Multi-species Fisheries Management:
A Comprehensive Impact Assessment of the Sandeel Fishery Along the English East Coast

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Executive summary

Sandeels form a significant part of the diet of many ‘high profile’ predators (e.g. birds, marine mammals, cod) and are the target of the largest fishery within the North Sea (Figure I-1 & I-2). The most extensive sandeel fishing grounds, the Dogger Bank, lies off the eastern coast of England. Substantiated by scientific evidence demonstrating the importance of sandeels to the breeding success of seabirds in Scotland (Rindorf et al 2000; Wright 1996), there are concerns that local depletion of this sandeel stock might have undesirable indirect impacts upon other predators of sandeels and fisheries of importance to the UK (Anon. 2003) and the North Sea ecosystem as a whole (e.g. Monaghan, 1992). This research uses empirical analysis to investigate the direct and indirect impacts of sandeel fisheries on the Dogger Bank and modelling approaches to evaluate the possible impacts of selected options for localised management.

The main objective was to produce a spatially explicit, multi-species model that can be used to explore how alternative sandeel fishery management options for the Dogger Bank might impact sandeels and their predators. Three multi-species models are presented. The foundations of the models are underpinned by data and knowledge from field investigations in to the ecology of sandeels and their predators undertaken from 2004-2006 and from previous Defra funded projects MF0315, MF0317 and MF0318.

This report summarises the main scientific findings, approaches taken, how successfully the objectives were met and the actions taken to overcome problems during the course of the investigation. Detailed scientific accounts of methods and findings are given in scientific papers and technical documents and are referenced throughout. The report is structured around the 5 objectives, which form a logical sequence connecting field investigations to modelling (Figure I-3). An overview of the main scientific findings is given below.

To tailor the application of models to management questions relating to the Dogger Bank, local scale data was collected during 8 research surveys. Using novel and established techniques, data was collected from 2 sites, allowing us to compare the effects of local scale depletion of sandeels in a heavily fished area with a more natural, less heavily fished area (Figure 2.1). Because the two sites are not identical in terms of their physical and environmental conditions, natural differences in sandeel abundance, distribution and predation impacts make comparisons more challenging. Nonetheless, there are several clear differences that shed light on the impacts of fisheries on sandeels and their predators.

Satellite tracking data from commercial sandeel vessels confirms that Grid 1 (North east) is much more heavily fished than Grid 2 (South west) (Engelhard et al. submitted) and that the distribution of effort is linked with availability of sandeels in the water column and the population density. Many more sandeel schools were found in Grid 1 than Grid 2, and the distribution was typified by the clustering pattern commonly found in small schooling fishes.

Acoustic methods revealed the topographic details of the study sites enabling insight to environmental conditions influencing the spatial distribution of sandeels. The presence or absence of sandeel schools in the water column during daytime (and hence availability to fisheries) is related to the availability of suitable sandeel habitat, salinity, temperature and feeding demands. Analyses from gut evacuation rates of sandeels and day-time dredge experiments indicate that given the right environmental conditions sandeels will emerge from the sediment each day to feed in the water column (Righton and Neville in prep). Highest abundance of sandeels during the daytime was associated with optimum salinity conditions and increased with zooplankton abundance (van der Kooij et al. in prep). It was not possible to disaggregate the data to look at how differences in the environmental conditions might differentially influence spatial distribution

patterns of juveniles and adults. Understanding the environmental conditions determining the distribution and abundance of sandeels allows us to infer the wider distribution of sandeels, beyond that demarcated by intense fishing activity.

During early spring, smaller younger individuals that form the bulk of the fishery in later months, dominate the sandeel population in the heavily fished area (Grid 1). In the less heavily fished area (Grid 2), abundance is much lower, but the population contains more larger, older fish. Individual schools also tended to be larger. Analyses suggest that the high density area (Grid 1) may act as an important local nursery area for the population of sandeels spread over a wider area. Consistent with the distribution of sandeel abundance, fishing effort was shown to be considerably higher in Grid 1, although it was not possible to detect the finer scale spatial patterns that links fishing effort with localised abundance of sandeels at sandy banks, plates or ridges (Engelhard et al. submitted). This information was used to compare model predictions on the spatial distribution of fishing effort.

Although it was not feasible to use mass marking or acoustic tracking of sandeel schools for determining short and longer term movement patterns, analysis of day-night differences in distribution implies that at high densities, sandeels undertake daily migrations in the range of 5-15 km (Engelhard et al. submitted). Measuring predator movements was also troublesome because predators were too small to be tagged using electronic tags and insufficient recaptures from conventional tagging. In lieu of specific data, knowledge of behaviour and migration from previous studies was used to infer rules specifying in the model the movements of predators and their opportunities for feeding interactions.

Ten species of sandeel predators were recorded, eating a wide variety of different prey types and selecting prey between 1.5 to 3 times smaller that their own size. Although consumption of sandeels was highest where sandeels were most abundant (Grid 1), with the exception of lesser weever, the predators did not aggregate locally with sandeels. Whiting, lesser weever and grey gurnard dominated sandeel consumption and accounted for approximately 90% of the predation mortality, but their spatial distribution did not match well with that of sandeels. More sandeels were eaten by predators in Grid 1 than Grid 2. The shortfall in availability of sandeels in the diet of predators in Grid 2 was supplemented with other items; sprat as prey for whiting, and pelagic crustaceans (hyperiid amphipods) plus shrimps as prey for weeverfish (Pinnegar et al. 2006). This suggests that they are flexible predators, capitalising on available prey, which supports the use of opportunistic feeding rules in the model. Whiting appear to prey on sandeels mainly during the day when they are in the water column whereas weevers prey on them mainly at night time or mostly likely during times of emergence and burial (Engelhard et al. submitted). Plaice, mackerel and cod also eat sandeels frequently but because their local abundance is lower, the overall impact on the sandeel population is lower (Pinnegar et al. 2006, Engelhard et al. submitted). Data from 1991 year of the stomach suggest that overall the broad scale (North Sea) cod eat proportionally fewer sandeels than we would expect (negative selection).

Biochemical analyses of feeding preferences in marine mammals showed that porpoise and common seal have a relatively similar diet among individuals of the same species. The isotope signature of porpoises was consistent with a diet dominated by low trophic level fish species, especially sandeels and sprat. Seals isotope signature indicated a diet of larger fish, and less reliance on sandeels and sprat, confirming observations by Hall *et al.* (1998) that common seals preferentially consume demersal fish such as whiting and plaice.

Generally, the diet 'flexibility' and ability to substitute diet shortfalls with other prey items suggests that predatory fishes of the Dogger Bank are perhaps less crucially dependent on local sandeel abundance than, e.g., seabird colonies of Scotland (Frederiksen et al. 2005). This is supported by other research showing that predatory fish tend to be generalist feeders (Trenkel et al. 2005; Pinnegar et al. 2003) and hence less reliant on a particular prey resource. However, our investigations revealed that when predators' consumption of sandeels was high they generally showed better condition indices, thus growth and reproduction of predators could be directly influenced directly by the availability of sandeels as prey. This underlines the importance of a healthy sandeel population for the commercially important predatory fish species of the Dogger Bank. Sandeel–predator-condition links appeared strongest for lesser weever and plaice; intermediate for whiting and haddock; and weakest for grey gurnard and mackerel (and perhaps cod but data were extremely limiting).

Information on the predator-prey interactions derived from field investigations are at the centre of development of a spatially explicit, individual-based multi-species model (IBM) developed within this project. The model is a significant, ambitious advance in the field of multi-species modelling, the approach being regarded as leading edge (Walters and Martell 2005). Using a generalised structure that could be adapted to other species and fisheries of interest, a framework has been created which enables the incorporation of both feeding and movement of predators and the spatial behavioural dynamics of the fishery itself. The model is an exploratory tool for comparing the impact of alternative fisheries management options on the fate of sandeels and their predators, expressed through changes mortality and opportunity for growth in time and space. Development time proved insufficient to include elements of hydrographic modelling.

Although the framework of the program is completed, technical difficulties have prevented it from being used to evaluate fully the specified management options with sufficient confidence to be publishable. Primarily, the technical difficulties relate to limitations of the computer platform. Full evaluation of the proposed management and any further development would require the program to be moved to a specialist computational platform. Thus, the results presented are shown only to demonstrate the potential of this framework to explore management options such as seasonal and area closures, and limits based on total allowable catches.

The computational load of the model is considerable in comparison to highly aggregated models such as Ecopath with Ecosim (EwE), but the models are attempting to examine quite different aspects of the ecosystem function. The IBM is better able to incorporate behavioural data regarding migration/dispersion choices and investigate individual feeding choices, but focuses on a sub-set of the ecological groups and assumes constancy in non-modelled groups. EwE on the other hand does tackle the entire ecosystem but by necessity makes broad assumptions regarding migrations and feeding.

Data collected during the field elements of the project were used to parameterise an implementation of the IBM to demonstrate the ability of the framework to evaluate different management plans. The evaluations demonstrated that the size and composition of the predator population is potentially as important in determining sandeel abundance as the fishery. The results presented are not, however, intended as a definitive prediction of the effects of the management options evaluated, but rather demonstrate the potential of this framework to explore these types of questions.

Funding from M0323 partially supported the development and parameterisation of species (Daskalov and Mackinson 2004, Mackinson and Daskalov 2007) and size-based ecosystem models of the North Sea (Blanchard et al. a and b (in prep), allowing us to investigate the broader, ecosystem-scale impacts of sandeel fisheries using 2 additional complementary approaches. Due to technical difficulties in was not possible to use output from the IBM model to drive the ecosystem models so that the local and broad-scale impacts could be investigated simultaneously. This work is still intended for completion and publication.

Applied independently the EwE ecosystem model showed how over the longer term, increases in the abundance of sprat, Norway pout and herring (through the ecological process of competitive release), could help sustain populations of predators that were initially negatively impacted by fisheries depleting stocks of sandeels. This result is partially supported by the field observations showing that predators are able to substitute prey items by way of compensation. Increasing TAC to 1 million tonnes generally had negative effects, whilst seasonal closure appeared to provide no benefit at all because the abundance of juvenile sandeels is mostly governed by the abundance of zooplankton. Area closures had the widest ranging positive impacts to sandeels, their predators and fisheries.

A dynamic size spectrum model was developed for coupled benthic detritivore and fish predator communities, incorporating the effects size-based feeding interactions and prey quality (Blanchard et al. in prep). The model produces size spectra for both communties that are consistent with observed size spectra in the North Sea and enables baseline predictions of an unexploited ecosystem to be made that are consistent with existing ecological theory (Jennings and Mackinson, 2003).

Evaluation of the impacts of the recent size-selective exploitation pattern (over the 1990-2003 period) on the North Sea fish community revealed a 90-99% reduction in large fish (4-16 kg) compared to the unexploited baseline. This was accompanied by an increase in fish between 0.1 and 0.5 kg due to predatory release. Addition of a sandeel area closure (the same as that used in EwE except according to size rather than species) resulted in an even greater abundance of small fish with the largest positive impacts of this change cascading to predators between 0.1 and 1 kg. The effect of different prey quality on the biomass and abundance of size classes was small but detectable, with lower benthic prey quality scenarios resulting in marginally larger reductions (by about 1-2%) in large fish predators across all of the fishing scenarios. Further work on the effects of prey quality is required to fully evaluate the management implications of removing high energy prey (such as sandeels and other fish species) on predators

The EwE ecosystem model characterises the North Sea ecosystem with regard to the connections and interactions among 69 species assemblages ranging from plankton to marine mammals (Daskalov and Mackinson 2004, Mackinson and Daskalov 2007). Predation by the three main consumer groups (commercial gadoids, mackerel and horse mackerel) is comparable to the level of fishing mortality. Sandeels dominate both consumption and catches, and the quantity consumed and fished exceed more than twice the next most important prey species- the Norway pout. Data from the 1991 'Year of the Stomach' and other sources indicate that the main sandeel predators are whiting, minke whales, small demersal fish (e.g. weevers), seabirds, rays, haddock and gurnards and that these positively select sandeels in their diet. Ecosystem indicators are used highlight changes in the North Sea ecosystem over time and make comparisons with other UK shelf seas. The relative contribution of fishing to the total mortality of North Sea fish has increased concomitant with a decline in predatory fish and increased fishing. Further work is required to investigate possible links to changes in system biomass and functional attributes. (i.e. Is total system biomass and relative mortality linked to ecosystem function?) System level indicators suggest a greater stability and maturity of the North Sea compared to the other UK shelf seas, which may be related to the diversity and abundance of consumers (e.g. fish) in the food web. Such comparisons should be treated with caution since structural differences in the models can make comparisons unreliable (Pinnegar et al. 2005). Further work is need on such critical evaluation of the use of ecosystem scale characterisations.

Introduction

Rationale and background

Despite the importance of sandeels to the North Sea ecosystem (Figure I-1) and industrial fisheries (Figure I-2), scientific understanding of the local scale processes affecting their dynamics is limited. There are several characteristics of sandeel ecology that raise the importance of local processes.

- Sandeels have highly specific habitat requirements in terms of the sediment composition and proximity to areas of high planktonic productivity.
- Although highly mobile during the larval phase, adult sandeels are not thought to undergo any long distance migrations. Sandeels therefore are repeatedly found at highly specific locations and it is these patches that the fishery prosecutes.
- Because sandeels depend on such specific habitat and form clusters of schools, it makes them vulnerable to local depletion. Sandeel patches that are heavily exploited may take several years to fully recover.
- Sandeels are food fish for a large number of predatory fish as well as seabirds and marine mammals. It is well documented that the breeding success of some species of seabird is dependent upon local availability of sandeels (Rindorf et al. 2000), but the implications for predatory fish is relatively unknown. New information regarding the behaviour of cod from Defra project MF0317 has shown that North Sea cod are sedentary for much of the summer. The extent of this behaviour in other species of predatory fish is unknown, but if predatory fish are reliant on sandeel patches for extended periods then they will be vulnerable indirectly (and perhaps directly) to fishing activity of the sandeel fleet.

This project builds on the field and modelling work already conducted under MF0315, MF0317 and MF0318 by characterising and quantifying the ecological processes on the Dogger Bank that influence the vulnerability of sandeels to predation and fishing, and the indirect impacts on the predators of sandeels. This is achieved by analysis of ecological data from dedicated field investigations and from fishery data on effort and spatial movements of vessels. The data and knowledge is used to primarily to construct a local scale, spatially explicit multi-species model that is used to assess the direct and indirect impacts of selected local scale management scenarios. Ecosystem models are used to help evaluate the possible ecosystem knock- on effects of the management actions.

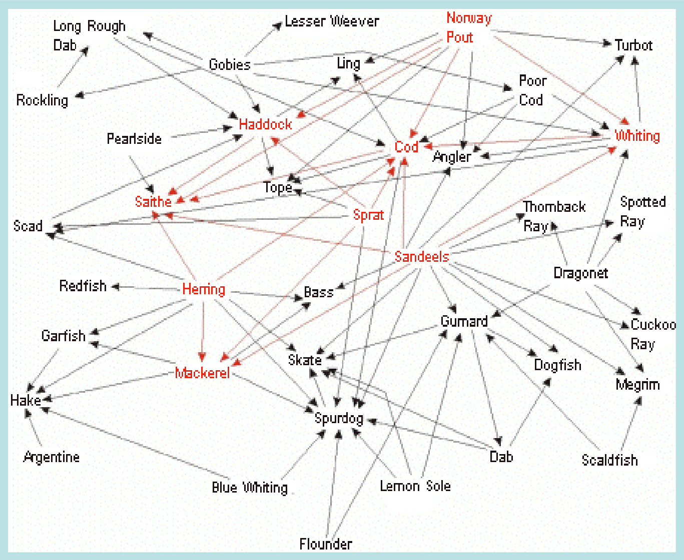


Figure I-1. Simplified web of feeding interactions in North Sea fish.

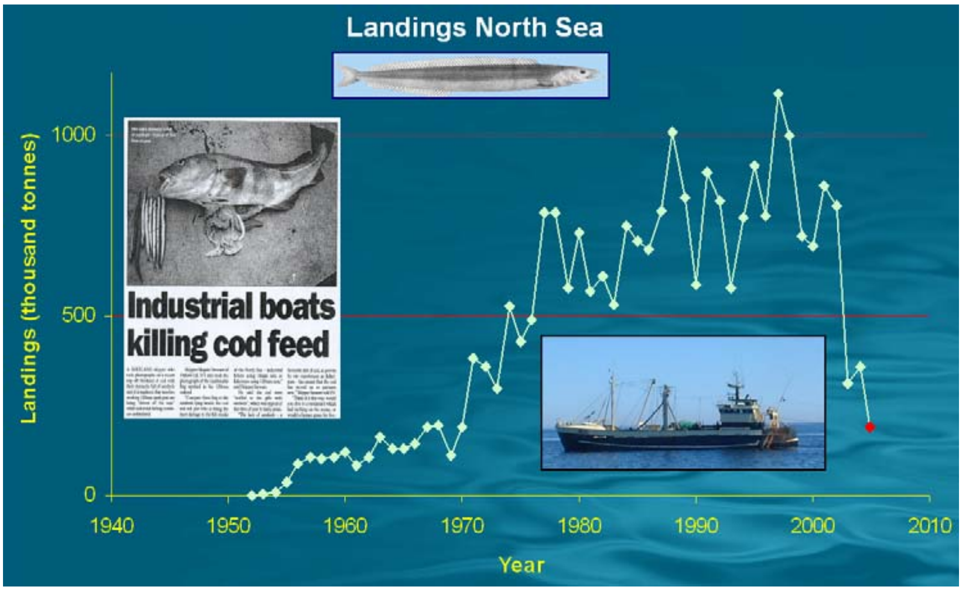
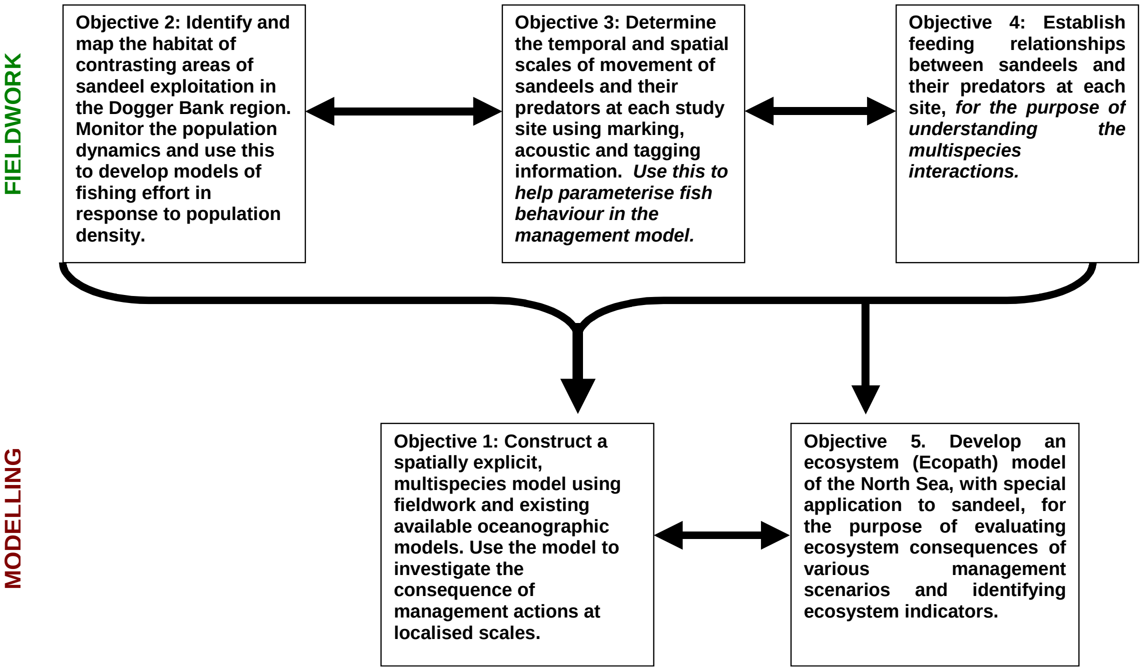


Figure I-2. Landings of North Sea sandeels

Objectives and structure of the report

This report summarises the main scientific findings, methods and approaches taken, how successfully the objectives were met, actions taken to overcome problems during the course of the investigation and the need for future work. The sections are structured around the 5 project objectives, which together form a logical sequence connecting field investigations to modelling (Figure I-3). Objectives 2, 3 and 4 are strongly related, together linking information on the spatial and temporal distribution and abundance dynamics of sandeels with that of their prey and fisheries. Results reported in objective 2, focus on the environmental control of sandeels distribution of fishing effort, while objectives 3 and 4 focus on predator movements and feeding. Throughout the sections reference is made to more detailed scientific papers and technical reports that form the comprehensive scientific outputs. At the beginning of each section, the key findings are summarises in bullet points.



Objective 2: Identify and map the habitat of contrasting areas of sandeel exploitation in the Dogger Bank region. Monitor the population dynamics and use this to develop models of fishing effort in response to population density.

Objective 3: Determine the temporal and spatial scales of movement of sandeels and their predators at each study site using marking, acoustic and tagging information. *Use this to help parameterise fish behaviour in the management model.*

Objective 4: Establish feeding relationships between sandeels and their predators at each site, *for the purpose of understanding the multispecies interactions.*

Objective 1: Construct a spatially explicit, multispecies model using fieldwork and existing available oceanographic models. Use the model to investigate the consequence of management actions at localised scales.

Objective 5. Develop an ecosystem (Ecopath) model of the North Sea, with special application to sandeel, for the purpose of evaluating ecosystem consequences of various management scenarios and identifying ecosystem indicators.

Figure I-3. Logical structure and connections between the project objectives

Objective 1: Construct a spatially explicit, multi-species model using fieldwork and existing available oceanographic models. Use the model to investigate the consequence of management actions at localized scales.

Key findings

- The type of multi-species model developed within this project is an exciting departure from those previously used within Cefas and the wider ICES community. The objective of the model is to understand how predators and fisheries respond at a local level to variations in sandeel abundance.
- It is an Individual-based model (IBM), which provides a way to represent the complex behavioural differences of individual fish in the ways they feed and move. Information from field data is used to parameterise the model.
- Although the framework of the program is completed, technical difficulties have prevented it from being used to evaluate specified management options with sufficient confidence to be publishable. Primarily, the technical difficulties relate to limitations of the computer platform. Full evaluation of the proposed management and any further development would require the program to be moved to a specialist computational platform.
- Despite the technical difficulties, the models' framework is well suited to addressing local scale management issue for the following reasons (i) It is highly flexible and can handle any number of species, it's output detailing the life history of each fish and each predation event, (ii) it has modules for feeding dependent growth of predators, seasonal migration patterns and the potential for fishing vessels to modify their behaviour based on their personal track record.

A recent study (Jensen et al. 2001) investigated the population dynamics and management scenario modelling of sandeels at a regional level. The data for this study came from a wide geographic region, but primarily from the Wee Bankie and Jutland/Little Fisher banks. The resulting management model was spatially resolved to five regions, covering the North Sea sandeel assessment area. The study concluded that fine scale (i.e. patch level) information regarding fishing and predation mortalities and hydrographic sea circulation were required. The field-work and modelling conducted during this project address this need by focussing on the dynamics and sandeels and their fisheries on the Dogger Bank.

Methods

The multi-species model developed within this project is an exciting departure from those previously used within Cefas and indeed in the wider ICES community, such as such as MSVPA (MultiSpecies Virtual Population Analysis). The spatial, individual multi-species model developed within this project has been designed to investigate how predators and fisheries respond at a local level to variations in sandeel abundance. A technical description of the model specification is given in Appendix 2 but essentially the model consists of individual fish and vessels moving round a number of discrete locations. The model uses the individual-based modelling approach (IBM), which provides a way to represent the complex behavioural differences of individual fish in the ways they feed and move. Fishing vessels are also treated as individuals. Their behaviour is controlled by simple rules based upon their surroundings and past performance. The model is flexible in that it can be adapted to represent the dynamics of other multi-species and fishery interactions. At any one timestep, fish feed on each other within the location they are currently residing in. Individuals then pass through routines dealing with residual natural mortality (disease, senescence and unaccounted mortality), growth and migration before finally being subject to the fishery itself. In principle, the model can cope with any number of individuals operating in a (potentially) unlimited spatial arena, but in practice, this is limited by computer memory. Computation time is extensive, the evaluations presented here were initialised with around 8 million individuals running on a weekly time step over 10 years and took in the order of 35 hours to complete.

The key functions of feeding and fishing are length rather than age related. This makes the enables the modelling of feeding dependent growth, an omission in previous multispecies models. In instances where multispecies feeding is not taking place (i.e. planktivorous species or life-history stages), growth is modelled deterministically through a Von Bertalanffy growth curve. Parameters for feeding dependent growth were taken from the report of an EU-funded program into multispecies feeding. During program testing a gross-mismatch between the growth potential under feeding-dependent growth and average (Von Bertalanffy) growth curves came to light in which fish grew up to 4 times larger than would be expected for a given age. It was not possible to reconcile this difference during the project and so the results presented below use Von Bertalanffy growth curves for all individuals.

Data from field-work investigation on the Dogger Bank (see objectives 2-4) were used to parameterise the model. This included parameterisation of the predator-prey links (who eats who and how much) and the prey size preference functions for predators. Data from previous Defra-funded studies were used to parameterise the migration functions and analysis of the VMS data went to parameterise the fishing vessel functionality.

Migration has been modelled as a type of Levy Flight, which is a probabilistic function which describes the likelihood of moving a particular distance in a given time-step. The migration module has been implemented such that changes in behaviour by both season and life-history stage (i.e. juvenile or adult dispersal/migration patterns) can easily be incorporated. Fish can either move in a directional manner, such as adult cod moving to/from spawning grounds, or in a random manner such as larval dispersal.

Fishing opportunities are governed by the management regime in place. After consultation with Defra, the following potential management plans were selected for evaluation;

1. Status quo fishing mortality.
2. Total closure of the North Sea sandeel fishery.
3. Total Allowable Catch (TAC)– this is the traditional management system for sandeels. TAC is applied to total landings for the whole North Sea. TAC limits of 1 million tonnes and 500 thousand tonnes were planned..
4. Area closure – representing the closure of areas 1A and 4 (Figure 1.1) (sandeel MPA)
5. Closed seasons. Representing a management tactic designed to prevent fishing on the recruiting ages by closing the fishery at a time when the new year class starts to become available to the fishery (e.g June, July)
6. Rotational MPAs closed to sandeel fishing. In this scenario, each patch would be open for fishing for a set period and then closed for a set period.

