Cephalopods as Prey. IV. Fishes

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Phil. Trans. R. Soc. Lond. B 1996 **351**, 1067-1081
doi: 10.1098/rstb.1996.0094

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SUMMARY

Predatory fishes that consume cephalopods have broad spectrum diets that include other groups, such as fishes and crustaceans. Extremely few fish predators feed on cephalopods to the virtual exclusion of other prey, although the tawny nurse shark *Nebrius ferrugineus* and the sicklefin weasel shark *Hemigaleus microstoma* may be exceptions, and some deep-living spiny dogfish may feed largely on cephalopods when they are available. Cephalopods are rarely taken in estuaries but they become more important prey on continental shelves and squids may be more dominant prey during their spawning aggregations. Cephalopods generally become more important components of the diets of larger predatory fishes, such as sharks, that inhabit the continental slope and rise. They may be important to pelagic fishes, such as swordfish and tunas in some parts of the oceans. Cephalopods are rarely taken by benthic Antarctic fishes but they are important prey of some pelagic fishes in the Arctic. Abundance and size of potential prey is critical, and the behaviour of both predator and potential prey is decisive, in prey choice. Factors such as prey switching with growth, between areas and at different times, have major influences on the diets of predators. There are extremely few studies that obtain rigorous enough data to allow quantitative analysis of the significance of cephalopods (or other prey) in the diets of predatory fishes and even the most comprehensive studies are not predictive because findings relate only to the time period of each study. Nevertheless, cephalopods are important components of most marine food webs and, furthermore, may play an indirect role in facilitating prey capture to secondary predators, and in providing rejecta to benthic scavengers.

1. INTRODUCTION

Fishes constitute about half the number of extant vertebrates, totalling an estimated 21 723 living species (Nelson 1984). Only 58% of modern fishes are marine (Cohen 1970 in Moyle & Cech 1982) and it is these groups that are most likely to prey on (or be prey of) cephalopods. Fishes vary in size from adults of 25 mm (*Trimma* spp.: Gobiidae) to the largest of fishes, whale sharks, which may attain 21 m. Teleosts pass through egg and larval stages and may attain > 1.5 m and > 50 kg (e.g. some Scombridae, Sparidae and Serranidae) and consequently, their niches change ontogenetically more extremely than marine mammals and birds. This paper aims to review the importance of cephalopods in the diets of fishes and investigate the existence of trends in relation to geographic locality, depth and size of predators. The purpose is to investigate whether there is any evidence from fish feeding studies to support the hypothesis that cephalopods are important in the ecology of the oceans, as has been suggested by studies of sperm whales (Clarke 1977).

2. METHODS

Quantitative comparisons between studies are difficult because different authors analyse and present their results in disparate ways. Furthermore, many studies do not identify cephalopods to species or even family level. Some of the more recent studies use their mandibles or 'beaks' (e.g. Pinkas *et al.* 1971; Smale 1986*a*, *b*), which has considerably improved understanding of cephalopods in food webs since the publication of appropriate guides (Clarke 1962, 1986; Smale *et al.* 1993). Nevertheless, identifications are often only to the family level, particularly if an area is poorly collected and the cephalopod fauna little known. On the other hand, some workers have used predators as 'samplers' of cephalopods (Rancurel 1970; Clarke 1977; Okutani & Tsukada 1988). Because of their specific interest, cephalopods have been described in detail in such studies, but the relative importance of cephalopods compared to other components of the diet is often not indicated. These constraints limit comparisons between studies, different species and different areas. Nevertheless, even those studies which do not provide accurate identification beyond the level of class may assist in assessing their relative importance in food webs. Many fish feeding studies have been multi-species in coverage of predators and are therefore suitable for assessing the 'big picture'.

In this review, the value of 10% mass (or other measures if mass or volume is not recorded) is considered important in any predator size group, or any locality. However, the limitations of this concept of importance will be discussed in more detail later. Predators at upper trophic levels will receive most attention because they are most likely to prey on cephalopods. The initial part of this review will investigate the role of cephalopods in the diets of fishes from different habitats to investigate trends in predator/prey interactions. Although this approach is convenient for assessing trends, many predators are able to move between habitats, so that grouping is somewhat arbitrary. However, some studies span a range of habitats and others do not clearly separate data by depth. Information on hunting by predators and aspects of cephalopod behaviour will be briefly reviewed later.

3. ESTUARINE FISHES

Studies of predatory fishes in estuaries have shown that cephalopods are either absent or minor components of the prey spectrum (Whitfield & Blaber 1978; Talent 1976, 1982; Snelson *et al.* 1984; Salini *et al.* 1992; Stillwell & Kohler 1993). This results from their being stenohaline (except *Loliguncula* spp.), and most occur in salinities of 27–38 parts per thousand and in areas of high water quality (Boletzky & Hanlon 1983). An apparent anomaly of *Sepia* sp. being recorded in a large proportion of eastern Cape estuaries of South Africa is attributable to their high salinity levels (Marais 1984).

4. CONTINENTAL SHELF FISHES

Very few feeding studies mention the occurrence of cephalopod larvae and small juveniles in stomach contents, although there are some (see Vecchione 1987). Hobson & Chess (1978) recorded squid larvae from the plankton of Enewetok Atoll and in the stomachs of nocturnal planktivores occasionally. Juvenile squids have also been recorded off the South African coast (Meyer & Smale 1991*a*).

(*a*) *Tropical seas*

Several studies in tropical seas have shown that cephalopods are relatively unimportant to fish predators (table 1). An exception is in northern Australia, where cephalopods are important to several species of teleost and chondrichthyan. Stevens (1984) suggested that *Nebrius concolor* (synonomized under *N. ferrugineus* by Compagno (1984)) may be a cephalopod specialist because all six studied had taken cephalopods and all those identified were octopods. *Hemigaleus microstoma* also appears to be a cephalopod specialist (Stevens & Cuthbert 1983; Stevens & McLoughlin 1991). Some 98% of stomachs contained cephalopods, mainly octopods (Stevens & Cuthbert 1983). A similar dominance of cephalopods was recorded in this shark by Salini *et al.* (1992; table 2). Salini *et al.* (1994) noted that prey may change in importance seasonally in the Gulf of Carpentaria and found that in one teleost, cephalopods changed from 6.2% dry mass in June to 60.9% in November–December.

(*b*) *Subtropical seas*

In subtropical waters off the south east United States cephalopods were important prey of vermilion snapper (Sedberry & Cuellar 1993), especially *Loligo plei*. While black sea bass, too, took significant volumes (7%) of cephalopod (Sedberry 1988), their importance to other species, such as whitebone porgy, was very minor (Sedberry 1989).

