



Ecosystem-based management objectives for the North Sea: riding the forage fish rollercoaster

M. Dickey-Collas^{1,2*}, G. H. Engelhard³, A. Rindorf⁴, K. Raab², S. Smout⁵, G. Aarts², M. van Deurs⁴, T. Brunel², A. Hoff⁶, R. A. M. Lauerburg⁷, S. Garthe⁸, K. Haste Andersen⁴, F. Scott^{3,9}, T. van Kooten², D. Beare¹⁰, and M. A. Peck⁷

¹ICES, Copenhagen, Denmark

²IMARES, IJmuiden, The Netherlands

³Cefas, Lowestoft, UK

⁴DTU-Aqua, Copenhagen, Denmark

⁵SMRU, University of St Andrews, UK

⁶IFRO, University of Copenhagen, Denmark

⁷IHF, University of Hamburg, Germany

⁸FTZ, University of Kiel, Germany

⁹European Commission Joint Research Centre, Ispra, Italy

¹⁰The World Fish Center, Penang, Malaysia

*Corresponding author: tel: +45 3338 6759; fax: +45 3393 4215; e-mail: mark.dickey-collas@ices.dk

Dickey-Collas, M., Engelhard, G. H., Rindorf, A., Raab, K., Smout, S., Aarts, G., van Deurs, M., Brunel, T., Hoff, A., Lauerburg R. A. M., Garthe, S., Haste Andersen, K., Scott, F., van Kooten, T., Beare, D., and Peck, M. A. Ecosystem-based management objectives for the North Sea: riding the forage fish rollercoaster. – ICES Journal of Marine Science, 71: 128–142.

Received 14 December 2012; accepted 23 April 2013; advance access publication 19 June 2013.

The North Sea provides a useful model for considering forage fish (FF) within ecosystem-based management as it has a complex assemblage of FF species. This paper is designed to encourage further debate and dialogue between stakeholders about management objectives. Changing the management of fisheries on FF will have economic consequences for all fleets in the North Sea. The predators that are vulnerable to the depletion of FF are Sandwich terns, great skua and common guillemots, and to a lesser extent, marine mammals. Comparative evaluations of management strategies are required to consider whether maintaining the reserves of prey biomass or a more integral approach of monitoring mortality rates across the trophic system is more robust under the ecosystem approach. In terms of trophic energy transfer, stability, and resilience of the ecosystem, FF should be considered as both a sized-based pool of biomass and as species components of the system by managers and modellers. Policy developers should not consider the knowledge base robust enough to embark on major projects of ecosystem engineering. Management plans appear able to maintain sustainable exploitation in the short term. Changes in the productivity of FF populations are inevitable so management should remain responsive and adaptive.

Keywords: biomass reserves, ecosystem approach, herring, sandeel, size based, sprat.

Introduction

The exploitation of forage fish (FF) is posing specific challenges to ecosystem-based management (Hilborn, 2011; Smith *et al.*, 2011), since fisheries remove large amounts of FF biomass from ecosystems and the FF populations are usually typified by varying productivity, thus are highly variable in abundance (Alder *et al.*, 2008). These planktivorous pelagic species which are often obligate schoolers play an important linking role in ecosystem energy transfer

through trophic levels (Rice, 1995; Bakun *et al.*, 2010). This linking role has been regularly highlighted, often based on research from upwelling systems (Pikitch *et al.*, 2012). The ecosystem approach to fisheries management requires the management of human activities within the ecosystem (de Young *et al.*, 2008). So, the move to integrated advice for ecosystem-based management (Sissenwine and Murawski, 2004) requires that scientific advisors respond to the changing demands of society (Rice, 2005), involve

all stakeholders, and be based on incentives and not control (Hilborn, 2004; Makino *et al.*, 2009). Scientists need to populate this debate with relevant information (Jennings and Le Quesne, 2012). Thus, fishers and managers need to be well informed of the consequences of management decisions. They also need to be aware of the breadth of potential management objectives. In Europe, fisheries managers appear reticent to engage in the discussion about management objectives beyond the sustainability of fisheries informed by single-species advice and environmental managers appear to be setting wide ranging objectives that may be too broad to be operational (van Hoof and vanTatenhove, 2009; Jennings and Rice, 2011). This could be seen as a failing to scope across management objectives in a constructive and appropriate manner (Jennings and Le Quesne, 2012).

The North Sea is an example of a region where fishing has substantially impacted on FF populations (Engelhard *et al.*, this volume). It also could be considered complex in term of its FF assemblage. Thus, it provides a good model to explore what is meant by ecosystem-based management objectives for a system with relatively large fisheries targeting FF fisheries. It also offers a perspective to managing human impact on FF to contrast with upwelling systems where many perceive that differing characteristics exist in ecosystem functioning and biodiversity, although this difference is currently being questioned (Fréon *et al.*, 2009; Madigan *et al.*, 2012). This paper will consider the context of FF fisheries including the role of FF for top predators, current fisheries management objectives, and practices, and explore the issues related to potential changes in management approaches to FF. It will do this by taking information from across studies of multispecies models, fieldwork on top predators, bioeconomic approaches, and discussing relevant issues using the North Sea as a case study. This paper is written by scientists, aware that the other prominent stakeholders have not contributed to its thesis; thus, it is meant to inform and stimulate further policy scoping rather than offering answers. It is designed to encourage further debate and dialogue.

The rollercoaster of FF productivity

It is well known that FF display fluctuations in their distribution and abundance (e.g. Reid *et al.*, 2001; Genner *et al.*, 2004; Rijnsdorp *et al.*, 2009). Due to their population characteristics and trophodynamic role, many FF stocks are bio-indicators of environment/climate-driven changes in marine systems worldwide (Fréon *et al.*, 2005). This variability makes it more difficult to manage sustainable exploitation. It is for this reason that we called this paper “riding the FF rollercoaster”. For a fish population to be productive, it requires a habitat that has the trophodynamic and physical/hydrodynamic conditions suitable for the species’ growth physiology and an expression of behaviour that allows life cycle closure (Petitgas *et al.*, 2013). Changes in trends of climate-induced, regional configurations will probably provoke shifts in species distributions (Beaugrand *et al.*, 2008) which may not be readily predictable (Cheung *et al.*, 2010, 2011). 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 systems (Lluch-Belda *et al.*, 1992; Schwartzlose *et al.*, 1999; Turre *et al.*, 2007). Atlantic and Pacific herring (*Clupea harengus* and *C. pallasii*) stocks have long-term cycles in abundance that correlate with changes in the strength and phase of oscillations in atmospheric climate indices (e.g. Hollowed and Wooster, 1992; Gröger *et al.*, 2010).

Various physical and biological processes, which are not mutually exclusive, have been postulated to cause shifts in FF productivity including optimal growth temperatures (Takasuka *et al.*, 2008), bottom-up control (Ware and Thomson, 2005; Rykaczewski and Checkley, 2008), top-down control (Frank *et al.*, 2005), wasp-waist and predator-pit dynamics (Cury *et al.*, 2000; Bakun, 2006), or intra-guild predation (Irigoien and de Roos, 2011). These processes act simultaneously with physical mechanisms (Twatwa *et al.*, 2005) and/or fishing (Ruiz *et al.*, 2006; Shelton *et al.*, 2006). Within European waters, expansion into higher latitudes or increases in the productivity of populations at the edge of their distribution have been documented in species such as European anchovy (*Engraulis encrasicolus*), sardine (*Sardina pilchardus*), and sprat (*Sprattus sprattus*; Alheit *et al.*, 2012; Petitgas *et al.*, 2012; Peck *et al.*, 2012). The drivers of this variable productivity of FF populations in the North Sea are discussed in Engelhard *et al.* (this volume).

Fisheries on FF in the North Sea

We define the FF in the North Sea as sprat, herring, sandeel (*Ammodytes* spp.), Norway pout (*Trisopterus esmarkii*), sardine, and anchovy. The first four of these FF are exploited by targeted fisheries, whereas the two latter species are considered occasional occupants of the North Sea and rarely occur at a large enough biomass to attract fisheries exploitation. We will not consider the role of cephalopods, krill, or the piscivorous mackerel (*Scomber scombrus*) or horse mackerel (*Trachurus trachurus*).

The fishery for herring has been the dominant FF fishery for the last 400 years up to the 1970s, when the catches of sandeel, Norway pout, and sprat increased (Figure 1). North Sea herring is a classic example of variability in productivity and slow management action leading to a stock collapse (Dickey-Collas *et al.*, 2010) which resulted in a much reduced fishing fleet for herring by the end of the 20th century. The recent catches of sandeel and Norway pout are much lower now than in the 1990s and the 1970s, respectively, due to a series of years with poor recruitment success associated with a subsequent rapid decline in spawning-stock biomass. For sandeels in particular, there appears to have been a decrease in productivity in northern areas of the North Sea where previous habitats of sandeels are no longer used and densities in the occupied areas are low (ICES, 2012b).

There are currently three main fishing techniques used to target FF in the North Sea. The industrial fishery (for meal and oil) uses midwater trawls with fine mesh nets (between 8 and 32 mm) and stores the catch of sandeel, Norway pout, sprat, and juvenile herring in tanks. The human consumption fishery on herring uses midwater trawls (mesh size 40–44 mm) deployed from single or paired trawlers, and either stores the catch in RSW (refrigerated seawater) tanks or freezes the catch onboard into blocks of sorted fish. There is also a purse-seine fishery on herring and sprat for human consumption in the eastern North Sea which stores the catch in RSW tanks.

