

Chapter 7

Trophic relationships, ecosystem variability and recruitment

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Abstract: Ontogenetic trends in trophic interactions involving squids of the genus *Illex* are reviewed generally. Trophic interactions are reviewed in more detail for each *Illex* species and fishery area to identify fish species potentially important in affecting recruitment of *Illex* through predator-prey type relationships. To further investigate such effects, data sets were created consisting of yearly estimates of abundances or abundance indices for *Illex* and for those fish species which interact with *Illex* as predators, prey, or competitors. Simple correlation analysis is applied to each data set to determine significant interactions. Such an approach assumes that those trophic interactions which affect *Illex* recruitment will be similar across ecosystems and will be evident despite the limitations of available data and effects of other interacting (e.g. abiotic) variables. Results, although not conclusive, suggest that, on the continental shelf in western boundary current systems, recruitment of *Illex* (*Illex illecebrosus* and *Illex argentinus*) may be affected by the abundance of predators and competitors. Recruitment of *I. illecebrosus* to a coastal fishery area near the limit of its distribution may be related to abundance of fish prey. No relationship with recruitment of *Illex coindetii* could be detected.

1 Introduction

Short-finned squid of the genus *Illex* grow rapidly and have a lifespan of about one year. As a result, the trophic role of *Illex* spp. is highly dynamic on a seasonal basis and also may shift considerably among years and geographical areas due to recruitment variation or due to spatial and temporal variation in the abundances of interacting species within the food web.

This review addresses the hypothesis that the relative abundances of species that have strong trophic interactions with *Illex* regulate, at least in part, the recruitment of *Illex* to various fishery areas. More specifically, we suppose that high levels of squid recruitment are associated either with a high abundance of prey and/or low abundance of competitors and predators. We address this hypothesis by first reviewing the trophic role of each of the three species of *Illex* considered here (*Illex illecebrosus*, *Illex argentinus* and *Illex coindetii*) with respect to interacting species of prey, competitors, or predators. We then use correlation analysis of annual data on the relative abundance of *Illex* and potentially interacting species (where available) to look for strong interactions. The availability of relative abundance data limited this correlation analysis to interactions within the continental shelf fish and squid community.

We recognize several potential difficulties with this type of quantitative approach.

- 1) If *Illex* recruitment is substantially influenced by environmental variation, then trophic interactions may be difficult to discern.
- 2) If important trophic interactions occur primarily between the youngest stages of *Illex* and other species during the oceanic phase of the life cycle, then abundance data concerning older life stages may be inadequate to discern the cause of recruitment variability.
- 3) If spatial and temporal aggregation of relative abundance data conceal the effects of local processes, then correlations based on aggregated data may be misleading;
- 4) If species that interact with *Illex* through competition for prey or through the sharing of predators are not considered, then important indirect trophic effects may be unmeasurable.

Nonetheless, while trophic interactions are complex and the interpretation of such interactions may be difficult due to indirect effects, we believe that a qualitative assessment of the importance of trophic interactions on *Illex* recruitment can be made with this approach, despite these potential difficulties.

To some degree, differences in the oceanographic regimes of the current systems where *I. illecebrosus*, *I. argentinus* and *I. coindetii* are distributed can be expected to affect the level of recruitment variability among the three species. Of the three, *I. illecebrosus* has the broadest range of distribution, and is closely associated with a large western boundary current system. This species displays the most extreme fluctuations in recruitment, particularly within the most northerly fishery areas. *Illex argentinus* is not as broad-ranging as *I. illecebrosus*, and is associated with a smaller western boundary current system. Annual fluctuations in its abundance levels are not as pronounced either. In both these western boundary current systems the cephalopod fauna is dominated by a single *Illex* species and a single species of *Loligo*. Fisheries in these areas are associated with the convergence of cold and warm currents. Further, *Illex* recruitment to these areas is seasonally specific, and associated with the seasonal productivity cycle.

In contrast, along the eastern central Atlantic coast *I. coindetii* is associated with an eastern boundary current (the Canary Current) and an oceanographic regime dominated by coastal upwelling that results in seasonally regular but highly variable periods of high productivity. Here, and in the Mediterranean Sea, the cephalopod fauna is more diverse than in the western boundary current systems and is dominated by loliginids. Pelagic fish species are also more prominent than in the two western Atlantic systems (Coelho 1985).

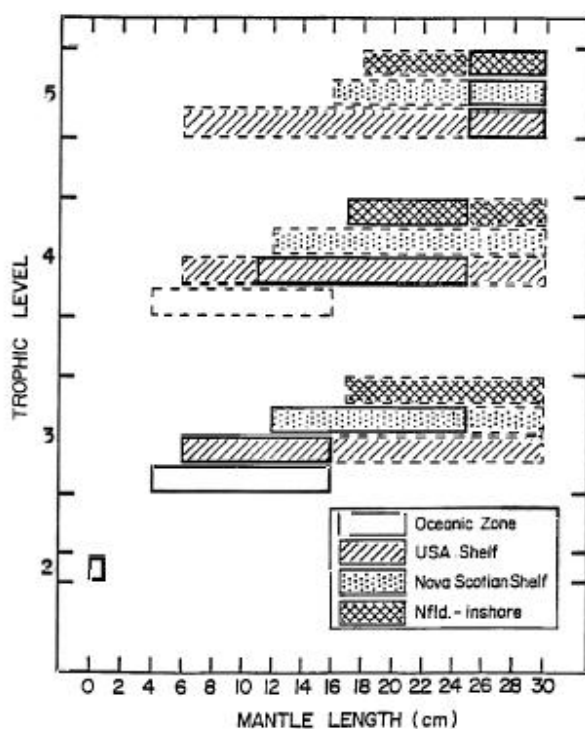


Figure 7.1. Diagrammatic representation of the ontogenetic progression of *Illex illecebrosus*, as a consumer, through the trophic pyramid; rectangles enclosed by solid lines represent primary trophic functioning for any size range and area; those enclosed by broken lines represent secondary trophic functioning.

Therefore, one might expect competition and niche partitioning to be more important for *I. coindetii* than for the other *Illex* species.

The three *Illex* species differ with respect to the present state of knowledge regarding their trophic interactions and structure of the relevant fish and squid communities. The quality and quantity of abundance data for all relevant species also varies considerably among these ecosystems and various fishery areas.

2 Ontogenetic changes in trophic relationships throughout the life cycle of *Illex*

While it is impossible to evaluate the effects of trophic interactions on *Illex* recruitment during the early (oceanic) portion of the squid life cycle because interacting species and their relative importance are not well known, it is possible to review trophic interactions qualitatively throughout the entire life cycle to identify critical stages at which recruitment could potentially be affected by trophic interactions.

In general, the trophic interactions involving *Illex* are quite dynamic, changing in less than a month at some stages. Such rapid changes in trophic position result from the life history of *Illex*, during which squid pass through the stages of planktonic paralarvae, epipelagic oceanic juveniles, neritic large juveniles and finally adults within a short life cycle of only about one year (Rodhouse and Hatfield 1990, Dawe and Beck 1992, *see Chapter 4*). Details of early trophic interactions are best known for *I. illecebrosus*.

Variability in recruitment of cephalopods could be related to starvation during a "critical period" (May 1974). In *Illex* such a critical period may be associated with transformation from particle-feeding paralarvae to predatory juveniles. It is not possible to address these hypotheses directly, but Froerman (1984) reported that most stomachs of small *I. illecebrosus* juveniles (less than 35 mm ML [mantle length]) were empty, so the transformation to juvenile may be the critical period.

The smallest juveniles found with food in their stomachs preyed, at the third trophic level (Fig. 7.1), upon crustaceans and chaetognaths (Froerman 1984). Larger juveniles, of 4–10 cm ML, preyed predominantly on chaetognaths but also, at the third and fourth trophic levels, on crustaceans (amphipods, euphausiids and shrimps) as well as on cephalopods and fish (Froerman 1984).

At about 11–16 cm ML, juveniles move onto the continental shelf and continue to function mainly at the third trophic level by preying upon crustaceans (Fig. 7.1). They also prey, at the fourth and fifth trophic levels, on fish and cephalopods, the latter mainly through cannibalism. Larger squid prey mostly on fish throughout summer-early fall and shift to cannibalism later in autumn (Squires 1957, Maurer and Bowman 1975, Ennis and Collins 1979, Vinogradov and Noskov 1979, Froerman 1984). Fish prey appears to be relatively unavailable on the Scotian Shelf (Fig. 7.1), where squid shift from a crustacean diet directly to cannibalism (Amaratunga 1983). The occurrence of cannibalism may reflect abundance of other suitable food types, especially fish prey.

In nature this squid is known to prey on such large fish as adult capelin (Dawe 1992). In captivity it may prey on fish as large as its own mantle length (O'Dor *et al.* 1980). However, most studies suggest that it, like other pelagic squids, usually preys on fish not larger than about 13 cm (Vovk 1974, Froerman 1984, Breiby and Jobling 1985, Dawe 1992).

Predators of larval and small juvenile *I. illecebrosus* are not known. Seabirds, dolphins and small whales may represent most of the predators between the continental shelf and the Gulf Stream. Predators of squid on the continental shelf and in coastal areas include such large predators as swordfish, tuna, sharks and cetaceans. Other predators include a variety of seabirds and fishes (Ennis and Collins 1979, Froerman 1984, Montecvecchi *et al.* 1988).

