mandible, (4) the maxilla, (5) the cleithrum, (6) the two hyoid bars forming the hyoid arch. Each of these elements performs as a mechanical unit during feeding.

Four major couplings can be defined in primitive teleosts. (1) Neurocranium–maxilla–mandible, (2) Hypaxial musculature–cleithrum–hyoid, (3) Cleithrum–hyoid–mandible, (4) Levator operculi–opercular series–mandible.

Salmo gairdneri: movements of the jaw during feeding

The cranial osteology and myology of *Salmo gairdneri* has been described elsewhere by several authors (Parker, 1893; Gregory, 1933; Tchernavin, 1938, 1948, 1953; Ballintijn & Hughes, 1965) and no comprehensive treatment will be presented here.

Characteristics of normal feeding movements (Fig. 2(a), (b), (c))

Movements of the neurocranium, maxilla, and mandible. (Fig. 1; open circles). As the distance between the jaws (as measured in Fig. 2(a)) increases in the feeding sequence, the maxilla swings through an arc of 31°, pivoting on its dorsal attachment to the neurocranium. The angle between the maxilla and the horizontal (φ: Fig. 1) reaches a maximum 0·005 sec after the distance between the jaws reaches its maximum value. Maxillary swing is thus temporally correlated with mouth opening.

The distance between the jaws, however, is a function of two variables: neurocranial lifting and mandibular depression. Both neurocranial lifting and mandibular depression also correlate temporally with maxillary swing.

Anatomically, the maxilla articulates dorsally with the neurocranium in a peg and socket joint; the medial process of the maxilla articulating anteriorly with the premaxilla which is immovably attached to the neurocranium (Tchernavin, 1953), and posteriorly with a large

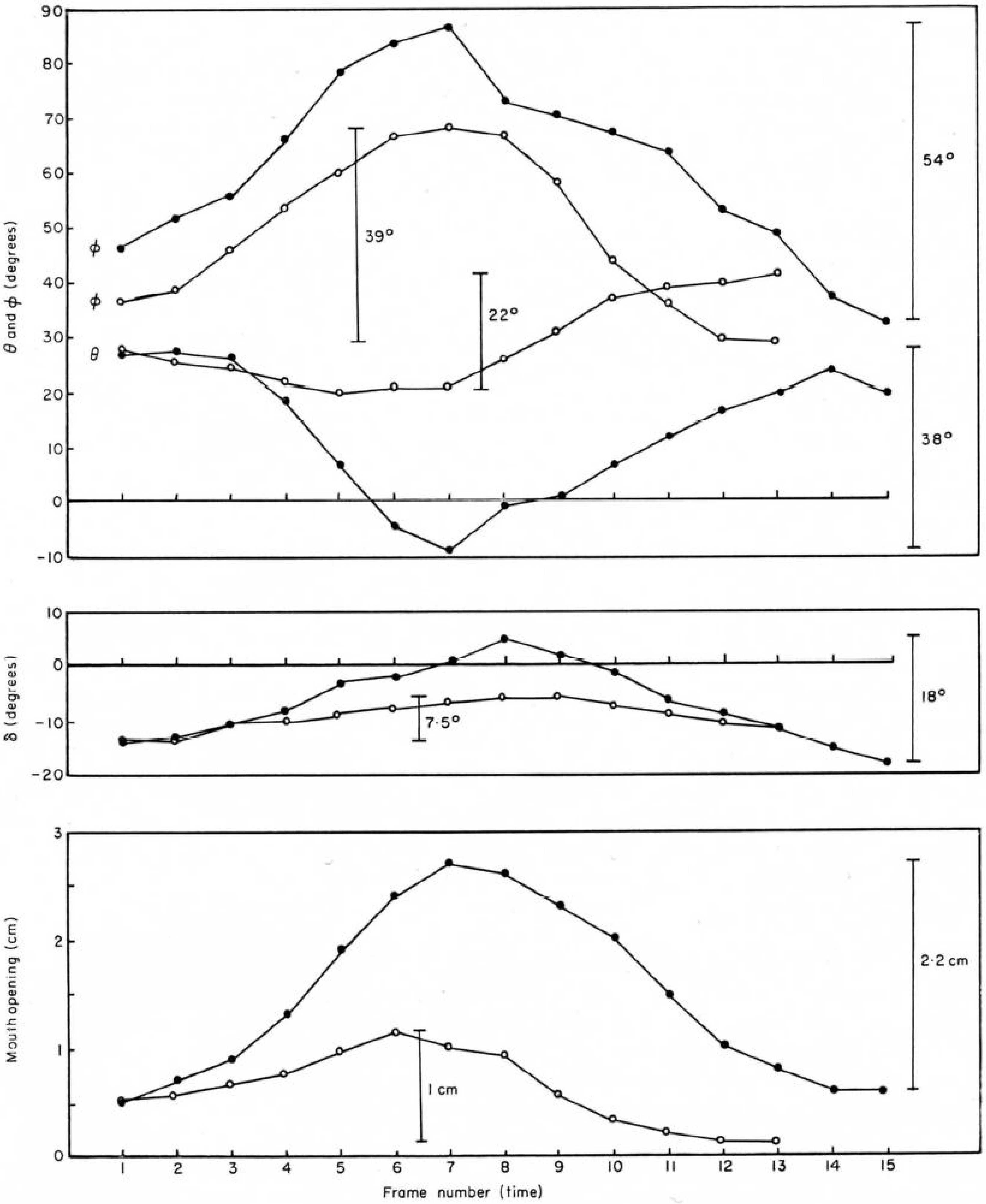

FIG. 1. *Salmo gairdneri*. Graphic representation of the angle of the neurocranium (δ), the maxilla (φ), the mandible (θ), and mouth opening during feeding. These symbols are used later (Fig. 18; Table I) in a mechanical model of the primitive teleost jaw, δ, φ, and θ are measured as shown in Fig. 18. Open circles represent feeding in a normal trout, closed circles feeding in a trout with bilaterally removed maxillomandibular ligaments. Time between frames is 0·005 sec. Bars represent the amplitude of excursion.

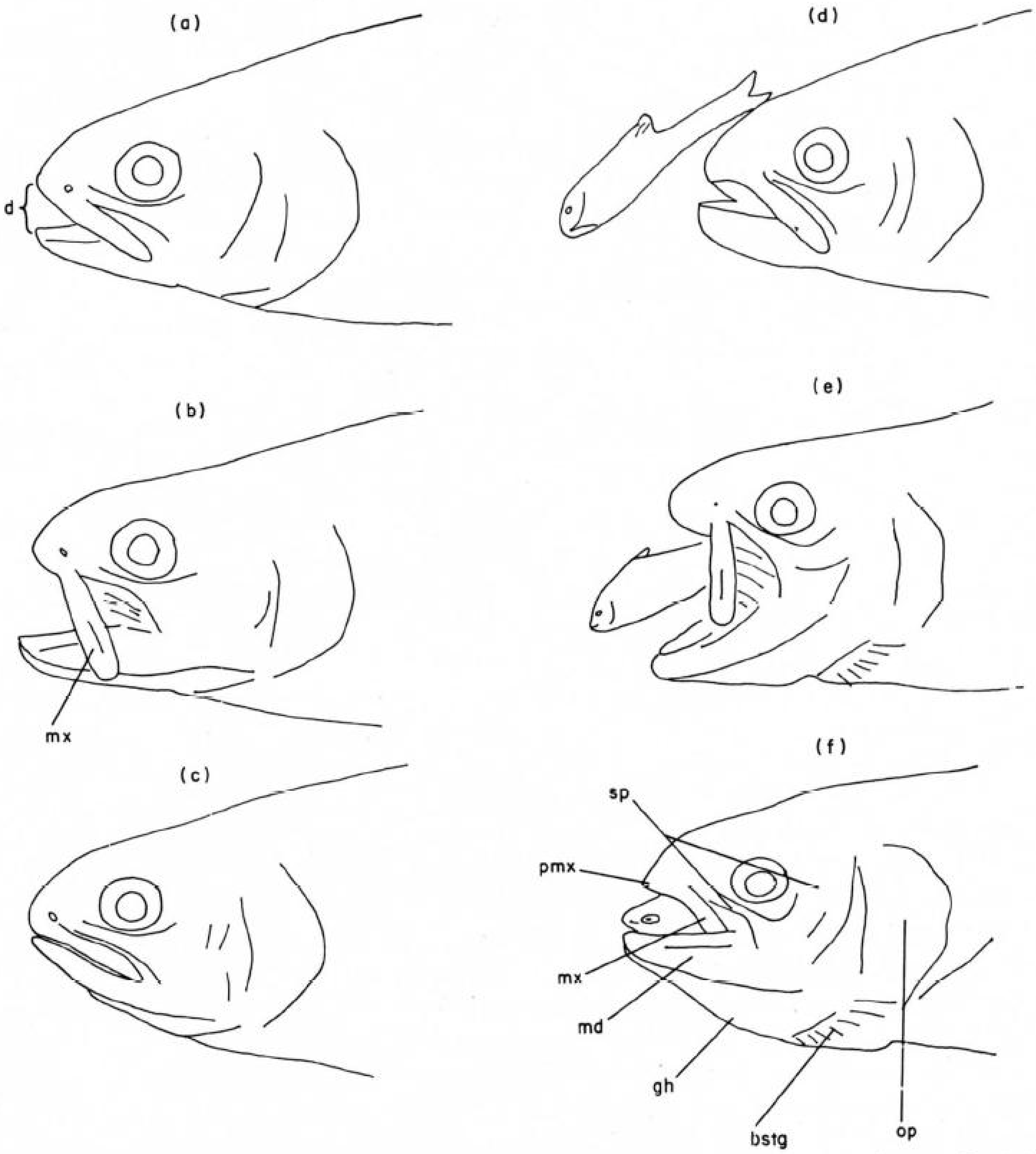

FIG. 2. Representative frames from 16 mm films showing jaw movements in the trout, *Salmo gairdneri.* (a), (b), (c) Frames 1, 7, and 13 respectively of a "coughing sequence" in a normal specimen. Movements of the jaw in this sequence are identical to those during feeding. (d), (e), (f) Frames 1, 7, and 13 respectively of a feeding attempt in a specimen with bilaterally removed maxillomandibular ligaments. Time between sequential film frames was 0·005 sec. A comparison of (b) and (e) shows that the initially large anterior swing of the maxilla increases after the maxillo-mandibular ligament has been cut.

Abbreviations: bstg, branchiostegal rays; *d*, the distance between the jaws measured from the anteroventral aspect of the premaxilla to the anterodorsal aspect of the mandible as seen in a lateral view; gh, geniohyoideus; md, mandible; mx, maxilla; op, opercle; pmx, premaxilla; sp, suspensory apparatus.

bulbous palatal process. The distal fan shaped aspect of the maxilla is attached to the coronoid process of the mandible by a flat wide maxillomandibular ligament. Mandibular depression has been widely evoked as causing maxillary swing in many groups of fishes (Tchernavin, 1953: *Salmo*; Alexander, 1966: *Idus*; Alexander, 1967: *Gasterosteus*; Roberts, 1969: *Hoplias*; Liem, 1970: Nandidae), while the effect of neurocranial lifting upon maxillary swing has been largely ignored.

Tchernavin (1953) did note that lifting the neurocranium will raise the anterodorsal aspect of the maxilla and thus passively increase φ, but no active swing of the maxilla has been attributed to neurocranial lifting. Measurements on the trout show that a fixed angular distance between the maxilla and the neurocranium is not maintained and that passive neurocranial lifting while maintaining a fixed angle between the maxilla and the neurocranium results in only a 6° increase in φ. The surprising degree of maxillary swing found during feeding must thus be due to a force exerted on the maxilla by either the mandible or the neurocranium.

Movements of the hyoid (Fig. 3(c), (d)). During feeding, hyoid depression begins as soon as the mouth is opened (Fig. 3(e)) and a relatively depressed condition is maintained throughout the sequence. An increase in hyoid depression may occur as the mouth closes on a prey at the end of a sequence. Once the prey has been trapped inside the mouth, attempts to force the prey back to the pharyngeal teeth and then into the esophagus produce movements very similar to those observed during feeding. The amplitude of hyoid movement also resembles that during feeding, but a depressed condition of the hyoid may not be maintained throughout the sequence.

The mandible–hyoid arch–cleithrum coupling. This coupling can adduct or abduct the mandible depending on the relative positions of the mechanical units (Fig. 4). In the early stages of the feeding sequence, the line of muscle contraction is superimposed upon a line drawn from the quadratomandibular articulation to the ventral tip of the cleithrum. No mechanical advantage is present. As the sequence progresses, the line of contraction swings below the working line and muscular contraction will abduct the mandible. Finally, adduction of the mandible swings the line of contraction above the working line and muscular contraction will adduct the mandible. The versatility of this coupling is due entirely to small changes in the relative positions of the mechanical units.

An additional series of events occurs when this coupling is active. Contraction of the sternohyoideus and geniohyoideus produces a torque on the hyoid (Fig. 4). The force of the sternohyoideus is transmitted to the ventral hypohyal through the urohyal–hypohyal ligament. The force resulting from contraction of the geniohyoideus is transmitted along the muscle insertion from the dorsal hypohyal to the ceratohyal. Maximum torque will result from the components of force acting in opposite directions at the ceratohyal and ventral hypohyal. This torque rotates the hyoid arch around the interhyal–hyomandibular articulation and results in hyoid depression (Fig. 4: frame 7).

The neurocranium and suspensory apparatus. As the neurocranium pivots on the anterior vertebrae, the suspensory apparatus swings with it carrying the quadratomandibular articulation (Tchernavin, 1953). Thus, as the angle β (Fig. 4) decreases, the quadratomandibular articulation is raised up above the line joining the ventral tip of the cleithrum and the previous position of the quadrate. This mechanism increases the mechanical advantage of the geniohyoideus and sternohyoideus. Neurocranial lifting can thus contribute to the mechanical efficiency of mandibular abduction.

