Energetics: The Costs of Living and Reproducing for an Individual Cephalopod

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Energetics: the costs of living and reproducing for an individual cephalopod

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SUMMARY

Cephalopods, like all other animals, have to decide how to allocate resources; maintenance processes, growth of somatic and reproductive tissues, and locomotor activity all have costs. We should like to be able to identify these costs and discover how efficiently cephalopods make use of the prey that they capture and digest. Cephalopods generally grow fast and mature rapidly; a first task is to determine how accurately laboratory studies reflect growth in the wild, because much of the information we need (such as food conversion efficiencies, excretion rates or the costs of locomotion) can be collected only from animals kept in the laboratory. Comparison of laboratory feeding and growth rates for octopods, sepioids and teuthoids with fisheries data suggests that data collected from cephalopods fed *ad libitum* in the laboratory may be used validly to construct energy budgets representative of individuals in the wild. The immediate cost of feeding (the specific dynamic action) has been thoroughly documented in *Octopus*, as has the longer-term elevation or depression of metabolic rate by feeding or starvation; it is assumed that similar costs will be found in squid. The cost of locomotion has been studied in both octopods and squid, but we have only limited data on how much time the animals spend moving, and how rapidly, in the wild. Excretory and faecal losses are assessed from laboratory studies, and maintenance costs estimated from feeding rates that just maintain body mass in the laboratory. Comparison of gross and net food conversion efficiencies suggest that squid convert food into tissues less efficiently than octopods, owing primarily to their greater time spent in locomotion. We present a representative series of energy budgets for octopods (based on *Octopus*) and squids (based on *Illex* and *Loligo*), for starving, feeding, migrating and maturing individuals. A major contrast is provided by *Nautilus*, which lives for ten or twenty years and grows only slowly. Finally we speculate on the possible biochemical and historical factors that may have limited the adaptive radiation of cephalopods, resulting in a group lacking herbivores, detritivores or filter-feeders but extremely successful as carnivores.

1. INTRODUCTION

All heterotrophic organisms must obtain energy and raw materials from the external world to fuel their existence. Some of this food will be utilized to build new tissue in growth or for reproductive products, some may be stored, and some will be oxidized to provide the energy to drive these processes, for locomotion or for maintenance.

There are two aspects of this fundamental process that are of particular interest. The first is how the organism balances the competing demands on food intake from the various physiological processes requiring energy or raw materials. The second is the overall impact a species or population makes on the world around it. The latter subject requires a knowledge of the size-structure and population dynamics and is dealt with elsewhere in this volume (Rodhouse & Nigmatullin, this volume). In this paper we examine the major patterns of energy flow through an individual cephalopod. We are concerned with the demands of that individual on the ecosystem in which it lives (that is, food consumption), and what the individual does with the food it ingests. We will be dealing solely with energetics at the level of the individual organism.

Physiological studies require the experimenter to keep organisms alive and in good condition in the laboratory. For cephalopods, and especially the larger or faster-swimming species, this is not always possible. Any generalizations will therefore be based on studies of a small (and not necessarily representative) subset of species, particularly of *Octopus*, *Sepia*, *Illex* and *Nautilus*. Although some clear generalities do emerge from these studies, the potential bias from studies of less active species must always be borne in mind.

2. THE ENERGY BUDGET

To understand the various physiological processes that act as sinks for the ingested food, and the shifting balances between them, it is first necessary to have a robust conceptual model of the energy budget of a representative individual cephalopod. The traditional formulation of the energy budget used by marine biologists has evolved from the 'balanced energy equation' proposed by Winberg and is based on a solid body of vertebrate (primarily mammalian) energetics (see recent discussion by Wieser 1994). It is:

$$C = R + P + G + F + U,$$

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where C is the energy ingested, R is the energy utilized in respiration, P and G are the amounts of energy invested in new somatic (P) or reproductive (G) tissues, F is the unabsorbed energy voided with the faeces, and U is the energy lost as nitrogenous and other waste compounds excreted in the urine.

This equation is both simple and intuitively reasonable. It divides the energy intake into units that can be measured easily and has the advantage of allowing the simple formulation of ecologically important concepts such as absorbtion efficiency or growth efficiency. Despite these undoubted strengths, however, the traditional formulation of the energy budget suffers from the serious disadvantage that it sets respiration (R) as an independent sink from production (somatic growth, P) or reproduction (G).

In reality respiration is a heterogeneous process, whose separate components may (and often do) vary independently. Respiration is a measure of the instantaneous demand for oxygen to act as an electron acceptor in the production of ATP (Clarke 1993). Under normal circumstances the rate of oxygen uptake by an organism is dictated by its requirement for ATP, and this ATP will almost certainly be needed for a variety of tasks including synthesis, turnover of cellular components, osmotic balance, information handling, detoxification and movement. At any one time an organism will thus be burning reserves to make ATP for a wide variety of possibly competing tasks.

Of particular interest in an ecological context are the thermodynamic costs of production, which may be presented as R_s (the costs of producing new somatic tissue, P_s) and R_g (the costs of synthesizing reproductive tissue, represented as G in the traditional equation (above) but given here as P_g). The terms R_s and R_g represent the fact that there are costs associated with the synthesis of new tissue. These costs include the thermodynamic costs of assembling new macromolecules (no chemical process is perfectly efficient) and those associated with the movement of the raw materials around the body and into cells. In general these costs are broadly tied to production as:

$$R_s = k(P_s)$$

and

$$R_g = k(P_g).$$

Parry (1983) has suggested that k is usually of the order 0.2–0.3; in other words it will cost a typical marine invertebrate about 120–130 kJ to produce 100 kJ of new tissue. The extra 20–30 kJ requires the consumption of reserves and can be measured as an increased oxygen consumption (in a respirometer) or as heat (in a calorimeter).

In episodic feeders the costs of growth (R_s and R_g) are believed to be a major component of the post-prandial increase in metabolism (the so-called specific dynamic action, SDA) (Jobling 1983). These costs can also lead to a longer-term elevation of resting metabolic rate (Wells *et al.* 1983*a*) which thereby complicates the precise estimate of the overall cost of growth, k (see §5*b* below). The other major components of overall respiratory demand are the costs of maintenance or basal turnover (R_m) and the costs of locomotor activity (R_a). R_m is defined as the respiratory cost of keeping the organism alive in the absence of growth, reproduction or locomotor activity. It comprises a variety of processes including protein, DNA and membrane turnover, osmotic work and in more complex organisms also activities such as circulation, maintenance of muscle tonus and behaviour such as vigilance (watching for approaching food or predators). R_m is often estimated by the maintenance respiration in the absence of either positive growth or shrinkage.

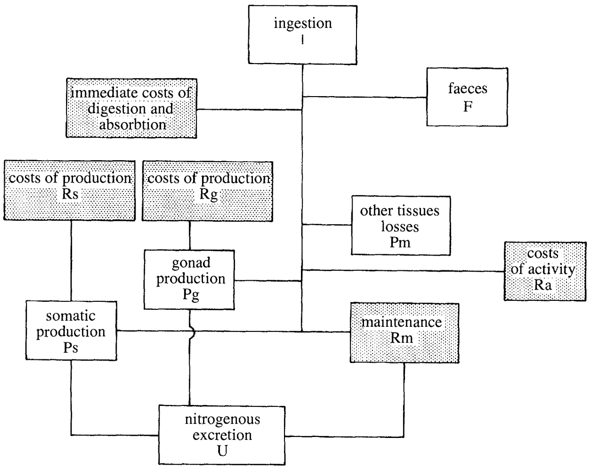

Figure 1. A diagrammatic representation of the energy budget of a cephalopod showing the partitioning of dietary energy. Boxes representing energy lost through respiration are shaded, showing the heterogeneous nature of respiratory demand. Only the major links are shown (for example, locomotor activity fuelled to a significant extent by protein would be expected to contribute to the nitrogenous excretion). Modified from Clarke (1987).

This breakdown of overall respiratory demand into its major components emphasizes the potential for a tradeoff within the organism between the use of a limited supply of energy for fuelling growth, reproduction, maintenance or activity. Such tradeoffs have long been described by fish physiologists (Calow 1985) and are at the heart of many ecological models for life-history evolution (Stearns 1992). The relative importance of these costs is far higher than in homeotherms, where these fluctuations are swamped by the costs of endothermy.

The breakdown of energy intake into the different physiological sinks is shown in figure 1. From this it can be seen clearly how the costs of maintenance processes (R_m) will influence food conversion efficiencies, a relation that was not apparent from the more traditional formulation, which includes R_m in an overall respiration term. It is now recognized that variations of R_m with latitude can have important consequences for patterns of investment in reproduction (Clarke 1987) and a tradeoff between the cost of basal processes and scope for growth has been shown clearly for some marine bivalves (Hawkins 1991). Similarly, R_a (costs of locomotor activity) will influence ecological growth efficiency, as will be seen later when comparing the active squids with the more sedentary octopods.

(*a*) *A note on units*

When constructing budgets, biological oceanographers interested in patterns of material or energy flux have traditionally used carbon or nitrogen as the unit. Ecologists have tended to use either energy (joules) or energy per unit time (power, watts) as their units, but to measure energy utilization as oxygen demand. We will use both ($1\ \mathrm{kJ\ d^{-1}} = 11.57\ \mathrm{mW}$).

3. GROWTH RATE IN CEPHALOPODS

Cephalopods typically grow fast and mature rapidly (although *Nautilus* and perhaps some deep-water forms are exceptions to this generalization). Because growth costs are therefore likely to dominate energy flux through an individual cephalopod, we will examine these first.

To construct an energy budget for a cephalopod in the sea and to assess its impact on the ecosystem, we need to know how much food is eaten to sustain the observed rate of growth. This cannot be established directly; there is at present no way that we can monitor food intake and growth throughout the lifetime of any cephalopod in its natural habitat. We can, however, measure food input and growth for certain species reared in the laboratory. The problem then becomes a matter of assessing the extent to which the laboratory results represent what may be going on in members of the same, and other, species living free in the sea.

An immediate difficulty is that although we can follow the growth of individuals in the laboratory, we are nearly always obliged to estimate individual growth in the wild from the average growth of members of a population. There is a potential trap here. Laboratory studies of cephalopods show that individuals at first grow exponentially and later logarithmically. There is no indication of asymptotic growth, for the curve is still concave upwards at the point where each individual reaches sexual maturity, spawns and dies (Forsythe & van Heukelem 1987). The sigmoid growth curve that is very often apparent from studies of populations arises because there is wide variation in the growth rates of individuals (Smale & Buchan 1981) and even of siblings reared under identical conditions (van Heukelem 1987). The fastest-growing individuals tend to mature first, so the mean growth rate is increasingly biased by the slower-growing animals; the mean growth curve is asymptotic even though no single individual ever follows this pattern (Alford & Jackson 1993).

A second difficulty arises because many cephalopods have a prolonged breeding season. Individuals of a number of species, particularly those that lay large eggs, may spawn several times during the course of a year (Mangold *et al.* 1993). Eggs, even eggs from the same spawning, may take very different lengths of time to hatch in cold water; recruits then join the stock over a period of months, depressing the apparent mean growth rate. This is not too much of a problem in studies on squid, where the growth rings on statoliths (and perhaps on the gladius) provide a means of ageing individuals, but it becomes serious in octopods, which tend to have a long breeding season and where no means of ageing wild-caught individuals currently exists.

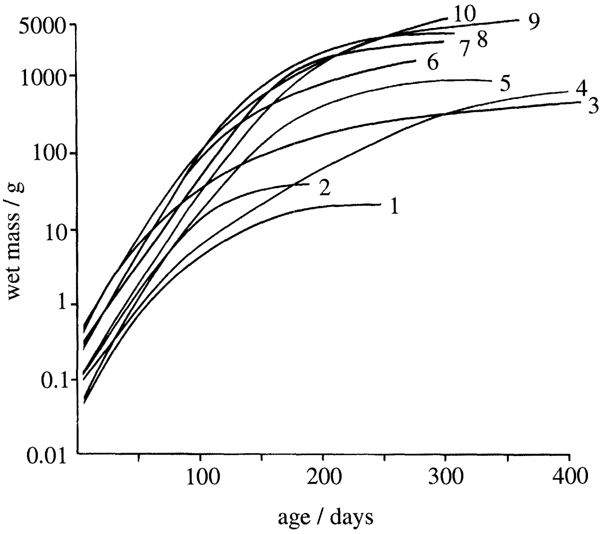

Figure 2. Laboratory growth curves for various species of octopus. 1, *Octopus joubini* (25 °C); 2, *O. digueti* (25 °C); 3, *Eledone moschata* (12–20 °C); 4, *O. bimaculoides* (18 °C); 5, *O. briareus* (25 °C); 6, *O. vulgaris* (Mediterranean, 18–22 °C); 7, *O. tetricus* (6–24 °C); 8, *O. maya* (25 °C); 9, *O. vulgaris* (South Africa, 20–25 °C); 10, *O. cyanea* (22–28 °C). Redrawn from Forsythe & van Heukelem (1987), where original sources are cited.

Because the problems of comparing wild and laboratory growth rates differ in octopods, sepioids and teuthoids, these three groups will be considered separately. It should be stressed that this is not a review of all the field growth estimates, or even of all the rearing experiments, that have been made (a list covering some 40 species that have been kept in laboratories is given by Boletzky & Hanlon (1983) and would undoubtedly be considerably longer now) but a selection, concentrating on those species where we can compare growth rates in the laboratory and in the wild.

(*a*) *Octopod growth in the laboratory and the wild*

A number of studies in which octopuses were reared in the laboratory and their growth monitored are summarized in figure 2. Most of these species lay large eggs and in most studies the growing individuals were fed *ad libitum*. The initial exponential growth phase shows clearly as a straight line on the semilogarithmic plot (figure 2) and a mean daily growth rate, G, can be calculated:

$$G = 100 \times (\ln M_2 - \ln M_1)/\Delta t,$$

where M_1 is the initial mass and M_2 is the mass after a growth period of Δt days.

Octopus vulgaris, *O. tetricus* and *O. cyanea* lay small eggs; the data for these species begin at the point when the larvae settle out from the plankton. In the initial phase, growth is rapid, typically in the range 4–8% body mass per day, later slowing progressively to as little as 0.5% before the onset of sexual maturity, at which point octopuses typically stop feeding and may even begin to lose mass (Forsythe & van Heukelem 1987; see also table 1).

Growth rate depends on temperature (Forsythe & Hanlon 1988*a*); species such as *O. vulgaris* in the Mediterranean grow fast in the summer and more slowly in the winter (Nixon 1969) whereas others like *Bathypolypus arcticus*, which lives at 4 ± 2 °C, grow by as little as 3.5 g per month and may take as long as 4 years to reach 70 g and complete their life cycle (O'Dor & Macalaster 1987).

Are similar rates of growth to be found in the sea? The limited data available would appear to suggest that they are. Because of the drop-out and recruitment problems discussed above, and our inability to age octopuses from their statoliths, the most valuable data come from individual animals through mark, release and recapture studies.

