Role as Consumers

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Role as consumers

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SUMMARY

Cephalopods are voracious, versatile predators. They generally have a short life span and a single spawning event followed by death. Populations are subject to dramatic fluctuations and their impact on prey populations is equally variable. The prehensile arms and tentacles of cephalopods, coupled with a highly evolved sensory system, allow them to occupy a broad trophic niche and migrations enable populations to exploit the temporal and spatial variability of production systems and populations of prey. Shoaling is a common behavioural feature of many species which facilitates prey capture and contributes to the impact of cephalopods on prey populations. Research on cephalopod stomach contents is hampered because the beak is used to bite the prey into small pieces so hard parts, which are usually needed for identification of prey species, are often rejected causing potential bias in estimation of diet. Cephalopods may also feed unnaturally in the presence of sampling gear. Despite these problems there is a growing body of data on cephalopod predation collected using direct observations, conventional visual analysis of stomach contents and serological methods. Most species feed on small crustaceans as juveniles and shift the diet to larger fish and other cephalopods during growth. This shift is accompanied by ontogenetic changes in the allometry of the brachial crown. There is increasing evidence that myctophid fishes are an important food resource for oceanic squid. The diet and stock size of some commercially exploited squid populations is sufficiently well known to quantify the impact of a single generation on the prey community. Where there is predation on commercial stocks of fish and crustaceans, the effect of cephalopod feeding on recruitment may be significant. Cephalopods are trophic opportunists in marine food webs from polar to equatorial seas.

1. INTRODUCTION

The cephalopods are active, fast-moving predators and they all feed on live prey. They are short-lived – generally having a lifespan of about one year – and they die after a terminal spawning event. To support this life-history strategy they feed voraciously, and with great versatility, on a wide range of prey to achieve high growth rates and maintain high rates of metabolism. These life-history and physiological traits enable the cephalopods to be opportunists in variable environments. Cephalopod populations respond rapidly to natural and anthropogenic environmental change in marine ecosystems and cephalopod fisheries show dramatic interannual fluctuations in recruitment and catch rates that are apparently unrelated to fishing effort (Beddington *et al.* 1990). These fluctuations can be expected to affect prey populations. Occasional plagues of cephalopods are well documented (Rees & Lumby 1954; Nesis 1983) and there is some evidence that where fish populations have been overexploited cephalopods may have filled the vacant trophic niche in the ecosystem and replaced fish as a commercial resource (Caddy 1983; FAO 1993).

The annual life cycle that is usual for many cephalopods means that their impact on prey populations is highly seasonal and in migratory species is spatially variable. The impact of cephalopods in marine ecosystems is subject to considerable interannual variation; when a strong cohort passes through a system, high rates of predation, coupled with high metabolic efficiency (manifested as growth efficiency), translate into substantial energy and nutrient flux to higher trophic levels and increased catch rates in the fisheries. Predation by a strong cohort of cephalopods on early stages of commercial fish is likely to be a variable affecting the recruitment success of fish stocks.

Here we explore the role of cephalopod populations as predators in marine ecosystems, especially in the context of their opportunistic life-cycle characteristics including the ability to prey on a wide range of prey species, short lifespan, high biomass turnover and semelparity. We confine ourselves to the coleoids – the squid, cuttlefish and octopus – and focus on the major fishery stocks and marine ecosystems.

2. MORPHOLOGICAL ADAPTATIONS

The cephalopod feeding apparatus is unique in the animal kingdom, possessing an extraordinary set of adaptations to facilitate prey handling and enable opportunistic feeding on a wide variety of prey types.

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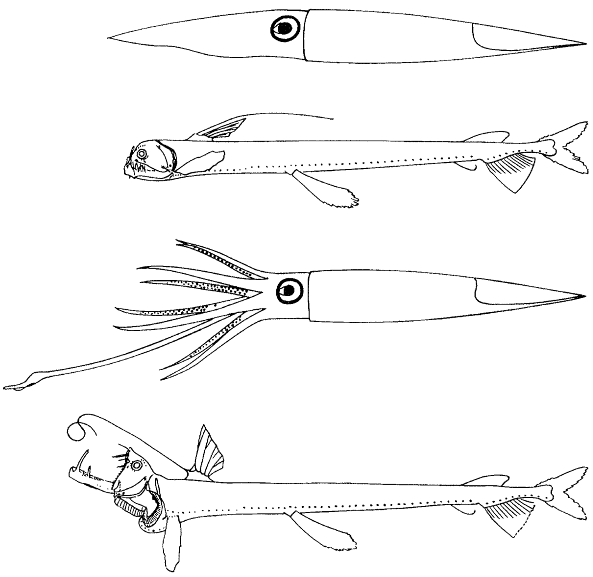

Figure 1. Comparison of the relative gape of the brachial crown of the squid *Illex* and the mouth of a midwater fish, *Chauliodis*, of similar size (both prey on midwater crustaceans and fishes).

An array of eight arms and, in squid and cuttlefish, two tentacles form the brachial crown, which surrounds the mouth (Boletzky 1993). In the octopuses the tentacles are absent and in some squids (eg. the Octopoteuthidae) they are shed during ontogenesis. The tentacles are extensible and employed in the initial capture of prey (Kier 1982). The brachial crown is effectively the functional mouth of cephalopods (Packard 1972), serving to capture, envelope and immobilize relatively large prey. This function is enhanced in many species, most notably the cirrate octopuses, by the presence of a web of skin between the arms. Compared with the fish mouth, the cephalopod brachial crown is large and considerably more versatile as a mechanism for capture and handling of prey. This is illustrated in figure 1, which compares a squid (*Illex*) with a fish (*Chauliodus*) of similar overall length. Both prey on midwater crustaceans and fishes; *Chauliodus* has a specially adapted jaw for handling relatively large prey items. As well as the size advantage of the squid brachial crown it is also much better at manipulating large, struggling prey than the fish mouth.

The prehensile arms and the tentacles of cephalopods are armed with suckers that are smooth and muscular in the octopuses (Kier & Smith 1990) and in the squids possess a chitinous ring usually furnished with small teeth that serve to prevent the sucker from slipping (Nixon & Dilly 1977). In some or all deep-sea members of the squid families Onychoteuthidae, Enoploteuthidae, Pyroteuthidae, Ancistrocheiridae, Octopoteuthidae, Gonatidae and Cranchiidae, some sucker rings develop during ontogenesis to form a chitinous hook, which facilitates grip on soft, fleshy prey such as fish and squid (Engeser & Clarke 1988). The mouth, which is relatively small, contains a chitinous beak, which masticates the food before it is swallowed. Species differences among the beaks of squid have not been related to diet (Clarke & Maddock 1988) but the shape of the beak dictates the area available for insertion of the mandibular muscle and hence its mass and biting force (Kear 1994). Beak morphology has been shown to differ markedly among sympatric Antarctic octopuses (Daly & Rodhouse 1994); this difference has probably arisen through the evolutionary process of character displacement. The buccal apparatus possesses a tongue-like radula adapted for rasping in the squids and for drilling in the incirrate octopuses (Altman & Nixon 1970; Mather & Nixon 1995). In some species the posterior salivary gland, which is associated with the buccal mass, produces cephalotoxin (Ghiretti 1959), and this paralyses the prey with the bite and is responsible for limited external digestion (Nixon 1985). The cephalopod alimentary tract is adapted to handle more than one meal at a time and for rapid digestion and high absorption efficiency (Boucher-Rodoni *et al.* 1987). Both the paralarval and the adult digestive systems are adapted for a carnivorous diet (Boucaud-Camou & Roper 1995). Prey is primarily visually located with the highly evolved eyes (Williamson 1995) but recently a 'lateral line' system has been discovered (Budelmann & Bleckman 1988) that is also implicated in prey detection and assists in prey location during darkness and in poor visibility.

3. BEHAVIOURAL ADAPTATIONS

(*a*) *Migration*

Given the seasonal variation and spatial patchiness of food resources in the oceans, coupled with the high metabolic requirements of cephalopods, a major selection pressure driving the evolution of migration has been the necessity to maximize feeding rate throughout the life cycle. Migration routes must therefore facilitate high feeding rates throughout the lifetime of a cohort.

The major ommastrephid populations exploited by fisheries and predators inhabit the western boundary currents and upwelling regions of the oceans and, during the course of the life cycle, make extensive migrations within these systems, exploiting latitudinal differences in the seasonality of production to maintain growth and maturation rates (Coelho 1985). Spawning in the *Illex* species complex takes place in tropical or subtropical regions of high productivity; the hatching rhynchoteuthions grow in meandering retention areas or in the polewards flow of the boundary current (O'Dor 1993). There is evidence that in some *Illex* species the migration subsequently splits, with one portion remaining at low latitudes and another portion, which is more variable interannually, migrating to productive areas in higher latitudes to grow and mature. This allows the stocks to exploit the more predictable, but less productive, low-latitude systems for the early life cycle and also allows at least part of the stock to exploit the less predictable, but more productive, higher-latitude systems during the later life cycle. During the growth phase of the life cycle some species of squid associate with warm core rings (Rowell *et al.* 1985; Vecchione & Roper 1986; Sugimoto & Tameishi 1992; Rodhouse *et al.* 1996), which are often features of enhanced productivity (Hitchcock *et al.* 1987). Once the squid approach maturity and readiness for spawning there is a return migration to the spawning area. The migration rate of a tagged *Illex illecebrosus* has been shown to average nearly 20 km d^{-1} (Dawe *et al.* 1981); *Ommastrephes bartrami* covers 5–10 km d^{-1} depending on the season (Araya 1983). Calculations show that feeding must continue during ommastrephid migrations as metabolic reserves are insufficent to meet the energy costs of swimming over the distances involved (A. Clarke *et al.* 1994). The squid must therefore track areas of production, which are variable both spatially and temporally, over the whole life cycle. Ommastrephids, and other squid, are cannibalistic; if poor feeding conditions are met during the migration, this behaviour may provide a mechanism for survival of at least part of the school (O'Dor & Wells 1987). However, cannibalism may be overestimated, as most evidence comes from samples taken with fishing gear, which causes bias (Breiby & Jobling 1985).

Many of the neritic cephalopods (loliginids, sepiids and octopodids) spawn in shallow water, where the young spend the early part of the life cycle, then migrate into deeper water as they grow and subsequently return to the shallows to spawn (see, for example, Mangold-Wirz 1963; Hatfield *et al.* 1990; Boucaud-Camou & Boismery 1991). This strategy places the newly hatched paralarvae and juveniles in the best position to prey on small planktonic crustaceans that are low in the food chain and are feeding on phytoplankton in the photic zone. Later they encounter larger prey in deeper water during the ontogenetic descent. There is evidence that some deepwater species may make upslope ontogenetic migrations over the life cycle (Villanueva 1992) but the role of these movements in relation to foraging has not been explained. Some neritic species also make horizontal migrations. *Loligo vulgaris reynaudii* migrates along the Cape Coast of South Africa (Augustyn *et al.* 1992) and these movements, driven by foraging requirements, are linked to local hydrographic conditions (Roberts & Sauer 1994). Feeding in this species continues until the squid are on the spawning grounds (Sauer & Lipiński 1991).

(*b*) ***Diurnal vertical migrations***

Many oceanic cephalopods make diurnal vertical migrations, which allow them to maximize the breadth of their trophic niche while minimizing the risk from predation in the upper, well-lit, layers of the water column. Most vertical migrations are towards the surface at dusk, returning to deeper layers at dawn (Clarke & Lu 1974, 1975; Lu & Clarke 1975*a*, *b*; Piatkowski *et al.* 1994). Because of these vertical movements, studies of feeding based on samples from fisheries that catch only at night (jiggers) or during daytime (trawlers) may bias estimates of diet (Tanaka 1993).

Vertical migration patterns differ between species and change with age and sexual maturity. In the South Atlantic immature and maturing *Illex argentinus* feed near the seabed on the Patagonian Shelf during the day and migrate to the surface at night. As they approach maturity they move into deeper water on the continental slope, where they remain near the bottom during the day and move up to depths of 200–300 m at night to feed on myctophids in the acoustic scattering layer (Nigmatullin 1989).

(*c*) ***Shoaling***

Shoaling behaviour in squid probably makes it easier for the individual to capture prey than when hunting individually and also reduces the likelihood of it being the victim of predation by being harder to locate and attack (Neill & Cullen 1974; Krause 1994). Many ommastrephids and loliginids are shoaling species, making them especially suitable for commercial exploitation; shoaling is probably a common feature of the behaviour of many species (Hanlon & Messenger 1996).

Where present, shoaling behaviour must influence the impact of cephalopods as predators. Attack by shoals is likely to be patchy in distribution, both temporally and spatially, and can potentially devastate prey densities locally.

4. METHODS OF ANALYSIS OF CEPHALOPOD DIET

Most studies of cephalopod diet have either been opportunistic observations or analyses performed as part of other fishery research. There are several specific problems of dietary analysis in cephalopods. The diameter of the oesophagus has been constrained during evolution because it passes through the brain, so although cephalopods are capable of capturing relatively large prey items, the beak bites off small pieces of tissue to swallow. Hard parts, which are usually necessary for identification of prey such as fish skeletons and crustacean integument, are thus often rejected. Furthermore, selective rejection will tend to bias data on prey species and size if, for instance, bones of small prey items are swallowed and those of larger specimens discarded. Voracious feeding behaviour, even when captured, means that cephalopods from net tows may have fed after capture so their stomach contents may not reflect natural diet. Breiby and Jobling (1985) have suggested that only the most digested stomach contents should be recorded in dietary studies in order to avoid bias caused by unnatural feeding in the presence of fishing gear.