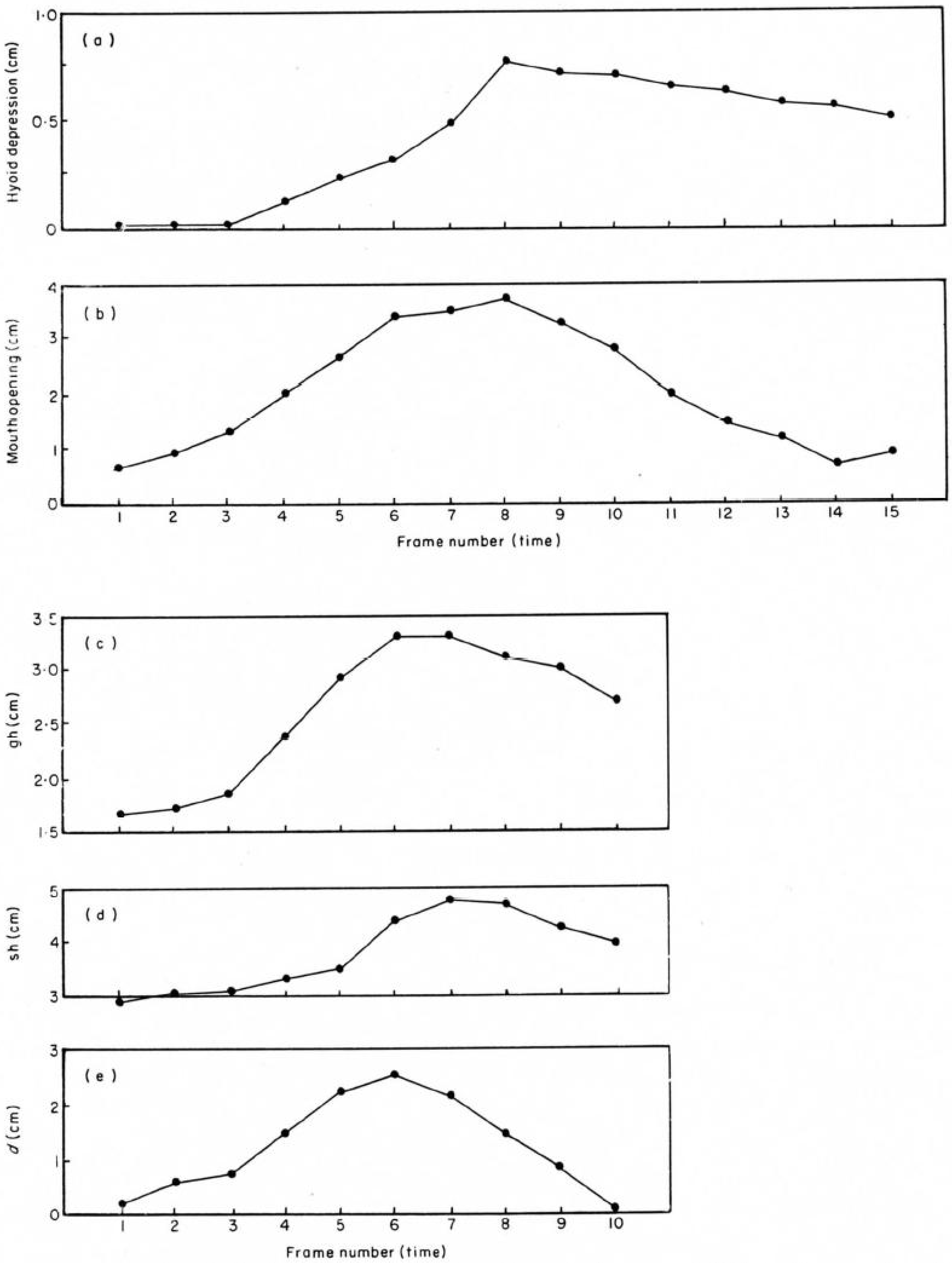

FIG. 3. *Salmo gairdneri*. (a) hyoid depression and (b) mouth opening in a trout with bilaterally removed maxillo-mandibular ligaments. (c) depression of the geniohyoideus (gh); (d) depression of the sternohyoideus (sh); (e) mouth opening (d) in a normal trout during a feeding sequence. Time between frames 0·005 seconds.

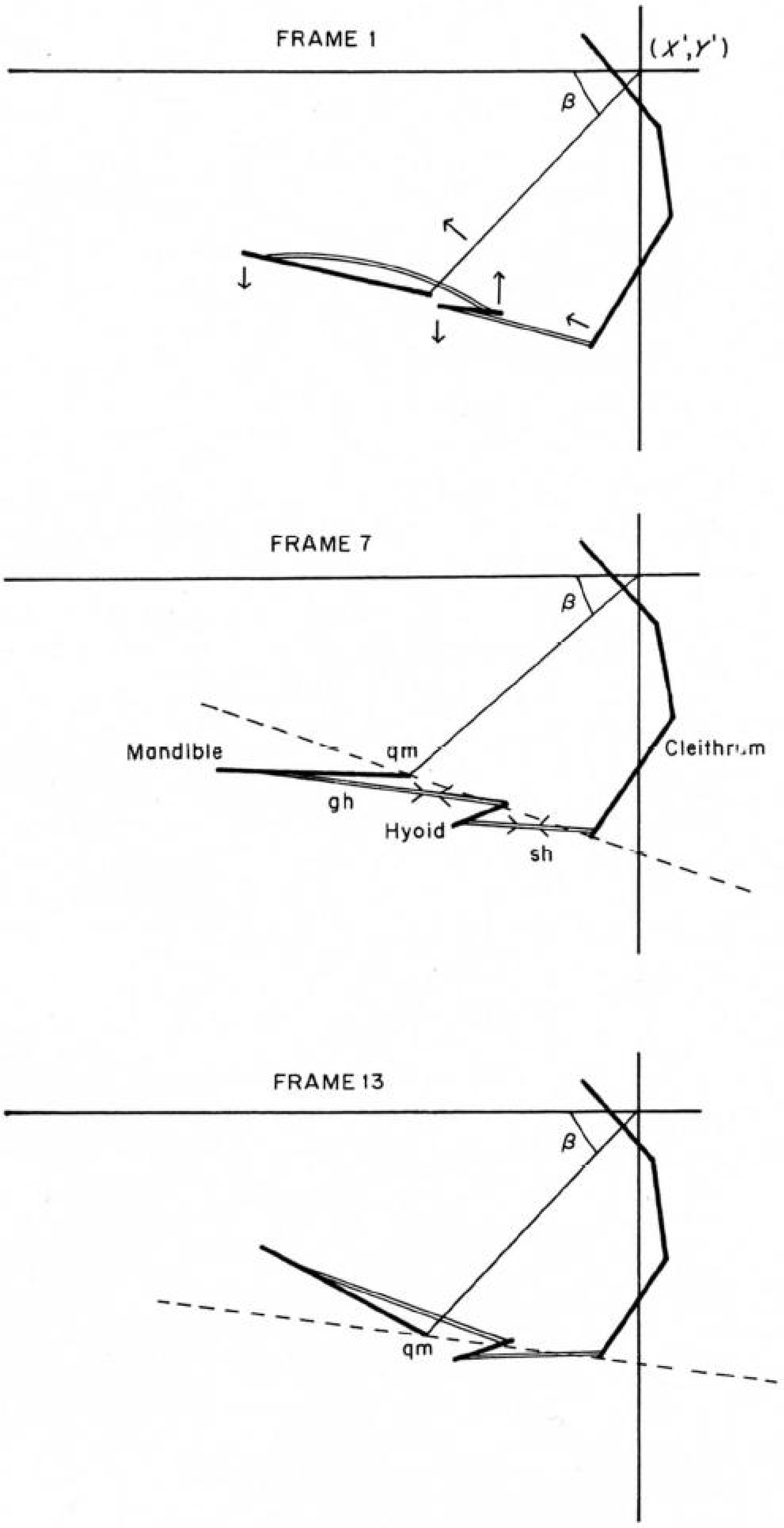

FIG. 4. *Salmo gairdneri.* Accurate diagrammatic representation of the positions of the mandible, hyoid, and cleithrum during feeding in a normal specimen.

Abbreviations: β, the angle between the horizontal and a line joining (*X′*, *Y′*) and fm; gh, geniohyoideus; qm, the quadratomandibular articulation; sh, sternohyoideus; (*X′*, *Y′*), the point of neurocranial bending on the vertebral column. The dashed line indicates the line between the ventral tip of the cleithrum and the quadratomandibular articulation and arrows indicate the direction of movement. Time between sequential frames was 0·005 seconds.

Suction. Dilation of the operculum (Fig. 5(a)), suspensory abduction, hyoid depression, neurocranial lifting, maxillary swing, and mandibular depression all increase the volume of the orobranchial cavity and cause a rapid influx of water carrying the prey into the mouth. The exact temporal sequence of these movements can accurately be determined only by a combination of electromyographic studies synchronized with high-speed cinematography, but a more qualitative analysis is possible by relating the measurements from different feeding sequences to the change in distance between the jaws—probably the most consistently predictable event during feeding. A comparison of Figs 3 and 5 shows that while hyoid depression is initiated as soon as the jaws begin to open and is maintained at near maximum depression throughout the feeding sequence, opercular dilation and suspensory abduction build slowly to a maximum value, peaking sharply after the jaws have begun to close. Nyberg (1971) noted this phenomenon in the bass and explained it as functioning to shift the low pressure center to the rear of the orobranchial cavity. This will move the prey nearer to the esophagus and facilitate deglutition.

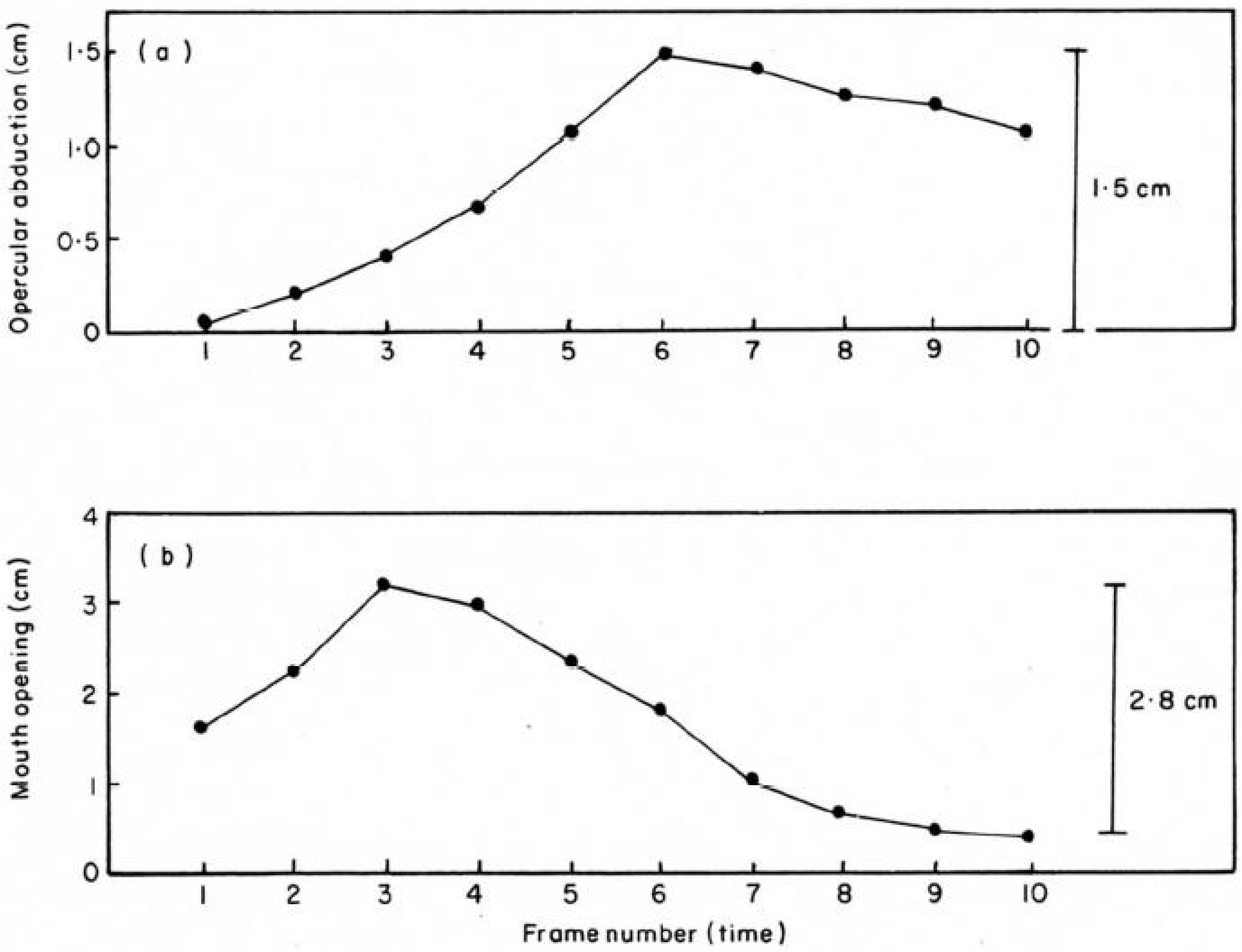

FIG. 5. Graphic representation of opercular expansion (a) and mouth opening (b) in *Salmo gairdneri* during feeding. Time between frames is 0·005 seconds.

Swinging the maxilla forward creates a tunnel which serves to extend the orobranchial chamber towards the prey, and may aid in trapping the prey within the mouth, thus generally increasing the efficiency of the suction mechanism. A more quantitative description of the increase in suction efficiency will be presented later.

Experimental analysis of the neurocranium–maxilla–mandible coupling (Fig. 2(d), (e), (f))

The maxillomandibular ligament was surgically bilaterally removed from a specimen of *Salmo gairdneri*. High-speed movies were then obtained of this specimen attempting to feed 24 hours later. The effects of this surgery are described below.

Movements of the neurocranium, maxilla, and mandible. Movement of all three of these mechanical units exhibits much greater amplitude than in a normal trout (Fig. 1; solid circles). Angular maxillary swing increases significantly, as does mandibular depression and neurocranial lifting. Maximum excursion of the maxilla occurs one frame before the maximum angle is achieved by the neurocranium, and simultaneously with maximum mandibular depression. Return of the maxilla to its final position seems to be achieved primarily by elastic recoil in the connective tissue between the mandible and the maxilla.

Suspensory abduction begins shortly after the mouth opens and as the distance between the jaws increases, the quadratomandibular joints are displaced laterally by suspensory abduction. This movement is transmitted to the distal aspect of the maxilla located lateral to the dentary. As the maxilla swings on its neurocranial pivot, extreme mandibular depression results in the distal aspect of the maxilla swinging out beyond the mandible (Fig. 2(e)). This instantly releases the lateral component of force on the maxilla resulting from suspensory abduction and the maxillaries both move medially and into the mouth. As the mouth is closed, the maxillaries are trapped within the orobranchial chamber and prevent complete closing of the mouth (Fig. 2(f)).

The effects of incomplete mandibular adduction are dramatic. No successful prey captures by the trout were recorded despite numerous attacks. This agrees well with Liem's (1970) results on nandids which showed that maxillomandibular ligament removal allowed successful initial capture of the prey, but that eventual escape invariably occurred.

General conclusions

The initation of a normal feeding sequence in the trout is characterized by rapid elevation of the neurocranium and depression of the mandible. Concomitant with these events is an immediate depression of the hyoid. Opercular expansion and suspensory abduction are initiated later in the feeding sequence after the mouth has begun to close. The hyoid may remain depressed and the suspensory apparatus abducted well after the prey has entered the orobranchial chamber.

It can be inferred that mandibular depression is initiated by the levator operculi–opercular series–mandible coupling (Liem, 1967, 1970; Liem & Osse, 1975), and that subsequent mandibular depression is at least partially due to forces exerted by the cleithrum–hyoid–mandible coupling.

The surprising discovery that maxillary swing increases after the ligamentous connection to the mandible is severed indicates that the hitherto supposed correlation between mandibular depression and maxillary movement must be reevaluated. Mandibular depression contributes only marginally to maxillary swing and the primary function of the maxillomandibular ligament is to restrain and guide maxillary motion. The coronoid process of the mandible provides a site of maxillomandibular ligament insertion and is thus critical to the stabilization of maxillary swing.

