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CAN RHYNCHOTEUTHIONS SUSPENSION FEED? (MOLLUSCA : CEPHALOPODA)

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CEPHALOPODA
OMMASTREPHID
SQUID
ILLEX ILLECEBROSUS
LARVAE
FILTER FEEDING

ABSTRACT. — The unique rhynchoteuthions of the ommastrephid squids are the smallest decapodan cephalopod hatchlings and have never been successfully reared. Based on anatomical and behavioural observations a mechanism of suspension feeding is proposed which depends on direct interception and inertial impaction on the mucus coated body surface. Mucus is transferred to the mouth area by ciliary motion and by observed cleaning behaviours. Suspension feeding is suggested to be a supplement to raptorial feeding but may be a critical "bridge" between small yolk reserves and the minimum development required for effective predation. Loss of ciliature through contact with vessel walls may prevent feeding in culture.

CEPHALOPODA
OMMASTRÉPHIDÉS
ILLEX ILLECEBROSUS
LARVES
FILTREUR

RÉSUMÉ. — La larve, ou rhynchoteuthion, des Calmars de la famille des Ommastrephidae est la plus petite de toutes celles des Céphalopodes Décapodes et n'a pas encore pu être élevée en aquarium. A partir d'observations d'anatomie et de comportement, il est suggéré que les larves pourraient se nourrir de particules en suspension. Les particules sont interceptées directement ou, dû à l'inertie même des particules, adhèrent à la couche de mucus couvrant la surface du rhynchoteuthion. Le mucus est transféré à la bouche par mouvements ciliaires et par un mode de nettoyage actif. Il est aussi suggéré que l'ingestion de particules en suspension supplémente l'alimentation par prédation mais peut aussi servir comme mécanisme intermédiaire entre les réserves alimentaires contenues dans le vitellus et le développement d'une prédation efficace. La perte de cils vibratils par contact avec les parois des bacs pourrait empêcher l'alimentation chez les larves en culture.

INTRODUCTION

The success of ommastrephid squid in the open ocean may result from reproductive adaptations which permit a life cycle isolated from land masses. They produce some of the smallest cephalopod eggs (ca. 0.8 mm) which yield unique « rhynchoteuthion » hatchlings less than 2 mm in total length with only two pairs of arms and a proboscis which later divides to form the tentacles of the adults. The small size of the eggs may be an adaptation to retaining the eggs in the upper water layers. All cephalopod eggs are probably denser than seawater, but ommastrephids produce neutrally buoyant egg masses by embedding small eggs in large volumes of gel produced by the nidamental glands (O'Dor & Balch, 1985). The advantages of small eggs may have provided a selective pressure producing embryos which hatch out too small to follow the usual cephalopod habits; rhynchoteuthions are the only cephalopod hatchlings which show sufficiently distinct developmental changes to make the term larvae attractive (Boletzky, 1974).

All cephalopod hatchlings which have been successfully reared begin to feed immediately as raptors (Boletzky & Hanlon, 1983), but all attempts to rear rhynchoteuthions on apparently suitable prey have failed (Balch *et al.*, this volume). Furthermore, no identifiable stomach contents have been found in wild-caught rhynchoteuthions. Based on extensive observations of rhynchoteuthion behaviour, but with no direct evidence, this paper will examine a possible mechanism which would allow rhynchoteuthions to feed on suspended particles during the critical period of transition from yolk reserves to normal predation.

Labarbera (1984) has reviewed suspension feeding mechanisms and emphasizes that three types of processes are required : 1) water transport past feeding structures, 2) particle capture and 3) particle transport to the mouth for ingestion. He also argues that actual sieving by a mesh finer than the particles is a mechanism used often by biologists but infrequently by organisms because of its high energy cost. A surface covered with a sticky collector like mucus can be nearly as effective at a lower cost by capturing particles through « direct interception ». This is the key element in the present hypothesis.

MATERIALS AND METHODS

Illex illecebrosus rhynchoteuthions were obtained from egg masses spawned in captivity and incubated as described in Balch *et al.* (this volume). The specimens for light and electron microscopy hatched after 5 days at 26 °C. Specimens for scanning electron microscopy were fixed in Bouin's solution and dehydrated in acetone. After critical point drying, they were fixed to an aluminum stub and sputter-coated with a 60/40 mixture of gold/palladium. Photographs were taken with a Nanolab 2 000 SEM and Kodak Pan-X film.