There is a complex set of policies implemented by the EU to address management concerns and targets such as the Common Fisheries Policy (CFP) and the Marine Strategy Framework Directive (MSFD; EU Commission, 2008). Norway has its own policies that broadly mirror those of the EU. The EU has adopted the maximum sustainable yield (MSY) concept for its fisheries targets. The MSFD has developed criteria and standards for determining “good environmental status” (GES) of the European marine waters, some of which directly germane to FF and their contribution to biological diversity (descriptor 1), their maintenance

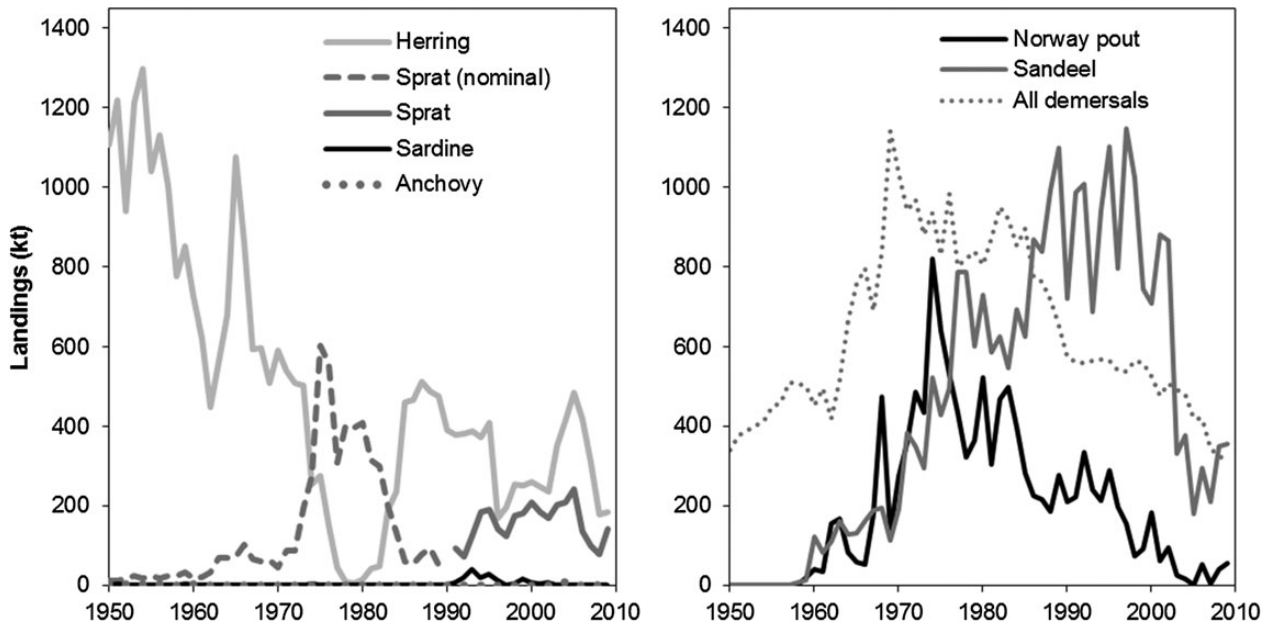


Figure 1. Trends in landings of North Sea FF species by the human consumption and industrial fisheries 1950–2009. Sprat (nominal) refers to a period when doubts exist about the species identification of reported landings. All demersals refer to the biomass of all other finfish landings.

within safe biological limits (descriptor 3), and their role in foodweb structure and function (descriptor 4; EU Commission, 2010). The MSFD says that fish can be exploited up to, but not beyond, levels compatible with MSY.

Within the North Sea, all management measures are now supposed to conform to MSY and the precautionary approach. As a result of the precautionary approach, management must ensure a certain threshold biomass of FF in the North Sea preventing an impairment of recruitment and accounting for reasonable natural mortality of the stock (equivalent to the amount required by natural predators). The precautionary principle is embedded in the advice by the use of buffers on these biomass reference points. These buffers vary with the strength of the knowledge base used to inform management (i.e. when less is known, bigger buffers are applied, and when more is known, smaller buffers are applied to biomass limits). This is interpreted by ICES (who provide the fisheries management advice) as managing stocks with a harvest control rule where the target fishing mortality at high biomasses is F_{MSY} .

Herring fisheries are managed through a multinational management plan which sets target fishing mortalities to be executed by the combined fleets. These targets are used to create the total allowable catch (TAC) for human consumption and a catch limit (bycatch ceiling) for the industrial fishery. The TAC is partitioned into northern and southern segments (Area IVa + IVb and Areas IVc and VIIId; Figure 2a). For short-lived stocks, the MSY approach is considered to be “escapement fishing” where the fishery each year aims to reduce the stock size to a biomass consistent with having a specific, low probability of impairing recruitment and that is a sufficient resource for predators. Norway pout, sandeels, and sprat are considered short-lived species and thus are managed with escapement rules rather than F_{MSY} . Sandeel catches in EU waters are managed through seven area TACs which are set at the beginning of every year (Figure 2) according to an escapement strategy. Norway has implemented an experimental management scheme for sandeels in the Norwegian waters with alternating closure and opening of fishing grounds from year to year. They keep half the fishing

grounds open in any one year and set a preliminary TAC for these grounds which is updated in the middle of the fishing season based on an acoustic estimate of sandeel abundance. According to this scheme, Norway has set a catch for Norwegian waters the last 2 years despite ICES recommending that no catch should be taken in the northeastern area of the North Sea (assessment area 3, ICES, 2012c). The Norway pout fishery is managed by the setting of a preliminary annual TAC according to the escapement rule. A preliminary TAC is varied within year as information on year-class strength becomes available in August. Sprat catches were managed by “within”-year advice determined by a survey index, but a collapse in the confidence of this method, resulted in no clear advice being given in recent years. There is now no consistent approach to the management of sprat catches. No management measures are in place for catches of sardine or anchovy. Anchovy catches used to be incidental but when the distribution is more widespread some minor targeted fisheries do take place (Cheung *et al.*, 2012; Petitgas *et al.*, 2012).

There are also technical measures used for the conservation of FF, or the bycatch of their fisheries (EU, 1998). Closed areas exist for Norway pout, herring, and sprat fisheries (Figure 2b and c). There are minimum landing sizes of the human consumption fishery on herring (20 cm); and percentage bycatch rules (dependent on mesh size) for industrial fisheries that catch sandeels, Norway pout, and sprat. Fisheries on sandeel stocks off Scotland, which were thought to have decreased the abundance of sandeels thus impacting the breeding success of kittiwake (*Rissa tridactyla*) populations, were closed in 2000 (Daunt *et al.*, 2008).

There is no evidence that the fisheries that target FF in the North Sea disturb the seabed in detrimental manner. Some are extremely “clean” in that they only target one species, e.g. herring or sandeels. Sprat and Norway pout fisheries can have substantial bycatch of other commercial species and, as a result, their bycatch is monitored and fishers must abide by bycatch ceilings. This approach is supposed to limit the impact of these small-mesh fisheries on non-target species.

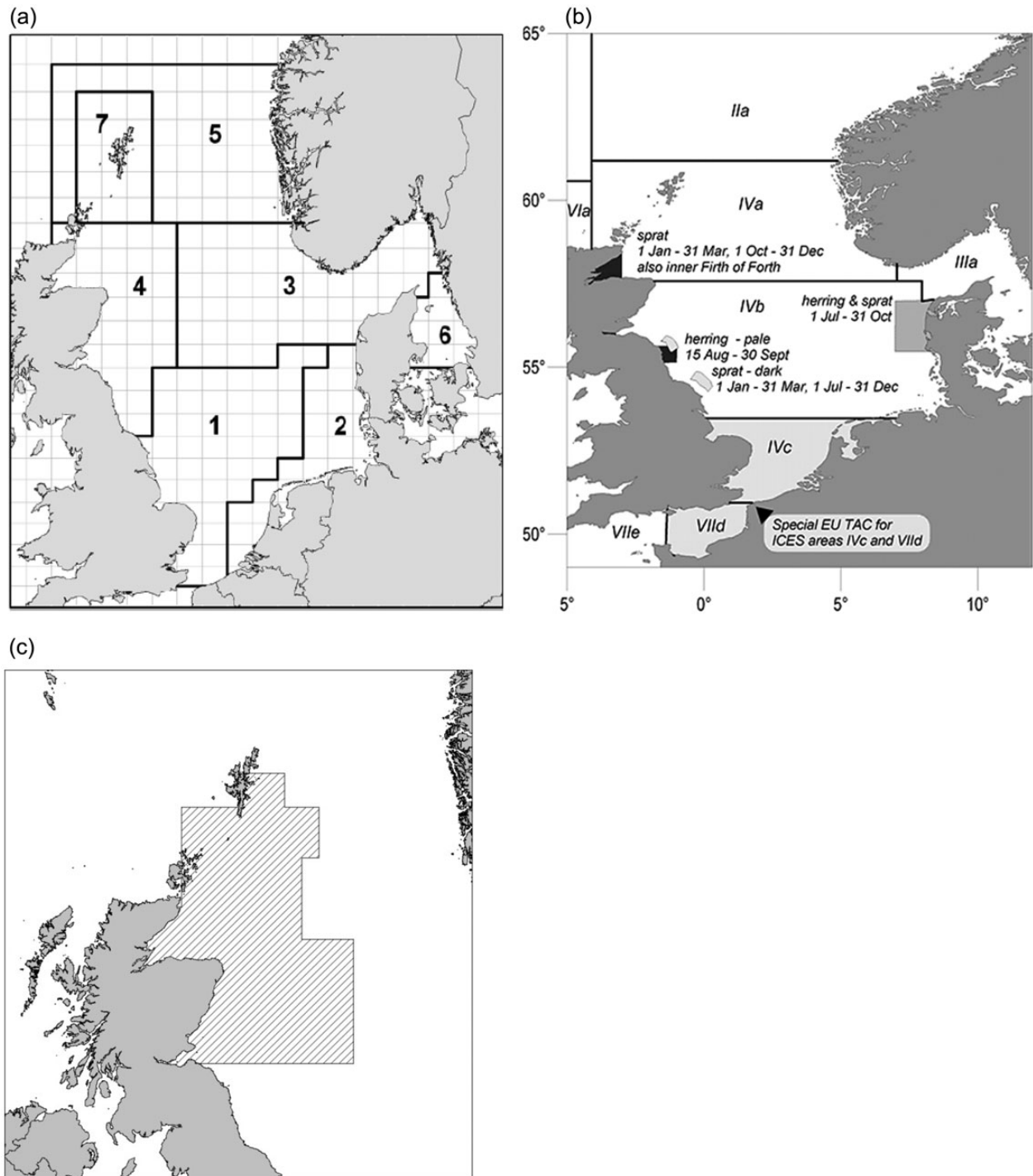


Figure 2. Spatial management of FF in the North Sea. (a) Management and assessment areas of sandeel currently used by ICES. 1, Dogger Bank area; 2, South Eastern North Sea; 3, Central Eastern North Sea; 4, Central Western North Sea; 5, Viking and Bergen Bank area; 6, Division IIIa East (Kattegat); 7, Shetland area. (b) ICES and closed areas to fishing on herring and sprat. Black, sprat fishery closures to protect juvenile herring; pale areas, closures on the herring fisheries. The shaded area to the west of Denmark is closed to the juvenile herring and the sprat fishing. (c) Closed area for fishing for Norway pout.

Predators reliant on FF in the North Sea

Energy-rich FF form a substantial component of predator diets (Hall *et al.*, 1998; Hammond and Grellier, 2005) and prey availability may impact predator condition and life history (Hjernquist and Hjernquist, 2010; Smout *et al.*, this volume). The majority of

the mortality on FF comes from the top predators compared with the fisheries (Figure 3; ICES, 2012a). The method used to estimate the removal did not account for the potential higher yield if a young fish was allowed to grow rather than caught; hence, the estimates of the costs of natural mortality are minimum values.

The proportion of FF biomass removed by fisheries has decreased with time to <20% of the biomass per year (Figure 3). The majority of the removal of FF from the system is by other finfish. Removals by marine mammals are small compared with other sources and seabirds have removed less than 10%. Very few elasmobranchs are included in the analysis.

Our analysis suggests the fishery takes around 20% of the total removal of FF, thus a doubling of the catch of FF would at most lead to a 13% reduction in the available biomass of FF for predators. At the same time, the reduced FF biomass would mean more food for small juvenile FF-sized predators. Further, not all the diet of the predatory fish comes from FF; some also prey on juvenile predatory fish and other food. Taken together, the current competition between predatory fish and the forage fishery is modest.

