ELSEVIER

Fisheries Research 52 (2001) 5–10

FISHERIES RESEARCH

www.elsevier.com/locate/fishres

Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview

U. Piatkowski[a,*], G.J. Pierce[b], M. Morais da Cunha[c]

[a]Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen, Scotland AB24 2TZ, UK
[b]Institut für Meereskunde an der Universität Kiel, Düsternbrooker Weg 20, 24105 Kiel, Germany
[c]Departamento de Recursos Marinhos, Instituto de Investigação das Pescas e do Mar, Av. Brasília 1449-006, Portugal

At present, world-wide traditional finfish stocks are decreasing due to overfishing and environmental changes (Caddy and Rodhouse, 1998). In response, cephalopods have gained increasing attention as an alternative to the traditional marine harvest and will gain a much larger importance in the future to supply mankind with marine living resources. In fact, total cephalopod landings have steadily increased since 1950s, peaking in 1997 at more than 3.3 million tonnes (FAO, 2000; Fig. 1).

Although increased cephalopod landings may partly reflect increased market demand, particularly in the Far East nations, there is evidence that overfishing finfish stocks has positively affected cephalopod populations. Data from fifteen FAO key areas reveal that, with the exception of the north-east Atlantic, cephalopod landings have increased significantly over the last 25 years, while groundfish catches have risen more slowly, remained stable, or declined (Caddy and Rodhouse, 1998). Species replacement has been suggested as an underlying factor in changing fishery patterns in the Saharan Bank fishery, with cephalopods replacing sparids as the main target species (Balguerías et al., 2000).

Despite these economic and ecological key positions of cephalopods, their overall role in the marine environment, their significance as food resources for higher trophic levels such as marine mammals and birds, and their impact as predatory consumers of finfish and invertebrates are only beginning to be studied (Clarke, 1996a). In comparison with other marine groups, such as crustaceans, fishes or marine mammals, ecological studies on cephalopods are strikingly sparse. Two major shortcomings are responsible for this: (1) cephalopods are difficult to catch and mostly taken as by-catch in surveys targeting other taxa; (2) they have complicated life cycles and distribution patterns which are only roughly understood for a few species. Consequently, it is of great importance to intensify field and laboratory studies on trophic interrelationships where cephalopods are involved, because they will help to elucidate cephalopod ecology and form the basis for further ecosystem modelling.

Among the terms of reference addressed by the International Council for the Exploration of the Sea (ICES) Working Group on Cephalopod Fisheries and Life History during the last decade, one focused on trophic interrelationships in which cephalopods are involved. This work resulted in a Theme Session on *Impact of cephalopods in the food chain and their interaction with the environment* which was held at the 1998 ICES Annual Science Conference in Cascais, Portugal. The topics that had been proposed for this session included all aspects of cephalopod feeding ecology, the importance of predators of cephalopod stocks, in particular marine mammals, and the

* Corresponding author.
E-mail address: g.j.pierce@abdn.ac.uk (G.J. Pierce).

PII: S0165-7836(01)00226-0

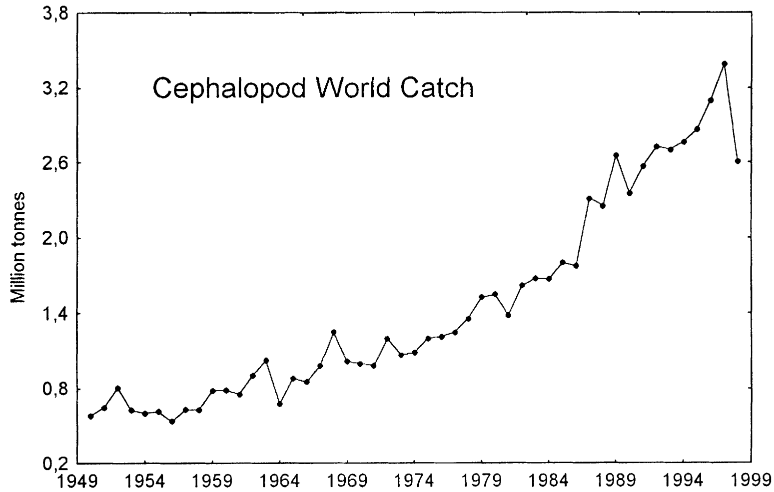

Fig. 1. Cephalopod world catch (from FAO, 2000).

interactions between cephalopod stocks and the physical environment. Another important subject was the human influence on cephalopod stocks due to fishing. Of the 43 presentations given at this Theme Session, seven plus three additional papers were chosen for the present volume to cover research on cephalopod trophic ecology from all parts of the world's oceans. This issue is not meant to summarise our present knowledge of cephalopods in the world's oceans. Instead, it illustrates specific aspects of the role of cephalopods in marine food chains, one of the major subjects of current research on cephalopods. The 10 papers can be divided into three broad topics: (a) the abundance of cephalopod stocks; (b) their importance as food for predators and (c) their importance as consumers.