In subtropical south west Indian Ocean waters of Natal, South Africa, cephalopods are of minor importance to inshore fishes (Joubert & Hanekom 1980, table 1), midwater predators (van der Elst 1976) and deeper living reef fishes (Garratt 1986). Sharks generally prey on teleosts or other chondrichthyans and cephalopods are of minor importance, although loliginids, sepiids and octopods have been recorded (Bass *et al.* 1973; Cliff *et al.* 1989, 1990; Cliff & Dudley 1991*a*, *b*, 1992; Dudley & Cliff 1993).

(*c*) *Temperate seas*

Cephalopods are not recorded as prey of demersal fishes in temperate waters off the west coast of Scotland (Gibson & Ezzi 1987), perhaps because of the small size of the fish (14–263 mm standard length) or low abundance of cephalopods. In the Irish Sea off the Isle of Man, Lyle (1983) reported that *Sepiola atlantica* was a minor prey of spotted dogfish *Scyliorhinus canicula*.

In cool temperate Pacific waters off southern California, three kelp bed teleosts were found to switch between benthic and pelagic prey, including squid. Although squids made up a maximum of 8% of prey volume overall, their seasonal contribution was up to 26% in summer for kelp bass (Love & Ebeling 1978). Further north, off British Columbia, spiny dogfish (*Squalus acanthias*) took squid and octopods as minor prey of adults (Jones & Geen 1977).

Edwards & Bowman's (1979) Atlantic study showed squid was important to 10 predators (table 1). Hacunda (1981) recorded no cephalopods in the diets of eight demersal fish of 150–552 mm TL from the Gulf of Maine. Bowering & Lilly (1992) found that although cephalopods (including *Gonatus* sp.) were minor prey (0.6–2% prey weight) there was a clear trend of cephalopods increasing in importance from the shelf to deeper waters of the slope, particularly at 801–1000 m. Langton and Bowman (1980) found that with the exception of *Urophycis regia* or spotted hake, which had 11% by mass of *Loligo* and *Rossia*, the other 15 fishes took few or no cephalopods. Sedberry (1983) showed that cephalopods were seasonally important in five of nine species studied in the Middle Atlantic Bight and *Illex illecebrosus* was an important prey. Cephalopods were minor prey of sandbar sharks, but ommastrephids were recorded offshore at > 100 m depth (Stillwell & Kohler 1993). McEachran *et al.* (1976) found that cephalopods were minor items in the diet of four skate species on the shelf off northeastern North America.

In the Benguela, Payne *et al.* (1987) worked on two hakes, *Merluccius capensis* and *M. paradoxus*, and found that both were opportunistic, that cephalopods were of lesser importance after Crustacea and fish, and that prey varied by locality and size of predator, as was also found by Roel & MacPherson (1988) off Namibia. Punt *et al.* (1992) confirmed the opportunistic feeding and found that cephalopods were more important for medium sized *M. capensis*, but that *M. paradoxus* relies more heavily on cephalopods, particularly larger predators. Their estimates of annual consumption

Table 1. *Selected multispecies feeding studies showing the number of species studied, the number of stomachs, the area, the group (Chondrichthyes or Telostei), the number of cephalopod predators, the number in which cephalopods were important* (> 10%), and the source

(P.O. = Pacific, I.O. = Indian, A.O. = Atlantic Oceans, T.S. = Tasman Sea, A.S. = Arafura Sea U.S.A. = United States of America, S.A. = South Africa.)

no. species	no. stomachs	area	group	cephalopod predators	cephalopods important	reference
continental shelf fishes						
tropics						
233	> 2000	Marshall Ids. P.O.	C, T	5	1	Hiatt & Strasburg (1960)
212	5526	West Indies P.O.	C, T	29	5	Randall (1967)
102	1547	Hawaii P.O.	T	8	0	Hobson (1974)
27	459	Madagascar I.O.	T	2	0	Harmelin-Vivien & Bouchon (1976)
79 (40 N > 5)	4143	G. Carpentaria, Australia	C, T	30	9	Salini *et al.* (1994)
6	45	Aldabra I.O.	C	5	1	Stevens (1984)
17	2625	N. Australia T.S., A.S.	C	16	10	Stevens & McLoughlin (1991)
3	268	N. Australia, T.S., A.S.	C	3	2	Lyle (1987)
11	679	G. Carpentaria, Australia	C	8	5	Salini *et al.* (1992)
subtropics						
30	3608	Natal, I.O.	T	3	0	Joubert & Hanekom (1980)
temperate						
15	783	W. Scotland, A.O.	C, T	0	0	Gibson & Ezzi (1987)
3	341	California P.O.	T	2	1	Love & Ebeling (1978)
80	> 25000	U.S.A., A.O.	C, T	> 21	10	Edwards & Bowman (1979)
8	660	U.S.A., A.O.	C, T	0	0	Hacunda (1981)
15	7391	U.S.A., A.O.	T	8	1	Langton & Bowman (1980)
9	4818	U.S.A., A.O.	C, T	7	5	Sedberry (1983)
19	2590	S.A., A.O. & I.O.	T	13	5	Meyer & Smale (1991*a*, *b*)
6	580	S.A., I.O.	C	6	2	Smale & Cowley (1992)
14	1026	S.A., A.O.	C	11	2	Ebert *et al.* (1991)
10	2181	S.A., I.O.	C, T	9	7	Nepgen (1982)
6	1819	S.A., I.O.	T	6	4	Smale (1986*a*)
4	478	S.A., I.O.	T	4	4	Smale (1986*b*)
10	1030	Alaska, P.O.	T	3	0	Rosenthal *et al.* (1988)
26	1542	Antarctic, S.O.	T	1	0	Targett (1981)
19	1609	Antarctic, S.O.	T	3	0	Daniels (1982)
slope and rise fishes						
6	3137	Mediterranean	T	2	0	Macpherson (1979*a*)
4	1282	Mediterranean	T	1	0	Macpherson (1979*b*)
5	500	Rockall Trough, A.O.	T	5	2	Mauchline & Gordon (1984*a*)
12	2999	Rockall Trough, A.O.	T	11	4	Mauchline & Gordon (1984*b*)
15	330	Rockall Trough, A.O.	C	10	6	Mauchline & Gordon (1983)
16	499	U.S.A., A.O.	C, T	5	2	Sedberry & Musick (1978)
32	1336	A.O.	C, T	4	1	Crabtree *et al.* (1991)
15	764	S.A., A.O	C	13	12	Ebert *et al.* (1992)
5	431	U.S.A., P.O.	T	4	2	Pearcy & Ambler (1974)
2	143	U.S.A., P.O.	C	2	1	Cross (1988)
70	2800	Hawaii, P.O.	T	2	0	Clarke (1982)
3	1841	Tasmania, P.O.	T	0	0	Young & Blaber (1986)
15	3998	Tasmania, P.O.	C, T	8	1	Blaber & Bulman (1987)

revealed that *M. capensis* may account for 465000–563000 tonnes and *M. paradoxus* 89000–425000 t of cephalopods. For comparison, the consumption of all prey for each species was estimated at 3450000–4328000 t and 962000–1877000 t, respectively. Ommastrephids, *Sepia* spp. and *Loligo* were the important cephalopods taken (Punt *et al.* 1992), but Lipinski *et al.* (1992) note that *Todaropsis* and *Lycoteuthis* are also important.

