

FOOD, FEEDING AND GROWTH IN CEPHALOPODS

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Abstract

Cephalopods play an important role in the food web of the oceans. While their predators are fairly well known, little is known about their prey and almost nothing about these caloric values. Stomach contents analysis and rearing experiments provide information of about 50 species out of the 700 known to exist. Crustaceans are the main food item, followed by fish and molluscs, including cephalopods. In many species, prey change with increasing size of the predator while others prefer the same food, e.g. crustaceans, during their whole life cycle.

Young benthic octopuses eat 10 to 20% of their own body weight per day. In later stages the food intake decreases to 5-2%. In young pelagic squids, the food intake is about 50% and 10-20% in subadult and adult animals. Their higher food intake can be related to the higher metabolic costs.

The conversion rate is very high: on a wet weight basis, 20-60% of the ingested food is used for growth. Food intake depends on temperature while conversion rate does not, but both seem to be dependent upon food quality, at least in some species.

Growth is very fast in young animals, slows down in subadults and adults and stops altogether or even declines in mature animals, especially in octopodid females.

The question of whether growth models obtained from laboratory data can be applied to growth in field populations is discussed.

Introduction

Elucidating the role of high-level predators in marine ecosystems is one of the urgent problems in fisheries biology, as has been clearly shown during the discussions of the workshop on 'The Biology and Resource Potential of Cephalopods' held in Melbourne in March 1981. There is no doubt that cephalopods are high-level predators, and the vital role that they play in the food web of the oceans, in pelagic as well as in benthic communities, has become increasingly evident during the last two decades. Cephalopods are heavily preyed upon by fish, birds and marine mammals, especially by whales, some of which depend almost exclusively upon squids as food (Clarke, 1977, 1980). A good deal is known about cephalopod predators, and analysis of their stomach contents allow us to make fairly realistic estimations of the stock size of some cephalopods. But our knowledge of the prey of cephalopods in the field is still poor. The range of prey organisms is wide, as representatives of nearly all marine phyla figure among them. The most important appear to be crustaceans, fish and molluscs, including cephalopods. A wealth of information exists on the food of maintained and reared cephalopod species (Boletzky, 1974a; Yang *et al.* 1980; Boletzky & Hanlon, this volume). However, even for these species,

verifications from field observations are scarce. Under laboratory conditions, cephalopods may accept food that they never encounter in their habitat.

As recent work shows (for a review, see Mangold, *et al.*, in press) the growth of cephalopods is fast. The life cycles are short, varying from about 6 months in small species to one, two or three years in larger ones. A few species of very large adult size may live for five or six years. Cephalopods are semelparous animals, reproducing once in their life time, although this 'once' may span quite a long period in some species. Indeed, spawning may be interrupted for several weeks (Mangold-Wirz, 1963; Boletzky, 1974a; Hixon, 1980).

If we ever hope to establish an 'energy balance sheet' between the predators and the prey of cephalopods, we have to determine specific energy budgets for growing cephalopods to adult size. This certainly will vary among different species and may depend, among other factors, on the kind of prey that each species eats. I do not intend to cover the whole topic here—it would indeed be a gigantic task. This paper constitutes a mini-review treating only certain aspects of food, feeding behaviour and feeding rate, conversion rate and growth for a few species. It includes some of my own published and unpublished results and

the results of an international group of scientists working on the energy budget of *Octopus vulgaris* (Wells, *et al.*, in press a,b,c). Finally, I shall try to summarize the present state of knowledge in these fields which currently is limited and rather patchy.

Material and Methods

Experiments were carried out principally on three species of the family Octopodidae easily obtained in the region surrounding Banyuls-sur-mer, France, namely: *Octopus vulgaris*, *Eledone moschata* and *E. cirrhosa*. *Eledone moschata* was reared from eggs laid in the laboratory to sexual maturity and spawning (see also Boletzky, 1975a). The other two species, having planktonic hatchlings, were collected by bottom trawls and reared from early benthic stages to spawning. Animals were kept either isolated or in small batches. In most experiments the octopods were fed crabs (*Carcinus mediterraneus*), but in some cases, different prey were offered, namely bivalves (*Mytilus galloprovincialis*, *Venus verrucosa*, *Tapes* spp.), gastropods (*Haliotis tuberculata*, *Patella coerulea*) and fish (*Sardina pilchardus*, *Engraulis* spp. and related species). Bivalves were provided for *O. vulgaris* based on shells collected beside occupied dens in the area of Banyuls-sur-mer (Ambrose, pers. comm.).

By way of comparison, rates for growth, daily feeding and food conversion (gross growth efficiency) were calculated according to Choe (1966):

$$A. \text{ daily growth rate} = \frac{w_2 - w_1}{tW} \times 100$$

where w_1 is the initial wet body weight, w_2 the final weight, W the average weight, and t the numbers of days.

$$B. \text{ food conversion rate} = \frac{w_2 - w_1}{FI} \times 100$$

where FI is the total food intake in grams of wet weight.

$$C. \text{ feeding rate} = \frac{FI}{tW} \times 100$$

Results and Discussion

A. FOOD, FEEDING AND GROWTH

1. Food preferences

a. Food preferences in three species of Octopodidae in experimental work.

