

# 3

## Feeding and Digestion in Cephalopods

EVE BOUCAUD-CAMOU

Laboratoire de Zoologie  
Université de Caen  
14032 Caen, France

RENATA BOUCHER-RODONI

Station Biologique  
29211 Roscoff, France

I. Summary and Perspectives .....	149
II. Introduction .....	150
III. Feeding .....	151
A. Food .....	151
B. Feeding Habits .....	152
C. Prey Capture .....	153
D. Feeding Organs .....	155
E. Killing the Prey .....	158
F. Food Intake .....	160
IV. Digestion .....	164
A. Structure of the Digestive Organs .....	164
B. Physiology of Digestion .....	170
References .....	180

### I. Summary and Perspectives

Since Bidder's review (1966), the knowledge about feeding and digestion in cephalopods has steadily increased. The diet and feeding habits of species such as the common benthic hunters, octopods and sepioids, as well as of other less common cephalopods such as *Nautilus*, cirrate octopods, and oceanic squids, are becoming better known. Accordingly, rearing and laboratory maintenance of cephalopods are in progress.

Anatomists and ethologists have studied in detail the mode of prey capture and ingestion of food in some species. The different stages of attack and the functioning of organs such as the suckers and the different parts of the buccal mass have been thoroughly analyzed. Thus, the part played by the different feeding organs

(for example, in drilling holes through shelled molluscs) and the neural control of food intake are now well established in *Octopus*.

The poison glands of cephalopods have always deserved much attention. A number of biological amines, enzymes, and true toxins such as cephalotoxins, eleidosin, and tetrodotoxin have been recognized in the posterior salivary glands of various cephalopods.

As far as digestion is concerned, the fine structure of digestive organs turns out to be very similar among the species investigated by electron microscopy (*Sepia* and octopods). Digestive enzymes such as chymotrypsin, cathepsin, various peptidases, amylases, chitinases, and lipases have been recognized in the alimentary tract and organs. The digestive gland and the salivary glands (in octopods) are considered the most important site of digestive-enzyme synthesis. The digestive gland is also one of the main organs concerned with digestive absorption, at least in *Octopus* and *Sepia*. Moreover, in *Sepia*, the ancestral process of intracellular digestion has been maintained.

Thus it appears, from these data, that most of the cephalopods investigated (mainly Octopodidae and Sepioidae) present very similar digestive features, and are, from a digestive point of view, more closely related to other molluscs than previously assumed. The primitive "multipurpose" digestive cell of molluscs (Purchon) was maintained in the cephalopods' digestive gland, in which a single type of cell performs various functions, such as secretion, absorption, intracellular digestion, and excretion.

In spite of increasing data on the digestive processes in cephalopods, there is still an urgent need for more information on digestive enzymes, their nature and localization, and their involvement in intracellular digestion. We need to know more about neural and hormonal control of digestion. Most of the studies have been restricted to a few species (mostly octopods and sepioids), and very little is known about digestion in teuthoids. Such a gap must be filled as soon as possible in order to obtain a more complete picture of digestion in cephalopods. This should not be difficult because of increasing success in laboratory maintenance of squid.

## II. Introduction

Cephalopods stand apart from other molluscs because of the extensive development of their central nervous system. They have been competing with fishes since the emergence of vertebrates. Various feeding methods have been developed in other molluscan classes, whereas cephalopods are all predaceous carnivores, either benthic or nectonic hunters. Thus they have come a long way from their primitive, deposit-feeding molluscan ancestors.

Related to their mode of feeding, cephalopods have been known to have

### 3. Feeding

evolved  
lar enzym  
molecule  
that intra

#### A. Food

Cephala  
ceans, fis

#### 1. Diets

Direct c  
have been  
and some  
determine  
1967; Wel  
cephalop  
Some larg  
(Fields, 19  
1978; Wor  
Shrimps,  
stomach co  
ceans are n  
fishes, poly  
gastropods)  
present in th  
published da  
caught with  
if it repres  
(1966). As th  
ceans first, th  
small mesope  
also feed on p  
P. S. Jacquem  
N. A. Solis,

#### 2. Diets in C

Boletzky ar  
feeding cepha

evolved a *vertebrate* mode of digestion, with *pancreatic* secretion of extracellular enzymes and *intestine-like* absorption (in the caecum and intestine) of small molecules. Although this scheme holds largely true, recent observations suggest that intracellular digestion also occurs in some species.

### III. Feeding

#### A. Food

Cephalopods are active predators that feed on moving, living animals. Crustaceans, fishes, and molluscs are their usual prey.

##### 1. Diets in the Wild

Direct observations of cephalopods feeding, generally made by scuba divers, have been restricted to common coastal species such as octopuses, cuttlefishes, and some loliginids (Boletzky and Hanlon, 1983). The diet of octopuses can be determined from the discarded remains around the holes they inhabit (Altman, 1967; Wells, 1978), but the most common way to gather information on the cephalopod diet is by examining stomach contents of freshly caught animals. Some large-scale studies have been made on commercial catches of squid (Fields, 1965; Nigmatullin and Ostapenko, 1976; Loukashkin, 1977; Guerra, 1978; Worms, 1979; Karpov and Cailliet, 1979).

Shrimps, prawns, and crabs are the most commonly found crustaceans in the stomach contents of coastal, bottom-living cephalopods, whereas pelagic crustaceans are more commonly found in the stomachs of oceanic forms. Various fishes, polychaetes, cephalopods (and, in the stomachs of octopods, bivalves or gastropods) have also been recognized. Occasionally, chopped seaweed is also present in the stomach (Bidder, 1966; Lane, 1974; E. Boucaud-Camou, unpublished data). It is still difficult to decide whether the seaweed is accidentally caught with the prey and remains undigested due to lack of suitable enzymes, or if it represents a correction of the carnivorous diet, as suggested by Bidder (1966). As the cephalopods grow, the nature of their prey changes: small crustaceans first, then larger crustaceans, fish, etc. However, throughout their lives, small mesopelagic oegopsids feed mainly on copepods and some large oegopsids also feed on planktonic crustaceans in subadult and adult stages (N. M. Erhardt, P. S. Jacquemin, B. F. Garcia, D. G. Gonzales, B. J. M. Lopez, C. J. Ortiz, and N. A. Solis, unpublished observations, 1981).

##### 2. Diets in Captivity

Boletzky and Hanlon (1983) compiled all the diets that have been used for feeding cephalopods maintained in captivity. Captive cephalopods are usually

fed the same prey they hunt in the wild (living crabs, shrimps, fishes, and for the younger ones, mysids and copepods). They can also be fed organisms they do not encounter in their natural habitat, such as *Artemia salina* for very young animals, or prey they do not preferentially attack, such as *Gammarus* for young *Sepia* or bivalves for *Octopus*.

Moreover, captive cephalopods may accept dead food. *Octopus* and *Eledone* can easily be fed pieces of crabs, fishes, or molluscs. *Nautilus* seems to accept almost all sorts of food, even of nonmarine origin, such as pieces of chicken or dog meat (Bidder, 1966; Boletzky, and Hanlon, 1983). Nevertheless, this species also eats live Crustacea (Ward and Wickstein, 1980).

Decapods, which commonly hunt very mobile prey, are more reluctant to accept dead food. However, it has been reported that frozen shrimps, freshly killed fishes, or even pieces of fish have been captured by squid or cuttlefishes (Boucaud-Camou, 1973; Boletzky and Hanlon, 1983). This is also the case for *Illex illecebrosus* which, when fed in aquaria with dead capelins thrown in the tank, attack them before they reach the bottom (Bradbury and Aldrich, 1969; Boucher-Rodoni, 1975). All cephalopods, however, although occasional scavengers, feed preferentially on live prey in the wild as well as in laboratory tanks.

### B. Feeding Habits

Cephalopods inhabit all levels of the seawater column, some species being benthonic, some nectobenthonic, and some pelagic. In spite of these ecological differences, their feeding ethology is almost the same throughout the class. All of them (young as well as adults) feed mainly on live Crustacea, molluscs (cephalopods included), and fishes of adequate size inhabiting their normal ranges. They swim in pursuit of their prey, which they capture with their arms and/or tentacles. Some benthic species, such as *Sepia* buried in the sand, or octopuses in their home, or cirrate octopods in *open umbrella-like* posture, can occasionally catch prey without pursuit.

Traditionally, cephalopods are considered dim-light feeders. *Octopus vulgaris* and *Sepia officinalis* are reported to be more active at night (Denton and Gilpin-Brown, 1960; Wells, 1965; Altman, 1967). Teuthoids will attack bait and are caught by squid-jigging at dusk or dawn, or when attracted by lights during the night hours. In *Octopus*, nevertheless, Nixon (1969a), using an automatic food dispenser, recorded a majority of responses between 0900 and 2100, and only some attacks during darkness. Wells (1978) points out that this species seems to be an opportunist, prepared to feed at any time. We also found that various species of cephalopods will accept food at any time of day (*O. vulgaris*, *O. cyanea*, *Eledone cirrhosa*, *S. officinalis*, *I. illecebrosus*, *Loligo vulgaris*, *L. forbesi*). As far as teuthoids are concerned, Vovk (1972) reported seasonal and diel variations in feeding of *Loligo pealei*, a species that was found to feed most

### 3. Feeding and D

intensely during night. Such is a

#### C. Prey Capture

In coleoid cephalopods, feeding is initiated (Young, 1965). *Octopus* (Wells, 1978) uses its tentacles, if pre

#### 1. Arms and T

In all cephalopods, the arms encircle the bu

*Nautilus* has suckers on its arms; they can adhere to the prey by a muscular sheath

Octopods have a web between their arms by a web and p... side are numbe... (1932). The cirr... *cirri* as well as

Decapods have two rows of suckers with two rows of suckers co

The suckers are used for capturing prey (1977). The suckers are arranged in a firm ring (Hunt, 1969). The suckers are covered with c... the processes a... (Nixon and Di... well developed cells (probably... (Graziadei, 1969). The suckers is p... gelatinous anir

The suckers are used for capturing prey proposed the f

1. In the in... the suck...
2. The infu... may act

intensely during daylight hours (maximum at about 1600) and less during the night. Such is also the case for *Loligo opalescens* (Karpov and Cailliet, 1978).

### C. Prey Capture

In coleoid cephalopods, which are mostly active hunters, the attack is visually initiated (Young, 1961; Messenger, 1968), although touch is important in *Octopus* (Wells, 1978). In all cases the prey is captured with the aid of arms and tentacles, if present. *Nautilus* seems to hunt chiefly by smell and touch.

#### 1. Arms and Tentacles

In all cephalopods, "those who bear their feet on their head," the arms encircle the buccal orifice.

*Nautilus* has 19 pairs of digital tentacles, without suckers but ridged so that they can adhere to the prey. These tentacles can be completely retracted into a muscular sheath (Bidder, 1966).

Octopods have eight slender and mobile subequal arms connected at their base by a web and provided with one or two rows of sessile suckers. The arms on each side are numbered from one to four (from dorsal to ventral) (Robson, 1929-1932). The cirrate octopods, which have a very deep web, possess two rows of *cirri* as well as suckers.

Decapods have eight arms, generally shorter than those of octopods, provided with two rows of stalked suckers. In addition they have two extensible tentacles with suckers concentrated on a terminal club.

The suckers of various cephalopods have been well studied by Nixon and Dilly (1977). The sucker has a chamber, the acetabulum (Fig. 1), lined by a chitinous, firm ring (Hunt and Nixon, 1981). Above the acetabulum lies the infundibulum, covered with cuticular polygonal processes, each provided with a peg. Actually, the processes are formed by aggregations of rods making numerous minute pores (Nixon and Dilly, 1977). The infundibulum is encircled by a rim, particularly well developed in octopods. Muscles are attached to the acetabulum. Sensory cells (probably mechano- and chemoreceptors) are present in the infundibulum (Graziadei, 1962, 1964; Nixon and Dilly, 1977). In many squid the inner ring of the suckers is provided with sharp teeth, which are presumably used to adhere to gelatinous animals or to retain food particles (Nixon and Dilly, 1977).

The suckers are indeed powerful organs of attachment. Nixon and Dilly (1977) proposed the following stages in the functioning of the sucker:

1. In the initial impact upon the prey, a hermetic seal is formed by the rim of the sucker.
2. The infundibular surface comes into contact with the prey. The fine pores may act either by adhesion and/or suction.

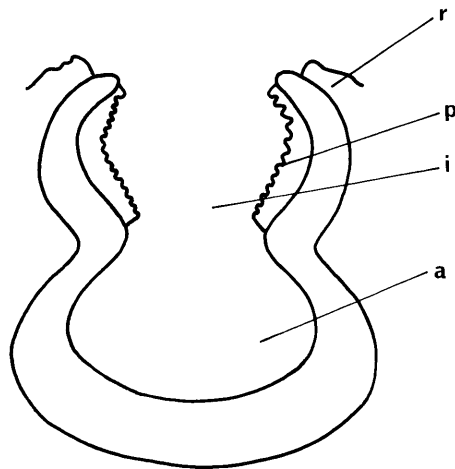


Fig. 1. Sagittal section through a small sucker of *Octopus*. a, acetabulum; i, infundibulum; p, peg; r, rim. (Drawing made from a photograph of Nixon and Dilly, 1977.)

3. The suction effect is produced by the contraction of the muscles of the sucker.

## 2. Modes of Prey Capture

**a. Decapoda.** *Sepia officinalis* captures fast-moving prey with its two long tentacles. Messenger (1968) distinguished three components in the attack process, which is visually initiated:

1. Attention: marked by color changes, erection of the first and second pair of arms, movement of eyes and head. The animal positions itself in the axis of the prey.
2. Positioning: the animal swims until it is about one mantle length away from the prey (the *attacking distance*).
3. Seizure: the tentacles are ejected very quickly, prey being seized within 30 msec. The prey is then carried further away from the animal for another 30 msec before being brought back to the mouth in about 150 to 300 msec.

Little is known about prey capture in other decapods. Whereas it seems clear that some loliginids and the ommastrephids behave like *Sepia*, others may capture prey in different ways (Messenger, 1977). In the ommastrephid *I. illecebrosus*, for instance, the sessile arms are used for initial prey capture (Bradbury and Aldrich, 1969).

In *Octopus*, too, the attack is determined by a moving object, perception of which is generally monocular and accidental (Messenger, 1968). Wells (1978)

## 3. Feeding and

has described the animal facing together with color changes. Crabs are trapped in the web until the

In cirrate octopods show octopods and Brundage, hunting by passing. Indeed, deep-sea animals plankton. Its tactile sense

In *Nautilus* form a cone of tentacles (Biddond) senses are

## D. Feeding O

### 1. Anatomy of

The first part within the circle rotate or protrude lined with a glass lips and in some. From the buccal with their muscles support strong

Within the space side to the dorsal lateral lobes.