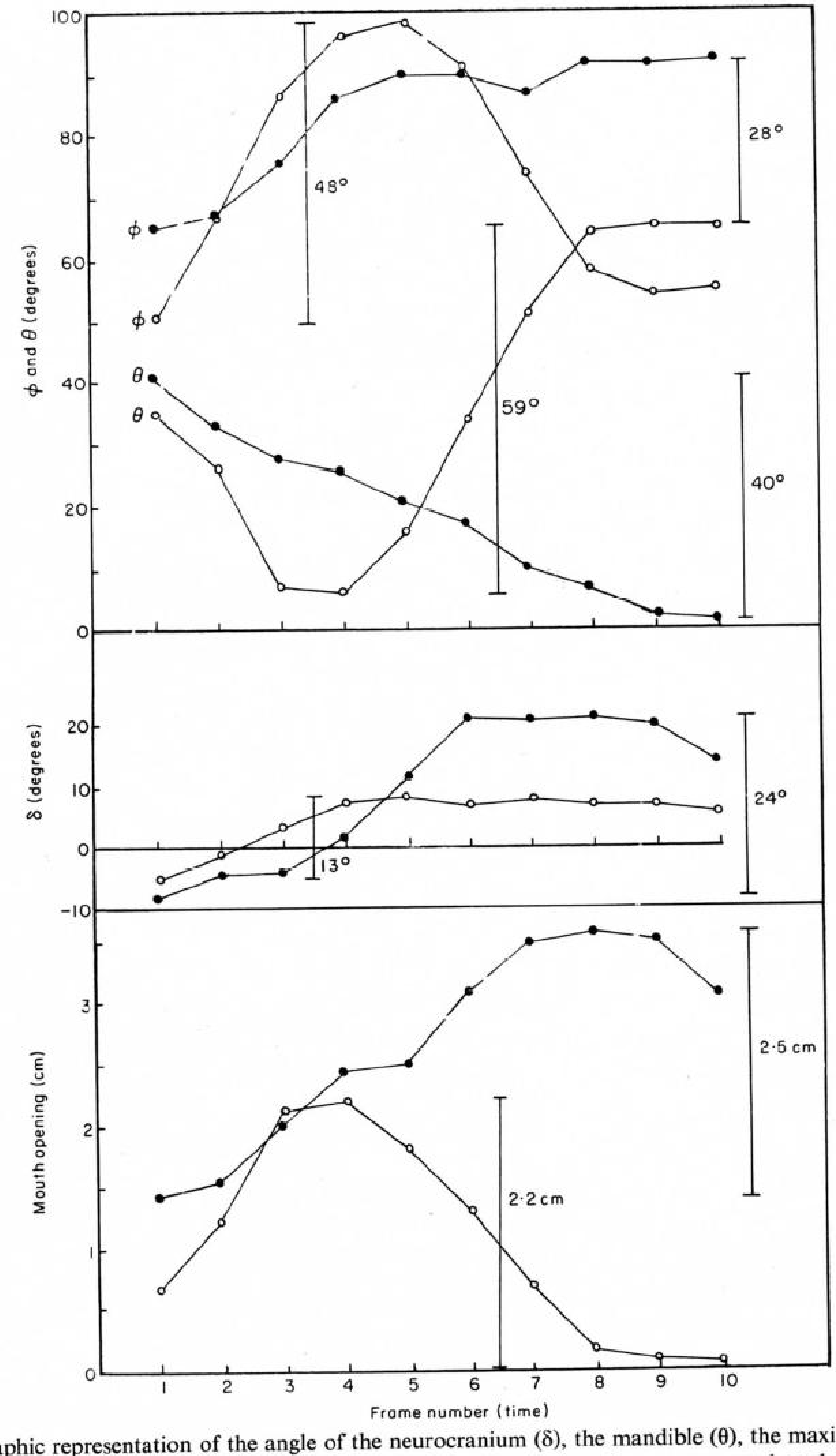

FIG. 6. Graphic representation of the angle of the neurocranium (δ), the mandible (θ), the maxilla (φ), and the distance of mouth opening during feeding of *Hoplias malabaricus*. δ, θ, and φ are measured as shown in Fig. 13. Open circles represent feeding movements in a normal specimen; solid circles represent movements in a specimen with bilaterally removed maxillomandibular ligaments. Time between frames is 0·005 sec. Bars represent the amplitude of excursion.

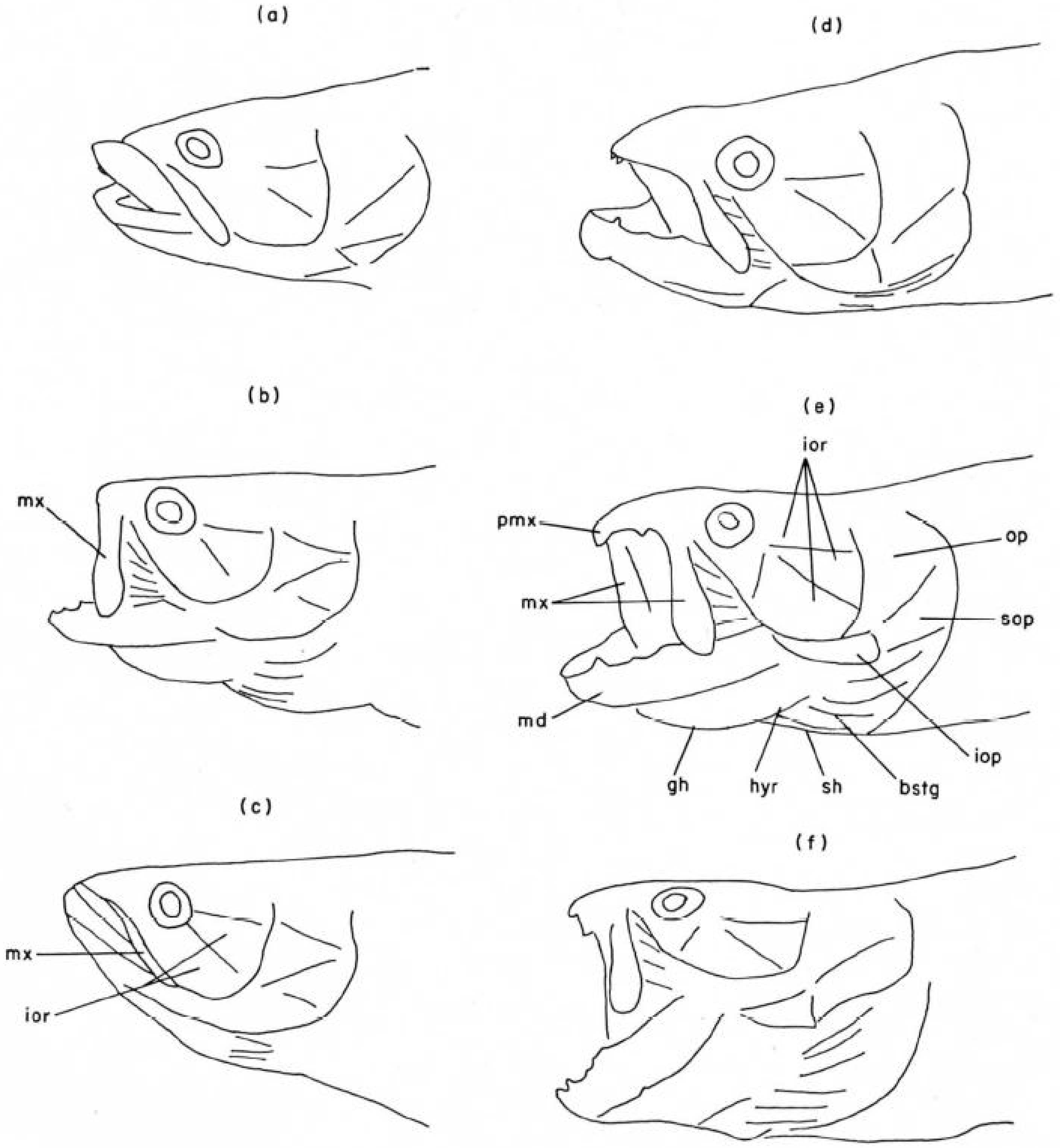

FIG. 7. Representative frames from 16 mm films showing jaw movements in *Hoplias malabaricus.* (a), (b), (c) frames 1, 5 and 10 respectively of a feeding sequence in a normal specimen. (a) The prey can be seen lodged between the jaws from a previous feeding. (b) Maximum expansion of the jaw elements. The maxilla has swung anteriorly past the vertical and the hyoid is extremely depressed. (c) The lower jaw is adducted against the neurocranium which is maintained in an elevated position. Note that the maxilla has returned to the infraorbital pocket. (d), (e), (f) Frames 1, 5, and 10 respectively of severe head shaking in a specimen with bilaterally removed maxillomandibular ligaments. (d) The right maxilla is between the mandibular rami. (e), (f) Elevation of the neurocranium and mandibular depression in an attempt to extricate the maxilla.

Abbreviations: bstg, branchiostegal rays; gh, geniohyoideus; hyr, hyoid ramus; iop, interopercle; ior, infraorbitals md, mandible; mx, maxilla; op, opercle; pmx, premaxilla; sop, subopercle.

Time between sequential film frames was 0·005 seconds.

Hoplias malabaricus: *movements of the jaw during feeding*

Alexander (1964) has briefly considered the cranial myology of *Hoplias* and Roberts (1969) has described the cranial osteology in considerable detail.

Characteristics of normal feeding movements (Fig. 7(a), (b), (c)).

Movements of the neurocranium, maxilla, and mandible. (Fig. 6; open circles) Movements of these mechanical units exhibit consistently greater amplitudes than comparable movements in the trout. Lifting of the neurocranium occurs synchronously with mandibular depression and both of these movements reach a maximum value at the same time. Correlated with the increase in distance between the jaws is an extreme swing of the maxilla around the neurocranial articulation. The maxilla swings through a 45° arc and may swing past the vertical in some sequences (Fig. 7(b)). The maximum angle of the maxilla occurs

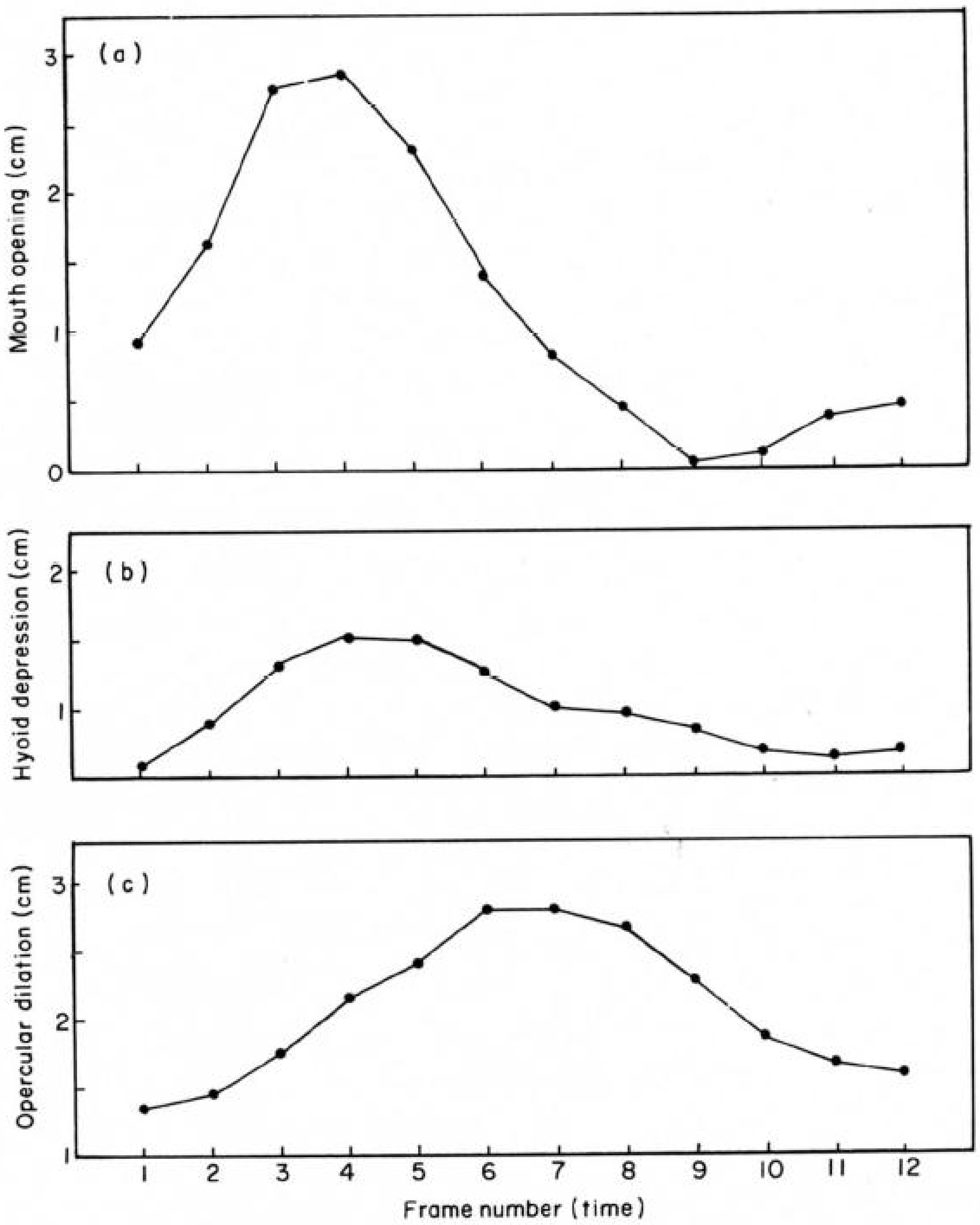

FIG. 8. Graphic representation of mouth opening (a), hyoid depression (b), and opercular abduction (c) in one feeding sequence of *Hoplias malabaricus*. Time between frames is 0·005 seconds.

one frame (0·005 sec) after the neurocranium and the mandible have reached their maximum angular swing.

The dorsal articulation of the maxilla consists of a long medial process which extends medially posterior to the premaxilla which is immovably attached to the neurocranium. A palatine-ectopterygoid–accessory ectopterygoid complex forms the posterior border of the maxillary–neurocranial articulation. Numerous strong thin strands of connective tissue extend anterodorsally from the maxilla to the posterior aspect of the premaxilla. As the maxilla pivots, the medial process rotates within the neurocranium and restricts maxillary swing to a nearly parasagittal plane.

As the mouth closes, the neurocranium maintains an elevated condition and the mandible is rapidly adducted against the upper jaw (Fig. 6; θ, open circles). The mandible is adducted through a 59° arc to close the mouth while the neurocranium is maintained at a 12° angle to the horizontal. The maxilla returns to its initial position as the distance between the jaws decreases.

Movements of the hyoid. As in the trout, hyoid depression begins as soon as the jaws begin to open and reaches a maximum shortly after the maximum distance between the jaws is achieved (Fig. 8(a), (b)). The hyoid is maintained in a relatively depressed condition even after the prey has entered the mouth and the jaws have closed.

The mandible–hyoid arch–cleithrum coupling. Throughout the numerous feeding sequences, the line of contraction represented by the geniohyoideus and sternohyoideus muscles never rose above the line between the quadratomandibular articulation and the ventral tip of the cleithrum (Fig. 9). Torque on the hyoid is very great, however, and the hyoid rami achieve almost a vertical position during the feeding sequence. Abduction of the suspensorium begins shortly after the mouth opens and spreads the two hyoid rami through lateral forces on the interhyals. When the sternohyoideus and geniohyoideus contract, the hyoid arch is twisted about the interhyal and will assume almost a vertical position as a result of antagonistic forces between the geniohyoideus and sternohyoideus. This results in a dramatic increase in volume of the orobranchial chamber. The extreme curvature of the geniohyoideus muscle (Fig. 7(b)) is probably the result of pressure from the basihyal which has been moved caudoventrally by rotation of the hyoid around the interhyal–suspensorial articulation.

