

The early life of *Sepia officinalis*, and the contrast with that of *Octopus vulgaris* (Cephalopoda)

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Abstract

The egg and hatchling of *Sepia officinalis* L. is relatively large, compared with those of other cephalopods. We review the information on growth, chromatophores, behaviour, prey capture, colour and body patterns of this sepiid, for correlation with changes in morphology and development of its central nervous system. We compare the early life of *S. officinalis* with that of the common octopod, *Octopus vulgaris*, Cuvier 1797. *Sepia officinalis* is initially benthopelagic but subsequently is mostly benthic in habit. *Octopus vulgaris* enters the plankton immediately after hatching and spends several weeks there before it settles to a life spent mostly on the bottom.

Key words: *Sepia*, hatchling, behaviour, brain, morphology

INTRODUCTION

The coastal-living *Sepia officinalis* L. produces relatively large eggs compared with those of many other cephalopods (e.g. Hochberg, Nixon & Toll, 1992) and at hatching the young animal closely resembles a miniature adult, and exhibits many adult habits and behavioural traits (Wells, 1958; Hanlon & Messenger, 1988). Our knowledge of the embryonic development of this species has been reviewed (Fioroni, 1990), and there is currently a considerable body of information available about the early part of the life cycle. We have extensively reviewed the literature to try to give a full account of the first few weeks of life of the post-hatchling, and to allow us to correlate changes in morphology and the central nervous system with habits and behaviour.

The terminology used to describe young cephalopods has varied. The exception is the embryonic period which Naef (1921, 1923, 1928) divided into stages; a system which is widely accepted. Young & Harman (1988) introduced a nomenclature for the early life of cephalopods, including the term 'paralarva' for the planktonic young of Teuthida and Octopoda. Also in 1988, Hanlon & Messenger named the early stages for *S. officinalis* as follows: hatchling for animals up to 1 week, early juvenile up to 7 weeks, and late juvenile up to 17 weeks. Where possible the exact age, or these terms, have been used in this paper.

Sepia officinalis is known from the eastern Atlantic,

from the North Sea and into the Mediterranean (Roper, Sweeney & Nauen, 1984), but the exact southern limit of this species is not certain.

ANIMALS AND METHODS

Specimens of *S. officinalis*, captured in the Bay of Naples, Italy, and off Plymouth, U.K., were measured. Two recently hatched young were preserved, sectioned serially in the sagittal and horizontal planes, and stained with haematoxylin and eosin. An arm and a tentacle from a 12-day-old hatchling were fixed in formalin, washed, taken through graded ethanol, ethanol and 'Freon 113' mixtures, and finally 'Freon 113' before being critical-point dried (Boyde, 1974). Each specimen was attached to an aluminium rivet, given evaporated, electrically conductive coatings of carbon and gold and then examined with a Cambridge Stereoscan S4-10.

In *Sepia* the mantle length (ML) is measured on the dorsal surface from the posterior apex of the mantle to its anterior-most point, and the total length (TL) from the posterior end of the mantle to the tip of the tentacular club.

The techniques described by Wirz (1959) were used to measure the lobes of the central nervous system of *S. officinalis* captured in Banyuls-sur-Mer (France) and Naples (Italy), and were followed by Frösch (1971), in newly-hatched specimens of this species caught in the same areas. Maddock & Young (1987) also made a

quantitative study of 30 lobes of the brain of *S. officinalis* and with similar results to those of Wirz (1954, 1959) although the methods used were different. In this paper the data from Wirz (1954, 1959) and from Frösch (1971) are used, as the same method was employed in both studies, so making direct comparison possible between the volumes of the lobes of the central nervous system in animals of different sizes. (Papers cited below by K. Wirz, K. Mangold-Wirz and K. Mangold are all by the same author.)

RESULTS

Sepia officinalis

The observations and results presented in this section are restricted to the hatchlings and young of the coastal cuttlefish, *S. officinalis*, except where otherwise indicated.

Spawning and hatching

Aristotle (384–322 BC, see translation by Thompson, 1910) was the first to record the spawning habits of *Sepia* in the Mediterranean. In this sea mature *S. officinalis* migrate to spawning grounds in inshore waters (Mangold-Wirz, 1963), and tagged animals were found to move at about 0.23 km/day (Ezzeddine-Najai, 1995). Many adults return to the grounds they left as juveniles, although some enter neighbouring areas, and this may allow for genetic interchange between populations (Boucaud-Camou & Boismery, 1991). The migrations show a close link with temperature but other extrinsic and/or intrinsic factors are probably also involved (see Boletzky, 1983).

During a 2-year study in the Netherlands (Delta area) mature adults were found to enter one area but not another, even when these areas were in close proximity: adults (462) and eggs were recorded in Oosterschelde and seven adults but no eggs in Westerschelde where the salinity (30‰) was the same, and three adults but no eggs in Grevelingen where the salinity was lower (28‰) (Paulij, Bogaards & Denucé, 1990). These authors demonstrated experimentally that eggs kept in salinities of more than 29.8‰ had a higher percentage rate of hatching success than those kept in lower salinities. Embryonic growth was found to be slower in salinities of 29–32‰ (Palmegiano & D'Apote, 1983). An increase in temperature results in a decrease in the time taken for development, and the oxygen content of the sea water around the eggs also has a role in their development (see Boletzky, 1983).

The attributes of a spawning ground necessary for the successful development, growth of the embryo and hatching, and for the survival of the hatchling and post-hatchling, include a sandy substrate (with rocks and/or pebbles) with sea grass or algal beds, a water depth of between 5 and 60 m, a salinity of 28‰ or more,

and a temperature of between 9.5°C and 20°C (Mangold-Wirz, 1963; Richard, 1969; Paulij *et al.*, 1990; Boucaud-Camou & Boismery, 1991). Such conditions, or closely similar ones, must continue for the duration of the embryonic and early stages of life of the cuttlefish.

The behaviour of the adults suggests that they have some capacity to detect differences in the nature of the surrounding sea water but how they monitor salinity or other extrinsic factors in the search for a suitable site for egg-deposition, or possess a 'homing' response, is currently not known. A 'lateral line' system is present in young cuttlefish and it is extremely sensitive to small water movements (Bleckmann, Budelmann & Bullock, 1991). There are putative chemoreceptor cells in each sucker (Graziadei, 1964), and sensory cells in the epithelium (Sundermann, 1983) and in the olfactory organs (see Fioroni, 1990; Wildenburg, 1991).

Spawning takes place shortly after copulation, while the male remains in visual contact with the female (see Boletzky, 1983). Each egg is laid singly and the female attaches it to seaweed, eventually often forming small clusters. Eggs are laid at intervals over several hours, and some individuals spawn over much longer periods (Boletzky, 1975). Each egg-case is black, 25–30 mm long and 12–14 mm in diameter. The ovum is 6 × 5 mm to 9 × 7 mm and contains a large quantity of yolk (see Boletzky, 1983). A long time is spent as a late embryo, (between embryonic stages XVIII and XX; Naef, 1928), during which 80% of the total growth takes place (Fioroni, 1964, 1990). Development to hatching in sea water takes 40–45 days at 20°C and 80–90 days at 15°C (see Boletzky, 1983). Eggs laid in March develop in 90 days whereas those laid in July, when the temperature is higher, hatch in 40 days (Bouchaud, 1991a). Fioroni (1990) reviewed the major contributions to the literature of the studies of ontogenesis of *S. officinalis* since the study of the processes of development by Kolliker (1844).

