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Structures and movements of the buccal and pharyngeal jaws in relation to feeding in *Diplodus sargus*

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ABSTRACT

The present paper studies the possibly different feeding strategies of *Diplodus sargus* to crustaceans, molluscs, worms, and small fish. The buccal jaws are built strongly and bound together by numerous ligaments. The dentition is heterodont: incisors in front and molars in the middle and hind parts. The principal originality of the musculature of this species is the forward insertion of the adductores mandibulae. These are very thick and insert on both the upper and lower jaws, so that contraction of any individual muscle acts on the buccal pieces as a whole, which thus constitute a remarkable crushing device. The pharyngeal jaws are frail as in primitive perciforms: the lower ones are well separated, being bound only anteriorly, while the upper ones consist of the second and third pharyngobranchials and a posterior toothed plate. When feeding on crabs, *Diplodus sargus* always sucks in the prey and seizes it with the buccal jaws. Mouth opening is accompanied by extensive protrusion of the mouth, with or without neurocranial elevation. Mouth sucking and seizing movements vary little. Once seized, the prey is usually moved to the molars and crushed. The crushing movements may be fast and ample or slow. In the latter case, deformation of the prey is observable. Crushing usually results in the crab being broken into pieces. The pharyngeal jaws grip one part of the prey and shift it to the oesophagus, then seize the second part. *Diplodus sargus* adapts its feeding behaviour to the type of prey. A snail, for instance, is crushed by the buccal or pharyngeal teeth, the pieces of shell are ejected, and the soft parts conveyed with diffculty to the oesophagus by the pharyngeal jaws. A fish on the other hand, is sucked tail first into the mouth cavity and quickly shifted to the digestive tract by the pharyngeal bones. Behaviour toward different prey differs by the presence or absence of parts of the sequence of feeding movements (for example crushing) or by the fact that certain movements or parts of the sequence are repeated. The variability of any movement in the sequence is the same whatever the sort of prey. Crushing occurs between the buccal incisors and molars and was observed twice between the pharyngeal teeth. Usually, it seems, the latter are involved in transport only. In transport, the left and right pharyngeal jaws may perform different functions: their movements, unlike the symmetrical movements of the buccal jaws, sometimes differ.

Introduction

In Acanthopterygians, suction is the most widespread means of processing food items in the buccal cavity (Lauder, 1983*a*; Van Leeuwen & Muller, 1984). Efficient sucking requires fast, broad movements of the parts of the head (mouth, suspensorium or cheeks, buccal floor, opercles, neurocranium). It also requires that the continuum formed by the buccal and opercular cavities adopts the shape of a truncated cone, the shorter base of which is the circular mouth aperture (Osse & Muller, 1980; Muller *et al*., 1982). Acanthopterygians are among the best equipped in this respect, having developed buccal protrusion [i.e. forward protrusion of the premaxillaries (Eaton, 1935; Alexander, 1967; Liem, 1970, 1979; Pietsch, 1978; Lauder & Liem, 1981)]. Food is not usually handled by the buccal jaws, but in the hind part of the branchial basket by the pharyngeal jaws (Liem, 1986; Liem & Sanderson, 1986; Vandewalle *et al*., 1992).

In the species of the families at the head of the list, such as serranids, the pharyngeal jaws merely process food from the buccal cavity to the oesophagus (Vandewalle *et al*., 1992). The reinforced pharyngeal jaws of the embiotocids moreover transform food (Liem, 1986). That latter function is increased further in labrids whose pharyngeal jaws are very powerful.

Sparids are acanthopterygians whose feeding strategy does not seem to match exactly the general acanthopterygian pattern. They are said to crush their prey between the buccal jaws. The aim of this paper is to describe feeding in one sparid species, *Diplodus sargus* (L. 1758), and explain this behaviour in terms of morphology and of buccal and pharyngeal jaw movement kinematics.

We will also shed light on the roles of the buccal and pharyngeal jaws in the handling of different sorts of food and on the phyletic position of sparids among perciforms.

Materials and methods

The present study is based on 36 living or dead *Diplodus sargus* specimens (7·7 to 18·3 cm S.L.) caught in the Bay of Calvi (Corsica) and the Gulf of Lion (France). Twenty-nine specimens (four cleared with trypsin and stained with alizarin, method of Taylor and Van Dijk, 1985), were dissected under a Wild M5 stereomicroscope and used for drawings. Buccal skeletal pieces and pharyngeal jaws were photographed with a JEOL SM 840 A scanning electron microscope.

Four individuals (10·1 to 13·7 cm S.L.) were trained to feed and filmed in a narrow corridor of a plexiglass experimental tank. They were fed with small crabs (*Carcinus maenas*, maximum cephalothoracic diameter 7 mm); porcelain crabs (*Porcellana longicornis*), shrimp (*Crangon crangon*) abdomens with their cuticle, snails (*Lymnaea stagnalis*, *Bithynia leachii*), earthworms (*Lumbricus terrestris*), and small fish [*Xiphophorus maculatus* 3·5 to 4 cm long]. Shrimp abdomens without their cuticle were used to test the reactions of *Diplodus sargus* to soft food (without a carapace). Fish were anaesthetized with MS 222 (Sandoz) and a hypodermic syringe was used to mark their buccal and pharyngeal jaws and skull roof with lead bits (**Fig. 1**). Despite special efforts, it is clear that standardization of marker localization on different fishes was incompletely reached. After suitable recovery the fish were filmed. Movements of the pharyngeal and buccal jaws were thus measured with respect to the neurocranium, considered immobile. X-ray plates were used to ascertain the locations of the lead markers, which were further confirmed by dissection.

Food items were impregnated with high-density barium sulphate (EZ-EM inc. Westburg, NY, U.S.A.) to make it possible to locate them from outside the oesophagus. Some of the crabs were marked with lead dorsally and ventrally for measuring possible crushing.

Both long side walls and the bottom of the feeding corridor of the experimental tank were of thin (3 mm) plexiglass. This, and the fact that the corridor did not contain much water, reduced X-ray absorption.

X-ray films (Agfa-Gavaert 30, 80 ASA) were made during feeding, in lateral and dorso-ventral views, on Gevapan 30 negative film (80 ASA) at 50 frames s^{-1} using a Sirecon 2 image amplifier equipped with an Arriflex 16 mm camera. X-rays were generated by a Siemens Tridoros 800 Optimatic (40 mA, 39 KV for lateral and 43 KV for dorso-ventral views). The distance between the X-ray tube and the amplifier was 1 m.

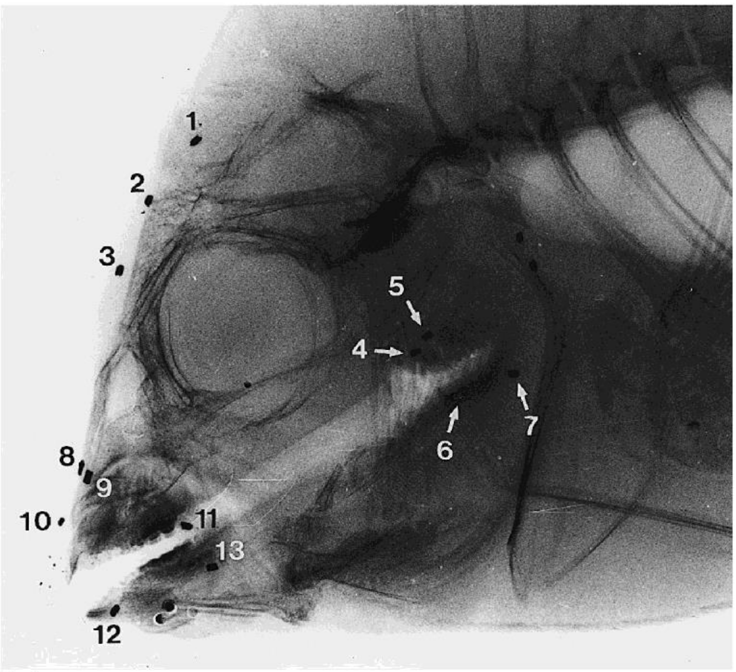
Positions of the lead markers were observed and digitized with an Analysis DF 16C NAC projector and a graphic analysis table (AGMEE, University of Liège). Software designed by V. Bels (University of Liège, Functional Morphology) was used to enter marker coordinates for each frame and to calculate distances between two successive markers and the angles determined by three points. The measuring error was calculated from the data obtained by locating 10 times (on the graphic table) a same point chosen at random. Forty-seven sequences filmed along a lateral axis and six sequences filmed along a vertical axis were analysed: 15 sequences of fish catching a crab or a porcelain crab, nine sequences of feeding on a shrimp abdomen with its carapace, five sequences with a shrimp without cuticle, 14 sequences of feeding on a gastropod (eight *Lymnaea*, six *Bithynia*), eight sequences of catching a worm, and two sequences of feeding on a fish.

Three individuals (standard length 10·5 to 12·6 cm) were trained to feed in a narrow experimental tank equipped with a mirror placed at a 45° angle beneath it. Food was identical to that used in cineradiographic observations. Cinematographic recordings were made on Kodak Eastman (400 ASA) negative films at 200 frames/s, using a Photosonics 1 PL camera. Fifteen sequences were analysed: four sequences of feeding on crabs (2) or porcelain crabs (2); four sequences with shrimps with (2) or without (2) cuticle; three sequences with gastropods (two *Lymnaea*, one *Bithynia*); one sequence with an earthworm; two sequences with a fish.

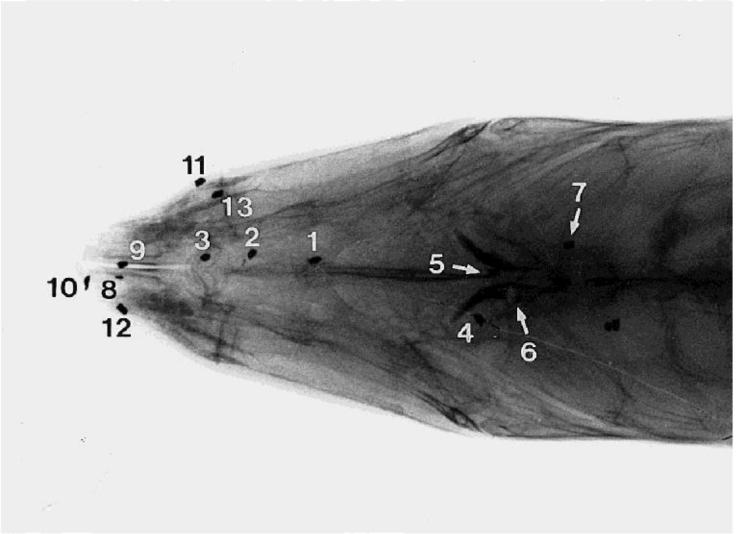
For the diagrams in **Figs 10** to **17**, all the measurements (**Fig. 9**) on the different specimens were given a coefficient equal to the quotient of the standard length of the 13·7 individual by their own standard length.

Fig. 1. *Diplodus sargus*. Radiographs showing a lateral (a) and a dorsal (b) view of the skull of a specimen marked with small lead bits inserted into its skeleton. Lead markers are numbered as follows: 1, 2, 3, neurocranium; 4, left upper pharyngeal jaw; 5, right upper pharyngeal jaw; 6, left lower pharyngeal jaw; 7,

right lower pharyngeal jaw; 8, processus ascendens of the left premaxilla; 9, between the left and right processi ascendentes of the premaxillae; 10, anterior end of the left premaxilla; 11, posterior end of the right premaxilla; 12, anterior end of the left dentary; 13, posterior end of the right dentary.



