



Trophic role of Atlantic cod in the ecosystem

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Abstract

As the world's oceans continue to undergo drastic changes, understanding the role of key species therein will become increasingly important. To explore the role of Atlantic cod (*Gadus morhua* Gadidae) in the ecosystem, we reviewed biological interactions between cod and its prey, predators and competitors within six ecosystems taken from a broad geographic range: three are cod-capelin (*Mallotus villosus* Osmeridae) systems towards cod's northern Atlantic limit (Barents Sea, Iceland and Newfoundland–Labrador), two are more diverse systems towards the southern end of the range (North Sea and Georges Bank–Gulf of Maine), and one is a species-poor system with an unusual physical and biotic environment (Baltic Sea). We attempt a synthesis of the role of cod in these six ecosystems and speculate on how it might change in response to a variety of influences, particularly climate change, in a fashion that may apply to a wide range of species. We find cod prey, predators and competitors functionally similar in all six ecosystems. Conversely, we estimate different magnitudes for the role of cod in an ecosystem, with consequently different effects on cod, their prey and predator populations. Fishing has generally diminished the ecological role of cod. What remains unclear is how additional climate variability will alter cod stocks, and thus its role in the ecosystem.

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Introduction

The Atlantic cod (*Gadus morhua* Gadidae) is an important species in many of the world's ocean systems from an economic, ecological and cultural perspective (Jensen 1972; Garcia and Newton 1997; Kurlansky 1997; FAO 1998). It is a species facing notable changes within the ecosystems in which it lives, and documenting the role of cod in the ecosystem will be important as these systems continue to change. As overfishing of the world's fish stocks (Garcia and Newton 1997; FAO 1998) and climate change scenarios continue to be expressed (ACIA 2005; IPCC 2007), examining how marine fishes will respond remains a critical issue. In many respects, cod is one of the few fish species for which we should be able to do this and, as such, serves as an example species. Comparable species from other ecosystems (be they ecological or economic or cultural equivalents) may not have had the level of study that cod has had. Thus scientists and managers in those systems may be informed by the insight obtained from an examination of cod.

Our focus here is twofold: to review the extent to which cod dynamics and distribution can be influenced by interactions with predators, prey and/or competitors, and to explore the extent to which changes in cod stock size can affect other species in the ecosystem. We highlight the extent to which population change, particularly due to fishing and climate variability, may affect the interactions between cod and other members of its ecosystem.

To help us explore the role of cod in the ecosystem, we review biological interactions between cod and its prey, predators and competitors within six ecosystems (Table 1; Fig. 1). These six examples are from a broad geographic range: three are cod-capelin (*Mallotus villosus* Osmeridae) systems towards cod's northern limit across the top of the Atlantic (Barents Sea, Iceland and Newfound-

land-Labrador), two are more diverse systems towards the southern end of the species' range on either side of the Atlantic (North Sea and Georges Bank-Gulf of Maine), and one is a species-poor system with an unusual physical and biotic environment (Baltic Sea). We then attempt a synthesis of the role of cod in these and other ecosystems and speculate on how the role of cod might change in response to a variety of influences, particularly climate change.

Comparison of case studies from major cod ecosystems

For each of six ecosystems (Fig. 1), we describe the diet of cod and the way that changes in the abundance or availability of prey have affected the cod's diet and recruitment, growth and mortality. Of considerable interest is the extent to which changes in the size of cod populations have affected the dynamics of prey populations. We also overview some changes in predator populations, and discuss ways in which these predators may have affected cod dynamics, especially recruitment but also the mortality of adults. The possibility of competition is also discussed. In some instances, we highlight phenomena that are particularly well studied within a specific cod population or ecosystem, but less so in others.

It is not our intent to compile an extensive review of the prey and predators of cod or of cod catch and population dynamics. The diversity of the food of cod has been described in delightful detail by some early investigators (Zatsepin and Petrova 1939; Brown and Cheng 1946; Hansen 1949; Popova 1962; Rae 1967). More recent studies tend to report cod prey in a more quantitative and aggregated manner. The predators of cod are less thoroughly documented. Pálsson (1994) and Methven (1999) have compiled informative lists and reviews of this information for several ecosystems.

Table 1 Key parameters for cod in the six example ecosystems.

	Baltic Sea	North Sea	Barents Sea	Iceland	Newfoundland/ Labrador	Gulf of Maine/ Georges Bank
Years of peak abundance	Early 1980s	1970	Mid-1930s and mid-1940s	Around 1930 and mid-1950s	Early 1960s	Late 1960s
Current cod B/L as % of peak cod B/L	12 (B)	20 (B)	35 (B) 40 (L)	30 (B) 35 (L)	2 (B)	10–15% (B)
Peak cod B/L as % of total fish B/L during cod peak	32 (B)	4 (B)	25 (B)	50 (L)	NK	25–30% (B)
Current cod B/L as % of current total fish B/L	4 (B)	1 (B)	25 (B)	25 (L)	NK	5–10% (B)
Thermal type of ecosystem	Temperate enclosed	Temperate	Boreal	Boreal	Boreal	Temperate
General interaction strengths in ecosystem	Moderate–strong	Moderate–weak	Strong	Strong	Moderate–strong	Weak
Cod growth dependant on forage fish	Moderate	No	Strongly suspected	Strongly suspected	Possible	Not Likely
Cod recruitment dependant on zooplankton	Maybe	Maybe	Maybe	Maybe	NK	Not likely
Forage fish predation on cod eggs/juveniles	Strong	Maybe	Moderate	Maybe	NK	Minimal
Marine mammal predation on cod	Minimal	Minimal	Moderate	Strongly	Suspected	Moderate-minimal
Predatory release of cod prey as cod decline	Yes	Possible	Suspected	Yes	Yes	Some
Increase in invertebrate fisheries after cod decline?	No – salinity too low for crustaceans	Yes	Possible	Yes	Yes	Possible

B, biomass; L, landings; NK, not known.

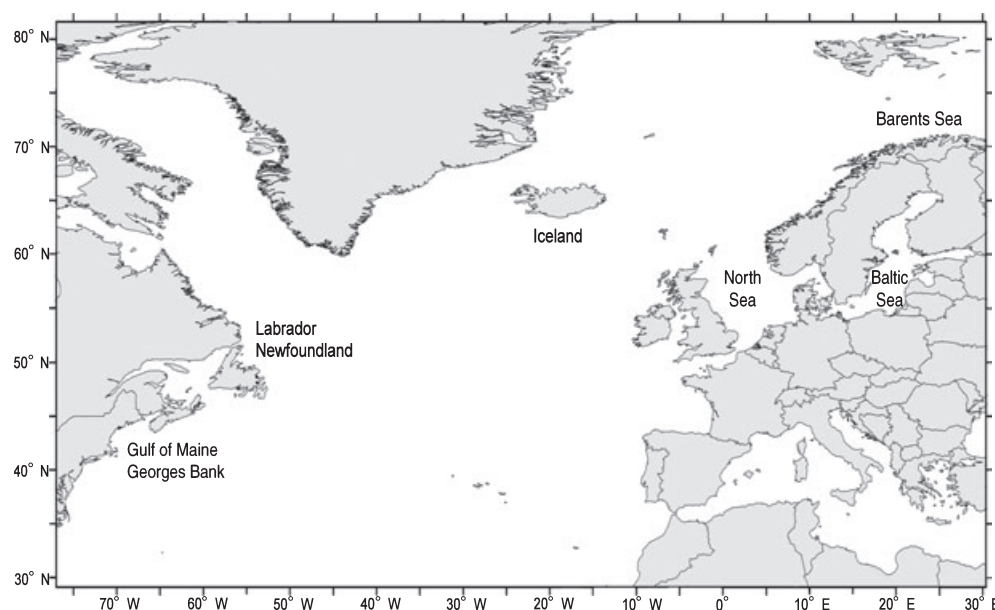


Figure 1 Location of the six ecosystems examined in this study.

Baltic Sea

The Baltic is a unique marine system as it is the world's largest brackish water sea. Salinity is generally $<20\text{‰}$, with a declining gradient from south to north, where it is close to zero. Furthermore, salinity varies interannually mainly as a result of sporadic inflows of saline water from the North Sea. Cod concentrates in the southern areas and can spawn successfully only where the salinity is above 11‰ (Westin and Nissling 1991). A further physical feature of the Baltic Sea is that the bottom water in the deepest parts is often oxygen depleted. As these are generally the areas preferred by cod for spawning and feeding, the level of dissolved oxygen is an important factor for the stock dynamics of cod in this area.

The fish community in the Baltic Sea is very simple as it is dominated by three main species: cod, herring (*Clupea harengus* Clupeidae) and sprat (*Sprattus sprattus* Clupeidae) (Sparholt 1994). Cod, herring and sprat are very important for the commercial fishery with annual landings of around 0.5–1.0 million tonnes. Cod catches peaked in 1984 and the stock is currently depleted (ICES 2003b, 2005b). The sprat stock now dominates (landings of 340 000 tonnes in 2002) the Baltic whereas herring is depleted, with the management system attempting to rebuild herring and cod. The propor-

tion of cod relative to all fish biomass in the ecosystem is 4% at present, but has been as much as 30% in the 1980s when the cod stock peaked and sprat were concurrently sparse (Table 1).

Species interactions in the Baltic have been investigated during the last two decades by several entities, including International Council for the Exploration of the Sea (ICES) Groups, European Commission projects and individual scientists (see Köster *et al.* 2003 for a detailed review). Cod eat herring and sprat, while herring and especially sprat eat cod eggs. These interactions seem to result in at least two semi-stable states of the ecosystem: one dominated by sprat that keeps cod down via cod egg predation and another dominated by cod via predation on sprat. This is shown by direct measurement of the diet composition, calculations of total amounts consumed and by historical stock assessments. Other interactions that might indirectly influence cod are less well studied. For example, a large sprat stock seems to depress the herring stock by food competition (Möllmann and Köster 2002; Möllmann *et al.* 2003, 2005). Salmon (*Salmo salar* Salmonidae) are also present in the system and can eat a notable amount of sprat (Karlsson *et al.* 1999; Hansson *et al.* 2001). The growth of salmon is related to the biomass of sprat, implying that this species benefits from the sprat dominated state. However, there are also indications

that a large sprat stock increases the incidence of the so-called M74 disease in salmon, perhaps via a B-vitamin esterase in sprat, negatively affecting the salmon stock. Thus, cod directly or indirectly influences sprat and herring stocks, herring growth, and salmon growth and health.

Climate variability has meant increased precipitation and river run off and less frequent inflows from the North Sea, resulting in a lower salinity in the Baltic Sea. This negatively influences not only the cod recruitment but also the amount of the marine copepod *Pseudocalanus elongatus* (Clausocalanidae), which is an important prey for herring and sprat. Thus these phenomena influence the production of these two forage fish species and indirectly the production of cod. Due to a very long turnover time for the water (around 30 years), the Baltic Sea is highly vulnerable to eutrophication, and this has been very pronounced in the 20th century. Thurow (1997) showed that herring and sprat biomass increased in the 1900s at a time corresponding approximately to the intensification of eutrophication, also ultimately influencing cod stocks. Thus, although the Baltic Sea fish community is simple in terms of number of fish species, it is quite complicated in terms of stability and interactions.