Towards the end of development the black egg capsule becomes thinner, due to an increase in the volume of perivitelline fluid; the late embryo within can apparently detect light changes, as under laboratory conditions hatching consistently took place during periods of darkness, and after the transition from light to dark (Paulij *et al.*, 1991). Some internal yolk remains at hatching to provide food during the first 24–48 h of independent life (Wells, 1958). The presence of mysids or similar small crustaceans is essential since in the absence of suitable prey the hatchlings will die in three days (Bouchaud, 1991b).

Behaviour of the young cuttlefish after hatching

After hatching the young moves amongst the seaweed on the bottom (Hanlon & Messenger, 1988) probably to avoid visual predators. The hatchling can attach itself to the substrate by means of a 'sucker' formed by the antero-ventral surface of the mantle and the postero-

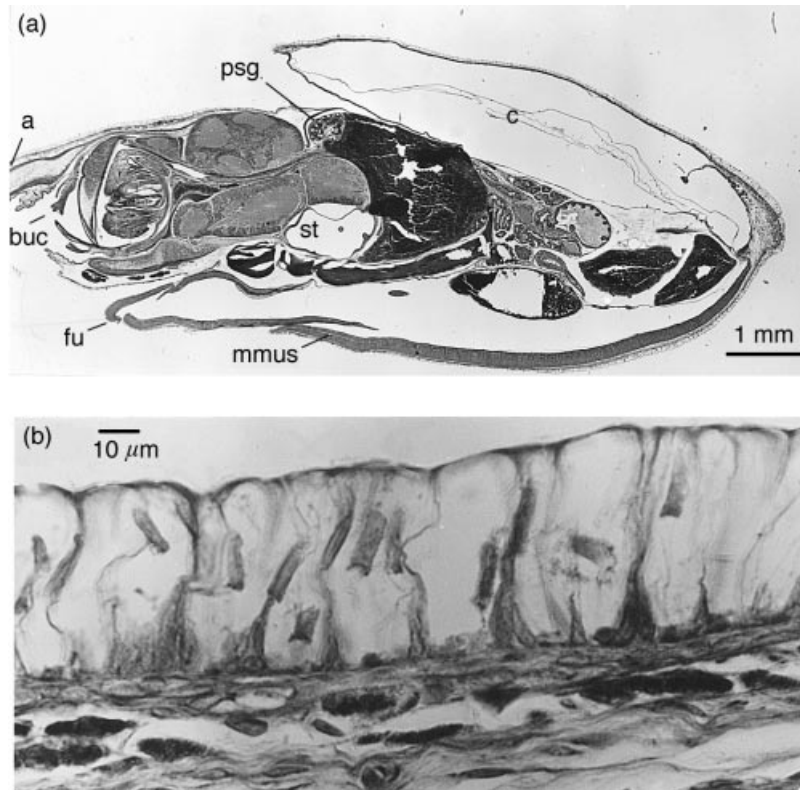


Fig. 1. *Sepia officinalis*. (a) A medial sagittal section of hatchling (8.5 mm ML) to show its main features. (b) Epithelial cells at higher magnification (haematoxylin and eosin). a, arm; buc, buccal mass; c, cuttlebone; fu, funnel; mmus, mantle muscle; psg, posterior salivary gland; st, statocyst.

ventral surface of the large ventral arms IV (Bather, 1895; Naef, 1923; Boletzky, 1974; Hanlon & Messenger, 1988). Sand-covering behaviour is established at hatching; in this the animal blows sand from beneath its body using the funnel, and gradually sinks deeper into the substrate until partially covered (Hanlon & Messenger, 1988). The hatchling spends the greater part of its time resting on the bottom (Wells, 1958). During daylight hours it usually sits on, or is buried in, the substrate; at dusk it becomes active in the water column (Hanlon & Messenger, 1988) at a time when the zooplankton is present.

Hatchlings swim vigorously, backwards or forwards equally well, sinuous waves passing with great rapidity along the fins (Bather, 1895). Juveniles and adults raise and lower each fin by serial contraction of the muscles, and the waves produced move from one end of the fin to the other (Boycott, 1958). If irritated the cuttlefish shoots backwards by jet propulsion and can eject ink shortly after hatching (Bather, 1895). Dr A. M. Bidder (pers. comm.) saw a cuttlefish, within 30 min of hatching, eject ink to form a 'pseudomorph' from behind which it foiled her efforts to capture it. When laboratory-reared hatchlings were released into the sea they moved away in different directions, and showed no tendency to school or pair; furthermore only single individuals were encountered underwater (Hanlon & Messenger, 1988).

Growth and morphological changes

A newly-hatched *S. officinalis* in many respects resembles the adult externally. Internally the organ systems are present (Figs 1, 2) and morphological differentiation, including the gonads (Fioroni & Sundermann, 1983), is quite well advanced (Fioroni, 1964, 1990). However the proportions of several organs and structures differ from those of the adult.

At hatching, the mantle length (ML) ranges from 6.0 to 10.2 mm, the total length (TL) from 13.6 to 17.0 mm, and the body weight is about 150 mg; the hatchling of the cuttlefish is larger than that of most other cephalopods (Fioroni, 1964, 1982, 1990; see Hochberg, Nixon & Toll, 1992). The ML and total body weight have been monitored from hatching to 30–40 days old in the laboratory (Richard & Declair, 1969; see Boletzky, 1983; Boucaud-Camou, Yim & Tresgot, 1985), and in several animals from 7 to 56 days (Hanlon & Messenger, 1988). The size of the cuttlefish has been monitored through its life cycle in its natural habitat (Le Goff & Daguzan, 1991).

Sagittal sections of the hatchling (8.5 mm ML) show the main features to be mostly well developed (Fig. 1) but some features appear disproportionately large. The epithelial cells are relatively large (Figs 1b, 2, 3) and some are ciliated. Those of a loliginid, *Alloteuthis subulata*, are also relatively large (unpubl. obs.).

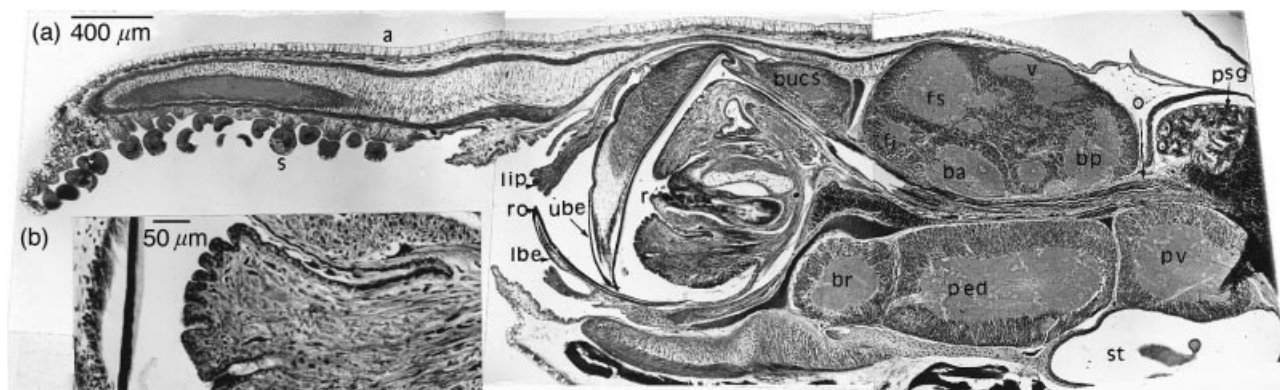


Fig. 2. *Sepia officinalis*. (a) Another medial sagittal section of the same hatchling as in Fig. 1 to show a dorsal arm, the buccal region and the brain. a, arm; ba, anterior basal lobe; bp, posterior basal lobe; br, brachial lobe; bucs, superior buccal lobe; fi, inferior frontal lobe; fs, superior frontal lobe; lbe, lower beak; o, oesophagus; ped, pedal lobe; psg, posterior salivary gland; pv, palliovisceral lobe; r, radula; ro, rostrum of beak; s, sucker; st, statocyst; ube, upper beak; v, vertical lobe. (b) The salivary papilla at higher magnification.