Knowledge of the biomass and production of cephalopod stocks is fundamental to understand their importance in energy and material flow in marine ecosystems. Indeed, a second volume arising from the 1998 Theme Session focuses on environmental influences on cephalopod abundance (Balguerías et al., 2000; Dawe et al., 2000; Koueta et al., 2000; O'Dor and Hoar, 2000; Sakurai et al., 2000). "Cephalopod production and biomass" was also the theme of an international symposium held in Aberdeen (UK) in July 2000 under the auspices of the Cephalopod International Advisory Council (CIAC).

Two papers in the present volume highlight the problems associated with measuring and understanding changes in the distribution and abundance of cephalopod populations. Denis and Robin (this issue) examine French data on the cuttlefish fishery in the English Channel. In common with many cephalopod fisheries, this fishery has by-catch (trawl) and directed (artisanal coastal trap nets) components. Seasonal patterns in the fishery data are shown to reflect the underlying migration patterns and (short) lifecycle of the species and it is concluded that data from trawl fishing can provide abundance indices. This is important because few European countries (with the notable exception of Portugal) direct research survey effort at monitoring cephalopod abundance. The application of GIS and spatial statistical techniques has highlighted the patchy spatial distribution of abundance in cephalopod stocks. Consequently, overall stock abundance may be a poor predictor of the local importance of cephalopods, and predators and prey. Research on factors underlying spatial distribution tends to emphasise the role of environmental factors (e.g. Pierce et al., 1998; Waluda and Pierce, 1998) but such relationships are difficult to quantify. The paper by Bellido et al. (this issue) shows how relatively recent developments in statistical methods, specifically generalised additive models can help to quantify the non-linear empirical spatial relationships found between local cephalopod abundance and environmental variables. It also provides a framework under which both spatial and temporal (in this example seasonal) patterns could be modelled simultaneously.

The importance of many cephalopod species as predators is not well-known, in part reflecting problems in collecting good data. The beak of cephalopods is used to bite the prey into small pieces so that 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, eating fish captured in the net as well as exhibiting cannibalism (see Rodhouse and Nigmatullin, 1996, for a recent review).

In the Northern Atlantic, various studies have quantified the diet and food consumption of squids (Macy, 1982; Breiby and Jobling, 1985; Maurer and Bowman, 1985; Collins et al., 1994; Pierce et al., 1994; Rocha et al., 1994; Pierce and Santos, 1996; Rasero et al., 1996; Coelho et al., 1997; Dawe et al., 1997; Lordan et al., 1998; Piatkowski et al., 1998). There are also a few such studies on cuttlefish (Castro and Guerra, 1989, 1990; McQuaid, 1994; duSel and Daguzan, 1997; Blanc et al., 1998; Koueta and Boucaud-Camou, 1999). In octopods, more attention has been given to predatory behaviour than diet per se (Nixon, 1979; Guerra and Nixon, 1987; Grisley et al., 1996, 1999; Runham et al., 1997; Fiorito and Gherardi, 1999), although diets have been studied, e.g. using serological methods (Boyle et al., 1986; Grisley and Boyle, 1988). Studies on predatory behaviour of other cephalopods include Porteiro et al. (1990) and Nicol and O'Dor (1985) for squid and Bergstrøm (1985) and Guerra et al. (1988) for sepioids. The present volume includes results from a new study of the diet of the commercially important ommastrephid squid *Illex argentinus* from the SW Atlantic (Mouatt et al., this issue). The most important prey were crustaceans (hyperiid amphipods and euphausiids), especially in smaller size classes of squid, although there was evidence of cannibalism in larger individuals. Feeding apparently occurred mainly around dusk, although dos Santos and Haimovici (1997) recorded feeding activity in this species during both the day and the night off Brazil.