Given the choice of live crustaceans (mainly crabs), shelled molluscs or fish, *O. vulgaris*, *E. moschata* and *E. cirrhosa* from the Banyuls area invariably take the crabs and ignore the other food items at all growth stages. If no crabs are offered, the three octopods will accept molluscs and/or fish, but only after several days or weeks of starvation. Bivalves are preferred over gastropods. Bivalves are torn open or are killed by boring a hole in the shell and injecting poison from the posterior salivary glands. All animals fed over various periods of time on molluscs and/or fish, ignored these prey when crabs were co-offered and the crabs were devoured immediately. The preference for a crab diet in the laboratory was noted by Taki (1941) for *O. vulgaris* in Japanese waters and by Altman & Nixon (1970) in the Mediterranean.

Eledone cirrhosa from the North Sea feeds on a wide variety of crustaceans: crabs, shrimps and lobsters. Molluscs, when offered, were rarely accepted (Boyle & Knobloch, 1981).

b. Food preferences of *O. vulgaris* and *E. cirrhosa* in the sea.

Guerra (1978) analysed the stomach contents of *O. vulgaris* from the Catalanian Sea: 80% of the food consisted of crustaceans (27 species were identified), 12% were fish and 8% were cephalopods (3 species). Sanchez (1981a) found crustaceans to be the main food of *E. cirrhosa* in the same area, and Moriyasu (1981) who analysed the stomach contents of several hundred specimens of *E. cirrhosa* from the Northern coast of the Western Mediterranean, confirmed the observations of Sanchez. Moriyasu noted that although seasonal changes in the composition of the diet occurred, the main food organisms were crustaceans.

There are two studies on prey of *O. vulgaris* from the northwest African coast. Nigmatullin & Ostapenko (1976) analysed over 2000 stomach contents of animals caught at depths

ranging from 15 to 80 m. The diet consisted mainly of crustaceans (frequency: 61.5%; volume: 53.6%) followed by fish (29.5% and 25.5% respectively). Only 6.3% (9.5% in vol.) of the food was shelled molluscs and another 6.0% (7.5%) consisted of cephalopods, including the same species. Nigmatullin & Ostapenko indicated the percentage of crustaceans (mainly crabs) may be overestimated, since most octopuses came from day catches and since they consider crabs to be 'day time' prey whereas fish are taken mostly at night. According to Hatanaka (1979), gastropods and bivalves are the most important prey (45-60%), while fish, crustaceans and cephalopods account for 19-34%, 7-16% and 4-13% respectively. This author also noted that prey vary with time of the day and depth.

The southeastern African reef population of *O. vulgaris* investigated by Smale & Buchan (1981), preys mainly on the pelecypod, *Perna perna* which is extremely abundant in this area. In the western Atlantic, *O. vulgaris* also seems to feed primarily on shelled molluscs (Arnold & Arnold, 1969; Wodinsky, 1969; Hochberg & Couch, 1971).

As is typical of most *Octopus* species, *O. vulgaris* is an opportunistic predator. Analysing stomach contents is a tedious task, and the stomachs are often empty. However, stomach contents do yield valuable information on the food of a predator even though some food items may be digested faster than others and leave no trace, at least not identifiable ones.

Examination of the gastropod and bivalve shells found in the den of an *Octopus* may give good evidence of what an *Octopus* has eaten. However, octopuses are known to collect shells and stones to protect their dens, hence, the possibility remains that the shelled molluscs present around a den may not actually have been eaten by the owner of the den. On the other hand, crustacean remains are often carried away and leave no traces in den middens which may then lead to an overestimation of the mollusc prey. Stomach contents may mainly reveal the abundance of different prey, e.g. a pure mollusc diet if no crustaceans are available. However, food preferences do exist, at least under laboratory conditions, and they

may well reflect a natural preference in the field. As far as *O. vulgaris* of the Catalanian Sea goes, there seems to be little doubt that crustaceans are the preferred prey.

c. General remarks on natural diets in Sepioids and Teuthoids.

To our knowledge, there is only one published analysis of the stomach contents of the nectobenthic cuttlefish, *Sepia officinalis*. The species accepts fish as readily as crustaceans, and molluscs, other than cephalopods, may occur in its diet as well as polychaetes (Najai & Ktari, 1979). The stomach contents of the benthic sepiolid *Rossia pacifica* consist mainly of crustaceans: about 80% (Brocco, 1970; Hochberg & Fields, 1980). The same holds for another member of the family, *Sepietta oweniana* (Summers & Bergström, 1983). For diets in captivity of the sepioids see Boletzky & Hanlon (this volume).

