

# SUCTION FEEDING STRATEGIES OF TWO SPECIES OF MEDITERRANEAN SERRANIDAE (*SERRANUS CABRILLA* AND *SERRANUS SCRIBA*)

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## ABSTRACT

A comparative study of the suction feeding strategies in *Serranus cabrilla* and *Serranus scriba* was carried out. Several specimens from both species were filmed at high speed. From these films, kinetics of the suction movements and dynamic parameters, such as volume increase/time, were calculated. A simulation model of the hydrodynamics of suction feeding was used to calculate velocities, accelerations and pressure waves. Simulation results are within the range of those previously found with experimental methods for other species. The results showed that feeding strategies are different. *S. cabrilla* is feeding as from an ambush, with a sudden big head expansion whereas *S. scriba* expands its head more gradually. The gradual increase could be related to a feeding mode in which an important component of the feeding flow is contributed to swimming. These differences are discussed in the context of the ecology of the species.

## INTRODUCTION

In the last twenty years, an extensive literature on teleostean feeding mechanisms has been produced. Papers deal with different but strongly interrelated aspects of feeding, *e.g.*, the sequence of muscle activity, kinematics, bucco-pharyngeal pressures and hydrodynamics. Several comprehensive articles reviewing the subject are available (see for instance, Osse, 1969; Lauder, 1983, 1985; Muller *et al.*, 1982; Muller & OSSE, 1984; OSSE *et al.*, 1985; Aerts, 1990).

We can safely assume that evolutionary changes in head morphology are a reflection of modifications of the predatory feeding function in different actinopterigian fishes (Schaeffer & Rosen, 1961). Teleostean suction feeding can essentially be represented as a model of head expansion and flow. The details of the mechanism have been largely modified, however, by different ecological demands. Closely related species may have very similar morphologies and

distributions and may have roughly similar food preferences. Nevertheless, they may have developed specific adaptations with respect to different strategies of prey capture (see Casinos, 1978;1981 for an example). The term ecomorphology has been used to indicate studies which elaborate on such situations (Alexander, 1988; Barel, 1983; Bock, 1990).

Serranidae have a wide distribution in tropical and subtropical sea waters, including the Mediterranean basin. In the latter, the genus *Serranus* is represented by four species. Two of them, the comber (*Serranus cabrilla* (Linné, 1758)) and the painted comber (*Serranus scriba* (Linné, 1758)) are, in spite of their differences in coloration, very similar in many respects. They use to share the same coastal waters and it is possible to see them at the same rock-wall, although their preferential habitats are somewhat different. *Serranus scriba* prefers to live close to *Posidonia* and other marine fields of Phanerogams (the eel grass, *Zostera* sp.), while *Serranus cabrilla* lives mainly among the cavities and spaces produced by fallen rock (field observation data), and also between Phanerogam fields. Both species can be found at similar depths (from 5 to 20 m), but *Serranus cabrilla* also occurs in deeper waters (40 m, Bruslé & Bruslé, 1975). They show territorial and non gregarious behaviour, often trying to capture similar prey. The stomach contents of several specimens of *Serranus scriba* (Robins & Starck, 1961) show that this species catches mainly mobile preys. No adequate information is available specifically on *S. cabrilla* preferences from the point of view of prey mobility. Both species are synchronic hermaphrodites and their reproduction takes place during the same summer months (Robins & Starck, 1961; Bruslé & Bruslé, 1975). The external and internal morphology and the size of the two species are very similar (B ENMOUNA *et al.*, 1983, 1984a, 1984b). The main quantitative structural differences are found in the mobile parts of the splanchnocranium: (1) the suspensorium is longer in *Serranus scriba*, (2) the hyomandibula is more massive and its posterior joint on the skull is longer in *Serranus scriba*, (3) the processus ascendens of the premaxillae is shorter while the angle between the two arms is larger in *Serranus cabrilla*, (4) the adductores mandibulae, levator hyomandibulae, levator arcus palatini and sternohyoideus muscles are broader and longer in *Serranus scriba*. Some other aspects of the head morphology and timing of feeding of *Serranus scriba* and *Serranus cabrilla* have been dealt with elsewhere (Benmouna *et al.*, 1986, 1989; Vandewalle *et al.*, 1992). The aim of the present paper is to characterize in both serranid species similarities and differences in feeding behaviour and feeding biomechanics, in order to try to explain some of their specializations in cephalic morphology.