As in other ecosystems, cod in the Baltic is a generalist, eating whatever is available (Sparholt 1994). Herring and sprat constitute about half the diet, with the isopod *Saduria entomon* (Chaetiliidae) accounting for another third. Other invertebrates such as the polychaete *Harmothoe sarsi* (Polynoidae) and the macroplanktonic crustacean *Mysis mixta* (Mysidae) make up a small percentage of the diet for large cod, but can constitute up to two-thirds of the diet for small cod. Juvenile cod constitute a small percentage of the diet of large cod, with other fish constituting ~10% (Fig. 2). Annual variation in the diet reflects variation in abundance of the prey field.

In the 1980s, cod consumed about 1.5 million tonnes per year (Sparholt 1994), and ate significantly more herring and sprat than was taken by the commercial fishery. Recently, consumption has dropped to around 300 000 tonnes due to the reduced size of the cod stock.

Growth of cod in this ecosystem has been related to available biomass of cod prey items (Gislason 1999) and there is evidence of density-dependent effects (ICES 2003d, 2005b), with consequences for maturity and fecundity. The variation in weight at age in the period 1977–1997 was a factor of about 1.5.

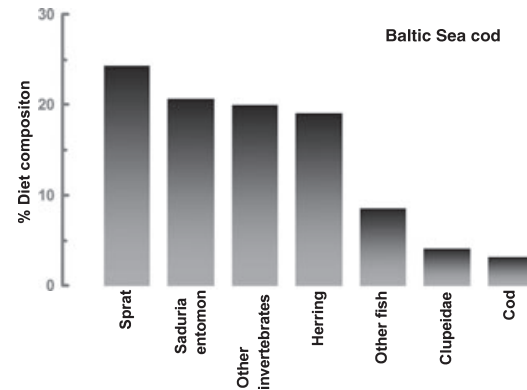


Figure 2 Diet of cod (average diet composition by weight per length group) in the Baltic Sea (adapted from Sparholt 1996b). Based on 43 544 cod stomachs sampled in 1977–1990.

A model of harvest strategies for all the commercial fisheries in the Baltic shows, somewhat surprisingly, that revenue is maximized by fishing down the cod stock and thus increasing the catch of herring and sprat (Gislason 1999). The price of cod was assumed in the model to be 10 times the price of herring and sprat. However, the effects of predation on cod eggs by herring and sprat were not included, because they have only been investigated recently. The conclusion would probably be very different if this interaction was included.

Cannibalism seems to be a significant regulatory mechanism for the cod stock in periods when the cod stock is large. A Ricker type stock–recruitment curve results from the assumption that production of 0-group cod is proportional to cod spawning stock biomass (SSB) (Sparholt 1995, 1996a,b) with recruitment (at age 3) peaking at a spawning stock size of 550 000 tonnes. This observation would indicate some form of compensation, notably via consumption of juveniles.

Total consumption of juvenile and adult cod by harbour porpoises (*Phocoena phocoena* Phocoenidae) and grey (*Halichoerus grypus* Phocidae), harbour (*Phoca vitulina* Phocidae), and ringed (*Phoca hispida* Phocidae) seals is estimated to be only about 2000 tonnes per year (ICES 1990). However, the biomass of seals may have been an order of magnitude or more greater a century ago, and total fish (mostly herring and sprat) consumption by these marine mammals has been estimated for that time to be 320 000 tonnes per year (Thurow 1997). The proportion of cod in the diet at that time was not

known, but it is suspected that the mortality on cod must have been significant. Seabirds are not major predators on cod in the Baltic. Some cormorants (*Phalacrocorax* spp. Phalacrocoracidae) take juvenile cod periodically, but only in very small amounts (ICES 1990).

Cod is the dominant medium-sized (30–100 cm in length) predator in the Baltic. Salmon is the only predator that might be of some significance as competitor. However, such competition is likely minor as the biomass of salmon is about 10 000 tonnes (ICES 2004c) compared to a biomass of cod of over 1 million tonnes in the early 1980s and over 0.5 million tonnes until its decline after 1986.

North Sea

Cod has been one of the most important fish stocks in the North Sea, socioeconomically speaking, for at least the last two decades. The fluctuations in stock size and in catches of cod have been described in detail elsewhere, but we would be remiss without noting the gadoid outburst from the mid-1960s to the mid-1980s, where cod and other gadoids, such as haddock (*Melanogrammus aeglefinus* Gadidae), whiting (*Merlangius merlangus* Gadidae), saithe (*Pollachius virens* Gadidae) and Norway pout (*Trisopterus esmarki* Gadidae), exhibited peak abundances (Cushing 1980). The reason for the outburst was good recruitment in some of those years (Hislop 1996). Now the cod stock is both growth and recruitment overfished, with the spawning stock size below pre-1960s levels (ICES 2004a). The total biomass of fish in the North Sea is about 10 million tonnes (Andersen and Ursin 1977; Sparholt 1990, ICES 2003a, 2005a,c), so cod only constitutes a small proportion of the North Sea fish community (Table 1) and is therefore not expected to have a large impact on the rest of the system. This may have been different historically, before heavy fishing on the stock began and the stock was at a higher level of abundance.

A significant amount of research effort has been devoted to studies of multispecies interactions in the North Sea for the past two to three decades. ICES has coordinated major stomach sampling projects, in 1981 and 1991. In both years about 100 000 stomachs from cod, haddock, whiting, saithe, mackerel (*Scomber scombrus* Scombridae), rays (*Raja* spp. Rajidae), gurnards (*Eutrigla gurnardus* Triglidae) and horse mackerel (*Trachurus trachurus* Carangidae) were collected and analysed (in

addition to a lesser amount for other species; ICES 1997, 1989). The primary objective was to obtain input data for the MultiSpecies Virtual Population Analysis (MSVPA) model for the North Sea (Sparre 1991).

As in other ecosystems, cod in the North Sea eat what is available within the size range of what they are capable of ingesting (ICES 1997, 1989). Small cod eat mainly crustaceans, gradually increasing the proportion of fish in the diet with ontogeny. All age groups eat some Annelida as well. The most important crustaceans are Caridae, Astacidea, Anomura and Brachyrrhyncha (ICES 1997, 1989). The most important fish species are herring, Norway pout, haddock, whiting, sandeel (*Ammodytes* spp. Ammodytidae) and dab (*Limanda limanda* Pleuronectidae) (Fig. 3). The available evidence indicates that cod and other species studied in the North Sea do not alter their preferences for particular prey, and that the consumption of a given prey species by an individual cod is generally proportional to the abundance of the prey. Indications of this can be seen in Fig. 3 where herring increases in importance by a factor of about 5 from 1981 to 1991, coinciding with a recovery of the North Sea herring stock from a spawning stock size of 195 000 tonnes in 1981 to 980 000 tonnes in 1991 (ICES 2004c).

Norway lobster (*Nephrops norvegicus* Nephropidae) is an important food item of cod and constitutes about 5% of its food by weight in the North Sea. This means that cod probably eat more *Nephrops*

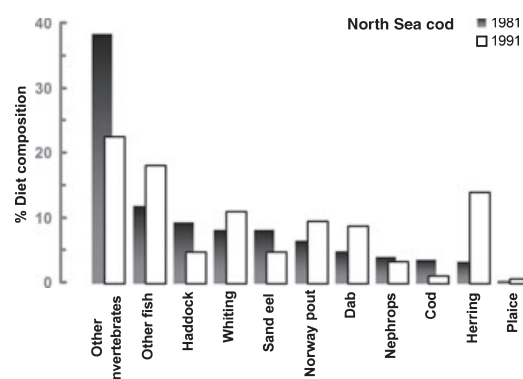


Figure 3 Food composition (by weight) of North Sea cod in 1981 and 1991 based on ICES Stomach Sampling Projects (1981: 11 471 cod sampled; 1991: 9719 cod sampled) (ICES 1989, 1997). The values are calculated based on data averaged by cod age; weighting is by stock numbers by age (ICES 2005a) and stomach content weight by age.

than are caught commercially. There is an increasing trend in the commercial landings of *Nephrops* in the last couple of decades, which may be due to release from predation as the cod stock has decreased (ICES 2003e). Thus the dynamics of the *Nephrops* stocks in the North Sea seem to depend strongly on the dynamics of cod, as is the case in the Irish Sea (Brander 1988; Brander and Bennett 1989) and probably other areas where they co-occur. Norway lobster is the only commercially important prey species for which cod is the main predator.

Cod is a cannibal in the North Sea; as such, it is one of the main predators of its own juveniles. As elsewhere, at the youngest ages, predation generally dominates cod mortality, while the fishery takes over at the older ages. According to the MSVPA model (ICES 2003a, 2005a,c), predation mortality is about 1–1.5 per year on 0-group, about 0.5 on 1 group 0.1–0.2 on 2–6 group and 0 on older cod. The main predators are cod, whiting, gurnards, grey seals and sea birds (ICES 2002, 2003a, 2005a,c), with a potentially high predation mortality of 0-group cod given the caveats of MSVPAs (ICES 2003a). Fig. 4 shows natural mortality of 0-group cod with and without grey gurnards included. The role of grey gurnard as a predator on 0-group was analysed in more detail by Floeter *et al.* (2005), highlighting the importance of this more recently prominent piscivore.

It has been claimed that herring and sprat eat cod eggs and larvae in the North Sea (Cushing 1980; Daan *et al.* 1985), but the phenomenon is not as well investigated in this area as it is in the Baltic, where it is clearly shown to be important for cod

recruitment (see Baltic Sea). The other main pelagic species, mackerel, is well investigated via the two large ICES stomach sampling projects and has been analysed in the MSVPA model; the results indicate that it does not seem to interact much with the cod stock. Cushing (1980) discusses the release of food with the declining pelagic stocks as a possible factor, but the data and knowledge are not conclusive.

The role of marine mammals as predators of cod is not well understood. Among all cetaceans and pinnipeds, only grey seals have been included in the North Sea MSVPA but they are responsible for a relatively small amount of the mortality experienced by cod. There is little information about food items of other seals and of whales. This topic merits further investigation.

Although entirely unclear, there is little evidence for competition between North Sea cod and other fish species. Assuming production in the North Sea is limited, that the growth of cod did not display a density-dependent decline during the 'gadoid outburst' when the cod and other gadoid stocks (potential food competitors) were very large is indicative of limited competition. This interpretation is further confounded by changes in North Sea plankton associated with leading climate indicators (Beaugrand *et al.* 2003). The potential for competition should be further explored by the analysis of dietary overlap between cod and the other main predators (whiting, haddock, saithe and mackerel).

Barents Sea

Cod is the main piscivore in the Barents Sea (Bogstad *et al.* 2000), with the fluctuations in stock size and in catches of Northeast Arctic cod¹ further described elsewhere (Nakken 1994; Hylen 2002). The stock abundance is about one-third of the peak level and somewhat below the long-term (1946–2005) mean (Table 1; ICES 2007); however, the stock is at present in a healthy state, with current SSB above B_{pa} .