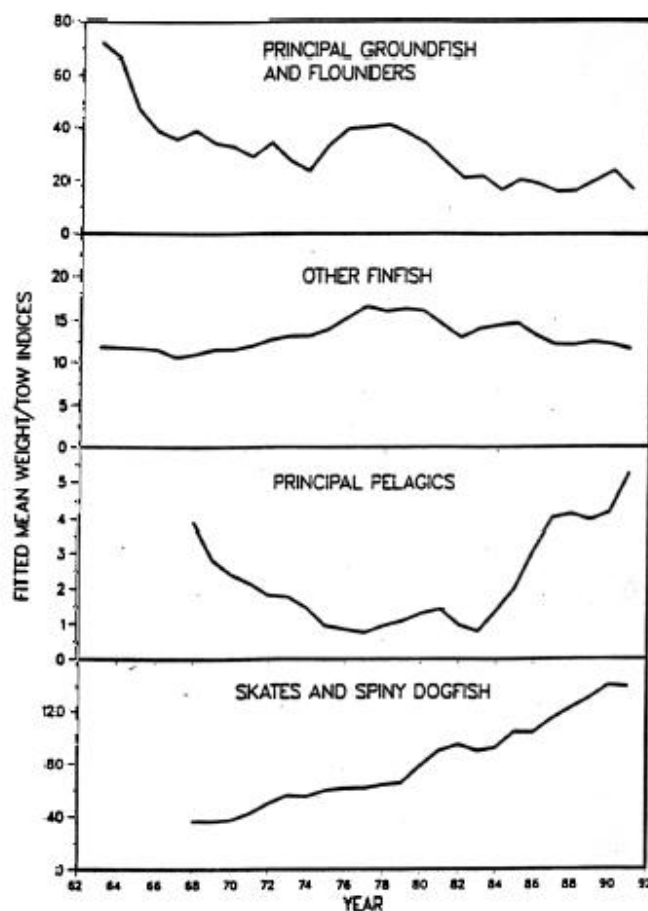


Figure 7.2. Trends in indices of aggregate abundance (catch in weight per survey/trawl/haul) for four species groups, reflecting the major changes in fishery resources, 1962–1991 (from Conservation and Utilization Division, Northeast Fisheries Science Center, 1992)

3 *Illex illecebrosus* in the northwest Atlantic

3.1 U.S. fishery area

The short-finned squid fishery area in U.S. waters encompasses the entire northeastern continental shelf from Cape Hatteras in the south to Georges Bank and the Gulf of Maine in the north (Tibbetts 1977). This region is highly productive, perhaps 2–4 times more productive than most continental shelf ecosystems (Sissenwine 1986). Since fish and other predators consume much of the fish production (Sissenwine 1986), this may be a predator-controlled ecosystem (Edwards and Bowman 1979, Sissenwine 1986). In such an ecosystem prey abundance and inter-specific competition would be expected to have an effect on piscivorous short-finned squid.

The structure of the fish and squid community off the northeastern USA has changed considerably over time, largely due to effects of over-exploitation. Edwards and Bowman (1979) attributed a decrease in predation pressure, a consequence of heavy exploitation, to a decline in total fish biomass, a decrease in mean

size of almost all species, and an increase in the abundance of small fish during 1963–1974. Also, the abundances of some long-lived bottom dwellers declined, whereas populations of some smaller species (e.g. sand lance, *Ammodytes* sp.) increased. In more recent years, the abundance of principal groundfish (gadoids - including silver hake [*Merluccius bilinearis*] and flounders) has remained at a very low level, whereas principal pelagics (mackerel [*Scomber scombrus*] and herring, *Clupea harengus*) have increased considerably in abundance (Fig. 7.2). Elasmobranchs, especially spiny dogfish (*Squalus acanthias*), have increased steadily in abundance, whereas there is no pronounced recent trend for other finfish. On Georges Bank, two major fish predators, silver hake and spiny dogfish, have accounted for a substantial portion of the total predation pressure on other fish species (Edwards and Bowman 1979, Sissenwine *et al.* 1984).

3.1.1 Trophic interactions

Silver hake interacts closely with *I. illecebrosus* as a predator and competitor, and also as a prey species. It represents the only fish prey identified to species by Vinogradov and Noskov (1979) and one of three fish prey species identified by Froerman (1984).

Predation on squid, especially by silver hake of about 21–55 cm, has been reported for June–July and October–December (Vinogradov 1972). The importance of such predation is uncertain. Edwards and Bowman (1979) reported that squid represented only 2.2 percent of the silver hake diet and Jensen and Fritz (1960) reported that squid prey of silver hake was *Loligo*.

Silver hake, being predominantly piscivorous, may affect *I. illecebrosus* more through competition for fish prey than through direct predation. Silver hake smaller than 20 cm prey primarily on crustaceans but they also cannibalize juveniles and include American sand lance (*Ammodytes americanus*) in their diet. Larger silver hake also commonly prey upon clupeids (especially herring, *C. harengus*), mackerel (*S. scombrus*), butterfish (*Peprilus triacanthus*), Atlantic argentine (*Argentina silus*), Muller's pearlsides (*Maurolucus muelleri*) and metallic lanternfish (*Myctophum affine*) (Vinogradov 1972, Bowman and Michaels 1984).

During summer on the continental shelf, it is likely that the most intense competition between *I. illecebrosus* and silver hake would be for juvenile silver hake. Other fish species known to be preyed upon by *I. illecebrosus* are either oceanic, not particularly abundant, or not prominent in the diet (Froerman 1984). The limited data on size of fish prey presented by Jensen and Fritz (1960) suggest that silver hake up to 50 cm may prey on fishes smaller than 13 cm. Cohen and Grosslein (1981) noted that age-0 silver hake (0–16 cm) are within the prey size range of age-2 silver hake (24–29 cm) in particular, and they estimated that age-2 silver hake consumed about 1.507×10^8 fish (178 000 t) annually on Georges Bank. This biomass represented slightly more than the total fish consumption by all age groups of cod on Georges Bank.

Loligo pealei, like silver hake, interacts with *I. illecebrosus* at all three levels (Vovk 1974, Vinogradov and Noskov 1979, Maurer and Bowman 1985). It is likely to be important as both a predator and a prey species but to what extent is uncertain. Cephalopod remains in the stomachs of either squid species have not been identified so the relative importance of interspecific predation versus cannibalism is unknown. However, *L. pealei* may interact most closely with *I. illecebrosus* as a prey species and competitor since it reportedly preys more heavily on fish than on squid whereas the reverse is true for *I. illecebrosus* (Maurer and Bowman 1985). The intensity of competition between these squids, especially for fish, is unknown, because the composition of the *L. pealei* fish diet has not been described. However, they probably share common species and sizes (mostly <13 cm) of fish prey since they are sympatric opportunistic predators which exhibit similar seasonal and size-related shifts in their diets (Vinogradov and Noskov 1979, Maurer and Bowman 1985).

Spiny dogfish is important as a predator and as a competitor for fish prey. Dogfish smaller than 60 cm in particular prey upon small squids (19 percent by weight of the diet) and these smaller dogfish may consume up to 179 000 t of squid (*I. illecebrosus* and *L. pealei*) annually (Waring 1984). Dogfish are opportunistic predators, however, shifting their diet with changes in abundance of prey (Bowman *et al.* 1984). Bowman and Eppli (1984) described small dogfish (<60 cm) as having a mixed diet of ctenophores, crustaceans, squid and fish, whereas larger dogfish were predominantly piscivorous. Fish prey included demersal as well as pelagic species, with Atlantic mackerel and sand lance being particularly important, when they were abundant.

Data on size relationships between dogfish and its fish prey (W.J. Overholtz, National Marine Fisheries Service, Woods Hole, MA, *unpubl. data*) show that dogfish of all sizes (21–100 cm) consume small (≤ 13 cm) fish. In fact, dogfish as large as 80 cm may consume more small than large (>13 cm) fish. It is unknown, however, how frequently small fish occurred in stomachs of the various size groups of dogfish.

Atlantic cod (*Gadus morhua*) is a voracious omnivorous predator which preys heavily upon fish (Bowman and Michaels 1984). Unlike the hakes, cod shift their diet to become piscivorous at two years of age and within a length range of about 23–26 cm (Cohen and Grosslein 1981). Fish prey size is quite variable and cod larger than 100 cm include small (<13 cm) fish in their diet (Edwards and Bowman 1979). A size relationship between cod and its fish prey indicates however that those cod within the 22–75 cm length range prey most heavily on fish smaller than 13 cm (Fig. 7 of Edwards and Bowman 1979). This would approximately represent cod age groups 2 (Cohen and Grosslein 1981) to 7 or 8 (on the Scotian Shelf, Kohler 1964) although there is great variability in size-at-age, especially for older cod (W. J. MacEachern, Biological Sciences Branch, Department of Fisheries and Oceans, Dartmouth, Nova Scotia, Canada, *unpubl. data*).

Atlantic cod represents a component of the total predation pressure on juvenile fish, but it is difficult to evaluate its importance as a competitor of *I. illecebrosus* for fish prey. This is because a broad size range of cod includes a very broad size range of fish in its diet. Furthermore, the fish prey spectrum of Atlantic cod is represented by about 30 species and includes demersal as well as pelagic fishes. It is evident however that predation pressure on small (<13 cm) fish by Atlantic cod is not nearly as great as that by silver hake.

White hake (*Urophycis tenuis*) larger than 30 cm preys heavily on fish, mostly of the same species as silver hake. The smallest white hake for which fish prey species could be identified (41–45 cm) preyed primarily on small silver hake and secondarily on clupeids. These fish prey remained predominant up to predator sizes of 71–75 cm, at which size mackerel and redfish became important (Bowman and Michaels 1984). Since fish represent about 78 percent (Langton and Bowman 1980) or 89 percent (Bowman and Michaels 1984) of food consumed, white hake is also a potentially important competitor of *I. illecebrosus* for fish prey. Squids of unknown species represent about 2 percent by weight of the white hake diet (Edwards and Bowman 1979).

Data on stomach contents indicate that a variety of other fish species interact with *I. illecebrosus* as predators or competitors (Vinogradov 1972, Maurer and Bowman 1975, Edwards and Bowman 1979, Langton and Bowman 1980, Langton 1982, Bowman and Michaels 1984). Squid predators also include such large fishes as swordfish (*Xiphias gladius*), several sharks (Edwards and Bowman 1979) and probably bluefin tuna, *Thunnus thynnus* (Scott and Scott 1988), as well as some small cetaceans (Froerman 1984). However none of these species are included in our subsequent analysis either because they are of less importance than the species described in detail due to their diets or low abundances, or because data on their abundances are lacking. Other fish prey than those described may be important in the *I. illecebrosus* diet but have not yet been identified in stomach contents. If so, these would likely include such small forage species as sand lance and butterfish, as well as juveniles (O-group) of the locally most abundant species (e.g. cod, haddock [*Melanogrammus aeglefinus*] and herring).