Van Heukelem (1973) branded, released and recaptured 11 *O. cyanea*, ranging in mass from 430 to 1218 g, and compared their rates of growth over 14–74 d with the growth of similar individuals fed *ad libitum* in the laboratory. The fastest-growing animal in the wild grew 28% more rapidly than the average laboratory-fed octopus; the slowest grew only half as rapidly. Two factors that may have influenced these measurements are that the marked individuals had been fasting before release, so that they were not perhaps in optimal condition when returned to the sea, and the slowest-growing individuals were sexually mature when recaptured. Yarnall (1969) kept two *O. cyanea*, initial masses 980 and 1180 g, on an enclosed area of reef for 24–33 d; the first grew at 2.3% and the second at 1.7% per day. Van Heukelem (1973) also quotes an experiment by Itami (1964) who released a number of *O. vulgaris*, average mass at release 342 g. The average mass of individuals recaptured 38–47 d later was just over 1000 g, an instantaneous daily growth rate of 2.5%. A single individual weighing 2250 g when recaptured 244 d later had averaged 0.77%.

These rates of growth fall within the ranges found in laboratory studies with animals of the same size and species fed *ad libitum*. They suggest that the growth of octopuses in the sea is not normally limited by the availability of prey.

The difficulty of establishing meaningful rates of growth from population studies has meant that relatively few such studies have been undertaken. Large samples, more than 30000 individuals in all, of *Eledone cirrhosa* from the Golfe de Lion, France, were collected by Mangold-Wirz (1963) and Moriyasu (1983). The animal here grows to a maximum of around 800 g in 18–22 months. Unfortunately, *E. cirrhosa* does not survive well at surface temperatures in the Mediterranean, so we have no aquarium growth studies from Mediterranean laboratories to compare with the growth curves derived from commercial captures. Individuals from a North Sea population sampled by Boyle & Knobloch (1982) did, however, feed and grow in aquaria. The maximum growth rate deduced from these studies was close to the summer growth rate of this population in the wild, and this in turn was close to the growth rates found in the Mediterranean studies. These results would indicate that although growth rates plainly follow temperature in an individual, or in individuals taken from the same population (see table 1), genetic differences between populations or species underlie compensation for the effects of temperature.

More laboratory data are available for *Octopus vulgaris*; here, for once, we have corresponding population growth data. Mangold-Wirz (1963) collected field data from some 900 octopuses in the Mediterranean. Her growth curves for males and females are compared with those from laboratory animals in figure 3. It is encouraging that the growth curves from fisheries data fall neatly within the range of variation shown by laboratory studies.

The conclusion from these studies, as from the release and recapture experiments, is that octopuses grow at about the same rates in the laboratory and in the sea. The implication is that food does not limit the rate of growth in the wild, so that studies of the energy budgets of octopuses fed *ad libitum* in the laboratory are likely to yield data that can be applied to the same species in the sea.

(*b*) *Sepioid growth in the laboratory and the wild*

Sepioids, like the large-egged octopods, have proved relatively easy to rear in the laboratory, for with rare exceptions (*Heteroteuthis*, *Idiosepius*, *Sprirula*) the large hatchlings have no pelagic phase (Boletzky & Hanlon 1983).

Most laboratory data come from *Sepia officinalis*, which has been reared successfully for up to seven consecutive generations. Individuals reared at 22 °C reached 100 g in about 120 d, an instantaneous relative growth rate close to 5%. Mean size at sexual maturity, achieved in 10–14 months, increased, and fertility fell, in successive generations. Fertility was low even in the first generation; the seventh, which included individuals of 2.6 and 2.9 kg, showed no sexual behaviour at all. Possible reasons for these trends are discussed by Forsythe *et al*. (1994). They range from lighting regimes to the absence of the symbiotic bacteria that normally appear to participate in the maturation of the nidamental glands. Survival from hatching was excellent at 50% and there was no conscious selection for large animals. This study serves as a warning that, even when rearing experiments are outstandingly successful, culture conditions may lead to a redistribution of resources within the cephalopod body.

As with octopods, the growth rate of laboratory-cultured sepioids depends on temperature; there is also a wide variation in the growth rates of individuals from the same batch of eggs even when food is available *ad libitum* (Forsythe *et al.* 1994). *Sepia officinalis* has been the subject of a number of tagging experiments, but these were made to trace migratory patterns and no data for individual growth have been reported (Le Goff & Daguzan 1991; Boucaud-Camou & Boismery 1991).

There are few data for the growth rate of sepioids in the wild against which to compare the laboratory

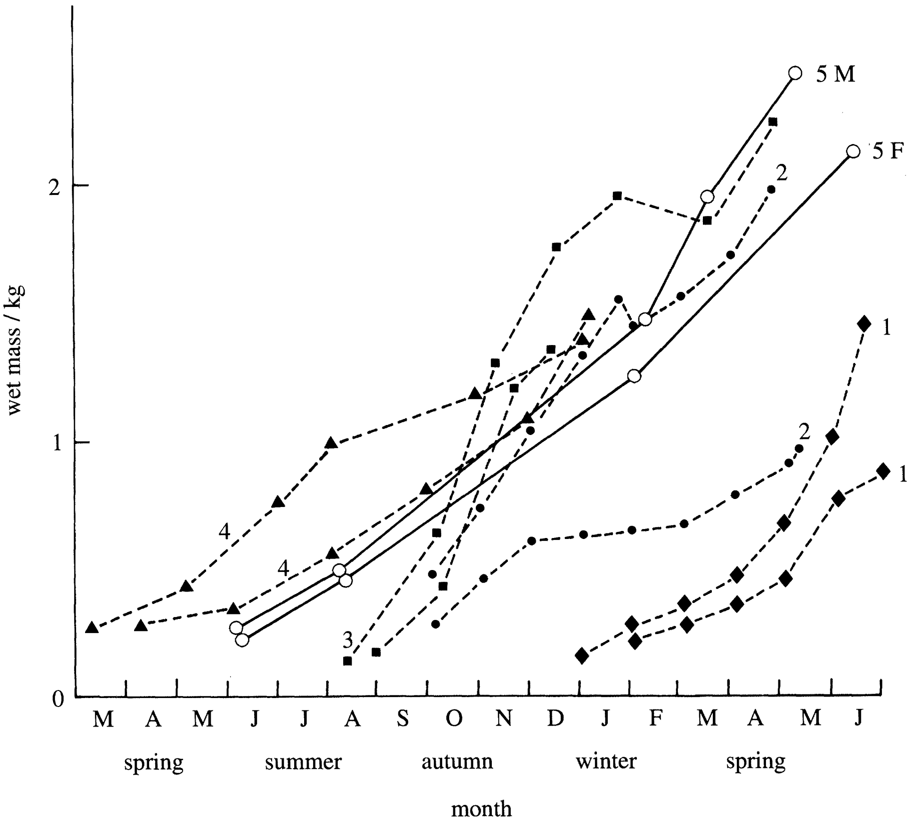

Figure 3. Comparison of laboratory and field growth data for *Octopus vulgaris*. Sources: 1, Mangold & Boletzky (1973); 2, Nixon (1966), extremes for a sample of 12, Naples; 3, Lo Bianco (1909); 4, Vevers (1961), 2 males; 5, K. Mangold-Wirz, fisheries data for males (M) and females (F) plotted separately. Redrawn from Wells (1978) with field data from Mangold-Wirz (1963) added.

growth rates, although E. Boucaud-Camou (personal communication) reports that growth in wild *Sepia officinalis* is generally faster than in the laboratory. In the Mediterranean, generations of *Sepia officinalis* appear to alternate. Large animals move inshore early in the year, laying eggs that hatch in spring. The young from these eggs spawn in the following summer, at an age of 14–16 months. The young from these late spawners grow throughout the following year and spawn in spring at an age approaching two years (Boletzky 1983).

(*c*) *The growth of squid in the laboratory and the wild*

The littoral and shallow subtidal octopuses that have proved to live well in isolation in aquaria are solitary beasts that would normally establish dens in the wild, leaving these only to forage or seek mates. Living conditions in the laboratory can be made to resemble their normal circumstances in the wild. This is practically impossible for squids, which normally live in large shoals in open water. Squids can be kept in laboratories, but they are very easily damaged by handling, require a lot of space and are probably always relatively stressed compared with laboratory octopuses (Hanlon *et al.* 1983).

A notable exception is *Sepioteuthis lessoniana*, which hatches at a much larger size than most loliginids. *Sepioteuthis* and *Loligo opalescens*, a more typical squid, are the only species so far to have been cultured throughout the life cycle, from hatching to spawning.

One consequence of the difficulty of keeping squids is that we have relatively little data on the growth rates of teuthoids in the laboratory. In particular we lack data on the food intake and growth of individuals, because the animals appear to become stressed by isolation and because they cannot be handled repeatedly to measure their mass.

We do, on the other hand, have a great deal of information from fisheries because several species are commercially important. The fact that the animals tend to travel in large schools of more or less uniform size means that it is often possible to follow the growth of cohorts from recruitment to spawning, although the earliest part of the life history is generally more difficult to study because the larvae are always pelagic and some are rarely caught. A major development has been the realization that, with caution (Rodhouse & Hatfield 1990*a*), it is possible to read the age of individual squids from the daily growth rings in their statoliths and use these data to validate the growth rates determined from fishery size-frequency observations.

The growth rates of some squids and sepioids that have been reared successfully in the laboratory are shown in figure 4. As with octopods, growth is at first exponential and then logarithmic. Daily relative growth rates in the laboratory are generally similar to those found in octopods. *Sepioteuthis lessoniana* represents

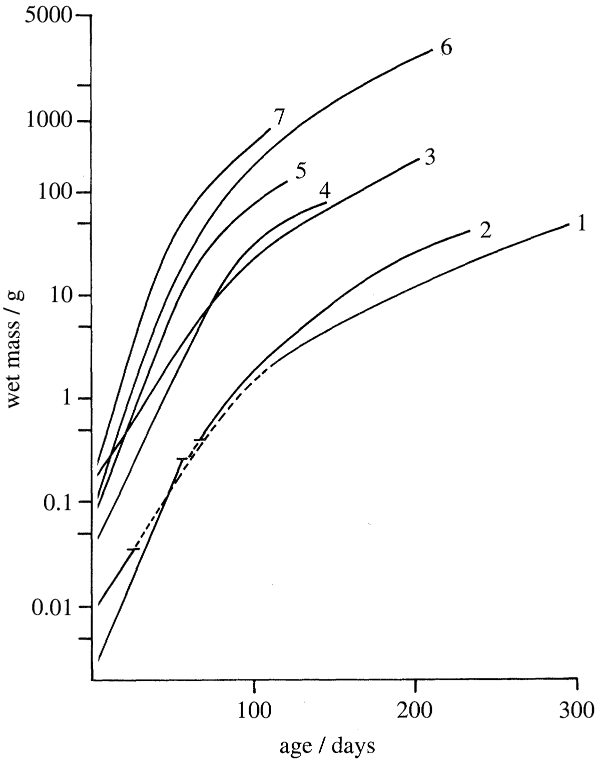

Figure 4. Laboratory growth curves for squid and cuttlefish species. 1, *Loligo forbesi* (15–18 °C); 2, *L. opalescens* (15–18 °C); 3, *Sepia officinalis* (21 °C); 4, *Sepioteuthis sepiodea* (23–27 °C); 5, *Sepia esculenta* (25–29 °C); 6, *Sepioteuthis lessoniana*; 7, *Sepia subaculeata* (25–29 °C). Redrawn from Forsythe & van Heukelem (1987) with data from Hanlon (1990) added.

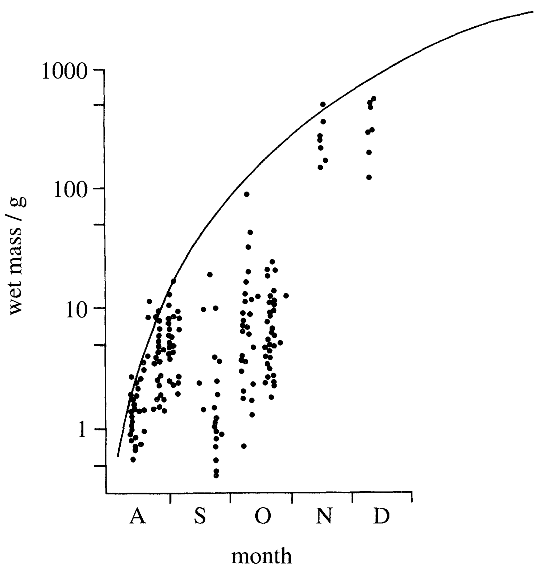

Figure 5. Comparison of laboratory growth in *Sepioteuthis lessoniana* (solid line) with field data for body mass against time for wild squid captured in the vicinity of Kominato Marine Biological Station in 1977. Redrawn from Segawa (1987) with laboratory data from Hanlon (1990) added.

the high end of the spectrum, with daily relative growth rates of 7–12 % at 25 °C (Hanlon 1990). These very fast rates continued throughout the life cycle; individual *Sepioteuthis* typically attained a mass of 1 kg within 5–6 months, representing an overall daily relative growth rate of approximately 7 %.

The only other laboratory growth rate data available for squid are for *Loligo opalescens* (Yang *et al.* 1986). At 15 °C laboratory-held squids grew at 8.4 % per day, slowing to 5.6 % by the end of the first two months, and 1.6 % when approaching maturity at 8 months and 50 g body mass.

The economic importance of squid has meant that considerable numbers have been tagged to trace migration paths. To date well over one million individuals have been tagged and released, largely by Japanese fishery scientists in the north Pacific: between 1927 and 1989, 830000 *Todarodes pacificus* alone were so marked (see Nagasawa *et al.* (1993) for a summary of tagging experiments on cephalopods). Unfortunately these experiments are dependent upon returns from commercial fishing vessels and so have only rarely yielded information on growth rates.

One exception is *Ommastrephes bartrami*. Individuals tagged in the northwest Pacific grew in mantle length by up to 8 cm per month, 3 out of the 6 individuals recovered having grown faster than the maximum of 4 cm per month calculated from length-frequency data (Araya 1983) in this study or the 0.61–1.6 mm d^{-1} found by Murata *et al.* (1988). Based on length-mass relations established for *Illex argentinus* (Rodhouse & Hatfield 1990*b*) and assuming a mean mantle length of 350 mm, these data suggest growth rates of 2.6 % per day in terms of mass. This low relative growth rate reflects the large size of these mature individuals.

In attempting to derive individual growth trajectories from field data, the difficulties produced by a prolonged period of recruitment may be compounded by the often dramatic effect of small differences in temperature on the rate of growth during the exponential phase. In places where there is a considerable seasonal increase in temperature, the later-hatched individuals can actually overtake those hatched earlier in the season by the time sexual maturity is reached (Forsythe 1993).