The interactions between cod and the two most abundant planktivorous species, herring and capelin, combined with variability in climate (temperature, inflow) to a large extent govern the dynamics

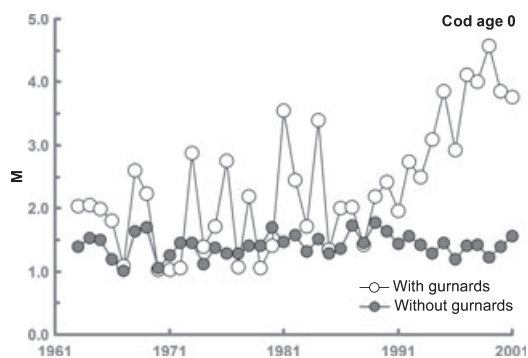


Figure 4 Natural mortality ($M = M_1 + M_2$) of 0-group cod in the North Sea as estimated from MSVPA, with and without gurnards included as a predator (adapted from ICES 2003a).

¹The Northeast Arctic cod stock is the same species, *Gadus morhua*, being compared to other cod stocks in the other ecosystems; it is not to be confused with Arctic or polar cod *Boreogadus saida* referred to here and in other ecosystems as cod prey/competitors.

of the Barents Sea ecosystem (Hamre 1994; Hjermann *et al.* 2007). Cod is a predator on capelin, herring and young cod (Bogstad *et al.* 1994; Bogstad and Gjosæter 2001; Johansen 2003), while herring prey on capelin larvae. Fig. 5 shows a simplified Barents Sea food web. Abundant year classes of herring have a strong adverse effect on capelin recruitment while they are present in the Barents Sea at ages 0–3 (Gjosæter and Bogstad 1998), indirectly influencing the cod stock. In periods with low capelin abundance, cod switch to krill and amphipods as prey (Bogstad and Mehl 1997). Low capelin abundance has also been shown

to influence individual growth of Northeast Arctic cod (Mehl and Sunnanå 1991).

Russian qualitative cod stomach content data (frequency of occurrence for the main prey species, degree of fullness) show that the abundance of herring in cod stomachs in the 1980s and 1990s was much lower than in the 1950s and 1960s (Ponomarenko and Yaragina 1979; Gjosæter and Bogstad 1998), a difference which cannot be explained only by the difference in abundance of young herring between those two periods (ICES 2006a). Additionally, the occurrence of cod cannibalism declined strongly from the early 1960s to the

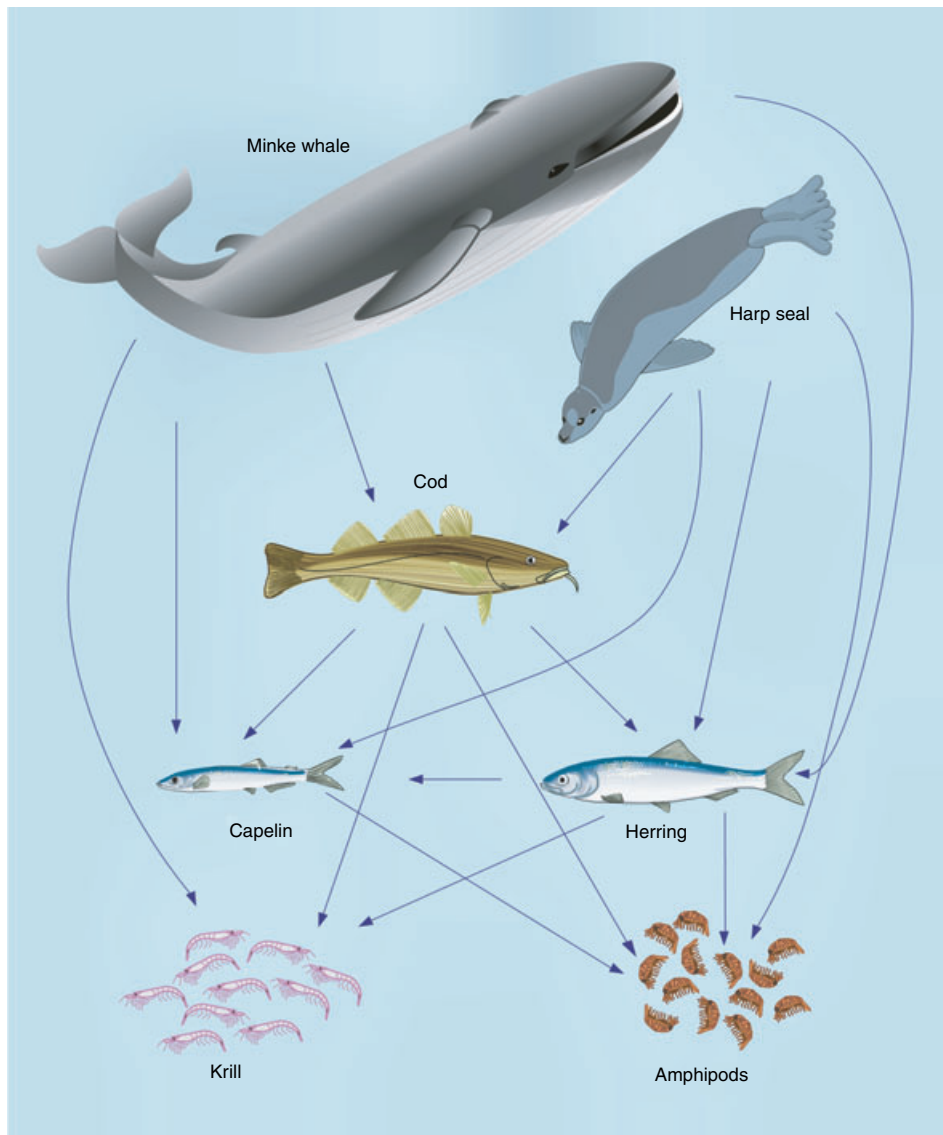


Figure 5 A simplified Barents Sea food web.

1970s (Ponomarenko *et al.* 1978; Yaragina *et al.* 2008), and the limited amount of Russian quantitative stomach content data for the 1950s (Bogstad *et al.* 1994) indicate that the level of cod cannibalism was much higher in the 1950s than in the 1980s. These differences in the importance of juvenile cod and herring as cod prey are partly due to different size composition in the cod stock (more larger, piscivorous cod in the 1950s and 1960s), but could also be due to changes in geographical distribution of either predator or prey.

Quantitative stomach content data have been collected by Norway and Russia since 1984, and a joint Norwegian–Russian stomach content database (Mehl and Yaragina 1992) has been established. The annual consumption of various prey species by cod was calculated based on diet composition, amount of food eaten and a model for stomach evacuation rate (Bogstad and Mehl 1997). An updated time series for the period 1984–2006 is

given in ICES (2007). Figs 6–8 show the variation in diet composition for cod aged 1–2, 3–6 and 7+ respectively. More details on the consumption by the various age groups are given below.

The diet of cod aged 1 and 2 is dominated by krill and amphipods (*Themisto* spp. Hyperiididae), northern shrimp (*Pandalus borealis* Pandalidae) and capelin. A more detailed study of the diet of cod aged 0–2 was carried out by Dalpadado and Bogstad (2004). They found that the 0- and 1-group cod feed mainly on crustaceans, with krill (Euphausiidae) and amphipods composing up to 70% of their diet. A shift in the diet from crustaceans to fish was observed from ages 1 to 2. The diet of a 2-year-old cod mainly comprised capelin and other fish, and to a lesser degree, krill and amphipods. **Shrimp was also an important prey in cod aged both 1 and 2.**

Cod aged 3–6 prey mainly on capelin, but in years of low capelin abundance, amphipods, krill, shrimp and fish species other than capelin [cod,

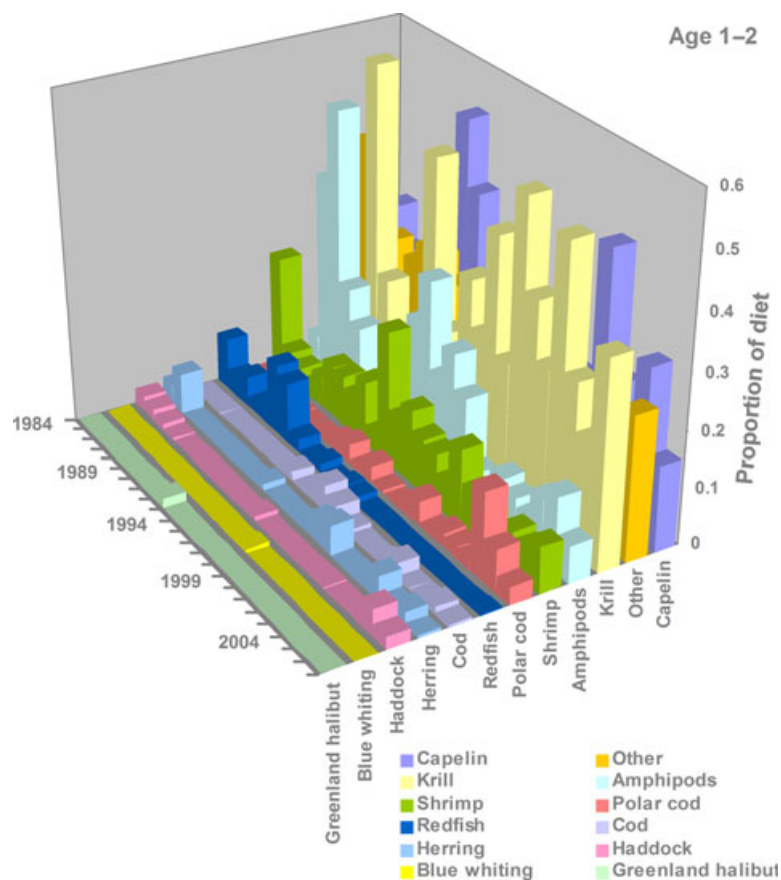


Figure 6 Diet composition (proportion, by weight) for cod aged 1–2 in the Barents Sea 1984–2006 (adapted from ICES 2007).