In the south east Atlantic off southern Africa, cephalopods, mainly *Sepia*, were important prey of only one shelf-dwelling skate, *Raja alba*, and one deeper-water species, *Bathyraja smithii*. Other skates took crustaceans and fish predominantly (Ebert *et al.* 1991).

Coastal temperate teleosts of the Indian Ocean off South Africa exhibit marked ontogenetic, seasonal and size-related changes in diets, but larger individuals that are mainly piscivorous feed on cephalopods, especially *Loligo vulgaris reynaudii* and *Octopus* spp. and, to a lesser extent, *Sepia* spp. (tables 1 and 2; Nepgen 1982; Smale & Bruton 1985; Smale 1986*a*, *b*), while those inhabiting rocky reefs feed on both octopods and

Table 2. *Selected predators showing relative proportions of different prey in their diets and dominant cephalopods taken*

(S.W. = south west, N.W. = north west, S.E. =south east, S.W. = south west, O. = ocean, A.B. = Algoa Bay, E.L. = East London, N.R. = not recorded.)

predator species	area	depth	no SC	cephalopod %M	fish %M	other %M	dominant cephalopod taxa	reference
continental shelf fishes								
Epinephelus marginatus	S.W. Indian O.	4–40 m	90	48.1	24.3	27.6	*Octopus*, *Loligo*, *Sepia*	Smale (1986*b*)
Petrus rupestris	S.W. Indian O.	5–40 m	113	10	89.8	0.2	*Octopus*, *Loligo*, *Sepia*	Smale (1986*b*)
Seriola lalandi	S.W. Indian O.	2–30 m	206	64.7	35.3	0.01	*Loligo*, *Sepia*	Smale (1986*a*)
Squalus megalops	S.E. Atlantic O.	50–450	53	31.8	65.7	2.5	*Octopus*	Ebert *et al.* (1992)
Hemigaleus microstoma	N. Australia	offshore	14	94.7	< 0.1	5.2	*Octopus*, *Sepiolid**	Salini *et al.* (1992) *Stevens & Cuthbert (1983)
slope and rise fishes								
Centroscyllium fabricii	S.E. Atlantic O.	150–700	45	8.3	27.3	64.1	unidentified	Ebert *et al.* (1992)
Centroscyllium fabricii	N.W. Atlantic O.	abyss, slope, rise	9	81.5	13.6	4.9	*Pholidoteuthis adami*	Crabtree *et al.* (1991)
Centroscymnus coelolepis	S.E. Atlantic O.	660–1016	71	71.2	13.5	15.4	Octopoteuthis, Lycoteuthis	Ebert *et al.* (1992)
Deania calcea	S.E. Atlantic O.	620–640 m	61	74	25	1	Ommastrepidae	Yano (1991)
Deania calcea	S.E. Atlantic O.	475–900	62	16.3	82.5	1.2	unidentified	Ebert *et al.* (1992)
Squalus acanthius	S.E. Atlantic O.	120–500	121	11.9	86.5	2.1	*Todarodes angolensis*	Ebert *et al.* (1992)
Squalus cf. mitsukurii	S.E. Atlantic O.	150–550	211	18.7	80.4	0.9	*Todarodes angolensis*	Ebert *et al.* (1992)
pelagic fishes								
Thunnus albacares	S.W. Indian O., A.B.	inshore	422	2	97	1	Loligindae, Ommastrephidae, Octopoda	Smale (1986*a*)
Thunnus albacares	S.W. Indian O., A.B.	shelf edge	63	27	72	1	*Lycoteuthis*, *Loligo*, *Omastrephes*	Smale (1986*a*)
Thunnus albacares	S.W. Indian O., E.L.	inshore & shelf edge	129	5	94	1	Ommastrephidae, Octopoda, Lycoteuthidae	Smale (1986*a*)
Thunnus albacares	Eastern Pacific O.	pelagic	18	13	36	52	*Dosidiscus*, *Argonauta Thysanoteuthis*	Blunt (1968)
Thunnus albacares	E.C. Atlantic O.	oceanic	132	27	72	1	Ommastrephidae, Enoploteuthidae, Octopoda	Pelczarski (1990)
Thunnus albacares	E.C. Atlantic O.	oceanic	520	12	69	19	*Illex*, *Ommastrephes*, *Argonauta*	Dragovich (1970)
Thunnus albacares	N.W. Atlantic O.	oceanic	16	14	85	1	Ommastrephidae, Octopoda	Dragovich (1970)
Thunnus albacares	C.W. Atlantic O.	oceanic	39	5	94	1	Ommastraphidae	Dragovich (1970)
Thunnus obesus	E.C. Atlantic O.	oceanic	23	19	81	0.5	Ommastrephidae, Octopoda, Cranchiidae	Pelczarski (1990)
Thunnus obesus	Eastern Pacific O.	pelagic	40	63	22	15	*Dosidiscus gigas*	Blunt (1968)
Xiphias gladius	Portugal	N.R.	37	22.3	62.8	15	*Illex*, *Taningia*	Moreira (1990)
Xiphias gladius	N.W. Atlantic O.	200+ m	151	67	33	< 1	Ommastrephidae, Octopoteuthidae	Stillwell & Kohler (1985)
Xiphias gladius	Florida Straits	< 200 m(?)	65	90	< 10	< 3	*Illex*, *Ommastrephes*, *Onychoteuthis*	Toll & Hess (1981)
Alepisaurus ferox	Central Pacific O.	150–200	24	23	76	2	*Japetella*, *Bolitaena*, *Moroteuthis*	Moteki *et al.* 1993
Alepisaurus ferox	Hawaii	220–250	40	19	52	29	*Japetella*, *Onykia*, *Bolitaena*	Moteki *et al.* 1993

squids (Nepgen 1982; Buxton 1984; Smale 1986*a*, *b*; Buxton & Clarke 1989). Predation on *Loligo* was seasonal (Smale & Bruton 1985; Smale 1986*a*, *b*), mostly when the squids aggregate inshore for spawning.

