Antarctic Science 6 (2): 139–142 (1994)

Embryonic development of cephalopods at low temperatures

S.v. BOLETZKY

Observatoire Océanologique de Banyuls, URA 117 CNRS, Laboratoire Arago, 66650 Banyuls-sur-Mer, France

Abstract: No information is available on the embryonic development of Southern Ocean cephalopods. Estimations of developmental times can only be made by extrapolation using data from other geographical areas. Based on known relationships between environmental temperature and embryonic development time, it appears that below 5°C even the smallest squid eggs measuring 0.6–1.0 mm in diameter need one to two months to develop to hatching. At *c.* 2°C, the embryonic development of these small eggs would probably cover between three and five months. Very large octopod eggs are known to develop over time spans of at least one year. Protection of the developing embryos either by long-lasting capsules laid at appropriate spawning sites, or by active 'brooding' (incirrate octopods) is required for embryonic survival and hatching success. The physiological conditions controlling the onset of hatching at very low temperatures are unknown; postponement of hatching appears to be common in cold waters.

Received 5 July 1993, accepted 2 September 1993

Key words: Cephalopoda, spawning, development, embryos, hatching, coldwater

Introduction

Antarctic cephalopods spend part or all of their life at very low temperatures, much like Arctic and abyssal cephalopods (Rodhouse & Clarke 1985, Rodhouse *et al.* 1992). They must be cold adapted and, for the lowest temperatures experienced, they probably depend on compensating mechanisms that prevent the physiological processes from coming to a standstill (Johnston 1990, Clarke 1991).

The question whether such compensating mechanisms exist in the embryo of cold adapted cephalopod species remains to be answered by future studies in developmental physiology. The importance of this question for cold water ecology and population studies becomes clear when the embryonic phase is included in calculations of life cycles; in some species it covers a few weeks, in others several months, or a whole year, or more. At the population level, the obvious consequences of a long embryonic phase can be further magnified in the age structure of a population by the occurrence of multiple spawning.

Very little is known about embryonic development of cephalopods at very low temperatures; that it takes about one year from the zygote stage to hatching in *Bathypolypus arcticus* at temperatures below 10°C (O'Dor & Macalaster 1983) is one of the rare data available. A developmental duration of 10–11 months was observed in *Octopus conispadiceus* at temperatures ranging from 2.2–17.2°C (Ito 1983). A similar time span (*c.* 11 months) was recorded in the embryo of *Nautilus belauensis* at temperatures higher than 18°C (Arnold *et al.* 1990) but it seems likely that *Nautilus* development takes much more than one year at the lower temperatures of deep water spawning sites. The examples mentioned above illustrate the fact that both 'brooding' (*Bathypolypus*, *Octopus*) and 'non-brooding' (*Nautilus*) types of reproductive behaviour are compatible with the requirements of extremely long embryonic development (Boletzky 1986a). In the first instance, which represents the spawning mode of the 'incirrate' octopods (Octopoda Leach, 1818 *sensu* Young 1989), survival of the brooding female to the end of embryonic development is required for hatching success (because in the absence of the female the embryos, which are surrounded only by the egg chorion, are rapidly suffocated by fouling organisms). In the second instance, the essential requirements of embryo protection are met by the production of protective egg cases and the capacity of the spawning female to either release them in midwater far from coastlines, or to deposit them on an appropriate substrate. These spawning sites reflect ecological conditions that may be compromises between conflicting requirements; for example, spawning sites must guarantee sufficient water movement for oxygenation of the eggs, yet must be sheltered from strong wave action.

This paper briefly surveys embryological aspects and the ecological implications of development at low temperatures in cephalopods. Experimental approaches to the developmental physiology of cephalopod embryos at low temperatures are also discussed.

Rate of development as a function of temperature

The inverse relationship between environmental temperature and duration of embryonic development in marine poikilotherms has been known for a long time (Clarke 1982, Johnston 1990, Naef 1928).