Slightly more is known of the diet of some loliginid and ommastrephid species. In general, juveniles eat crustaceans while subadults and adults prey mainly on fish and squids. Worms (1979) was unable to find any crustaceans in the stomach contents of *Loligo vulgaris* of more than 100 mm mantle length. Macy (1982) showed very clearly the correlation between the size of *L. pealei* and the composition of its diet. He also showed that slight differences exist in this relationship between in- and offshore populations. Loukashkin (1976) and Karpov & Caillet (1978) analysed the stomach contents of *L. opalescens*, a key species in the food web of the pelagic and benthic communities along the coast of California. *Lolliguncula panamensis* exhibits a clear preference for fish diet (Squires & Barragan, 1979) as does the ommastrephid, *Ommastrephes bartrami* (Araya, this volume). An exhaustive list of food items for the squid *Illex illecebrosus* is given by O'Dor (1983). Besides crustaceans, fish and squids, *I. illecebrosus* occasionally eats gastropods, pteropods and chaetognathes.

Several authors reported on the diet of the jumbo squid, *Dosidicus gigas*, a particularly voracious predator (Nesis, 1970, 1983; Hochberg & Fields, 1980; Erhardt *et al.*, this volume). Pelagic fish and squids seem to be the

main diet; small animals often feed on small crustaceans, subadults and adults prey heavily on the pelagic red crab, *Pleuroncodes planipes*. Pelagic molluscs also figure among the prey items. It should be noted that in some areas (Gulf of California), populations feed on small pelagic crustaceans during all stages of their life cycle, thus breaking the general pattern; an example of opportunistic feeding behaviour.

Mesopelagic oegopsids of small adult size (*Abrahaia*, *Abrahiopsis*, *Pterygioteuthis*, *Pyroteuthis*) eat small crustaceans, mainly copepods, during their entire life cycle (Mangold, unpublished).

2. Feeding rate

It is well known that within the normal range of temperature adaptation of a species, higher temperatures lead to greater food intake, although exceptions occur among the cephalopods (Boletzky, 1975b). As an example for the rule, *O. vulgaris* fed *ad libitum* over several weeks ingested 40 to 83% of all crabs offered at 20°C, ate only 29 to 31% at 15°C, while those at 10°C ingested as little as 12 to 15% (Mangold & Boletzky, 1973). Accordingly, the daily growth rate varied between 1.14 and 5.08% at 20°C, between 0.69 and 2.74% at 15°C and between 0.35 and 1.42 at 10°C. Similar results were obtained with *E. moschata* (Mangold, 1983b), although the overall means at the three temperatures were lower for subadult animals than in *O. vulgaris*.

In *E. cirrhosa* and *O. salutii*, however, food intake was at its highest between 15 and 18°C and then decreased with increasing temperatures. Both species are adapted to cooler waters than *O. vulgaris* and *E. moschata* (Mangold & Boletzky, 1973; see also Boyle & Knobloch, 1982b).

The daily feeding rate for all four species of Octopodidae decreased with increasing size, a fact already known for *O. vulgaris* (Nixon, 1966) and many other species (Choe, 1966; Van Heukelem, 1976; Joll, 1977 and others) and recently confirmed by Boyle & Knobloch (1982b) for *E. cirrhosa*.

Food intake also depends on food availability and size at least in some species. Borer (1971 a, b) showed that doubling the number of

prey for *O. briareus* and *O. bimaculoides* greatly increased food intake while reduction in food size decreased it. Food intake may also be dependent upon physiological limits such as the duration of the digestive processes (O'Dor *et al.*, 1980).

At least two other factors may influence food intake. One of them is the quality of food. When *O. vulgaris* of comparable initial size (300 to 350 g) were fed *ad libitum* over several weeks on either the crab (*Carcinus mediterraneus*), the limpet (*Patella coerulea*), the bivalve *Venus verrucosa* or the sardine (*Sardina pilchardus*), but otherwise maintained under strictly identical conditions (temperature rising from 10 to 13.5°C, normal day/night cycle), the mean feeding rate for animals fed on crabs was 3.6%, on limpets and *Venus* it was 2.5%, but on fish it was as low as 1.6%. These are preliminary results, based on wet weight relations. Further studies need to be conducted on a larger scale and also evaluated in terms of calorific values.

In the squid, *Illex illecebrosus*, however, the daily feeding rate was higher when fish (*Fundulus* spp.) rather than crustaceans (*Crangon* spp.) were offered *ad libitum* (Hirtle *et al.*, 1982). Although the squid ate a larger number of crustaceans, the total amount of food intake was higher with fish and the growth rate was higher on a fish diet. When the same quantities (weight) of fish or crustaceans were ingested, the daily growth rates were comparable. *Illex* seems to convert fish and crustaceans into cephalopod with a similar efficiency.