In some cases the growth of a cohort of individuals shows up clearly from length-frequency data gathered over a period of months (Hayashi 1993). In others there is so much scatter that it is impossible to pick out any clear peaks. Such a case is shown in figure 5. The apparent average growth rate of *Sepioteuthis* shown here is very far below that achieved in the laboratory by Hanlon (1990). If one assumes, however, that the growth of the first hatchlings of the season is represented by the greatest mass in each succeeding month, the two curves are not dissimilar. The fact that *Sepioteuthis*, like *Sepia* and the octopods, can growth as fast in the sea as in the laboratory was confirmed when the statoliths of cultured and wild-caught squid were compared (Jackson 1994); plots of mass-at-age (from statoliths) for *Sepioteuthis lessoniana* reared in Galveston from Japanese stock, and for the same species taken from the sea off Australia, were almost identical.

Growth in the wild, however, may not always be as rapid as can be achieved by individuals fed *ad libitum* in the laboratory. Observations on *Loligo opalescens* from California by Fields (1965) and Spratt (1978) suggested much slower growth than achieved by Yang *et*

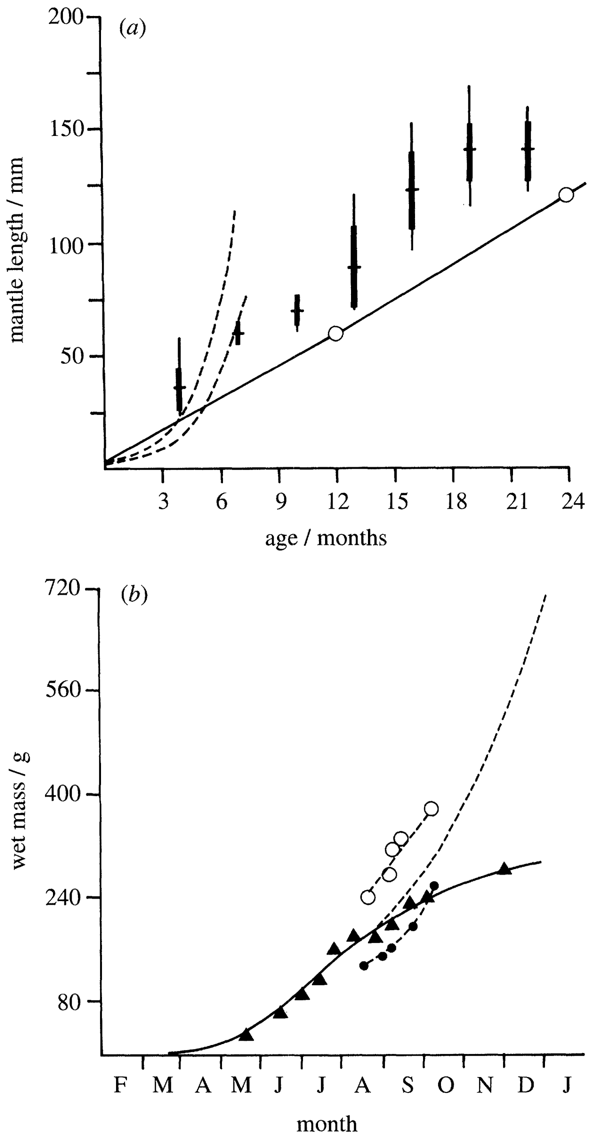

Figure 6. Comparison of field and laboratory growth rate data for squid. (*a*) *Loligo opalescens*. Dashed lines show laboratory data; bars show growth (mean, standard deviation and range) at three-month intervals derived from statolith ring counts (Spratt 1978), and open circles population data from Fields (1965). (*b*) *Illex illecebrosus*. Solid line shows growth in wild-caught individuals (mean values). Circles show data for laboratory squid fed *ad libitum*: filled circles, population mean; open circles, data for a single tagged individual. The dashed lines are extrapolated from laboratory data: (*a*) from Yang *et al.* (1986), (*b*) from O'Dor *et al.* (1980).

al. (1986) in the laboratory (figure 6*a*). The slow growth identified by Fields (1965) may have been the result of sampling bias: the individuals were collected only on or near the spawning grounds, where growth may have been slowed by gonad maturation. The estimates of age by Spratt (1978) depended on the assumption that the major statolith increments were formed monthly, whereas recent work suggests that fortnightly increments are also possible (see Yang *et al.* 1986).

A comparison of wild-caught and laboratory-cultured *Illex illecebrosus* by O'Dor *et al.* (1980) also suggested much slower growth rates in the sea (figure 6*b*). Further studies in which age and growth history were assessed from statoliths (Dawe & Beck 1992) indicated, however, that the apparent slowing down of growth seen in the 1977 population considered by O'Dor may have been due to a combination of an unusually successful breeding season and successive recruitment from younger cohorts. Statoliths showed that individuals in the sea grew at rates close to those seen in the laboratory. Growth curves derived from statolith increments in field samples of *Illex argentinus* from the South Atlantic by Rodhouse & Hatfield (1990*a*, *b*) also indicated growth rates similar to those of *I. illecebrosus* held in the laboratory (O'Dor 1983). Boyle & Ngoile (1993) studied the growth of *Loligo forbesi* in the North Atlantic and concluded that the growth rates of loliginids in the field are comparable with those achieved (by other loliginids) in the laboratory.

Taken overall, squid studies, like those on sepioids and octopuses, appear to show that these animals can, and generally do, grow as rapidly in the sea as in laboratories, where they are generally fed *ad libitum*. Overall we conclude, on the evidence available, that studies of growth, conversion rates and the effects of maturation made in the laboratory are likely to yield data that can be applied directly to the energy budgets of cephalopods in the sea.

(*d*) ***Energy invested in growth***

There are two ways in which the energy invested in growth by a cephalopod might be estimated. The first is to measure growth in tissue mass and estimate energy requirements from the energy content of the new tissue and a knowledge of the cost of growth. The second is to measure the gross conversion efficiency, which is a measure of the amount of cephalopod growth per unit of food eaten.

The latter is the traditional approach, but is confounded by the simultaneous demands of maintenance (or 'standard') metabolism and any activity costs (see §2 above). Nevertheless there is a considerable body of data based on this approach, and this will be examined below (see §5).

Most data for the energy content of cephalopod tissues are concerned with their value for the food industry and are difficult to use in an ecological context; data for whole 'octopus' and whole 'squid', ranged from 3.31 to 4.06 kJ g^{-1} (fresh mass) (from O'Dor & Wells (1987), who provide a useful compilation). A detailed study of the biochemical composition and energy content of the major tissues of *Illex argentinus* suggested overall mean energy contents for sexually mature adults of 5.49 kJ g^{-1} (fresh mass) in males and 6.57 kJ g^{-1} in females (Clarke *et al.* 1994). The difference between the two sexes was related to the greater lipid content of ovaries compared with testes; the overall higher values compared with the octopus data collated by O'Dor & Wells (1987) may reflect the large, lipid-rich digestive gland present in mature, premigratory *Illex argentinus*.

As well as estimating the energy content of new tissue we must also allow for the metabolic costs of synthesizing that tissue (Parry 1983). This matter is discussed in §5*b* below.

4. MAINTENANCE COSTS IN CEPHALOPODS

Before proceeding to a comparison of measured growth rate data with food conversion data we need to see whether we can estimate the costs of maintenance in resting cephalopods. This is because gross conversion rates include maintenance costs that the animal has to meet even without growing, and these costs must be subtracted to avoid confounding the comparison. A baseline, against which to measure the costs of growth alone, can be established in one of three ways. One is to measure the routine oxygen uptake of animals that are just maintaining their mass; a second is to note the drop in mass of starving animals, which should also reflect maintenance needs; a third is to determine the feeding rate at which body mass just remains unchanged from the results of steady feeding at a range of rations.

Of the three, the last is by far the best because metabolic rates change with the time since the last meal (Wells *et al.* 1983*a*, *b*). The 'steady mass' figure will include the cost of feeding sufficient to maintain activity in search of food (which may of course be reduced under aquarium conditions) as well as body maintenance costs; although different from a hard physiological definition of basal metabolism (see Clarke 1987, 1993) this is ecologically a more meaningful measure of maintenance costs. Estimates of maintenance metabolism in *Octopus vulgaris* have been made using all three approaches.

(*a*) *Maintenance costs in* Octopus

Wells *et al.* (1983*a*) measured the oxygen consumption of 341 *Octopus vulgaris* weighing between 250 and 1200 g, over a temperature range of 18–24 °C. Oxygen uptake varied with both body mass and temperature:

$$V_{O_2} = 0.107 M_f^{0.72} \times 1.059^T,$$

where M_f is the fresh mass of the individual in grams and T is the temperature in °C. Overall the average mass-specific oxygen uptake was 72 ml kg^{-1} h^{-1}, but this varied with both activity and the time since the last meal. Thus 59 animals classified as fasting (that is, not fed for 36 h) and resting averaged 53 ml kg^{-1} h^{-1}, 31 animals classed as fasting and active consumed on average 65 ml kg^{-1} h^{-1}, and 79 fed but resting animals utilized 76 ml kg^{-1} h^{-1}. In the majority of these experiments the animals were fed rations that would roughly maintain their body mass, so the overall figure of 72 ml kg^{-1} h^{-1} is probably our best estimate of the cost of maintaining a steady body mass. This is the figure that we shall use as R_m (maintenance metabolic rate) in our energy budget. If the standard oxycalorific conversion is used (1 ml oxygen consumed is equivalent to 4.8 calories or 20.1 J utilized (Elliot & Davison 1975)), together with the data for the energy content of crab and octopus flesh and the assimilation efficiencies given in O'Dor & Wells (1987), this rate of oxygen consumption is equivalent to a food intake of about 1.3 % body mass per day.

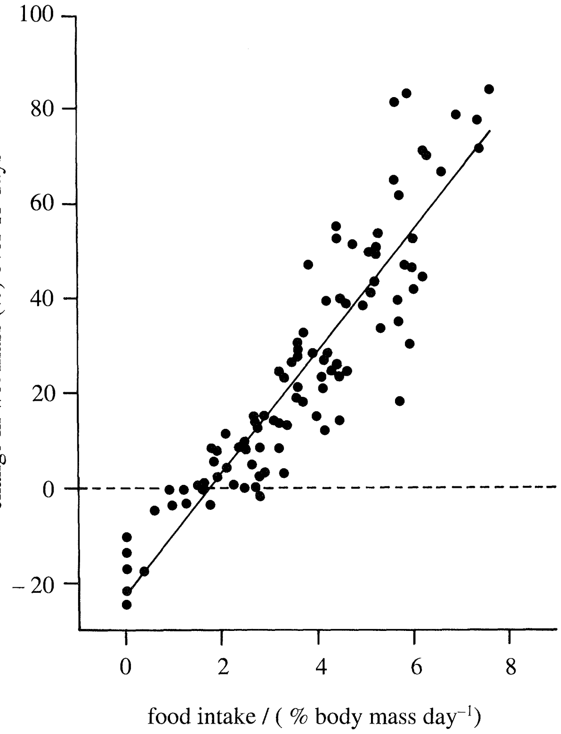

Figure 7. Relation between food intake (percentage of body mass ingested per day) and growth rate (percentage change in mass over 15 d) in *Octopus cyanea*, ranging from 67 to 6480 g in initial mass. The horizontal line at zero growth rate represents the best estimate of maintenance ration averaged over all sizes (1.8 % body mass per day). Redrawn from van Heukelem (1973).

Measurements of the daily loss of mass in starving *Octopus vulgaris* have shown that the rate depends on temperature. Mangold & Boletzky (1973) found decreases in body mass of 0.44 % per day at 10 °C, 0.79 % at 15 °C, 1.60 at 20 °C and 1.79 % at 25 °C. Nixon (1966) measured an average rate of 1.0 % in 6 animals (the temperature was not stated, but could have been as low as 14 °C) and 1.7 % in a further 5 animals starved at about 24 °C (M. Nixon, personal communication).

Ellis (1984) fed *Octopus vulgaris* of average mass 550 g, and held at 24 C, at a range of rations ranging from 0.5 to 30 g of crabs per day; the break-even point for change in mass was at 10 g d^{-1}, equivalent to 1.8 % body mass per day. This is similar to the 1–2 % body mass per day required for *Octopus tetricus* to maintain a steady body mass at 17–24 °C (Joll 1977). The most extensive data are for *O. cyanea* and *O. maya* held at 25 °C (van Heukelem 1973, 1983) which indicated 1.8 % body mass per day as the break-even point to maintain a steady body mass; data for *O. cyanea* are shown in figure 7.

(*b*) *Maintenance costs in* Illex

Illex illecebrosus in respirometers can rest on the bottom; submarine observations have confirmed that this species also does so in the sea. In deeper water such

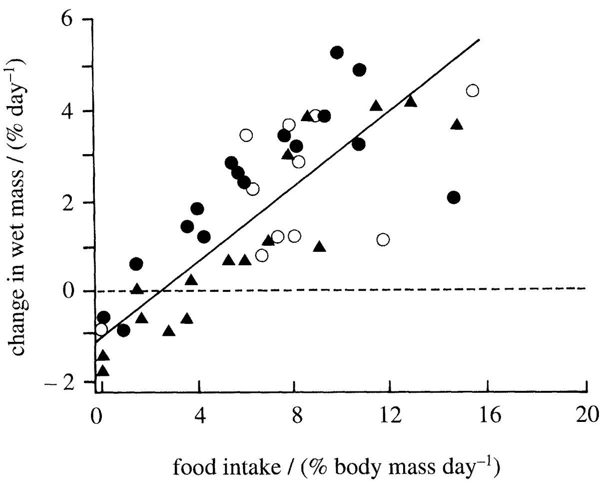

Figure 8. Relation between daily growth rate (percentage change in body mass) and feeding rate (percentage of body mass ingested per day) in *Illex illecebrosus* fed on fish. Body masses are indicated as follows: filled circles, 75–89 g; open circles, 90–99 g; triangles, over 100 g. The horizontal line at zero growth rate represents the best estimate of maintenance ration. From Hirtle *et al.* (1981).

non-buoyant oceanic squid have to swim all the time, and their maintenance requirements would be significantly higher than the minimum values observed in some laboratory studies. The metabolic rate of one ammoniacal squid, *Histioteuthis*, has been reported; it is predicted at around one fifteenth of that of *Illex*.

Captive *Illex illecebrosus* fed either crustacean or fish flesh showed the expected positive relationship between ration and growth rate (data for the fish diet are shown in figure 8). Linear regression of growth as a function of intake provided estimates of maintenance ration from the break-even point (ration for zero growth) for *Illex illecebrosus* at 7 °C as 1.0 % body mass per day when fed crustaceans, and 2.6 % when fed fish (Hirtle *et al.* 1981). Members of a school of *Illex illecebrosus* unlucky enough to be elbowed aside so that they failed to feed lost body mass at a rate of 1.3 % per day (Hirtle *et al.* 1981).