A comparison of rates of development at different (constant) temperatures in six common cephalopod species illustrates

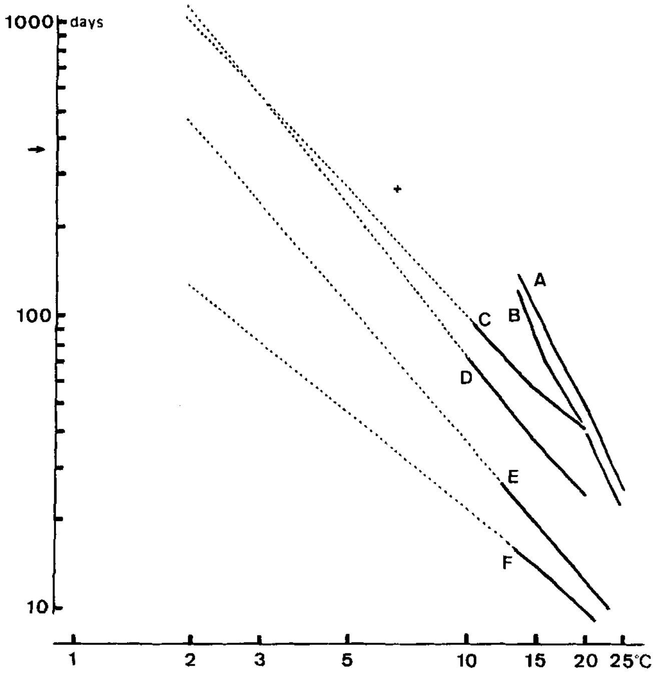

Fig. 1. Length of embryonic development at different temperatures, in double logarithmic representation. The solid lines are copied from Boletzky (1987, fig. 2.1 a) and represent the following species: A=*Sepia officinalis*, B=*Octopus vulgaris*, C=*Sepiola robusta*, D=*Loligo vulgaris*, E=*Loligo pealei* (from Summers 1983), F=*Illex illecebrosus* (from O'Dor 1983). Dotted lines are extrapolations, + represents data from Summers & Colvin (1989) on *Rossia pacifica*. The arrow at left marks one year on the time axis.

this common rule (Boletzky 1987) and also draws attention to considerable variation between species (Fig. 1). This variation is related to the respective size of the eggs. Thus in *Illex illecebrosus*, the egg measures *c.* 0.9 × 0.7 mm in diameter and hatches within about 0.5 month at 13°C (O'Dor 1983). At the same temperature, eggs of *Loligo pealei* (1.6 × 1.0 mm) take nearly 1 month (Summers 1983), and eggs of *Loligo vulgaris* (2.2 × 1.6 mm) about 1.5 months to hatching (Boletzky 1987). *Sepiola* eggs of a similar size (2.3 × 1.8 mm) show a much slower development with about 2.5 months to hatching at 13°C, and 2 months at 15°C (Boletzky 1983). The slightly larger eggs of *Sepietta oweniana* develop to hatching in about 2 months at 13°C, 2.5 months at 10°C and 5.5 months at nearly 7°C (Bergstrom & Summers 1983). The much larger eggs of the sepiolid *Rossia macrosoma* (6.5 x 5.0 mm) take more than three months to hatch at 15°C (Boletzky & Boletzky 1973). In *Rossia pacifica*, which has eggs similar in size to those of *R. macrosoma*, embryonic development lasts from 4.5–5 months at 10°C, and at winter temperatures of 6–7°C, viable embryos with yolk reserves have remained unhatched for up to nine months after spawning (Summers & Colvin 1989).

Extrapolation of the solid lines in Fig. 1 to lower temperatures (dotted lines) suggests hypothetical developmental times ranging from *c.* 1–6 months at 5°C and *c.* 4–12 months at 2°C for decapodan species with egg sizes between about 1 mm and 2.5 mm. No extrapolation is attempted for *Sepia officinalis* and *Octopus vulgaris;* indeed no sepiid has ever been observed in cold water.

Neither *Octopus* nor other Octopodinae species with very small eggs (similar to those of *Octopus vulgaris*) appear to live in cold water. Apart from the previously mentioned *Octopus conispadiceus*, which produces very large eggs (see Hochberg *et al.* 1992 for a review of egg sizes in octopods), it appears that *Octopus dofleini* can spawn at water temperatures around 5°C but the eggs then need one and a half years to develop to hatching (Kubodera 1991). This is surprising since the eggs of *O. dofleini* are not extremely large; they measure 6–8 mm in length and (given the large adult size) belong to the category of 'relatively small' eggs developing into planktonic hatchlings (Boletzky 1987).

Flexibility of the hatching stage

In nearly all cephalopods in which embryonic development has been studied, the hatchlings have some yolk (in the so-called inner yolk sac) when leaving the egg case (Boletzky 1987). This nutrient reserve is sufficient to keep the young animal alive for some time after hatching if no food is available. The greater the volume of yolk left, the longer the duration of the reserves; the lower the environmental temperature, the slower the absorption of the remaining yolk. Normally hatched *Rossia macrosoma* survived for nearly three months without food when maintained at a temperature of 8–9°C (Boletzky, unpublished results). In developmental terms, this situation may be similar to the effect of postponed hatching at very low temperature as observed in *Rossia pacifica* (Summers & Colvin 1989). Within the range of temperature adaptation of cephalopod species, there seems to be a generalized developmental tendency to postpone hatching when water temperatures are close to the lower range limit (Boletzky 1987).