## MATERIAL AND METHODS

The specimens studied were captured in the wild from different places of the Western Mediterranean (Corsica and Catalonia). They were trained during several weeks to feed both on the same prey items consisting of pieces (about 5-10 mm long) of fresh shrimps and small fishes under conditions needed for filming. Filming conditions involved a high level of illumination, restricted, but sufficient space for swimming movements, and the presence of a mirror below the fish, placed at an angle of 45 °. This mirror permitted to record both lateral and ventral views.

Animals were filmed with a Photosonics 1PL high speed 16 mm camera at speeds of 100 and 200 frames per second, using a continuous light source of 2 kW. This protocol was considered a reasonable compromise between filming requirements and experimental stress. Films were analyzed with a L-W International high-speed projector.

The feeding action from seven specimens of each species was recorded. Films were used to calculate time differences in the sequence of movements related to prey intake. These data, in graphic form, show how the velocity of mouth opening and the expansion of the buccal cavity is related to the time of prey passage, in the sense of Muller & Osse (1984).

The most representative sequences of each species, performing all movements in a way which enabled a thorough analysis, were selected. This selection included sequences where the fish was in a completely parasagittal view, catching the prey before it arrived at the bottom. In order to characterize the feeding action of each species from these sequences, an average typological feeding action was made, trying to obtain a mean pattern in velocity and acceleration. All the measurements were scaled to body length, to avoid size variability of different animals (see figure 1). Measurements were repeated three times and, although the same errors could be made, a rough analysis showed they were negligible.

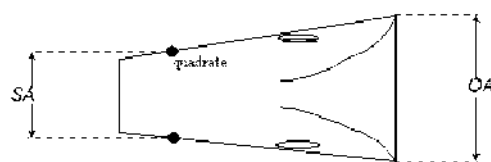
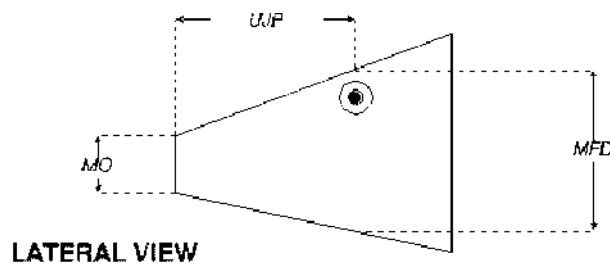
Changes in head volume were calculated by means of the ellipse method (Drost & VAN DEN Boogart, 1986), using an X-Y tablet connected to a personal computer to digitize the coordinates of the ellipse radii and to perform the calculations. As stated by Drost & van den Boogart (1986) a 5-10% error is possible, depending on the form of the object and the perpendicularity of the views. A large part of the error is systematic. Systematic errors in the experimental conditions of this research will be standard for both species due to their similarity (see above). The ellipse model is an extremely comprehensive and relatively easy model. The most important sources of error are the choices of a line defining the limits of the opercular and branchiostegal valve apertures and the assumption that the cross-sectional area of the head of the fish approaches the shape of an ellipse.

The feeding action was simulated by visualizing the fish head as an expanding truncated cone pointing anteriorly, in which the surface increase of the gape, the length, the diameter increase at the level of the opercula, and the time course of these moments were used to calculate velocities, accelerations and pressures of the flow during feeding (Muller & Osse, 1984). Accelerations of water and pressure peaks as a function of time were calculated by means of the hydrodynamical model of suction feeding described by Muller *et al.* (1982). They were obtained from dynamic simulations at the snout level. The program with which the simulations were made was written by P. Aerts for MS-DOS-computers and later modified by C.V. This modified program calculated an adjusted curve for the gape and opercular movement by minimum-squares approximation. The input data were measured from the films by means of an X-Y tablet. Small errors in position may produce large errors in the calculated accelerations and these deviations are still more important in calculated pressures. It can however be expected that such errors will be similar for both two species compared in this paper, as quoted above.