(a)



(b)

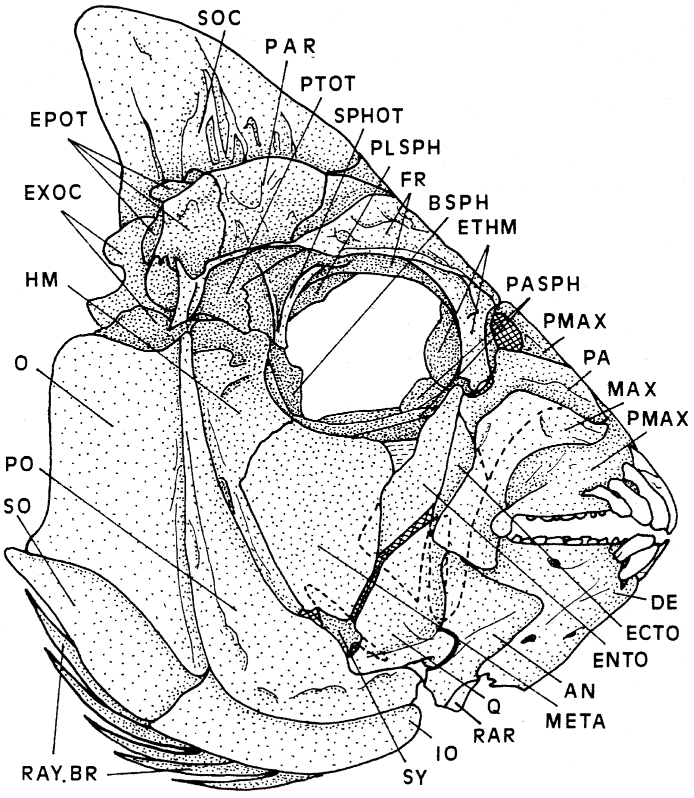
Results

ANATOMY

BUCCAL JAWS AND ASSOCIATED MUSCULATURE

The mandible consists of dentaries and angulars (**Fig. 2**). The latter are fused posterioventrally with the retroarticulars and bear the coronomeckelians medially (**Figs 3, 6**). The quadrato-angular articulations are strong (**Fig. 2**). Anteriorly, the angulars sink deeply into the dentaries (**Figs 3, 6**). Dentaries and angulars are held tightly together by fibres running along the outer face of the mandible [**Fig. 5(a), Li 5**]. Medially, they limit a large cavity we shall call the 'angulo-dentary cavity' (**Fig. 3**). Dentaries are broad and thick and cling to one another via a broad symphysis. They are fastened together by short fibres (**Figs 3, 5**). Posteriorly, their external symphysis are linked to the internal faces of the maxillaries by a strong ligament [Li 4, **Fig. 5(a)**].

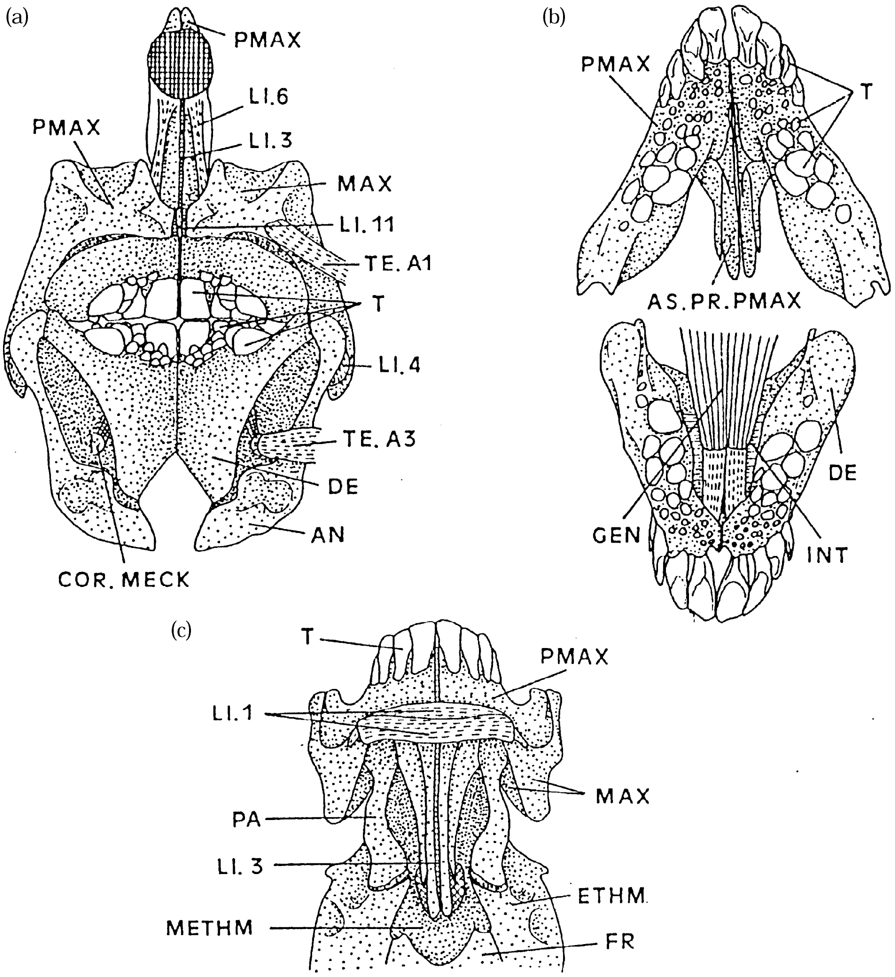
Fig. 2. *Diplodus sargus*. Lateral view of the skull. Suborbitals series, nasal and extrascapulars have been removed. Cartilages are squared and hidden outlines of some pieces of the suspensorium are in dotted lines. AN, Angular; BSPH, basiphenoid; DE, dentary; ECTO, ectopterygoid; ENTO, entopterygoid; EPOT, epiotic; ETHM, lateral ethmoid; EXOC, exoccipital; FR, frontal; HM, hyomandibula; IO, interopercle; MAX, maxilla; META, metapterygoids; O, opercle; PA, palatine; PAR, parietal; PASPH, parasphenoid; PLSPH, pleurosphenoid; PMAX, premaxilla; PO, pre-opercle; PTOT, pterotic; Q, quadrate; RAR, retroarticular; RAY BR, branchiostegal rays; SPHOT, sphenotic; SO, subopercle; SOC, supraoccipital; SY, symplectic.



Like the dentaries, the left and right premaxillaries cling to one another via a broad surface and by short ligamental fibres along the processus ascendentes (**Fig. 3**). Anteriorly the maxillaries overlap, but posteriorly they form a groove into which the premaxillaries fit (**Figs 3, 5**). Premaxillaries and maxillaries are united by ligamentous fibres (Li 2, Li 6).

Fig. 3. *Diplodus sargus*. (a) Posterior view of the buccal jaws; (b) premaxillae in ventral view and dentaries, dorsal view; (c) dorsal view of the upper jaws, palatines and anterior neurocranium. Cartilage is squared. AN, Angular; AS PR PMAX, premaxilla ascendant process; COR MECK, corono-meckelian; DE,

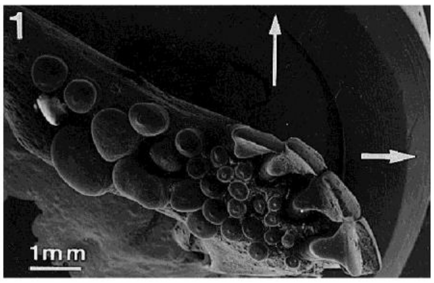
dentary; ETHM, lateral ethmoid; FR, frontal; GEN, geniohyoideus; INT, intermandibularis; LI 1, dorsal ligament between the maxillae; LI 3, ligament between the ascendant process of the premaxillae; LI 4, ligament between the maxilla and the dentary; LI 6, internal ligament between the maxilla and the premaxilla; LI 11, internal ligament between the maxillae; MAX, maxilla; METHM, mesethmoid; PA, palatine; PMAX, premaxilla; T, teeth; TE A1, TE A3 tendon of A1 and A3.

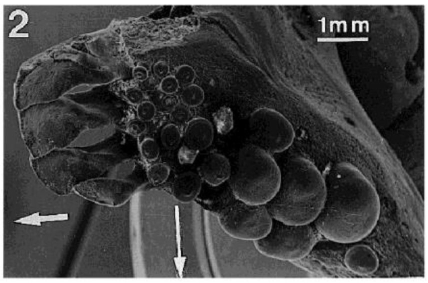


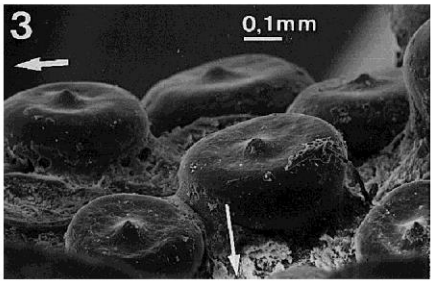
The maxillaries are fastened together by Li 1, which passes over the premaxillaries [**Fig. 5(a)**], and by the very short Li 11, which unites them behind the posterior processes of the premaxillaries (**Fig. 3**). The maxillaries are surmounted by very thick palatines, forming a strong articulation with the dumpy ethmoideal region (**Fig. 2**). This articulation is subvertical (**Fig. 2**).

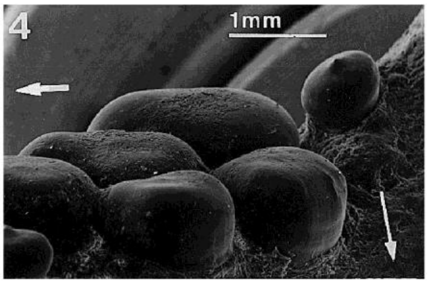
The dentaries and premaxillaries are broadened medially, forming a flattened tooth-bearing surface. There are two sorts of teeth: each half-mandible bears four incisors followed by three to four rows of molars increasing in size from front to rear (**Figs 3, 4**). When observed under high magnification, the smaller molars show a depression with a small, conspicuous point in the middle. The bigger molars are less concave and their point is smaller or lacking (**Fig. 4**).

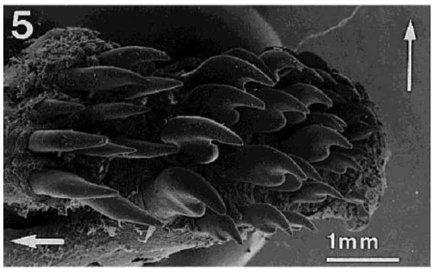
Fig. 4. *Diplodus sargus*. SEM photographs of the buccal and pharyngeal teeth. 1, Right premaxilla; 2, left dentary; 3, 4, details of the left dentary teeth; 5, left upper pharyngeal jaw; 6, lower pharyngeal jaw.

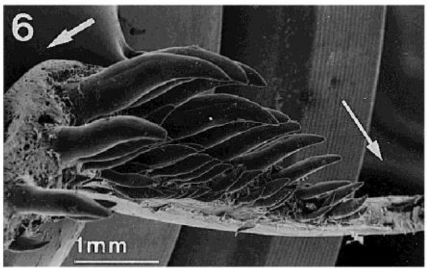












When the mouth is closed, the incisors are in contact. The molars are not, but the outer ones are closer than the inner ones. Seen from behind, the molars seem to form an oval.

Mouth opening is produced, as in other acanthopterygians, by the action of classically arranged and inserting muscles: the sternohyoideus, the levator operculi, the epaxial and hypaxial muscles, and sometimes the geniohyoidei [**Fig. 5(a)**]. Individual or simultaneous contraction of these muscles results in lowering of the lower jaw, which makes the upper jaw protrude by frontward projection of the premaxillary (Osse, 1969; Vandewalle, 1972; Liem, 1973, 1978).

As in all teleosts, the adductores mandibulae close the mouth (Osse, 1969; Liem, 1970; Lauder & Liem, 1981). They insert posteriorly on the suspensorium (hyomandibula, metapterygoid, quadrate, preopercular) and anteriorly on the maxillary and mandible.