We have the tools to estimate “who takes” FF, but we have less information on “who needs” FF and how much they require. Local depletions of FF can negatively affect the survival, breeding, or condition of top predators (Boyd *et al.*, 1994; Rindorf *et al.*, 2000; Haug *et al.*, 2002; Piatt *et al.*, 2007; Harding *et al.*, 2011). However, detecting or quantifying competition between top predators and fisheries is difficult on the scales at which the North Sea fisheries are usually managed. Reduced availability of FF will only impact top predators if FF comprise a large proportion of the diet and predators are unable to substitute that proportion by alternative prey. Furthermore, these effects are likely to be of greatest importance to the conservation of a species if a substantial proportion of the population resides in the North Sea and/or the global abundance of a species is low. Current understanding makes it difficult to account for these factors in a quantitative manner, especially when dealing with migrating predators and prey, localized food depletions and a lack of information about prey preferences and consumption rates of predators (Smout *et al.*, this volume). Engelhard *et al.* (this volume) further discuss the impacts of predators on FF and here we consider the management of FF in relation to the top predators. We estimated the potential vulnerability of predators to depletions of FF by accounting for the distribution

of predators, the proportion of FF in the diet, and any reports of impacts of reduced FF abundance on growth, survival, or breeding success of predators (Table 1). The first two categories are comparable with those used by Furness and Tasker (2000), who produced vulnerability scores of seabirds based on size, cost of foraging, foraging range, spare time in daily budget, ability to dive, and ability to switch diet. Whereas their categories were specific to seabirds, our categories apply to fish, seabirds, and mammals and hence needed to be more general.

The distributional contribution was defined as the summed effect of whether the species is globally scarce (1) or not (0) and whether a significant proportion of the population resided in the North Sea (1) or not (0). The diet contribution was defined as 0 if the proportion in the diet was low (<20%), 1 if the proportion was medium (20–50%), and 2 if the proportion was high (>50%). Documented effects on growth or reproduction resulted in a scoring of either 0 (no effects documented), 1 (effects of food abundance on growth documented), or 2 (effect of FF abundance on reproductive output documented) for recorded impacts. The total scoring was the sum of scores obtained from distributional aspects, dietary aspects, and documentation of effects, except when the dietary aspect score was 0, in which case the distributional score was also set to 0. Hence, the maximum score of any species was 6. The scoring on recorded impacts is used both in the total scoring and to compare the vulnerability score of the distribution and dietary vulnerability to the presence of documented effects. Whether the species is a widespread or local feeder is also scored as this indicates whether widespread or local management measures are likely to be most appropriate.

In general, seabirds are the most vulnerable to FF depletions; seabirds have the most recorded incidents where depletions in FF coincided with reductions in the reproductive output. Of the local predators, six of seven had reported effects of low prey abundance. This may partly be linked to the greater availability of data for local seabirds, but for marine mammals, this does not seem a likely explanation. The score on reported effects was positively

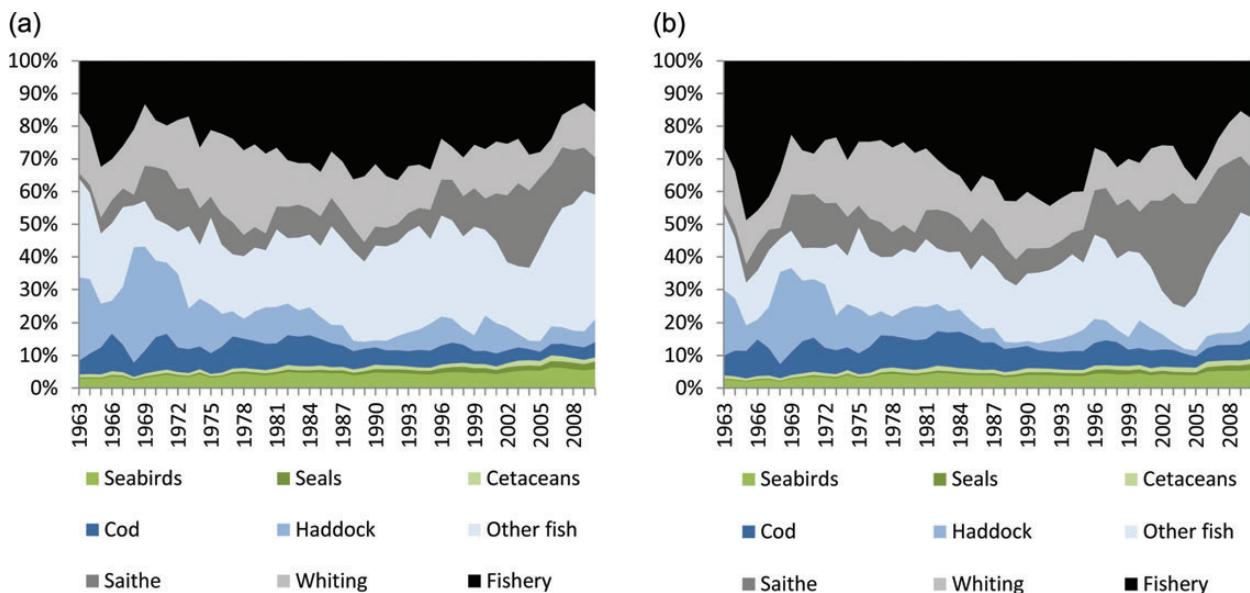


Figure 3. Removals by different predators and the fishery of North Sea FF per year (1963–2010). (a) Proportion of FF removed as a percentage of total removals by weight per year. (b) Proportion of value (Euros) of removals of FF by source per year (right). Output from the SMS model (ICES, 2011).

correlated with the diet score (correlation = 0.58, $p = 0.005$), indicating that a large proportion of FF in the diet together with a local distribution greatly increases the probability of recording effects of FF shortage. The four most vulnerable species are Sandwich terns, great skua, European shag, and common guillemots (scores >3 in Table 1). The species ranked with medium vulnerability are minke whale, grey seal, razorbill, and black-legged kittiwake. Fish are generally less vulnerable than birds with an average vulnerability score of 1.0 and with no fish species having a score of >2. Marine mammals are intermediate with an average score of 1.6. We have not considered issues such as the return of bluefin tuna or grey whales to the North Sea. These charismatic species were once common and a healthy population of FF would be crucial for their return. Our synthesis was also limited to species with adequate information on their North Sea diet. There may be additional vulnerable species in the area which can be identified, e.g. many elasmobranchs or cephalopods. This manuscript also did not consider the behavioural interactions (temporal and spatial) that will impact on the productivity, mortality, and distribution of FF and their predators.

Exploring short-term economic consequences of management options for North Sea fisheries on FF

Fisheries management is carried out through the management of human behaviour; thus, it should account for the economic and social drivers responsible for that behaviour. Here, we consider economic drivers but acknowledge that the optimization techniques often used in economic studies may not accurately reflect human behaviour as social norms and values also play a role (de Young *et al.*, 2008; Richter, 2011). The price per tonne of herring, sprat, and sardine for human consumption has fluctuated over the last 60 years reaching the lowest value in the 1990s (Figure 4a, adjusted to prices in 2000). The price of industrial catches has increased throughout the time-series, although a short peak occurred during the herring closure (Figure 4b). The value of the landed catch (human consumption and industrial) has been variable, from €125 million to €625 million per year first sale and is now low compared with the last 60 years (Figure 4c). The number of EU vessels operating in the North Sea that target FF for human consumption has been greatly reduced from thousands in the early 20th century to hundreds by the mid-century to ~100 ships in the 2010s (Figure 4d). The decline in vessels that execute the industrial fishery has been extremely rapid in the last 20 years.

There has been a lack of bioeconomic analysis of the pelagic and industrial fisheries in the North Sea probably due to the challenge of compiling datasets and combining them with multispecies models. In a first step to help understand the economic consequences of decisions about the management of fisheries on FF, an economic module that included the FF fleet in the North Sea was added to a multispecies production model (Larkin, 1966; Quinn and Deriso, 1999; Collie *et al.*, 2003). The bioeconomic model includes the total Danish North Sea fishery to evaluate the short-term trade-offs for the Danish fishery, representing a specific European fishery, of changing the forage fishery management in the North Sea.

The economic module is based on the FcubEcon model (Hoff *et al.*, 2010) that finds the effort allocation, providing the maximum total profit for the fishery in the year following a base year, between the fleet segments included in the fishery. This model originally used the single-species Baranov equation for short-term projections of targeted stocks. In the present context, this has

been replaced by a Schaefer multispecies stock projection model, including species interactions (for details on the model refer to the Supplementary Appendix). Inclusion of species interactions in bioeconomic models, having a high level of detail on the economic side as the FcubEcon model has, is still rare, and thus the model offers a contribution to the ongoing discussion on the optimal management of fisheries, where it is necessary not only to consider the commercially most valuable species and/or the species being targeted, but also these species' prey and predators.

The model asks what the optimal effort allocation will be between the included fleet segments 1 year ahead, given certain management restrictions. We use 2007 as the base year. In the present context, the restrictions were: (i) increasing the fishing mortalities of herring, sprat, sandeels, and Norway Pout one by one to F_{MSY} (thus providing four scenarios) and (ii) limiting the fishing mortalities of the four FF species one by one to below half the levels in 2007 (thus providing another four scenarios). All scenarios are constrained by demanding that the Danish catches of other species must not exceed the Danish quotas in 2007 (except for blue whiting, mackerel, and horse mackerel; see below for a further discussion of this), thus securing that when changing the FF management, this does not imply that other species are suddenly overfished (the non-Danish forage fishery fleet segments almost exclusively target FF and thus the quotas of other fish have not been limited for these segments.)

In each scenario, the outcomes were compared with the *status quo* situation in 2007, i.e. to the actual economic outcome for the included fleet segments in 2007. The scenarios are meant as "outer limits" of actual management actions; it is clear that increasing the fishing mortality of one species to F_{MSY} from one year to the next may be unrealistic given that this might lead to unsustainable catches. However, this is in part prevented by only allowing the effort of the fleet segments to vary but not the fleet segments sizes (capacity), i.e. the number of vessels are kept constant. Thus, it is not possible to fish more than what is actually physically possible for the existing forage fishery fleet. This also means that for Norway pout and sandeels, it was only possible to increase the fishing mortality to be close to, but not exactly equal to, F_{MSY} .

Price and cost data included in the model are based on data collected for STECF (the European Commission's Scientific Technical and Economic Committee on Fisheries). As the optimization is short term (1 year ahead), price and cost data are kept fixed (i.e. not influenced by market dynamics). The year 2007 was chosen as the baseline year, as the data provision was best for this year (for details on input data to the model refer to the Supplementary Appendix).