The initial gape movement was used as the reference point of the other movements. The parameters derived from the films were: time and amount of mouth opening; jaw protrusion; mouth floor depression; suspensorial abduction; opercular opening; volume increase of the buccal and opercular cavities in time, and time of opening of the opercular valve.

**Fig. 1.** Movements or measurements, units and indices used in this study.

MOVEMENT	or	UNIT	INDEX USED
MEASUREMENT			
body mass (BM)		g	directly
body length (BL)		cm	directly
mouth opening (MO)		cm	MO/BL
upper jaw protrusion (UIP)		cm	UIP/BL
mouth floor depression (MFD)		cm	MFD/BL
suspensorium abduction (SA)		cm	SA/BL
opercular abduction (OA)		cm	OA/BL
volume (V)		cc	(V/BM)*100



The centre of the eye was used as a point of reference to measure the protrusion and the mouth floor depression. Suspensorial abduction was measured as the distance between left and right quadrate bone.

## RESULTS

The results are shown separately for each of the parameters studied.

### SNAPPING EFFICACY

A good parameter to characterize feeding in different species is to compare the timing of opening and closing of the mouth and the opercular valves together with the moment of prey intake for successful and unsuccessful snaps. We considered the total time as the period between the starting point of the mouth opening and the final moment of the opercular valve closure.

Table 1 shows differences in mouth closing time, moment of opening of the opercular valve and total time between *Serranus scriba* and *Serranus cabrilla*. Results show that all the suction movements are faster in *S. cabrilla* than in *S. scriba* : in the first case the average is about 120 ms, whilst it is about 190 ms for the latter species. When total time is compared by means of an

ANOVA test, notwithstanding the small number of observations, they appeared as statistically different ( $p < 0.05$ ).

In *S. cabrilla* the start of opercular opening coincides with buccal closing time but in *S. scriba* it does not. In the latter species the opercular opening started before the closure of the mouth (about 25 ms before on average) in three cases and in one case there was a small delay between the opening (105 ms) of the opercular valve and the mouth closing (100 ms).

**Table 1.** Times of the feeding actions of the different sequences analysed.

Species	Mouth closing time (ms)	Moment of opening of the opercular valve (ms)	Total time (ms)
<i>S. cabrilla</i>	85	85	125
<i>S. cabrilla</i>	25	25	75
<i>S. cabrilla</i>	145	145	195
<i>S. cabrilla</i>	30	30	80
<i>S. cabrilla</i>	50	50	120
<i>S. cabrilla</i>	40	40	100
<i>S. cabrilla</i>	50	50	170
<i>S. scriba</i>	120	95	170
<i>S. scriba</i>	195	140	245
<i>S. scriba</i>	100	105	160
<i>S. scriba</i>	70	50	190
Means:			
<i>S. cabrilla</i>	42.5	42.5	117.5
<i>S. scriba</i>	121.25	97.50	191.25

Time is 0 ms at the moment of jaw opening. Different times correspond to different specimens. See text for further explanation.

## APPROACHING THE PREY

In *S. scriba* the swimming movement towards the prey starts at a large distance and only when the prey is very close to the fish, the suction feeding act starts. In *S. cabrilla*, the action is different: there is no real pursuit of the prey. The prey is slowly followed until a short distance to the prey is reached. At that moment, swimming speed increases simultaneously with the suction feeding action to capture the prey. *S. scriba* starts suction at a distance approximately three times larger than *S. cabrilla*.

## KINETICS

The measurements are explained in figure 1. Figure 2 shows the relative timing of the most relevant movements (relative to body length) during the feeding process for each species, using the indices shown previously. The movement of each structure is analyzed separately.

**Mouth opening:** The opening process is faster in *S. cabrilla* than in *S. scriba*. Nevertheless, the steep slopes of the closing of the mouth are similar in both species as shown in the plot. In *S. cabrilla*, the maximum gape is about 30% larger than in *S. scriba*.