The salivary glands' duct, with buccal orifice. small teeth; large can be everted

The odontophore which lies the radular sac. The radular sac, octopods to decapods

has described how an octopus catches moving prey. First, the head is raised, and the animal faces the disturbance. There is a smooth approach to the prey, together with color changes, followed by a jet-propelled forward leap on the prey. Crabs are trapped in the interbranchial web, covered by arms, and gathered in the web until the octopus returns home to eat.

In cirrate octopods the cirri are thought to be tactile organs. Photographs often show octopods with the cirri erected, the arms and web being expanded (Roper and Brundage, 1972). This *open umbrella-like* posture is interpreted as a form of hunting by passive drifting, the cirri acting as receptors to detect water movements. Indeed, the tactile sense must be dominant in the search for prey in such deep-sea animals. *Argonauta* is a pelagic octopod that swims slowly among the plankton. Its arms bring to the mouth any small prey touching them. Only the tactile sense seems to be involved (Lacaze-Duthiers, 1892; Young, 1960).

In *Nautilus* swimming in search of food, a group of tentacles are spread to form a *cone of search*. The food is then brought to the mouth by another set of tentacles (Bidder, 1962). In the aquarium both chemical (first) and tactile (second) senses are involved in the food search (Haven, 1972).

#### D. Feeding Organs

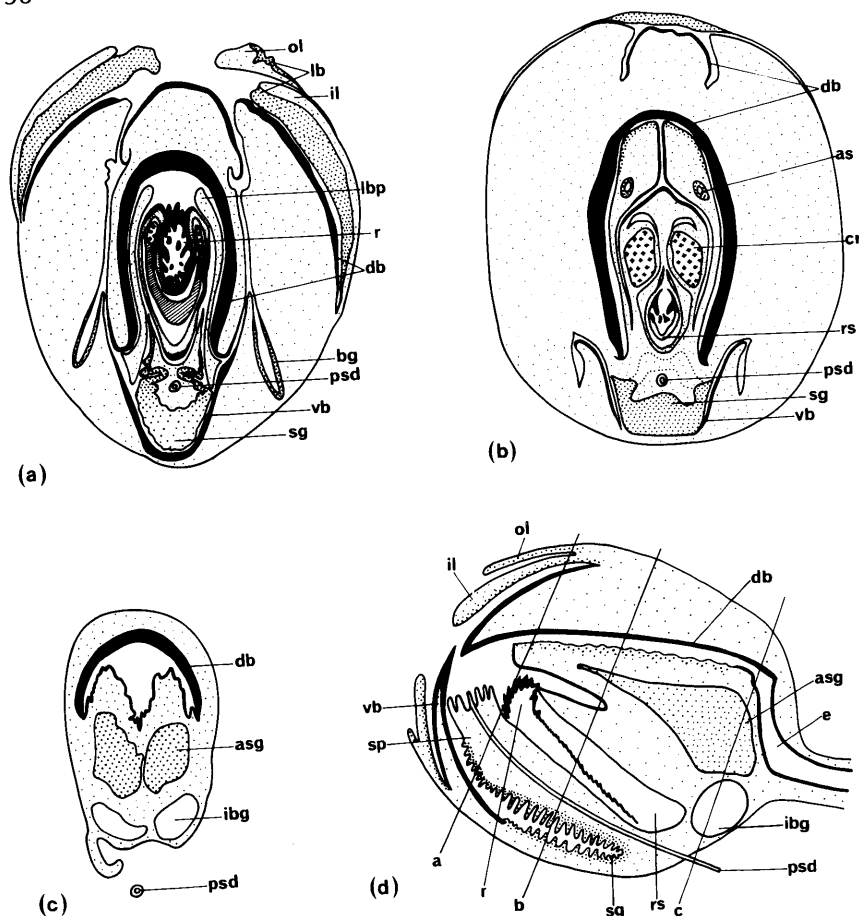
##### 1. Anatomy of the Buccal Mass

The first part of the digestive tract consists of the buccal mass, which lies within the circle of the arms. Bathed in a blood sinus, it is very mobile and can rotate or protrude to bite. The buccal orifice is surrounded by two lips (Fig. 2) lined with a glandular epithelium. In decapods a buccal membrane encircles the lips and in some genera is developed in the females into a copulatory pouch. From the buccal opening protrude the hard extremities of a pair of beaks that, with their muscles, form the buccal mass (Fig. 3). The lateral wings of the beaks support strong muscles, which form the wall of the buccal mass (Fig. 2).

Within the space made by the jaws, three organs are found from the ventral side to the dorsal side (Fig. 2): the salivary papilla, the odontophore, and the lateral lobes.

The salivary papilla is a muscular organ. In its axis runs the posterior salivary glands' duct, which opens at the extremity of the salivary papilla, close to the buccal orifice. In *Octopus* the papilla is covered by a thin cuticle forming very small teeth; larger teeth are present at the extremity of the salivary duct, which can be everted in order to drill shells (Nixon, 1980).

The odontophore, supported by two cartilages, is folded in an axial groove, in which lies the radular sac, containing the odontoblasts and the radula (Fig. 3). The radular sac, well developed in *Nautilus*, shows a trend to reduction from octopods to decapods, decreasing in size from *Loligo* to *Sepia* and *Sepiola* (Gabe



**Fig. 2.** Buccal mass of *Sepia officinalis*. (a), (b), (c) Transverse sections through the plates a, b, and c, (d) Sagittal section. asg, anterior salivary gland; as, anterior salivary gland duct; bg, buccal glands; cr, radular cartilage; db, upper (dorsal) beak; ibg, inferior buccal ganglia; il, inner lip; lb, labial gland; lbp, lateral lobe; r, radula; rs, radular sac; sg, submandibular gland; sp, salivary papilla; vb, lower (ventral) beak. (After Boucaud-Camou, 1973, modified.)

and Prenant, 1957). However, the radula is totally absent in cirrate octopods (Robson, 1929–1932).

The lateral lobes are paired muscular organs, forming between them a narrow passage for food. On the inner face of each lobe is the opening of one of the paired anterior salivary glands.

The esophagus leaves the buccal mass dorsally. Ventrally lie the inferior

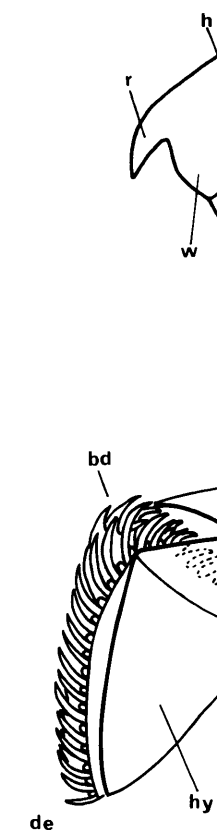
### 3. Feeding and Digestion

buccal ganglia and the buccal mass in the buccal mass is

### 2. Beaks and Radula

Both the beak and the radula are produced by odontoblasts producing the beaks (Ducros, 1966).

These hard parts are the radula, and both have



**Fig. 3.** Beaks and radula. bd, beak; de, bending plane; de, distal end of rostrum; w, wing.



buccal ganglia and the anterior salivary glands, which are more or less embedded in the buccal mass in decapods, whereas they are external in octopods (Fig. 2).

## 2. Beaks and Radula

Both the beak and the radula are chitinous sclerotized structures (Jeuniaux, 1963; Ducros, 1966; Hunt and Nixon, 1981) secreted by specialized cells: The odontoblasts produce the radula (Gabe and Prenant, 1957) and the beccublasts produce the beaks (Dilly and Nixon, 1976).

These hard parts resist digestion and remain intact in the stomachs of predators, and both have been used for systematic identification. Clarke (1962) gave a

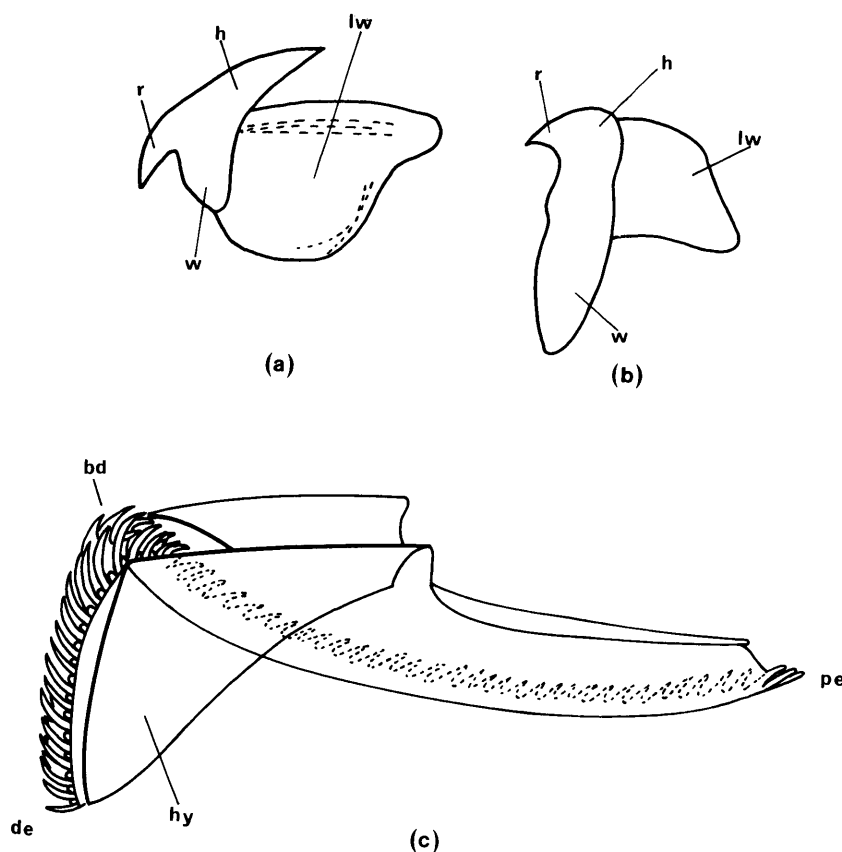


Fig. 3. Beaks and radula of *Sepia officinalis*: (a) upper beak (b) lower beak, (c) radula. bd, Bending plane; de, distal end; h, hook; hy, hyaline shield; lw, lateral wall; pe, proximal end; r, rostrum; w, wing.

determination key to the family or genera; Mangold and Fioroni (1966) set up a key including all Mediterranean species; Aldrich et al. (1971) determined the families and sometimes the genera by examining the structure of the radula.

The beaks have been used to estimate animal size, weight, and sex (Clarke, 1962; Mangold and Fioroni, 1966). In *Octopus* Nixon (1969b, 1973) found a correlation between several radular parameters (weight, teeth) and total body weight.

### 3. Glands of the Foregut

Two categories of glands discharge their secretion into the buccal cavity:

1. Diffuse glands within the buccal mass, consisting of single gland cells or of small groups of cells. In *Octopus* (Capurro, 1961) and in *Sepia* and *Sepiolo* (Boucaud-Camou, 1968), they are on the lips (labial glands), on the salivary papilla (lingual glands), and in the buccal epithelium (buccal glands).
2. Conspicuous tubular glands: the submandibular gland, lying beneath the salivary papilla (Fig. 2), the anterior salivary glands (Fig. 2), and the posterior salivary glands. The latter are actually within the visceral mass close to the digestive gland, but their common duct opens in the buccal cavity through the salivary papilla (Fig. 2).

In *Sepia* and *Sepiolo*, three cell types have been recognized in labial, buccal, submandibular, and anterior salivary glands: mucous cells (A) with acid polysaccharidic secretion, salivary cells (B) with glycoprotein secretion and enterochromaffin cells (C). Mucous cells are predominant in labial and buccal glands, A, B, and C cells are present in submandibular glands, whereas the anterior salivary glands contain only B and C cells (Boucaud-Camou, 1968). In *Octopus* the histochemical nature of the secretion seems to be very similar (Capurro, 1961).

On the contrary, the posterior salivary glands of octopods are very different from those of decapods, at least of sepioids. In octopods the glands have various types of mucous cells and enterochromaffin cells. In *Sepia* and *Sepiolo* only one type of cell, which has a tryptophan-rich proteinaceous secretion exists, and no enterochromaffin cells occur (Boucaud-Camou, 1968). No data on histology are available for teuthoids.

### E. Killing the Prey

#### 1. Methods of Killing

The cephalopods, feeding almost exclusively on living animals, paralyze or kill them before eating. Although the immobilization of the prey is not a prereq-

### 3. Feeding and Digestion

quisite of its ingestion, it is an advantage in the case of

Very active hunters, such as *Teutho*, severing the spinal cord (Romeo, 1969); other prey such as *Stomatopoda* poisoning.

On the other hand, *Sepia* eating. It has long been known that it actually poison glands, and to some fishes (Romeo, 1969) topuses that have the ability to poison a crab after capture.

*Sepia* bites its prey, and the prey is often paralyzed and discharged in a closed state (Romeo, 1960).

#### 2. Poisons of the Prey

As is usually the case with the cephalopods, the poisons are amines, enzymes, and

**a. Biologically Active Amines.** Several amines have been detected in *Sepia* and *Eledone*: octopamine, tyramine, and acetylcholine. The presence has been reported in 1922; Vialli and Ersland (1953) concentration of the amines (Ducros, 1976). How they act upon crabs has been reported (1953).

Few data are available on octopamine, and tyramine and noradrenaline (Killick, 1973). Actin on the glands of *Sepia* (Boucaud-Camou, 1968).

**b. Enzymes.** Several enzymes are related to amines, such as proteolytic enzymes (Cannon, 1952) have been

quisite of its ingestion (Altman and Nixon, 1970; Young, 1965a), it is a real advantage in the case of very voluminous or mobile prey.

Very active hunters such as teuthoids, which feed on fishes, kill their prey by severing the spinal cord (Bidder, 1950; Fields, 1965; Bradbury and Aldrich, 1969); other prey such as crustaceans are cut into pieces. There is no evidence for poisoning.

On the other hand, in *Sepia* and in octopods, the prey is poisoned before eating. It has long been demonstrated that the posterior salivary glands are actually poison glands. Extracts have been shown to be toxic to crustaceans and to some fishes (Romijn, 1935; Ghiretti, 1960; Nicol, 1966). Moreover, octopuses that have their posterior salivary gland nerve sectioned are unable to poison a crab after catching it (Young, 1965a).

*Sepia* bites its prey, thus introducing the poison. In *Octopus* and in *Eledone*, the prey is often paralyzed without any detectable wound, the poison being discharged in a closed compartment formed by the interbrachial web (Ghiretti, 1960).

## 2. Poisons of the Posterior Salivary Glands

As is usually the case for venoms, the secretion of the posterior salivary glands of cephalopods appears to be a mixture of several substances: biologically active amines, enzymes, and nonenzymatic polypeptides.

**a. Biologically Active Amines.** A number of biologically active amines have been detected in the posterior salivary glands of some octopods (*Octopus* and *Eledone*): octopamine, 5-hydroxytryptamine, tyramine, noradrenaline, histamine, and acetylcholine (Endean, 1972). For at least some of them, their presence has been related to the secretory activity of the chromaffin cells (Verne, 1922; Viali and Erspamer, 1938; Matus, 1971; Ducros, 1971). Actually, a high concentration of the amines occurs in the secretory nerve trunks (Arluison and Ducros, 1976). However, it seems established that the amines have an excitatory action upon crabs but are not responsible for the death or paralysis (Ghiretti, 1953).

