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Forage fish, their fisheries, and their predators: who drives whom?

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The North Sea has a diverse forage fish assemblage, including herring, targeted for human consumption; sandeel, sprat, and Norway pout, exploited by industrial fisheries; and some sardine and anchovy, supporting small-scale fisheries. All show large abundance fluctuations, impacting on fisheries and predators. We review field, laboratory, and modelling studies to investigate the drivers of this complex system of forage fish. Climate clearly influences forage fish productivity; however, any single-species considerations of the influence of climate might fail if strong interactions between forage fish exist, as in the North Sea. Sandeel appears to be the most important prey forage fish. Seabirds are most dependent on forage fish, due to specialized diet and distributional constraints (breeding colonies). Other than fisheries, key predators of forage fish are a few piscivorous fish species including saithe, whiting, mackerel, and horse-mackerel, exploited in turn by fisheries; seabirds and seals have a more modest impact. Size-based foodweb modelling suggests that reducing fishing mortality may not necessarily lead to larger stocks of piscivorous fish, especially if their early life stages compete with forage fish for zooplankton resources. In complex systems, changes in the impact of fisheries on forage fish may have potentially complex (and perhaps unanticipated) consequences on other commercially and/or ecologically important species.

Keywords: climatic drivers, fishing impacts, forage fish, intraguild interactions, pelagic fish, predator–prey interactions.

Introduction

Forage fish are planktivorous pelagic species that often form the major avenue for transforming zooplankton production into food available to higher trophic levels (Cury *et al.*, 2000; Alder *et al.*, 2008; Bakun *et al.*, 2010). They are typically obligate schoolers and respond strongly to climatic changes (Corten, 1999; Tourre *et al.*, 2007; Rijnsdorp *et al.*, 2010). As they all feed mainly on zooplankton, forage fish may compete with each other for food leading to potentially complex interactions. Apparent mutualism may also arise where forage fish share common predators, and predators are likely to compete for forage fish leading to possible effects of one predator on other predators. Humans are often among the most important "predators" of forage fish and forage fish catches for fishmeal, fishoil, and human consumption across the world make up 30% of all landed capture fisheries (Tacon and Metian, 2009). This paper uses examples from the North Sea to examine the interrelationships between different forage fish species and their environment, predators, and fisheries. This is of interest because many studies to date have focused on simpler systems dominated by one or two forage fish species, but the North Sea offers a wider portfolio of interacting species whose productivity oscillates in response to both the environment and each others' dynamics.

Here, we highlight six species in the North Sea's forage fish portfolio. One of these (herring *Clupea harengus*) supports an important targeted fishery for human consumption; three (sandeel *Ammodytes marinus*, sprat *Sprattus sprattus*, and Norway pout *Trisopterus esmarkii*) that support a substantial industrial fishery for fishmeal and fishoil; and two (European sardine *Sardina pilchardus* and European anchovy *Engraulis encrasicolus*) that exist at low abundance and have only been recently exploited (Dickey-Collas *et al.*, 2010; Engelhard *et al.*, 2011). All the six forage fish are planktivorous, feeding mostly on zooplankton and ichthyoplankton (including fish eggs and larvae), and to some extent on phytoplankton. They are fairly short-lived, mostly maturing at ages of 1 or 2 years (less often 3 years) and with a longevity of ∼3–5 years (Boulcott *et al.*, 2007; Petitgas, 2010); within the North Sea, herring are the longest living (up to 20 years), maturing after 2 or 3 winters (Petitgas, 2010). Sprat, sandeel, and anchovy are spring or summer spawning, with Norway pout, sandeel, and herring spawning in autumn and winter (Daan *et al.*, 1990; Lambert *et al.*, 2009; Petitgas, 2010; Rijnsdorp *et al.*, 2010). Sprat, sardine, Norway pout, and anchovy all spawn pelagic eggs, whereas the eggs of herring and sandeel are demersal (Russell, 1976; Sparholt *et al.*, 2002).

The North Sea has displayed rapid rates of warming over the last half century and the temperature has increased >1°C over the past 100 years (Belkin, 2009). The period since the late 1980s has been associated with a sustained positive phase of the North Atlantic Oscillation index (Beaugrand, 2004) which is associated with a warmer winter climate, stronger winds, and more oceanic inflows from the North Atlantic into the North Sea, both resulting in warmer sea temperature, especially in winter (Pingree, 2005). These changing climatic conditions were associated with a strong increase in annual primary production at the end of the 1980s in the southern North Sea (Reid *et al.*, 1998; Beaugrand and Reid, 2003; McQuatters-Gollop *et al.*, 2007) and a change in phytoplankton species composition (Edwards *et al.*, 2001, 2006a; Leterme *et al.*, 2005). Furthermore, the dominant members of the zooplankton community have shifted from copepod species with cold-temperate water affinities before the late 1980s to warm-temperate species (Beaugrand, 2004). The decrease in the cold-water calanoid copepod *Calanus finmarchicus* in the North Sea has led to a 70% decrease of total zooplankton biomass between the 1960s and the post-1990s (Edwards *et al.*, 2006b). The number and the abundance of warm-temperate zooplankton species have increased (e.g. Johns *et al.*, 2005) along with meroplankton (Kirby *et al.*, 2007). Hence, it is likely that there have been substantial changes in forage fish productivity as a result of changes in prey composition and availability.

There is often a perceived conflict between the demands of the ecosystem for prey fish and fisheries exploiting those forage fish populations. Various studies in the North Sea suggest that, with the reduction in fishing pressure in recent years, populations of pelagic fish are now regulated through bottom-up mechanisms (Kenny *et al.*, 2009; Fauchald *et al.*, 2011). In contrast, Mackinson *et al.* (2009) reported that populations of both pelagics and demersals are still forced primarily by fisheries. The total abundance of pelagic or planktivorous fish has increased since 1990 and there have been suggestions of a shift from a demersal- to a pelagic-dominated fish community (Heath, 2005; Engelhard *et al.*, 2011). There has been little consideration of how other top predators (such as seabirds and marine mammals) impact forage fish populations in the North Sea system.

This paper synthesizes our current understanding of the factors driving the dynamics of forage fish populations in the North Sea. It describes (i) climatic and environmental drivers, (ii) interactions between different forage fish, (iii) predator–prey interactions, and (iv) the dynamics of the fisheries. It also briefly considers the role of forage fish on ecosystem stability and energy flow. This synthesis attempts to answer the question: "when many forage fish species are present, who drives whom?" in the North Sea and, by doing so, provides information for the development of management objectives of North Sea forage fisheries (Dickey-Collas *et al.*, 2013).

Climatic and environmental drivers

Forage fish populations typically respond strongly to climate-driven changes in marine systems, owing to the short lifespans and rapid reproductive turnover of these species, and strong coupling to phytoplankton and zooplankton production. Previous studies have detected global synchrony in the low frequency (20–30 years) cycles in commercially important small pelagic species of anchovy and sardine within upwelling and oceanic systems (Lluch-Belda *et al.*, 1993; Schwartzlose *et al.*, 1999; Tourre *et al.*, 2007). Similarly, it has been suggested that cycles in the strength of North Sea herring recruitment co-vary with the Atlantic Multidecadal Oscillation (Gröger *et al.*, 2010) and that recruitment variations in Norwegian spring-spawning herring are related to the temperature fluctuations of Atlantic water masses flowing into the Barents Sea (Toresen and Østvedt, 2000). There may be some degree of recruitment synchrony in North Sea forage fish, as suggested by synchronous serial poor recruitments in the early 2000s in herring, sandeel, and Norway pout; however, the evidence is based on a short time-series only and is not fully conclusive (ICES, 2007).