Behavioural observations were made in either a plastic petri dish filled with seawater over a Zeiss inverted microscope or in a vertical flow-through swim chamber (3 mm square and 78 mm high, made from microscope slides) through a Zeiss dissecting microscope. In each set-up the ocular could be replaced with an RCA TC 2011/N low-light video camera connected to a Sony SLO-323 Beta recorder to make a permanent record. A Vicon Industries Model V240 Date/Time Display Generator added a time base to the nearest 0.1 s. Frame-by-frame analyses were made of behaviours. Over 20 hours of video were made from 80 hours of observation.

RESULTS

Rhynchoteuthions exhibited behaviours which could be associated with each of Labarbera's (1984) three processes. Since particle capture is the most critical step, and the type of capture determines the requirements for the other processes, it will be discussed first. Rhynchoteuthions have no obvious

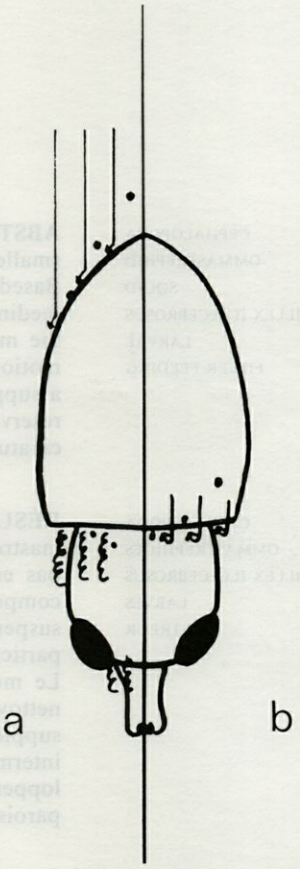
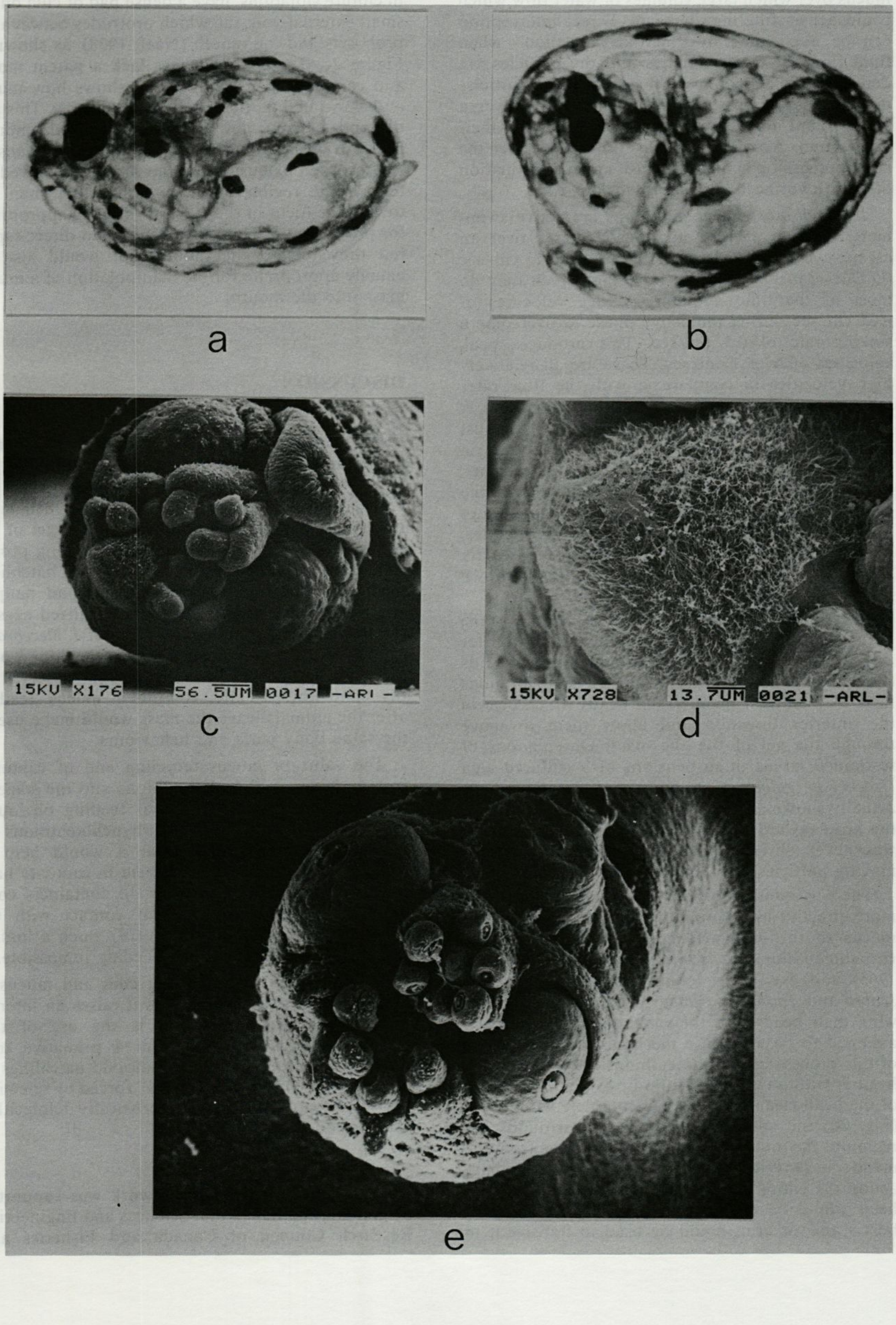


