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The Role of Cephalopods in the World's Oceans: General Conclusion and the Future

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The role of cephalopods in the world's oceans: general conclusions and the future

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1. INTRODUCTION

In this volume we have considered the problems of investigation special to cephalopods. Almost all our knowledge of their general biology is restricted to the shelf-living, muscular, negatively buoyant (the Loliginidae and Octopodidae) or gas-supported species (the Sepiidae and Nautilidae) and members of the Ommastrephidae which move on to the continental shelves at certain seasons. These species of the continental shelves comprise only about 15% of all cephalopod genera and live in water of less than 300 m depth, which covers only 6% of the Earth's surface. They do not represent the majority of cephalopod species or much of their total biomass; 85% of genera are spread in the upper 2000 m and across the bottom of the deep oceans, which occupy 66% of the Earth's surface. Over 40% of these genera are neutrally buoyant by oil or chemical means and may have very different lifestyles from the forms we know from shallow water. Improvement of our knowledge of the ecology of deep water forms is hindered by our poor direct sampling methods and rests largely upon sampling from stomachs or regurgitations of the predators that eat cephalopods.

Although studies on anatomy and physiology show that cephalopods have evolved many mechanisms in parallel with fish (Packard 1972), from the complex information assembled here we can conclude that muscular cephalopods are different from other nekton, including fish, in many details of their biology and ecology (Boyle & Boletzky, Rodhouse & Nigmatullin, Wells & Clarke). Their populations show wide fluctuations of abundance (Boyle & Boletzky), largely because they usually grow rapidly to maturity, in one or two years, they carry few food reserves (Rodhouse & Nigmatullin), have little overlap of generations and their migratory patterns make them particularly susceptible to changes in oceanographic conditions. On the other hand, they show great resilience to fluctuations in conditions by their capacity to vary their growth rates, extend their breeding seasons, vary the depth of their spawning grounds and maintain complex recruitment patterns (Boyle & Boletzky).

Cephalopods in general have developed special means to collect sufficient nutrients to fuel their growth and high metabolic activity in an environment having seasonal fluctuation in food and a varying biomass spectrum (Rodhouse & Nigmatullin). They maintain a capacity to take small food while increasing the maximum size they eat during growth. As Rodhouse & Nigmatullin have shown, by their development of arms with adhesive structures, cephalopods have effectively expanded their food collection apparatus from the mouth to such proportions that they can capture, hold and devour animals approaching or even exceeding their own size. This has considerable advantages over the mouth of the fish and changes our usual concept of the nutrient chain progressing through ever larger animals. Cephalopods have a capacity to catch, ingest and digest animals of most phyla in their environment, and can switch from one to another as required. They migrate to optimum feeding grounds, but this increases their demand for energy. They are regular cannibals and thus obtain access to food accumulated through several mouths, from several size groups of food organisms and this may, perhaps, facilitate migrations through areas which are deficient in food organisms of other phyla (Boyle & Boletzky).

2. SIZE OF CEPHALOPODS

Consideration of the role of cephalopods should not neglect reference to their size. Reference to the giants of 20 m is usually considered against a background of inshore species comparing to middle-sized fish of 500 mm or so. Midwater oceanic fish and cephalopod species are usually thought of as small. However, while most of the midwater fish have maximum lengths less than about 200 mm, the majority of the cephalopods in midwater, the ommastrephids, histioteuthids, octopoteuthids, cranchiids, etc. mature at much larger size. While the fish and cephalopods caught by midwater research nets, between mouth areas of 7 m^2 and 50 m^2, look roughly the same size, the majority of the fish are mature and the majority of the cephalopods are very young stages. It is difficult to quantify the marked difference between midwater fishes and cephalopods in this respect, but figure 1 shows an attempt for species caught off Madeira. The comparison is made between the maximum fork lengths of the fish species and the maximum lengths from the tips of the arms to the apex of the body of the cephalopods (often called 'standard length'; they are calculated here from mantle lengths and are regarded as a more realistic length to compare with the fish length, as much muscle usually lies in the arms and head). The large pelagic species, such as tuna, sharks and billfish, lie above 1000 mm, while