Of the North Sea forage fish, herring has been most extensively studied with respect to drivers of productivity, which seems to be linked to temperature (Corten, 1999; Gröger *et al.*, 2010). Time-series analyses have suggested that herring year-class strength is determined by differences in mortality rates occurring between the early to late larval stages (Nash and Dickey-Collas, 2005; Payne *et al.*, 2009). During the critical, early larval phase, colder temperatures have been linked to increased productivity (Fässler *et al.*, 2011). Physiological modelling also indicated that climate-driven changes in bottom-up factors will affect the survival and growth of herring larvae, by delaying the timing of autumn spawning resulting in less favourable conditions for larval growth and survival during the following months (Hufnagl and Peck, 2011). In juveniles, warmer temperatures promote faster growth rates up to ∼15–16°C in the laboratory (Bernreuther *et al.*, 2012) and likewise are correlated with faster growth and higher weight-at-age in the field (Brunel and Dickey-Collas, 2010). In adults, the growth rate and the asymptotic weight are both reduced at warmer temperatures (Brunel and Dickey-Collas, 2010), patterns that evidently reflect both direct (physiological) and indirect (trophodynamic) climatic impacts. Thus, the environmental needs change with the age of the fish and can even be contradictory, with the eggs and larvae needing rather cold and productive waters, juvenile growth rate benefiting from warmer temperatures, and adults requiring given conditions to trigger spawning, which can be delayed by climatic change and result in larvae living in unfavourable conditions. The temperature of the North Sea in the last 3 years has reduced to the average of the late 20th century.

In sprat, likewise, environmental requirements change between consecutive life stages (Peck *et al.*, 2012). Coupled biophysical modelling of the early life stages highlighted that the first feeding success of larvae is influenced by the interrelationships between temperature, prey biomass, and turbulence (Daewel *et al.*, 2008). Still, model-based estimates of larval survival in relatively warm and cold years were similar (Daewel *et al.*, 2011). This finding agrees with a previous field investigation where no relationships were found between sprat larval growth rate and either food availability or oceanographic conditions (Valenzuela and Vargas, 2002), but not with earlier fieldwork where larval growth was positively correlated with primary production (chlorophyll content) and vicinity to a tidal front (Munk, 1993). Combined field and laboratory data on sprat ecophysiology suggest that optimal thermal windows for growth and survival are wider for eggs (5–17°C) than for young early-feeding larvae (5–12°C); later on as larvae become able to capture larger prey, thermal windows expand again to include warmer temperatures, and early juveniles display highest rates of feeding and growth at 18–22°C (Peck *et al.*, 2012). With a warming temperature regime, sprat are therefore expected (at least towards the north of the species' range) to accelerate growth rates but also to show a more density-dependent regulation of recruitment (through top-down control of zooplankton resources) acting during the late-larval and juvenile stages, particularly when sprat stocks are at high levels (Peck *et al.*, 2012).

In sandeels, recruitment strength has been positively correlated with the abundance of adult *C. finmarchicus* (Arnott and Ruxton, 2002; van Deurs *et al.*, 2009); the mechanism suggested to explain this covariance is through the importance of copepod eggs as food for larval sandeels, and a reduction in *C. finmarchicus* that may have resulted from climate-driven warming. In contrast to sandeels, evidence from biophysical modelling, genetics, and time-series analyses suggested that warming has increased the productivity of relict populations of North Sea anchovy (Petitgas *et al.*, 2012). Little is known about the recruitment processes in Norway pout and sardine, although warming temperatures appear to be associated with an increased abundance of sardine, which has southern biogeographical affinity, and a decrease in the northerly species, Norway pout (Engelhard *et al.*, 2011).

In summary, climate variability and changes in physical (bottom-up) forcing are demonstrated drivers of the dynamics of forage fish in the North Sea. This is to be expected as other examples from around the world confirm the strong coupling between forage fish populations and the spatial and temporal dynamics of phyto- and zooplankton production, and confirm the direct effect of temperature on rates of growth, reproduction, and survival.

Interactions between forage fish

Different forage fish species or specific life stages can strongly influence each other through trophic interactions. These include (i) density-dependent competition for the same food resources, both between and within species; (ii) cannibalism; and (iii) intraguild predation (IGP), defined as a species not only competing for food but also preying upon another species. For IGP, growth and survival chances of the predatory forage fish species may either be positively or negatively correlated with the abundance of the prey species, because both must share the same food resources but one may benefit from the other by preying upon it (Polis and Holt, 1992). Apart from trophic interactions, forage fish may also influence each other through (iv) parasitism or disease, in specific cases where parasites or pathogens are shared between species; and through (v) behavioural interactions, not discussed here owing to a paucity of information. Various factors influence the strength of trophic interactions between forage fish: degree of habitat overlap in space and time, degree of diet overlap, intensity of IGP, and population density.

Within temperate systems such as the North Sea, strong seasonality in phyto- and zooplankton production often limits the growth season of forage fish to short time windows during a year (Sydeman and Bograd, 2009; Varpe and Fiksen, 2010). Thus, to understand the degree of food competition among forage fish, it is critical to examine the degree of spatial overlap in feeding areas during the growth season. However, caution is necessary when interpreting a lack of spatial overlap as a lack of interaction, as spatial displacement may be a result of intraguild interactions, if the degree of competition and levels of IGP are severe enough.

The degree of spatio-temporal and diet overlap can be different depending on the life stages (Figure 1). As adults, North Sea herring show little spatial overlap with sprat: during spring and summer, herring are concentrated in the northern North Sea and in autumn they occur on spawning grounds in the west (Figure 1a), whereas North Sea sprat are concentrated in the south and southeast (Figure 1b), with occasional increases in nearshore waters off Scotland. Sprat do, however, show significant spatial overlap with juvenile herring, which have nursery areas mainly in the southeastern North Sea, Skagerrak, and adjacent estuaries; often they even form mixed schools with juvenile herring (e.g. Maes and Ollevier, 2002). Sprat show also more diet overlap with juvenile than adult herring: whereas the latter feed on euphausiids and *C. finmarchicus* in summer (Last, 1989), herring juveniles feed less on *C. finmarchicus* but predominantly on smaller copepods (*C. helgolandicus* and *Temora longicornis*), hyperiids, crustacean larvae, and post-larvae of sprat (Last, 1987, 1989); small copepods (especially *T. longicornis*) also predominate the diet of sprat (Last, 1987; De Silva, 1973). The distribution of adult herring does overlap significantly with Norway pout (Figure 1c) and the herring spawning grounds partly coincide with areas of high sandeel abundance (Figure 1d).

There is a reasonable body of published evidence for inter- and intraspecific trophic interactions among North Sea forage fish; Table 1 gives an overview for herring, sprat, sandeel, and anchovy (evidence seems limited for Norway pout and sardine). Studies quantifying dietary overlap (lightest-grey shading in Table 1) are relatively few. A comparison between herring, sprat, and anchovy revealed that dietary overlap was highest between anchovy and herring compared with the species pairs anchovy–sprat and sprat–herring (Raab *et al.*, 2012). Hence, food competition, where it occurs, is likely more intense between anchovy and herring than in the other species pairs, although anchovy is considered more generalist (Raab *et al.*, 2012). Although anchovies are still at comparatively low abundance in the North Sea, their abundance has markedly increased since the mid-1990s (Petitgas *et al.*, 2012).