For the upper end of the temperature range the opposite tendency prevails, so that hatching occurs at the earliest possible moment, as soon as the outer yolk sac is empty. So far all observations suggest that hatching prior to complete emptying of the outer yolk sac is premature. However, in octopus hatchlings, the possibility exists that prematurely hatched animals ingest the remaining outer yolk sac, so the nutrient reserve is not wasted (Opresko 1974). This behaviour could provide an important 'emergency exit' for the offspring when a brooding female dies before the young animals hatch out normally. In cold environments such a mechanism would allow the organism to bypass the long terminal phase of 'normal' yolk absorption, which is particularly long in embryos developed from large eggs.

The pre-hatching phase is characterized by a peculiar process, which was first described by Portmann (1926).

Except in the two octopodid species *Octopus maya* and *Eledone moschata* (Boletzky 1975), cephalopod embryos shift the yolk from the outer to the inner yolk sac during late embryonic stages. This yolk transfer is concomitant with (but independent of) the continuing yolk absorption. The latter is achieved by the yolk syncytium, which delivers the nutrients to the body tissues via the blood (Boletzky 1975). Yolk transfer is not necessary in the embryos of many oegopsid squids because they never have a fully formed outer yolk sac (Naef 1928, O'Dor 1983, Arnold & O'Dor 1990).

Considering the obvious flexibility of 'yolk management' in cephalopod embryos during the later embryonic stages, incorporation of a large yolk reserve in the inner yolk sac or in the digestive system (crop of octopus hatchlings) would indeed provide a means to shorten the embryonic phase at low temperatures, as suggested above. However, this mechanism has thus far been observed only at relatively high temperatures in cephalopods of temperate and tropical zones. The examples cited from the sepiolid genus *Rossia* indeed suggest that at low temperatures the opposite tendency exists, with lengthening of the pre-hatching phase. Although this tendency seems surprising, it might have a regulatory function where food supply shows seasonal fluctuations (cf. Clarke 1982).

Protection of the embryo

Since at low temperatures cephalopod embryos take a long time to develop, longterm protection is vital. In the cold water octopodids (mostly from subfamilies Eledoninae and Bathypolypodinae; see also Voss 1988) the embryos are protected by the 'brooding' mother individual. The example of *Bathypolypus arcticus* (O'Dor & Macalaster 1983) demonstrates that this phase may cover one half of post-hatching life (ie. one third of the whole female life cycle). This situation is probably not exceptional since all cold water octopuses eggs are large, generally larger than the eggs of *Octopus dofleini* mentioned earlier (Kuehl 1988).

In all the decapods and in the cirrate octopods the embryos develop inside egg cases. In the sepiolid subfamily Rossiinae and in all the cirrate octopods the outermost envelope becomes a rigid egg shell soon after spawning (Boletzky 1982, 1986a) or during spawning (in cirrates). Aquarium observations indicate that *Rossia* egg shells do not decay after hatching nor are they colonized by sessile organisms (Boletzky, unpublished observation). Such a highly resistant egg case allows the embryo to live for many months like a sessile organism!

In contrast, all squid egg masses, whether they are structured capsules or amorphous jelly masses (as in the Ommastrephidae), tend to decay rapidly after hatching, and they are often colonized by other organisms while the embryos are developing. The protective value of the envelopes obviously decreases with time. The longevity of such egg masses is likely to be limited to a few months. This suggests that only relatively small eggs, which develop to hatching within 1–2 months, permit 'jelly spawning' in very cold waters. Floating egg masses are faced with the risk of stranding, so the selection of spawning sites should assist in keeping this risk to a minimum. Where these conditions cannot be met by a species, the alternative solution of spawning in warmer waters might be inevitable.

Experimental approaches

Given the scarcity of field data on cephalopod spawning in cold waters, the various questions raised above may be approached by using the classic methods of experimental zoology. For medium to small sized benthic cephalopods, non-traumatic capture of living animals for aquarium maintenance at low water temperatures is possible (cf. O'Dor & Macalaster 1983), provided that shipboard tanks with temperature control are available to avoid temperature shock. Longterm maintenance in land based coldwater aquaria may then allow animals to survive and reproduce.

