The Role of Cephalopods in the World's Oceans: An Introduction

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The role of cephalopods in the world's oceans: an introduction

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1. INTRODUCTION

The object of this volume is to summarize our present knowledge of the role of cephalopods in the oceans and adjacent seas. Only in the last three decades have we become aware of their ecological importance, and we are at present on the brink of an expansion of their utilization by man. The role of cephalopods in the life of man must depend ultimately upon their role in the ocean. Man poses the threat of a major predator from outside their ecosystem as he has with the fish, but cephalopods are very different from fish in many aspects of their life (Boyle & Boletzky; Rodhouse & Nigmatullin), and their commercial exploitation will bring about very different responses and pose very different problems. Man asks, 'What can they give us?' What he must also ask is, 'What could we ultimately lose from their careless exploitation?' This volume presents information upon which a first attempt to answer these questions can be based.

At present, cephalopods contribute only 3% to the tonnage of global fisheries, but their total value lies third, below only shrimps and tuna (Clarke, figure 3*b*, p. 1106). Progressive increase in the annual tonnage of fish removed from the oceans has been achieved only by increased effort, with a consequent increase in the threat to fish stocks, many of which are now declining. Almost all exploited fish, except the tuna, live over the continental shelves and attempts to increase the harvesting of open ocean fisheries have been met by three major difficulties. Midwater fish of comestible size are few, so that only low value, industrial species are harvestable. Bottom fish are larger but they are extremely slow growing so that their uncontrolled exploitation will quickly reduce their stocks and be short-lived. All oceanic fish, but particularly the bottom fish, are difficult and expensive to harvest. As pressures on fish continue to increase, man's attention will certainly turn to the most underexploited, sizable midwater residents of the deep oceans, the cephalopods.

Our knowledge of cephalopods comes from the interest sparked by local, artisanal shelf fisheries and from their suitability as physiological test beds to study the fundamental functions of nervous systems, blood-brain barriers, sense organs, etc. Both the fisheries and the physiology have involved only the members of three shelf-living families, the Loliginidae, the Sepiidae and the Octopodidae, and one family, the Ommastrephidae, which moves seasonally on to the continental shelves. These are all muscular animals that are either supported in the water by a shell containing a partial vacuum (the sepiids), or have to swim continuously to stay at a particular level in the water, i.e. they are negatively buoyant. However, most species of cephalopod do not live on the continental shelves, have not been exploited for food and have very different bodies and lives to those few that have been the focus of our investigations. Most oceanic species attain neutral buoyancy by retention of either ammonia, chloride or special oils (Clarke *et al.* 1979) and have a less energetic lifestyle than their shelf-living counterparts. Far fewer fisheries biologists, or indeed ecologists, have studied cephalopods rather than fish and, among the cephalopods, least is known about the oceanic, neutrally buoyant and most prolific forms.

The contributors to this volume describe the current status of our knowledge of the role of cephalopods in the ocean, with the intention of exposing deficiencies in our knowledge and providing a base from which future work can spring. In the course of this re-examination we have found that cephalopods occupy and are equipped to fill a special place in the ocean ecostructure and this is detailed here for the first time.

The initial selection of topics for this issue was strictly limited to the natural role of cephalopods in the sea. Principally, this was thought to embrace their role as consumers, providers and transporters of nutrients, chemicals and energy. To determine each of these roles, information is needed on cephalopod interaction with other species, the ecosystem and their own growth, size, life cycles, migrations and energetics. Such a consideration of the whole animal aspects takes us part way and is a necessary preliminary to considering chemical and energy fluxes. However, immediately chemical and energy fluxes are addressed, large inadequacies in our knowledge become evident. The most basic is the paucity of knowledge on chemical constituents of cephalopods; the storage, transport and dissipation or concentration of the very substance of the animals. The other product, energy, has been studied in more detail and in the contribution by Wells & Clarke, a new synthesis of published and new work gives a foundation for future understanding of the energetics of muscular cephalopods, including those having shells containing gas.

Whole animal considerations naturally divide into studies of populations, distribution and migrations, reviewed by Boyle & Boletzky, cephalopods as consumers, reviewed by Rodhouse & Nigmatullin and

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cephalopods as food for predators, reviewed by Croxall & Prince, Klages, Clarke and Smale. Although relatively straightforward, these studies are also in their infancy, but here an outline of the present state of knowledge is presented.