Table 7.1. Abundance data for species with potentially important interactions with *I. illecebrosus* in the U.S. fishery area, 1973–1988

Species/Series	Series Description
<i>Illex illecebrosus</i>	
illexr	Short-finned squid, mean number of recruits (> 10 cm) per tow ^a
illexp	Short-finned squid, mean number of pre-recruits (< 10 cm) per tow ^a
<i>Loligo pealei</i>	
loligor	Long-finned squid, mean number of recruits (> 8 cm) per tow ^a
loligop	Long-finned squid, mean number of pre-recruits (< 8 cm) per tow ^a
<i>Peprilus triacanthus</i>	
butter	Atlantic butterfish, mean number per tow ^a
<i>Melanogrammus aeglefinus</i>	
gbhad0	Georges Bank haddock, Age-1 numbers lagged 1 year ^b
<i>Clupea harengus</i>	
herr0	Herring, of Age-1 numbers lagged 1 year ^b
<i>Merluccius bilinearis</i>	
nshake0	Northern silver hake, numbers of Age-1 lagged 1 year ^b
nshake1	Northern silver hake, numbers of Age-1 ^b
nshake2+	Northern silver hake, numbers of Age-2 and older ^b
sshake0	Southern silver hake, numbers of Age-1 lagged 1 year ^b
sshake1	Southern silver hake, numbers of Age-1 ^b
sshake2+	Southern silver hake, numbers of Age-2 and older
<i>Squalus acanthias</i>	
spdog	Spiny dogfish, mean weight per tow ^c
<i>Urophycis tenuis</i>	
whake	White hake, mean weight per tow ^a
<i>Gadus morhua</i>	
gbcod0	Georges Bank cod, mean numbers of age-1 per tow lagged 1 year ^a
gbcod23	Georges Bank cod, mean number of age-2 and age-3 per tow ^a
gbcod4+	Georges Bank cod, mean number of age-4 and older per tow ^a
<i>Ammodytes americanus</i>	
slance	American sand lance, mean number per tow ^a

^a Based on NEFSC fall surveys

^b VPA (virtual population analysis) estimates, from Northeast Fisheries Science Center (1990)

^c Based on NEFSC spring surveys

3.1.2 Relationship of community change to *Illex illecebrosus* recruitment on the northeastern US Shelf

To explore the relationship between community change and short-finned squid recruitment, we examined a data set consisting of 19 series of species abundances on the northeast U.S. shelf during 1973–1988 (Table 7.1). Of these series, seven represented potentially important fish prey (butter, gbhad0, herr0, nshake0, sshake0, gbcod0, and slance), while three represented potentially important squid prey (loligop, illexp, and loligor). A total of seven series represented potentially important predators (nshake2+, sshake2+, spdog, whake, gbcod23, gbcod4+, and *Loligor*), while a total of eight series represented potential competitors (nshake1, nshake2+, sshake1, sshake2+, spdog, whake, gbcod23, and loligor).

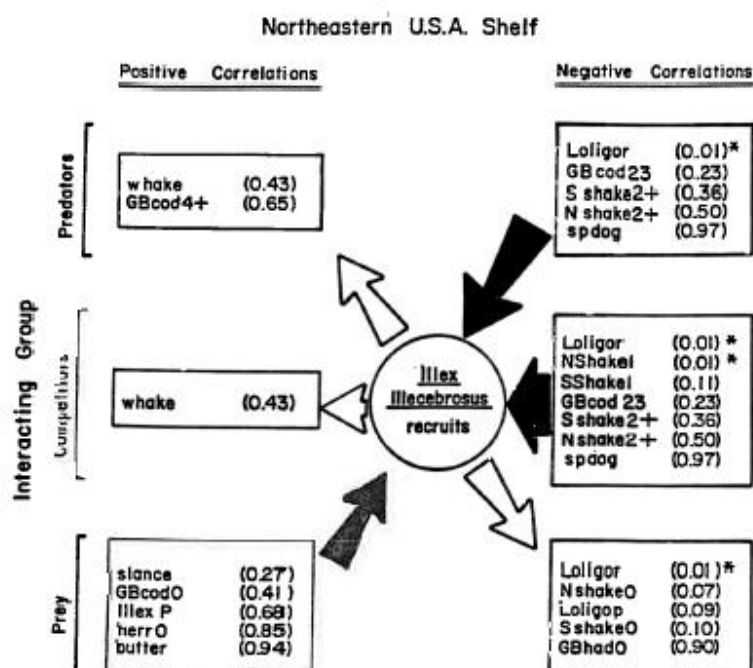


Figure 7.3. Schematic representation of the relative importance of three types of trophic interactions on *Illex illecebrosus* recruitment on the northeastern U.S. shelf, based on the occurrence of positive versus negative correlations with relevant fish stocks and age groups (p-values marked by * were judged to be statistically significant); thickness of the dark arrows represents relative importance of interactions which could affect *I. illecebrosus* recruitment. See Table 7.1 for definitions of interacting groups.

We calculated Pearson correlation coefficients for the 171 pairs of series to look for empirical evidence of strong community-level interactions. We found that a total of 23 correlations were significantly different from 0 at the 0.05 level of significance (Table 7.2). This was more than twice as many significant correlations as would be expected by chance alone. The significant negative correlations between dogfish and other major piscivores (age 2+ silver hake and age 4+ Georges Bank cod) suggest that competition for fish prey may be intense.

There was a significant positive correlation between the *I. illecebrosus* pre-recruit series and the age-0 Georges Bank haddock and age-4 and older Georges Bank cod series (Table 7.2). The positive correlation with the haddock series suggests that greater availability of juvenile haddock is associated with higher levels of *I. illecebrosus* pre-recruit abundance in this area. This positive association may be due to a set of environmental factors that have a common effect on haddock and *I. illecebrosus* recruitment. It may also reflect the rapid growth *I. illecebrosus* pre-recruits and their transition to opportunistic piscivory. In contrast, the positive correlation with the adult cod series suggests that cod survival may improve when squid prey are readily available, although it is unlikely that adult cod abundance is an important determinant of *I. illecebrosus* pre-recruit abundance.

Table 7.2. Significant correlations between abundance series for species with potentially important interactions with *I. illecebrosus* in the U.S. fishery area

Series	Pearson correlation coefficient	Probability of Type I error
illexr and loligor	-0.589	0.0164
illexr and nshake1	-0.593	0.0156
illexp and gbhad0	0.899	0.0001
illexp and gbcod4+	0.799	0.0002
loligor and loligop	0.527	0.0361
loligor and gbcod0	-0.601	0.0138
butter and nshake2+	-0.637	0.0079
butter and sshake2+	-0.606	0.0128
gbhad0 and gbcod4+	0.638	0.0078
herr0 and spdog	0.521	0.0387
nshake0 and sshake0	0.735	0.0018
sshake0 and nshake2+	0.559	0.0301
sshake0 and sshake2+	0.571	0.0062
spdog and gbcod4+	-0.704	0.0023
spdog and shake2+	-0.589	0.0031
nshake1 and sshake1	0.806	0.0002
nshake1 and sshake2+	0.571	0.0208
nshake1 and sshake0	0.814	0.0002
sshake1 and nshake0	0.577	0.0244
sshake1 and sshake0	0.907	0.0001
sshake1 and nshake2+	0.789	0.0003
sshake1 and sshake2+	0.831	0.0001
nshake2+ and sshake2+	0.895	0.0001

Consideration of all interactions that could potentially affect *I. illecebrosus* recruitment (Fig. 7.3) appears to support this proposed importance of competitive and predatory interactions. Although most correlations were weak, there were seven negative, versus two positive, correlations with competitors or predators. There were five negative and five positive correlations with potential prey.

There was a significant negative correlation between the *I. illecebrosus* recruit series and the *L. pealei* recruit series and northern silver hake age 1 series. The negative association with the *L. pealei* index suggests that competitive and predatory interactions between the two primary squid species of the northeastern U.S. shelf are important determinants of *I. illecebrosus* recruitment to this area. The negative association with the silver hake age-1 index suggests that competitive interactions with silver hake are also important determinants of *I. illecebrosus* recruitment on the northeastern U.S. shelf.

Competitive and predatory trophic interactions appear to be important determinants of *Illex* recruitment to the northeast U.S. shelf area. While the variability of *Illex* recruitment is lower in this area than in the Scotian Shelf and Newfoundland areas, presumably due to shorter migration distances for juveniles and adults,

Illex recruitment to this area appears to be episodic, with alternating periods of high and low abundance. This variability in recruitment may be due to the fact that the *Illex* population has to "invade" the marine food web of the U.S. shelf each year through its seasonal inshore migration. Some obvious potential determinants of the success of this migration are the relative abundances of predators and competitors of *I. illecebrosus*. While the dynamics of the trophic interactions between these species are complex, the observed negative associations suggest that high relative abundances of competitors and predators may reduce the invasibility of this food web by *I. illecebrosus* recruits. In particular, many of the competitors and predators of *Illex* in this area were heavily exploited by fisheries during the late 1960s and early 1970s, most notably on Georges Bank. Substantial reductions in the biomass of *Illex* predators and competitors during this period may have produced an open niche for *Illex* to utilize by the mid-1970s. It appears that as the abundance of *Illex* predators and competitors was reduced, *Illex* landings and the relative abundance of *Illex* recruits dramatically increased (Figs. 7.4 and 7.5).

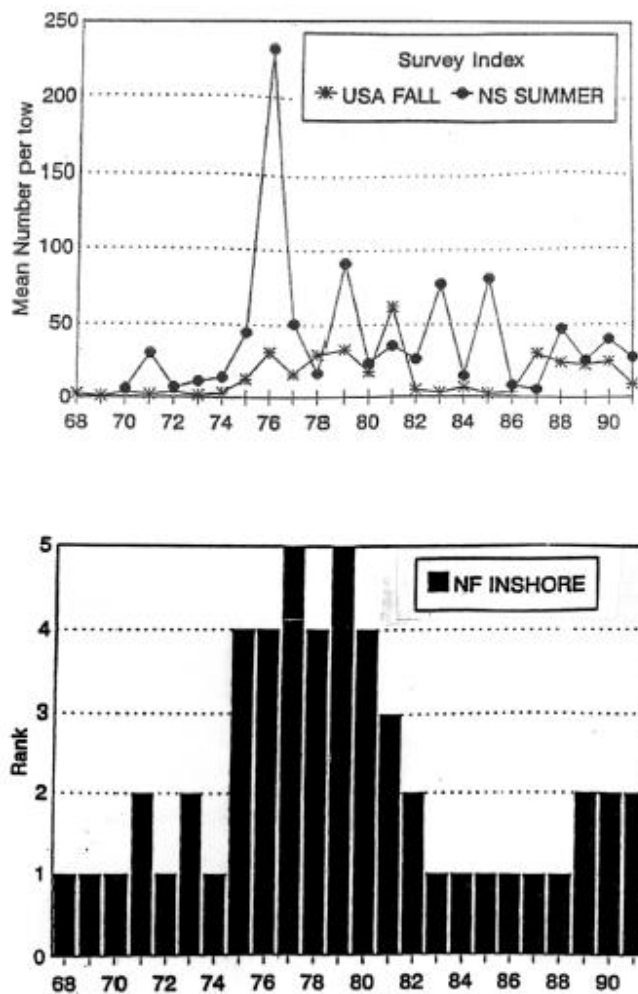


Figure 7.4. Trends in relative abundance (recruitment indices) for *Illex illecebrosus* by fishing area, 1968–1991, based on bottom trawl catch numbers per tow for each of the U.S. shelf and Scotian Shelf (top) and based on qualitative ranking for Newfoundland (bottom)