Suction. Correlation of hyoid depression, mouth opening, and opercular dilation and suspensorial abduction indicates that these events all occur in a definite sequence during feeding. As the distance between the jaws increases, hyoid depression is initiated and only after the mouth is nearly closed does opercular dilation reach a maximum value (Fig. 8). Lateral expansion of the suspensorium has not been measured directly but several sequences show extreme suspensorial movements which occur synchronously with opercular dilation.

An important additional mechanism that acts to increase suction efficiency has been discovered in *Hoplias*. As the maxillaries swing forward they do not swing in a strictly parasagittal plane. Rather, the planes of maxillary swing intersect at a point about 10 cm in front of the head. Ciné-film in which the sagittal plane of *Hoplias* is perpendicular to the film plane show that as the mouth is opened, the distal aspect of the maxilla swings anteriorly towards the sagittal plane so that the effective cross-sectional area of the mouth is decreased. Measurements indicate that maxillary swing decreases the cross-sectional area by a factor of 10 to 15 percent. Since the flow rate of water entering the mouth is proportional to the cross-sectional area times the velocity of flow, given a constant flow rate, a

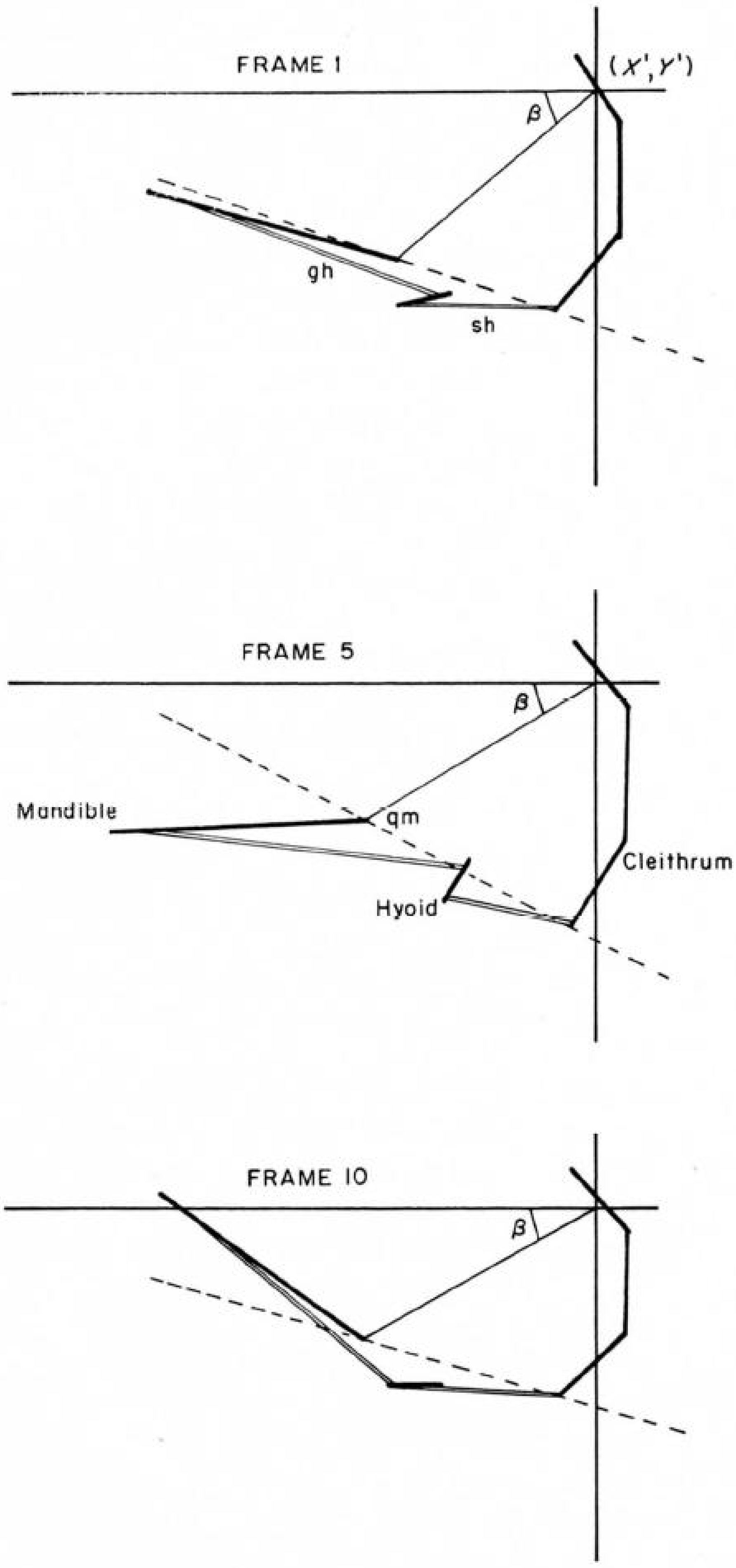

FIG. 9. Accurate diagrammatic representation of the relationship between the mandible, hyoid, and cleithrum during a feeding sequence of *Hoplias malabaricus*. Abbreviations as in Fig. 4.

decrease in cross-sectional area will result in an increased velocity of water flow. This added velocity may be useful in bringing prey within the reach of the anterior premaxillary and mandibular teeth where it could be grabbed when the mouth is closed. Several sequences were observed in which the attack was apparently initiated too far from the prey or the prey attempted vigorously to escape. In these cases, the initial attack only served to bring the prey to the anterior portion of the mouth and coughing movements were necessary to move the prey back into the orobranchial chamber.

Experimental analysis of the neurocranium–maxilla–mandible coupling (Fig. 7(d), (e), (f)).

The maxillomandibular ligament was bilaterally removed from a specimen of *Hoplias malabaricus*. No feeding sequences were recorded as the specimen refused to feed after surgery. Several sequences were obtained, however, of jaw movements following surgery.

Movements of the neurocranium, maxilla, and mandible. (Fig. 6; solid circles) Lifting of the neurocranium and mandibular depression are both temporally correlated with maxillary swing. Since the ligamentous connection to the mandible has been severed, the swing of the maxilla must be attributed to neurocranial lifting. As in the trout, opening the mouth frequently caused one or both of the maxillaries to swing inside the lower jaw. This was due to the extreme movements of the lower jaw and neurocranium which resulted in the distal portion of the maxilla swinging out beyond the mandibular rami and into the oral cavity. As the jaw closed, the maxilla was caught inside the mouth. Violent head shaking was observed and as the lower jaw was depressed and the head lifted, the maxilla swung outside the mandibular rami and returned to its initial position.

In *Hoplias*, the distal portion of the maxilla usually rests inside the infraorbital bones in a pocket lined medially by fascia covering the adductor mandibulae and laterally by the infraorbital bones (Fig. 7(b), (c)). Surprisingly, after the maxillomandibular ligament has been cut and the specimen has attempted to open its mouth, the maxillaries usually return to their normal position in the infraorbital pocket. Presumably a medial force is exerted on the maxillaries by the neurocranium–maxillary articulation and this force guides the maxilla into the infraorbital pocket.

The magnitudes of neurocranial lift and mandibular depression consistently exceed those of a normal feeding sequence and repeated "lifting sequences" were observed as the specimen attempted to extricate the maxilla from its mouth. As a result, no complete sequences of jaw opening and closing were observed. The extreme head movements, however, were very useful in determining the range of possible movements and in observing the action of certain couplings during jaw opening.

Movements of the hyoid. The cleithrum–hyoid arch–mandible coupling is an important coupling active during extreme mandibular abduction. The hyoid arch achieves almost a vertical position and the geniohyoideus can clearly be seen extending from the tip of the mandible posteriorly to the insertion on the ceratohyal and hypohyal. Contraction of the geniohyoideus and sternohyoideus would, in addition to placing a torque on the hyoid, strongly abduct the mandible.

The interopercular, through contraction of the levator operculi and subsequent dorsal movement of the opercular series, can transmit a distal force to the articular ventral to the quadratomandibular articulation and also abduct the mandible. This coupling is probably active only in the initial stages of mandibular abduction since the mechanical advantage of the geniohyoideus and sternohyoideus increases greatly as the lower jaw drops.

Hyoid movements during extreme "lifting sequences" follow the pattern of the other jaw elements: the magnitude of extension tends to increase as the sequence progresses.

General conclusions

Hoplias can be characterized as a suction feeder. Rapid and extreme hyoid depression as soon as the mouth begins to open followed by suspensorial abduction and opercular dilation are all adaptations to a suction mode of feeding. Following capture of the prey, the suspensorium and operculum return quickly (0·015 sec) to their initial position while the hyoid remains depressed for a considerable period of time.

The cleithrum–hyoid–mandible coupling activated by contraction of the geniohyoideus and sternohyoideus seems to be an important coupling mediating mandibular abduction, although the levator operculi–opercular series–mandible coupling is almost certainly initially active and increases the mechanical advantage of the former coupling.

Maxillary swing is primarily due to neurocranial lifting although the evidence here is less clear than in the case of *Salmo gairdneri*.

Amia calva: *movements of the jaw during feeding* (*Figs 10, 11*).

Anatomical couplings

Gosline (1969, 1971), Patterson (1973) and Allis (1897) have all considered the cranial anatomy of *Amia* to some degree. Allis' work represents an extremely detailed account of the muscles and nerves of the head of *Amia calva*, and Gosline and Patterson have relied heavily on this for their accounts of the cranial anatomy of *Amia*. Gosline (1969: 192) states, "In *Amia*, then, the interopercle has no special attachment to the mandible and none whatsoever to the angular . . .", and Gosline (1971: 66–67) writes, "In the 'holostean' *Amia*, lowering of the mandible appears to be entirely associated with, and dependent on, the lowering of the floor of the mouth." Patterson (1973: 245) concurs with Gosline and remarks, "the interopercular . . . serves to transmit the pull of the levator operculi muscle to the ceratohyal ((in) *Amia*)."

The implication, then, is that no direct coupling exists between the levator operculi, the opercular series, and the mandible in *Amia*, and that the hyoid must be of fundamental importance in opening the jaw. Gosline (1969, 1971) has proposed several systems which may be operative in *Amia* to mediate jaw opening and has relied heavily for his data on Allis (1897).

Gosline and Patterson seem to have misinterpreted Allis, however, since Allis (1897: plate 20, figure 1) clearly shows the presence of an interoperculomandibular ligament. Allis also illustrates three other important ligaments, all originating from the uppermost branchiostegal ray and inserting separately on the mandible, hyoid, and interopercular. It is thus possible that the uppermost branchiostegal ray provides another link from the opercular series to the mandible.

My own dissections reveal an extremely thick interoperculomandibular ligament. This ligament extends from the anteroventral tip of the interopercular to the retroarticular and angular and has a wide insertion on the mandible. This insertion is ventral to the quadratomandibular articulation and could exert a strong force on the distal aspect of the mandible which would rotate the lower jaw around the quadratomandibular articulation. It thus seems that *Amia*, like the teleosts, has a musculoskeletal coupling that mediates mandibular abduction through contraction of the levator operculi.

This coupling, in fact, may be highly efficient since the opercular series of *Amia* is tied very closely together by strong connective tissue, and any force on the opercular exerted by contraction of the levator operculi would be immediately transferred to the mandible.

Movements of the neurocranium, maxilla, and mandible (Fig. 10).

High-speed ciné-film (200 frames per second) of *Amia calva* feeding support the above anatomical inferences and shed further doubt on Gosline's (1969, 1971) proposed jaw movements in *Amia*.

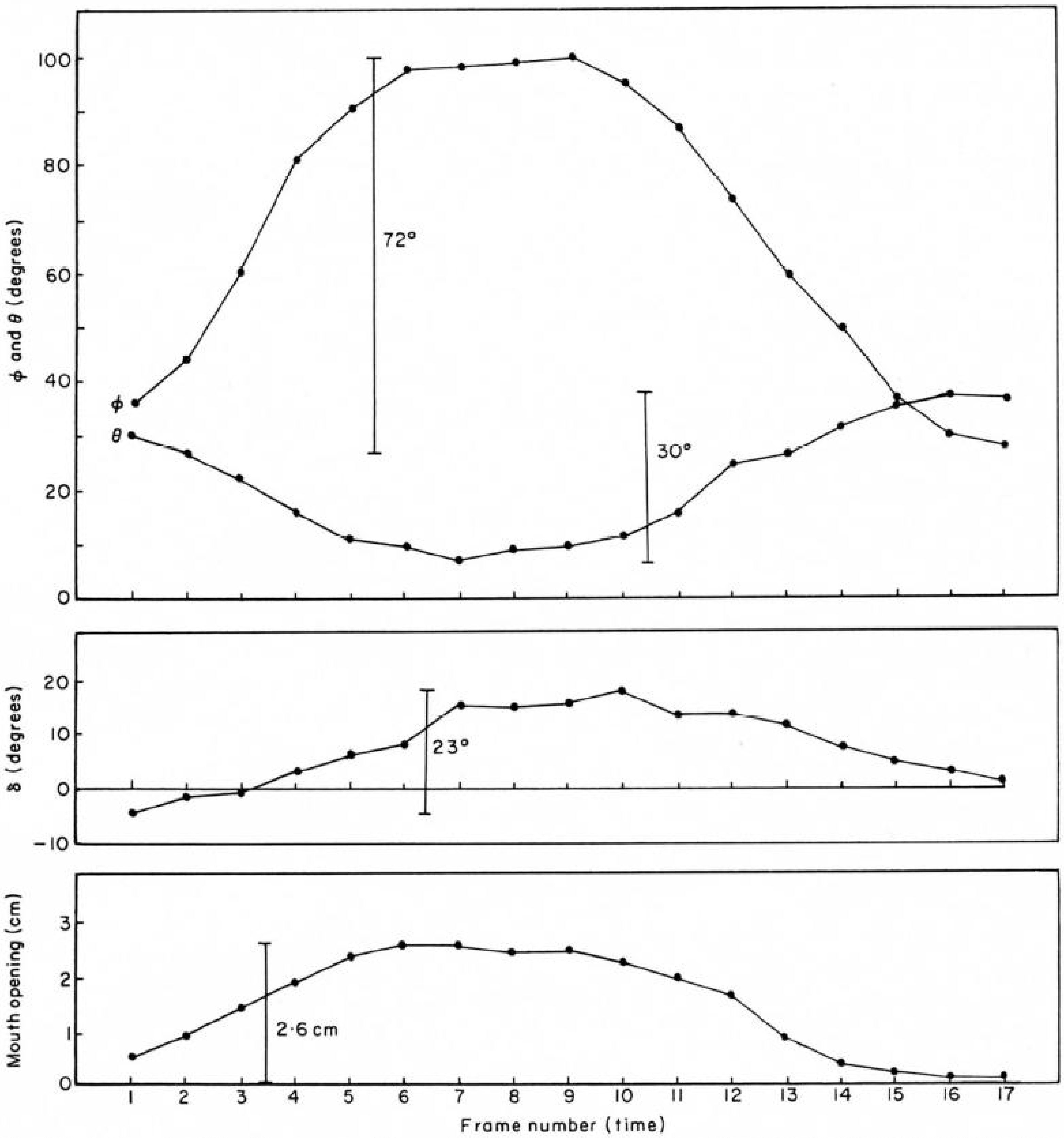

FIG. 10. *Amia calva*. Graphic representation of the angle of the neurocranium (δ), maxilla (φ), mandible (θ), and the distance of mouth opening during a feeding attempt. δ, φ, and θ are measured as shown in Fig. 13. Time between frames is 0·005 seconds and bars represent the range of excursion.