Few data are available for decapods. Attempts to detect 5-hydroxytryptamine, octopamine, and tyramine in *Sepia* and *Loligo* were unsuccessful, although dopamine and noradrenaline have been detected in both species (Juorio and Killick, 1973). Actually, there are no chromaffin cells in the posterior salivary glands of *Sepia* (Boucaud-Camou, 1968).

**b. Enzymes.** Some of the enzymes detected in octopods' salivary glands are related to amine metabolism (Endean, 1972). Other enzymes are lytic: proteolytic enzymes (Ghiretti, 1950; Morishita, 1974a,d) and hyaluronidase (Romanini, 1952) have been found in octopus glands. These enzymes are probably

involved in diffusion of poison, but their possible role in digestion is still disputed (Arvy, 1960) (see Section II,B).

**c. Toxins.** Eledoisin, a polypeptide with a vasodilatory and hypotensive effect upon mammals, has been found in *Eledone* (Erspamer and Anastasi, 1962), but the significance of this substance in the salivary glands is obscure (Endean, 1972).

Cephalotoxin, a glycoprotein, has been demonstrated to be responsible for the paralysis and killing of crabs by *Octopus* and *Sepia* (Ghiretti, 1959, 1960). Actually, at least two cephalotoxins,  $\alpha$  and  $\beta$ , occur in *Octopus* glands. They have a high carbohydrate content and act on synapses by inhibiting transmission (Cariello and Zanetti, 1977). Indeed, it has become more and more evident that all cephalotoxins from various cephalopods are not identical in their chemical composition, even though they show the same properties against crustaceans (Songdahl and Shapiro, 1974).

Tetrodotoxin has been identified as the toxin (maculotoxin) occurring in the venom of the blue-ringed octopus, *Haplochromis maculosa*, whose bite is lethal to man (Sheumack et al., 1978).

## F. Food Intake

### 1. Parts Played by the Different Feeding Organs

The prey, captured with the arms and/or tentacles, eventually paralyzed by cephalotoxin secretion, is kept in front of the mouth by the arms during the whole duration of the meal. The food is swallowed by cephalopods with the help of different mouthparts, mainly the beaks and radula.

The arms are used by *Octopus* in dismembering the crab, but the removal of tissue from inside the skeleton and the swallowing of food are the result of the interaction between the beaks and radula (Altman and Nixon, 1970). A detailed study of the movements of the *Octopus* isolated buccal mass during the *bite* cycle confirms that the beak mechanism is responsible for chopping the flesh of the prey into small pieces (Boyle et al., 1979). The upper beak and the radula work together in the more delicate phases of the cleaning process; the lower beak is more important than the upper one in breaking the food into small pieces (Altman and Nixon, 1970). The functions of the radula may differ according to the prey and the feeding procedure, whether boring holes in shells or eating crabs (Altman and Nixon, 1970). However, the radula is not essential for feeding normally, because after ablation octopuses can still feed both by drilling into shellfish and by cleaning out crabs' exoskeletons (Nixon, 1980). *Sepia* has quite powerful jaws, probably related to its predatory activity, but the radula is not very impor-

### 3. Feeding and Digestion

tant and probably important (Bidder, 1973). Bidder (1955) observed that the food is bitten by the radula, which is a cat [p. 12]. The radula is an important part in the process of lubricating the food by the mucus.

What is swallowed is only a very small amount of food. Cephalopods (sepia) have a very small exoskeleton.

Octopods are known for their hole boring into shells. The hole boring into shells is done before the food is swallowed.

### 2. Shell Drilling

When feeding, octopods always succeed in feeding. An animal can use the beak in some cases, then pulling out the food. Taylor, 1961; Armon, 1979a,b, 1980). The species of *Octopus* that there were no records of *Murex* shells could be drilled by octopod *E. cirrhosa* on crustacean prey (Boucaud-Camou, 1979).

Each animal sees the shell in relation to its intraindividual preferences suggest the influence of the environment.

The hole-boring is done using chemical secretion. The drilled is quite irregular and with the rasping action. So, the rasping action might exist and facilitate the hole-boring.

Rasping is more important during the first 2 minutes of a burst of rapid rasping.

tant and probably here also nonessential for food ingestion (Boucaud-Camou, 1973). Bidder (1950) indicated, as far as *Loligo* and *Alloteuthis* are concerned, that the food is bitten by the beaks and swallowed without any rasping action by the radula, which is "... a tongue, used in swallowing like the rough tongue of a cat [p. 12]." The lateral palps, with their irregularly set teeth, play an important part in the passage of the food towards the esophagus (Young, 1965b), lubricated by the mucous secretion from the glands of the buccal mass.

What is swallowed by cephalopods is mainly flesh for *Octopus* and *Eledone*; only a very small amount of skeletal material is to be found in the gut. Other cephalopods (sepioids and teuthoids) swallow not only flesh, but also at least part of the exoskeleton of crab, the backbone of fish, and the pen of squid.

Octopods are known for two particular alternative (optional) feeding habits: hole boring into shellfish, and partial external digestion of crab flesh inside the exoskeleton before ingestion.

## 2. Shell Drilling by Octopus

When feeding upon shelled gastropods and bivalves, the octopus does not always succeed in forcing the body of the prey out of the shell. In such a case the animal can use the alternative feeding procedure of drilling a hole (or more than one in some cases) through the calcareous shell, secreting mucus into the hole, then pulling out the body of the prey and eating it (Fujita, 1916; Pilson and Taylor, 1961; Arnold and Arnold, 1969; Wodinsky, 1969, 1973; Nixon, 1977, 1979a,b, 1980). This behavior was well established for Atlantic and Pacific species of *Octopus*. For the Mediterranean *Octopus* Wells (1978) indicated that there were no records of shell drilling until Nixon (1977) found that *Mytilus* and *Murex* shells could be drilled by *O. vulgaris* in the Mediterranean (Naples). The octopod *E. cirrhosa* has also been reported to be able to bore holes through crustacean prey (Boyle and Knobloch, 1981).

Each animal seems to have a tendency to drill in some particular area of the shell in relation to its lip (Arnold and Arnold, 1969). The existence of inter- and intraindividual preferences in the placing of the holes leads Wodinsky (1969) to suggest the influence of learning.

The hole-boring gastropods are known to achieve regularly shaped holes, using chemical secretion to dissolve the shell. With *Octopus* the shape of the hole drilled is quite irregular, and its size varies with the thickness and hardness of the shell and with the size of the octopus. The mechanism of boring is a mechanical rasping action. Some softening chemical secretion from the salivary glands might exist and facilitate the drilling procedure (Nixon et al., 1980).

Rasping is more or less continuous, rapid at the beginning (10 rasps/min during the first 2 min), then the rate decreases rapidly (2-4 rasps/min). Another burst of rapid rasping occurs at the end. Each individual rasp is 0.3 to 0.4 sec in



gestion in octopus, but the summaries of these Japanese papers do not mention the possibility of these enzymes being used for external digestion.

Although predigestion seems to be an accepted procedure as far as a crab meal is concerned, there are still no indications that such a process is used when fish or molluscs are fed to the animals. Wells (1978) suggested that the secretion injected into the holes drilled through the calcareous shell of bivalves or gastropods could, to some extent, loosen the attachment of the columella muscle as in a crab meal.

#### 4. Control of Food Intake

Food intake is the result of a complex procedure involving capture of prey, sometimes digging holes through shells, eventually poisoning and sometimes predigesting the food, biting, and rasping before swallowing a meal. The whole procedure is achieved by the combination of the mechanical action of the arms and buccal mass and the chemical action of the salivary glands. A complex neural control exists for all the sequences of events. Young (1965a,b, 1971) described the neural control of eating in octopuses by a series of neural centers: the superior buccal lobe, the inferior buccal and the subradular ganglia. By a series of complementary surgical experiments, Young (1965b) showed that the superior buccal lobe is the initiator of the whole feeding sequence, and that the inferior buccal and subradular ganglia cannot mediate the responses necessary for eating without connections to the superior buccal lobe.

In *Octopus* and *Sepia* the whole procedure of eating prey is initiated by secretion from the posterior salivary glands. Their innervation was studied in *Octopus* by many authors (Bogoraze and Cazal, 1946; Young, 1965a,b; Ducros, 1971, 1972a,b,c; Martin and Barlow, 1972). These glands receive axonal projections directly from the superior buccal lobe to the epithelium of the secretory tubules and projections from the subradular ganglion to the circular muscular fibres surrounding the tubules. The salivary papilla, responsible for the injection of the poison, is controlled by the subradular ganglia (Young, 1965a,b; Boyle et al., 1979). The mechanical actions of the beaks are controlled by the inferior buccal ganglion alone, as shown by an *in vitro* study of the mandibular movements of octopuses (Boyle et al., 1979).

A regulation of the quantity of food eaten exists in all cephalopods that have been studied so far. They all reject any excess food: it is impossible, by offering food, to overfeed experimentally a cephalopod. According to Nixon (1965, 1966), in octopuses the signal of repletion might come from the crop, the animal stopping to feed "just before the crop is filled to its functional maximum." The brain receives information from the anterior part of the digestive tract via the sympathetic nerves. Nevertheless, little is known about the initiation and control of the process. Peristaltic movements of the esophagus and crop can be initiated either by direct mechanical stimulus (Bidder, 1957) or by electrical stimulation

of the sympathetic nerves (Young, 1971). In the females of some species, a relationship seems to exist between gonad maturation and food intake, the animals decreasing their rate of feeding at the approach of mating and spawning. According to Wodinsky (1977) food intake might be under the hormonal control of optic glands' secretion, which in the drilling octopus (*O. hummelincki*) seems also to be responsible for the shift from the *boring* to the *pulling* mode of feeding after egg laying in females.

#### IV. Digestion

##### A. Structure of the Digestive Organs

##### 1. Digestive Tract

In the cephalopods, the digestive tract is U-shaped (Fig. 4). The descending branch (or anterior part), lined with a chitinous cuticle, includes the esophagus and the stomach. The esophagus of *Nautilus* is not lined by a cuticle (Fukada, 1980). In *Nautilus* and in the octopods, the esophagus is distended into a crop (Fig. 4). The ascending branch (or posterior part) includes the caecum and the rather short intestine, which have their folded mucosa lined with a ciliated and glandular epithelium. The caecum has a spiral form, the lumen is largely filled with *leaflets*, permanent folds of the mucosa. Each face of a leaflet is covered with ridges and grooves running parallel to the free edge. In some teuthoid families (including the Loliginidae), the caecum may be enlarged by a simple sac (Fig. 4). The anus lies just posterior to the funnel in the Coleoidea, but at the posterior end of the mantle cavity in *Nautilus* (Bidder, 1966). The ink sac discharges its secretion by a duct opening in the intestine not far from the anus.

The esophagus ends and the intestine begins at the bend of the U, in the vestibule where the stomach and the caecum open. Sphincters enable both the caecum and the stomach to be isolated from the rest of the digestive tract. The two *digestive ducts*<sup>1</sup> that is, the ducts originating from the digestive gland, join together just before reaching the axis of the spire in the caecum. A groove, the *digestive groove*<sup>1</sup> leads from this opening to the vestibule, thus making a free passage from the midgut gland to the stomach (Bidder, 1966). The groove and sphincter systems enable the substances present in the stomach to enter the digestive ducts or the intestine and the reverse flow from the digestive ducts to reach the stomach directly, thus bypassing the caecum. This anatomical layout must be kept in mind in order to understand the digestive processes of the cephalopods.

<sup>1</sup>We follow Bidder's nomenclature (Bidder, 1976).

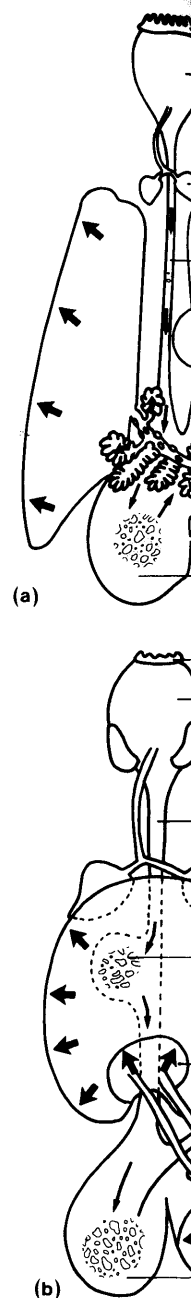


Fig. 4. The digestive tract of *Nautilus vulgaris*. (The ink sac is not shown). c, caecum; cr, crop; cs, digestive gland; i, intestine; arrow, course of solid particles.



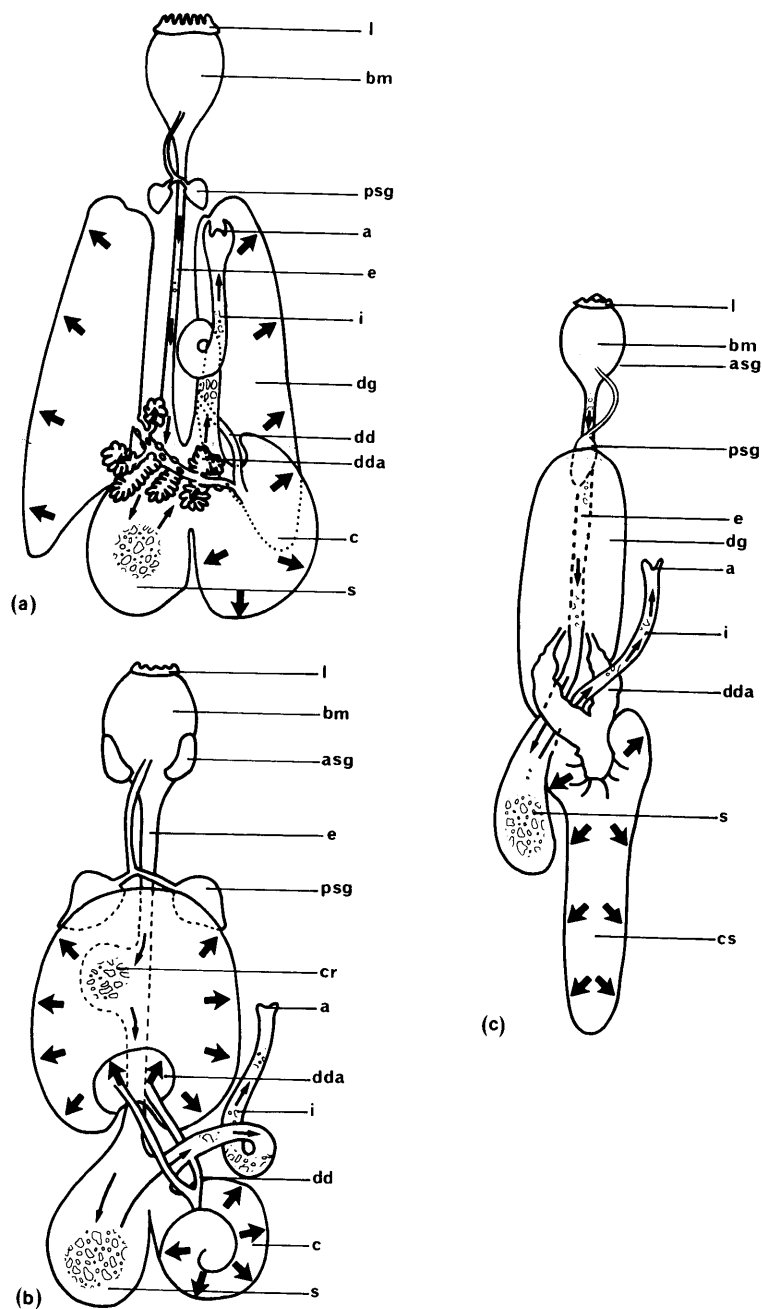


Fig. 4. The digestive organs of (a) *Sepia officinalis*, (b) *Octopus vulgaris*, and (c) *Loligo vulgaris*. (The ink sac is not represented.) a, Anus; asg, anterior salivary gland; bm, buccal mass; c, caecum; cr, crop; cs, caecal sac; dd, digestive duct; dda, digestive ducts' appendages; dg, digestive gland; i, intestine; l, lips; e, esophagus; psg, posterior salivary gland; s, stomach; thin arrow, course of solid particles in the digestive tract; thick arrow, sites of absorption.

