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A LOWER LIMIT TO ADULT SIZE IN COLEOID CEPHALOPODS: ELEMENTS OF A DISCUSSION

S. v. Boletzky

CNRS, Observatoire Océanologique, Laboratoire Arago, F-66651 Banyuls-sur-Mer, boletzky@obs-banyuls.fr

ABSTRACT

The smallest living cephalopods are coleoids weighing less than 1 gram when adult (the pygmy squid *Idiosepius* spp., several pygmy species of the genus *Octopus*), and there are slightly larger species among sepiolid (*Sepiola* spp.) and loliginid (*Pickfordiateuthis* spp.) squid, sepiid cuttlefish (e. g. *Sepia pulchra*); moreover there are dwarf males in three pelagic octopod genera (*Argonauta*, *Tremoctopus*, *Ocythoë*). A common biological feature of these small species are short life-spans, the minimum being 3 months in *Idiosepius*. Small adult size of a female, along with a short life-span, limits individual fecundity. The adaptive responses to this limitation vary widely among species or groups. The most striking difference appears in the respective egg sizes. In pygmy squid, an individual ovum measures less than 1 mm in diameter, whereas in pygmy octopus, ovum sizes vary between 5 and 12 mm depending on the species. In both cases, maturation and release of eggs covers several weeks. If *Idiosepius* demonstrates that very small eggs giving rise to very small hatchlings permit rapid attainment of small adult size, within a very short life-span, the high fecundity of *Idiosepius* suggests massive juvenile mortality, probably relating to the planktonic post-hatching phase. A suggestive difference in fecundity appears within the octopodids: *Octopus fitchi* has a planktonic post-hatching phase and has a higher fecundity than pygmy species devoid of a planktonic phase.

1. INTRODUCTION

Two decades after the major reviews by Peters (1983) and Schmidt-Nielsen (1984), the issue of body size in animal ecology and related questions of adaptation continue to sustain interest in the underlying evolutionary mechanisms. Blanckenhorn (2000) reviewed the selective advantages of small body size in various organisms and focused attention on the viability disadvantages of large body size and on sexual selection against large body size. It is well known that phenotypic plasticity may allow some dwarfism, or stunting, especially in isolated populations submitted to certain environmental conditions, e. g. in landlocked forms of salmonids and other fish (Roff 1992: 235). The examples from bony fishes are of potential interest to evolutionary considerations on cephalopods, as cephalopods and fish appear to share some consequences of paleo-ecological interactions (Packard 1972, O'Dor & Webber 1986). When small adult size has become a species-specific, genetically determined feature, however, the foregoing body size evolution has to be considered beyond the domain of phenotypic plasticity (Maurer *et al.* 1992). The aim of this paper is a reassessment of some features of reproduction and development relating to the evolution of very small adult size in different coleoid cephalopods.

Given the large size of cephalopod eggs, the advantages of a small adult size are only available at the condition of an extended individual spawning activity accommodated in the group-typical scope of terminal reproduction (Boyle & Boletzky 1996). Until recently, the pygmy squid *Idiosepius pygmaeus*, which measures about 10-15 mm in dorsal mantle length (ML) and weighs less than 1 gram (Lewis & Choat 1993), was considered to represent the lower end of the coleoid size spectrum. Chotiyaputta *et al.* (1991)

showed that adults of *Idiosepius thailandicus* are even smaller than *I. pygmaeus*. The issue broadened when Norman (1997-98, 2000) called attention to the fact that a very different assortment of benthic cephalopods have similar small adult sizes, namely various pygmy octopuses some of which are also fully mature at weights less than one gram. Only slightly larger sizes are observed among the loliginid squids, namely in *Pickfordiateuthis pulchella* (Voss 1953), among the bobtail squids of the genus *Sepiola* (Naef 1923), and among the sepiid cuttlefish, e. g. *Sepia pulchra* of the so-called Hemisepius species group (Roeleveld & Liltved 1985).

A peculiar case that has to be considered separately are the dwarf males in the closely related pelagic octopod genera *Argonauta*, *Tremoctopus*, *Ocythoë* (Boletzky 1999, 2002). Males of *Ocythoë* are somewhat larger than those of the first two genera and differ in that they use empty tests of *Salpa* as floating homes (Naef 1923).