10 fishing vessels were allowed to fish the area, all targeting sandeels. This represents approximately 5% of the real fleet (ICES. WGNSSK: 2006). Parameterisation of the vessels' fishing power and characteristics (towing speed etc) came from analysis of VMS data (see section 2.6)

The original intention was do divide the Dogger Bank into 7 discrete areas which are shown in figure 1.2. The model also has one generic area called “outside” which holds any individuals which migrate out of the main areas. The initialisation files give the user the opportunity to place individuals in space and for the purposes of the runs presented here individuals have not been placed randomly. In order to limit the computation to a level possible on a desktop PC (see NOTE 1) the simulations presented here are limited to just the NW Riff and Dogger1 areas. Cod and sandeels have been placed in both locations, plus some individuals starting in the “outside” location. Haddock, whiting and dab were placed in both locations whilst lesser weevers, plaice and gurnards are only found in the “NW riff” area.

The output from the model consists of an annual summary of population status (total stock biomass, spawning stock biomass, recruits and landings), and a complete output of all living individuals every 6 months, detailing their weight, length, age, location. There is also a file detailing each mortality event stating which individual died, it’s weight, length and age at death, how it died and if it was eaten, then which fish had eaten it. For the model runs presented here this totals approximately 8GB of data and the detail regarding who eats what, where and when is almost as detailed as the results of the field data. For the purposes of this report, summary statistics regarding stock status, and overall feeding relationships are presented.

The long run-times and memory limitation mean that full evaluation of all the proposed plans could not be achieved. 1 Even in this reduced specification the computer ran out of memory after a few years (4-7 depending upon the management configuration). One solution to this problem was to considerably reduce the size of the starting populations but this meant the size of some predator populations were unfeasibly small. Presented below are examples of program output, but due to the lack of full evaluation these results are designed for demonstration purposes only and are in no way intended as final results. The management scenarios presented are

a) total closure in both areas,
b) open fishery in both areas
c) one area closed, one area open
d) one area permanently open, the other area open in a rotational fashion (1 years open, 2 years closed).

Results

Figures 2.1 and 2.2 show the total stock biomass trajectories for scenarios a) and b) showing markedly different stock developments for a variety of species with the different management regimes. Figures 2.3 and 2.4 show the type of detailed information at the level of the individual that the model produces. These are the growth trajectories of individual dab which , once a critical weight is reached (relating to the start of multispecies feeding) show a cyclical pattern which is closely related to the availability of sandeels as a prey item.

NOTE 1: Due to the potentially long run-times, the model was tested with few individuals and only brought up to size for the final runs. At this point it was discovered that the model quickly reached the technical limits of the computer system used which was a dual-processor (3.0ghz) workstation with 4GB ram operating with Windows XP. It transpires that the Windows operating system will allocate a maximum of 2GB to any one application, which capped the number of individuals that the system could handle at any one time. The starting values for the population sizes used were in proportion to those observed in the field, in order to model the system on a 1:1 basis would have entailed several billion individuals whereas in reality the 2GB limit capped the model run to about 20 million individuals. Table 1.1 gives the starting population numbers.

Table 1.1 Starting number of individuals by species.

Cod	81
Haddock	130
Plaice	75
Gurnard	374
Lesser Weaver	1450
Sandeel	5389007
Other-food (large)	500000
Other-food (medium)	1000000
Other-food (small)	200000

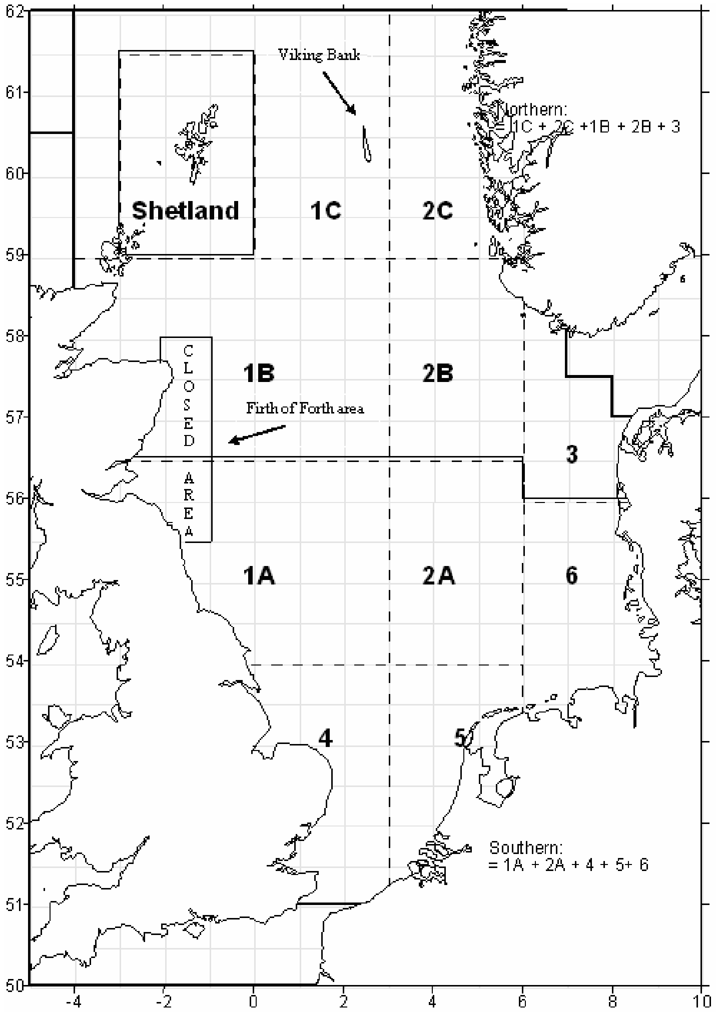


Figure 1.1. Fishing areas. Area 1A and 4 are taken as the Area closure (MPA) scenario.

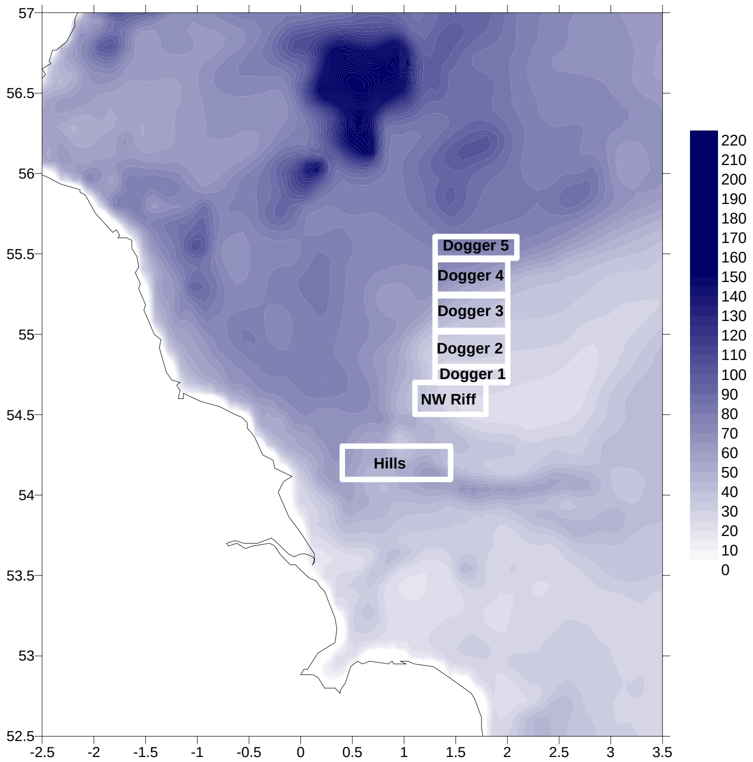


Figure 1.2 Layout of locations used in model implementation.

Future directions.

The IBM model framework is an exciting step forward in multispecies modelling and represents what is probably the most advanced model of its kind given the range of biological and physical factors that it encompasses. As it stands, the model is a useful tool to investigate the potential impacts of management plans and whilst it is capable of dealing with single-species, single-area models this type of scenario would probably be better served by simpler, more computationally rapid models. The model is best suited to investigating complex situations entailing multiple species, fleets, areas and migration behaviours.

Whilst the model is fully operational, its development should not be considered to be complete. Ideally the program should be transferred to a more suitable computational platform (e.g. Linux) which would ease the memory limitation problems encountered. Run-time could be considerably reduced were the program to run on a computer cluster and again a move in computation platform would greatly assist in this. As computational power increases with time, the model will be able to effectively handle more individuals although the volume of output will increase accordingly and more effective means of output storage and processing would be advantageous.

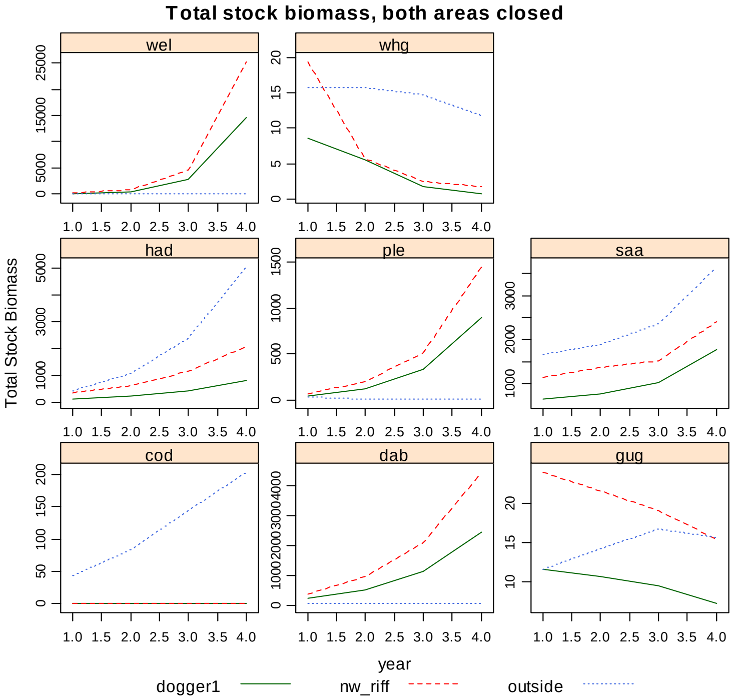


Figure 2.1 Total stock biomass for scenario where both patches are closed.

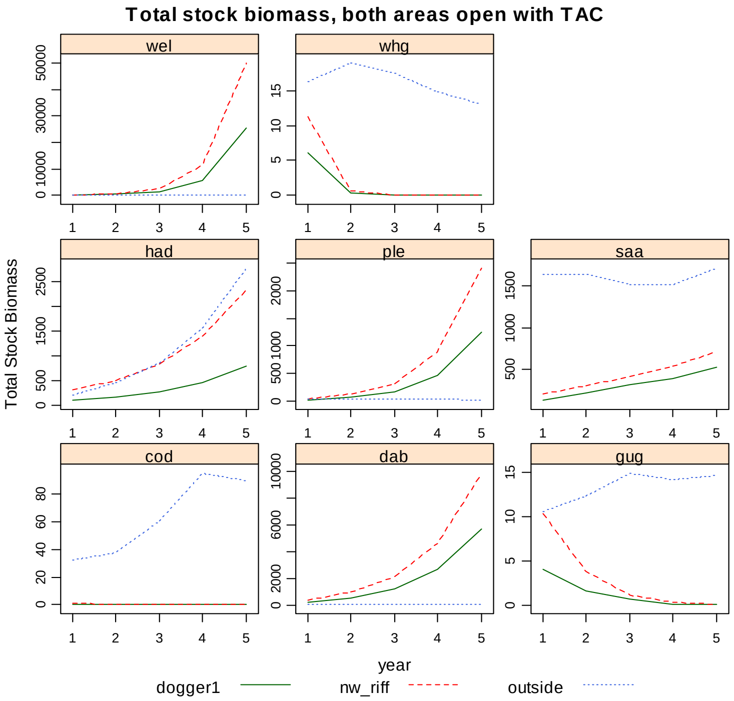


Figure 2.2 Total stock biomass for scenario where both patches are open.

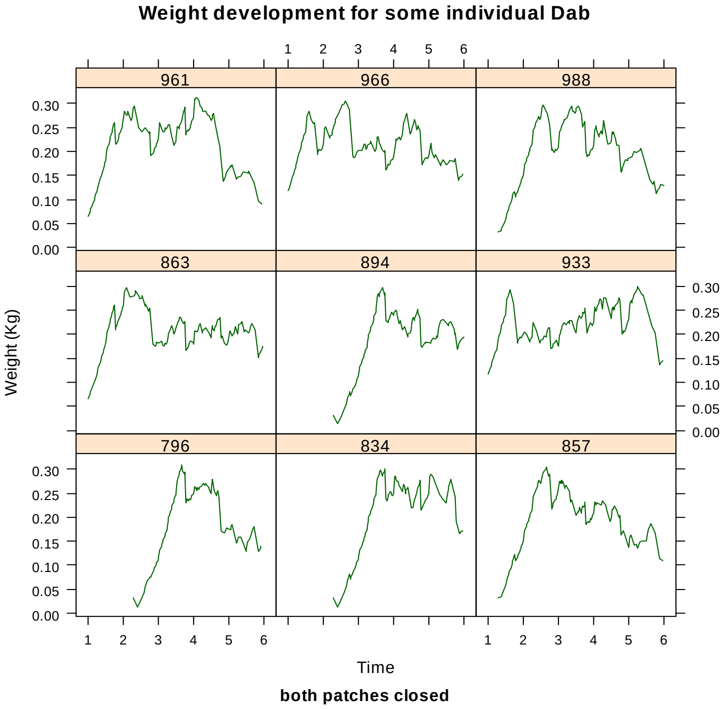


Figure 2.3 Weight development for selected individual Dab where both patches were closed.

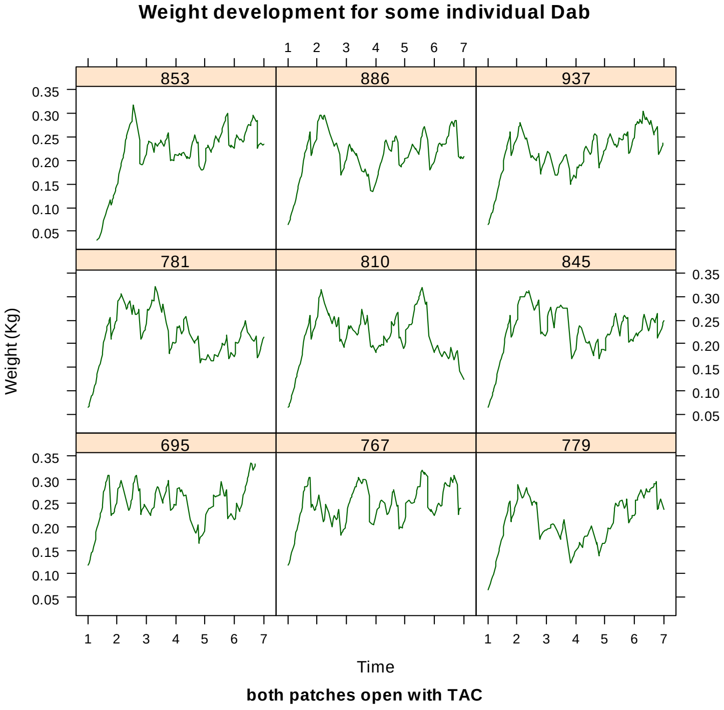


Figure 2.4 Weight development for selected individual Dab where both patches were open.

		Patch	Manageme	cod	dab	gug	had	ple	saa	wel	whg
a)	Both closed	Combined	Closed	0	6,910	23	2,861	2,336	4,174	39,865	2
b)	Both open	Combined	Open	0	7,281	1	1,858	1,367	932	16,869	0
c)	One open, one closed	dogger1	Closed	0	2,637	6	633	809	1,467	14,631	1
		nw_riff	Open	0	4,622	0	1,505	884	1,079	14,855	0
d)	One rotational, one closed	dogger1	Open	0	2,591	0	460	486	406	4,708	0
		nw_riff	Rotational	0	4,775	1	1,417	965	852	15,016	0

Table 2.1 Total stock biomass at the start of year 4 for the 4 scenarios

Objective 2: Identify and map the habitat of contrasting areas of sandeel exploitation in the Dogger Bank region. Monitor the population dynamics and use this to develop models of fishing effort in response to population density.

Key findings

- Between spring 2004 and autumn 2006, thirty-five days per year were to collect data on the environment, sandeels and their predators from a heavily fished area (Grid 1) and a lightly fished area (Grid 2) to the west side of the Dogger Bank.
- Acoustic methods revealed the topographic details of the study sites enabling insight to physical and environmental conditions influencing the spatial distribution of sandeels. There is a trade-off between the ability to perform high-resolution acoustic surveys and the need to survey large areas.
- Sandeels show a highly localised distribution both within the North sea and within the Dogger Bank region. Sandeel schools were much more abundant and clustered in their distribution in Grid 1. Although the schools in Grid 2 were fewer in number and more dispersed, they were found to be larger in size and acoustic energy indicating higher numbers of fish per school.
- During spring, their fine-scale distribution during the day (when feeding in the water column) differs notably from that during the night (when buried in the seabed) suggesting extensive diurnal feeding migrations occur at a scale of 5–10 km daily (Engelhard et al. submitted)
- Daytime distribution of sandeels is linked to hydrography (especially sea surface salinity), temperature and local biological parameters, notably zooplankton abundance (van der Kooij et al. in prep).
- Analysis of satellite tracking from commercial sandeel vessels shows that fishing effort is highly localised. It matches the spatial distribution of sandeel abundance well between the two grids, but not at the fine scale of a few km. Effort is primarily matched with local topographical features (Engelhard et al. submitted).
- Fishing occurs chiefly, during daytime between April and June at times when the majority of sandeels are in the water column feeding (Righton & Neville in prep) and hence available to capture.
- Sandeel nursery areas may be even more confined than adult localised distributions. The ‘high density’ grid 1 was apparently crucial as a local nursery area to the wider area.

2.1 Field survey methods overview

Between spring 2004 and autumn 2006, thirty-five days per year were to collect data on sandeels and their predators from a heavily fished area (Grid 1) and a lightly fished area (Grid 2) to the west side of the Dogger Bank (Figure 2.1). Surveys times were chosen to match the start and end of the main sandeel fishing season. At each sampling station, biological samples were taken to ascertain plankton abundance, sediment type, water column structure, seabird abundance, nocturnal sandeel density in the sediment and predator abundance. While steaming between the stations, hydroacoustics were utilized to estimate the abundance of sandeels in the water column. An extensive stomach-sampling programme of fish predators was used to determine the consumption of sandeels by fish predators. Five full stomachs were sampled per 5 cm length class of predator. Stomach contents were sorted to species where possible, and the weight and length of prey type was recorded. These data were used to characterise predator-prey interactions and parameterize the feeding functions within the multi-species management model and ecosystem models.

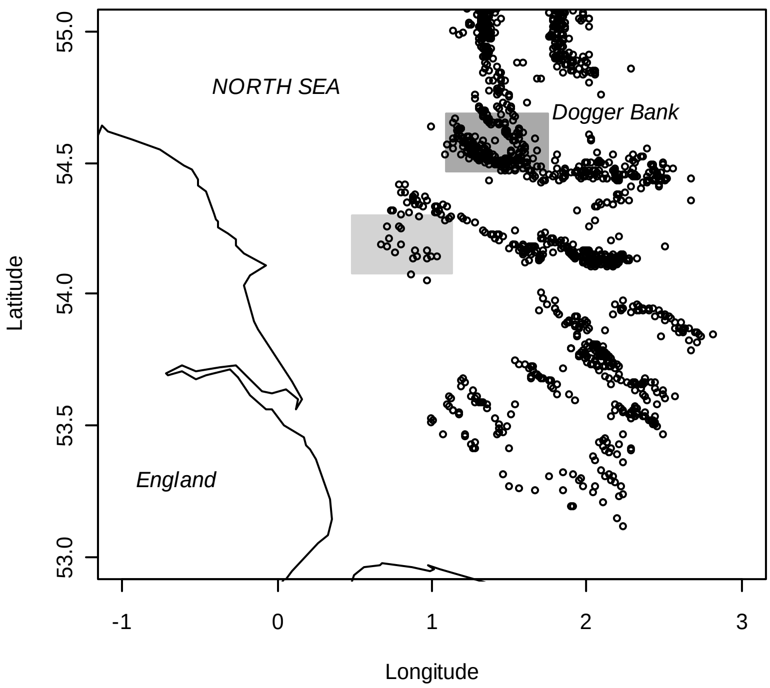


Figure 2.1. Map of the Dogger Bank study area, showing the locations of 'Grid 1' (dark grey) and 'Grid 2' (light grey). Symbols indicate distribution of sandeel fishing effort during the peak season (April–June) of 2005; note marked difference in effort between the two grids. Grid 1 is situated on the "North West Riff", at the southwest corner of the Dogger Bank. Grid 2, lies about 35 nautical miles southwest of site 1 in an area known as "The Hills". Each grid covers and area of about 800 km^2, and Grid 2 (The Hills), an equally sized but relatively unfished area. Each grid has 30 biological sampling stations arranged in a regular pattern.

2.2 Bathymetry and topographic features of the survey grids.

Methods

Over several cruises a combination of swathe bathymetry (Simrad EM3000 multi-beam sonar), acoustic ground discrimination data (QTC) and sediment samples (Hammond grab) were collected to develop a high resolution topographical map of the grids.

Results and discussion

Detailed bathymetry maps were created from the multi-beam data (Figure 2.2). In addition, the multi-beam data proved to be a useful tool to obtain quick insight into fine scale features of the seabed substrate over large areas (Figure 2.3). Apart from bathymetry, the multi-beam sonar also records raw backscatter data that contains information on the sediment structure. Overlaying the backscatter on the bathymetry allowed us to visualise the topography (Figure 2.4) and infer that the sediments on the ridges tended to be coarser. The distribution of sandeels schools in relation to the seabed was visualised (Figure 2.5), but unfortunately, this method is at present too data intensive to be used to survey large areas. Building on previous investigations, attempts to detect sandeels in the sediment at night on a large scale (survey grid scale) using acoustic ground discrimination proved unsuccessful and highlighted the difficulties of this method.

Single beam acoustic ground discrimination methods were used to identify suitable sandeel habitat and on one survey sediment samples were taken. Attempts to determine sediment characteristics by manual sieving of the Hammond grab samples while at sea were not successful enough to produce results at the level of detail required because of the low contrast in the sediment composition of the region. Storage and detailed sediment analysis was not deemed cost-effective, and so we relied up outputs from previous investigations (M0317) and recently published work (Holland et al 2005) to infer the habitat quality of sandeels.

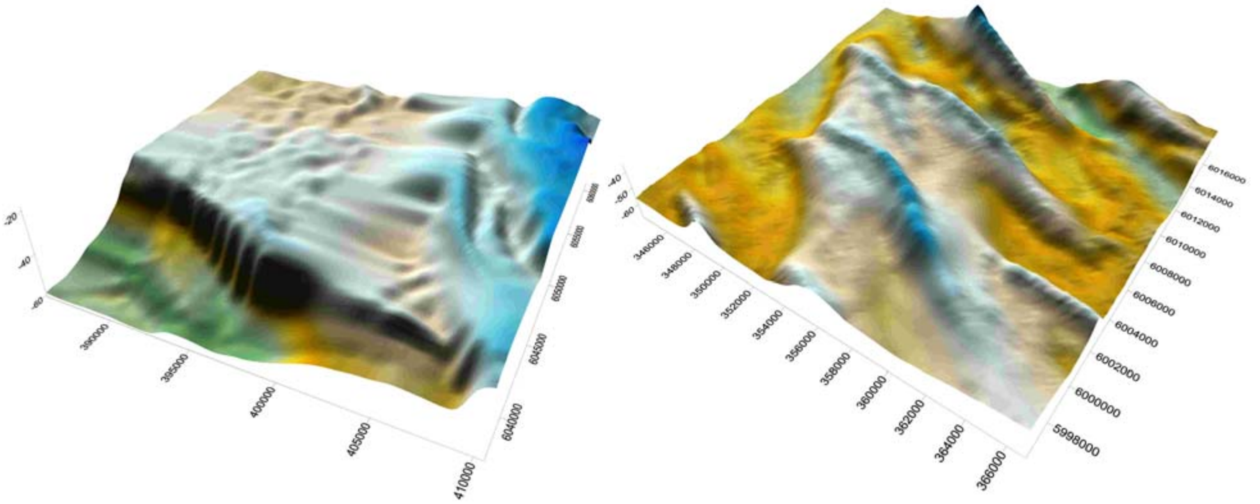


Figure 2.2. Detailed bathymetry maps of grid 1: Northwest Riff (left) and grid 2: The Hills (right)

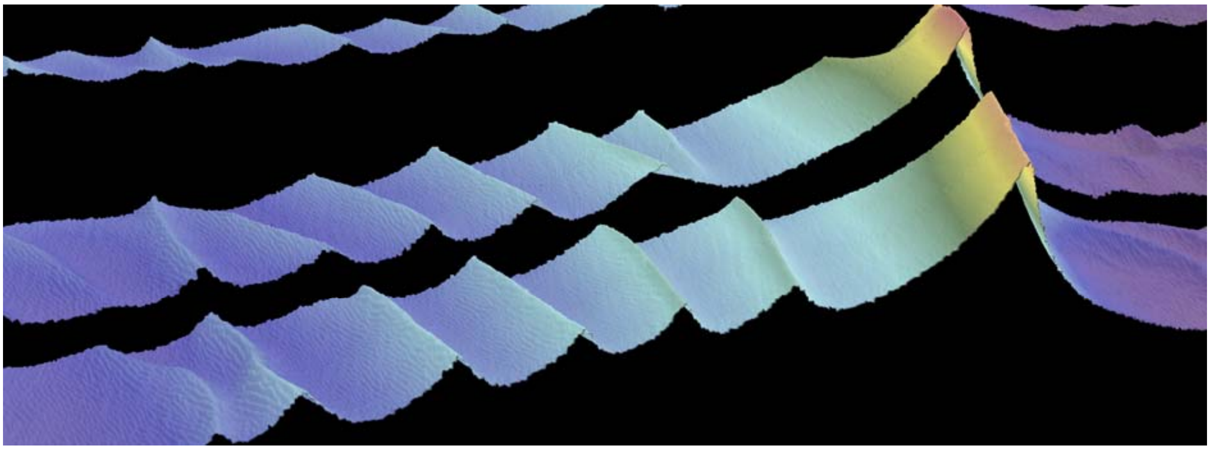


Figure 2.3. Detail of multibeam data from grid 2, displaying large and small sand ridges with small sand ripples.