The remainder of this special issue concerns the role of cephalopods as prey, for various predators in different parts of the world. The role of smaller fish as predators of cephalopods is probably less well-understood than the role of sharks, swordfish, birds and mammals, although this topic was recently reviewed by Smale (1996). Previous large-scale studies in the ICES area have suggested that cephalopods are a relatively minor part of fish diet (ICES, 1988; Hislop et al., 1983, 1991; Daan, 1989; Hislop, 1997) and with the notable exception of Hislop et al. (1991), cephalopods eaten were usually not identified to species. However, from the perspective of their effect on cephalopod populations, such interactions could be very important.

Daly et al. (this issue) enumerated the cephalopod prey in stomach contents of 17 demersal fish species in UK waters. The cephalopods were found to be mostly species of little or no commercial value and small adult body size, e.g. Sepiolidae, *Alloteuthis* spp., although some small *Loligo* spp. were also recorded. Generally, as found in previous work, cephalopods were a minor component of the diet. The data were used to estimate *Loligo* consumption by cod *Gadus morhua* in UK waters. Although the estimate is based on a small data set and some assumptions must be made to complete the calculations, amounts of post-recruit squid eaten by cod could be of the same order of magnitude as recent population estimates for *Loligo* in UK waters (Pierce et al., 1996). Velasco et al. (this issue) quantified cephalopods in the stomach contents of 27 species of fish from the southern Bay of Biscay. As was the case in UK waters, cephalopods formed only a small proportion of the diet of most species, although in large specimens of monkfish *Lophius piscatorius* cephalopods comprised 17% (by volume) of the diet. Both small cephalopods (Sepiolidae, *Alloteuthis* spp.) and larger species (e.g. the squids *Illex coindetii*, *Todaropsis eblanae* and *Loligo* spp.) were recorded. The incidence of *Alloteuthis* spp. and octopods in fish stomachs was correlated with the abundance in surveys of these species, although this was not the case for other cephalopod categories.

There have been many more previous studies on the role of cephalopods in the diets of seabirds (e.g., Rodhouse, 1989; Furness, 1994; Piatkowski and Pütz, 1994; Cherel and Weimerskirch, 1995, 1999; Cherel and Klages, 1998; Cherel and Kooyman, 1998; Rodhouse et al., 1998; Imber, 1999) and marine mammals (notably numerous papers by Malcolm Clarke and co-authors). Three new reviews on predators of cephalopods are collected in Clarke (1996a), covering seabirds (Croxall and Prince, 1996), seals (Klages, 1996) and cetaceans (Clarke, 1996b).

Piatkowski et al. (this issue) describe the cephalopods eaten by king penguins *Aptenodytes patagonicus*) in the Falkland (Malvinas) Islands during the austral winter, showing that the diet includes squid of coastal and oceanic waters, with the ommastrephid squid *Martialia hyadesi* being the most important in terms of biomass. This squid species is now targeted by commercial fisheries and the authors discuss the potential impact of the fishery on king penguins.

Mori et al. (this issue) recorded squids from the stomach contents of northern fur seals *Callorhinus ursinus* in the western and central North Pacific. The most important squid prey numerically was *Watasenia scintillans*. The size of squid taken suggested that fur seals targeted mature female squid migrating into shallow waters off Japan for spawning.

Dos Santos and Haimovici (this issue) catalogued the instance of cephalopods in stomachs of marine mammals along the Brazilian coast. A wide range of cephalopod species was recorded, with a greater diversity being found in diets of mammals from offshore waters as compared to those from inshore waters.

Bjørke (this issue) reviews information on the amounts of the Arctic squid *Gonatus fabricii* eaten, in Norwegian waters, by sperm whales *Physeter macrocephalus*, northern bottlenose whales *Hyperoodon ampullatus*, long-finned pilot whales *Globicephala melas* and hooded seals *Cystophora cristata*. The importance of this squid as a source of food for sperm whales and northern bottlenose whales may help to explain the presence of these mammals in Norwegian waters. It may be noted that *Gonatus* spp. have also been identified as an important part of the diet of Greenland halibut (*Reinhardtius hippoglossoides*) off the Atlantic coast of Canada (Dawe et al., 1998).

Santos et al. (this issue) reviews both published and previously unpublished data on the amounts of cephalopods eaten by sharks, swordfish and sperm whales in different parts of the world, making calculations based on various assumptions about diet, energetic requirements and population sizes of the predators. The traditional approach was based on comparison of results from ‘‘minimum’’ and ‘‘maximum’’ figures, but now modern computer sampling techniques (specifically, the bootstrap) allow estimation of confidence limits for amounts of cephalopods eaten. The example given for the latter methodology is based on dietary data for sperm whales in the NE Atlantic, taken from Santos et al. (1999). Although confidence limits appear discouragingly wide, the computations are useful to show where the data are most imperfect, allowing research priorities to be identified.