2. ADULT LIFE STYLE IN COLEOIDS

Coleoids may be very active nektonic swimmers, slow hoverers (sometimes macro-planktonic rather than nektonic), or bottom-dwelling crawlers/sitters/diggers (nevertheless being able to swim up for feeding or escape).

The small loliginid squid *Pickfordiateuthis pulchella* (Brakoniecki 1996) lives as an active swimmer in shallow waters, close to the bottom, whereas oegopsid squids (Laptikhovsky 1999) [and the dwarf males of *Argonauta*, *Tremoctopus* and *Ocythoë*] are fully pelagic. In contrast to these variants of nektonic life style, the pygmy squid *Idiosepius* spp. (Nabhitabhata 1998), the sepiid cuttlefish, e. g. *Sepia pulchra*, and all the Octopodidae including pygmy octopuses are bottom dwellers. However, there are important differences between their respective benthic behaviours. *Idiosepius* spp. adhere (dorsally) to e. g. eelgrass blades (*Zostera*) or fronds of *Ulva* (Fig. 1, Sasaki 1923). *Sepia pulchra* can adhere (ventrally) to hard substrates (Boletzky & Roeleveld 2000), whereas both the sepiolid squids and the octopodids use their suckers to attach themselves to hard substrates (Fig. 2), and most of them also bury in soft substrates (Boletzky 1996).

3. POST-HATCHING LIFE STYLE IN COLEOIDS

Newly hatched cephalopods in general tend to adopt the adult life style as far as that is possible in very small hatchlings. Two exceptions are known: the pygmy squid genus *Idiosepius*, and a large number of octopodid species in genera like *Octopus*, *Scaeurgus*, *Eledone* (Boletzky 1977). Newly-hatched pygmy squid measure about 1 mm ML and start out as planktonic young (Nabhitabhata 1998), they grow to larger size, while tentacles develop, before they adopt the adult life style. In octopodids, the general rule is that species producing eggs smaller than 10% of adult ML have young which live as active swimmers in the plankton until their short arms grow longer than the mantle and their body size reaches several times that of a hatchling. Conversely, octopodids hatched from eggs bigger than 10% adult ML, as those shown in Fig. 2, are long-armed crawl-away young which adopt the adult mode of bottom life immediately after hatching (Boletzky 1974). This seems to be the predominant mode in pygmy octopuses (see *4.2.2.* for the exceptional case of *Octopus fitchi*).

4. SPAWNING MODES AND CONSTRAINTS ON GAMETE PRODUCTION AT VERY SMALL SIZE

Male gametes (spermatozoa) are so small that even minute testicular sizes are adequate for mass production of sperm, as demonstrated by the dwarf males of *Argonauta* and allied genera (Naef 1923). Yet sperm production is always protracted regardless of male size. Constraints due to size limitations in very small males might be more tangible in the sperm packing and transfer systems (spermatophoric glands, hectocotylus) than in the gamete production system (testis) (Boletzky 2001). In contrast, female gametes (ova) are so large that ovarian space limitations in small individuals are likely to generate higher constraints than the size limitations on the egg packing system (oviducal and nidamental glands producing protective envelopes). Therefore, only the females of pygmy cephalopods are discussed here.