An alternative approach for determining maintenance metabolism is to determine an empirical relation between metabolic rate (usually measured as oxygen uptake) and activity (usually measured as swimming speed). The fitted equation can then be solved for zero activity. This technique suffers from the disadvantage that it is usually difficult to control for the effects of any recent feeding. Indeed experiments on swimming squid made in tunnel respirometers always use fasting squid (to keep the respirometers clear of contaminating faeces) and hence will underestimate metabolic rates in the wild. Nevertheless this is an alternative approach to the food ration techniques discussed above; a similar answer would give us confidence in our estimates.

Relations between metabolic rate and swimming activity in *Illex illecebrosus* are provided by DeMont & O'Dor (1984) and Webber & O'Dor (1986). Solving these for a squid of mass 0.5 kg and zero swimming velocity, and converting mass and oxygen consumption to common units by using measured energy contents (Clarke *et al.* 1994) and the standard oxycalorific conversion, suggests maintenance energy intake rates of 1.56 and 2.53 % body mass per day, respectively.

It is encouraging that these two approaches agree so well; we will take the maintenance ration of a typical squid to be 2.5 % body mass per day. (This figure is, of course, an artificial underestimate in that no squid can survive at zero activity; real ecological maintenance costs will be higher than this.)

5. FEEDING RATES AND CONVERSION EFFICIENCIES

For many purposes one of the most useful energetic measures is the gross conversion efficiency, which expresses the amount of food intake required to fuel a unit amount of growth. This is a measure both of the overall efficiency of the organism at converting food to tissue and of the impact of the individual on its environment. As such it has been widely used in energetic studies. It should be recognized, however, that any value calculated for gross growth efficiency will vary with circumstances (for example how much energy is being used for locomotor activity) and is also dependent on food intake itself. It can easily be seen from the empirical relations in figures 7 or 8 that the higher the food intake, the greater the proportion available for ecologically useful processes such as growth.

In table 1 we list gross conversion rates that have been reported for cephalopods. These data are for animals that have passed the early exponential growth phase but may not yet have achieved sexual maturity. In young stages very high relative growth rates may be achieved (see §9*c* below) and although feeding rates increase with temperature, there is no empirical evidence that food conversion rates change detectably with temperature (Mangold & Boletzky 1973; van Heukelem 1983). There are, however, theoretical reasons to expect an increase in growth efficiencies in polar compared with tropical species, and some empirical evidence from crustaceans suggests that this is the case (Clarke 1987).

Of particular interest are estimates of feeding rates in the wild. Mather & O'Dor (1991) followed individual *Octopus vulgaris* in Bermuda. Their six tagged and weighed octopuses lost mass slowly at 26 °C on an estimated prey intake of 1.2 % body mass per day. Other individuals gained body mass at around 1.4 % per day; at a conversion rate of 50 % this would imply a prey intake of 2.8 % body mass per day. Mather & O'Dor point out that in this particular environment, where predator pressure may have been high, the octopuses were foraging for only about 11 % of each 24 h.

In squids, estimates have to be made from stomach contents with digestive rates and diurnal patterns of feeding taken into account. Very few such studies have been made. The feeding rate for *Loligo opalescens* has been measured in this way by Karpov & Cailliet (1978), yielding an overall figure of 14.4 % body mass per day for animals of commercial size; this is close to the 15–18 % found by Yang *et al.* (1986) in laboratory

Table 1. *Growth rates, feeding rates and gross conversion rates of cephalopods*

(Growth rates are expressed as relative growth rate (%) per day, and feeding rates as % body mass ingested per day; conversion rate has been calculated from data in original publications as 100 × [final mass − initial mass]/mass of food consumed, presented as range with mean in parenthesis; * indicates field data; ND, not determined.)

species	temperature (°C)	relative growth rate (% per day)	mass range (g)	food intake (% body mass/day)	conversion rate (%)	food	reference
Octopods							
Eledone moschata	15	0.8	250	3.4	37	*Carcinus*	Mangold 1983*b*
Eledone cirrhosa	15	0.7	250	2.0	35	*Carcinus*	Boyle & Knobloch 1982
Octopus cyanea	24	2.5	500	6.0	48	crabs	van Heukelem 1973
Octopus dofleini	12	1.0	2700	1.3	69	crabs, bivalves	Hartwick 1983
Octopus maya	25	4.1	300	9.2	40	crabs	van Heukelem 1976
Octopus vulgaris	10	0.9	300	1.6	56	crabs	Mangold & Boletzky 1973
	15	1.7	300	3.3	55	crabs	Mangold & Boletzky 1973
	20	2.9	300	5.4	48	crabs	Mangold & Boletzky 1973
	20	ND	300	3.6	50	crabs	Mangold 1983*a*
	20	ND	350	1.6	25	sardines	Mangold 1983*a*
	20	ND	350	2.5	20	limpets, *Venus*	Mangold 1983*a*
	20	ND	350	ND	40	lobsters	Smale & Buchan 1981
	20	ND	ND	ND	24	mussels	Smale & Buchan 1981
						mussels	
Sepioids							
Sepia officinalis	ND	3.2	60	7.5	43	—	Pascual 1978
	24	6.5	ND	11.0	59	shrimps	Forsythe *et al.* 1994
Sepiola affinis	13	2.4	2	6.4	38	—	Gabel-Deickert 1995
Squid							
Illex illecebrosus	7	1.3	104	5.2	35	fish	Hirtle *et al.* 1981
	10	1.2	171	3.7	33	fish	O'Dor *et al.* 1980
Loligo forbesi	15	1.9	232	6.7	28	fish	O'Dor *et al.* 1980
	14	0.7	(10 or 60)	4.6	16	crustaceans, fish	Hanlon 1990
		1.4	60	4.6	22	crustaceans, fish	Forsythe & Hanlon 1988*b*; Hanlon *et al.* 1989
Loligo opalescens	15	1.7	50	15	13	crustaceans,	Yang *et al.* 1986
	18	ND	14*	ND	ND	fish	Karpov & Cailliet 1978
Sepioteuthis lessoniana	25	7	100	ND	25	crustaceans, fish	Hanlon 1990
Sepioteuthis sepioidea	ND	2.1	50	ND	15	crustaceans, fish	La Roe 1971
Todarodes pacifica	16	0.6	384	3.3	19	fish	Sakurai *et al.* 1993

Table 2. *Growth rates and growth efficiencies in* Octopus maya *and* Illex illecebrosus

(Intake expressed as % body mass d^{-1}; relative growth rate expressed as % d^{-1}; maintenance metabolism expressed as % body mass d^{-1}; data for *Octopus maya* from van Heukelem (1976) and data for *Illex illecebrosus* from Hirtle *et al.* 1981. I, intake; G, growth; R_b, basal metabolism.)

	energy intake, I (% bm d^{-1})	growth rate, G (% d^{-1})	gross conversion $k1$, G/I (%)	$(I-R_b)$ (%)	net conversion $k2$, $G/(I-R_b)$ (%)
Octopus maya (R_b = 1.8 % d^{-1}, 25 °C)					
	4	1.4	35	2.2	64
	8	4.3	54	6.2	69
	12	7.0	58	10.2	69
Illex illecebrosus fed fish (R_b = 2.6 % d^{-1}, 7 °C)					
	4	0.6	15	1.4	43
	8	2.2	28	5.4	41
	12	4.0	30	9.4	43
Illex illecebrosus fed crustaceans (R_b = 1.0 % d^{-1}, 7 °C)					
	4	0.9	23	3.0	30
	8	2.1	26	7.0	30
	12	3.4	28	11.0	31

studies. Erhardt (1991) made a similar study of the much larger *Dosidicus gigas* and concluded that these animals were consuming 13.1 % of their body mass per day. Plainly, large schools of squid can have a very considerable impact on the fish or crustaceans that have the misfortune to share the same patches of ocean.

Because so many variables contribute to the final figure computed for gross conversion efficiency, the data in table 1 should be regarded only as first approximations. It is nevertheless striking that squids convert food less efficiently (and perhaps eat more) than octopods. This is as one would expect given the higher maintenance plus activity costs of squid compared with octopods.

(*a*) *Net growth efficiencies in cephalopods*

In table 2 we compare the growth efficiencies of an octopod (*Octopus maya*) and a squid (*Illex illecebrosus*). It can be seen immediately that *Illex* requires a significantly greater energy intake than *Octopus* to fuel a given rate of growth, a difference related primarily to the greater activity costs in a squid compared with a more sedentary octopus.

The second feature of interest in this comparison is the impact of maintenance metabolism, R_m. When this is corrected for, the net conversion efficiency remains the same for all levels of food intake (table 2). This in turn implies that metabolic costs of growth are independent of meal size. These costs are associated with the post-prandial rise in oxygen consumption, and a longer-term elevation in resting metabolic rate (Wells *et al.* 1983*a*).

(*b*) *Costs of growth*

In all animals there is a rise and then a fall in metabolic rate after a meal, traditionally referred to as the specific dynamic action (SDA) according to Rubner (1902). For animals that feed episodically (such as fish or cephalopods taking a single discrete food item) metabolic rate may return to prefeeding levels before the next meal is taken. For organisms such as grazers or suspension feeders, which may feed essentially continuously, feeding activity will often induce a long-term increase in metabolic rate (A. Clarke, unpublished data). Cephalopods, although carnivores, consume large quantities of prey and also show an overall increase in resting metabolic rate when feeding regularly (Wells *et al.* 1983*c*).

The SDA response comprises a suite of metabolic costs, including mechanical costs (moving food along the gut), digestion costs (synthesis and excretion of enzymes into the gut, absorption of digested food) and synthesis costs (Jobling 1983; Houlihan *et al.* 1990). The latter include both anabolic and catabolic processes, which continue even in starving animals (Wieser 1994) and which must be largely responsible for the longer-term elevation in metabolic rate noted above.

The rise and fall in oxygen uptake has been followed in *Octopus vulgaris*, where its magnitude has been shown to depend on the size of the meal consumed (Best 1981; Best & Wells 1983, 1984; Ellis 1984; Wells *et al.* 1983c). Uptake peaked at 1–2 h after capture of a crab and remained elevated for 8–12 h (figure 9*a*). The total short-term (SDA) oxygen cost of devouring a crab was in the order of 8.9 ml O_2 g^{-1} flesh mass (Wells *et al.* 1983*c*). This equates to 178 J g^{-1} flesh; on the assumption that the energy content of the edible portion of crab flesh is 4.19 kJ g^{-1} (O'Dor & Wells 1987) the immediate (SDA) cost works out at 4.3 % of the energy content of the ingested food. A problem in evaluating this cost is that the routine metabolic rate taken as a baseline varies with the recent feeding history of the individual concerned. The animal illustrated in figure 9*a*, for example, had been starved for 3 d before the first feed. Each of the four (similarly sized) meals given led to a further rise and fall in oxygen uptake, but the baseline rose as well. This is a reversible effect: routine metabolic rate can double or treble with regular feeding and declines when the animal is starved (figure 9*b*).

This study of *Octopus vulgaris*, the most detailed analysis of the metabolic costs of feeding for a marine invertebrate yet undertaken, suggests that a meal has two effects on metabolic rate. The first is the classic

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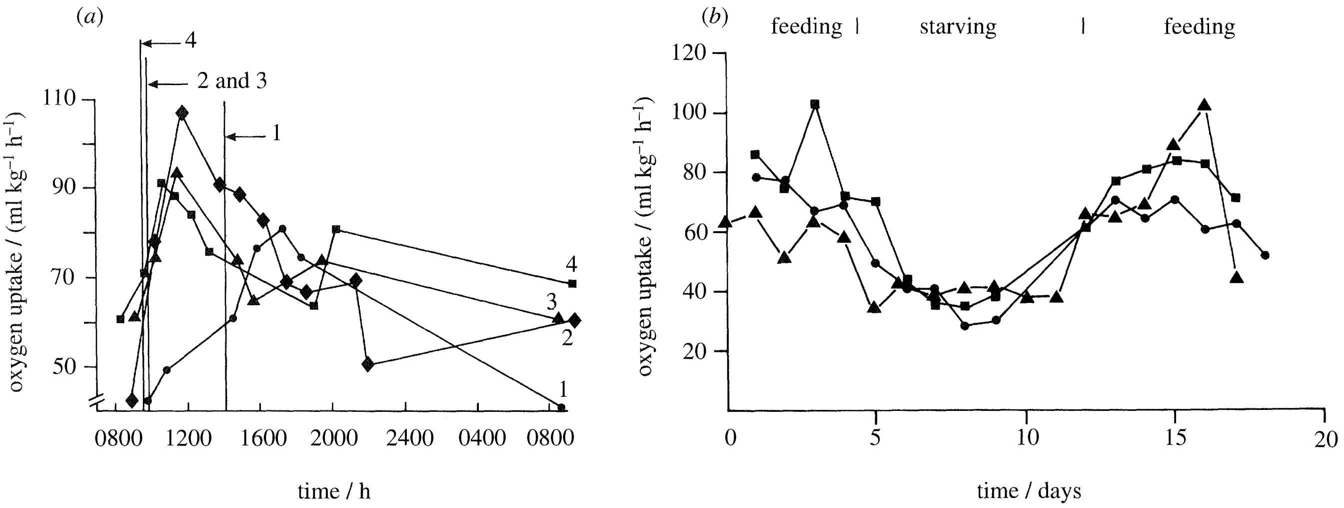

Figure 9. Specific dynamic action and longer-term effects of feeding in *Octopus vulgaris*. (*a*) The rise and fall in oxygen consumption in a single individual on four successive days after a period of starvation; the vertical lines show the time of feeding. The baseline rises progressively. (*b*) The longer-term experiment with observations made every 24 h (before a daily feed), during starvation and when feeding was resumed. Animals averaged 499 g in mass. Redrawn from Wells *et al.* (1983*c*).

SDA response immediately after a meal and the second is a longer-term, but still reversible, increase in routine metabolic rate.

The estimate of the total cost of processing a meal based on the short-term SDA alone (4.3 % of the ingested energy) is small; Houlihan *et al.* (1990) estimated that in *Octopus* growing at 6 % body mass d^{-1} over 90 % of the protein synthesized after a meal was incorporated as growth in the short term. When the long-term doubling of metabolic rate is added to the total cost, however, the figure for *Octopus* rises to 18 % of the energetic value of the food eaten. Crab flesh is protein-rich, with very little lipid or carbohydrate; one might expect an efficient conversion into similarly protein-rich *Octopus* flesh. On this basis the data for *Octopus* incorporating both the short- and long-term effects of feeding, are comparable with Parry's (1983) estimate of 20–30 % of the newly synthesized tissue in other invertebrate animals.

The problem is where to allocate the immediate and long-term costs of feeding in any energy budget. Food fuels activity and a number of other less expensive physiological processes, and the rise and fall in metabolic rate associated with feeding is associated with a rise and fall in growth or activity fuelled by that feeding. The logical answer would therefore seem to be to divide these costs between the two major sinks in proportion to their energetic requirements.