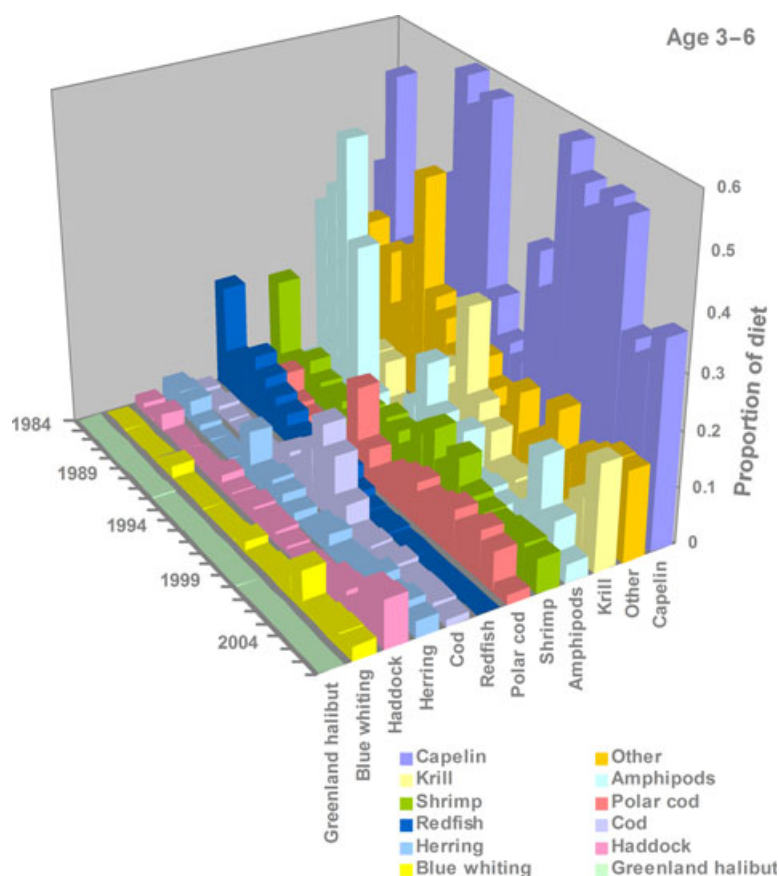


Figure 7 Diet composition (proportion, by weight) for cod aged 3–6 in the Barents Sea 1984–2006 (adapted from ICES 2007).

herring, Arctic or polar cod (*Boreogadus saida* Gadidae), haddock, redfish (*Sebastes* spp. Scorpaenidae) and in some years blue whiting (*Micromesistius poutassou* Gadidae)] are also important. Cod aged 7+ generally prey on a variety of fish species, with capelin as the main prey. The proportion of krill and amphipods in the diet of 7+ cod in years with low capelin abundance is much lower than in younger cod. The percentage of fish prey in the diet is generally proportional to the abundance of those fish in the sea. This clear ontogenetic shift towards piscivory is typical of cod (Pálsson 1994). During its spawning migration, mature Northeast Arctic cod mainly feeds on adult herring and on Norway pout (Michalsen *et al.* 2008).

Other abundant piscivorous fish species in the Barents Sea are haddock, deep-sea redfish (*Sebastes mentella* Scorpaenidae), Greenland halibut (*Reinhardtius hippoglossoides* Pleuronectidae), long rough dab (*Hippoglossoides platessoides* Pleuronectidae) and

thorny skate (*Raja radiata* Rajidae). Bogstad *et al.* (2000) found that while cod on average consumed 4.7 million tonnes of prey in the period 1990–1996, the five other species mentioned consumed about 2.0 million tonnes of prey, assuming the same consumption/biomass ratio for these species as for cod. Of these 2.0 million tonnes, less than half is fish prey. However, it should be kept in mind that the biomass of deep-sea redfish and Greenland halibut was much larger in the 1960–1970s than it is at present (ICES 2007).

Individual growth and size at the age of Northeast Arctic cod show strong variations (ICES 2007), and growth has been shown to be positively related to capelin abundance (Mehl and Sunnanå 1991). Variations in growth have a strong effect on fecundity and atresia; skipped spawning has even been observed in years with low condition factor (Marshall *et al.* 1998). Both growth in length and weight at length showed much less decline during

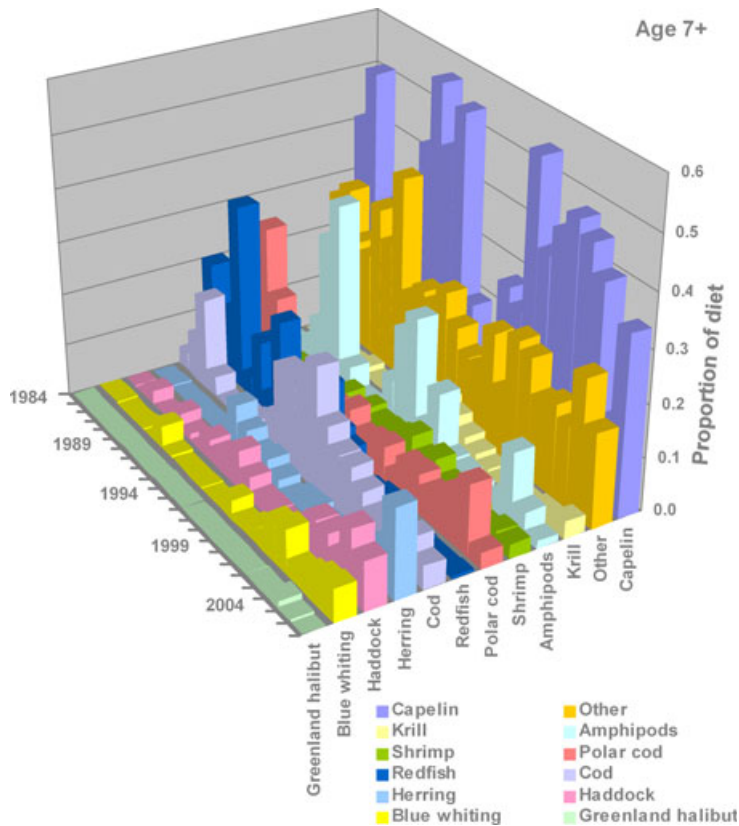


Figure 8 Diet composition (proportion, by weight) for cod age 7 and over in the Barents Sea 1984–2006 (adapted from ICES 2007).

the second and third capelin collapses (mid-1990s and early 2000s) than during the first collapse in the late 1980s (Gjosæter *et al.* 2008). The reason for this difference may be that more, other fish prey was available for cod in the mid-1990s, while in the 1980s, cod had to switch to less nutritious food such as krill and amphipods. A tentative conclusion is that cod may compensate for the absence of capelin by feeding on other fish species if this is possible.

Cod is also an important prey item for the two most abundant marine mammal stocks: minke whale (*Balaenoptera acutorostrata* Balaenopteridae) and harp seal (*Phoca groenlandica* Phocidae) (Fig. 9). Nilssen *et al.* (2000) calculated that harp seals in the Barents Sea eat approximately 100 000 tonnes of cod annually in years with high capelin abundance, and 300 000 tonnes annually in years with low capelin abundance. Folkow *et al.* (2000) found that minke whales eat about 250 000 tonnes annually. These calculations were based on abundance estimates, stomach content data from the first half of the 1990s and bioenergetics models. Except for cod cannibalism, these two marine mammal

stocks are the most important predators of cod aged 1+, and the estimates of consumption of cod by harp seal and minke whale are fairly close to the estimates of biomass removed by a natural mortality of 0.2 y^{-1} (Bogstad *et al.* 2000).

Predictions of interspecies interactions from the various multispecies models created for the Barents Sea ecosystem sometimes produce contradictory results. Schweder *et al.* (2000) found that capelin catches decreased with increasing whale abundance, while Bogstad *et al.* (1997) found that capelin catches increased with increasing minke whale abundance, due to strong indirect effects. Hamre (2003) argues that a large cod stock may reduce the average obtainable catch of all three fish stocks, including cod, significantly. The models by Bogstad *et al.* 1997 and Schweder *et al.* 2000 did not test different levels of fishing mortality for cod, but Hamre's results differ from those obtained using single species models for Northeast Arctic cod (e.g. Nakken *et al.* 1996). There should be enough contrast in the data to investigate to what extent prey switching actually occurs. This is a key factor in explaining differences of the modelled outcomes

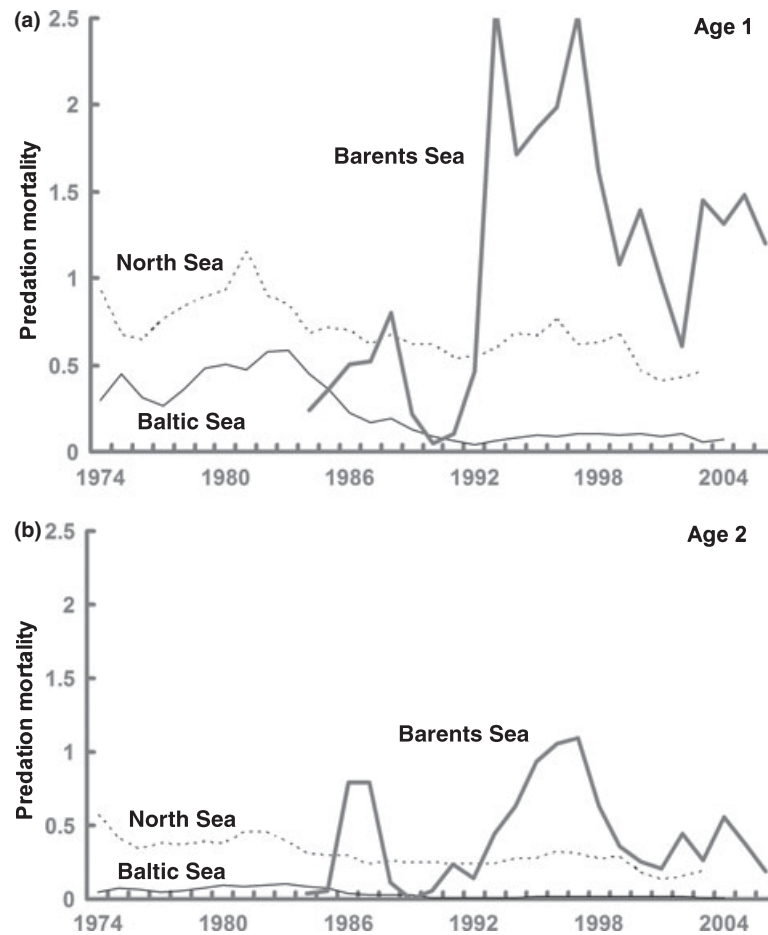


Figure 9 Predation mortality (M2) on (a) age 1 and (b) 2 cod in the North Sea, the Baltic Sea and the Barents Sea (adapted from ICES 2005b,c, 2007).

and how the ecosystem may respond as cod abundance changes.

Iceland

The fluctuations in stock size and catches of Icelandic cod are described elsewhere (Schopka 1994), with cod the most abundant piscivore in Icelandic waters. As with cod in many other areas, cod in Icelandic waters is currently close to historical low levels (Table 1, ICES 2006b).

The main prey species for Icelandic cod is capelin (Pálsson 1983, 1994; Magnússon and Pálsson 1989, 1991a), but shrimp is also an important prey for cod (Pálsson 1983, 1994; Magnússon and Pálsson 1989, 1991b). From the perspective of the prey, cod is the main fish predator on capelin (Pálsson 1997), and Stefánsson *et al.* (1998) found

a highly significant negative correlation ($P < 0.01$) between juvenile cod abundance and each of three different abundance indices for shrimp. This is quite likely due to predation mortality on shrimp by cod. Management of Icelandic cod and shrimp in a multispecies context has been addressed (Stefánsson *et al.* 1994; Danielsson *et al.* 1997).