Pelagic cephalopods are difficult to observe directly in the field; the inshore species, which are sometimes encountered by divers, are either cryptic in their behaviour, or wary, and difficult to observe behaving naturally. Rapid digestion rates ensure that many specimens have little or no food in the stomach and material that has passed beyond the stomach is visually unidentifiable.

A further problem in interpretation of gut contents is that food items in the guts of the prey might appear to have been consumed directly, for example when squid have been feeding on planktivorous fish, and if mistaken for primary prey will bias estimates of actual prey. Such items are likely to be relatively small and present in large numbers, but given the trophic niche width of many cephalopods it may be difficult to distinguish between these and prey consumed directly.

Despite the problems of studying cephalopod diet, there is a growing body of knowledge. Visual studies of squid diet have relied on hard parts of prey species for identification of prey to species level. Fish otoliths, fragments of crustacean integument and eyes, cephalopod beaks and sucker rings can usually be identified; otoliths and beaks are used to calculate body size of prey items by means of independently derived allometric equations (see, for example, Rodhouse *et al.* 1992*b*). When these hard parts are absent it is usually possible to discriminate between more general categories from the presence or absence of fish scales and bones and from the appearance of muscle and other tissue in the stomach. Gut contents have been visually analysed in paralarvae as small as 2 mm in mantle length (ML) by staining the whole specimen with Alcian Blue and clearing with trypsin (Vecchione 1991). Prey of octopuses has been determined by analysis of gut contents (Ambrose 1984; Iribarne *et al.* 1991; Cortez *et al.* 1995) and also by direct observation of feeding and by analysis of the hard parts of prey in middens (Mather 1991). However, Cortez *et al.* (1995) point out that analysis of middens and direct observations of feeding have failed to record piscivory by octopuses whereas gut contents have usually revealed fish remains.

Serological screening of cephalopod digestive tracts has provided a powerful means of testing for specific prey species (Grisley & Boyle 1985, 1988). The method employs antibodies from a host vertebrate that has been injected with proteins (antigens) from a prey species. This is a useful technique for testing for presence or absence of specific prey species and has been used to determine whether the northern octopus *Eledone cirrhosa* preys on several crustacean species (Boyle *et al.* 1986) and to screen a number of Antarctic squid for evidence of predation on Antarctic krill, *Euphausia superba* (Kear 1992). Time and cost constraints preclude the use of serology for routine screening for large numbers of prey species, but many gut samples can be screened quickly for a specified prey. Serology has a significant advantage over conventional analysis of gut contents because proteins retain antigenic sites for some time during digestion, making it possible to detect prey that is no longer visually recognizable (Kear & Boyle 1992). It has potential, for instance, for focusing on the role of cephalopods as predators on particular commercial fish species.

If DNA can withstand passage through the gut and sequences can be amplified by polymerase chain reaction (PCR), as seems likely from vertebrate studies (Höss *et al.* 1992), it may prove possible to use molecular genetic markers to identify prey items in the gut contents and faeces of cephalopods. It should be emphasized that serology, and any future molecular genetic methods, provide accurate qualitative data but these can only be quantified in terms of percentage occurrence in the samples and not at the level of the individual.

Naturally occurring stable isotopes of nitrogen found in animal tissues differ according to prey species and trophic level and provide a means of assessing their level in the food web. The ratio of ^{15}N to ^{14}N ($\delta^{15}N$) in a small sample of *Loligo pealei* has been determined as part of a food-web analysis on the Georges Bank in the western Atlantic (Fry 1988); the species was found to occupy a position intermediate between trophic levels 3 and 4. This is closely similar to the level occupied by planktivorous fish in the pelagic system and also by isopods and large polychaetes in the benthos.

5. THE PREY OF CEPHALOPODS

Nixon's (1987) comprehensive review of cephalopod prey, based on stomach contents and direct observation, covered a large number of species representing several families and provided ample evidence that cephalopods are broadly opportunistic in their predatory behaviour. Most marine phyla, including unexpected forms such as cnidarians (Heeger *et al.* 1992), have been recorded. There are many instances of a squid species feeding on different diets in different geographical locations (see, for example, Ivanovic & Brunetti 1994; Lipiński & Linkowski 1988); these observations emphasize that few, if any, are specialist predators. Direct observation of octopuses in shallow water also indicates that, when foraging, they appear to be unselective in their choice of prey type (Mather 1993).

(*a*) *Neritic cephalopods*

The squids and cuttlefishes in coastal and shelf waters feed primarily on crustaceans, fish and other cephalopods (including conspecifics). Juveniles and subadults mostly prey on crustaceans and shift their diet to fish and cephalopods as they grow (Breiby & Jobling 1985; Le Mao 1985; Lipiński 1987; Castro & Guerra 1990; Guerra *et al.* 1991; Lipiński *et al.* 1991; Collins *et al.* 1994; Pierce *et al.* 1994). Cannibalism seems to be related to poor feeding conditions (Ennis & Collins 1979). Recent records of benthic species in the diet of *Todarodes pacificus* caught in bottom trawls over the continental shelf (Tanaka 1993) indicate the breadth of the feeding spectrum of this species. Benthic organisms may be more important to neritic squid than has generally been realized, especially during the daytime, when their vertical migrations may take them near the seabed and when sampling by jigs is less effective.

The sepiolids feed almost exclusively on mysids and decapod shrimps and ignore crabs and fish. In the Gullmar Fjord, Sweden, *Sepietta oweniana* feeds in the hyperbenthic zone, primarily on the euphausiid *Meganyctiphanes norvegica* and on a pandalid shrimp, probably *Pandalus borealis*, late in the year (Bergström 1985).

Newly hatched octopuses feed in the water column on planktonic crustaceans and then settle to the seabed after a few weeks' growth and switch the diet to nectobenthic crustaceans and benthic molluscs (Nixon

Table 1. *Myctophid species and an assessment of their importance in the diet of oceanic ommastrephids*

ommastrephid species	myctophid species	oceanic region	contribution to total diet	source
Martialia hyadesi	*Krefftichthys anderssoni* *Electrona carlsbergi* *Protomyctophum bolini*	Southern Ocean (Atlantic sector)	frequency of occurrence 77 % (diet dominated by myctophids)	Rodhouse *et al.* 1992*b*; Kear 1992
Sthenoteuthis oualaniensis	*Symbolophorus evermanni* *Myctophum nitidulum* *M. aurolaternatum* *Hygophum reinhardtii* *H. proximum* *Notoscopelus resplendens* *Diogenichthys laternatus* *Ceratoscopelus townsendi* *Benthosema suborbitale* *Triphoturus mexicanus*	eastern Pacific	frequency of occurrence 19–89 % (increases with ML); 41–77 % of biomass (proportion increases with ML)	Shchetinnikov 1992
Sthenoteuthis oualaniensis	Myctophidae	Arabian Sea	predominant items in stomach contents are myctophid remains	Zuev *et al.* 1994; Snÿder 1995
Ommastrephes bartrami	Myctophidae	central Pacific (North of Hawaiian island)	frequency of occurence of fish 33 % (mostly myctophids); 38 % of biovolume consumed is fish (mostly (myctophids)	Seki 1993*a*, *b*
Ommastrephes bartrami	*Myctophum phengodes* *Ceratoscopelus warmingii* *Lepidophanes guentheri* *Symbolophorus* spp *Protomyctophum* spp *Diaphus* spp	southwest Atlantic	frequency of occurrence 32 % (Second in importance after cephalopods)	Lipiński & Linkowski 1988
Ommastrephes bartrami	Myctophidae	North and South Atlantic	fish, dominated by myctophids and juvenile saurids, are the most numerous prey in specimens > 50–80 mm ML	Gaevskaya & Nigmatullin 1976
Illex coindetii	*Ceratoscopelus maderensis* *Mictophum punctatum* *Lampanyctus cocodrilus* *Notoscopelus elongatus*	Mediterranean (Catalan Sea)	frequency of occurrence of myctophids 6–17 % (varies seasonally); numerical proportion of myctophids in diet 2–17 % (varies seasonally)	Sanchez 1982
Illex argentinus	*Gymnoscopelus nicholsi* *Protomyctophum tenisoni* *Lampichthys procerus*	southwest Atlantic	frequency of occurrence of myctophids 0–72 % (varies with location on the Patagonian Shelf)	Ivanovic & Brunetti 1994
Illex illecebrosus	Myctophidae	northwest Atlantic	numerical proportion of fish that are myctophids 45 % (fish dominate diet of squid > 220 mm ML)	Froerman 1984
Dosidicus gigas	Myctophidae	eastern Pacific (Gulf of California)	0–38 % of biomass consumed is myctophids (varies with the seasonal migration)	Ehrhardt 1991
Dosidicus gigas	Myctophidae	eastern Pacific (open ocean west of Ecuador, Peru and northern Chile)	70 % of biomass consumed is myctophids	Nesis 1970
Todarodes angolensis	*Lampanyctodes hectoris*	southeast Atlantic	frequency of occurrence 50–64 %	Lipiński 1992
Todaropsis eblanae	*Lampanyctodes hectoris*	southeast Atlantic	frequency of occurrence 49 %	Lipiński 1992

1985; Villanueva 1994). Whereas squid and cuttlefish preying on pelagic crustaceans ingest the exoskeleton, octopus paralyse their prey with cephalotoxin; after limited external digestion, the flesh is consumed and the exoskeleton rejected. In South Africa *Octopus vulgaris* feed mostly on mussels. Small mussels are opened by pulling the valves apart; large ones are drilled first and then pulled apart (McQuaid 1994). Large octopuses (over 1 kg) feed on larger, more mobile prey and the proportion of fish and cephalopods in the diet increases with body size (Nigmatullin & Ostapenko 1976; Guerra 1978; Villanueva 1993).

Natural octopus densities have demonstrable effects on community structure in the subtidal. On the California coast *Octopus bimaculatus* consumes various gastropods, chitons, bivalves and crustaceans (Ambrose 1986). Over a period of five years, during which a natural decline in octopus density of 80% was documented, total prey abundance, especially of snails and hermit crabs, increased by 500%.

Octopus predation on pelagic organisms may be more common than is generally recognized. *Octopus rubescens* has recently been seen from a submersible feeding on euphausiids at 200 m off Santa Cruz, California (Laidig *et al.* 1995).

(*b*) *Oceanic cephalopods*

The diet of oceanic species is also dominated by crustaceans, fish and cephalopods. Newly hatched paralarval and early juvenile phases of the oceanic squids mostly feed on planktonic crustaceans, especially copepods. A study in the Gulf of Mexico showed that the micronektonic cephalopod assemblage preys mainly on the copepod *Pleuromamma* sp. (Passarella & Hopkins 1991). Although other copepods and euphausiids were also important, *Pleuromamma* was probably selected by the juvenile cephalopods because it is highly bioluminescent. The cranchiids in the community had fewer stomach contents than the muscular species, possibly reflecting a lower food demand in this buoyant group.

At the Antarctic Polar Frontal Zone in the South Atlantic immature *Brachioteuthis* sp. feed primarily on copepods (Rodhouse *et al.* 1996) and in the Croker Passage, Antarctica, *Galiteuthis glacialis* of ML less than 104 mm feed on copepods and small euphausiids (Hopkins 1985).

It has been postulated that the rhynchoteuthion larvae of ommastrephids might suspension-feed on phytoplankton in the immediate post-hatching period after the yolk reserves are exhausted and before effective raptoral behaviour is established (O'Dor *et al.* 1985). Mucus coating the surface of the mantle could trap particulate food and cilia on the mantle could transport this towards the head. This may explain the absence of animal remains in the stomach contents of wild-caught specimens but there is no better direct evidence to support the idea. Phytoplankton have never been found in the rhynchoteuthion stomach; the paralarval digestive system appears to be adapted for carnivory (Boucaud-Camou & Roper 1995).

Subadults of most species shift their diet from microplanktonic forms to macroplanktonic or micronektonic crustaceans including euphausiids, hyperiid amphipods, mysids and decapods. In *Illex illecebrosus*, *I. argentinus*, *I. coindetii*, *Nototodarus gouldi* and *Todarodes pacificus*, with distributions close to and over the continental shelf, crustaceans may remain an important food into full adult size. Where the distributions of *Todarodes pacificus* and *Ommastrephes bartrami* overlap there appears to be niche separation, with *O. bartrami* feeding on fish and *T. pacificus* feeding on crustaceans (Araya 1983). The *Illex* spp., *Nototodarus gouldi* and *T. pacificus* are also opportunists and will readily take fish and cephalopods when available.

Adults of the larger oceanic squid are primarily piscivorous and also feed on cephalopods, including conspecifics, but the extent of cannibalism in natural conditions is questionable (Breiby & Jobling 1985). Some epipelagic forage fishes, e.g. the scomberesocids and exocoetids, are consumed, but myctophids are probably the most important fish prey for many of the larger ommastrephids over the deep ocean and at the edges of the continental shelves (table 1) and they have also been recorded in the diet of histioteuthids (Voss *et al.* 1996) and lycoteuthids (Voss 1962). Although myctophids are of greatest importance for the oceanic ommastrephids they also make a significant contribution to the diet of the shelf and near-shelf forms such as the *Illex* spp., *Todarodes* spp. and *Dosidicus gigas* when they are feeding offshore.