The 'cuttlebone' develops early in embryogenesis (Naef, 1923; see Fioroni, 1990) and eight or nine completed chambers are present at hatching (see Boletzky, 1983). At this time the cuttlebone forms the major portion of the mantle (Fig. 1). After hatching the septa are more closely spaced, and 15 septa are present in a month-old animal (Naef, 1923). In another study 6–14 septa were found in animals of 1–19 days old (Ré & Narciso, 1994). With growth of the animal the cuttlebone becomes relatively smaller and the proportion changes. The volume forms only about 9% of a mature animal of 1000 g total weight (Denton & Gilpin-Brown, 1973). The cuttlebone is calcified and its lamellar structure provides an indication of growth as the septa are laid down at fairly regular intervals (Choe, 1963; Denton, 1974; Boletzky & Wiedmann, 1978), although this process is influenced by temperature (Richard, 1969). A group of young *S. officinalis* (1–19 days old) had 6–14 lamellae present in their cuttlebones, with differences of 2–5 lamellae in animals of the same age, and a relationship between the number of lamellae and the length of the animal was found (Ré & Narciso, 1994); from this study the cuttlebone appears to reflect growth of the animal rather than chronological age.

The cuttlebone is important for the neutral buoyancy of the animal (see Denton & Gilpin-Brown, 1973; Denton, 1974; see Mangold & Bidder, 1989). In darkness liquid is pumped out of the chambers by the siphuncular membrane so the animal becomes more buoyant; in daylight the reverse takes place and as the volume of fluid increases in the chambers so buoyancy is reduced and the cuttlefish rests on the bottom or buries itself (Denton, 1974). Changes in buoyancy recorded in the laboratory (Denton & Gilpin-Brown, 1961a, b) correspond to those observed in the sea, the young being on or near the bottom during the day and in the water column during the hours of darkness (Hanlon & Messenger, 1988). The relatively large size of the cuttlebone of the hatchling is perhaps a reflection of the

importance of buoyancy in the early life of the animal. Cuttlebones (6–9 mm long) of hatchlings implode at pressures equivalent to depths of 50–100 m, whereas those from larger animals (47–170 mm) do so at pressures equivalent to depths of 150–200 m (Ward & Boletzky, 1984). These depths are somewhat greater than those usually inhabited by *S. officinalis* of these size classes, so the strength of the cuttlebone provides a margin of safety (Denton, 1974).

The funnel is approximately half the length of the mantle of a hatchling (Fig. 1a). The muscles of the funnel and of the ventral mantle wall are thick and well developed, and provide for the jet propulsive movements observed in the newly-hatched animal in the laboratory (Bather, 1895). At a mantle length of 35 mm the funnel forms a smaller proportion of the cuttlefish. The relatively large size of the funnel in the hatchling indicates that it is an active and mobile animal at this stage.

The arms diminish in length in the order IV > III > II > I (Tompsett, 1939). Ventral arms IV are longest and largest at the time of hatching (Bather, 1895), and remain so throughout the life of the cuttlefish; they are 39–50% of the ML in specimens of 34–42 mm ML (Adam, 1941). The brachial nerve is large and extends along the length of the arm, and it is encircled by muscles. Some tissues of the arms have a loose organization (Figs 2, 3a).

Arm suckers, with well-developed muscles, are numerous at embryo stage XX (Naef, 1923, 1928). There is a main circular muscle and a thickened suction pad and the suckers are capable of adhering to a foreign surface at hatching (Nolte & Fioroni, 1983). The suckers extend to the tips of the arms at hatching (Fig. 2), as they do in the adult. The main features of the suckers in a 12-day-old specimen (Nixon & Dilly, 1977) are already present in those of the hatchling (Schmidtberg, 1997). The cells of the sucker are relatively large at hatching (Fig. 3b). The chitinous inner ring of the

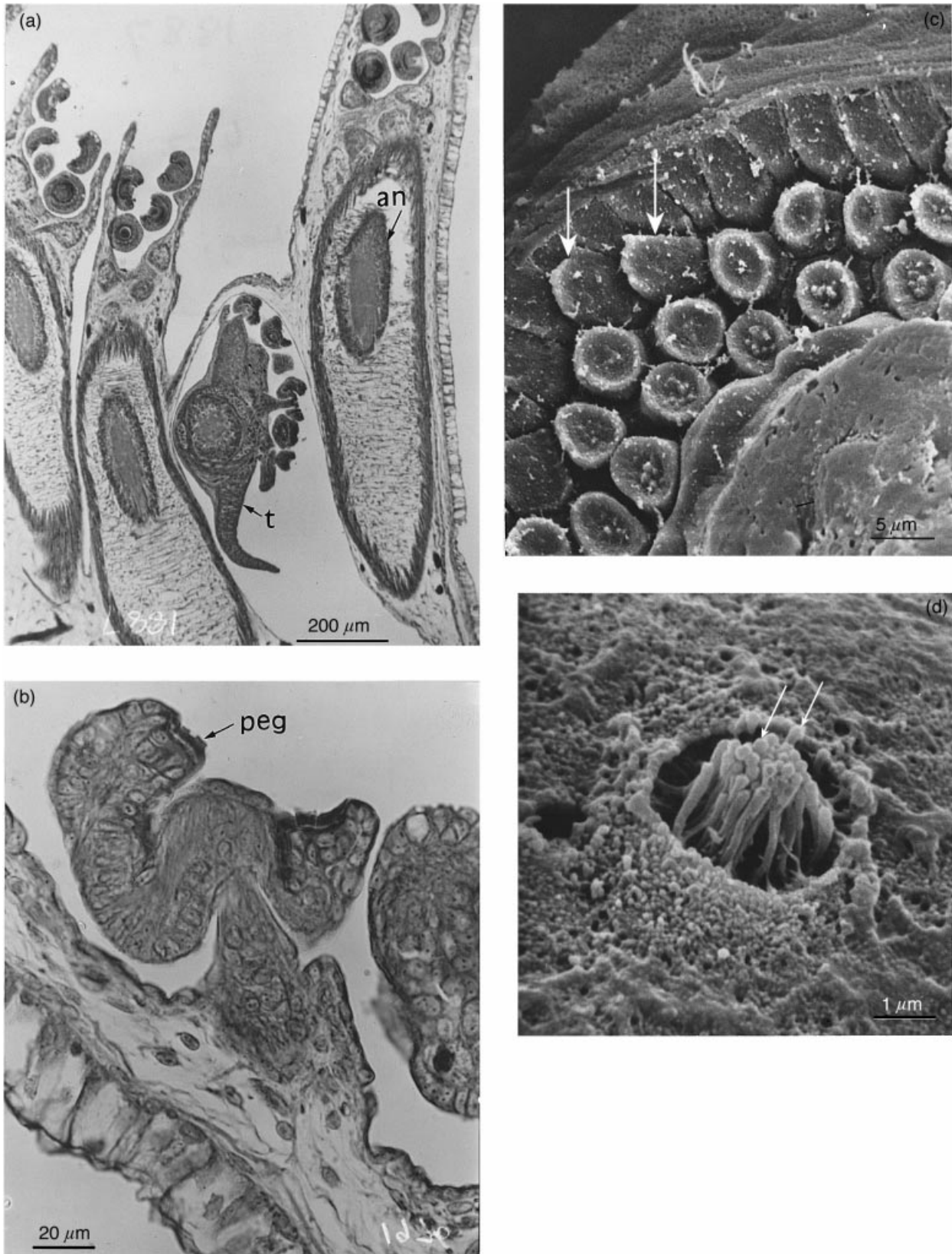


Fig. 3. *Sepia officinalis* (a) Three arms, cut sagittally, of hatchling in Fig. 1, and a tentacle, cut transversely. The latter has densely organized muscles surrounding the tentacular nerve. an, arm nerve; t, tentacle. (b) A sucker at higher magnification. Scanning electron micrographs of (c) an arm sucker to show processes developing into pegs (arrows); and (d) cilia at higher magnification on the outer surface of the sucker (arrows).