The embryological origin is ectodermic for the buccal mass, the anterior part of the esophagus, and the salivary glands. The digestive duct from the crop (if present) and posterior part of the esophagus to the anus, the midgut gland, and the ink sac are of meso- and endodermic origin, except for the anus itself, which is ectodermic (Boletzky, 1967, 1978).

## 2. Midgut Gland

In the Coleoidea the midgut gland is divided into two unequal parts connected in series: The anterior one is the large brown digestive gland (*liver*) and the posterior one, the so-called *pancreas*, which actually consists of appendages developed from the paired digestive ducts. For this reason their proposed name is *digestive ducts' appendages* (Bidder, 1976). In the octopods they are enclosed in the digestive gland capsule (Fig. 4). In the decapods they lie within the kidney sac, thus covered with a coelomic epithelium, enclosing only the outer layer of the gland in the loliginids. In the sepioids each tubule is covered with the coelomic epithelium. Actually, the two epithelia, the inner endodermal as well as the outer coelomic one, are very similar to each other and to the renal appendages' epithelium.

The internal epithelium serves in both excretion and digestive absorption; the external one seems involved in ion regulation and urine formation (Boucaud-Camou, 1972, 1973; Schipp and Boletzky, 1975, 1976; Donaubauber and Schipp, 1978).

In *Nautilus* the complex midgut gland is not divided into two parts (Bidder, 1976).

**a. Structure of the Digestive Gland.** The digestive gland, in addition to its digestive functions, is also the site of storage of fuel reserves. Its color is often brownish due to the presence of carotenoid pigments of dietary origin (Fox, 1966; Altman and Nixon, 1970). The digestive gland of squid, which feed mainly on fish, is not as rich in carotenoids as that of the preferentially crustacean eaters *Eledone*, *Octopus*, and *Sepia* (Fisher et al., 1956). The digestive gland of octopuses fed exclusively on fish becomes greenish (Altman and Nixon, 1970).

Of paired embryological origin, the digestive gland is often a single organ in the adult, except in some species where the two lobes are still distinct (*Sepia*). In *Nautilus* the midgut gland is divided into three to five lobes. The digestive gland is covered by a thin muscular and connective tissue envelope, often transparent. The gland itself consists of tubules, the largest of which end in a pair of wide lumina, which in turn open into the digestive ducts. The tubules are lined with a glandular epithelium that lies on a thin sheath of well-vascularized and innervated muscular and connective tissue. Several cell types have been described in the digestive gland of the cephalopods (Cuénot, 1907; Bidder, 1957; Boucaud-

## 3. Feeding and Digestion

Camou, 1968; Boucaud-Camou, 1972, 1973). In some species (*Sepia*, *Eledone*), if not all, of the various types of digestive cell (*boules*) contain teinaceous inclusions and masses containing

### b. Histological

rhythmic activities of individual cells. The changes of the digestive gland and their relative activities

The digestive gland is involved in digestion. Bidder (1976) described the digestive gland cells in *Nautilus* (Camou (1973), Boucaud-Camou and Boucher-Rodoni (1975), Boucaud-Camou (1976)). In this case, by electron microscopy, the size of the boules and the brown bodies. The chemical characteristics (Boucaud-Camou, 1972, 1973) and slighter fluctuations (Rodoni and Mangano, 1975) of the boules, follow

### 3. Innervation

Young (1971) proposed two centers of the superior buccal ganglia and important peripheral lobes (ganglia) serve the inferior buccal ganglia and interbuccal connectives and the radula. For nerves, which arrive at the crop wall an important

The gastric ganglia, ducts, and the intestine CNS not only by the represents the only

Camou, 1968; Boucher-Rodoni, 1976; Schipp and Pfeiffer, 1980). In some species (*Sepia*, *Eledone*, *Octopus*) and probably in all coleoid cephalopods, most, if not all, of the various cell forms are functional stages of a single cell type, the digestive cell (*boules cell*) (Boucaud-Camou and Yim, 1980; Boucher-Rodoni, 1981). The mature digestive cell is characterized by the *boules*, large proteinaceous inclusions, and by the frequent occurrence of *brown bodies*, large masses containing crystals, often included in a vacuole (Fig. 5).

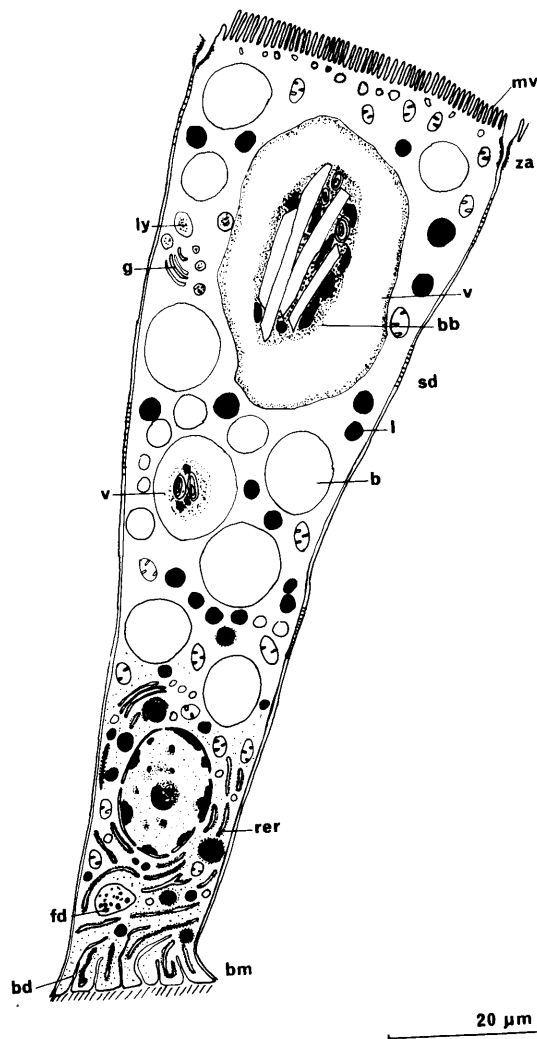
**b. Histological Changes Related to Digestion.** The digestive gland shows rhythmic activities as a whole, but these are not closely synchronized within individual cells. This explains the difficulty in understanding the structural changes of the digestive gland, in that different types of inclusions are present and their relative abundance is quite variable.

The digestive gland cells undergo some histological changes that can be related to digestion. Bidder (1950, 1957) was the first to notice the changes in the digestive gland cell during digestion. Further studies were made by Boucaud-Camou (1973), Boucher-Rodoni (1976), Boucher-Rodoni and Mangold (1977), Boucaud-Camou and Yim (1980), often on a numerical basis and, in the last case, by electron microscopy. From these studies, it appears that the number and the size of the boules are related to digestion, but such is not the case for the brown bodies. The rhythmicity of the boules' secretion as well as their histochemical characters suggest that they could be the digestive enzymes' carrier (Boucaud-Camou, 1973). Later, the number of boules increases slowly, showing slighter fluctuations, which could be related to further enzyme release (Boucher-Rodoni and Mangold, 1977). The enzymes may be secreted by fragmentation of the boules, followed by exocytosis (Boucaud-Camou and Yim, 1980).

### 3. Innervation

Young (1971) pointed out that in octopods, the digestive tract is controlled by two centers of the central nervous system (CNS), the superior buccal lobes (or superior buccal ganglia in decapods) and the palliovisceral lobes, and by an important peripheral ganglion, the gastric ganglion (Fig. 6). The superior buccal lobes (ganglia) send nerves directly to the posterior salivary glands and, via the inferior buccal ganglia (which are connected to the superior buccal lobes by interbuccal connectives) to the anterior salivary glands, the muscles of the jaws, and the radula. From the inferior buccal ganglia also issue the sympathetic nerves, which arrive in the gastric ganglion. They form in the esophagus and crop wall an important plexus including nuclei (Alexandrowicz, 1928).

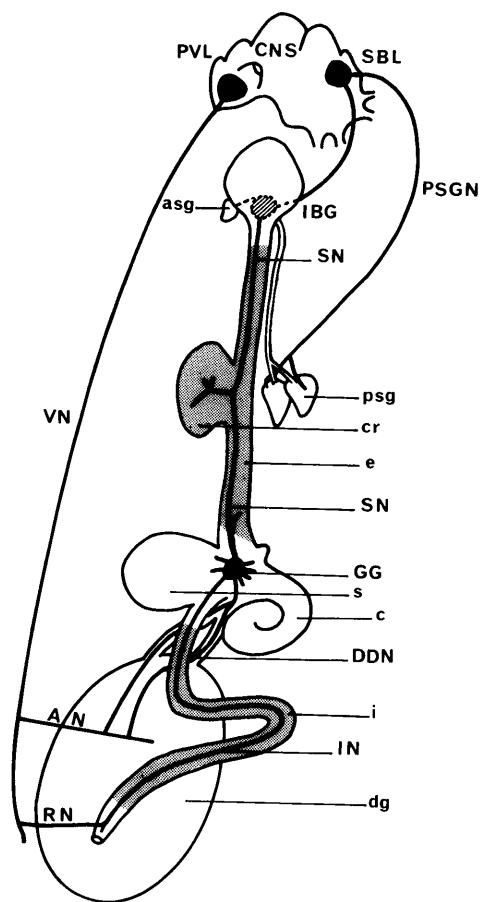
The gastric ganglion sends nerves to the stomach, the caecum, the digestive ducts, and the intestine. In *Octopus* the gastric ganglion is connected with the CNS not only by the sympathetic nerves, but also by the visceral nerves. This represents the only direct connection between CNS and gastric ganglion in *Sepia*,



**Fig. 5.** Digestive cell (or boule cell) from the digestive gland of *Sepia officinalis*. bb, Brown body; b, boule; bd, basal infoldings; bm, basal membrane; fd, ferric deposit; g, Golgi apparatus; l, lipids; ly, lysosome; mv, microvilli; rer, rough endoplasmic reticulum; sd, septate junction; v, vacuole; za, zonula adherens (apical belt desmosome). (After Boucaud-Camou, 1973.)



**Fig. 6.** Diagram of the digestive system of *Sepia officinalis*. The brain is figured as seen from the ventral side. Not all represented in the same section. (After Best, 1981.) A, anterior salivary gland; PVL, palliovisceral lobe; ps, intestine plexus; GG, gastric ganglion; DDN, digestive nerve; RN, rectum; VN, ventral nerve.



**Fig. 6.** Diagram of the innervation of the gut of *Octopus*. (After Boucher-Rodoni, 1981.) The brain is figured as seen from the right side. (After Young, 1971.) The digestive organs are not all represented in the same perspective but are distributed to make the drawing as clear as possible. (After Best, 1981.) All the nerves, even if some are paired in reality, are represented as single structures. The digestive organs are indicated as in Fig. 4. The esophagus and crop plexus and the intestine plexus are dotted. CNS, central nervous system; SBL, superior buccal lobe; PVL, palliovisceral lobe; psg, posterior salivary glands; PSGN, posterior salivary glands' nerves; asg, anterior salivary glands; IBG, inferior buccal ganglion; SN, sympathetic nerves; GG, gastric ganglion; DDN, digestive ducts' nerves; i, intestine; IN, intestinal nerves; RN, nerves of the rectum; AN, abdominal nerves; VN, visceral nerves.



*Loligo* (Pignero and Rocca, 1969), and *Sepia* (Boucher-Rodoni, 1981), the proteolytic activity is partially thiol dependent. It is located among the proteins with a high electrophoretic  $R_f$  and a medium molecular weight (Boucher-Rodoni, 1981).

Morishita (1978) identified a chymotrypsin-like enzyme in the digestive juice of *Octopus*, originating from the posterior salivary glands. Rothe et al. (1970) found a chymotrypsin-like activity in the *Magensaft* of *Sepia*, and Boucaud-Camou (1974) located such an activity inside the vacuoles and at the boules level in the digestive gland cells of the same species. A slight, occasional, similar activity seems to exist in the digestive gland of *Eledone* (Boucher-Rodoni, 1981). A tryptic activity was recorded in the digestive gland of *Loligo* (Pignero and Rocca, 1969). A strong proteolytic activity with optimum acid pH exists in the digestive juice, in the digestive gland, and in the posterior salivary glands of most species investigated. This activity can be related to the presence of cathepsin-like enzymes. Such enzymes were identified in the digestive gland extract of *Loligo* (Pignero and Rocca, 1969) and of *Octopus* (Morishita, 1972a,b,c). A carboxypeptidase A-like activity was found in the digestive gland of *Loligo* (Pignero and Rocca, 1969) and in the digestive juice and posterior salivary glands extract of *Octopus* (Morishita, 1978). Dipeptidase activities have been found in most of the digestive organs investigated (Sawano, 1935; Romijn, 1935; Bidder, 1966 for review).

Sawano (1935) and Takahashi (1960) have found proteolytic activity at acidic and basic pH in the digestive ducts' appendages extract of *Octopus* and *Todarodes*, respectively. These results are, however, probably due to contamination of the gland by digestive gland secretion. The caecum extract has been found to display a proteolytic activity at pH 8 in *Sepia* (Boucaud-Camou, 1973) and in *Todarodes* (Takahashi, 1960).

The differences recorded by the authors in enzyme composition might to some extent be the result of different stages of digestion or of life cycle at the sampling time. The influence of digestion on enzymatic activities is shown by the important variations recorded in the total proteolytic activity of the digestive gland of *Eledone* and *Sepia* during one digestive cycle (Boucher-Rodoni, 1981). As for the importance of the life cycle, Sakaguchi (1968) reported a strong activity in the digestive gland and in the posterior salivary glands of *Octopus*. After spawning in females, enzymatic activity decreases considerably in both organs.