In a 500 g *Octopus* growing at 2 % body mass d^{-1}, new somatic tissue adds 30.4 kJ d^{-1}, whereas activity costs only 1.6 kJ d^{-1}. The increase in metabolic rate on feeding is approximately twofold (an increase of 17.28 kJ d^{-1}) so the total cost of feeding is 17.28 + 1.05 (SDA), i.e. 18.33 kJ d^{-1}. Of this, 95 % (17.41 kJ d^{-1}) is attributable to growth and 5 % (0.92 kJ d^{-1}) to activity.

In squids a far higher proportion of the daily intake goes to fuel locomotion. A 40 g *Loligo* growing at 2 % body mass per day adds 4.87 kJ d^{-1} to its tissues but meanwhile expends 1.37 kJ d^{-1} swimming. The appropriate allocation of feeding costs (5.92 kJ d^{-1}) would therefore appear to be 78 % (4.62 kJ d^{-1}) to growth and 22 % (1.30 kJ d^{-1}) to swimming. In migrating *Illex*, almost all of the energy intake goes to fuel long bouts of rapid swimming.

6. OTHER METABOLIC COSTS: ACTIVITY

The cost of locomotor activity is one aspect of the energy budget that clearly distinguishes squids from octopods. We will therefore treat these separately.

(*a*) *Costs of activity in* Octopus

Octopus vulgaris walks on its arms, although occasionally it swims for short distances. We know nothing about the cost of swimming, but we can measure the cost of walking. Octopus will walk at rates of around 0.34 km h^{-1} for an hour or more in an exercise wheel. The oxygen cost (including a small oxygen debt, which is paid off within 15 min at the end of a run) for a 500 g *Octopus* is 252 ± 8 ml O_2 kg^{-1} km^{-1} at 22 °C, elevating metabolic rate by a factor of 2.4 over the resting maintenance value (Wells *et al.* 1983*b*).

To interpret such experimental data in ecological terms we need to know how much time an octopus spends moving about at this speed in the wild; this is much more difficult. Mather & O'Dor (1991) kept a continuous watch on several octopuses in the wild in Bermuda, and established that they were active for about 11 % of every 24 h. The temperature was 27 °C and these 200 g octopuses grew at 1.4 % body mass d^{-1}. Mather & O'Dor estimated that the same individuals could have maintained their mass by hunting for 6 % of the day, and achieved growth of 2 % body mass d^{-1} by hunting for about 13 % of the time. If we allow normal activity in the wild to approximate to 50 % of the measured cost of continuous activity in an exercise wheel (the animals stop to grope between rocks and to eat prey as they go along), and if we translate the data

Table 3. *A comparison of swimming performance and respiratory metabolism for squids* (Loligo opalescens *and* Illex illecebrosus) *and a fish* (*salmon*: Oncorhynchus nerka)

(From O'Dor (1982) and Webber & O'Dor (1985, 1986); data in parentheses are for the best-performing squid.)

measure	unit	*Loligo*	salmon	*Illex*	salmon
temperature	°C	14	15	15	15
total length	m	0.20	0.19	0.42	0.37
total fresh mass	g	41	55	400	500
maximum oxygen consumption	$\mathrm{ml\ kg^{-1}\ h^{-1}}$	1075	691	—	—
maximum speed	$\mathrm{m\ s^{-1}}$	1.0	1.6	—	—
critical speed	$\mathrm{m\ s^{-1}}$	0.30 (0.36)	0.77	0.76	1.35
standard oxygen consumption	$\mathrm{ml\ kg^{-1}\ h^{-1}}$	254	50	313	40
active metabolic rate	$\mathrm{ml\ kg^{-1}\ h^{-1}}$	664 (862)	627	1047	480
maximum aerobic scope	$\mathrm{ml\ kg^{-1}\ h^{-1}}$	410 (608)	577	734	440
gross cost of transport	$\mathrm{J\ kg^{1}\ m^{-1}}$	12.5	2.6	7.6	1.9
net cost of transport	$\mathrm{J\ kg^{-1}\ m^{-1}}$	7.8	2.0	5.4	1.7

to a 500 g *Octopus* at 22 °C, the cost of activity needed to maintain mass and to grow at 2 % body mass $\mathrm{d^{-1}}$ would be 0.7 and 1.6 $\mathrm{kJ\ d^{-1}}$, respectively. Part of the cost of feeding must be added to these locomotor costs (see §5b above).

(*b*) *Costs of activity in* Illex *and* Loligo

As with octopus, we have data for fasted squid swimming in respirometers, and more limited data on activity in the wild. *Loligo opalescens* (O'Dor 1982) and *Illex illecebrosus* (Webber & O'Dor 1985, 1986) both exhibited an optimum speed at which the cost of transport was minimal (figure 10). In table 3 the swimming performance and respiratory metabolism of these squids are compared with salmon of similar size (a squid of 400 g will be carrying an average of around 100 g of water as it jets, so for these purposes it is roughly equivalent to a fish with 25 % greater mass).

In the very large pool at Dalhousie University, *Illex illecebrosus* swam continuously, generating jet pressures corresponding to 0.15 $\mathrm{m\ s^{-1}}$ and 400 ml $\mathrm{O_2\ kg^{-1}\ h^{-1}}$, equivalent to a daily food intake of 3.8 % body mass to fuel locomotion (Webber & O'Dor 1986). On migration, *Illex illecebrosus* travel at around 20 $\mathrm{km\ d^{-1}}$, averaging 0.23 $\mathrm{m\ s^{-1}}$. This is not their most economical speed (figure 10), which is closer to 0.6 $\mathrm{m\ s^{-1}}$. O'Dor (1988) points out that they would migrate most economically if they swam at 0.6 $\mathrm{m\ s^{-1}}$ for 50 % of the time, slowing down to feed and lowering their metabolism to a standard or maintenance rate of *ca.* 313 ml $\mathrm{O_2\ kg^{-1}\ h^{-1}}$.

No equivalent information is available for *Loligo opalescens*. We do, however, have data from telemetred *L. vulgaris* swimming off South Africa (O'Dor *et al.* 1996). Male squid of 80 g mass averaged 0.17 $\mathrm{m\ s^{-1}}$; at this speed the net cost of transport (after deduction of maintenance metabolic rate) for *L. opalescens* at 15 °C would be 3.84 $\mathrm{kJ\ d^{-1}}$ (44.4 mW) (O'Dor 1982). A share of the cost of feeding must be allocated to locomotor costs, as discussed in §5 above.

7. OTHER METABOLIC COSTS: EXCRETION AND EGESTION

Van Heukelem (1976) collected the faeces from *Octopus cyanea*. Six animals of mean mass 1380 g produced an average of 2.7 $\mathrm{g\ d^{-1}}$. At 28 % dry mass and 1.86 $\mathrm{kcal\ g^{-1}}$ faeces, this represented a loss of 5.89 $\mathrm{kJ\ d^{-1}}$.

Octopuses also shed sucker cuticles (the small round discs of sucker cuticle can generally be seen in any tank harbouring octopuses). Why octopuses shed these discs is unknown; the assumption must be that it is necessary to ensure the proper functioning of the many sense organs or the suppleness of the suckers. Van Heukelem's octopuses shed 2.4 g of discs each day; the material was very watery with a dry matter content of only 3 %. At 4.68 $\mathrm{kcal\ g^{-1}}$ the shedding of these discs of cuticle represents a further loss of only 0.34 $\mathrm{kJ\ d^{-1}}$. There must also be a considerable, but so far unquantified, loss of mucus both from the body surface and with the faeces.

Cephalopods are ammonotelic, with two thirds (*Octopus*) or three quarters (*Illex*) of nitrogen excreted in this form, mainly through the gills; the rest is urea with a little uric acid (Andrews 1988; Hoeger *et al.* 1987; Boucher-Rodoni & Mangold 1994). There is an efficient recovery of carbohydrates (and possibly amino acids) from the ultrafiltrate produced from the branchial heart appendages through the walls of the pericardial ducts (Harrison & Martin 1965). Urine in the renal sacs contains substantial quantities of protein, much of which may come from the mesozoan parasites that are always present. Because these animals must obtain their nourishment from their host, the protein lost in this way has to be included in any budget. Tait (1986) measured a protein concentration of 515 $\mathrm{mg\ l^{-1}}$ in the urine of immature animals, rising to 1407 $\mathrm{mg\ l^{-1}}$ in mature females. Starving animals showed 662 $\mathrm{mg\ l^{-1}}$, a figure not statistically different from that of young, growing octopuses.

Wells & Wells (1990) measured urine production in *Octopus vulgaris*; 15 fasted animals averaged 11.1 ± 3.3 % and 7 fed animals 14.0 ± 4.0 % body mass $\mathrm{d^{-1}}$. Daily energy losses in octopus urine would thus amount to 1.44 $\mathrm{kJ\ kg^{-1}\ d^{-1}}$ (immature and starving animals) and 3.06 $\mathrm{kJ\ kg^{-1}\ d^{-1}}$ (mature females). No equivalent information is available for squids. In the budgets to follow it has again been assumed that squid metabolism will resemble that of octopuses. It is further assumed that losses in urine and faeces will be proportional to metabolic rate.

8. COSTS OF REPRODUCTION

The function of an adult organism is to produce sufficient eggs or sperm of sufficient quality to ensure that its genes are carried forward to the next generation. The energetics of an organism can thus be seen as the mechanism preparing it for a maximum investment in reproduction. Again there is a striking contrast between the squids and octopods in their reproductive energetics, so we will treat the two groups separately.

Although the fecundity and egg size of a given individual or species is of fundamental significance to its reproductive ecology, what concerns us here is the energetic investment. For a review of fecundity and egg size in cephalopods see Mangold (1987).

(*a*) *The energetic cost of reproduction for* Octopus

Cephalopod life cycles generally terminate with reproduction. As the animal matures, resources are allocated to the growth of the gonads and associated structures, eventually at the expense of other tissues. *Octopus vulgaris* has been particularly well studied. This species spawns once and dies. The onset of sexual maturity is associated with a secretion of the optic glands, which simultaneously accelerates the growth of the gonads and their ducts, and catabolism of muscle and other tissues (Wells & Wells 1959; O'Dor and Wells 1973, 1978). The breakdown of muscle floods the bloodstream with amino acids, increasing the metabolic rate as after feeding. However, the animals have by now ceased to feed. They waste away faster than in normal starvation (Tait 1986) and die within 1–4 months, depending on the temperature.

Octopus vulgaris is perhaps an extreme case. Octopuses laying smaller numbers of larger eggs can produce more than one clutch in a season before expiring, as does *Sepia*. Deep-water cirromorph octopods have eggs of a range of sizes in the oviducts and may, like *Nautilus*, continue to produce eggs over a number of years (Villañeuva 1992).

It is easy enough to weigh gonads and other tissues to estimate the proportion of resources allocated to the gonads and the rest of the body. What we cannot do is distinguish between rises in metabolic rate associated with gonadial and other growth. We have to assume that the cost of growing gonads is the same as the cost of growing guts and muscle, knowing that this may not be true because eggs, for example, contain a much higher proportion of lipid than most somatic tissues.

The assumption of an equal cost may well be erroneous for a second reason. In *Octopus* gonadial growth is associated with a threefold increase in the concentration of many amino acids and proteins in the urine. Extra energy is thus lost from the system in excretion during gonadial growth, adding to the effect of an increased metabolic rate, mentioned above (O'Dor & Wells 1978; Tait 1986). In squids and cuttlefish, the large nidamental glands and their output during spawning must represent an additional substantial drain on resources (Clarke *et al.* 1994).

There appears to be rather little information on the energy invested in reproduction by octopods. Van Heukelem (1976) analysed a single female *Octopus cyanea* in detail. This individual had a body mass of 600 g close to spawning, of which 80 g was eggs. Bomb calorimetry gave energy contents of 19 kJ g^{-1} for octopus flesh and 22.45 kJ g^{-1} for eggs (both on a dry mass basis). Allowing for water contents, the distribution of energy in this individual immediately before spawning was 2100 kJ in flesh and 982 kJ in her eggs. *Octopus* only rarely feeds while guarding eggs; during this period the female shrank to 384 g (721 kJ). This indicates that of the energy contained in body tissue immediately before spawning, 32 % went into eggs and 45 % into metabolic costs while brooding. *O. cyanea* produces a large number of planktonic young. In contrast, *O. maya* produces a smaller number of larger, benthic, offspring; however, the energy expended in reproduction appears to be about the same (van Heukelem 1976).

Male *Octopus vulgaris* begin to produce spermatophores at a body mass of around 250 g, and continue to do so until they die. Although males show the same sensecent changes as females in advanced maturity, the testes rarely exceed 0.01 % of the male's own body mass. There has been no attempt to assess the number or energy value of the spermatophores produced during a lifetime, nor the amount of time spent roaming in search of females. Because the animals die at about the same age and mass as females, the assumption must be made that the costs of reproduction are similar, although somewhat differently apportioned because the males expend energy seeking mates whereas impregnated females withdraw and brood eggs.

(*b*) *The energetic cost of reproduction for* **Illex**

Rodhouse & Hatfield (1990*b*, 1992) and Hatfield *et al.* (1992) provide a thorough analysis of the growth of different tissues within maturing *Illex argentinus*. Clarke *et al.* (1994) used these data and a measurement of tissue energy content to estimate investment in reproduction. *Illex argentinus* feeding before migration to the spawning grounds are actively growing as well as maturing gonads. Between the age of 300 and 350 d, a representative female will incorporate an average of 22 g carbon (or 935 kJ) into new tissue. Of this the majority goes to form new somatic tissue (23 % to the mantle, 17 % to the head, arms, tentacles and viscera), with the digestive gland being the major recipient (46 %). Reproductive tissues, although growing fast, receive only 16 % of the ingested carbon (Clarke *et al.* 1994). Males are smaller and growing more slowly; they accumulate only 6 g (250 kJ) between the ages of 300 and 350 d, of which 5.7 % goes into reproductive tissues. Ommastrephid squid thus represent a pattern of resource allocation during reproduction totally different from that of octopuses. Being fast-swimming pelagic organisms, they cannot afford to utilize muscle tissue to fuel the production of eggs or sperm until they are close to the spawning grounds, but must continue to feed. Of the energy they ingest, only a small fraction goes towards reproductive tissues; the remainder fuels continuing growth. No samples of *Illex argentinus* were available for this study from the spawning grounds to see whether mantle tissue is utilized at the final stages of gonad maturation, although growth appears to slow significantly during migration and to cease entirely just before arriving on the spawning grounds (Arkhipkin 1993). Recent evidence for the tropical *Photololigo* suggests that some squid may utilize mantle tissue immediately before spawning (Moltschaniwskyj 1995).

9. POWER BUDGETS FOR REPRESENTATIVE CEPHALOPODS

We now have enough information to construct preliminary power budgets for representative cephalopods. Because the patterns of energy utilization in octopods and squids are so different, we will construct budgets for each, exemplified by *Octopus vulgaris*, and a 'typical' squid, derived mainly from *Loligo opalescens* and *Illex illecebrosus*. We will base the budgets on the division of energy intake shown in figure 1 and discussed in §2. We have not attempted to construct budgets for a sepioid, for data on the costs of digestion or locomotion are not available; however, we would expect budgets for sepioids to be intermediate between the two extremes represented by the largely sedentary *Octopus* and the perpetually active squids.