**Upper jaw protrusion:** This movement is more variable. Compared to the previous movement, a long retained protrusion after jaw closure can be assumed in *S. cabrilla*, whilst this is absent in *S. scriba*. The maximum protrusion is achieved at the same time the mouth floor arrives at its

deepest point in both species. Moreover, in *S. scribea*, the protrusion movement reaches a minimum value at the end of the movement, which is below the starting level. In *S. cabrilla* the start and end values are similar. Protrusion to lengthen the reach of the predator is more important in *S. cabrilla* than in *S. scribea*, as shown in figure 2.

Mouth floor depression: This movement develops faster in *S. cabrilla*, but in *S. scribea* the depression continues longer and the floor of the mouth returns to one half of its initial position, followed by a second and less important excursion coinciding with the final part of the feeding act. The amplitude of the movement of the mouth floor depression is similar in both species.

Suspensorium abduction: Abduction was measured as the lateral displacement of the quadrate. The suspensoria abduct earlier in *S. cabrilla* than in *S. scribea*. In the latter species some early movements are probably present previous to the complete abduction. The return movement to the starting point differs considerably, being slower in *S. scribea*. The amplitude of suspensorium abduction is larger in *S. scribea* than in *S. cabrilla*.

Opercular abduction: This movement starts at least 40 ms later in *S. scribea* than in *S. cabrilla*, although plots (see figure 2) show a similar pattern in both species. The maximum excursion is somewhat bigger in *S. cabrilla*, while the slopes before and after this point are very similar in both species.

## DYNAMICS

In spite of unavoidable errors of the ellipse method such calculations provide a proper approximation of the changes of volume in the head of the fishes during suction feeding.

Volume increase: figure 3 shows the volume increase of the buccal cavity plus the opercular cavity against time, during suction feeding in both species. In *S. cabrilla* volume increase is faster and considerably (about 50 ms on average) earlier than in *S. scribea* and also returns earlier to the starting value. In the former species, the volume peak is achieved in almost half the time of the latter, in which half of the maximum volume increase is still present when the opercular valve already opens up. The *S. scribea* curve also shows a small early peak, which may be related to some early suspensoria and mouth floor movements. Something similar happens in the perch: some suspensorial adduction takes place before the real abduction movement, as described by OSSE (1969).

In spite of the differences in the timing of the movement of the morphological units, the volume variation is similar in both species, taking into account the early reduction of volume in *S. scribea*. The maximum volume increase reached in *S. cabrilla* is larger than that in *S. scribea*.

Velocities, accelerations and mouth pressures: Calculations of water velocity (permitting the calculation of accelerations and pressure variations) at the snout level, were done by computer simulation every  $46 \times 10^{-4}$  seconds for *Serranus cabrilla* and every  $96 \times 10^{-4}$  seconds for *Serranus scribea*, depending upon the movement time. Results of these simulations in both species are shown in figure 3.

In almost 20 ms, the velocity of the water entering the mouth of *S. cabrilla* reaches a value of up to  $-8 \text{ m}\cdot\text{s}^{-1}$  (the minus sign is only a convention, meaning water is going in). Quickly, the water velocity falls to  $-2 \text{ m}\cdot\text{s}^{-1}$ , and is accelerated again to a new minimum of almost  $-4 \text{ m}\cdot\text{s}^{-1}$ . Then,

water velocity is annulled (about 100 ms after the start of the movement) and very fast it arrives to a value of  $4 \text{ m} \cdot \text{s}^{-1}$ , indicating that water is going out of the oropharyngeal cavity.