**b. Carbohydrate Digestion.** Goddard (1968) found an increase in the blood glucose concentration after a meal, more or less steep according to the carbohydrate content of the food. An amylasic activity exists at almost the same locations as the proteolytic activity: gut lumina (Boucaud-Camou, 1969, 1973 in *Sepia*), digestive gland (Romijn, 1935 in *Sepia* and *Eledone*; Takahashi, 1960, 1963 in *Todarodes*; Boucaud-Camou, 1969, 1973, 1974 in *Sepia*; Boucher-

Rodoni, 1981 in *Sepia* and *Eledone*), caecum contents, and tissue extract, (Takahashi, 1960, 1963 in *Todarodes*; Romijn, 1935 in *Sepia* and *Loligo*; Boucaud-Camou, 1969, 1973, 1974 in *Sepia*). Again no activity can be detected in the cuticularized esophagus and stomach epithelia. Such is also the case in the anterior and posterior salivary glands of *Sepia* (Boucaud-Camou, 1973). Romanini (1949, 1951, 1952) identified hyaluronasic and amylolytic activities in the posterior salivary glands of octopods.

The digestive gland here again displays a strong activity. In *Sepia* an amylase has been histochemically localized in the lumina of the tubules and in the boules cells, mainly in the distal and middle region of the cell (Boucaud-Camou, 1973). Cellulase is present in digestive gland extract of *Octopus* (d'Aniello and Scardi, 1971). Oshima et al. (1930) and Okutani and Kimata (1964) found an important chitinolytic activity in the digestive gland and in the stomach of *Todarodes pacificus* and *Octopus dofleini*.

Positive results in digestive ducts' appendages were obtained by Romijn (1935), but they were not entirely confirmed by Boucaud-Camou (1974) who noted some occasional activity, but only in the lumina of the tubules of *Sepia*. This activity is probably due to contamination by digestive gland secretion.

**c. Lipid Digestion.** There is not much information available about lipid digestion in cephalopods. As far as gut content is concerned, caecal fluid has been investigated and has given positive results (Romijn, 1935). Digestive gland and caecum are again the main organs concerned with this activity in the different species (Romijn, 1935; Takahashi, 1960, 1963; Boucaud-Camou, 1973, 1974; Boucher-Rodoni, 1981). A lipolytic activity was noted by both Takahashi (1960) and Romijn (1935) in the digestive ducts' appendages due probably here also to contamination by digestive gland secretion. Boucaud-Camou (1974) identified nonspecific esterase activities in the digestive gland, which probably correspond to the lipasic activities found by the different authors. The sites of esterase activity often surround the lipid inclusions of the boules cells. Such an enzymatic film surrounding lipid droplets is known in other groups such as bivalves (Reid, 1966, 1968) and phoronidians (Vandermeulen and Reid, 1969). These enzymes might be more involved in the utilization of reserves than in food digestion (Boucaud-Camou, 1973).

Lipid digestion requires emulsifiers to be efficient. Very little is known so far on the subject, except the negative results obtained by Vonk (1947) in the intestine and digestive gland of *Loligo*.

## 2. Absorption

**a. Sites of Absorption.** The caecum has long been considered the main absorptive organ in cephalopods, on the basis of microscopic anatomy and cytol-

## 3. Feeding and Digestion

ogy. The surface of the mucosa, and the apical part of the cell (Boucaud-Camou, 1950).

Indeed, by using place in the caecum (Péquignat, 1973; Boucher-Rodoni, 1977) has shown the top of the leaflet ridge (Fig. 7). In *Octopus* (Boucaud-Camou, 1973) in *Sepia* (Boucaud-Camou, 1973) and intestine are present.

On the contrary, the results (Falloise, 1960) a long time by authors.

Bidder (1957) shows that enters the digestive



Fig. 7. A stylized diagram of the caecum of *Sepia*. The ridges are marked by dots (chymotrypsin particles) into mucous cells. The mucous cells are figured



ogy. The surface of the caecal epithelium is enlarged by the numerous folds of the mucosa, and the occurrence, related to digestion, of lipid droplets in the apical part of the cell suggests an absorptive function (Enriques, 1902; Bidder, 1950).

Indeed, by using radiolabeled food, it has been shown that absorption takes place in the caecum, at least in *Sepia* and in *Octopus* (Boucaud-Camou and Péquignat, 1973; Boucaud-Camou et al., 1976). In *Sepia* Boucaud-Camou (1977) has shown the polarity of the mucosa. Absorption actually occurs at the top of the leaflet ridges, whereas digestive enzymes are active within the grooves (Fig. 7). In *Octopus* the absorptive role of the caecum seems more important than in *Sepia* (Boucaud-Camou et al., 1976). In the Loliginidae the large caecal sac and intestine are probably the main organs of absorption (Bidder, 1950).

On the contrary, the role of the digestive gland in absorption was disputed for a long time by authors who used carmine suspension and obtained conflicting results (Falloise, 1906; Cuénot, 1907; Gariaeff, 1915).

Bidder (1957) showed by the same method (carmine suspension) that food enters the digestive gland and that the digestive cells can actually perform an

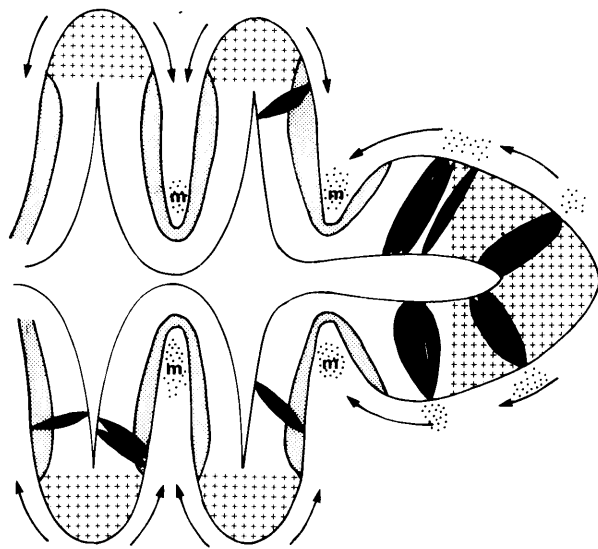


Fig. 7. A stylized drawing of the extremity of a primary leaflet, summarizing the functions of the caecum of *Sepia officinalis* L. The absorption sites, situated on the top of the leaflet's ridges are marked by crosses, the areas of lytic activities (acid phosphatase, esterase, chymotrypsin) are dotted. The arrows represent the ciliary currents which gather the undigested particles into mucous strings (m), further eliminated by the intestine (Bidder, 1950). The mucous cells are figured in black. (From Boucaud-Camou, 1977.)

absorptive function, at least in *Octopus* and in *Sepia*. Later, Boucaud-Camou and Péquignat (1973), using radiolabeled food, demonstrated that food was absorbed by the digestive gland in *Sepia*, and this occurs very early during digestion. Moreover, the digestive gland, which retains 80% of the labeled food, thus appeared as the main absorptive organ. Further studies on *Octopus* gave results very similar to those obtained with *Sepia* (Boucaud-Camou et al., 1976). In *Loligo* no absorption has been shown to take place in the digestive gland (Bidder, 1950, 1966). Nevertheless, A. M. Bidder (personal communication) thinks that it is not impossible that absorption may still be found, but only at the very end of digestion.

Most surprising was the finding of the absorptive function of the digestive ducts' appendages. In *Sepia* they are always the most labeled organ, thus showing the highest specific activity (Boucaud-Camou and Péquignat, 1973). It is indeed the internal epithelium that retains the larger part of the radioactivity.

In *Octopus* and *Sepia* the intestine does not seem to play a noticeable role in digestive absorption. However, its histological structure is very close to that of the caecum, and it has been shown that some absorption may occur in its epithelium in *Eledone* (Tritar, 1970a). In *Loligo* the intestine plays an important part in fat absorption (Bidder, 1950), and this might also be true for some other teuthoids.

**b. Absorption of Small Molecules.** Tritar (1970a, 1971) studied the absorption of amino acids in the intestine of *Eledone moschata* and Tritar and Peres (1974), the absorption of glucose in the intestine of *S. officinalis*. They found a weak absorption of these substances in both species. Indeed, Tritar (1970b) found a better absorption of glycine in the caecum of *Eledone*.

Boucaud-Camou and Péquignat (1973), and Boucaud-Camou et al. (1976) followed the absorption of [ $^3\text{H}$ ]glycine in the digestive system of *Sepia* and *Octopus* by scintillation counting and autoradiography. The results showed that glycine is absorbed mainly by the digestive ducts' appendages, the digestive gland, and the caecum.

**c. Absorption of Large Molecules and Particles: Intracellular Digestion in the Digestive Gland.** Bidder (1957), using carmine, found that food penetrates the digestive gland of *Octopus* and *Sepia*. In order to determine whether particles are actually absorbed by the digestive cells, ferritin was used as a tracer by Boucaud-Camou and Yim (1980) and followed both by electron and light microscopy. It was thus demonstrated that the digestive cells can capture large molecules by pinocytosis and digest them intracellularly in heterolysosomes. In *E. cirrhosa*, ferritin appears to be absorbed by a similar process (Boucher-Rodoni, 1981). In *Nautilus* small fragments of food are digested in the digestive gland (Bidder, 1966).

### 3. Feeding and Digestion

#### 3. Excretion Related

The labeling of ingested residues of the intracellular body vacuoles (Bidder, Camou et al., 1976).

Boucaud-Camou and of the brown-body vacu deposits from the meta boules in the cytoplasm larger, collecting the re and of heterogenous orig into the digestive tubule off, the brown body is passes to the caecum and strings. The formation a of feeding.

Some metallic elements vanadium, are known (Miramand and Guary, that some heavy metals Miramand, personal com act as a means of detox

#### 4. Digestive Processes

**a. Movement of Food** the esophagus by peristalsis. In *Nautilus*, food can be partially broken down by the gland and perhaps the sa and, through the digestive *Sepia* and in octopods. digestion is achieved everywhere the larger part of the caecum undergoes f *Loligo* food does not see take place chiefly in the

**b. Duration of Digestion** from one species of cephalopods is highly influenced by the longer in benthonic species

## 3. Excretion Related to Digestion

The labeling of ingested food by radioelements or by carmine shows that the residues of the intracellular digestion are finally collected in the large brown-body vacuoles (Bidder, 1957; Boucaud-Camou and Péquignat, 1973; Boucaud-Camou et al., 1976).

Boucaud-Camou and Yim (1980) have made a detailed study of the formation of the brown-body vacuole. The crystals of the brown body (probably uric acid deposits from the metabolism of the digestive gland) appear directly in small boules in the cytoplasm and are later included in a vacuole that grows larger and larger, collecting the residues of the intracellular digestion, both of endogenous and of heterogenous origin. When the brown-body vacuole is mature it protrudes into the digestive tubule, swelling the apical part of the cell. The vacuole bursts off, the brown body is liberated within the lumen of the digestive tubule and passes to the caecum and intestine, from which it is eliminated among mucous strings. The formation and excretion of brown bodies also occurs in the absence of feeding.

Some metallic elements that can occur as pollutants, cadmium, mercury, and vanadium, are known to be concentrated in the digestive gland of *Octopus* (Miramand and Guary, 1980). Further, from autoradiographic studies, it appears that some heavy metals such as americium are concentrated in brown bodies (P. Miramand, personal communication). It is thus clear that the brown body could act as a means of detoxification.

## 4. Digestive Processes

**a. Movement of Food.** From the buccal cavity the food is passed through the esophagus by peristaltic muscular action to the stomach. In octopods and in *Nautilus*, food can be stored in the crop. In the stomach the food is at least partially broken down by the action of enzymes originating from the digestive gland and perhaps the salivary glands. The digestive fluid then enters the caecum and, through the digestive ducts' appendages, the digestive gland, at least in *Sepia* and in octopods. In *Nautilus* it enters the midgut gland. In these species digestion is achieved eventually by intracellular processes in the digestive gland, where the larger part of the digested food is absorbed. The food that has entered the caecum undergoes final stages of digestion and is then absorbed there. In *Loligo* food does not seem to reach the digestive gland, and absorptive processes take place chiefly in the large caecal sac and intestine (Bidder, 1966).

**b. Duration of Digestion.** The total time necessary to digest a meal varies from one species of cephalopod to the other, and within the same species it is highly influenced by the temperature. At a given temperature digestion lasts longer in benthonic species than in pelagic. The size of the meal seems to have

but little effect on the total duration of digestion, provided, of course, that the meal is not too small.

For a similar mode of life and at the same temperature, digestion seems to be more rapid and more efficient in cephalopods than in fishes (Boucher-Rodoni, 1973b, 1975). The rate of digestion, that is, the quantity of food digested per hour, depends on the total duration of digestion (hence on the temperature) and on the size of the meal. The food intake of a small animal is larger relative to its size than that of a large animal (Nixon, 1966; Mangold and Boletzky, 1973; Van Heukelem, 1976; Joll, 1977; Boyle and Knobloch, 1982), but the quantity digested at a given hour always represents a fairly constant percentage of the quantity ingested (Boucher-Rodoni, 1975).

In all cephalopods in which digestion was studied experimentally by following the quantitative evolution of the food in the gut, the rate of digestion appears to be very high during the first few hours and to slow down later (Fig. 8). Thus digestion is particularly efficient in cephalopods during the first few hours. This initial rapid digestion lasts, in octopods, as long as there is food in the crop.

It has been noted that animals can, and often do, take a new meal before the digestion of the previous one is completed (Bidder, 1966; Boucher-Rodoni, 1973b). It might be that it is at the end of the rapid stage of digestion that animals can feed anew. This is in agreement with Nixon (1966), who suggests that the signal of repletion, in *Octopus*, might come from the crop. When the organ is full, the animal stops eating, and when the organ is empty, the animal can eat again. Such a role might be played by the stomach in decapods (Boucaud-Camou, 1973). Moreover, digestion proceeds in successive phases, in stomach, caecum, and (at least in the octopods and sepioids) in the digestive gland. This possibility of the digestion of two meals in parallel makes the digestive process of cephalopods potentially of remarkable efficiency.

**c. Control of Digestive Processes.** In *Octopus* Best (1981) shows that there is neural control of the digestive gland secretion during feeding, via the sympathetic nerves. This does not seem to be the case for the abdominal and rectal nerves, which are branches of the visceral nerves, other connections between gastric ganglion and CNS (Fig. 6).

As far as hormonal control of digestion is concerned, only one study is known so far (Ledrut and Ungar, 1937). They isolated a secretin-like substance from the caecum of *Octopus*, which induces hypersecretion by the midgut gland. A hormonal link is not excluded by the work of Best (1981), in which it was shown that the activity of the digestive gland of about half of artificially fed octopuses, with the organ isolated from all nervous input, resembled that of normally fed controls.