Relative to the 2007 *status quo*, the North Sea forage fleet gained net income when the fishing mortality of the forage species was set equal to F_{MSY} (Table 2). The gain relative to *status quo* is almost equal when sprat, Norway pout, and sandeels were fished at F_{MSY} , whereas the gain was less when herring was fished at F_{MSY} . In the scenarios where the FF fishing mortalities were limited to below 0.5 F_{2007} , the total North Sea forage fishery fleet obtained a lower contribution margin (revenue minus variable costs) relative to the *status quo* scenario (run 1, Table 2).

One of the reasons that the landings values were higher in the scenarios where the FF were fished at F_{MSY} was that the catches increased in all FF-targeted species and on some industrial species. This is because it is not possible to reach F_{MSY} for the FF without also fishing more on blue whiting, mackerel, and horse mackerel. This highlights the complex nature of the multispecies and technical fleet interactions; aiming to achieve MSY exploitation

Table 1. Qualitative consideration of vulnerability of top predators to depletions of North Sea FF.

Predator name	Distribution in North Sea (local or widespread)	Distributional sensitivity	Total FF in diet	Reported effects of low FF abundance?	Total vulnerability
Minke whale <i>Balaenoptera acutorostrata</i>	Widespread	Medium	62% [1]	No evidence reported for the North Sea	3
Grey seal <i>Halichoerus grypus</i>	Local	Medium	42% [2]	Condition of breeding females linked to sandeel abundance [3]	3
Common Seal <i>Phoca vitulina</i>	Local	Medium	49% [4,5]	Pupping date associated with prey abundance [6]	2
Harbour Porpoise <i>Phocoena phocoena</i>	Widespread	Medium	6% [2]	Poor nutritional status of stranded animals [7]	0
Striped dolphin <i>Stenella coeruleoalba</i>	Widespread	Low	16% [8]	No evidence reported	0
Great skua <i>Catharacta skua</i>	Local during breeding	High	10–95% [9,10]	Reproductive success influenced by local sandeel availability [11]	6
European shag <i>Phalacrocorax aristotelis</i>	Local	Medium	98% [9,10]	Reproductive performance strongly depends on local sandeel availability [14]	5
Sandwich tern <i>Sterna sandvicensis</i>	Local	Low	99% [9,10]	Highly vulnerable to changes in local food supply (especially clupeids): reproductive performance, breeding numbers and breeding distribution [12]	4
Common guillemot <i>Uria aalge</i>	Local during breeding	Low	70% [2]	Reproductive performance influenced by local abundance and quality of sandeel and sprat [13]	4
Razorbill <i>Alca torda</i>	Widespread	Low	68% [2]	Reproductive output probably limited by local FF availability [15]	3
Black-legged kittiwake <i>Rissa tridactyla</i>	Local during breeding	Low	36% [2]	Reproductive performance strongly depends on local sandeel availability [16]	3
Atlantic puffin <i>Fratercula arctica</i>	Widespread	Low	71% [2]	No evidence reported for the North Sea	2
Northern gannet <i>Morus bassanus</i>	Widespread	Low	34% [2]	No evidence reported	1
Lesser black-backed gull <i>Larus fuscus</i>	Widespread	Medium	7–25% [9,10]	No evidence reported	0
Northern fulmar <i>Fulmarus glacialis</i>	Widespread	Low	15% [2]	No evidence reported	0
Whiting <i>Merlangius merlangus</i>	Widespread, substock structure	Low	30% [2]	Positive correlations between local sandeel abundance and condition [17]	2
Cod <i>Gadus morhua</i>	Widespread, substock structure	Low	21% [2]	Positive correlation between abundance of small fish and growth in the North Sea [18]	2
Saithe <i>Pollachius virens</i>	Widespread	Low	41% [2]	No evidence reported	1
Horse mackerel <i>Trachurus trachurus</i>	Widespread	Low	34% [2]	No evidence reported	1
Starry ray <i>Amblyraja radiata</i>	Widespread	–	24% [2]	No evidence reported	1
Grey Gurnard <i>Eutrigla gurnardus</i>	Widespread	Low	23% [2]	No evidence reported	1
Haddock <i>Melanogrammus aeglefnus</i>	Widespread, substock structure	Low	20% [2]	Positive correlation between egg production and total feeding level [19]	0

Summed scores of vulnerability rating each predator according to distribution in the North Sea (0 or 1); distributional sensitivity [whether it has a global population of less than 100 000 individuals (0 or 1) and a large proportion more than 25% of the global population resides within the North Sea (0 or 1)], diet proportion (low 0: <20%, medium 1: 20–50%, high 2: >50%), and documented effects on growth or reproduction (no effects 0, effects of food abundance on growth 1, effect of FF abundance on reproductive output 2). Increasing shading indicate relatively higher scores for each category considered and total assessed vulnerability, the sum of distributional sensitivity, diet proportion score, and score on reported effects, except where the diet proportion score was zero, in which case the total vulnerability was set to zero. 1. Windsland *et al.* (2007); 2. ICES (2011); 3. Smout *et al.* (this volume); 4. Sharples *et al.* (2009); 5. Cunningham *et al.* (2004); 6. Reijnders *et al.* (2010); 7. MacLeod *et al.* (2007); 8. Santos *et al.* (2008); 9. BWPI (2004); 10. Mendel *et al.* (2008); 11. Furness (2007); 12. Stienen (2006); 13. Wanless *et al.* (2005); 14. Rindorf *et al.* (2000); 15. Mitchell *et al.* (2004); 16. Frederiksen *et al.* (2004); 17. Engelhard *et al.* (this volume); 18. Rindorf *et al.* (2008); and 19. Hislop and McKenzie (1976).

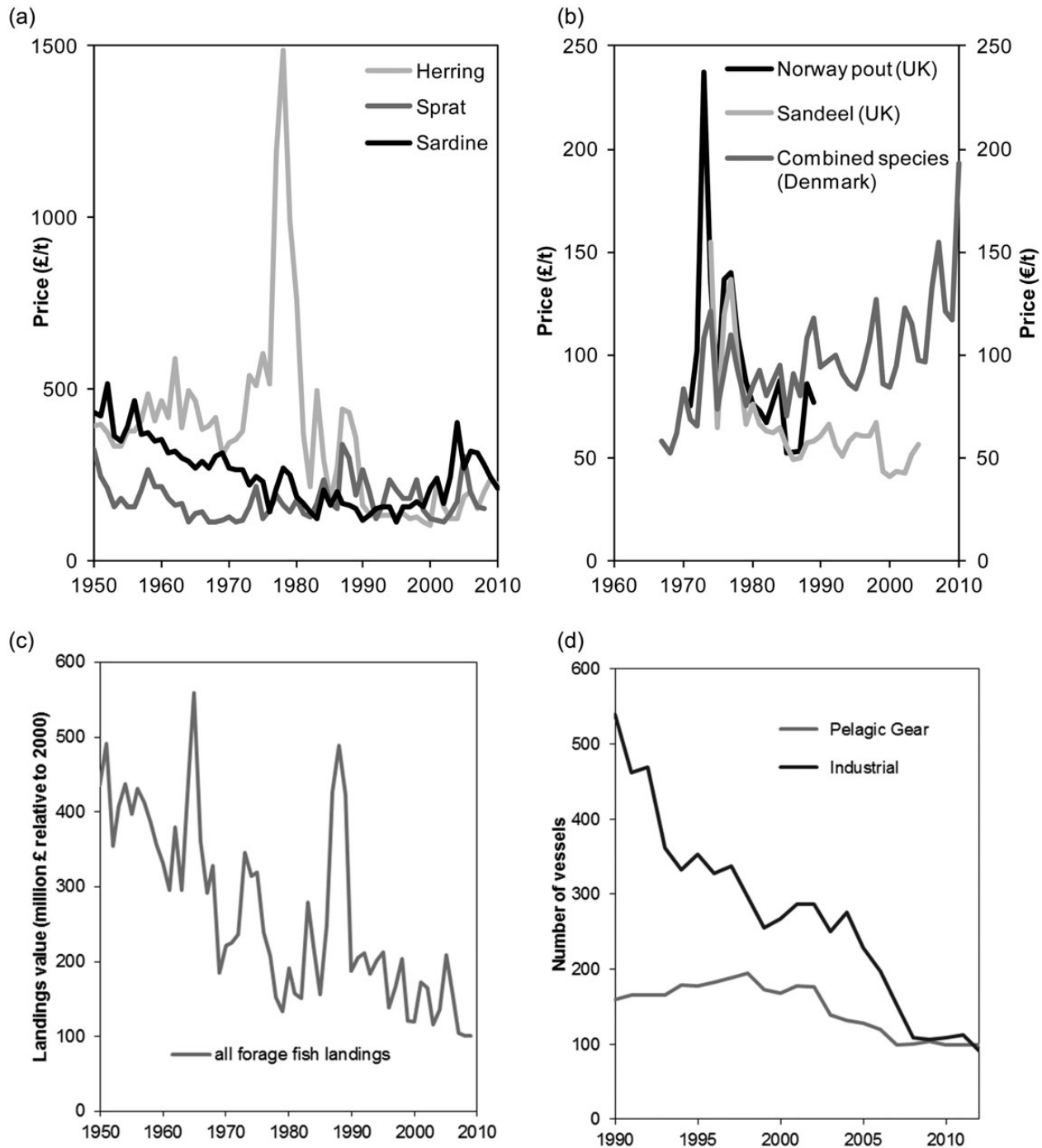


Figure 4. Trends in prices of North Sea FF species. (a) Inflation adjusted prices human consumption species herring, sprat, and sardine (UK prices, £). (b) Inflation adjusted prices industrial species, including Norway pout and sandeels (UK prices, £), and mixed species for the Danish industrial fishery (€). The Danish “mix” consisted of sandeels, herring, sprat, haddock, whiting, and Norway pout during 1967–1977, and sandeels, sprat, Norway pout, and blue whiting during 1978–2010. All prices are expressed in the value of £ or € for the year 2000. (c) The trend in the value of landings of FF from the North Sea (1950–2010) incorporating price adjustment. Data from EU FISHSTAT, Cefas, and DTU-Aqua. (d) Number of EU vessels targeting FF in the North Sea (1990–2012), data from EU fleet register and DTU-Aqua.

for one species will usually result in changes in the exploitation of other bycatch species, such as mackerel.

Similar results were obtained when we examined the country with the largest industrial fleet (Denmark, Table 3). When fishing the FF species in turn at F_{MSY} in 2008, the total Danish fleet was predicted to increase its income compared with 2007.

If, on the other hand, the FF fishing mortalities were limited to below $0.5 F_{2007}$, the earnings of the total Danish fleet, in three of the four scenarios, decreased or stayed equal to the *status quo* value (restrictions on sprat, herring, and Norway pout fishing mortality). However, the model suggested that restricting the sandeel fishing mortality would result in an increase in the

Table 2. Total economic indicators (million €) for the North Sea forage fishery fleet.