Cephalopods are important to a few demersal teleosts, particularly those that feed in the water column. While *Loligo* is important inshore, *Lycoteuthis* is more dominant near the shelf break (Meyer & Smale 1991*a*, *b*). In the south west Indian Ocean, cephalopods (*Loligo*, *Octopus* spp. and *Sepia* spp.) are of importance to larger individuals of two skate species (Smale & Cowley 1992). *Todarodes angolensis* and *Loligo vulgaris reynaudii* are important to small cowsharks (Ebert 1994), and off the south eastern Cape *Loligo* was important to several other chondrichthyans (Smale 1991; Sauer & Smale 1991).

In cool temperate waters of Alaska, octopods were minor prey of rockfish (Rosenthal *et al.* 1988), suggesting that the pelagic cephalopods taken by pomfrets are unavailable to them. Similarly, in the Antarctic, cephalopods were taken extremely rarely, but the octopod *Graneledone* was recorded (Targett 1981), and krill dominated the prey. Daniels (1982) also found that cephalopods were a very minor dietary component and clearly, squid are of little importance in the diets of coastal Antarctic fishes (Kock 1987).

5. FISHES OF THE SLOPE AND RISE

Cephalopods were found to be unimportant to halibut in the eastern Bering Sea shallower than 200 m, but they were dominant for fishes of 30–70 cm length deeper than 200 m. Gonatids, particularly *Berryteuthis magister* and *Gonatopsis* sp. dominated the diet (Yang & Livingston 1988).

In the Mediterranean, Macpherson (1979*a*, *b*) showed that cephalopods were very rare prey, although *Sepietta oweniana* and *Alloteuthis media* were recorded. Cephalopods are seasonally important to *Scymnorhinus licha*, with *Sepietta owenia* and *Histioteuthis reversa* being recorded (Matllanas 1982). The diet of *Centroscymnus coelolepis* at 1419–2251 m was dominated by unidentified cephalopods, Histioteuthidae and Ommastrephidae (Carrassón *et al.* 1992). In the same study, a smaller shark, *Galeus melastomas*, preyed mainly on crustaceans, but cephalopods became more dominant (up to 37 % mass) at deeper stations at 984–1584 m (Carrasón *et al.* 1992), suggesting that cephalopods may be more abundant at greater depths.

In the north Atlantic, cephalopods were generally not important prey of berycomorphid and percomorphid fishes from the Rockall Trough (table 1; Mauchline & Gordon 1984*a*; Gordon & Duncan 1987). Cephalopods were also minor prey in terms of frequency and number in macrourid fishes from the Rockall Trough, with the exception of four (Mauchline & Gordon 1984*b*). Sharks and chimaeroids from the Rockall Trough, especially *Apristurus* spp, *Centroscymnus coelolepis* and *C. crepidator*, preyed fairly commonly on cephalopods (table 1; Mauchline & Gordon 1983).

A study of the mid-Atlantic coast of U.S. fishes revealed that cephalopods were second in importance to fish in the diet of the eel *Synaphobranchus kaupi*. *Antimora rostrata*, *Phycis chesteri* and *Coryphaenoides armatus* also took cephalopods and *Illex* was important (Sedberry & Musick 1978, table 1).

A study of fish from the rise and abyss of the western north Atlantic, showed that only four of 32 species had cephalopod remains in their stomachs, and the shark *Centroscyllium fabricii* had the most, particularly *Pholidoteuthis adami* and unidentified species (Crabtree *et al.* 1991). Benthic rattails, *Coryphaenoides armatus*, at 200–2760 m took pelagic fish and cephalopods when large, especially Enoploteuthidae, Histioteuthidae and Gonatidae (Haedrich & Henderson 1974).

In the south east Atlantic off Namibia at 200–500 m, *Genypterus capensis* > 60 cm took significant quantities of cephalopods, particularly *Todarodes sagittatus* (Macpherson 1983). Of nine species of skate of the south east Atlantic deep slope, four had cephalopod remains, but crustaceans and fish were more important prey items (Ebert *et al.* 1991). *Bathyraja smithii* took the most cephalopods including *Pholidoteuthis boschmai*, *Sthenoteuthis oualaniensis* and *Octopus* sp. (Ebert *et al.* 1991). While squaloid sharks (*Squalus* spp.) in shallower waters fed mainly on fish, cephalopods were important food of the deeper water shark genera (Ebert *et al.* 1992, tables 1 and 2). Although most of the cephalopods were unidentified in this study, *Moroteuthis robsoni*, *Lycoteuthis* cf *diadema*, *Octopoteuthis* sp., *Todarodes angolensis* and *Abraliopsis* sp. were identified. Cephalopods were found to be very important prey of the squaloid sharks *Deania calceus* and *D. crepidalbus* from the slope off Namibia (Yano 1991).

Small midwater fish such as Zoarcidae generally do not take cephalopods, or they make up trace contributions to the diets (e.g. Anderson 1981). Similarly, Pacific macrourid fishes will often take prey other than cephalopods, although two species, *Coryphaenoides armatus* and *C. filifer*, took large amounts of cephalopods, including *Gonatopsis borealis*, *G. magister*, *Gonatus fabricii* and *Octopoteuthis sicula* (Pearcy & Ambler 1974). Cross (1988) found that two scyliorhinid shark species (*Apristurus brunneus* and *Parmaturus xaniurus*) in the north east Pacific took 11.2 and 1.8 % mass of cephalopods with *Gonatus*, *Abraliopsis* and *Loligo* being recorded. In the central north Pacific, Wilson & Seki (1994) recorded six cephalopod taxa in the 101 stomachs of dogfish *Squalus mitsukurii* (20 % mass) that had taken mesopelagic and benthic prey.

Clarke's (1982) study of stomiatoid fishes from Hawaii revealed that three families were considered planktivores while a further six were nekton feeders, that most of the latter were principally or exclusively piscivorous and only two species had traces of cephalopods. Many vertically migrating mesopelagic fishes fed on relatively large and pigmented or opaque crustaceans but few other taxa, and translucent prey were rarely taken (Clarke 1980). Young & Blaber (1986) similarly found that three small mid-water fish species associated with the slope off Tasmania preyed mainly on crustaceans or fish, but not cephalopods. In a later study of demersal and pelagic fishes of the upper slope (420–550 m), Blaber & Bulman (1987) found cephalopods to be minor prey of eight species and important in one, *Genypterus blacodes* (table 1).