As most recently highlighted by the CIAC Symposium on Cephalopod Biomass and Productivity, there is world-wide interest in the large biomass of cephalopods in the global oceans, and its importance in marine food webs, especially at higher trophic levels, and to major international and regional fisheries. The papers collected in this issue demonstrate that this is an active and vigorous research field.

One key point is that, in short-lived fast growing species such as squid, the standing crop (biomass) per se is not necessarily a good indicator of the level of predation or exploitation that may be supported by a population, since the rate at which biomass is generated must also be considered. In most cephalopod populations, the entire standing crop is replaced every year (see Boyle and Boletzky, 1996). A corollary of the lack of ‘‘buffering’’ in cephalopod populations is that abundance may fluctuate widely from year to year, so that predators — and fisheries — must be able to turn to alternative resources in years of low abundance. Most of the studies in the present volume report ‘‘snapshots’’ of the trophic interactions taking place and a target for future investigations will be to understand the dynamics of predator responses to fluctuations in the abundance of cephalopod populations, particularly in those predators (such as sperm whales) that apparently specialise in feeding on cephalopods.

References

Balguerías, E., Quintero, M.E., Hernández-González, C.L., 2000. The origin of the Saharan Bank cephalopod fishery. ICES J. Mar. Sci. 57, 15–23.

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

Blanc, A., DuSel, G.P., Daguzan, J., 1998. Habitat and diet of early stages of *Sepia officinalis* L. (Cephalopoda) in Morbihan Bay, France. J. Mollus. Stud. 64, 263–274.

Boyle, P.R., Boletzky, S.v., 1996. Cephalopod populations: definitions and dynamics. Phil. Trans. R. Soc. Lond. B 351, 985–1002.

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. Assoc. UK 66, 867–879.

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

Caddy, J.F., Rodhouse, P.G., 1998. Cephalopod and groundfish landings: evidence for ecological change in global fisheries. Rev. Fish Biol. Fish. 8, 431–444.

Castro, B.G., Guerra, A., 1989. Feeding patterns of *Sepia officinalis* (Cephalopoda: Sepioidea) in the Ría de Vigo (NW Spain). J. Mar. Biol. Assoc. UK 69, 545–553.

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

Cherel, Y., Klages, N., 1998. A review of the food of albatrosses. In: Robertson, G., Gales, R. (Eds.), Albatross Biology and Conservation. Surrey Beatty and Sons, Chipping Norton, pp. 113–136.

Cherel, Y., Kooyman, G.L., 1998. Food of emperor penguins (*Aptenodytes forsteri*) in the western Ross Sea, Antarctica. Mar. Biol. 130, 335–344.

Cherel, Y., Weimerskirch, H., 1995. Seabirds as indicators of marine resources: black-browed albatrosses feeding on ommastrephid squids in Kerguelen waters. Mar. Ecol. Proc. Ser. 129, 295–300.

Cherel, Y., Weimerskirch, H., 1999. Spawning cycle of onychoteuthid squids in the southern Indian Ocean: new information from seabird predators. Mar. Ecol. Prog. Ser. 188, 93–104.

Clarke, M.R. (Ed.), 1996a. The role of cephalopods in the world's oceans. Phil. Trans. R. Soc. Lond. B 351 979–1112.

Clarke, M.R., 1996b. Cephalopods as prey. 3. Cetaceans. Phil. Trans. R. Soc. Lond. B 351, 1053–1065.

Coelho, M., Domingues, P., Balguerias, E., Fernandez, M., Andrade, J.P., 1997. A comparative study of the diet of *Loligo vulgaris* (Lamarck, 1799) (Mollusca: Cephalopoda) from the south coast of Portugal and the Saharan Bank (Central-East Atlantic). Fish. Res. 29, 245–255.

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.

Croxall, J.P., Prince, P.A., 1996. Cephalopods as prey. 1. Seabirds. Phil. Trans. R. Soc. Lond. B 351, 1023–1043.

Daan, N. (Ed.), 1989. Data base report of the Stomach Sampling Project 1981. ICES Co-operative research Report 164. International Council for the Exploration of the Sea, Copenhagen.