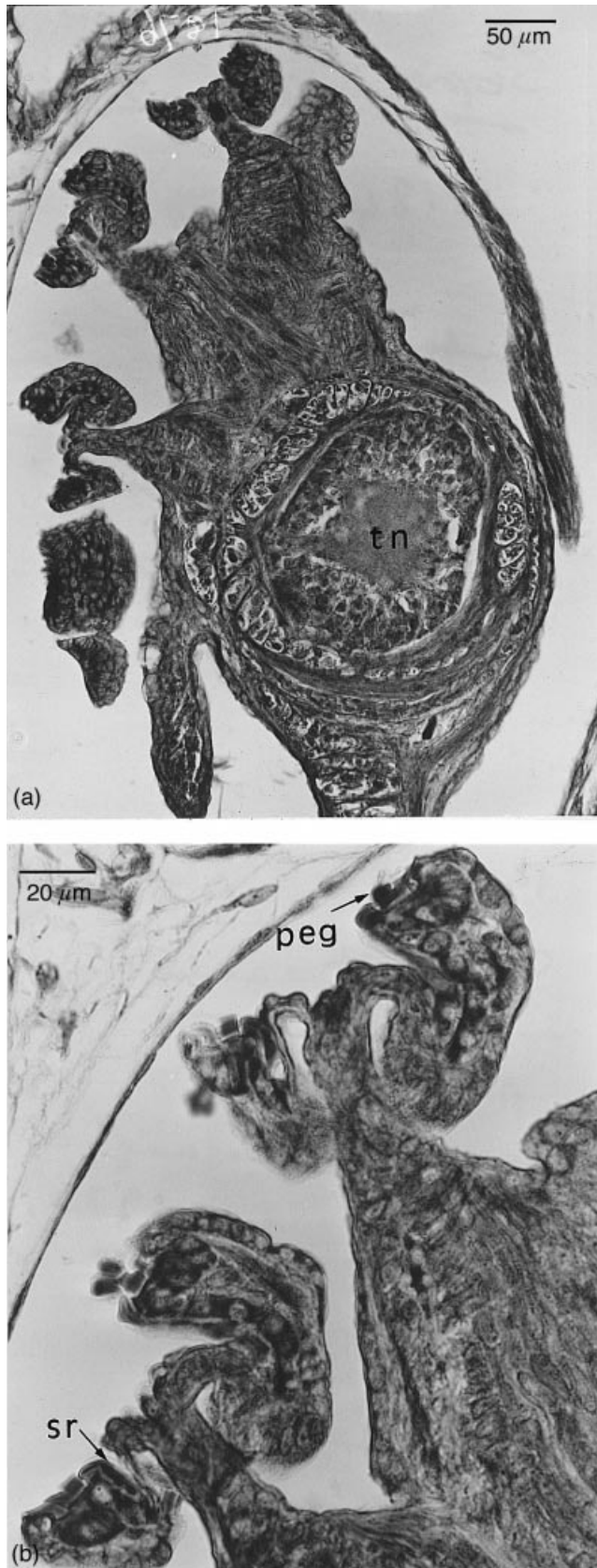


Fig. 4. *Sepia officinalis*. (a) Transverse section through tentacular club and its suckers (same hatchling as in Fig. 1), and (b) sucker at higher magnification. sr, sucker ring; tn, tentacle nerve.

sucker (Hunt & Nixon, 1981) has wide, blunt projections on one half and a few conical ones on the remaining half in a young cuttlefish of 12 days (8.5 mm ML). The infundibulum has two to three rings of polygonal processes, each with a projecting peg; the innermost, and earliest formed, ring of processes has the largest pegs (Fig. 3c) (Nixon & Dilly, 1977). At the periphery the radially arranged processes are elongated and represent the early stages of development of the pegs. The outer epithelium of the sucker has cilia (0.5–2.5 mm in length) which protrude from the surface (Fig. 3d). Ciliated sensory cells in arm suckers have been described in the newly-hatched cuttlefish by Sundermann (1983, 1991), and in juveniles by Graziadei (1964).

Histological sections of a tentacle of a hatchling show a relatively large nerve surrounded by dense muscle tissues (Fig. 3a) and in this it is like the juvenile and adult (Nixon & Dilly, 1977). In the hatchling the tissues of the tentacle differ markedly from those of its arms, as the former are dense and the latter of much looser organization (Figs 3a, b, 4). The importance of the tentacles and their capacity to elongate very rapidly is seen during the successful capture of prey shortly after hatching (Wells, 1958). In the loliginid squid, *Loligo pealei*, the transverse muscles of the tentacles produce extremely rapid extension for prey capture, and the ultrastructural characteristics include transverse striation of the muscle cells and short sarcomeres indicative of specialization for fast contraction (see Kier, 1991). The suckers of the tentacular club are well developed and are borne on longer stalks than those of the arms. In a 12-day-old animal the tentacular club has suckers of varying sizes (Fig. 5a). The infundibular surface of some suckers shows little differentiation into discrete pegs, but in others there are rings of well-defined pegs with developing pegs at the periphery, and a toothed, chitinous, inner ring (Fig. 5b, c). On the outer surface of the sucker there are pores from which a few cilia (20 µm long) emerge (Fig. 5b), eight being visible in one group (Fig. 5d). Graziadei (1964) found that a small sucker (3 mm diameter) of an adult had three principal types of sensory cells, including some 600 touch receptors and 100 chemoreceptors.

Capture and ingestion of prey, and the digestive tract

In the laboratory newly-hatched *S. officinalis* were observed by Naef (1923) "with tentacle clubs ready to catch a *Mysis* [a prawn-like malacostracan]. Such prey can be caught with great accuracy at a distance of 1–2 body lengths. The sudden extension and retraction of the club brings the prey to the mouth held by the suckers". Hatchlings will usually capture prey even on the first presentation; when suitable prey approaches, the young cuttlefish moves to the correct distance from which its tentacles, when projected, can reach the prey (Wells, 1958; Messenger, 1977; Hanlon & Messenger, 1988). The hatchling initially recognizes prey 'innately' and its response is visual since mysids swimming behind