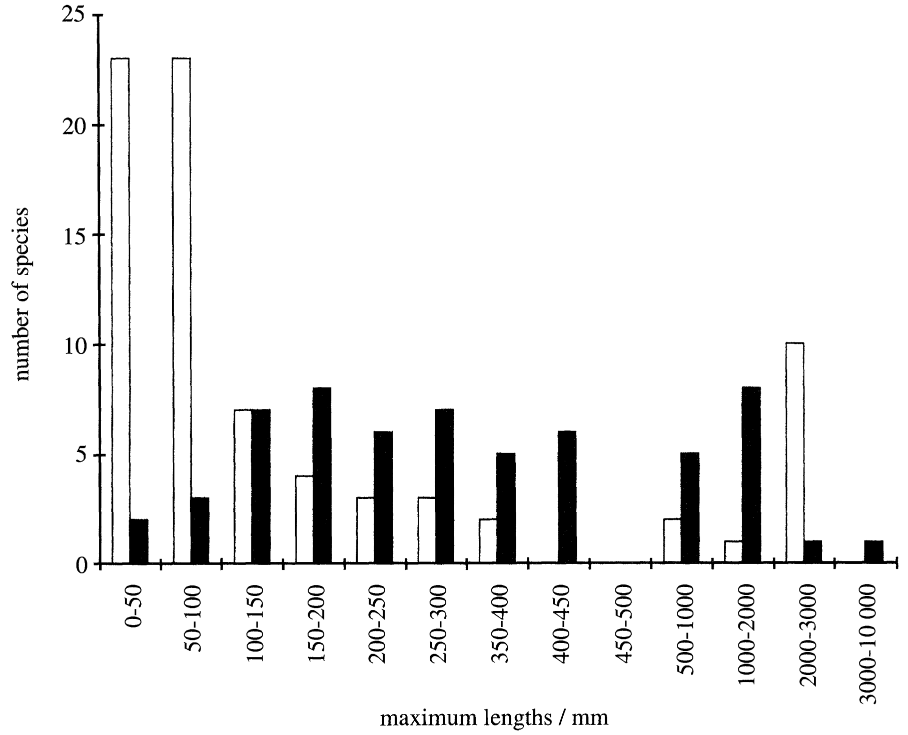

Figure 1. A histogram of the maximum lengths, extracted from the literature, of 76 fish species (fork lengths; open squares) and 62 cephalopod species (standard lengths derived from mantle lengths; closed squares) occurring in midwaters off Madeira. The fish above 1000 mm are represented by the large pelagic fishes such as sharks, tunas, swordfish, billfish and sailfish and there may be a few more than the 11 species shown.

most of the midwater fish lie below 100 mm. Most cephalopods lie between these groups.

That this is so is also supported by the comparison of net-caught cephalopods with specimens of the same families collected from sperm whale stomachs (Clarke, figure 1, p. 979), which shows the large gap between the sizes of cephalopods caught in nets and the sizes of cephalopods in the same waters. It is therefore very likely that cephalopods comprise a much greater part of the biomass in midwater than is recognized in most models of the oceanic biota. This biomass might equal or even exceed that of fish.

3. ENVIRONMENTAL IMPACT

Boyle & Boletzky draw attention to our lack of detailed knowledge on the effect that the presence and migration of cephalopods has on the distribution of chemicals and energy. For example, the annual movement of hundreds of millions of ommastrephid individuals, during phases of high growth, on to the Continental shelves of the world must make an enormous mass available as food for neritic species of many phyla, as well as removing a much greater biomass when they return to deep water to spawn. These cephalopods are the basis for the main fisheries of the world, so we have some slight idea of the magnitude of their effect, but we have no idea of the causes of their natural fluctuations.

The impact on their animate environment of shoaling, migrating squids and even perambulating octopods, can be very considerable. They include in their food many commercial species (Rodhouse & Nigmatullin). Although impact by large squids may be more recognized, there is no doubt that the impact of the more numerous, more voracious and more active early stages must have a greater effect. Juveniles may consume up to 72% of their body weight per day and they attack the smaller stages of the commercial stocks. A strange feature of our sampling is that only rarely do our samplers collect paralarvae and they provide little evidence for their prodigious numbers and immense impact.

An estimate of the consumption by squids worldwide is $2–4 \times 10^9$ t (Rodhouse & Nigmatullin). Overall, the squids greatly exceed the octopods in importance, although muscular octopods on the shelves and neutrally buoyant, pelagic and bathy-benthic octopods are widespread and, in some regions and in some years, their numbers may reach plague proportions and have devastating effects on local commercial crustaceans (Rodhouse & Nigmatullin).

Little has been done on any chemical concentrating mechanisms special to cephalopods, although Caurant (1995) noted that squids are well known as cadmium accumulators and may be a significant source of this element to their predators.