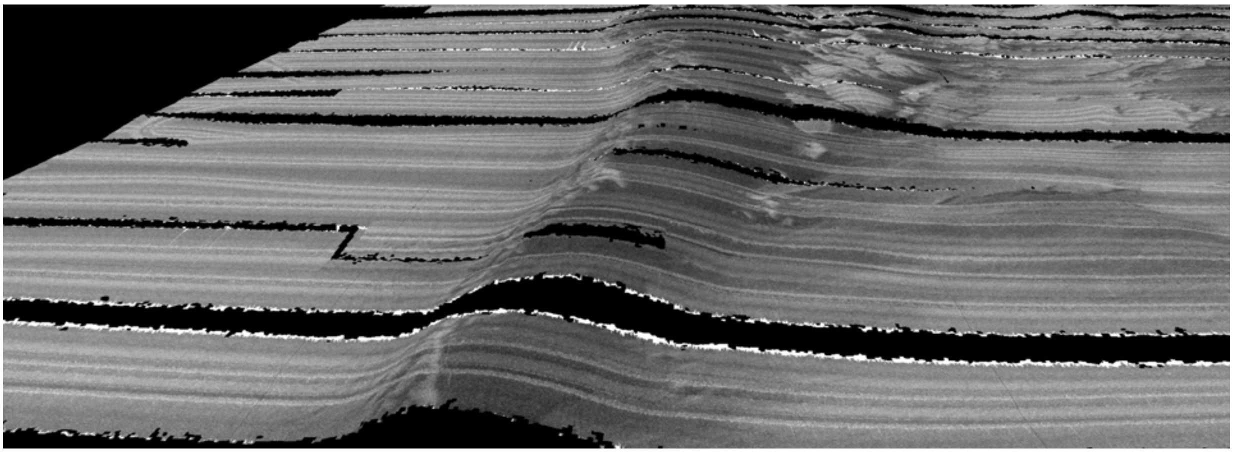


Figure 2.4. Detail of grid 1 seabed: swathe bathymetry with backscatter overlaid. Dark shade on top of bank represents coarser (sandy) substrate.

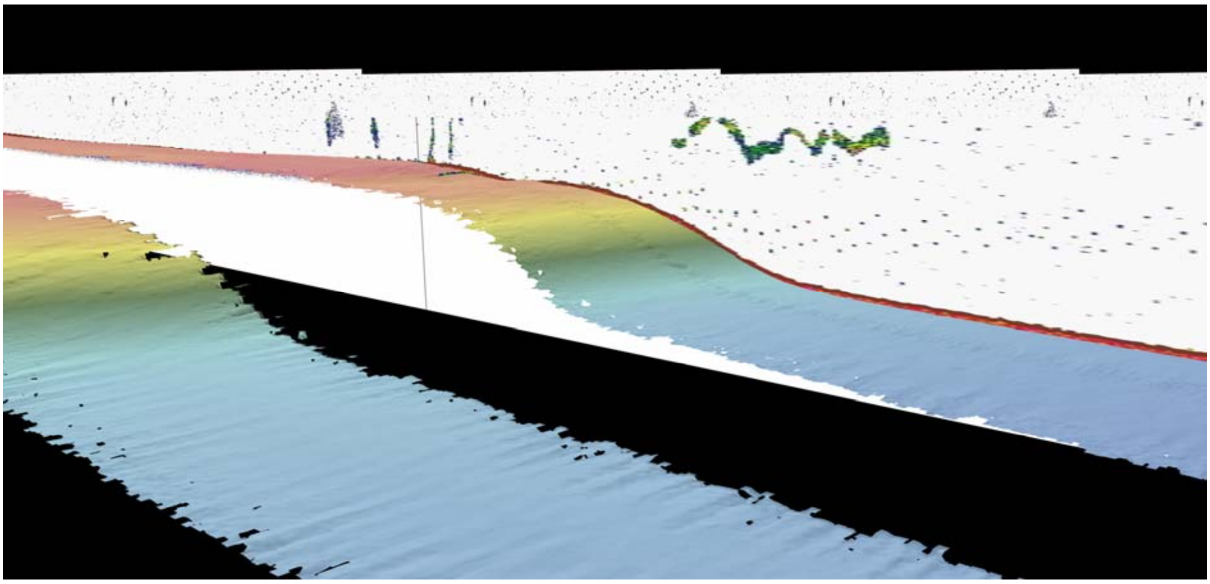


Figure 2.5. Echogram curtain with sandeel schools (blue and green marks) overlaid over bathymetry.

2.3 Aggregation patterns and structural characteristics of sandeels schools

Methods

Acoustic data were collected using a calibrated split-beam scientific echosounder (Simrad EK60) at two different frequencies (38 kHz and 120 kHz) between 5 am and 10.30 am when sandeels forage in the water column. The vessel speed was between 4 and 8 knots depending on weather conditions. Sandeel schools were classified by their shape, position in the water column, and by comparing the strength of the echo traces detected by two different acoustic frequencies (Mackinson, et al. 2005). Sandeels are detected far more strongly by the 120 kHz transducer primarily because they have no swimbladder. Echoview software (SonarData Pty Ltd) was used to select sandeel schools using a detection threshold of –65 dB, and to export a variety of school metrics.

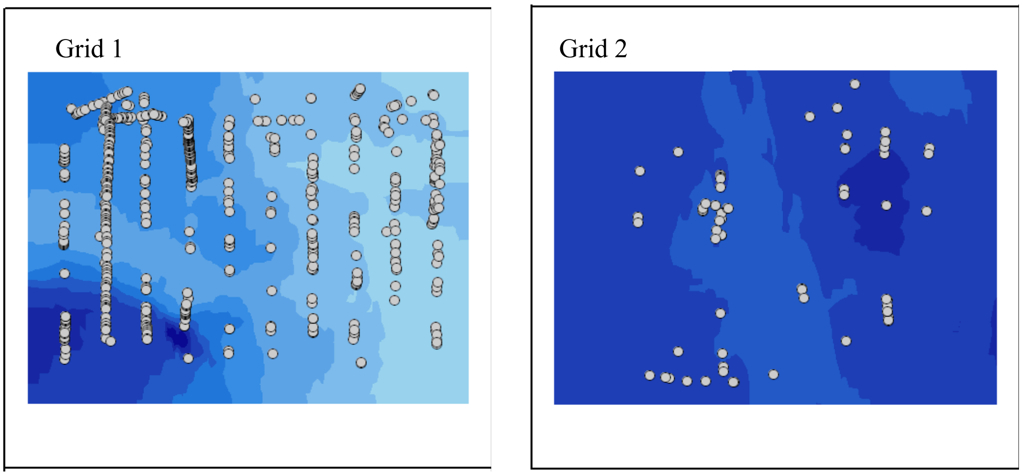


Figure 2.6. Comparison of the distribution of sandeel school locations in relation to bathymetry. All schools identified in the surveys 2004-2006 are plotted.

To compare the spatial distribution of sandeel schools between the two grids, GPS location, school depth (sea surface to school centre), distance from the seabed, seabed depth beneath the school, distance from nearest sandeel school (NND) (Mackinson et al. 1999; Viscido et al., 2005), and mean average distance to all other sandeel schools within grid (ISD) were determined. In addition, morphological parameters were calculated and used to compare the school structure between the two grids (length, height, 2D perimeter and area, 3D area and volume, elongation, compactness, horizontal roughness coefficient, vertical roughness coefficient, fractal dimension, uneveness, and rectangularity).

Results and discussion

In each year a greater number of schools were identified in Grid 1 (total of 611) than in Grid 2 (total of 90) (Figure 2.6). In 2004, no schools at all were identified in Grid 2, which corresponds with a particularly low overall abundance estimate that year.

Table 2.1. Comparison of spatial distribution parameters for sandeel schools.

Parameter	Mean (standard deviation)							
	Grid 1				**Grid 2**			
	All years n=611	2004 n=91	2005 n=129	2006 n=393	All years n=90	2004 (no sandeels)	2005 n=25	2006 n=65
School depth (m)	25.83 (7.85)	21.36 (3.54)	26.97 (6.77)	26.66 (8.62)	37.45 (11.29)		36.55 (7.71)	37.79 (12.52)
Distance from seabed (m)	9.78 (7.87)	5.09 (3.56)	8.58 (10.09)	11.25 (7.27)	13.66 (11.03)		11.91 (6.44)	13.83 (12.27)
School depth (% of total depth, m)	74.20 (17.07)	81.39 (11.49)	79.21 (19.32)	70.91 (16.50)	73.45 (20.16)		75.63 (12.49)	73.16 (22.12)
NND (km)		0.68 (1.33)	0.60 (1.24)	0.22 (2.62)			1.58 (0.50)	0.91 (1.50)
ISD (km)		15.90 (7.31)	22.71 (4.72)	13.55 (6.80)			14.75 (3.49)	22.92 (4.32)
Cluster Coefficient		0.04 (0.06)	0.03 (0.06)	0.02 (0.13)			0.11 (0.03)	0.04 (0.06)

Table 2.2. Comparison of the structural characteristics of sandeels schools

Parameter	Mean (standard deviation)		
	All (*n* = 701)	Grid 1 (*n* = 611)	Grid 2 (*n* = 90)
NASC	244.62 (564.2)	239.6 (579.2)	278.73 (450.54)
Height_mean	1.64 (1.11)	1.62 (1.08)	1.76 (1.29)
Corrected_length	20.1 (17.45)	19.91 (17.73)	21.38 (15.47)
Corrected_perimeter	157.99 (173.08)	148.72 (144.66)	220.91 (295.97)
Corrected_area	31.84 (45.54)	30.5 (40.06)	40.97 (72.23)
Image_compactness	77.83 (90.3)	72.92 (81.53)	111.14 (131.5)
Horizontal_roughness_coefficient	0.000017 (0.000035)	0 (0)	0 (0)
Vertical_roughness_coefficient	0.000003 (0.000007)	0 (0)	0 (0)
3D_school_area	284.94 (470.47)	268.33 (401.45)	397.67 (788.38)
3D_school_volume	41.22 (108.28)	40.03 (98.87)	49.29 (158.53)
Elongation	17.14 (19.36)	17.13 (19.86)	17.23 (15.67)
Fractal dimension	2.2 (1.35)	2.18 (1.43)	2.33 (0.49)
Uneveness	22.11 (23.68)	21.88 (24.27)	23.71 (19.27)
Rectangularity	1.19 (0.38)	1.21 (0.41)	1.09 (0.08)

The depth of the seabed is far greater in Grid 2, and consequently the mean depth of the sandeel schools is also greater than in Grid 1. However, the position of the school as a percentage of the total depth was almost identical in both grids (~74 %) suggesting relative depth within the water column is more important than actual depth. Sandeels were far more abundant in Grid 1, and the distance between schools was far less. The differences in abundance between 2004, 2005 and 2006 caused the clustering to change. Where there were relatively high numbers of schools (2006 - 393 schools) the clustering was found to be greater.

For many of the individual school parameters there was little difference between the two grids (Table 2.2). However, the values for acoustic energy (NASC), perimeter, area, and 3D school area for the sandeel schools were much greater in Grid 2, so although the schools in this grid were fewer in number, the schools were found to be larger and contain more acoustic energy indicating schools with higher numbers of sandeels.

2.4. Sandeel distribution during day and night

Methods

This consisted of (1) at night, sampling sandeels in the seabed by dredge; (2) from morning to midday, observing sandeels in the water column by means of acoustics; and (3) during morning or afternoon, sampling sandeel predators (and their stomach contents) caught by Granton trawl.

Results and discussion

During autumn surveys, sandeels were often recorded in the seabed (by dredge) but virtually none were observed acoustically in the water column, in line with the hibernation behaviour of sandeels from September to early April (Macer 1966). During spring surveys however (coinciding with the feeding season), sandeels were frequently observed in the water column by day, and in the seabed by night. The two study grids differed markedly in sandeel numbers, which were far higher in the heavily fished Grid 1 than in Grid 2 (Table 2.3). In addition, observed sandeel numbers were considerably higher in May 2005 and especially 2006, than in April–May 2004. Indeed, in 2004 sandeel abundance in the North Sea is generally known to have been particularly low (e.g. Frederiksen et al. 2005).

Table 2.3. Day and night sandeel abundance compared between study grids and years (means ± SE of values for 60 stations). Day abundance: numbers in the water column observed through acoustics; night abundance: numbers in the sediment measured by dredge (corrected for dredge inefficiency following Mackinson et al. 2005). Data from Engelhard et al. (submitted).

Study season	Day abundance (sandeels per 1000 m^2)		Night abundance (sandeels per 1000m^2)	
	Grid 1	Grid 2	Grid 1	Grid 2
April–May 2004	212 ± 85	0	502 ± 178	134 ± 25
May 2005	3583 ± 1347	449 ± 266	695 ± 187	290 ± 67
May 2006	4244 ± 2972	241 ± 97	2263 ± 612	321 ± 136

There was also a very localised sandeel distribution at the finer spatial scale of stations within study grids. Notably, during spring marked day–night differences in sandeel spatial distributions were found (Figure 2.7). These suggested that sandeels undertake extensive, horizontal diurnal movements during spring (Engelhard et al. submitted). Movements were most prominent in the 'high density' Grid 1 (at a scale of about 10 km daily), although less so in the 'low density' Grid 2 (up to 5 km daily). This scale is larger than recorded previously (Kühlmann & Karst 1967; Hobson 1986), but sandeels were, in accordance with earlier studies, found to move between shallower grounds at night and deeper waters during the day. Night sandeel locations were often characterised by medium to fine sands, previously described as preferred sandeel burying habitats (Wright et al. 2000; Holland et al. 2005). Characteristics of daytime sandeel locations are described below in section 2.5. Overall, our results are consistent with the idea that sandeel diurnal movements are motivated by local distributions of suitable night shelter and day feeding opportunities (Reay 1970; Wright et al. 2000).

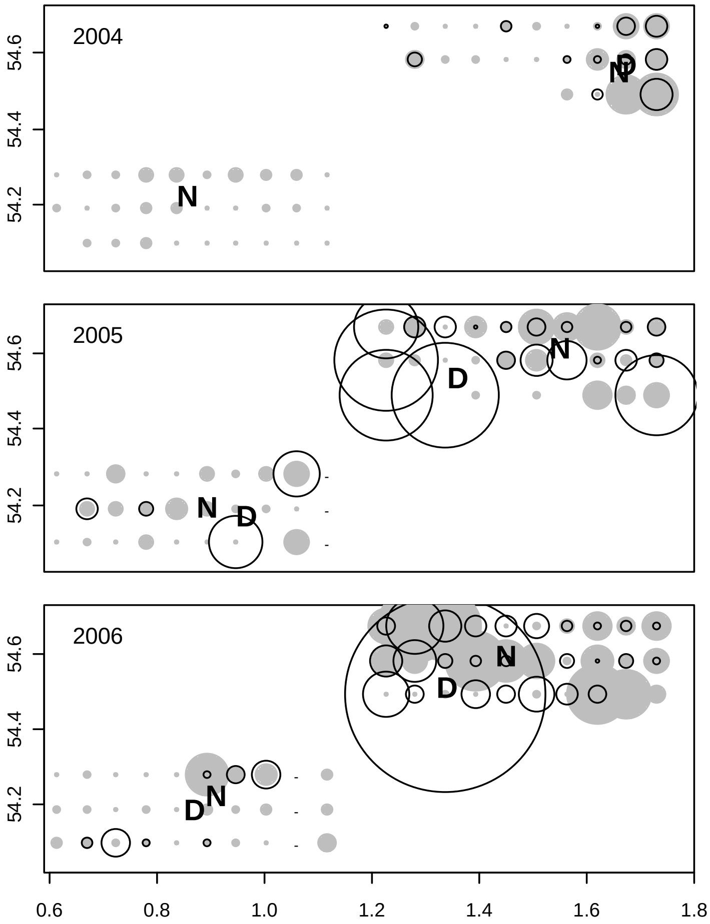


Figure 2.7. Day and night distributions of sandeels in the two study grids, as observed during April–May 2004 (*top*), May 2005 (*middle*), and May 2006 (*bottom*). Size of grey symbols proportional to night (seabed) sandeel numbers; areas of open symbols proportional to day (in-water) sandeel numbers (same scale for day and night). Hyphens indicate grid points not surveyed in the given year. Letters D and N mark the within-grid centres of gravity of sandeel distribution during day and night, respectively. From Engelhard et al. submitted.

2.5. Linking sandeel distribution to environmental parameters.

Methods

Plankton and oceanographic data were sampled on the stations of the study grids. Zooplankton samples were taken vertically using a ringnet (200 µm) from the surface to 4m above the seabed, and vertical salinity and temperature profiles were collected on the same stations using a CTD mounted on the ringnet. Sandeel day distribution and densities in the watercolumn were derived from fisheries acoustics, and numbers of sandeels in the seabed at night was used as a proxy for suitable habitat. We used generalised additive models (GAMs) to investigate the assumed relationships between the dependent variable (spring sandeel densities) and covariates, in this case zooplankton, quality of night habitat and various hydrographic features, through a series of additive and unrestrictive smooth functions. A GAM is a non-parametric multiple regression technique, with advantage over conventional regression methods because it is not dependent on specific functional relationships and is less restrictive in its assumptions about the underlying statistical distribution of the data. A two stage model was implemented, firstly modelling the presence or absence of sandeels in relation to the environmental variables, and secondly, given that sandeels are present, their abundance. Different combinations of covariates as well as varying smooth functions were explored to acquire the best model, and model performance was tested using established statistical criteria.

*Results and discussion (*van der Kooij et al. in prep)

Spring sandeel distribution during the day was significantly related to bottom temperature (with optimum at ~8.7ºC) and suitable night -time habitat. In addition clear patterns in relation to surface salinity and bottom depth were observed. Abundance of sandeels was best explained by bottom temperature (again with optimum at ~8.7ºC) and surface salinity (optimum at ~35ppt). As expected, a positive relation was found between zooplankton densities and sandeel abundance. Although not significant, some patterns in the difference between surface and bottom temperature emerged indicating that more sandeels were found in more stratified waters (Figure 2.8).

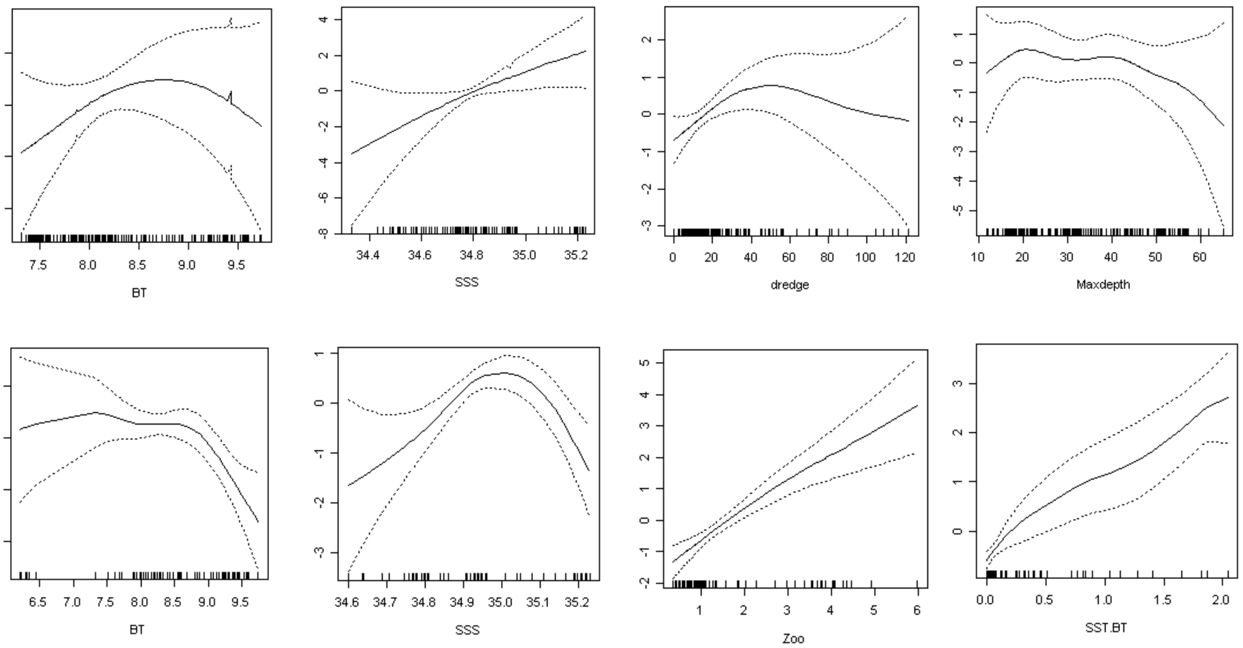


Figure 2.8. GAM regressions for sandeel daytime presence/absence (top graphs) and sandeel daytime abundance (bottom graphs) as a function of various environmental variables. BT=bottom temperature, SSS=sea surface salinity, dredge=square root of sandeel abundance in dredge (at night), Maxdepth=bottom depth, Zoo=square root of zooplankton densities and SST.BT=difference between surface and bottom temperature. Dashed lines represent standard error ranges around the covariate main effects and tick-marks on x-axis represent location of data points.

These results confirm suggestions postulated by Reay (1970) and Wright et al. (2000). However the two stage modelling approach undertaken in the present study conveyed a more in-depth insight into the ecological behaviour of sandeels in the area area and the relative importance of the various environmental factors on sandeel distribution and abundance.

2.6. Temporal and spatial distribution of sandeel fishing effort.

Methods

Satellite tracking data for commercial sandeel vessels operating on the Dogger Bank were obtained from Danish authorities and analysed to investigate the patterns in fishing effort.

Results and discussion

The Dogger Bank sandeel fishery is, perhaps unsurprisingly, found to be tightly related to sandeel life-history. It is highly localised both within the North Sea and within the Dogger Bank region (Figure 2.1), linked to the very localised abundance of sandeels at shallower sandy banks or ridges. Sandeel fishing effort differed substantially between our two study grids; averaged over 2002–2005, effort was over 40 times higher in Grid 1 than in Grid 2. This was in accordance with far higher sandeel numbers observed in Grid 1 during our surveys. It was mainly during March–June that far greater effort occurred in Grid 1; in the other months there was very little effort in either grid (Figure 2.9). Clearly, there is a close match between the seasonality of the fishery and that of sandeels feeding in the water column.

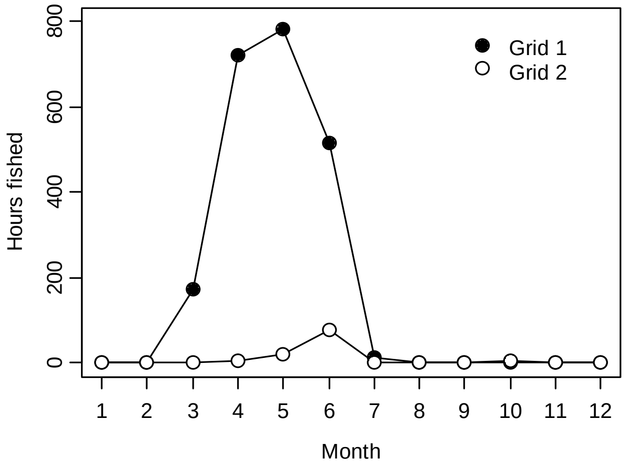


Figure 2.9. Monthly sandeel fishing effort (number of hours fished by Danish sandeelers, averaged over January 2002–August 2006) expended in Grids 1 and 2. From Engelhard & Bell 2006.

Fishing effort shows distinct day–night differences in movements by sandeel fishing vessels. Vessel speeds characteristic of trawling (2–4.5 knots) occurred far more frequently during day than night, consistent with targeting of sandeel schools when these are swimming freely in the water column. By contrast, vessel speeds characteristic of steaming (>4.5 knots) occurred more commonly at night, implying that darkness hours when sandeels are buried in the seabed (Figure 2.10).

Interestingly, effort distribution only matched that of sandeel numbers at moderately fine spatial scale (between Grid 1 and 2).Within-grid scale of sampling stations, effort distribution did not correlate well with day sandeel distributions despite most trawling occurring during daylight; neither were there clear links with night sandeel distributions (Figure 2.11). Generally, only weak (P>0.05) correlations were found between sandeel numbers (day or night) measured at stations, and the number of hours fished locally in corresponding months (Engelhard & Bell 2006). Rather, the ‘centres of gravity’ of effort distribution within grids tended to be intermediate between those for the day and night sandeel distributions (Figure 2.11). Nevertheless, effort distribution was highly localised but it appeared to be primarily matched with local topographical features—fishers closely following the shallower ridges and sandy banks. Our previous, acoustic studies revealed that good sandeel catches may generally be obtained here (Mackinson & van der Kooij 2006). Indeed, fishing location choices frequently incorporate knowledge on catch rates during previous years or weeks (Rijnsdorp et al. 2000). We recognise that our acoustic data provide only ‘snap-shots’ of sandeel abundance at the time of surveys, and may not necessarily be good indicators over the longer time-span of a fishing season. Accounting for this, it appears that fishers have ‘imperfect’ knowledge of where precisely the highest concentrations of sandeel schools are found at the time of fishing, perhaps partly due to the high mobility of sandeels during their diurnal migrations. In spite of fishing being concentrated during daylight there were no indications that fishers actively follow diurnally migrating sandeel schools (Engelhard et al. submitted).