(*a*) *Preliminary power budgets for* Octopus

Four budgets have been constructed from the data available for *Octopus* discussed above. One budget is for a starving animal, last fed several days ago (starving), a second is for an animal feeding but showing zero net growth (maintenance), a third (growing) for an individual growing at 2 % body mass per day, a typical rate for a individual growing wild in the sea, and the fourth for a female just before egg-laying (mature). These budgets are shown in table 4. The estimated necessary feeding rates (as loss of mass at starvation) correspond well with the observed gains and losses reported in §§4 and 5 above.

(*b*) *Preliminary power budgets for* Illex *and* Loligo

The budgets outlined above for a representative octopus can be derived from data collected from *Octopus vulgaris* and *O. cyanea* both of 500 g body mass and kept at 22–24 °C. Parallel information for a 'typical' squid must be patched together from studies of several species of two genera, *Illex* and *Loligo*, one an oegopsid, the other a myopsid. Most of the information comes from *L. opalescens* of around 40 g and *Illex illecebrosus* of ten times that mass. Temperatures ranged from 7 to 15 °C. Some values, such as the cost of digestion and assimilation or the energetic value of faeces and urine, known for *Octopus*, are not available for squid. The budgets we have constructed should therefore be regarded as considerably less reliable than those made for *Octopus*.

The budget for an active but starving squid of 40 g body mass at 14 °C is based on metabolic data for *Loligo opalescens* (O'Dor 1982) and activity costs based on an average speed of 0.8 body lengths s^{-1} (O'Dor *et al.* 1996). The estimate of energy lost is based on excretion in *Octopus* scaled to the estimated total metabolic rate of the squid.

The estimated budget for a feeding squid under similar conditions assumes that regular feeding raises the metabolic rate (in addition to the immediate postprandial rise in respiration), and that the cost of digestion is the same as in *Octopus*.

The 'migrating – zero growth' budget is based on *Illex* swimming from Nova Scotia to Florida in 100 d and is an order of magnitude larger than that for *Loligo*. O'Dor (1988) has pointed out that these squid

Table 4. *Preliminary power budgets for 500 g* Octopus vulgaris *at 22 °C. Data are presented both as* $kJ\ d^{-1}$ *and* mW *(conversion* $1\ kJ\ d^{-1} = 11.57\ mW$*); for derivation of values, see text.* Octopus *flesh was assumed to contain* $3.06\ kJ\ g^{-1}$ *fresh mass*

	starving		maintenance		growing		mature	
	$kJ\ d^{-1}$	mW	$kJ\ d^{-1}$	mW	$kJ\ d^{-1}$	mW	$kJ\ d^{-1}$	mW
maintenance metabolism	12.7	147.2	17.3	200.2	17.3	200.2	17.3	200.0
costs of activity	0.7	8.1	0.7	8.1	2.5	28.9		
energy content of new tissue	—	—	—	—	30.4	351.7	—	—
costs of synthesis/breakdown	0.9	10.4	1.2	13.9	17.4	20.3	19.6	226.8
excretory losses	0.5	6.1	0.7	8.1	1.4	16.2	1.5	17.4
faecal and sucker losses	2.2	25.7	3.1	35.9	6.2	71.7	2.2	25.5
total power requirement	17.0	196.7	23.0	266.2	77.6	897.8	40.6	469.7
absorption efficiency (%)	—		93 %		93 %		—	
ingestion	nil	(no tissue)	24.7	285.8	83.4	965.4	40.6	469.7
ingestion (% body $kJ\ d^{-1}$)	−1.1 %	(own tissue)	1.6 %		5.5 %		— −2.7 %	(own tissue)
net conversion efficiency	nil	(no feeding)	nil	(no growth)	46.0 %		nil	(no feeding)
gross conversion efficiency	nil	(no feeding)	nil	(no growth)	36.5 %		nil	(no feeding)

Table 5. *Preliminary power budgets for squids, based on 40 g* Loligo opalescens *at 14 °C and 400 g* Illex illecebrosus *at 15 °C. Presentation as for table 4*

	Loligo				Illex	
	starving		growing		mature migrating	
	kJ d^{-1}	mW	kJ d^{-1}	mW	kJ d^{-1}	mW
maintenance metabolism	4.87	56.3	4.87	56.3	60.1	695.3
costs of activity	1.37	15.85	2.67	30.89	70.5	815.3
energy content of new tissue	—	—	2.8	32.4	—	—
costs of synthesis/breakdown	—	—	4.62	53.5	—	—
excretory losses	0.46	5.32	1.12	12.96	4.0	46.3
faecal losses	0.7	8.1	1.68	19.44	6.0	69.4
total power requirement	7.04	81.45	1.84	206.41	140.5	1625.6
absorption efficiency (%)	—		86 %		86 %	
ingestion	nil	(not feeding)	20.74	240.01	163.4	1890.5
ingestion (% body kJ d^{-1})	−5.03 %	(own tissue)	14.81 %		11.7 %	
net conversion efficiency	nil	(not feeding)	17.64 %		nil	(no growth)
gross conversion efficiency	nil	(not feeding)	13.57 %		nil	(no growth)

cannot migrate on their own bodily reserves and must eat on the way; he further suggested that the most readily available food is their own kind, the school feeding on itself as it goes along. Clarke *et al.* (1994) estimated that reserves in the digestive gland of *Illex argentinus* before migration could, in the absence of feeding, fuel migrations lasting only 14 d (males) or 21 d (females).

For construction of the energy budget in migrating *Illex* the metabolic rate was taken as 2.2 times the maintenance level found by Webber & O'Dor (1985) to allow for the long-term effects of regular feeding; this could even be an underestimate because of the very high rate of feeding. Costs of activity were estimated on the basis of 50 % of 24 h spent travelling at the most economical speed with the remainder 'hovering' at maintenance rates.

These budgets are presented in table 5. Again the 'bottom line' figures agree with observations made in §§4 and 5 above. The mass loss figure of 5 % body mass d^{-1} for a starving *Loligo opalescens* is high compared with that for *Illex* (estimated at *ca.* 2.5 %) but the *Illex* were much larger (by a factor of ten) and held at 7 °C rather than 14 °C. Ingestion for growing *Loligo opalescens* at 14.8 % body mass d^{-1} is almost identical with the 14.4 % body mass d^{-1} estimated by Karpov & Cailliet (1976) from field studies.

(*c*) *The impact of juveniles*

It should be stressed that all the daily budgets outlined above for both octopuses and squid are for animals that have passed the exponential phase of their growth; indeed, all are from animals approaching sexual maturity and the end of their life cycles. Typical daily growth rates in the first few months after hatching are in the range 5–8 % body mass d^{-1} (Forsythe and van Heukelem 1987), with species such as *Sepia subaculeata* (Choe 1966) and *Sepioteuthis lessoniana* (Hanlon 1990; Segawa 1990) reaching 13 % body mass d^{-1}. Juveniles have very high metabolic rates (Segawa 1991) because they are so small; they must consume relatively large quantities of prey to sustain the observed rates of growth. There is a considerable literature on what young cephalopods will eat in captivity (see, for example, references in Segawa (1993) and Yang *et al.* (1986)), but actual figures for the mass of prey consumed are more difficult to come by because attempts at culture have generally aimed to provide food *ad libitum* to groups of individuals. Hanlon (1990) estimated a feeding rate of 20 % body mass d^{-1} for *Loligo forbesi*; Choe (1966) calculated figures close to 30 % body mass d^{-1} for three species of *Sepia*. Segawa (1990) found that the per gram food consumption of *Sepioteuthis* peaked at around 1 g, individual animals then consuming up to an amazing 60 % (fish) or 72 % (mysids) of their own body mass daily at 25 °C.

It would be fascinating to assemble comparable daily budgets for juveniles, the more so because most cephalopods spend most of their lives as very small animals. Voracious as the subadults are, it is clear that the real impact of cephalopods in the sea probably comes from their activities early in life when they are numerous and growing at prodigious rates. At the moment the physiological data needed to construct such budgets are unfortunately almost entirely lacking.

(*d*) *Life in the slow lane*: **Nautilus**

Most of the coleoids we know about grow fast, breed in a single season and then die, aged one or two years. *Nautilus*, in contrast, grows slowly, is iteroparous and lives for ten or twenty years.

Estimates of growth rates have been made from mark, release and recapture studies, from growth in aquaria, from the decay of radionuclides in the shell and from the rate of chamber formation. Estimates vary with the method and the species concerned; *N. macromphalus* probably takes 5–6 years to reach sexual maturity, the larger *N. belauensis* 11–15 years (Landman & Cochran 1987; Ward 1987).

Sexual maturity is marked by a series of changes,

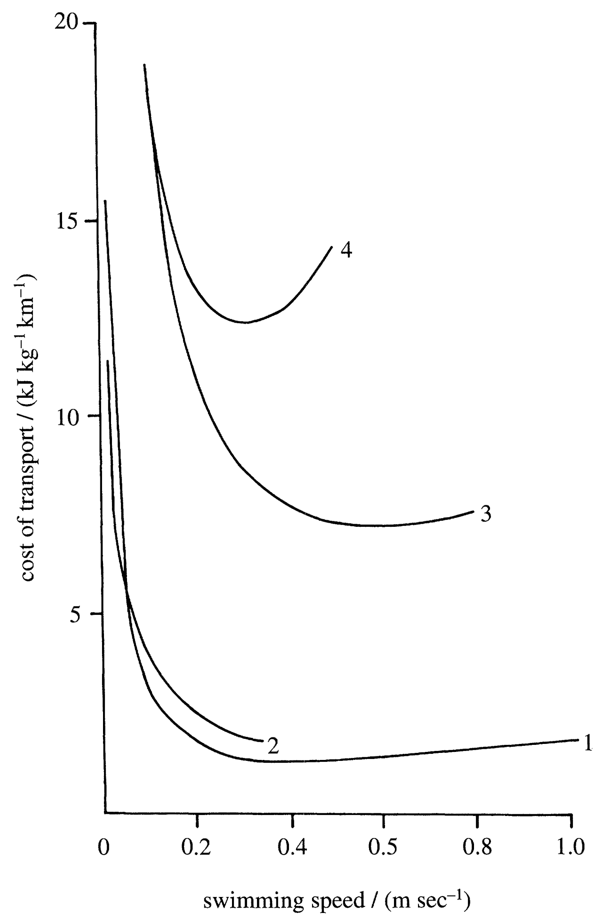

Figure 10. Relation between the gross cost of transport (kJ kg^{-1} km^{-1}) and swimming speed (m s^{-1}) in two species of squid, a fish, and *Nautilus*. 1, Salmon, *Oncorhynchus nerka*, 500 g; 2, *Nautilus pompilius*, 500 g; 3, *Illex illecebrosus*, 400 g; 4, *Loligo opalescens*, 40 g. Redrawn from O'Dor (1988).

including relative enlargement of the body chamber, which becomes wider and more rounded (particularly in males) and thickening of the apertural edge with development of a black band of pigment along the margin. The last septum is thicker than the rest and laid down unusually close to the one before (Collins & Ward 1987).

Quite how long *Nautilus* lives after reaching sexual maturity is unknown. Saunders (1983) reports a *N. belauensis* recaptured 4 years after release as a mature animal. Juveniles are comparatively rare; of 2387 *N. belauensis* caught and released in Palau, 80% were mature and there was no evidence of any segregation of size by depth. This, and the very low fecundity, maybe only ten or twenty huge eggs in a year (by the 25% of the animals that are females; all populations so far investigated have shown an overwhelming proportion of males) imply that the *Nautilus* may live for 10 years or more after attaining maturity. The animal is thus potentially very vulnerable to overfishing, as records from the Philippines appear to show (Ward 1987).

As well as growing very slowly, *Nautilus* moves around slowly (but very economically). In captivity, *Nautilus* is only intermittently active (Zann 1984). Active periods, typically one or two in any hour, lasted from 20 min during the night to less than 5 min at midday (Wells *et al.* 1992). Similar behaviour was seen in a telemetred animal in a cage on the seabed, but when the same animal was released it became considerably more active (O'Dor *et al.* 1993). While active at 20 °C in a swim-tunnel, *Nautilus* can consume up to 100 ml O_2 kg^{-1} h^{-1}, corresponding to an aerobically sustainable speed of 16 cm s^{-1}; higher speeds up to around 25 cm s^{-1} lead to the accumulation of an oxygen debt (O'Dor *et al.* 1990). Having no fins, *Nautilus* can only move by jet propulsion (there is no indication that it can use the arms for locomotion). Jet propulsion is inherently expensive and particularly so in *Nautilus* where the ejectable mass is so small (Chamberlain 1987). The animal is, however, neutrally buoyant and can use its ventilation stream both for respiration and for locomotion. Provided that it swims slowly (at less than 5 cm s^{-1}) *Nautilus* is actually more economical than a salmon (O'Dor *et al.* 1990) (figure 10).

Interestingly, this is the speed at which it chooses to move for most of the time when it is free in its natural habitat on the sea bed (at 22 °C). At this rate the oxygen consumption of an adult animal would indicate a food requirement of less than 1 g (*ca.* 3.5 kJ) per day. *Nautilus* has a very substantial crop, as befits an animal that is plainly a scavenger as well as a predator adapted to sweep up tiny prey as well as more substantial items (hermit crabs appear to be a favourite food item (Ward 1987)); a cropful (50 g) would last it for six weeks or more (O'Dor *et al.* 1993).

Nothing whatever is known about the rate of feeding by *Nautilus* in the wild, and we lack any other physiological data to enable the construction of an energy budget. Nevertheless we do know enough to conclude that *Nautilus* lives an exceedingly low-energy lifestyle.

10. SOME FINAL THOUGHTS

Although cephalopods are undoubtedly a very successful group in modern seas, and have been dominant in the past, a consideration of their energetics gives clues to possible constraints on what a cephalopod can do.

(*a*) *Metabolic substrates*

As with other muscles required to deliver high power, squid mantle muscle is rich in mitochondria; it also shows a number of parallel adaptations to insect flight muscle (Storey & Storey 1983). The muscles of more sluggish cephalopods, such as *Octopus* or *Nautilus*, have lower mitochondrial contents and lower activities of oxidative enzymes (Hochachka *et al.* 1978). The terminal electron acceptor is usually oxygen (that is, metabolism is primarily aerobic).

In common with many molluscs, however, cephalopods are capable of anaerobic metabolism, coupling fermentation of carbohydrate through glycolysis to the hydrolysis of phosphagen reserves such as arginine phosphate. In this case a typical electron acceptor would be octopine (Storey & Storey 1983). This mechanism allows for a rapid production of ATP per unit time, but is a very inefficient use of reserves (providing a low ATP yield per unit of glucose). It is possible that in the more sluggish species of cephalopod, such as *Octopus*, such anaerobic pathways may provide the primary (or even sole) source of power for infrequent bursts of swimming. The subsequent oxidation of anaerobic electron acceptors accumulated during a burst of activity contributes to the oxygen debt observed after activity in *Octopus* (Wells *et al.* 1983*b*).