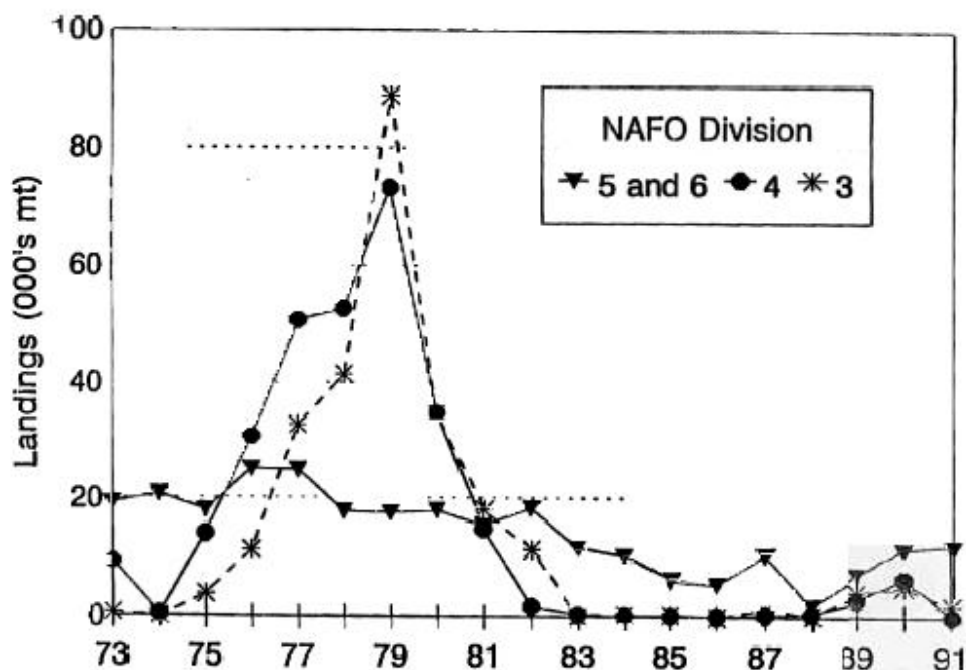


Figure 7.5. Trends in annual landings of *Illex illecebrosus* by fishing area, 1973–1991

3.2 Scotian Shelf

The fish and squid community of the Scotian Shelf is somewhat similar to that of the northeastern U.S. shelf, with a similar assemblage of demersal fishes (Gabriel 1992), and with short-finned squid interacting with dogfish and, more closely, with silver hake. However, the Scotian Shelf is not nearly as productive as the northeastern U.S. shelf. Primary productivity in grams carbon per metre squared is about 102–128 on the Scotian Shelf and slope (Sinclair *et al.* 1984), whereas it varies between about 260 and 470 throughout the more southern area, with the maximum on Georges Bank (O'Reilly and Busch 1984). The Scotian Shelf then is not able to support as large a total biomass of predatory fishes as is the more productive area to the south. Some predators and competitors of *I. illecebrosus* further south are uncommon on the Scotian Shelf. These species include long-finned squid (Dawe *et al.* 1990) and bluefish (Scott and Scott 1988). Predatory fishes common to both continental shelf ecosystems are generally more abundant on the northeastern U.S. shelf. Also, most fish function as predators at a lower trophic level on the Scotian Shelf than to the south, by relying heavily upon crustaceans rather than fish as prey (Waldron 1983).

Species assemblages of squid and bottom fishes on the Scotian Shelf are segregated spatially as well as by differences in depth, temperature, salinity or substrate preference (Scott 1982, Waldron 1983, Sinclair *et al.* 1984). Trophic interactions, then, are a function not only of prey distribution and prey preference, but also of predator habitat preferences.

Waldron (1983) noted that over the period 1970–80, redfish abundance declined in response to warming while squid, red hake and haddock increased. It appears that the gadoids (haddock, pollock and cod) increased from 1975 to 1980. Sinclair *et al.* (1984) showed that total fish and squid biomass was relatively stable during 1970–1981 but there was considerable variation for individual species and some groups.

The short-finned squid is not a fixed component of the fish and squid community on the Scotian Shelf, as it is off the USA. Rather it is one of several migrating species (including mackerel and dogfish) that occupy the continental shelf of such northern areas only during the most productive period of the year (April to November). We hypothesize, then, that in the Canadian fishery areas, short-finned squid recruitment and interaction with fish species will be a function of environmental variation, with squid abundance, and that of some of its predators, prey or competitors, co-varying as an adaptive response to environmental variation (Dawe and Warren 1993, *see Chapter 6*).

3.2.1 Trophic interactions

Many of the studies of trophic interactions on the U.S. continental shelf have included the Scotian Shelf (Scott and Tibbo 1968, Vinogradov 1972, Vinogradov and Noskov 1979, Froermer 1984, Waring 1984) or the western portion of the Scotian Shelf (Edwards and Bowman 1979, Grosslein *et al.* 1980, Langton and Bowman 1980, Langton 1982, Durbin *et al.* 1983, Bowman *et al.* 1984, Bowman and Michaels 1984).

Illex illecebrosus probably interacts most closely with silver hake on the Scotian Shelf, as was concluded for the northeastern U.S. shelf. Silver hake spawn on the banks of the Scotian Shelf in July to October and juveniles aggregate at the slope-water/shelf-water frontal zone (Sherstyukov 1991) where they interact closely with short-finned squid. Although fish prey is never predominant in the stomachs of *I. illecebrosus* from the Scotian Shelf, silver hake (probably O-group) represents the most common continental shelf fish prey species found. Other fish prey consist mostly of oceanic species (Vinogradov and Noskov 1979, Amaratunga 1983, Froermer 1984).

Predation by silver hake on molluscs (predominantly *I. illecebrosus*) is apparently opportunistic (Swan and Clay 1979). Waldron (1988) showed that molluscs (mostly squid) were an important component of the diet in 1981 and 1982 (about 50 percent and 30 percent respectively by weight) but were virtually negligible as a silver hake prey item during 1983–1986, when short-finned squid were in very low abundance on the Scotian Shelf (Figs. 7.4 and 7.5). Dupouy *et al.* (1982) suggested that only silver hake larger than about 40 cm prey upon squid. Waldron (1988, 1992) found that this predation by silver hake increases progressively from about 6–7 percent by weight at ages 2 and 3 to average about 20 percent by weight for age groups 4–10.

Silver hake is likely the most important competitor of short-finned squid for all components of the diet. Both species prey on crustaceans (especially euphausiids), fish (especially silver hake) and short-finned squid. Furthermore, these predators have a close physical association in spring and early summer as they move onto the shelf (Sinclair *et al.* 1984), as well as throughout summer and fall on the shelf (Waldron 1988). They appear to compete for fish most intensely during October–December (Swan and Clay 1979). This agrees with Waldron (1988), who showed that in the fall, silver hake prey most heavily on fish but very little on squid.

Waldron (1988, 1992) showed that all ages of silver hake prey on fish to some extent and that this predation increases with age. Percent by weight of fish in the diet was very low for age groups 0 (5.5 percent) and 1 (8.1 percent) but it increased with predator age to high levels of 63–86 percent for age groups 6–10. Of the identified fish prey, unspecified gadids were most important for age group 1, myctophids were most important for age groups 2 and 3, but also prevalent for age-group 4, and silver hake were most important (cannibalism) for the older age groups (4–10). Sand lance was of minor importance for age groups 4–8 and a few other fishes were uncommon.

Table 7.3. Abundance data for species with potentially important interactions with *I. illecebrosus* on the Scotian Shelf. Numbers-at-age represent VPA estimates.

Species/Series	Series Description
<i>Illex illecebrosus</i>	
Illex	Short-finned squid, July Survey, mean numbers per tow, 1970–1992 (provided by J. Simon, Scotia Fundy Region, Department of Fisheries and Oceans, Canada)
<i>Gadus morhua</i>	
4Xcod0	NAPO Division 4X cod, age-1 numbers lagged 1 year, 1947–1990 (from Campana and Hamel 1992)
4Xcod4+	NAPO Division 4X cod, age-4 and older numbers, 1948–1991 (from Campana and Hamel 1992)
4Vcod0	NAPO Division 4V cod, age-1 numbers lagged 1 year, 1969–1990 (from Mohn and MacEachren 1992)
4Vcod4+	NAPO Division 4V cod, age-4 and older numbers, 1970–1991 (from Mohn and MacEachren 1992)
<i>Melanogrammus aeglefinus</i>	
4Xhad0	NAFO Division 4X haddock, age-1 numbers lagged 1 year, 1947–1990 (from Hurley <i>et al.</i> 1992)
4TVWhad0	NAFO Division 4 TVW haddock, age-1 numbers lagged 1 year, 1947–1990 (from Zwanenburg 1992)
<i>Clupea harengus</i>	
4Wxher0	NAFO Division 4WX herring, age-1 numbers lagged 1 year, 1964–1990 (Stephenson <i>et al.</i> 1992)
<i>Merluccius bilinearis</i>	
4Wsil0	NAFO Division 4W silver hake, age-1 numbers lagged 1 year, 1976–1990 (from Waldron <i>et al.</i> 1992)
4Wsil1	NAFO Division 4W silver hake, age-1 numbers, 1977–1991 (from Waldron <i>et al.</i> 1992)
4Wsi12+	NAFO Division 4W silver hake, age-2 and older numbers, 1977–1991 (from Waldron <i>et al.</i> 1992)
4Wsi14+	NAFO Division 4W silver hake, age-4 and older numbers, 1977–1991 (from Waldron <i>et al.</i> 1992)
4VWXsil0	NAFO Division 4VWX silver hake, Canada/USSR Survey, mean number of age-0 per tow, 1981–1990 (from Sherstyukov 1991).
<i>Pollachius virens</i>	
4VWX5Zpo14+	NAFO Division 4VWX5Z pollock, age-4 and older numbers, 1974–1991 (from Annand and Beanlands 1992)
<i>Squalus acanthias</i>	
4VWXspdog	NAFO Division 4VWX spiny dogfish, July Survey, mean numbers per tow, 1970–1992 (provided by J. Simon, Scotia Fundy Region, Department of Fisheries and Oceans, Canada)

Table 7.4. Significant correlations between abundance series for species with potentially important interactions with *I. illecebrosus* on the Scotian Shelf

Series	Pearson correlation coefficient	Probability of Type I error
4VWX5ZpoI4+ and 4VWXspdog	0.486	0.0407
4VWX5ZpoI4+ and 4Wsi12+	0.636	0.0107
4VWXspdog and 4Wsil2	0.597	0.0186
4VWXspdog and 4Wsi12+	0.713	0.0028
4Wsill and 4Wsill +	0.825	0.0001
4Wsi12+ and 4Wsill+	0.606	0.0166
4Wsi12+ and 4Wsil2	0.847	0.0001
4Xcod4 + and 4Wxher0	0.479	0.0114
4Xcod0 and 4Vcod0	0.588	0.0040
4Wsii0 and 4VWXsii0	0.657	0.0390

The other most likely predator on or competitor of *I. illecebrosus* is dogfish, which also (further south) preys upon crustaceans, fish and squid. However we have no data on the diet of dogfish on the Scotian Shelf.