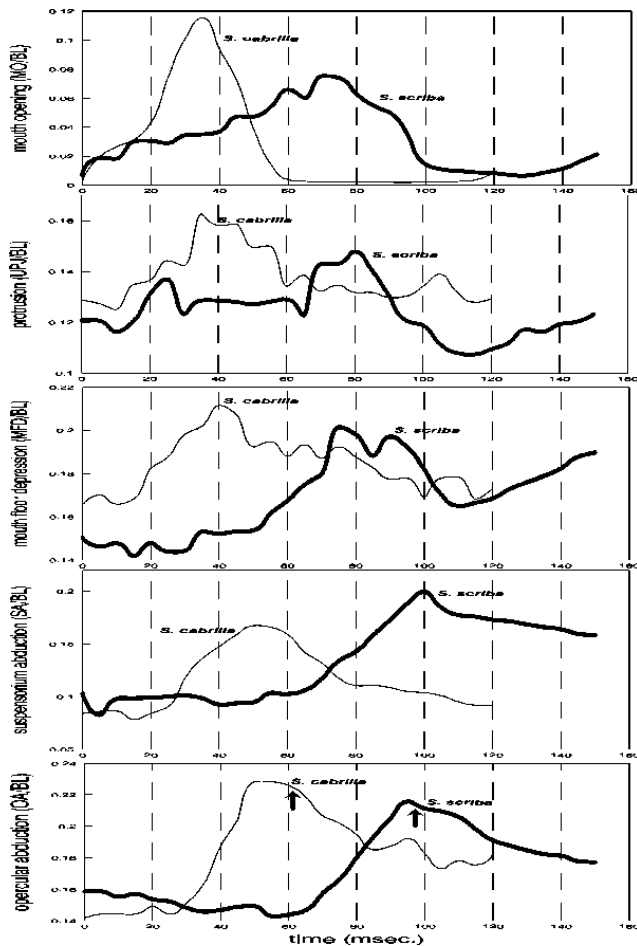
The maximum water velocity ( $-4 \text{ m} \cdot \text{s}^{-1}$ ) for *S. scriba* is only about a half of that found for *S. cabrilla*. From this moment on, it decreases slowly until almost 0 (at about 90 ms). A second and smaller acceleration takes place later ( $-2 \text{ m} \cdot \text{s}^{-1}$ ), to be annulled quickly and the water out flow through the gills starts. The feeding action in *S. scriba* takes about 30 ms longer than in *S. cabrilla*.

As expected both outlines of the pressure graphs closely follow the velocity patterns seen above. *S. cabrilla* shows two successive pressure drops, with values of approximately - 14 kPa and - 7 kPa, which coincide with both accelerations described above (about 75 ms for acceleration and 70 ms for pressure). This small difference may reflect the real situation or a standard error of measurement. The outflow of water may be due to the positive pressure of less than 4 kPa. There is a very small positive peak between both negative peaks, which could be due to the fact that the opercular valve is still closed and that the fish approaching the prey creates a pushing effect. The graph finishes with another positive peak, higher than 4 kPa, which may indicate the final expulsion of all the water.

The *S. scriba* negative peak is achieved later. Its value is only - 4 kPa. Afterwards, there is a new, and smaller, negative peak. The positive peak is smaller than 1 kPa.



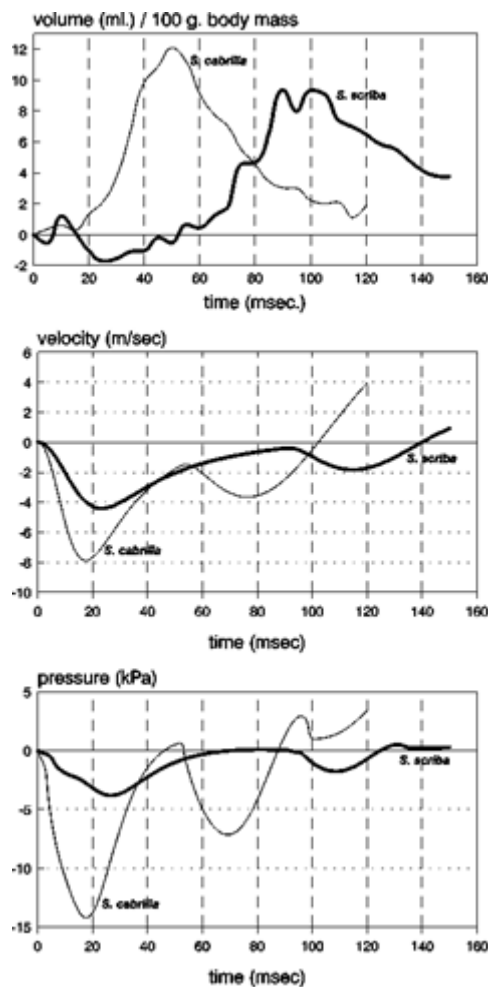
**Fig. 2.** A comparison of the kinematics of feeding in *Serranus cabrilla* and *S. scriba*.