The ecology of the deep-ocean mesopelagic system is poorly understood but the role of ommastrephid squid as predators, and for transferring energy and nutrients from the mesopelagic community to higher trophic levels, may be far more important than has been appreciated. Some myctophids migrate close to the surface at night. They are primarily planktivores feeding mostly on copepods, small euphausiids and hyperiid amphipods (Kozlov & Tarverdieva 1989). Although they are preyed on by demersal fish, including scorpaenids, gadoids, merluciids and macrourids, there is little evidence of predation by epipelagic fish. It is possible that in the open ocean most predation pressure comes from epipelagic ommastrephid squid. At the Antarctic Polar Frontal Zone in the South Atlantic, cephalopods, especially *Martialia hyadesi*, which is a myctophid predator (Rodhouse *et al.* 1992*b*), fill the trophic niche of epipelagic fish, which are apparently absent (Rodhouse & White 1995); there are probably similar food webs in other oceanic regions. The mesopelagic fishes, myctophids, gonostomatids and sternoptychids, form a continuous layer (the deep scattering layer) across all the major oceans and are probably the most abundant vertebrates on earth (Mann 1984). The standing stock biomass of mesopelagic fishes in the productive regions of the open ocean has been estimated to be 7–14 g m^{-2} and production to be 3.5–7 g m^{-2} a^{-1}; this value is comparable with the fish production on many continental shelves of 5–10 g m^{-2} a^{-1} (1 g $\approx$ 1 kcal) so they are an abundant prey resource for oceanic cephalopods.

The deep-living benthopelagic cirrate octopuses have more specialist feeding habits than the incirrate

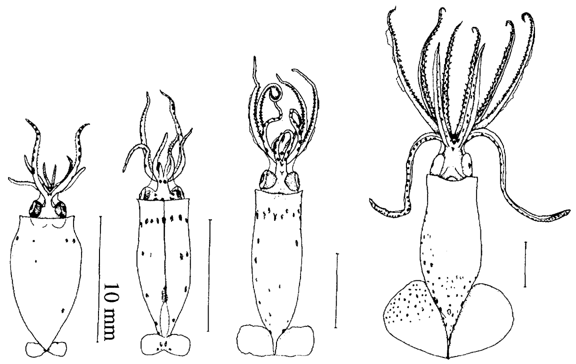

Figure 2. *Gonatus madokai*: ontogenetic phases drawn with the mantle at the same size to illustrate the positive allometric growth of the brachial crown (from Kubodera & Okutani 1977).

octopuses, preying largely on small epibenthic forms such as copepods and also polychaetes (Vecchione 1987; Villanueva & Guerra 1991).

6. ONTOGENETIC SHIFT OF FOOD RELATIONS

In the usual single-year life cycle of a cephalopod, feeding shifts rapidly from the small prey, low in the food chain, of newly hatched paralarvae to large prey, high in the food chain, eaten by adults. Cephalopods thus occupy a wide range of ecological niches and trophic levels during their short life cycle. Growth is frequently accompanied by ontogenetic descent in pelagic cephalopods as they increase in size and ability to capture and subdue larger prey (Rodhouse & Clarke 1985, 1986)

Pelagic biomass spectra in marine ecosystems are characterized by peaks of biomass separated by regions of low biomass (Boudreau & Dickie 1992). These peaks are separated by one or more orders of magnitude of difference in body size and are composed of characteristic groups of organisms. In high latitudes, for instance, they pass in order of increasing size from diatoms (10^4–10^6 μm^3) to cyclopoid copepods (2×10^6–3×10^7 μm^3), calanoid copepods (1–50 mm^3), euphausiids (50 mm^3–1 cm^3), and salps and small fish (1–10 cm^3) (Witek & Krajewska-Soltys 1989). At small body sizes benthic biomass spectra may have peaks of biomass that correspond with troughs in the pelagic spectra (Warwick *et al.* 1986). The rapidly growing cephalopod must track across the biomass spectrum, in a single year in most cases, and span the troughs in the biomass spectrum if it is to increase the size of its prey as it grows.

The ontogenetic shift in squid diet from crustaceans to fish has already been described and is well illustrated by Breiby & Jobling's (1985) study of *Todarodes sagittatus* in Norwegian waters. This shift largely reflects the taxonomic composition of pelagic biomass spectra with increase in body size. However, where the relationship between cephalopod size and prey size has been examined in detail, a poor correlation has often been found. Minumum prey size commonly remains constant over a large range in body size whilst maximum prey size increases. Breadth of trophic niche thus increases with growth. In *Loligo pealei* there is a marked ontogenetic increase in the size range of prey taken as well as an increase in the mean size of prey from *ca.* 8% of mantle length at a ML of 31 mm to *ca.* 20% of mantle length at a ML of 211 mm (Vovk 1985).

Benthic octopus species commonly have a planktonic larval phase after hatching. This strategy has possibly evolved partly in response to the discrepancy between pelagic and benthic biomass spectra, enabling benthic species during the planktonic phase to feed on small crustaceans; these occupy a peak in the pelagic biomass spectrum which is absent in the benthic system. There is strong positive allometry of arm growth in the second half of the planktonic life of *Octopus vulgaris* (Villanueva *et al.* 1995) when the arms increase in length rapidly in relation to the rest of the body.

Ontogenetic changes in the allometry of the brachial crown in squid may reflect adaptation to the peaked structure of pelagic biomass spectra. Illustrated ontogenetic series of most squid species, e.g. *Gonatus madokai* (Kubodera & Okutani 1977) (figure 2), show positive allometric growth of the arms in relation to overall body size. Allometric equations for several Southern Ocean squid species have mantle length exponents for arm length of over 1.5 and in some cases approaching 2.0. This rapid relative growth of the brachial crown relative to overall body growth has probably evolved in response to the need to shift predation from one peak in the biomass spectrum to the next, accommodating the transition between diets differing in body size by at least one order of magnitude (Rodhouse & Piatkowski 1995). Discontinuities in allometric growth of the brachial crown of juvenile squid (Kubodera & Okutani 1977; Vidal 1994) indicate that dramatic changes in the size of the cephalopod predator, relative to its prey, occur in some species during early growth.

7. QUANTITATIVE IMPACT ON PREY POPULATIONS

There are few cephalopod populations for which sufficient data are available to attempt a quantitative estimate of prey consumption, but when data on stock size are available with knowledge of the digestion rate of the species (Jobling 1985) an estimate of consumption rate of a population can be made. By combining this with information on the relative contribution of different prey types to diet, the impact of the population on the prey community can be assessed. By using an energetics approach the impact on the prey resource of a population of squid, with a one-year life cycle and producing a single brood per year, can be demonstrated by modelling the lifetime energetics of a cohort and incorporating allometric data on size relations of squid and their prey. The digestion-rate method has been applied to the *Illex illecebrosus* and *Loligo pealei* populations in the northwest Atlantic (Maurer & Bowman 1985); there are sufficient laboratory and field data available to construct a model of the lifetime energetics of a cohort of *Illex*

Table 2. *Estimates of prey consumption* (*t*) *by* Illex illecebrosus *and* Loligo pealei *on the US Eastern Continental Shelf* (*from Maurer & Bowman 1985*)

	Year 1			Year 2		
	spring	summer	autumn	spring	summer	autumn
Illex illecebrosus						
Crustaceans	4659	37695	17636	63	95559	7718
Squid	16	141103	21501	3	75021	23895
Fish	574	25350	7288	3	32395	11054
Loligo pealei						
Crustaceans	35650	53574	5788	21570	3586	32868
Squid	1196	12210	554	—	1693	313599
Fish	18838	32397	22081	63090	15776	251035

argentinus in the southwest Atlantic and *Loligo forbesi* in the northeast Atlantic.

(*a*) ***Digestion-rate method*: Illex illecebrosus *and* Loligo pealei**

Maurer & Bowman (1985) collected *Illex illecebrosus* and *Loligo pealei* from trawl catches between the Gulf of Maine and Cape Hatteras (Eastern US Continental Shelf) over two seasons, identified stomach contents to the lowest taxa possible and determined the proportion of different prey types. Food consumption was calculated by using an exponential model:

$$\mathrm{d}S/\mathrm{d}t = R - \alpha S,$$

where S is the mass of food in the stomach, R is the rate of food intake, and α is the instantaneous rate of gastric evacuation. Assuming the relationship between temperature and gastric evacuation time was the same for squid as fish (Fange & Grove 1979), they calculated α thus:

$$\alpha = a\mathrm{e}^{bT} = 0.1818\mathrm{e}^{0.0747T},$$

where T is temperature in °C. The mean daily ration ($\bar{D}$) was then estimated from the modified Bajkov equation (Eggers 1979):

$$\bar{D} = 24\alpha\bar{S}$$

and expressed as percentage body mass. The food consumption of the population was estimated by multiplying the daily ration (% body mass) of each size group of squid by the appropriate estimate of standing stock biomass for each squid species and expanding to quarterly consumption.

Estimates of prey consumption by each squid species over two years are shown in table 2. Crustaceans, mostly euphausiids, dominated the diet of both species in the spring, whereas in the summer and autumn fish and squid became more important. Of these, fish was more important for *Loligo* and squid was more important for *Illex*. *Loligo* is potentially most important as a consumer of pre-recruit fish, especially in autumn. Small *Loligo* (ML < 100 mm), which are assumed to take most pre-recruits, accounted for an estimated 80% and 75% of fish consumption in the autumn of the two years, respectively, so consumption of pre-recruits was about 17.6 kt in year 1 and 188 kt in year 2. Fish species with pre-recruits within the size range available to *Loligo* included cod, haddock, yellowtail flounder, silver hake, butterfish, scup, mackerel, herring, menhaden and sand-lance. Cannibalistic consumption of pre-recruit squid by *Loligo* was estimated to be 443 t in the autumn of year 1 and 235 kt in year 2. Cannibalism did not appear to be related to population biomass in *Illex* and was probably a function of the availability of alternative prey. These data illustrate the potential effect of squid predation on the recruitment success of commercial stocks.

(*b*) ***Energetics method*: Illex argentinus**

We examine here the winter-spawning, south Patagonian Shelf stock of *Illex argentinus* and estimate food consumption for a hypothetical pre-exploitation cohort from hatching until its post-spawning extinction after one year. No single model has been proposed that provides a satisfactory fit to squid growth throughout the lifespan but for this purpose Uozumi & Shiba's (1993) logistic fit to winter-hatched (June–August) female *I. argentinus* growth has been chosen. This seems to fit early growth well but provides a relatively poor fit for older squid, for which a linear model is most appropriate (Rodhouse & Hatfield 1990). Survivorship is modelled according to the method of Caddy (1991), who proposed a scheme of changing natural mortality rate with age for fish populations and subsequently extended the concept to short-lived invertebrates (Caddy 1996). Mortalities (M-at-age) ranging from a value of 106.3 post hatching to 3.9 in the last six months of the life of the cohort are assumed. Mean fecundity is taken to be 200000 eggs per female, spawned at the end of the life cycle before post-spawning death (Rodhouse & Hatfield 1990). This is a conservative estimate, which ignores the potential total fecundity that would be realized if the previtellogenic oocytes present in the ovary at maturity were to mature and be spawned in a multiple spawning process (Laptikhovsky & Nigmatullin 1993). A spawning stock of 60 kt (*ca.* 50 million females) is assumed; this value is the overall mean recorded by Basson *et al.* (1996) over a three-year period. Daily feeding rate (FR, g d^{-1}) is predicted from O'Dor and Wells' (1987) multiple regression equation for *Illex illecebrosus*:

$$\mathrm{FR} = 0.058M^{0.79} \times 1.082^{T},$$

where M is body mass in grams and T is temperature in °C. The temperature regime experienced by the

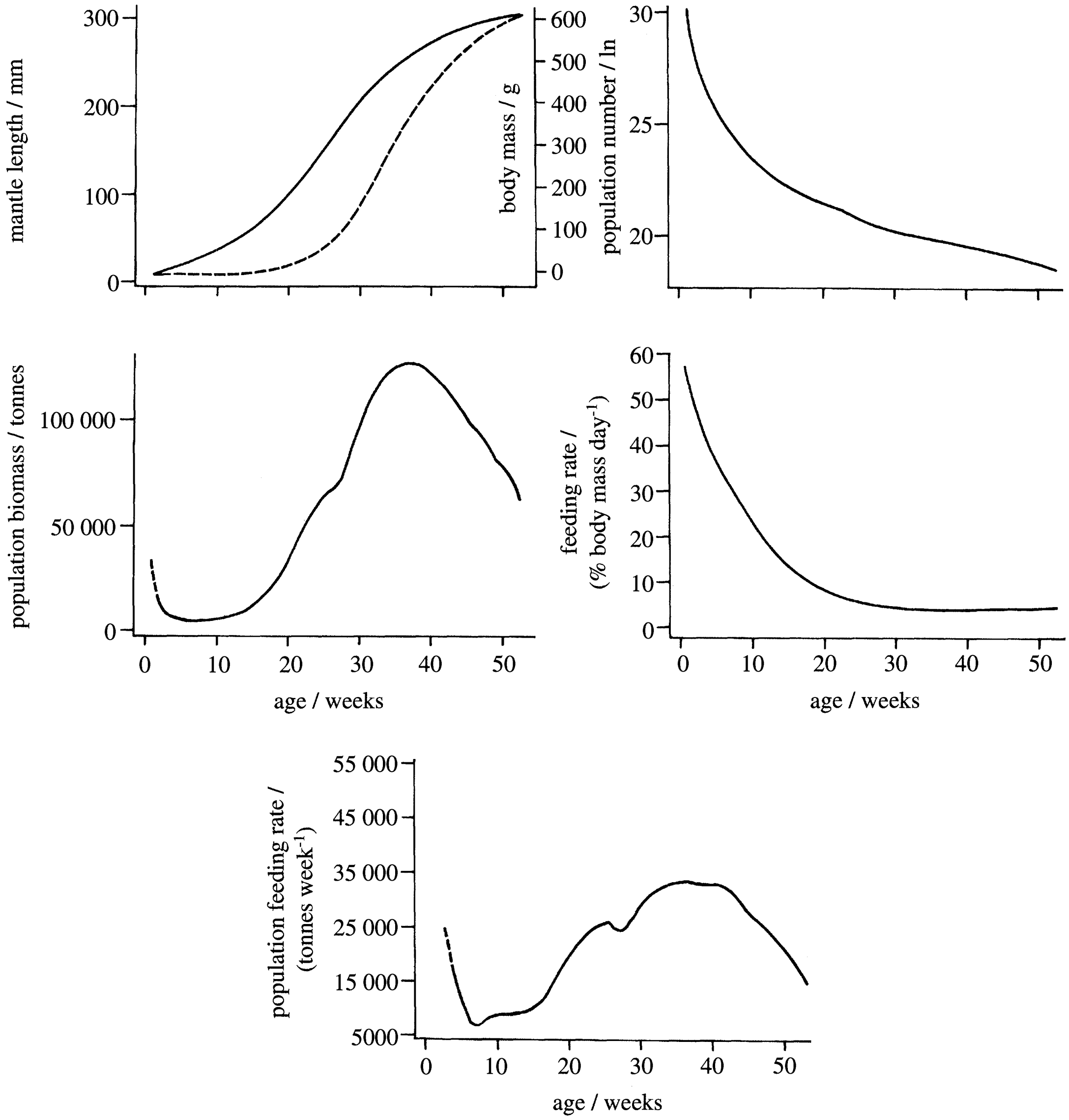

Figure 3. Lifetime energetics of an *Illex argentinus* cohort from the winter-spawning southern Patagonian Shelf population.

cohort is based on the assumption of a hatch date of 1 July, 90 d in the waters of the Brazil Current (15 °C), 90 d on the North Patagonian Shelf (12 °C), 120 d on the South Patagonian Shelf (10 °C) and a further 60 d on the North Patagonian Shelf edge–slope (12 °C) before spawning.