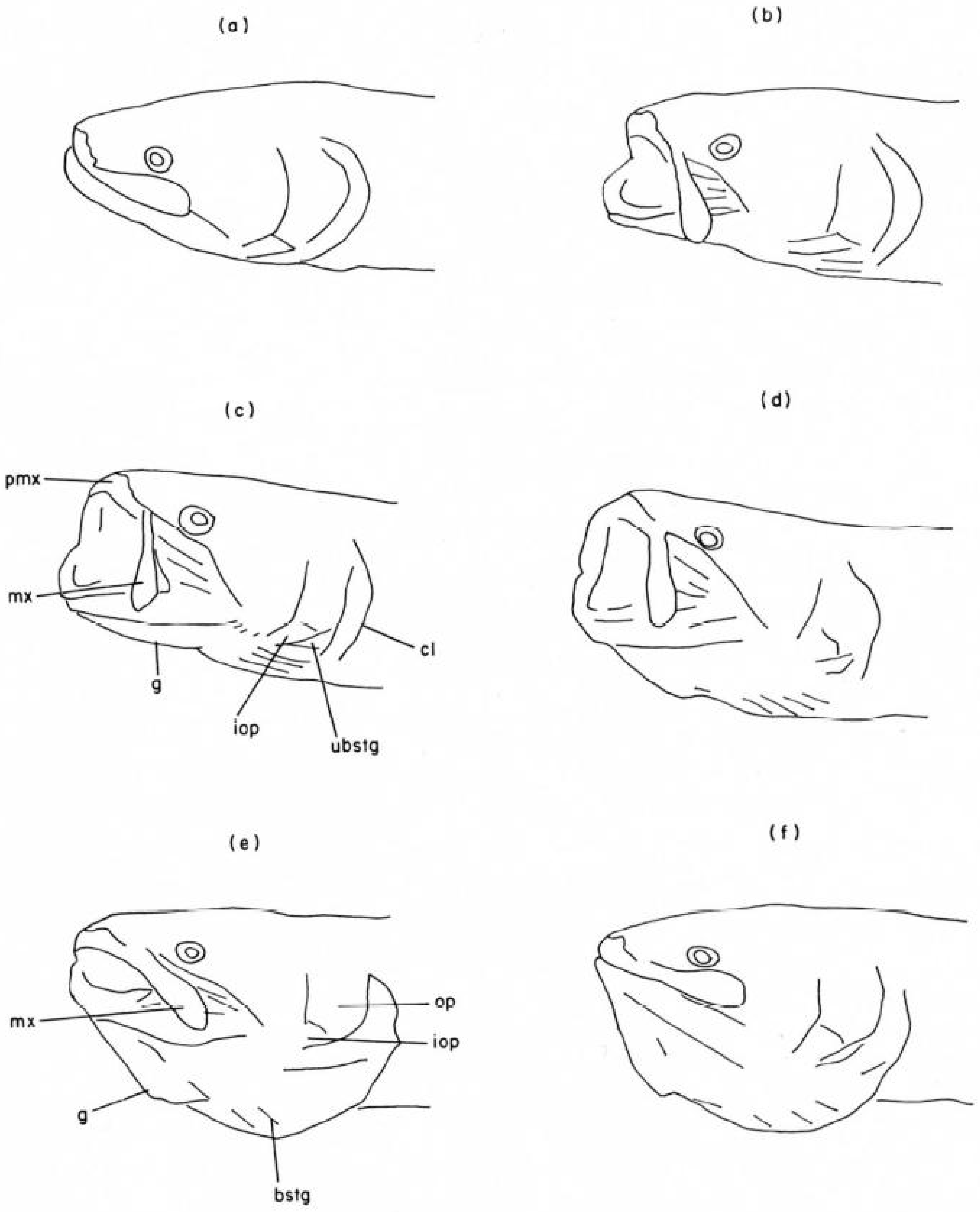

FIG. 11. Representative frames from 16 mm films showing jaw movements in *Amia calva*. (a), (b), (c), (d), (e), (f) Frames 1, 3, 6, 8, 13, 17 respectively of a feeding sequence. Note the extremely rapid opening of the mouth ((a) and (b)) with relative inactivity of the ventral head couplings. (c) The mouth has reached its maximum gape and the maxilla has swung anteriorly into a nearly vertical position. (d), (e), (f) as the mouth closes, the ventral expansion of the head reaches its maximum.

Abbreviations: bstg, branchiostegal rays; cl, cleithrum; g, gular plate; iop, interopercle; mx, maxilla; op, opercle; pmx, premaxilla; ubstg, upper branchiostegal ray.

Time between sequential film frames was 0·005 seconds.

Opening of the mouth occurs extremely rapidly. Within 0·025 seconds the distance between the jaws has nearly reached its maximum. Extreme forward swing of the maxillary occurs and is correlated with neurocranial lifting and mandibular depression.

Closing of the mouth follows a similar pattern to that observed in *Hoplias* and, to some extent, in *Salmo*: the mandible is adducted against the neurocranium which is maintained in an elevated position.

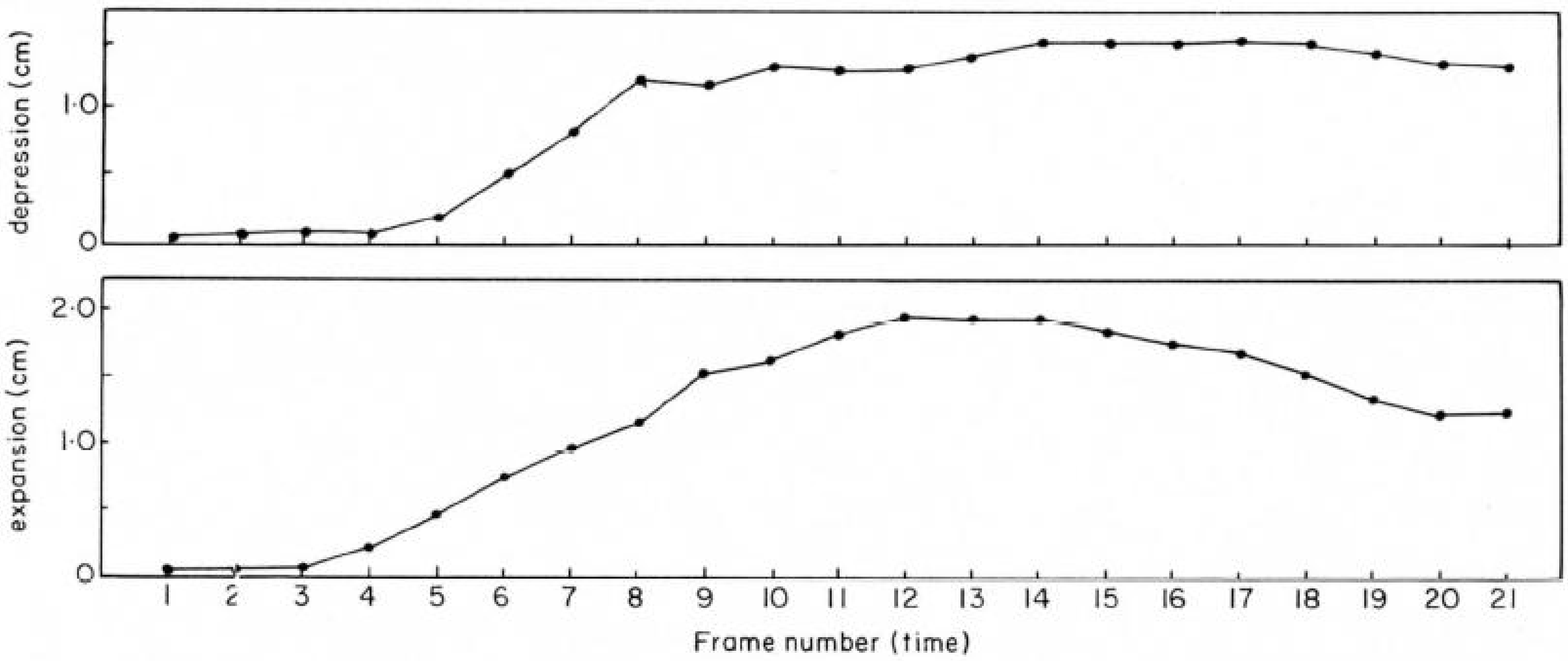

FIG. 12. Gular depression and branchiostegal expansion during a feeding sequence. The frame numbers correspond to those in Figs 10 and 11. Notice that gular depression begins before branchiostegal expansion and that both of these events reach a maximum well after the mouth has begun to close.

Movements of the gular plate, operculum, and branchiostegal rays (Figs. 11, 12).

Initial expansion of the branchiostegal rays preceeds depression of the gular plate by several frames. Early in the feeding sequence (Fig. 11:C), the mouth has opened yet the gular plate is still retracted between the mandibular rami and the branchiostegals have only just become visible. As the branchiostegals expand ventrally, the suspensorium is abducted and dilation of the operculum occurs. The gular plate becomes visible at about the fifth frame probably as a result of geniohyoideus and sternohyoideus contraction and is rapidly depressed as the mouth closes. Gular plate depression and the ventral displacement of the branchiostegal rays only becomes evident in the late stages of mouth opening and reaches a peak after the jaws have closed (Figs 10, 12). In addition, several film sequences have been obtained of chewing motions after the prey has been captured in which the jaws remain closed but extreme movements of the gular, hyoid, and branchiostegal rays occur. These observations indicate that mouth opening and ventral expansion of the orobranchial chamber are relatively independent events. Gosline's (1971) suggestion that "lowering of the mandible seems to be entirely associated with, and dependent upon, the lowering of the floor of the mouth" is contradicted by the sequence of jaw movements. In all probability, *Amia* can to some extent mediate the sequence of movements governed by the action of the levator operculi, geniohyoideus, and sternohyoideus by contraction of the adductor mandibulae. The exact timing of adductor contraction could mediate the degree of jaw opening when ventral expansion of the orobranchial chamber occurs. Electromyographic evidence and additional feeding sequences will be necessary, however, before this hypothesis can be tested.

The observed rapid opening of the mouth before the hyoid is visible supports the anatomical inference that the levator operculi–opercular series–mandible coupling is active during feeding. The presence of a strong interoperculomandibular ligament, the firm connections between the opercular elements, and the observed rapid opening of the mouth when no other couplings can be seen active, strongly suggests that coupling four is active during feeding and may, in fact, be the primary force causing mandibular abduction.

General conclusions

Analysis of feeding movements in *Amia calva* strongly indicates that the levator operculi–opercular series–mandible coupling is extremely important during feeding.

Movements of the neurocranium, maxilla, and mandible during feeding in *Amia* are very similar to those in *Salmo* and *Hoplias*.

The extreme ventral depression of the gular plate and branchiostegal rays after the mouth has begun to close is very unlike teleost feeding movements.

Cinematographic evidence indicates that the levator operculi coupling and the couplings associated with movements of the hyoid, branchiostegal rays, and gular plate represent two relatively independent movements of the jaws.

Mechanical analysis of the neurocranium–maxilla–mandible coupling

The amount of angular maxillary swing in *Salmo*, *Hoplias*, and *Amia* is far greater than would have been expected solely on the basis of an anatomical analysis of the head. In all three fishes, the maxilla articulates dorsally with the neurocranium in a peg and socket joint and ventrally with the mandible via a thick maxillomandibular ligament. Connective tissue covers the area between the side of the head and the maxilla, and because of its elastic properties acts to oppose maxillary motion.

Maxillary swing can only be due to a force applied at one of the two attachments on the jaw. The effects of cutting the mandibular connection have been described for *Salmo* and *Hoplias* and I have indicated that maxillary swing increases when this attachment is severed. As an additional aid in understanding the relationships and mutual functional influences of the neurocranium, maxilla, and mandible, the fish jaw has been modelled as a series of mechanical linkages.

Mechanical model (Fig. 13: Table 1)

The neurocranium, l, pivots around (X', Y'), the estimated point of vertebral bending, and forms and angle δ with the horizontal. l is mechanically defined as the line between (X', Y') and the articulation between the neurocranium and the maxilla, (X_0, Y_0). r, the distance from the quadratomandibular articulation to the mandibular attachment of the maxillomandibular ligament (x, y), pivots about the quadratomandibular joint and forms an angle θ with the horizontal. The maxillomandibular ligament, D, extends from (x, y) on the mandible to a point (X_1, Y_1) on the medial aspect of the maxilla (see Fig. 13 and Table I).

It is now possible to derive two equations from this model which will express the angle of the maxilla relative to the horizontal,φ, as a function of θ, δ, and the lengths of the bony elements and the coordinates of their attachments.

Applying the law of cosines,

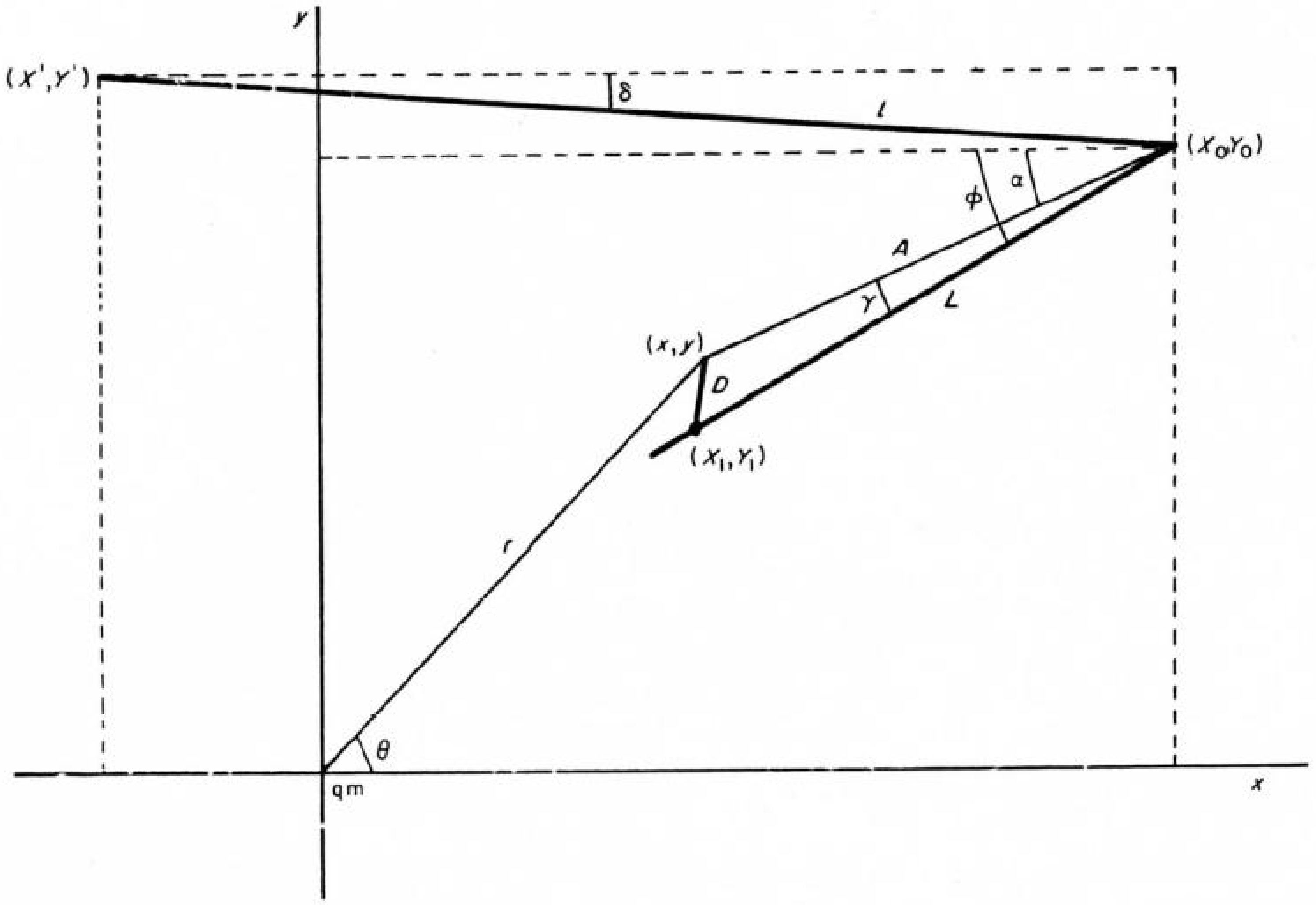

FIG. 13. Mechanical model of the jaw of *Hoplias*, *Amia* and *Salmo*. This model is used to derive equations (see text). Predicting the position of the maxilla, L, as a function of the angle of the neurocranium, δ, and the angle of the mandible, θ.