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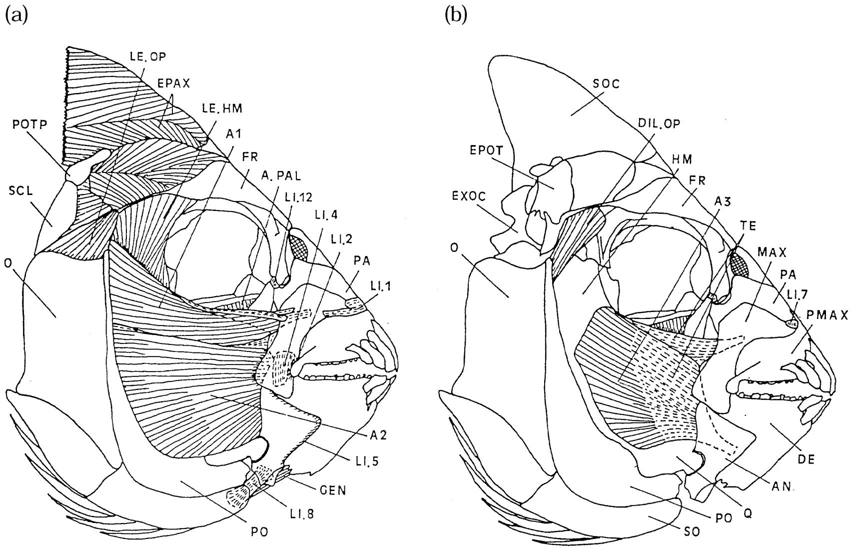
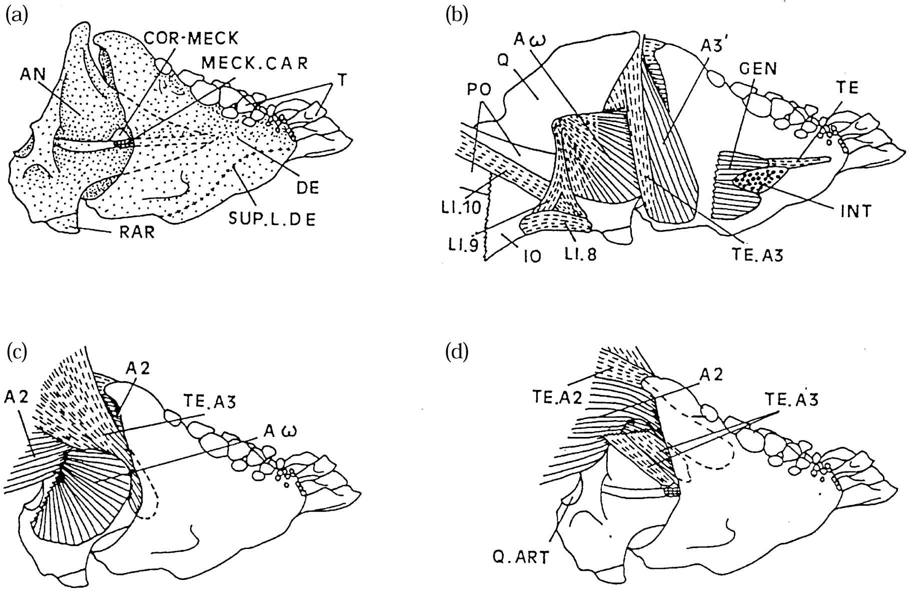
Fig. 5. *Diplodus sargus*. (a) Lateral view of the cephalic muscles; (b) lateral view of the head to show the third adductor mandibulae. Squared areas are cartilages and thick dotted lines are the outlines of hidden ligaments, tendons or muscles. A1, A2, A3 sections of the adductor mandibulae; AN, angular; A PAL, adductor arcus palatini; DE, dentary; DIL OP, dilatator operculi; EPAX, epaxial musculature; EPOT, epiotic; EXOC, exoccipital; FR, frontal; GEN, geniohyoideus; HM, hyomandibula; LE HM, levator hyomandibulae; LE OP, levator operculi; LI 1, dorsal ligament between the maxillae; LI 2, external ligament between the premaxilla and the maxilla; LI 4, ligament between the maxilla and the dentary; LI 5, ligament between the dentary and the angular; LI 7, ligament between the anterior part of the palatine and the maxilla; LI 8, ligament between the angular and the interopercle; LI 12, ligament between the lateral ethmoid and the entopterygoid; MAX, maxilla; O, opercle; PA, palatine; PMAX, premaxilla; PO, preopercle; POTP, posttemporal; Q, quadrate; SCL, supracleithrum; SO, subopercle; SOC, supraoccipital; TE, tendon.



In *D. sargus*, the anterior joints are complicated. The A1 adductor is attached by two tendons to the medial and outer faces of the maxillary [**Fig. 5(a)**]. The external tendon is surmounted by another tendon which lines the major part of the upper area of A1 [**Fig. 5(a)**]. The A2 adductor is a big muscle joining the entire posterior edge of the angular (over the quadrate-mandibular joint) with the inner face of the angulo-dentary cavity [**Figs 5(a), 6**]. Moreover, A2 is attached by a tendon to the apex of the dentary, and by an aponeurosis to A1 (**Fig. 6**). The A3 adductor inserts above on the medial face of the maxilla by means of a thin tendon which fuses with the inner tendon of A1 [**Fig. 5(b)**] and ventrally by a broad tendon of which the majority of fibres attach to the coronomeckelian and in the angulo-dentary cavity (on the side of the dentary) (**Fig. 6**). The upper fibres of this tendon depart from the others, pass above them and insert ventrally on the angular. Some also extend into the A3' bundle which in turn attaches to the inner face of the mandible, outside the angulo-dentary cavity (**Fig. 6**). The Aω adductor extends from the quadrate to the angular. Next to Aω, several ligaments link the angular, quadrate, interopercular, and hyoid bars one to another (**Fig. 6**).

A thick intermandibular muscle joins both dentaries just above their connection area (**Fig. 6**).

Fig. 6. *Diplodus sargus*. Inner lateral views of the left lower jaw. (a) Skeleton; (b–d) three successive planes deeper and deeper in the musculature; in (b) the geniohyoideus and intermandibular muscles have been cut. A2, A3, A3', Aw sections of the adductor mandibulae; AN, angular; COR MECK, corono-meckelian; DE, dentary; GEN, geniohyoideus; INT, intermandibularis; IO, interopercle; LI 8, ligament between the angular and the interopercle; LI 9, ligament between the interopercle and the quadrate; LI 10, ligament between the angular and the hyoid bar; MECK CAR, Meckel's cartilage; PO, preopercle; Q, quadrate, Q ART, place of the quadrate-mandible articulation, RAR, retroarticular; SUP L DE, superior limit of the contact area of the dentaries; TE, tendon; TE A2, TE A3, tendons of A2 and A3.



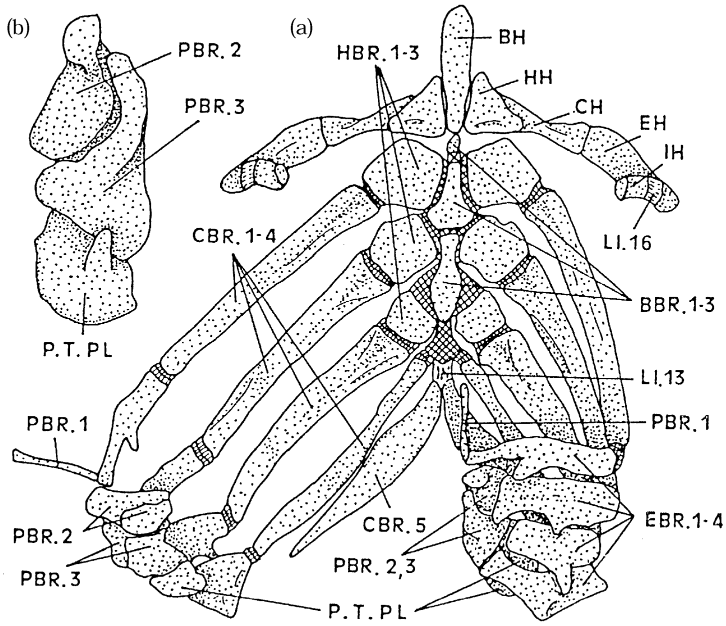
PHARYNGEAL JAWS AND ASSOCIATED MUSCULATURE

The first three branchial arches are complete and consist of a basibranchial and a pair each of ceratobranchials, epibranchials, and pharyngobranchials (**Fig. 7**). The next branchial arch consists of ceratobranchials and epibranchials only and the fifth is reduced to ceratobranchials alone (**Fig. 7**).

The fifth ceratobranchials are each covered by a dorsal toothed plate and constitute the lower pharyngeal jaws (**Figs 4, 7**). The latter are independent of each other. They are linked anteriorly to the branchial copula by a ligament [**Fig. 7(a)**] and posteriorly to the fourth cerato- and epibranchials by muscles [**Fig. 8(d)**]. Their teeth are arranged in three rows, the largest ones lying in the inner row (**Fig. 4**). The teeth are conical, unicuspid and bent sideward.

The upper pharyngeal jaws hang opposite the lower ones. Each consists of a second pharyngobranchial and a third pharyngobranchial bearing a ventral tooth plate, and a third associated posterior tooth plate (**Fig. 7**). These three pieces are associated only by membranes and by short ligaments linking the epibranchials to one another and to the second and third pharyngobranchials.

Fig. 7. *Diplodus sargus.* (a) Dorsal view of the branchial basket and hyoid bars; the posterior left upper part has been unfolded; (b) dorsal view of the parts of the left upper pharyngeal jaw. Squared areas are cartilage. BBR.1–3, 1st, 2nd and 3rd basibranchial; BH, basihyal; CBR 1–4, 1st, 2nd, 3rd and 4th ceratobranchial; CBR5, 5th ceratobranchial; CH, ceratohyal; EBR 1–4, 1st, 2nd, 3rd and 4th epibranchials; EH, epihyal; HBR 1–3, 1st, 2nd and 3rd hypobranchials; HH, hypohyal; IH, interhyal; LI 13, ligament between the 5th ceratobranchial and the medial branchial cartilage; LI 16, ligament between the interhyal and the epihyal; PBR 1, PBR 2, PBR 3, 1st, 2nd and 3rd pharyngobranchials; PBR 2, 3, 2nd and 3rd pharyngobranchials; P T PL, posterior toothed plate.



The teeth on the upper pharyngeal jaws are almost bicuspid and are compressed laterally (**Fig. 4**). The teeth borne by the second and third pharyngobranchials are turned respectively backward and backward inward, forming a 45° angle with the previous ones (**Fig. 4**). The posterior plate bears only a few small teeth.

Most muscles involved in the movements of the branchial basket, and consequently of the pharyngeal jaw apparatus, closely resemble those described for other perciforms (Liem, 1970, 1973; Vandewalle, 1972; Liem & Osse, 1975; Elshoud-Oldenhave, 1979; Lauder, 1983*a*; Vandewalle *et al.*, 1992). They are listed with their insertions and presumed biological roles in **Table I.** However, several anatomical features and particularities are worthy of note:

- the adductor muscles of the first three branchial arches appear to be missing;
- the adductor of the fourth arch lies along the postero-anterior face of the fourth cerato- and epibranchials and not on their front face [**Fig. 8(d)**];
- the adductor of the fifth arch is independent of the fourth arch and of the posterior levatores;
- there are no obliqui transversi;
- the branchial basket hangs from the parasphenoid in a peculiar way: by a fibrous pad (**Fig. 8**) attaching dorsally to the parasphenoid and ventrally to the aponeurosis shared

by two new special muscles lining the parasphenoid to the left and right. These muscles run from the dorsal extremities of the second pharyngobranchials, go around the fibrous pad and fuse together posteriorly.

Fig. 8. *Diplodus sargus*. Views of the dorsal branchial musculature and hyoidean bars. (a) General view of the muscles; (b) view of the musculature after removal of the fibrous part and of the muscles attached to it. (c) Ventral view of the fibrous pad. (d) Posterior view of the peculiar muscles joining the left fourth and fifth epi and ceratobranchials. AD 4, AD 5, Adductores of the 4th and 5th branchial arches; CBR 4, CBR 5, 4th and 5th ceratobranchials; DEP PBR 2, depressor to the 2nd pharyngobranchials; EBR 1, EBR 4, 1st and 4th epibranchials; I LE E 1, I LE E 2, I LE E 3, I LE E 4, insertions of the 1st, 2nd, 3rd and 4th levatores externi; I LE I.2, I LE I 3, insertions of the 2nd and 3rd levatores interni; I LE P, insertion of the levator posterior; LI 14, fibrous pad between the parasphenoid and the superior central part of the branchial basket; LI 15, ligament between the fibrous pad (LI.14) and the aponeurosis of the depressor of the 2nd pharyngobranchials; OBL D 3, 4, 3rd and 4th obliqui dorsales; OBT 5, obturator of the least branchial slit; PBR 1, PBR 2, PBR 3, 1st, 2nd and 3rd pharyngobranchials; RE D, retractor dorsalis; SPH, sphincter oesophagi; TR D A, transversus dorsalis anterior; TR D P, transversus dorsalis posterior.