One further role of the cephalopods is their place as secondary and primary hosts of parasites and this interacts with the consumer and predator sections, but sometimes has a special interest to man's utilization of fish. As a comprehensive review of the subject has been published elsewhere (Hochberg 1990) it will not be treated here.

2. HISTORY

Considerable difficulties hinder our understanding of the role of cephalopods in the past. Fossil evidence depends on organisms having a skeleton. Almost the only fossil records of cephalopods are their calcareous remains and these are not preserved in acid environments, a limitation to preservation of shells and statoliths as it is with fish otoliths. Statoliths are found with fish otoliths in deposits back to the Jurassic. Much of the present deep ocean had not been formed before the Jurassic so that many of the fossils are shelf animals. Comparison with living cephalopods is the only way to draw conclusions on their lifestyle. Only *Nautilus*, *Spirula* and sepiids have calcareous shells, whereas fossil cephalopods nearly all have calcareous shells which are of a great variety of shapes. While the buoyancy studies of Denton & Gilpin-Brown (1973) have led to a much better understanding of the function of many fossil shells, the shapes of many more cannot just be interpreted in terms of buoyancy without much more knowledge of the animals within or around the shells. Fossil records cannot be used to give estimates of population numbers and numbers relative to other phyla because their 'beds' have accumulated over thousands or even millions of years. Information on the diet and feeding apparatus, the lifestyle and the growth, is minimal. From their shells, we know individuals had about the same range in length and biomass as the living cephalopods.

Since their appearance in the Cambrian, cephalopods have evolved to include the largest invertebrates (over 20 m) and to become common predators in all shallow and deep seas. For much of life's history, over 200 million years, they were probably the top predators of the marine environment. We can be reasonably sure that the animals having these calcareous shells, which bestow neutral buoyancy, were muscular, rich in protein and must have provided a high energy food source for the larger predators which later appeared; first they became the food of cartilaginous and later teleost fishes and then also of the reptiles, crocodilians, icthyosaurs, plesiosaurs and pliosaurs. As these predators disappeared they were augmented and replaced by the birds and marine mammals.

After the Jurassic the coleoids, the recent group to which the living cephalopods belong, became dominant. All the fossil remains so far described, including the statoliths (Clarke & Fitch 1979), are from muscular cephalopods, either with gas-filled shells or with no shells at all. No record has so far been published of members of the prolific neutrally buoyant group of deep sea families depending on ammonia or on sulphate displacement. At some stage, and this may have been much earlier than the evidence from fossils suggests, cephalopods developed chemical methods of buoyancy and more active jet-swimming, which enabled them to colonize the deep ocean from top to bottom. Their physical environment was diversified, the environmental niches available were multiplied and the overall abundance of cephalopods could vastly increase. As we have described fossil statoliths in the Jurassic and Cenozoic, and they occur in all living ammoniacal squids, there is every possibility that further collections may indicate how long ammoniacal teuthoids and other families of intestate cephalopods have been in existence.

The decline of fossil records of cephalopods and the increase in those of the bony fishes suggests that the fishes became more successful than the cephalopods and replaced them as a dominant predator after the Jurassic. This impression is partly given by the replacement of ancient shelled cephalopods, which leave a clear fossil record, by forms with no external shells. However, an idea of the relative numbers of cephalopods and teleost fish can be obtained, in particular localities, by comparing the numbers of fish otoliths with squid statoliths as they are all of the same material and of about the same size (Clarke & Maddock 1988). In the Jurassic of southern England the cephalopod statoliths outnumbered the fish otoliths by about 8:1 (range in six sites of 1:2–44.6:1) while in the North American Cenozoic deposits teleost fish outnumbered squids 441:1 (range in six sites of 20:1–1300:1). Cartilaginous fish do not have otoliths. Besides a replacement of the cephalopods by the more numerous fishes, there grew an interdependence between these two mobile and diverse groups reflected by detailed parallels in their evolution (Packard 1972). While they both evolved to more adequately fit the same marine physical environment with its numerous niches, much stimulus to cephalopod evolution also came from their interaction with fish and later with other higher vertebrate predators, the reptiles, seals, cetaceans and birds.

