FEEDING AND DIGESTION OF YOUNG SEPIA OFFICINALIS L. (MOLLUSCA : CEPHALOPODA) DURING POST-HATCHING DEVELOPMENT

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E. BOUCAUD-CAMOU, M. YIM and A. TRESGOT

Laboratoire de Zoologie, Université de Caen, Caen, 14000 Caen Cedex

CEPHALOPODA
SEPIA OFFICINALIS
FEEDING
DIGESTION
POST-EMBRYONIC DEVELOPMENT
EARLY JUVENILE

ABSTRACT. — A whole variety of studies on feeding and digestion in very young animals has shown there are three phases in the life of the cuttlefish *Sepia officinalis*. During the embryonic phase, food is only provided by the yolk, which is digested by the intracellular enzymatic activities of the yolk syncytium. During the post-embryonic phase, which begins with the first meal, the embryonic mode of nutrition (yolk digestion) comes to coexist with the post-embryonic mode (capture of small crustaceans and extracellular digestion in the digestive tract). The progressive differentiation of the digestive gland is closely related to exogenous feeding. The transition to the juvenile-adult phase is characterized by changes in the diet (greater variety of prey) and by the acquisition of an « adult » pigmentation and physiology in the digestive gland. This time is marked by other changes (in the blood and nervous system) and seems to constitute a critical period in the life of *Sepia officinalis*.

CEPHALOPODA
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NUTRITION
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JUVÉNILES

RÉSUMÉ. — Un ensemble de recherches sur la nutrition et la digestion chez les très jeunes animaux a permis de caractériser trois phases dans la vie de la Seiche *Sepia officinalis* L. Pendant la phase embryonnaire, la nutrition se fait uniquement aux dépens du vitellus, digéré grâce à l'activité enzymatique intracellulaire du syncytium vitellin. Pendant la phase post-embryonnaire qui commence au premier repas, les modes de nutrition embryonnaire (digestion intracellulaire du vitellus) et post-embryonnaire (capture de petits Crustacés et digestion extracellulaire dans le tractus digestif) vont coexister un certain temps. La différenciation progressive de la glande digestive est en relation étroite avec l'alimentation exogène. Le passage à la phase juvénile-adulte se caractérise par un changement de régime alimentaire (proies plus variées), l'acquisition d'une pigmentation et d'une physiologie « adultes » par la glande digestive. Il constitue dans la vie de la Seiche une période critique qui est marquée par d'autres changements au niveau du sang et du système nerveux.

INTRODUCTION

Although there is a lot of data available on the food and feeding habits of several young cephalopods that have been successfully reared in the laboratory (see the review of Boletzky and Hanlon, 1983, Boucher-Rodoni *et al.*, 1986 and Nixon, 1985), very little is known about the process of digestion in post-hatching cephalopods. Actually, most of the studies on digestion have been carried out on subadult and adult cephalopods (Boucaud-Camou and Boucher-Rodoni, 1983; Boucher-Rodoni *et al.*, 1986). The digestive gland has been shown to play an oustanding role in the digestive processes, being the main organ for both enzyme synthesis and digestive absorption. Moreover, conspicuous cytological changes in the gland can be related to the state of digestion (Boucaud-Camou and Boucher-Rodoni, 1983). Over the past years, our laboratory has

investigated the digestive processes of *Sepia officinalis* and made several studies of the early young (Yim, 1978, Boucaud-Camou and Yim, 1980, Yim and Boucaud-Camou, 1980, Boucaud-Camou, 1982, Tresgots, 1982), with various methods, such as histology, electron microscopy, histoenzymology and organ cultures using young *S. officinalis* reared in the laboratory under controlled conditions. We focused on the digestive gland because of its important role, and because it is the only digestive organ that is not fully developed at hatching. It is very different in colour and cytological structure when compared to the « adult » gland. This paper summarises all these results in an attempt to build a picture of the processes of feeding and digestion of an early juvenile cephalopod.

HATCHLINGS

Hatchling *Sepia officinalis* look like miniature adults and have the same benthic mode of life. The external yolk is fully digested but a large amount of yolk remains in the inner yolk sac. The space occupied in the adult by the digestive gland is largely occupied by yolk; the anterior lobe of the yolk sac, lined by the yolk syncytium, separates the paired lobes of the gland (Yim, 1978; Boucaud-Camou, 1982). The digestive cells are still undifferentiated; most of the cells are immature (Boucaud-Camou and Yim, 1980; Yim and Boucaud-Camou, 1980). At hatching, the digestive gland is still developing (multiplication stage) as shown by the many mitoses (Yim and Boucaud-Camou, 1980). Some « brown bodies » can also be seen; these are large inclusions in the cytoplasm, containing crystals. A few cells display synthetic activity, forming secretory granules : these are the « synthesizing cells » (Boucaud-Camou and Yim, 1980).

