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“VENTRAL ADHESION” TO HARD SUBSTRATES: A THIGMOTACTIC RESPONSE IN SEPIID CUTTLEFISH (MOLLUSCA, CEPHALOPODA)

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CEPHALOPODS
CUTTLEFISH
SEPIA
BEHAVIOUR
ECOLOGY
EVOLUTION

ABSTRACT. – The adhesive “settling” response to hard substrates observed in young cuttlefish involves well defined dermal structures of the ventral surface of the mantle and ventral arms, which are able to act as a set of suckers. This behaviour, which was first described more than a century ago, is probably a common sepiid feature characterizing the early post-hatching phase. In some species, generally small to medium-sized, it is retained in the adult stage. Ventral adhesion allows an individual to immobilize itself on a hard substrate and thus resist the shearing forces of moving water. This paper reports on aquarium experiments demonstrating the efficiency of ventral adhesion in newly hatched *Sepia officinalis*, provides some information on ventral adhesion in the dwarf cuttlefish *Sepia pulchra* and addresses the question of the evolutionary origin of this behaviour.

CÉPHALOPODES
SEICHES
SEPIA
COMPORTEMENT
ÉCOLOGIE
ÉVOLUTION

RÉSUMÉ. – Chez de jeunes Seiches, alors qu’elles sont posées au fond, la réaction spécifique vis-à-vis d’un substrat dur fait intervenir des structures tégumentaires précises de la surface ventrale du manteau et des bras ventraux, qui forment alors un ensemble de ventouses. Ce comportement a été décrit pour la première fois il y a plus d’un siècle; il représente probablement un caractère juvénile commun à toutes les Seiches de la famille des Sepiidae. Chez certaines espèces, généralement de taille petite ou moyenne, il est conservé jusqu’au stade adulte. Ce comportement adhésif permet à l’animal de s’immobiliser sur un substrat dur sans être emporté par les mouvements de l’eau. Cet article rend compte d’expériences effectuées en aquarium qui démontrent l’efficacité de l’adhésion ventrale chez les animaux fraîchement éclos (*Sepia officinalis*), apporte quelques données sur l’adhésion ventrale chez la Seiche naine *S. pulchra* et propose une discussion sur les éléments permettant d’envisager l’origine évolutive de ce comportement.

INTRODUCTION

Cuttlefish of the family Sepiidae are essentially bottom-dwelling, but they can leave the sea floor during foraging or migration. Under the influence of light, cuttlefish normally remain in physical contact with the bottom and in some species (e.g. *Sepia officinalis*), the animals bury in sandy substrates and remain quiescent till dusk (for literature see Boletzky 1996). This lifestyle is generally termed benthic or nekto-benthic (Boletzky 1977). Nixon & Mangold (1998) call the early post-hatching behaviour of *Sepia officinalis* benthopelagic.

Bather (1895) described a special benthic behaviour in newly hatched individuals : “For a day

or two after its escape from the egg-capsule, the young *Sepia officinalis* attaches itself to the floor of the glass vivarium, or to other flat substances. The adhesion is effected by a definite area on the ventral surface of the body and of the postero-ventral arms, which area acts like a sucker, or in some ways like the foot of a gastropod.... The area has a distinct border not identical with the fins, but about one-third or half way between them and the median ventral line. The area is flat and colourless, except for a few pale yellow chromatophores such as are also found on the funnel and just within the pallial cavity. It is bordered by the ordinary chromatophores”. Bather (loc. cit.) suggested : “This development of a ventral sucker is no doubt with the object of preventing the young cuttle-fish from being swept far away by currents,

and is paralleled by the suckers in the young of many other animals, e.g., in tadpoles".

Naef (1928 : 231) provided a complementary description based on his own observations : "The ventral side shows the flat mantle shield, sharply bordered by the lateral ridges. The latter can flatten out, or can be raised as sharp edges or narrow folds. When the animal sits on a flat bottom (e.g. in a glass vessel), the ventral shield is closely applied to the substrate and thus forms an effective surface of adhesion. The latter is enhanced by the lateral ridges or folds, so that the skin musculature acts like a flat sucker. The ventral arms, with their ventral surfaces enlarged by the lateral edges, participate in this action. Thus the young animals can not only (like the adults) bury in sand by a combination of jetting and fin movements, they can also attach themselves to hard substrates (rock), protecting themselves by color and form mimicry, namely using chromatophore patterns and skin papillation".