In squid, however, sustained swimming is powered aerobically, with anaerobic mechanisms used only for extreme situations such as predator avoidance or prey capture. Hochachka *et al.* (1975) suggested that the metabolism of squid mantle muscle during sustained swimming is fuelled primarily by carbohydrate, in direct contrast to the lipid fuel typical of vertebrate muscle. The problem with this is that squid typically contain very low levels of carbohydrate (Clarke *et al.* 1994); these reserves would be depleted by only a few minutes of sustained activity (Storey & Storey 1983; O'Dor & Webber 1986). This indicates quite clearly that such activity must be fuelled by either lipid or protein. Studies of lipid-metabolizing enzymes in squid, however, have suggested that their ability to utilize lipid as a metabolic substrate is limited (Mommsen & Hochachka 1981; Ballantyne *et al.* 1981). Dietary studies of *Octopus* have also suggested that absorption efficiencies for lipid (45–75 %) are much lower than for protein or carbohydrate (95 % or more) (O'Dor *et al.* 1984).

Although the lipid content of cephalopod muscle is generally low (summarized by Storey & Storey (1983)), some species of squid feed on lipid-rich prey such as zooplankton or myctophid fish and can accumulate substantial quantities of lipid in the digestive gland (Clarke *et al.* 1994). This would indicate that the biochemical machinery exists for the digestion and absorption of lipid in squid. Furthermore, the reserves of lipid typical of squid would sustain locomotor activity for several days in the absence of feeding (O'Dor & Webber 1986; Clarke *et al.* 1994). The evidence thus points to lipid as an important fuel for sustained swimming in squid, despite the apparent inefficiency of the metabolic machinery for utilizing lipid. This intriguing paradox needs resolving.

Measurements of nitrogen (primarily ammonia) excretion, and in particular O:N ratios, indicate that cephalopods utilize significant quantities of protein (Boucher-Rodoni & Mangold 1985; Segawa & Hanlon 1988). Furthermore, O'Dor *et al.* (1978) have suggested that under conditions of starvation, energy may be derived from metabolism of muscle protein. Certainly cephalopods (indeed molluscs in general) are notable for their ability to withstand large changes in body size, and a direct utilization of protein is more efficient energetically than a conversion to lipid or carbohydrate. *Octopus* also utilizes muscle protein during the production of its ovary (O'Dor & Wells 1978).

Taken together, these observations would suggest that cephalopods retain the ability to utilize carbohydrate, lipid and protein as metabolic substrates, with lipid and protein fuelling routine aerobic metabolism and carbohydrate providing substrate for burst (anaerobic) activity.

(*b*) ***Feeding and prey in cephalopods***

All living cephalopods are carnivores. If there were herbivorous or filter-feeding cephalopods in the past, none has survived. It is perhaps worth considering why this might be, since other molluscs have successfully exploited a much wider range of foods.

The essential equipment for both filter-feeding and herbivory exists even in coleoids. There is a beak and a radula; the animals could eat plants, even grind the cellulose cell walls to release the contents. There are gills; other molluscs exploit the use of a current created by the gills to trap particles in mucus that is fed in a rope out of the mantle and into the mouth. However, no living cephalopod uses the mouthparts or the gills to do these things.

Instead, the animals have specialized in an active predatory lifestyle. Here they have one great advantage over fish, their principal competitors. The spread of the arms of cephalopods means that they can tackle prey as large as themselves, seizing and biting bits off. They are good at catching other animals, although the passage of the gut through the brain in cephalopods means that all prey must be eaten in small pieces. The ancestors of modern coleoids exploited this advantage, but to do so fully they had to be fast and manoeuvrable. Here the cephalopods run into a problem: jet propulsion is inherently energetically extravagant compared with undulant swimming.

One consequence can be seen in the energy budgets outlined in tables 4 and 5. The energy demands of *Octopus*, let alone of squid, are very great by the standards of other invertebrates, even of fish; only the more energetic fish even approach them. The ancestors of the squids (and the octopods that later developed from them) were inevitably driven to an increasingly muscular mantle (cutting off the possibility of filter feeding) and a move towards ever more streamlined shapes. Herbivores generally need large guts to process large volumes of material, and this is incompatible with the power demands of jet propulsion. Once the ancestors of the modern coleoids had modified sufficiently to compete successfully with fish, they were committed to a carnivorous existence.

(*c*) ***Competition with fish***

An interesting evolutionary experiment appears to have taken place in the Southern Ocean. Here the original shallow-water fish fauna was eradicated by an extinction event sometime in the Cainozoic (Eastman 1993), probably associated with the onset of glaciation (Clarke & Crame 1989). Subsequently there has been a spectacular radiation of a single group of fish, the Notothenioidea (Eastman 1993), a largely demersal group which has secondarily lost a functional swimbladder. As a result the Southern Ocean lacks the schools of active, midwater pelagic schooling fish which are major predators of plankton in most other seas (Clarke & Johnston 1996). Perhaps it is this evolutionary accident that has created an ecological opportunity for the fast-growing but less efficient cephalopods to become such an important group ecologically in parts of the Southern Ocean (Rodhouse & White 1995).

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REFERENCES

Alford, R. A. & Jackson, G. D. 1993 Do cephalopods and larvae of other taxa grow asymptotically? *Am. Nat.* **141**, 717–728.

Andrews, E. B. 1988 Excretory systems of molluscs. In *The Mollusca* vol. 11 (*Form and function*) (ed. E. R. Trueman & M. R. Clarke), pp. 381–448. San Diego: Academic Press.

Araya, H. 1983 Fishery biology and stock assessment of *Ommastrephes bartrami* in the North Pacific Ocean. *Mem. Vict. Mus.* **44**, 269–283.

Arkhipkin, A. 1993 Age, growth, stock structure and migratory rate of prespawning short-finned squid *Illex argentinus* based on statolith ageing investigations. *Fish. Res.* **16**, 313–338.

Ballantyne, J. S., Hochachka, P. W. & Mommsen, T. P. 1981 Studies on the metabolism of the migratory squid, *Loligo opalescens*: enzymes of tissues and heart mitochondria. *Mar. Biol. Lett.* **2**, 75–85.

Best, E. M. H. 1981 Aspects of the digestive system and its control in *Octopus vulgaris*. Ph.D. thesis, University of Cambridge, U.K.

Best, E. M. H. & Wells, M. J. 1983 The control of digestion in *Octopus* 1: The anticipatory response and the effect of severing the nerves to the gut. *Vie Milieu* **33**, 135–142.

Best, E. M. H. & Wells, M. J. 1984 The control of digestion in *Octopus* 2: The role of internal stimuli. *Vie Milieu* **34**, 1–7.

Boletzky, S. von 1983 *Sepia officinalis*. In *Cephalopod life cycles*, vol. 1. *Species accounts* (ed. P. R. Boyle), pp. 31–52. London: Academic Press.

Boletzky, S. von & Hanlon, R. T. 1983 A review of the laboratory maintenance, rearing and culture of cephalopod molluscs. *Mem. Natl. Mus. Vict.* **44**, 147–187.

Boucaud-Camou, E. & Boismery, J. 1991 The migrations of the cuttlefish, *Sepia officinalis* L. In *Acta 1st Int. Symp. Cuttlefish Sepia* (ed. E. Boucaud-Camou), pp. 179–189. Caen: Centre de Publications de l'Université de Caen.

Boucher-Rodoni, R. & Mangold, K. 1994 Ammonia production in cephalopods, physiological and evolutionary aspects. *Mar. Freshw. Behav. Physiol.* **25**, 53–60.

Boyle, P. R. & Knobloch, D. 1982 On growth of the octopus, *Eledone cirrhosa*. *J. mar. biol. Ass. U.K.* **62**, 277–296.

Boyle, P. R. & Ngoile, M. A. K. 1993 Assessment of maturity state and seasonality of reproduction in *Loligo forbesi*, Cephalopoda: Loliginidae, from Scottish waters. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 37–48. Tokyo: Tokai University Press.

Calow, P. 1985 Adaptive aspects of energy allocation. In *Fish energetics: new perspectives* (ed. P. Tytler & P. Calow), pp. 13–31. London: Croom Helm.

Choe, S. 1966 On the growth, feeding rates and efficiency of food conversion for cuttlefishes and squids. *Korean J. Zool.* **9**, 12–20.

Clarke, A. 1987 Temperature, latitude and reproductive effort. *Mar. Ecol. Prog. Ser.* **38**, 89–99.

Clarke, A. 1993 Seasonal acclimitization and latitudinal compensation in metabolism: do they exist? *Funct. Ecol.* **7**, 139–149.

Clarke, A. & Crame, J. A. 1989 The origin of the Southern Ocean marine fauna. In *Origins and evolution of the Antarctic biota* (ed. J. A. Crame) (Geological Society Special Publication no. 47), pp. 253–268. London: Geological Society.

Clarke, A. & Johnston, I. A. 1996 Evolution and adaptation of Antarctic fishes. *Trends Ecol. Evol.* **11**, 212–218.

Clarke, A., Rodhouse, P. G. & Gore, D. J. 1994 Biochemical composition in relation to the energetics of growth and sexual maturation in the ommastrephid squid *Illex argentinus*. *Phil. Trans. R. Soc. Lond.* B **344**, 201–212.

Clarke, A., Rodhouse, P. G., Holmes, L. J. & Pascoe, P. L. 1989 Growth rate and nucleic acid ratio in cultured cuttlefish *Sepia officinalis* (Mollusca: Cephalopoda). *J. exp. mar. Biol. Ecol.* **133**, 229–240.

Collins, D. & Ward, P. D. 1987 Adolescent growth and maturity in *Nautilus*. In: *Nautilus. The biology and palaeobiology of a living fossil* (ed. W. B. Saunders & N. H. Landman), pp. 421–432. New York: Plenum Press.

Dawe, E. G. & Beck, P. C. 1992 Population structure, growth and sexual maturation of short-finned squid at Newfoundland, Canada based on statolith analysis. ICES CM 1992 K: 33 Shellfish Committee. (23 pages.)

DeMont, M. E. & O'Dor, R. K. 1984 The effects of activity, temperature and mass on the respiratory metabolism of the squid, *Illex illecebrosus*. *J. mar. biol. Ass. U.K.* **64**, 535–543.

Eastman, J. T. 1993 *Antarctic fish biology: evolution in a unique environment*. London: Academic Press. (322 pages.)

Ehrhardt, N. M. 1991 Potential impact of a seasonal migratory jumbo squid *Dosidicus gigas* stock on a Gulf of California sardine *Sardops sagax coerulea* populations. *Bull. mar. Sci.* **49**, 325–332.

Elliot, J. M. & Davison, W. 1975 Energy equivalents of oxygen consumption in animal energetics. *Oecologia, Berl.* **19**, 195–201.

Ellis, S. L. 1984 The cost of feeding and growth in *Octopus vulgaris*. B.Sc. thesis, University of Dalhousie.

Fields, W. G. 1965 The structure, development, reproduction, and life history of the squid *Loligo opalescens* Berry. *Calif. Dept. Fish Game, Fish. Bull.* **131**, 1–108.

Forsythe, J. W. 1993 A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 133–143. Tokyo: Tokai University Press.

Forsythe, J. W., DeRusha, R. H. & Hanlon, R. T. 1994 Growth, reproduction and life span of *Sepia officinalis* Cephalopoda: Mollusca cultured through seven consecutive generations. *J. Zool.* **233**, 175–192.

Forsythe, J. W. & Hanlon, R. T. 1988*a* Effect of temperature on laboratory growth, reproduction and life span of *Octopus bimaculoides*. *Mar. Biol.* **98**, 369–379.

Forsythe, J. W. & Hanlon, R. T. 1988*b* Growth of the Eastern Atlantic squid, *Loligo forbesi* Steenstrup, 1856 Mollusca: Cephalopoda. *Aquacult. Fish Mgmt* **20**, 1–14.

Forsythe, J. W. & Heukelem, W. F. van 1987 Growth. In *Cephalopod life cycles*, vol. 2. *Comparative reviews* (ed. P. R. Boyle), pp. 135–156. London: Academic Press.

Gabel-Deickert, A. 1995 Reproductive patterns in *Sepiola affinis* and other Sepiolidae. *Bull. Inst. Oceanogr. Monaco* **16**, 73–83.

Hanlon, R. T. 1990 Maintenance, rearing and culture of Teuthoid and Sepioid squids. In *Squid as experimental animals* (ed. D. J. Gilbert, W. J. Adelman & J. M. Arnold), pp. 35–62. New York: Plenum Press.

Hanlon, R. T., Hixon, R. F. & Hulet, W. H. 1983 Survival, growth, and behaviour of the loliginid squids *Loligo plei*, *Loligo pealei*, and *Lolliguncula brevis* Mollusca: Cephalopoda in closed seawater systems. *Biol. Bull. mar. Biol. Lab, Woods Hole* **165**, 637–685.

Hanlon, R. T., Yang, W. T., Turk, P. E., Lee, P. G. & Hixon, R. F. 1989 Laboratory culture and estimated life span of the Eastern Atlantic squid, *Loligo forbesi* Steenstrup, 1856 Mollusca: Cephalopoda. *Aquacult. Fish. Mgmt* **20**, 15–34.

Harrison, F. M. & Martin, A. W. 1965 Excretion in the cephalopod *Octopus dofleini*. *J. exp. Biol.* **42**, 71–92.

Hartwick, B. 1983 *Octopus dofleini*. In *Cephalopod life cycles*, vol. 1. *Species accounts* (ed. P. R. Boyle), Ch. 17, pp. 277–291. London: Academic Press.

Hatfield, E. M. C., Rodhouse, P. G. & Barber, D. L. 1992 Production of soma and gonad in maturing female *Illex argentinus* (Mollusca: Cephalopoda). *J. mar. biol. Ass. U.K.* **72**, 281–291.

Hawkins, A. J. S. 1991 Protein turnover: a functional appraisal. *Funct. Ecol.* **5**, 222–233.

Hayashi, S. 1993 Growth and maturation of the firefly squid *Watasenia scintillans* Berry in Toyama bay and adjacent waters of the sea of Japan. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 173–178. Tokyo: Tokai University Press.

Heukelem, W. F. van 1973 Growth and lifespan of *Octopus cyanea*. *J. Zool.* **169**, 299–315.

Heukelem, W. F. van 1976 Growth, bioenergetics and lifespan of *Octopus cyanea* and *Octopus maya*. Ph.D. thesis, University of Hawaii.

Heukelem, W. F. van 1983 *Octopus cyanea*. In *Cephalopod life cycles*, vol. 1. *Species accounts* (ed. P. R. Boyle), Ch. 17, pp. 267–276. London: Academic Press.

Hirtle, R. W. M., DeMont, M. E. & O'Dor, R. K. 1981 Feeding growth and metabolic rates in captive short-finned squid, *Illex illecebrosus*, in relation to the natural population. *J. Shellfish Res.* **1**, 187–192.