In many octopodid females, the amount of food ingested is drastically reduced or even stops altogether about 1 to 4 weeks before spawning. Growth may then stop rather abruptly and even may become negative. Brooding females of most species lose weight (Buckley, 1977, for *O. vulgaris*) although occasionally they may accept some food.

3. Conversion rate

While food intake is dependent upon temperature, food conversion or gross growth efficiency is not (Mangold & Boletzky, 1973; Van Heukelem, 1976; Pascual, 1978). Food conversion is also largely independent of the

size of the animals, but it appears to be lower in maturing individuals, especially in females of octopodid species. Mangold & Boletzky (1973) found that 20 to 80% (overall mean 55%) of the ingested food (crabs) was used for growth in *O. vulgaris*, whatever the temperature. More recent experiments gave slightly lower values, with an overall mean of 50% (Mangold, 1983a). In *E. moschata*, food conversion rate ranges between 18 and 70% (Mangold, 1983b) while in *E. cirrhosa* from the North Sea, the values lie between 10 and 70%, with an overall mean of 37% (Boyle & Knobloch, 1982b). These figures are very similar to those obtained for *E. cirrhosa* in the Mediterranean (Mangold, unpublished). In *O. cyanea* and *O. maya*, average food conversion rates are close to 40% (Van Heukelem, 1976). The overall mean for the small *O. joubini* was also found to be 40% (Forsythe, 1981; Forsythe & Hanlon, 1980), whereas in *O. tetricus* it is 47%, closer to the figures for *O. vulgaris* (Joll, 1977). It should be emphasised, however, that food conversion is highly variable, even with the same diet; not only between individuals of a species, but also on a temporal basis within individual octopuses (Mangold & Boletzky, 1973).

Preliminary results suggest that gross growth efficiency in *O. vulgaris* seems to be dependent upon food quality. When fed *ad libitum* on either crabs, sardines, limpets or clams, the food conversion averaged 50% when the food was crabs, a mainly proteic diet. In animals fed on sardines, a fatty diet, or on limpets or clams, relatively rich in carbohydrates, the conversion rates were distinctly lower about 25 and 20% respectively.

Smale & Buchan (1981) showed that in both males and females of *O. vulgaris*, conversion rates were higher when the animals were fed mussels (*Perna perna*) and rock lobsters (*Panulirus homarus*) than when fed on mussels only (males: 40.1 and 23.5%; females: 40.3 and 23.7% respectively).

Ingested food is used in two ways, for growth and for maintenance (the food required to keep an animal at a constant weight). Maintenance costs can be subdivided into energy used for standard metabolism, for specific organ activity (such as digestion and assimilation) and addi-

tional energy used in locomotory activity (Warren, 1971). The maintenance requirement decreases per unit body weight (Joll, 1977), it is dependent upon temperature, doubling or trebling with a rise of 10°C, and it is very likely to be higher in nectonic squids than in benthic octopuses (LaRoe, 1971; O'Dor *et al.*, 1980).

Gross growth efficiency in cephalopods is among the highest reported in the literature (Van Heukelem, 1976). On a wet weight basis, about 20 to 60% of the ingested food is used for growth. In *O. cyanea* and *O. maya*, gross growth efficiency is 40%; 55% of the ingested food is used in maintenance, only 5% (feces) is not absorbed (Van Heukelem, 1976). In *O. vulgaris*, the maintenance costs seem to be lower, about 45% on a crab diet, with 5% not absorbed. This difference, resulting in a higher gross growth efficiency (about 50%) may be simply due to the difference in temperature, since this species lives in cooler waters. It may also be due to a lower activity level. On an ashfree, caloric basis, the figures for conversion, maintenance and unabsorbed food for *O. cyanea* on a crab diet are 60, 36 and 4% respectively (Van Heukelem, 1976).

Wells *et al.* (1983, a,b,c) established the metabolic costs in *O. vulgaris* by measuring oxygen consumption. The standard metabolic rate in starving, inactive animals of 300 to 400 g at 21-22°C is about 56 ml O₂ Kg⁻¹ h⁻¹. The 'routine' metabolism (mean values from starved resting and active animals and from fed resting animals, *n* = 341) is 75 ml O₂ Kg⁻¹ h⁻¹. Feeding raises the metabolism in two ways. The capture, ingestion, digestion and assimilation of a prey (crab) causes an increase in oxygen uptake that lasts about 6 hours and peaks during the 1st to 3rd h after capture. This short-term (6 h) cost of assimilating the 10 to 12 g of flesh from a 20 g crab is in the order of 9 ml O₂ g⁻¹. There is also a long-term effect of feeding. Feeding a starved octopus in the 300 to 500 g size range a 20 g crab each day results in a progressive rise in oxygen consumption over the first 2 to 4 days following the first meal. Small animals do treble their oxygen uptake, larger ones double it. After these 2 to 4 days, the oxygen consumption decreases a little or remains steady. The size of the meal greatly affects oxygen consump-

tion. While very small meals (less than a 10 g crab for an octopus of 300 to 500 g) causes only a slight increase, very large meals (several crabs of 20 to 30 g each) produce a very large increase, both in the short and the long term. After several days of heavy feeding, following a starvation period, the animals cut down their food intake (Mangold, unpublished; Wells *et al.*, 1983, c). Compared to the costs of feeding, the costs of locomotion in this rather inactive species are low, although they are high per hour: 253 ml O_2 Kg^{-1} Km^{-1} for an octopus of 500 g travelling at 22°C at 0.34 Km h^{-1} (Wells *et al.*, 1983, a,b). Feeding is definitely the most important factor that determines the daily energy requirement in this species (Wells *et al.*, 1983, c).