When an animal is thus attached to a hard substrate, the distal end of the funnel emerges with its orifice on one side, between the posterior rim of the flat ventral arm and the anterior rim of the mantle "sucker" (Boletzky 1974 : Pl. IX, Fig. 5). Thus respiratory water exchange between the mantle cavity and the surrounding sea water continues normally when the animal adheres to a hard surface : water is taken in through the lateral slits between the collar and the mantle rim and is expelled through the funnel.

The observation that the adults of some medium-sized and of dwarf cuttlefish attach themselves to a hard substrate exactly like the young animals (Adam & Rees 1966, Roeleveld & Liltved 1985) raises previously unexpected questions about the evolutionary origin of this behaviour pattern. Indeed, what had generally been thought of as a typical juvenile adaptation (Boletzky 1974) may stem from a morphological condition related originally to small adult size. Here we discuss the biological and autecological role of this peculiar behaviour and address the question of the likely structural prerequisites for its establishment in the sepiid ancestor.

MATERIAL AND METHODS

Adults of *Sepia pulchra* were observed in their natural environment (by SCUBA diving) and in the aquarium. *Sepia pulchra* Roeleveld & Liltved is a very small species of the "Hemisepius group" (Khromov *et al.* 1998) known only from the Cape Peninsula, South Africa. The animals become sexually mature at a size of about 20 mm in mantle length (ML).

Sepia officinalis juveniles, from hatching to several months in age, were observed in the aquarium. This

species, which occurs in the eastern North Atlantic between 20 and 60°N and throughout the Mediterranean, becomes sexually mature at sizes above 80-90 mm ML. Hatchlings were tested in a glass tube (inner diameter 15 mm) connected to a seawater supply, thus allowing one to vary the water flow through the tube by means of the inlet-tap.

Hatchlings and advanced juveniles of *Sepia orbignyana*, reared in the aquarium, and hatchlings of *Sepia elegans*, were observed in the aquarium. These two species live in roughly the same area as *S. officinalis*, but stay at greater depths throughout their life cycles (Khromov *et al.* 1998).

RESULTS

Field and laboratory observations of adult Sepia pulchra

In the field, most individuals of *Sepia pulchra* observed by SCUBA diving at depths ranging from 15 to 50 m were seen adhering to vertical rock faces in the head-down position (W. R. Liltved, pers. comm.), as shown in Figure 1. Both the ventral shield of the mantle and the lower surfaces of the ventral arms participate in the formation of a tripartite ventral "sucker". In the aquarium, animals were also seen to use the ventral mantle shield alone for adhesion (Roeleveld & Liltved 1985 : Fig. 12). When this variant occurs, the animal erects itself prominently above the surface of the substrate. Such an attitude would seem to be less suited for effective adhesion under strong water movement, as found in the high energy coastline of South Africa, than the combined use of ventral mantle shield and ventral arms.

Laboratory observations of hatchlings and juveniles

Newly hatched *Sepia officinalis*, *S. orbignyana* and *S. elegans* showed very similar adhesive behaviours. The only notable difference observed was the stronger expansion of the tegumental ridges in the ventral mantle "sucker" in the hatchlings of *S. elegans* and *S. orbignyana*. This is noteworthy since these two species appear to "lose" their adhesive behavior at advanced juvenile stages earlier than young *S. officinalis* (this hypothesis remains to be tested, however).

Experiments related to the adhesive behaviour were done with *Sepia officinalis* only. In the laboratory, it is easy to observe this behaviour in newly hatched cuttlefish, especially when the water of a container holding the animals is set in motion (e.g. a round basin in which the water is

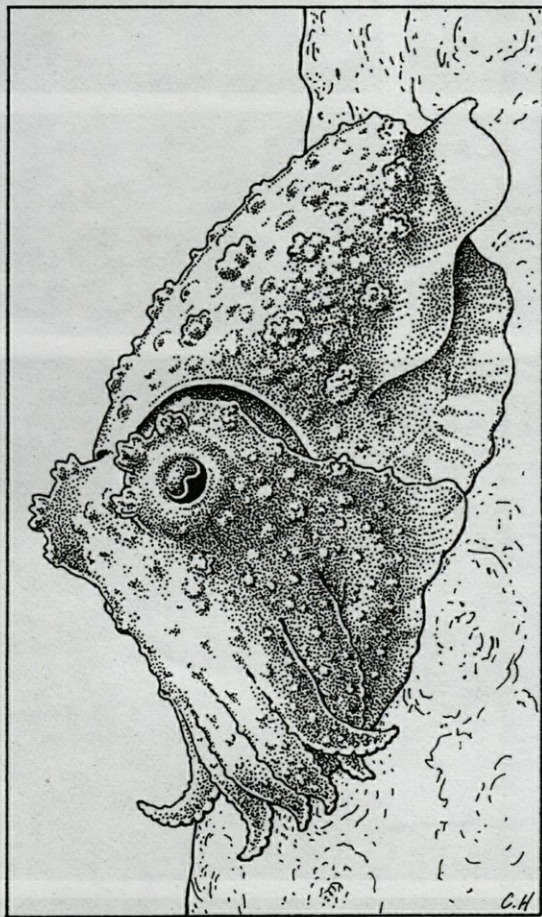


Fig. 1. – Mature female *Sepia pulchra* (ML 19 mm) attached to a vertical rocky surface (after Roeleveld & Liltved 1985, Fig. 12).