Dupouy *et al.* (1982) reported that cod and pollock, especially those larger than 50 cm, preyed more heavily on squid than did silver hake or haddock. These two gadoids likely also compete with squid for crustacean and fish prey, to some extent. It is unknown to what extent hakes other than silver hake (e.g. white hake and red hake) prey upon or compete with squid on the Scotian Shelf.

It is not known why short-finned squid do not appear to prey upon a-group juveniles of other abundant resident species such as cod, haddock, and pollock. These species spawn on the banks of the Scotian Shelf at various times during November to May and larvae tend to be retained over the banks (O'Boyle *et al.* 1984). Perhaps short-finned squid simply do not interact closely with a-group fish of any species other than silver hake on the Scotian Shelf. Alternatively predation on these other juvenile fishes may not yet have been detected.

3.2.2 Relationship of community change to *Illex illecebrosus* recruitment on the Scotian Shelf

We assembled a data set consisting of 15 series of species abundances on the Scotian Shelf during 1948–1991 (Table 7.3) to examine whether there was evidence of strong community interactions between *I. illecebrosus* and other species. A total of seven of these series represented potentially important fish prey of *I. illecebrosus*; these series were 4Xcod0, 4Xhad0, 4Vcod0, 4TVWhad0, 4Wxher0, 4Wsi10, and 4VWXsil0. A total of five series were considered to be potentially important predators of *I. illecebrosus* (4Xcod4+, 4Vcod4+, 4VWX5Zpol4+, 4Wsil4+, and 4VWXspdog), and a total of four series represented potential competitors (4VWX5Zpol4+, 4Wsil1, and 4Wsil2+, and 4VWXspdog).

Pearson correlation coefficients were calculated for all interactions to look for evidence of strong community interactions (Table 7.4). Ten of the 105 correlations were significant at the 0.05 probability level, twice as many as would be expected by chance alone. All ten significant correlations were positive. Positive correlations between predatory fishes (dogfish, silver hake and pollock) suggest that competition is not intense. No correlations with the *Illex* series were significantly different from 0 at the 0.05 level of significance.

The lack of significant correlations of the *I. illecebrosus* series with any of the other series suggests that the relative abundance of *I. illecebrosus* on the Scotian Shelf may not be substantially affected by the other species included in the analysis. One interpretation of this lack of correlation between *I. illecebrosus* and other species abundance indices is that the important determinant of *I. illecebrosus* abundance on the Scotian Shelf could be environmental variation. In particular, the chance occurrence of favourable conditions for paralarval and juvenile dispersal through Gulf Stream waters could be an important mechanism that affects *I. illecebrosus* abundance on the Scotian Shelf. Alternative conclusions could include a lack of spatial or seasonal concordance between the *I. illecebrosus* survey series and the VPA (virtual population analysis) estimates of numbers at age or inadequate data for other community members.

There is some suggestion that predation or competition may affect *I. illecebrosus* recruitment because five of the seven relevant interactions produced negative correlations (Fig. 7.6). However, this is less compelling than was the structure of the correlation matrix for such interactions on the northeastern U.S. shelf. Abundance of potential fish prey was not important to squid recruitment on the Scotian Shelf. Indeed, six of seven correlations with potential prey were negative, suggesting that survival of young fish may be enhanced by low abundance of squid.

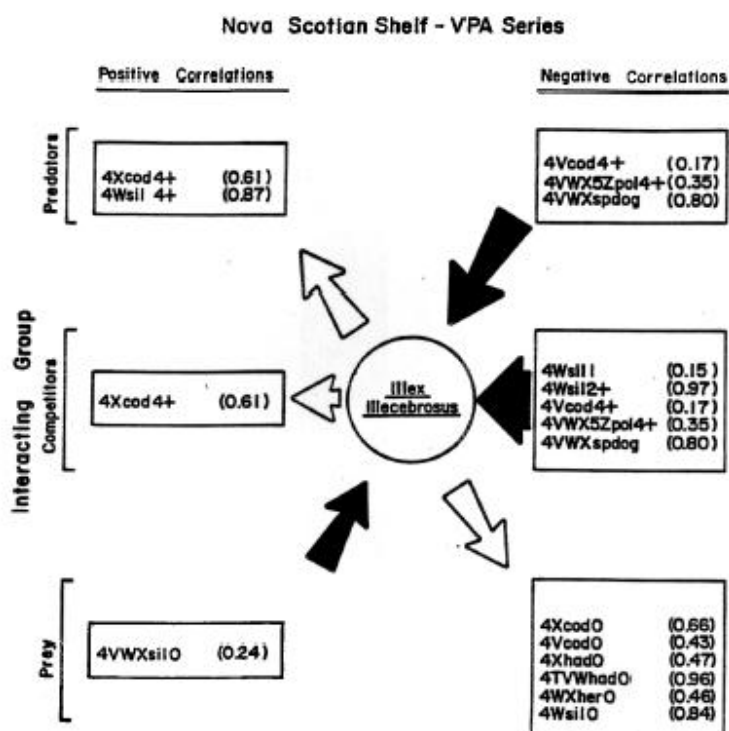


Figure 7.6. Schematic representation of the relative importance of three types of trophic interactions on *Illex illecebrosus* recruitment on the Scotian Shelf, based on the occurrence of positive versus negative correlations with relevant fish stocks and age groups; values in parentheses represent p-values. Thickness of the dark arrows represents relative importance of interactions that could affect *I. illecebrosus* recruitment. See Table 7.3 for definitions of interacting groups.

3.3 Newfoundland coastal waters

The fishery area for *I. illecebrosus* at Newfoundland differs from those previously described in that it is comprised of shallow-water areas very near shore rather than continental shelf waters. *I. illecebrosus* occurs to some extent both inshore and offshore in all three fishery areas, but in some years it appears to become particularly abundant in near-shore waters at Newfoundland. The highly variable and sometimes great abundance of *I. illecebrosus* in near-shore waters of Newfoundland may be related to the suggested role of this habitat as a nursery area for juvenile fishes. Also, several species of small planktivorous forage fishes may be seasonally abundant in these waters whereas predators are not particularly abundant.

We hypothesize, therefore, that availability of suitable fish prey, rather than abundance of predators or competitors, is the type of interaction most likely to affect recruitment of *I. illecebrosus* at Newfoundland. We expect that at Newfoundland in particular, because it is the most northern fishery area, such an interaction would be a result of co-variation of species abundances in response to environmental variation. We further suggest that the Newfoundland area may represent a marginal habitat for this species and that *I. illecebrosus* is abundant at Newfoundland only in years when environmental variation results in an adequate supply of suitable prey and only during the warmest period of the year (July to November) (O'Dor and Coelho 1993, *see Chapter 11*).

3.3.1 Trophic interactions

Atlantic cod and capelin (*Mallotus villosus*) appear to interact most closely with *I. illecebrosus* in nearshore Newfoundland waters. Capelin is relied upon heavily as prey (Squires 1957) during July–September (Dawe 1992), but particularly in July, when it is locally most abundant (Methven and Piatt 1991). Adult capelin are probably not limiting as prey in July but the observed decline in predation on fish and increase in cannibalism after July (Dawe 1988) suggest that availability of fish prey in general becomes limiting. Predation on capelin continues, to some extent, into September, but after July 0-group Atlantic cod (mostly 1–9 cm) represents the most common fish prey, as indicated by otoliths recovered from squid stomachs (Dawe 1992). Otoliths from sand lance (*Ammodytes* sp.) that are mostly 3–9 cm also represent a regular component of the otoliths recovered from squid stomachs, whereas 0-group juveniles (mostly less than 13 cm) of Arctic cod (*Boreogadus saida*), herring and hakes may be relatively prominent in some years. Redfish is preyed upon only on the south coast of Newfoundland and a variety of other fishes are rarely represented by recovered otoliths (Dawe 1992).

Atlantic cod also interacts with short-finned squid as a predator and competitor at Newfoundland. Adult Atlantic cod seasonally migrate to shallow near-shore waters in spring. They co-exist with *I. illecebrosus* throughout the squid fishing season, but especially in summer because in late summer and autumn cod tend to move to deeper waters to avoid warm temperatures (Templeman and Fleming 1956). Although capelin (*M. villosus*) represents the main prey of cod in inshore waters, short-finned squid represents an important component of the diet in years when squid are abundant (Lilly and Osborne 1984, Methven and Piatt 1989). Predation by cod on short-finned squid is unlikely to be especially intense at any time due to differences in temperature preference that would maintain some segregation between these species. Cod prefers temperatures of 0–5°C (Templeman and May 1965), whereas *I. illecebrosus* prefers temperatures greater than 5°C (Hurley 1980, Dawe and Warren 1993). Cod may be more important as a competitor for fish prey than as a direct predator since, like *I. illecebrosus*, it relies heavily upon capelin in July (Templeman 1965) and subsequently includes juvenile cod and sand lance in its diet (Methven and Piatt 1989).

Table 7.5. Abundance data for species with potentially important interactions with *I. illecebrosus* in Newfoundland coastal waters; numbers-at-age represent VPA estimates for cod and hydroacoustic estimates for capelin.

Species/Series	Series Description
<i>Illex illecebrosus</i> <i>Illex</i>	Newfoundland inshore short-finned squid ranked abundance index, 1948–1992
<i>Gadus morhua</i> 3NOcod3 +	NAFO Division 3NO cod, age-3 and older numbers, 1959–1991 (from Baird <i>et al.</i> 1992a)
2J3KLcod3 +	NAFO Division 2J3KL cod, age-3 and older numbers, 1962–1991 (from Baird <i>et al.</i> 1992b)
3NOcod2 +	NAFO Division 3NO cod, age-2 and older numbers, 1959–1991 (from Baird <i>et al.</i> 1992a)
2J3KLcod2 +	NAFO Division 2J3KL cod, age-2 and older numbers, 1962–1991 (from Baird <i>et al.</i> 1992b)
3NOcod0	NAFO Division 3NO cod, age-3 numbers lagged 3 years, 1956–1988 (from Baird <i>et al.</i> 1992a)
2J3KLcod0	NAFO Division 2J3KL cod, age-2 numbers lagged 2 years, 1960–1989 (from Baird <i>et al.</i> 1992b)
<i>Mallotus villosus</i> 3Lcap	NAFO Division 3L capelin, age-1 and older numbers, 1982–1992 (from Miller 1992)
2J3Kcap	NAFO Division 2J3K capelin, age-1 and older numbers, 1981–1992 and 1983–1992 (from Miller 1993)

Spiny dogfish represents another potential predator on, and competitor of, short-finned squid. Dogfish may be very abundant during July–November (especially during July–August) of some years (Templeman 1944). There are few data on predation by dogfish on squid at Newfoundland, but we presume that predation may be intense in years of high squid (and dogfish) abundance. Like cod and *I. illecebrosus*, dogfish prey heavily upon capelin in July and include other fish (especially herring and cod) in their diet afterward. However, only large dogfish (≥ 55 cm) occur in Newfoundland waters, and they consume fish as large as 30 cm (Templeman 1944, 1984). Therefore, and because capelin availability is apparently not limited in July, we believe that competition between dogfish and squid is not intense. In any event, we have no data on abundance of dogfish at Newfoundland.