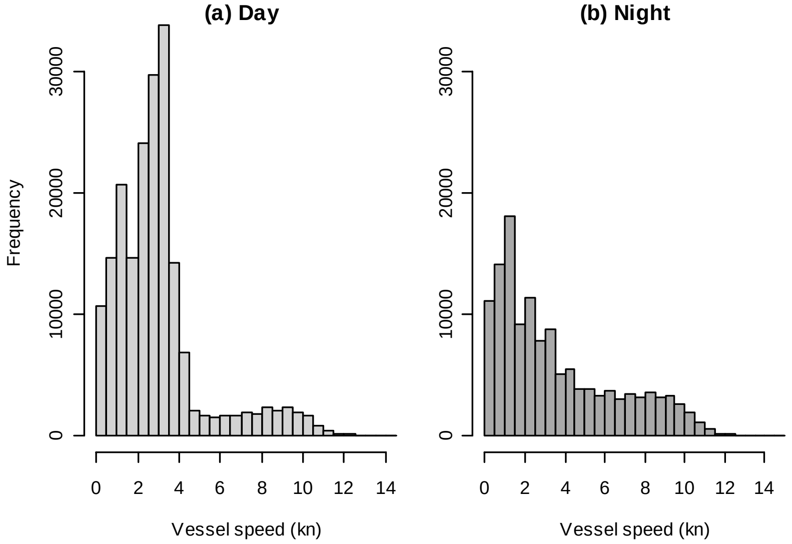


Figure 2.10. Frequency distributions of vessel (net) speeds in VMS observations of 107 sandeelers during (a) daylight and (b) darkness hours. From Engelhard & Bell 2006.

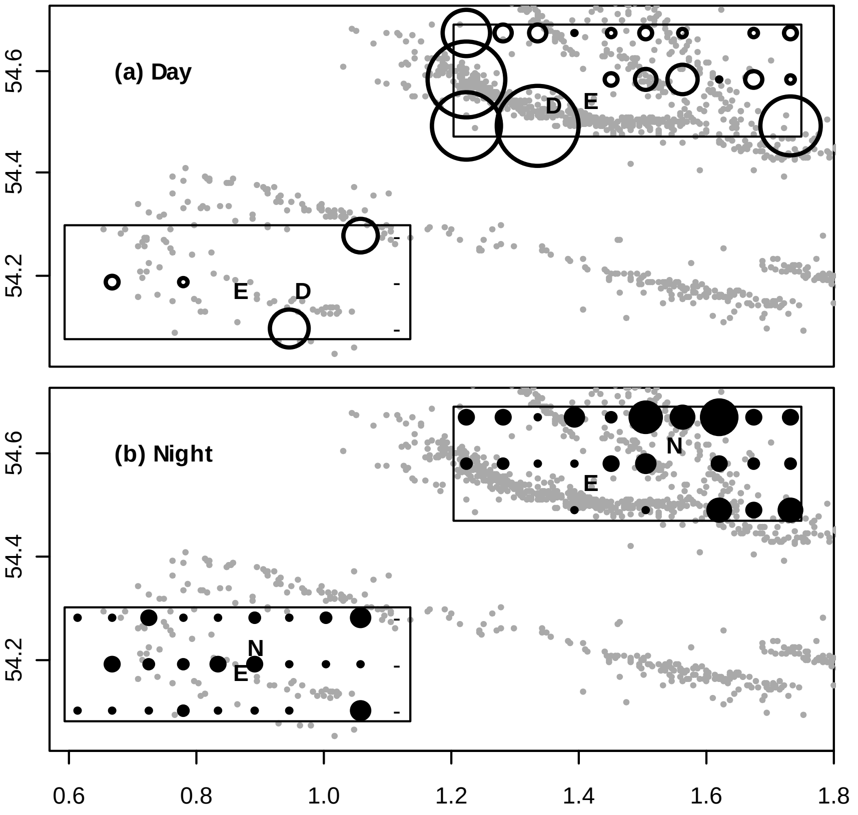


Figure 2.11. Fine-scale distribution of sandeel fishing effort, compared with day and night sandeel distributions in the two study grids (rectangles). Small grey dots each represent approximately 3 h fished by sandeelers in April–June 2005. Size of open symbols in (a) proportional to day (in-water) sandeel numbers measured acoustically during the May 2005 survey; size of closed symbols in (b) proportional to night (in-seabed) sandeel numbers measured by dredge. Hyphens indicate unsampled stations. Letters E, D and N mark the within-grid centres of gravity of fishing effort, day and night distributions of sandeels, respectively. From Engelhard et al. submitted.

2.7. Feeding periodicity of sandeels

The above-mentioned day–night differences in sandeel distributions clearly indicated diurnal migrations during the feeding season, but left open the question of feeding periodicity, i.e. what fraction of sandeels tends to participate in feeding migrations each day. The question is highly relevant if acoustics data on sandeels are to be used for stock assessment purposes, and was addressed by 2 approaches.

(i) Gut evacuation experiment [initial experiment funded by Defra M0317]
Approach 1 was a gut evacuation experiment carried out within Grid 1 in June 2001 aboard RV *Corystes*. At 13:30, which is towards the end of the sandeel daily foraging period, 230 sandeels were caught by trawl and held in a 2-m deck tank containing fresh filtered seawater. Over the next 24 h, 10 fish were sacrificed each hour, frozen and returned to the lab, where their gut contents were examined. Indeed, gut evacuation was indicated by a continual decline of the mean weight of gut contents throughout the experimental period (Figure 2.12), and it appears that after about 12 h approximately 50% of the gut is evacuated (Righton & Neville in prep.).

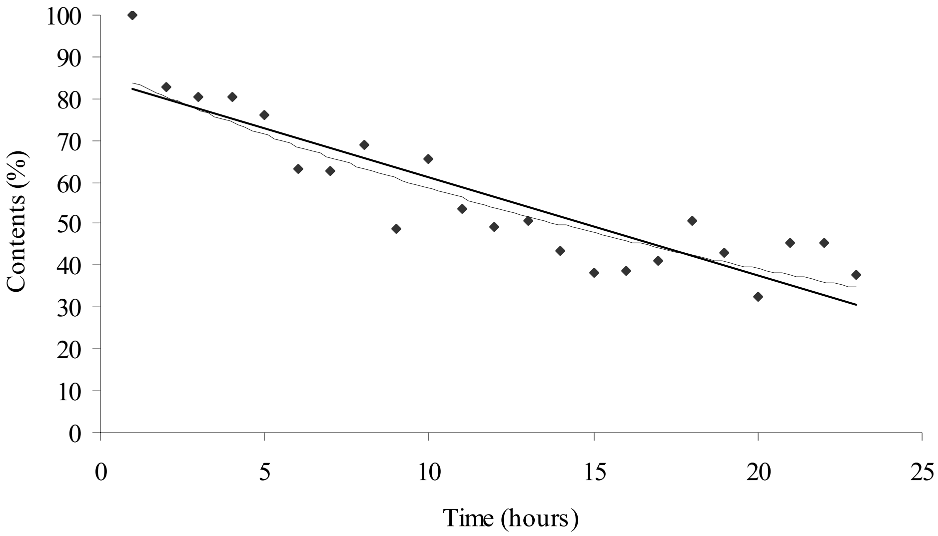


Figure 2.12. Percentage weight of mean gut contents, assuming at hour one the gut is 100% full. From Righton & Neville in prep.

(ii) 24-h dredge experiment
Approach 2 for examining sandeel feeding periodicity was an experiment whereby 24 dredge hauls were repeated at the same site but at different periods of the day (Figure 2.13). Sandeel numbers in the seabed were highest at night, lowest at midday, and intermediate during morning and evening hours. The relative densities indicated that during daylight hours, at least 77% of sandeels had moved from the seabed to feed in the water column.

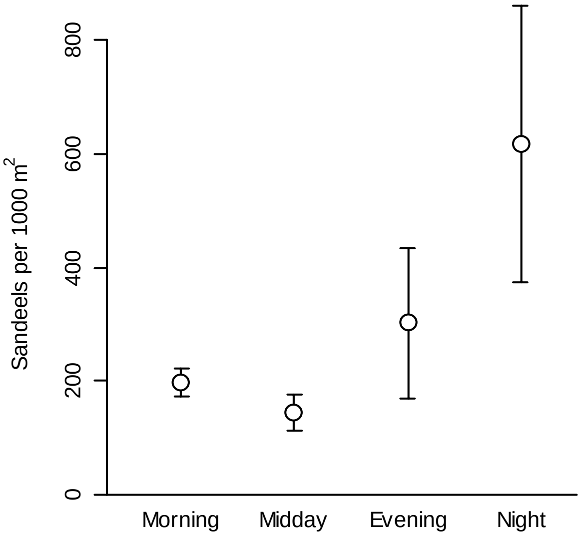


Figure 2.13. Density of sandeels in the sediment (mean ± SE), as sampled by dredge at different times of the day (20–21 May 2006). Six dredges were carried out per period, all within an area of 2 km^2.

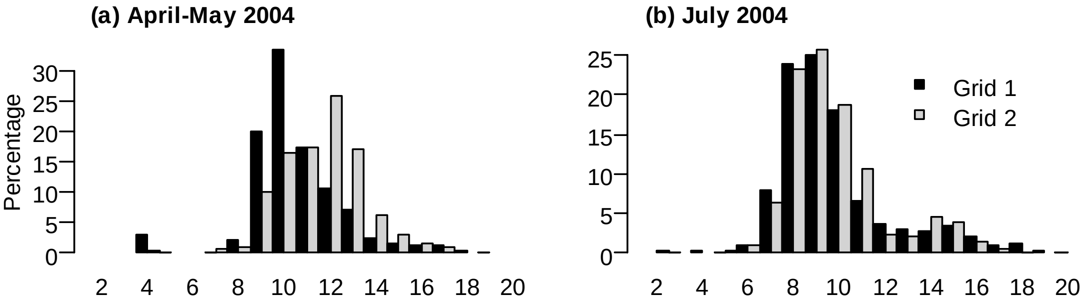
Combined these two approaches show that each day of the feeding season, the majority of sandeels are expected to participate in feeding migrations. The gut evacuation experiment shows that well within 24 h of feeding, most gut contents are evacuated and sandeels are thus likely motivated again to go out feeding; and the 24-h dredge experiment shows that by midday, only a small fraction of sandeels (about 23%) are still in the seabed.

The results of the 24-h dredge experiment are also relevant in assessment context. If sandeel abundance is to be derived from day-time acoustics data (as in Mackinson et al. 2005), then we propose that acoustic sandeel abundance estimates from morning, midday and evening data are to be inflated, respectively, by factors 1.5, 1.3 and 2.0 to obtain total (in-water and in-seabed) sandeel abundance (Engelhard et al. submitted).

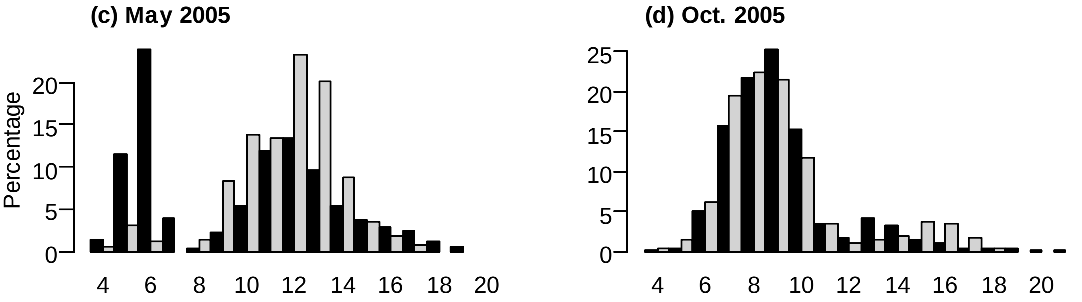
2.8. Size composition of sandeels in the two study grids.

There was evidence that the ‘high density’ Grid 1 not only has generally higher sandeel numbers, but also can crucially function as nursery area in contrast to Grid 2. This becomes clear if length frequency distributions (from data collected by dredge) are compared between grids, years and seasons (Figure 2.14). Firstly, it should be noted that in Grid 1, owing to far higher general sandeel abundance, total numbers in any size class were almost always higher than in Grid 2. However, during our spring surveys (Figure 2.14, left-hand graphs) we observed far higher relative (and absolute) numbers of small (<8 cm) sandeels in Grid 1 than in Grid 2; in fact, hardly any small sandeels were observed in the latter grid at all (Figure 2.14). The size difference between grids was especially pronounced in spring 2005, when a strong incoming year-class was highly abundant in Grid 1 but almost absent from Grid 2—notice that this year-class strongly contributed to the considerable increase in sandeel abundance from 2004 to 2005. During our summer 2004 and autumn 2005 surveys, the size differences observed between grids in spring had virtually disappeared, although it was still present to some extent during autumn 2006 (Figure 2.14, right-hand graphs).

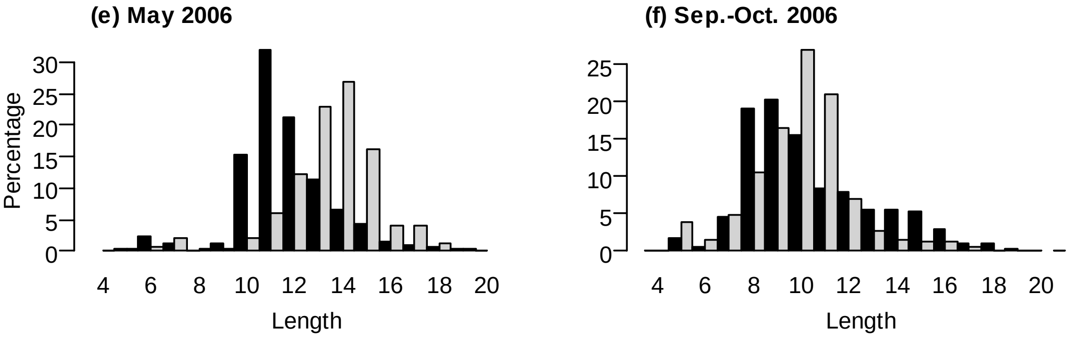
Overall this implies that during the spring feeding season, small (young) sandeels differ from larger (older) individuals in that they are more limited in where they occur, being almost restricted to the apparently ‘high quality’ Grid 1. Most likely this relates to differences in feeding behaviour between juveniles and adults. Later in the year when the feeding season has finished, juveniles apparently partly disperse out of these ‘nursery areas’ and their distribution becomes more similar to that of adults. In this context it is important to note that relatively confined ‘core areas’ can be of crucial importance for successful recruitment in sandeels, with implications for stock dynamics.


(a) April-May 2004

(b) July 2004


(c) May 2005

(d) Oct. 2005


(e) May 2006

(f) Sep.-Oct. 2006

Figure 2.14. Length frequencies of sandeels in Grid 1 (black bars) and Grid 2 (grey bars), as observed during 3 spring surveys (left) and 3 summer or autumn surveys (right) in 2004, 2005 and 2006.

Objective 3: Determine the temporal and spatial scales of movement of sandeels and their predators at each study site using marking, acoustic and tagging information. Use this to help parameterise fish behaviour in the management model.

Key findings

- Changes in the day-night distribution patterns (reported in objective 2) were used to infer the movements of sandeels because technical problems prevented the use of mass-marking and acoustics to track their short-medium term movements.
- The movements of fish predators were inferred from previous experiments since the fish predators captured during the surveys were too small to be tagged with electronic tags and results from conventional tagging were insufficient. Predator movement rules are used in the multi-species IBM used for evaluating management scenarios.
- Large uncertainties in bird sighting data meant that it was not possible to accurately relate bird movements and distribution to that of sandeels.

In addition to the knowledge of sandeel and fish predator movements gained from our survey work on distribution patterns (described in objective 2), the field programme was designed to use innovative techniques to investigate the short to medium term movement patterns of sandeels and their fish predators. This work was acknowledged as a risk in the project proposal. Unfortunately, technical problems with acoustic equipment on-board the RV Endeavour, and low occurrence of suitably sized predatory fish meant that the planned studies were either unsuccessful or could not be undertaken. This necessitated changes to the program: these changes were agreed with Defra. Alternative approaches were also largely unsuccessful. Instead, the scale of movements of sandeels was determined by comparing the locations of sandeel densities during the night and day, measured during acoustic and fishing surveys during the project fieldwork. For predators, the best information comes from predator behaviour rules developed through previous Defra (M0317) and EU investigations (CODYSSEY).

3.1 Temporal and spatial scales of sandeel movement

A feasibility study was undertaken to identify candidate methods for mass marking of adult sandeels at sea. However, none of the candidate methods (e.g. the use of fluorescent dyes to mark sandeels, the use of tetracycline to mark otoliths) were either legitimate (due to the transfer of chemicals into the human food chain) or practical on a large-scale due to cost. Wire tagging of individuals was also considered, but the likelihood of recapture and detection of these devices in such abundant animals was so low as to be unsuitable. Small-scale marking experiments would not have been cost-effective use of ship given the likely low recapture rates and therefore an unlikely avenue for the delivery of worthwhile results.

Cefas Endeavour carries a the Simrad SH80 sonar which is a high-resolution unit designed to track the movement of fish shoals. Although a computer program that enabled us to target track fish schools using was developed and successfully tested, the sonar unit suffered from repeated technical problems which prevented the collection of data suitable for analysis within this project. These technical problems were overcome at the end of 2006, and the methods have subsequently proven successful. Successful application of the technique relies on finding clusters of schools in a localised area, and while it was not possible to use the method to track sandeel schools within this project, the movements of herring and sprat schools in the Irish Sea were tracked during another project for proof of concept.

3.2 Movement of predators

Predatory fish

Whilst depletions in the local abundance of sandeels has been linked to reduced breeding success for specific colonies (Rindorf et al. 2000), little work has been conducted on the dependence of predatory fish on particular patches of sandeel. It is generally assumed that the predators will either switch prey type or change location in response to reduced sandeel availability. Project MF0317 demonstrated that, for long periods within summer, cod within the North Sea remain static and are thus potentially much more vulnerable to local depletion of sandeels.

During the first field season it became apparent that the predators at the study sites were not of a suitable size (>40cm) to be fitted with acoustic 'pinger' tags. We consulted with Defra in March 2005 and agreed to a change in research program from using acoustic tags to traditional tags. In total 562 fish were tagged, mostly whiting, gurnard and dabs (see Annexe 2). The results are insufficient to glean any meaningful information: only 3 tags have been returned - 1 plaice after 35 days and shrank 7mm, 1 dab - 209 days and shrank 1mm, 1 plaice - 215 days and grew 23mm. The recapture positions of the recaptured fish were estimated, so cannot be used as reliable indicators of movement.

Movement parameters of predatory fish were therefore estimated using data from mark-recapture experiments undertaken in previous years, held on the Cefas 'Tagfish' database*. In total, release and recapture information for 3742 cod tagged in the southern North Sea were available. Recapture data for cod tagged spanned mostly between early 1960's to mid-1980's with 70% of ICES div IVc cod recaptured during the 1980's. Any recaptures of cod that occurred within 90 days of release were excluded. This was to ensure that the movements measured were those of cod with sufficient time to migrate to different areas between the spawning and feeding periods, and that any same quarter recaptures remaining were of cod that had been at liberty for over a year after their release. Recaptured cod were all released during quarters 1 and 4 (n=1785). Finally recaptures were placed into size categories dependent on the length of cod at recapture: smaller than 50cm (classed as 'juvenile') or larger than 50 cm (classed as 'adult'). Maturity ogives derived from International Bottom Trawl Survey (ICES, 2005) data collected between 1977 and 2005 confirmed that this split was consistent with mean size at 50% maturity.

The results of the analysis suggest that cod migrate to feeding grounds during spring and remain there during summer before migrating back to spawning grounds in autumn (Figure 3.1). For cod in the southern North Sea, the mean bearing of movement is north in spring and south in autumn, at a speed of ~4 km per week. Adult cod travelled further and faster than juveniles, which tended to be caught close to their point of release even after a year at liberty. These data support the results of recent experiments using electronic and acoustic tags (Righton et al., 2001) that show residence on feeding grounds in the summer months and migration in spring and autumn. Similar results have been described for plaice (Bolle et al., 2005).

These results were used as the basis of size-based movement rules for predatory fish, and were subsequent incorporated in the multi-species IBM:

- Predatory fish smaller than 40cm were assumed to behave like juvenile cod, and not migrate between feeding and spawning grounds;
- Predatory fish large enough to spawn (>50cm) were assumed to behave similarly to cod, and migrate annually between spawning grounds in the south and feeding grounds on the Dogger Bank;
- Predatory fish could move at a speed between 0.3 body lengths per second and 0.9 body lengths per second (the range of sustainable swimming speed over short-periods ~ 1 day) in random directions during the feeding season

- The swimming speed was chosen so that horizontal movements of all predatory fish during the summer followed a Levy flight pattern. A Levy flight is a specialised random walk where the probability of step length l is modelled as $P(l)=\alpha l-\mu$, where μ can take a value between 1 and 3, and α is a tuning parameter. An optimal forager feeding on patchy prey would be expected to have an exponent of 2 (the Levy flight).

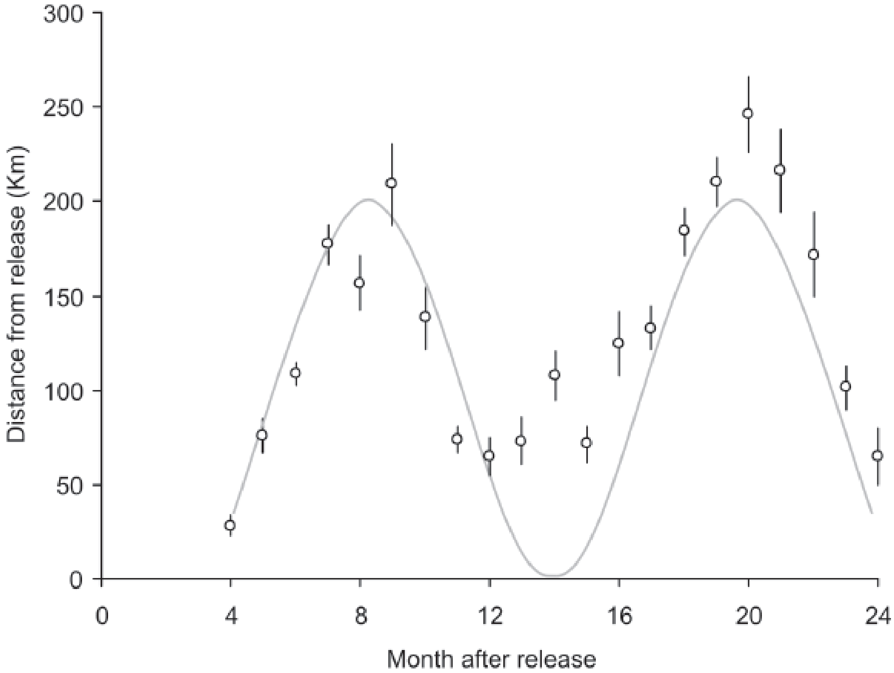


Figure 3.1. Mean distance between release and recapture positions of cod tagged and released in ICES area IVc in the spawning season. Lines of best fit were calculated by co-varying the parameters of sinusoidal wave (frequency, amplitude and offset) and using a least-squares minimisation routine.

*Note: this work was undertaken under project codes MF0158 and MF0154, and is in press in the Journal of the Marine Biological Association (UK).

Predatory seabirds

Using standard protocols, bird-sighting information was collected for the purpose of mapping the distribution and movement of seabirds and relating this to the distribution of sandeels during the daytime. The data was found to be inadequate due to large uncertainties exist due to errors in identification of species, determining directions of movement and counting in variable visibility conditions.

Weighted for numbers seen together, the 1657 sightings represent 3135 birds. Almost 90% of records were accounted for by four species: kittiwake, guillemot, fulmar and gannet. All breed in large numbers on coastal cliffs within a couple of hours flying time of the grid area. There were no obvious patterns: one cruise had more birds overall in grid 1, one had more in grid 2 and one had them almost equal. Higher winds were associated with more birds. However, when wind direction was considered, the largest single total occurred in winds described as light or variable. Matching the sea state, there was further evidence that fewer birds were seen in calm weather while the largest numbers were seen in the roughest conditions.

Objective 4: Establish feeding relationships between sandeels and their predators at each site, for the purpose of understanding the multi-species interactions.

Key findings

- The stomach contents of 14,351 individual fish belonging to 34 species were examined on six research cruises in 2004, 2005 and 2006. This information is used directly in the multi-species IBM to specify the predator-prey interactions.
- The total sandeel consumption by predators was tightly linked to sandeel numbers; more were consumed in years of high sandeel abundance.
- Whiting accounted for 42% of all sandeels consumed, lesser weever (50%) and Grey gurnard (6%).
- In spring sandeels were much more important to predators (especially whiting and lesser weeverfish) in grid 1 (north-east), as compared to at grid 2 (south-west), and this coincides with the greater abundance of sandeels in Grid 1.
- The shortfall in availability of sandeels in the diet of predators in Grid 2 is supplemented with other items; sprat as prey for whiting, and pelagic crustaceans (hyperiid amphipods) plus shrimps as prey for weeverfish (Pinnegar et al. 2006). *(NOTE: this supports the results of the Ecoystem model predictions in Objective 5).*
- Sandeels comprised only a small part of the diet of plaice and haddock.
- Sandeels were selected by predators more often than would be expected given their availability in the environment. This result is influenced by the uncertainties in estimating availability (Pinnegar et al. 2006).
- Clear seasonal differences were observed in predator diets for all species. Although still and important prey item, sandeels were consumed less during autumn when they are known to be buried in the sediment. Whiting ate more crabs and sprat during this time.
- Whiting feeding preferences at our sites on the Dogger Bank closely matched dietary preferences across the whole region as recorded during a Fishery-Science Partnership (FSP) project in October 2006.
- Fish predators consumed preys that were from 1.5 to 3 times smaller in length. Cod, Lesser Weever and Dab consumed prey that were on average slightly larger and haddock consumed prey that were slightly smaller than the overall average of 2.5.
- Feeding size “preferences” by predator-prey size categories were calculated. Whiting had a higher peak preference with predators selecting prey that were approximately 2 times smaller compared to Gurnard and Lesser Weever (approximately 1.25 times smaller). Difficulties in measuring prey availability means the predators may experience a different prey-field from that we can measure. The data on size selectivity by predator are incorporated directly in the multi-species IBM and size-spectra models reported under objectives 1 and 5.
- Our study of predator prey size ratios during the course of this project has also allowed us to partake in general ecology studies resulting in the following publications: Brose et al. 2005, 2006.
- The spatial distribution of consumption by lesser weevers matched that of the distribution of sandeels at night, whilst that of whiting more closely matched the daytime distribution. These findings support knowledge of the strategies used by the predators (Engelhard et al. in prep).
- Generally, diet data suggested that predatory fishes of the Dogger Bank are perhaps less crucially dependent on local sandeel abundance than, e.g., seabird colonies of Scotland (Frederiksen et al. 2005). This is because predatory fish tend to be generalist feeders (Trenkel et al. 2005; Pinnegar et al. 2003) and hence less reliant on a particular prey resource.
- Where predators ate more sandeels they tended to have better condition indices. This link was strongest for lesser weever and plaice; intermediate for whiting and haddock; and weakest for grey gurnard and mackerel (and perhaps cod but data were extremely limited). Predator condition is well-known to relate to survival and reproduction. This underlines the importance

of a healthy sandeel population for the commercially important predatory fish species of the Dogger Bank (Engelhard et al. in prep.)