Abbreviations: (X', Y'), the estimated point of neurocranial bending on the vertebral column; (X_0, Y_0), the maxilla–premaxilla articulation; (X_1, Y_1), the point of maxillomandibular ligament attachment to the maxilla; (qm), the quadratomandibular articulation; (x, y), the point of maxillomandibular ligament attachment to the mandible; D, the maxillomandibular ligament; L, the maxilla; l, the neurocranium; r, the distance from the quadratomandibular articulation to (x, y); A, the distance between (x, y) and (X_0, Y_0); δ, the angle of the neurocranium with respect to the horizontal; φ, the angle of the maxilla with respect to the horizontal; α, the angle between the horizontal and line A; γ, the angle between lines A and L; θ, the angle of the mandible with respect to the horizontal. See Table I for exact measurements.

$$D^2 = A^2 + L^2 - 2AL\cos\gamma \quad \text{Thus,}$$

$$\gamma = \arccos\left(\frac{(A^2+L^2) - D^2}{2AL}\right) \tag{1}$$

Now, $A^2 = (X_0 - X)^2 + (Y_0 - Y)^2$

$$\begin{aligned} A^2 &= (X_0 - r\cos\theta)^2 + (Y_\theta - r\sin\theta)^2 \\ &= X_0^2 + r^2\cos^2\theta + Y_0^2 + r^2\sin^2\theta - 2r(X_0\cos\theta + Y_0\sin\theta) \\ &= X_0^2 + Y_0^2 + r^2 - 2r(X_0\cos\theta + Y_0\sin\theta) \end{aligned}$$

Substituting this last expression for A^2 into equation (1),

$$\gamma = \arccos\left(\frac{L^2 + X_0^2 + Y_0^2 + r^2 - 2r(X_0\cos\theta + Y_0\sin\theta) - D^2}{2L(X_0^2 + Y_0^2 + r^2 - 2r(X_0\cos\theta + Y_0\sin\theta))^{\frac{1}{2}}}\right) \tag{2}$$

TABLE I

Symbols and values used in the mechanical model of the primitive teleost jaw

Symbol	Description	*Hoplias*	*Salmo*	*Amia*
(X', Y')	Point of neurocranial bending on the vertebral column.	$X'=-1{\cdot}4$ cm $Y'=1{\cdot}6$ cm	$X'=-1{\cdot}9$ cm $Y'=2{\cdot}1$ cm	$X'=-3{\cdot}1$ cm $Y'=3{\cdot}2$ cm
(X_0, Y_0)	Maxilla–premaxilla articulation.	—	—	—
(X_1, Y_1)	Point of maxillomandibular ligament attachment to the maxilla.	—	—	—
(x, y)	Point of maxillomandibular ligament attachment to the mandible.	—	—	—
(qm)	The quadratomandibular articulation.	—	—	—
D	The length of the maxillomandibular ligament.	0·46 cm	0·46 cm	0·80 cm
L	The length of the maxilla from (X_0, Y_0) to (X_1, Y_1)	1·5 cm	1·5 cm	3·2 cm
l	The length of the neurocranium from (X', Y') to (X_0, Y_0).	3·1 cm	4·1 cm	7·5 cm
r	The distance from (x, y) to (qm).	1·0 cm	1·3 cm	2·8 cm
A	The distance between (x, y) and (X_0, Y_0).	—	—	—
δ	The angle of the neurocranium below the horizontal.			
φ	The angle of the maxilla below the horizontal.			
α	The angle between the horizontal and line A.			
γ	The angle between lines A and L.			
θ	The angle between r and the horizontal. Change in θ represents mandibular depression.			

Also, $\tan\alpha=\left(\frac{Y_0-Y}{X_0-X}\right)$ and $X=r\cos\theta$ and $Y=r\sin\theta$

$$\text{so,}\quad \alpha=\arctan\left(\frac{Y_0-r\sin\theta}{X_0-r\cos\theta}\right) \tag{3}$$

If δ is initially negative, $X_0=X'+l\cos\delta$ and
$Y_0=Y'+l\sin\delta$

Substituting these equations into equations (2) and (3) we obtain

$$\gamma=\cos^{-1}\left(\frac{L^2+(X'+l\cos\delta)^2+(Y'+l\sin\delta)^2+r^2-2r((X'+l\cos\delta)\cos\theta+(Y'+l\sin\delta)\sin\theta)-D^2}{2L((X'+l\cos\delta)^2+(Y'+l\sin\delta)^2+r^2-2r((X'+l\cos\delta)\cos\theta+(Y'+l\sin\delta)\sin_{\theta}))^{\frac{1}{2}}}\right)$$

(equation 4) and,

$$\alpha=\tan^{-1}\left(\frac{(Y'+l\sin\delta)-r\sin\theta}{(X'+l\cos\delta)-r\cos\theta}\right) \tag{5}$$

Since $\varphi=\alpha+\gamma$, the angle of the maxilla (φ) can now be expressed as a function of the angle of the neurocranium (δ), the angle of the mandible (θ), and the lengths and positions of the bones and ligaments of the jaw.

Predictions from the model

Careful dissection of preserved specimens, detailed measurements of the anaesthetized fish prior to filming (in *Salmo* and *Hoplias*), and correlation of these measurements with prints made from 16 mm ciné-film enabled the constants in equations (4) and (5) to be obtained (Table I). These values reflect, as nearly as possible, the actual values in the specimen used for filming. The values of θ and δ for each frame (Figs 1, 6, 10) were then inserted into equations (4) and (5) and the resulting angle of the maxilla calculated.

In *Salmo gairdneri*, the maximum angle of the maxilla, 68°, was predicted to within 0·5° by this model (Fig. 14(b)). The predicted value for the total angular range of maxillary swing, 34°, also agrees well with the actual value of 39°: the discrepancy resulting mostly from a failure of the model to predict the position of the maxilla accurately in the final few frames.

If the angle of the neurocranium is held constant at its initial value of $-13{\cdot}5°$, the predictive capacity of the model declines drastically (Fig. 14(b): crosses). A range of only 23° occurs and the peak angle of the maxilla is predicted as 49° instead of 67·5°. This maximum value also occurs two frames before the actual maximum. Thus, although the angle through which the neurocranium pivots is only 7·5°, it appears from the model that the contribution of the neurocranium to maxillary swing is substantial. If the contribution of the neurocranium is eliminated, then the change in angle of the maxilla as a function of time only slightly approximates maxillary movement. It is important to note, however, that the model does predict that the mandible also contributes to maxillary motion. Depression of the mandible in a freshly dead specimen will move the distal aspect of the maxillary anteriorly, thus changing the angle with respect to the horizontal. The maximum angle achieved in this case is roughly the same as that predicted by the model, 49°.

With respect to maxillary movement in *Hoplias malabaricus*, the model predicts neither the range of angular excursion nor the general pattern of maxillary movement (Fig. 14(a)). This is primarily the result of frame four where no real value of γ in equation four could be found. This indicates that D^2 was not large enough to reduce the size of the numerator to a value less than the denominator. Anatomically this result suggests that D, the maxillomandibular ligament, must stretch during the feeding sequence to allow the maxilla to swing out to its observed position.

The length of D necessary to fit the model exactly to the observed curve of maxillary swing can be calculated by solving equation four for D, and applying the observed values of θ, φ, and δ to equations four and five (Fig. 15(a)). From the model one would predict that the maxillomandibular ligament must stretch to just over twice its initial length if the observed amount of maxillary swing is to occur. An examination of the length of the maxillomandibular ligament during feeding from the prints of the 16 mm ciné-film confirms that some stretching must occur, but quantification is impossible without the model.

In the trout, *Salmo gairdneri*, a similar analysis (Fig. 15(b)) indicates that the maxillomandibular ligament only needs to stretch to about 10% of its original length to achieve the observed amount of maxillary swing. In much of the feeding sequence the ligament is not even stretched to its resting length.

In *Amia calva* (Fig. 14(c)) the model fails to predict the angle of the maxilla accurately. Five frames have no real value since the fixed length of the maxillomandibular ligament was

FIG. 14. Graphic representation of the actual angle of the maxilla (solid circles) and the angle predicted from the model (see text) (open circles). Crosses represent the angle of the maxilla predicted if the angle of the neurocranium is held constant at its initial value. (a) *Hoplias malabaricus*. One value could not be calculated since the equations gave no real solution. (b) *Salmo gairdneri*. (c) *Amia calva*. Dashed lines indicate that no real value could be calculated since the equations gave no real solutions. Time between frames is 0·005 seconds.

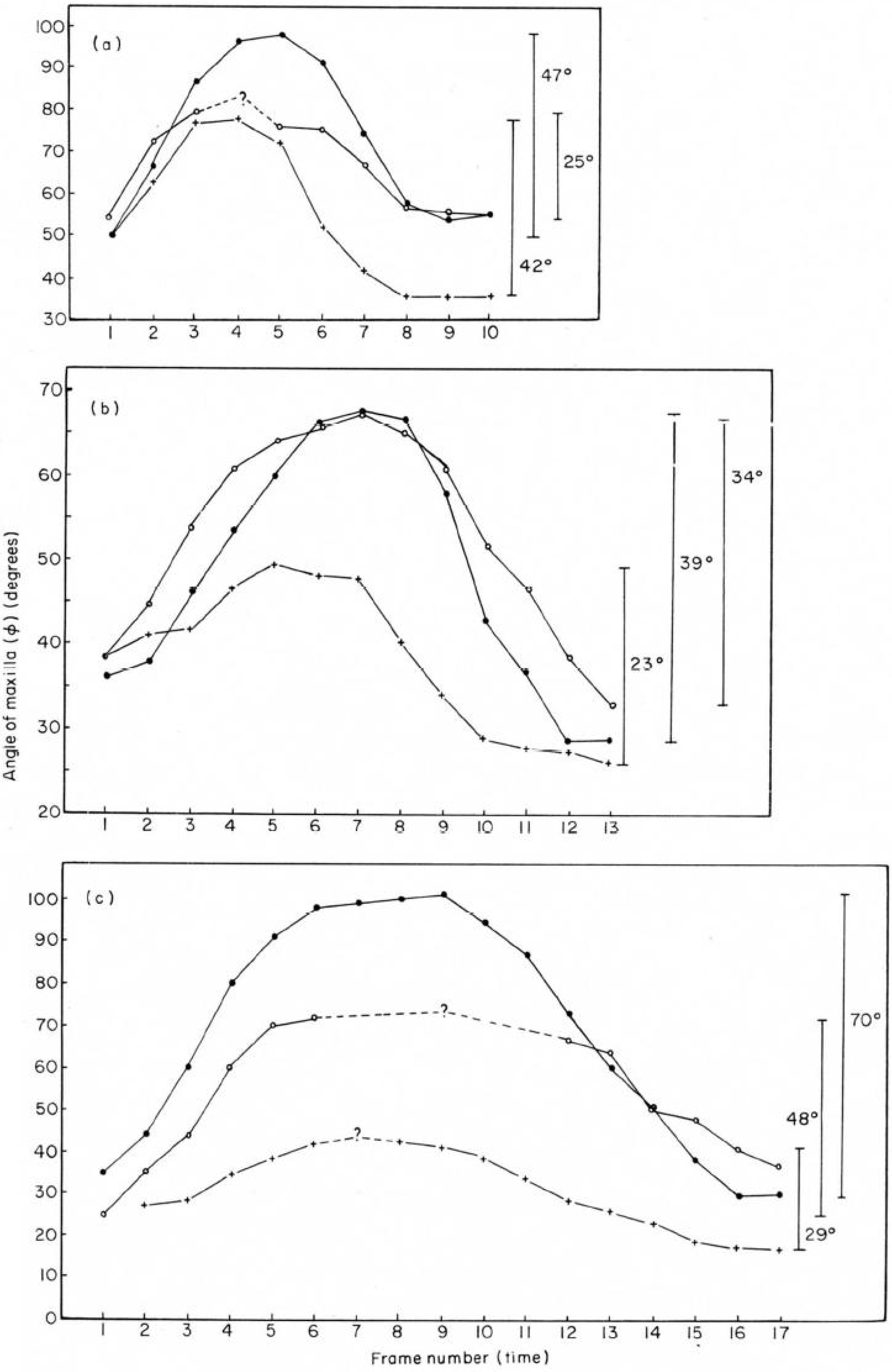
(a)
(b)
(c)
47°
25°
42°
39°
34°
23°
70°
48°
29°
?
Angle of maxilla (ϕ) (degrees)
Frame number (time)
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

FIG. 14.