Chlamydoselachus anguineus (frilled shark) from 50–200 m off Japan are significant predators of cephalopods (60.5% frequency) (Kubota *et al.* 1991). Nearly whole *Todarodes pacificus* were found, while the rest of the cephalopods (*Onychoteuthis*, *Gonatus*, *Histioteuthis* spp., *Todarodes*, *Sthenoteuthis*, *Chiroteuthis* spp. and *Mastigoteuthis*) were identified from beaks. Fishes were found in only 10.5% of the stomachs. Although this bathypelagic shark is believed to be a slow swimmer, it had taken both fast-swimming muscular squids (Ommastrephidae) and slow-moving histioteuthids. Seigel (1978) noted that another shark, *Squaliolus laticaudus*, found at 200–500 m in oceanic waters, preys on *Chiroteuthis laticaudus*, *Chiroteuthis imperator*, *Histioteuthis* and mid-water fishes. He suggested that it migrates towards the surface at night, following its prey.

In the Red Sea, Waller & Baranes (1994) found that the diet of smooth hound shark, *Iago omanensis*, taken from 150–450 m included 47.2% by number cephalopods, of which *Enigmoteuthis dubia* and (?*Abralia*) *steindachneri* dominated. Cephalopods were the most important prey overall except in summer.

6. PELAGIC FISHES

In the cool temperate waters of the Pacific, large pomfret feed mainly on fish in the north west and cephalopods in the north east (Savinykh 1994). Marked seasonal changes occurred and squid, *Berryteuthis anonychnus*, dominated the prey, but *Gonatopsis* was also recorded. Pearcy *et al.* (1993) found that small *Gonatus* spp. squids dominated and usually comprised 75% or more of the prey of pomfrets, and in other areas *Berryteuthis anonychnus* was recorded. The impact of this fish is considerable because it is widely distributed and abundant in the north Pacific (Seki & Bigelow 1993). Cephalopod prey was also dominant in salmonids in this region (Pearcy *et al.* 1988) and opportunistic changes in prey were noted.

Because of their economic importance, the highly migratory tunas have received considerable attention from fisheries biologists (Sund *et al.* 1981). Although sympatric tuna species show overlap in prey taken, the considerable differences result from them feeding at different water depths (Kornilova 1980). There are ontogenetic changes in swimming depth (Talbot & Penrith 1968; Blackburn 1965; Kornilova 1980), the species attain different maximum sizes and have several morphological differences, such as gill raker size (Magnuson and Heitz 1971), that also influence prey selection. Prey choice varies according to locality, depth and time, but fishes generally dominated the diets and cephalopods were usually the second or third most important prey group (Dragovich 1970; Pinkas *et al.* 1971; Dragovich & Potthoff 1972; Perrin *et al.* 1973; Mathews *et al.* 1977; Kornilova 1980; Smale 1986*a*; Pelczarski 1990). However, Blunt (1968) in his study, observed that cephalopods, particularly *Dosidicus gigas*, were a large part of the diet of *Thunnus obesus* (table 2).

Regional differences have also been noted in the Indian Ocean in studies of yellowfin tuna in the south west (Smale 1986*a*), compared to tropical waters (Kornilova 1980). The dominance of fish prey in tuna diets inshore may be a result of the greater relative abundance of clupeoid fishes there. At the edge of the continental shelf, cephalopods were considerably more important as prey (table 2; Smale 1986*a*).

In the temperate waters off California, Pinkas *et al.* (1971) recorded the dominance of anchovy in the diets of three species of tuna, but they also recorded cephalopods, especially *Loligo opalescens*, inshore, and oceanic species offshore. Also off California, Morejohn *et al.* (1978) recorded 19 species of fish which fed on market squid, including several pelagic fish predators.

Lancetfish, *Alepisaurus ferox*, are often taken with tunas on deep-set longlines, and they also feed on cephalopods as a secondary prey item; prey dominance in the diet depends on locality (table 2; Moteki *et al.* 1993).

Dolphin fishes (Coryphaenidae) feed on surface prey including cephalopods, but they are less important than fishes, and diet varies markedly at different localities (Hida 1973; Manooch *et al.* 1984) and at different sizes. Furthermore, they prey on animals associated with *Sargassum* to a much greater extent than is found in tunas (Manooch *et al.* 1984).

Most billfishes are considered pelagic, to feed in similar ways and are often thought to be competitors for food (Nakamura 1985). Often the cephalopod component of the diet is largely muscular squids, such as loliginids and ommastrephids (DeSylva & Davis 1963; Ovchinnikov 1970; Nakamura 1985). Maksimov's (1971) study of sailfish in the Atlantic showed that squids and octopods contributed up to a maximum of 61% frequency of occurrence. Voss (1953) found that adult sailfish took mainly fishes, while cephalopods contributed 16.8%, and that these were mainly argonauts (*Argonauta argo*) and ommastrephid squids that are probably epipelagic (Roper *et al.* 1984). Jolley (1977) recorded a similar prey spectrum to Voss (1953).

Swordfish, *Xiphias gladius*, are epi- and meso-pelagic and may descend to 550 or 650 m (Nakamura 1985). In the western north Atlantic, Scott & Tibbo (1968) found that although cephalopods were important, fish dominated the prey. Stillwell & Kohler (1985) found that cephalopods were more important than fishes in swordfishes from the western north Atlantic. Ommastrephidae contributed to at least 46% of the prey mass and 10 other families were recorded (Stillwell & Kohler 1985). Swordfish from the straits of Florida ($n = 65$) preyed largely on aggregating cephalopods, and of the 15 species of squid found, *Illex* was the single most important prey (Toll & Hess 1981). Off the Portuguese coast, Moreira (1990) found the main prey types to be fish, cephalopods and crustaceans. Ommastrephids were the dominant of six families of cephalopod recorded (Moreira 1990). Guerra *et al.* (1993) working on swordfish in the north east Atlantic found 17 species of pelagic cephalopod, and ommastrephids dominated. Hernandez-Garcia's (1995) study of swordfish from the central and north east Atlantic, found substantial regional differences in the prey choice. In the Straight of Gibraltar fish dominated, but off the Canary Islands, cephalopods dominated the diet. He recorded 15 families and 26 species of cephalopod and he showed that cephalopods were more important in oceanic waters. Off the Azores, however, cephalopods and fishes contributed almost equally to swordfish diets, in terms of mass (Clarke *et al.* 1995).