The principal features of the lifetime energetics of a cohort of winter-spawned *Illex argentinus* from the model are illustrated in figure 3. Cohort biomass peaks at about 38 weeks and declines thereafter. It is assumed that spawning occurs at age 52 weeks and is rapidly followed by catastrophic mortality. In a cohort's lifetime, individual biomass increases over five orders of magnitude (from less than 0.01 g to over 600 g), population biomass changes over two orders of magnitude (from *ca.* 3 kt to over 125 kt) but weekly population feeding rate changes over less than one order of magnitude (from over 6 kt to *ca.* 33 kt).

The picture that emerges of *Illex argentinus* diet is that this is a highly opportunistic predator that consumes crustaceans (hyperiid amphipods and euphausiids) until it reaches a ML of about 200 mm, when it may shift to preying on fish (myctophids, *Engraulis anchoita* and *Merluccius hubbsi*), cephalopods (*Loligo gahi* and *L. sanpaulensis*) if available, and conspecifics. However, when these larger prey are not available, feeding on small crustaceans, especially hyperiids, continues beyond this size. On the northern Patagonian Shelf, fish and cephalopods appear to play a greater part in the diet than on the southern part (Ivanovic & Brunetti 1994).

Illex argentinus from the winter-spawning stock on the south Patagonian Shelf are predicted here to reach a mantle length of 200 mm in week 30 (figure 3) this prediction agrees well with Rodhouse & Hatfield (1990) and Rodhouse *et al.* (1995). Lifetime prey consumption by a cohort is estimated to be 1.06 Mt. If only crustaceans are consumed below a ML of 200 mm then a minimum of 0.41 Mt of crustaceans are consumed during the first 30 weeks and these will range in size from copepods consumed soon after hatching to larger euphausiids, etc., in the juvenile–subadult phase. The remaining 0.65 Mt consumed during adult life will be made up of a combination of

Table 3. *Selected records of cephalopod predation on commercial resource species of fish and crustacean identified to species level*

cephalopod species	resource species	geographical area	source
Sepia officinalis	*Pagellus acarne*, *Pagellus erythrinus*, *Pagellus canariensis*, *Dentex macrothalmus*, *Otoperca aurita*, *Trachurus trachurus*, *Decapterus punctatus*, *Sardinella aurita*, *Scomber colias*, *Parapenaeus longirostris*	NW Africa	Nigmatullin 1975
Loligo forbesi	*Sprattus sprattus*, *Clupea harengus*, *Pleuronectus platessa*	Ireland	Collins *et al.* 1994
	Clupea harengus, *Micromesistius poutassou*	Irish Sea	Pierce *et al.* 1994
	Merlangius merlangus, *Melanogrammus aeglefinus*	Irish Sea & off Lisbon, Faroes	Pierce *et al.* 1994
	Sardina pilchardus, *Merluccius merluccius*, *Macromesistius poutassou*, *Trachurus trachurus*	Galician coast, Spain	Rocha *et al.* 1994
	Trachurus pictoratus, *Boops boops*, *Lepidopus caudatus*	Azores	Martins 1982
Loligo vulgaris	*Clupea harengus*	off Lisbon	Pierce *et al.* 1994
	Macromesistius poutassou	off Lisbon	Pierce *et al.* 1994
	Sardina pilchardus, *Sprattus sprattus*, *Merluccius merluccius*, *Macromesistius poutassou*, *Trachurus trachurus*, *Ammodytes tobianus*	Galician coast, Spain	Rocha *et al.* 1994
	Trachurus trachurus, *Scomber colias*, *Pagellus acarne*, *Sardinella anrita*, *Dentex macroptalinus*, *Mugil cephalus*	NW African coast	Nigmatullin 1975
Loligo opalescens	*Merluccius gayi*	Monterey Bay	Hixon 1983
Loligo pealei	*Anchoa mitchiei*, *Ammodytes americanus*, *Breortia tyrannis*, *Cynoscion regalis*	NW Atlantic	Macy 1982
Loligo vulgaris reynaudii	*Engraulis capenses*, *Merluccius capensis*	South Africa	Lipiński 1992
Todarodes sagittatus	*Melanogrammus aeglefinus*	Scotland	Pierce *et al.* 1994
	Trisopterus esmarkii, *Merlangius merlangus*	Shetland Islands	Joy 1989
	Micromesistius poutassou, *Trisopterus minutus*	Rockall Bank	Joy 1989
	Mallotus mallotus, *Sebastes mentella*, *Clupea harengus*	Barents Sea	Sennikov *et al.* 1986
	Chlorophtalmus atlantica, *Pasapenaeus longirostris*, *Plesionica heterocampus*	Mauritania	Nigmatullin 1972
Todarodes pacificus	*Goloabias sanza*, *Sardina ivasi*	NW Pacific	Shevtzov 1978
Nototodarus gouldi	*Sardinops pilchardus*	Bass Strait	O'Sullivan & Cullen 1983
Illex coindetii	*Engraulis encrasicholus*	Catalan Sea	Sanchez 1982
	Scomber colias, *Parapenaeus longirostrus*	NW African coast	Nigmatullin 1972
Illex argentinus	*Merluccius hubbsi*, *Engraulis anchoita*	Patagonia Shelf	Angelescu & Prenski 1987
Illex illecebrosus	*Merluccius bilinearis*	NW Atlantic	Froerman 1984
Dosidicus gigas	*Sardinops sagax caerulea*	Gulf of California	Ehrhardt 1991
Kondakovia longimana	*Euphausia superba*	Antarctic	Nemoto *et al.* 1988
Moroteuthis knipovitchi	*Euphausia superba*	Antarctic	Nemoto *et al.* 1988
Moroetuthis ingens	*Euphausia superba*	Antarctic	Nemoto *et al.* 1988
Moroteuthis robsoni	*Euphausia superba*	Antarctic	Nemoto *et al.* 1988
Alluroteuthis antarcticus	*Euphausia superba*	Antarctic	Nemoto *et al.* 1988
Galiteuthis glacialis	*Euphausia superba*	Antarctic	Nemoto *et al.* 1988; Lu & Williams 1994
Gonatus antarcticus	*Euphausia superba*	Antarctic	Nemoto *et al.* 1988
Brachioteuthis ?picta	*Euphausia superba*	Antarctic	Nemoto *et al.* 1988
Psychroteuthis glacialis	*Euphausia superba*	Antarctic	Lu & Williams 1994
Octopus vulgaris	*Hommarus gammarus*, *Cancer pagurus*	English Channel	Rees & Lumby 1954
	Pagellus acarne, *Pagellus canariensis*, *Dentex filosus*	NW Africa	Nigmatullin 1975; Nigmatullin & Ostapenko 1976
Eledone cirrhosa	*Hommarus gammarus*, *Cancer pagurus*, *Nephrops norvegicus*, *Pandalus borealis*	North Sea	Boyle 1983

crustaceans, fish and cephalopods, the relative proportions of which probably depend on availability but will be mostly crustaceans in the winter-spawning stock on the southern part of the shelf.

(*c*) ***Energetics method*: Loligo forbesi**

Pierce & Santos (1996) took a different approach to estimating predation by *Loligo forbesi* in Scottish waters. Daily feeding rate (FR) was estimated by using an equation derived from data given by O'Dor and Wells (1987) for *Loligo pealei* and *Illex illecebrosus*:

$$\mathrm{FR} = 0.0683 + 0.0474\,M,$$

where M is body mass in grams. The squid population size at monthly intervals was estimated by using the difference equation model:

$$N_t = (N_{t+1} + C_t)\,/\,(1 + r_t - m),$$

where N_t is the population at the start of month t; r_t is the recruitment in month t expressed as a proportion of N_t; C_t is the commercial catch in month t; m is the monthly mortality expressed as a fixed proportion of N_t. Population food intake was estimated from:

$$I = N_t \times P_i \times F \times T_t,$$

where I is the monthly food intake in tonnes; P_i is the proportion by mass of prey type i in the diet; F is the mean mass of food eaten daily per individual; T_t is the number of days in month t. Monthly food intake was summed to give annual food consumption.

Depending on the value of m used (0.04 or 0.16), the population's consumption was estimated to be 9–16 kt of food in year 1 of the study and 3–5 kt in year 2. In year 1 the food included 1.7–3.0 kt of sandeels, 1.6–2.7 kt of *Trisopterus* spp. and 1.0–1.7 kt of *Merlangius merlangus*. The diet was dominated by fish, but the estimates do not include consumption by prerecruits, which must be substantial and is probably dominated by crustaceans.

(*d*) ***A global estimate***

Using data from various sources, we can attempt a tentative estimate of global consumption by cephalopods. For this purpose we will consider only subadults and adults. Nesis (1985), drawing on data given by Voss (1973) and Clarke (1983), estimated the global standing stock biomass of mesopelagic squid to be 150–300 Mt; Nigmatullin (1990) estimated the global stock of oceanic epipelagic squid and slope–shelf edge squid to be 30–50 Mt and 8–15 Mt, respectively. Although published data are not available, an estimate of the stock of sepiids and octopus on the continental shelves, based on world catch, is some 5–10 Mt. Total biomass thus falls in the range 193–375 Mt. The feeding rate of subadult and adult cephalopods is 1–12% body mass per day (Clarke & Wells, this volume). As mesopelagic squid, with comparatively low metabolic and feeding rates, dominate the standing stock ,we assume a mean feeding rate of 3% body mass per day. Global daily consumption by cephalopods is thus estimated at 5.8–11.2 Mt. Although individual populations of cephalopods may show dramatic annual fluctuations in biomass we assume that the global biomass is quasi-stable because the seasonal dynamics of temperate populations are approximately six months out of phase in the northern and southern hemispheres, because many abundant species spawn year-round in the tropical regions and because in the polar regions at least some species probably have life cycles in excess of one year. Global annual consumption by cephalopods is thus estimated at 2.09–4.03 Gt.

8. IMPACT ON COMMERCIAL STOCKS

The role of cephalopods as predators on fish and crustaceans clearly implicates them as a factor influencing natural mortality and recruitment success in stocks of commercially exploited species. In turn, the status of fish stocks may influence recruitment success of some of the commercial cephalopods (Dawe & Brodziak 1996). The short, semelparous life history of cephalopods, the fact that populations usually produce only one or two broods per year, and that these often undertake feeding and spawning migrations, means that they are likely to affect prey stocks at quite specific times and locations. Numerous studies of cephalopod stomach contents have identified remains of commercial fish and crustacean species (table 3). Among the fishes, clupeids, scombrids, gadoids are prevalent in the diet of a number of squid feeding on the continental shelves, as are penaeid prawns; commercially exploited species of crab and lobster are attacked by octopuses; and Antarctic krill, which support one of the the largest crustacean fisheries, are eaten by several squid species. The short cephalopod life cycle compared with that of most fish species means that within the one-year lifespan of an individual it can rapidly shift roles between prey and predator, as for instance in the *Illex argentinus*–*Merluccius hubbsi* system in the southwest Atlantic (Roper *et al.* 1984) and the *Illex illecebrosus*–*Merluccius bilinearis* system in the northwest Atlantic (Dawe & Brodziak 1996).

The impact of a squid population on a commercial fish stock at a specific geographic location and season is well illustrated by the migration of *Dosidicus gigas* into the Gulf of California, where it shifts its diet during June, July and August to the California sardine, *Sardinops sagax caerulea* (Ehrhardt 1991). At the start of the migration, near the entrance to the bay, the squid feed on myctophids, red crab and conspecifics. As they migrate into the bay the diet shifts to penaeid postlarvae and sardine until at the peak of sardine predation in July it contributes up to 80% of total diet. In 1980 and 1981 there were especially conspicuous migrations of *D. gigas* into the Gulf of California and in 1980 an estimated 60 kt of sardines were consumed. A subsequent decline in sardine landings in 1981 was probably attributable to this increased predation pressure.