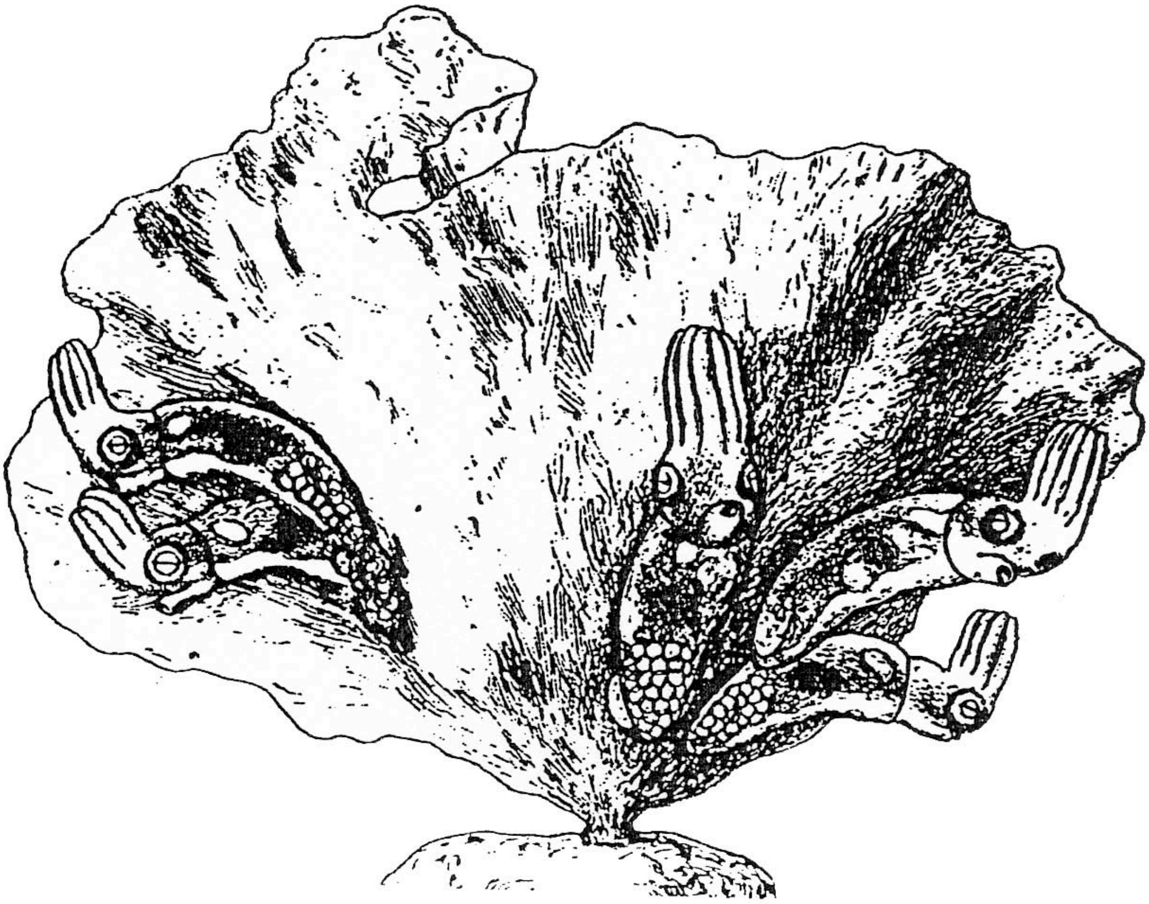

Fig. 1 Adults of *Idiosepius paradoxus*, in their typical resting position (arms raised), adhering to the underside of a frond of *Ulva* sp. by means of their dorsal mantle sucker (from Sasaki 1923; there given as *I. pygmaeus*). Note the concentrations of eggs in the posterior part of the mantle in the lower two individuals and in the female at the upper left (ca 3x nat. size)

4.1. Decabrachia

The large size of an ovary containing mature ova can be recognized in a sketch (Fig. 1) showing adult *Idiosepius paradoxus* as observed by Sasaki (1923; species originally given as *I. pygmaeus*). Natsukari (1970), Nabhitabhata (1998) and Kasugai (2000) described egg laying in different species of *Idiosepius* and noted some interesting spawning variants within and among species. The eggs are very small (ca 0.9 x 0.7 mm in *I. pygmaeus*), but compared to the small size of the reproductive organs, they are so large that only a limited number of them can be stored in the ovary and oviduct. Hylleberg and Nateewathana (1991a, b) described the general anatomy of the visceral mass, including the sexual duct glands in both sexes, showing how large the nidamental glands are in females. Lewis and Choat (1993) published some illustrations of the histological aspect of ovaries with immature and mature eggs, which fill the cavity occupying the posterior part of the female visceral mass.