Cod growth is dependent on capelin abundance in Icelandic waters (Steinarsson and Stefánsson 1996). The ICES North Western Working Group (NWWG) used capelin biomass and mean weight of the year class in the previous year to predict weight at age of cod during the period 1991–2003 (ICES 2004b). However, the relationship between capelin biomass and mean weight increase of cohorts seems to be much weaker in recent years, most likely due to changes in the spatial distribution of capelin or uncertainties in the estimation of capelin stock size.

Also, predictions of capelin biomass were not available to NWWG in 2004–2006. Thus, in recent years, NWWG set the weight at age in the predictions equal to the *status quo* (last year of observation; ICES 2006b). The share of capelin in the diet in recent years has been reduced as has total consumption and mean weight at age (H. Björnsson, MRI, Iceland, pers. comm.).

The approach used in 1991–2003 implies that the process relating capelin biomass to cod weight at age is more or less instantaneous. An alternative analysis using growth rates shows that growth is high during the years preceding the high capelin biomass. This suggests that the factors and processes causing high growth rates of cod and eventually high weight at age are also causing the biomass of capelin to increase. The two may thus be indirectly rather than causally linked. The variability in capelin stock size has been lower in Icelandic waters than in the Barents Sea (Gjosæter *et al.* 2002; Vilhjálmsón 2002). Cod is the main predator on capelin in Icelandic waters, followed by minke, humpback and fin whales (Vilhjálmsón 2002). The annual consumption of capelin by cod may amount to about 1.5 times the cod biomass.

Stomach content data for marine mammals in Icelandic waters are scarce. Out of 68 minke whale stomachs sampled, one was almost full of cod and another contained cod or cod-like species together with euphausiids (Sigurjónsson *et al.* 2000). Codfishes (Gadidae) were also an important prey item for harp seals in coastal areas off Northern Iceland in the period February to May (Hauksson and Bogason 1995). Thus, it is suspected that marine mammals may be important predators of cod in this ecosystem. Some multispecies models show that not only may cetaceans have a considerable impact on future yields from Icelandic cod (Stefánsson *et al.* 1997a), but seals may also have an even greater impact (Stefánsson *et al.* 1997b). The consensus is that marine mammals likely influence the cod stock, but to what degree remains to be validated.

Eastern Newfoundland–Labrador

The 'northern' cod stock off southern Labrador and eastern Newfoundland crashed during the late 1980s and early 1990s and since the mid-1990s has remained at about 2% of the level seen in the early 1960s (Lilly *et al.* 2005; Table 1). Other changes in the Newfoundland–Labrador ecosystem included concurrent declines in most other demersal

fish, including species that were not targeted by commercial fishing (Atkinson 1994; Gomes *et al.* 1995); a surge in snow crab (*Chionoecetes opilio* Oregoniidae) and especially in northern shrimp (Lilly *et al.* 2000); an increase in the abundance of harp seals from fewer than 2 million individuals in the early 1970s to more than 5 million in the late 1990s (Healey and Stenson 2000); and numerous changes in the biology of capelin, the dominant forage fish in the area (Carscadden *et al.* 2001). It has been asserted that the collapses of cod (Hutchings and Myers 1994; Myers *et al.* 1996) and other demersal fish (Haedrich and Fischer 1996) were due entirely to fishing, but there is also recognition that the cooler water temperatures of the last three decades of the 20th century, and especially of the early 1990s, may have contributed substantially to the various changes observed in cod (Parsons and Lear 2001; Drinkwater 2002) and other components of the ecosystem (Narayanan *et al.* 1995; Colbourne and Anderson 2003). It has been difficult to isolate and quantify the relative impacts of fishing, climate variability and species interactions.

The upper trophic levels of this Arcto-boreal ecosystem were historically dominated by three species (capelin, cod and harp seals) that were linked trophically (Lilly 1987; Hammill and Stenson 2000) and exploited commercially (Templeman 1966). The importance of capelin to cod was always evident from the vast shoals of cod that migrated into the traditional inshore fishing grounds in pursuit of capelin that had approached the coast to spawn (Akenhead *et al.* 1982). Food habits studies supported the role of capelin as a major prey, but also revealed a wide variety of additional prey that changed gradually as cod grew and also differed spatially, seasonally and annually (Lilly 1987, 1991). The major prey for small cod is crustaceans, notably hyperiid amphipods in the north and euphausiids on Grand Bank. For medium-sized cod (30–70 cm), the major prey are schooling planktivorous fish, the most important of which is capelin, but Arctic (polar) cod are eaten in the north, herring are consumed in inshore waters, and sand lance (*Ammodytes dubius* Ammodytidae) are important on Grand Bank. Larger cod tend to feed on medium-sized fish and crabs, especially toad crabs (*Hyas* spp. Oregoniidae) and small snow crabs. Other notable prey species, such as northern shrimp, bank clam (*Cyrtodaria siliqua* Hiatellidae) or short-finned squid (*Illex illecebrosus*

Ommastrephidae), are moderately important only in certain seasons or years depending upon their relative abundance.

As in the Barents Sea and Icelandic waters, capelin seems to be an important food item for cod. A compilation of diet data for a study of biomass flows (Bundy *et al.* 2000) concluded that capelin comprised about 60% of the diet of large (>35 cm) cod on an annual basis during the period 1985–1987. The importance of capelin was further emphasized by the observation that, over a series of years, the quantity of capelin in the stomachs of cod caught during the autumn off eastern Newfoundland increased with the abundance of capelin. Additionally, during years of low capelin abundance, the cod were not able to compensate fully by feeding more intensively on other prey (Lilly 1991).

Earlier management-driven hypotheses explored whether exploitation of capelin would result in a reduction in the growth rate of cod or a decline in the proportion of the cod migrating inshore (where they would be accessible to the traditional inshore fishery). The approach was not to construct exploratory, heuristic models but rather to conduct empirical analyses to reveal relationships that could then be built into predictive models (Shelton 1992). Despite the expectation that linkages among species would be strong in a system with few abundant members, it proved difficult to find evidence of such links. Only weak evidence could be found of a positive relationship between capelin biomass and success of the inshore cod fishery (Akenhead *et al.* 1982; Lear *et al.* 1986). Similarly, neither Akenhead *et al.* (1982) nor Millar *et al.* (1990) found a significant relationship between cod growth and capelin biomass. It was felt by several authors (Akenhead *et al.* 1982; Shelton *et al.* 1991) that measurement error may be high, given the complexities and limitations of quantifying fish abundances and vital rates, and that the potential for Type II error was high. Krohn *et al.* (1997) found, however, that with the inclusion of data from the early 1990s, capelin biomass explained some of the variability in cod growth and condition.

The role of capelin in the collapse of cod during the early 1990s remains unclear. Estimates of capelin biomass from offshore hydroacoustic surveys declined dramatically from 1991 onward, and the capelin changed their autumn distribution towards the southeast (Carscadden and Nakashima 1997). It has been suggested that these changes, together with changes in the timing of capelin

migrations, made the capelin less accessible to cod, thereby contributing to low condition and possibly an increase in the mortality of the cod (Atkinson and Bennett 1994; Lilly 2001). However, cod distribution also changed during the early 1990s, such that most of the cod remaining during the latter stages of the collapse seemed to have undiminished access to capelin, at least in the offshore during the autumn (Lilly 1994; Taggart *et al.* 1994; O'Driscoll *et al.* 2000). It has been hypothesized that the change in cod distribution came about from a southward redistribution of fish (Atkinson *et al.* 1997; Rose *et al.* 2000), not spatial differences in mortality (Hutchings 1996). Rose *et al.* (2000) further hypothesized that the redistribution of the cod was a response to the redistribution of capelin, and Atkinson *et al.* (1997) and Rose *et al.* (2000) hypothesized that the change in distribution of the cod resulted in the cod becoming more accessible to trawlers, thereby contributing to the cod collapse. However, dramatic changes in distribution of capelin and cod did not occur during a cold period in the mid-1980s (Lilly 1994; Atkinson *et al.* 1997). There remains uncertainty regarding the extent to which the low water temperatures and extensive ice cover of the early 1990s contributed to changes in the abundance and distribution of capelin, the distribution of cod, the feeding success of the cod, and the mortality of cod from natural causes and fishing (Lilly *et al.* 2005 and references therein).

The predators of cod tend to change as the cod grow (Lilly 1987; Pálsson 1994; Bundy *et al.* 2000). Very small cod are eaten by squid, various demersal fish (such as sculpins) and some seabirds. Larger juveniles have many predators: demersal fish, most notably larger conspecifics and Greenland halibut; harp seals and hooded seals (*Cystophora cristata* Phocidae); certain toothed whales, such as harbour porpoise and pilot whales (*Globicephala melaena* Delphinidae); and probably minke whales. Large cod seem to have few natural predators, but seals can prey upon them by belly-feeding, a mode of predation whereby the seal takes a bite from the cod's abdomen, consuming the liver and some of the other abdominal organs, but generally leaving the rest of the carcass and the head (Lilly *et al.* 1999).

The predator that has attracted most attention is the harp seal (Bundy *et al.* 2000; Hammill and Stenson 2000). There was speculation that seals contributed to the collapse of the cod stock (Atkinson and Bennett 1994), but it is generally thought that their contribution was small. However, the

total mortality of cod in the offshore has remained very high since the moratorium on directed fishing in 1992, and analyses of tagging data have revealed that adult cod in the inshore experienced high mortality in addition to that caused by the reopened fishery in 1998–2002 (Lilly *et al.* 2005). It is possible that the seals could be maintaining cod in a 'predator pit' (Shelton and Healey 1999). It has been concluded by some authors (DFO 2003; Rice *et al.* 2003), based on the large size of the harp seal population, the known predation by harp seals on cod and the paucity of information pointing to other factors, that predation by harp seals is a contributing factor to the high mortality of cod. It must be emphasized, however, that there is very little information on harp seal diet in the offshore, where most of the seal foraging is thought to occur. The little information available for hooded seals indicates that they too could be important predators on cod (McLaren *et al.* 2001).

The role of cod within an ecosystem may become more apparent when cod biomass declines, as happened off Labrador and eastern Newfoundland. The surge in snow crab and particularly northern shrimp is consistent with a release from predation pressure from cod (Lilly *et al.* 2000; Bundy 2001; Worm and Myers 2003) and other demersal fish, but it is difficult to separate the influence of predator release from the effects of environmental change. It has been postulated that the increase in both snow crab and northern shrimp was related to improved recruitment associated with the cold water during the 1980s and 1990s (Parsons and Colbourne 2000). It may also be noted that there is no evidence that capelin or any other finfish increased following the cod collapse.

The degree to which competition with other species has influenced the dynamics of cod is difficult to determine. It has been suggested (Anderson and Rose 2001) that Arctic cod might be a competitor of pelagic juvenile cod, and may have had a larger impact during the cold years of the early 1990s when Arctic cod expanded its distribution southward (Lilly *et al.* 1994). Most concerns regarding competition are focused on the harp seal, which is estimated to have consumed about 3 million tonnes of food per year in the northern cod stock area during the late 1990s (Hammill and Stenson 2000; Stenson and Perry 2001). Most of this food was pelagic planktivores, notably capelin, so the potential for competition with cod exists. However, cod and seals share

capelin and other planktivores (Arctic cod, sand lance, herring) with numerous additional predators, including other demersal fish, several species of baleen whales and birds (Bundy *et al.* 2000; Carscadden *et al.* 2001).