IGP plays an important role in forage fish dynamics (Irigoien and de Roos, 2011), as forage fish are known to feed extensively on fish larvae and fish eggs, in the North Sea (Hardy, 1924; Daan *et al.*, 1985) and elsewhere (Ellis and Nash, 1997; Plounevez and Champalbert, 2000; Plirú *et al.*, 2012). Fish eggs can be especially important as food source in late winter/early spring when few alternative food sources may be available (Segers *et al.*, 2007; Plirú *et al.*, 2012). In

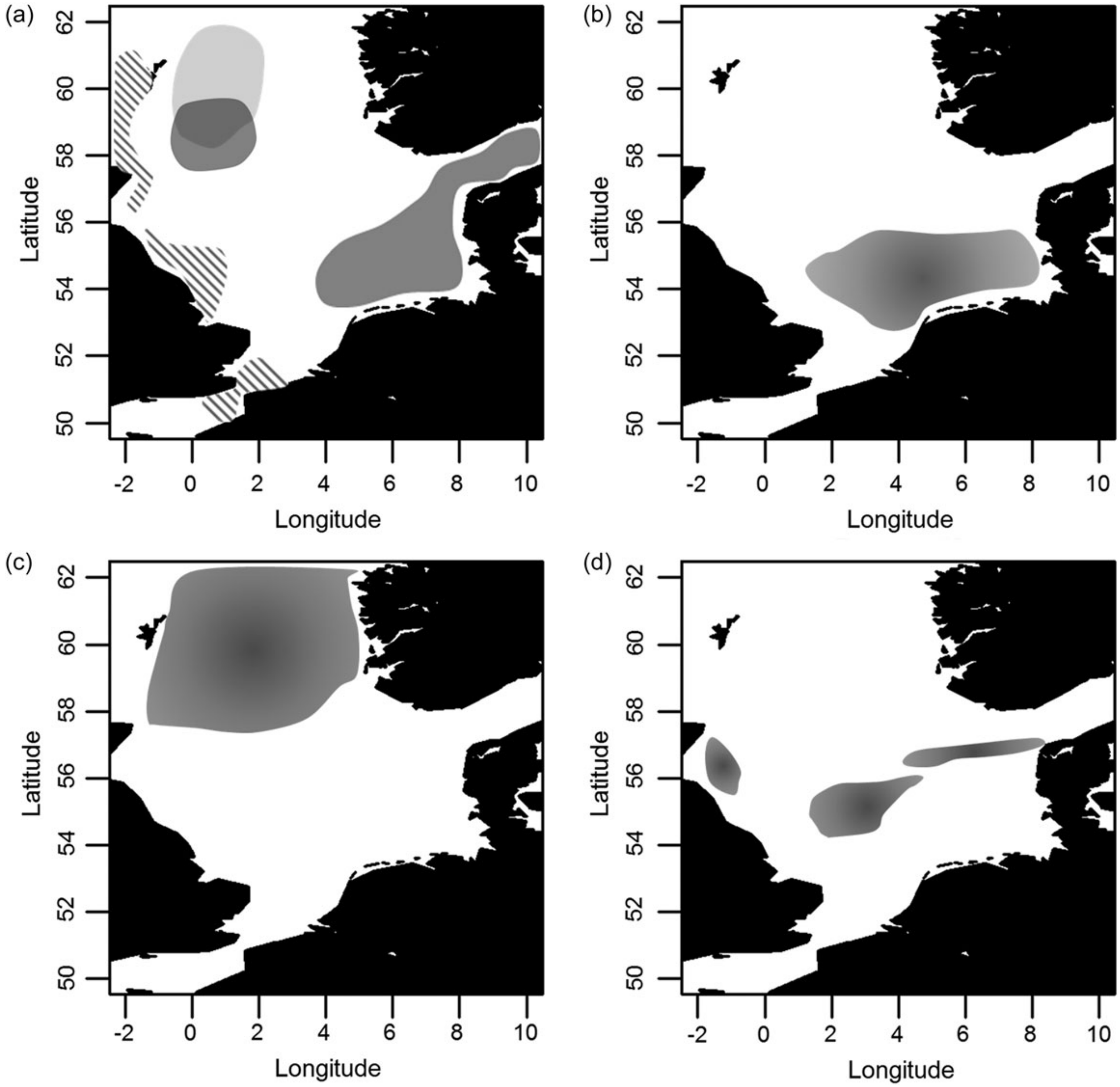

Figure 1. Schematic distribution maps showing the areas of highest concentrations within the North Sea for four forage fish species. (a) Herring, distinguishing between juveniles (dark grey), adult herring during summer (light grey), and autumn spawning areas (hatched). (b) Sprat. (c) Norway pout. (d) Sandeel. The sketches are based on a combination of data from the International Bottom Trawl Surveys (IBTS), acoustics, and commercial catches.

the North Sea, herring and anchovy feed on eggs and larvae of other forage fish species (see darkest-shaded cells in Table 1). In some years, herring prey extensively on sandeel larvae and post-larvae during spring (Hardy, 1924; Pommeranz, 1981; Hopkins, 1989), when sandeel larvae may form the second-most important food item to herring in the southern North Sea (Savage, 1937), but in other years, sandeel forms a small proportion of the diet. Several authors have speculated that intraguild interactions between herring, gadoids, and possibly sandeels might explain the beginning and the end of the gadoid outburst in the North Sea, because the very high recruitment levels of gadoids in the late 1960s–1970s partly coincided with the depletion and collapse of North Sea herring; similarly, sandeels increased when herring collapsed (Cushing, 1980; Hislop, 1996). Other studies suggest links between population dynamics of fish in the North Sea, but often using a correlative approach and their findings should be interpreted with care (Walters and Collie, 1988; Myers, 1998).

Cannibalism occurs in the herring- and anchovy-like fish (families Clupeidae and Engraulididae; Smith and Reay, 1991) but has mainly been described for other regions than the North Sea, e.g. anchovies *Engraulis* spp. off South Africa, California, and Japan (Hunter and Kimbrell, 1980; Valdes *et al.*, 1987; Takasuka *et al.*, 2004). The evidence is limited for North Sea forage fish, although 2- and 3-year-old herring consumed eggs and occasionally larvae

Table 1. Overview of studies on intra- and interspecific trophic interactions between North Sea forage fish.

Predator: **Prey:**	**Herring**	**Sprat**	**Sandeel**	**Anchovy**
Herring	Density-dependence (Heath *et al.*, 1997; Nash *et al.*, 2009); absence of density-dependence (Brunel and Dickey-Collas, 2010)	Similar diets of crustaceans and copepods (De Silva, 1973); however, herring may be more specialised on copepods (Raab *et al.*, 2012)	–	IGP by anchovy on herring eggs and larvae (North Sea: Raab *et al.*, 2012; Mediterranean Sea: Plounevez and Champalbert, 2000)
Sprat	IGP by herring on sprat (Savage, 1937; Pommeranz, 1981; Hopkins, 1989; Last, 1989)	Density-dependence (Maes *et al.*, 2005)	–	IGP by anchovy on sprat eggs and larvae (North Sea: Raab *et al.*, 2012; Mediterranean Sea: Plounevez and Champalbert, 2000)
Sandeel	Herring can prey extensively on sandeel (Hardy, 1924; Savage, 1937; Pommeranz, 1981; Hopkins, 1989; Last, 1989)	–	Density-dependence (Arnott and Ruxton, 2002)	IGP by anchovy on sandeel eggs and larvae (North Sea: Raab *et al.*, 2012; Mediterranean Sea: Plounevez and Champalbert, 2000)
Anchovy	Similar diets of copepods and crustacans, but anchovy are more generalist than herring (Raab *et al.*, 2012)	Similar diets of copepods and crustacans, but anchovy are more generalist than sprat (Raab *et al.*, 2012)	–	Cannibalism (observed in congener *Engraulis japonicus* off Japan: Takasuka *et al.*, 2004)

Lightest shading, interspecific trophic competition or diet overlap; *mid-grey shading*, intraspecific density-dependence or cannibalism; *darkest shading*, IGP. Note that white cells reveal absence of evidence, not evidence of absence.

of herring, but much more substantially those of plaice *Pleuronectes platessa* (Daan *et al.*, 1985). North Sea clupeids, in general, commonly consume fish eggs and larvae (see above section on IGP) so unless they discriminate between their own species' and other species' larvae, cannibalism is likely to occur frequently.

Intraspecific density-dependence is known for various North Sea forage fish stocks (mid-grey shaded cells in Table 1). Density-dependent growth has been suggested for North Sea herring (Heath *et al.*, 1997; Nash *et al.*, 2009; but see Brunel and Dickey-Collas, 2010) and has been attributed to both habitat and food limitation. Sprat and herring in the central Baltic Sea appear to be subject to both intra- and interspecific density-dependence: body condition of these two species was strongly influenced by density of sprat, and to a lesser extent, to density of herring, apart from abiotic factors such as salinity (Casini *et al.*, 2011).