Parameters of the feeding motion are: mouth opening, upper jaw protrusion, mouth bottom depression, suspensorial abduction and opercular abduction. In both species studied, all parameters are represented as a function of body length (dimensionless indices) and plotted against time. Arrows in the opercular plot show moment of water outflow. Time in milliseconds.

**Fig. 3.** Volume change (cumulative), water velocities and pressure peaks, plotted against time.





For both species, volume change is calculated for a theoretical fish of 100 g body mass. Velocities and pressures were obtained by computer simulation. See text for details.

## DISCUSSION

In both species the movements of the cephalic structures follow the same sequence and, if the maximum gape is considered as an important point of reference, they arrive at a similar final position. But there are some differences as well. *S. scriba* shows the slowest mouth opening movement, while the other movements take place at nearly the same speed in both species. To judge this compare the slopes of the graphs of figure 2. However, a considerable delay is observed with respect to the movements in *S. cabrilla*. *S. scriba* combines suction action with swimming to catch the prey. With these combined characteristics, *S. scriba* achieves the smallest values for volume increase and pressure drop. This is in agreement with the visual observation that *S. scriba* lives habitually in open waters with plenty of posidonia, close to the rocks, whilst *S. cabrilla* is usually observed among rocks (see Introduction). This ecological preference provides *S. scriba* with more space for pursuing the prey than fishes in rocky ecosystems, where swimming movements are more restricted and quick turning is necessary. Such ecological preferences apparently show up in details of the feeding process. According to Muller & Osse

(1984) suction feeding from an ambush would require more velocity suction (as observed in *S. cabrilla*) than suction feeding after pursuit, where the water flow into the mouth is for a large part due to forward motion of the fish and less to suction.

Benmouna *et al.* (1984a) show that the angle between the premaxilla and its processus ascendens is smaller in *S. scriba* than in *S. cabrilla*, while the maxilla of *S. scriba* is longer than that of *S. cabrilla*. According to these morphological characteristics, a larger mouth opening (or a more anterior position) in *S. scriba* was expected (Benmouna *et al.*, 1983). However, this has not been observed. Due to the relatively low film speed it cannot be excluded that the films did not register the maximum mouth opening. Both species are able to change from one habitat to the other, although this behaviour is observed more frequently in *S. cabrilla*. As *S. scriba* is preparing to catch the prey at some distance, it will have time to adjust its movements and also the size of its mouth opening to obtain the prey. Unfortunately, the low number of sequences analyzed does not permit a statistical analysis.

The model we used assumes that gill resistance is negligible in fish suction feeding and because that assumption has been criticized (Lauder, 1983, 1986; Lauder *et al.*, 1986), our results on volume increase, water acceleration and pressure drops, require a comparison with previous papers.

The maximum values of volume increase are about 12 ml in *S. cabrilla* and 9 ml in *S. scriba*, for a hypothetical fish of 100 g body mass. The reverse would be expected, given the more well developed musculature in *S. scriba* (Benmouna *et al.*, 1984b). Casinos (1981) estimated volume increase by means of high speed film analysis and obtained values of 6.3 ml/100 g for *Gadus callarias* and 4.6-4.7 ml/100 g for *Pollachius virens* and *Motella tricirrata*. Our data are of the same order of magnitude. Unfortunately, we have no data about the contributions to volume increase caused by the abduction of the suspensoria and the depression of the mouth floor, neither do we know how the position of the axis of the mouth cavity changes with movements of the cranium and the pectoral girdle. From the first two movements, we calculated indices which show that in *Serranus cabrilla*, the species with the largest increase of volume, there is a small contribution of suspensorial abduction and a larger from mouth floor depression.

We found instantaneous, calculated velocities of - 8 m/s and - 4 m/s when water is entering the mouth. These values are much higher than those obtained by Casinos (1981) (-0.13 m/s and - 0.15 m/s). Differences in predatory behaviour and habitat between Gadidae and Serranidae may explain these differences in velocity. It should also be taken into account that the accuracy of the method employed in the present kinetic analysis is higher than that of the method used in the past. Measurements were taken directly from the films without the aid of frame analysis systems (Casinos, 1981) and the time interval is reduced to a few milliseconds.