Scenario	Total landings value	Total crew cost (CC)	Total variable cost ex. CC	Contribution margin	Net income
(1) <i>Status quo</i> , 2007	253	64	74	115	25
(2) Sprat: $F = F_{MSY}$	506	124	122	259	170
(3) Herring: $F = F_{MSY}$	421	108	106	208	118
(4) Nor. P: $F = 0.93F_{MSY}$	577	146	158	274	184
(5) Sandeel: $F = 0.9F_{MSY}$	577	146	158	274	184
(6) Sprat: $F \leq 0.5F_{2007}$	174	42	25	107	17
(7) Herring: $F \leq 0.5F_{2007}$	139	35	25	79	-11
(8) Nor. P: $F \leq 0.5F_{2007}$	169	41	26	102	12
(9) Sandeel: $F \leq 0.5F_{2007}$	184	46	67	70	-20

Table 3. Economic indicators (million €) for the total Danish fleet operating in the North Sea.

Scenario	Effort	Landings value	Total crew cost (CC)	Total variable cost ex. CC	Contribution margin	Net income
(1) <i>Status quo</i> , 2007	21 466	197	57	64	76	6
(2) Sprat: $F = F_{MSY}$	35 554	281	70	83	128	58
(3) Herring: $F = F_{MSY}$	33 247	303	79	104	120	50
(4) Nor. P: $F = 0.93F_{MSY}$	39 478	358	93	121	144	74
(5) Sandeel: $F = 0.92F_{MSY}$	39 478	358	93	121	144	74
(6) Sprat: $F \leq 0.5F_{2007}$	15 696	123	30	23	70	0
(7) Herring: $F \leq 0.5F_{2007}$	20 453	136	33	31	72	2
(8) Nor. P: $F \leq 0.5F_{2007}$	20 207	139	33	30	76	6
(9) Sandeel: $F \leq 0.5F_{2007}$	25 659	190	46	51	94	23

total Danish fleet earnings compared with *status quo*, thus implying that it would have been economically optimal for the Danish forage fishery fleet to catch less of the original *status quo* catches. So it appears that the total Danish North Sea fleet would be affected by changes to the management of FF stocks. It probably, thus, follows that the other European North Sea fleets would be affected. This exercise of linking a simple economic model to a multispecies production model suggests that any likely change in the management of fisheries on FF will have consequences not only for that fleet but also for demersal fleets.

Generic questions about the management of fisheries on FF in the North Sea

High-profile discussions about the management of FF worldwide have tended to focus on the need to conserve more FF as a result of their role as prey for top predators (Cury *et al.*, 2012; Smith *et al.*, 2011). Much less discussion has focused on the ability of FF to graze down other fish species, change trophic pathways, or the role of FF in providing cheap, sustainable protein to promote food security (Bundy *et al.*, 2009; Tacon and Metian, 2009). Informal discussions have started in Europe on the impact of having large FF populations. The current management of fisheries in the North Sea is based on single-species exploitation targets and limits. Certain, pertinent questions arise when considering exploiting FF in an ecosystem.

Is FF biomass or the mortality rate a more appropriate management tool?

Management objectives for the marine ecosystem have often been set in terms of biomass, e.g. a minimum acceptable stock size for fish aimed at optimizing productivity and avoiding irreversible reductions due to Allee effects (Chen *et al.*, 2002). To sustain biodiversity and meet conservation objectives, lower limits for fish

biomass can also be based on the requirements of predator populations for food resources (Candy and Constable, 2008). These targets are often based on single-species production or population models. When managing FF as an ecosystem component, it is necessary to account for the requirements of predators and also account for predators in any projected management action. The allocation of a specific amount of biomass for predators (maintain a biomass reserve) is not the only approach to secure sufficient prey for the predators. There are a range of approaches across the world (Pikitch *et al.*, 2012). Management can incorporate a rate of removal by predators into our understanding of population dynamics (account for variable predation rates). This takes the requirements of predators into the core modelled and projected dynamics of the populations as is now the case for North Sea cod, whiting, and herring (ICES, 2012c).

Fisheries management manages people (the fishers) that exploit the natural resources; therefore, it is easier to manage based on exploitation rate targets (e.g. fishing mortality) rather than by biomass targets which may fluctuate depending on ecosystem productivity and multispecies interactions. The approach of the precautionary reserve for predators is usually based on the estimates of population size, total consumption, and diet composition. Simple approaches to estimate the reserves of FF involve estimating target abundances of key prey species and may be effective in conjunction with adaptive management in relatively simple systems (Constable, 2011). Where population size, total consumption, and diet composition remain fairly constant, so will the reserve required, such as in long-lived species with a reasonably constant intake and specialized in a single prey species (e.g. European shag; BWPi, 2004; Mendel *et al.*, 2008). However, simple biomass reserves are more problematic when applied in a complex system with many trophic links such as the North Sea (Yodzis, 1994; 1998; 2001). Here, most predators have a wider diet and their populations, food intake, and diet composition may change significantly over time. For these species in this and other regions, the “minimum safe level” required

depends on properties of the ecosystem that change with time such as the abundance of predator species or the availability of food resources. The majority of the North Sea top predators have a broad diet of more than one prey species and their diet composition is likely to change in response to changes in food availability. In addition, populations of both prey and predators are subject to stochastic effects which may bounce populations away from the target, e.g. variable recruitment. It is also possible that provision for a multitude of predators may be mutually incompatible.

Rather than seeking to follow and engineer absolute target abundance levels, ecosystem managers may instead opt to monitor and respond to rates of change in the productivity. The concept of ecosystem equilibrium as a management tool in fisheries has long been discredited, and we all now accept that the productivity of various components of any ecosystem will change over time and often outside human control. Thus aiming at some pristine “historical target” biomass might not be an achievable goal especially when considering more than one species. Methods that incorporate changes in productivity rates and react via changes to removal rates are generally more resilient to changes in vital processes (Kell *et al.*, 2005). Management through rates involves setting aside a proportion of the prey to a given predator (via incorporation of realistic natural mortalities in the population models) then estimating the amount which can be removed by anthropogenic sources. This approach still assumes that the predators have primacy over the fisheries, but the relative changes in the ratio of fishing to natural mortality are presumed to be known. This builds our knowledge into the evidence basis for management action, rather than treating biomass as a management target. Unfortunately, we currently do not have robust approaches to project natural mortality rates in models of catch options for fisheries. Instead, forward projections incorporate recent estimates. This approach combines the amount of alternative food and the preference for the specific prey into estimations thus eliminating inconsistencies in the amount available and the amount eaten. Here, management can be through target exploitation rates (reference points), with limit reference points providing a backup under unpredicted situations.

In other parts of the world, control rules have been fashioned that provide target F_s that respond to changes in productivity and biomass (Alaskan herring, California sardine, Southern Ocean krill; Pikitch *et al.*, 2012). This provides added protection at lower biomass but it could be questioned if this approach provides primacy to the predators always. In the North Sea context where lower F_s only kick in below a buffered limit biomass, we assume (perhaps incorrectly) that our knowledge base is as good at high biomass compared with low biomass, as commercial catch tuning indices are not used in the stock assessments (other than for sandeel). Thus hyperstability of cpue is an unlikely danger for management.

To become completely operational, we may well have to consider a more dynamic approach. “Acceptable” levels of prey availability may involve more than one type of prey, so that targets or limits cannot be simple point estimates for one prey species but instead have to be represented as curves or surfaces in multidimensional prey space. To predict where “good” and “bad” regions for a predator lie, within such a space, we must parameterize a “metric” of predator success (e.g. foraging success or survival) to prey abundance. To fit a multidimensional function data over a range of prey abundances and combinations of these are required, creating a considerable demand for additional data. Estimation is easier when some *a priori* notion of the functional form and the

meaning of its parameters exists (Smout *et al.*, 2010) but can also be attempted with smoothing approaches if there is no clear expectation of the nature of the response surface (Smout *et al.*, *this volume*). These functions can potentially be used in combination with models of fish stock dynamics which might not explicitly include predators, to set limits for management to sustain biodiversity targets for the predators.

When operating a responsive fisheries management predominantly through target exploitation rates, it is probably more robust to provide dynamic advice about the prey requirement of predators. The reserve biomass approach has its merit when knowledge of predator–prey dynamics is missing or stability is a correct assumption. However, when the requirements change over time and the knowledge base is strong (such as in the Barents, Baltic, and North Seas), the removal rate approach prevents changes in productivity or predator preferences from impacting on the management of the fishery. Managing for production and fishing mortality can enable fisheries to continue operating sustainably, even against a background of environmental change, but it requires a tolerance and a preparedness to respond to the fluctuations in FF populations. The drawback to this approach is the large requirement for data and knowledge, the need for ongoing monitoring and the existence of a management regime that is responsive and adaptive. It is not a “resource light” solution.

Should FF be management as a pool of species (a portfolio)?

This question is linked to the question above. Management of a single “FF” pool made up of inter-replaceable fish species could simplify management decisions. However, before making such a leap in strategy, there are other considerations about productivity and ecosystem functioning that may be relevant to consider such as the differences between species in the response to climatic drivers, their role as energy transporters between spatial areas (horizontal transport) and trophic levels (vertical transport). The strength and direction of response of each species to the same change in an environmental driver will differ (Engelhard *et al.*, *this volume*) as the North Sea is the southerly geographic limit for sandeels and the northern limit for sprat, anchovy, and sardine. FF species in the North Sea exhibit different behaviours. The way each species transfers energy within the ecosystem also varies. Sandeels, Norway pout, and sprat can be considered resident throughout their life stages, whereas herring migrate across and out of the North Sea and potentially can transfer large amounts of energy to other waters. The vertical energy transfer is impacted by energy conversion efficiency (fish tissue production/consumption) and has been proposed as a major determinant of food chain length (the energy-flow hypothesis, e.g. Yodzis, 1984; Rand and Stewart, 1998). Low energy conversion efficiency results in less energy available for production at higher trophic levels. Although strict comparisons between studies are difficult due to different approaches, the conversion efficiency appears to vary among the FF species found in the North Sea from 6–17% in clupeids (De Silva and Balbontin, 1974; Stewart and Binkowski 1986; Varpe *et al.*, 2005) to >17% in sandeels (Gilman, 1994; Sun *et al.*, 2010). Consequently, the production of the highest trophic levels may depend on the species composition of the FF community. In the North Sea, with our current understanding and tools, we suggest that FF should not be managed as a pool of species, but considered separate populations in a dynamic system.

Should considerations of ecosystem resilience and stability be taken into account?

The relationship between stability and ecosystem complexity is the subject of a long debate in ecology. May (1973) showed that in randomly constructed model communities, higher complexity leads to less stable communities which are more prone to species extinctions. This counterintuitive conclusion and its apparent violation in nature (e.g. in coral reef systems or tropical rain forests) has inspired much research on the subject (McCann, 2000). Increasingly, it is thought that generally weak interactions among species tend to stabilize foodwebs, whereas strong interactions destabilize them (McCann *et al.*, 1998). This is relevant to how FF should be treated in ecosystem-based management. Weak interactions occur when predators on FF are opportunistic generalists, feeding on whichever species happen to be abundant. Strong interactions occur when specific FF species have specific predators that depend on that specific prey species.