A further mechanism linking the dynamics of different forage fish species is through the transfer of shared parasites and disease. The protist *Ichthyophonus hoferi* is an important internal parasite in herring but is also prevalent in sprat; an epizootic from 1991–1993 contributed to a drop in herring biomass in the 1990s (Mellergaard and Spanggaard, 1997) and may have also affected sprat (Rahimian, 1998). A flatworm, *Pseudanthocotyloides heterocotyle*, likewise occurs internally in herring and sprat and possibly in anchovy (Rahimian *et al.*, 1999). Ectoparasites often have several host species (e.g. the sea louse *Caligus elongatus*) but pelagic fish tend to have fewer ectoparasites than benthic fish, possibly limiting their impact on forage fish (Rohde *et al.*, 1995). Fish mortalities caused directly by parasites are seldom observed, probably because a heavy parasite load leads to starvation or disorientation before the fish dies from the parasite itself (Möller, 1987). The importance of parasitism and pathogens in forage fish dynamics is probably highly underestimated; marine viruses, in particular, are ubiquitous in the marine environment and are currently considered to form a major source of mortality in populations of marine organisms (review, Suttle, 2007).

Dependencies of predators on forage fish

Top predators consuming forage fish in the North Sea include piscivorous fish, seabirds, and marine mammals and a range of studies have shown that forage fish can exert bottom-up control on top predators (e.g. Cury *et al.*, 2011; Smith *et al.*, 2011). These bottom-up effects can be expected to be strongest in cases where a predator is a specialist relying to a great extent on the availability of the particular forage fish. Specialization in some cases only applies to part of the predator's life history or to certain times of the year, e.g. for kittiwakes *Rissa tridactyla* where a shortage of appropriately sized prey during the breeding season may result in breeding failures due to high chick mortality (Wanless *et al.*, 1998; Frederiksen *et al.*, 2004). Even where predators appear to be generalists because their diet contains a variety of prey species, their condition can be strongly influenced by one prey type if this is of high calorific value (Wanless *et al.*, 2005). For example, the availability of sandeels (a high energy prey; Hislop *et al.*, 1991) appears to be linked to better body condition of fish predators (whiting *Merlangius merlangus*, grey gurnard *Eutrigla gurnardus*, and weever *Echiichthys vipera*) and also grey seals *Halichoerus grypus* (Engelhard *et al.*, 2013a, b). In some cases, the predator requires a "balanced diet" that includes several different prey types (Onthank and Cowles, 2011).

Some predators have a restricted spatial distribution for all or part of their life history. This may be due to the limited availability of suitable habitat, and restrictions may operate differently according to age, size, or season (Martin *et al.*, 2010). Restricted spatial usage is especially the case for those marine mammals and seabirds that are central-place foragers and must return to land to rest or provision their offspring, such as grey seals and harbour seals

Table 2. Documented evidence on dependencies of North Sea top predators on forage fish.

		Proportion of forage fish in diet					
Predator name	**Mobility**	**Herring**	**Sprat**	**Sandeel**	**Norway pout**	**Forage fish total**	**Reported effects of low forage fish abundance**
Marine mammals							
Minke whale *Balaeonoptera acutorostrata*	M	6%	0%	56%	0%	62% [1]	No evidence reported for the North Sea
Harbour seal *Phoca vitulina*	IB	6%	0%	37%	6%	49% [2,3]	Later pupping dates [4], which in turn are associated with higher likelihood of breeding failure and lower pup weights [20]
Grey seal *Halichoerus grypus*	IB	0%	0%	41%	1%	42% [5]	Condition of breeding females linked to sandeel abundance [6]
Striped dolphin *Stenella coeruleoalba*	M	0%	0%	3%	13%	16% [7]	No evidence reported
Harbour porpoise *Phocoena phocoena*	M	3%	0%	2%	1%	6% [5]	Poor nutritional status of stranded animals [8].
Seabirds							
Sandwich tern *Sterna sandvicensis*	I	High	High	High	Low	99% [9,10]	Highly vulnerable to changes in local food supply (especially clupeids): reproductive performance, breeding numbers and breeding distribution [12]
Shag *Phalacrocorax aristotelis*	I	Low	Low	High	Low	98% [9,10,11]	Reproductive output probably limited by local sandeel availability at Isle of May [13]
Great skua *Catharacta skua*	IB	Low	Low	10–95%	Low	10–95% [9,10]	Reproductive success influenced by local sandeel availability [14]
Puffin *Fratercula arctica*	IB	8%	8%	55%	0%	71% [5]	No evidence reported for the North Sea
Guillemot *Uria aalge*	IB	14%	15%	42%	0%	70% [5]	Provisioning of chicks influenced by local abundance and quality of sandeel and sprat [15]
Razorbill *Alca torda*	IB	9%	22%	37%	1%	68% [5]	Reproductive output probably limited by local sandeel availability at Isle of May [16]
Kittiwake *Rissa tridactyla*	IB	2%	6%	28%	0%	36% [5]	Reproductive performance strongly dependent on local sandeel availability [17]
Gannet *Morus bassanus*	IB	11%	4%	18%	0%	34% [5]	No evidence reported
Lesser black-backed gull *Larus fuscus*	M	High	Low	Low	Low	7–25% [9,10]	No evidence reported
Northern fulmar *Fulmarus glacialis*	M	0%	2%	11%	2%	15% [5]	No evidence reported
Predatory fish							
Saithe *Pollachius virens*	M	17%	0%	5%	19%	41% [5]	No evidence reported
Horse-mackerel *Trachurus trachurus*	M	3%	13%	17%	0%	34% [5]	No evidence reported
Whiting *Merlangius merlangus*	M	6%	6%	7%	10%	30% [5]	Positive correlations between local sandeel abundance and condition [18]
Starry ray *Amblyraja radiata*	M	0%	0%	18%	5%	24% [5]	No evidence reported
Grey gurnard *Eutrigla gurnardus*	M	0%	2%	12%	9%	23% [5]	Positive correlations between local sandeel abundance and condition [18]
Cod *Gadus morhua*	M	8%	2%	4%	7%	21% [5]	Positive correlation between overlap with sandeel and growth in the North Sea [19]
Haddock *Melanogrammus aeglefinus*	M	0%	0%	15%	5%	20% [5]	No evidence reported
Mackerel *Scomber scombrus*	M	2%	3%	10%	3%	18% [5]	No evidence reported

Table shows, for each predator species, the levels of mobility; proportion of diet made up by each of four forage fish species, and all species combined; and documented cases of effects of low forage fish abundance on top predators. Mobility describes the potential of the predator to relocate to different feeding areas in response to localized prey shortages: I, immobile year-round; IB, immobile during the breeding season only; M, mobile year-round. Diet proportions refer to the percentage composition by mass of a particular prey type, averaged over 1 year and over the North Sea: note that local and seasonal percentages can be substantially higher or lower. Shading of species cells indicates high likelihood of effects of low forage fish availability, resulting from both a low potential to relocate and a high (>20%) proportion of forage fish in the diet. Shading of diet indicates >20% (light grey) or >50% (dark grey), and shading of reported effects indicates those on condition or growth (light grey) and on reproductive success (dark grey). Literature sources: [1] Windsland *et al.* (2007); [2] Sharples *et al.* (2009); [3] Cunningham *et al.* (2004); [4] Reijnders *et al.* (2010); [5] ICES (2011); [6] Engelhard *et al.* (2013b); [7] Santos *et al.* (2008); [8] MacLeod *et al.* (2007); [9] BWPi (2004); [10] Mendel *et al.* (2008); [11] Harris and Wanless (1991); [12] Stienen (2006); [13] Rindorf *et al.* (2000); [14] Furness (2007); [15] Wanless *et al.* (2005); [16] Mitchell *et al.* (2004); [17] Frederiksen *et al.* (2004); [18] Engelhard *et al.* (2013a); [19] Rindorf *et al.* (2008); [20] Pomeroy *et al.* (1999).