Since the velocities for serranids were reached in 5 and 15 ms, respectively, accelerations ought to be - 1600 and -266 m \* s<sup>-2</sup>. Muller & Osse (1984) calculated an acceleration of - 1000 m \* s<sup>-2</sup> in adult pipefishes.

The pressure values obtained from *S. cabrilla* (- 14 kPa and - 7 kPa) are higher than those of *S. scriba* (- 4 kPa). Drost *et al.* (1988) gave a range of values of pressure fall of - 5 to - 65 kPa for adult predatory fishes. Van Leeuwen & Muller (1983) simulated and also measured values from - 4 to - 40 kPa. Casinos (1981) found a range of - 0.12 to - 17 kPa for three different species of

Gadidae, values changing according to the species and the water temperature. In the same study, positive pressures, which cause outflow of water through the branchial openings, were registered. The range was 0.03-0.08 kPa. For *S. cabrilla* and *S. scriba* we obtained positive pressure values clearly less than 4 kPa. Therefore, negative pressures are in the same range both using experimental or modeling methods, but positive pressures are not. The higher value of the calculated positive pressures might well reflect the more detailed data in the present study.

It can be expected that the faster the volume increase is, the bigger the pressure drop. The difference in the calculated negative pressure values between the two species of *Serranus* studied is not unexpected in comparison with other cases. In his study on Gadidae, Casinos (1981) found the smallest drops of pressure in *Pollachius virens*, a species combining suction and swimming to catch the prey, as is the case in *S. scriba*.

Some data about the ecology of the serranid species can be used to explain the kinetics analyzed. In the introduction we quoted the prey preferences of *S. scriba* (Robins & Starck, 1961) and this characteristic could be the reason for an approach from a distance. The present detailed data depict *S. cabrilla* more as an ambush hunter with sudden suction, and *S. scriba* more as a pursuit hunter. It is true that the same kind of food was given to both species studied and that the characteristics of the food perhaps were more close to the normal food of *S. scriba* than to that of *S. cabrilla*. Unfortunately, the stomach contents of both species do not allow an assessment of food preferences. Further observations in the natural habitat are needed to establish this suggestion. Although it is true that the natural conditions in which the studied species live and feed are different from the experimental conditions, the comparison of the above feeding parameters allows an equivalent approach to the biology of the species as is required in any ecomorphological research. It has been postulated elsewhere (BOCK, 1990) that a proper determination of the adaptive significance of features depends on a combination of both laboratory and field studies. Here we made field observations and studied the details of the feeding actions in the laboratory.