Dawe, E.G., Dalley, E.L., Lidster, W.W., 1997. Fish prey spectrum of short-finned squid (*Illex illecebrosus*) at Newfoundland. Can. J. Fish. Aquat. Sci. 54 (Suppl. 1), 200–208.

Dawe, E.G., Bowering, W.R., Joy, J.B., 1998. Predominance of squid (*Gonatus* spp.) in the diet of Greenland halibut (*Reinhardtius hippoglossoides*) on the deep slope of the northeast Newfoundland continental shelf. Fish. Res. 36, 267–273.

Dawe, E.G., Colbourne, E.B., Drinkwater, K.F., 2000. Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). ICES J. Mar. Sci. 57, 1002–1013.

dos Santos, R.A., Haimovici, M., 1997. Food and feeding of the short-filnned squid *Illex argentinus* (Cephalopoda: Ommastrephidae) off southern Brazil. Fish. Res. 33, 139–147.

duSel, G.P., Daguzan, J., 1997. A note on sex ratio, length and diet of a population of cuttlefish *Sepia officinalis* L. (Mollusca: Cephalopoda) sampled by three fishing methods. Fish. Res. 32, 191–195.

FAO, 2000. Total production 1950–1998. FAO Homepage (former FAO Yearbook of fisheries statistics "Catches and landings").

Fiorito, G., Gherardi, F., 1999. Prey-handling behaviour of *Octopus vulgaris* (Mollusca: Cephalopoda) on bivalve preys. Behav. Process. 46, 75–88.

Furness, R.W., 1994. An estimate of the quantity of squid consumed by seabirds in the eastern North Atlantic and adjoining seas. Fish. Res. 21, 165–178.

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

Grisley, M.S., Boyle, P.R., Key, L.N., 1996. Eye puncture as a route of entry for saliva during predation on crabs by the octopus *Eledone cirrhosa* (Lamarck). J. Exp. Mar. Biol. Ecol. 202, 225–237.

Grisley, M.S., Boyle, P.R., Pierce, G.J., Key, L.N., 1999. Factors affecting prey handling in lesser octopus (*Eledone cirrhosa*) feeding on crabs (*Carcinus maenas*). J. Mar. Biol. Assoc. UK 79, 1085–1090.

Guerra, A., Nixon, M., 1987. Crab and mollusc shell drilling by *Octopus vulgaris* (Mollusca: Cephalopoda) in the Ria de Vigo (north-west Spain). J. Zool. Lond. 211, 515–523.

Guerra, A., Nixon, M., Castro, B.G., 1988. Initial stages of food ingestion by *Sepia officinalis* (Mollusca: Cephalopoda). J. Zool. Lond. 214, 189–197.

Hislop, J.R.G., 1997. Data base Report of the Stomach Sampling Project 1991. ICES Co-operative Research Report 219. International Council for the Exploration of the Sea, Copenhagen.

Hislop, J.R.G., Robb, A.P., Brown, M.A., Armstrong, D.W., 1983. A preliminary report on the analysis of the whiting stomachs collected during the 1981 North Sea Stomach Sampling Project. International Council for the Exploration of the Sea CM 1983/G: 59.

Hislop, J.R.G., Robb, A.P., Bell, M.A., Armstrong, D.W., 1991. The diet and food consumption of whiting (*Merlangius merlangus*) in the North Sea. ICES J. Mar. Sci. 48, 139–156.

ICES, 1988. Report of the Meeting Co-ordinators in the Stomach Sampling Project 1985–1987. International Council for the Exploration of the Sea CM 1988/G: 27.

Imber, M.J., 1999. Diet and feeding ecology of the Royal Albatross *Diomedea epomophora* — king of the shelf break and inner slope. Emu 99, 200–211.

Klages, N.T.W., 1996. Cephalopods as prey. 2. Seals. Phil. Trans. R. Soc. Lond. B 351, 1045–1052.

Koueta, N., Boucaud-Camou, E., 1999. Food intake and growth in reared early juvenile cuttlefish *Sepia officinalis* L. (Mollusca: Cephalopoda). J. Exp. Mar. Biol. Ecol. 240, 93–109.

Koueta, N., Castro, B.G., Boucaud-Camou, E., 2000. Biochemical indices for instantaneous growth estimates in young cephalopod *Sepia officinalis* L. ICES J. Mar. Sci. 57, 1–7.

Lordan, C., Burnell, G.M., Cross, T.F., 1998. The diet and ecological importance of *Illex coindetii* and *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Irish waters. S. Afr. J. Mar. Sci. 20, 153–163.