Fig. 1. — a, A schematic illustration of the streamlines and possible impaction points for particles on a rhynchoteuthion during jetting; b, of the flow pattern during mantle refilling.

Fig. 2. — a and b, A live sequence of a rhynchoteuthion withdrawing its head into the mantle. During withdrawal the mantle lip cleans the surface of the head, and when the head is fully withdrawn the lip, with accumulated mucus, lies directly over the mouth region. c, An overview of the ciliated pad on the yolk sac protruding between the proboscis and arms of a stage XVII embryo. d, A detail of the same specimen as in c showing accumulated mucus and particles on the ciliated pad. e, A similar view of a stage XX embryo after the pad has withdrawn (c-e SEM).


a
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15KV X176 56.5UM 0017 -ARL-
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15KV X728 13.7UM 0021 -ARL-
d
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sieving structures but do have large areas covered in mucus over which large volumes of water flow which could act as filtering elements. Direct interception can be augmented by "inertial impaction" when fluid flows at high velocities and the particles are denser than the medium. In this mechanism particles move across streamlines as the fluid flows over a surface and impact on the surface due to their momentum. As will be shown, water flow over the rhynchoteuthion is relatively fast, and a combination of these two mechanisms is plausible.

I. illecebrosus rhynchoteuthions are active swimmers and can average up to 5.6 cm/sec over an escape cycle with peak velocities of up to 15 cm/sec (O'Dor *et al.*, 1985). Even hovering, which they do most of the time, requires average velocities of 0.62 cm/sec during the active phase to overcome a sinking rate of 0.5 cm/sec. This produces peak velocities of over 1 cm/sec. These are all relatively high velocities in comparison with the flow rates over most biological filter elements (Rubenstein & Koehl, 1977). It seems clear that some particles must adhere to the mucus coated mantle as shown in Figure 1a as the animal accelerates with each jet. The other likely place for inertial impaction is on the head near the lip of the mantle where the water being taken in changes direction and accelerates. The inertia of particles with densities significantly greater than water would cause impaction as shown in Figure 1b.

Accepting that there is water flow and some particle capture, a mechanism is required to transfer the particles to the mouth. Like other young squids (Boletzky, 1982), *I. Illecebrosus* rhynchoteuthions have cilia on their mantles and heads which beat in the anterior direction and allow them to move through the gel of the egg mass. Observations of restrained larvae in suspensions of a cultured alga *(Isochrysis galbana)* at high magnification have actually shown algae trapped in mucus moving over the head toward the mouth. Even though ingestion was never observed there is clearly a means of moving particles over the surface of the head.