Lewis and Choat (1993) provided evidence that female *Idiosepius pygmaeus* kept under optimal aquarium conditions providing a large food supply spawn massively during more than two weeks: "Oocyte synthesis and maturation occur continuously after sexual maturation has been reached. Senescence and death are not related to an exhaustion of reproductive potential. On average, captive female *I. pygmaeus* with access to unlimited food produced 640 eggs in 11 batches over 18 d. When reproductive output was expressed as a ratio of dry female body weight, on average, specimens had incorporated five times their body weight into eggs and egg coatings". These authors found very high maxima in some individuals: "Remarkably, the maximum observed output was more than double these averages. Two sepioids laid more than 1150 eggs, while one specimen laid 1215 eggs in 12 batches over the course of 25 d. The greatest number of egg batches laid by a completely satiated sepioid was 19”. The final adult phase is preceded by post-hatching development to maturity that takes 1.5 to 2 months (Jackson 1988). Prior to this post-hatching growth phase, about two weeks of embryonic development have elapsed (Natsukari 1970, Yamamoto 1988). This sequence makes up a life cycle that covers about 3 months.

Compared to such a high reproductive output, the roughly 100 to 200 eggs produced by some small sepiolid squids within a life cycle of about 6 months (egg to egg) represent a relatively modest performance (Gabel-Deickert 1995). As will be shown below (**5**), this difference can be viewed in relation to post-hatching life style.

Nothing is known about the reproductive output of *Sepia pulchra* and other small cuttlefish of the Hemisepius group. As for the smallest teuthid squids, fecundity estimations exist only for species of *Abraliopsis*, in which Laptikhovsky (1999) found potential fecundities of several thousand eggs per female.

In the representatives of the Decabrachia considered up to here, a common feature of female organs is the presence of paired nidamental and accessory glands, in addition to the oviducal glands present in all coleoid cephalopods. Only in some enoploteuthid squids the nidamental glands are lacking and the very large oviducal glands form a likely “replacement”, as described by Naef (1923). Whatever the specific modifications, oviducal and nidamental glands produce gelatinous wrappings as a protection for the eggs, which are abandoned by the female after spawning.

4.2. Octobrachia

4.2.1. Cirroctopoda

That encapsulated eggs are abandoned after spawning is true also in the finned octopuses of the order Cirroctopoda, one of the two orders of the Octobrachia (which lack discrete nidamental glands, their likely homologs being incorporated as parts of the oviducal glands). No pygmy cirroctopods are known to date.

4.2.2. Octopoda

In all the finless octopuses of the order Octopoda, the paired oviducts of the females have oviducal glands similar to the gland of the unpaired oviduct in cirroctopods. But in contrast to the cirroctopods, the secretory product of the oviducal glands in octopods does not wrap the eggs entirely, it only embeds the extremity of the chorion, which is drawn out into a stalk (opposite the micropyle). These essentially unprotected eggs are actively brooded by the spawning female until the young hatch. Some of the pelagic octopods are rather small as adults, e. g. *Eledonella pygmaea* of the family Bolitaenidae, but duration of spawning and total fecundity are not yet known (Hochberg *et al.* 1992).

Among the bottom-living Octopodidae, the smallest species (the true pygmy octopuses *sensu* Norman) belong to the genus *Octopus* (Norman, 2000). Of these, *Octopus chierchiae* is the only species that has been studied throughout its reproductive phase. Rodaniche (1984) made aquarium observations (temperatures ranging 25-29°C) on seven individuals, 4 females and 3 males, which were sexually mature when captured. All the females spawned between 10 and 50 days after capture, and all the spawned eggs measured ca 3.8 x 1.2 mm. One female spawned three times fertile eggs. A few days before laying the first and second batch, respectively, she had mated with one of the males. The third batch was laid 83 days after the second mating. This female died nearly nine months after capture, about two weeks after the last young hatched. One female spawned three fertile and one unfertile batch (the second one, consumed after one month) and died about eight months after capture, two weeks after the last young of the fourth batch of eggs hatched. Invariably the hatchlings were benthic “crawl-away” young measuring 3.5 mm ML.