Perhaps the most important predator of *I. illecebrosus* at Newfoundland is the pilot whale (*Globicephala melaena*), which will prey exclusively on this squid when available (Mercer 1975). Other large predators include bluefin tuna (Butler 1971) and (presumably) sharks. However these large predators have been in very low abundance at Newfoundland for many years. The northern gannet (*Sula bassanus*) also includes *I. illecebrosus* in their diet at Newfoundland, when available (Montevecchi *et al.* 1988), but total annual consumption would not be great. Further, we have no data on abundances of any such large predators and seabirds.

Table 7.6. Significant correlations between abundance series for species with potentially important interactions with *I. illecebrosus* at Newfoundland

Series	Spearman correlation coefficient	Probability Type I error
<i>Illex</i> and 3NO cod 0	0.408	0.0182
2J3KL cod 3+ and 3NO cod 3+	0.664	0.0001
3NO cod 2 + and 3NO cod 3 +	0.949	0.0001
2J3KL cod 2+ and 3NO cod 3+	0.667	0.0001
3NO cod 0 and 3NO cod 3 +	0.683	0.0001
2J3KL cod 0 and 3NO cod 3 +	0.575	0.0009
3NO cod 2+ and 2J3KL cod 3+	0.573	0.0011
2J3KL cod 2 + and 2J3KL cod 3 +	0.999	0.0001
3NO cod 0 and 2J3KL cod 3 +	0.504	0.0072
2J3KL cod 0 and 2J3KL cod 3 +	0.602	0.0007
2J3KL cod 2+ and 3NO cod 2+	0.576	0.0011
3NO cod 0 and 3NO cod 2+	0.733	0.0001
2J3KL cod 0 and 3NO cod 2 +	0.538	0.0021
3NO cod 0 and 2J3KL cod 2+	0.511	0.0064
2J3KL cod 0 and 2J3KL cod 2 +	0.614	0.0005
2J3KL cod 0 and 3NO cod 0	0.586	0.0008
3L cap and 2J3KL cod 3+	0.733	0.0158
3L cap and 2J3KL cod 2+	0.733	0.0001
3L cap and 2J3KL cod 0	0.976	0.0001
3L cap and 3NO cod 2 +	-0.800	0.0096

3.3.2 Relationship of community change to *Illex illecebrosus* recruitment in Newfoundland coastal waters

We assembled a data set consisting of nine series of species abundances in Newfoundland coastal waters within the period 1948–1992 (Table 7.5) to look for evidence of strong community interactions between *I. illecebrosus* and other community members. A total of two of these series represented potentially important fish predators off *I. illecebrosus*: 3NOcod3+ and 2J3KLcod3+. A total of two series were considered to have potentially important competitive interactions with *I. illecebrosus*: 3NOcod2 + and 2J3KLcod2 +. A total of four series were considered to be potentially important prey: 3Lcap, 2J3Kcap, 3NOcod0, and 2J3KLcod0.

Spearman correlation coefficients were calculated between all 36 series pairs to look for direct evidence of strong community interactions. Spearman correlation coefficients were used because the Newfoundland short-finned squid index (Fig. 7.4) is integer-valued and ranges between one (low abundance) and five (high abundance). Although twenty correlations were significant, eleven times the number expected by chance alone, most were between series of Atlantic cod (Table 7.6). The four significant correlations between cod and capelin series suggest that predator-prey relationships may be important in Newfoundland coastal waters.

One significant correlation with the *Illex* series was found, that with the 3NOcod0 series (Table 7.6). This positive association suggests that relative abundance of *I. illecebrosus* in coastal Newfoundland waters improves when cod prey are abundant and readily available. Two other correlations with fish prey were positive but weak, whereas none were negative (Fig. 7.7). This is consistent with the suggestion that *I. illecebrosus* recruitment may be related to availability of fish prey. Jpredation and competition appear to be unimportant.

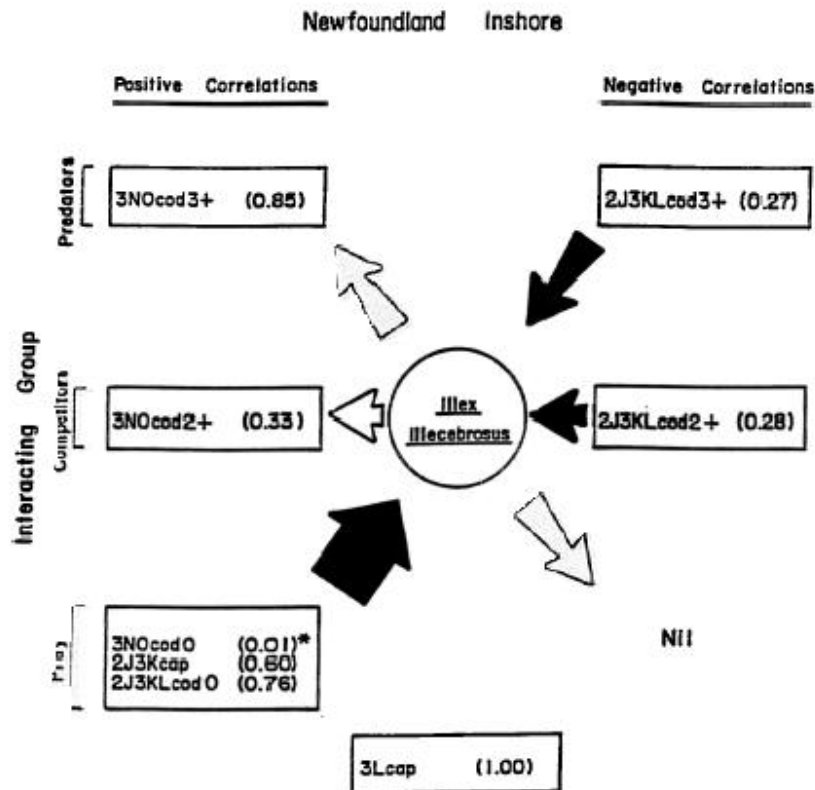


Figure 7.7. Schematic representation of the relative importance of three types of trophic interactions on *Illex illecebrosus* recruitment in Newfoundland coastal waters, based on the occurrence of positive versus negative correlations with relevant fish stocks and age groups (p-values marked by an asterisk were judged to be statistically significant); thickness of the dark arrows represents relative importance of interactions that could affect *I. illecebrosus* recruitment. See Table 7.5 for definitions of interacting groups.

4 *Illex argentinus* on the Patagonian Shelf

The population of *I. argentinus* in the southwest Atlantic is remarkably similar to that of *I. illecebrosus* in the northwest Atlantic (Coelho *et al.* 1985, Hatanaka *et al.* 1985). Each of these species is closely associated with a western boundary current system (*see Chapter 6*). Both species have several spawning peaks within the year (Lange and Sissenwine 1983, Brunetti and Comas 1989a,b, Arkhipkin 1990) with the major peak, in winter, supporting fisheries on the continental shelf throughout the most productive (summer to autumn) season (Coelho 1985, Hatanaka 1985).

Perhaps the most obvious difference between these two species is in the latitudinal range of their distributions. The broad range of distribution of *I. illecebrosus* has been related to its great recruitment variability in the most northern fishery areas (Hatanaka *et al.* 1985, O'Dor and Coelho 1993). In contrast, *I. argentinus*, with a more limited distributional range, has relatively stable annual recruitment, similar to that of *I. illecebrosus* in its most southern fishery area. This implies that mechanisms which affect recruitment of *I. argentinus* to the Patagonian Shelf may be similar to those affecting recruitment of *I. illecebrosus* to the northeastern U.S. shelf.

Table 7.7. Biomass estimates (x1000 t) for most abundant bottom fishes and squids on the Patagonian Shelf

Species	FAO (1983)				Prenski and Angelescu (1993)		Nakamura (1986)
	1973	1978/79	1978	1981/82	Summer	Autumn	
<i>Merluccius hubbsi</i> (common hake)	2302	3919	1154	1758	370	1038	3912– 3927
<i>Micromesistius australis</i> (southern blue whiting)	768	532	421	406	2668	1841	3247
<i>Macrouronus magellanicus</i> (Patagonian whiphake)	-	424	242	350	1377	1240	2069
<i>Merluccius australis</i> (Patagonian hake)					368	609	934
<i>Illex argentinus</i>	-	4-3	6-	23-	1741	413	2605
<i>Loligo</i> spp.	-	33	16	1	2	62	-

The fish and squid community of the Patagonian Shelf (FAO 1983, Nakamura 1986, Csirke 1987, Prenski and Angelescu 1993) is basically similar to that of the northeastern U.S. shelf, being dominated by hakes and (sometimes) by squid belonging to the genera *Illex* and *Loligo*. However there are several differences between the two ecosystems.

The Patagonian Shelf, the widest continental shelf in the world (Nakamura 1986), is considerably larger than the northeastern U.S. shelf; it supports a total fish and squid biomass in the order of 200 million tons (Inada 1986). The squid and demersal fish community is characterized by a great diversity of gadiform fishes, with 45 species represented (Nakamura 1986), but with total abundance dominated by only a few species. Common hake (*Merluccius hubbsi*) is by far the most abundant bottom fish, with landings representing about two-thirds of the total fish catch (Inada 1986, Podestá 1990). Patagonian whiphake (*Macrouronus magellanicus*) and *I. argentinus*, along with common hake and southern blue whiting, comprise about half the total standing stock of bottom fishes and squids (Inada 1986). Biomass estimates for these most abundant fishes and squids are highly variable, but provide a general idea of the relative magnitude of these resources (Table 7.7). There are two species of *Loligo*, *L. gahi* and *L. sanpaulensis*, the former species being more abundant and broadly dispersed (to the south), whereas the latter has a more northern, coastal distribution (Hatanaka 1986). The maximum catch of *L. gahi* was 80 000 t in 1988 (Hatfield and Rodhouse 1991). Total *Loligo* biomass is apparently much lower than that of *I. argentinus* (Table 7.7).