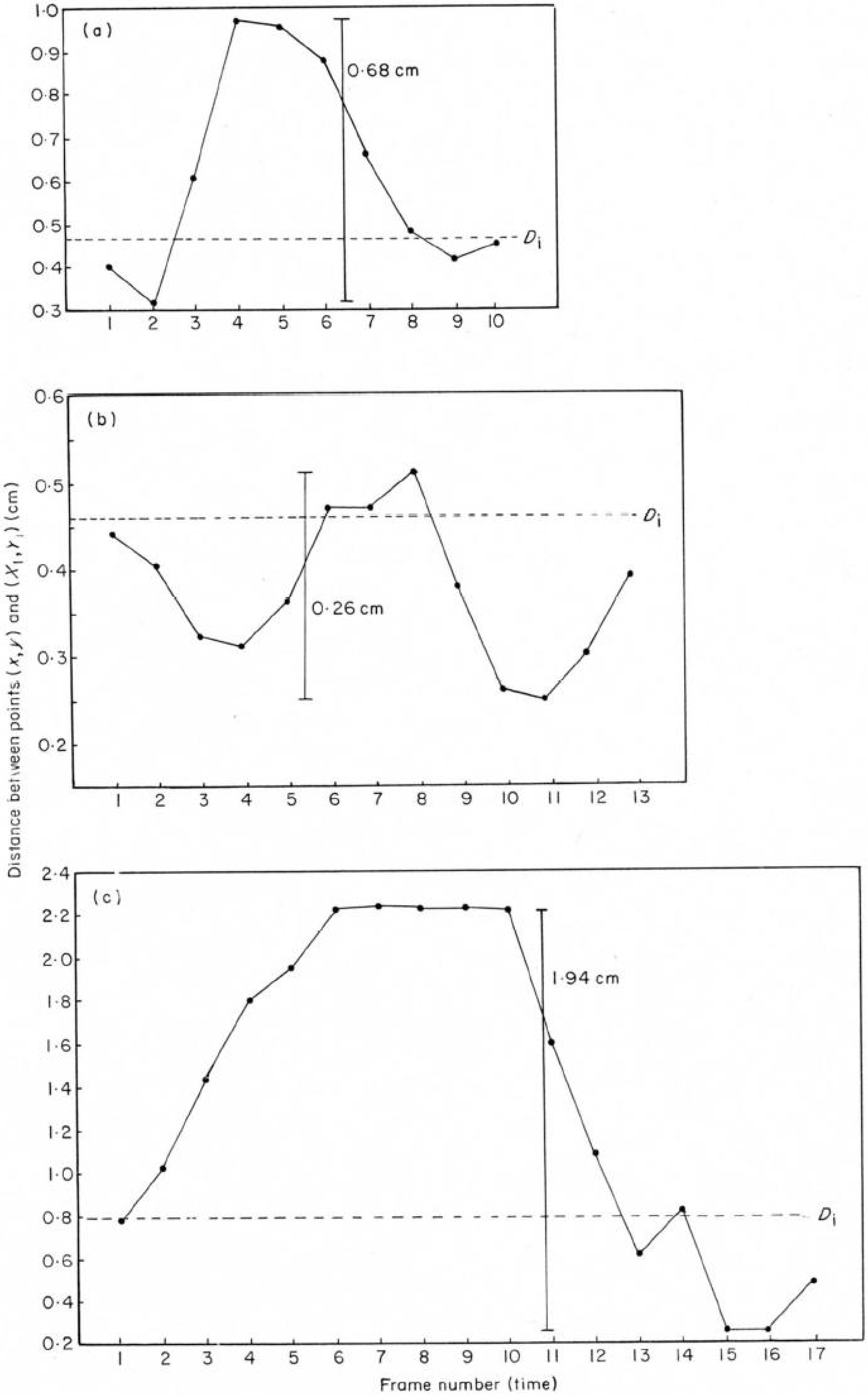
(a)
0·68 cm
D_i
(b)
0·26 cm
D_i
(c)
1·94 cm
D_i
Distance between points (x, y) and (X_1, Y_1) (cm)
Frame number (time)
1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
0·2
2·4
2·2
2·0
1·8
1·6
1·4
1·2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17

FIG. 15.

insufficient to calculate γ with the given values of θ and δ. The maxillomandibular ligament must stretch 2·8 times its original length (Fig. 15(c)) if the model is fitted exactly to the observed angular maxillary swing. The remarkable amount of deformation occurring in the maxillomandibular ligament during feeding must be due to a strong anterior force exerted on the ligament by the distal aspect of the maxilla.

Assumptions of the model

Four major assumptions have been made. (1) The maxillomandibular ligament has been approximated as a one-dimensional rigid length. (2) The effect of the connective tissue between the cheek and the maxilla has not been taken into account. Elastic recoil of this connective tissue (*Salmo* and *Amia*) or contraction of the A1 division of the adductor mandibulae (*Hoplias*) may act to restore the maxilla to its resting position more quickly than predicted by the model (e.g. Fig. 14(b)). (3) (X', Y') is assumed to be a fixed point. (4) Movements of the linkage elements are assumed to occur within a plane defined by the points (X', Y'), (X_0, Y_0), and the quadratomandibular articulation.

Anker (1974) constructed a model of the stickleback jaw and was forced to make many of the same assumptions. The effect of his assumptions is impossible to ascertain, however, since he did not test his model against the actual movements of the jaw.

Assumption one has broad mechanical implications for jaw movements. If the maxillomandibular ligament were actually one-dimensional, considerable angular movement of the mandible would be necessary before the mandible became sufficiently depressed to transmit a strong force to the maxilla. This would invert triangle (x,y), (X_0, Y_0), (X', Y'), (Fig. 13) so that $\varphi = \alpha - \gamma$. In fact, this never occurs and the maxilla always swings in front of the mandible and is not propelled by it.

The actual maxillomandibular ligament in *Salmo*, *Hoplias*, and *Amia* is flexible and is roughly trapezoidal in shape, the longer dorsal base attaching to the mandible along the dorsal margin of the coronoid process and dentary, while the ventral base of the ligament attaches laterally to the distal aspect of the maxilla. The effect of this unique structure is to compensate for the flexibility of the ligamentous tissue. If a force is applied to the upper left hand corner of the ligament (Fig 16(a)) (mandibular adduction), the maxilla will feel an immediate force of almost equal magnitude as the ligament takes up strain, since at least one point of ligamentary attachment to the maxilla is in line with the direction of applied force.

As the mouth is opened, the anterior component of the force resulting from mandibular depression will be transmitted to the maxilla so that the distal aspect moves anteriorly. This will occur approximately at the time the point of maxillomandibular ligament attachment to the mandible furthest from the quadratomandibular joint swings below a line drawn between the quadratomandibular joint and the furthest point of ligamentous attachment to the maxilla. Thus, the contribution of the mandible to maxillary motion is a direct consequence of the trapezoidal shape of the maxillomandibular ligament. If the ligament were more of a one-dimensional shape (Fig. 16(b)), excessive mandibular depression would be necessary before a force was exerted on the maxilla. At the same time.

FIG. 15. Graphic representation of the change in length of the maxillomandibular ligament, *D*, with respect to time if equations four and five (see text) are fitted exactly to the actual movement of the maxilla. D_i is the rest length of the maxillomandibular ligament. (a) *Hoplias malabaricus*. (b) *Salmo gairdneri*. (c) *Amia calva*.

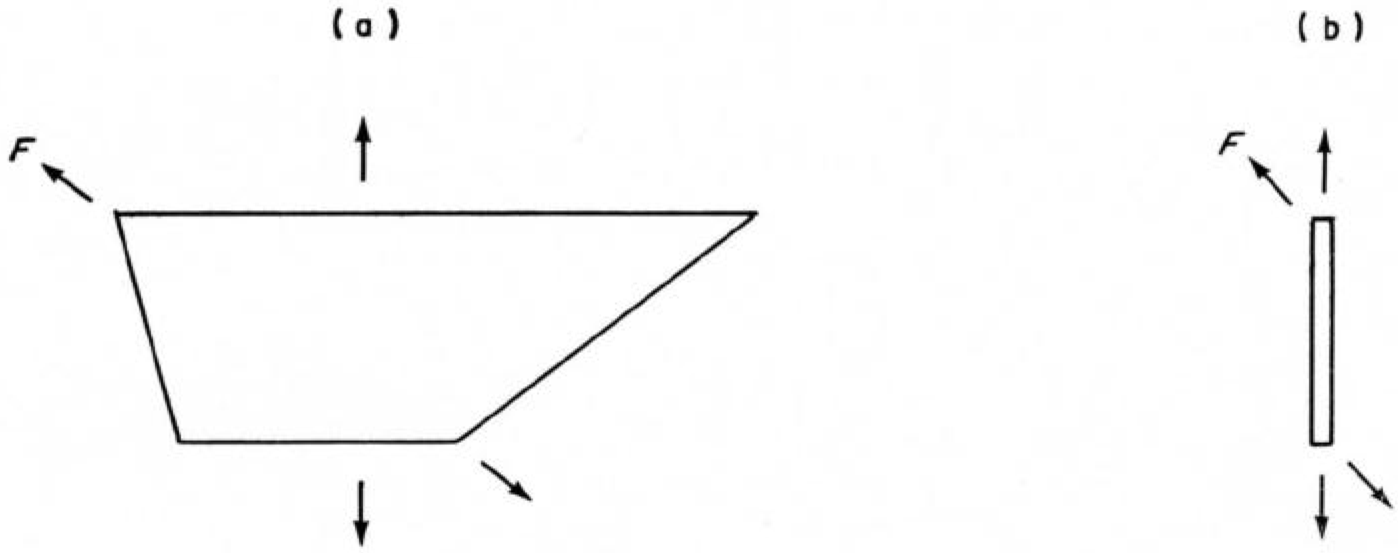

FIG. 16. Diagrammatic representation of the shape of two ligaments: (a), the maxillomandibular ligament in *Hoplias*, *Salmo*, and *Amia*; (b) a small rectangular ligament for comparison. *F* indicates the direction of a theoretical applied force. The upper and lower bases of both ligaments attach to bony elements: the upper base attaching to the mandible, the lower to the maxilla. The force *F* will exert an immediate pull on the lower right hand corner of the trapezoidal ligament while a delay will occur in the rectangular ligament.

however, the contribution of the mandible to maxillary motion is by no means sufficient to produce the observed angular swing of the maxilla.

The mechanism of maxillary motion

The exact cause of the extreme swing of the maxilla during feeding is unknown. I have shown that mechanically, the mandible can cause small amplitude movements of the maxilla and that severing the ligamentous connection between the maxilla and the mandible actually increases the swing. Mandibular depression, then, is not obligatorily linked to maxillary motion.

Movement of the neurocranium appears to be the most critical factor in producing maxillary swing. Only two possible explanations exist: (1) that factors external to the neurocranium (e.g. gravity) produce the swing, or, (2) that internal deformation within the neurocranium somehow produces a force on the maxilla. The first explanation is unlikely since the weight of the maxilla in water is negligible and the maxilla must overcome the opposing force exerted by the lateral connective tissue to the cheek. The second hypothesis is intriguing, and some support is found in the anatomy of the maxilla—neurocranial articulation. In all three species, a flattened medial process of the maxilla extends into a small socket behind the premaxilla and anterior to the palate. If movement of the suspensorium as the neurocranium was lifted were slightly delayed, a torque on the medial process of the maxilla would result. This torque might be sufficient to swing the distal aspect of the maxilla anteriorly.

General conclusions

Mandibular depression can result in small amplitude initial movements of the maxilla.

The mechanical model of the jaw becomes an increasingly inaccurate predictor of maxillary swing as the observed amplitude of swing increases.

Mandibular adduction can act to restore the maxilla to its initial position.

In large amplitude movements of the maxilla, the maxillomandibular ligament stretches to over twice its initial length.

Suction feeding

Most authors who have discussed suction feeding in fishes (e.g. Alexander, 1967; Liem, 1970; Nyberg, 1941) have concentrated on the relationship of protrusibility to suction feeding in advanced fishes, and little has been written on suction feeding in "primitive" teleosts.

Qualitatively, suction is created by an expansion of the orobranchial chamber (involving a large number of interrelated movements) and opening of the mouth. In *Salmo*, *Hoplias* and *Amia*, one conspicuous feature of jaw opening is the large degree of maxillary swing. The significance of this movement in feeding appears to be fourfold. First, the anterior swing of the maxilla extends the orobranchial chamber forward towards the prey, thus increasing the efficiency of suction. Secondly, since the maxilla has sharp teeth along its length, the toothed portion of the jaw is extended towards the prey. Thirdly, as the maxillaries swing forward, they may pivot towards each other and thus increase the velocity of flow, an aspect of maxillary swing has been confirmed in *Hoplias*. Finally, the extension of the maxillaries along the sides of the mouth prevents water from entering the orobranchial chamber from the side and increases the flow of water from the region directly in front of the predator, presumably the area where the prey is located.

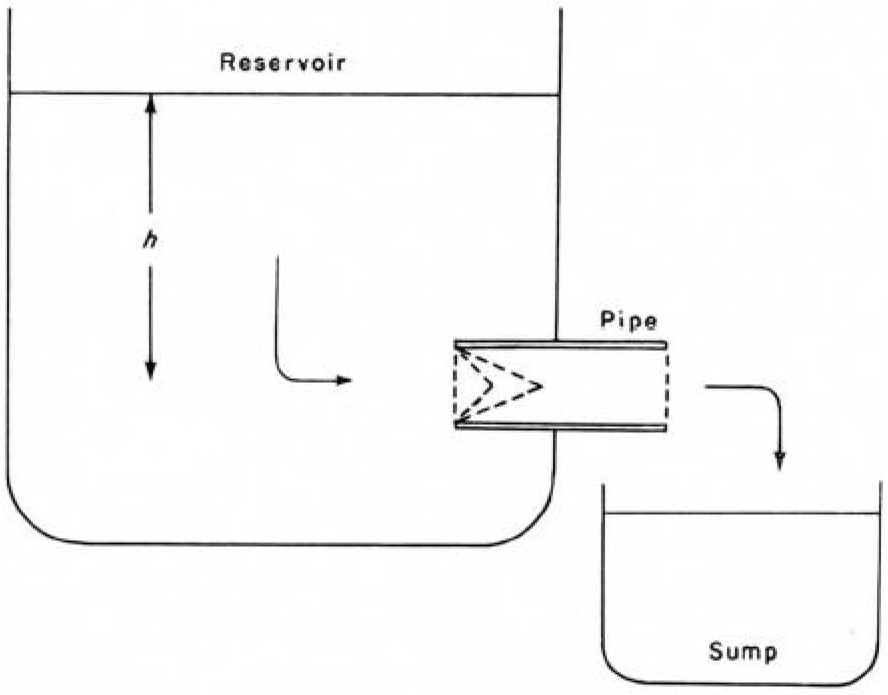

FIG. 17. Diagram of an experiment designed to test the effect of inlet geometry on the rate of water flow through a pipe. Water is maintained at a constant level in the reservoir and flow into the sump is measured in cm^3/5 seconds. The experiment was conducted for three different inlet geometries: a round opening, an opening with a one centimetre notch, and an opening with a two centimetre deep notched inlet. *h* is the height of the water above the inlet centre.

The effect of maxillary swing upon the rate of flow has been quantified by an experiment which measures the flow of water into a pipe as a function of inlet geometry (Fig. 17). The shape of the inlet was chosen to represent three possible configurations of jaw elements during feeding. The round pipe opening corresponds to the shape of the jaw when the maxilla is maximally extended, the one centimetre notch to the position of the maxilla at the middle of the feeding sequence, and the two centimetre notch in the end of the pipe represents a condition where no maxillary swing occurs (see Fig. 2(b); Fig. 7(b); Fig. 11(b)). The pipe diameter remained constant.

The results of these experiments (Fig. 18) show that the round pipe opening allows 15–20% more flow than the two centimetre notched opening. This represents a highly significant increase in water flow, and indicates that the round opening is a far more efficient opening than a notched opening for suction feeding.

Quantitatively, for the experimental apparatus depicted in Fig. 17,

$Q = C_d A\sqrt{2gh}$ where,
Q = rate of water flow
C_d = orifice coefficient
A = cross-sectional area of the pipe
g = gravitational constant
h = height of water above the pipe centre

From the data in Fig. 18, the orifice coefficient, C_d, for the round pipe is 0·79.