Apart from temporary cessation of feeding during the days when the young hatched out, the brooding female *O. chierchiae* fed regularly. The individuals surviving for more than seven months grew to sizes about two to three times the ML they had at the time of capture. The female which spawned four times measured 8 mm ML at capture, 24 mm ML at death. The actual size of the eggs (close to 4 mm) did not change with time. Thus relative egg size, expressed as a percentage of adult ML, decreased from an egg length index of 44 to an index of 15. But the number of eggs laid in each batch increased from an initial 6, through 13 (second, unfertile batch) and 20 (third batch) to a final complement of 30 eggs, i. e. a total of 69 eggs were produced. The female which spawned three times grew from 10 mm ML to 25 mm ML and produced a total of 70 eggs (13 + 22 + 35).

The relative egg size at the outset of spawning in *O. chierchiae* is very high. It may be even higher in the likely twin species *O. zonatus* from the Caribbean coast of Columbia (Voss 1968). Similar size relations exist in *O. micropyrsus*, which grows to 25 mm ML. The eggs of this species measure 10-12 x 5-6 mm (Hochberg & Fields 1980). Haaker (1985) observed and photographed a female with a batch of 4 eggs in her den. Probably due to disturbance, one animal hatched out and proved to be a large crawl-away young with long arms (close to 10 mm ML according to the original document). The very large size of the eggs compared to the body size of the female (Fig. 2) suggests that individual eggs are laid at intervals of several days thus allowing submature ovarian eggs to reach their full size. Hochberg (pers. obs. in Hochberg *et al.* 1992) observed batch sizes of 25 to 45 eggs. To produce such large batches, a female must spawn over several weeks.

A different egg size relationship exists in *Octopus fitchi*, another very small species. Adult females reach a size of 30 mm ML and produce 150-300 eggs measuring 5 x 2 mm, which must take many days to be laid (Hochberg 1980, Hochberg *et al*. 1992). According to Voight (pers. comm. 1986) the adults may reach a size of 36 mm ML. The relative egg size (egg length index) thus is close to 20% according to Hochberg, about 14% according to Voight. From what is known of other octopodids, one would expect that such relatively large eggs (with an egg length index higher than 10) release benthic crawl-away young (Boletzky 1974). This is not what happens in this species. The hatchlings of *O. fitchi* are planktonic (Hochberg 1980, confirmed by Voight pers. comm. 1986).

5. FECUNDITY AND POST-HATCHING MORTALITY: A PRECARIOUS BALANCE

The apparently exceptional condition of *Octopus fitchi* is interesting in several respects. A close look at the planktonic hatchlings reveals some suggestive differences when compared to planktonic hatchlings of other octopodids. They measure 2.0 mm ML, a body size that is very small for an animal hatched from an egg that measured about 5 mm when laid (to give a more typical example: *Octopus salutii* produces eggs of the same size, and the hatchlings have an ML of at least 3.5 mm). Clearly this small body size is morphometrically compensated by a development of robust arms. Each arm has 14-16 suckers, more than any planktonic hatchling of comparable size (Gabe 1975, Boletzky 1977). The arms of a "young posthatchling" measuring 2.0 mm (Hochberg *et al.* 1992, Fig. 263e) indeed appear strikingly thicker and longer than the arms of any other planktonic young octopus shortly after hatching (where normally arms are about 50% of ML). These peculiarities suggest that *O. fitchi* represents an intermediary situation, with hatchlings being "quasi crawl-away" young in terms of morphometrics (Boletzky 1977). If they had about 20 suckers on each arm, one would readily place them with benthic young octopuses. That a young octopus with such a well developed arm crown has a planktonic life style is surprising, but it also recalls the fact that undeniable crawl-away young may sometimes be