The most abundant pelagic fish is probably anchovy (*Engraulis anchoita*), with Argentinean catches ranging from about 10 000 to 41 000 t during 1972–1982 (Table 4 of Nakamura 1986). The families Serranidae (especially *Acanthistius brasiliensis*) and Sciaenidae are also abundant, each representing annual catches by Argentina of about 20 000 t (Nakamura 1986).

The total fishery resources of the Patagonian Shelf have probably not been as heavily exploited as those of the northeastern U.S. shelf. However, Prenski and Angelescu (1993) noted that some species subjected to directed fisheries (including southern blue whiting, Patagonian hake and *I. argentinus*) have decreased in biomass between 1978 and 1987 whereas some unexploited fishes, including spiny dogfish (*S. acanthias*) have increased in biomass. Such community change is remarkably similar to the northeastern U.S. shelf.

Illex argentinus has a very broad distribution on the Patagonian Shelf (Coelho 1985, Hatanaka *et al.* 1985, Brunetti and Comas 1989a,b, Brunetti and Ivanovic 1992), so it interacts with all of the most abundant fishes and squids, whether over a very broad area (e.g. common hake) or within various more localized regions. Although there is a greater diversity of abundant cephalopods on the Patagonian Shelf (Hatanaka 1986), *Illex* is clearly much more dominant than on the northeastern U.S. shelf (Table 7.4).

4.1.1 Trophic interactions

Ontogenetic trends in the prey spectrum of *I. argentinus* are similar to those already described for *I. illecebrosus*. The main prey type for squid less than 20 cm ML is crustacea, with fish and squid dominating the diet of larger squid (Koronkiewicz 1986, Santos 1992). Fishes represent the predominant prey of adult squid off southern Brazil (Santos 1992), whereas squid (cannibalism) reportedly predominates to the south, over most of the Patagonian Shelf (Koronkiewicz 1986). In that latter study, feeding intensity was greatest in summer and cannibalism increased in prominence in autumn, when feeding intensity declined. *I. argentinus* appears to play a more important role as a prey item of predatory fishes than does *I. illecebrosus*, representing about 75 percent by weight of all food consumed by those predatory fishes between 46°S and 50°S (Prenski and Angelescu 1993).

Illex argentinus clearly interacts most closely and in all capacities with the very abundant common hake. As on the North American shelf, *Illex* co-exists with both juveniles and adults of the most common hake species on the Patagonian Shelf, especially in frontal zones over the slope and at tidal fronts on the shelf (Podestá 1990). *I. argentinus* is the only consistent prey of common hake in all areas of the Patagonian Shelf (Ishino *et al.* 1983), representing as much as 55 percent by weight of all food consumed (Prenski and Angelescu 1993). Angelescu and Prenski (1987) noted that large hake (≥ 50 cm total length), in particular, prey on squid whereas smaller hake feed mostly on zooplankton and micronecton. They showed however that smaller common hake, especially 15–40 cm, also prey to some extent on smaller (2–21 cm) *I. argentinus*. Podestá (1990) noted that *I. argentinus* becomes more prevalent in common hake stomachs during late fall as common hake migrate northward along the shelf-break. Indeed, he suggested that this squid may play an important role in transferring energy from lower trophic levels to hake.

Common hake represents the only known continental-shelf fish prey species of *I. argentinus*, off southern Brazil, with other known fish prey consisting of slope-oceanic species (Santos 1992). Common hake likely compete with *I. argentinus* for juvenile hake as well as anchovy and myctophids. The latter (especially anchovy) represent the most important fish prey of common hake on the Patagonian Shelf (Prenski and Angelescu 1993) and, although there are no data on fish prey of *I. argentinus* in that area, these predators likely share a common prey spectrum of small fishes.

Patagonian hake, in particular those larger than 50 cm (Angelescu and Prenski 1987), also reportedly preys on *I. argentinus* in middle and southern portions of the Patagonian Shelf (Ishino *et al.* 1983) although Prenski and Angelescu (1993) did not note this predation. The importance of Patagonian whiphake as a predator of *I. argentinus* is unclear. Angelescu and Prenski (1987) suggested that this species is planktivorous, whereas Ishino *et al.* (1983) suggested that it is a predator in the middle and southern Patagonian Shelf. Furthermore, Prenski and Angelescu (1993) reported that *I. argentinus* represented between 22 percent and 51 percent of its diet. It is also unclear to what extent whiphake may compete with *I. argentinus* for fish, but Prenski and Angelescu (1993) listed a variety of fishes (and *Loligo gahi*) as components of its diet. Similarly, we consider southern blue whiting to be a potential predator and competitor in part because it is second in overall abundance to common hake (Table 7.7). Although it is reportedly planktivorous on the Patagonian Shelf, congeneric blue whiting is

predatory in other areas, as noted later (MacPherson 1978, P. Sánchez, Instituto de Ciencias del Mar de Barcelona, Spain, *unpubl. data*). Other fishes which prey upon *I. argentinus* and may compete with it for fish include southern cod (*Notothenia ramsayi*) and elasmobranchs (skates and dogfish). Other less abundant fishes also include *I. argentinus* as small components of their diets (Prenski and Angelescu 1993). There are no data on trophic interactions among squid species but we presume that *Loligo* sp. may serve as predators, competitors and prey of *Illex*, as was true on the northeastern U.S. shelf.

4.1.2 Relationship of community change to *Illex argentinus* recruitment on the Patagonian Shelf

We assembled relative abundance data for the period 1975–1985 to look for evidence of strong community interactions between *I. argentinus* and potentially important competitors or predators on the Patagonian Shelf; we have no data on abundances of prey. For this period, a total of seven indices of relative abundance were available (Table 7.8). Pearson correlation coefficients were calculated between all series pairs to look for evidence of strong community interactions. Whereas one significant correlation would be expected due to chance alone, three significant interactions were found (Table 7.9). All three significant correlations were positive and were among the main predatory fishes, suggesting that competition among major predatory fishes is not intense.

No significant correlations were found between the *I. argentinus* series and potentially important competitors or predators. However, we do note that five of the six interactions produced negative, but weak, correlations (Fig. 7.8). This, too, was similar to our results from the North American continental shelf and suggests that abundance of predators and competitors may affect *I. argentinus* recruitment.

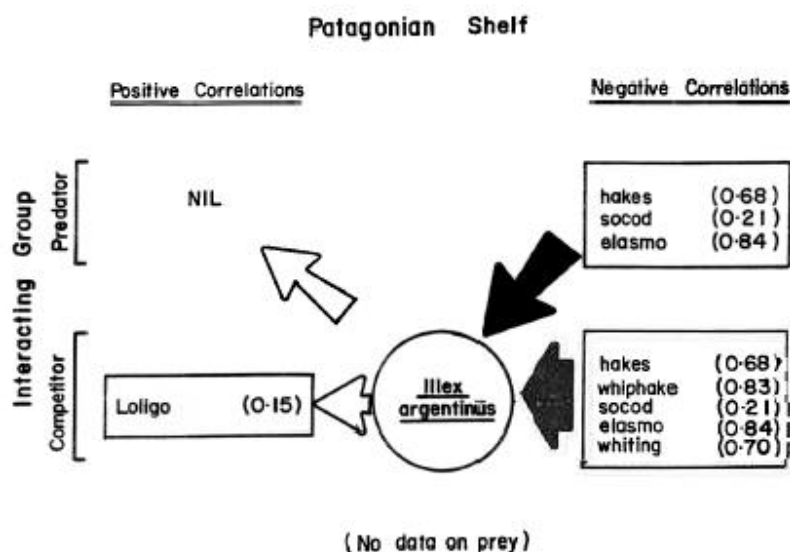


Figure 7.8. Schematic representation of the relative importance of three types of trophic interactions on *Illex argentinus* recruitment on the Patagonian Shelf, based on the occurrence of positive versus negative correlations with relevant fish stocks and age groups; thickness of the dark arrows represents relative importance of interactions that could affect *I. argentinus* recruitment. See Table 7.8 for definitions of interacting groups.

Table 7.8. Abundance data for species with potentially important interactions with *I. argentinus* on the Patagonian Shelf, 1975–1985 (taken or calculated from Csirke 1987); catch-per-unit-effort (CPUE) is expressed as metric tons per day fished.

Species/Series	Series description
<i>Illex argentinus</i> illex	<i>I. argentinus</i> estimates of total number of recruits, 1978–1985
<i>Loligo</i> spp. loligo	<i>Loligo</i> spp. CPUE
<i>Merluccius</i> spp. hakes	Common hake and Patagonian hake CPUE
<i>Micromesistius australis</i> whiting	Southern blue whiting CPUE
<i>Macruronus magellanicus</i> whiphake	Patagonian whiphake CPUE
<i>Notothenia</i> spp. socod	Southern cod CPUE
<i>Elasomobanchii</i> elasma	Sharks and rays CPUE

Table 7.9. Significant correlations between abundance series for species with potentially important interactions with *Illex argentinus* on the Patagonian Shelf.

Series	Pearson correlation coefficient	Probability of Type I error
hakes and socod	.773	.0053
hakes and elasma	.895	.0002
socod and elasma	.886	.0003

5 *Illex coindetii* in the central eastern Atlantic and the Mediterranean Sea

5.1 Central eastern Atlantic

Illex coindetii is of some commercial value as a by-catch between Galicia, or northwest Spain (González *et al.* 1992a), and Angola (Bianchi 1992a,b). Unlike *Illex* species in the western Atlantic, it is neither a dominant species within the fish-squid community, nor is it a dominant cephalopod (Bas 1975, Burukovski *et al.* 1979, Coelho and Borges 1982). Loliginids are more abundant than ommastrephids throughout this area, as is typical of eastern boundary currents (Coelho 1985).

Earlier we briefly compared characteristics of the ecosystem associated with the Canary Current and those of Atlantic western boundary current system (*see Section 1.0*), and more detail is available elsewhere (Wooster *et al.* 1976, Hempel 1982, Parrish *et al.* 1983, Coelho 1985, *see Chapter 6*). In the Canary Current system, the seasonal productivity cycle, closely related to upwelling events, is greatly affected by irregular temporal and local processes. Variability in upwelling and productivity appears to affect recruitment of at least one short-lived planktivorous fish, the sardine, *Sardina pilchardus* (Robles *et al.* 1992). The season of most intense upwelling varies between northwest Africa and Galicia (Wooster *et al.* 1976). Spawning for both of the dominant ommastrephid squids in the Galician fishery (*I. coindetii* and *Todaropsis eblanae*) appears to peak in spring/summer (Mario Rasero, Instituto de Investigaciones Marinas, Vigo, Spain, unpubt. data). Therefore, larvae and small juveniles of both species would be most abundant during the summer period of maximum upwelling and productivity in that area.