4. PRESENT AND POSSIBLE FUTURE EXPLOITATION

The total world catch of all fisheries went from 65.2 mt in 1970 to 98.1 mt in 1994, showing an increase of 50%, while in the same period cephalopod catches went from 1 mt to 2.8 mt, showing an increase

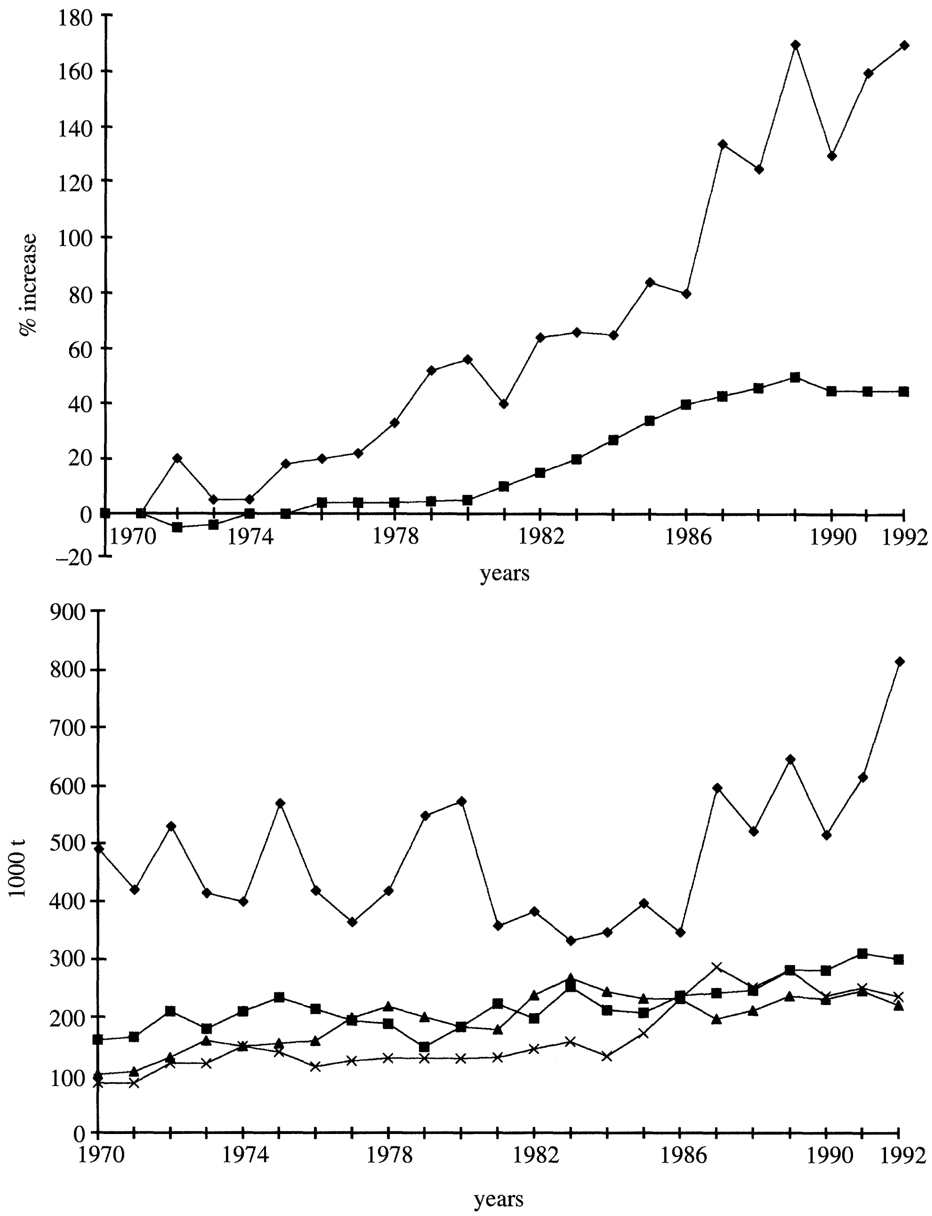

Figure 2. (*a*) Comparison of world landings of all commercial marine species (closed squares) and the cephalopod landings (closed diamonds). (Extracted from FAO statistics.) (*b*) Trends in the landings of cephalopods by major categories: oceanic squid (closed diamonds), octopus (closed aquares), cuttlefish (closed triangle) and neritic squid (crosses). (Extracted from FAO statistics.)

of 180% (figure 2). The composition of the catch of cephalopods in this period shows the importance of 'oceanic squid', but nearly all these are ommastrephids with *Todarodes pacificus* and *Illex argentinus* by far the largest components. While an increase in catch of the exploited families probably will take place, as the current level of fish stocks reduce, their increase is likely to be achieved by expansion of the fisheries into the less fished regions of the oceans which are evident in figure 3. However, eventually man is likely to turn to other species and other families to replace fish stocks which overfishing may reduce irreversibly.