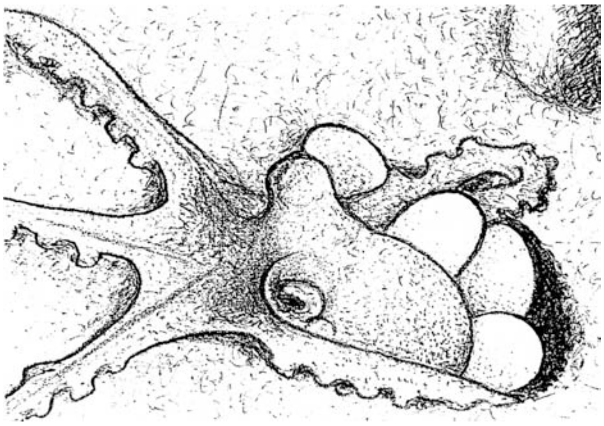

Fig. 2 Brooding female of *Octopus micropyrsus*, with 4 eggs attached inside her den by chorion stalks that are not visible (drawn from a photograph by Haaker 1985). Note the very large size of these eggs (containing embryos at late developmental stages). The situation shown in the original photograph was described as an accidental exposure of the animal, since the diving assistant "had broken a short horizontal mudstone pinnacle riddled with piddock clam bores, and had found a small octopus guarding eggs at the inner end of an empty piddock hole" (ca 2x nat. size)

excellent swimmers or drifters (Boletzky 1977).

A striking difference between *O. fitchi* and *O. chierchiae*, which are comparable in both adult size and egg size, is the respective fecundity. The much higher fecundity of *O. fitchi* of course suggests a higher juvenile mortality in planktonic young, provided that *O. fitchi* and *O. chierchiae* have comparable longevities. The data of Rodaniche (1984) suggest a longevity close to 1 year in *O. chierchiae*, this would plead for a position far below the D line in Fig. 3. It seems very unlikely that *O. fitchi* has a greater longevity, so a higher mortality can be assumed. A conceivable scenario would be something close to Cx in Fig. 3, with a life-span of only about 6 months.

That juvenile mortality in planktonic young cephalopods may be very high can be inferred from the high fecundity of *Idiosepius*. The adult life style probably minimizes exposure to potential predators (Sasaki 1923, Moynihan 1983), so the greatest proportion of the several hundred hatchlings produced by a female is likely to die during the first weeks of planktonic life. Assuming a mortality on the order of 95% for the first month after hatching, the offspring of a single female would have dwindled away to about 30 advanced juveniles that remain after 1 month. This number of individuals would be sufficient to complete a life cycle of about 3 months if mortality in advanced juveniles and pre-spawning adults drops to about 60% per month. Such a decrease in mortality rates seems more likely than a 90% mortality per month throughout post-hatching life (cf. "I?" close to line A in Fig. 3).

In small sepiolid squids, a series of field samples interpreted on the basis of growth rates observed in aquarium cultures suggested an average monthly mortality of 50%, but the actual mortality rates appeared lower than average during the first two months after hatching (Boletzky 1983). This relates well to the fact that sepiolid hatchlings are already benthic and hide in sandy bottom during the day. Thus small sepiolids may maintain a cycle covering about 6 months with less than 100 hatchlings per female. Gabel-Deickert (1995) observed an overall mean fecundity of 100 eggs per female in *Sepiola affinis*, slightly more in *S. intermedia*, with individual fecundities ranging from 25 to 349 in *S. affinis*, 47-184 in *S. intermedia*, spawning lasting about one month, rarely up to two months under aquarium conditions. Although body size of the female generally continues to increase after the onset of spawning, this terminal growth adds only a few mm ML (Boletzky 1975). It is noteworthy that the same is true in the much larger cuttlefish *Sepia officinalis* when spawning begins at the minimal size allowing sexual maturity (Boletzky 1987).

Although cephalopod embryos are well protected by elaborate mechanisms of encapsulation or by active brooding (Boletzky 2001), very little is known about actual pre-hatching mortality, especially with regard to predominant causes and ranges of variation under natural conditions. Such uncertainties must be taken into consideration for an assessment of post-hatching mortality in relation to fecundity. Thus a simple graphical representation as in Fig. 3 (which assumes embryonic mortalities close to zero) may need to be accompanied by different scenarios considering various causations of embryonic mortality, which may differ with short or long spawning phases, high or low environmental temperatures, high or low exposure to overall disturbance and/or predation.