There are several large pelagic shark species and some feed on cephalopods. In the north west Atlantic, however, Stillwell and Kohler (1982) found that although *Illex illecebrosus* and *Loligo pealei* occur inshore in high abundance, they were minor prey of makos (*Isurus oxyrinchus*), while bluefish (*Pomatomus saltatrix*) made up 86% by frequency of occurrence (FO) of the diet inshore. On the other hand, blue sharks (*Prionace glauca*) off California were found to take more than 12 cephalopod taxa; *Loligo opalescens* dominated the diet inshore in the squid's spawning season, while histioteuthids and other offshore species were recorded offshore (Tricas 1979; Harvey 1989).

Off New South Wales, Australia, cephalopods were found to be more dominant (61%FO)in blue sharks but less important to makos (22.2%FO) and tiger-sharks, *Galeocerdo cuvieri*, while smooth hammerhead sharks, *Sphyrna zygaena*, had 72%FO of cephalopods (Stevens 1984). Off eastern Australia, Dunning *et al.* (1993) examined cephalopod predation by sharks, and six of the nine studied contained cephalopods. They showed that hammerheads, *Sphyrna leweni*, fed largely on mesopelagic cephalopods, while blue sharks, *Prionace glauca*, took oceanic squids, although this shark was also found to feed on the shelf, supporting the findings of Tricas (1979) and Harvey (1989). Bigeye thresher, *Alopias superciliosus*, a shark of the slope and open sea (Stillwell & Casey 1976), preys on fish and cephalopods, but squid were the most common prey (66% frequency) and these were mainly ommastrephids, probably *Illex* (Gruber & Compagno 1981).

7. HABITAT SUMMARY

The importance of cephalopods as prey increases from absent or very rare in estuaries, to their greater importance on the continental shelf, particularly in some temperate waters. Prey choice is strongly influenced by availability and, as a result, switching is found in virtually all predators. While many benthic predators on the shelf feed largely on benthic cephalopods (e.g. *Sepia* and *Octopus*), pelagic muscular squids (e.g. *Loligo* spp.) may be favoured by pelagic predators. Numerous studies have shown that squids are important prey to fishes seasonally (Sedberry 1983; Smale & Bruton 1985), and this often coincides with the prey's spawning season (Tricas 1979; Sauer & Smale 1991). In those studies that do not examine seasonal variation in prey choice, the cephalopod portion of the diets of fishes may be swamped by other prey during the rest of the year and the importance of cephalopods at a particular time may be overlooked. Although the arbitrary value of 10% was used to indicate importance, even lower levels than this may be critical to survival of predators in periods of limited availability of other prey. This arbitrary level is therefore a simplification of complex interactions in the sea.

Prey switching from oceanic cephalopods to shelf forms by highly mobile predators has been demonstrated repeatedly, although there is often a greater portion of the diet made up by schooling teleosts, such as clupeids, in coastal areas (e.g. Pinkas *et al.* 1971; Tricas 1979; Smale 1986*a*; Yang & Livingston 1988).

Like their pelagic counterparts, numerous smaller species of deep-sea fishes appear to feed mainly on crustaceans. Larger predators, particularly squaloid sharks, feed largely on cephalopods and in several studies there was a trend for cephalopods to become more important in diets in deeper waters of the slope, compared to shelf waters (Yang & Livingston 1988; Carrassón *et al.* 1992; Ebert *et al.* 1992). Sampling bias caused by regurgitation of stomach contents of benthic fishes when hauled to the surface needs to be overcome. This is particularly problematical with teleosts with swimbladders, and may be exacerbated by smooth prey such as cephalopods, which may have a higher rate of regurgitation. Regurgitation may be worse with line-caught sharks than trawled samples (Yano 1991).

In oceanic waters, cephalopods are more dominant components of the prey of large fishes including tunas, broadbills and sharks, where fast-moving muscular squids are often taken by these powerful predators (Smale 1986*a*; Stillwell & Kohler 1993; Hernandez-Garcia 1995). Although absolute or relative abundance of potential prey may influence prey choice, energy values and other factors are important, and will be discussed below.

8. PREDATOR/PREY BEHAVIOUR

Although predators are generally called opportunistic, there are constraints to their choice of prey, one of which is size (Cohen *et al.* 1993). Some schooling predators are able to attack aggregating squids, while lone hunters may be best suited to attack solitary prey such as octopods (Smale 1986*a*, *b*; Sauer & Smale 1991). Fish predators have a variety of behaviours used to attack prey, such as slashing by broadbills and billfish (Nakamura 1985), the use of the threshers' tail to stun prey (Gruber & Compagno 1981), chasing from behind by blue sharks (Tricas 1979) and ambush by less mobile predators (Smale *et al.* 1995).

Deep-sea demersal fishes can obtain pelagic prey by feeding on prey whose vertical distribution extends close to the bottom; migrating into the water column to feed; or feeding on carcasses that sink to the bottom (Cross 1988). Epibenthic and benthic fishes are thought to scavenge to some degree on carcasses arriving from surface waters and because of this behaviour they may be attracted to baits (e.g. Bagley *et al.* 1994; Priede *et al.* 1994). Vertical migration in the sea is well documented in a variety of taxa and this allows even deep-dwelling demersal fishes to attack vertically migrating prey, including cephalopods (Pearcy & Ambler 1974; Sedberry and Musick 1978).

Major advances have been made in the understanding of the physiology of tunas and their behaviour in relation to the environment (Sund *et al.* 1981), and while it is now understood that even epipelagic fishes such as skipjack tuna can move (and feed) through the top 200–250 m of the water column (Dizon *et al.* 1978), how this relates to feeding on particular groups of prey is currently unclear.

Tunas are generally thought to be opportunistic and take whatever is in the area most abundantly, provided it is of appropriate size (Alverson 1963). Mathews *et al.* (1977) also noted that prey size taken was smaller for small tunas, and that faster-moving muscular squids (such as Ommastrephidae) were taken by these predators, compared to the deeper-living gelatinous squids taken by *Alepisaurus*, such as Histioteuthidae, Bathyteuthidae and Cranchiidae. Furthermore, *T. albacares*, which inhabits shallow waters, preys more heavily on Ommastrephidae, while deeper-dwelling *T. obesus* takes more deeper-living cephalopods, such as *Octopoteuthis* (Kornilova 1980).