Phoca vitulina and all seabird species during the breeding season (e.g. Wanless *et al.*, 1988; Matthiopoulos *et al.*, 2004). Such restrictions may limit the size of predator populations through intraspecific competition for space and local resources (Matthiopoulos *et al.*, 2008). The accessibility of prey that is far from the forager's base of operations may also be very much reduced, because the predators may be unable to adaptively move to areas where prey is more plentiful or extend their foraging range to increase their harvest when the overall density of prey is low (Daunt *et al.*, 2002). Therefore, spatially restricted foragers are particularly sensitive to fluctuations in the local food supply on which they rely, which might arise from global changes in the stock or from the activities of a local fishery (Furness, 2002; Wanless *et al.*, 2005; Matthiopoulos *et al.*, 2008).

In Table 2, we summarize information about predatory species in the North Sea, identifying those that are potentially most sensitive to variations in the availability of forage fish, as species where (i) the range of the predator is spatially restricted and (ii) forage fish form more than 20% of predator diet. Further, the table highlights cases where effects on growth, condition, or reproductive success have been documented. Typically, documented effects apply to species also found to be most sensitive based on the above criteria (Table 2), indicating that the sensitivity rating here reflects the actual sensitivity of the species and can be used to predict where effects are likely though relationships have not yet been documented. In general, seabirds tend to show the greatest sensitivity, with large proportions of forage fish in the diet and restricted foraging ranges during breeding when birds are often highly concentrated (see also Furness, 2002, 2007; Frederiksen *et al.*, 2004; Wanless *et al.*, 2005; Cury *et al.*, 2011). They are followed by the two seal species, while predatory fish and cetaceans are probably less sensitive to local forage fish abundance. Unfortunately, sufficient information on diet is lacking for a long list of species, and hence their sensitivity cannot be evaluated.

Of the forage fish species examined here, sandeel is clearly the most important to seabirds, of which only a single species, lesser black-backed gull *Larus fuscus*, does not have sandeel as most important forage fish species in the diet (Harris and Wanless, 1991; BWPi, 2004; Mendel *et al.*, 2008; ICES, 2011). The same is true for both seal species (Cunningham *et al.*, 2004; Sharples *et al.*, 2009), whereas the importance of sandeel to cetaceans varies (MacLeod *et al.*, 2007; Windsland *et al.*, 2007; Santos *et al.*, 2008). The importance of forage fish to predatory fish is more variable, with sandeel being the most important forage fish in the diet of five predatory fish species; herring and Norway pout of about equal importance to cod and saithe; and herring, sprat, sandeel, and Norway pout all about equally important to whiting (Engelhard *et al.*, 2008; ICES, 2011). However, the diet of the predatory fish species generally does not contain more than 20% of any "single" forage fish species, and hence their sensitivity is substantially lower than in the case of seabirds (Table 2).

Impacts of predators on forage fish

Forage fish are heavily impacted by predation, often by multiple predator species. Their natural mortality is substantially higher than the value of 0.2 often assumed in fish stock assessments (Table 3). Hence, though some of the species are also subject to substantial fishing mortality, the ratio of fishing mortality F to natural mortality M, often used as an indication of overexploitation when values exceed 1, has been in the range of 0.46–0.77 in the past decade, except Norway pout which has been extremely lightly exploited in recent years.

Table 3. Contrasting fishing and natural mortality in North Sea forage fish during the last decade: removals by fishing as % of total removals (natural and fishing combined); natural mortality (M); fishing mortality (F); and ratio of F/M (index of exploitation level, with values >1 considered to signify overexploitation)

	Removals by fishing as % of total	M	F	F/M
Herring	16%	0.41	0.19	0.46
Norway pout	4.5%	1.70	0.14	0.08
Sandeel	19%	0.89	0.49	0.56
Sprat	19%	1.23	0.95	0.77

The figures shown are averages over a ten-year period (2001–2010) of annually estimated values (source: ICES, 2011). Removals in % include fish of all ages; M, F, and F/M are averaged for 1-year olds and older to avoid the effect of extremely high 0-group mortality in all species.

For predators to exert top-down control over their prey, they must be responsible for a large part of the variation in prey mortality. This is likely to occur only in the most predominant predator species (in terms of biomass) and only if their predation impact is substantial. Defining potential top-down controllers as any predators (including humans) that on average are responsible for at least 20% of the removals of a prey species, only three predators remain: saithe predating herring and Norway pout, and horse mackerel and mackerel both predating sprat (Figure 2, based on ICES, 2011). Whiting and saithe approach 20% of predation mortality on Norway pout. Though several predators predate heavily on sandeel, none of them is singly responsible for at least 20% of the biomass removals, and hence any change in predation mortality from one source is likely to be dampened by variation in that induced by other sources. The fishery is currently, based on the above definition, not listed as likely to induce a strong top-down control on the four forage fish species; in the recent past, however, removals by the fishery have exceeded 20% for long periods, in particular for herring (Figure 2) where F has also historically exceeded M by more than 100% (Dickey-Collas *et al.*, 2010).

Although at the larger North Sea-wide scale, no single predator species appears to exert significant top-down control over forage fish, evidence suggests that at localized scales, predators can have substantial impact. This is especially likely when predators exhibit so-called "aggregative responses" (Temming *et al.*, 2007), defined as many individuals aggregating at sites where prey is locally more concentrated. On the Dogger Bank, three predators (whiting, lesser weever, grey gurnard) showed aggregative responses to patches of high sandeel density, where they were responsible for over 80% of observed sandeel predation events (Engelhard *et al.*, 2008); likewise, aggregative responses by whiting and haddock to sandeel concentrations, and significant predation, were observed off the Scottish coast (Temming *et al.*, 2004).

Commercial importance of forage fish

For over five centuries, forage fish have been a key element in the commercial fisheries of the North Sea. During the previous six decades, the total forage fish landings (consisting almost entirely of only four species) have almost consistently been higher than those for all demersal fish combined (representing well over 30 species; Figure 3). Herring has played an especially important role in the economic and political development of Northern Europe, with countries going to war over access to the fishery; it is said that Amsterdam was "built on herring bones" (Poulsen, 2006).