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

Maurer, R.O., Bowman, R.E., 1985. Food consumption of squids (*Illex illecebrosus* and *Loligo pealei*) off the northeastern US. NAFO Sci. Counc. 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.

Nicol, S., O'Dor, R.K., 1985. Predatory behaviour of squid (*Illex illecebrosus*) feeding on surface swarms of euphusiids. Can. J. Zool. 63, 15–17.

Nixon, M., 1979. Hole-boring in shells by *Octopus vulgaris* Cuvier in the Mediterranean. Malacologia 18, 431–443.

O'Dor, R.K., Hoar, J.A., 2000. Does geometry limit squid growth? ICES J. Mar. Sci. 57, 8–14.

Piatkowski, U., Pütz, K., 1994. Squid diet of emperor penguins (*Aptenodytes forsteri*) in the eastern Weddell Sea, Antarctica during late summer. Antarct. Sci. 6, 241–248.

Piatkowski, U., Hernández-García, V., Clarke, M.R., 1998. On the biology of the European flying squid *Todarodes sagittatus* (Lamarck, 1798) (Cephalopoda: Ommastrephidae) in the central eastern Atlantic. S. Afr. J. Mar. Sci. 20, 375–383.

Pierce, G.J., Santos, M.B., 1996. Trophic interactions of squid in Scottish waters. In: Greenstreet, S.P.R., Tasker, M.L. (Eds.), Aquatic Predators and their Prey. Fishing News Books, Oxford, pp. 58–64.

Pierce, G.J., Boyle, P.R., Hastie, L.C., Santos, M.B., 1994. Diets of squid *Loligo forbesi* and *Loligo vulgaris* in the northeast Atlantic. Fish. Res. 21, 149–164.

Pierce, G.J., Bailey, N., Robin, J.-P., 1996. Stock assessment for *Loligo* spp. in the northeast Atlantic. International Council for the Exploration of the Sea CM 1996/K: 23.

Pierce, G.J., Bailey, N., Stratoudakis, Y., Newton, A., 1998. Distribution and abundance of the fished population of *Loligo forbesi* in Scottish waters: analysis of research cruise data. ICES J. Mar. Sci. 55, 14–33.

Porteiro, F.M., Martins, H.R., Hanlon, R.T., 1990. Some observations on the behaviour of adult squids, *Loligo forbesi*, in captivity. J. Mar. Biol. Assoc. UK 70, 459–472.

Rasero, M., González, 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. Assoc. UK 76, 73–87.

Rocha, F., Castro, B.G., Gil, M.S., Guerra, A., 1994. The diets of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in northwestern Spanish Atlantic waters. Sarsia 79, 119–126.

Rodhouse, P.G., 1989. Cephalopods in the diet of wandering albatrosses and sea-surface temperatures at the Sub-Antarctic Front. Sci. Mar. 53, 277–281.

Rodhouse, P.G., Nigmatullin, C.M., 1996. Role as consumers. Phil. Trans. R. Soc. Lond. B 351, 1003–1022.

Rodhouse, P.G., Olsson, O., Anker Nilssen, P., Murray, A.W.A., 1998. Cephalopod predation by the king penguin *Aptenodytes patagonicus* from South Georgia. Mar. Ecol. Prog. Ser. 168, 13–19.

Runham, N.W., Bailey, C.J., Carr, M., Evans, C.A., Malham, S., 1997. Hole-drilling in crab and gastropod shells by *Eledone cirrhosa* (Lamarck, 1798). Sci. Mar. 61, 67–76.

Sakurai, Y., Kiyofuji, H., Saitoh, S., Goto, T., Hiyama, Y., 2000. Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) due to changing environmental conditions. ICES J. Mar. Sci. 57, 24–30.

Santos, M.B., Pierce, G.J., Boyle, P.R., Reid, R.J., Ross, H.M., Patterson, I.A.P., Kinze, C.C., Tougaard, S., Lick, R., Piatkowski, U., Hernández-García, V., 1999. Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990–1996. Mar. Ecol. Prog. Ser. 183, 281–294.

Smale, M.J., 1996. Cephalopods as prey. 4. Fishes. Phil. Trans. R. Soc. Lond. B 351, 1067–1081.

Waluda, C.M., Pierce, G.J., 1998. Temporal and spatial patterns in the distribution of squid *Loligo* spp. in UK waters. S. Afr. J. Mar. Sci. 20, 323–336.