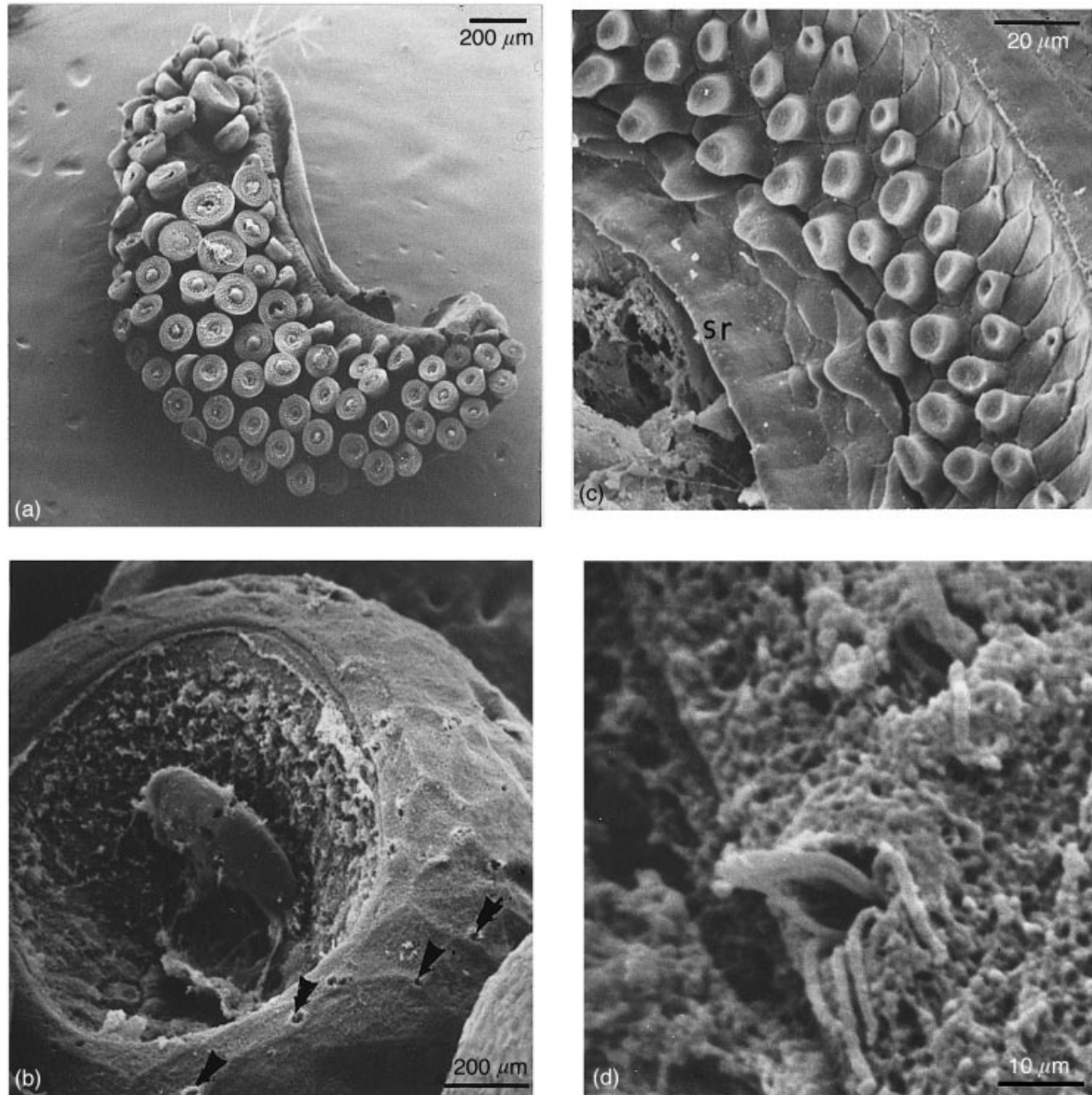


Fig. 5. *Sepia officinalis*. Scanning electron micrographs of (a) tentacle club of 12-day-old animal; (b) a sucker at higher magnification (arrows indicate cilia on the outer surface). (c) A well-developed club sucker showing the infundibular surface with cuticular inner ring and pegs, note those just developing at the periphery. sr, sucker ring. (d) Higher magnification of the club in (a) to show cilia protruding from the outer surface of a sucker.

a glass screen are as likely to be attacked as when swimming freely. Immobile prey is rarely attacked (Wells, 1958).

Prey is not attacked for 24–48 h after hatching, a period correlated with the absorption of yolk (Wells, 1958), although ingestion of food may occur before all of the yolk is used (see Fioroni, 1990). In the laboratory the first presentation of *Mysis* does not elicit colour changes, eye movements or other reactions from the hatchling. Then within about 2 min the eye nearest to the mysid turns sharply towards the prey, a few seconds later the whole animal moves, still on the bottom, to face the mysid. The two eyes then rotate forwards towards the prey, the cuttlefish flushes darkly, hovers,

by means of fins and funnel, and remains facing the mysid. The cuttlefish pales, jets straight and fast to within about 5 mm of the prey, then projects its tentacles to capture the mysid with the suckers of the clubs. This mode of attack does not appear to change with experience, but there is a marked reduction between the time of presentation of the *Mysis* and the first reactions of the cuttlefish (this reduces from 154 s to 5–6 s). No changes were detected in the number of attacks made on *Mysis* by cuttlefish of up to 14 days old. However, mysids presented behind glass were attacked almost continuously for as long as 6 h, in spite of the absence of any reward (Wells, 1958).

Fast-moving prey, such as mysids, prawns or fish fry,

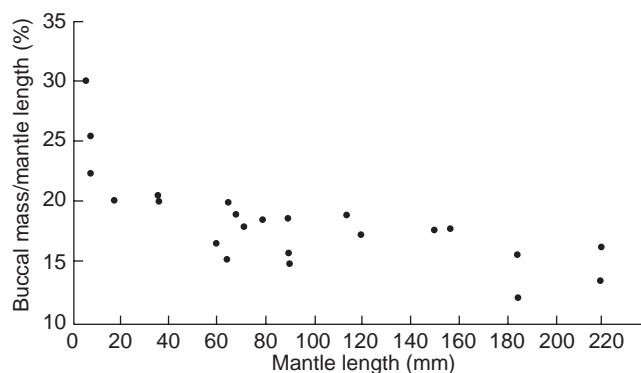


Fig. 6. The buccal mass as a percentage of the mantle length in relation to the mantle length.

are generally captured with the tentacles, but slow-moving prey such as a crab is usually 'jumped on' and seized by the arms or the tentacles (Wilson, 1946; Messenger, 1968; Duval, Chichery & Chichery, 1984; Chichery & Chichery, 1991a). Prawns removed 5 s or more after capture are moribund and the limbs exhibit convulsive movements (Messenger, 1968). Both crabs and prawns are immobilized by a toxin (Ghiretti, 1959, 1960) that is functional at hatching (E. Boucaud-Camou in Boucher-Rodoni, Boucaud-Camou & Mangold, 1987). A crab is usually wounded in the proximal joint of the hind pereopod (Chichery & Chichery, 1988). Juvenile and adult cuttlefish use the beak to bite the prawn near the point of flexure with the abdomen (Wilson, 1946).

The diet of *S. officinalis*, caught off Banyuls-sur-Mer in the western Mediterranean, has been followed from hatching to the late juvenile stage. It consists mainly of small crustaceans, which commonly swarm in large schools just above the bottom, and the young cuttlefish may either remain on the bottom to capture mysids by tentacular strikes, or move to take them in the water column (Hanlon & Messenger, 1988). Off the coast of northern France (Luc-sur-Mer) the stomachs of hatchlings and early juveniles (6–30 mm ML) were found to contain the remains of crustaceans (mainly of the shrimps *Crangon vulgaris* and *C. fasciatus*) which formed 75% of their diet, with fishes 15% and cephalopods 5% (Henry & Boucaud-Camou, 1991). Off the French coast, in the Normano-Breton Gulf, early juveniles (up to 20 mm ML) fed on mysids (35%) and amphipods (65%) (Le Mao, 1985), but dietary changes take place with growth and late juveniles (20–45 mm ML) feed mainly upon amphipods and caridean shrimps (Guerra, 1985). The diet is similar in these areas, but the species consumed may differ. The size and spectrum of prey eaten increases as the cuttlefish grows but the smallest diameter of each skeletal piece ingested has to be small enough to pass along the oesophagus, especially where the latter passes through the brain (Guerra, Nixon & Castro, 1988).