**d. Food Conversion.** Cephalopods are rapidly growing animals (Nixon, 1966, 1969a; Choe, 1966; Wells and Wells, 1970; Richard, 1971; Mangold and

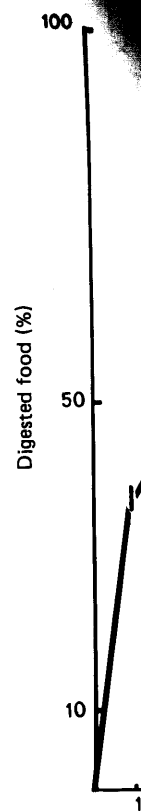


Fig. 8. Quantitative evolution of food digestion during the digestive cycle. The digestive organ is empty 12 h after the beginning of the meal.

Boletzky, 1973; Van Heukelem, 1976; Joll, 1977; Boyle and Knobloch, 1982). Food conversion, and conversion of food into animal tissue, is also a remarkable feature. Food conversion, temperature and in some species (Borer, 1971; Mangold and Boletzky, 1973; Bidder, 1966; Boucher-Rodoni, 1973a; Mangold and Boletzky, 1973). The relationship between food intake and growth period, shows that 25% of the food is converted into tissue (Nixon, 1966). The food con-

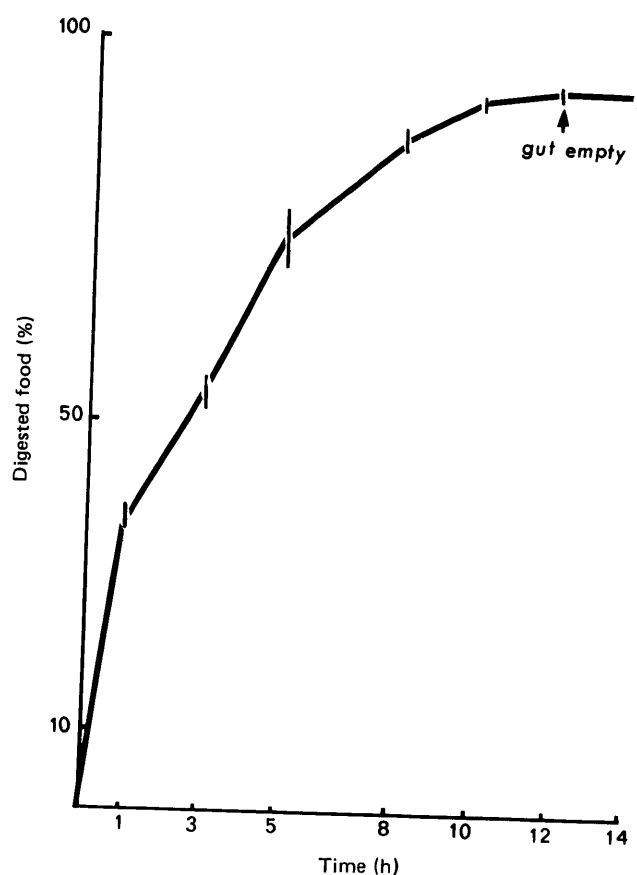


Fig. 8. Quantitative evolution of the food in the gut of *Octopus cyanea* during one digestive cycle. The digested food is expressed as a percentage of the quantity ingested. The gut is empty 12 h after the beginning of the meal. (After Boucher-Rodoni, 1973b.)

Boletzky, 1973; Van Heukelem, 1973). During growth, feeding, digestion, absorption, and conversion are the successive stages leading to transformation of food into animal tissue. The food intake in most cephalopods is determined by temperature and in some by density of food available (Richard, 1966, 1971; Borer, 1971; Mangold and Boletzky, 1973). Digestion is rapid and efficient (Bidder, 1966; Boucher-Rodoni, 1973b, 1975). Food conversion into body tissue is also a remarkably efficient procedure in cephalopods in comparison with that of fish, for instance (Choe, 1966; Nixon, 1966, 1969a; Boucher-Rodoni, 1973a; Mangold and Boletzky, 1973; Mangold, 1983). In *Octopus* the relationship between food intake and changes in body weight, over a 1 to 7.5 month period, shows that 25 to 55% of the food is incorporated into body tissue (Nixon, 1966). The food conversion efficiency, that is

$$\frac{\text{final body weight} - \text{initial body weight}}{\text{total food intake}} \times 100$$

can vary considerably from one species to another, within the same species from one animal to the other, and within the same animal from one period to the other. In *Sepia esculenta*, for instance, Choe (1966) recorded conversion rates ranging from 9 to 71% of the ingested food, with a mean value of 38.7%.

A first attempt was made to try to go into more detail concerning assimilation and conversion efficiencies in two species: *E. cirrhosa* and *I. illecebrosus* (Boucher-Rodoni, 1973a), using total nitrogen and caloric content energy budgets. The results, despite some inherent, inevitable errors (sacrifice method, mucous strings in feces, parasites, etc.) show that absorption efficiency (or coefficient of digestibility) is nearly always above 90%. When nitrogen was used as a criterion, conversion efficiency was higher in the crab-fed octopods than in the fish-fed (capelins) teuthoids, and when caloric content was considered, it was higher in *Illex*. The figures for conversion, maintenance, and unabsorbed food in *Octopus cyanea*, on a caloric basis, are respectively 60, 36, and 4% (Van Heukelem, 1976).

One would expect that these high food conversion rates are probably biased values, in that they are drawn from experimental conditions, and do not reflect the real life conditions in nature, which might be important for animals with such elaborate behavior. However, recapture of branded animals after a few weeks in the wild shows that laboratory growth results are reasonably close to those in nature, at least as far as *Octopus* is concerned (Itami, 1964; Van Heukelem, 1973). Boyle and Knobloch (1982) showed for *Eledone* a growth rate similar in the aquarium and *in situ*. *Illex* seems to grow even faster in captivity than in nature, especially at the end of the life cycle (O'Dor et al., 1980).

##### 5. Evolution of Digestive Processes

Cephalopods may be considered to have evolved from a molluscan ancestor, a crawling form inhabiting shallow waters and probably feeding on detritus. The radula would be important in feeding, the jaws scarcely developed. The midgut would be simple and particulate food would penetrate the midgut gland, where extra- and intracellular digestion would take place. This action of the midgut gland persists in *Nautilus* (Table I).

Two important evolutionary steps led to the present cephalopod digestive system: the development of powerful jaws (correlated with acquisition of predatory habits) and the division of the midgut gland into a stomach, where extracellular digestion of large pieces of food takes place, and a caecum allowing further digestion and providing an important absorptive surface. The old molluscan alternate secretion-absorption phases in the digestive gland allow only a slow digestive process, even if the subdivisions of the gut increase the digestive

TABLE I  
Evolution of Digestive Processes in Some Cephalopods

Species	Life-style	Duration of digestion at a given temperature	State of food entering the digestive gland	Sites of absorption		
				Digestion in the digestive gland	Digestive duct's appendages	Caecum

TABLE I

## Evolution of Digestive Processes in Some Cephalopods

Species	Life-style	Duration of digestion at a given temperature	State of food entering the digestive gland	Digestion in the digestive gland	Digestive gland	Sites of absorption Digestive duct's appendages	Caecum
<i>Nautilus pompilius</i>	Benthic		Pieces of food <sup>c</sup>	?	++	?	?
<i>Sepia officinalis</i>	Nectobenthic	20 h at 15°C	Fluid and fine particles <sup>b</sup>	Intracellular <sup>i</sup>	++ <sup>e</sup>	++ <sup>e</sup>	+ <sup>e</sup>
<i>Eledone cirrosa</i>	Benthic	15 h at 20°C <sup>d</sup> 30 h at 10°C 20 h at 15°C <sup>f</sup> 15 h at 20°C	Fluid juice and fine particles?	Intracellular? <sup>i</sup>	++ <sup>i</sup>	?	?
<i>Octopus vulgaris</i>	Benthic	16 h at 14°C <sup>g</sup> 12 h at 18–19°C <sup>h</sup> 14–15 h at 23°C <sup>b</sup> 4–6 h at 18°C <sup>a</sup>	Fluid juice <sup>b</sup>	?	++ <sup>b,g</sup>	+ <sup>g</sup>	++ <sup>g</sup>
<i>Loligo vulgaris</i>	Pelagic		Food does not enter the organ <sup>a</sup>	No digestion	— <sup>a</sup>	?	++ <sup>a</sup>

<sup>a</sup> Bidder, (1950).<sup>b</sup> Bidder, (1957).<sup>c</sup> Bidder, (1966).<sup>d</sup> Boucaud-Camou, (1973).<sup>e</sup> Boucaud-Camou and Péquignat, (1973).<sup>f</sup> Boucher-Rodoni (1975).<sup>g</sup> Boucaud-Camou et al., (1976).<sup>h</sup> Boucher-Rodoni and Mangold, (1977).<sup>i</sup> Boucaud-Camou and Yim, (1980).<sup>j</sup> Boucher-Rodoni, (1981).





- Bogoraze, D., and Cazal, P. (1946). Remarques sur le système stomatogastrique du poulpe (*Octopus vulgaris* Lam.). *Arch. Zool. Exp. Gen.* **84**, 115-131.
- Boletzky, S. v. (1967). Die embryonale Ausgestaltung der frühen Mitteldarmanlage von *Octopus vulgaris* Lam. *Rev. Suisse Zool.* **74**, 555-562.
- Boletzky, S. v. (1978). Gut development in cephalopods: a correction. *Rev. Suisse Zool.* **85**, 379-380.
- Boletzky, S. v., and Hanlon, R. T. (1983). A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. *Mem. Natl. Mus. Victoria, Melbourne*.
- Borer, K. T. (1971). Control of food intake in *Octopus briareus* Robson. *J. Comp. Physiol. Psychol.* **75**, 171-185.
- Boucaud-Camou, E. (1968). Étude histologique et histochimique de l'appareil digestif de *Sepioloa atlantica* d'Orbigny et *Sepia officinalis* L. *Bull. Soc. Linn. Normandie* **9**, 220-243.
- Boucaud-Camou, E. (1969). Localisation d'activités amylasiques et protéasiques dans l'appareil digestif de *Sepia officinalis* L. *C. R. Hebd. Seances Acad. Sci. Ser. D* **269**, 2564-2566.
- Boucaud-Camou, E. (1972). Étude infrastructurale du pancréas de *Sepia officinalis* L. *Bull. Soc. Zool. Fr.* **97**, 197-205.
- Boucaud-Camou, E. (1973). "Étude de l'appareil digestif de *Sepia officinalis* L. (Mollusque Céphalopode). Essai d'analyse expérimentale des phénomènes digestifs." Ph.D. Dissertation, Univ. of Caen, France.
- Boucaud-Camou, E. (1974). Localisation d'activités enzymatiques impliquées dans la digestion chez *Sepia officinalis* L. *Arch. Zool. Exp. Gen.* **115**, 5-27.
- Boucaud-Camou, E. (1977). Structure et fonction de l'épithélium caecal de *Sepia officinalis* L. *Biol. Cell.* **29**, 55-60.
- Boucaud-Camou, E., and Péquignat, E. (1973). Étude expérimentale de l'absorption digestive chez *Sepia officinalis* L. *Forma & Functio* **6**, 93-112.
- Boucaud-Camou, E., and Yim, M. (1980). Fine structure and function of the digestive cell of *Sepia officinalis* (Mollusca: Cephalopoda). *J. Zool.* **191**, 89-105.
- Boucaud-Camou, E., Boucher-Rodoni, R., and Mangold, K. (1976). Digestive absorption in *Octopus vulgaris* (Cephalopoda: Octopoda). *J. Zool.* **179**, 261-271.
- Boucher-Rodoni, R. (1973a). "Nutrition, digestion et transfert énergétique chez les Céphalopodes *Eledone cirrosa* (Lamarck) et *Illex illecebrosus* (Lesueur)." Ph.D. Dissertation, Univ. of Geneva, Switzerland.
- Boucher-Rodoni, R. (1973b). Vitesse de digestion d'*Octopus cyanea* (Cephalopoda: Octopoda). *Mar. Biol. (Berlin)* **18**, 237-242.
- Boucher-Rodoni, R. (1975). Vitesse de digestion chez les Céphalopodes *Eledone cirrosa* (Lamarck) et *Illex illecebrosus* (Lesueur). *Cah. Biol. Mar.* **16**, 159-175.
- Boucher-Rodoni, R. (1976). Étude histologique du tube digestif de deux Céphalopodes *Eledone cirrosa* (Octopoda) et *Illex illecebrosus* (Teuthoidea), au cours de la digestion. *Cah. Biol. Mar.* **17**, 254-260.
- Boucher-Rodoni, R. (1981). "Étude de la glande digestive de deux Céphalopodes, au cours de la digestion et au cours du cycle de vie." Ph.D. Dissertation, Univ. of Paris XI, France.
- Boucher-Rodoni, R., and Mangold, K. (1977). Experimental study of digestion in *Octopus vulgaris* (Cephalopoda: Octopoda). *J. Zool.* **183**, 505-515.
- Boyle, P. R., and Knobloch, D. (1981). Hole boring of crustacean prey by the octopus, *Eledone cirrhosa* (Mollusca, Cephalopoda). *J. Zool.* **913**, 1-10.
- Boyle, P. R., and Knobloch, D. (1982). On growth of the octopus *Eledone cirrhosa*. *J. Mar. Biol. Ass. U.K.* **62**, 277-296.
- Boyle, P. R., Mangold, K., and Froesch, D. (1979). The mandibular movements of *Octopus vulgaris*. *J. Zool.* **188**, 53-67.