Although *Loligo vulgaris* is the most abundant pelagic squid throughout the Canary Current system, *I. coindetii* apparently interacts spatially most closely with *T. eblanae* (Coelho and Borges 1982, González *et al.* 1992a, M.L. Coelho, Universidade do Algarve, Portugal, unpubl. data). In Galician waters *I. coindetii* is more abundant at 100–300 m depths whereas *T. eblanae* is more abundant at 300–500 m depths. *Todaropsis eblanae* is usually the more abundant ommastrephid squid, especially prior to 1984. During 1973–1983 *I. coindetii* was virtually absent from Galician waters (González *et al.* 1992b, 1994). *I. coindetii* is the most abundant of the ommastrephid squids off northwest Africa (Hernandez-Garcia 1991).

The fish communities of eastern boundary current ecosystems are characterized by a high ratio of pelagic to demersal species (Parrish *et al.* 1983, Coelho 1985). The most abundant pelagic fish species include pilchard or sardine (*S. pilchardus*), anchovy (*Engraulis encrasicolus*), horse mackerel (*Trachurus* sp.), other mackerels (*Scomber japonicus* and *S. scombrus*) and tunids (*Sarda sarda*, *Thunnus alalunga*, and *T. thynnus*).

The demersal fish community off northwest Africa is dominated by porgies (Sparidae) on the shelf and hakes, especially *Merluccius senegalensis* and *M. merluccius*, over the outer shelf and slope (Bravo de-Laguna 1982, Bianchi 1992a, 1992b). Off northwest Spain, *I. coindetii* and *T. eblanae* are taken in the multispecies bottom trawl fishery directed for blue whiting (*Micromesistius poutassou*), hake, horse mackerel and monkfish (*Lophius* spp.).

5.1.1 Trophic interactions

Data on trophic interactions involving *I. coindetii* are scant and there are no published data on abundances of potentially interacting species. The potentially most important predators and competitors include cetaceans, hakes, blue whiting, and other squids (Burukovski *et al.* 1979, González 1994, Ch. Nigmatullin, AtlantNIRO, Kaliningrad, Russia, unpubl. data). Fish prey noted to date have included outer continental shelf and slope forms (Burukovski *et al.* 1979). In Galician waters the most common fish prey of both *I. coindetii* and *T. eblanae* appears to be blue whiting (Rasero *et al.* 1996). Of the other *I. coindetii* fish prey, the most common species include *Aphya minuta*, *Gadiculus argenteus* and *Argentina sphyraena*. Fewer fish prey species have been

identified in the diet of *I. coindetii* from West African waters than from Galician waters. Fish prey from that more southern area include myctophids and four other fishes (*see Chapter 4*), none of which have been identified in stomachs from the more northern area. There are no data on the relative importance of those fish prey to the West African *I. coindetii* diet.

5.1.2 Relationship of community change to *Illex coindetii* recruitment in the central eastern Atlantic

We are unable to investigate the possible effects of changes in abundances of interacting fish species because we have no data on species abundances. Even a very crude analysis, using nominal catches as indices of abundances, is not possible because catches of *I. coindetii* are reported as part of total ommastrephid squid catches. However, increase in abundance of *I. coindetii* in Galician waters since 1983 coincided with overfishing of predatory fishes, especially European hake, *M. merluccius* (González *et al.* 1992b).

5.2 Mediterranean Sea

Illex coindetii occurs throughout the Mediterranean and Black seas and is taken as by-catch in bottom trawl fisheries, especially in the western Mediterranean (Roper *et al.* 1984). In these areas *I. coindetii* is not associated with a well-defined current system, but upwelling events occur in localized areas (*see Chapter 6*). The cephalopod-fish community of the Mediterranean Sea is basically similar to that of the central eastern Atlantic (Mangold-Wirz 1963, Roper *et al.* 1984). Of the squids, the loliginids (especially *Loligo vulgaris*) are most abundant but *I. coindetii* probably interacts more closely with *T. eblanae* (which appears to be less abundant [Martin 1991]). Pilchard and the European anchovy (*Engraulis encrasicolus*) are the most abundant pelagic fishes whereas demersal fisheries are dominated by the Sparidae, the Mullidae, and to a lesser extent by blue whiting (*Micromesistius poutassou*), European hake (*M. merluccius*) and picarels (*Maena* spp.) (Northridge 1984, Martin 1991). *Illex coindetii* is taken as a by-catch in the fishery for European hake and blue whiting off the Spanish Mediterranean coast (P. Sánchez, Instituto de Ciencias del Mar, Barcelona, *unpubl. data*).

5.2.1 Trophic interactions

Predators of *I. coindetii* in the Mediterranean Sea may include other squids, especially *Todarodes sagittatus* and *Loligo vulgaris*, which are generally larger than *I. coindetii*. Data are scant on diets of commercial fishes but *I. coindetii* is one of four cephalopods which, as a group, occurs in about 17–20 percent of large blue whiting (>24 cm) stomachs off the Spanish Mediterranean coast (MacPherson 1978, P. Sánchez *unpubl. data*). *Illex coindetii* interacts spatially and temporally with blue whiting and so both likely compete for crustacean and fish prey (MacPherson 1978, Sánchez *unpubl. data*). *Illex coindetii* likely also competes with other squids and with piscivorous hakes, but we have no relevant data on diets to support this.

Sánchez (1982) and Sánchez *et al.* (*see Chapter 4*) provide data on the prevalence of fish in general in the *I. coindetii* diet and on species composition of the fish prey spectrum. That predation on fish (as opposed to cannibalism) by large squid was very high, especially in autumn, suggested that fish prey is not limiting. Predation on fish generally was quite high, as in Galician waters, and some fish prey were common to diets from both areas (*Micromesistius poutassou*, *Gadicuius argenteus* and *Maurolicus muelleri*). Ten other fishes were identified in stomachs from the western Mediterranean (*see Chapter 4*). However, we have no data on their relative importance in the diet. Also we have no data on abundance of fish prey.

5.2.2 Relationship of community change to *Illex coindetii* recruitment in the Mediterranean Sea

We assembled a data set consisting of monthly landings of hake, blue whiting, and *I. coindetii* in the Mediterranean Sea from 1984 to 1991 to look for evidence of strong community interactions between these species. The hake and blue whiting represented potentially important predators and competitors of *I. coindetii*. Landings of these species provided a rough measure of relative abundance of the recruited portion of their populations.

Pearson correlation coefficients were calculated between the three pairs of series. A total of two correlations were significantly different from 0 at the 0.05 level of significance; these were between hake and *I. coindetii* with $\rho=0.504$ and $\text{Pr}(\text{Type I error})=0.0001$ and between blue whiting and *I. coindetii* with $\rho=-0.330$ and $\text{Pr}(\text{Type I error})=0.001$.

The fact that monthly landings of both hake and blue whiting were significantly correlated with *I. coindetii* landings suggests that trophic relationships between these species could be important determinants of *I. coindetii* abundance, provided that the pattern of fishing effort was stable during 1984 to 1991. The positive correlation between hake and *I. coindetii* could indicate that abundances of both species are affected by a common environmental mechanism or that *I. coindetii* and hake share similar prey species whose individual abundances are only loosely coupled with hake and *I. coindetii* predation pressure. In contrast, the negative correlation between blue whiting and *I. coindetii* may indicate strong competitive or predatory interactions. In this case, either direct predation or the depletion of a shared prey species could be the important trophic interaction.

Alternatively, these associations could be due to common seasonal trends in species availability or fishing effort directed at these species. To examine whether these associations would also be evident on an annual basis, we pooled the monthly landings to form annual landings series for each of the species. We calculated Pearson correlation coefficients between the three pairs of annual landings series and found that the hake and *Illex* series were significantly positively correlated with $\rho=0.723$ and $\text{Pr}(\text{Type I error}) = 0.043$ and that the whiting and *Illex* series were significantly negatively correlated with $\rho=-0.711$ and $\text{Pr}(\text{Type I error}) = 0.048$. Overall, the results of the annual analysis were concordant with the monthly analysis and suggested that the associations were not due to seasonal effects.

6 Summary and recommendations

Although the results of each of our analyses were inconclusive, our comparative study suggested generally that abundance of predators and competitors appears to affect *Illex* spp. recruitment in western boundary continental shelf ecosystems. This conclusion is based on the predominance of negative interactions involving *I. illecebrosus* on the northeastern U.S. shelf and Scotian Shelf, as well as *I. argentinus* on the Patagonian Shelf. The apparent importance of predatory and competitive interactions is consistent with the hypothesis that fast-growing, short-lived species increase in abundance in stressed ecosystems where predatory fishes have declined (Sherman 1980). If this hypothesis holds for *Illex* spp., it could be due to competitive interactions where an *Illex* sp. fills a trophic niche vacated by predatory fishes. Alternatively, it could reflect an increase in abundance of a prey species (*Illex* sp.) in response to both a decrease in abundance of total predators as well as the resultant increase in availability of secondary production to such prey species (Sherman 1980). In either case, *Illex* species, being annual, would be capable of responding more rapidly than any fish species to such ecosystem changes.

The Newfoundland coastal fishery area is unique in that in relation to the spawning area it represents a particularly remote area and predatory fishes are not very abundant. In this fishery area absolute abundance of fish prey may be related to *I. illecebrosus* recruitment. It seems logical and adaptive that recruitment to such a

remote area would be related to availability of suitable prey. It would also be logical and adaptive if this predator-prey relationship was regulated by the environment. This seems likely, particularly since both the predator and most of the fish prey represent a common (and the current) year-class.

Illex coindetii is also unique in that it represents a rather minor component of a very diverse and temporally irregular ecosystem. For this reason, and because data on *Illex* and fish species abundances were inadequate, we failed to demonstrate any effect of trophic interactions on *I. coindetii* recruitment (if any such effect exists).

As noted earlier, even our most convincing results (*I. illecebrosus* on the northeastern U.S. shelf), are not conclusive. Rather, our general findings should be used as working hypotheses in more extensive future studies. Future efforts should focus on more detailed quantitative studies of trophic interactions and the effects of such interactions on squid growth and mortality. For all predators, age- and size-specific studies of energetic requirements should be pursued. Effort should also be directed towards quantifying the daily ration for each diet component. Extensive time series of high quality data on squid and fish abundances will also be required.

The comparative approach used here should be extended through a multinational collaborative study. Such a comparative study should focus on ecologically closely related species, rather than a phylogenetic group (e.g. genus). For example, a study of squid recruitment dynamics within western boundary current ecosystems should include *Todarodes pacificus* rather than *I. coindetii* (with *I. illecebrosus* and *I. argentinus*).

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