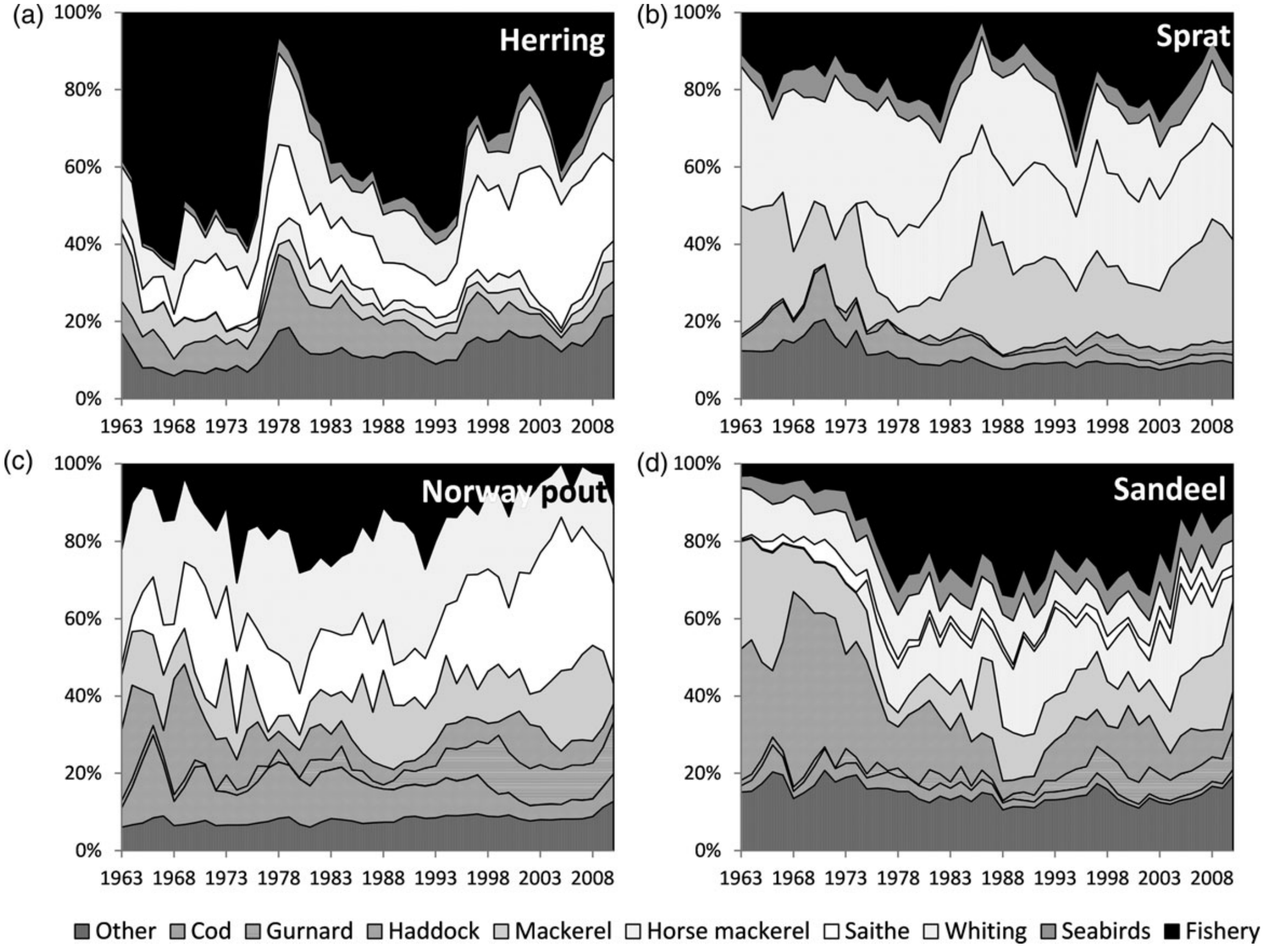

Figure 2. North Sea forage fish: biomass removals by different sources of predation, including the dominant predatory fish, seabirds, and the fishery (data from ICES, 2011). Only predators accounting for more than 5% of the total removals in at least 1 year are included.

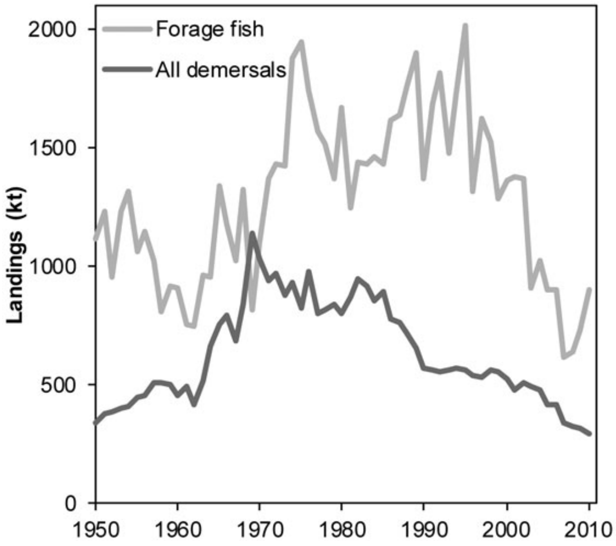

Figure 3. Total international landings of forage fish taken from the North Sea, compared with those for all demersal fish species combined. Forage fish include herring, sprat, sardine, anchovy, sandeel, and Norway pout; demersal fish include human consumption species only. Source: ICES catch statistics (ICES, 2011; Lassen *et al.*, 2012) extracted using FishStat Plus software (FAO, 2012).

Four forage fish species have been considered economically important, and the landings of each of these have fluctuated over the past 60 years (Figure 4).

Herring was the most important forage fish fishery before the 1970s, when the population collapsed due to unsustainable fishing during a time of reduced productivity (Figure 4a). As previously mentioned, it is the only forage fish that is predominantly taken for the human consumption market; this was also the case historically but not during the 1950s–1960s when adults were fished for human consumption and juveniles for reduction to fishmeal and fishoil. In this period, the majority of all industrial landings from the North Sea was comprised by herring (Madsen, 1978), and the biomass removals of herring by the fisheries well exceeded those by other mortality sources (Figure 2a). The stock has recovered since the 1980s as a result of a fisheries closure followed by close monitoring and enforcement of management advice and is currently considered to be sustainably fished, now supporting a fishery carried out mainly by Norway, Denmark, the Netherlands, and Scotland (Dickey-Collas *et al.*, 2010, 2013).

In the 1960s and 1970s when herring declined, industrial fisheries for other forage fish species increased. There was rapid growth in the industrial fishery for sprat, although the high landings statistics for the 1970s and the 1980s (Figure 4a) should be taken *cum grano salis*,

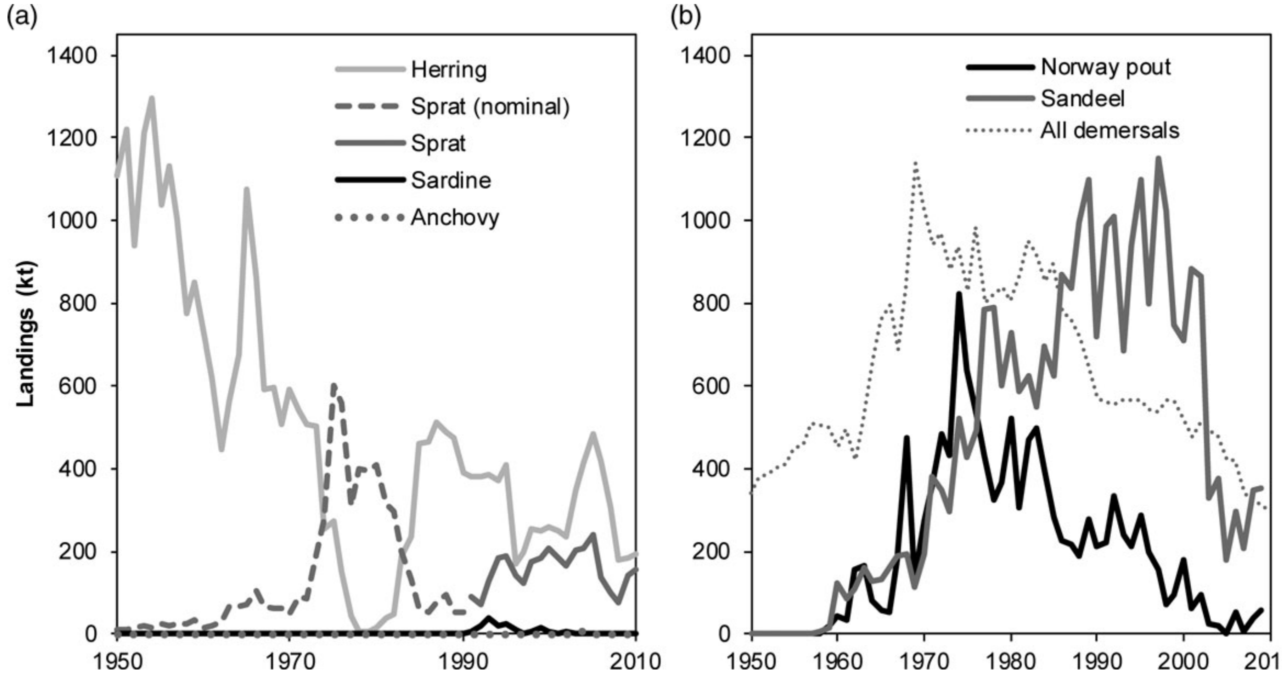

Figure 4. Trends in the international landings of six forage fish species from the North Sea (ICES Subarea IV). (a) Herring, sprat, sardine, and anchovy. (b) Norway pout and sandeel. For comparison, the total international landings of demersal (non-forage) fish species are also shown in Figure 4b (dotted line). Source: ICES catch statistics (ICES, 2011) extracted using FishStat Plus software (FAO, 2012).

as it is suspected that large amounts of juvenile herring were misreported as sprat at that time (Dickey-Collas *et al.*, 2013). Monitoring of the species composition of the sprat fishery was greatly improved in the early 1990s. Since 1991, between 100 and 200 kt of sprat have been landed in most years.