- Bradbury, H. E., and Aldrich, F. A. (1969). Observations on feeding of the squid *Illex illecebrosus* (Lesueur, 1821) in captivity. *Can. J. Zool.* **47**, 913-915.
- Capurro, S. (1961). Ricerche istochimiche sui mucopolisaccaridi degli epiteli del canale alimentare di *Octopus vulgaris* Lam. *Ann. Mus. Civ. Stor. Nat. Genova* **72**, 249-284.
- Cariello, L., and Zanetti, L. (1977).  $\alpha$  and  $\beta$  cephalotoxins: two paralyzing proteins from posterior salivary gland of *Octopus vulgaris*. *Comp. Biochem. Physiol. C* **57**, 169-174.
- Choe, S. (1966). On the growth, feeding rates and the efficiency of food conversion for cuttlefishes and squids. *Kor. J. Zool.* **9**, 72-80.
- Clarke, M. C. (1962). The identification of cephalopod "Beaks" and relation between size and total body weight. *Bull. Br. Mus. (Nat. Hist.) Zool.* **8**, 421-480.
- Cuénot, L. (1907). Fonctions absorbante et excrétrice du foie des Céphalopodes. *Arch. Zool. Exp. Gen.* **7**, 227-245.
- d'Aniello, A., and Scardi, V. (1971). Attività cellulasica nel polipo (*Octopus vulgaris*). *Boll. Soc. Ital. Biol. Sper.* **47**, 481-483.
- Denton, E. J., and Gilpin-Brown, J. B. (1960). Daily changes in the buoyancy of the cuttlefish. *J. Physiol.* **151**, 36P-37P.
- Dilly, P. N., and Nixon, M. (1976). The cells that secrete the beaks in octopods and squids (Mollusca: Cephalopoda). *Cell Tissue Res.* **167**, 229-242.
- Donaubauer, H. H., and Schipp, R. (1978). The localization of enzyme activities in the pancreatic appendages of *Sepia officinalis* L. (Cephalopoda) *Histochemistry* **59**, 29-44.
- Ducros, C. (1966). Tannage quinonique du bec, de la plume et des dents radulaires chez le Calmar, *Loligo vulgaris* Lamarck. *Bull. Soc. Zool. Fr.* **91**, 331-332.
- Ducros, C. (1971). L'innervation des glandes salivaires postérieures chez *Octopus vulgaris*. *Arch. Anat. Microsc. Morphol. Exp.* **60**, 27-36.
- Ducros, C. (1972a). Étude ultrastructurale de l'innervation des glandes salivaires postérieures chez *Octopus vulgaris*. I. Les troncs nerveux du canal salivaire. *Z. Zellforsch. Mikrosk. Anat.* **132**, 35-49.
- Ducros, C. (1972b). Étude ultrastructurale de l'innervation des glandes salivaires postérieures chez *Octopus vulgaris*. II. Innervation de la musculature du canal et des glandes. *Z. Zellforsch. Mikrosk. Anat.* **132**, 51-65.
- Ducros, C. (1972c). Étude ultrastructurale de l'innervation des glandes salivaires postérieures chez *Octopus vulgaris*. III. Innervation des tubules de la glande. *Z. Zellforsch. Mikrosk. Anat.* **132**, 67-78.
- Endean, R. (1972). Aspects of Molluscan pharmacology. In "Chemical Zoology" (M. Florkin, and B. T. Sheer, eds.), Vol. 8, pp. 421-466. Academic Press, New York & London.
- Enriques, P. (1902). Il fegato dei Molluschi e le sue funzioni. Ricerche prevalentemente microscopiche. *Mitt. Zool. Stn. Neapel* **15**, 281-406.
- Erspamer, V., and Anastasi, A. (1962). Structure and pharmacological actions of eledoisin, the active endecapeptide of the posterior salivary glands of *Eledone*. *Experientia* **18**, 58-59.
- Falloise, A. (1906). Contribution à la physiologie comparée de la digestion. La digestion chez les Céphalopodes. *Arch. Int. Physiol.* **3**, 282-296.
- Fields, W. G. (1965). The structure, development, food relations, reproduction and life history of the squid *Loligo opalescens* Berry. *Bull. Calif. Dep. Fish Game Fish* **13**, 1-108.
- Fisher, L. R., Kon, S. K., and Thompson, S. Y. (1956). Vitamin A and carotenoids in certain Invertebrates. V. Mollusca: Cephalopoda. *J. Mar. Biol. Ass. U.K.* **35**, 63-80.
- Fox, D. L. (1966). Pigmentation of molluscs. In "Physiology of Mollusca" (K. M. Wilbur, C. M. Yonge, eds.), Vol. 2, pp. 249-274. Academic Press, New York & London.
- Fujita, S. (1916). On the boring of pearl oysters by *Octopus (Polypus) vulgaris* Lamarck. *Dobutsugaku Zasshi* **28**, 250-257.

## 3. Feeding and Digestion

- Fukada, Y. (1980). Observations on the feeding of the squid *Illex illecebrosus* (Lesueur, 1821) in captivity. *Can. J. Zool.* **47**, 913-915.
- I. Obata, T. Okutani, Gabe, M., and Prenant, M. (1961). Étude histochimique du radulaire de quelques Céphalopodes. *Univ. Kharkov* **48**, 1-10.
- Gariaeff, V. P. (1915). The salivary gland of the squid *Illex illecebrosus*. *Sper.* **26**, 776-780.
- Ghiretti, F. (1950). Enzymi del radiale. *Sper.* **26**, 776-780.
- Ghiretti, F. (1953). Les enzymes du radiale. *Int. Physiol.* **61**, 10-11.
- Ghiretti, F. (1959). Cephalopods. *Nature* **124**, 1-10.
- Ghiretti, F. (1960). Toxicity of the radularia. *Nature* **124**, 1-10.
- Goddard, C. K. (1968). Structure and function of the radularia. *Nature* **227**, 275-285.
- Graziadei, P. (1960). Ricerche sulla fisiologia del radiale. *Ital. Anat. Embriol.* **1**, 1-10.
- Graziadei, P. (1962). Recherches sur la physiologie du radiale. *Comp. Biochem. Physiol.* **31**, 1-10.
- Graziadei, P. (1964). Recherches sur la physiologie du radiale. *Comp. Biochem. Physiol.* **37**, 1-10.
- Guerra, A. (1978). Sobre la fisiología del radiale. *Investig. Pesquera* **42**, 1-10.
- Haven, N. (1972). The ecology of the squid. *Nature* **235**, 75-80.
- Hunt, S., and Nixon, M. (1976). The structure and function of the beaks of the squid. *Comp. Biochem. Physiol.* **73**, 1-10.
- Itami, K. (1964). Marking of the beaks of the squid. *Nature* **204**, 1-10.
- Jeuniaux, C. H. (1963). The structure and function of the beaks of the squid. *Nature* **200**, 1-10.
- Joll, L. M. (1977). Growth of the beaks of the squid. *Aust. J. Freshwater Res.* **28**, 1-10.
- Juorio, A. V., and Killick, J. (1978). The structure and function of the beaks of the squid. *Physiol. A* **44**, 1059-1065.
- Karpov, K. A., and Cailliet, J. M. (1978). The structure and function of the beaks of the squid. *Physiol. A* **44**, 1059-1065.
- Karpov, K. A., and Cailliet, J. M. (1979). The structure and function of the beaks of the squid. *Physiol. A* **45**, 1-10.
- Karpov, K. A., and Cailliet, J. M. (1980). The structure and function of the beaks of the squid. *Physiol. A* **46**, 1-10.
- Berry, in relation to the structure and function of the beaks of the squid. *Calif. Coop. Oceanogr. Fish. Res.* **10**, 37-56.
- Kozlovskaya, E. P., and V. (1978). The structure and function of the beaks of the squid. *Comp. Biochem. Physiol.* **73**, 1-10.
- Lacaze-Duthiers, H. (1892). Recherches sur la physiologie du radiale. *Arch. Zool. Exp. Gen.* **10**, 37-56.
- Lane, F. W. (1974). "Kinetics of the structure and function of the beaks of the squid. *Calif. Coop. Oceanogr. Fish. Res.* **10**, 37-56.
- Ledrut, J., and Ungar, G. (1978). The structure and function of the beaks of the squid. *Physiol. A* **44**, 1059-1065.
- Loukashkin, A. (1977). On the structure and function of the beaks of the squid. *Physiol. A* **43**, 1-10.
- the knowledge of its function. *Rep.* **18**, 109-111.
- Mangold, K. (1983). Food habits of the squid. *Nature* **301**, 1-10.
- Victoria, Melbourne.

- Fukada, Y. (1980). Observations by SEM. In "Nautilus macromphalus in Captivity." (T. Hamada, I. Obata, T. Okutani, eds.) pp. 23-33. Tokai Univ. Press, Tokyo, Japan.
- Gabe, M., and Prenant, M. (1957). Recherches sur la gaine radulaire des Mollusques. VI. L'appareil radulaire de quelques Céphalopodes. *Ann. Sci. Nat. Zool.* **19**, 587-602.
- Gariaeff, V. P. (1915). The structure of the digestive tract of some Cephalopoda. *Trav. Soc. Natl. Univ. Kharkov* **48**, 1-122.
- Ghiretti, F. (1950). Enzimi delle ghiandole salivari posteriori dei Cefalopodi. *Boll. Soc. Ital. Biol. Sper.* **26**, 776-780.
- Ghiretti, F. (1953). Les excitants chimiques de la secretion salivaire chez les Céphalopodes. *Arch. Int. Physiol.* **61**, 10-21.
- Ghiretti, F. (1959). Cephalotoxin: the crab-paralysing agent of the posterior salivary gland of Cephalopods. *Nature (London)* **183**, 1192-1193.
- Ghiretti, F. (1960). Toxicity of *Octopus* saliva against Crustacea. *Ann. N.Y. Acad. Sci.* **90**, 726-741.
- Goddard, C. K. (1968). Studies on the blood sugar of *Octopus dofleini*. *Comp. Biochem. Physiol.* **27**, 275-285.
- Graziadei, P. (1960). Ricerche sulla innervazione del canale alimentare di *Sepia officinalis*. *Arch. Ital. Anat. Embriol.* **65**, 169-177.
- Graziadei, P. (1962). Receptors in the suckers of *Octopus*. *Nature (London)* **195**, 57-59.
- Graziadei, P. (1964). Receptors in the sucker of the cuttlefish. *Nature (London)* **203**, 384-386.
- Guerra, A. (1978). Sobre la alimentacion y comportamiento alimentario de *Octopus vulgaris*. *Investigation Pesquera* **42**, 351-364.
- Haven, N. (1972). The ecology and behavior of *Nautilus pompilius* in the Philippines. *Veliger* **15**, 75-80.
- Hunt, S., and Nixon, M. (1981). A comparative study of protein composition in the chitin-protein complexes of the beak, pen, sucker disc, radula and oesophageal cuticle of cephalopods. *Comp. Biochem. Physiol. B* **68**, 535-546.
- Itami, K. (1964). Marking and release study in the *Octopus*. *Aquaculture* **12**, 119-125.
- Jeuniaux, C. H. (1963). "Chitine et chitinolyse." Masson, Paris.
- Joll, L. M. (1977). Growth and food intake of *Octopus tetricus* (Mollusca: Cephalopoda) in aquaria. *Aust. J. Freshwater Res.* **28**, 45-56.
- Juorio, A. V., and Killick, S. V. (1973). The distribution of monoamines and some of their acid metabolites in the posterior salivary glands and viscera of some cephalopods. *Comp. Biochem. Physiol. A* **44**, 1059-1067.
- Karpov, K. A., and Cailliet, G. P. (1978). Feeding dynamics of *Loligo opalescens*. *Fish. Bull.* **169**, 45-65.
- Karpov, K. A., and Cailliet, G. M. (1979). Prey composition of the market squid, *Loligo opalescens* Berry, in relation to depth and location of capture, size of squid and sex of spawning squid. *Calif. Coop. Oceanogr. Fish. Invest. Rep.* **20**, 51-57.
- Kozlovskaya, E. P., and Vaskovsky, V. E. (1970). A comparative study of proteinases of marine Invertebrates. *Comp. Biochem. Physiol.* **34**, 137-142.
- Lacaze-Duthiers, H. (1892). Observation d'un argonaute de la Méditerranée. *Arch. Zool. Exp. Gen.* **10**, 37-56.
- Lane, F. W. (1974). "Kingdom of the *Octopus*." Sheridan, New York.
- Ledrüt, J., and Ungar, G. (1937). Action de la sécrétine chez l'*Octopus vulgaris*. *Arch. Int. Physiol.* **44**, 205-211.
- Loukashkin, A. (1977). On biology of the market squid, *Loligo opalescens*, a contribution toward the knowledge of its food habits and feeding behaviour. *Calif. Coop. Oceanogr. Fish. Invest. Rep.* **18**, 109-111.
- Mangold, K. (1983). Food, feeding habits and growth in some cephalopods. *Mem. Natl. Mus. Victoria, Melbourne*.

- Mangold, K., and Fioroni, P. (1966). Morphologie et biométrie des mandibules de quelques Céphalopodes méditerranéens. *Vie & Milieu A* **17**, 1139-1196.
- Mangold, K., and Boletzky, S. von (1973). New data on reproductive biology and growth of *Octopus vulgaris*. *Mar. Biol. (Berlin)* **19**, 7-12.
- Martin, R., and Barlow, J. (1972). Localisation of monoamines in nerves of the posterior salivary gland and salivary center in the brain of *Octopus*. *Z. Zellforsch. Mikrosk. Anat.* **125**, 16-30.
- Matus, A. I. (1971). Fine structure of the posterior salivary gland of *Eledone cirrosa* and *Octopus vulgaris*. *Z. Zellforsch. Mikrosk. Anat.* **122**, 111-121.
- Messenger, J. B. (1968). The visual attack of the cuttlefish *Sepia officinalis*. *Anim. Behav.* **16**, 342-357.
- Messenger, J. B. (1977). Prey, capture and learning in the cuttlefish, *Sepia*. *Symp. Zool. Soc. London* **38**, 347-376.
- Miramand, P., and Guary, J. C. (1980). High concentrations of some heavy metals in tissues of the mediterranean *Octopus*. *Bull. Environ. Contam. Toxicol.* **24**, 783-788.
- Morishita, T. (1972a). Studies on the distribution of proteolytic enzymes in the internal organs of *Octopus*. *Bull. Jpn. Soc. Sci. Fish.* **38**, 839-843.
- Morishita, T. (1972b). Studies on some properties of proteolytic enzyme from *Octopus* liver. *Nippon Suisan Gakkaishi (Bull. Jpn. Soc. Sci. Fish.)* **38**, 1051-1056.
- Morishita, T. (1972c). On the existence of cathepsins A, B, and C in *Octopus* liver. *Nippon Suisan Gakkaishi (Bull. Jpn. Soc. Sci. Fish.)* **38**, 1057-1060.
- Morishita, T. (1974a). Participation in digestion by the proteolytic enzymes of the posterior salivary gland in *Octopus*. I. Confirmation of the existence of protein digestive enzymes in the posterior salivary gland. *Nippon Suisan Gakkaishi (Bull. Jpn. Soc. Sci. Fish.)* **40**, 595-600.
- Morishita, T. (1974b). Participation in digestion by the proteolytic enzymes of the posterior salivary gland in *Octopus*. II. Isolation and purification of the proteolytic enzymes from the posterior salivary gland. *Nippon Suisan Gakkaishi (Bull. Jpn. Soc. Sci. Fish.)* **40**, 601-607.
- Morishita, T. (1974c). Participation in digestion by the proteolytic enzymes of the posterior salivary gland in *Octopus*. III. Some properties of purified enzymes from the posterior salivary gland. *Nippon Suisan Gakkaishi (Bull. Jpn. Soc. Sci. Fish.)* **40**, 917-925.
- Morishita, T. (1974d). Participation in digestion by the proteolytic enzymes of the posterior salivary gland in *Octopus*. IV. Purification and some properties of proteolytic enzymes from the digestive juice. *Nippon Suisan Gakkaishi (Bull. Jpn. Soc. Sci. Fish.)* **40**, 927-936.
- Morishita, T. (1978). Studies on the protein digestive enzymes of octopus, *O. vulgaris* Cuvier. *Bull. Fac. Fish. Mie Univ.* **5**, 197-282.
- Nicol, J. A. C. (1966). Special effectors: luminous organs, chromatophores, pigments and poison glands. In "Physiology of Mollusca" (K. M. Wilbur, and C. M. Yonge, eds), Vol. 1, pp. 353-381. Academic Press, New York & London.
- Nigmatullin, C. M., and Ostapenko, A. A. (1976). Feeding of *Octopus vulgaris* Lam. from the Northwest African coast. *ICES, C. M.* 1976/K, 6.
- Nixon, M. (1965). Some observations on the food intake and learning in *Octopus vulgaris*. *Pubbl. Stn. Zool. Napoli* **34**, 329-339.
- Nixon, M. (1966). Changes in body weight and intake of food by *Octopus vulgaris*. *J. Zool.* **150**, 1-9.
- Nixon, M. (1969a). The time and frequency of responses by *Octopus vulgaris* to an automatic food dispenser. *J. Zool.* **158**, 475-483.
- Nixon, M. (1969b). Growth of the beak and radula of *Octopus vulgaris*. *J. Zool.* **159**, 363-379.
- Nixon, M. (1973). Beak and radula growth in *Octopus vulgaris*. *J. Zool.* **170**, 451-462.
- Nixon, M. (1977). Hole-boring by *Octopus vulgaris* Cuvier from the Mediterranean sea. *Eur. Malacol. Congr. UME Amsterdam* **6**, 79.
- Nixon, M. (1979a). Has *Octopus* a second radula? *J. Zool* **187**, 291-296.