3. THE OCEAN

The main marine ecological zones are the shoreline, the littoral zone or continental shelves from the shore to about 300 m, which now comprises only 8% of the total ocean bed, the relatively steep continental slope from 300–2000 m and the ocean deeper than 2000 m, which covers over 90% of the ocean floor, extends to over 7000 m depth and covers 66% of the surface area of the Earth.

Penetration of light into the sea concentrates the smaller food organisms in the upper 300 m and leads to a stratification of vertical migrators and non-migrators in the upper 1000 m of the deep sea. Few cephalopods

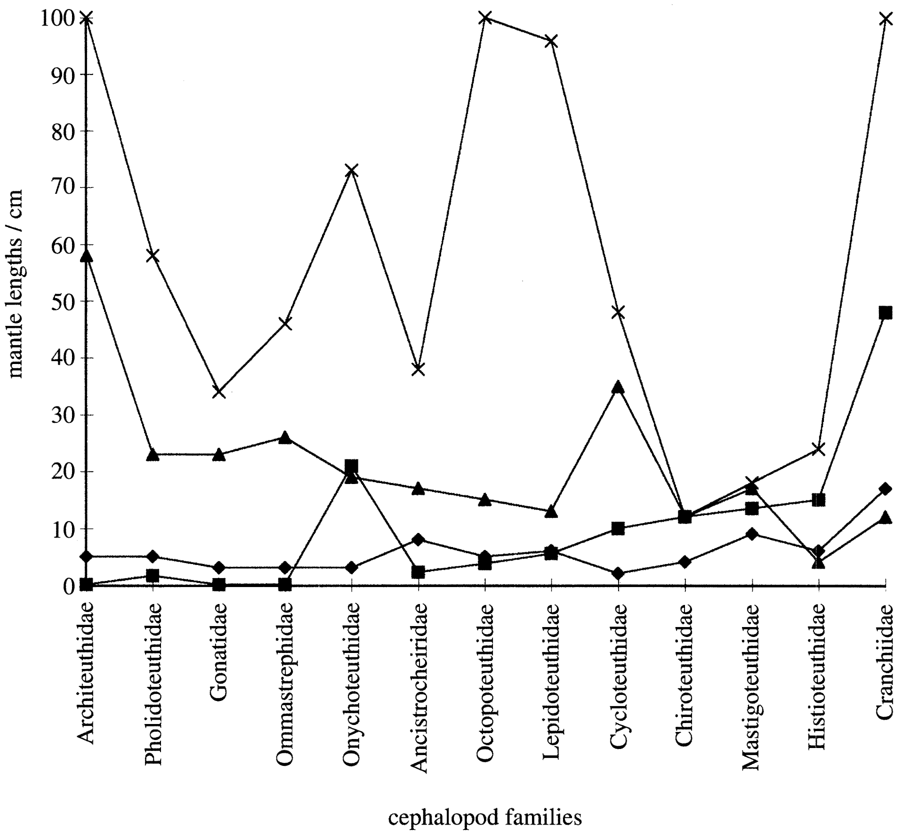

Figure 1. The mantle lengths of squids of various families caught in nets and by sperm whales. The limits of the range of complete specimens found in sperm whale stomachs for each family, are shown by closed triangles and crosses. Estimation of lengths from beaks show that these grow much larger. The maximum mantle length for squids of each family caught in almost 600 research net hauls with a mouth area of 9 m^2 (closed diamonds) and 57 research net (RMT 50) hauls with a mouth area of 50 m^2 (closed squares) are also shown.

are caught between 1500 m from the surface and 100 m from the bottom. A diverse cephalopod fauna is associated with the bottom in both shallow and deep seas but these have special adaptations to handle the abrasive qualities of rock and sand and silt in suspension. In shallow seas most of the species have secondary skins protecting the eye lenses, leading to a major taxonomic division in the squids of the predominantly shelf-living Myopsida and the oceanic Oegopsida.