Large pelagic squids are not easily amenable to such experiments. However, it is possible to extract viable gametes from freshly caught individuals, to obtain artificially fertilized eggs, to embed them in 'nidamental' jelly prepared from lyophilized nidamental glands, and to keep these egg masses in culture (Arnold & O'Dor 1990). Although these successful experiments were made with very small squid eggs at high temperatures, so that the complete embryonic development covered only a few days, it is conceivable that similar procedures could be used for cultures at very low temperatures. One shortcoming of this method is that the artificially prepared jelly is not necessarily providing the same conditions for hatchlings when emerging from the chorion as the naturally produced nidamental jellies. The internally decaying jelly of natural egg masses may indeed provide a provisional living space for the hatchlings as long as the surface of the egg mass is intact (O'Dor *et al.* 1985). This problem requires large scale experiments similar to those described by Balch *et al.* (1985).

Conclusion

From the available data on cephalopod embryogenesis at low temperatures, and from estimations based on data extrapolation, an inescapable conclusion seems to be that at temperatures below 5°C no cephalopod can complete its embryonic phase in a period of less than one month. For species producing medium to large sized eggs, an embryonic phase of several months to one year or more is probably common in cold waters.

That cephalopod embryogenesis ends with a poorly defined hatching stage has been stated before (Boletzky 1987). It seems more appropriate to view the end of embryonic development as a phase of 'hatching competence', which may vary in length from a few hours in the smallest hatchlings when exposed to high temperatures (Arnold & O'Dor 1990) to several months in large hatchlings when exposed to very low temperatures (Summers & Colvin 1989). Thus far, nothing seems to indicate that cold adapted cephalopods have developed mechanisms of embryonic phase compression in the sense of terminal shortening (unless one considers the incorporation of virtually all the yolk reserves in the embryonic body, as is typical of many oegopsid squids, as the result of an original cold adaptation, which subsequently proved adaptive also for temperate and warm conditions). Future developmental studies will perhaps modify the picture drawn here. However, if true compensating mechanisms exist in cold adapted cephalopods, it is highly likely that in many species their effects on population dynamics are partly counterbalanced by multiple spawning, especially in species producing very large eggs (Boletzky 1982, 1986b, Kuehl 1988, Villanueva 1992). An embryonic phase covering one year or more combined with protracted individual spawning activity covering several months may be the typical ingredients of many cold water cephalopod life cycles. While species producing small eggs may have developmental times close to those of bony fishes at low temperatures (Johnston 1990), here the teleost cephalopod analogy does not apparently hold throughout the cephalopod class. Large cephalopod eggs undergoing slow development at low temperatures are probably more comparable to shark eggs.

Acknowledgements

I am grateful to Paul Rodhouse for the opportunity to present a tentative cold water essay from the Mediterranean. Special thanks to Roger Villanueva for many inspiring discussions and for his critical reading of the manuscript. The helpful comments of Andrew Clarke and an anonymous reviewer are also gratefully acknowledged.

References

Arnold, J.M. & O'Dor, R. 1990. *In vitro* fertilization and embryonic development of oceanic squid. *Journal of Cephalopod Biology*, **1**, 21-36.

Arnold, J.M., Awai, M. & Carlson, B. 1990. Hatching of *Nautilus* embryos in the Waikiki Aquarium. *Journal of Cephalopod Biology*, **1**, 117.

Balch, N., O'Dor, R.K. & Helm, P. 1985. Laboratory rearing of rhynchoteuthions of the ommastrephid squid *Illex illecebrosus* (Mollusca: Cephalopoda). *Vie et Milieu*, **35**, 243-246.

Bergstrom, B. & Summers, W.C. 1983. *Sepietta oweniana*. *In* Boyle, P.R. *ed. Cephalopod Life Cycles, vol. I.* London: Academic Press, 75-91.

Boletzky, S.v. 1975. A contribution to the study of yolk absorption in the Cephalopoda. *Zeitschrift fur Morphologie der Tiere*, **80**, 229-246.

Boletzky, S.v. 1982. On eggs and embryos of cirromorph octopods. *Malacologia*, **22**, 197-204.

Boletzky, S.v. 1983. *Sepiola robusta*. *In* Boyle, P.R. *ed. Cephalopod Life Cycles, vol. I.* London: Academic Press, 53-67.

Boletzky, S.v. 1986a. Encapsulation of cephalopod embryos: a search for functional correlations. *American Malacological Bulletin*, **4**, 217-227.

Boletzky, S.v. 1986b. Reproductive strategies in cephalopods: variation and flexibility of life-history patterns. *Advances in Invertebrate Reproduction*, **4**, 379-389.