- Isotopic signatures of some of the main predatory fish species (weeverfish, gurnard, haddock and plaice) revealed that over the longer term, the diet of predators of in grid 1 includes more small sandeels and planktonic prey. The difference was not apparent for whiting, whose 'average' diet may be broadly similar across their range because of their higher mobility resulting in them being less constrained by local prey resources. However, differences in the isotope signature with size of whiting, show that prey types changes throughout their life.
- Porpoise and common seal exhibited little variability in their isotope signature, suggesting a relatively similar diet among individuals of the same species. Porpoises signature was consistent with a diet dominated by low trophic level fish species, especially sandeels and sprat. Seals isotope signature indicating a diet of larger fish, and less reliance on sandeels and sprat, confirming observations by Hall *et al.* (1998) that common seals preferentially consume demersal fish such as whiting and plaice.

Although a considerable amount is known about who eats whom in marine systems, much less is understood about the dynamics, and specifically how diets of marine consumers relate to changes in the abundance of their prey in the environment (Greenstreet et al. 1998). Many marine fishes are opportunistic predators and readily switch feeding preferences in space as well as in time, either on a seasonal (Greenstreet et al. 1998) or interannual (Jennings & Kaiser 1998, Link & Garrison 2002) basis.

In this section we consider the extent to which predatory fish species on the Dogger Bank are reliant on sandeels, as opposed to other prey resources – and hence whether demersal fish resources (and their fisheries) are likely to be impacted 'bottom up' by over-exploitation of the sandeel stock.

Stomach sampling exercises in the North Sea have tended to look at variability in predation patterns over large geographic scales (Floeter & Temming 2003; Hislop et al. 1997), and there have been few studies that have looked for local-scale patterns of variability within a few km^2. Macer (1966) examined the stomach contents of whiting, cod and plaice on the Dogger Bank in 1961 and 1962, specifically to determine the importance of sandeels. In areas where sandeels were locally concentrated, whiting and cod were found to consume this prey in large numbers. In other areas, sandeels were much less important as a food item, suggesting that predators were relatively opportunistic. Since the 1960s, the North Sea has experienced major changes in fish communities (Greenstreet & Hall 1996) and zooplankton assemblages (Beaugrand et al. 2002), thus it is highly likely that there have also been major changes food-webs and predator-prey relationships.

4.1 Stomach content analysis

The stomach contents of 14,351 individual fish belonging to 34 species were examined on six research cruises in 2004, 2005 and 2006 (Appendix 3). Predatory fish were sampled using a standard Granton-trawl (20 minute tows, horizontal opening of the net 18.1m, vertical opening 1.8m) and up to five fish in each 5cm length class were taken from the total catch at each station and their stomachs examined.

The diets of all species were found to vary markedly and consistently between the two sampling grids, even though they were separated by only 28km (see Pinnegar et al 2006). In spring sandeels were much more important to predators (especially for whiting and lesser weeverfish) at grid 1 (north-east), as compared to at grid 2 (south-west), and this coincides with the greater abundance of sandeels at the northern grid (Grid 1), as well as the greater incidence of sandeel fishing at grid

1. At grid 2, the apparent 'shortfall' in the availability of sandeels seems to have been made up by sprat as prey for whiting, and pelagic crustaceans (hyperiid amphipods) plus shrimps as prey for weeverfish (Figure 4.1). Euphausiids, mysids and pelagic amphipods ('EMA') were consumed in large numbers by many predators, especially grey-gurnard, but despite the large numbers consumed, their biomass as a component of the diet was always small. Plaice and haddock tended to consume a wide variety of benthic preys including bivalve molluscs, echinoderms, shrimps, crabs and polychaetes. Sandeels comprised only a small part of the diet in these species and there were some differences in the relative importance of benthos types at each of the different sampling grids (Figure 4.1).

Clear seasonal differences were observed in predator diets for all species. Diets were much more diverse during autumn research cruises, as compared to those in the spring. At both sampling grids, whiting ate substantially more crabs, sprat and hyperiid amphipods ('EMA') during the autumn period but far less sandeel. Sandeels bury themselves in the sediment during autumn/winter months and are thus less accessible to predators, even though they are more abundant in real terms than is the case during the spring. Grey gurnard consumed substantially fewer planktonic crustaceans ('EMA') during the autumn months and more shrimps, crabs or fish (sandeels, dragonets, gobies) even though hyperiid amphipods were much more abundant at this time of year. Lesser weeverfish diets were much more diverse during the autumn period although a high proportion of stomachs were always empty in this species, which is an 'ambush predator'. Polychaetes and cephalopods were particularly important prey at grid 2 during this season, whereas sandeels remained an important – but less dominant, prey at grid 1. For plaice, polychaetes became more important (at both sites) during the autumn period, for haddock crabs were more apparent, although sample sizes (numbers of available stomachs) were relatively small for this species.

As part of this study, we used Chesson's prey-preference index to examine whether predators on the Dogger Bank simply consume prey items in proportion to their availability in the environment (see Pinnegar et al. 2006). Our results confirm that several prey items, most notably sandeels, were selected by predators more often than would be expected given their availability in the environment. However, caution must be exercised in interpreting preference indices, because the survey data used as an estimate of numbers of prey in the environment (i.e. availability), do not necessarily provide a true picture of the ecosystem. All sampling gears are selective and the choice of sampling method can greatly affect the perception of the structure and dynamics of the ecological community in a given area (Pinnegar et al. 2006).

The stomach data collected as part of this project has subsequently been compared with additional data collected as part of a Fishery-Science Partnership (FSP) project, to examine whether whiting feeding patterns along the North East coast of the United Kingdom vary throughout the year and in space (see Stafford et al. 2007). This study found that whiting feeding preferences at our sites on the Dogger Bank, closely matched dietary preferences across the whole region for individuals sampled over soft substrates in October 2006 (large numbers of mysids, amphipods and euphausiids were consumed, fish formed only a small part of the diet). However, whiting stomachs collected by the FSP project in rocky areas, were nearly always empty or they contained crabs and/or pipefish (see *Fishing News,* 2 March 2007).

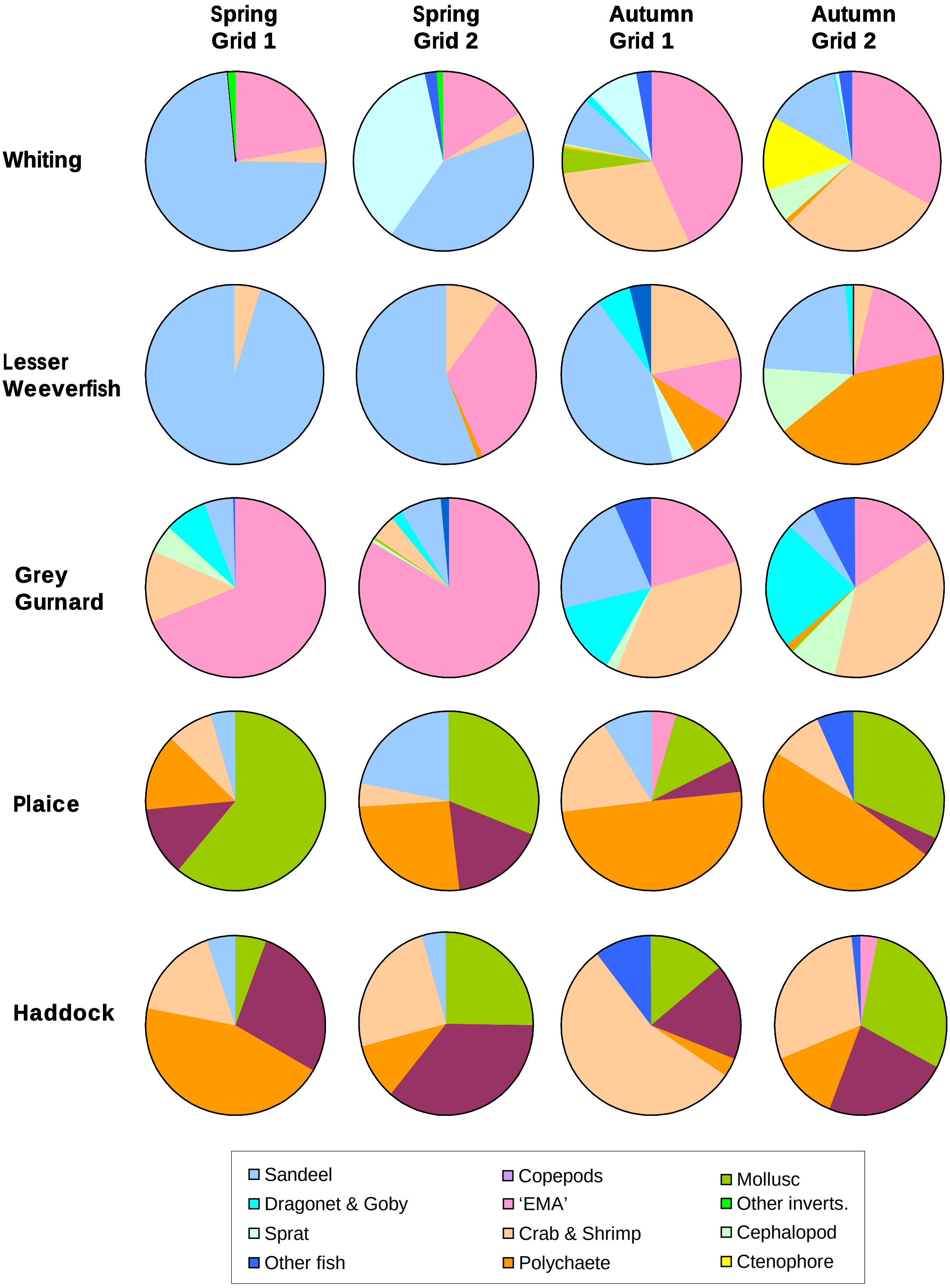


Figure 4.1. Diet composition (% of individual prey items consumed) by whiting, weeverfish, grey-gurnard, plaice and haddock in the spring (research cruise CEnd-07-2005) and autumn (research cruise CEnd-16-2005).

4.2 Predator-prey size relationships

Although there are clearly species–specific differences in the feeding interactions and diets of predators (see above), it is well known that the feeding behaviour of fish is also strongly dependent on body size (Jennings et al. 2002). Relationships between the size of predators and their prey (logarithm of the predator length/prey length) were calculated for the primary predator species on the Dogger Bank using the stomach contents data collected from two springs cruises in 2005 and

2006. Predator-prey length ratios (PPLR) were used to evaluate whether there were species-specific differences in the average prey size predators consumed and whether some species had a wider range of prey sizes than others.

Stomach contents data of main fish predators and length frequency data of all individuals sampled in the community (collected during two research cruises on Dogger Bank and the Hills in the spring of 2005 and 2006) were used to estimate predator-prey size ratios and the availability of the full size range of all prey in the fish community (known as the prey size spectrum), respectively. Analyses of stomach contents data were restricted to "fish" prey only, and for digestion stages 0 and 1 only. This was an attempt to avoid biases associated with longer digestion times of larger prey items. Only prey lengths > 6 cm were included in the analyses, as lengths smaller than these created outliers in the distributions. These were mostly attributed to 0-group fish that may have very high local abundances that cannot be captured by the prey size spectrum.

For each predator species (Table 4.1), the frequency distributions of all individual predator and prey length combinations, expressed as $\log_{10}$ (predator length:prey length) were constructed. All distributions passed tests for normality assumptions. The mean and associated standard deviation of $\log_{10}$ (predator length:prey length) was calculated for each species that had sufficient information. The $\log_{10}$ predator-prey length ratios showed that predators were on average 2.5 times larger than their prey (Table 4.1). There were slight differences between years for all species, possibly due to differences in prey availability. Although this holds across species, Lesser Weever had relatively larger prey items compared to their own size than the other species, whereas Haddock consumed relatively smaller prey than the other species. Overall fish predators consumed preys that were from 1.5 to 3 times smaller in length. Cod, Lesser Weever and Dab consumed prey that were on average slightly larger and haddock consumed prey that were slightly smaller than the overall average.

One problem in using predator–prey size ratios to parameterise size "preference" for predators feeding on smaller prey is that by fitting distributions to observed predator-prey size ratios directly from stomach contents data, the effects of the availability of the prey in the environment are confounded with the "true" size preference of predators. The size-based feeding relationships in conjunction with our field estimates of the prey availability (by size classes and irrespective of species) allowed for the construction of size-preference functions. Abundance density (numbers per m2) in each 5 cm length class was calculated to estimate the prey abundance-size spectrum of fish in the environment during 2005 and 2006. Abundance density (numbers per m^2) at length was calculated for each tow by dividing the total the abundance of individuals caught-at-length by the area swept during the tow. Area swept was calculated as distance covered on the ground multiplied by trawl or dredge wing width for each tow. Linear regressions were fit to the overall $\log_{10}$ abundance density versus $\log_{10}$ length class relationships for each year and the fitted equations were used to calculate availability of prey sizes in the environment (Figure 4.2).

Feeding size "preferences" by predator-prey size categories were calculated according to Chesson's Index (Chesson, 1978) by removing the effect of relative availability of size classes in the environment. There was only sufficient data to calculate preference indices for Whiting, Gurnard and Lesser Weever (Figure 4.3). Whiting had a higher peak preference with predators selecting prey that were approximately 2 times smaller compared to Gurnard and Lesser Weever (approximately 1.25 times smaller). The width of the size preference function for Gurnard during 2006 was shifted more towards the left, was much wider, and is probably a result of very high abundances of smaller prey in their stomach contents during spring 2006 and perhaps reflecting high local densities of smaller prey items that were not captured by our sampling methods. Our results on the width of the size preference (Figure 4.3) are consistent with the findings of Floeter and Temming (2005), preference values were very sensitive to the slope of the size-spectrum calculated. The fact that it is difficult to sample prey densities of the very small organisms (plankton, zooplankton and fish larvae) in the field (see Pinnegar et al. 2006) means that the prey availability estimates used in this study (and in all other similar studies) may not represent the true prey-field experienced by individual predator.

The prey preference functions were directly used as parameters in the multi-species individual-based (see objective 1) and dynamic size-spectrum models (see objective 5), thereby linking the output from our field studies with modelling approaches for investigating fisheries management implications.

Table 4.1. Mean and standard deviation of log10 predator length:prey length (PPLR) for the main Dogger Bank predator species based on data collected during spring of 2005 and 2006. A smaller value means that on average predators consume relatively larger prey.

Species	**2005**	**2006**	**Years Pooled**
	Mean log10 PPLR (+/-standard deviation)	**Mean log10 PPLR (+/-standard deviation)**	**Mean log 10 PPLR (+/-standard deviation)**
Cod	Insufficient data	0.393 (0.115)	0.393 (0.116)
Haddock	Insufficient data	0.489 (0.098)	0.489 (0.098)
Whiting	0.442 (0.107)	0.387 (0.096)	0.404 (0.103)
Gurnard	0.448 (0.096)	0.423 (0.093)	0.432 (0.094)
Lesser Weever	0.215 (0.055)	0.168 (0.061)	0.182 (0.063)
Plaice	0.466 (0.088)	0.408 (0.09)	0.442 (0.093)
Dab	Insufficient data	0.295 (0.073)	0.295 (0.074)
Species Pooled	0.434 (0.111)	0.386 (0.111)	0.402 (0.113)

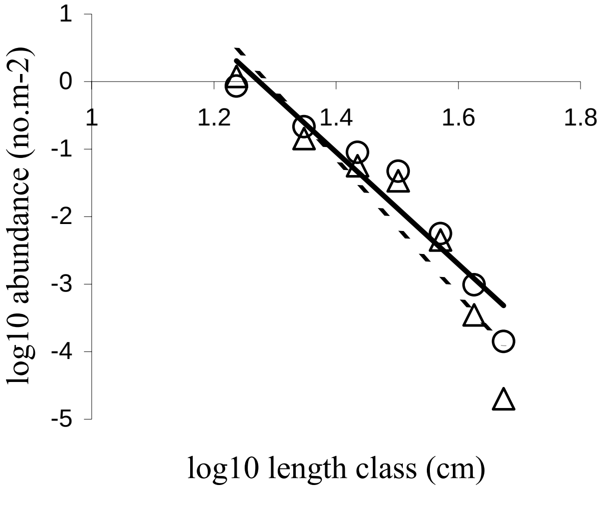


Figure 4.2. Log10 abundance (numbers.m^{-2}) versus log10 length class (cm) relationships for 2005 (Cend 07-05) and 2006 (Cend 11-06) used to estimate prey size spectra. Circles and solid line correspond to the 2005 data and fitted regression equation: log10(abundance) = 10.6 – 8.29

log10(length). Triangles and dotted line correspond to the 2006 data and fitted regression equation: log10(abundance) = 12.7 – 9.9 log10(length).

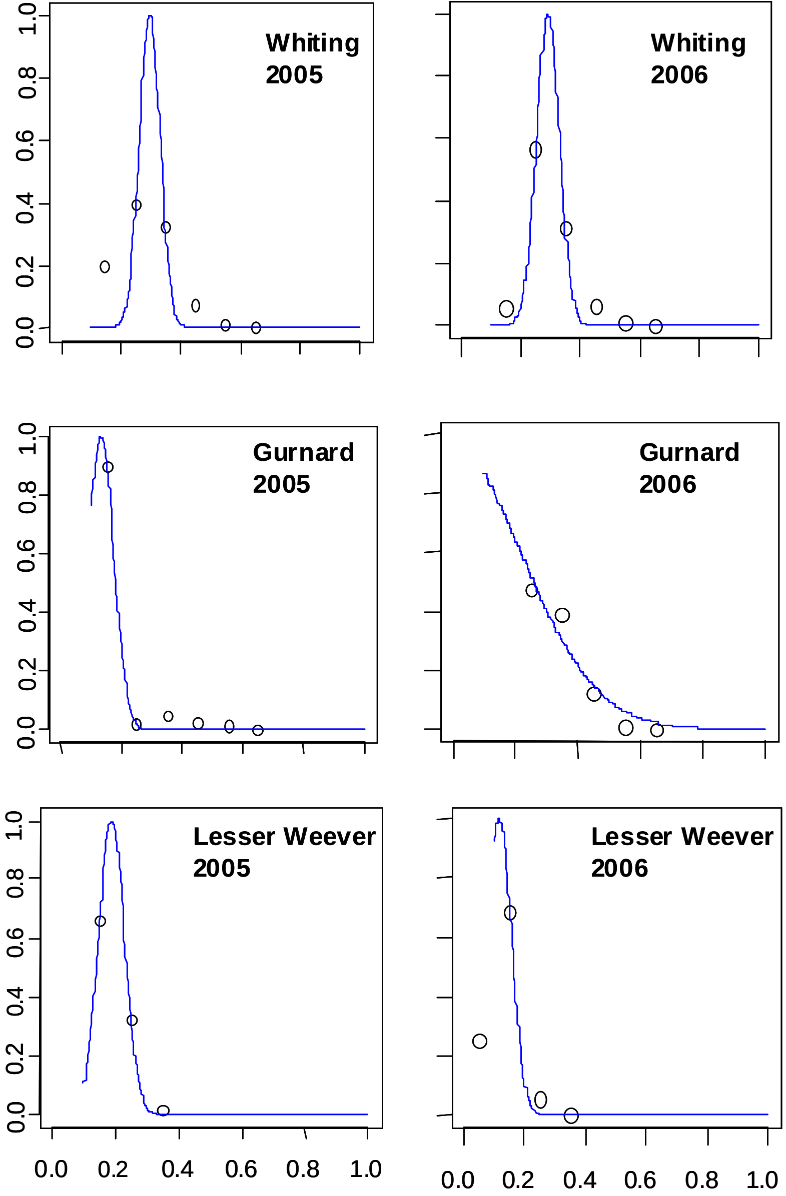


Figure 4.3. Plots of estimated preference indices as a function of log10 (predator length:prey length, PPLR) (circles) fitted with Gaussian probability distribution functions for 2005 and 2006. (y-axis, preference index, x –axis log10 (predator length:prey length)

Our study of predator prey size ratios during the course of this project has also allowed us to partake in general ecology studies resulting in the following publications Brose et al. 2005, 2006.

4.3 Spatial analysis of feeding patterns

For our 3 spring surveys coinciding with the sandeel feeding season, we examined how the spatial distributions of sandeels during day (whilst in the water column) and night (whilst in the seabed) might relate to the actual consumption of sandeels by predatory fish species. In addition we estimated the total sandeel consumption in 'numbers per station' (Engelhard et al. in submitted).

Within our study grids, sandeels were consumed by 10 fish species, 9 of which are of commercial significance. However, 3 of these dominated the total sandeel consumption; these were whiting (42% of all sandeels consumed, averaged over the 3 seasons), lesser weever (50%) and grey gurnard (6%). A fourth species, dab, is very abundant but apparently only rarely eats sandeels (none of 102 dab stomach-sampled in 2004, but a few individuals in 2005 and 2006); however owing to their very high abundance their total sandeel consumption might still be fairly high (unfortunately our stomach data are limited). Five of the other 6 predator species were far less common (or rare) locally so that their total sandeel consumption was far lower, however sandeels did comprise an important part of their diet (present in 5–50% of all stomachs examined, including empty stomachs). These were, in decreasing order of abundance, plaice, mackerel, greater sandeel, cod and turbot. Finally, haddock only infrequently ate sandeels (1–4% of stomachs examined).

The total sandeel consumption by predators was tightly linked to sandeel numbers. Not only were far fewer sandeels consumed by predatory fish during the ‘low sandeel density’ season of 2004 than in 2005 and 2006, but also there were far more sandeels consumed in the ‘high sandeel density’ Grid 1 than in Grid 2. The latter is illustrated in Figure 4.4 for the May 2005 survey (from Engelhard et al. submitted). Total sandeel consumption by all predators combined (Figure 4.1b) was far higher in Grid 1, and so was the number of sandeels eaten per predatory fish (Figure 4.1c).

This pattern of higher total and per-predator sandeel consumption in Grid 1 remained consistent for each of the “main” predatory species, whiting (Figure 4.4e-f), lesser weever (Figure 4.4h-i) and grey gurnard (Figure 4.4k-l). This ‘match’ appears tightest for weeverfish, given that the spatial distribution of weevers themselves, as well as of total and per-weever sandeel consumption were found to closely coincide with the *night* distributions of sandeels (there were far weaker relationships with sandeel day distributions). This strongly corroborates the concept that weevers are ‘ambush predators’ that lie mostly buried in sandy seabed but become active at night, when they may target sandeels during twilight when these break loose from the schools to enter the sediment, or vice versa during dawn (cf. Hobson 1986). By contrast, sandeel consumption by whiting was (at least within study grids) significantly related with daytime sandeel numbers (Engelhard et al. submitted), indicating that these predators with their fairly mobile, visual hunting tactics target free-swimming schools of sandeels in the water column (cf. Pedersen 2000). Similar analyses suggested that grey gurnard exhibit some predation on sandeels during both day and night (Engelhard et al. submitted).

Even though predators ate more sandeels where these were more abundant, they did not aggregate locally with sandeels: for example, note that both whiting (Figure. 4.1d) and grey gurnard (Figure. 4.1j) occurred in higher numbers in the ‘low sandeel density’ Grid 2, where they apparently could readily eat different prey types than sandeels (cf. Pinnegar et al. 2006; and compare with Figure 4.1). Weevers were exceptional (Figure. 4.1g), being spatially tightly linked with (night) sandeel distributions. Generally, diet data suggested that predatory fishes of the Dogger Bank are perhaps less crucially dependent on local sandeel abundance than, e.g., seabird colonies of Scotland (Frederiksen et al. 2005).