Creation and movement of the continents has changed the shape, area and depths of the ocean with consequent changes to areas of continental shelves, currents and upwelling areas, all with influence on cephalopod evolution and relative abundance of different species and families. Broad, shallow shelves favoured the expansion of forms such as the Ammonoidea, Nautiloidea and Belemnoidea, but they must have been restricted to the upper few hundred metres in oceanic waters.

Today, cephalopods are numerically a small part of the shelf fauna being vastly outnumbered by fish of similar size, except at certain seasons and localities. In oceanic waters they are more diverse in structure and play a more important role than in shallow seas.

4. DEFICIENCIES IN DATA

Our low level of understanding of cephalopod ecology comes from a paucity of taxonomists and ecologists attracted to the group; until two decades ago these numbered less than about 30 worldwide, while there must have been well over 50 times that number working on sea fish. This was a reflection of the relative economic importance of the two groups, but decline in fish stocks, increase in the total value of cephalopod fisheries and the realization that it is desirable for us to know more about fish, bird and sea mammal food are now changing our attitudes towards cephalopod studies.

Lack of data is also due to man's inadequacy in catching oceanic cephalopods. While the kinds and sizes of net usable from a research ship catch many hundreds of fish with one haul in midwater, it usually catches less than eight cephalopods (Clarke & Lu 1974). We can now be sure that this is not a true reflection of the relative abundance, biomass and ecological importance because, as it has become possible to use larger nets and nets provided with lights (Clarke & Pascoe 1996), more and larger cephalopods have been caught. However, even then, we obtain a mere reflection of what is revealed to be present in the sea by the presence of cephalopods in the diets of their predators. Such studies show that, not only are

Table 1. *Classification of living cephalopods*

Class	**Cephalopoda**	**Cuvier 1798**
Subclass	**Nautiloidea**	**Agassiz 1847**
Family	Nautilidae	Blainville 1825
Subclass	**Coleoidea**	**Bather 1888**
Order	**Sepiida**	**Naef 1916**
Family	Spirulidae	Owen 1836
Family	Sepiidae	Keferstein 1866
Order	**Sepiolida**	**Clarke 1988**
Family	Sepiadariidae	Naef 1912
Family	Sepiolidae	Leach 1817
Family	Idiosepiidae	Appellof 1898
Order	**Teuthida**	**Naef 1916**
Suborder	**Myopsida**	**Orbigny 1845**
Family	Pickfordiateuthidae	Voss 1953
Family	Loliginidae	Steenstrup 1861
Suborder	**Oegopsida**	**Orbigny 1845**
Family	Lycoteuthidae	Pfeffer 1908
Family	Enoploteuthidae	Pfeffer 1900
Family	Ancistrocheiridae	Clarke 1988
Family	Pyroteuthidae	Clarke 1988
Family	Octopoteuthidae	Berry 1912
Family	Onychoteuthidae	Gray 1849
Family	Cycloteuthidae	Naef 1923
Family	Gonatidae	Hoyle 1886
Family	Psychroteuthidae	Thiele 1921
Family	Lepidoteuthidae	Naef 1912
Family	Pholidoteuthidae	Voss 1956
Family	Architeuthidae	Pfeffer 19
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	Grimalditeuthidae	Pfeffer 1900
Family	Joubiniteuthidae	Naef 1922
Family	Cranchiidae	Prosch 1849
Order	**Vampyromorpha**	**Pickford 1939**
Family	Vampyroteuthidae	Thiele 1915
Order	**Octopoda**	**Leach 1818**
Suborder	**Cirrata**	**Grimpe 1916**
Family	Cirroteuthidae	Keferstein 1866
Family	Stauroteuthidae	Grimpe 1916
Family	Opisthoteuthidae	Verrill 1896
Suborder	**Incirrata**	**Grimpe 1916**
Family	Bolitaenidae	Chun 1911
Family	Amphitretidae	Hoyle 1886
Family	Idioctopodidae	Taki 1962
Family	Vitreledonellidae	Robson 1932
Family	Octopodidae	Orbigny 1845
Family	Tremoctopodidae	Brock 1882
Family	Ocythoidae	Gray 1849
Family	Argonautidae	Naef 1912
Family	Alloposidae	Verrill 1882

cephalopods numerically much commoner than our inadequate sampling can show, but many species grow to a much greater size than our nets will catch (figure 1). In fact, in the deep sea, many grow larger than most of the midwater fish species. Our nets catch only immature specimens, while many large predators consume adults of exotic forms in quantities considered large by even commercial fishery standards. Sperm whales alone, for example, probably consume annually more than twice the mass of all fish landed by man (Clarke, p. 1060).