In the Bering Sea the trophic ecology of the gonatid *Berryteuthis magister* is linked to the Alaska pollack, *Theragra chalcogramma*; there are sufficient data to quantify the role of squid predation. *B. magister* grows to a maximum ML of about 350 mm during a lifespan

Table 4. *Major cephalopod populations and their key prey species in the world's major marine ecosystems*

Sherman *et al.*'s (1993) classification of large marine ecosystems is used.)

marine ecosystem	Teuthoidea	prey species of adult	*Sepioidea and Octopoda*	prey species of adult
Bering Sea/Gulf of Alaska	*Berryteuthis magister*[13]	[a] *Thysanoessa* spp., *Theragra chalcogramma*	*Octopus dofleini*	no data
California Current	*Dosidicus gigas*[1]	no data	*Octopus dofleini*	no data
	Loligo opalescens[14]	[b] *Euphausia pacifica*, *Thysanoessa spinifera*		
Gulf of California	*Dosidicus gigas*[1]	[c] *Sardinops sagax caerulae*		
Gulf of Mexico/Caribbean Sea	*Illex coindetii*[15]	no data		
	Loligo pealei[2]	no data		
Eastern U.S. Continental Shelf/ Scotian Shelf/Newfoundland shelf	*Illex illecebrosus*[3]	[d] *Meganyctiphanes norvegica*, Myctophidae, Merluceidae		
	Loligo pealei[2]	*Merluccius bilinearis*, euphausiids		
West Greenland Shelf	*Gonatus fabricii*	no data		
Insular Pacific–Hawaiian	*Nototodarus hawaiiensis*	no data		
Humboldt Current	*Dosidicus gigas*[1]	no data		
Patagonian Shelf	*Illex argentinus*[4]	[e] *Themisto gaudichaudii*, *Euphausia lucens*, *Gymnoscopelis nicholsi*		
	Loligo gahi[13]	[f] euphausiids		
Brazil Current	*Illex argentinus*[4]	[e] *Themisto gaudichaudii*, *Euphausia lucens*, *Gymnoscopelis nicholsi*		
Northeast Brazil Shelf	*Loligo sanpaulensis*	[t] Fish		
East Greenland Shelf/Iceland Shelf	*Gonatus fabricii*	no data		
	Todarodes sagittatus[5]	no data		
	Illex illecebrosus[3]	no data		
Faroe Plateau/Norwegian Shelf	*Todarodes sagittatus*[5]	[g] *Meganyctiphanes norvegica*, *Clupea harengus*		
Barents Sea	*Gonatus fabricii*	[h] *Scorpaenide*, *Scopelarchidae*		
	Todarodes s. sagittatus[5]	no data		
North Sea	*Loligo forbesi*	[i] *Merlangius merlangus*, *Trisopterus* sp., Ammodytidae, Clupeidae	*Sepia officinalis*[9]	no data
	Todarodes sagittatus[5]	[i] *Melanogrammus aeglefinus*		
	Todaropsis eblane	[i] Clupeidae, Gadidae		
Celtic–Biscay Shelf/Iberian Coastal/Mediterranean Sea	*Loligo vulgaris*	[i] Ammodytidae, *Atherina presbyter*	*Sepia officinalis*[9]	[o] *Palaemon* sp., *Pisidia longicornis*, *Liocarcinus* sp., *Lesuerigobius friesii*
	Loligo forbesi	as for North Sea		
	Illex coindetii[15]	[q] *Maurolicus muelleri*, *Engraulis encrasicholus*	*Eledone cirrhosa*[10]	[u] *Alpheus glaber*, *Gonoplax rhomboides*
	Todarodes sagittatus[5]	no data	*Octopus vulgaris*[11]	no data
	Todaropsis eblanae	[s] *Micromesistius poutassou*		

Canary Current	*Loligo vulgaris*	no data	*Sepia officinalis*[9]	no data
	Illex coindetii[15]	no data	*Octopus vulgaris*[11]	no data
	Todarodes sagittatus[5]	no data		
	Todaropsis eblanae	no data		
Guinea Current	*Illex coindetii*[15]	no data	*Sepia officinalis*[9]	no data
	Todarodes sagittatus[5]	no data		
Benguela Current	*Loligo vulgaris reynaudi*[6]	[p]*Engraulis capensis*	*Sepia officinalis*[9]	
	Todarodes angolensis	[p]*Lampanyctodes hectoris*	*Sepia australis*	[p]Pterygosquilla armata
	Todaropsis eblanae	[p]*Lampanyctodes hectoris*		
Agulhas Current	*Loligo vulgaris reynaudi*[6]	[j]*Bregmaceros* sp., *Nereis* sp.		
	Todarodes angolensis	no data		
Somali Coastal Current	*Loligo duvauceli*	no data	*Octopus cyaneus*	no data
Arabian Sea/Red Sea	*Loligo duvauceli*	no data	*Sepia pharaonis*	no data
			Octopus cyaneus	No data
Bay of Bengal	*Loligo duvauceli*	No data	*Sepia pharaonis*	No data
	Sepioteuthis lessoniana	no data	*Octopus aegina*	no data
			Octopus cyaneus	no data
South China Sea/Sulu–Celebes Sea/Indonesian Seas	*Loligo chinensis*	no data	*Sepia pharaonis*	no data
	Loligo duvauceli	no data	*Sepia latimanus*	no data
	Sepioteuthis lessoniana	no data	*Sepia esculenta*	no data
			Octopus aegina	no data
			Octopus cyaneus	no data
Northern Australian Shelf			*Sepia pharaonis*	no data
			Sepia latimanus	no data
			Octopus cyaneus	no data
Southern Australian Shelf	*Nototodarus gouldi*[16]	[k]*Sardinops neopilchardus*, *Leionura atun*, *Leptochela sydniensis*		
New Zealand Shelf	*Nototodarus sloani*[7]			
East China Sea	*Sepioteuthis lessoniana*	no data	*Sepia esculenta*	no data
	Loligo edulis[17]	[x]fish, [z]*Spratelloides gracis*	*Sepiella japonica*	no data
	Todarodes pacificus[8]	no data	*Octopus aegina*	no data
			Octopus cyaneus	no data
Yellow Sea	*Todarodes pacificus*[8]	no data	*Sepiella japonica*	no data
			Octopus aegina	no data
Kurushio Current	*Loligo bleekeri*	no data		
	Todarodes pacificus[8]	[cc]*Myctophium* spp., *Engraulis* japonicus		
	Thysanoteuthis rhombus	no data		

Table 4 (*cont.*)

marine ecosystem	Teuthoidea	prey species of adult	*Sepioidea and Octopoda*	prey species of adult
Sea of Japan	*Sepioteuthis lessoniana*	[aa]fish	*Sepia esculenta*	[v]fish
	Loligo bleekeri	[w]fish	*Sepiella japonica*	no data
	Loligo edulis[17]	[y]*Engraulis japonica*	*Octopus conispadiceus*	no data
	Todarodes pacificus[8]	[bb]*Maurolicus muelleri japonicus*, *Parathemisto japonica*	*Octopus dofleini*	[dd]*Eopsetta grigorjewi*, Gymnochanthus sp., *Neptunea* sp., *Nordotis discus hannai*, *Chlamys farreri akazara*, *Solen* sp., *Loligo bleekeri*
			Octopus vulgaris[11]	no data
Oyashio Current	*Berryteuthis magister*[13]	[ff]*Thysanoessa longipes*		
Sea of Okhotsk	*Berryteuthis magister*[13]	no data		
	Todarodes pacificus[8]	[gg]*Euphausia pacifica*		
Antarctic	*Moroteuthis knipovitchi*	[l]*Euphausia superba*	Pareledone spp.	[n]crustaceans, polychaetes, benthic molluscs
	Knodakovia longimana	[l]*Euphausia superba*		
	Psychroteuthis glacialis	[l]*Euphausia superba*		
	Alluroteuthis antarcticus	[l]*Euphausia superba*		
	Mesonychoteuthis hamiltoni	[l]*Euphausia superba*		
	Gonatus antarcticus	[l]*Euphausia superba*		
Subtropical gyre: North and South Atlantic	*Ommastrephes bartrami*[19]	no data		
	Sthenoteuthis pteropus	no data		
	Thysanoteuthis rhombus	no data		
Subtropical gyre: North and South Pacific	*Ommastrephes bartrami*	[r]Ommastrephidae, *Myctophum* sp.		
	Sthenoteuthis oualaniensis	[ee]*Symbolophorus evermanni*, *Myctophum nitidulum*		
	Thysanoteuthis rhombus	no data		
Subtropical gyre: Northern Indian Ocean	*Sthenoteuthis oualaniensis*	no data		
	Thysanoteuthis rhombus	no data		
Subtropical gyre: Southern Indian Ocean	*Ommastrephes bartramii*[19]	no data		
	Sthenoteuthis oualaniensis	no data		
	Thysanoteuthis rhombus	no data		
Antarctic Circumpolar Current	*Martialia hyadesi*[12]	[m]*Krefftichthys anderssoni*		

Total annual world catch (t): [1]121 643, [2]22 200, [3]24 008, [4]310 300, [5]6921, [6]6271, [7]29 060, [8]537 943, [9]22 257, [10]3542 (recorded as *Eledone* spp.); [11]72 496, [12]1252 (FAO 1995); [13]65 613 (Falkland Islands Government Fisheries Department statistics 1994); [14]*ca.* 9000 in 1984, effort recently increased; [15]*ca.* 10 000, [16]*ca.* 39 000, [17]*ca.* 5000, [18]*ca.* 6100, [19]*ca.* 187 000 (Roper *et al.* 1984)

Sources: [a]Kuznetsova & Fedorets 1987; [b]Karpov & Caillet 1978; [c]Ehrhardt 1991; [d]Froerman 1984; [e]Ivanovic & Brunetti 1994; [f]Guerra *et al.* 1991; [g]Breiby & Jobling 1985; [h]Wiborg *et al.* 1984; [i]Pierce *et al.* 1994; [j]Sauer & Lipiński 1991; [k]O'Sullivan & Cullen 1983; [l]Nemoto *et al.* 1988; [m]Rodhouse *et al.* 1992*b*; [n]Daly, unpublished; [o]Castro & Guerra 1990; [p]Lipiński 1992; [q]Sanchez 1982; [r]Seki 1993*a*, *b*; [s]Rasero *et al.* 1996; [t]Andriguetto & Haimovici 1996; [u]Sanchez, 1981; [v]Natsukari & Tashiro 1991; [w]Sato 1991; [x]Tashiro *et al.* 1981; [y]Ogawa 1982; [z]Tashiro 1977; [aa]Segawa 1993; [bb]Okiyama 1965; [cc]Okutani 1962; [dd]Maruyama & Tamura 1959; [ee]Shchetinnikov 1992; [ff]Fedorets & Kun 1988; [gg]Shevtsov 1978.

of two years. There are three broods per year, which spawn in spring, summer and winter; the egg stage lasts some four months. Mean standing stock biomass of subadult and adult *B. magister* is estimated at 640 kt and the ratio of production to biomass is estimated to be approximately 3.0, giving an annual production of 1.92 Mt per year (Radchenko 1992). The feeding rate of *B. magister* is estimated at 1.1 % body mass per day; analysis of stomach contents has shown that 10–15 % of the daily food ration of *B. magister* consists of *T. chalcogramma* ranging in size from 50 to 150 mm (Kuznetsova & Fedorets 1987). The feeding rate of the total *B. magister* stock is calculated to be some 7040 t d^{-1}, of which *T. chalcogramma* makes up 700–1056 tonnes. The total annual food consumption of the *B. magister* stock is thus 2.5 Mt, of which T. *chalcogramma* contributes 250–375 kt.

The impact of octopus populations on commercial crustacean stocks is most apparent in fisheries where octopus enter commercial traps or pots to attack crabs and lobsters after capture. Studies in Scottish waters used observations on commercial creels, supported by serological methods, to reveal that the octopus *Eledone cirrhosa* preys on commercial species of lobster, crab and prawn (*Homarus gammarus*, *Nephrops norvegica*, *Cancer pagurus* and *Pandalus borealis*) (Boyle 1986; Boyle *et al.* 1986). In New Zealand, *Octopus maorum* is a significant predator on the rock lobsters *Jasus edwardsii* and *J. verreauxi*; it is responsible for a loss of up to 20 % of the takeable catch (Ritchie 1972). In Australia, *Octopus tetricus* has been estimated to eat 195000 legal-sized western rock lobsters (*Panulirus longipes cygnus*) in the fishery during a single season (Joll 1977). In 1899, 1900 and again in 1950 plagues of *Octopus vulgaris* invaded the English Channel and the creel fishery for crabs and lobsters on the English and French coasts was devasted (Rees & Lumby 1954). The observed impact of octopus in these fisheries serves to illustrate the potential effect on natural populations. Significantly greater losses must be sustained by juvenile and adult crabs and lobsters outside the traps.

9. FOOD RELATIONS OF CEPHALOPODS IN THE MAJOR MARINE ECOSYSTEMS

Cephalopods are widespread in the world's oceans from the polar regions to the tropics and they support several industrial and numerous artisanal fisheries. We document here (table 4) the major cephalopod stocks and, where known, the key prey species of the adult form. Given almost ubiquitous cannibalism among the cephalopods, predation on conspecifics is not included in the table. We include both stocks that are currently exploited and those that are considered to have potential, and we examine the role of cephalopods in systems that are already to some extent managed. We largely ignore cephalopod families that are undoubtedly significant contributors to oceanic biomass such as the histioteuthids, enoploteuthids, ancistrocheirids and octopoteuthids. Apart from data from predators (Clarke 1980) little is known about stock size of these forms and virtually nothing is known about their predatory behaviour.