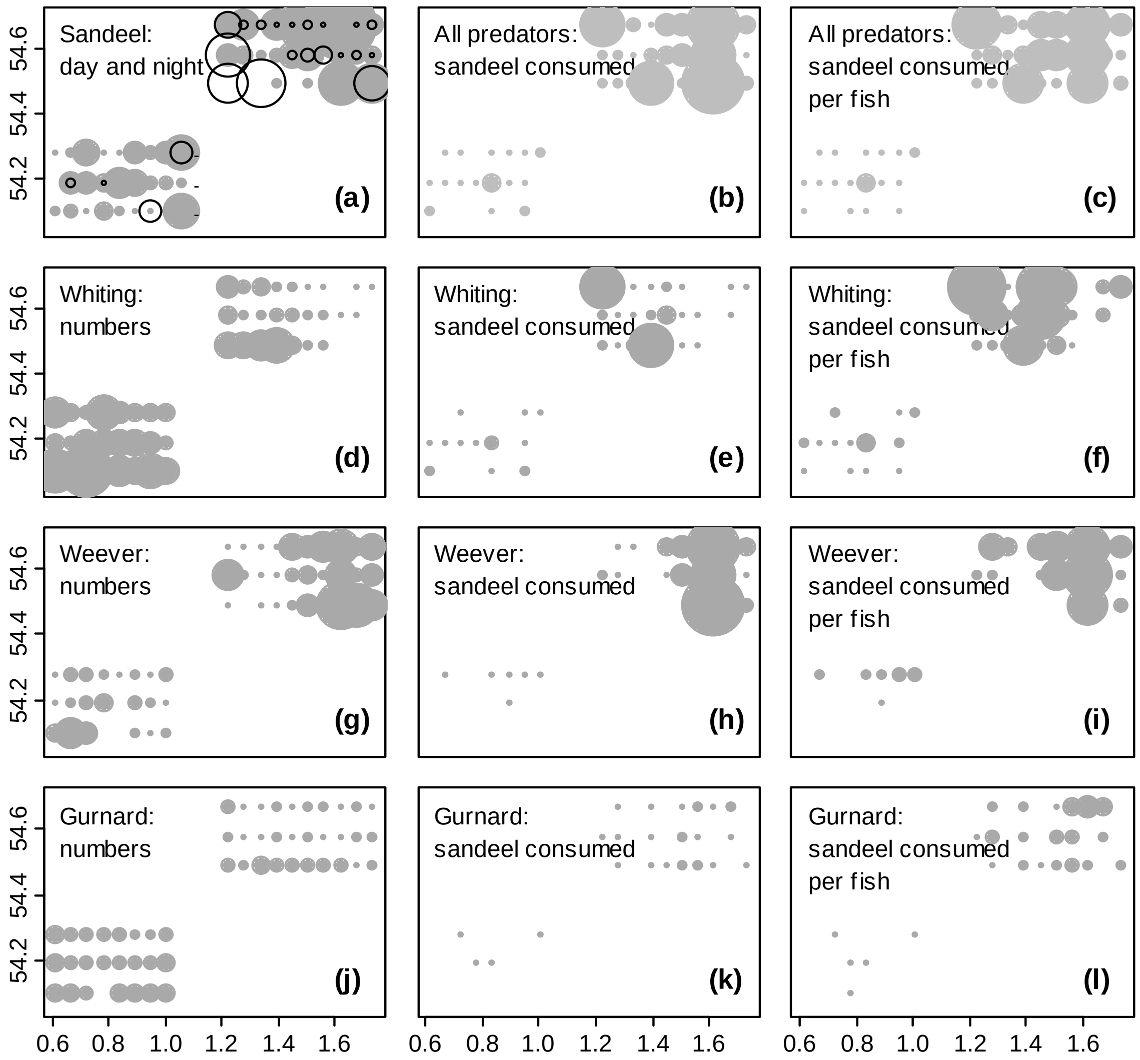


Figure 4.4. Comparison of the spatial distribution during May 2005 of (a) sandeels during day (open circles) and night (grey), with that of (b) all sandeels consumed by predatory fishes, and (c) the number of sandeels consumed per predator. Graphs exclude dab. (d–f) Whiting: Distribution of fish numbers, total sandeel consumption, and sandeel consumption per individual fish. (g–i) Ibid. for lesser weever, and (j–k) ibid. for grey gurnard. Scales of predator numbers, total sandeel consumption, and sandeel consumption per individual predator consistent among graphs.

4.4 Sandeels and predator condition

Comparisons of sandeel-rich with sandeel-poor years, and of the sandeel-rich with sandeel-poor grid sites, revealed that where and when sandeels were more abundant, predators not only ate more sandeels but also generally showed better condition indices (Figure 4.5, from Engelhard et al. in prep.). The link between sandeel and predator condition appeared strongest for lesser weever and plaice; intermediate for whiting and haddock; and weakest for grey gurnard and mackerel (and perhaps cod but data were extremely limited).

Predator condition is well-known to relate to survival and reproduction. This underlines the importance of a healthy sandeel population for the commercially important predatory fish species of the Dogger Bank.

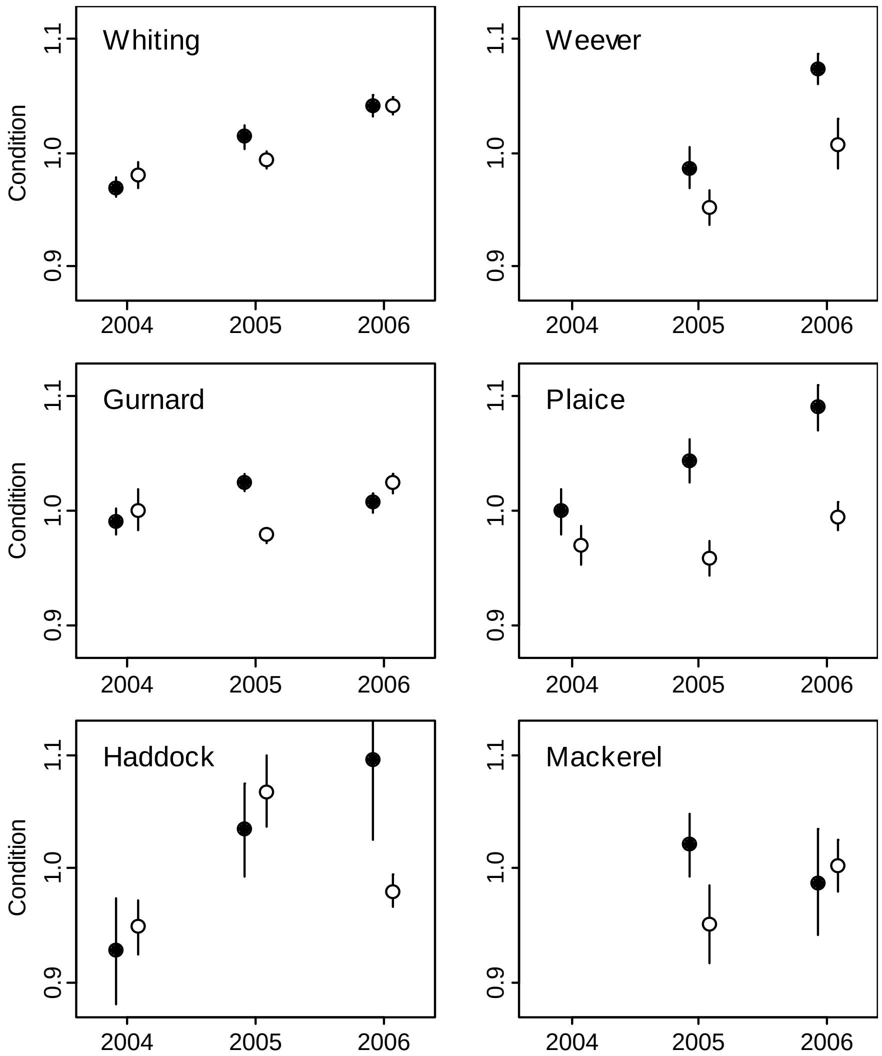


Figure 4.5. Comparison of Le Cren's condition indices of sandeel predators observed within Grid 1 ('high sandeel abundance', *closed symbols*) and Grid 2 ('low sandeel abundance', *open symbols*) during the 2004, 2005 and 2006 surveys characterised by low, medium and high sandeel abundance, respectively. Means and standard errors (by sampling station) are shown. From Engelhard et al. in prep.

4.5 Stable isotope analysis

Many fish species regurgitate their food upon capture, or feed only intermittently and thus their stomachs are nearly always empty when captured (Bowman 1986). This can make analysis of dietary preferences very difficult. Furthermore, gut contents data only offer a brief snapshot of feeding habits over the past 24-48 hours, by contrast - the signature of stable isotopes, locked-away in the tissues of a consumer, may reflect diet integrated over a year or more in some fish species (Hesslein et al. 1993) and thus is much less subject to seasonal bias.

During two research cruises in 2005 (Cend-07-2005 and Cend-16-2005), 863 samples of fish muscle tissue were collected for analysis of stable isotopes. Typically, at each trophic transfer, stable carbon isotope ratios (expressed as $\delta^{13}C$) are enriched by 1-2‰, whereas stable nitrogen isotope ratios ($\delta^{15}N$) increase by ~3.4‰. In aquatic ecology, $\delta^{13}C$ values have been used most often to discern between primary food sources (e.g. macroalgae, seagrasses, phytoplankton), whereas $\delta^{15}N$ values have allowed the accurate determination of trophic level (e.g. Pinnegar et al. 2002).

Analyses of fish tissue samples was conducted at Iso-Analytical Limited, Cheshire. Preliminary results revealed that small and large sandeels were not significantly different in terms of $\delta^{15}N$ in different seasons, but sandeels were significantly depleted in ^{13}C in spring compared to autumn, particularly so for small sandeels. This difference may reflect the selection of substantially different planktonic prey items in spring compared to autumn, and possibly the selection of diatoms in May/April by small sandeels which have rapid tissue turnover rate, and thus quickly assimilate the signature of a new prey source (see section on fatty acids – below). Sprat exhibited very variable isotopic signatures (particularly in autumn). Individuals were very depleted in ^{13}C in autumn (i.e. opposite to sandeels) and a similar pattern was exhibited by the goby *Pomatoschistus minutus*.

Analysis of the main predatory fish species (gurnard, haddock plaice, weeverfish and whiting) revealed that feeding was relatively similar at each of the two sampling sites in the spring, and that there were not significant differences in the isotopic signature of similar sized fish from the two grids (Table 4.2), in spite of clear differences in short-term stomach content data (see section above). In autumn, by contrast, there were significant differences in the $\delta^{13}C$ of gurnard, haddock, plaice and weeverfish at the two sampling grids, suggesting that there may be fundamental long-term disparities in the feeding preferences of animals at the two sites throughout the year, with individuals at grid 1 typically more depleted in ^{13}C than at grid 2 (Table 4.3). The more 'negative' $\delta^{13}C$ values at grid 1, are consistent with a diet which includes more small sandeels or plankton prey, whereas less 'negative' $\delta^{13}C$ values at grid 2 are consistent with greater reliance on benthic prey-types. It is possible that the significant differences in autumn, as opposed to spring – when the stomach contents were most different, may reflect a lag in the accommodation of a new isotopic signature because of slow tissue turnover rates. Whiting are the most mobile of the species considered, and the 'average' diet of individuals may be broadly similar across their range because the species is not constrained by local prey resources.

In the spring, whiting did exhibit a significant relationship between body length (in cm) and $\delta^{15}N$ at both sampling grids, inferring that larger animals fed at higher trophic levels. Plaice and haddock exhibited a significant relationship between $\delta^{13}C$ and body size, suggesting a change in the prey types being targeted throughout the animals lives. Fewer body size - $\delta^{13}C$ or $\delta^{15}N$ relationships were apparent in the autumn although larger grey-gurnards were typically enriched in ^{13}C at grid 2 and there was a weak relationship between $\delta^{15}N$ and body size for plaice at grid 1.

Table 4.2. Spring 2005 (research cruise CEnd-07-2005). Difference between the isotope signature at sampling grids 1 and 2 (± 1 SE).

Species	Size range (cm)	$\delta^{13}C$ (‰)			$\delta^{15}N$ (‰)		
		Grid 1	Grid 2	P	Grid 1	Grid 2	P
GUG	20-28	-18.27 ± 0.14	-18.53 ± 0.41	0.57	13.21 ± 0.40	13.37 ± 0.09	0.71
HAD	32-39	-18.27 ± 0.23	-17.71 ± 0.15	0.09	12.14 ± 0.41	12.21 ± 0.36	0.91
PLE	25-33	-16.95 ± 0.17	-17.12 ± 0.18	0.50	13.51 ± 0.47	12.35 ± 0.25	0.07
WEL	11-14	-18.92 ± 0.07	-18.38 ± 0.24	0.08	13.29 ± 0.08	13.87 ± 0.15	0.01*
WHG	26-31	-17.58 ± 0.04	-17.57 ± 0.26	0.97	14.08 ± 0.09	14.22 ± 0.27	0.64

Table 4.3. Autumn 2005 (research cruise CEnd-16-2005). Difference between the isotope signature at sampling grids 1 and 2 (± 1 SE).

Species	Size range (cm)	δ^{13}C (‰)			δ^{15}N (‰)		
		Grid 1	Grid 2	P	Grid 1	Grid 2	P
GUG	20-28	-18.45 ± 0.23	-17.68 ± 0.22	0.05*	13.12 ± 0.15	13.22 ± 0.48	0.85
HAD	32-39	-17.98 ± 0.13	-16.98 ± 0.02	<0.01*	12.95 ± 0.25	13.28 ± 0.17	0.31
PLE	25-33	-17.45 ± 0.14	-16.50 ± 0.08	<0.01*	12.57 ± 0.22	12.51 ± 0.43	0.91
WEL	11-14	-18.70 ± 0.15	-18.15 ± 0.03	0.01*	13.11 ± 0.11	13.37 ± 0.08	0.11
WHG	26-31	-17.54 ± 0.18	-17.26 ± 0.14	0.25	14.66 ± 0.39	14.48 ± 0.38	0.75

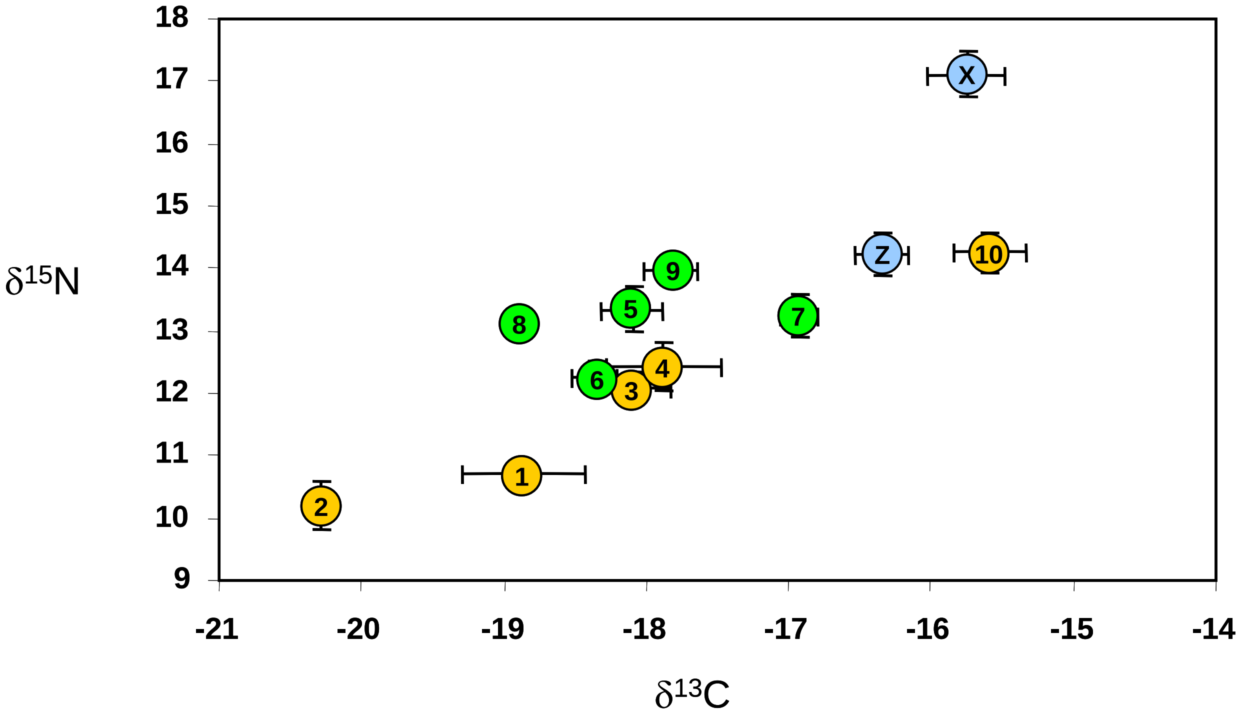


Figure 4.6. Stable isotope signatures of marine mammals (X = common seal, Z = harbour porpoise) and potential 'prey' animals (1 = large sandeels, 2 = small sandeels, 3 = gobies, 4 = sprat, 5 = grey-gurnard, 6 = haddock, 7 = plaice, 8 = lesser-weeverfish, 9 = whiting, 10 = brown shrimp) in spring 2005 (± 1 SE).

As part of project M0323 stable isotope analysis was also carried out on marine mammal tissues, in particular those of harbour porpoise *Phocoena phocoena* and common seal *Phoca vitulina*. Harbour porpoises are found throughout the North Sea and are known to be the most abundant cetacean species in the region (Hammond et al. 2002). In recent years, porpoise populations are thought to have increased (Hammond & Macleod 2006) in the southern North Sea, however concern has been raised about the possible implications for porpoise populations, given a decline in the availability of sandeels since 2002 (McLeod et al. 2006). Around 30,000 common seals are known to exist in the North Sea, including large populations at haul-out sites in Lincolnshire and North Norfolk. These animals are thought to forage over large distances, and to regularly visit offshore sites including the Dogger Bank. They are thought to be more reliant on sandeels as a key prey (Hall *et al.* 1998), in comparison with the larger, and more abundant grey seal *Halichoerus grypus*.

Porpoise muscle samples (n = 10) were obtained from animals that were accidentally caught in fishing nets off the coast of Bridlington (the nearest point on the mainland to our sampling sites), between 2000 and 2003. Samples had originally been retained for analysis of persistent pollutants (see Law et al. 2006). Seal samples (n = 6) were obtained from dead animals, collected along the Lincolnshire and north Norfolk coasts in August/September 2002, by the Institute of Zoology-London, during an outbreak of Phocine Distemper Virus (PDV).

Both species (porpoise and common seal) exhibited little variability in their isotope signature, suggesting a relatively similar diet among individuals of the same species (Figure 4.6). Porpoises exhibited low $\delta^{15}N$ values, consistent with a diet dominated by low trophic level fish species, especially sandeels and sprat (assuming a per trophic-step enrichment of ~3‰ for $\delta^{15}N$ and 1-2‰ for $\delta^{13}C$). Seals exhibited higher $\delta^{15}N$ values (and enriched $\delta^{13}C$ values), indicating a diet of larger fish, and less reliance on sandeels and sprat. The two predators were clearly selecting very different prey items. Our results seem to infer that common seals preferentially consume demeral fish such as whiting and plaice (Figure 4.6), rather than sandeels, thus confirming observations by Hall *et al.* (1998).

The isotope signatures of mammals in the present study are consistent with those reported by Das et al (2003) for animals on the French, Belgian and Dutch coasts, possibly indicating similar and consistent feeding patterns throughout the North Sea. Evans *et al.* (1997) suggested that changes in harbour porpoise abundance during the 1980s might be related to annual variation in sandeel populations since spawning stock biomass of sandeels declined markedly from 1984–92, when porpoise populations also apparently declined. Similarly, McLeod et al. 2006, demonstrated that more porpoises starved to death in low sandeel years (2002 and 2003) compared to other periods.

4.6 Fatty-acid analysis

Fatty acid profiles have been widely used to elucidate the diets of fish, marine mammals and seabirds. Stable isotopes and fatty acid profiles (FAS) can be complementary, especially as they provide insights about the diet of predators over different time scales (Hobson & Clark 1992, Käkelä et al. 2005). Ingested triglycerides and lipids are broken down in the body into free fatty acids and monoglycerides. Fatty acids are stored without substantial modification in adipose tissue (Iverson *et al.*, 1995). It has been demonstrated that specific fatty acids or combinations of them are associated with certain taxonomic classes of phytoplankton (Sargent, 1976, 1978). Such differences are passed-on up the food chain and hence differences in fatty acid composition are also detectable in higher trophic level animals that have fed on different diets. Profiles may change significantly in only 3 weeks in adult cod (*Gadus morhua*) (Kirsch *et al.*, 1998). In seabirds, large changes have been recorded in blood plasma FAS, after only 5 days following a switch of diet, although adipose tissue and muscle react slightly more slowly (Käkelä et al. 2005).

During the research cruise Cend-07-2005 (May 2005) samples of small (~10cm) and large sandeels (16-18cm) were taken from night-time dredge stations for processing by colleagues at University of Glasgow. Total lipids were extracted and analyzed using a gas-liquid chromatograph, including both flame ionization (FID) and mass detection. Analysis revealed that small sandeels from the Dogger Bank were particularly rich in polyunsaturated fatty acids (PUFA), especially 22:6n-3 and 20:5n-3, but contained few long chain monounsaturated fatty acids (MUFA)), compared to the other pelagic fish analyzed by Käkelä et al. (2005) as well as larger sandeels from the same site. These PUFAs are characteristic of a diet that includes phytoplankton, and in particular diatoms, which predominate in this part of the North Sea during the spring (when the small sandeels were caught). North Sea phytoplankton is dominated by dinoflagellates in the autumn, which are characterized by the presence of C18:4 (n-3) and C18:5 (n-3) fatty acids. Larger sandeels exhibited more of the 20:1n-9 and 22:1n-11 fatty acids than was the case with smaller animals, however they were still very different to other pelagic and demeral fish from the same region (see Käkelä et al. 2005; 2006).

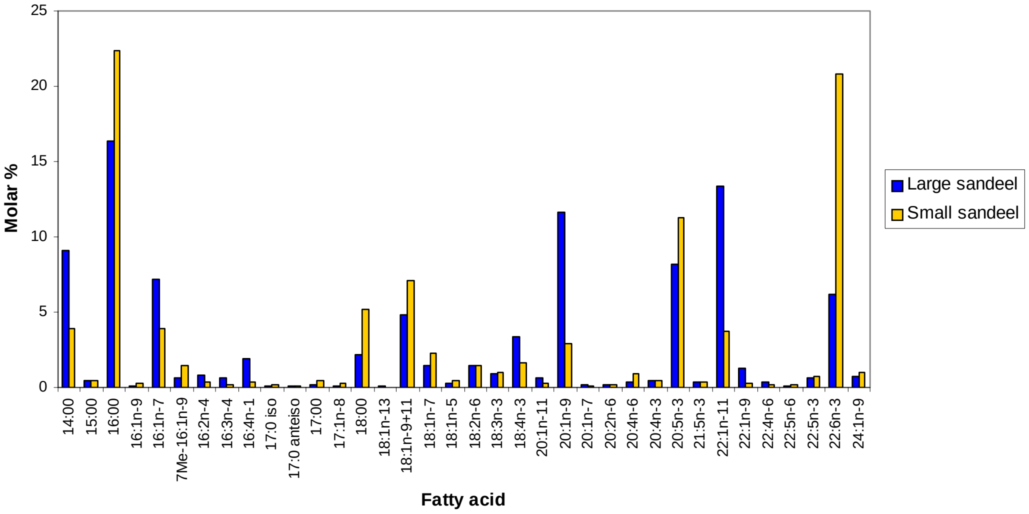


Figure 4.7. Proportions of the major fatty acids (mol%) in tissue samples of large (n = 12, 16 to 18 cm) and small (n = 11, 10 to 18 cm) sandeels from the Dogger Bank. Identified fatty acids are abbreviated as follows: [carbon number]:[number of double bonds] n-[position of the first double bond calculated from the methyl end] (e.g. 22:6n-3).

Colleagues at University of Glasgow have subsequently used the fatty acid profiles from our sandeel samples to examine differences in the feeding preference of great skuas *Stercorarius skua* (a kleptoparasitic seabird) throughout the northern North Sea (Käkelä et al. 2006). In the North Sea, declining fish stocks, changes in technical measures, and the beginning of a recovery programme for cod *Gadus morhua* have reduced the amount of fishery discards in recent years (Votier et al. 2004a). There are fears that short-term changes in food supply, due to sudden reduction in discard rates, may result in breeding failures of longlived seabirds (Oro et al. 1996) or a switch in diet, with severe impacts on other species (Oro & Furness 2002, Votier et al. 2004b).

Interestingly, the FAS of plasma samples in dead skuas collected at Foula in the Shetlands, showed a temporal shift towards larger values of long chain MUFA and smaller values of phytoplankton type PUFA from 2002 to 2003. The long chain MUFA are characteristic for herring and mackerel and originate from pelagic zooplankton, whereas the main fish species representative for the phytoplankton type PUFA without the long chain MUFA in the diet of North Sea seabirds is small size sandeel (Table 3). The year 2003 was exceptional in Shetland as the population of sandeels collapsed to the lowest level on record. Work is on-going at University of Glasgow (in collaboration with CEFAS) to examine the diets of other seabird species using FAS, in particular species such as kittiwakes *Rissa tridactyla* which are thought to be heavily reliant on healthy sandeel populations.

Objective 5. Develop an ecosystem (Ecopath with Ecosim - EwE) model of the North Sea, with special application to sandeel, for the purpose of evaluating the ecosystem consequences of various management scenarios and identifying ecosystem indicators.

Key findings

- Partially supported by the funding under this project, species and size-based models of the North Sea ecosystem have been constructed (Daskalov and Mackinson 2004, Mackinson and Daskalov (in prep), Blanchard et al. a and b (in prep). The EwE model represents 69 functional and 12 fisheries.
- Sandeels dominate both consumption and catches in the North Sea, with the amount consumed and caught exceeding more than twice the next most important prey species- the Norway pout.
- Data from the 1991 'Year of the Stomach' and other sources indicate that the main sandeel predators in the North Sea are whiting, minke whales, small demersal fish (e.g. weevers), seabirds, rays, haddock and gurnards and that these positively select sandeels in their diet.
- The relative contribution of fishing to the total mortality of North Sea fish has increased concomitant with a decline in predatory fish and increased fishing.
- System level indicators suggest a greater stability and maturity of the North Sea compared to the other systems that may be related to the diversity and abundance of consumers (e.g. fish) in the food web. However, further work is need on such critical evaluation of the use of ecosystem scale characterisations
- Our study of trophic indicators from ecosystem models during the course of this project has also allowed us to contribute to science resulting in the following publications, Cury et al. 2005, Daskalov et al. submitted.
- Due to technical difficulties in was not possible to use output from the IBM model to drive the ecosystem models so that the local and broad-scale impacts could be investigated simultaneously. This work is still intended for completion and publication.
- Evaluation of the broad scale impacts of alternative sandeel management scenarios using the EwE model specified using data from the Dogger Bank, revealed that the 'release' of sandeel competitors, could help sustain population of predators that were initially negatively impacted by fisheries depleting stocks of sandeels. Increasing TAC to 1 million tonnes generally had negative effects, whilst seasonal closure appeared to provide no benefit at all because the abundance of juvenile sandeels is mostly governed by the abundance of zooplankton. Area closures had the widest ranging positive impacts to sandeels, their predators and fisheries.
- Dynamic size-spectra models are used to represent the seasonal flux of energy from plankton to large fish predators (through size-based feeding) and the effects of fishing on different parts of the size-spectrum. A dynamic size spectrum model was developed for coupled benthic detritivore and fish predator communities, incorporating the effects of high and low quality prey (Blanchard et al. in prep). The model produces size spectra for both communties consistent with observed size spectra in the North Sea and predicts baseline predictions that are consistent with existing ecological theory.
- Evaluation of the impacts of the recent exploitation pattern (1990-2003) on the size structure of the fish community revealed that compared to the unexploited baseline there was a 90-99% reduction in large fish (4-16 kg), accompanied by an increase in fish between 0.1 and 0.5 kg due to predatory release.