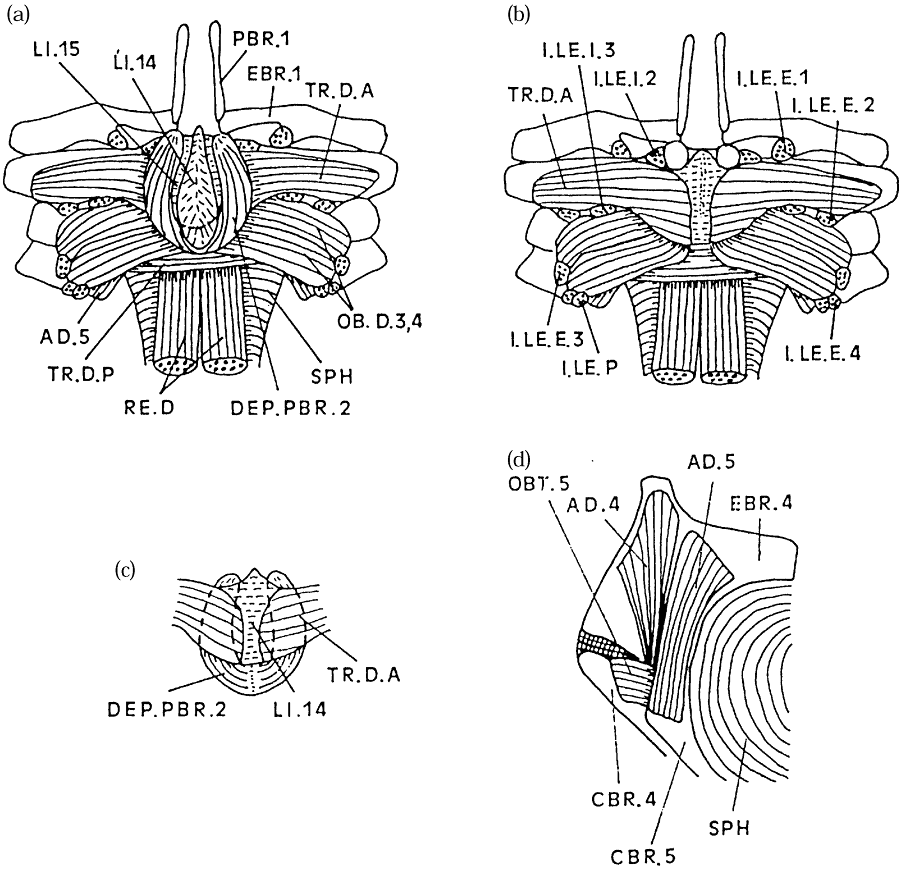
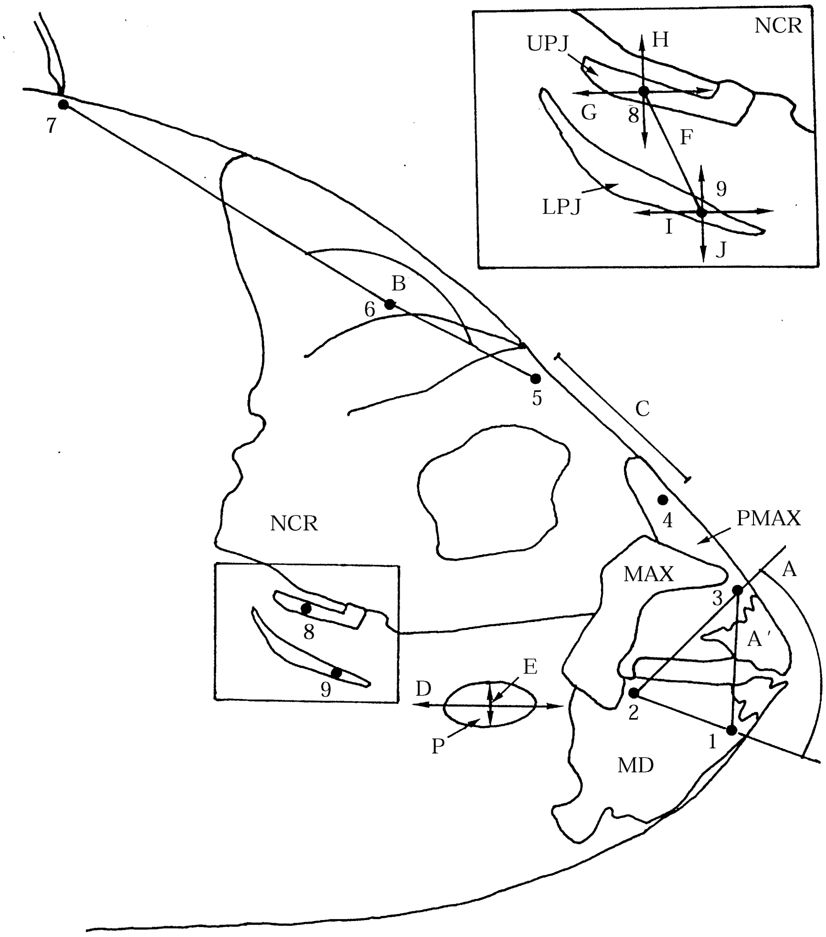


Table I. Insertions of branchial muscles

Name	Proximal insertion	Distal insertion	Main role
1st, 2nd, 3rd levatores externi	Prootic	Posterior tip of the 1st, 2nd, 3rd epibranchial	Elevation and protraction of epibranchials and upper pharyngeal Jaw
4th levator externus	Superior edge of prootic and pterotic	Posterior tip of the 4th epibranchial	
2nd, 3rd levatores interni	Pterotic	2nd, 3rd pharyngobranchials	Elevation of the upper pharyngeal jaw
Levator posterior	Posterior point of the pterotic	Posterior tip of the 4th epibranchial	Elevation of the 4th epibranchial and the lower pharyngeal jaw
Pharyngocleithralis externus	5th ceratobranchial	Anterior end of the cleithrum	Depression of the lower pharyngeal Jaw
Pharyngocleithralis internus	5th ceratobranchial	Middle part of the cleithrum	Retraction of the lower pharyngeal jaw
Transversus dorsalis anterior	2nd epibranchial	Median aponeurosis between the left and right muscles and ligament 14	Bringing closer to one another the upper pharyngeal jaws
Transversus dorsalis posterior	4th right epibranchial	4th left epibranchial	
3rd obliquus dorsalis	3rd epibranchial	Upper side of the 3rd pharyngobranchial	Controlling the angles between the 3rd and 4th epibranchials, and upper pharyngeal jaw
4th obliquus dorsalis	4th epibranchial	Upper side of the 3rd pharyngobranchial	
Depressor of the 2nd pharyngobranchial	Anterior dorsal end of the 2nd pharyngobranchial	Aponeurosis between left and right muscles	Depression, retraction and bringing closer to one another the pharyngobranchials
1st, 2nd, 3rd obliqui dorsales	1st, 2nd, 3rd hypobranchials	1st, 2nd, 3rd ceratobranchials	Controlling the angles between the hypobranchials and ceratobranchials
Rectus communis	Lateral edge of the urohyal	5th ceratobranchial through a membrane	Depression and protraction of the lower pharyngeal Jaw
Rectus ventralis	3rd hypobranchial	4th ceratobranchial	Bringing together the 3rd and 4th branchial arches
Transversus ventralis anterior	4th right ceratobranchial	4th left ceratobranchial	Bringing together of the right and left lower pharyngeal Jaws
Transverse ventralis posterior	5th right ceratobranchial	5th left ceratobranchial	
5th obturator	4th ceratobranchial	5th ceratobranchial	Straightening the 4th branchial slit
4th, 5th adductores	4th, 5th ceratobranchial	4th, 5th epibranchial	Reduction of the angle between the 4th or 5th ceratobranchials and the 4th or 5th epibranchials
Retractor dorsalis	Mesial side of the 3rd pharyngobranchial	1st, 2nd, 3rd vertebra	Retraction of the upper pharyngeal Jaws
Sternohyoideus	Urohyal	Cleithrum	Retraction of the branchial basket
Geniohyoideus	Mandible	Hyoidean bar	Protraction of the branchial basket

Fig. 9. *Diplodus sargus*. Schematized lateral view of the outline of the head, neurocranium and buccal and pharyngeal jaws. Digitalized points 1 to 9 are an example of the position of the lead markers. Letters A to J represent the distances and angles measured between the markers whose variations are shown in the **Figs 10** to **17**. LPJ, Lower pharyngeal jaw; MAX, maxilla; MD, mandible; NCR, neurocranium; P, prey; PMAX, premaxilla; UPJ, upper pharyngeal jaw. Points: 1 and 2, mandible; 3 and 4, premaxilla; 5 and 6, neurocranium; 7, first ray of the dorsal fin; 8 and 9, pharyngeal jaws. Letters: A, angle formed by the points 1, 2 and 3 measuring the gape of the mouth; A', distance between points 1 and 3 measuring the gape of the mouth; B, angle formed by the points 5, 6 and 7 measuring the elevation of the neurocranium; C, distance between the points 4 and 5 measuring the protrusion; D and E, horizontal and vertical displacement of the prey; F, distance between the points 8 and 9 proportional to the gape between the pharyngeal jaws. G and H, horizontal and vertical displacements of the point 8 or of the right upper pharyngeal jaw; I and J, horizontal and vertical displacements of the point 9 or of the right pharyngeal jaw.



MOVEMENTS

We shall first describe in detail how a crab or porcelain crab (both being called 'crab') is caught, then consider other sorts of food. The words 'hammering' and 'crushing' refer to movements involving mouth opening and closing or series of such movements. When the prey lies between the pharyngeal jaws, the movements are called 'transport' if they do not involve any observable modification of the shape of the prey.

CATCHING A CRAB

Whether motionless or not, on the bottom or in open water, the prey is sucked in (there is a conspicuous displacement of the prey toward the predator) and seized between the buccal jaws by incisors or molars. The prey is sometimes missed (**Fig. 10**), in which case the predator tries again. Sometimes a prey is captured and rejected immediately. Just after it is seized, the prey is often correctly positioned. This is perceptible from the outside by the various movements opening and closing the mouth (**Fig. 11**). Meanwhile the pharyngeal jaws are drawn back and apart.

Fig. 10. *Diplodus sargus*. Diagrams related to gape of the mouth (a), neurocranial elevation (b) and upper jaw protrusion (c) in the case of a failed attempt to catch a crab followed by a successful one. The measuring error is shown in the upper left-hand corner.

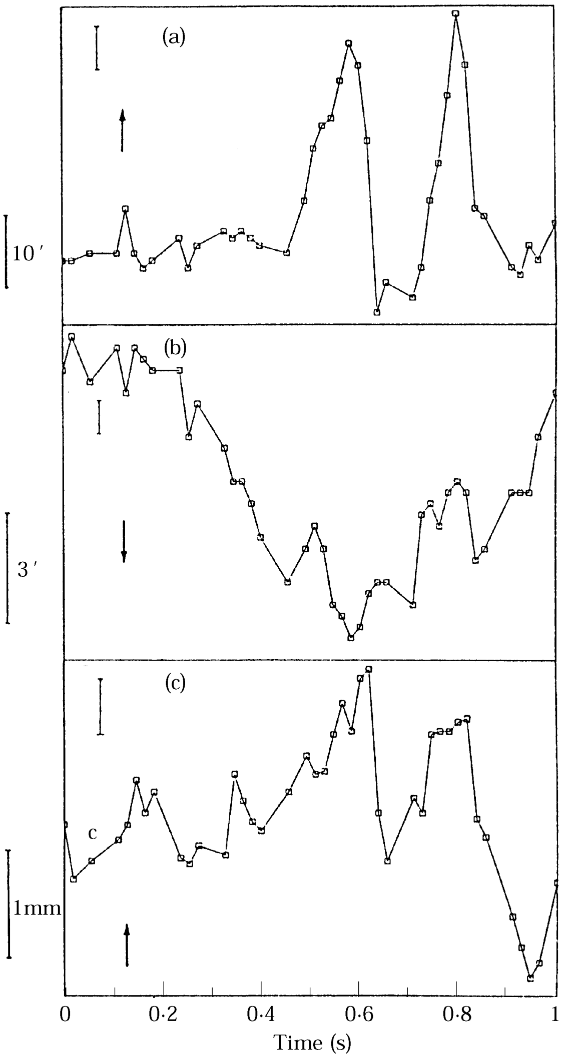
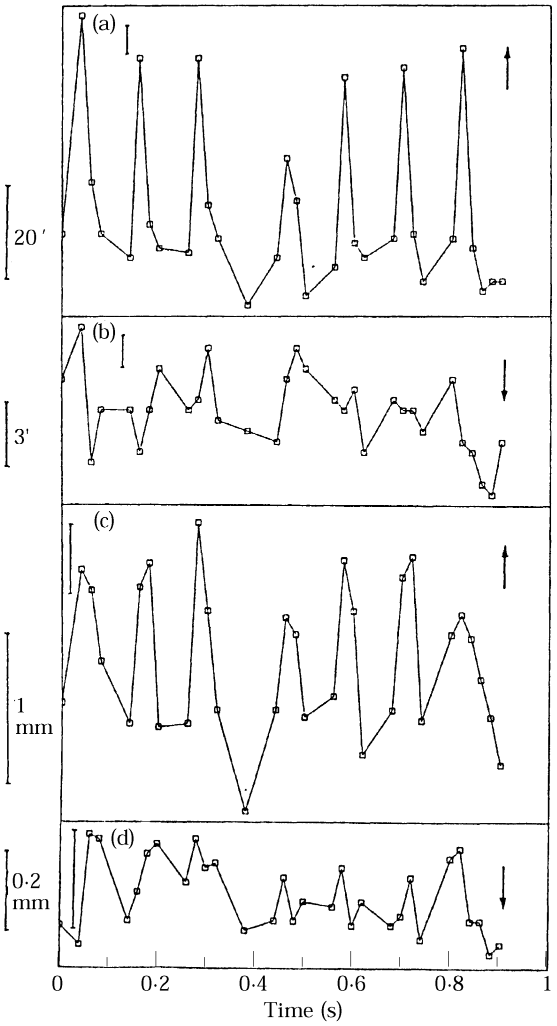


Fig. 11. *Diplodus sargus*. Diagrams related to gape of the mouth (a), neurocranial elevation (b), upper jaw protrusion (c) and damage to a crab (d) during fast crushing movements. Crushing of the prey does not seem to be severe.



