

SQUID, OCTOPUS AND THE LIVING CEPHALOPODS

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Keywords: Cephalopods, squid, octopus, cuttlefish, nautilus, life-history, production, management, aquaculture.

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Summary

Modern shell-less coleoid cephalopods are distributed from pole to pole and range from surface dwelling tropical forms with adults the size of a grain of rice to 30m giants in the deep oceans. They compete with fishes in nearly all marine niches, although, there are only one tenth as many species, perhaps reflecting their relatively recent radiation since the disappearance of the dinosaurs. Cephalopods have been called 'racing snails' because they have undergone dramatic adaptations of their molluscan heritage to remain the only invertebrates among the large pelagic predators. This has made them more interesting to physiologists than to fishers. Perhaps it seems obvious that fishers focus on fish, as fish biomass appears to exceed that of cephalopods globally, but short life cycles and rapid growth suggest that cephalopod annual production may actually be greater. This maybe a fact the other marine mammals are hiding from us! Cephalopod fisheries continue to expand while fish fisheries are in decline, and it is interesting to speculate on whether the short-lived cephalopod 'weeds' are displacing the fish 'trees' in ocean ecosystems as we 'clear-cut' (over-fish) them. If so, is the process reversible or can we look forward to 21st century menus filled with cephalopods? Rapid growth and high feed efficiency, along with increasing acceptance of cephalopods as food globally,

suggests that some species will also become important in aquaculture - unless their colorful antics turn them into pets instead!

1. Introduction

Cephalopods have often been compared to fishes since Packard declared that, "Squid functionally are fish", in a review of the limits of convergent evolution. This is certainly true in terms of three dimensional form, but recent improvements in aging techniques for squid have made it clear that in the forth dimension, time, squid operate very differently (see Bibliography for additional references). Although the living fossil, nautilus, is an exception, the adage, "Live fast, die young", is generally appropriate. The modern coleoid cephalopods have lost their external molluscan shells and transformed their mantle cavities into muscular pumps that drive powerful jet propulsion systems. The jet is inherently less efficient than undulatory fish propulsion, but can be coupled to respiration allowing higher power outputs to compensate. To maintain such systems most cephalopods are effective predators with high feeding and growth rates, that mature reproduce and die in less than two years (see Pörtner *et al.* 1994). This has many consequences for marine ecosystems as well as for how we think about and describe cephalopods. Their phylogeny and relations to fossil ancestors going back the Cambrian have been a fascination since the beginnings of biology and geology, but there are still un-described species and unseen giants from the deep ocean where they dominate.

In many ways the latter half of the 20th century has been a golden age for cephalopod science. Giant axons and big brains made them targets for physiologists and behavioralists (examples in the Bibliography), whose efforts are finally bringing some understanding of what it takes to allow these 'racing snails' to be the only invertebrates still competing directly with vertebrates. The Cephalopod International Advisory Council (CIAC) has provided a bridge between basic biology and commercial activity with a series of volumes (listed in the Bibliography) on topics ranging from beak (for stomach content analysis) and larval identification to biogeography, fisheries and management. Clarke has recently synthesized much of this information on cephalopods and their role in the ecosystem in a special theme publication which points to their increasing importance in heavily exploited seas of the future.

2. Taxonomy

Current classifications put the total number of cephalopod species at over 700 from up to 50 families (Table 1). Figure 1 shows the basic features of squids, as an example, with many cephalopod standard features characterized. Although it is generally recognized that many 'cosmopolitan' species, such as *Octopus vulgaris*, are probably complexes, there is considerable debate over whether it is most appropriate to divide these into subspecies, species or even genera. It seems likely that modern DNA techniques will reveal a large number of cryptic taxa, but these have not yet been widely applied in cephalopods. The final species count could go as high as 1000, if the 'splitters' have their way. The number of reproductively isolated 'populations' and 'stocks' that must be considered from either a biodiversity or fishery management perspective is obviously much higher, at least double, based on spatial isolates, and

perhaps as much as an order of magnitude, if temporal isolates (seasonal breeding groups) prove to be significant.