Some 95 % of the biomass yield of the world's marine fisheries is caught within the geographical limits of about 50 large marine ecosystems that have been defined on the basis of distinct bathymetry, hydrography, productivity and trophic dependence of their populations (Sherman *et al.* 1993). These systems broadly correspond to management units. We adopt them here because they match the biogeographic range of many cephalopod species. Because there are large stocks of ommastrephids in the oceanic regions, we also add the major subtropical gyres and the Antarctic Circumpolar Current (ACC) to the list. Cephalopod species included are identified by Roper *et al.* (1984) as being of commercial, or potential commercial, interest or are important in predator diets (Clarke 1980; Rodhouse *et al.* 1987, 1990, 1992*a*; Rodhouse & Prince 1993).

Table 4 highlights the lack of data on the prey of several cephalopod species that already form important fisheries worldwide, and lack of knowledge of their role in the marine food web in these ecosystems.

10. CONCLUSION

We have focused here on the fast-swimming, muscular cephalopods that generally form shoals (at least in the squids), usually have a one-year life cycle and are semelparous. The Ommastrephidae and Loliginidae form the basis of the major cephalopod fisheries and play an important part in the trophic structure of the world's marine ecosystems. Judging by their role in the diet of predators (Clarke 1983) other families including the Histioteuthidae, Onychoteuthidae and Octopoteuthidae are probably shoaling and are undoubtedly important in oceanic food webs but, because they are not sampled by fisheries, knowledge of their trophic biology is limited by lack of data. The ammoniacal, buoyant species that are generally solitary and usually occur in deep water are assumed to be animals of low metabolic rate (Wells 1994). They too are important in oceanic food webs but virtually nothing is known about their diet.

The trophic biology of the fast-growing, short-lived, semelparous species has faced special selection pressures because of the need to maintain high growth and maturation rates in order to complete the life cycle and spawn successfully within a tight time schedule. Failure to feed successfully for even short periods is disastrous for animals with such high metabolic rates and low levels of metabolic reserves. The evolution of cephalopod feeding has taken place in the context of a highly unstable adaptive landscape. Selection pressures arise from the temporally and spatially variable trophic environment in marine habitats, owing to seasonality in the production cycle and geographical patchiness in the distribution of production. Adaptations arising from these selection pressures include a spawning season or seasons timed in relation to the annual production cycle, migrations that track optimum feeding conditions in time and space, and ontogenetic modulation of the morphology of the feeding structures. However, perhaps the most significant feature of the evolution of the cephalopods, in this context, is trophic opportunism facilitated by a uniquely versatile feeding apparatus, the brachial crown, which is controlled by a sophisticated nervous system and linked to a highly developed sensory system dominated by the eyes (Budelmann 1995).

The prehensile arms and tentacles of cephalopods, armed with variations on suckers, toothed and naked sucker rings, hooks, cirri and enveloping webs, have enabled most species to achieve great breadth of trophic niche by freeing them from some of the constraints that limit the size and form of their prey. We see, for instance, that adult ommastrephids can feed equally effectively on relatively small macroplanktonic euphausiids or on fish that may be up to the same length as their own mantle or even larger, and they switch prey type according to availability by using the versatile prey-handling capability of the arms and tentacles. Also pelagic squid feed on benthos and benthic octopuses feed on pelagic organisms. Trophic flexibility in the cephalopods is a necessary adjunct to their high metabolic rate and short life cycle, which, taken together, adapt them for the role of ecological opportunists.

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REFERENCES

Altman, J. S & Nixon, M. 1970 Use of beaks and radula by *Octopus vulgaris* in feeding. *J. Zool.* **161**, 25–38.

Ambrose, R. F. 1984 Food preferences, prey availability, and the diet of *Octopus bimaculatus* Verril. *J. exp. mar. Biol. Ecol.* **77**, 29–44.

Ambrose, R. F. 1986 Effects of octopus predation on motile invertebrates in a rocky subtidal community. *Mar. Ecol. Prog. Ser.* **30**, 261–273.

Angelescu, V. & Prenski, L. B. 1987 Ecología trófica de la merluza común del Mar Argentino (Merlucciidae, *Merluccius hubbsi*). Parte 2. Dinámica de la alimentatión analizada sobre la base de las condiciones ambientales, la estructura y las evoluciones de los efectos en su área de distributión. *Serie Contribuciones INIDEP* (Instituto Investigaciones y Desarrollo Pesquero, Mar del Plata, Argentina) no. 561. [In Spanish.]

Araya, H. 1983 Fishery, biology and stock assessment of *Ommastrephes bartrami* in the north Pacific Ocean. *Mem. natl. Mus. Vict.* **44**, 269–283.

Augustyn, C. J., Lipiński, M. R. & Sauer, W. H. H. 1992 Can the *Loligo* squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. *S. Afr. J. Mar. Sci.* **12**, 903–918.

Basson, M., Beddington, J. R., Crombie, J., Holden, S. J., Purchase, L. V. & Tingley, G. A. 1996 Assessment and management techniques for migratory annual squid stocks: the *Illex argentinus* fishery in the Southwest Atlantic as an example. *Fish. Res.* (In the press.)

Beddington, J. B., Rosenberg, A. A., Crombie, J. A. and Kirkwood, G. P. 1990 Stock assessment and the provision of management advice for the short fin squid fishery in Falkland Islands waters. *Fish. Res.* **8**, 351–365.

Bergström, Bo. I. 1985 Aspects of natural foraging by *Sepietta oweniana* (Mollusca, Cephalopoda). *Ophelia* **24**, 65–74.

Boletzky, S. v. 1993 The arm crown in cephalopod development and evolution: a discussion of morphological and behavioural homologies. *Am. Malacol. Bull.* **10**, 61–69.

Boucaud-Camou, È. & Boismery, J. 1991 The migrations of the cuttlefish (*Sepia officinalis*) in the English Channel. In *Acta 1st International Symposium on the cuttlefish* Sepia (ed. È. Boucaud-Camou), pp. 179–189. Caen: Centre de Publications de l'Université de Caen.

Boucaud-Camou, È. & Roper, C. F. 1995 Digestive enzymes in paralarval cephalopods. *Bull. mar. Sci.* **57**, 313–327.

Boucher-Rodoni, R., Boucaud-Camou, È. & Mangold, K. 1987 Feeding and digestion. In *Cephalopod life cycles: comparative reviews*, vol. 2 (ed. P. R. Boyle), pp. 85–108. London: Academic Press.

Boudreau, P. R. & Dickie, L. M. 1992 Biomass spectra of aquatic ecosystems in relation to fisheries yield. *Can. J. Fish. aquat. Sci.* **49**, 1528–1538.

Boyle, P. R. 1983 *Eledone cirrhosa*. In *Cephalopod life cycles: comparative reviews*, vol. 1 (ed. P. R. Boyle), pp. 365–386. London: Academic Press.

Boyle, P. R. 1986 A descriptive ecology of *Eledone cirrhosa* (Mollusca: Cephalopoda) in Scottish waters. *J. mar. biol. Ass. U.K.* **66**, 855–865.

Boyle, P. R., Grisley, M. S. & Robertson, G. 1986 Crustacea in the diet of *Eledone cirrhosa* (Mollusca: Cephalopoda) determined by serological methods. *J. mar. biol. Ass. U.K.* **66**, 867–879.

Breiby, A. & Jobling, M. 1985 Predatory role of the flying squid (*Todarodes sagittatus*) innorth Norwegian waters. *NAFO Sci. Coun. Stud.* **9**, 125–132.

Budelmann, B. U. 1996 Active marine predators: the sensory world of cephalopods. *Mar. Freshw. Behav. Physiol.* **25**, 59–75.

Budelmann, B. U. & Bleckmann, H. 1988 A lateral line analogue in cephalopods: water waves generate microphonic potentials in the epidermal head lines of *Sepia* and *Loliguncula*. *J. comp. Physiol.* A **164**, 1–5.

Caddy, J. F. 1983 The cephalopods: factors relevent to their population dynamics and to the assessment and management of stocks. In *Advances in assessment of world cephalopod resources*. (*FAO Tech. Pap.* no. 231) (ed. J. F. Caddy), pp. 416–449. Rome: FAO.

Caddy, J. F. 1991 Death rates and time intervals: is there an alternative to the constant natural mortality axiom? *Rev. fish Biol. Fish.* **1**, 109–138.

Caddy, J. F. 1996 Modelling natural mortality with age in short-lived invertebrate populations: application of a strategy of gnomic time division. *Aquat. Living Resourc.* (In the press.)

Castro, B. G. & Guerra, A. 1990 The diet of *Sepia officinalis* (Linnaeus, 1758) and *Sepia elegans* (D'Orbigny, 1835) (Cephalopoda, Sepioidea) from the Ria de Vigo (NW Spain). *Sci. Mar.* **54**, 375–388.

Clarke, A., Rodhouse, P. G. & Gore, D. J. 1994 Biochemical composition in relation to the energetics of growth and sexual maturation in the ommastrephid squid *Illex argentinus*. *Phil. Trans. R. Soc. Lond.* B **344**, 201–212.

Clarke, M. R. 1980 Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. *Discovery Rep.* **37**, 1–34.

Clarke, M. R. 1983 Cephalopod biomass - estimation from predation. *Mem. natl. Mus. Vict.* **44**, 95–107.

Clarke, M. R. & Lu, C. C. 1974 Vertical distribution of cephalopods at 30° N 23° W in the north Atlantic. *J. mar. biol. Ass. U.K.* **54**, 969–984.

Clarke, M. R. & Lu, C. C. 1975 Vertical distribution of cephalopods at 18° N 25° W in the north Atlantic. *J. mar. biol. Ass. U.K.* **55**, 165–182.

Clarke, M. R. & Maddock, L. 1988 Beaks of living coleoid cephalopoda. In *The Mollusca*, vol. 12, *Paleontology and neontology of cephalopods* (ed. M. R. Clarke & E. R. Trueman), pp. 123–131. London: Academic Press.

Coelho, M .L. 1985 Review of the influence of oceanographic factors on cephalopod distribution and life cycles. *NAFO Sci. Coun. Stud.* **9**, 47–57.

Collins, M. A., De Grave, S., Lordan, C., Burnell, G. M. & Rodhouse, P. G. 1994 Diet of the squid *Loligo forbesi* Steenstrup (Cephalopoda:Loliginidae) in Irish waters. *ICES J. mar. Sci.* **51**, 337–344.

Cortez, T., Castro, B. G. & Guerra, A. 1995 Feeding dynamics of *Octopus mimus* (Mollusca: Cephalopoda) in northern Chile waters. *Mar. Biol.* **123**, 497–503.

Daly, H. I. & Rodhouse, P. G. 1994 Comparative morphology of two sympatric *Pareledone* species from South Georgia. *Antarct. Sci.* **6**, 163–169.

Dawe, E. G., Beck, P. C., Drew, H. J. & Winters, G. H. 1981 Long distance migration of a short-finned squid (*Illex illecebrosus*). *J. Northw. Atl. Fish. Sci.* **2**, 75–76.

Dawe, E. G. & Brodziak, J. 1996 Trophic relationships, ecosystem variability and recruitment. In *Squid recruitment dynamics* (ed. P. G. Rodhouse, E. G. Dawe & R. K. O'Dor), Rome: FAO. (In the press.)

Eggers, D. M. 1979 Comment on some recent methods for estimating food consumption by fish. *J. Fish. Res. Bd Can.* **36**, 1018–1019.

Ehrhardt, N. M. 1991 Potential impact of a seasonal migratory jumbo squid (*Dosidicus gigas*) stock on a Gulf of California sardine (*Sardops sagax caerulea*) population. *Bull. mar. Sci.* **49**, 325–332.

Engeser, T. S. & Clarke, M. R. 1988 Cephalopod hooks, both recent and fossil. In *The Mollusca*, vol. 12, *Paleontology and neontology of cephalopods* (ed. M. R. Clarke & E. R. Trueman), pp. 133–151. London: Academic Press.

Ennis, G. P. & Collins, P. W. 1979 Food and feeding of the short finned squid, *Illex illecebrosus*, during its seasonal occurrence in the Newfoundland area. *ICNAF select. Pap.* **5**, 25–29.

Fange, R. & Grove, D. 1979 Digestion. In *Fish Physiology*, vol. 8 (ed. W. S. Hoar, D. J. Randall & J. R. Brett), pp. 161–260. New York: Academic Press.

FAO 1993 Review of the state of marine fishery resources. *FAO Fish. Tech. Pap.* no. 335. Rome: FAO. (136 pages.)

FAO 1995 *Fishery statistics*, vol. 76, *Catches and landings*. Rome: FAO. (687 pages.)

Fedorets, Yu. A. & Kun, M. S. 1988 Food spectrum and feeding of the commander squid *Berryteuthis magister* near the Kurile Islands in 1987. In *Resources and the biological basis of rational exploitation of commercial invertebrates* (Abstracts of reports of All-Union conference, 22–24 November 1987, Vladivostok), pp. 70–72. Vladivostok. [In Russian.]

Froerman, Yu. M. 1984 Feeding spectrum and trophic relationships of short-finned squid (*Illex illecebrosus*) in the Northwest Atlantic. *NAFO Sci Coun. Stud.* **7**, 67–75.

Fry, B. 1988 Food web structure on Georges Bank from stable C, N and S isotopic compositions. *Limnol. Oceanogr.* **33**, 1182–1190.

Gaevskaya, A. V. & Nigmatullin, Ch. M. 1976 Biotic relationships of *Ommastrephes bartrami* (Cephalopoda, Ommastrephidae) in the North and South Atlantic. *Zool. Zh.* **55**, 1800–1810. [In Russian.]

