DWARF CEPHALOPODS: CONDITIONS OF REPRODUCTION AT SMALL SIZE

Boletzky, Sigurd v.

Observatoire Océanologique de Banyuls, F-66651 Banyuls-sur-Mer (E-mail: boletzky@arago.obs-banyuls.fr)

The oldest fossils supposed to represent a cephalopod (*Plectronoceras* of the Upper Cambrian) are chambered shells measuring 15-20 mm in length. Thus the body size was in the same range as the adult size of the smallest living cephalopods, *Idiosepius pygmaeus*. Only slightly larger are some dwarf sepiids (e. g. *Sepia pulchra*, *Metasepia* spp.), the smallest sepiolids (*Sepiola* spp.), some loliginid squids (*Pickfordiateuthis* spp.) and members of several pelagic squid families, some octopods (e. g. *Octopus micropyrsus* among the bottom-living forms; dwarf males in the pelagic *Argonauta*, *Tremoctopus*, *Ocythoë*).

A common biological feature of very small cephalopod species is a life-span of less than one year, with a minimum of about 3 months in *Idiosepius*. (The life span of dwarf males in pelagic octopods is unknown). The small adult size of the females, along with their 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 *Idiosepius pygmaeus*, the ovum measures about 1 mm in diameter, whereas in *Octopus micropyrsus*, it mesures 8-10 mm in length, 4-5 mm in width. In both cases, however, maturation and release of eggs is prolonged; i. e. this *terminal reproduction tends to multiple spawning*.

During embryonic development, a very large part of the yolk mass stored in the ovum is used for the production of embryonic cell complexes and for the subsequent formation of functional organs. But some yolk remains in the so-called inner yolk sac; its volume is a function of (1) the speed of yolk absorption during late embryonic stages, and (2) the point of time when hatching actually occurs. The only species in which the young hatch without a yolk reserve are medium-sized octopods producing very large eggs (*Octopus maya*, *Eledone moschata*). Hatchlings of *E. moschata* can survive for 2 to 3 weeks without food, i. e. the early juvenile metabolism can function according to the adult "emergency program" (using muscular proteins as an energy source). This is an exceptional capacity for an early juvenile metabolism.

Adult size may be attained rapidly when hatchlings are relatively large due to strong embryonic growth based on a large amount of yolk in the egg (e. g. *Octopus micropyrsus*). However, *Idiosepius* shows that even small eggs giving rise to small hatchlings permit rapid growth to adult size, within a very short life-span.

A comparative analysis of all cephalopod embryos large and small suggests one generalization: embryogenetic mode and juvenile design require a minimal ovum size above 0.5 mm. This generalization is essential for any hypothesis on the likely reproductive mode of the earliest cephalopods, which were dwarfs.

The focus of this paper is on biological aspects of size limitations in the evolution of cephalopods, with special emphasis on the secondary size reductions that must have occurred, and on their functional limits.