During the first days of life, growth is still slow (Fig. 1). Newly hatched *Sepia* may not capture prey for up to three days while continuing nutrition (embryonic phase, Boucher *et al.*, 1986), the nutriments being provided exclusively from the yolk by the digestive activity of the yolk syncytium. This fact is illustrated by the strong proteolytic activity of the yolk syncytium, contrasting with the weak activity of the digestive gland (Boucaud-Camou, 1982). The digestive activity of the yolk syncytium is intracellular as shown by the strong positive reaction for such lysosomal enzymes as acid phosphatase (Boucaud-Camou, 1982) and dipeptidylaminopepti-

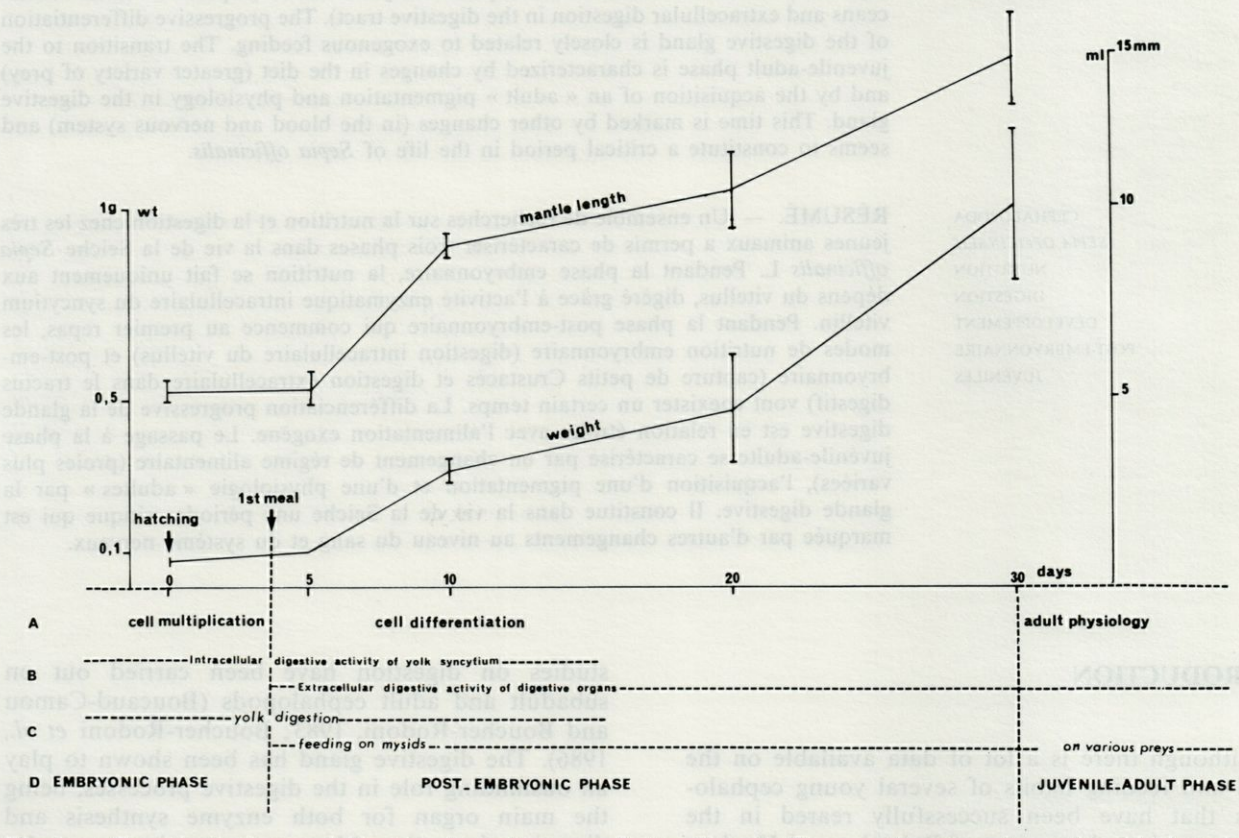

Fig. 1. — Growth, feeding and digestion in early young *Sepia officinalis*. The growth curves size and weight have been drawn from the data of Yim (1978). Each point is the mean of measures from 10 animals reared in the laboratory and fed on mysids. A : state of the digestive gland. B : mode of digestion; C : food; D : phases of the life cycle.
wt = fresh weight, ml = dorsal mantle length

dase II (Boucaud-Camou, unpublished results), and negative reactions for such extracellular enzymes as chymotrypsin (Boucaud-Camou, 1982).