We should ask which species of cephalopod might become of interest to man for food? As touched on by Croxall & Prince, Klages, Clarke and Smale, there is clear evidence, mainly from estimated consumption of their predators, that there are large cephalopod resources in the open ocean available for exploitation. Table 1 lists the medium to large cephalopods with large populations already exploited or with potential for exploitation, including the deep-water species. Because their tissues contain ammonia, many oceanic squids are distasteful and only likely to be valuable for industrial processing. However, experiments are being carried out to remove this defect on a commercial scale. The ommastrephids, which are already the greatest contributor to the shelf commercial cephalopod fisheries, and include a few species not moving into shelf waters, have no ammonia and good firm flesh.

Four Atlantic species: *Sthenoteuthis pteropus*, *Ommastrphes bartrami*, *Martialia hyadesi* and *Todarodes sagittatus*; four Indo-Pacific species: *Sthenoteuthis oualaniensis*, *Ommastrephes bartrami*, *Nototodarus philipinensis* and *Dosidicus gigas*; and the circum-polar, sub-Ant-

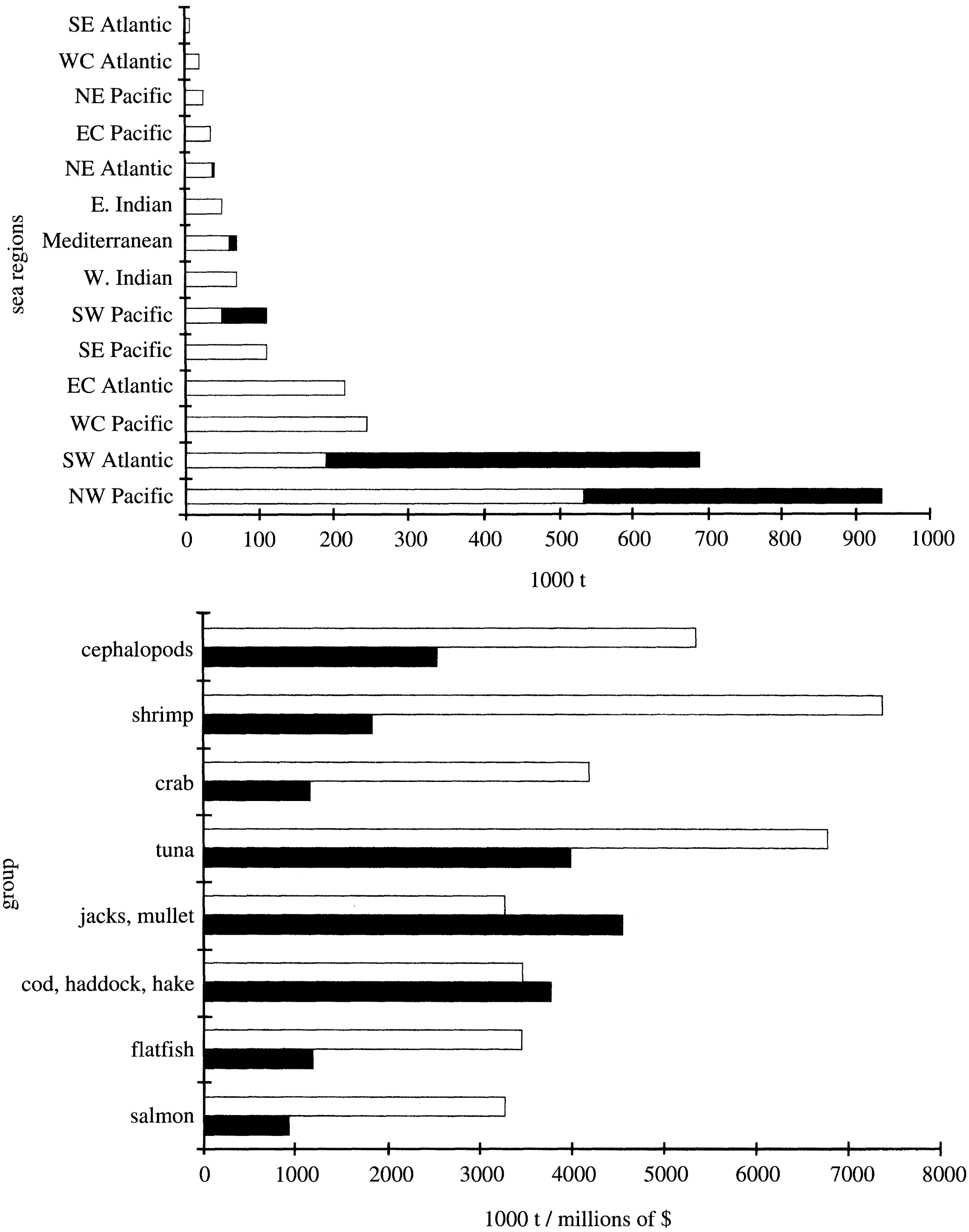

Figure 3. (*a*) World distribution of cephalopod catches, neritic (open squares) and oceanic (closed squares). (Extracted from FAO statistics.) (*b*) Estimated total landed (closed squares) and values (open squares) of selected marine groups. (Extracted from FAO statistics.)

arctic *Todarodes filippovae* have large unexploited or underexploited populations. Their capture in deep water will need minor developments in catching technique, but major effort in detection techniques to find where they congregate for feeding and spawning. Very large increases in tonnages of high quality cephalopods could result. Experiments with gill-netting proved successful near sea mounts but has now been banned. The only other oceanic families with high quality flesh and large populations are the Thysanoteuthidae, Gonatidae and Pholidoteuthidae. *Thysanoteuthis* produced a very large catch with drift-jigging in the North Pacific (up to 100 million yen in value) and gonatids are widespread in the Arctic and North Pacific and can be caught by development of present methods. *Pholidoteuthis*, however, is among many others listed in table 1 which are probably living on the Continental slope in canyon areas which man has failed to fish effectively. None of these are catchable without major development in fishing techniques and nearly all of them would need processing. Before these are utilized, catching the cosmopolitan Histioteuthidae could be considered. This family is a major contributor to many diets of oceanic cetaceans, birds, seals and fish from the Arctic to the Antarctic. They shoal in midwater mainly at 200–800 m but no method has yet been designed to catch them in large numbers, although they are sluggish. However, one large commercial catch has already been made in the North Atlantic (Okutani, personal communication).