Gulf of Maine–Georges Bank

As at many other places around the globe, cod in the Gulf of Maine–Georges Bank ecosystem are no longer one of the biomass dominants of the fish community, only comprising around 5–10% of the total fish biomass in the ecosystem (Table 1; Serchuk *et al.* 1994). Despite this, the species remains a key component of regional fishery landings and is still an ecologically important organism. The history of the US northwest Atlantic cod fishery and subsequent changes in the fish community are well documented (Serchuk and Wigley 1992; Serchuk *et al.* 1994; Murawski *et al.* 1997; Fogarty and Murawski 1998), with cod currently around 25–30% of historical levels. Fish biomass is now dominated by elasmobranch and pelagic species in the ecosystem. Although there has been some sign of recovery in other groundfish stocks, cod stocks have remained at low levels.

The diet of cod has also been well documented for this part of the Atlantic, namely describing the generalist feeding nature of this species (Langton and Bowman 1980; Langton 1982; Bowman and Michaels 1984; Vinogradov 1984; Link and Almeida 2000; Link and Garrison 2002a). These studies have shown that cod typically eat the same main types of food across the Gulf of Maine and Georges Bank, despite local changes in habitat. Usually, the diet represents local, ambient benthos augmented by seasonal migrations of small pelagic forage fish (i.e. Atlantic herring, Atlantic mackerel). Link and Garrison (2002a) showed a notable change in the diet composition across the past three decades, principally reflecting changes in the relative abundance of the prey field (Fig. 10). As herring and mackerel declined in this ecosystem during the 1970s, sand lance (*Ammodytes* spp. *Ammodytidae*) replaced those small pelagics as the dominant component in the diet (Fogarty *et al.* 1991). As herring and mackerel began to recover in the late 1980s, those two species again comprised a significant portion of the diet. The ontogenetic shift in the diet observed in this ecosystem confirms the common change from benthivory to piscivory as cod grow (Link and Garrison 2002a).

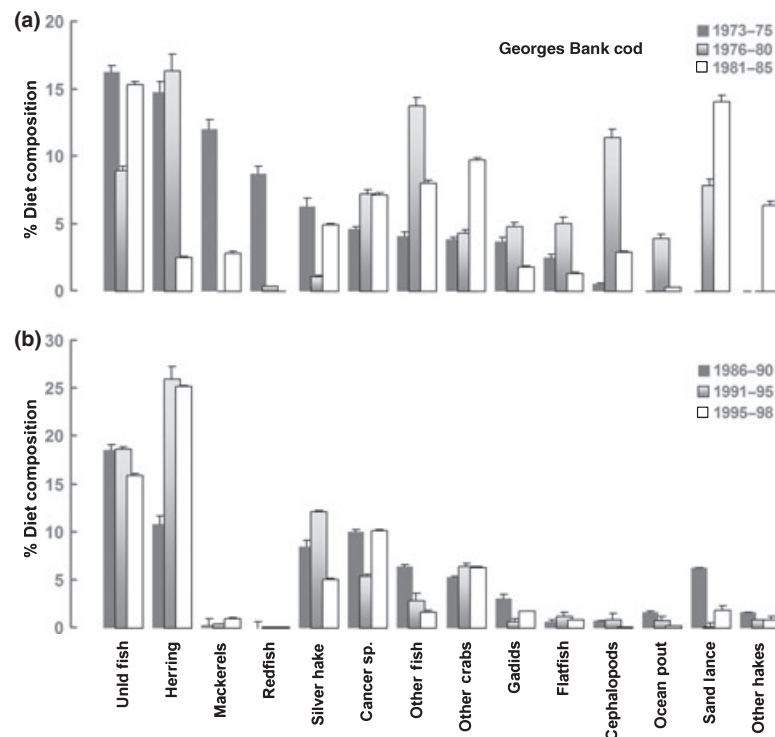


Figure 10 Percentage diet composition (by weight) of cod at Georges Bank, Gulf of Maine ecosystem, 1973–1998: (a) for 1973–1985 and (b) for 1986–1998 (adapted from Link and Garrison 2002a).

Several studies have examined the relationship among ~~cod consumption, diet and feeding to cod growth, recruitment and reproduction~~ (Mayo *et al.* 1998; O'Brien 1999; O'Brien and Munroe 2000; NEFSC (Northeast Fisheries Science Center), unpublished data). No detectable changes attributable to diet-related considerations have been observed in growth rates, density dependence or stock–recruitment relationships. Most of the effects on the cod stocks have been attributed to overfishing (Serchuk and Wigley 1992; Serchuk *et al.* 1994; Murawski *et al.* 1997).

The prominence of cod in this ecosystem has diminished. Link and Garrison (2002b) show that the amount of energy flowing through the cod population has declined notably, with cod consuming about one-third of what the population once did on Georges Bank (Fig. 11). Cod used to be the dominant piscivore in the ecosystem, but that is no longer true. Other gadoids (i.e. hakes) and a suite of elasmobranchs consume a much higher amount of fish than cod. Essentially, there are less cod and the cod that are present are smaller than historically speaking. The sum result of this stock (in abundance and size) is that cod eat less than before. However,

cod are still one of the top 10 fish predators in the ecosystem.

Some populations of cod predators have increased over the past four to six decades, whereas most have steadily declined. Species such as sharks, Atlantic halibut (*Hippoglossus hippoglossus* Pleuronectidae), large hakes and larger cod are much less abundant generally and in this ecosystem than they were 40+ years ago (NEFSC 1998). Whether the observed decline in cod stocks caused declines in the populations of cod predators is unknown, but not strongly suspected. Other cod predators, such as goosefish (*Lophius americanus* Lophiidae) or sea raven (*Hemitripterus americanus* Cottidae), have increased, but generally do not consume large amount of biomass and cod do not comprise a large portion of their diet. Conversely, whether the increases in some other cod predators have resulted in cod populations being stuck in a 'predator pit', ultimately hindering stock recovery, is unknown. There was some suspicion that highly abundant elasmobranchs such as spiny dogfish (*Squalus acanthias* Squalidae) or winter skate (*Raja ocellata* Rajidae) significantly prey upon cod, but this has been disproven (Tsou and Collie 2001a,b; Link *et al.* 2002). However, the role of small pelagic

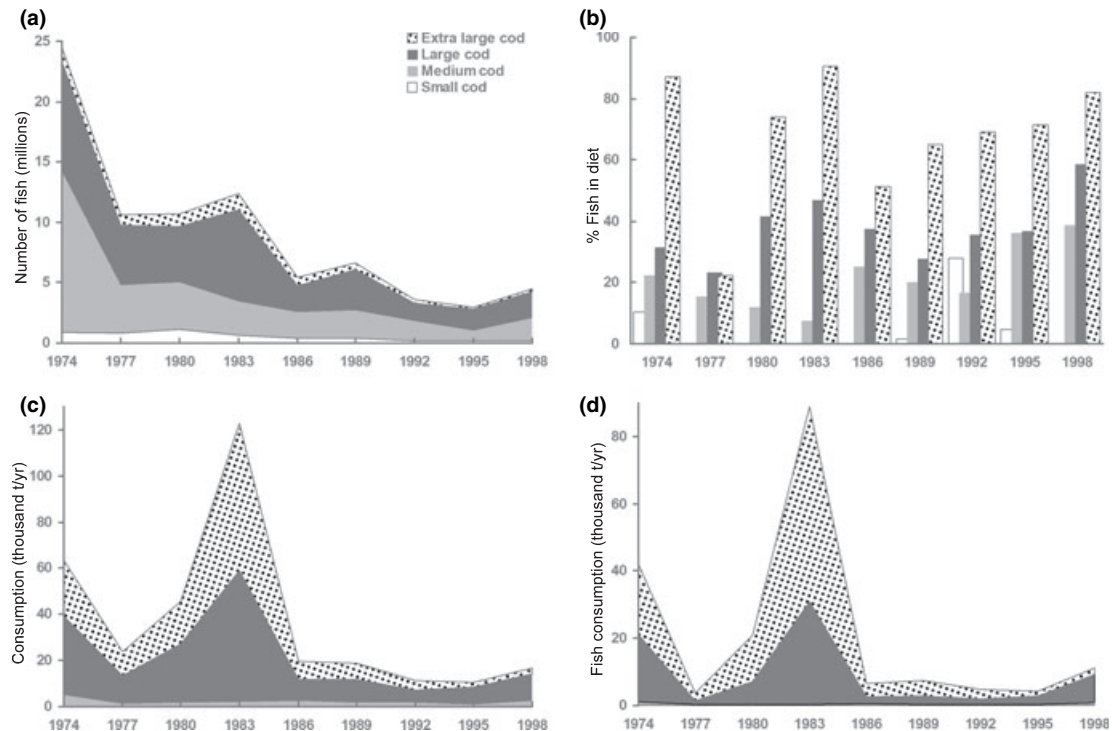


Figure 11 Cod abundance and diet at Georges Bank, Gulf of Maine ecosystem. (a) Minimum swept area abundance of different size classes of cod across the time series; (b) mean proportion of fish (% weight) in the diet of cod; (c) total amount of food consumed by cod and (d) total amount of fish consumed by cod (adapted from Link and Garrison 2002b).

fish feeding upon larval stage cod remains a key issue, with the magnitude of this process potentially significant but currently unresolved (Garrison *et al.* 2000, 2002).

Multispecies models (Tsou and Collie 2001a,b; Link and Garrison 2002b; Link 2003) suggest that, like elsewhere, the earliest life-history stages experience the most predation mortality. How predation mortality of these early life stages has impacted on cod recruitment is unclear, but is suspected to be secondary to recruitment overfishing. Link (1999, 2002) had shown how complex the food web of this ecosystem can be, and ultimately questioned how feasible it might be to predict specific effects of species interactions beyond a general, aggregate biomass level (Link 2003).

There is a suite of potential cod competitors (Garrison and Link 2000a,b; Link *et al.* 2002). However, competition is generally difficult to quantify in the field. There are four requirements that must be fulfilled to demonstrate competition: spatiotemporal overlap, similarity of resource utilization (i.e. diet), limiting resources and notable population impacts of the interaction. Given these

difficulties and assumptions for demonstrating competition, the first two items can be shown, but Georges Bank is a highly productive ecosystem (Cohen *et al.* 1982; Sissenwine *et al.* 1984), suggesting that resources may not be limiting. It is also unclear whether opposite directions of population trajectories among cod and potential competitors are causal or just inversely correlated in this system. Arguably, some of the bigger competitors of cod in this ecosystem are the fisheries for small pelagics, shrimp and decapods (Worm and Myers 2003). Yet, there is limited evidence that cod could not switch to alternate prey and are in fact resource limited. Thus although the concept merits further investigation, the evidence to date suggests that it is unlikely that competition is currently limiting cod stocks in this ecosystem.