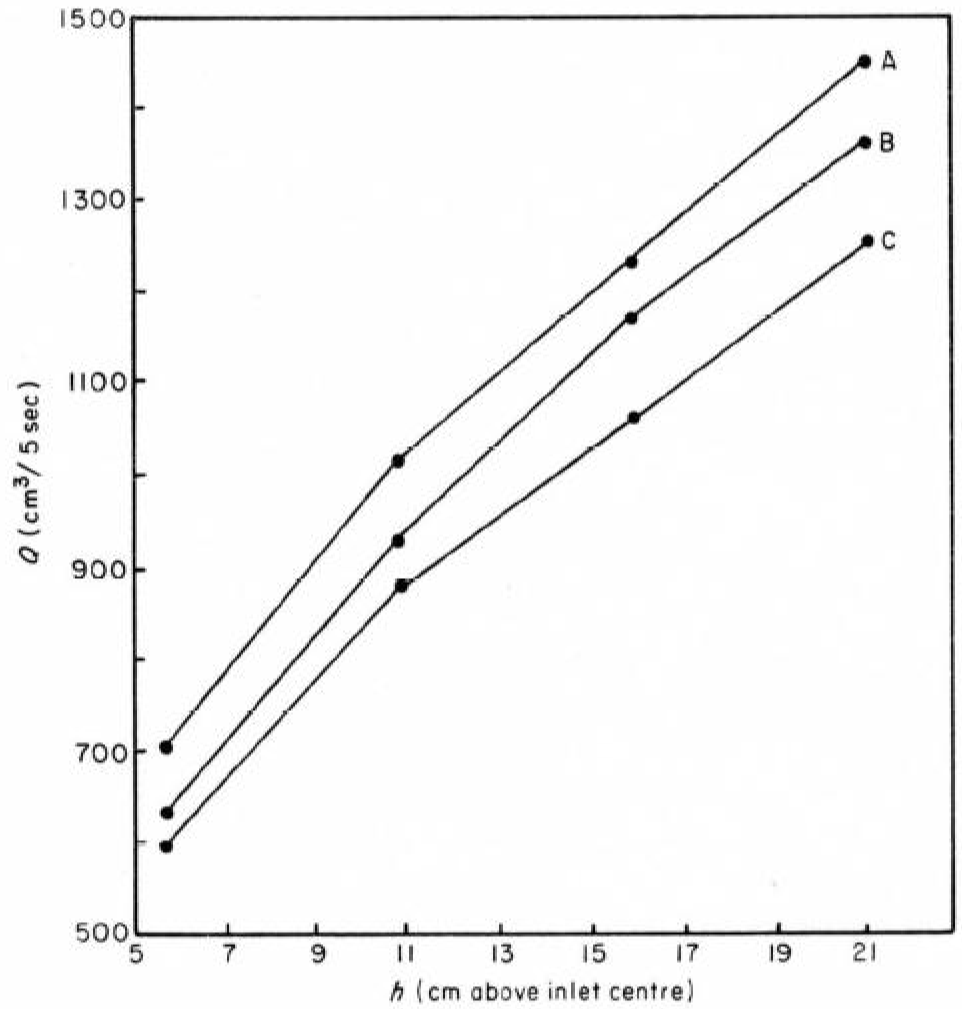

FIG. 18. Rate of flow through a pipe (Q) as a function of water height, h, (pressure) above the pipe inlet. A, Rate of flow through a pipe with a round opening. B, Flow, through a pipe with a one centimetre deep notch. C, Flow through a pipe with a two centimetre notched inlet. Changing the inlet configuration by notching the end of the pipe results in a 15–20% decrease in flow.

Discussion

Comparative analysis of feeding mechanisms

Alexander (1967) has noted three possible feeding strategies in fishes. The predator may (1) actively pursue the prey, swimming up to it with mouth open and surrounding the prey. (2) The fish may swim towards the prey and expand the buccal cavity as the prey nears the mouth. In this case, both forward body velocity and the creation of a low pressure centre inside the mouth are used to capture prey. Finally, (3) the predator may remain essentially stationary and rapidly expand the volume inside the mouth to draw prey in. This is suction feeding.

Of the three fishes considered in this study, only *Hoplias* can be considered a suction feeder. The trout, *Salmo gairdneri*, uses method two and moves towards the prey, opening the mouth as the prey is approached. *Amia calva* also seems to use the second method of capturing prey.

Despite the different modes of feeding in *Salmo* and *Hoplias*, the feeding mechanisms are quite similar. Adaptations to suction feeding in *Hoplias* primarily involve greater amplitude and speed of jaw movements than those found in *Salmo*, while the basic pattern of events remains the same. The sequence of jaw movements during feeding in *Hoplias* and *Salmo* is as follows: (1) The mouth begins to open, and hyoid depression starts. (2) As the mouth continues to open, the maxilla swings anteriorly and the hyoid is depressed further. At this time suspensory abduction and opercular dilation begin. (3) Mouth opening, maxillary swing, and hyoid depression reach a near simultaneous maximum while suspensorial abduction and/or opercular dilation reach their maximum value somewhat later. (5) The mouth closes while the neurocranium maintains an elevated position, the hyoid remains in a relatively depressed condition, and the suspensorium and operculum remain abducted. (6) The hyoid is retracted and the suspensorium and operculum slowly return to their initial positions.

In *Hoplias*, the amount of hyoid depression is much greater than in the trout, opening and closing of the jaw occurs much more rapidly, and suspensory and opercular abduction are both more rapid and greater in magnitude. These characteristics adapt *Hoplias* to rapidly creating a low pressure centre within the mouth for the purpose of drawing prey in.

The general feeding pattern described above has also been found in advanced teleosts. Liem (1970: Fig. 49) in a study on nandids found that depression of the hyoid coincided with mouth opening and that as the mouth closed, the hyoid was retracted. In addition, suspensory abduction began as the mouth opened and maintained a maximally abducted condition until well after the jaws had closed. Nyberg (1971: Fig. 3) in the largemouth bass *Micropterus*, and Alexander (1969: Fig. 3) in *Idus*, have also concluded that the sequence of events during feeding falls into the general pattern described above. Liem & Osse (1975: Fig. 5)have found that hyoid depression coincides with jaw opening in *Perca fluviatilis* and electromyograms of *Tilapia melanopleura* indicate a similar sequence of jaw movements to those found in primitive teleosts.

Thus the general sequence of jaw movements during feeding seems to be extremely similar within the Teleostei, indicating that a certain relatively well defined sequence of jaw movements has been very successfully used by many fishes to capture food. Within the overall pattern of movement, however, differences in couplings may exist which distinguish the basal teleostean groups from the more advanced fishes yet still allow similar overall patterns of movement.

One example of this is the levator operculi–opercular series–mandible coupling. Liem (1970) noted the extreme mechanical efficiency of this coupling in the Nandidae, and Liem & Osse (1975) have indicated that mandibular depression in the perch and cichlids is caused primarily by contraction of the levator operculi which rotates the mandible around the quadratomandibular articulation by applying a caudodorsal force to the interoperculo-mandibular ligament. The primary mechanism for lower jaw depression in advanced teleosts thus seems to be the action of the levator operculi coupling. In *Hoplias* and *Salmo*, the cleithrum–hyoid–mandible coupling plays a significant role in mandibular depression. Action of the levator operculi during the initial stages of mouth opening acts to depress the mandibular symphysis and greatly increases the mechanical advantage of the geniohyoideus and sternohyoideus muscles. In *Hoplias* especially, the geniohyoideus and sternohyoideus are in excellent position to apply a strong caudal force to the tip of the mandible 0·005 sec after the mouth opens. Complete opening and closing of the mouth in *Hoplias* has been observed to occur in 0·03 sec. The evidence thus indicates that while the general pattern of jaw movement in the primitive teleosts investigated here conforms to that observed in more advanced teleosts, different couplings are responsible for producing similar movements.

In contrast to the teleost feeding mechanism, the "holostean" (used in this discussion as indicating an evolutionary grade) *Amia calva*, has a very different sequence of jaw movements during feeding. As noted earlier, misunderstandings of the anatomy of *Amia* have resulted in an interpretation of possible amiid (and holostean) feeding mechanics based on the absence of the levator operculi coupling. Analysis of movies of *Amia* feeding, however, reveals the following sequence of events: (1) Rapid mouth opening accompanied by maxillary swing. (2) Slight depression of the gular plate and slight expansion of the branchiostegal rays at the time the mouth has reached maximum gape. (3) Closing of the mouth accompanied by extreme gular depression and branchiostegal expansion. (4) Maintenance of the extreme expansion of the ventral portions of the head well after the mouth is closed. Jaw opening and closing in *Amia* takes approximately 0·075 sec.

Major differences occur between this sequence and the one previously presented for teleosts. Hyoid depression is not synchronized with mouth opening and closing, and extreme ventral expansion of the branchiostegal rays occurs and is maintained well after the mouth is closed. The evidence from the films indicates that in *Amia*, the levator operculi–opercular series–mandible coupling is extremely effective and is relatively independent of couplings associated with the ventral aspect of the head.

One puzzling aspect of the feeding sequence common to both *Amia* and the teleosts is the maintenance of an extremely expanded operculum, suspensory apparatus, and (in *Amia*) branchiostegal system after the mouth has closed. In fact, the maximum expansion of the volume inside the head is only achieved as the mouth is closed. In a suction feeding fish the optimum time to create the lowest pressure inside the mouth should be when the mouth is wide open. Perhaps lateral and ventral expansion of the head after the mouth is closed serves to move the prey posteriorly and facilitate deglutition, and dilation of the operculum may allow water sucked into the mouth to pass out the side of the head as the prey is carried back towards the esophagus. While these explanations rationalize the maintenance of an abducted suspensorium and operculum late in the feeding sequence, they do not explain why in many cases the maximum volume inside the mouth only occurs well after the jaws have begun closing.

It has commonly been assumed (e.g. Alexander, 1969) that opercular abduction contributes to the creation of suction during feeding. The fact that opercular dilation often reaches a maximum after the jaws have closed indicates that this conclusion may not be true. Further evidence has been found in ciné-film taken of *Osteoglossum* feeding (Keith Thomson, pers. comm.). *Osteoglossum* is not a suction feeder and utilizes forward body velocity only to engulf its prey. In spite of this mode of feeding, substantial opercular abduction occurs during the strike. This observation lends further support to the suggestion that opercular abduction is not obligatorily linked to a suction mode of feeding.

Evolution of the "holostean" and teleostean jaw

A comparative study of the feeding mechanics in teleosts is interesting because the effect of morphologic differences between fishes upon feeding patterns can be assessed and because basic "improvements" in the mechanics of feeding can be charted from basal groups to advanced groups. Perhaps more importantly, though, the examination of basal generalized teleosts (and *Amia*) can give substantial new insights into the evolution of the actinopterygian jaw. The significance of anatomical features in fossil fishes can best be interpreted in light of the functional significance of the nearest equivalent features in living fishes. The best living examples to choose for comparison with generalized fossil fishes are the morphologically generalized members of the basal teleostean superorders and *Amia calva*, a surviving "holostean."

Rosen (1973, 1974), Greenwood *et al.* (1966), and Gosline (1971) all consider the Salmoniformes to be a generalized basal teleostean group. Roberts (1969, 1973) considers *Hoplias* to be a generalized characoid and Rosen (1973) has placed the Ostariophysi at the base of the Euteleostei. *Amia* is the most generalized living "holostean" and is more closely related to teleosts than *Lepisosteus* (Patterson, 1973). *Amia*, *Salmo* and *Hoplias* all share the primitive characteristic of a maxilla included in the gape and articulated with the neurocranium in a peg and socket joint.

Several aspects of jaw structure should now be reconsidered in light of information available on living fishes. Generalized palaeoniscoid carnivores (e.g. *Pteronisculus*) possessed a jaw structure indicating primarily a "biting" habit (Schaeffer & Rosen, 1961). That palaeoniscoids could also open their mouth widely is inferred from fossils preserved with the jaws wide open and the neurocranium at a substantial angle to the vertebral axis. It can thus be supposed that an epaxial musculature–neurocranium–upper jaw coupling was active during feeding and instrumental in increasing the distance between the jaws.

Schaeffer (1956) found a virtually complete statistical association between the presence of a coronoid process on the mandible and the occurrence of a free maxillary in "subholostean" fishes. This association may be explainable in light of the functional conclusions presented earlier. The coronoid process allows the attachment of the maxillomandibular ligament to the mandible and is necessary for the stability of maxillary movement during feeding. Fishes possessing a free maxillary and no coronoid process would, on the basis of the functional relationships elucidated for *Salmo* and *Hoplias*, have had considerable difficulty feeding.

Schaeffer & Rosen (1961) have explained the development of a coronoid process in terms of increased torque available for mandibular adduction. The insertion of the adductor mandibulae on the coronoid process of the mandible increases the efficiency of adduction because the coronoid process transforms the mandible from a straight lever system into a bent lever. However, Liem (1970) has found an extremely large coronoid process which does not serve as an insertion for the adductor mandibulae in nandid fishes.

The two above explanations of the significance of the coronoid process at the holostean grade are not mutually exclusive. The advantage of a coronoid process could have been two-fold, allowing both increased efficiency of mandibular adduction and also increased forward expansion of the orobranchial chamber. The advantage of maxillary swing during feeding would at least partially have been realized by Triassic holosteans even if only a limited amount of maxillary swing was initially present.

A number of predaceous palaeoniscoid fishes, however, while having the maxilla fixed immovably to the cheek also possessed a fairly well developed coronoid process (e.g. the

Amblypteridae, Gardiner, 1967). In this case, the principle advantage of the coronoid process probably was related to the efficiency of mandibular adduction. The presence of the coronoid process as an improvement in the biting mechanism may also have been a potentially powerful preadaptation (*sensu* Bock, 1959) which provided an insertion point for the maxillomandibular ligament. In the transition to the holostean adaptive level, fishes with a coronoid process (initially developed to improve the biting mechanism) would then have been preadapted for the successful utilization of a free maxillary in the feeding mechanism. In addition, the anatomical coupling necessary to produce angular maxillary swing around the maxillo–neurocranial articulation, the epaxial musculature–neurocranium–upper jaw coupling, was already present in the palaeoniscoid jaw.

A real biomechanical improvement in the predaceous feeding mechanism may thus have been obtained through the smooth integration of a preexisting coupling with a morphological innovation. The free maxillary, propelled forward by neurocranial lifting increased the versatility of the feeding mechanism, and concomitant changes in jaw structure such as increased lateral suspensorial mobility and the differentiation of an interopercular bone undoubtedly contributed significantly to the development of a suction feeding mechanism.

The significance of the differentiation of the interopercular bone at the holostean grade, and the presumed concomitant differentiation of the interoperculomandibular ligament and the levator operculi muscle, may not lie so much in the improvement in efficiency of mouth opening (although this almost certainly would have occurred) as in the potential independence of anatomical couplings. The interopercular and the accompanying ligamentous and muscular elements of the levator operculi coupling would have allowed the ventral couplings of the head to assume new functions to some extent independent of mouth opening. In palaeoniscoid fishes the gape was probably increased primarily through two sets of couplings: the epaxial muscles–neurocranium–upper jaw coupling and the cleithrum–hyoid–mandible couplings mediated by contraction of the sternohyoideus, interhyoideus, and hypaxial muscles. Mandibular depression was thus probably caused by contractions of the ventral head and body musculature, and movements of the hyoid presumably accompanied the muscle contractions.

At the holostean level, the levator operculi coupling removed the constraints of jaw opening functions from the ventral head couplings and allowed reasonably independent movements of the hyoid and ventral muscles. This condition occurs in *Amia calva*, where the movements of the hyoid, gular, and branchiostegal rays are not primarily linked with mandibular depression.

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