Applying the area closure used in the EwE scenario resulted in a greater abundance of small fish with the largest positive impacts cascading to predators sized between 0.1 and 1 kg. Different prey quality had a small effect on the biomass and abundance of size classes, with lower benthic prey quality scenarios resulting in marginally larger reductions (by about 1-2%) in large fish across all of the scenarios. Further work on the effects of prey quality is required to fully evaluate the management implications of removing high energy prey (such as sandeels and other fish species) on predators.

Acknowledging ecological interactions, such as predation, is key to an ecosystem approach to fisheries. Trophic interactions raise two concerns for fisheries management. The first is the decline in the food resource of commercially and functionally important stocks causing possible negative impacts. The second is the indirect effect of decreasing fish biomass on ecosystem functioning (e.g. trophic cascade, Daskalov et al. 2007).

5.1 Ecopath model of the North Sea ecosystem

Methods

Trophic models based on Ecopath with Ecosim methodology are widely used for the quantification of food webs and analyses of ecosystem dynamics (Christensen et al. 2000). The approach provides a common platform for model development that will enables comparisons of the North Sea with other marine ecosystems through the derivation of various system indicators. By simulating changes in the food web through time, the approach also makes it possible to investigate the ecosystem scale consequences of alternative fisheries management scenarios.

The present model is one of the most detailed Ecopath models constructed. The model structure was set to 69 functional groups including 3 mammal, 1 bird, 45 fish, 14 invertebrate, 2 microbial, 1 autotrophic, discards and detritus groups (Appendix 4). The commercially important target fish species were divided into juvenile and adult groups (e.g. cod, whiting, herring). The model is parameterised with estimates of biomass, production and consumption rates and diet composition compiled from data and literature sources (Daskalov and Mackinson 2004, Mackinson and Daskalov in prep). The model also contains information about landings and discards taken with various fishing gears grouped in 12 categories e.g. demersal trawls, pelagic trawls, drift nets, etc. This information is used to formulate and simulate different fisheries management scenarios.

5.1.1 Ecosystem indicators

Ecosystem indicators are needed to evaluate the interactions between the different components, and of structural ecosystem changes resulting from exploitation. We analysed selected descriptive indicators (both groups and system level) to characterise the role of sandeels in the system, to compare the present model to past and future states and other UK coastal ecosystems.

Results

Indicator: Biomass

Biomass estimates were compared to historical data (Sparholt, 1990; Mackinson, 2002, Fig. 1). Total fish biomass in the North Sea was estimated ~26 million tons by the late 19th century (Mackinson, 2002) and ~ 11 million tons in 1991 (Daskalov and Mackinson 2004). The biggest change (between 50 and 100%) was in exploited target species e.g. gadoids (cod, haddock, saithe), horse mackerel, herring and flatfish. Total fish biomass seems to stabilise at ~ 10-11 million tons in the 1980-1990s (Sparholt 1990) however there was a change in the relative importance of different stocks, with pelagic groups and some flatfish increasing and demersal groups decreasing (Daskalov and Mackinson in prep).

Indicator: Mortality

The main prey groups in the North Sea ecosystem model are juvenile gadoids, Norway pout, clupeids (sprat and herring) and sandeel. The highest predation overall is caused by commercial gadoids, mackerel and horse mackerel, and it is comparable to the level of fishing mortality

(Figure 5.1). The main predators of sandeel are mackerel, whiting, baleen (minke) whales and small demersal fish (e.g. weevers). These predators are positively selective for sandeel as are seabirds, rays, haddock and gurnard (Figure 5.2). Fishing accounts for approximately 25% of the total explained mortality of sandeels in the model with total ‘consumption by fisheries being 800,000 $t.y^{-1}$and consumption of predators being 2,000,000 $t.y^{-1}$ (Figure 5.3). Comparison with an unpublished model of the North Sea in 1974 (Christensen unpubl.) indicates that the contribution of fishing to the total mortality of fish has increased, whilst that caused by predation has decreased (Figure 5.4). Investigating the links between changes in the relative contributions of fishing and predation to total mortality and changes in system biomass and function are important topics for future investigation.

Indicator: Niche overlaps and mixed trophic impacts.

Measuring the similarities in the diets of predators and prey provide indicators on competitive interactions and provide insight in to how species might be expected to respond to changes in the abundance of their predators and competitors. Sandeels compete for food with a range of other fish and non-fish. Juveniles, small fish and invertebrate share the same predators as sandeel (Figure 5.5)

The mixed trophic impact is an indicator of the relative direct and indirect impacts of a change in the biomass of one component on other components of the ecosystem (Ulanowicz and Puccia, 1990). The estimation shows that sandeels affect positively (via their productivity or bottom-up effect) the sandeel fisheries and their main predators: baleen whales, rays, gurnards, whiting, haddock, mackerel and seabirds, and negatively (through predation, top-down effect) zooplankton (direct effect) and competitors like sprat, herring and Norway pout and jelly-plankton.

Cross system comparisons

Several ecosystem indicators (details are given in Cury et al. 2006) were used describe the North Sea ecosytem in terms of productivity, complexity/connectance, trophic efficiency and ecosytem health and to compare to other UK marine ecosystems (Figure 5.6): English Channel (Stanford and Pitcher, 2000), Western English Channel model (Araujo et al., 2005), and Irish Sea (Lees and Mackinson 2007). The values of most of the indicators in the North Sea are higher than in the other systems (e.g. biomass, efficiency, connectance and cycling) that indicate greater stability and maturity of the North Sea compared to the other systems. This is probably due to the greater geographical extend and dominance of predator groups. On the other hand the productivity indicators (e.g. primary production, system’s throughput and ascendancy) are higher in the Channel systems and the Irish Sea. The utilisation of primary production, mainly by zooplankton, is also higher in the Irish Sea and western Channel that is reflected in the higher level of primary production to support the catch (a measure of the efficiency of the trophic transfer from primary producers to fish). However comparisons of indicators based on primary production are not robust enough because of the high uncertainty of determination of primary production in the different systems. Comparisons are also made difficult by uncertainties associated with structural differences in the models (Pinnegar et al. 2005).

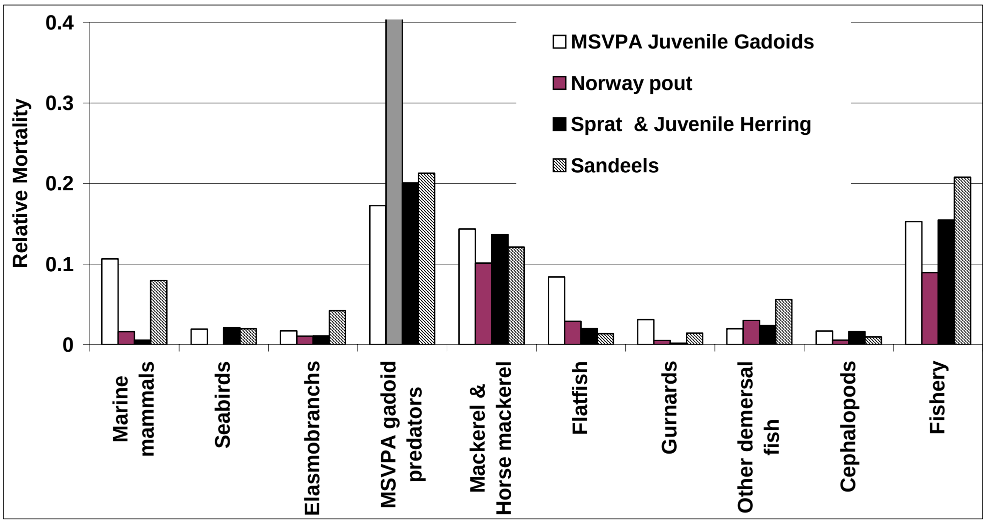


Figure 5.1. Mortality caused by the main predator and the fisheries (shown on the x-axis). Columns are the main prey groups

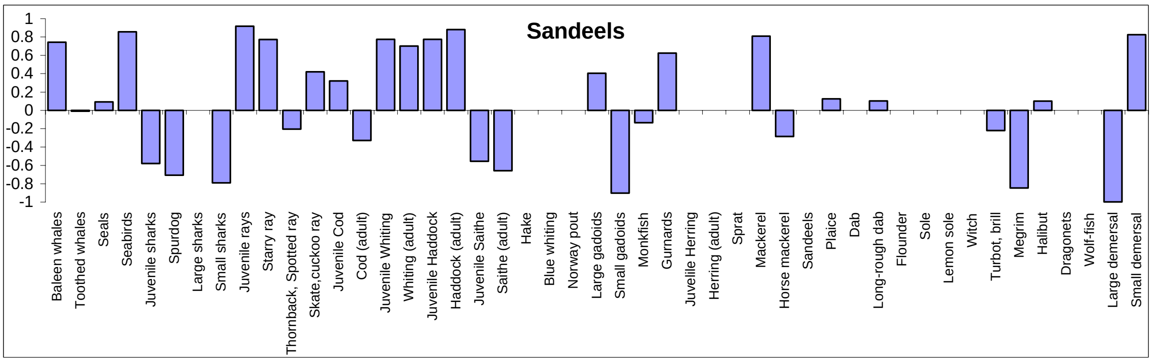


Figure 5.2. Selectivity of different predators for sandeel: positive selectivity means preference and negative- avoidance.

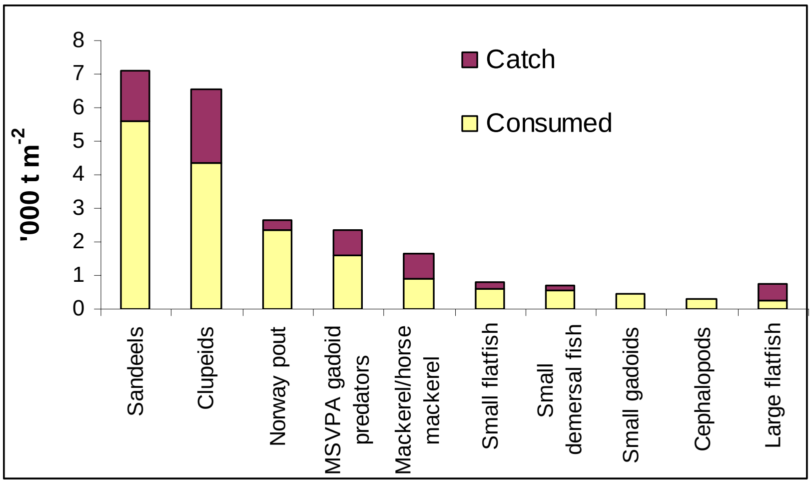


Figure 5.3. Contribution of consumption by predators and removal by fisheries for prey groups that share the same predators (predator overlap >40%). The figure demonstrates the overall importance of sandeels as a prey and that the fishery removal amounts to about 35% of that consumed by predators.

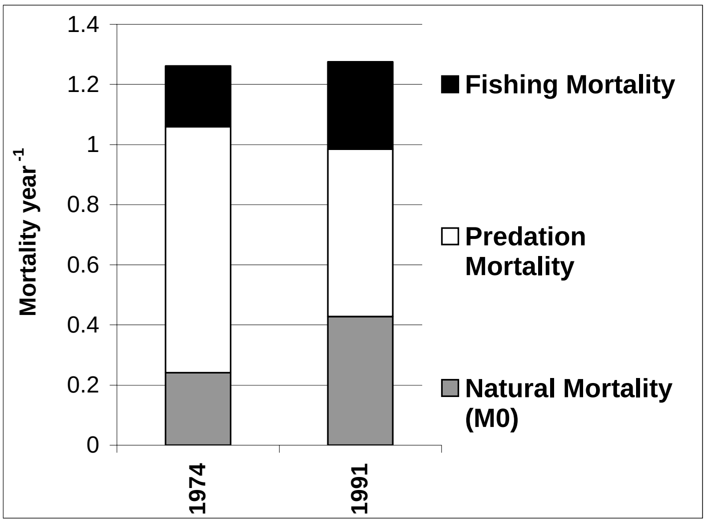


Figure 5.4. Mortality in the whole fish community

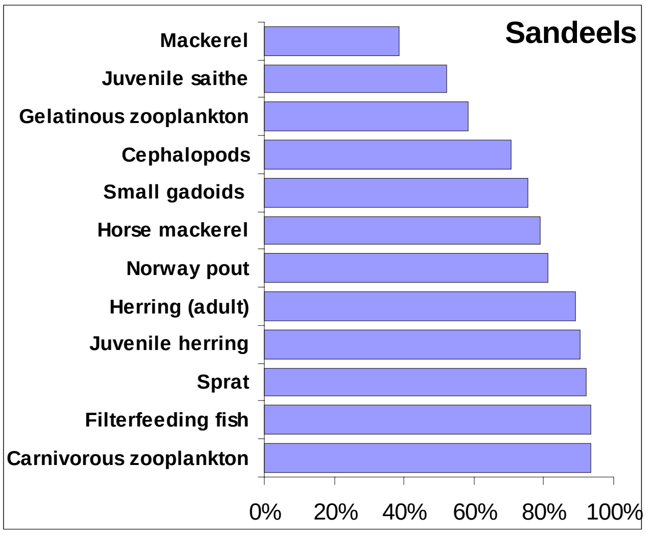


Figure 5.5. Overlap of prey: Indicates the degree to which other groups share the same prey as sandeel, and thus allows us to identify food competitors.

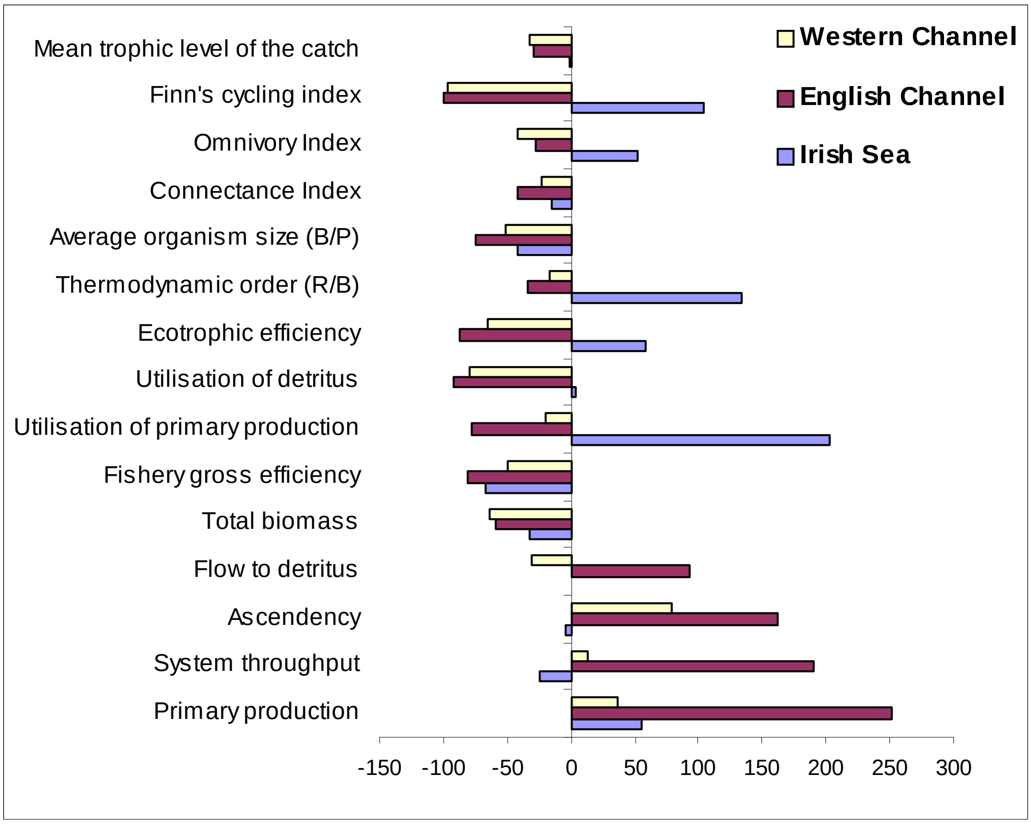


Figure 5.6. Comparing whole-system indicators of the North Sea with 3 other UK coastal seas in % difference from the North Sea.

5.1.2 Evaluation of management scenarios using the EwE model

Methods: model specification and setup

The North Sea ecosystem model (described in above) was adapted for application to evaluating the ecosystem-wide consequences of the defined local-scale sandeel fishery management scenarios. Using information from output of MSVPA (2005), sandeels were divided in to adult and juvenile (<12.6 cm, 7.4g from MSVPA) components, thus allowing for exploring the impacts of size selection by predators and fisheries. The diet composition of the key predators of sandeels on the Dogger Bank (whiting, gurnard, weevers, cod, haddock, dab and plaice) recorded from field investigations was input to the model. For whiting, cod and haddock, diet information was separated by size (adult and juvenile) reflecting ontogenetic changes in diet.

Important technical assumptions in the specification and application of the model are (i) that the densities of fish in the model reflect local scale relative densities. i.e. that the relative abundance of the fish groups on the Dogger Bank is similar to that found throughout the whole North Sea, (iii) all fish are distributed evenly throughout, which implies that all prey are available to all predators in space (i.e. there is no representation of the fine-scale spatial differences in overlap of predators and prey). (iv) catch and by-catch compositions of each fishing fleet specified in the model remain stable, (iv) the relative influence of top-down and bottom-up factors controlling the strength of interactions between predator and prey are specified in the model by a ‘vulnerability’ parameter. This parameter is parameterised through fitting model predictions to observed time trends in the relative abundance of species. The reliability of the 10 year predictions are strongly conditioned on the assumption that these remain stable. Unfortunately there is no way to determine otherwise and thus this is an inherent feature of our simplified understanding and modelling of the complex dynamics we know to be important.

Important consideration for interpretation are (i) the model predictions only account for changes in the population dynamics resulting from the direct impact of fisheries and indirect trophic interactions. (ii) the 'time frame' represented by the model is not of concern since we are interested in investigating the relative consequences of alternative management actions rather than the specific details of population trends in time (iii) the directions of response are generally robust whilst interpretation of the rates and magnitude of predicted responses should be taken with caution.

The model was used to investigate the impacts of the proposed managements scenarios in two ways. First as a standalone tool, representing each of the scenarios using the best available approach and second as tool driven by the outputs of the IBM model (Table 5.1). *Due to technical difficulties in was not possible to use output from the IBM model to drive the ecosystem models so that the local and broad-scale impacts could be investigated simultaneously. This work is still intended for completion and publication.*

Results of the stand-alone simulations are evaluated in terms of the impacts on sandeels (Figure 5.7), sandeel fisheries (Figure 5.8), their main fish predators (Figure 5.9a), 'high-profile' predators (Figure 5.10) competitors (Figure 5.9b, 5.9c), the sandeel fishing fleet and fleets dependent on other species (i.e cross fishery interactions) (Figure 5.11)

Table 5.1 Setup of the management scenarios using EwE and when driven by the IBM model

Scenario	EwE Standalone implementation	IBM driven
Status quo	Constant removal of sandeels at the catch specified in the model (approx 750,000 t adult sandeels and 65,000 t juv. Sandeels, which equates to F of 0.97 and 0.07 respectively).	
TAC	Constant removal of sandeel at the specified levels, 1 million t and 0.5 million t. Split between adult and juveniles in proportion to status quo proportions. Note: TAC of 1 million t is the only scenario evaluated that increases the catch from the baseline value in the model.	B, F or Effort driven for sandeels B or F driven for predators
Total closure of the North Sea	Relative fishing effort of sandeel trawlers is set to zero. There is some residual mortality because sandeels are still caught incidentally by other gears.	B, F or Effort driven for sandeels B or F driven for predators
Closed seasons to prevent fishing on juveniles	Fishing mortality on juvenile sandeels set to zero. Adults remain at status quo.	B, F or Effort driven for sandeels B or F driven for predators
7. MPA (closure of area 1A and 4 to sandeel fishing)	Represented as a 45% proportional reduction in the relative effort of the sandeel fleet. Closure of area 1A and 4 (Figure 1.1), results in a loss of 45% of fishable grounds. Assuming that there are few other suitable grounds there is unlikely to be a significant redistribution of effort, and so the reduction of effort represents the expected loss of effort from the spatial closure. Other fleets need	B, F or Effort driven for sandeels B or F driven for predators

	to have their relative efforts/ catches reduced if by closing the sandeel areas the other fleets loose opportunity (catches) overall. However, we might assume that their effort is displaced and catch in maintained.	

Results and discussion

Increasing the fisheries take of sandeels from the status quo to 1 million t per year results in across the board negative impacts to sandeels (Figure 5.7 and 5.8), their predators and the fisheries on the predators (Figure 5.11, 5.10). However, the negative impact did not appear to be sustained for all predator species, with the biomass of whiting, haddock, plaice, dab and cod starting to increase toward the end of the 10 year period. The explanation behind this observation involves the ecological dynamics of competitive release and predator functional response. Fish sharing a similar diet to sandeels (e.g. sprat, herring, Norway pout) ‘fill the gap’ left by the depleted sandeel population. ‘Released’ from competition, their increasing biomass (Figure 5.9c) is available to their predators (which are often the same as those of sandeel). In trying to maintain their consumption requirements, the predators consume relatively more of these prey in lieu of having less sandeels to eat (Table 5.2). This enables the predators to increase in number and ‘recover’ from the initial decline. The release of sandeel competitors is beneficial to the fisheries dependent upon them (Figure 5.9b)

The substitution of one prey item by another is a facet of predators trying to maintain consumption requirement by adapting their intake of each prey item in proportion to it’s abundance and availability (vulnerability in the model). Field-evidence for predators making up a shortfall in their consumption of sandeels is presented under objective 4. Because the model does not account for prey quality, it cannot be inferred that the diet substitution is equally beneficial for the predator. Indeed, our field-investigations reveal that the condition of predators is lower when sandeels are consumed less (see objective 4 section 4.4).

Closure of the entire North Sea to sandeel fishing has strong positive effects for the sandeel predators and the fisheries dependent upon them. It is also strongly beneficial for sprats (a competitor), which are taken as a by-catch of the sandeel fishery. Predators benefit from the increased abundance of both. This type of response is the rationale that has supported the development of forage fish management plans in the USA, the principal goal of which is to conserve stock of small fish important to top predators (e.g Herring in Washington and Alaska, Small pelagics in Florida). i.e. create the right food conditions for predators and their populations are more likely to strive.

Even though the adult stock might be strongly dependent on the survival of juvenile sandeels, the effects of stopping fishing for juveniles (seasonal closure) are minor. This is because the dynamics of juvenile sandeels in the model are largely dependent on the bottom-up processes (ie. most tightly linked to the abundance and availability of zooplankton). Since we are only investigating the impact of fisheries, there is little effect. For comparison, Figure 5.12 predicts changes in the abundance of sandeels in response to changes in the abundance of zooplankton over a 12 year period. This highlights the importance of environmental effect on the dynamics of juvenile sandeels. Analyses of field data (section 2.6) suggest that the wider spatial distribution of adult sandeels is linked to local abundance of juveniles in high-density areas. So, although the model predicts that removing fishing on juveniles has little benefit to the overall population size of adults, it might influence the spatial distribution of the adult population. If resilience of the stock is linked to opportunity for sandeels to have a spatial refuge from fishing, this might be an important factor.

Closing area 1A and 4 (MPA scenario) has positive consequences for by-catch species from the sandeel fishery (.g. sprat, herring, Norway pout), who's fishing mortality is also reduced in proportion to the area closed (e.g. Figure 5.9c). Since many of the by-catch species are also competitors of sandeels, competitive release results in their biomass increasing, to the benefit the fisheries and predators dependent upon them.