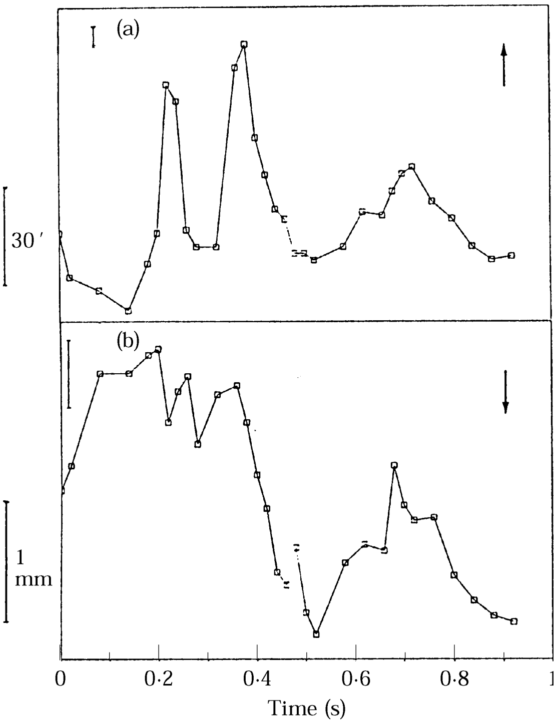
Suction begins shortly after the mouth begins to open. The prey arrives between the buccal jaws while the mouth is still partly closed. Mouth opening is always fast (about 0·2 s) and its amplitude reaches 50° (**Fig. 10**). In the case of several successive suctions, when the prey is seized wrongly (for example by the appendages), the subsequent mouth openings are less wide than the first, perhaps because the prey is closer. After a missed catch, the fish opens its mouth as quickly as at the first attempt. The mouth always begins to close quickly, but the end of the movement may be slower (**Fig. 10**), possibly due to the presence of the prey between the jaws.

Each time the mouth opens, protrusion occurs to a variable degree. When the mouth closes, protrusion decreases and disappears. When the mouth opens twice in succession, effacement of protrusion due to a first closure may be stopped to allow the second protrusion to begin. Mouth opening may or may not be accompanied by elevation of the neurocranium. If so, elevation may be sustained between two successive openings (**Figs 10** and **11**). Once seized, the prey is either subjected to hammering movements (2 to 8) or sent to the pharyngeal jaws. In the latter case, it is immediately returned to the mouth and seized either by the incisors (seen once) or by the molars (observed six times). It is then subjected to crushing movements. There is no observable difference between crushing by molars and crushing by incisors.

These successive movements are variable. In most cases, they are swift, ample, and in very quick succession (**Fig. 11**), but sometimes they are smaller and slower. They are always accompanied by protrusion, the extent of which is not always proportional to the gaping of the mouth (**Fig. 11**).

It is often hard to appreciate the impact of jaw movements on the prey during crushing. The prey may be shifted. If the movements are swift, the effect of mouth closure on the crab cannot be observed (**Fig. 12**). When closing is slower, however, deformations produced by the jaws are often conspicuous and the crushing of crabs marked dorsally and ventrally with lead can be recorded (**Fig. 12**). In many cases, the crab does not recover its initial thickness (**Fig. 11**), which suggests that its structures undergo plastic deformation.

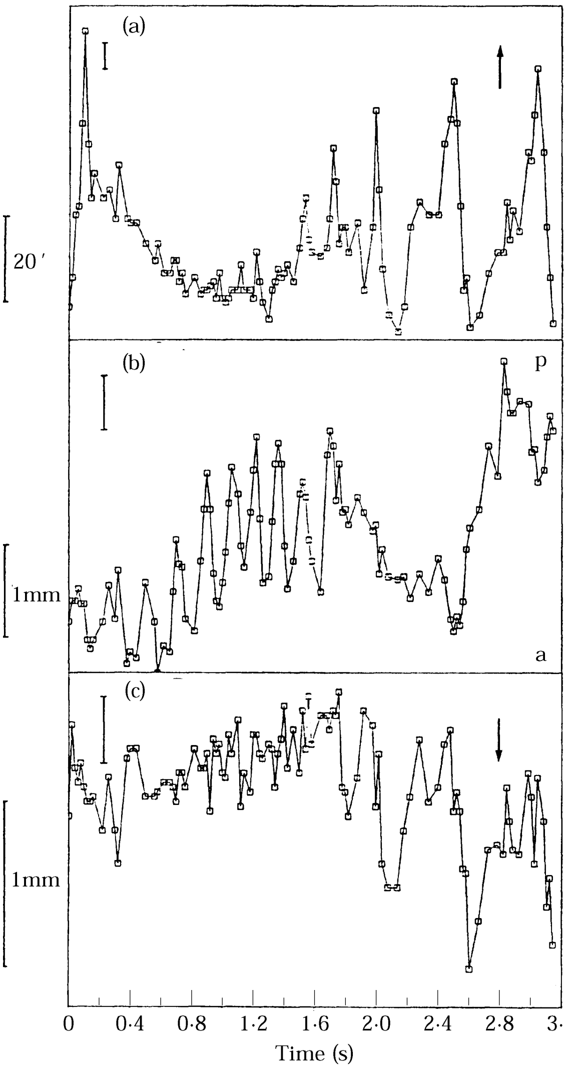
Fig. 12. *Diplodus sargus*. Diagram illustrating two movements of positioning a crab between the buccal jaws followed by crushing. (a) Gape of the mouth; (b) severe crushings of the prey at 0·5 and 0·9 s.



Crushing movements were never observed while the pharyngeal jaws were active. **Figure 13**, for example, shows a crushing cycle followed by a period during which the buccal jaws rest while holding the crab. Meanwhile, the pharyngeal jaws are moving (probably conveying a small, inconspicuous prey item to the oesophagus). Later, their activity slows down while crushing movements resume.

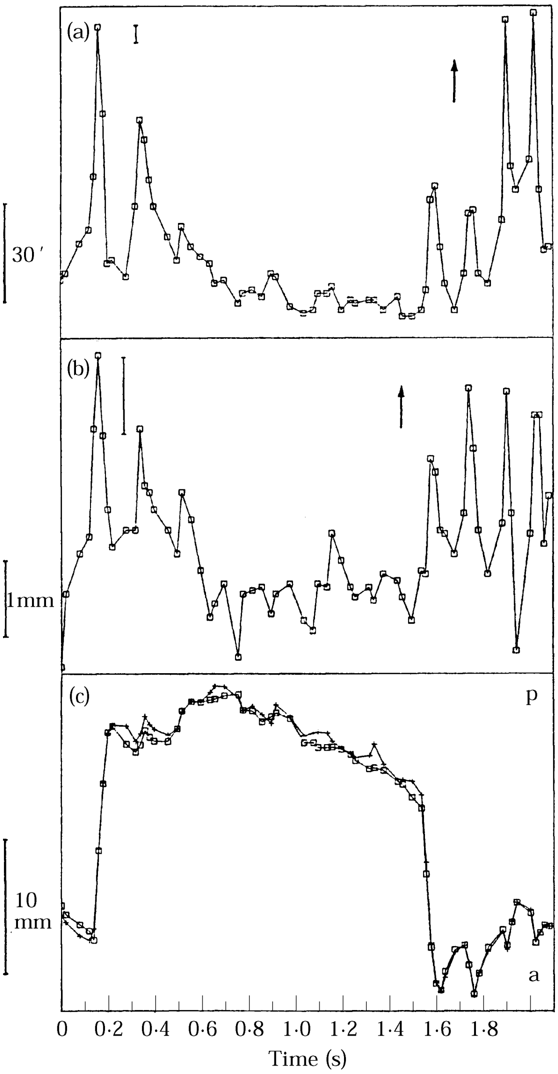
Next, the prey may or may not seesaw between the buccal and pharyngeal jaws. One variably wide opening of the mouth and subsequent closing is associated with each backward motion. The crab reaches the pharyngeal jaws when the mouth has just closed (**Fig. 14**). A second and even a third buccal movement may ensue; probably for pushing the prey between the pharyngeal jaws (**Fig. 14**). When the prey moves forward, the mouth aperture is widest just before the prey arrives between the buccal jaws. After a seesaw, the prey usually stops between the buccal parts crushing it (**Fig. 14**).

Fig. 13. *Diplodus sargus*. Diagrams showing gape of the mouth (a), horizontal movements of the right upper pharyngeal jaw (b) and crushing of a crab (c). a, Anterior; p, posterior.



Finally, the prey is seized by the pharyngeal jaws and conveyed into the oesophagus. It is always seized when the upper pharyngeal jaws are in their forward position (**Figs 15** and **16**). At this stage, only transport movements are observed. Upon its final arrival between the pharyngeal jaws, the prey is often in more than one piece (nine cases), the carapace and thorax seeming to be separated from the rest of the body. Each part is conveyed separately to the oesophagus (in three to five movements) (**Figs 15** and **16**). Several attempts are generally required before the pharyngeal jaws grip the prey (**Fig. 16**). During these attempts and subsequent transport, the upper pharyngeal jaws keep moving back and upward or forward and downward (**Figs 15** and **16**) but the amplitude of their displacements is not constant. Movements of the left and right pharyngeal jaws may also differ [**Fig. 15(e)**].

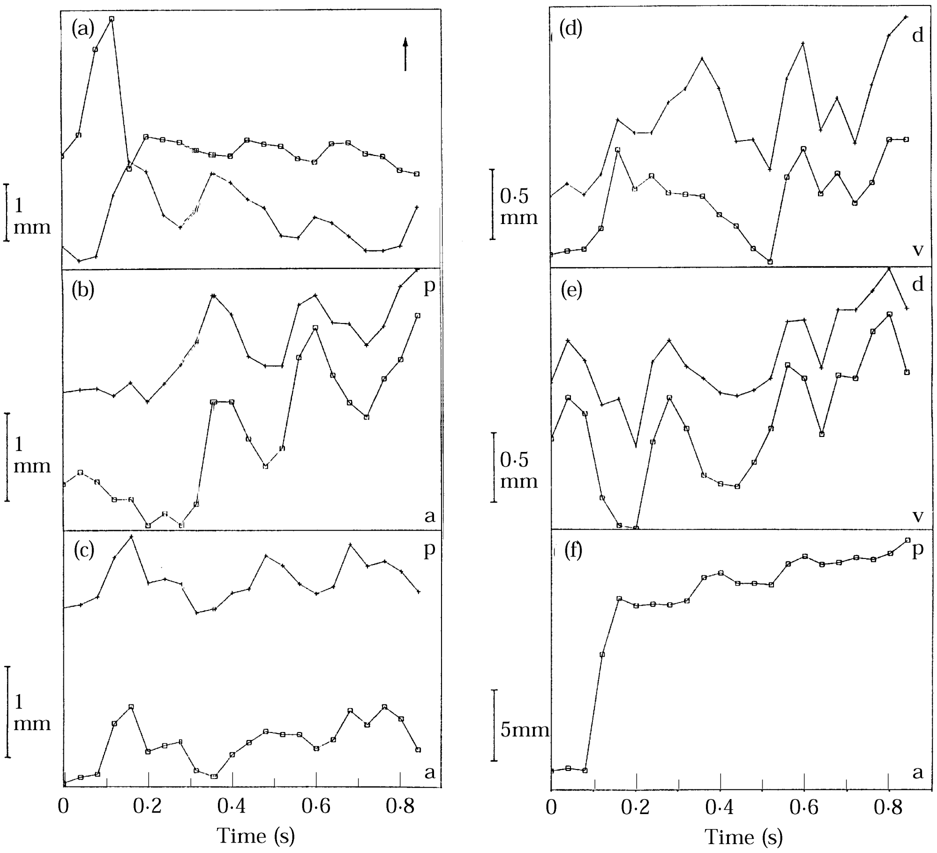
Fig. 14. *Diplodus sargus*. Diagram showing events during transport of a crab from the mouth to the pharyngeal jaws and its rejection toward the buccal jaws: gape of the mouth (a), upper jaw protrusion (b) and prey displacements (c). Each of the curves in (c) represents the displacements of a lead marker on the crab. The prey is not yet dislocated into two parts. a, Anterior; p, posterior.