Conceptually, the marine pelagic foodweb is often thought to be structured predominantly by size-dependent feeding relationships, where size of individuals, more so than the species they belong to, determines the type and strength of interaction between them (e.g. Andersen and Beyer, 2006). This approach, by playing down the importance of species differences in favour of size differences, tends implicitly to lead to generalist predators, weak links, and hence stable systems. Even when the species concept is to some degree implemented, external disturbances of the ecosystem tend to be strongly damped (Andersen and Pedersen, 2009; Zhang *et al.*, 2012). From this work, it could be concluded that the various species of FF, because they generally span similar size ranges, could be treated as one pool of interchangeable individuals (see above). However, some of the key differences between the species give reason for concern that such a homogeneous interpretation of the FF community may be a dangerous oversimplification. Although the species may be homogeneous in terms of their size range, they may differ strongly in their behaviour, spatial and temporal availability, and quality as a prey. Hence, it may be that while on the level annual dynamics of the entire North Sea, things may appear homogeneous, in more detail, each predator population may be interacting only with a single FF as prey depending on location or time of year, leading to strong, destabilizing interactions. While simulation frameworks are available that can deal with complex ecosystems, these generally involve compiling a data-rich representation of the ecosystem under study. No general, ecological theory exists which can produce generic theoretical expectations for ecosystem stability when both spatial, temporal, and life-history variation is taken into account.

So far, we have mainly considered the intrinsic stability of an ecosystem, i.e. its tendency to persist if undisturbed. Another essential aspect of ecosystem persistence is its resilience, i.e. its capacity to buffer disturbances, without shifting into another state (Holling, 1973). The resilience of an ecosystem increases with the diversity of species residing at different trophic levels (within different feeding guilds). Smith *et al.* (2011) emphasized this character of resilience highlighting the prime importance of FF species diversity. This work suggests that in terms of the North Sea ecosystem, a difference in the impact of harvesting different FF species on other trophic groups likely exists. This interspecific variation in impacts of fishing on FF has important consequences referring to ecosystem-based management. The principal aim of ecosystem-based management is to ensure that human activity maintains a healthy ecosystem.

Hence, the management of FF stocks should be species specific and aim for resilience and thereby enhance the likelihood of sustainability and a stable ecosystem (Pikitch *et al.*, 2004).

Maintaining a certain pool of FF biomass regardless of species is not sufficient to ensure the ecosystem role of FF. On the other hand, when a large proportion of the FF species in a system are at low abundance, to be precautionary, the abundance of the remaining dominant species should be maintained, probably by reducing fisheries exploitation. The lack of other FF is likely to increase natural mortality on the remaining species and make the predators particularly sensitive to a decrease in the remaining species.

Should fishing for FF be used as ecosystem engineering?

Fishing brings about changes in the abundances of target populations and bycatch species. The use of projections of catch in management illustrates that we consider ourselves able to manipulate fish populations through managing fisheries. Fishing has led to indirect and unpredicted effects on the targeted populations and the ecosystem, such as the removal of top predators releasing more FF for exploitation or “surplus-yield” (Parsons, 1992; Yodzis, 2001). In Europe, there are often requests for certain trophic groups to be overexploited to increase catching opportunities on other trophic groups. In theory, management action that impacts on multi-trophic coupling could be used to actively change the abundance and biomass of some ecosystem components. Under the precautionary approach, all management action should be carried out with an assessment of risk. Our current understanding of the system is such that we cannot predict, e.g. recruitment in the medium term (5–10 years) and hence the consequences of our actions, or assess the associated risk. We currently apply adaptive management that responds to monitoring rather than determining an ecosystem state as an objective.

Although theory and practice in freshwater lakes and coastal wetlands suggest that ecosystem engineering can result in some demonstrable targets (Martin, 1979; Mitsch and Jørgensen, 1989), the experience within marine foodwebs so far is that it is difficult to manipulate them to achieve specific multispecies dynamics or targets (e.g. the Baltic Sea, Gislason, 1999; Lindegren *et al.*, 2010). Clearly, foreseeing the consequences of bio-engineering in multispecies systems is difficult, but even in simpler systems, the intuitive negative relation between predator–prey abundance, may not hold (Pine *et al.*, 2009). Even if possible, this type of ecosystem engineering requires that society and stakeholders can agree on a target ecosystem state. The MSFD determines that the marine ecosystem should have GES and that all exploited species should be at MSY, with normal foodweb interactions. This reduces greatly the scope for active wide-scale ecosystem engineering that favours particular trophic groups. Since FF play a key role in the North Sea ecosystem and given the complex ecosystem feedbacks, targeting a top predator in an attempt to alter other ecosystem components (including the abundance of FF) may appear theoretically attractive to some stakeholders, but is likely to have unforeseen and perhaps unwanted consequences.

Much of the knowledge base on FF dynamics comes from studies of so-called “wasp waist” systems (Pikitch *et al.*, 2012). Projecting the possible effects of management action using the knowledge developed from these systems may not be appropriate for coastal, shelf seas with a wide diversity of FF species available. Omnivory is common in the North Sea and trophic and behavioural interactions are complex. However, the current perception of distinct differences in the trophic structure between systems is now being

challenged as the concept of wasp-waist organisms in upwelling systems is being explored (Fréon *et al.*, 2009; Madigan *et al.*, 2012).

Conclusion

Recent fisheries advice from ICES suggests that the FF in the North Sea are being sustainably managed and that policy measures ensure that biomass of the stocks is maintained above limit biomasses (ICES, 2012c). This management is completely single species in nature and does not account for species interactions nor for the consequences of those measures for non-assessed or less commercial species in the North Sea. The management of fisheries with and without existing management plans is responsive to monitoring and can be adaptive if necessary. However, this is not really ecosystem management. Society values other components of the ecosystem as well, namely the top predators and other aspects of ocean health (De Young *et al.*, 2008).

Through this manuscript, we have illustrated that changing management of fisheries on FF will have economic consequences for all fleets in the North Sea. We list the predators that our initial scoping suggests may be particularly vulnerable to depletions in FF. In general, seabirds were the most vulnerable group whereas no fish species had a high vulnerability score with marine mammals lying between the two groups. In terms of trophic energy flow, stability and resilience of the ecosystem, we recommend that FF be considered not simply as a pool of biomass (a portfolio) but as separate species by both managers and modellers. Following the precautionary approach, we consider the knowledge base on FF and their role in the ecosystem as incomplete and that embarking on any major projects of ecosystem engineering through selective fishing should be avoided. Management plans appear to maintain sustainable exploitation in the short term and management should remain responsive and adaptive within the medium term. This can allow management to respond to the changes that will inevitably occur in the productivity of FF populations. We encourage modelling exercises and comparisons of management strategies that allow researchers to consider which measure(s) (e.g. from maintaining reserves of biomass for top predators to more integral monitoring rates) is (are) most robust under the ecosystem approach. We also want to encourage all attempts to further develop bioeconomic models of the North Sea fleets, especially considering the small-mesh and pelagic trawl fleets. When exploiting FF, society is increasingly demanding that sustainability be not only defined by exploitation rate or biomass limits but also by maintaining a healthy marine ecosystem. FF populations naturally fluctuate greatly, thus our management measures must respond as we ride the FF rollercoaster.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Acknowledgements

Thanks to Hans Mose Jensen for creating maps and to Richard Nash (IMR, Norway) for comments on the manuscript. This research was supported by the EU FP7 grant FACTS (Forage Fish Interactions), grant agreement no. 244966.

References

Alder, J., Campbell, B., Karpouzi, V., Kaschner, K., and Pauly, D. 2008. Forage fish: from ecosystems to markets. *Annual Review of Environment and Resources*, 33: 153–166.

- Alheit, J., Pohlmann, T., Casini, M., Greve, W., Hinrichs, R., Mathis, M., O'Driscoll, K., *et al.* 2012. Climate variability drives anchovies and sardines into the North and Baltic Seas. *Progress in Oceanography*, 96: 128–139.
- Andersen, K. H., and Beyer, J. E. 2006. Asymptotic size determines species abundance in the marine size spectrum. *The American Naturalist*, 168: 54–61.
- Andersen, K. H., and Pedersen, M. 2009. Damped trophic cascades driven by fishing in marine ecosystems. *Proceedings of the Royal Society of London, Series B*, 277: 795–802.
- Bakun, A. 2006. “Wasp-waist” populations and marine ecosystem dynamics, navigating the “predator pit” topographies. *Progress in Oceanography*, 68: 271–288.
- Bakun, A., Babcock, E. A., Lluch-Cota, S. E., Santora, C., and Salvadeo, C. J. 2010. Issues of ecosystem-based management of forage fisheries in “open” non-stationary ecosystems: the example of the sardine fishery in the Gulf of California. *Reviews in Fish Biology and Fisheries*, 20: 9–29.
- Beaugrand, G., Edwards, M., Brander, K., Luczak, C., and Ibanez, F. 2008. Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecology Letters*, 11: 1157–1168.
- Boyd, I. L., Arnould, J. P. Y., Barton, T., and Croxall, J. P. 1994. Foraging behavior of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology*, 63: 703–713.
- Bundy, A., Heymans, J. J., Morissette, L., and Savenkoff, C. 2009. Seals, cod and forage fish: a comparative exploration of variations in the theme of stock collapse and ecosystem change in four Northwest Atlantic ecosystems. *Progress in Oceanography*, 81: 188–206.
- BWPi. 2004. The birds of the western Palearctic. Interactive DVD Birdguides, Shrewsbury.
- Candy, S. G., and Constable, A. J. 2008. An integrated stock assessment for the Patagonian toothfish (*Dissostichus eleginoides*) for the Heard and McDonald Islands using CASAL. *CCAMLR Science*, 15: 1–34.
- Chen, D. G., Irvine, J. R., and Cass, A. J. 2002. Incorporating Allee effects in fish stock-recruitment models and applications for determining reference points. *Canadian Journal of Fisheries and Aquatic Sciences*, 59: 242–249.
- Cheung, W. L., Dunne, J., Sarmiento, J., and Pauly, D. 2011. Integrating ecophysiology and plankton dynamics into projected changes in maximum fisheries catch potential under climate change in the Northeast Atlantic. *ICES Journal of Marine Science*, 68: 1008–1018.
- Cheung, W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., Zeller, D., and Pauly, D. 2010. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Global Change Biology*, 16: 24–35.
- Cheung, W. W. L., Pinnegar, J., Merino, G., Jones, M. C., and Barange, M. 2012. Review of climate change impacts on marine fisheries in the UK and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 22: 368–388.
- Collie, J. S., Gislason, H., and Vinther, M. 2003. Using AMOEBA to display multispecies, multifleet fisheries advice. *ICES Journal of Marine Science*, 60: 709–720.
- Constable, A. J. 2011. Lessons from CCAMLR on the implementation of the ecosystem approach to managing fisheries. *Fish and Fisheries*, 12: 138–151.
- Cunningham, L., Sharples, R. J., and Hammond, P. S. 2004. Diet of Harbour Seals in the UK. SCOS, St Andrews.
- Curry, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quinones, R. A., Shannon, L. J., and Verheye, H. M. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, 57: 603–618.
- Curry, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J. M., Furness, R. W., Mills, J. A., *et al.* 2012. Global seabird response to forage fish depletion—One-third for the birds. *Science*, 334: 1703–1706.