Table 1. *Medium to large cephalopods having large populations*

ecosystem		family	genus	species	Atlantic	Pacific	Indian Ocean	Antarctic	Arctic	Adult length	flesh	palatability	Fisheries indust	artis	exploitation	estimated stock × 1000 t
continental shelves		Octopodidae	Octopus	9 species	X	X	X			< 5 m	firm	good		X	under	
		Sepiidae	Sepia	many	X	X	X			1 m	firm	good		X	under	
		Loliginidae	Loligo	many	X	X	X			1 m	firm	good		X	under	
			Sepioteuthis	3 species	X	X	X			0.5 m	firm	good		X	under	
		Ommastrephidae	Todarodes	pacificus		North				0.75 m	firm	good	X		over/recovering	
				sagittatus	X					0.75 m	firm	good			under	
			Nototodarus	gouldi		Australasia							X		satsfactory	
				sloanii		N.Z.							X		satisfactory	
				philippinensis		China sea									under	
			Illex	illecebrosus	Northwest					0.40 m	firm	good		X	over	
				argentinus	Southwest					0.40 m	firm	good	X		satisfactory	
				coindeti	East					0.40 m	firm	good		X	satisfactory	
			Todaropsis	eblanae	X					0.40 m	firm	good		X	under	
			Martialia	hyadesi	Southwest					0.75 m	firm	good			not exploited	
continental slopes (on bottom, in canyons) (cephalopods not caught)	upper 500 m	Loliginidae	Loligo	many	X	X	X			1 m	firm	good		X	under	
	below 500 m	Octopodidae	Benthoctopus	few	X	X	X		X	1 m	firm	good			not exploited	
			Bathypolypus	few	X	X	X			1 m	firm	good			not exploited	
		Alloposidae	Alloposus	mollis	X	X	X			3 m	gelly	not			not exploited	
		Architeuthidae	Architeuthis	several	X	X	X			20 m	soft	not			not exploited	
		Octopoteuthidae	Octopoteuthis	rugosa	X	X	X			0.5 m	soft	not			not exploited	
			Taningia	danae	X	X	X			2 m	soft	not			not exploited	
		Lepidoteuthidae	Lepidoteuthis	grimaldii	X	X	X			1.5 m	soft	not			not exploited	
		Pholidoteuthidae	Pholidoteuthis	2 species	X	X	X			1 m	firm	poss. good			not exploited	
		Cycloteuthidae	Cycloteuthis	akimushkini	X	X	X			0.75 m	soft	not			not exploited	
		Cranchiidae	Megalocranchia	several	X	X	X			1 m	firm	not			not exploited	
			Teuthowenia	3 species	X	X	X			0.5 m	firm	not			not exploited	
oceanic midwater (may spawn on slopes and seamounts very few caught)	often above 200 m	Ommastrephidae	Ommastrephes	bartrami	X	X	X			1.5 m	firm	good	X		under	380
			Sthenoteuthis	pteropus	X					1 m	firm	good			not exploited	1600–2500
				oualaniensis		X	X			0.75 m	firm	good			not exploited	300
			Dosidicus	gigas		Southeast				3 m	firm	good	X		under	1300–18000
			Todarodes	filippovae	X	X	X			0.75 m	firm	good			not exploited	
		Thysanoteuthidae	Thysanoteuthis	rhombus	X	X	X			1.5 m	firm	very good	X		under	
(some netting over seamounts discontinued)	below 200 m	Onychoteuthidae	Kondakovia	longimana				X		2 m	soft	?			not exploited	
			Moroteuthis	robsoni	X	X	X			1 m	firm	poss. good			not exploited	
			Moroteuthis	robusta		North				3 m	firm	poss. good			not exploited	
			Onychoteuthis	boreali-japonicus	X	X				0.3 m	firm	good			not exploited	130
		Cranchiidae	Mesonychoteuthis	hamiltoni				X		6 m	soft	poss. good			not exploited	1500
		Histioteuthidae	Histioteuthis	about 10 species	X	X	X	X		1 m	soft	not			not exploited	
		Gonatidae	Gonatus		X	X		X	X	0.6 m	firm	good			under	6000
			Berryteuthis			X				0.6 m	firm	good			under	
			Gonatopsis			X				0.6 m	firm	good			under	

The increased utilization of these oceanic species might have very far-reaching effects on the oceanic ecosystem and much caution should be exercised before such developments take place. The short life cycles and terminal spawning of many cephalopods may make heavy exploitation during particular seasons more devastating to the stocks than for longer living fish species but, on the other hand, it might make planning of less destructive exploitation easier.

5. THE ROLE OF CEPHALOPODS

In this issue we have shown the importance of cephalopods as predators and as food of top predators in and above the sea, particularly the deep oceans of the world. Population mass estimates are preliminary but commensurate with fish.

One way of assessing the role of cephalopods in the sea is to ask, 'What would happen if cephalopods were removed or even just reduced?' To attempt this we must first know the position in the energetic heirarchy held by cephalopods, mainly squids, in the oceans.

The contributions by Croxall & Prince, Klages, Clarke and Smale summarize their position in outline. Muscular cephalopods generally derive energy from crustaceans in their early lives and from fishes, up to their own size, in their later lives. They also cannibalize their own species and other cephalopods (Rodhouse & Nigmatullin).

Many oceanic birds, particularly petrels, prey on larval and juvenile squids but a few of the larger birds, such as albatrosses, take larger stages. Muscular squids, as they become sub-adults and mature, are consumed by large fish, like billfish, broadbills and tunnas, and marine mammals including sperm whales, beaked whales and elephant seals (The papers on predation). These cephalopods are the fast food store for the large oceanic predators. They convert and concentrate slow- and fast-growing oceanic resources rapidly into high energy food for large predators. By taking full advantage of high seasonal fluctuations in production for their own growth during their annual or biannual lives, they provide a ready and steady long-term supply for their predators. On the other hand, the neutrally buoyant squids such as the Histioteuthidae, Octopoteuthidae and Cranchiidae probably greatly outweigh the muscular squids and also provide energy to the same predators but not over the Continental shelves. The energy per mass of these may be as little as one half the energy of muscular squid (Clarke *et al.* 1985), but their total biomass and stored energy probably greatly exceeds those of muscular squids in the deep oceans. The papers on predation show what