Hochachka, P. W., French, C. J. & Meredith, J. 1978 Metabolic and ultrastructural organisation in *Nautilus* muscles. *J. exp. Zool.* **205**, 51–62.

Hochachka, P. W., Moon, T. W., Mustafa, T. & Storey, K. B. 1975 Metabolic sources of power for mantle muscle of a fast swimming squid. *Comp. Biochem. Physiol.* **52B**, 151–158.

Hoeger, U., Mommsen, T. P., O'Dor, R K. & Webber, D. 1987 Oxygen uptake and nitrogen excretion in two cephalopods, octopus and squid. *Comp. Biochem. Physiol.* **87A**, 63–67.

Houlihan, D. F., McMillan, D. N., Agnisola, C., Genoino, I. T. & Fott, L. 1990 Protein syntehsis and growth in *Octopus vulgaris*. *Mar. Biol.* **106**, 251–259.

Itami, K. 1964 Marking and release study in the octopus. *Aquiculture* **12**, 119–125. [In Japanese.]

Jackson, G. D. 1994 Statolith age estimates of the loliginid squid, *Loligo opalescens* Mollusca, Cephalopoda: corroboration with culture data. *Bull. mar. Sci.* **54**, 554–557.

Jereb, P., Ragonese, S. & Boletzky, S. von (eds). 1990 *Squid age determination using statoliths*. Proceedings of the International Workshop held in the Instituto di Tecnologia della Pesca e del Pescado ITPP-CNR Mazara del Vallo, Italy, 9–14 October 1989. N.T.R. – I.T.P.P. Special Publications, no. 1. (128 pages.)

Jobling, M. 1983 Towards an explanation of specific dynamic action (SDA). *J. Fish. Biol.* **23**, 549.

Joll, L. M. 1977 Growth and food intake of *Octopus tetricus* Mollusca: Cephalopoda in aquaria. *Aust. J. mar. Freshw. Res.* **28**, 45–56.

Karpov, K. A. & Cailliet, G. M. 1978 Feeding dynamics of *Loligo opalescens*. *Fish. Bull.* **169**, 45–65.

Landman, N. H. & Cochran, J. K. 1987 Growth and longevity of *Nautilus*. In *Nautilus. The biology and palaeobiology of a living fossil* (ed. W. B. Saunders & N. H. Landman), pp. 401–420. New York: Plenum Press.

La Roe, E. T. 1971 The culture and maintenance of the Loliginid squids *Sepioteuthis sepioidea* and *Doryteuthis plei*. *Mar. Biol.* **9**, 9–25.

Le Goff, R. & Daguzan, J. 1991 Étude des déplacements de las seiche commune L. dans le golfe du Morbihan au cours de la période de la reproduction, In *La seiche – the cuttlefish* (ed. E. Boucaud-Camou), pp. 167–177. Acta 1st Int. Symp. Cuttlefish *Sepia*. Caen: Centre de Publications de l'Université de Caen.

Lo Bianco, S. 1909 Notizie biologiche riguardanti specialmente il periodo di maturità sessuale degli animali del Golfo di Napoli. *Mitt. zool. Stat. Neapel.* **19**, 513–761.

Mangold, K. 1983*a* *Octopus vulgaris*. In *Cephalopod life cycles*, vol. 1. *Species accounts* (ed. P. R. Boyle), pp. 335–364. London: Academic Press.

Mangold, K. 1983*b* *Eledone moschata*. In *Cephalopod life cycles*, vol. 1. *Species accounts* (ed. P. R. Boyle), pp. 387–400. London: Academic Press.

Mangold, K. 1983*c* Food, feeding and growth in cephalopods. *Mem. Natl. Mus. Vict.* **44**, 81–93.

Mangold, K. 1987 Reproduction. In *Cephalopod life cycles*, vol. 2. *Comparative reviews* (ed. P. R. Boyle), pp. 157–200. London: Academic Press.

Mangold, K. & Boletzky, S. von 1973 New data on reproductive biology and growth of *Octopus vulgaris*. *Mar. Biol.* **19**, 7–12.

Mangold, K., Young, R. E. & Nixon, M. 1993 Growth versus maturation in Cephalopods. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 697–704. Tokyo: Tokai University Press.

Mangold-Wirz, K. 1963 Biologie des céphalopodes benthiques et nectoniques de la mer Catalane. *Vie Milieu* **13** (suppl), 1–285.

Mather, J. & O'Dor, R. K. 1991 Foraging strategies and predation risk shape the life history of juvenile *Octopus vulgaris*. *Bull. mar. Sci.* **49**, 253–269.

Moltschaniwskyj, N. A. 1995 Multiple spawning in the tropical squid *Photololigo* sp.: what is the cost in somatic growth? *Mar. Biol.* **124**, 127–135.

Mommsen, T. P. & Hochachka, P. W. 1981 Respiratory and enzymatic properties of squid heart mitochondria. *Eur. J. Biochem.* **120**, 345–350.

Moriyasu, M. 1983 Étude biométrique de la croissance d'*Eledone cirrhosa* Lam., 1798 Cephalopoda, Octopoda du Golfe de Lion. *Oceanol. Acta.* **6**, 35–41.

Murata, M., Nakamura, Y., Kubota, S., Hashiba, T. & Yamaguchi, H. 1988 Some biological aspects of the neon flying squid, *Ommastrephes bartrami* caught by Japanese gillnetters in the North Pacific. *Nippon Suisan Gakkaishi* **54**, 1573–1581.

Nagasawa, K., Takayanagi, S. & Takami, T. 1993 Cephalopod tagging and marking in Japan: a review. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 313–329. Tokyo: Tokai University Press.

Nixon, M. 1966 Changes in body weight and intake of food by *Octopus vulgaris*. *J. Zool.* **150**, 1–9.

Nixon, M. 1969 The lifespan of *Octopus vulgaris*, Lamarck. *Proc. malacol. Soc. Lond.* **38**, 529–540.

O'Dor, R. K. 1982 Respiratory metabolism and swimming performance of the squid, *Loligo opalescens*. *Can. J. Fish. aquat. Sci.* **39**, 580–587.

O'Dor, R. K. 1983 *Illex illecebrosus*. In *Cephalopod life cycles*, vol. 1. *Species accounts* (ed. P. R. Boyle), pp. 175–199. London: Academic Press.

O'Dor, R. K. 1988 The energetic limits on squid distributions. *Malacologia* **29**, 113–119.

O'Dor, R. K., Durward, R. D., Vessey, E. & Amaratunga, T. 1980 Feeding and growth in captive squid, *Illex illecebrosus*, and the influence of food availability on growth in the natural population. *ICNAF select. Pap.* **6**, 15–21.

O'Dor, R. K., Forsythe, J. W., Webber, D. M., Wells, J. & Wells, M. J. 1993 Activity levels of *Nautilus* in the wild. *Nature, Lond.* **362**, 626–627.

O'Dor, R. K. & Macalaster, E. G. 1987 *Bathypolypus arcticus*. In *Cephalopod life cycles*, vol. 1. *Species accounts* (ed. P. R. Boyle), pp. 401–410. London: Academic Press.

O'Dor, R. K., Mangold, K., Wells, M. J., Wells, J. & Boucher-Rodoni, R. 1984 Nutrient absorption, storage and remobilization in *Octopus vulgaris*. *Mar. behav. Physiol.* **11**, 239–258.

O'Dor, R. K. & Webber, D. M. 1986 The constraints on cephalopods: why squid aren't fish. *Can. J. Zool.* **64**, 1591–1605.

O'Dor, R. K., Webber, D. M., Sauer, W. H. H., Roberts, M. J. & Smale, M. J. 1996 High resolution 3-D tracking of squid on spawning grounds with radio-telemetry. *Proc. 13th Internat. Symp. Biotelem.* (In the press.)

O'Dor, R. K. & Wells, M. J. 1973 Yolk protein synthesis in the ovary of *Octopus* and its control by the optic gland gonadotropin. *J. exp. Biol.* **59**, 665–674.

O'Dor, R. K. & Wells, M. J. 1978 Reproduction versus somatic growth: hormonal control in *Octopus vulgaris*. *J. exp. Biol.* **77**, 15–31.

O'Dor, R. K. & Wells, M. J. 1987 Energy and nutrient flow. In *Cephalopod life cycles*, vol. 2. *Comparative reviews* (ed. P. R. Boyle), pp. 109–133. London: Academic Press.

O'Dor, R. K., Wells, M. J. & Wells, J. 1990 Speed, jet pressure and oxygen consumption relationships in free-swimming *Nautilus*. *J. exp. Biol.* **154**, 383–396.

Parry, G. 1983 The influence of cost of growth on ectotherm metabolism. *J. theor. Biol.* **107**, 453–477.

Pascual, E. 1978 Crecimiento y alimentacion de tres generaciones de *Sepia officinalis* in cultivo. *Inv. Pesq.* **42**, 421–442.

Rodhouse, P. G. & Hatfield, E. M. C. 1990*a* Age determination in squid using statolith growth increments. *Fish. Res.* **8**, 323–334.

Rodhouse, P. G. & Hatfield, E. M. C. 1990*b* Dynamics of growth and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 Teuthoidea: Ommastrephidae. *Phil. Trans. R. Soc. Lond.* B **329**, 229–241.

Rodhouse, P. G. & Hatfield, E. M. C. 1992 Production of soma and gonad in maturing male *Illex argentinus* (Mollusca: Cephalopoda). *J. mar. biol. Ass. U.K.* **72**, 293–300.

Rodhouse, P. G. & White, M. G. 1995 Cephalopods occupy the ecological niche of epipelagic fish at the Antarctic Polar Frontal Zone. *Biol. Bull. mar. Biol. Lab., Woods Hole* **189**, 77–80.

Rubner, M. 1902 *Die Gesetze des Energieverbrauches bei der Ernährung*. Leipzig: Deuticke.

Sakurai, Y., Ikeda, Y., Shimizu, M. & Shimazaki, K. 1993 Feeding and growth of captive adult Japanese common squid, *Todarodes pacificus*, measuring initial body size by cold anaesthesia. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 467–476. Tokyo: Tokai University Press.

Saunders, W. B. 1983 Natural rates of growth and longevity of *Nautilus belauensis*. *Palaeobiology* **9**, 280–288.

Segawa, S. 1987 Life history of the oval squid, *Sepioteuthis lessoniana* in Kominato and adjacent waters of central Honshu, Japan. *J. Tokyo Univ. Fish.* **74**, 67–105.

Segawa, S. 1990 Food consumption, food conversion and growth rates of the oval squid *Sepioteuthis lessoniana* by laboratory experiments. *Nippon Suisan Gakkaishi* **56**, 217–222.

Segawa, S. 1991 Body size and oxygen consumption rate of the oval squid, *Sepioteuthis lessoniana*. *Nippon Suisan Gakkaishi* **57**, 1651–1656.

Segawa, S. 1993 Field and laboratory studies of the Japanese oval squid, *Sepioteuthis lessoniana*. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 499–511. Tokyo: Tokai University Press.

Segawa, S. & Hanlon, R. T. 1988 Oxygen consumption and ammonia excretion in *Octopus maya*, *Loligo forbesi* and *Lollijuncula brevis*. *Mar. behav. Physiol.* **13**, 389–400.

Smale, M. J. & Buchan, P. R. 1981 Biology of *Octopus vulgaris* off the East coast of South Africa. *Mar. Biol.* **65**, 1–12.

Spratt, J. D. 1978 Age and growth of the market squid, *Loligo opalescens* Berry,in Monterey Bay. In *Biological, oceanographic, and acoustic aspects of the market squid, Loligo opalescens Berry* (ed. C. W. Recksick & H. W. Frey). *Calif. Dept. Fish Game, Fish. Bull.* **169**, 35–44.

Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press. (249 pages.)

Storey, K. B. & Storey, J. M. 1983 Carbohydrate metabolism in cephalopod molluscs. In *The Mollusca*, vol. 1 (ed. P. W. Hochachka), pp. 91–136. London: Academic Press.

Tait, R. W. 1986 Aspects physiologiques de la sénescense post-reproductive chez *Octopus vulgaris*. Ph.D thesis, University of Paris VI.

Vevers, H. G. 1961 Observations on the laying and hatching of octopus eggs in the Society's aquarium. *Proc. zool. Soc. Lond.* **137**, 311–315.

Villañeuva, R. 1992 Continuous spawning in the cirrate octopoda *Opistoteuthis agaizii* and *O. vossi* – features of sexual maturation defining a reproductive strategy in cephalopods. *Mar. Biol.* **114**, 265–275.

Ward, P. D. 1987 *The natural history of* Nautilus. Boston: Allen and Unwin.

Webber, D. M. & O'Dor, R. K. 1985 Respiration and swimming performance of short-finned squid, *Illex illecebrosus*. *NAFO Sci. Coun. Stud.* **9**, 133–138.

Webber, D. M. & O'Dor, R. K. 1986 Monitoring the metabolic rate and activity of free-swimming squid with telemetered jet pressure. *J. exp. Biol.* **26**, 205–224.

Wells, M. J. 1978 *Octopus: physiology and behaviour of an advanced invertebrate*. London: Chapman and Hall.

Wells, M. J., O'Dor, R. K., Mangold, K. & Wells, J. 1983*a* Diurnal changes in activity and metabolic rate in *Octopus vulgaris*. *Mar. behav. Physiol.* **9**, 275–287.

Wells, M. J., O'Dor, R. K., Mangold, K. & Wells, J. 1983*b* Oxygen consumption in movement in *Octopus*. *Mar. behav. Physiol.* **9**, 289–303.

Wells, M. J., O'Dor, R. K., Mangold, K. & Wells, J. 1983*c* Feeding and metabolic rate in *Octopus*. *Mar. behav. Physiol.* **9**, 305–317.

Wells, M. J. & Wells, J. 1959 Hormonal control of sexual maturity in *Octopus*. *J. exp. Biol.* **36**, 579–588.

Wells, M. J. & Wells, J. 1990 Urine production in *Octopus vulgaris*. *J. exp. Biol.* **152**, 383–385.

Wells, M. J., Wells, J. & O'Dor, R. K. 1992 Life at low oxygen tensions: the behaviour and physiology of *Nautilus pompilius* and the biology of extinct forms. *J. mar. biol. Ass. U.K.* **72**, 313–328.

Wieser, W. 1994 Cost of growth in cells and organisms; General rules and comparative aspects. *Biol. Rev.* **68**, 1–33.

Yang, W. T., Hixon, R. F., Turk, P. E., Krejci, M. E., Hulet, W. H. & Hanlon, R. T. 1986 Growth, behaviour and sexual maturation of the market squid, *Loligo opalescens* cultured throughout the life cycle. *Fish. Bull.* **84**, 771–798.

Yarnall, J. L. 1969 Aspects of the behaviour of *Octopus cyanea* Gray. *Anim. Behav.* **17**, 747–754.

Zann, L. P. 1984 The rhythmic acitivity of *Nautilus pompilius* with notes on its ecology and behaviour. *Veliger* **27**, 19–28.