Subclass Nautiloidea	Agassiz, 1848
Order Nautilida	Agassiz, 1848
Family Nautilidae	Blainville, 1825
Subclass Coleoidea	Bather, 1888
Superorder Decabrachia	Boettger, 1952
Order Spirulida	Stolley, 1919
Family Spirulidae	Owen, 1836
Order Sepiida	Zittel, 1895
Family Sepiidae	Keferstein, 1866
Family Sepiariidae	Fischer, 1882
Order Sepiolida	Fioroni, 1981
Family Sepiolidae	Leach, 1817
Family Idiosepiidae	Appellöf, 1898
Order Teuthida	Naef, 1916
Suborder Myopsina	Orbigny, 1841
Family Pickfordiateuthidae	Voss, 1953
Family Loliginidae	Lesueur, 1821
Suborder Oegopsina	Orbigny, 1845
Family Lycoteuthidae	Pfeffer, 1908
Family Enoploteuthidae	Pfeffer, 1900
Family Ancistrocheiridae	Pfeffer, 1912
Family Pyroteuthidae	Pfeffer, 1912
Family Octopoteuthidae	Berry, 1912
Family Onychoteuthidae	Gray, 1849
Family Walvisteuthidae	Nesis/Nikitina, 1986
Family Cycloteuthidae	Naef, 1923
Family Gonatidae	Hoyle, 1886
Family Psychroteuthidae	Thiele, 1920
Family Lepidoteuthidae	Pfeffer, 1912
Family Architeuthidae	Pfeffer, 1900
Family Histioteuthidae	Verrill, 1881
Family Neoteuthidae	Naef, 1921
Family Bathyteuthidae	Pfeffer, 1900
Family Ctenopterygidae	Grimpe, 1922
Family Brachioteuthidae	Pfeffer, 1908
Family Batoteuthidae	Young/Roper, 1968
Family Ommastrephidae	Steenstrup, 1857
Family Thysanoteuthidae	Keferstein, 1866
Family Chiroteuthidae	Gray, 1849
Family Mastigoteuthidae	Verrill, 1881
Family Promachoteuthidae	Naef, 1912
Family Joubiniteuthidae	Naef, 1922
Family Cranchidae	Prosch, 1847
Superorder Octobrachia	Fioroni, 1981
Order Octopodida	Leach, 1818
Suborder Cirrina	Grimpe, 1916
Family Cirroteuthidae	Keferstein, 1866
Family Stauroteuthidae	Grimpe, 1916
Family Opisthoteuthidae	Verrill, 1896
Suborder Incirrina	Grimpe, 1916
Family Bolitaenidae	Chun, 1911

Family Amphitretidae	Hoyle, 1886
Family Idioteuthidae	Taki, 1962
Family Vitreledonellidae	Robson, 1932
Family Octopodidae	Orbigny, 1840
Family Tremoctopodidae	Tryon, 1879
Family Ocythoidae	Gray, 1849
Family Argonautidae	Tryon, 1879
Family Alloposidae	Verrill, 1881
Order Vampyromorphida	Pickford, 1939
Family Vampyroteuthidae	Thiele, 1915

Table 1. Living Class Cephalopoda Cuvier, 1797 to Family (Voss, NA, Vecchione, M and Toll, RB 1998. *Systematics and Biogeography of Cephalopods*. Smithsonian Contributions to Zoology 586:1-599.)