The buccal mass is almost one-third of the length of the mantle in a newly hatched animal (Fig. 1), but its proportion diminishes with growth. The antero-

posterior length of the buccal mass, as a percentage of the mantle length, falls from 31.5% at hatching to about 15% in an adult (Fig. 6). The main features of the buccal mass are present at hatching (see Nixon, 1985). The mandibular muscles are well developed and the muscle fibres are densely organized (Fig. 2a). The beaks are partially tanned. The oral borders of the beaks lack denticles, such as are present on those of the planktonic paralarvae of *L. vulgaris* and *O. vulgaris* (Boletzky, 1971). The radula is complete, with simple cone-like teeth present along its entire length (from the radular sac to the distal end of the radular ribbon: Fig. 2a). The newly-formed teeth, emerging from the radular sac, are larger than the older, earlier-formed, teeth at the distal end of the ribbon. The salivary papilla is a prominent feature of the buccal complex (Fig. 2b), and it carries the single duct from the paired posterior salivary glands. There are no denticles on the tip of the posterior salivary gland duct or on the anterior face of the salivary papilla (Fig. 2b) such as there are in *O. vulgaris* (Nixon, 1979). The lateral buccal palps extend from the front of the buccal cavity back to the entrance to the oesophagus, and, with the buccal complex, are capable of considerable movement. These palps bear small, backward-pointing, teeth on their antero-medial borders. The oesophagus is deeply folded, and it has a cuticular lining, which is already present at hatching. The cuticle consists of α -chitin (Rudall, 1965; Rudall & Kenchington, 1973).

The paired posterior salivary glands, which lie immediately behind the brain (Figs 1, 2a), are fully functional in the newly hatched animal (E. Boucaud-Camou in Boucher-Rodoni *et al.*, 1987). Each gland consists of ramifying tubules lined with a single type of secretory cell (Koueta & Boucaud-Camou, 1986). Among the secretory product is a glycoprotein, cephalotoxin, which immobilizes crustaceans and is secreted by both *S. officinalis* and *O. vulgaris* (Ghiretti, 1959, 1960). Lytic enzymes are also present, and these are usually involved in the facilitation of the penetration and spread of a toxic substance once it has entered the prey (Koueta & Boucaud-Camou, 1986). Boucaud-Camou & Roper (1995) investigated digestive enzymes in paralarvae of oegopsid squids (Enoploteuthidae, Ommastrephidae) and octopods (*Octopus* sp., *Japetella*) and found high proteolytic activity in the digestive gland and in the posterior salivary glands. These authors comment that the "strong proteolytic and weak amylolytic activities suggest (but not absolutely prove) carnivorous habits" and "The young seem especially equipped to digest proteins". Confirmation of a carnivorous diet in *S. officinalis* comes from the almost exclusive presence of crustaceans in the stomachs of hatchlings captured in the sea (Henry & Boucaud-Camou, 1991).

The digestive gland of *S. officinalis* is in two parts, being divided by the yolk sac (Boucher-Rodoni *et al.*, 1987), and lacks colour at hatching (Richard & Declair, 1969). The structure of the gland undergoes changes and at 5 days its cells show increasing activity, and large

protein inclusions or 'boules' appear; in an early juvenile, 20–30 days after hatching, the structure and colour of the digestive gland is similar to that of an adult (Boucaud-Camou *et al.*, 1985). The sequence of the appearance of different cell types and the changes in feeding indicate three stages of development of the digestive gland: a multiplication stage, from hatching to day 5, a maturation stage, from day 5 to day 30, and the adult stage, after day 30 (Boucaud-Camou & Yim, 1980).

The digestive process takes 4–6 h at 23 °C in animals 5–30 days old; this is faster than in adults at the same temperature, in which it takes 10–12 h (Boucaud-Camou & Yim, 1980). The conversion rate of food is 35–50% under normal conditions and does not appear to be related to water temperature, but hatchlings reared under continuous light showed a marked increase in food conversion efficiency when transferred to a cycle of 9 h light and 15 h dark (Pascual, 1978). The improvement in food conversion under the latter regime may have been due to an increase in prey capture during the hours of darkness, as this is the time when the hatchlings are in the water column (Hanlon & Messenger, 1988).

Chromatophores and chromatic behaviour

Chromatophores begin to develop in the embryo; brown ones appear first, followed by the yellow chromatophores, and the dorsal surface is much more heavily pigmented than the ventral surface (Fioroni, 1965). All the arms are pigmented by embryo stage XVII, and at a later stage the tentacles become pigmented; when it hatches, the cuttlefish is opaque and has a full complement of densely packed chromatophores (Fioroni, 1990). Iridocytes develop at embryo stage XVIII (Fioroni, 1965). Hanlon & Messenger (1988) made a detailed study of the coloration and body patterns and their relation to behaviour in *S. officinalis*, and estimated that a hatchling (7 mm ML) has approximately 400–500 chromatophores mm⁻² on the dorsal surface of the mantle that are fairly uniformly spaced. An early juvenile (15–20 mm ML) has some 200–500 chromatophores mm⁻², but in an animal of 220 mm ML the number of chromatophores is only 35–50 mm⁻², demonstrating a marked reduction in their recruitment and density. The ventral mantle surface has only 20 chromatophores mm⁻². The chromatophores are neurally controlled and participate in numerous components contributing to the complex patterning of the skin, making the chromatic behaviour of the hatchlings comparable with that of adults (Hanlon & Messenger, 1988).

During the day the hatchlings usually remain motionless, and are so successful at concealing themselves against their background, by general matching of colour, texture and patterning, that they are frequently overlooked by predatory fishes and human divers (Hanlon & Messenger, 1996). When *S. officinalis* (hatchlings to late juveniles) were transferred from the

laboratory into the sea human observers had great difficulty in finding them, especially after glancing away momentarily: this is beautifully illustrated in a series of colour photographs in which it is almost impossible to detect the young cuttlefish (Hanlon & Messenger, 1988). Flight and threat patterns are displayed and these can misdirect predators; and the young cuttlefish can escape from behind a discrete plume of ink and mucus, 'pseudomorph', and these authors commented "that hatchlings and juveniles are almost wholly concerned with concealment and predator evasion".

Receptors

The eyes first appear at embryo stage XV, and are well developed at hatching; light and transmission electron microscopy show that differentiation of the retina occurs in the last phases of embryonic life (Lemaire & Richard, 1978). The eyes form a relatively large proportion of the head, although the numerous chromatophores in the skin around them tends to obscure their size (Fioroni, 1965). The hatchling, like the adult (Messenger, 1973), can estimate the distance from which the tentacles could be ejected to capture the prey (Messenger, 1977). The eyes are important for perceiving different light intensities from the substrate, so the chromatophores are regulated to generate appropriate patterns for camouflage or crypsis (Hanlon & Messenger, 1988; Marshall & Messenger, 1996).

The paired statocysts have two separate receptor systems; a macula and statolith system, which detects gravity (linear acceleration), and a crista and cupula system with sensory hair cells, which respond to rotational movements (angular acceleration) (Budelman, 1977; Williamson, 1991). The statocysts form a large portion of the head at hatching (Fig. 1), but their subsequent growth is at a slower rate than the rest of the animal (Maddock & Young, 1984; Nixon & Young, in prep.). The internal features of the statocysts are simpler in a newly-hatched cuttlefish than in a juvenile, and only hamulus 4 is well formed and projects into the cavity (Bülow & Fioroni, 1989). Nevertheless the statocysts of *S. officinalis* show greater differentiation at hatching than do those of *L. vulgaris* (see Fioroni, 1990). The remaining hamuli develop rapidly in the days immediately after hatching; the features of this statocyst suggest a need to monitor faster pitching and rolling movements, perhaps associated with the buoyancy system of the cuttlebone (Young, 1989). The cuttlefish can sense low frequency 'sound', and, although no experiments were carried out to elucidate which sensory organ system detects vibration, it is highly likely that it is the statocyst (Packard, Karlsen & Sand, 1990).