Ghiretti, F. 1959 Cephalopotoxin: the crab-paralyzing agent of the posterior salivary glands of cephalopods. *Nature, Lond.* **183**, 1192–1193.

Grisley, M. S. & Boyle, P. R. 1985 A new application of serological techniques to gut contents analyses. *J. exp. mar. Biol. Ecol.* **90**, 1–9.

Grisley, M. S. & Boyle, P. R. 1988 Recognition of food in *Octopus* digestive tract. *J. exp. mar. Biol. Ecol.* **118**, 7–32.

Guerra, A. 1978 Sobre la alimentatión y el comportamiento alimentario de *Octopus vulgaris*. *Invest. pesq.* **42**, 351–364.

Guerra, A., Castro, B. G. & Nixon, M. 1991 Preliminary study on the feeding by *Loligo gahi* (Cephalopoda: Loliginidae). *Bull. mar. Sci.* **49**, 309–311.

Hanlon, R. T. & Messenger, J. B. 1996 *Cephalopod behaviour*. Cambridge University Press.

Hatfield, E. M. C., Rodhouse, P. G. & Porebski, J. 1990 Demography and distribution of the Patagonian squid *Loligo gahi* d'Orbigny, 1835 during the austral winter. *J. Cons. perm. int. Explor. Mer.* **46**, 306–312.

Heeger, T., Piatkowski, U. & Möller, H. 1992 Predation on jellyfish by the cephalopod *Argonauta argo*. *Mar. Ecol. Prog. Ser.* **88**, 293–296.

Hitchcock, G. L., Langdon, C. & Smayda, T. J. 1987 Short-term changes in the biology of a Gulf Stream warm-core ring: phytoplankton biomass and productivity. *Limnol. Oceanogr.* **32**, 919–928.

Hixon, R. F. 1983 *Loligo opalescens*. In *Cephalopod Life cycles: comparative reviews*, vol. 1 (ed. P. R. Boyle), pp. 95–114. London: Academic Press.

Hopkins, T. L. 1985 Food web of an Antarctic midwater ecosystem. *Mar. Biol.* **89**, 197–212.

Höss, M., Kohn, M., Pääbo, S., Knauer, F. & Schröder, W. 1992 Excrement analysis by PCR. *Nature, Lond.* **359**, 199.

Iribarne, O. O., Fernández, M. E. & Zucchini, H. 1991 Prey selection by the small Patagonian octopus *Octopus tehuelchus* d'Orbigny. *J. exp. mar. Biol. Ecol.* **148**, 271–282.

Ivanovic, M. L. & Brunetti, N. E. 1994 Food and feeding of *Illex argentinus*. *Antarct. Sci.* **6**, 185–193.

Jobling, M. 1985 'Digestion rate' methods for the estimation of daily ration in cephalopods. In *Marine biology of the polar regions and effects of stress on marine organisms* (ed. J. S. Gray & M. W. Christiansen), pp. 269–279. Chichester: John Wiley & Sons Ltd.

Joll, L. M. 1977 The predation of pot caught western rock lobster (*Panulirus longipes cygnus*) by octopus. Report no. 29, Department of Fisheries and Wildlife, Western Australia. (58 pages.)

Joy, J. B. 1989 *The fishery biology of ommastrephid squids in Shetland waters*. MSc thesis, University of Aberdeen.

Karpov, K. A. & Caillet, G. M. 1978 Feeding dynamics of *Loligo opalescens*. *Calif. Dept. Fish. Game, Fish Bull.* **169**, 45–66.

Kear, A. J. 1992 The diet of Antarctic squid: comparison of conventional and serological gut contents analyses. *J. exp. mar. Biol. Ecol.* **156**, 161–178.

Kear, A. J. 1994 Morphology and function of the mandibular muscles in some coleoid cephalopods. *J. mar. biol. Ass. U.K.* **74**, 801–822.

Kear, A. J. & Boyle, P. R. 1992 Loss of meal antigenicity during digestion in Sepia officinalis (Cephalopoda: Sepiodea). *J. mar. biol. Ass. U.K.* **72**, 543–551.

Kier, W. M. 1982. The functional morphology of the musculature of squid (Loliginidae) arms and tentacles. *J. Morph.* **172**, 179–192.

Kier, W. M. & Smith, A. M. 1990 The morphology and mechanics of octopus suckers. *Biol. Bull. mar. Biol. Lab., Woods Hole* **178**, 126–136.

Kozlov, A. N. & Tarverdieva, M. I. 1989 Feeding of different species of Myctiophidae in different parts of the Southern Ocean. *J. Ichthyol.* **29**, 160–167.

Krause, J. 1994 Differential fitness returns in relation to spatial position in groups. *Biol. Rev.* **69**, 187–206.

Kubodera, T. & Okutani, T. 1977 Description of a new species of Gonatid squid, *Gonatus madokai*, n. sp., from the Northwest Pacific, with notes on morphological changes with growth and distribution in immature stages (Cephalopoda: Oegopsida). *Jap. J. Malacol.* (*Venus*) **36**, 123–151.

Kuznetsova, N. A. & Fedorets, Yu. A. 1987. Feeding of the commander squid *Berryteuthis magister*. *Biologia moriya* (*USSR*) **1**, 71–73. [In Russian with English abstract.]

Laidig, T. E., Adams, P. B., Baxter, C. & Butler, J. L. 1995 Feeding on euphausiids by *Octopus rubescens*. *Calif Fish Game* **81**, 77–79.

Laptikhovsky, V. V. & Nigmatullin, Ch. 1993 Egg size, fecundity and spawning in females of the genus *Illex* (Cephalopoda: Ommastrephidae). *Fish. Res.* **16**, 313–338.

Le Mao, P. 1985 Place de la seiche *Sepia officinalis* (mollusque, cephalopoda) dans les chaines alimentaires du golfe Normano-Breton. *Cah. Biol. mar.* **26**, 331–340.

Lipiński, M. R. 1987 Food and feeding of *Loligo vulgaris reynaudii* from St Francis Bay, South Africa. *S. Afr. J. mar. Sci.* **5**, 557–564.

Lipiński, M. R. 1992 Cephalopods and the Benguela ecosystem: trophic relationships and impact. *S. Afr. J. mar. Sci.* **12**, 791–802.

Lipiński, M. R. & Linkowski, T. B. 1988 Food of the squid *Ommastrephes bartramii* (Lesueur, 1821) from the south-west Atlantic Ocean. *S. Afr. J. mar. Sci.* **6**, 43–46.

Lipiński, M. R., Roeleveld, M. A. & Augustyn, C. J. 1991 Feeding studies on *Sepia australis* with an assessment of its significance in the Benguela ecosystem. In *La seiche*, 1*st International Symposium on the cuttlefish* Sepia (ed. È. Boucaud-Camou), pp. 117–129. Caen: Centre de Publications de l'Université de Caen.

Lu, C. C. & Clarke, M. R. 1975*a* Vertical distribution of cephalopods at 40° N 53° W and 60° N 20° W in the north Atlantic. *J. mar. biol. Ass. U.K.* **55**, 143–163.

Lu, C. C. & Clarke, M. R. 1975*b* Vertical distribution of cephalopods at 11° N 20° W in the north Atlantic. *J. mar. biol. Ass. U.K.* **55**, 369–389.

Lu, C. C. & Williams, R. 1994 Contribution to the biology of squid in the Prydz Bay region, Antarctica. *Antarct. Sci.* **6**, 223–229.

Macy, W. K. 1982 Feeding patterns of the long-finned squid, *Loligo pealei*, in New England waters. *Biol. Bull. mar. Biol. Lab., Woods Hole* **162**, 28–38.

Mangold-Wirz, K. 1963 Biologie des cephalopodes benthiques et nectoniques de la Mer Catalane. *Vie Milieu* **13** (suppl.), 1–25.

Mann, K. H. 1984 Fish production in open ocean ecosystems. In *Flows of energy and materials in marine ecosystems* (ed. M. J. R. Fasham), pp. 435–458. New York: Plenum Press.

Martins, H. R. 1982 Biological studies of the exploited stock of *Loligo forbesi* (Mollusca: Cephalopoda) in the Azores. *J. mar. biol. Ass. U.K.* **62**, 799–808.

Maruyama, K. & Tamura, T. 1959 Food habit of an octopus, *Octopus dofleini*, in Hakodate Bay. *Aquaculture* **7**, 48–54.

Mather, J. A. 1991 Foraging, feeding and middens of juvenile *Octopus vulgaris*. *J. Zool.* **224**, 27–39.

Mather, J. N. 1993 Octopuses as predators: implications for management. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 275–282. Tokyo: Tokai University Press.

Mather, J. A. & Nixon, M. 1995 *Octopus vulgaris* (Cephalopoda) drills the chelae of crabs in Bermuda. *J. mollusc. Stud.* **61**, 405–406.

Maurer, R. O. & Bowman, R. E. 1985 Food consumption of squids (*Illex illecebrosus* and *Loligo pealei*) off the Northeastern United States. *NAFO Sci. Coun. Stud.* **9**, 117–124.

McQuaid, C. D. 1994 Feeding behaviour and selection of bivalve prey by *Octopus vulgaris* Cuvier. *J. Exp. mar. Biol. Ecol.* **177**, 187–202.

Natsukari, Y. & Tashiro, M. 1991 Neritic squid resources and cuttlefish resources in Japan. *Mar. Behav. Physiol.* **18**, 149–226.

Neill, S. R. St. J. & Cullen, J. M. 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. *J. Zool.* **172**, 549–569.

Nemoto, T., Okiyama, M., Iwasaki, N. & Kikudi, T. 1988 Squid as predators on krill (*Euphausia superba*) and prey for sperm whales in the Southern Ocean. In *Antarctic Ocean and resources variability* (ed. D. Sahrhage), pp. 292–296. Berlin: Springer-Verlag.

Nesis, K. N. 1970 The biology of the giant squid of Peru and Chile, *Dosidicus gigas*. *Oceanology* **10**, 140–152.

Nesis, K. N. 1983 *Dosidicus gigas*. In *Cephalopod life cycles: comparative reviews*, vol. 1 (ed. P. R. Boyle), pp. 215–231. London: Academic Press.

Nesis, K. N. 1985 *Oceanic cephalopods*. Moscow: Nauka. (285 pages.) [In Russian.]

Nigmatullin, Ch. M. 1972 Feeding of ommastrephid squids off West Africa coast. *Trudy AtlantNIRO* **42**, 152–155. [In Russian.]

Nigmatullin, Ch. M. 1975 Feeding of mass cephalopods in Spanish Sahara and Mauritanian Shelf. *Trudy AtlantNIRO* **58**, 177–186. [In Russian with English abstract.]

Nigmatullin, Ch. M. 1989 Las especies de calamar mas abundantes del Atlantico Sudoeste y sinopsis sobre la ecologia del calamar (*Illex argentinus*). *Frente Maritimo* **5**, 71–82. [In Spanish.]

Nigmatullin, Ch. M. 1990 Squid stocks of the world ocean and the possibility of its exploitation for the U.S.S.R. In *5th All-Union Conference on the Commercial Invertebrates, Minsk (Naroch), 9–13 October 1990: thesis of the reports*, pp. 86–87. Moscow: VNIRO. (In Russian).

Nigmatullin, Ch. M. & Ostapenko, A. A. 1976 Feeding of *Octopus vulgaris* Lam. from the northwest African coast. *ICES* C.M. 1976/K:6.

Nixon, M. 1985 Capture of prey, diet and feeding of *Sepia officinalis* and *Octopus vulgaris* (Mollusca: Cephalopoda) from hatchling to adult. *Vie Milieu* **35**, 255–261.

Nixon, M. 1987 Cephalopod diets. In *Cephalopod life cycles: comparative reviews*, vol. 2 (ed. P. R. Boyle), pp. 201–219. London: Academic Press .

Nixon, M. & Dilly, P. N. 1977 Sucker surfaces and prey capture. *Symp. Zool. Soc. Lond.* **38**, 447511.

O'Dor, R. K., Helm, P. & Balch, N. 1985 Can rhynchoteuthions suspension feed? (Mollusca, Cephalopoda). *Vie Milieu* **35**, 267–271.

O'Dor, R. K. 1993 Big squid, big currents and big fisheries. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 385–396. Tokyo: Tokai University Press.

O'Dor, R. K & Wells, M. J. 1987 Energy and nutrient flow. In *Cephalopod life cycles: comparative reviews*, vol. 2 (ed. P. R. Boyle), pp. 109–133. London: Academic Press.

Ogawa, Y. 1982 Evaluation of the influence of changes in prey abundance on catch fluctuations of 'Shiroika', *Loligo edulis*, in coastal waters of the southwestern Japan Sea. *Bull. Jap. Soc. Fish. Oceanogr.* **41**, 11–16. [In Japanese with English summary.]

Okiyama, M. 1965 On the feeding habit of the common squid *Todarodes pacificus* Steenstrup, in the off-shore region of the Japan Sea. *Bull. Jpn Sea Regional Fish. Res. Lab.* **14**, 31–41. [In Japanese with English abstract.]

Okutani, T. 1962 Diet of the common squid, *Ommastrephes* *sloani pacificus* landed around Ito Port, Shizuoka Prefecture. *Bull. Tokai Region Fish. Res. Lab.* **32**, 41–47.

O'Sullivan, D. & Cullen, J. M. 1983 Food of the squid *Nototodarus gouldi* in Bass Strait. *Aust. J. mar. freshw. Res.* **34**, 261–285.

Packard, A. 1972. Cephalopods and fish: the limits of convergence. *Biol. Rev.* **47**, 241–307.

Passarella, K. C. & Hopkins, T. L. 1991 Species composition and food habits of the micronektonic cephalopod assemblage in the eastern Gulf of Mexico. *Bull. mar. Sci.* **49**, 638–559.