Vertical movements of other large predators have been confirmed using acoustic tags (Tricas 1979; Carey & Robinson 1981; Nelson 1990; Klimley 1993) and have been related to feeding behaviour (Sciarrotta & Nelson 1977; Stillwell & Kohler 1985). Carey & Scharold (1990) showed that blue sharks have the deepest dives during the day down to > 400 m, but they were confined to depths near the thermocline at night. Carey & Scharold (1990) suggested that the diving may be related to hunting either visually or to searching for scent trails, and that blue sharks may be hunting deep-dwelling cephalopods below the thermocline. Juvenile mako sharks appear to use the mixed layer mainly (Holts & Bedford 1993), whereas larger individuals may penetrate the thermocline more readily (Carey & Scharold 1990), which may reflect differences in prey choice. It seems likely that with the increased power and sophistication of such equipment and development of multi-function tags, finer details of movements and recorded feeding events will help to resolve questions of feeding selectivity and other aspects of feeding behaviour that at present remain enigmatic, particularly if the movements of predators and abundance and location of prey are monitored simultaneously.

To avoid predation, cephalopods have evolved a suite of defenses best suited to their environment (Hanlon & Messenger, 1996). Most benthic octopods, for example, can camouflage themselves with the substrate when they emerge to hunt. When threatened, they may ink and flee, or they may retreat into caves (Hanlon & Messenger 1996). Octopods are not always consumed whole, and some predators may remove their arms only. A study off South Africa (Smale & Buchan 1981; Smale unpublished) found that a high percentage of *Octopus vulgaris* living on rocky reefs had parts of their arms removed, probably by moray eels. However, some scyliorhinid sharks also use this technique of removing an arm if they are unable to consume the whole animal (Smale unpublished). It appears that the morphology and behaviour of eels and some scyliorhinid sharks are highly suited to attacking octopods that escape into small caves and crevices, as has also been suggested for the tawny nurse shark (Stevens 1984).

The octopod *Ameloctopus litoralis* has evolved the defense of arm autotomy but has lost the ink sac, which is probably a result of selective pressure associated with its form of foraging from within lairs with the elongated arms, although several species of *Octopus* also share the character of arm autotomy while retaining the ink sac (Norman 1992). With reduction of emergent foraging behaviour in *Ameloctopus*, the decoy or pseudomorph function of ink is presumably no longer beneficial and the alternative decoy of arm loss is used instead (Norman 1992). Voss (1988) suggested that the loss of the ink sac in deep-water octopods, such as the Cirrata and most of the Bathypolypodidae, may be explained by their living in lightless depths, where ink would no longer function as a defence against predation.

Squids are thought to be especially vulnerable to predation during mating and spawning behaviour. Defenses of neritic squid include camouflage, schooling behaviour, protean behaviour and inking (Hanlon & Messenger 1996), and it appears that during mating the efficacy of these defences may be reduced. Sauer & Smale (1991) examined the stomach contents of sharks and teleosts near spawning aggregations of squid and recorded several that had preyed on reproductively active individuals. Fishes have been recorded on video recorders attacking and ambushing living, actively spawning squid (Sauer & Smale 1991; Smale *et al.* 1995). No dead or moribund *Loligo vulgaris reynaudii* were found around the spawning areas, and no post-spawning mortality was seen, in contrast with *Loligo opalescens* (Vaughan & Recksiek 1978).

Luminescence is a well-known phenomenon, particularly in oceanic and bathypelagic families of cephalopod (Herring 1978; Young 1983). Although the functions are thought to be complex, luminescent organs are primarily weapons of offence and/or defence in most animals (Young 1983). Nielsen *et al.* (1989) noted that slow-swimming cephalopods in the genera *Heteroteuthis*, *Brachioteuthis*, *Cranchia* and *Gonatus* were taken by the pelican eels *Eurypharynx pelecanoides* collected in a depth range of 500–2750 m off Iceland, and suggest that they and other prey may have been attracted within striking distance by the luminous lure. Signaling between conspecifics also occurs, but there is a degree of danger in such communication (Morin 1983; Young 1983). Although studies of the role of luminescence in such interactions are still in their infancy, they should provide fascinating insight into the vulnerability of different groups and the evolution of different forms of luminescence.

In addition to their direct role in food webs, cephalopods may also play an indirect, facultative role to fish predators. For example, groupers or serranids are known to form feeding associations with octopods (and other primary predators) whereby the octopod manages to gain access to crevices to attack potential prey, such as shrimps. The groupers learn to forage with the primary predators and benefit by attacking prey escaping from the octopod, thereby gaining access to organisms that would otherwise be unavailable to them (Diamant & Shpigel 1985). Quantified observations in the Gulf of California revealed that octopus are very important as primary predators and are followed whenever they moved over the reef by day (Strand 1988), showing that this behaviour may be considerably more widespread than hitherto realized. Their indirect role in feeding associations would clearly be undetected without *in situ* observation, thereby illustrating another limitation of attempting to understand ecological interactions from a single perspective, such as examination of stomach contents of predators.

Scavenging of fish heads is a common feeding strategy of demersal fishes (Meyer & Smale 1991*b*; Smale & Cowley 1992). Squids have frequently been observed to decapitate large fishes on which they prey, before eating the rest of the body. The heads and other remains are allowed to drop to the bottom (Lipinski 1987; Smale personal observation). Scavenging of these fish heads therefore provides an energy source for benthic scavenging fishes. Often these prey are pelagic planktivores, so a direct energy pathway from the epipelagic zone to deeper-dwelling fishes is provided. In the open ocean, this may have a significant contribution to the rain of organic particles and carcasses in the food web of the deep sea (Marshall 1979). Macpherson (1983) found hake heads in kingklip stomach contents off Namibia and argued that this was a specialized form of predation. A more parsimonious explanation is that the demersal fish scavenge the fish heads rejected by other predators, such as squid.

9. OPTIMAL FORAGING

Optimal foraging theory is a concept that was initiated from consideration of 'where should an animal feed to get the most food, and what items should it pursue?' (Hughes 1980). Although the theory has been criticized, the question remains and has profound influence on how predation is considered. Implicit is the question of prey choice and decisions predators have to make about which prey to attack. The relevance to predation studies is in the interpretation of results of stomach content analyses to try to understand the predator's behaviour. It is also relevant to answer the question of whether the stomach contents of any particular species give insight into the abundance of different prey in the wild (the logical extension of the premise that 'predators are opportunistically taking whatever is most abundant in the wild'). Given the fact that different prey species have different costs of capture and handling, and different energy rewards in terms of calorific values (Batchelor & Ross 1984; Clarke *et al.* 1985; Blaber & Bulman 1987), the assumption that predators are truly opportunistic and feed on whatever is available is highly unlikely. Until there is better understanding of the cost versus benefit, the breadth of choice, how predators perceive prey and which prey are vulnerable to particular predators, the use of terms like 'opportunistic' have little value in our understanding of predator/prey interactions, other than indicating a fairly broad trophic niche.