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## REFERENCES

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

- ALEXANDER, R.McN., 1988. The scope and aims of functional and ecological morphology. *Neth. J. Zool.* **31**: 3-22.
- BAREL, C.D.N., 1983. Towards a constructional morphology of cichlid fishes (Teleostei, Perciformes). *Neth. J. Zool.* **33**: 357-424.
- BENMOUNA, H., P. VANDEWALLE & M. CHARDON, 1983. Étude morphofonctionnelle de la région céphalique de deux espèces de Serrans méditerranéens. Première approche. *Rapp. Comm. Int. Mer Médit.* **28**(5): 119-122.
- Benmouna, H., I. Trabert, P. Vandewalle & M. Chardon, 1984a. Comparaison morphologique du neurocrâne et du splanchnocrâne de *Serranus scriba* (Linné, 1758) et *Serranus cabrilla* (Linné, 1758) (Pisces, Serranidae). *Cybiurn* **8**: 71-93.
- Benmouna, H., M. Chardon & P. Vandewalle, 1984b. Comparaison morphologique de la musculature céphalique de *Serranus scriba* (LINNÉ, 1758) et *Serranus cabrilla* (LINNÉ, 1758) (Pisces, Serranidae). *Cybiurn* **8**: 15-33.
- Benmouna, H., M. Chardon & P. Vandewalle, 1986. Mouvement de prise de nourriture chez *Serranus cabrilla* (Pisces, Serranidae). *Rapp. Comm. Int. Mer Médit.* **30**: 222.
- Benmouna, H., M. Chardon & P. Vandewalle, 1989. Feeding movements in a serranidfish: *Serranus scriba* (L.). In: H. SPLECHTNA & H. HILGERS (Eds): *Trends in Vertebrate Morphology* :156-159. Gustav Fischer Verlag, Stuttgart-New York.
- BOCK, W.J., 1990. From Biologische Anatomie to Ecomorphology. *Neth. J. Zool.* **40**: 254-277.
- BRUSLÉ, J. & S. BRUSLÉ, 1975. Comparaison des périodes de maturité sexuelle de trois espèces de serrans méditerranéens. *Bull. Soc. Zool. France* **100**: 115-116.
- CASINOS, A., 1978. The comparative feeding mechanism of gadidae and macrouridae. I. Functional morphology of the feeding apparatus. *Gegenbaurs morph. Jahrb.* **124**: 434-449.
- CASINOS, A., 1981. The comparative feeding mechanism of gadidae and macrouridae. II. Mechanics of the feeding action. *Gegenbaurs morph. Jahrb.* **127**: 246-262.
- DROST, M.R. & J.G.M. VAN DEN Boogaart, 1986. A simple method for measuring the changing volume of small biological objects, illustrated by studies of suction feeding by fish larvae and of shrinkage due to histological fixation. *J. Zool., Lond. (A)* **209**: 239-249.
- DROST, M.R., M. MULLER & J.W.M. OSSE, 1988. A quantitative hydrodynamical model of suction feeding in larval fishes: The role of frictional forces. *Proc. R. Soc. Lond. (B)* **234**: 263-281.
- LAUDER, G.V., 1983. Prey capture hydrodynamics in fishes: Experimental test of two models. *J. exp. Biol.* **104**: 1-13.
- LAUDER, G.V., 1985. Aquatic feeding in lower vertebrates. In: M. HILDEBRAND, D.M. BRAMBLE, K.F. LIEM & D.B. WAKE (Eds): *Functional Vertebrate Morphology*: 210-229. The Belknap Press (Harvard University Press), Cambridge Massachusetts.
- LAUDER, G.V., 1986. Aquatic prey capture in fishes: experimental and theoretical approaches. *J. exp. Biol.* **125**: 411-416.
- LAUDER, G.V., P.C. WAINWRIGHT & E. Findeis, 1986. Physiological mechanisms of aquatic prey capture in sunfishes: functional determinants of buccal pressure changes. *Comp. Biochem. Physiol. A*, **84**: 729-734.
- MULLER, M. & J.W.M. OSSE, 1984. Hydrodynamics of suction feeding in fish. *Trans. Zool. Soc. Lond.* **37**: 51-135.

MULLER, M., J.W.M. OSSE & J.H.G. Verhagen, 1982. A quantitative hydrodynamical model of suction feeding in fish. *J. theor. Biol.* **95**: 49-79.

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

OSSE, J.W.M., M. MULLER & J. L. Van Leeuwen, 1985. The analysis of suction feeding in fish. In: H.-R. DUNCKER & G. FLEISCHER (Eds): *Functional Morphology in Vertebrates*: 217-221. Gustav Fischer Verlag, Stuttgart-New York.

ROBINS, C.R. & W.A. STARCK, II, 1961. Materials for a revision of *Serranus* and related fish genera. *Proc. Acad. Nat. Sci. Phila.* **113**: 259-314.

SCHAEFFER, B. & D.E. ROSEN, 1961. Major adaptative levels in the evolution of the actinopterygian feeding mechanism. *Am. Zool.* **1**: 187-204.

Vandewalle, P., M. Havard, G. Claes, & F. De Vree, 1992. Mouvements des mâchoires pharyngiennes pendant la prise de nourriture chez *Serranus scriba* (Linné, 1758) (Pisces, Serranidae). *Can. J. Zool.* **70**: 145-160.

Van LEEUWEN, J.L. & M. MULLER, 1983. The recording and interpretation of pressures in prey-sucking fish. *Neth. J. Zool.* **33**: 425-475.