Regular movements of the lower pharyngeal jaws are sometimes hard to observe and to associate with prey movements (**Fig. 16**), but in other cases the movements are perfectly measurable. The lower pharyngeal jaws always remain in a posterior and low position during prey capture (**Fig. 15**). This produces a wide gape between the upper and lower pharyngeal jaws. During prey transport, the lower pharyngeal jaws may be up and aft or down and aft and then up and fore or down and fore (**Fig. 15**). There is no significant difference between the movements of the left and right lower pharyngeal jaws. The lower pharyngeal jaws always move backward while the upper ones move forward (**Fig. 15**), but the vertical component of the movements of the lower pharyngeal jaws is by no means regular (**Fig. 15**).

Fig. 15. *Diplodus sargus*. Diagrams showing the rearward displacements of a crab and its transport between the pharyngeal jaws. (a) Gape of the mouth (□) and gape between upper and lower pharyngeal

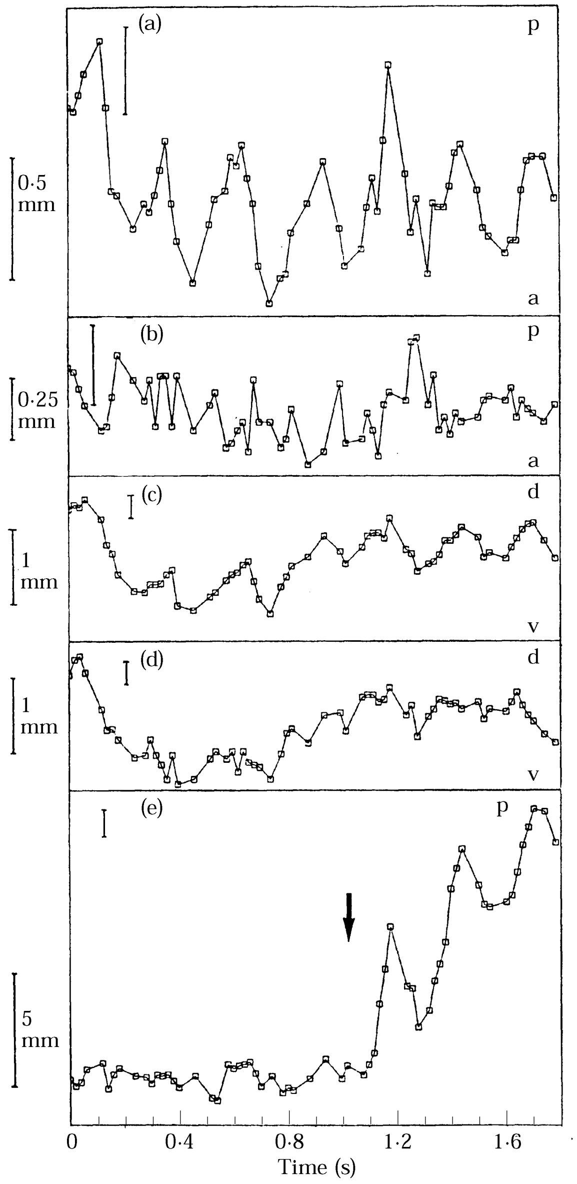
jaws (+); (b) horizontal movements of the left (+) and right (□) upper pharyngeal jaws; (c) horizontal displacements of the left (+) and right (□) lower pharyngeal jaws; (d) vertical movements of the left (+) and right (□) upper pharyngeal jaws; (e) vertical movements of the left (+) and right (□) lower pharyngeal jaws; (f) displacement of part of the prey from mouth to oesophagus. a, Anterior; d, dorsal; p, posterior; v, ventral.



Movements of the upper pharyngeal jaws are almost always more ample than those of the lower ones. The prey is always moved to the oesophagus when the upper pharyngeal jaws move backward and upward and the lower ones shift forward (when the movements are measurable), whatever the vertical movements may be (**Figs 15** and **16**). The prey is stopped or moves slightly forward while the upper pharyngeal jaws move upward and the lower ones move backward (when the movements are measurable). Once between the pharyngeal jaws, neither the prey nor parts of it are ever rejected to the buccal jaws or outside.

After deglutition some ample movements of the upper pharyngeal jaws continue to be recorded while the lower pharyngeal jaws appear to rest.

Fig. 16. *Diplodus sargus*. Diagrams showing attempts to seize a crab with the pharyngeal jaws and subsequent transport of a part of the prey to the oesophagus. Horizontal (a) and vertical (c) movements of the right upper jaw, horizontal (b) and vertical (d) movements of the right lower jaw, and in (e) variation of the gape between two lead markers on the two parts of the prey, showing that first both parts of the prey arrive simultaneously near the pharyngeal jaws, followed by transport of just one part to the oesophagus. The arrow indicates the prey seizing by the pharyngeal jaws. a, Anterior; d, dorsal; p, posterior; v, ventral.



In two recorded instances, one part of the prey was seen between the pharyngeal jaws while the other part was still between the buccal bones. The latter did not move during transport of part of the prey to the oesophagus.

Dorso-ventral recording of feeding on a crab did not reveal any lateral widening or straightening of the buccal jaws during seizing and crushing. No lateral or asymmetrical movement of the pharyngeal jaws was observed.

FEEDING ON OTHER PREY

The movements of the buccal and pharyngeal jaws closely resemble those observed with a crab prey. Behaviour toward other sorts of prey is variable.

GASTROPODS

Lymnaea is sucked in and seized by the incisors (all recorded cases). Then it is either crushed immediately by the incisors or shifted to the pharyngeal jaws. In the latter case, it is quickly brought back forward and crushed by the incisors or the molars. Crushing consists of only one movement which breaks the shell, as attested by the observed rejection of shell fragments. In two cases where the prey was brought backward, it was seized by the pharyngeal jaws and shell fragments were immediately rejected outside before the prey was brought back forward.

Then the prey, shell-less or nearly so, may seesaw several times from the buccal to the pharyngeal jaws, possibly halting for crushing between the buccal jaws or for a tentative grasping by the pharyngeal jaws. When seized, it is shifted to the oesophagus. In the course of the shift, five *Lymnaea* specimens were cut into at least two conspicuous pieces. Many movements (15 to 21) are needed to bring the prey or pieces of it into the oesophagus. It even occurred three times that after numerous attempts to shift the prey backward, part of it was ultimately rejected through the mouth. Such rejection is very swift: the prey moves from the pharyngeal jaws to the outside in 0·1 s (**Fig. 17**). When the items leave, the pharyngeal jaws begin to separate, they go on doing so, the mouth begins to open and the gape reaches its maximum after the prey is already outside (**Fig. 17**).

Dorsal observations show asymmetrical movements (amplitude and orientation) of the upper pharyngeal jaws while a piece of *Lymnaea* passes between them.

Bithynia is always sucked in and grasped by the incisors. One of the following then occurs: (1) the prey is crushed by the molars; (2) it is thrown out, sucked in again, and crushed by the molars; (3) it is shifted to the pharyngeal jaws. In the latter case, it is brought back to the mouth and hammered by the molars.

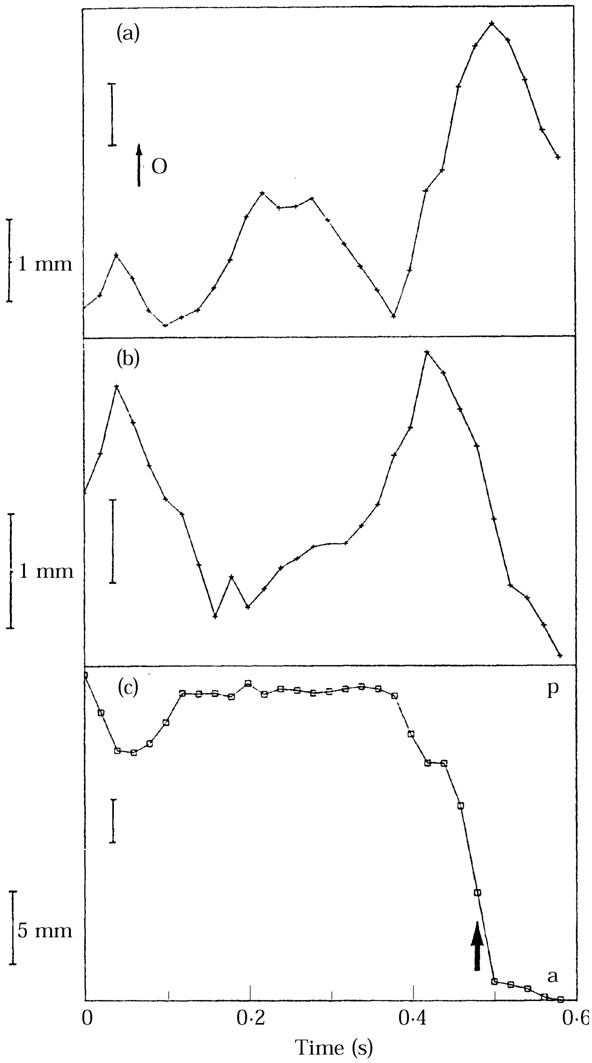
If several attempts prove unsuccessful, the prey is rejected for good. This occurred in all cases but one, in which the shell broke into pieces at the fourth attempt. The prey was then treated like a *Lymnaea* and it entered the oesophagus in one piece after 16 transport movements.

Rejection movements are very similar to those described above.

SHRIMP ABDOMEN WITH ITS CUTICLE

Food in open water or lying on the bottom is sucked in and seized by the incisors (five cases) which crush it, or brought backward directly (four cases). If the food is grasped by the pharyngeal jaws, it is sent into the oesophagus. If not, it is brought back to the buccal jaws between which it suffers a number of crushing movements (one to six), sometimes by the molars but more often by the incisors. Several seesaws between the buccal and pharyngeal jaws may occur. Finally the shrimp is seized by the pharyngeal jaws, at which time it is in one or several pieces with or without a cuticle. In the latter case the carapace is rejected like the shell pieces of *Lymnaea*. The shrimp abdomen or the pieces of it are transported into the oesophagus in five to eight movements if the cuticle is preserved, and in up to 12 movements if it is not.

Fig. 17. *Diplodus sargus*. Diagrams showing rejection of a morsel of Lymnea. Gape of the mouth (a), gape between the upper and lower pharyngeal jaws (b), displacements of the rejected item (c). The big arrow indicates the time when the prey leaves the buccal cavity.



SHRIMP ABDOMEN WITHOUT ITS CUTICLE

Food lying in open water or on the bottom is either seized by the incisors (twice) or shifted directly to the pharyngeal jaws (three times). If seized by the incisors, food is immediately sent backward. It may then seesaw several times between the mouth and the pharyngeal jaws or be seized immediately by the pharyngeal jaws. During a seesaw, food does not stop at the level of the buccal jaws and seems not to be crushed there.

Once seized by the pharyngeal jaws, the shrimp abdomen is shifted to the oesophagus in several transport movements (nine to 13) and remains undivided.