6. DISCUSSION

The undeniable flexibility of adult size in cephalopods is not a unique phenomenon. The cephalopodan feature of uninterrupted terminal reproduction notwithstanding, this flexibility reminds one of what Peters (1983: 129) observed in other poikilotherms: "Unlike homeotherms, many poikilotherms do not have a fixed maximum size but continue to grow throughout their lives". When terminal growth is rather inconspicuous (as in the small sepiolids), there is still some, though not much, additional space becoming available for the production and storage of ova. In contrast, *Octopus chierchiae* adds a large volume of ovarian space during its final growth phase, as can be seen from the increase in batch size (the size of individual ova remaining unchanged). In an evolutionary perspective, this large variation raises the question of the most likely adult size and egg size in the immediate ancestor of the species considered, and it also raises questions about stability versus variation of egg size between speciation events (Boletzky 1997).

Whatever the special evolutionary history that has led to extremely small adult sizes in different cephalopod lineages, a common denominator seems to

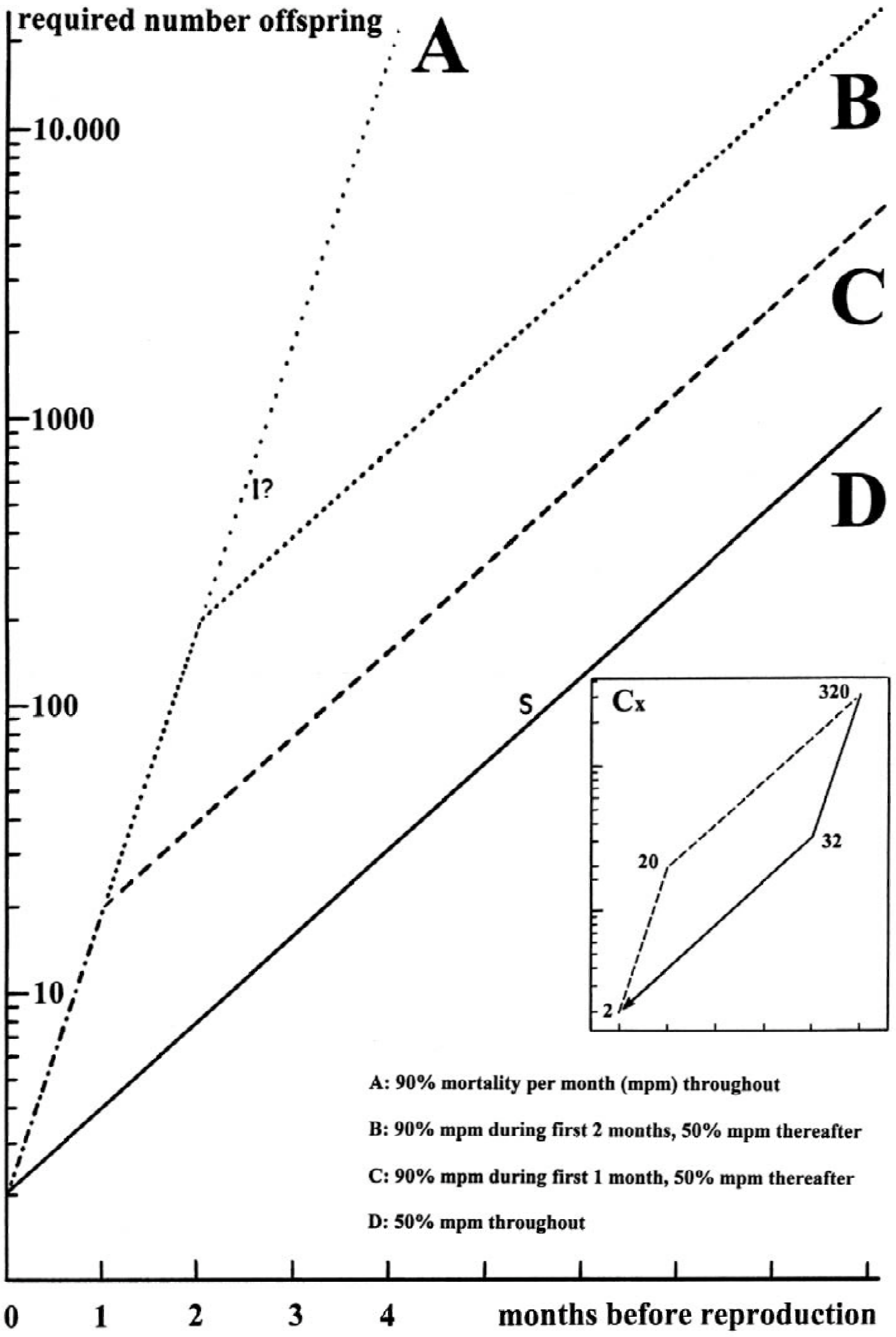

Fig. 3 A diagram illustrating the link between fecundity and post-hatching mortality for different life-spans, considering that one female individual must produce enough offspring to insure the survival, on an average, of two individuals (one of each sex) to reproduce. If embryonic mortality is considered negligible (a questionable simplification, as pointed out at the end of section **5**), hatchling numbers are close to the respective number of eggs produced by a spawning female. The mortality rate A (90% mortality per month [mpm]) seems unlikely for large species with life-spans greater than a few months (to give an example, 2 million hatchlings would be required in a post-hatching life-span of 6 months). "I?" indicates a conceivable position for *Idiosepius pygmaeus*; however, this situation appears unlikely for reasons given in section **5**. B may represent various octopus species having a rather long planktonic phase with high mortality; under such conditions a post-hatching life-span of 12 months (2 months 90% mpm + 10 months 50% mpm) would require about 200,000 hatchlings at the outset. C represents a similar pattern, but having a shorter phase of high mortality; an example (Cx) is given in the inset, possibly corresponding to the condition of *Octopus fitchi* (see **5**). With regard to the (artificial) trajectories of B and C, one should note that the likely higher mortality during the first month after hatching (solid line and arrow in Cx) has the same numerical effect as the (unlikely) inverse course showing a higher mortality during the last month before reproduction (broken line in C and Cx). "S" indicates the approximate position of *Sepiola* spp. (see **5**)