Generalities, comparisons and synthesis

Basic cod feeding ecology

The cod ecosystem overviews above and various reviews of cod feeding habits (ICES 1992; Pálsson

1994; Methven 1999) reveal that cod have a broad diet consisting mainly of crustaceans and teleost fish. It has been demonstrated repeatedly that the diet of cod shifts ontogenetically. Small cod tend to feed on small crustaceans, such as mysids, euphausiids, amphipods and small shrimp. Medium-sized cod feed on larger crustaceans and small fish, especially planktivorous fish that are sometimes referred to as 'forage fish' (capelin, sand lance, herring, Arctic cod and other juvenile gadoids such as hakes). Large cod feed on crabs and medium-sized demersal and forage fish. Forage fish may be replaced or supplemented by squid or the juveniles of larger fish. Other taxa found in the diet include ctenophores, cnidarians, polychaetes, gastropods, bivalves and echinoderms, but these are seldom found in large quantities and perhaps, particularly in the case of ctenophores and brittle stars, indicate poor feeding conditions. Differences in biotic communities across ecosystems and the subgeographies within ecosystems, and across seasons within those ecosystems, alter the realized local prey field, but the general pattern described here is consistent for cod wherever cod feeding habits have been described.

The gradual change in diet with increasing predator size is considered to be a consequence of energetic advantage associated with the obtaining of large prey items, constrained by the cost of acquiring the prey and a morphological limitation on maximum prey size (Kerr 1971; Scharf *et al.* 2000). This increasing prey size involves not only a change in taxa but also an increase in individual size within a taxon (Pálsson 1983; Lilly 1984; Scharf *et al.* 2000). Despite this tendency for increasing prey size, even the largest cod eat a wide size range of prey, and never entirely stop eating large zooplankton, shrimp and benthic invertebrates. Indeed, individual large cod may be found with several thousands of euphausiids in their stomachs (Lilly 1987; Scharf *et al.* 2000).

Do differences in diet translate into broad impacts on cod populations? One area where diet quality can be critical is seen in the interaction between cod and forage fish. Forage fish are clearly very important to the northern stocks (c.f. Newfoundland, Barents Sea, Iceland examples). Climate effects on forage fish are suspected or known in these locales; e.g. concern about changed migration patterns for capelin north of Iceland and in the Barents Sea due to environmental variability (Gjøsæter 1998; Vilhjálmsson 2002). In the more southerly stocks, this may not be as strong a consideration, but is an

obvious climate-related change to the prey field that could have significant effects on cod populations.

Further evidence of diet impacts on cod populations is unclear. Some studies indicate that a more 'balanced' diet, specific diet components or simply a greater availability of food increase cod growth (Brown *et al.* 1989; Mehl and Sunnanå 1991; Jobling *et al.* 1994; Clark *et al.* 1995; Krohn *et al.* 1997; Lambert and Dutil 1997; Dutil and Lambert 2000; Rose and O'Driscoll 2002; Mello and Rose 2005). Other investigators indicate that spawning ceases or is curtailed if inadequate food is present (Kjesbu 1994; Burton *et al.* 1997; Lambert and Dutil 2000). Lambert and Dutil (1997) and Swain (1999) suggested that, combined with overfishing, changes in cod diet are responsible for declines in cod stocks and distribution shifts. However, the growth and mean size of cod in the Georges Bank–Gulf of Maine ecosystem have remained relatively constant across time despite large changes to the abundance of those stocks (Mayo *et al.* 1998; O'Brien 1999; O'Brien and Munroe 2000).

Conversely, many studies have related how much, but not what, cod eat relative to the reproductive state, recruitment and growth of cod. Yaragina and Marshall (2000) found the liver condition index of Northeast Arctic cod to be positively correlated with the frequency of occurrence of capelin in cod stomachs. The total lipid energy for mature females in the stock is proportional to the total egg production (Marshall *et al.* 1999). Link and Burnett (2001) show that the amount of food eaten by cod is related to the maturity state, with food consumption greater post-spawning to recover depleted energy reserves. Cod growth has been shown to be dependent on capelin abundance in both Icelandic waters (Steinarsson and Stefánsson 1996) and the Barents Sea (Mehl and Sunnanå 1991) and on the total amount of prey in the Baltic Sea (Gislason 1999). Additionally, basic bioenergetic considerations can affect cod growth, recruitment, reproductive success and physiology (Jobling *et al.* 1994; Krohn *et al.* 1997; Lambert and Dutil 1997, 2000; Brander 2000; Dutil and Lambert 2000; Dutil *et al.* 2003).

Cannibalism

Bogstad *et al.* (1994) compared cod cannibalism in the Barents Sea, Icelandic waters and the Newfoundland area. They found that the proportion of cod in cod diet increases with cod size. On average,

the proportion was <1% for cod <50 cm, and increased to 5–9% in cod >100 cm. The maximum prey size was about 50% of the predator length, and the range of prey size increased with predator size. For all these areas, cod stomachs have been sampled annually, and the year-to-year variability in the frequency of occurrence of cod in cod stomachs was found to be large. Uzars and Plikshs (2000) and Neuenfeldt and Köster (2000) found similar results for Baltic cod, but predation on cod aged 2 and older (>15 cm) seem to be less frequent than in the other areas.

For the North Sea and the Baltic, predation mortality (M2) has been calculated using MSVPA (ICES 2003a,d, 2005a–c). Estimates of cannibalism mortality are also provided for Northeast Arctic cod by the Arctic Fisheries Working Group (ICES 2007). Fig. 9 shows the predation mortality (M2) for cod aged 1 and 2 for these areas. The M2 values were highest for Northeast Arctic cod and lowest for Baltic cod. For the Barents Sea and the Baltic Sea, M2 is only due to cannibalism. For the North Sea, cannibalism accounts for 50–70% of the predation on cod aged 1 and about 90% of the predation on cod aged 2. Link and Garrison (2002a,b) noted that cannibalism is a less important factor currently than it may have been historically for Georges Bank, but with cod still comprising a small but notable 2–5% of the diet of cod. Similar values have been observed for other ecosystems (ICES 1992; Pálsson 1994; Methven 1999). It is likely that the convergence of spatiotemporal overlap among juveniles and adults, coupled with the extent of alternate prey, influence the degree of cannibalism by cod.

Cod prey and other fisheries

What are the impacts of cod feeding on the rest of the food web? To answer these questions, one must understand at a basal level the amount of food eaten by cod. By scaling individual consumption of cod to population levels, total removals of prey can be estimated (Sparre 1991; Sparholt 1994; Bogstad and Mehl 1997; Link and Garrison 2002b). Removals relative to prey population sizes can then provide an assessment of the mortality induced by cod. Thus, what are the implications of changing cod stock size for prey populations of cod? In some instances, cod appear to regulate prey populations. The more simple ecosystems (Iceland, Barents, Newfoundland–Labrador, Baltic) tend to have fewer species but stronger species interactions and, in

those cases, alterations to cod stocks are cascaded to their prey. This is seen as a prey population expands (if cod abundance declines) or declines (if cod abundance increases, but only to a point; e.g. Baltic sprat versus cod). Conversely, in some ecosystems this is not seen at all. Fewer instances in the more complex North Sea and Georges Bank–Gulf of Maine ecosystems show a change in cod prey populations related to a change in cod abundance (e.g. *Nephrops* in the North Sea).

Because of the broad and omnivorous nature of cod feeding, it is likely more feasible to list those benthivorous and piscivorous fish species or marine mammals from the same ecosystem that are not potential competitors of cod. Some researchers have shown that the dietary overlap (a unitless proportion ranging from 0 to 1) among cod and other species generally ranges from 0.2 to 0.7 for the entire fish community (Garrison and Link 2000a,b). Yet in most instances, competition is indeterminate and suspected to be a minor element affecting cod competitors and cod.

As the predatory role of cod changes in the ecosystem, there are major implications for fisheries management. For instance, the abundance and fisheries landings for some forage fish have had an inverse relationship to cod stocks (e.g. Baltic sprat). But arguably the major observation is that of the interaction between cod and major crustacean prey (Bogstad *et al.* 2000; Lilly *et al.* 2000; Bundy 2001; Worm and Myers 2003; Parsons 2005). Cod predation is a larger source of shrimp mortality than fishing in the Barents Sea and Icelandic waters (Magnússon and Pálsson 1991b; Bogstad *et al.* 2000). In the Newfoundland–Labrador area, where there was a collapse in cod and a surge in shrimp, cod took far more shrimp than the fishery during most of the 1980s, but by the late 1990s, the fishery for shrimp far exceeded removals by cod (Lilly *et al.* 2000). An inverse relationship between cod biomass and shrimp (particularly *Pandalidae*) abundance has been found (Stefánsson *et al.* 1998; Lilly *et al.* 2000; Worm and Myers 2003). The *Nephrops* fishery in the North Sea and the Irish Sea (Brander 1988; Brander and Bennett 1989) has also shown an inverse relationship to cod stock size. In many instances, the decline in cod has had a markedly positive impact on shrimp, crab and lobster fisheries. However, Hanson and Lanteigne (2000) indicate that cod was not an important source of natural mortality for American lobster, and there is similarly limited evidence in the Georges Bank–Gulf of

Maine ecosystem (Link and Garrison 2002a; Worm and Myers 2003).

It is highly conceivable that several fisheries could be competing with cod, particularly for small pelagic fishes and economically valuable invertebrates (Jakobsson and Stefánsson 1998), as in the case of the *Nephrops* fishery in the North Sea and the Irish Sea (Brander 1988; Brander and Bennett 1989). In the latter case, a mixed fishery model was used to estimate the joint yield for cod and *Nephrops*, and European Union fisheries management policy was altered to allow cod biomass to be reduced in order to benefit the *Nephrops* stock. In instances where the relationship is strongly suspected, a precautionary approach should be adopted to include this possibility.

Cultivator effects

A wide range of organisms preys on eggs and larvae of cod (Pálsson 1994). Here we focus on trophic loops, wherein cod prey on forage species but these forage species may, in turn, depress the recruitment of cod by preying on the cod's early life stages (eggs, larvae or early juveniles) or by competing with those early life stages for food. In the Baltic Sea, for example, herring and especially sprat prey on cod eggs (Köster and Möllmann 2000), and it is thought that the system alternates between two semi-stable states, one dominated by sprat and the other by cod (Köster *et al.* 2003). Similarly, there is evidence from the North Sea (Daan *et al.* 1994) and the southern Gulf of St Lawrence (Swain and Sinclair 2000) that recruitment of cod is more successful when the biomass of planktivorous pelagic fishes is low. The evidence is unknown or unclear for the other ecosystems we examined (Table 1).

The existence of such 'cultivation' effects (Walters and Kitchell 2001) is also less clear in the case of juveniles. The presence of trophic loops (Rice 1995), with cod preying on the adults or juveniles of another species and the larger individuals of that other species preying on juvenile cod, has often been reported. For example, cod off eastern Newfoundland and in the Gulf of St Lawrence prey on short-finned squid (Lilly and Osborne 1984), and squid feed on juvenile cod (Dawe *et al.* 1997). Cod prey on juvenile Greenland halibut (Lilly 1991) and Greenland halibut feed on juvenile cod (Bowering and Lilly 1992; Hovde *et al.* 2002). Despite the existence of such trophic loops, we are not aware of examples where a cod decline has been followed by an

increase in another piscivore, which has then depressed the recruitment of cod.