O'Dor *et al.* (1980) observed that captive *Illex illecebrosus* which had ingested a large meal, more than 20% of their own body size, refused to eat the next day. Meals of about 10% body weight were regularly accepted.

The same authors (1980) compared values for feeding rates, growth rates and conversion efficiency of *I. illecebrosus* with the corresponding values from *O. vulgaris* for animals of the same size range and at comparable temperatures. Growth, in *Illex*, is slightly faster, but the conversion rate is lower. Squids have to eat about twice as much as an octopus. The low conversion rate is partly due to the higher activity of the squid, hence higher maintenance costs, but it may also depend on the quality of food which was fish (*Fundulus*) for *Illex* and crabs (*Carcinus*) for *Octopus* (but see Hirtle *et al.*, 1982).

4. Growth

Data on growth are available from two sources, field and laboratory studies, the former mostly carried out during fishery surveys for commercially important species. For convenience, in field studies, growth is usually expressed as increase in length, the standard measurement being the dorsal mantle length. In laboratory studies, growth in decapod cephalopods is mostly measured in terms of increase in length while for octopods, weight measurements prevail. In both types of studies few authors record growth by indicating both

length and weight (Boletzky, 1975a; Hanlon, 1975; Opresko & Thomas, 1975; Forsythe, 1981, for octopods; Richard, 1971; Hixon, 1980; Amaratunga, 1980, for decapods).

The difference in shape of the growth curves for length and weight measurements depends upon the body proportions, especially the development of the arm apparatus in many octopodid species (see Forsythe, 1981).

In field studies, growth and age can only be accurately correlated when there is clear evidence that a single year class from a stable population is under study, an almost ideal situation. In species where the spawning season is prolonged or extends throughout the year, this may prove to be an impossible task (see Mangold & Boletzky, 1973). Field growth studies are also biased by the sampling methods, e.g. the lack of postembryonic and juvenile stages in the catches.

In laboratory studies, growth and age can be linked only when the actual ages of the animals are known (i.e., those species reared from hatching onwards). All these species have large eggs and benthic young (Boletzky & Hanlon, this volume) with the exception of one species with planktonic hatchlings, *Loligo opalescens*, which was successfully reared from hatching to spawning in Galveston (Yang *et al.*, 1980, 1983 and Hanlon, pers. comm.). For species reared from wild-caught stages onward, the growth over a given period of time can be accurately determined, but the link with age remains approximate.

As reported in the above sections on feeding and conversion rates, growth is determined by many factors. High variability makes it almost impossible to compare controlled laboratory growth with growth in natural populations. Many cephalopods do not live in the same habitat (e.g. depth) or area during their whole life cycle. A number of species migrate to stay in similar temperature regimes, while others, very clearly, encounter different temperatures during their life time, e.g. those that live in shallow temperate waters where differences in temperature between summer and winter affect their daily food intake as well as their metabolic costs.

Levels of activity may be different in wild and

captive animals, especially in nektonic species, and this certainly influences their metabolism.

Food is overabundant in most laboratory experiments (but see Boletzky, 1974b, 1979) whereas in the sea animals may not experience such ideal conditions on a sustained basis. If the growth pattern within a population of a species is different from that of individuals of the same species obtained in the laboratory, it may not be possible to determine which factors are responsible for the difference.

O'Dor, *et al.* (1980) found that growth rates of field populations of *I. illecebrosus* are well below those in animals maintained in the laboratory. The authors estimated that the activity level of the captive animals kept in a large pool was probably comparable to that of field animals (temperatures were approximately the same), and they concluded that food intake must account for the difference. It seems, indeed, that the population does not feed *ad libitum* during late summer and autumn because its main prey, capelin (*Mallotus villosus*), and other fish species, are scarce. Hixon (1980) also found that the growth rate in three species of loliginid squid, *Loligo pealei*, *L. plei* and *Lolliguncula brevis* in the Gulf of Mexico was distinctly higher when calculated from laboratory results than from field data.

However, for other species, such as *E. cirrhosa* in the North Sea, *O. cyanea* in Hawaii and *O. vulgaris* in the Catalonian Sea, growth rates of animals reared in the laboratory are comparable to those of wild animals (Boyle & Knobloch, 1982b; Van Heukelem, 1976; Mangold, 1983a).