Paired olfactory organs are present in the late embryo (Naef, 1923). Each organ lies posterior to the eye, and in front of the inhalant channel of the mantle (Tompsett, 1939). One type of ciliated epithelial cell, and two types of sensory cell are present (see Fioroni, 1990; Sunderman, 1991; Wildenburg, 1991). The olfactory organs

may be concerned in detecting chemical stimuli, including ink, as in *Loligo opalescens* (Gilly & Lucero, 1992; Lucero, Farrington & Gilly, 1994).

Ciliated cells are found in the epithelium around the outside of the sucker (Nixon & Dilly, 1977). In addition to ciliated cells, secretory cells are present on the surfaces of the head, arms, mantle, funnel, collar, olfactory pit, and funnel cartilage (Sundermann, 1991).

Epidermal lines of cells were first described in embryos by Naef (1928). Four epidermal lines are present on each side of the head (antero-posterior) and continue on to the arms, except the two shortest lines which run below each eye. More recent studies of embryos and post-embryos, with light and transmission electron microscopy, show the lines to consist of hair cells indicating a possible mechanoreceptor system (Sundermann, 1983). Each line consists of hair cells with kinocilia (up to 20 µm long) and an axon extending from the base, the hair cells being surrounded by accessory cells (Budelmann & Bleckmann, 1988). Single-hair cells and groups of hair cells alternate (Sundermann, 1983).

Stimulation of an epidermal line on the head of *S. officinalis* (10–16 mm ML) results in receptor potentials with features similar to lateral line microphonic potentials in fishes and amphibians; thus these lines of hair cells may provide a receptor system for the detection of small water movements (Budelmann & Bleckmann, 1988; Budelmann, Riese & Bleckmann, 1991). Calculations have shown that the sensitivity of these cells is such that a juvenile cuttlefish (about 30 mm ML) should be able to detect a moving fish, 1 m in body length, at a distance of 30 m. These young cuttlefish can find and capture prey in complete darkness, but the partial destruction of the epidermal lines reduces the rate of prey capture significantly (Budelmann *et al.*, 1991).

The central nervous system

The central nervous system grows throughout life in cephalopods (Wirz, 1959; Young, 1963; Packard & Albergoni, 1970; Giuditta *et al.*, 1971). The various lobes of the central nervous system of *S. officinalis* can be distinguished at hatching (Fig. 2a); quantitative studies show some to be well developed at this stage (Frösch, 1971) but others less so when compared with the brains of adults (Wirz, 1959). The relative volumes of some of the lobes change as the animal grows; these changes are mostly minor, but in a few lobes they are marked (Table 1).

The basal (and pedal) lobes are concerned with orientation, locomotion, prey capture, and chromatic and postural behaviour (Boycott, 1961). The basal lobes form 39% of the total brain volume at hatching (Frösch, 1971) but only 26% in animals of 70–185 mm ML (Wirz, 1954, 1959). Electrical and chemical stimulation of the basal lobes in late juveniles show that they are involved in movements of the head, eyes, buccal mass,

Table 1. The volumes of various lobes of the brain as a percentage of the total brain volume (except the optic lobes) at hatching (H) and juvenile/adult stage (J/A) (Wirz, 1959; Frösch, 1971; Nixon & Mangold, 1996)

Central nervous system	Stage	<i>Sepia officinalis</i>	<i>Octopus vulgaris</i>
Inferior frontal lobe	H	1.1	2.5
	J/A	0.9	3.0
Superior frontal lobe	H	4.4	3.6
	J/A	3.4	3.1
Subvertical lobe	H	2.2	0.8
	J/A	1.3	0.6
Vertical lobe	H	6.9	2.0
	J/A	11.9	5.0
Anterior basal lobes	H	8.5	8.8
	J/A	5.6	3.2
Posterior basal lobes	H	30.6	26.7
	J/A	20.4	15.2
Brachial lobes	H	4.6	8.3
	J/A	7.8	17.5
Pedal lobes	H	23.9	16.6
	J/A	18.1	18.0
Palliovisceral lobe	H	19.4	25.9
	J/A	22.1	24.1

arms, tentacles, and fins, and in the control of respiration, locomotion, swimming, and chromatophores (Boycott & Young, 1950; Boycott, 1961; Chichery & Chanelet, 1976, 1978). The relatively large proportion of the brain occupied by these lobes at hatching is in accord with the fact that the hatchlings are active in capturing prey, and generating complex body patterns for concealment or threat (Hanlon & Messenger, 1988).

The gross morphology and organization of the lateral basal lobes and the chromatophore lobes appear almost identical in hatchlings and adults, and the posterior chromatophore lobe in the suboesophageal mass shows little change between 7 and 112 days post-hatching (Hanlon & Messenger, 1988). This reflects the large number of chromatic and body patterns displayed by hatchlings with the numerous chromatophores they already possess.

The anterior basal lobe in juveniles, as in adults (Boycott, 1961), is concerned with the capture of prey: lesions in the central part of the lobe result in poor orientation of the cuttlefish towards its prey, and inaccurate ejection of the tentacles (Chichery & Chichery, 1991a, b). This lobe is important for prey capture at all stages of the life of *S. officinalis*.

The pedal lobe is also concerned with orientation, locomotion, prey capture, chromatic and postural behaviour. It forms about 24% of the total brain volume at hatching (Frösch, 1971) and 18% in adults of 70–185 mm ML (Wirz, 1954, 1959). In late juveniles electrical stimulation of the anterior part of the pedal lobe results in movements of the arms and tentacles, and of the posterior pedal lobe in retraction of the head and movements of the funnel (Boycott, 1961). The brachial lobe occupies 5% of the total brain volume at hatching (Frösch, 1971) and 8% in adults (Wirz, 1954, 1959).

Table 2. Comparison of various aspects of the early life, habits, and habitats of *Sepia officinalis* and *Octopus vulgaris*. The ML is measured between the anterior edge and the posterior apex of the mantle in *Sepia officinalis* (Roper & Voss, 1983), and in *Octopus vulgaris* it is measured from the mid-point between the eyes to the posterior apex of the mantle (Mangold-Wirz, 1963). The sources for the data for *Octopus vulgaris* are from Mangold (1983), Schmidtberg (1992), Villanueva (1994, 1995), Villanueva, Nozals & Boletzky (1995), a review by Nixon & Mangold (1996), Lenz (1997), and Wildenburg (1997)