given a rotatory movement). The effect of adhesion is immediately recognizable in comparison to the animals not attached to the substrate, which are flushed around with the swirling water. If the water movement is not too strong, such drifting animals can often be seen to “drop out” of the moving water and settle on the bottom.

A simple method to observe young animals while adhering to the substrate is to place them in a wide glass tube filled with sea water and plugged to a supply tap. By gradually increasing the water flow in the tube, one can follow the reaction of the settled animal under the pressure of the water current (Pl. I A-F). In particular, the contraction of the ventral arms is enhanced by an increasing water flow (Pl. I C, F). The effect of this contraction, which is assumed to improve the sucker effect of the ventral arms, does not appear to improve stream-lining of the body, however.

At advanced juvenile stages (up to a body size close to 30 mm ML), *Sepia officinalis* can still be observed to adhere to a hard substrate (Pl. I I), and the elevation of the tegumental ridges deli-

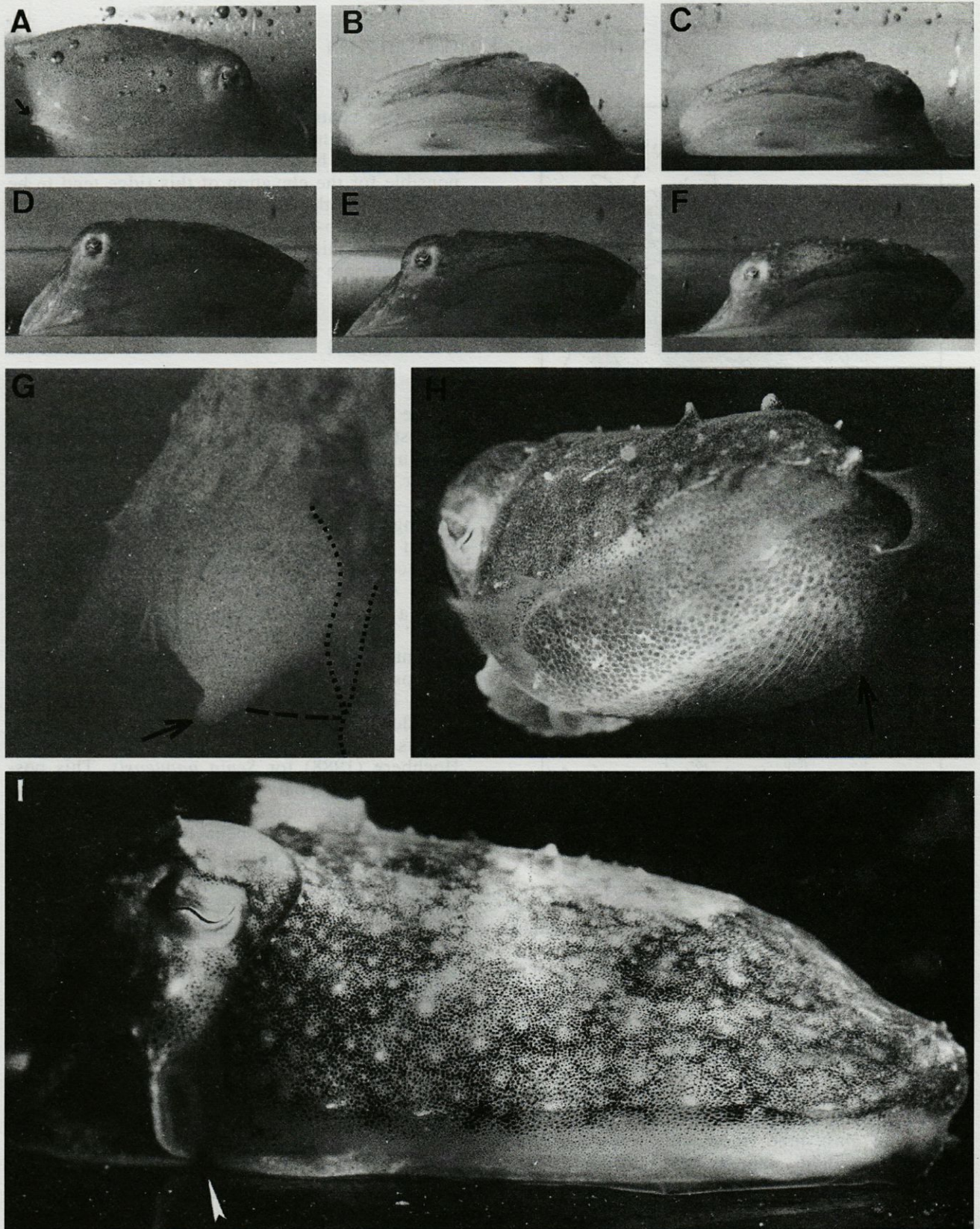
miting the ventral mantle shield can be seen even before the animal settles (Pl. I G). During slow swimming or hovering, the dermal muscles responsible for the elevation of this ridge tend to be relaxed. Thus the limit between the ventral shield and the ventro-lateral area below the fins is generally recognizable only from the difference in chromatophore patterns (Pl. I H).