be the extension of oogenesis, which allows production of more ova than a very small body can hold at one time. Whether individual eggs are large or small is a matter of the respective adaptive value of one or the other ovum size within a given longevity for a given life style in a given habitat. The smallest ovum sizes known in living coleoids (ca 0.8 mm) suggest that much smaller sizes would not be viable, probably because of developmental constraints imposed by the conserved cephalopodan program of embryogenesis (Boletzky 1989). Larger eggs have greater potential for yolk storage, which may improve survival ability (Goulden *et al.* 1987). The longer the individual reproductive activity, the more critical the effects of "bet hedging" (Stearns 1992) relating to the residual reproductive value and the "cost of reproduction" (Calow 1979).

Given the uniform pattern of cephalopod embryogenesis, which is related to strong yolk accumulation, even the smallest known eggs are so large relative to a very small adult (*Idiosepius* spp.) that the instantaneous holding capacity of the ovary may be insufficient to counterbalance a likely high post-hatching mortality (cf. "balanced mortality" hypothesis, Price 1974). If early mortality is due mainly to high exposure to predators during planktonic life, one may wonder why egg size has not increased for development of a benthic juvenile similar to those of small sepiolid squids. A similar question may be asked relating to *Octopus fitchi*: why does the "virtually benthic" hatchling live in the plankton where mortality is likely higher than on the bottom ? The reason for that is not known, but it seems at least conceivable that the planktonic life style offers some assets (e. g. higher food availability for extremely small, juvenile predators) that may or may not be honored by natural selection. Whether one or the other solution has been achieved should also depend on the ancestral condition from which adaptive improvements can be derived. Put simply, what is extant is what has escaped extinction. Why it has escaped extinction can only be inferred from data viewed in the framework of life history theory, which attempts to explain patterns in reproductive effort: "It assumes that increasing effort yields the benefits of increased offspring production and the costs of decreasing chances of parental survival and that selection has favored an optimization of levels of effort relative to these costs and benefits" (Winkler & Wallin 1987).

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