## 3. Feeding and Dig

- Nixon, M. (1979b). H. *acologia* **18**, 43.
- Nixon, M. (1980). The **190**, 53-57.
- Nixon, M., and Dilly, 447-511.
- Nixon, M., Maconnac *Octopus. J. Zool.*
- O'Dor, K. R., Durwar *captive squid (Ill population. ICN*
- Okutani, K., and Kim *Distribution of c Gakkaishi (Bull.*
- Oshima, K., Satodate, *cephalopods. J.*
- Pignero, A., and Roc *Loligo vulgaris*
- Pilson, M. E. Q., an *1366-1368.*
- Reid, R. G. B. (1966). *L. Comp. Biochem*
- Reid, R. G. B. (1968) *Comp. Biochem*
- Richard, A. (1966). *Sepia officinalis*
- Richard, A. (1971). *sexuelle de Sep Lille, France.*
- Robson, C. G. (1929- *London.*
- Romanini, M. G. (19 *Octopus vulgaris*
- Romanini, M. G. (19 *anteriori e poste*
- Romanini, M. G. (195 *ori degli octopo*
- Romijn, C. (1935). *373-431.*
- Roper, C. F., and Br *nisms: new biol Contrib. Zool. 1*
- Rothe W., Pfeleiderer, *Protease mit ch fisch). Hoppe-S*
- Sakaguchi, H. (1968). *Jpn. Soc. Sci. F*
- Sawano, E. (1935). *34, 101-126.*

- Nixon, M. (1979b). Hole-boring in shells by *Octopus vulgaris* Cuvier in the Mediterranean. *Malacologia* **18**, 431-443.
- Nixon, M. (1980). The salivary papilla of *Octopus* as an accessory radula for drilling shells. *J. Zool.* **190**, 53-57.
- Nixon, M., and Dilly, P. N. (1977). Sucker surfaces and prey capture. *Symp. Zool. Soc. London* **38**, 447-511.
- Nixon, M., Maconnachie, E., and Howell, P. G. T. (1980). The effects on shells of drilling by *Octopus*. *J. Zool.* **191**, 75-88.
- O'Dor, K. R., Durward, R. D., Vessey, E., and Amaratunga, T. (1980). Feeding and growth rates in captive squid (*Illex illecebrosus*) and the influence of food availability on growth in the natural population. *ICNAF sel. Papers* **6**, 15-22.
- Okutani, K., and Kimata, M. (1964). Studies on chitinolytic enzymes present in aquatic animals. III. Distribution of chitinase in digestive organs of a few kinds of aquatic animals. *Nippon Suisan Gakkaishi (Bull. Jpn. Soc. Sci. Fish.)* **30**, 574-576.
- Oshima, K., Satodate, K., and Ithya, S. (1930). Existence of proteinase and amylase in the viscera of cephalopods. *J. Dep. Agric. For. Sapporo Univ.* **99**, 40.
- Pignero, A., and Rocca, E. (1969). Proteolytic and peptidasic activities of a particulate fraction of *Loligo vulgaris* Lamarck hepatopancreas. *Comp. Biochem. Physiol.* **29**, 1271-1275.
- Pilson, M. E. Q., and Taylor, P. B. (1961). Hole drilling by *Octopus*. *Sciences (N.Y.)* **134**, 1366-1368.
- Reid, R. G. B. (1966). Digestive tract enzymes in the Bivalves *Lima hians* Gmelin and *Mya arenaria* L. *Comp. Biochem. Physiol.* **17**, 417-433.
- Reid, R. G. B. (1968). The distribution of digestive tract enzymes in Lamellibranchiate Bivalves. *Comp. Biochem. Physiol.* **24**, 727-744.
- Richard, A. (1966). La température, facteur externe essentiel de croissance pour le Céphalopode *Sepia officinalis* L. *C. R. Hebd. Seances Acad. Sci. Ser. D* **263**, 1138-1141.
- Richard, A. (1971). "Contribution à l'étude expérimentale de la croissance et de la maturation sexuelle de *Sepia officinalis* L. (Mollusque Céphalopode)." Ph.D. Dissertation, Univ. of Lille, France.
- Robson, C. G. (1929-1932). "A Monograph of the Recent Cephalopoda," 2 Parts. Brit. Museum, London.
- Romanini, M. G. (1949). Attività ialuronidasi delle ghiandole salivari anteriori e posteriori di *Octopus vulgaris* e di *Octopus macropus*. *Boll. Soc. Ital. Biol. Sper.* **25**, 1179-1180.
- Romanini, M. G. (1951). Azioni istochimicamente rivelabili dei fermenti delle ghiandole salivari anteriori e posteriori di *Octopus vulgaris*. *Boll. Soc. Ital. Sper.* **27**, 1082-1083.
- Romanini, M. G. (1952). Osservazioni sulla ialuronidasi delle ghiandole salivari anteriori e posteriori degli octopodi. *Pubbl. Stn. Zool. Napoli* **23**, 252-270.
- Romijn, C. (1935). Die Verdauungsenzyme bei einigen Cephalopoden. *Arch. Neerl. Zool.* **1**, 373-431.
- Roper, C. F., and Brundage, W. L., Jr. (1972). Cirrate octopods with associated deep-sea organisms: new biological data based on deep benthic photographs (Cephalopoda). *Smithsonian Contrib. Zool.* **121**, 1-46.
- Rothe W., Pfeleiderer, G., and Zwilling, R. (1970). Zur Evolution der Endopeptidasen. XI. Eine Protease mit chymotryptischer Spezifität aus dem Magensaft von *Sepia officinalis* (Tintenfisch). *Hoppe-Seylers Z. Physiol. Chem.* **351**, 629-634.
- Sakaguchi, H. (1968). Studies on digestive enzymes of devilfish. *Nippon Suisan Gakkaishi (Bull. Jpn. Soc. Sci. Fish.)* **34**, 716-721.
- Sawano, E. (1935). Proteolytic enzymes in *Polypus vulgaris* Lamarck. *Sci. Rep. Zool. Inst. Tokyo* **34**, 101-126.

- Schipp, R., and Boletzky, S. v. (1975). Morphology and function of the excretory organs in Dibranchiate Cephalopods. *Fortschr. Zool.* **23**, 89-111.
- Schipp, R., and Boletzky, S. v. (1976). The pancreatic appendages of Dibranchiate Cephalopods. I. The fine structure of the "pancreas" in Sepioidea. *Zoomorphologie* **86**, 81-98.
- Schipp, R., and Pfeiffer, K. (1980). Vergleichende cytologische und histochemische Untersuchungen an der Mitteldarmdrüse dibranchiater Cephalopoden (*Sepia officinalis* L. und *Octopus vulgaris* Lam.). *Zöol. Jb. Anat.* **104**, 317-343.
- Sheumack, D. D., Howden, M. E. H., Spence, I., and Quinn, R. J. (1978). Maculotoxin a neurotoxin from the venom glands of the octopus *Hapalochlaena maculosa* identified as tetrodotoxin. *Science (Washington, D.C.)* **199**, 188-189.
- Songdahl, J. M., and Shapiro, B. I. (1974). Purification and composition of a toxin from the posterior salivary gland of *Octopus dofleini*. *Toxicon* **12**, 109-115.
- Takahashi, T. (1960). Biochemical studies on the viscera of cuttlefish, *Ommastrephes sloani pacificus*. III. *Nippon Suisan Gakkaishi* (Bull. Jpn. Soc. Sci. Fish.) **26**, 500-507.
- Takahashi, T. (1963). Studies on the viscera enzymes of cuttlefish, *Ommastrephes sloani pacificus*. *J. Fac. Fish. Prefect. Univ. Mie* **5**, 384-411.
- Tritar, B. (1970a). L'absorption du glyco-colle par l'intestin de l'Eledone (*Eledone moschata* Lamarck). Effets de la durée et de la concentration. *J. Physiol. (Paris)* **62**, (Suppl. 1), 223.
- Tritar, B. (1970b). Recherche sur l'absorption digestive des acides aminés chez les Céphalopodes (Mollusques). I. La cinétique de l'absorption du glyco-colle par le caecum spiral de l'Eledone *moschata* Lamarck. *Ann. Inst. Michel Pacha* **3**, 8-13.
- Tritar, B. (1971). Recherches sur l'absorption intestinale des acides aminés chez les Céphalopodes: absorption comparée du glyco-colle, de la L. méthionine et de la L. histidine par l'intestin d'Eledone *moschata* Lamarck. *C. R. Seances Soc. Biol. Ses Fil.* **165**, 887-890.
- Tritar, B., and Peres, G. (1974). Recherche sur l'absorption intestinale des glucides chez les mollusques Céphalopodes: influence de la température et de la solution administrée sur l'absorption du glucose par l'intestin de la Seiche (*Sepia officinalis* L.). *Ann. Inst. Michel Pacha* **7**, 1-12.
- Vandermeulen, J. H., and Reid, R. G. B. (1969). Digestive tract enzymes in Phoronida. *Comp. Biochem. Physiol.* **28**, 443-448.
- Van Heukelem, W. F. (1973). Growth and life-span of *Octopus cyanea* (Mollusca: Cephalopoda). *J. Zool.* **169**, 299-315.
- Van Heukelem, W. F. (1976). "Growth Bioenergetics and Life-Span in *Octopus cyanea* and *Octopus maya*." Ph. D. Thesis, Univ. of Hawaii, Honolulu.
- Verne, J. (1922). Contribution histologique à l'étude de la sécrétion de la glande salivaire postérieure des Céphalopodes. *C. R. Assoc. Anat.* **17**, 309-320.
- Vialli, M., and Erspamer, V. (1938). Ricerche istochimiche sulla ghiandola salivare posteriore di *Octopus vulgaris*. *Mikrochemie* **24**, 253-261.
- Vonk, H. J. (1947). La présence d'acides biliaires et la résorption des acides gras chez les Invertébrés. *Bull. Soc. Chim. Biol.* **29**, 94-96.
- Vovk, A. N. (1972). Feeding habits of the North American squid, *Loligo pealii* Lesueur). *Fr. Tr. Atl. Navchmo-Issled Inst. Rybn. Khoz. Okeanogr.* **42**, 141-151.
- Ward, P., and Wickstein, M. D. (1980). Food sources and feeding behavior of *Nautilus macromphalus*. *Veliger* **23**, 119-124.
- Wells, M. J. (1965). Learning by marine invertebrates. *Adv. Mar. Biol.* **3**, 1-62.
- Wells, M. J. (1978). "Octopus: Physiology and Behaviour of an Advanced Invertebrate." Chapman & Hall, London.
- Wells, M. J., and Wells, J. (1970). Observation on the feeding, growth rate and habits of newly settled *Octopus cyanea*. *J. Zool.* **161**, 65-74.
- Wilson, D. P. (1951). "Life of the Shore and Shallow Sea." Nicholson & Watson, London.

## 3. Feeding and Digestion

- Wodinsky, J. (1969). Penetration of food into the digestive tract of the cuttlefish, *Sepia officinalis*. *Proc. Zool. Soc. London* **133**, 47-50.
- Wodinsky, J. (1973). Mechanism of food intake in the cuttlefish, *Sepia officinalis*. *Proc. Zool. Soc. London* **133**, 47-50.
- Wodinsky, J. (1977). Hormonal control of food intake and secretion. *Sciences (Paris)* **216**, 101-102.
- Worms, J. (1979). "L'Utilisation de la nourriture: l'étude d'une population de mollusques." Ph.D. Dissertation, University of Paris.
- Young, J. Z. (1960). Observations on the feeding habits of the cuttlefish, *Sepia officinalis*. *Proc. Zool. Soc. London* **133**, 47-50.
- Young, J. Z. (1961). Learning by the cuttlefish, *Sepia officinalis*. *Proc. Zool. Soc. London* **136**, 32-36.
- Young, J. Z. (1965a). The feeding habits of the cuttlefish, *Sepia officinalis*. *Biol. J. Linn. Soc.* **43**, 581-593.
- Young, J. Z. (1965b). The feeding habits of the cuttlefish, *Sepia officinalis*. *Biol. J. Linn. Soc.* **249**, 27-44.
- Young, J. Z. (1971). "The Feeding Habits of the Cuttlefish, *Sepia officinalis*." Press (Clarendon), Oxford.

- Wodinsky, J. (1969). Penetration of the shell and feeding on Gastropods by *Octopus*. *Am. Zool.* **9**, 997-1010.
- Wodinsky, J. (1973). Mechanism of hole boring in *Octopus vulgaris*. *J. Gen. Psychol.* **88**, 179-183.
- Wodinsky, J. (1977). Hormonal inhibition of feeding and death in *Octopus*: control by optic gland secretion. *Sciences (N.Y.)* **198**, 948-951.
- Worms, J. (1979). "L'Utilisation des prises commerciales en biologie des pêches. Application à l'étude d'une population de *Loligo vulgaris* (Cephalopoda, Teuthoidea) du golfe du Lion." Ph.D. Dissertation, Univ. of Montpellier, France.
- Young, J. Z. (1960). Observations on *Argonauta* and specially its method of feeding. *Proc. Zool. Soc. London* **133**, 471-479.
- Young, J. Z. (1961). Learning and discrimination in the *Octopus*. *Biol. Rev. Cambridge Philos. Soc.* **36**, 32-96.
- Young, J. Z. (1965a). The nervous pathways for poisoning, eating and learning in *Octopus*. *J. Exp. Biol.* **43**, 581-593.
- Young, J. Z. (1965b). The buccal nervous system of *Octopus*. *Phil. Trans. R. Soc. London Ser. B* **249**, 27-44.
- Young, J. Z. (1971). "The Anatomy of the Nervous System of *Octopus vulgaris*." Oxford Univ. Press (Clarendon), Oxford.