DISCUSSION

The few observations so far available tend to suggest that ventral adhesion is a generalized pattern in sepiid hatchlings and early juveniles, no matter what the adult behaviour(s) related to substrate. No quantitative data are yet available regarding duration of adhesion, current speeds or age of the animals involved, and could be taken into account in future analyses. Adult animals of *Sepia orbignyana* and *S. elegans* are known to lack a sand digging behaviour and appear to “lose” the ventral adhesive behaviour; they keep in contact with hard or soft substrates only with the tips of the ventral arms, the mantle remaining nearly horizontal due to the near-neutral buoyancy provided by the cuttlebone (Boletzky 1989, 1996). This is the “bipod posture” described by Roper & Hochberg (1988) for *Sepia papuensis*. This posture is possible only in fairly still water. If the hatchlings live under similar conditions as the adults, their adhesive behaviour may appear of minor importance, unless it is used to stabilize the body in a vertical position similar to that observed in adult *S. pulchra*.

Viewed against adult behaviour patterns in other species, such as the bipod posture mentioned above, the ventral adhesion in adult *Sepia pulchra* may be interpreted as a paedomorphic character related to very small adult size. Conversely, the ventral adhesion observed as a juvenile character in larger species could be interpreted as a juvenile adaptation derived from a pattern that was not originally restricted to the juvenile phase (in the immediate ancestor). The observation that in *S. typica*, a closely related species, each of the ventro-lateral ridges of the mantle is differentiated into a series of small sucker-like structures (Roeleveld 1972) could be used as an argument to support either one or the other hypothesis.

It should not be overlooked that ventral suction has also been observed in some larger species outside the “Hemisepius group”, especially *Sepia tuberculata* (max. ML 80-90 mm) and *S. papillata* (max. ML 140 mm), which have slightly different types of ventral “suckers”. In *S. tuberculata* “the ventral side of the mantle shows the characteristic lateral pads with their wrinkled surface; similar pads are present on the ventral arms” (Adam &



Pl. I. – A-F, Newly hatched *Sepia officinalis* (ML 8-9 mm) introduced into a glass tube (inner diameter 15 mm). A, animal settling down in still water; arrow points at tegumental ridge. B, animal attached to the bottom in water current coming from the left (caudal) side. C, same as B, but water current stronger; note “shortening” due to stronger contraction of arms (enforcing adhesion of ventral arm surfaces). D, animal attached to the bottom in still water. E, same animal “streamlining” in water current coming from the left (cephalic) side. F, same as E, but in stronger current (cf. C). G, Advanced juvenile *Sepia officinalis* (ML 28 mm), hovering just above the bottom of the aquarium, in latero-anterior view; in this close-up, the tegumental ridge on the right side of the ventral mantle surface (arrow) is very prominent (broken line marks lower mantle surface beyond focus, dotted lines mark lateral edges of arms closer than focus). H, Advanced juvenile *Sepia orbignyana* (ML 25 mm) hovering above the bottom of an aquarium (latero-caudal view); the limit between the ventral “shield” and the ventro-lateral mantle surfaces below the (undulating) fins is distinct (arrow) without forming a ridge. I, *Sepia officinalis*, same individual as in G, attached to the glass bottom of an aquarium; note the funnel (arrow head) emerging between the left ventral arm and the anterior mantle rim forming the ventral “sucker”.