There is another behaviour which may be even more effective in cleaning the head and transferring mucus to the mouth. There are reports of other rhynchoteuthions (*Todarodes pacificus*; Okiyama, 1965) and even large cranchiid squids (*Cranchia scabra* and *Taonius megalops*; Dilly, 1972) withdrawing their heads into their mantles. This has been assumed to be a defense mechanism. Observations of this process in rhynthoteuthions show that as the head is withdrawn the mantle lip wipes the surface of the head clean (Fig. 2a). On complete withdrawal (Fig. 2b) the contracted mantle lip surrounds the region of the mouth. Since all of the mucus from the mantle is moved toward the mantle lip by ciliary action the entire mucus collection from mantle and head would be collected at a site where the proboscis and/or arms could be used to transfer it to the mouth. Stage XVII embryos, which often hatch in culture situations, have a dense pad of cilia on the small external yolk sac which protrudes between the proboscis and the mouth (Naef, 1928), as shown in Figure 2c. These early stages lack a patent mouth and cannot feed, but Figure 2d shows how mucus and associated particles collect in this area. This pad disappears from view in more advanced embryos (Fig. 2e) but may still play a role in mucus transfer. All recorded extensions of the proboscis moved up toward the region of the mouth rather than out toward the focus of the eyes as would be appropriate for prey capture. This movement could direct captured prey toward the mouth, but would also be equally appropriate for the manipulation of a mucus mass into the mouth.

DISCUSSION

These observations do not prove that rhynchoteuthions are suspension feeders, but do provide circumstantial evidence that they have the capacity for it. There is also a logical progression of behaviour from the ciliary locomotion through the gel of the egg mass to the type of suspension feeding proposed. Durward *et al.* (1980) suggested that hatchlings might feed on micro-organisms, copepod nauplii, etc. which colonize the gel and unfertilized eggs in the large (up to 1 meter) egg masses of *I. illecebrosus* as they move to the outside. Such behaviour would certainly supplement the small yolk reserves of rhynchoteuthions, and continued mucus feeding after the animals leave the mass would make use of the same body parts and behaviours.

The value of mucus recycling and of captured food particles to rhynchoteuthions and the stage at which they change to raptorial feeding obviously require further investigation. If rhynchoteuthions are dependent on this mechanism it would help to explain why attempts to rear them in captivity have failed. Cephalopods kept in small containers commonly lose surface cilia from contact with the container walls (Hulet *et al.*, 1979). Such a loss of cilia would make suspension feeding impossible.

If suspension feeding using cilia and mucus is important for rhynchoteuthions it raises an interesting eveolutionary question : is the use of this common molluscan mechanism a primative trait retained by these smallest cephalopod hatchlings or is it a "re-invention of the wheel" forced by selection for small egg size to characteristically telolecithal cephalopods ?

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REFERENCES

Boletzky S.V., 1982. Structure tégumentaire de l'embryon et mode d'éclosion chez les Céphalopodes. *Bull. Soc. Zool. Fr.,* **107** : 475-482.

Boletzky S.V., 1974. The "larvae" of Cephalopoda : a review; *Thalassia Jugoslavica,* **10** : 45-76.

Boletzky S.V. & R.T. Hanlon, 1983. A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. *Mem. Nat. Mus. Victoria,* **44** : 147-187.

Dilly P.N., 1972. *Taonius megalops,* a squid that rolls up into a ball. *Nature,* Lond., **237** : 403-404.

Durward R.D., E. Vessy, R.K. O'Dor & T. Amaratunga, 1980. Reproduction in the squid, *Illex illecebrosus* : First observations in captivity and implications for the life cycle. *Int. Comm. N. W. Atl. Fish. Sel. Papers,* **6** : 7-13.

Hulet W.H., M.R. Villoch, R.F. Hixon & R.T. Hanlon, 1979. Fin damage in captured and reared squids. *Lab. Animal Sci.,* **29** : 528-533.

Labarbera M., 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. *Amer. Zool.,* **24** : 71-84.

Naef A., 1928. Die Cephalopoden. Fauna Flora Golf Neapel, **35** (2) : 1-357.

O'Dor R.K. & N. Balch, 1985. Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. *N. Atl. Fish. Org. Sci. Coun. Studies,* **9** : 69-76.

O'Dor R.K., E.A. Foy, P.L. Helm & N. Balch, 1986. The locomotion and energetics of hatchling squid, *Illex illecebrosus. Amer. Malacol. Bull.,* **4** : 55-60.

Okiyama M., 1965. Some information on the eggs and larvae of the common squid, *Todarodes pacificus* Steenstrup. *Bull. Jap. Sea Reg. Fish. Res. Lab.,* **15** : 39-53. (Fish. Res Board Can. Transl. Ser. No. 811).

Rubenstein D.I. & M.A.R. Koehl, 1977. The mechanisms of filter feeding : some theoretical considerations. *Amer. Nat.,* **111** : 981-994.

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