Piatkowski, U., Rodhouse, P. G., Murphy, E. J., White, M. G., Bone, D. G. & Symon, C. 1994 Nekton community of the Scotia Sea as sampled by the RMT25 during austral summer. *Mar. Ecol. Prog. Ser.* **112**, 12–28.

Pierce, G. J., Boyle, P. R., Hastie, L. C. & Santos, M. B. 1994 Diets of squid *Loligo forbesi* and *Loligo vulgaris* in the northeastern Atlantic. *Fish Res.* **21**, 149–163.

Pierce, G. J. & Santos, M. B. 1996 Trophic interactions of squid in Scottish waters. In *Aquatic predators and their prey* (ed. S. P. R. Greenstreet & M. L. Tasker), pp. 58–64. Oxford: Blackwell Scientific Publications.

Radchenko, V. I. 1992 The role of squids in the Bering Sea pelagic ecosystem. *Oceanology* **32**, 762–767.

Rasero, M., Gonzalez, A. F., Castro, B. G. & Guerra, A. 1996 Predatory relationships of two sympatric squid, *Todaropsis eblanae* and *Illex coindetii* (Cephalopoda: Ommastrephidae) in Galician waters. *J. mar. biol. Ass. U.K.* **76**, 73–87.

Rees, W. J. & Lumby, J. R. 1954 The abundance of *Octopus* in the English Channel. *J. mar. biol. Ass. U.K.* **33**, 515–536.

Ritchie, L. D. 1972 Octopus predation on pot caught rock lobster, Hokianga area, N.Z. September–October 1970. *Fisheries Technical Report. New Zealand Marine Department*, no. 81. (40 pages.)

Roberts, M. J. & Sauer, W. H. H. 1994 Environment: the key to understanding the South African chokka squid (*Loligo vulgaris reynaudii*) life cycle and fishery. *Antarct. Sci.* **6**, 249–258.

Rocha, F., Bernardino, G. C., Maria, S. G. & Guerra, A. 1994 The diets of *Loligo vulgaris* and *L. forbesi* (Cephalopoda: Loliginidae) in northwestern Spanish Atlantic waters. *Sarsia* **79**, 119–126.

Rodhouse, P. G., Arnbom, T. R., Fedak, M. A., Yeatman, J. & Murray, A. W. A. 1992*a* Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. *Can. J. Zool.* **70**, 1007–1015.

Rodhouse, P. G., Barton, J., Hatfield, E. M. C. & Symon, C. 1995 *Illex argentinus*: life cycle, population structure, and fishery. *ICES mar. Sci. Symp.* **199**, 425–432.

Rodhouse, P. G. & Clarke, M. R. 1985 Growth and distribution of young *Mesonychteuthis hamiltoni* Robson (mollusca: cephalopoda): an Antarctic squid. *Vie Milieu* **35**, 223–230.

Rodhouse, P. G. & Clarke, M. R. 1986 Distribution of the early-life phase of the Antarctic squid *Galiteuthis glacialis* in relation to the hydrology of the Southern Ocean in the sector 15° to 30° E. *Mar. Biol.* **91**, 353–357.

Rodhouse, P. G., Clarke, M. R. & Murray, A. W. A. 1987 Cephalopod prey of the wandering albatross *Diomedea exulans*. *Mar. Biol.* **96**, 1–10.

Rodhouse, P. G. & Hatfield, E. M. C. 1990 Dynamics of growth and and maturation in the cephalopod *Illex argentinus* de Castellanos, 1960 (Teuthoidea: Ommastrephidae). *Phil. Trans. R. Soc. Lond.* B **329**, 229–241.

Rodhouse, P. G. & Piatkowski, U. 1995 Fine-scale distribution of juvenile cephalopods in the Scotia Sea and adaptive allometry of the brachial crown. *Mar. Biol.* **124**, 111–117.

Rodhouse, P. G. and Prince, P. A. 1993 Cephalopod prey of the black-browed albatross *Diomedea melanophrys* at South Georgia. *Polar Biol.* **13**, 373–376.

Rodhouse, P. G., Prince, P. A., Clarke, M. R. & Murray, A. W. A. 1990 Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. *Mar. Biol.* **104**, 353–362.

Rodhouse, P. G., Prince, P. A., Trathan, P. N. *et al.* 1996 Cephalopods and mesoscale oceanography at the Antarctic Polar Front: satellite tracked predators locate pelagic trophic interactions. *Mar. Ecol. Prog. Ser.* **136**, 37–50.

Rodhouse, P. G. & White, M. G. 1995 Cephalopods occupy the ecological niche of epipelagic fish at the Antarctic Polar Frontal Zone. *Biol. Bull. mar. Biol. Lab.*, *Woods Hole* **189**, 77–80.

Rodhouse, P. G., White, M. G. & Jones, M. R. R. 1992*b* Trophic relations of the cephalopod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Antarctic Polar Front, Scotia Sea. *Mar. Biol.* **114**, 415–421

Roper, C. F. E., Sweeney, M. J. & Nauen, C. E. 1984 *FAO species catalogue*, vol. 3. *Cephalopods of the world. An annotated illustrated catalogue of species of interest to fisheries.* (*FAO Fish. Synopsis*, no. 125.) Rome: FAO. (277 pages.)

Rowell, T. W., Trites, R. W.& Dawe, E. G. 1985 Distribution of short-finned squid (*Illex illecebrosus*) larvae and juveniles in relation to the Gulf Stream frontal zone between Florida and Cape Hatteras. *NAFO Sci. Coun. Stud.* **9**, 77–92.

Sanchez, P. 1981 Regimen alimentaire d'*Eledone cirrhosa* (Lamarck, 1798) (Mollusca, Cephalopoda) dans la mer Catalane. *Rapp. Comm. int. Mer Medit.* **27**, 209–212.

Sanchez, P. 1982 Regimen alimentario de *Illex coindetti* (Vernay,1837) en el mar Catalan. *Inv. Pesq.* **46**, 443–449.

Sato, M. 1991 [On the feeding habit of *Loligo bleekeri*.] Ika-rui Shigen Gyokaikyo Kento Kaigi Kenkyu Hokoku (Heisei 2-nendo). *Hokkaido Region Natn. Fish. Res. Inst. Kushiro*, pp. 84–90. [In Japanese.]

Sauer, W. H. H. & Lipiński, M. R. 1991 Food of squid *Loligo vulgaris reyaudii* (Cephalopoda: Loliginidae) on their spawning grounds off the eastern cape, South Africa. *S. Afr. J. mar. Sci.* **10**, 193–201.

Segawa, S. 1993 Field and laboratory feeding studies of the Japanese oval squid, *Sepioteuthis lessoniana*. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 499–511. Tokyo: Tokai University Press.

Seki, M. P. 1993*a* Trophic relationships of *Ommastrephes bartramii* during winter migrations to subtropical waters north of the Hawaiian Islands. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 523–529. Tokyo: Tokai University Press.

Seki, M. P. 1993*b* The role of the neon flying squid, *Ommastrephes bartrami*, in the North Pacific pelagic food web. *Bull. int. N. Pac. Fish. Comm.* **53**, 207–215.

Sennikov, A. M., Shimko, B. P., Mukhin, S. G. & Bliznichenko, T. E. 1986 Biology and distribution of the winter spawning group of arrow-squid *Todarodes sagittatus* in the North-West Atlantic. In: *Resources and perspectives of using of squids of World ocean*, pp. 29–46. Moscow: VNIRO. [In Russian.]

Shchetinnikov, A. S. 1992 Feeding spectrum of squid *Stenoteuthis oualaniensis* (Oegopsida) in the eastern Pacific. *J. mar. biol. Ass. U.K.* **72**, 849–860.

Sherman, K., Alexander, L. M. & Gold, B. D. (eds) 1993 *Large marine ecosystems.* Washington, D.C.: American Association for the Advancement of Science. (376 pages.)

Shevtsov, G. A. 1978 [Pacific squid *Todarodes pacificus* Steenstrup, 1880 (Cephalopoda, Ommastrephidae) in the North-West Pacific (biology, distribution and stock assessment).] *Avtoreferat dissertatsii na soiskanie uchionoy stepeni kandidata biologicheskikh nauk*. Vladivostok. (25 pages.) [In Russian.]

Snÿder, R. 1995 The giant form of *Sthenoteuthis oualaniensis* from the Arabian Sea. M.Sc. thesis, University of Aberdeen. (70 pages + appendix.)

Sugimoto, T. & Tameishi, H. 1992 Warm-core rings, streamers and their role on the fishing ground formation around Japan. *Deep-Sea Res.* **39**, suppl. 1, S183–S201.

Tanaka, Y. 1993 Japanese common squid (*Todarodes pacificus*) preys on benthic polychaete (*Nereis pelagica*). In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 555–558. Tokyo: Tokai University Press.

Tashiro, M. 1977 [Biology and fishery of the loliginid squid, *Loligo edulis*, in the coasta[waters of northwestern Kyushu.] *Nihonkai Block Shiken Kenkyu Shiroku* **1**, 81–98. (In Japanese.]

Tashiro, M., Tokunaga, T., Machida, S. & Takata, J. 1981 Distribution of a squidfish, *Loligo edulis* Hoyle, in the East China Sea. *Bull.Nagasaki Prefect. Inst. Fish.* **7**, 21–30. [In Japanese with English title.]

Uozumi, Y. & Shiba, C. 1993 Growth and age composition of *Illex argentinus* (Cephalopoda: Oegopsida) based on daily increment counts in statoliths. In *Recent advances in cephalopod fisheries biology* (ed. T. Okutani, R. K. O'Dor & T. Kubodera), pp. 591–605. Tokyo: Tokai University Press.

Vecchione, M. 1987 A multispecies aggregation of cirrate octopods trawled from north of the Bahamas. *Bull. mar. Sci.* **40**, 78–84.

Vecchione, M. 1991 A method for examining the structure and contents of the digestive tract in paralarval squids. *Bull. mar. Sci.* **49**, 300–308.

Vecchione, M. & Roper, C. F. E. 1986 Occurence of larval *Illex illecebrosus* and other young cephalopods in the Slope/Gulf Stream interface. *Proc. biol. Soc. Wash.* **99**, 703–708.

Vidal, E. A. G. 1994 Relative growth of paralarvae and juveniles of *Illex argentinus* (Castellanos, 1960) in Southern Brazil. *Antarct. Sci.* **6**, 275–282.

Villanueva, R. 1992 Deep-sea cephalopods of the north-western Mediterranean: indications of up-slope ontogenetic migration in two bathybenthic species. *J. Zool.* **227**, 267–276.

Villanueva, R. 1993 Diet and mandibular growth of *Octopus magnificus* (Cephalopoda). *S. Afr. J. mar. Sci.* **13**, 121–126.

Villanueva, R. 1994 Decapod crab zoeae as food for rearing cephalopod paralarvae. *Aquaculture* **128**, 143–152.

Villanueva, R. & Guerra, A. 1991 Food and prey detection in two deep-sea cephalopods: *Opisthoteuthis agassizi* and *O. vossi* (Octopoda: Cirrata). *Bull. mar. Sci.* **49**, 288–299.

Villanueva, R., Nozals, C. & Boletzky, S. v. 1995 The planktonic life of octopuses. *Nature, Lond.* **377**, 107.

Voss, G. L. 1962 A monograph of the Cephalopoda of the North Atlantic, I: The family Lycoteuthidae. *Bull. mar. Sci. Gulf Caribb.* **12**, 264–305.

Voss, G. L. 1973 *Cephalopod resources of the world.* (*FAO Fisheries Circular* no.149.) Rome: FAO. (75 pages.)

Voss, N. A., Nesis, K. N. & Rodhouse, P. G. 1996 The cephalopod family Histioteuthidae (Oegopsida): Systematics, biology and biogeography. In *Systematics and biogeography of cephalopods* (ed. N. A. Voss, M. Vecchione, R. Toll & M. Sweeney). *Smithson. Contrib. Zool.* (In the press.)

Vovk, A. N. 1985 Feeding spectrum of longfin squid (*loligo pealei*) in the northwest Atlantic and its position in the ecosystem. *NAFO Sci. Coun. Stud.* **8**, 33–38.

Warwick, R. M., Collins, N. R., Gee, J. M. & George, C. L. 1986 Species size distributions of benthic and pelagic metazoa: evidence for interaction. *Mar. Ecol. Prog. Ser.* **34**, 63–68.

Wells, M. J. 1994 The evolution of a racing snail. In *Physiology of cephalopod molluscs* (ed. H. O. Pörtner, R. K. O'Dor & D. L. Macmillan), pp.1–12. Basel: Gordon & Breach.

Wiborg, K. F., Gjøsaeter, J. & Beck, I. M. 1984 *Gonatus fabricii* (Lichtenstein). Investigations in the Norwegian Sea and western Barents Sea, June-September 1982 and 1983. *Fisken Hav.* **2**, 1–11.

Williamson, R. 1995 A sensory basis for orientation in cephalopods. *J. mar. biol. Ass. U.K.* **75**, 83–92.

Witek, Z. & Krajewska-Soltys, A. 1989 Some examples of the epipelagic plankton size structure in high latitude oceans. *J. Plankt. Res.* **11**, 1143–1155.

Zuev, G. V., Nikolsky, V. N. & Chesalin, M. V. 1994 The biology and resources of the purpleback flying squid (*Sthenoteuthis oualanienesis*) in the Arabian Sea. In *Biogeochemical processes in the Arabian Sea* (U.S. C.I.S. Arabian Sea workshop, Sevastopol, Crimea, Ukraine, Sept. 20–25, 1993), pp. 167–172. MHI UNAS.