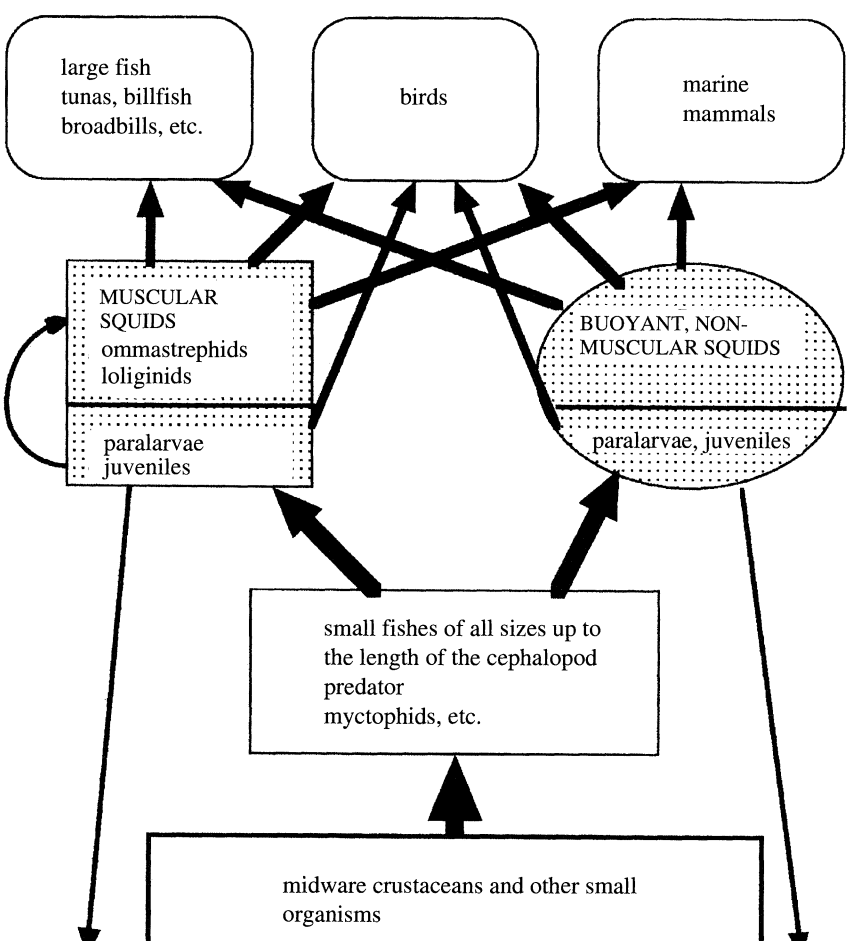

Figure 4. A summary of the role of cephalopods in the world's oceans and seas as expressed by their position in the energetic heirarchy.

eats these low energy cephalopods but we have almost no information of their food, their energetics, their growth or their life cycles and spawning. We do not even know where they spawn or what the spawn looks like.

Loss of energy from the 'cephalopod level', which does not reach the top predators and mainly enhances the energy of the benthic ecosystem, includes some from death at spawning, unhatched or consumed spawn, scraps as a biproduct of their feeding (e.g. fish heads), shedding of mucus, etc. and loss in faeces (Wells & Clarke). All this may considerably enhance productivity of the benthos in specific areas.

From figure 4 and the fact that most top predators include fish as well as muscular and buoyant cephalopods in their food, we can make tentative predictions of the effects of removal of cephalopods from the Continental shelves and the deep ocean. Removal of cephalopods from the shelves would have local influences on the muscular Loliginiidae, Sepiidae, Sepiolidae and Octopodidae; some crustacean and fish populations would increase because of the removal of these predators and others would decrease because a high energy source would disappear. Annual production would probably be reduced. The balance of species would change, but cephalopods represent only a small part of shelf life. Destruction of the other family occurring on the shelf seasonally, the Ommastrephidae, would have a much wider effect because they spend most of their lives in the deep ocean. Their serious reduction, as has happened in *Todarodes pacificus* and *Dosidicus gigas* from over-fishing or climatic changes must have very broad, but, as yet, unquantifiable effects on oceanic life. The removal of muscular cephalopods from the deep ocean would substantially reduce the food choice of many odontocetes, some pinnipedes, some large fish and many oceanic birds. They might be able to increase their predation on non-muscular squid and small fishes but, in either case, the energy aquired might not repay the extra energy required to gather the prey, and removal of cephalopods is likely to lead to reductions in these top predator populations. If the muscular cephalopods were removed by fisheries and then followed by removal of buoyant squids, impact on top predator populations would be greatly increased; over large areas of the deep oceans, populations of small midwater fish like myctophids would increase, and populations of the top predators, particularly cetaceans and seabirds globally and seals and fishes regionally, would decrease.