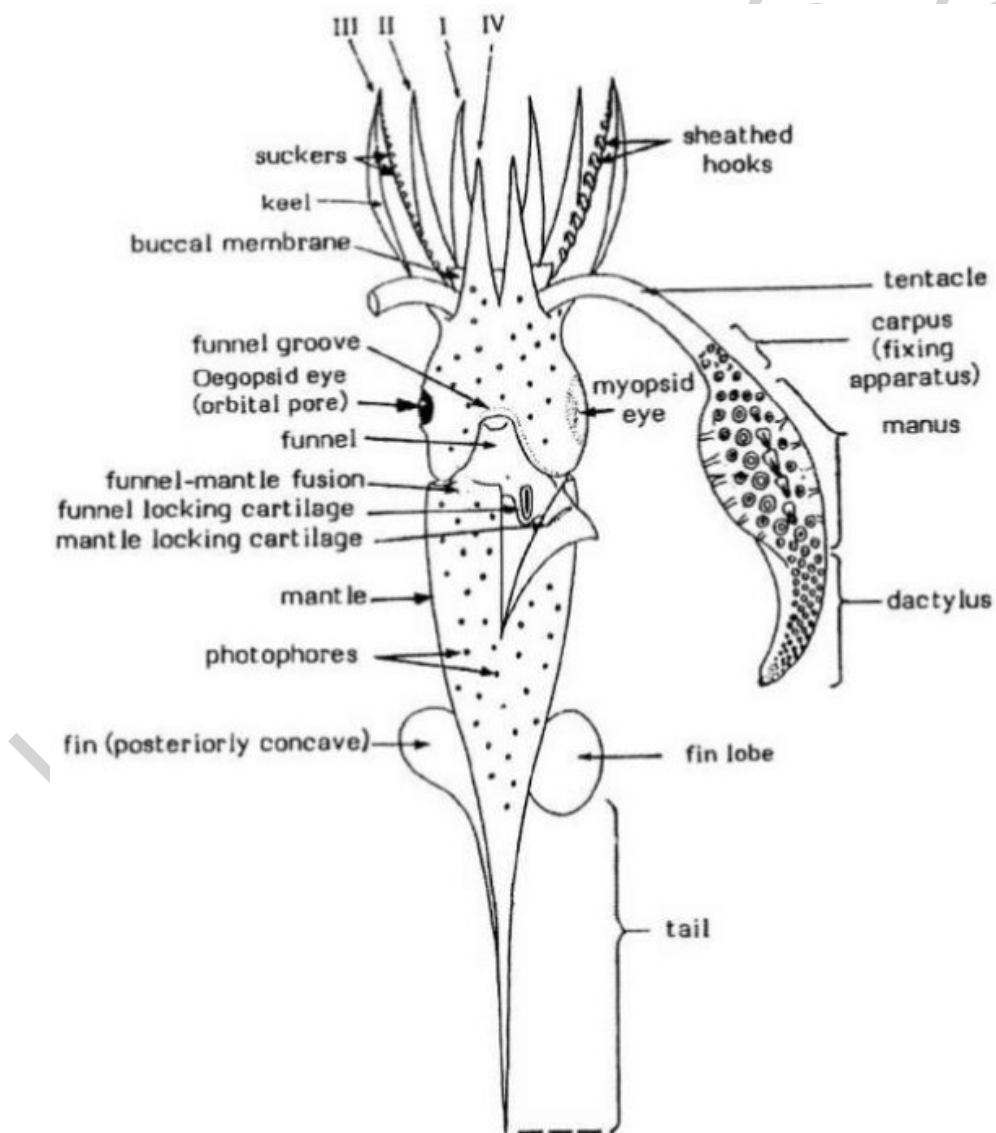


Figure 1. A composite diagram illustrating basic features of cephalopod anatomy, reproduced with permission from Roper C.F.E., Sweeney M.J. and Nauen C. (1984).

Cephalopods of the World, Vol 3, An Annotated and Illustrated Catalogue of Species of Interest to Fisheries. Fisheries Synopsis No. 125, 277 pp. Rome: FAO.

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Biographical Sketch

Ron O'Dor was born in 1944 in Kansas City, Missouri, USA. An AA in Chemistry from El Camino Junior College, Torrance, California led to an AB in Biochemistry at the University of California, Berkeley, followed by a PhD in Medical Physiology from the University of British Columbia, Canada, with a thesis on the isolation and characterization of salmon calcitonin, now an osteoporosis treatment. A Canadian Medical Research Council Fellowship to Cambridge University and Stazione Zoologica, Napoli, allowed studies of octopus gonadotrophin and reproductive physiology. He has been at Dalhousie University in Halifax since 1973, as Aquatron Laboratory Director and now Professor and Chair of Biology. His current research focus on radio-acoustic positioning and telemetry (RAPT) used to monitor behavior, bioenergetics and physiology *in situ* of cephalopods, including nautilus, cuttlefish, octopus and squid around the world: Canada, USA, Mexico, Azores, France, South Africa, Australia, Papua New Guinea and Japan. He is an FAO consultant on cephalopod fisheries, former president of the Cephalopod International Advisory Council, editor and author of *Squid Recruitment Dynamics* (1998), *Physiology of Cephalopod Molluscs* (1994) and *Recent Advances in Cephalopod Fishery Biology* (1993), as well as over 100 scientific articles.