- Daunt, F., Wanless, S., Greenstreet, S. P. R., Jensen, H., Hamer, K. C., and Harris, M. P. 2008. The impact of the sandeel fishery closure on seabird food consumption, distribution, and productivity in the northwestern North Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 362–381.
- De Silva, S. S., and Ballbontin, F. 1974. Laboratory studies on food intake, growth and food conversion of young herring, *Clupea harengus* (L.). *Journal of Fish Biology*, 6: 645–658.
- De Young, C., Charles, A., and Hjort, A. 2008. Human Dimensions of the Ecosystem Approach to Fisheries: an Overview of Context, Concepts, Tools and Methods. Fisheries Technical Paper 489. FAO, Rome. 165 pp.
- Deecke, V. B., Nykanen, M., Foote, A. D., and Janik, V. M. 2011. Vocal behaviour and feeding ecology of killer whales *Orcinus orca* around Shetland, UK. *Aquatic Biology*, 13: 79–88.
- Dickey-Collas, M., Nash, R. D. M., Brunel, T., Damme, C. J. G., van Marshall, C. T., Payne, M. R., Corten, A., et al. 2010. Lessons learned from stock collapse and recovery of North Sea herring: a review. *ICES Journal of Marine Science*, 67: 1875–1886.
- Engelhard, G. H., Peck, M. A., Smout, S., Rindorf, A., Raab, K., Aarts, G., Deurs, M., et al. this volume. Forage fish, their fisheries, and their predators: who drives whom? *ICES Journal of Marine Science*.
- EU. 1998. EU Council Regulation (EC) No 850/98 of 30 March 1998 for the conservation of fishery resources through technical measures for the protection of juveniles of marine organisms, L 125: 1–55 pp.
- EU Commission. 2008. Directive 2008/56/EC of the European Parliament and of the Council. Official Journal of the European Union, L 164/19: 19–40 pp.
- EU Commission. 2010. On criteria and methodological standards on good environmental status of marine waters. Official Journal of the European Union, L 232: 14–24.
- FAO. 2005. Review of the state of world marine fishery resources. FAO Fisheries Technical Paper, 457. FAO, Rome. 235 pp.
- Foote, A. D., Vikingsson, G., Øien, N., Bloch, D., Davis, C. G., Dunn, T. E., Harvey, P., et al. 2007. Distribution and abundance of killer whales in the North East Atlantic. Document SC/59/SM5 submitted to the Scientific Committee of the International Whaling Commission. 59th Annual Meeting, 28–31 May 2007, Anchorage, AK, USA. http://iwcofficeorg/_documents/sci_com/SC59docs/SC-59-SM5pdf.
- Foote, A. D., Vilstrup, J. T., de Stephanis, R., Verborgh, P., Nielsen, S. C. A., et al. 2011. Genetic differentiation among North Atlantic killer whale populations. *Molecular Ecology*, 20: 629–641.
- Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science*, 308: 1621–1623.
- Frederiksen, M., Wanless, S., Harris, M. P., Rothery, P., and Wilson, L. J. 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea Black-legged Kittiwakes. *Journal of Applied Ecology*, 41: 1129–1139.
- Fréon, P., Cury, P., Shannon, L., and Roy, C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: A review. *Bulletin of Marine Science*, 76: 385–462.
- Fréon, P., Aristegui, J., Bertrand, A., Crawford, R. J. M., Field, J. C., Gibbons, M. J., Tam, J., et al. 2009. Functional group biodiversity in Eastern Boundary Upwelling Ecosystems questions the wasp-waist trophic structure. *Progress in Oceanography*, 83: 97–106.
- Furness, R. W. 2007. Responses of seabirds to depletion of food fish stocks. *Journal of Ornithology*, 148(Suppl. 2): 247–252.
- Furness, R. W., and Tasker, M. L. 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series*, 202: 253–264.
- Genner, J. M., Sims, D., Wearmouth, V. J., et al. 2004. Regional climatic warming drives long-term community changes of British marine fish. *Proceedings of the Royal Society of London*, 271: 655–661.
- Gilman, S. L. 1994. An energy budget for northern sand lance, *Ammodytes dubius*, on Georges Bank, 1977–1986. *Fishery Bulletin*, 92: 647–654.
- Gislason, H. 1999. Single and multispecies reference points for Baltic fish stocks. *ICES Journal of Marine Science*, 56: 571–583.
- Greenstreet, S. P. R., Bryant, A. D., Broekhuizen, N., Hall, S. J., and Heath, M. R. 1997. Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. *ICES Journal of Marine Science*, 54: 243–266.
- Gröger, J. P., Kruse, G. H., and Rohlf, N. 2010. Slave to the rhythm: how large-scale climate cycles trigger herring (*Clupea harengus*) regeneration in the North Sea. *ICES Journal of Marine Science*, 67: 454–465.
- Hall, A. J., Watkins, J., and Hammond, P. S. 1998. Seasonal variation in the diet of harbour seals in the south-western North Sea. *Marine Ecology Progress Series*, 170: 269–281.
- Hammond, P. S., and Grellier, K. 2005. Grey seal diet composition and fish consumption in the North Sea. Department for Environment, Food and Rural Affairs, pp. 1–54.
- Hammond, P. S., Hall, A. J., and Prime, J. H. 1994. The diet of gray seals around Orkney and other island and mainland sites in North-Eastern Scotland. *Journal of Applied Ecology*, 31: 340–350.
- Harding, A. M. A., Welcker, J., Steen, H., Hamer, K. C., Kitaysky, A. S., Fort, J., Talbot, S. L., et al. 2011. Adverse foraging conditions may impact body mass and survival of a high Arctic seabird. *Oecologia*, 167: 49–59.
- Haug, T., Lindstrom, U., and Nilssen, K. T. 2002. Variations in minke whale (*Balaenoptera acutorostrata*) diet and body condition in response to ecosystem changes in the Barents Sea. *Sarsia*, 87: 409–422.
- Hilborn, R. 2004. Ecosystem-based fisheries management: the carrot or the stick? *Marine Ecology Progress Series*, 274: 275–278.
- Hilborn, R. 2011. Future directions in ecosystem based fisheries management: a personal perspective. *Fisheries Research*, 108: 235–239.
- Hislop, J. R. G., and McKenzie, K. 1976. Population studies of the whiting *Merlangius merlangus* (L.) of the northern North Sea. *Journal du Conseil International pour l'Exploration de la Mer*, 37: 98–111.
- Hjernquist, B., and Hjernquist, M. B. 2010. The effects of quantity and quality of prey on population fluctuations in three seabird species. *Bird Study*, 57: 19–25.
- Hoff, A., Frost, H., Ulrich, C., Damalas, D., Maravelias, C. D., Goti, L., and Santurtun, M. 2010. Economic effort management in multispecies fisheries: the FcubEcon model. *ICES Journal of Marine Science*, 67: 1802–1810.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4: 1–23.
- Hollowed, A. B., and Wooster, W. S. 1992. Variability of winter ocean conditions and strong year-classes of Northeast Pacific groundfish. *ICES Marine Science Symposia*, 195: 433–444.
- ICES. 2011. ICES Working Group on Multispecies Assessment Methods. ICES Document CM 2011/SSGSUE: 10. 235 pp.
- ICES. 2012a. Report of the Working Group on Multispecies Assessment Methods. ICES Document CM 2011/SSGSUE: 10. 153 pp.
- ICES. 2012b. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak. ICES Document CM 2011/ACOM: 13. 1383 pp.
- ICES. 2012c. Report of the ICES Advisory Committee, 2012. ICES Advice, 2011. Books, 1–11. 1685 pp.
- Irgoien, X., and de Roos, A. 2011. The role of intraguild predation in the population dynamics of small pelagic fish. *Marine Biology*, 158: 1683–1690.
- Jansen, O. E., Leopold, M. F., Meesters, E. H. W. G., and Smeenk, C. 2010. Are white-beaked dolphins *Lagenorhynchus albirostris* food specialists? Their diet in the southern North Sea. *Journal of the Marine Biological Association of the UK*, 90: 1501–1508.
- Jennings, S., and Le Quesne, W. J. F. 2012. Integration of environmental and fishery management in Europe. *ICES Journal of Marine Science*, 69: 1329–1332.