5. TAXONOMY

There are less than 650 known living species of cephalopod, and they occupy niches from the shore to the deepest ocean (Nesis 1987). Until the last two decades, the basic biology of even the inshore species was very poorly known and much still remains to be learnt to understand them as much as we do many fish species.

Taxonomy of the group has been especially difficult because of the few specimens, particularly of adults, available in collections. Even major grouping of families is still unsure, although recent accelerating activity is crystallizing much discussion. One generally accepted classification of living cephalopods is given in table 1.

6. DISTRIBUTIONS

The general ecological types of cephalopod and their niches can be listed as follows. The inshore coastal region is inhabited by Octopodidae on rocky or coral shores and the sepiolids on sand or mud. On the continental shelf, outside the wave zone, Loliginidae and Sepiidae predominate, but Ommastrephidae appear seasonally and return into deep water to spawn and live for most of their lives. This represents a major movement of protein, chemicals and energy on and off the shelf, which, in many parts of the world, has a major effect on predators and food organisms (Boyle & Boletzky). The continental slope and oceanic island slopes attract species for spawning on the bottom as well as specialized cephalopods adapted to the vertical mixing and canyon topography of this narrow zone. Off the shelf and free of the slope a few species, such as the blue *Onychia* or the transparent *Cranchia*, are adapted to life in brightly lit, surface waters. More species visit the shallow depths only after dark and probably spend the daylight hours in a fairly inactive state. Others remain at depths greater than 500 m for all, or most, of their lives (Clarke & Lu 1974; Lu & Clarke 1974, 1975). Some of the larger midwater squids, such as those in the Ommastrephidae and Onychoteuthidae, seasonally migrate horizontally for feeding and spawning. Some midwater species migrate over great vertical depths during growth and some of these probably spawn on the bottom. On and close to the bottom are benthic and bathypelagic forms and these possibly migrate across the bottom, but little is known of their behaviour. Movements and distributions of all these various cephalopods are reacted to by predators and have effects on numbers, distribution and evolution of their food species.

7. SPECIAL ADAPTATIONS

Cephalopods have developed large brains (Young, 1988), keen senses of sight, touch, balance and motion (Budelmann 1977), chemical discrimination and vibration detection. Together with fin-swimming, they developed jet propulsion for fast locomotion. A suite of skin colouring, reflecting and wrinkling devices were evolved for camouflage and complicated signalling. Most of these typical cephalopod devices have been studied in the inshore species of Loliginidae, Sepiidae, Sepiolidae and Octopodidae (Hanlon & Messenger 1995). They have been modified, expanded or simplified in the oceanic families and other developments have arisen for coping with the special conditions in the deep ocean, such as photophore diversification for camouflage against downwelling light (Young 1983) and for signalling (Herring 1988) and the perfection of several methods of buoyancy control.

Thus, apart from the partial vacuum system developed by early shelled cephalopods and now surviving in the Sepiida (Denton & Gilpin-Brown 1973), a fish-like air sac evolved in *Ocythoe* (Packard & Wurz 1994), and in many families, including the Histioteuthidae and Cranchiidae, there has been replacement of metallic ions with ammoniacal ions (Clarke *et al.* 1979) or, in some pelagic octopods such as *Japetella*, sulphate ions with chloride ions (Denton & Shaw 1961). Even special low density oils, similar in structure to squaline in elasmobranchs, were developed in the Gonatidae. Other cephalopods, such as the Ommastrephidae, are denser than seawater and swim to maintain their depth. These buoyancy methods affect both the energetics and the calorific values (Croxall & Prince 1982) of the animals concerned. General shape has largely been determined by the methods of swimming and of food capture.

Relevant to the study of food of cephalopods are the development of tentacles, arms, webs, suckers, and hooks and beaks (Rodhouse & Nigmatullin). These allow a very much bigger variation in food selection than the mouths of fish.

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