EARTHWORM

Feeding on an earthworm is variable. A worm 4 cm long was sucked in and brought immediately to the pharyngeal jaws which grasped it and transported it to the oesophagus in three movements.

A 3-cm worm was sucked in and seized by the pharyngeal jaws after 13 attempts. Then it was folded and conveyed to the oesophagus in three movements.

A 2-cm worm was sucked in as far as the pharyngeal jaws but not grasped. It was brought back forward and then backward. Three successive seesaws occurred without a halt and without any crushing by the buccal jaws. The food was then grasped by the pharyngeal jaws and transported into the oesophagus in three movements. A 7-cm worm was treated in the same way but it took seven movements to convey it to the oesophagus.

A 6-cm worm was drawn in. One end was seized by the pharyngeal jaws while the other remained grasped between the buccal jaws. After an unsuccessful attempt at transport, the worm was thrown back outside, sucked in again, grasped again by the pharyngeal jaws, and brought into the oesophagus in eight transport movements.

Three other seizings of a worm can be described as mixtures of the above sequences. In no case was the earthworm divided before entering the oesophagus.

FISH

The fish is sucked directly tail first into the buccal cavity (all cases). After a while, it is grasped by the pharyngeal jaws and transported whole into the oesophagus in nine to 11 movements.

Discussion

BUCCAL PARTS

One of the most significant improvements in the Acanthopterygei is upper jaw protrusion. During feeding, protrusion often accompanies opening of the mouth. The buccal skeletal transformations associated, in the course of evolution, with the tremendous adaptive radiation of the acanthopterygians may seem slight: minor changes in shape and proportion, differing insertions, division into bundles of some muscles, the presence or absence of certain ligaments. Such modifications, however, can greatly affect the degree of protrusion or even its setting in motion. In some cases protrusion seems to result solely from the lowering of the mandible (Liem, 1970). In other fishes, it appears to be caused by axial rotation of the maxilla, pushing the premaxilla forward (Alexander, 1967). It may sometimes be produced by neurocranial elevation (Liem, 1979). Protrusion is very slight in Blenniidae (Vandewalle *et al*., 1982) and very great in the labrid *Epibulus insidiator* (Pallas, 1770) which additionally possesses a movable quadrate enabling the mandible to protrude as well (Weastneat & Wainwright, 1989). Slight protruders most often grasp food before sucking it in while in *E. insidiator*, sucking is very powerful, as in most acanthopterygians, and the buccal jaws barely touch the food or not at all (Alexander, 1967; Osse, 1969; Lauder, 1980).

In acanthopterygians generally, the premaxillae are equipped with a processus ascendens and surmounted by the maxillae which support the palatines. The maxillae are bound to the mandible by ligament Li 4 and the premaxillae are surmounted by ligament Li 1 which links the left and right maxillae and/or palatines (Anker, 1974, 1978, 1987; Liem, 1981; Motta, 1984).

The premaxillae and the dentaries are often linked by short fibres. These allow modulation of the shape of the mouth, which becomes nearly circular when opened (Osse & Müller, 1980).

The adductores mandibulae are the most variable muscles. In *Blennius pholis* (Linné, 1758) they are so highly developed that they insert dorsally to the midline of the skull (Vandewalle *et al.*, 1982). In *Serranus scriba* (Linné, 1758) they are more slender (Benmouna *et al.*, 1984). *B. pholis* grubs up its food before sucking it in, a process that requires powerful muscles, while *S. scriba* sucks its food in directly.

In *D. sargus*, the dentaries and premaxillaries are thick and bound tightly together via broad contact areas and very short ligaments. The left and right maxillae are almost in contact below the processus ascendentes of the premaxillae. The maxillae overlap the premaxillae in two regions. The quadrato-mandibular joints are very well developed. Cohesion of the buccal bones is further reinforced by numerous ligaments.

With the buccal bones are associated powerful adductor muscles. The first three bundles are remarkable: each is in direct relation with both the upper and lower jaws so that contraction of any one muscle affects the whole buccal apparatus. This is not so in many acanthopterygians, where individual muscle functions are less imbricated because A1 inserts on the maxilla and the other adductores on the mandible. In *Diplodus sargus*, the upper and lower jaws close the mouth in the same way, whichever adductor may be contracting. This mouth closure pattern associated with the cohesion of the buccal skeleton seems to be 'designed' for crushing prey. Moreover, the very anterior insertion of A2 in the angulo-dentary cavity results in its action on both mandibular bones. In this crushing device, the role of the incisors could be to cut or break prey while the molars crush them, a behaviour observed in *D. sargus* towards snails and crabs. The smaller molars equipped with a central cuspid might produce cracks in carapaces and the larger ones crush them.

Despite the stiffness of the jaws, the left and right upper and lower jaws are not fused together, so that some relative motion is possible. The intermandibular and Aω adductor probably control these minute movements. The intermandibular could tighten the binding of the half-mandibles in order to increase the pressure on the prey, while Aω could draw them apart, a process previously suggested for other fishes (Vandewalle, 1972). However slight, such movements are very important in processing preys.

The musculo-skeletal apparatus of *D. sargus* is probably incapable of mouth movements such as described by Liem (1978, 1980) for cichlids. The latter fishes can distinctly direct the mouth to the left or right (Liem, 1980), keep the mouth closed while protrusion is still great (Liem, 1978), or even protrude the mouth at any time during opening or closing (Liem, 1980). Such movements were not observed in *D. sargus*, although the latter can surely protrude the mouth considerably during mouth opening. This could be guessed from the morphology of the premaxillae, with their large processus ascendentes, and is confirmed by observation of buccal movements. Even the amplitude of protrusion can be modulated. In *D. sargus* as in *E. insidiator* (according to Westneat & Wainwright, 1989) protrusion always accompanies mouth opening during prey catching. In the cichlid *Eretmodus cyanostictus* Boulenger, 1898 protrusion is delayed with respect to mouth opening (Liem, 1979). In other species, protrusion begins at the same time as mouth opening but ends after buccal closure (Liem, 1970; Elshoud-Oldenhave & Osse, 1976).

Cranial elevation may or may not occur when *D. sargus* opens its mouth. It can even be sustained during mouth closure. When measurable, neurocranial elevation ranges from 3 to 10 degrees, a finding congruent with Osse's observations (1976) on *Gymnocephalus cernua* (Linné, 1758) and Liem's observations (1979) on *E. cyanostictus*.

The inconstancy of cranial elevation during food capture suggests that this phenomenon does not directly affect the mouth movements or protrusion as in the cichlids *Spatodus erythrodon* Boulenger, 1901 and *Petrotilapia tridentiger* Trewawas, 1935 (after Liem, 1979, 1980). Nor, it seems, is protrusion produced by axial rotation of the maxilla as proposed by Alexander (1967). The maxilla is indeed held in a groove of the premaxilla, so that its ability to rotate axially is severely restricted. Mandible lowering is thus most probably the principal cause of buccal protrusion in *Diplodus sargus*, as in nandids (Liem, 1970).

During food aspiration, the time required to open and close the mouth is about 100 ms for *Stizostedion lucioperca* (Linné, 1758) (according to Elshoud-Oldenhave, 1979) and *Serranochromis robusta* (Gunther, 1864) (according to Liem, 1978), 125 ms for *G. cernua* (after Elshoud-Oldenhave & Osse, 1976), 300 to 400 ms for *E. cyanostictus* (after Liem, 1979), and 80 to 120 ms in three *Lepomis* species, depending on whether the prey is a fish or a worm (Lauder, 1980). The duration of the movements of the mouth is about 200 ms in *E. cyanosticus* in the case of tearing away a leg of a locust, but their amplitude is distinctly less than during suction (Liem, 1979). In *G. cernua*, the amplitude of these movements is also much less for seizing a worm on the bottom than for catching a fish in the open water (Elshoud-Oldenhave & Osse, 1976). Some variation is thus seen among acanthopterygians in the movements of the mouth during food catching. *D. sargus* is in no way special in its sucking and seizing movements: the duration of the mouth movements varies from 150 to 250 ms whatever the sort of prey. It is the same for shifting a prey from the buccal to the pharyngeal jaws or for bringing it forward. In the case of crushing, two types of buccal movement can readily be distinguished. One type consists of numerous, very fast (sometimes lasting less than 75 ms), and usually rather ample movements which probably require the working of many cephalic muscles. The second type consists of less frequent, slower, much less ample movements (lasting about 350 ms) (**Fig. 12**). To close the mouth, all the adductores mandibulae plus the intermandibular are probably recruited while a slight opening could result simply from prey elasticity. Lastly, when a piece of the prey is ejected from the posterior part of the mouth, the buccal movements are ample but relatively slow.

THE PHARYNGEAL BONES

The major evolutionary trend of the pharyngeal system in the acanthopterygians is the transformation from the complex structure of the Pristolepidae and Nandidae to the simplified architecture of the Cichlidae and Embiotocidae (Liem & Greenwood, 1981). In the former, the slender and independent fifth ceratobranchials are opposed to small pharyngobranchials hanging from the neurocranium; all these parts are toothed and there are additional toothed plates, the basihyal and third hypobranchials facing the parasphenoid. In the latter, the only toothed pieces are the fused fifth ceratobranchials facing the upper pharyngeal jaws articulating with the skull. The upper pharyngeal jaws consist of the left and right pharyngobranchials tightly fastened to one another and each followed by a posterior toothed plate. This simplification process is complete in the labrids and scarids, where the fused fifth ceratobranchials, articulating with the pectoral girdle, are opposed only to the third pharyngobranchials connected by joints to the neural skull (Liem & Greenwood, 1981).

The serranids occupy an intermediate position in this simplified scheme (Comes *et al.*, 1988; Vandewalle *et al.*, 1992). They have no teeth on the basihyal, the hypobranchials or the parasphenoid. The lower pharyngeal jaws are bound together anteriorly while the upper pharyngeal jaws hang from the neurocranium by the first pharyngobranchials and the levatores branchiales muscles as in nandids. Each consists principally of a posterior toothed plate and of second and third pharyngobranchials which are less developed than in cichlids and embiotocids (Liem & Greenwood, 1981).

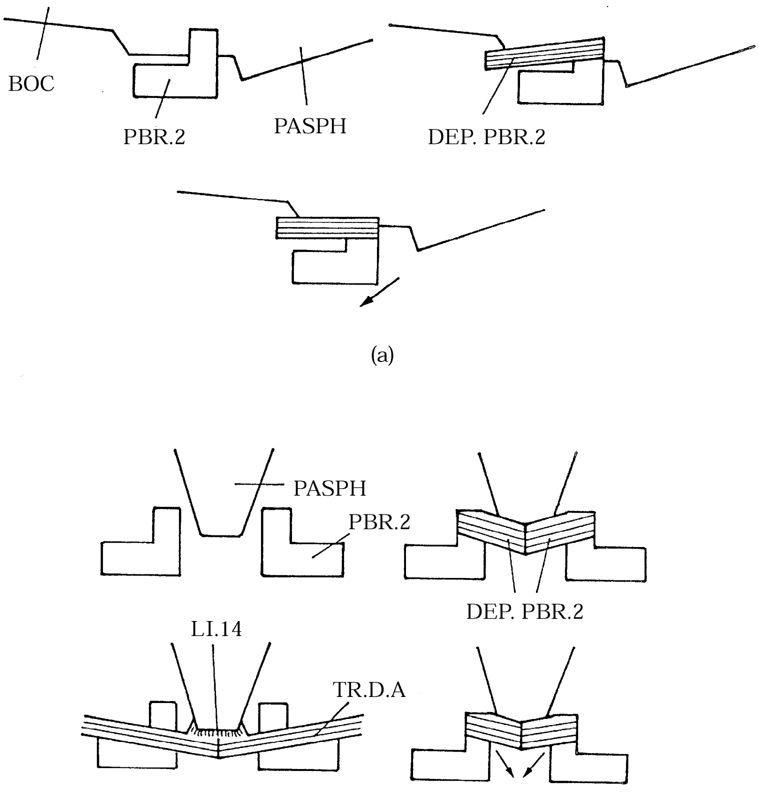
The skeletal organization of *D. sargus* closely resembles that of the serranids. The originality lies, in addition to hanging by the first pharyngo-branchials and levatores branchiales, in that there is a fibrous pad binding the parasphenoid to the dorsal muscles of the branchial basket. The pad probably restricts the freedom and motion of the upper pharyngeal jaws as compared to those of serranids, but differently than would a true joint. The comparison of the horizontal and vertical components of the displacement of the upper pharyngeal jaws in a 14 cm standard length *Serranus scriba* and a 13·7 cm standard length *D. sargus* show a clear difference: 2·4 and 2·8 mm for the serranid (Vandewalle, 1992) and only 1·4 and 1·4 mm for *D. sargus*.