Cod and marine mammals

The abundance of fish that might prey on cod juveniles has declined throughout most of the north Atlantic during the past few decades (Pauly *et al.* 1998; Christensen *et al.* 2003). This does not necessarily mean that the whole predator field has declined. The populations of some marine mammals, such as Northwest Atlantic harp seals (Healey and Stenson 2000) and Scotian Shelf grey seals (Bowen *et al.* 2003), have increased dramatically during recent decades as they have rebounded under less-intensive harvesting or culling. These and other mammals, such as minke whales, have not been adversely affected by the declines in cod populations, because cod is generally a small portion of their diet and they are sustained by other prey, most notably forage fish (Folkow *et al.* 2000; Hammill and Stenson 2000; Nilssen *et al.* 2000).

The mortality rate of juvenile cod in some of these areas is very high (Fu *et al.* 2001; Lilly *et al.* 2005). Depensation in the form of a 'predator pit' is possible (Shelton and Healey 1999), but seal diet data are generally insufficient to address the question adequately. Cod is, however, a more important prey for Barents Sea minke whales than for other marine mammal stocks (Folkow *et al.* 2000), although it seems to be less preferred as a prey species than herring and capelin (Haug *et al.* 1996; Skaug *et al.* 1997). Mammal predation on cod is also suspected to be high in Icelandic waters and other parts of the Barents Sea. However, this appears to be less of a factor in the other ecosystems we examined (Table 1). Nevertheless, there is evidence from various sources that the natural mortality of adult cod is unusually high in the northern Gulf of St Lawrence (Benoît and Chouinard 2004), the southern Gulf of St Lawrence (Chouinard *et al.* 2003), the eastern Scotian shelf (Fu *et al.* 2001) and inshore waters of eastern Newfoundland (Lilly *et al.* 2005). It has been concluded by some (Rice *et al.* 2003) that predation by seals has contributed to the high cod mortality and to the lack of recovery in these cod stocks.

When a cod stock is healthy, predation by marine mammals is but one of many sources of mortality to which the stock has become adapted. However, when a cod stock has been depleted by fishing, perhaps exacerbated by adverse environmental

conditions as hypothesized off eastern Canada (Dutil and Lambert 2000; Drinkwater 2002), rejuvenated populations of marine mammals have the potential to impede attempts to promote cod recovery. Such circumstances have led to calls for the deliberate reduction of mammal numbers. This inevitably raises questions about the ability of science to provide reliable information regarding the efficacy of such reductions (Yodzis 2001), the ability of humans to steer ecosystems into specific configurations, and the legal and ethical implications of attempting to do so (Molenaar 2002, 2003). Clearly this is an area that merits continued attention.

Most predators of cod do not exhibit a large dependence upon cod as prey. Rarely does the frequency of occurrence and per cent diet composition exceed 10–15% for cod as prey. Yet there are some exceptions. Scaling the amount of cod removed by predators demonstrates that, in some ecosystems, predation on cod can be a significant source of mortality, whereas in other locales, it is minor relative to other influences on cod stocks. Again, in simpler ecosystems with stronger species interactions, the potential for there to be significant 'predator pits' is likely higher than in more complex, more diffuse species interacting ecosystems.

Climate change

As noted above, the abundance of cod and its prey and predators have been affected not only by fisheries but by environmental variation. Of great interest is the potential impact of the global atmospheric warming that is currently occurring and is projected to continue (IPCC 2001, 2007). In the area of the North Atlantic, the intensity of warming is projected to vary geographically, with the greatest warming in the Arctic and Subarctic and possibly little or no warming in certain areas, such as the Labrador Sea.

Predictions regarding the extent to which this atmospheric warming will affect cod and interacting species require a downscaling from Global Circulation Models to regional physical oceanography, a process that is not yet well advanced for many areas where cod is found (Vilhjálmsen *et al.* 2005). Nevertheless, Drinkwater (2005) predicted future changes in the abundance and distribution of various cod stocks by coupling projections of temperature increase in shelf waters occupied by those stocks (IPCC 2001, 2007) with observed responses of cod to past temperature variability. He found that

cod will likely spread northwards along the coasts of Greenland and Labrador and occupy larger areas of the Barents Sea, whereas stocks in the southern range will decline (southern North Sea and Georges Bank) or even disappear (Celtic and Irish Seas). As noted by Vilhjálmsen *et al.* (2005), such predictions must be tempered by knowledge that the abundances of some cod stocks and the species with which they interact are now so altered from historic levels that cod populations may not respond to climate variability as they did in the past. Additional uncertainty arises from fisheries-induced evolutionary changes in life-history traits (Jørgensen *et al.* 2007), which might alter the manner in which species respond to environmental change.

The role of cod in the ecosystems of the future will depend not only on the abundance and distribution of cod, but also on the abundance and distribution of their prey and predators. It is possible that some ecosystems will migrate northward but remain similar to their present state. However, it is more likely that the various species within each ecosystem will respond differently to climate change (Rose 2005). Thus, predicting the role of cod under scenarios of climate change requires that one should consider the impact of climate change on abundance and distribution of each of the major interacting species and the extent of overlaps among them. We discuss just a few examples to illustrate the types of changes that investigators might be obliged to consider.

If climate change favours some prey species over others, then the prey field available to cod may become less favourable for cod condition. For example, in the East Newfoundland–Labrador area, the decline in capelin and the rise in northern shrimp may have been related, at least in part, to climate variability during the early 1990s. This change in prey availability has been hypothesized to have caused a reduction in cod condition, which, in turn, has contributed to the observed increase in the mortality of the cod (Rose and O'Driscoll 2002).

The impact of cod as a predator may change as a consequence of climate change. If cod becomes prominent in northern areas in which it is currently absent or in low abundance, then the potential prey species that are currently there may experience increased mortality. If an increase in temperature promotes population growth in those cold-water cod stocks that are now at low abundance, such as those on the Eastern Scotian Shelf and off Eastern Newfoundland–Labrador and West Greenland, then

those species that are thought to have increased as a result of predator release, such as sand lance on the Eastern Scotian Shelf and northern shrimp off Eastern Newfoundland–Labrador, might experience a decline. Conversely, if warming promotes a decline in cod stocks towards the southern end of the present cod distribution, then some prey stocks in those areas might increase. However, the relative importance of cod in the southern areas is already less than in the northern areas.

The consequences to cod as a prey taxa may also change as climate change affects the abundance and distribution of its predators. Of particular interest is the impact that reductions in sea ice might have on populations of seals that pup on ice (e.g. harp and hooded seals, and grey seals in some areas). Reductions in the extent or duration of sea ice might cause declines in seal populations, which, in turn, might promote increases in cod populations, particularly those highly depressed cod stocks that some hypothesize may be held in a predator pit by marine mammals and other predators.

Summary

The dominant factor in the dynamics of most cod stocks, at least during the most recent two to three decades, has been fishing (Table 2; Lilly *et al.* 2008). One way to compare the relative importance of several extrinsic factors on population dynamics is to investigate how much of the variation of a given population abundance or biomass can be explained by each of the factors. The results in Table 2, based on analyses of data from the Baltic, North and Barents Seas, show that the main impact on both

Table 2 Ratio of spawning stock biomass and growth and recruitment variance explained by the extrinsic factors: fishing, predation and climate.

Population	Factor	SSB	Recruitment
North Sea cod	Fishing	(-) 0.52	(-) 0.26
	Predation	(-) 0.12	(-) 0.16
	Climate		(-) 0.18
Baltic Sea cod	Fishing	(-) 0.21	(-) 0.43
Barents Sea cod	Fishing	(-) 0.25	(-) 0.33
	Predation	0	0
	Climate		(+) 0.18

(-) means a negative effect of the factor on the population and (+) means a positive effect. Adapted from ICES (2003c). SSB, spawning stock biomass.

SSB and recruitment was from fishing (ICES 2003c). Fishing accounted for 21–52% of the variance (ICES 2003c). For the period included within the study, climate and predation accounted for a smaller part of the variation. Several studies have shown that most cod stocks have a history of overfishing and are currently depressed or in the recovery stage (Schopka 1994; Fogarty and Murawski 1998; O'Brien and Munroe 2000; Hylan 2002; ICES 2003c; Lilly *et al.* 2008). This means that the abundance of cod is generally lower now and will likely continue to be for the near future. With excess fishing, the average size of cod will continue to be small. Additionally, as abundance is generally low, the distribution and range of these stocks are reduced. Thus, due to the direct effects of fishing on cod, it appears that the ecological role of cod is diminished relative to historical roles in many cod ecosystems. What remains unclear is how additional climate variability will alter cod stocks, and thus the role of cod in the ecosystem.

Additionally, cod recruitment by temperature for a set of cod stocks (Fig. 12) shows that, below 1 °C and above 10 °C, recruitment is very low and dome-shaped in between. The implication is that as the climate changes, particularly if global warming occurs as predicted (Turrell *et al.* 2003; Drinkwater 2005; IPCC 2007), then recruitment for cod is likely to diminish for stocks living at the upper temperature range and may increase for the stocks living at

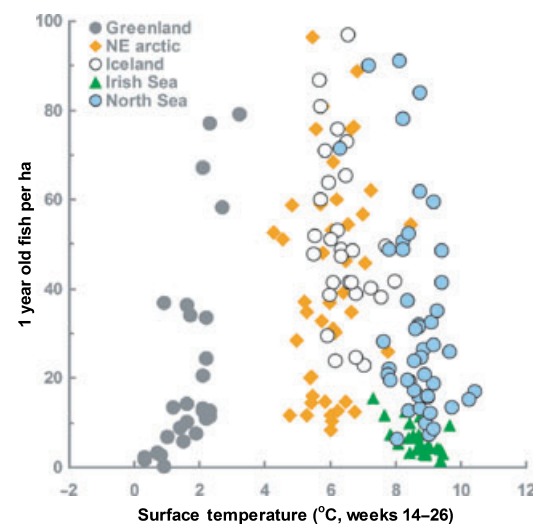


Figure 12 The relationship between recruitment and surface water temperature for different cod stocks (adapted from Brander (2000)).

the lower temperature range. Additionally, if the North Atlantic continues to warm, the range of cod will likely move northward, making cod a rarer organism in those ecosystems where it is already at the southern extreme of its range. Thus, it appears that the ecological role of cod will likely change in ecosystems in the southern and northern ranges of the present cod distribution due to climate changes.

Clearly, the magnitude or effects of the ecological role played by cod in these ecosystems is tightly coupled to their abundance. It is probable that based on densities alone, the declined cod stocks in all of these ecosystems have a much smaller role than they did in historical times. Conversely, any recoveries of cod imply an increased role of cod in an ecosystem. Beyond that, the specific impacts of any changes due to climate variability might remain difficult to predict.

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