At present we can only look at the problem locally, but to take one example, in the Antarctic the annual consumption of odontocetes is estimated at 14.4 mt and the squid taken by beaked whales alone are calculated to eat about 24 mt of krill, approaching the 33 mt of krill consumed by penguins (Kasamatsu & Joyce 1995). What if the Eastern cephalopod-eating nations managed to fish out *Dosidicus gigas* in the south east Pacific, *Todarodes sagittatus* in the North Atlantic or *Ommastrephes bartrami and Histioteuthis* spp. from the open ocean? What if all cephalopods disappeared or even just certain families in certain areas? Would we lose all the teuthophages such as *Physeter*, *Globicephalus*, *Grampus*, some seal species, some shark and tuna species, some albatross and penguin species? Or could some of these adapt to heavier fish-eating? We might assume the predators eating both fish and cephalopods would readily change to more fish. Where would these come from – the shelf or the deep sea? Ultimately, certainly the shelf, with consequent large losses to commercial fish stocks. Apart from that, there are already held to be some indications that as shelf-living fish stocks go down due to over-fishing, cephalopod catches go up (Boyle & Boletzky).

Perhaps of more academic interest is what would be the effect on parasite cycles if cephalopods were reduced? Are they so specific that the cephalopod predators may become healthier with large reductions in certain secondary hosts? Does the enormous production of eggs protect the parasites from serious reduction even if the hosts are much reduced in numbers?

6. THE FUTURE

The extension of cephalopod fisheries to include more oceanic species offers a chance to improve our knowledge by riding on the improvements in sampling that the industry can implement. But the industry must be made to recognize its own position as just another predator and its long-term dependence on a better understanding of the role of all cephalopods in the ocean. It must resist the temptation to regard the current target species as the only one of interest and as independent from its predators, its food and the complex structure it enhances. More cooperation between the industry and environmental biologists is a basic requirement for sustaining the industry and increasing our knowledge of the role of cephalopods.

Methods outlined in the papers on predation show the importance of cephalopods in the marine biosphere. They also illustrate the intangible nature of the results. Any but the most general conclusions are hampered by temporal, regional and sampling variations. Is there any point in continuing such investigations now that we have general pictures, if all we can hope to obtain is more of the same? There is still much to be learned about cephalopods by continuing such food analyses, but further progress will be greatly enhanced if substantial parts of well-defined ecosystems are studied in detail over several years. As a first attack, trophic links between the fish, cephalopods and vertebrate predators should be studied within representative areas. A start has been made for the Antarctic (e.g. British Antarctic Survey work quoted by Croxall & Prince and Klages), but while most studies have the same ultimate aim, concerted effort in smaller areas should be more illuminating. Areas could be (*a*) round an oceanic island group (e.g. Azores, Galapagos Islands), (*b*) over parts of the continental slope (see work off South Africa) or (*c*) in well-defined seas or bays. We desperately need to know more about the ammoniacal, neutrally buoyant cephalopods, particularly the Histioteuthidae, Octopoteuthidae and Cranchiidae, their growth rates, conversion rates and food. The methods of using beaks of cephalopods and otoliths of fish need to be further refined and this can best be achieved by studies within the areas selected (e.g. Smale *et al.* 1993).

Only such studies can provide the data for more sophisticated modelling of cephalopods in the ecosystem and a full understanding of their role, together with predictions of the affects of their exploitation. Man will certainly exploit cephalopods to an increasing degree. Before he develops techniques efficient in the open ocean, it is essential that a much better understanding of the likely effects is obtained so that some basis for regulation can be used in argument. In view of the difficulties confronting international regulation, the only safe way forward is to seek agreement to an international moratorium on oceanic cephalopod fishing until more research can form a basis for rational exploitation. If exploitation extends further into the deep ocean it will be very difficult to control or stop. The balance of the planet's marine life is at stake and all nations could be affected.

From this issue we can begin to see the role of cephalopods in the oceans, but much more work on all aspects is required and we hope that this will give a stimulus to fill in the detail and progress with the methodology. Probably the greatest gap in our knowledge concerns all aspects of the biology of neutrally buoyant oceanic squids which we only really know are there from predators' stomach contents, we can only catch in small numbers and we cannot keep alive.

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