In recent years, the largest, single-species fishery has been on sandeel; in the 1990s, landings in some years exceeded 1 million tonnes (Figure 4b). The industrial sandeel fishery in the North Sea rapidly expanded in the 1950s when both Denmark, Germany, and, slightly later, the UK were involved. However, this has been an essentially Danish and Norwegian fishery since the 1990s with ~75 and 20% of sandeel catches landed in Denmark and Norway, respectively (ICES, 2012). Landings peaked in 1997, but have decreased since then primarily due to a reduction in the productivity of sandeel in the northern North Sea where recruitment has decreased to less than half the average of earlier years. Reductions in catches in the central and southern North Sea have been less up to 2011, when the fishery was given a minimal catch owing to two consecutive years of historically low recruitment, although spawning biomasses were above the level thought to impair recruitment (ICES, 2012). Despite the substantial reduction in the fishery, landings of sandeel in 2009 were still higher than those for all demersal fish species combined (Figure 4b).

The Norway pout fishery exploits a population in the northern, relatively deeper region of the North Sea. The fishery grew rapidly in the 1960s–1970s, with landings exceeding those of herring and sandeel in some years (Figure 4b). Since that time, the fishery has greatly reduced, especially after a series of low recruitment years after 2000 when, despite a reduction in fishing mortality, the stock continued to decline. Following some years of particularly small landings compared with other species, the landings have started to increase again in response to a recent increase in recruitment. In contrast to the other exploited North Sea forage fish, fisheries for sardine and anchovy are much smaller. Their landings are almost negligible compared with the other four species (Figure 4a). If the North Sea continues to warm, these two species are expected to play an increased role in the fisheries (Alheit *et al.*, 2012; Petitgas *et al.*, 2012).

In conclusion, different forage fish species have each dominated fisheries catches at different periods: from historical times until the 1950s, human consumption fisheries for herring; 1950s–1960s, industrial fisheries for young herring; 1970s–1980s following herring collapse, industrial fisheries for Norway pout, sandeel, and sprat; 1990s–2000s, industrial fishery predominated by sandeel and human consumption fishery for herring reinstated. The changes in the relative importance of each species reflect not only changes in the abundance of the fish, but also changes in management measures taken to sustain populations and economic considerations such as the price and availability of markets as reviewed by Dickey-Collas *et al.* (2013).

Energy flows and ecological services of forage fish

Population dynamics of forage fish are affected by trophic cascades, induced by the exploitation of predator species (Frank *et al.*, 2005; Casini *et al.*, 2008). Such trophic cascades caused by the removal of top predators act by releasing forage fish from predation pressure, which may lead to an increase in forage fish abundance.

Foodweb models provide one way of assessing to what extent predators rely on forage fish as a food source, and/or how changes in the forage fish community (potentially driven by fisheries) might influence top predators. Most pelagic fish species grow several orders of magnitude over ontogeny, changing their ecological role as they grow, so that prey fish may compete, for example, with juvenile stages of their predators, possibly preventing them from reaching predatory size (Mylius *et al.*, 2001). Hence, to study the transfer of energy through a pelagic foodweb in a model, it needs not only to capture the size-based nature of the feeding interactions, but also the food-dependent growth of individuals. Generic models based on these principles have demonstrated how reductions in predator populations can lead to trophic cascades, with benefits for forage fish populations (Andersen and Pedersen, 2010). They have also demonstrated how fairly large changes in forage fish populations may have only modest effects on the productivity and size of predatory fish populations (Houle *et al.*, in press).

To illustrate the interconnectedness of the North Sea foodweb and the trophodynamic importance of the forage fish ensemble, we employed a size-based foodweb model parameterized and calibrated for the North Sea (Piet, 2010). The model is based on the same principles as the general model in Houle *et al.* (in press). The model describes the feeding interactions between individuals, as the combined results of not only the size of the individual fish (size-based function: Ursin, 1973) but also a species-specific spatial overlap matrix, derived from the co-occurrence of species in trawl survey catches. Consumed food is used for somatic growth in juveniles and partitioned between growth and reproduction in adults; growth and reproduction therefore depend on food intake and availability. Each species has a Beverton–Holt-type stock–recruitment relationship where the maximum recruitment was estimated by fitting the predicted spawning-stock biomass and yield of each species against the values reported by ICES (2012). The forage fish included in the model are herring, sprat, sandeel, and Norway pout, and the predators included are whiting, haddock, and cod. The outputs of the model are size-based patterns of growth, reproduction, and mortality for each species.

Simulations using this size-based foodweb model confirm that the general patterns observed by Houle *et al.* (in press) are borne out in the North Sea. The results suggest that forage fish constitute a significant fraction of the food for adult predators; on average ~50%, but as much as 75%, depending on the body size of the predator (Figure 5), with whiting being most reliant on forage fish, followed by cod and haddock. It should be noted that the proportion of forage fish in predator diet is probably overestimated slightly here, since the model does not include benthic food sources. Nevertheless, the simulation results imply that both adult growth and egg production of individual predators rely to a large degree on forage fish. Reductions in forage fish stock will therefore lead to smaller sizes of predatory fish and lower fecundity. However, as will be shown, some of these individual-level effects are countered at the population level by changes in the abundance of predators.

To examine how changes in the stock sizes of forage fish influence predator species, we calculated three scenarios with the model: a base scenario with current levels of fishing on all species (forage fish and predators), and two alternative scenarios where we either double, or halve, the fishing mortality on the forage fish. These scenarios reveal an emergent negative relationship between forage fish biomass and predator biomass, induced by the competition between forage fish and young predators. A change in forage fish mortality F has a direct impact on the biomass of forage fish and hence on total fish biomass: an increase in F leads to a decrease in the biomass of each of the four forage fish species, and a reduction in F to an increase in forage fish (Figure 6a). Intuitively, an increase

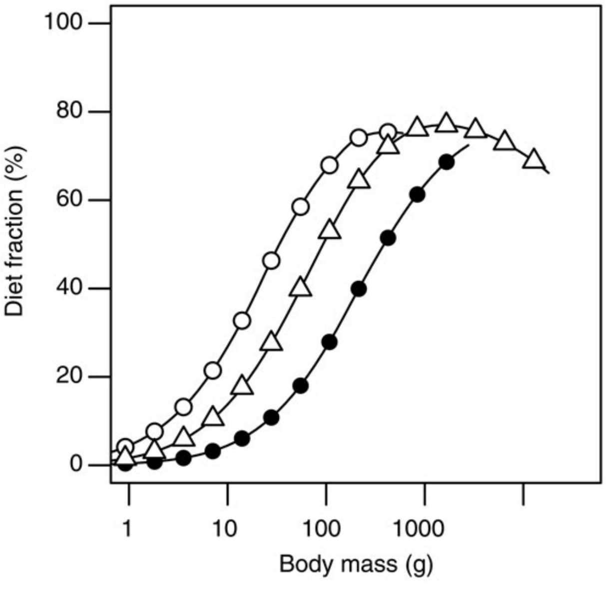

Figure 5. The fraction of diet consisting of forage fish as a function of body weight, for three predatory fish species: whiting (open circles), cod (triangles), and haddock (closed circles).

