

Mating, spawning, and death in oceanic cephalopods: a review

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A review is presented of the sexual and maturity-related characters of all cephalopod families, from Nautilidae to Argonautidae, with a special consideration of oceanic and deep-water families. The position of hectocotylus is discussed, as well as the presence/absence of a long distensible penis, the presence of special male and female characters predominantly developed during the maturation, the place of sperm attachment, and the type of eggs and embryonic development.

The hectocotylus is present in 58% of families and subfamilies of coleoid cephalopods. Probably in all coleoids lacking a hectocotylus, the spermatophores are transferred from male to female by the penis. The only family having both hectocotylus and penis is the Architeuthidae, the giant squids. There are 6 main types of male maturity-related characters: special modification of non-hectocotylized arm; elongation and enlargement of some arms; enlargement of some arm suckers; tail elongation; male sexual photophores; special male coloration.

The female maturity-related characters are more rare than the male ones, the most important are sexual photophores on arm ends or around the mouth. In most cases males are smaller than females and mature earlier, but some interesting exceptions are known to exist. There are at least 8 sites of sperm attachment in coleoids. The mating and spermatophore transfer may be very bizarre in some species. The eggs are usually laid either on the bottom or in the water (in rather firm or loose egg masses), but some species are ovoviviparous or the female brood eggs on her arms. A classification or reproductive strategies is presented. The fate of spent animals is discussed, with a particular attention to the arising to the surface of moribund spent females of many deepwater squids characterized by a gelatinous degeneration during the maturation. Their role in the feeding of seabirds is considered.

Спаривание, нерест и смерть у океанических головоногих моллюсков: обзор

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Дан обзор особенностей строения всех семейств головоногих моллюсков от Nautilidae до Argonautidae, связанных с созреванием, спариванием и нерестом. Специальное внимание уделено океаническим и глубоководным семействам. Обсуждаются расположение гектокотилия, присутствие/отсутствие длинного пениса, наличие специальных признаков, связанных с созреванием у самцов и самок, места прикрепления сперматофоров у самок, характер яиц и тип эмбрионального развития.

Гектокотиль имеется у представителей 58% всех семейств и подсемейств колеоидных головоногих. У видов, не имеющих гектокотилия, самец передает

самке сперматофоры с помощью пениса. Только у гигантских кальмаров Architeuthidae имеются и гектокотиль, и длинный пенис. У самцов имеется 6 основных типов признаков, связанных с созреванием: специальное видоизменение не-гектокотилизированной руки; удлинение и утолщение других рук; увеличение некоторых присосок на руках; удлинение хвоста; развитие особых половых фотофоров; специальная самцовая окраска. Специальные связанные с созреванием признаки самок немногочисленны, необходимо упомянуть о "женских" фотофорах на концах рук или вокруг рта у некоторых видов. У большинства видов самцы мельче самок и созревают раньше, но имеются примечательные исключения. Приведены краткие сведения об уходе и спаривании. Известно не менее 8 мест прикрепления сперматофоров на теле самок. У некоторых видов спаривание и перенос сперматофоров осуществляется очень необычными способами. Яйца либо откладываются на дно, либо выметываются в толщу воды (в прочных или рыхлых и легко распадающихся яйцевых массах), но некоторые виды живородящи, или самки вынашивают яйца на руках. Дана классификация типов репродуктивной стратегии. Обсуждается судьба головоногих моллюсков после нереста, в частности, всплытие к поверхности умирающих выбойных самок многих глубоководных кальмаров, испытывающих при созревании студенистое перерождение. Подчеркивается их значение в питании ныряющих морских птиц.

Mating and spawning are among the most important processes in the life history of animals. They are rather well known in coastal and neritic cephalopods, Sepiidae, Sepiolidae, Loliginidae and Octopodidae (Octopodinae), which can be studied both in aquaria and in the sea with scuba [reviews: Arnold, 1984; Boletzky, 1974, 1975a; Boletzky, Hanlon, 1983; Fioroni, 1978; Hanlon et al., 1983; Mangold, 1987, 1989; Okutani, 1990; etc.]. Among the non-coastal cephalopods, these processes were observed only in *Nautilus* [Arnold, 1987; Ward, 1983, 1987], *Illex* [Boletzky et al., 1973; O'Dor, 1983] and *Todarodes pacificus* [Hamabe, 1962] in aquaria. The information about mating and spawning of the majority of deep-water and oceanic cephalopod species is very scanty and obtained mostly by the investigation of specimens caught with trawls or extracted from the stomachs of sperm whales. Researchers attempting to collect data on these most important processes shall behave as detectives who gather information drop by drop and make conclusions based on circumstantial evidences. This way may lead to results, which in the future may prove to be wrong as, for example, Louis Dollo's [1912] discourse about benthonization and nektonization in modern and ancient cephalopods. Or the whole way of reasoning may be wrong, as, for example, the attempt to understand the ammonoid ecology on the basis of ecological study of modern *Nautilus* [Jacobs, Landman, 1993]. But today I do not see any other way to bring nearer to obscure truth than to collect dispersed, fragmentary, anecdotal, and in some cases unproven observations, and to try to reconstruct the whole picture.

On this way we will discuss the following

structures: (1) hectocotylus and terminal part of male reproductive apparatus destined for the transfer of spermatophores from male to female; (2) other male structures destined for luring females and preparing to transfer spermatophores; (3) female characters serving for the same purpose; (4) sites of attachment of spermatophores on female body, traces of spermatangia, etc.; (5) information about egg masses or at least habitats where mating and spawning may supposedly occur (Table 1). The sexual differences in relative dimensions of arms, tentacles, head, mantle, fin, etc., will not be discussed.

Because all three specific divisions of Cephalopoda — cuttlefishes, squids, and octopuses — contain both coastal/neritic and oceanic species, it is reasonable to describe the material systematically, without dividing families and subfamilies into neritic and oceanic ones. But of course the better known shallow-water families would be described in less detail. The classification is used as adopted in Nesis [1987], with minor new additions and corrections. Many details of structure and biology mentioned below are described in Nesis [1985, 1987] and will not be accompanied by special references.

SEXUAL CHARACTERS OF CEPHALOPODS

Class Cephalopoda Subclass Nautiloidea Order Nautilida Family Nautilidae

Nautilus has no hectocotylus. Males have a voluminous erectable copulative organ (spa-