	<i>Sepia officinalis</i>	<i>Octopus vulgaris</i>
Mature adults	Migrate—inshore shallow waters	Migrate—inshore shallow water
Breeding period, Mediterranean	Winter, spring and summer	Spring, summer, autumn
Spawning site	Spawning grounds	In crevices—inshore waters
Depth of spawning site	5–60 m	5–40 m
Bottom habitat	Rocks, pebbles, sand, mud associated with sea grass	Rocks, sand, mud
Number of eggs per individual	Up to 1000	100 000–500 000
Egg capsule length	25–30 mm	2 mm
Eggs	Laid singly and attached to algae or other objects on the substrate	Laid in strings and attached to roof or wall of den
Egg-care	None	Brooded in den by female
Embryo development	40–45 days at 20 °C	47–54 days at 21 °C
Mantle length at hatching	8–10 mm	2 mm
Total length at hatching	13.6–17.0 mm	2.9 mm
Weight at hatching	150–155 mg	1.0–1.4 mg
Weight	1000 mg (at 40 days)	200 mg (at 42 days)
Time of hatching	At transition from light to dark	? No observations
Hatchling	Opaque, resembles adult, and moves away from egg to inhabit the same bottom habitat	Translucent, with very short arms. At hatching young are expelled into water column by female.
Larva/paralarva type	Non-dispersive	Dispersive
Denticles on beaks (oral surface)	Absent	Present
Buccal mass length at hatching	30% of mantle length	60% of mantle length
Number of suckers on each arm	Numerous >20	3–4
Habitat		
daylight	On or near bottom	24 h in the plankton
darkness	In water column	
Response to light at hatching	Negative—buries itself or hides in daylight	Positive—moves toward light at hatching
Chromatophores		
at hatching	350–500 mm ⁻² on dorsal surface	70–80 total number per animal
in juvenile	200–500 mm ⁻² on dorsal surface	Massive increase at settlement
Chromatic and body patterns		
at hatching	As variable as in adult	No true patterning
in juvenile	Highly variable	Highly variable
Locomotion	Jet propulsion and swimming	Jet propulsion, ?passive drifting
Buoyancy	Cuttlebone forms a neutral buoyancy mechanism	May raft on surface film
Ink sac	Present	Present, silver coated
Ink ejection	At or shortly after hatching	Probable
Prey—in the sea	Crustaceans	Crustaceans—planktonic
Feeding	Predatory—“innate” response to shrimps	Predatory—planktotrophic
Mode(s) of prey capture		
tentacular strike	Present	Absent
arms	Present	Present
Paralysis of prey	Toxin(s) secreted by posterior salivary glands	Toxin(s) secreted by posterior salivary glands
Habits	Sand-covering, adheres to substrate by means of ‘sucker’ on antero-ventral surface of mantle and arms, enters water column in darkness	Entirely planktonic until close to time of settlement when it joins flotsam for short periods before finally settling
Settlement on bottom	Benthopelagic at hatching	At 33–54 days old (depending upon body weight)
Receptors		
Eyes	Present	Present
Extraocular light organs	Present	Present
Statocysts	Present	Present
Olfactory organs	Present	Present
Epidermal ciliated receptor cells	Present	Present
Lateral line analogue	Present	Present
Lifespan	12–24 (36) months	15–24 months

When this lobe is stimulated electrically there are movements in all of the arms (Boycott, 1961).

The vertical lobe system (the vertical, superior frontal and subvertical lobes) is concerned with learning and memory (see Young, 1965). The vertical lobe forms 7% of the total brain volume at hatching, and 12% in juveniles (Wirz, 1959; Frösch, 1971). Surgical removal of the vertical and/or superior frontal lobes from juveniles and adults impairs learning, and they will no longer follow a prawn as it passes out of sight (Sanders & Young, 1940). Newly hatched *S. officinalis*, when tested under the same experimental conditions, do not follow a prawn after it is lost from sight, and showed no ability to learn at 7 days old, though some is apparent at 1 month, with further improvement at 2 months; by 4 months learning, retention and hunting behaviour is exhibited (Messenger, 1973, 1977). Prey is first recognized 'innately' and the hatchling is "dominated by a built-in mechanism assuring attacks on mysids, at first coupled with almost complete inhibition of attacks on other moving objects" (Wells, 1958); this author also demonstrated that these young cuttlefish will continue to attack live mysids, even when behind glass (see earlier). A delay in learning this particular task is probably important as it allows innate attacks on appropriate prey to continue (Wells, 1958, 1962); if such attacks were inhibited then the capture of potential prey would be considerably reduced when food is essential for the rapid growth and development that takes place at this period.

The inferior frontal lobe occupies a relatively larger proportion of the brain at hatching than it does in a juvenile (Table 1). Stimulation of this lobe in juveniles results in some movements of the buccal mass (Boycott, 1961), progressive opening of the arms and grasping behaviour (Chichery & Chichery, 1991b). The buccal mass almost certainly has an active role as the hatchlings are more voracious than the juveniles.

DISCUSSION

Sepia officinalis and *Octopus vulgaris* inhabit the coastal regions of the eastern North Atlantic. *Sepia officinalis* is known to occur between 16°N and 59°N (see Boletzky, 1983) although there is no recent investigation of the geographical distribution of this species. *O. vulgaris* (*sensu stricto*) is now considered to occur from 30°N to 56°N or perhaps further south (F. G. Hochberg & K. Mangold, pers. comm.). After hatching the paralarva of the latter is entirely planktonic for several weeks, and so differs from the hatchling of *S. officinalis*, which spends only the hours of darkness in the water column. Around the time of settlement, and just after, the habits of *Octopus vulgaris* change as the animal moves from the plankton to live mostly on the bottom in coastal waters. Various aspects of the lives of these two species at and shortly after hatching can be compared in Table 2.

In the central nervous system some lobes of the brain

change their proportion in relation to the total brain volume between hatching and the juvenile stage (Table 1); differences and similarities are apparent between the two species. The brachial lobe is small relative to the total brain volume at hatching in both *S. officinalis* and *O. vulgaris*, but subsequently increases in proportion to the rest of the brain, especially in *O. vulgaris*, in which there is considerable growth of the arms and increase in the number of suckers around the time of settlement. The arms and suckers have a more complex role in the life of the octopus when settled on the bottom than when in the plankton. The pedal lobe of *S. officinalis* occupies a larger proportion of the brain at hatching than in the juvenile stage, whereas the reverse is so in the plankton-living hatchling of *O. vulgaris*. In hatchling *S. officinalis* this lobe is concerned with the ejection of the tentacles and capture of prey as well as other activities, whereas the latter has short arms and few suckers. At hatching the basal lobes (anterior and posterior) form a relatively larger part of the brain than at the juvenile stage of either species. These lobes are higher motor centres, concerned with movements of the head, eyes, buccal mass, arms, and tentacles, as well as with respiration, locomotion, swimming and chromatic control (Boycott, 1961). The relatively large size of these lobes in *O. vulgaris* and *S. officinalis* at hatching indicates that both species are active from the moment of emergence from the egg.

The vertical lobe system shows considerable development in the paralarva of *O. vulgaris*, while it is in the plankton, but by the time of settlement the lobe approaches the proportions found in the juvenile and adult stage (Nixon & Mangold, 1996). The vertical lobe system of *S. officinalis* takes almost four months to become well developed, and not until the end of this time is the learning curve comparable with that of the adult (Messenger, 1973, 1977). In *O. vulgaris* the subfrontal lobe also develops during its life in the plankton (Young, 1965, 1983; Messenger, 1973, 1977) in preparation for the increased use of the arms and suckers in the search for prey on the bottom.

The density of chromatophores is markedly different in the two species, being most densely packed in *S. officinalis*. These differences are reflected in the chromatophore and lateral basal lobes of the brain; in *S. officinalis* the gross morphology and organization of these lobes are very similar to those of the adult, but in *O. vulgaris* they are undifferentiated or poorly developed (Hanlon & Messenger, 1988). For its life in the plankton, *O. vulgaris* needs to be translucent and has few chromatophores. *S. officinalis* is benthopelagic and is highly successful at using complex body patterns to avoid detection by predators (Hanlon & Messenger, 1988).

Sepia officinalis increases in weight from 150 mg at hatching to 2 g at 50 days and 300 g at 150 days, furthermore it converts food efficiently (35–50%) (see Boletzky, 1983) (Table 2). Likewise *Octopus vulgaris* grows from 1–1.4 mg at hatching to 0.4 g at 50 days and 80 g at 150 days (Mangold 1983). The initial weight of

S. officinalis may be advantageous at least during this time.

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