The pharyngeal musculature is fairly constant in acanthopterygians (Winterbottom, 1974) including *D. sargus*. The principal differences among acanthopterygians concern muscle volume, length, and orientation, often related to the way of life (Liem & Greenwood, 1981; Barel, 1983; Gobalet, 1989), and the subdivision of muscles into bundles. The number of transversi dorsales varies from one to three (Winterbottom, 1974). Insertions also vary: the levator posterior inserts into the fourth epibranchial in *D. sargus*, but into the fifth epibranchial in other species (Yamaoka, 1978); in *S. scriba*, it is partly fused with the fifth adductor and the fourth levator externus (Vandewalle *et al.*, 1992).

In different fish some muscles may or may not be present. Sometimes certain muscles are fused. *D. sargus* has no obliquus posterior while this muscle is present in *S. scriba* (according to Vandewalle *et al.*, 1992) and in cichlids (Kaufman & Liem, 1982). In pomacentrids, it is almost completely fused with the obliquus dorsalis of the fourth arch (Lauder & Liem, 1983). No adductor was observed on the first three branchial arches of *D. sargus* while other species have one on each arch.

The main originality of the musculature of *D. sargus* is the 'depressor of the second pharyngobranchial' which is absent from Winterbottom's (1974) exhaustive list of the striated muscles of teleosts and which seems never to have been described previously. Contraction of this muscle could draw the second pharyngobranchials (**Fig. 18**) backward, downward, and to the midline and thus contribute to food handling by the upper pharyngeal jaws.

Fig. 18. *Diplodus sargus*. Schemas explaining the supposed role of the depressores muscles of the 2nd pharyngobranchials, lateral (a) and posterior (b) views. BOC, Basioccipital; DEP PBR 2, depressor to the 2nd pharyngobranchials; LI 14, fibrous pad between the parasphenoid and the superior central part of the branchial basket; PASPH, parasphenoid; PBR 2, 2nd pharyngo-branchial; TR D A, transversus dorsalis anterior.



(a)

(b)

The movements of the pharyngeal jaws have previously been described for several acanthopterygian species by Lauder (1983*a*,*b*), Liem (1986), Liem & Sanderson (1986), Aerts *et al.* (1986), Claes & De Vree (1991), Vandewalle *et al.* (1992). All are cyclic movements resulting from successive, ordered contractions of different muscles of the branchial basket (Liem, 1978, 1986; Lauder, 1983*a*,*b*; Liem & Sanderson, 1986; Claes & De Vree, 1989). Also in *D. sargus*, the movements of the upper pharyngeal jaws are approximately elliptical, elongated antero-posteriorly, and clockwise when observed from the right side. These gyrations may result from successive contractions of the levatores branchiales followed by contraction of the retractores dorsales. When observable, the movements of lower pharyngeal jaws are irregular, horizontal, vertical or elliptical (clockwise or trigonometric). The horizontal displacements certainly result mainly from contraction of the geniohyoidei followed by the pharyngocleithrales externi.

Seen laterally, the movements of the left and right upper pharyngeal jaws are not always identical. Such differences have been pointed out previously by Claes & De Vree (1989) and Vandewalle *et al.* (1992). These authors also mention occasional asymmetrical lateral movements, for example in *S. scriba*. Such laterally asymmetrical movements were observed in *D. sargus* only when it was processing a *Lymnaea.* Vandewalle *et al.* described in *S. scriba* individual displacements of the various elements of the upper pharyngeal jaws. Such displacements are possible in *D. sargus* too, since both species have a very similar arrangement of the upper pharyngeal jaws.

As the anatomical disposition of the upper pharyngeal jaws and of the obliquus dorsalis and levator posterior muscles, the mechanism of the depression of upper pharyngeal laws proposed by Wainwright (1989*a*,*b*) in haemulids is maybe the same for *D. sargus* as well.

FEEDING BEHAVIOUR

In acanthopterygians, suction feeding is the most widespread system (Alexander, 1967; Osse, 1969; Liem, 1970; Elshould-Oldenhave & Osse, 1976; Elshoud-Oldenhave, 1979; Lauder, 1980). Bulky prey, however, may be seized by the buccal jaws and progressively drawn backward to the oesophagus (Liem, 1970). Buccal suction movements, furthermore, may vary somewhat according to whether the prey is seized on the bottom or in open water (Elshoud-Oldenhave & Osse, 1976) or depending on the sort of prey (Liem, 1979; Lauder, 1980). But in most cases, variations in feeding behaviour concern the pharyngeal jaws.

Lauder (1983*a*,*b*) has shown that in so-called primitive acanthopterygians (Centrarchidae), the upper and lower pharyngeal jaws aroused only for food transport, performing elliptical movements, generally in phase with the anteroposterior direction. In *S. scriba* also, the pharyngeal jaws are used for food transport only, but progression of the prey results from a wide variety of different pharyngeal movements, necessarily comprising a backward displacement of one of the pharyngeal jaws (Vandewalle *et al.*, 1992). Variations in the transport mechanism seem to be independent of the sort of prey. *S. scriba* does not easily swallow prey without a carapace.

In more advanced acanthopterygians, the pharyngeal jaws transport and process food (Liem, 1978, 1986; Liem & Sanderson, 1986; Aerts *et al.*, 1986; Claes & De Vree, 1991). In cichlids, embiotocids, and labrids, Liem (1973, 1978, 1986) and Liem & Sanderson (1986) have described two seemingly stereotyped sets of pharyngeal movements: chewing movements in the shape of a figure eight and elliptical deglutition cycles. Upper and lower pharyngeal jaws are described as being in phase, contrary to the observations of Aerts *et al.* (1986) on the cichlid *Oreochromis niloticus* (Linné, 1758). Claes & De Vree (1991) have shown that the pharyngeal behaviour of this species changes according to the nature of the prey.

In *D. sargus*, different stages are distinguishable in feeding: sucking in, seizing by the buccal pieces, buccal crushing, backward shifting from the buccal cavity, bringing back to the mouth, rejecting outside, transport by the pharyngeal jaws. Except for buccal crushing, the movements composing each stage are similar whatever the food. Some stages, however, are not observed with all types of prey and with some prey certain stages may be repeated.

All types of food are sucked in. Then hard prey are always stopped by the buccal jaws. Prey with a supple carapace are stopped less often. Prey without a carapace are never stopped and directly reach the pharyngeal jaws. These differences in the handling of prey are probably related to the sensory (visual?) perception of the food before and during capture.

The carapace of crabs is hard but somewhat supple, probably requiring numerous fast or slow crushings which cease only when the prey is dislocated enough (often into at least two parts) to allow easy digestion.

In the case of a *Lymnaea* equipped with a non-supple shell, crushing is usually immediate. It is performed by the incisors which exert pressure on a pinpoint surface of the shell and break it. This is followed by rejection of at least most of the shell. In the molluscivorous cichlids, shell pieces are also rejected (Hoogerhoud, 1987); this lightens the fish and avoids the need for a larger swimbladder and thus for a larger abdominal cavity (Hoogerhoud, 1987). Although the dentition of cichlids is peculiar, whether crushing is performed by the buccal or the pharyngeal jaws has not been reported. The shell of a *Bithynia* is harder than that of *Lymnaea. D. sargus* can hardly crush it, so it will usually be rejected.

The movements of the buccal pieces toward a shrimp abdomen with its cuticle are unpredictable and the results of crushing are variable.

Crushing movements apparently cease while the pharyngeal jaws are working. Buccal and pharyngeal jaws are linked by geniohyoidei muscles, hyoidean bars and branchial arches. Displacements of anterior jaws may move the others or affect their movements. Efficient activity probably needs very precise movements and consequently the cephalic structures and especially the buccal jaws remain motionless or almost so.

Grasping by the pharyngeal jaws probably depends on various factors such as the position or hardness of the prey. All prey with teguments are easily seized and transported to the oesophagus. Prey without a tegument, such as a peeled shrimp abdomen or a shell-less *Lymnaea* are seized and transported with diffculty. Soft tissues are grasped by the sharp teeth and the movements of the pharyngeal jaws are hardly able to unhook them. Sometimes the fish must resort to ejecting the prey. More often the prey only seesaws one or several times between the pharyngeal and buccal jaws. Drucker & Jensen (1991) described a somewhat similar but faster movement during winnowing (separating food from debris) in embiotocids. With all prey but *Lymnaea*, the pharyngeal jaws do nothing but convey the prey to the oesophagus as in *S. scriba* (after Vandewalle *et al.*, 1992). With *Lymnaea* they were twice seen to break the shell and several times to cut the prey into two pieces during its shifting to the oesophagus. It is hard to judge whether this behaviour toward *Lymnaea* actually contributes to processing the prey and hence whether it constitutes progress with respect to primitive acanthopterygians.

In primitive teleosts (for example in *Esox lucius* L.), the lower pharyngeal jaws dominate food transport movements (Lauder, 1983*a*). In lower acanthopterygians, food transport is performed principally by the upper pharyngeal jaws (Lauder, 1983*b*; Wainwright, 1989*a,b*; Vandewalle *et al.*, 1993). That shifting of the function to the upper pharyngeal jaws is to be related to the development of the retractor dorsalis and of the ensemble of the levatores externi III and IV. Gallis (1993) highlights the importance of the development and fibres orientation of the retractor dorsalis in the feeding behaviour of the advanced acanthopterygian *Haplochromis piceatus*. At the very moment *D. sargus* seizes its prey, the upper pharyngeal jaws are placed antero-dorsally and the lower ones postero-ventrally. Once seized, the prey is brought to the oesophagus by rotational movements of the upper pharyngeal jaws principally. In labrids, the role of the lower pharyngeal jaws is probably more prominent because they remain more movable than the upper pharyngeal jaws. The lower pharyngeal jaws seem to be particularly efficient in transport and mastication thanks to their articulation on the pectoral girdle and to the large size of the levator posterior and levator externus 4 (Yamaoka, 1978; Liem & Greenwood, 1981; Liem & Sanderson, 1986; Stiassny & Jensen, 1987).

The importance of the upper pharyngeal jaws in feeding in *D. sargus* fully justifies the backward orientation of the teeth borne by the second pharyngo-branchials. The inwardly turned teeth of the third pharyngobranchials may additionally perforate certain soft tegments. They are perfectly opposed to the teeth of the lower pharyngeal jaws. The horizontal movements of the upper and lower pharyngeal jaws are performed in opposite directions, so that the arrangements of the teeth should favour tearing of the prey. The only prey seen to be transformed by the pharyngeal jaws is *Lymnaea*, which does not mean that other prey remain intact. While the orientation of the teeth of the lower pharyngeal jaws seems justified, it is hard to explain their arrangement in rows with increasing size from the outer to the inner row.

The problem of the temporal and functional relations between the movements of the buccal and pharyngeal jaws was apparently never discussed previously for acanthopterygians. It is clear that in all the observed feeding behaviour in *D. sargus*, no constant relation exists between buccal and pharyngeal jaw displacements.

Mouth opening associated to feeding always comprises protrusion, the amplitude and the timing of which varies considerably. When food lies between the buccal jaws, two types of reduction are observed, either slow 'crushing' movements or repeated fast 'hammering' movements.

As formerly demonstrated, the pharyngeal jaws of *D. sargus* can move in any direction, even asymmetrically as in *S. scriba* (Vandewalle *et al.*, 1992). All the observed movements followed more or less elliptical three-dimensional curves. These movements are not cyclical since the bones do not pass regularly by the same position. It is impossible to separate any type of movement of the pharyngeal jaws on a purely cinematical basis. However, movements can be separated on the basis of their biological result: transport, rejection and deglutition.

Conclusion

The food handling apparatus of sparids displays an original pattern of specialization toward a wide diet spectrum including shells. Instead of specializations of the pharyngeal jaws apparatus as in labrids and cichlids, they have developed different types of teeth (incisiform, molariform) and many particularities in the anterior jaws. Among perciforms they have elaborated an alternative food reduction pattern in conjunction with the buccal jaws own adaptive transformations. As not all perciform families have yet been investigated, it may be expected that other motor patterns and morphological transformations of the buccal and pharyngeal jaws will be described in future.

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