- Jennings, S., and Rice, J. 2011. Towards an ecosystem approach to fisheries in Europe: a perspective on existing progress and future directions. *Fish and Fisheries*, 12: 125–137.
- Kell, L. T., Pilling, G. M., and O'Brien, C. M. 2005. Implications of climate change for the management of North Sea cod (*Gadus morhua*). *ICES Journal of Marine Science*, 62: 1483–1491.
- Larkin, P. A. 1966. Exploitation in a type of predator–prey relationship. *Journal of the Fisheries Research Board of Canada*, 23: 349–356.
- Lindegren, M., Möllmann, C., and Hansson, L. A. 2010. Biomanipulation: a tool in marine ecosystem management and restoration? *Ecological Applications*, 20: 2237–2248.
- Lindstrom, U., Smout, S., Howell, D., and Bogstad, B. 2009. Modelling multi-species interactions in the Barents Sea ecosystem with special emphasis on minke whales and their interactions with cod, herring and capelin. *Deep Sea Research II: Topical Studies in Oceanography*, 56: 2068–2079.
- Lluch-Belda, D., Schwartzlose, R., Serra, R., Parrish, R. H., Kawasaki, T., Hedgecock, D., and Crawford, R. J. M. 1992. Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report. *Fisheries Oceanography*, 1: 339–347.
- Lonergan, M., Duck, C. D., Thompson, D., Mackey, B. L., Cunningham, L., et al. 2007. Using sparse survey data to investigate the declining abundance of British harbour seals. *Journal of Zoology*, 271: 261–269.
- MacLeod, C. D., Santos, M. B., Lopez, A., and Pierce, G. J. 2006. Relative prey size consumption in toothed whales: implications for prey selection and level of specialisation. *Marine Ecology Progress Series*, 326: 295–307.
- MacLeod, C. D., Pierce, G. J., and Santos, M. B. 2007. Starvation and sandeel consumption in harbour porpoises in the Scottish North Sea. *Biology Letters*, 3: 535–536.
- Madigan, D. J., Carlisle, A. B., Dewar, H., Snodgrass, O. E., Litvin, S. Y., Micheli, F., and Block, B. A. 2012. Stable isotope analysis challenges wasp-waist food web assumptions in an upwelling pelagic ecosystem. *Nature Scientific Reports*, 2: 6–54.
- Makino, M., Matsuda, H., and Sakurai, Y. 2009. Expanding fisheries co-management to ecosystem-based management: a case in the Shiretoko World Natural Heritage area, Japan. *Marine Policy*, 33: 207–214.
- Martin, G. E. 1979. Predator removal: effect on fisheries yields in Lake Victoria (East Africa). *Science*, 203: 646–648.
- May, R. M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton.
- McCann, K. 2000. The diversity-stability debate. *Nature*, 405: 228–233.
- McCann, K., Hastings, A., and Huxel, G. R. 1998. Weak trophic interactions and the balance of nature. *Nature*, 395: 794–798.
- MCCIP. 2012. *Marine Climate Change Impacts on Fish, Fisheries and Aquaculture*. Ed. by M. Frost, J. M. Baxter, P. J. Buckley, M. Cox, S. R. Dye, and N. Withers Harvey. Summary Report, MCCIP, Lowestoft. 12 pp.
- Mendel, B., Sonntag, N., Wahl, J., Schwemmer, P., Dries, H., Guse, N., Müller, S., et al. 2008. Profiles of seabirds and waterbirds of the German North and Baltic Seas. Distribution, ecology and sensitivities to human activities within the marine environment. *Naturschutz und Biologische Vielfalt 61*. Bundesamt für Naturschutz, Bonn - Bad Godesberg.
- Mitchell, P. I., Ratcliffe, N., Newton, S. F., and Dunn, T. E. 2004. *Seabird Populations of Britain and Ireland. Results of the Seabirds 2000 Census*. Poyser, London.
- Mitsch, W. J., and Jørgensen, S. E. 1989. Introduction to ecological engineering. *In Ecological Engineering: an Introduction to Ecotechnology*, pp. 3–12. Ed by W. J. Mitsch, and S. E. Jørgensen. John Wiley and Sons, New York.
- Parsons, T. R. 1992. The effect of predator removal on prey fish. *Marine Pollution Bulletin*, 25: 51–53.
- Peck, M. A., Baumann, H., Bernreuther, M., Clemmesen, C., Herrmann, J-P., Huwer, B., Kanstinger, P., et al. 2012. The ecophysiology of *Sprattus sprattus* in the Baltic and North Seas. *Progress in Oceanography*, 103: 43–57.
- Petitgas, P., Alheit, J., Peck, M. A., Raab, K., Irigoien, X., Huret, M., van der Kooij, J., et al. 2012. Anchovy population expansion in the North Sea. *Marine Ecology Progress Series*, 444: 1–13.
- Petitgas, P., Rijnsdorp, A. D., Dickey-Collas, M., Engelhard, G. H., Peck, M. A., Pinnegar, J. K., Drinkwater, K., et al. 2013. Impacts of climate change on the complex life cycles of fish. *Fisheries Oceanography*, 22: 121–139.
- Piatt, J. F., Harding, A. M. A., Shultz, M., Speckman, S. G., van Pelt, T. I., Drew, G. S., and Kettle, A. B. 2007. Seabirds as indicators of marine food supplies: cairns revisited. *Marine Ecology Progress Series*, 352: 221–234.
- Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., et al. 2004. Ecosystem-based fishery management. *Science*, 305: 346–347.
- Pikitch, E., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Essington, T., Heppell, S. S., et al. 2012. *Little Fish, Big Impact: Managing a Crucial Link in Ocean Food Webs*. Lenfest Ocean Program. Washington, DC. 108 pp.
- Pine, W. E., Martell, S. J. D., Walters, C. J., and Kitchell, J. F. 2009. Counterintuitive responses of fish populations to management actions: some common causes and implications for predictions based on ecosystem modeling. *Fisheries*, 34: 165–180.
- Quinn, T. J., and Deriso, R. B. 1999. *Quantitative Fish Dynamics*. Oxford University Press, New York. 560 pp.
- Rae, B. B. 1973. Additional notes on the food of the Common porpoise (*Phocoena phocoena*). *Journal of Zoology*, 169: 127–131.
- Rand, P. S., and Stewart, D. J. 1998. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 318–327.
- Reid, P. C., Borges, M. F., and Svendsen, E. 2001. A regime shift in the North Sea circa 1998 linked to changes in the North Sea horse mackerel fishery. *Fisheries Research*, 50: 163–171.
- Reijnders, P. J. H., Brousseau, S. M. J. M., and Meesters, E. H. W. G. 2010. Earlier pupping in harbour seals, *Phoca vitulina*. *Biology Letters*, 6: 854–857.
- Rice, J. 1995. Food web theory, marine food webs, and what climate change may do to northern marine fish populations. *In Climate Change and Northern Fish Populations*, pp. 561–568. Ed. by R. J. Beamish. Canadian Special Publication in Fisheries and Aquatic Science, 121.
- Rice, J. C. 2005. Implementation of the ecosystem approach to fisheries management—asynchronous co-evolution at the interface between science and policy. *Marine Ecology Progress Series*, 300: 265–270.
- Richter, A. P. 2011. *The coevolution of renewable resources and institutions—implications for policy design*. PhD thesis, Wageningen University, Wageningen.
- Rindorf, A., Jensen, H., and Schrum, C. 2008. Growth, temperature and density relationships of North Sea cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 456–470.
- Rindorf, A., Wanless, S., and Harris, M. P. 2000. Effects of changes in sandeel availability on the reproductive output of seabirds. *Marine Ecology Progress Series*, 202: 241–252.
- Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., and Pinnegar, J. K. 2009. Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science*, 66: 1570–1583.
- Ruiz, J., Garcia-Isarch, E., Huertas, I. E., et al. 2006. Meteorological forcing and ocean dynamics controlling *Engraulis encrasicolus* early life stages and catches in the Gulf of Cádiz. *Deep Sea Research II*, 53: 1363–1376.
- Ryckaczewski, R. R., and Checkley, D. M. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proceedings of the National Academy of Sciences*, 105: 1965–1970.
- Santos, M. B., Pierce, G. J., Learmonth, J. A., Reid, R. J., Ross, H. M., et al. 2004. Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992–2003. *Marine Mammal Science*, 20: 1–27.

- Santos, M. B., Pierce, G. J., Learmonth, J. A., Reid, R. J., Sacau, M., *et al.* 2008. Strandings of striped dolphin *Stenella coeruleoalba* in Scottish waters (1992–2003) with notes on the diet of this species. *Journal of the Marine Biological Association of the UK*, 88: 1175–1183.
- SCANS. 2006. Final Report Small Cetaceans in the European Atlantic and North Sea (SCANS-II). Life Project, LIFE04NAT/GB/000245. <http://biology.st-andrews.ac.uk/scans2/inner-finalReport.html>.
- Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., Fletcher, W. J., *et al.* 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science*, 21: 289–347.
- Sharples, R. J., Arrizabalaga, B., and Hammond, P. S. 2009. Seals, sandeels and salmon: diet of harbour seals in St. Andrews Bay and the Tay Estuary, southeast Scotland. *Marine Ecology Progress Series*, 390: 265–276.
- Shelton, P. A., Sinclair, A. F., Chouinard, G. A., Mohn, R., and Duplisea, D. E. 2006. Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 235–238.
- Sissenwine, M., and Murawski, S. 2004. Moving beyond “intelligent tinkering”: advancing an ecosystem approach to fisheries. *Marine Ecology Progress Series*, 274: 291–295.
- Smith, A. D. M., Brown, C. J., Bulman, C. M., Fulton, E. A., Johnson, P., Kaplan, I. C., Lozano-Montes, H., *et al.* 2011. Impacts of fishing low-trophic level species on marine ecosystems. *Science*, 333: 1147–1150.
- Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S., *et al.* 2010. The functional response of a generalist predator. *PLoS One*, 5: e10761. doi:10.1371/journal.pone.0010761.
- Smout, S., Engelhard, G., Rindorf, A., Matthiopoulos, J., and Pomeroy, P. this volume. The effect of prey availability on the mass of breeding grey seals at the Isle of May. *ICES Journal of Marine Science*.
- Spitz, J., Mouroucq, E., Leaute, J. P., Quero, J. C., and Ridoux, V. 2010. Prey selection by the common dolphin: fulfilling high energy requirements with high quality food. *Journal of Experimental Marine Biology and Ecology*, 390: 73–77.
- Stevick, P. T., Allen, J., Clapham, P. J., Katona, S. K., Larsen, F., *et al.* 2006. Population spatial structuring on the feeding grounds in North Atlantic humpback whales (*Megaptera novaeangliae*). *Journal of Zoology*, 270: 244–255.
- Stewart, D., and Binkowski, F. 1986. Dynamics of consumption and food conversion by lake-michigan alewives—an energetics-modeling synthesis. *Transactions of the American Fisheries Society*, 115: 643–661.
- Stienen, E. 2006. Living with gulls. Trading off food and predation in the Sandwich Tern *Sterna sandvicensis*. PhD Thesis, University of Groningen.
- Sun, Y., Liu, Y., Liu, X., and Tang, O. 2010. The influence of particle size of dietary prey on food consumption and ecological conversion efficiency of young-of-the-year sand lance, *Ammodytes personatus*. *Deep Sea Research II: Topical Studies in Oceanography*, 57: 1001–1005.
- Tacon, A. G. J., and Metian, M. 2009. Fishing for feed or fishing for food: increasing global competition for small pelagic forage fish. *Ambio*, 38: 294–302.
- Takasuka, A., Oozeki, Y., Kubota, H., and Lluch-Cota, S. E. 2008. Contrasting spawning temperature optima: why are anchovy and sardine regime shifts synchronous across the North Pacific? *Progress in Oceanography*, 77: 225–232.
- Tourre, Y. M., Lluch-Cota, S. E., and White, W. B. 2007. Global multi-decadal ocean climate and small-pelagic fish population. *Environmental Research Letters*, 2: 1–9.
- Twatwa, N. M., van der Lingen, C. D., Drapeau, L., Moloney, C. L., and Field, J. G. 2005. Characterising and comparing the spawning habitats of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. *African Journal of Marine Science*, 27: 487–499.
- Van Hoof, L., and vanTatenhove, J. 2009. EU marine policy on the move: the tension between fisheries and maritime policy. *Marine Policy*, 33: 726–732.
- Varpe, O., Fiksen, O., and Slotte, A. 2005. Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia*, 146: 443–451.
- Wanless, S., Harris, M. P., Redman, P., and Speakman, J. R. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series*, 294: 1–8.
- Ware, D. M., and Thomson, R. E. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science*, 308: 1280–1284.
- Windsland, K., Lindstrom, U., Nilssen, K. T., and Haug, T. 2007. Relative abundance and size composition of prey in the common minke whale diet in selected areas of the northeastern Atlantic during 2000–04. *Journal of Cetacean Research and Management*, 9: 167–178.
- Yodzis, P. 1984. Energy flow and the vertical structure of real ecosystems. *Oecologia*, 65: 86–88.
- Yodzis, P. 1994. Predator-prey theory and management of multispecies fisheries. *Ecological Applications*, 4: 51–58.
- Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *Journal of Animal Ecology*, 67: 635–658.
- Yodzis, P. 2001. Must top predators be culled for the sake of fisheries? *Trends in Ecology and Evolution*, 16: 78–84.
- Zhang, L., Thygesen, U. H., Knudsen, K., and Andersen, K. H. 2012. Trait diversity promotes stability of community dynamics. *Theoretical Ecology*, 6: 57–69.

Handling editor: Jason Link