10. ONTOGENETIC CHANGES IN DIET

In attempting to assess the importance of cephalopods to fishes, it needs to be remembered that they often exhibit extreme ontogenetic changes in diet. Teleosts modify their prey selection as they grow from larvae, through juveniles, up to their maximum size. Consequently, different prey organisms are important as teleosts and chondrichthyans grow (Pearcy & Ambler 1974; Mauchline & Gordon 1983; Meyer & Smale 1991*a*, *b*; Crabtree *et al.* 1991; Smale & Cowley 1992; Punt *et al.* 1992). Many top predatory teleosts feed on plankton such as mysids and euphausiids when small and only later in life do larger prey become important (Smale 1987). Concomitant with growth, many fishes of the shelf change their habitat. Some species move out of estuaries or shallow bays to deeper waters of the continental shelf, where predation on cephalopods becomes more important (Smale 1984; Smale & Bruton 1985).

11. REGIONAL DIFFERENCES IN DIET

Numerous studies show that in some areas, cephalopods are dominant in the diet, whereas in other localities they are uncommon or rare (Lee 1978; Langton & Bowman 1980; Smale 1986*a*; Gordon & Duncan 1987; Payne *et al.* 1987; Dubochkin & Kotlyar 1989; Meyer & Smale 1991*a*, *b*). Variations like these confound attempts to provide a concise comment about the role and importance of cephalopods. There are few, if any, studies that can relate abundance and distribution patterns of predators to predation patterns. This significantly reduces the understanding of the role and importance of cephalopods (or any other prey) in food webs. Studies that have attempted to investigate this include Payne *et al.* (1987) and Punt *et al.* (1992). Although they were not looking at the problem from the perspective of cephalopods alone, several of their findings are pertinent to this paper. These include their warning of the danger of extrapolating findings from one study to other time periods, and that pooling of data from different geographic areas and seasons may introduce substantial bias in estimates of consumption and daily ration. They note that changes in abundance of a predator are likely to lead to changes in natural mortality of the prey species, resulting in the altering of availability of prey. Consequently, consumption estimates collected at one time should not be used for another time period (Punt *et al.* 1992).

12. THE ROLE OF CEPHALOPODS IN THE DIETS OF FISHES

Caddy (1983) suggested that a marked increase in cephalopods in industrial fisheries was a result of the exploitation favouring their 'fast lane' life strategy over longer-lived fishes, for example in the western Sahara fishery. Although evidence is often constrained by the limited data available on catches of all species before and after such events, and possible changes in fishing strategy, other workers (e.g. Bello 1991) have suggested similar effects. Stillwell & Kohler (1985) noted more squid in the diet of broadbill in the western north Atlantic compared to previous work by Scott & Tibbo (1968), and suggest that this results from a steadily increasing abundance of squid along the continental margin. Whether this is a long-term fluctuation or a result of the decline of fish stocks is not yet clear. Nevertheless, it illustrates that studies of diet are pertinent to the time frame in which they were collected, as emphasized by Punt *et al.* (1992).

Fishes can provide important insights into the occurrence and seasonal patterns of squids. They are a relatively cheap alternative to sampling the cephalopod fauna, and with careful prey identification, they can provide useful information on cephalopods (Dunning *et al.* 1993). They can also help to improve understanding of natural mortality (Sauer & Smale 1991) and seasonality of spawning (Smale 1986*b*). Furthermore, they can provide rare or undescribed species from remote areas (Rancurel 1970; Okutani & Tsukada 1988) and may indicate the relative importance of different species in the environment. For example, *Lycoteuthis* was commonly found in predators at the edge of the Agulhas bank (Smale 1986*a*) and this was subsequently confirmed from deep trawls further west (Roeleveld *et al.* 1992).

In most, if not all, studies of fish predation, there are confounding factors, such as regurgitation and sampling bias, that limit our understanding of the process. On top of these constraints, there is presently no accurate knowledge of the biomass and size and spatial distribution of any single species of marine fish by which subsamples of stomach contents could be multiplied up to gain a clear understanding of the biomass of cephalopods taken by any one or a suite of predators. Some very preliminary attempts have been made in some instances (e.g. Domanevsky & Patokina 1986) but the value of these, other than a record of prey, is in doubt because no numbers were presented, biases were not discussed and time, space and regurgitation problems were not mentioned. Even in those instances where relatively large samples of commercial species have been studied, considerable caution is needed with interpretation of results (Punt *et al.* 1992). In many studies, the nature of the samples collected are opportunistic and few studies continue long enough to investigate seasonal or annual fluctuations (Punt *et al.* 1992). Although estimates of daily ration and annual consumption may be obtained, because of the fluctuating and dynamic nature of natural populations, which change as a result of environmental and anthropogenic effects, there are dangers in extrapolating consumption estimates to other periods of time. To try and reduce some of these shortcomings, Punt *et al.* (1992) suggest that before any large-scale stomach collection exercise is undertaken, it is advisable to perform simulation studies to assess sampling intensity required to achieve desired levels of accuracy and precision for predictions from multi-species model estimation procedures which make use of such data.

In conclusion, there are no fishes that are specialist cephalopod predators, with the possible exception of the siclefin weasel shark, *Hemigaleus microstoma* (Stevens & Cuthbert 1983; Salini *et al.* 1992). Cephalopods may make up a large proportion of the diet of other sharks and teleosts, for example, shallow-water tropical tawny nurse shark, *Nebrius ferrugineus* (Stevens 1984) and deep-living squaloid sharks, such as the Portuguese dogfish, *Centroscymnus coelolepis* (Carrassón *et al.* 1992; Ebert *et al.* 1992). As studies on broadbill swordfish have shown (Stillwell & Kohler 1985; Clarke *et al.* 1995), even those species that prey heavily on cephalopods are able to switch to other prey, probably when prey availability changes and it becomes necessary or more profitable energetically to switch. Consequently, although some species are highly suited and possibly prefer cephalopods, probably very few, if any, are specialized enough to depend on cephalopods. The vast majority of fishes that are able to prey on cephalopods take them as a part of fairly catholic diets. Nevertheless, the results of Punt *et al.* (1992) have shown that even in species such as hakes, which are generalist predators, very large quantities of cephalopods may be consumed, showing that cephalopods are important components of marine food webs.

I thank Malcolm Clarke, Peter Boyle and an anonymous referee for comments and suggestions on a draft of this paper. M. Eric Anderson and Martina Compagno Roeleveld kindly made available their reference libraries.

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