POST-EMBRYONIC PHASE

This begins with the first meal (exogenous feeding). The favourite prey animals are mysids, which are plentiful in summer, in warm coastal waters. Prey capture by early juvenile *Sepia officinalis* has been extensively studied (Wells, 1958, 1962; Boulet, 1964; Messenger, 1968, 1977). Prey is digested far more quickly than in the adult (max. 5 hours at 25 °C, Yim, 1978).

The first meal releases the secretory activity of the digestive gland : so-called « boules » (proteinaceous inclusions characteristic of most cephalopods; Boucaud-Camou and Boucher-Rodoni, 1983) appear together with a secretion filling the lumen of the tubules of the gland, which has grown considerably at the expense of the inner yolk sac (Yim and Boucaud-Camou, 1980). The glandular secretion displays high proteolytic activity. However, yolk digestion continues, due to the digestive activities of the yolk syncytium (Boucaud-Camou, 1982).

During the following days, the two modes of nutrition, embryonic (yolk) and post-embryonic (prey capture), coexist. Yolk reserves would help very young *Sepia* to survive if the amount of food available were not sufficient. However, if there is enough food, the growth curve becomes exponential. During this post-embryonic phase, the digestive cells progressively differentiate and, about ten days after hatching, the four cell differentiation stages present in the adult can be recognized, i.e. in addition to the *immature cells* and the *synthesizing cells* already present at hatching, the *resting cells* and the *mature digestive cells* (Yim and Boucaud-Camou, 1980, Boucaud-Camou and Yim, 1980).

Apparently, the cell differentiation is triggered by exogenous feeding. The digestive glands of hatchlings or late embryos maintained in organ cultures for more than ten days do not display the conspicuous changes that appear after feeding (secretion, « boules », vacuoles). The most striking feature in these cultures is the great number of brown bodies (Tresgots, 1982). Moreover, the digestive gland of animals unfed since hatching looks inactive (Boucaud-Camou, unpublished results).

As first noticed by Richard and Decleir (1969), the digestive gland is not tinted at hatching and becomes progressively pigmented to reach the « adult » brown colour at the end of the first month of life (Yim, 1978). Obviously, the pigmentation is related to feeding : organ cultures of hatchling digestive glands remain unpigmented (Tresgots, 1982).

TRANSITION TO THE JUVENILE-ADULT PHASE

By the end of the first month of life, the digestive gland has the same coulour, the same histological structure and the same histophysiology (number of the « boules ») as in the adult (Yim, 1978, Yim and Boucaud-Camou, 1980). By now, the young *Sepia* will have reached an average mantle length of 15 mm (Yim, 1978) and be able to catch a greater variety of prey : small crabs, shrimps and fishes. At about this time there occur changes in blood composition (Richard and Decleir, 1969) and in the nervous system (Chichery, 1976). These seem to mark the transition to the juvenile-adult phase (Boucher-Rodoni *et al.*, 1986), a stage that seems critical in the life of *Sepia officinalis* at least in the laboratory. It is then that high mortality often occurs; it might also occur in nature, and it should be taken into account in recruitment studies.

DISCUSSION AND CONCLUSION

Under the aspects of feeding and digestion we have tried to define three phases in the life of *Sepia officinalis*. The *embryonic phase* corresponds to embryonic development and ends, not at hatching, but with the first meal. During this stage there is only yolk digestion; the digestive gland is still developing (cell multiplication) and has no digestive function. The *post-embryonic phase* is characterized by the beginning of exogenous feeding, which induces the start of exponential growth, and by the development of the digestive activity of the digestive gland (cell differentiation). Our post-embryonic phase corresponds almost exactly to the « période post-embryonnaire » of Richard and Decleir (1969) but is slightly longer. We have not used the term "larval", for there are no true "larvae" in cephalopods (Boletzky, 1974). Especially in *S. officinalis*, early juveniles have the same mode of life as the adults. The juvenile-adult phase begins (long before the onset of sexual maturity) with the physiological maturity of the digestive gland (adult physiology), a more varied diet and other metabolic and physiological changes, which make the end of the post-embryonic life a critical stage. These phases might, perhaps, be suitable for all cephalopods, as suggested in an earlier review (Boucher-Rodoni *et al.*, 1986). Certainly work on other species (especially those with a planktonic stage) is needed, considering the different feeding and digestive events of this period with respect to the three phases defined in Figure 1.

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