A variety of different growth models have been proposed for cephalopods. Figure 1 illustrates 5 growth curves which have been applied to loliginid species only: (A) linear growth (*L. opalescens*, Fields, 1965); (B) asymptotic growth or von Bertalanffy type curve (*L. pealei*, Verrill, 1881); (C) cyclic growth (*L. vulgaris*, Tinbergen & Verwey, 1945); and (D) exponential growth (*L. vulgaris*, Mangold-Wirz, 1963; and *L. pealei*, Summers, 1971). The first four curves are based on data obtained from field populations. The fifth type (E) represents sigmoidal growth for *L. pealei*, *L. plei* and *Lolliguncula brevis* obtained from laboratory

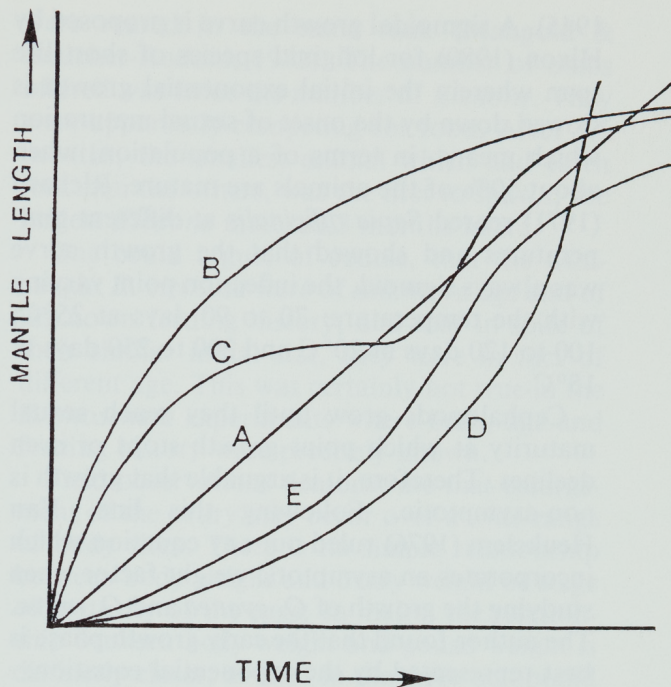


Figure 1. Growth curves for five loliginid species (after Hixon, 1980). A=linear growth (*Loligo opalescens*, Fields, 1965), B=asymptotic growth (*L. pealei*, Verrill, 1881), C=cyclic growth (*L. vulgaris*, Tinbergen & Verwey, 1945), D=exponential growth (*L. vulgaris*, Mangold-Wirz, 1963; *L. pealei*, Summers, 1971), E=sigmoidal growth (*L. pealei*, *L. plei*, *Lolliguncula brevis*, Hixon, 1980).

data (Hixon, 1980). The growth curve for *L. opalescens* reared in the laboratory is exponential (Yang *et al.*, 1980). Thus, for a given species, growth curves are different not only when laboratory and field studies are compared, but also when animals of the same species from different areas are compared.

However, most field data for octopods as well as for teuthoids fit a von Bertalanffy type curve (e.g. for *O. vulgaris*: Guerra, 1979; Pereiro & Bravo de Laguna, 1979; and Hatanaka, 1979; for *I. illecebrosus*: Squires, 1967; and *Amaratunga*, 1980; and for *I. coindetii*: Sanchez 1981b). According to Hixon (1980), this model probably does not account for growth of very young planktonic stages. A cyclic growth pattern probably occurs in species with a two year life span which live in waters with large temperature fluctuations, as e.g. *L. vulgaris* in the North Sea (Tinbergen & Verwey,

1945). A sigmoidal growth curve is proposed by Hixon (1980) for loliginid species of short life span wherein the initial exponential growth is slowed down by the onset of sexual maturation which means, in terms of a population, when about 50% of the animals are mature. Richard (1971) reared *Sepia officinalis* at different temperatures and showed that the growth curve was always sigmoid, the inflection point varying with the temperature: 70 to 90 days at 25°C; 100 to 120 days at 20°C and 200 to 250 days at 15°C.

Cephalopods grow until they reach sexual maturity at which point growth stops or even declines. Therefore, it is arguable that growth is non-asymptotic. Following this line, Van Heukelem (1976) ruled out any equation which incorporates an asymptotic weight factor when studying the growth of *O. cyanea* and *O. maya*. The author found that the early growth phase is best represented by the exponential equation:

$$W_2 = W_1 e^{kt}$$

where W_2 and W_1 are the final and the initial weights, T the time and k the instantaneous coefficient of growth. This exponential growth phase is very fast. The following phase which lasts more or less to sexual maturity is slower and best fitted by the equation:

$$W = ax^b$$

where a is the elevation, b the slope and x the age in days. This phase is called the logarithmic growth phase (straight line on a double log paper). Forsythe (1981) found the same growth pattern in *O. joubini* and pointed out the striking similarity in growth patterns for octopodid species of different life spans and very different adult sizes (Table 1).