Rees 1966 : 107, Pl. 27, Fig. 171); "... these curious formations function as suckers with which the animals, living in the tidal zone, adhere temporarily to the rocks, preventing them from being swept away by the waves" (J. H. Day in Adam & Rees 1966, footnote on p. 107). "The animal of *S. papillata* strongly resembles that of *S. tuberculata* in the oval pads on the ventral surface of the mantle" (Adam & Rees 1966 : 109; see also Roeleveld 1972, Fig. 12).

In pursuing speculations on the evolutionary origin of ventral adhesion, it may be useful to analyse the form/function complex so far considered. Could the typical form of the ventral arms and ventral mantle surface of cuttlefish have a function other than providing a flat surface for adhesion to a substrate? It is undeniable that ventro-lateral mantle ridges similar to those observed in cuttlefish exist in many octopods, but nothing is known of their function, let alone the question of their homology. On the other hand, ventro-lateral mantle ridges in *Metasepia* clearly have a special "locomotor" function related to the substrate, but so far nothing allows one to say whether it is a function derived from, or superimposed on, the "sucker" function. Whatever the answer, the mobile "ambulatory flaps" (Roper & Hochberg 1988) of these small sepiids are very likely homologues of the "sucker ridges" described above.

The only other instance of an adhesive behaviour (not involving brachial suckers) known in cephalopods, namely the "adhering habit" of *Idiosepius* (Sasaki 1923, Moynihan 1993), further highlights the peculiar condition of sepiid ventral adhesion. Indeed, the adhesive zone of the mantle in *Idiosepius* is different in position (dorsal) and histology (thick glandular epidermis). In contrast, the dermal structures allowing sepiids to become attached to a substrate are not recognizable in the epidermis (except by the ventral "pores" in *Sepia typica* and the wrinkled areas in *S. tuberculata* and *S. papillata*). Only contracted dermal musculature in the mantle ridge zones generally reveals the special function of these muscular elements *in vivo* and often also *post mortem* (especially in preserved specimens), whereas fully relaxed dermal musculature leaves virtually no trace of the ridges (their location then is recognizable only from chromatophore patterns, as shown in Pl. 1 H).

The neural mechanisms underlying the specific use of this musculature for ventral adhesion must somehow involve mechanoreceptors in the skin, and perhaps also proprioception, allowing the co-ordination of mantle and ventral arm components in ventral adhesion. It is still unknown how the animal distinguishes soft from hard substrates, but mechanoreception is probably involved in recognizing these differences. If mechanoreceptors

of the ventral integument provide the central nervous system with some information on substrate properties (such as roughness, cf. Hanlon & Messenger 1996 : 15), ventral adhesion must be the positive effect of ventral thigmotaxis (cf. Grimpe 1928). An incapacity to become attached, e.g. on a soft substrate, could provide the trigger for burial behaviour (see Boletzky 1996).

The evolutionary origin of ventral adhesion is inconceivable without the pre-existence of a dermal musculature that could have been "taken over" in an exaptation involving a specific behavioural response. Thus the most intriguing question remains the (phylogenetically preceding) first establishment of the respective dermal differentiation and its original function. Perhaps the presence of ventro-lateral ridges in the mantle integument of octopods provides a hint; the mantle ridges in octopus and cuttlefish are raised by contraction of localized dermal musculature, in a way similar to the erection of skin papillae. The latter exist in both octopus and cuttlefish as part of cryptic skin patterns. This observation raises an important question related to the great phyletic distance separating octopus and cuttlefish, namely whether the respective dermal structures are homologous or homoplastic features. Another question is whether the ventro-lateral mantle ridges may have resulted from a (single or convergent) homeotic transformation by which skin papillation was "exported" to surface areas not directly involved in cryptic patterning, but as part of a behaviour related to crypsis.

The autecological role (counteracting dispersal) of ventral adhesion in post-hatching *Sepia*, as already suggested by Bather (1895) and Naef (1928), would seem to indicate that early juveniles are behaviourally enhanced bottom-dwellers, notwithstanding their capacity to swim up actively (e.g. when pursuing prey). An early juvenile that "enters [the] water column in darkness" (Nixon & Mangold 1998) may take a high risk of being eaten by predatory fish such as *Serranus cabrilla* (Hanlon & Messenger 1988 : Pl. 9). Perhaps positive buoyancy due to sudden, severe underfeeding related to food shortage forces some young animals to leave the bottom (Boletzky 1993). The resulting exposure to potential predators is likely to limit the chances of survival of such individuals, until they find better foraging conditions, allowing them to recover neutral buoyancy. Most observations indeed suggest that healthy juveniles of *Sepia officinalis* (i.e. those able to maintain a neutral or slightly negative buoyancy) limit their excursions into the water column to brief attacks on moving prey (Boletzky 1983).

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