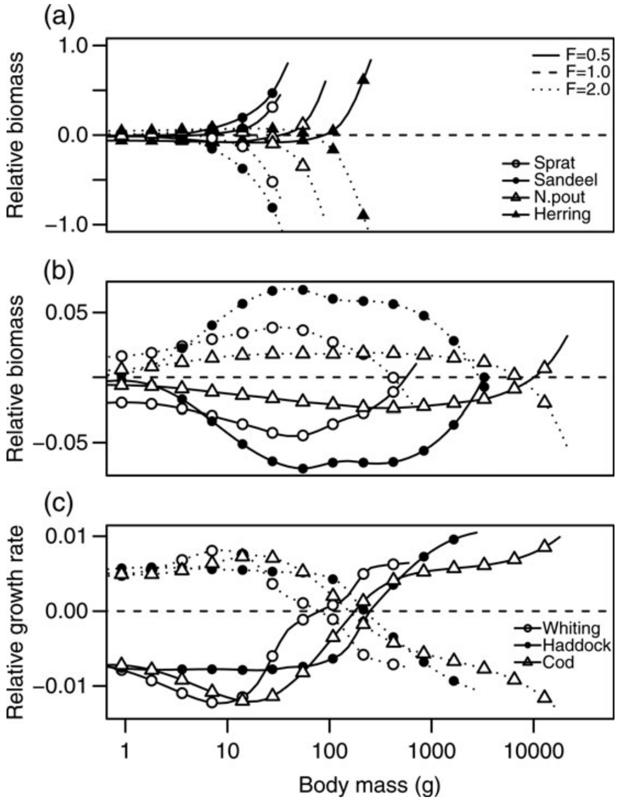

Figure 6. Modelled responses of a fish community to either doubling or halving the fishing mortality on four forage fish species (herring, sprat, sandeel, Norway pout), relative to a base case with $F = 1$ year^{-1}. Three scenarios are shown in each panel: a base case (horizontal dashed lines), halved fishing mortality (continuous lines), and doubled fishing mortality (dotted). Panel (a) shows, for each forage fish species, the change in biomass relative to the base case (proportion increase or decrease), as a function of individual fish size (x-axis). Panel (b) shows the change in biomass of the three predator species (open circles, whiting; triangles, cod; closed circles, haddock) relative to the base case, if F on forage fish is halved (continuous lines) or doubled (dotted). Notice that the changes in the biomass of the predatory fish are smaller than 5%. Panel (c) shows the change in growth rate of the predator species relative to the base case.

in the forage fish biomass (which could result from reduced *F* on forage fish) would be expected to lead to an increase in the biomass of the predator species. That, however, is not the case (Figure 6b). Conversely, the higher biomass of forage fish causes a fairly modest decrease in the biomass of cod, whiting, and haddock at most body sizes, with only the largest individuals of cod displaying an increase in biomass. This counterintuitive result can be understood by examining the growth rate of the predators (Figure 6c). When forage fish abundance is high, the growth rate is decreased for juvenile predators due to increased competition for food, resulting in slower growth, higher cumulative mortality, and therefore reduced numbers of larger predators. Even though in larger individual predators the growth rate is increased at high forage fish abundances (Figure 6c), leading to better growth at these sizes and a higher total egg production, these changes are more modest and not sufficient to offset the strong competitive effects acting upon the predators at the juvenile stages (Andersen and Pedersen, 2010). A reduction in fishing mortality on forage fish results in similar effects on predator populations as described for the increased fishing mortality, just with the opposite sign. Finally, it should be noted that the effects on the predator species are quite small (roughly ~25%) compared with the direct effects on the forage fish. In summary, these foodweb models predict that in response to decreased forage fishing mortality, forage fish stocks will show comparatively strong increases, the biomass of smaller predators will decline moderately, whereas the biomass and growth rates of larger predators will increase slightly.

Synthesizing the evidence: who drives whom?

Our review of the results of field, laboratory, and modelling studies helps reveal the multitude of ways in which North Sea forage fish populations are linked to climatic and planktonic drivers, to other forage fish species, and to predators and forage fish fisheries. This study has considered in a mostly qualitative manner the productivity and dynamics of a forage fish assemblage that is made up of six different species. By necessity and for brevity, we have excluded some factors that may also be important drivers of forage fish populations. Nevertheless, the broad evidence-base presented is the first to highlight the degree of interconnectedness of forage fish in the North Sea foodweb and the potential range in processes that will affect the productivity of specific populations.

The following issues became apparent when considering the forage fish, their fisheries, and their predators.

1. Climate-driven changes in North Sea forage fish populations via direct (abiotic) and indirect (trophodynamic/prey species) routes are clear and are exemplified most clearly in herring, anchovy, and sardine (e.g. Gröger *et al.*, 2010; Petitgas *et al.*, 2012). These three species also serve to highlight that, at the regional scale, there will be winners and losers expected from projected climatic warming (Rijnsdorp *et al.*, 2010; Petitgas *et al.*, 2013), the North Sea being close to the southern boundary in herring (hence negative effects of climate change), to the northern boundary in anchovy and sardine (hence positive effects).
2. Any single species consideration of climatic drivers is likely to fail if there are strong interactions between the forage fish species. Evidence of interactions among North Sea forage fish species is plentiful and we highlight both interspecific (competition, IGP) and intraspecific mechanisms (density-dependence and cannibalism) mechanisms, with some suggestion for interactions through shared parasites or disease. Most correlative investigations of time-series fail to account for these potential changes in drivers and any hysteresis in the system. Alternative outcomes are possible. When considering interactions, overlaps in space, time, and diet and the potential for IGP need to be considered either through process-based studies or field campaigns that simultaneously sample forage fish, predators, and spatio-temporal patterns in forage fish prey (including phyto-, zoo-, and ichthyoplankton).
3. Trophic dependence of (top) predators on forage fish is well publicized (e.g. Cury *et al.*, 2011; Smith *et al.*, 2011). We rank the dependence on forage fish for a range of seabirds, marine mammals, and predatory fish species in the North Sea. Seabirds were the most sensitive to variations in forage fish because of their specialized diets and limited foraging range (particularly at breeding colonies), followed by marine mammals, then predatory fish (which often display generalist diets). Among the forage fish species, sandeel was most "universally important" as a prey to predators.
4. The importance of top-down control of forage fish by predators was evidenced from the estimates from different foodweb models. The North Sea multispecies assessment clearly suggests that predators are predominant sources of mortality for forage fish (ICES, 2011). Key predators are a relatively small number of fish species including saithe, whiting, mackerel, and horse mackerel, whereas seabirds and seals have a far more modest effect on forage fish. Importantly, each of the key forage fish predators also support major human consumption fisheries (ICES, 2012), so that the removal of forage fish biomass by these species indirectly benefits society (Dickey-Collas *et al.*, 2013).
5. There is little doubt that fishing has been a major driver of forage fish dynamics in the North Sea, especially during the 1960s–1970s when industrial fisheries grew rapidly and the herring stock collapsed (Madsen, 1978) and during the 1980s–1990s when forage fish removals by the fisheries were substantial. Fortunately, sound management has contributed to the recovery of herring, and evidence indicates that, in recent years, fishing mortality on the different forage fish stocks has been in decline and is now relatively low (well below *M*). Foodweb models suggest that the increased biomass of forage fish stocks resulting from reducing fishing mortality may not necessarily lead to larger stocks of piscivorous fish; the reverse may be true if early life stages of predator fish compete with forage fish for limited zooplankton resources. This highlights that changes in the magnitude of fisheries removal of forage fish may have potentially complex (and perhaps unanticipated) consequences on other commercially and/or ecologically important species.

In conclusion, there is no simple answer to the question: "who drives whom?" for forage fish in the North Sea. The effective management of North Sea forage fish (Dickey-Collas *et al.*, 2013) will need to take into account climate-driven variations in productivity and the variety of interactions and trophic pathways highlighted in this study.

Acknowledgements

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