Boyle & Knobloch (1982b) constructed an ideal curve for *E. cirrhosa* from the North Sea for maximum growth rates from 10 to 1000 g, and this curve best fits the parabolic model. This model takes into account the relative slow growth in animals freshly brought from the sea and the decline in growth at sexual maturity.

We are thus confronted with at least half a dozen growth models. They may reflect real differences in growth patterns of different cephalopod species, or they may be biased by sampling methods (field studies) and the high adaptability of cephalopods to artificial laboratory conditions. The ability to rear species of all suborders, regardless of whether the young animals are benthic or planktonic may clear up this rather confusing picture. Indeed, laboratory experiments provide the raw material for such theoretical considerations. However, one must be extremely careful when trying to apply a model to natural populations. One of the main questions will be whether size

TABLE 1
Growth patterns of octopuses relative to size at spawning and life span.

Species	Size at spawning g	Life-span months	Authors*
<i>O. joubini</i>	20-30	5.5-6.5	Forsythe, 1981
<i>O. briareus</i>	500-1500	12	Hanlon, pers. comm.
<i>O. vulgaris</i>	500-3000 mean 1500	15-18	Mangold, 1983a
<i>O. maya</i>	700-6500 mean 3200	10	Van Heukelem, 1976
<i>O. cyanea</i>	700-6500 mean 3600	12-15†	Van Heukelem, 1976
<i>E. moschata</i>	250- 600 mean 400	15-18	Mangold, 1983b

* The authors quoted are those who described the 'exponential-logarithmic' growth pattern for 6 species. The size at spawning and the life-span have been indicated by other authors.

† From settlement.

classes in wild and reared populations can be compared with respect to their age structure.

B. FEEDING BEHAVIOUR AND SEXUAL MATURATION

It is well known that the females of many species of Octopodidae slow down their food intake several days or weeks before spawning (for a review see Wodinsky, 1978). There seems to exist a kind of 'interaction' between feeding behaviour, hence growth, and sexual maturation, or 'maturation versus somatic growth' as O'Dor & Wells (1978) put it.

As an example: I reared *E. moschata* from hatching to spawning. Animals that hatched over a period of 3 days from an egg mass laid by a single female were selected. Very early growth differed only slightly when the animals, fed *ad libitum*, were kept isolated. In animals that shared a tank, weight differences at the age of two months were 10 fold or higher (Mangold, 1983b), perhaps as the result of the establishment of a feeding hierarchy (see also O'Dor *et al.*, 1980, for *I. illecebrosus*). Table 2 shows the minimum and maximum weights for 10 animals kept isolated and for 10 animals that shared a 60 × 40 × 20 cm plexiglass tank provided with an adequate number of shelters.

It should be emphasized that even with isolated animals, the period of heavy feeding and rapid growth, was variable, as were the sizes and the ages at which sexual maturity was attained. Some females stopped eating at the age of 7.5 to 8 months and these, mostly of relatively small size, were the first to spawn. Others continued to feed intensively and spawned at a larger size and a greater age, 10 to 12 months (Mangold, 1983b).

In earlier experiments with wild-caught *E. cirrhosa* several animals of similar initial size

were reared in the same tank (Mangold & Boucher-Rodoni, 1973). The number of crabs offered was twice the number of *Eledone*. They were apparently competing for food. After 3.5 months, the smallest animal which had eaten less than the others, was the first to spawn; the largest *Eledone* matured 3 months later.

One could argue, of course, that the wild-caught *E. cirrhosa* were of unknown age and of unknown feeding history, and that in spite of their similar initial size, they were in fact of different age. This was certainly not true in the *E. moschata* experiments where both, age and feeding history were precisely known.

Field observations demonstrate that enlargement of the ovary may occur over a wide range of body sizes. There is no simple relationship between body weight and ovary weight or stage of maturity of the eggs. In males, the relationship between body weight and gonad weight is distinctly closer, at least in the three octopodid species studied: *O. vulgaris*, *E. cirrhosa* and *E. moschata* (Table 3). Thus, females of these three species become mature in the field at different sizes and very likely also at different ages. Several parameters are thought to influence the process of sexual maturation in cephalopods, namely light, temperature and food availability at different stages of the life cycle (Richard, 1971; Van Heukelem, 1976; Mangold, 1983a). Combined effects of these parameters can result in producing mature females at different sizes and ages.

But why do females hatched within 3 days of each other, from eggs laid by a single female, become mature at different sizes and ages when reared under strictly identical conditions as in my *E. moschata* experiments (Mangold, 1983b)? Several authors have noticed that females in captivity tend to mature precociously

TABLE 2

Minimum and maximum weights in grams attained by 10 isolated and 10 cohabitant specimens of *Eledone moschata* reared from hatching to 60 days.