Boletzky, S.v. 1987. Embryonic phase. *In* Boyle, P.R. *ed. Cephalopod Life Cycles, vol. II.* London: Academic Press, 5-31.

Boletzky, S.v. & Boletzky, M.V.v. 1973. Observations on the embryonic and early post-embryonic development of *Rossia macrosoma* (Mollusca, Cephalopoda). *Helgolander wissenschaftliche Meeresuntersuchungen*, **25**, 135-161.

Clarke, A. 1982. Temperature and embryonic development in polar marine invertebrates. *International Journal of Invertebrate Reproduction*, **5**, 71–82.

Clarke, A. 1991. What is cold adaptation and how should we measure it? *American Zoologist*, **31**, 81-92.

Hochberg, F.G., Nixon, M. & Toll, R.B. 1992. Order Octopoda Leach, 1818. *In* Sweeney, M.J., Roper, C.F.E., Mangold, K.M., Clarke, M.R. & Boletzky, S.v. *eds.* "Larval" and juvenile cephalopods: a manual for their identification. *Smithsonian Contributions to Zoology*, No. 513, 213-279.

Ito, H. 1983. Some observations on the embryonic development of *Paroctopus conispadiceus* (Mollusca: Cephalopoda). *Bulletin of the Hokkaido Regional Fisheries Research Laboratory*, **48**, 93-105.

Johnston, I.A. 1990. Cold adaptation in marine organisms. *Philosophical Transactions of the Royal Society of London*, **B 326**, 655-667.

Kubodera, T. 1991. Distribution and abundance of the early life stages of octopus, *Octopus dofleini* Walker, 1910 in the North Pacific. *Bulletin of Marine Science*, **49**, 235-243.

Kuehl, S. 1988. A contribution to the reproductive biology and geographical distribution of Antarctic Octopodidae (Cephalopoda). *Malacologia*, **29**, 89–100.

Naef, A. 1928. Die Cephalopoden (Embryologie). *Fauna e flora del Golfo di Napoli*, **35**, 1-357

O'Dor, R.K. 1983. *Illex illecebrosus*. *In* Boyle, P.R. *ed. Cephalopod Life Cycles, vol. I.* London: Academic Press, 175-199.

O'Dor, R.K. & Macalaster, E.G. 1983. *Bathypolypus arcticus*. *In* Boyle, P.R. *ed. Cephalopod Life Cycles, vol. I.* London: Academic Press, 401-410.

O'Dor, R.K., Helm, P. & Balch, N. 1985. Can rhynchoteuthions suspension feed? (Mollusca: Cephalopoda). *Vie et Milieu*, **35**, 267-271.

Opresko, L.K. 1974. *The early development of* Octopus briareus *Robson (Cephalopoda: Octopoda) and the organogenesis of the digestive system and its associated organs.* Ph.D. thesis, University of Miami, 154pp. [Unpublished.]

Portmann, A. 1926. Der embryonale Blutkreislauf und die Dotterresorption bei Loligo vulgaris. *Zeitschrift fur Morphologie und Okologie der Tiere*, **5**, 406-423.

Rodhouse, P.G. & Clarke, M.R. 1985. Growth and distribution of young *Mesonychoteuthis hamiltoni* Robson (Mollusca: Cephalopoda): an Antarctic squid. *Vie et Milieu*, **35**, 223-230.

Rodhouse, P.G., Symon, C. & Hatfield, E.M.C. 1992. Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. *Marine Ecology Progress Series*, **89**, 183-195.

Summers, W.C. 1983. *Loligo pealei*. *In* Boyle, P.R. *ed. Cephalopod Life Cycles, vol.* I. London: Academic Press, 115-142.

Summers, W.C. & Colvin, L.J. 1989. On the cultivation of *Rossia pacifica* (Berry, 1911). *Journal of Cephalopod Biology*, **1**, 21-32.

Villanueva, R. 1992. Continuous spawning in the cirrate octopods *Opisthoteuthis agassizii* and *O. vossi*: features of sexual maturation defining a reproductive strategy in cephalopods. *Marine Biology*, **114**, 265-275.

Voss, G.L. 1988. Evolution and phylogenetic relationships of deep-sea octopods (Cirrata and Incirrata). *In* Clarke, M.R. & Trueman, E.R. *eds. Paleontology and Neontology of Cephalopods* (vol. 12 of The Mollusca). San Diego: Academic Press, 253-276.

Young, J.Z. 1989. The angular acceleration receptor system of diverse cephalopods. *Philosophical Transactions of the Royal Society of London*, **B 325**, 189-237.