Day	1	15	30	45	60
isolated	0.3	0.96-1.06	2.15-2.45	4.81-5.32	9.50-10.52
sharing a tank	0.3	0.41-2.00	0.51-3.72	0.65-8.03	0.98-17.85

TABLE 3

Relationship between body weight and gonad weight, r , in males and females of *Octopus vulgaris*, *Eledone cirrhosa*, and *E. moschata*.

Species	n	r	Area	Authors
<i>O. vulgaris</i>				
males	519	0.935	Catalonian Sea	Mangold & Frösch, 1977
females	492	0.545		
<i>E. cirrhosa</i>				
males	63	0.904	North Sea	Boyle & Knobloch, 1982 a, b
females	286	0.560		
males	125	0.911	Catalonian Sea	Mangold, unpublished
females	1510	0.581		
<i>E. moschata</i>				
males	55	0.815	Catalonian Sea	Mangold, unpublished
females	63	0.661		

(Wells, 1978; Boyle & Knobloch, 1982b). This seems to be true for *E. moschata* as far as size is concerned; the mean size at spawning is smaller in captivity than in the field (Mangold, 1983b). But this still does not answer the above question, and I have no answer to offer at the present time.

What is known is that the feeding behaviour changes with the approach of sexual maturity when females begin to eat less and less regularly. Wodinsky (1978) showed that mature and brooding females of *O. vulgaris* along the east coast of America not only eat less, they also switch from boring holes into the shells of gastropods to pulling the prey out by force. According to this author, the production of the toxic secretion of the posterior salivary glands may be inhibited.

Concluding remarks

Cephalopods are voracious predators that feed on a wide variety of live prey. Food size spans a wide range from very small planktonic animals to prey equal or even larger in size to that of the predator. This general statement is based on stomach content analysis, feeding studies in rearing and maintenance experiments of about 50 species (Boletzky & Hanlon, this volume and personal observations). The most important food is crustaceans of all kinds, pelagic as well as benthic. Almost no information is available on the prey of the 650 or more

other cephalopod species known to exist, many of which are themselves important prey for marine mammals, birds and fish (Clarke, 1977, 1980). There is a serious lack in our knowledge as pointed out by Clarke (this volume). Not only should we know what cephalopods eat during their entire life cycle, we also have to know what the different food organisms represent in terms of caloric values.

Most species change food habits with growth. *Octopus* species often switch from small crustaceans to larger ones, while others eat small crustaceans during the whole life span (e.g. *O. cyanea*, Van Heukelem, 1976), still others may change food species as well. Squids usually feed on crustaceans in early stages whereas fish and fellow squids or other cephalopods are preferred later. However, some species do not conform to this general pattern. Food may vary with distribution and depth (inshore/offshore) rather than with size, as reported for *L. opalescens* by Karpov & Caillet (1978).

Food intake is dependent upon temperature, size of the predator (and prey), number of prey, quality of food; feeding behaviour changes in many octopodid females as sexual maturity approaches. Young octopuses eat as much as 10 to 20% of their own body weight per day; during this phase, their daily growth rate averages 6% (Van Heukelem, 1976; Forsythe, 1981; Mangold, 1983a,c and others). This high food intake corresponds to the first very fast (exponen-

tial) growth phase. Food intake and growth rate drop during the second (logarithmic) phase to about 5% and 2% respectively, and both slow down drastically with sexual maturity. Food intake in squids may be as high as 50% or higher in very early stages (Hurley, 1976, for *L. opalescens*) whereas in subadults and adults, it varies between 10 and 25% (LaRoe, 1971; Hanlon, 1978; O'Dor *et al.*, 1980; Hirtle *et al.*, 1982). The higher food intake in squids probably is related to higher metabolic costs associated with their higher activity.

Gross growth efficiency or food conversion in cephalopods is among the highest of all animals reported in the literature.

Growth in reared or cultured cephalopods may or may not follow a unique pattern. However, since growth is dependent upon many factors that are likely to vary in nature and to be different from the controlled environmental conditions in the laboratory, the application of a laboratory model to field population dynamics must be handled with great caution and can probably never be assured with certainty.

Animals of the same size in the laboratory and in the sea may be of different ages. Thus, determination of age in natural populations is one of the major problems to be solved. Several attempts have been made during the two last decades to obtain information from periodic structures such as beaks, statoliths and cuttlebones, but serious problems still remain. As shown for the cuttlebone, the periodicity of chamber formation not only changes with age, but also is dependent upon temperature and feeding conditions (Richard, 1969; Boletzky, 1974b, 1979). This is likely to be true for statoliths and beaks as well.

No attempt has been made in this paper to compare the state of the art on food, feeding and growth in cephalopods with that in fish, their primary competitors. Such a comparison would have demonstrated the enormous gaps in our knowledge of cephalopods. Only within the last two decades has the scientific community recognized the role of cephalopods in the food web of the oceans, their importance as a high quality protein resource for human consumption and their uniqueness as a research model.

It is now the common task of basic and applied research to fill the gaps.

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