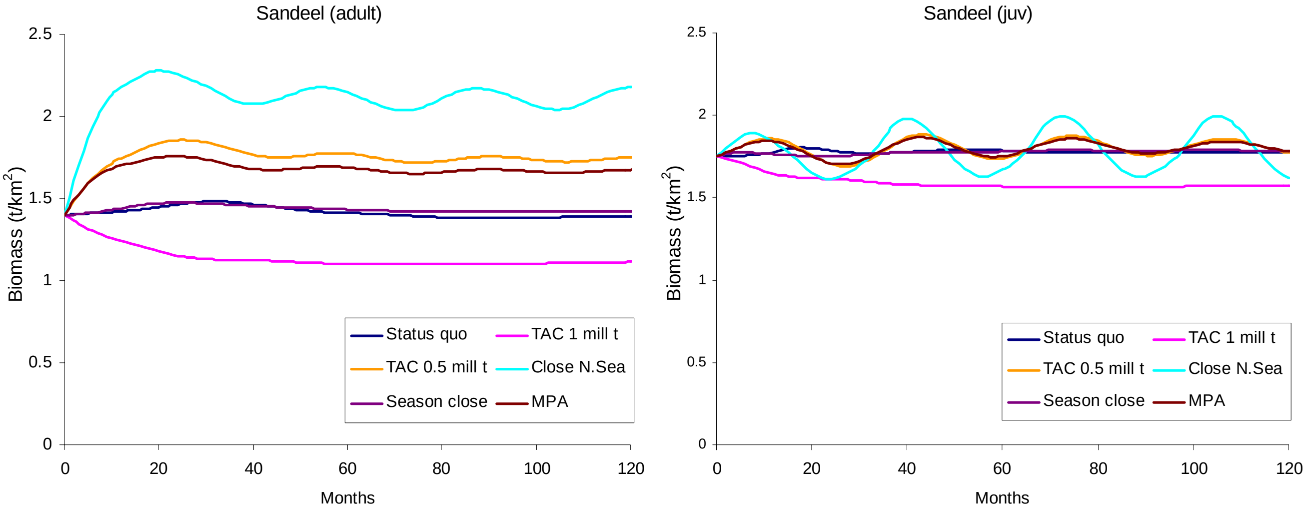


Figure 5.7. Biomass of adult and juvenile sandeels

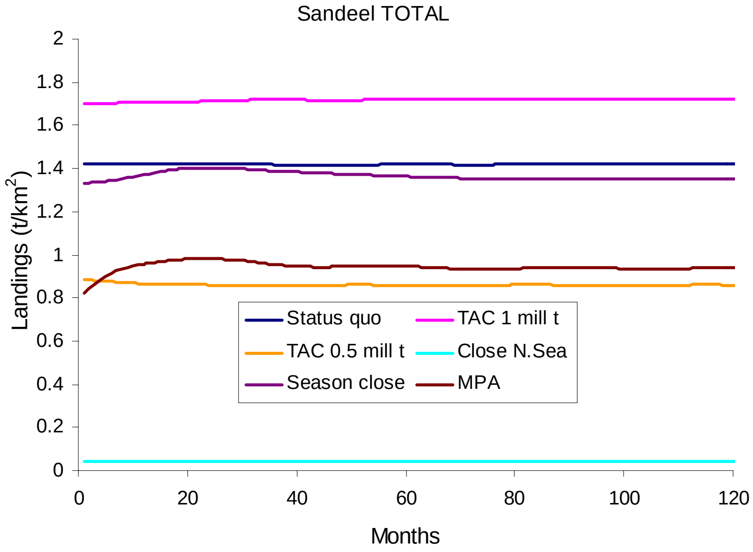


Figure 5.8. Landings by sandeel trawlers

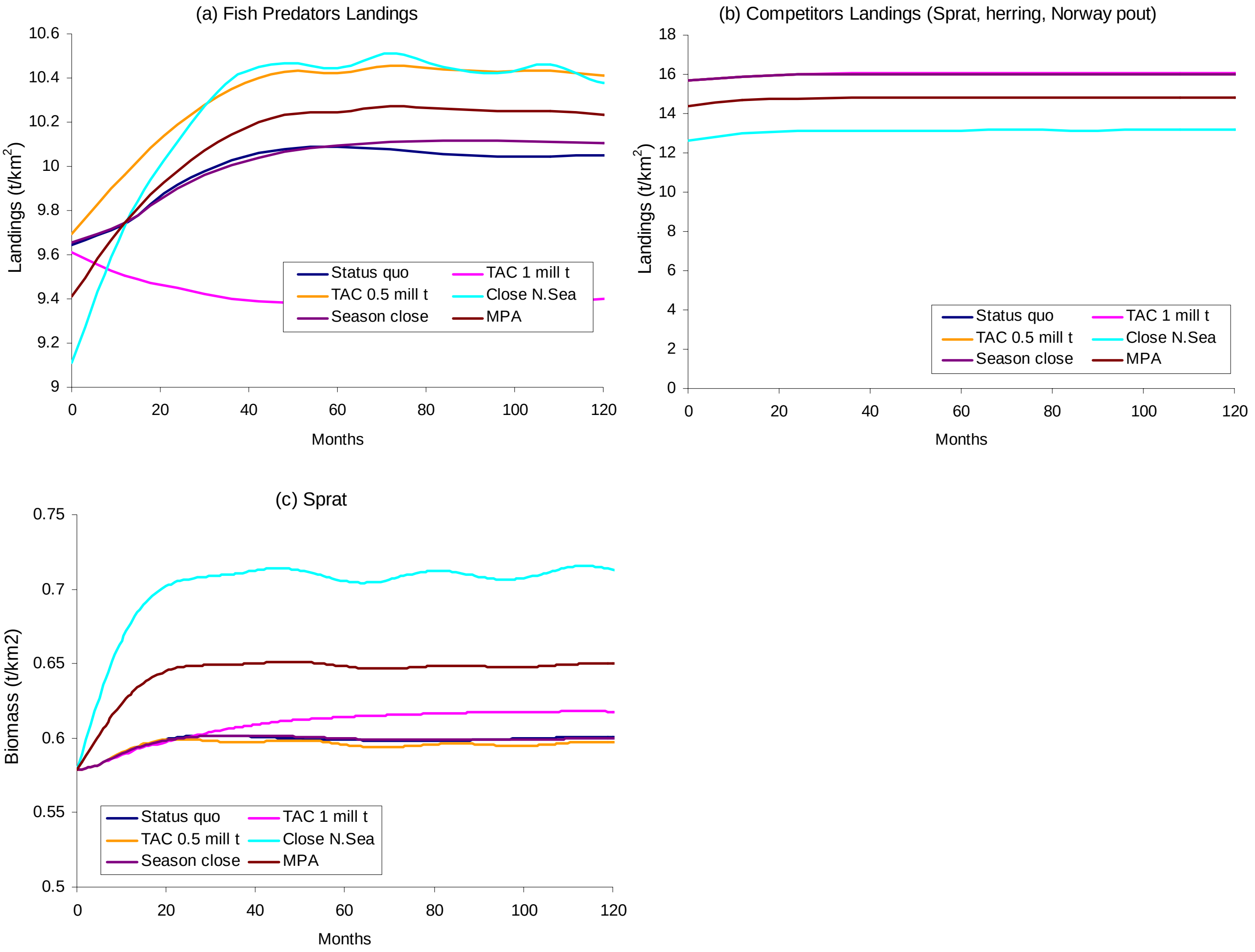


Figure 5.9. Impacts on (a) landings of key sandeel predators (b) landings of competitors (c) biomass of sprat (a key competitor)

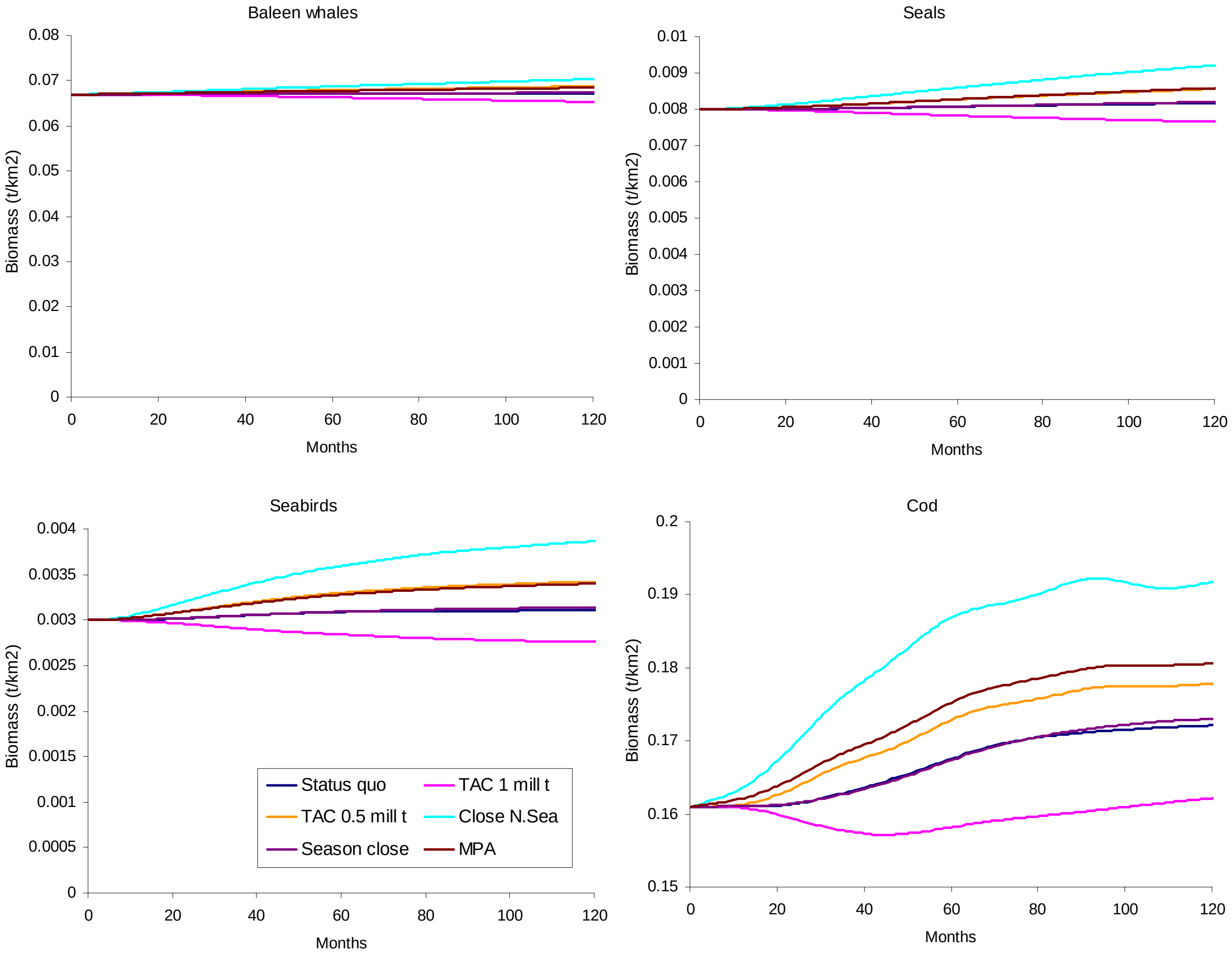


Figure 5.10. Predicted changes in the biomass of high profile fauna.

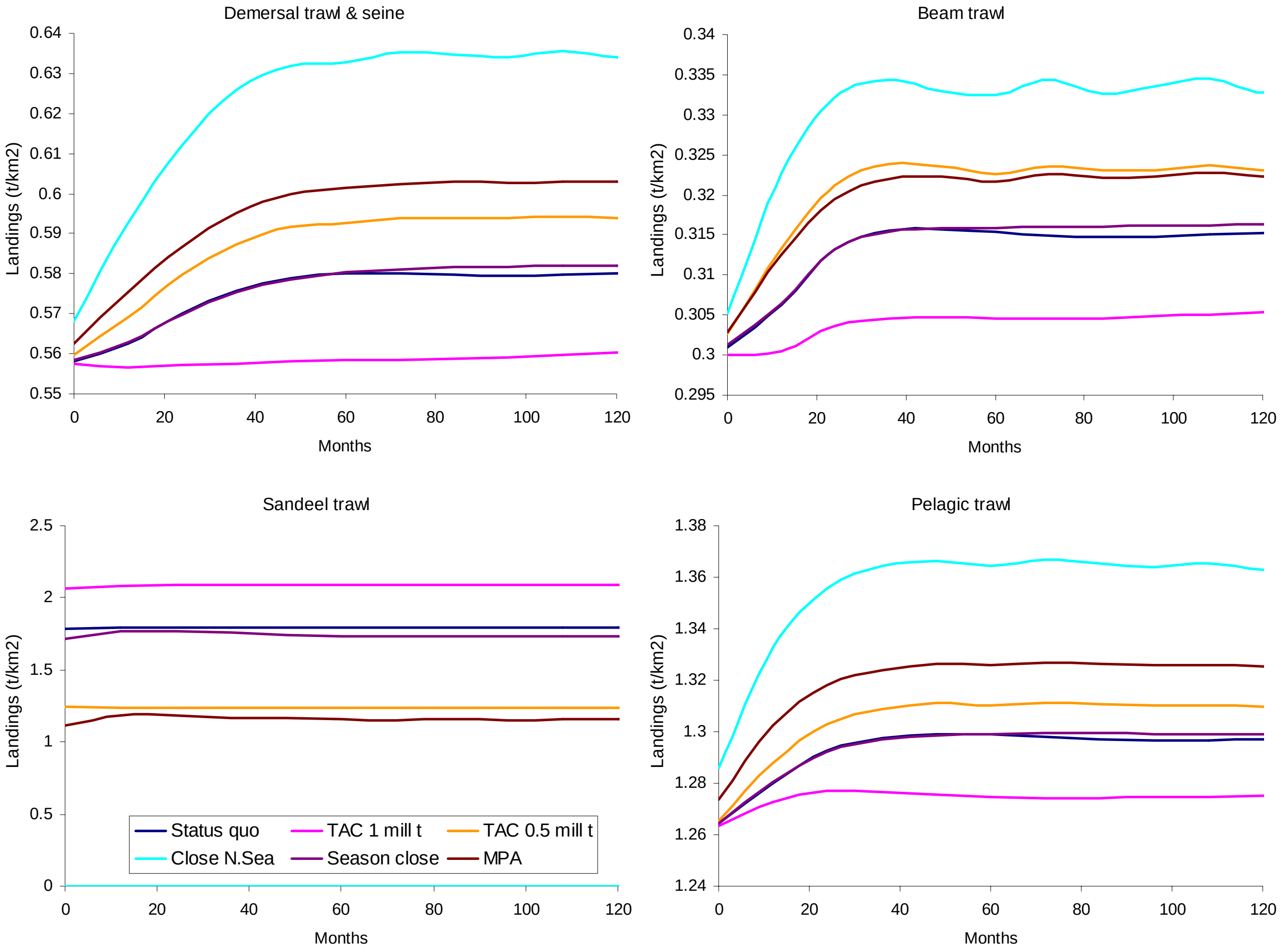


Figure 5.11. Impacts on the landings of main North Sea fleets

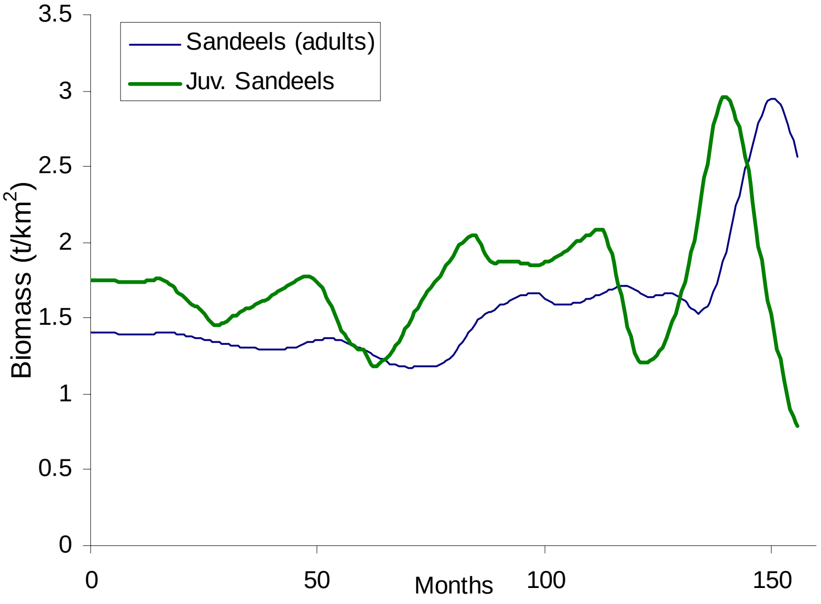


Figure 5.12. Predicted dynamics of juvenile and adult sandeels in response to changes in zooplankton.

Table 5.2. Consumption of sandeels by their predators at the end of 10 years.

Direction of change in consumption

	Baleen whales	Toothed whales	Seals	Seabirds	Juv. Cod	Cod (adult)	Juv. Whiting	Whiting (adult)	Juv. Haddock	Haddock (adult)	Gurnards	Mackerel	Plaice	Dab	Small demersal
Status quo	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
TAC 1 mill t	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TAC 0.5 mill t	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Close N.Sea	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+
Season close	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
MPA	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

Sandeels as a proportion of total comsumption

	Baleen whales	Toothed whales	Seals	Seabirds	venile Cod	Cod (adult)	uvenile Whiti	Whiting (adult)	uvenile Haddo	Haddock (adult)	Gurnards	Mackerel	Plaice	Dab	Small demersal
Status quo	65%	21%	29%	22%	27%	0.21%	66%	40%	23%	21%	42%	23%	28%	30%	43%
TAC 1 mill t	61%	19%	25%	19%	23%	0.17%	63%	37%	18%	18%	38%	19%	24%	27%	40%
TAC 0.5 mill t	68%	24%	30%	24%	28%	0.31%	67%	41%	26%	23%	42%	24%	30%	31%	43%
Close N.Sea	70%	25%	31%	23%	28%	0.30%	65%	38%	30%	24%	41%	25%	32%	31%	41%
Season close	70%	25%	32%	25%	29%	0.31%	67%	42%	28%	24%	43%	26%	31%	32%	44%
MPA	67%	23%	30%	23%	28%	0.31%	66%	40%	25%	22%	42%	24%	29%	31%	43%

5.2 Size-spectrum models

Although not an initial specified objective, the development of size-based ecosystem models was supported through this project (Blanchard et al. *in prep*). The size spectra approach relies on the principle that the distribution of body mass follows regular patterns and changes to this pattern can occur by fishing. These models were parameterised using data on the predator-prey size ratios from fieldwork and are used in the analysis of the ecosystem effects of the management scenarios.

In contrast to the species-based approach used in an Ecopath ecosystem model, a size-based model assumes that the size rather than the species most heavily influences the role of an individual in an ecosystem. Size-based models are simpler and less data-demanding compared to conventional multispecies and ecosystem models. They provide a useful tool for answering questions related to the effects of fishing on the structure of ecosystems and can complement traditional single-species, multi-species and more complex modelling approaches for addressing ecosystem-based fisheries management questions.

Dynamic size spectrum models were developed by Cefas using theory described in Benoît and Rochet (2004) and by developing new extensions to the theory. Dynamic size-spectra models are used to represent the seasonal flux of energy from plankton to large fish predators and the effects of fishing on different parts of the size-spectrum. Similar to the Ecopath model, they can eventually be used to contrast the historical changes that have occurred in the North Sea over time, either in a descriptive sense, by scenario testing, or by implementing time-series data for production and exploitation patterns.

Using the empirical data on predator and prey sizes taken from stomach contents and stable isotope samples collected during the field programme of M0323 (see section Objective 4), two models have been developed under the auspices of BECAUSE (EU FP6) with matched funding from M0323: 1)A dynamic size-spectrum model for the pelagic fish community based on Benoît & Rochet (2004) and 2) A new dynamic size spectrum model allowing for coupling between benthic and pelagic communities, incorporating the effects of high and low quality prey (Blanchard et al. in prep). . Appendix 5 shows the model equations and definitions and Appendix 6 shows parameter values for the coupled size spectrum model. Although most of these parameters represent fish and benthic detritivores generally, they have been approximated and validated for size-structured communities in the North Sea ecosystem.

5.2.1 Evaluation of management scenarios using the size-spectra model

Empirical analyses carried out during M0323 showed condition of predators was lower at certain times of the year and areas of Dogger Bank. A lowered condition factor could be linked with reduced quality and/or quality of prey food available. Fish prey, such as sandeels, are thought to have higher energy content compared to other prey items eaten on Dogger Bank. This is particularly the case for benthic invertebrates, due to the greater proportion of undigestible shell material (Cauffopé and Heymans, 2005).

We used the coupled size spectrum model to test how a twofold difference in benthic prey quality may impact the community when fishing occurs. Using a dynamic size-based model allowed us to investigate the effects of different fishing scenarios relative to the theoretical baseline of a pristine community. Three fishing scenarios were run with and without a difference in benthic prey quality: (i) no fishing, (ii) the average multispecies exploitation pattern of the North Sea during the 1990-2003 period, and (iii) a hypothetical sandeel MPA. The latter scenario is roughly equivalent to the scenario tested in the Ecopath with Ecosim model that resulted in the widest ranging positive impact to sandeels, their predators and fisheries.

Methods

The exploitation pattern during 1990-2003 in the North Sea was used as input for the model by deriving average fishing mortality–at-weight estimates for the pelagic-demersal community from MSVPA (ICES, 2005). For the area closure scenario (iii), a 45% reduction in the fishing mortality of sandeel, sprat, herring and Norway pout was assumed and then average F across species by size-class was calculated (Figure 5.13). Simulations were run for a period of 50 years (daily timestep) without any temporal variation in primary production or variability in fish recruitment.

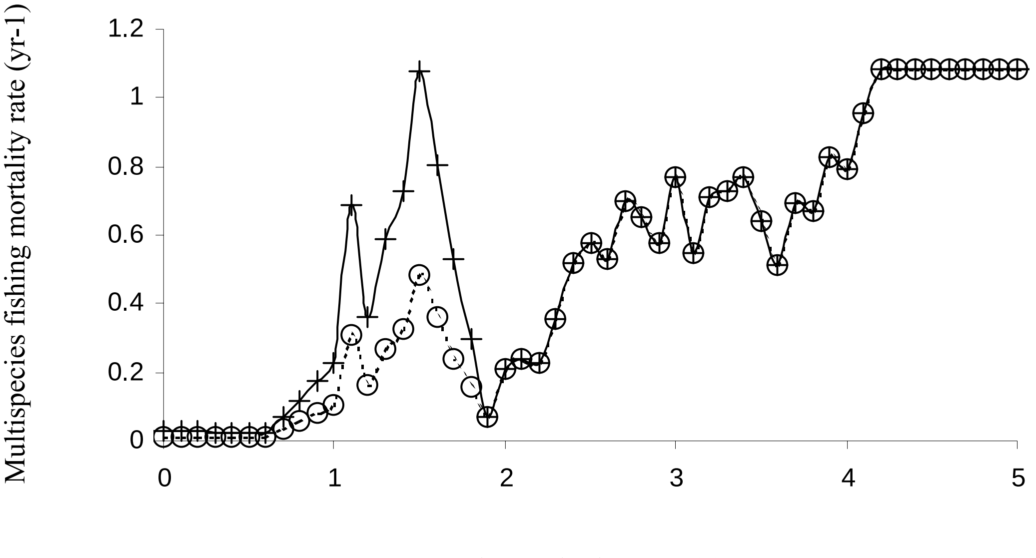


Figure 5.13: Fishing mortality at log10 body mass for the North Sea during the 1990-2003 period (ii, crosses and solid line) and for a hypothetical area closure scenario (ii, open circles and dotted line) assuming a 45% reduction in fishing mortality of sandeel, sprat, juvenile herring and Norway pout.

Results and Discussion

Baseline (without fishing) simulations showed that the fish community size spectrum slopes were –1.028 and –1.036 with and without differences in benthic prey quality, respectively (Figure 5.14). In the absence of any fishing impacts, when the "quality" of food in the benthic community was assumed to be lower, growth rates of fish predators were marginally slower.

The percent change in relative to the baseline was different for the two scenarios. A local area closure (as we defined it) resulted in a higher abundance of small fish (in the size classes occupied by sandeels, Norway pout and sprat along with juvenile fish of other species) compared to the 1990-2003 average. All scenarios predicted between 90 - 99% reduction in fish 4-16 kg compared to the unexploited baseline. These results are consistent with the findings reported in Jennings and Blanchard (2004) for the North Sea fish community. The differences between the two fishing scenarios were of comparable magnitude whether or not benthic prey were assumed to be lower quality (Table 5.3). The sandeel MPA benefited fish predators in the size range 0.5-1.0 kg the most and their biomass was not as greatly impacted with the closed area in place even though they experienced the same levels of fishing mortality as without the sandeel closure. The reduction in larger fish (>4 kg) was exacerbated when benthic prey quality was lower by around 1-2 %. We assumed that a twofold difference in the energy density of fish versus benthic invertebrate prey (Cauffopé and Heymans, 2005) was directly proportional to the fraction of food that would be converted into growth of the predators. There is very little work available on whether this holds true for the variety of prey types that fish encounter in their environment. Further work is required in this area to fully determine the management implications of removing high energy prey on predators.
Further work on size spectrum models, including model sensitivity tests, development of spatially explicit and stochastic models and linking size spectrum models with hydrodynamic processes is being carried out at Cefas under current and future Defra and EU projects.

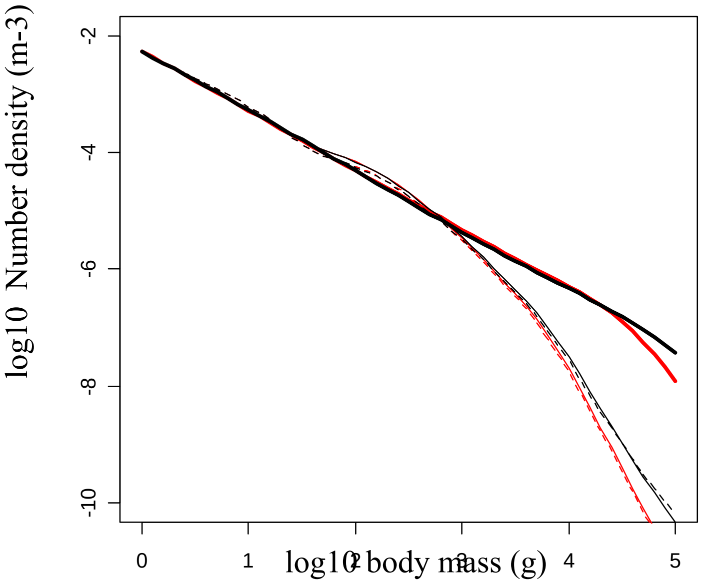


Figure 5.14: Fish community size spectra (black=equal prey quality, red=lower benthic prey quality) after 50 years without fishing (solid thick lines), under the 1990-2003 average fishing mortality (faint solid lines), and under a hypothetical sandeel MPA (faint dotted lines).

Table 5.3: Percent difference in biomass of different size classes of fish in the size spectrum compared to the unexploited baselines, with (A) and without (B) differences in benthic prey quality and for each fishing scenario.

A. Low Quality Benthic Prey, High Quality Fish Prey

	Multispecies F scenario	
Size range (kg)	1990-2003 average	sandeel MPA
0.01 - 0.1	1.14%	8.03%
0.1 - 0.5	20.63%	43.37%
0.5 - 1.0	-13.93%	-2.57%
1.0 - 4.0	-58.65%	-54.19%
4.0 - 16.0	-91.63%	-90.59%
16.0 - 66.0	-99.43%	-99.34%

B. Equal Prey Quality

	Multispecies F scenario	
Size range (kg)	1990-2003 average	sandeel MPA
0.01 - 0.1	-2.35%	4.23%
0.1 - 0.5	23.66%	46.85%
0.5 - 1.0	-3.61%	8.69%
1.0 - 4.0	-50.23%	-44.51%
4.0 - 16.0	-88.18%	-86.32%
16.0 - 66.0	-98.90%	-98.80%

Publication material generated by this project

Manuscripts

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Blanchard J.L., Jennings S., Law R., Castle M.D. (in prep) Does coupling promote stability of size-structured food webs?

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Appendix 1. Project objectives described in the proposal

1 Construct a spatially explicit, multi-species model.

1.1 Define biological and physical parameters to be collected during fieldwork.
1.2 Determine a fine-scale oceanographic modelling approach for use at study sites.
1.3 Investigate the consequence of management actions at localized scales.

2 Identify contrasting areas of sandeel exploitation in the Dogger Bank region.

2.1 Map the habitat structure of each site.
2.2 For sandeels and their predators, monitor population structure, recruitment, growth and mortality.
2.3 Monitor and develop models of fishing effort in response to population density.

3 Determine the temporal and spatial scales of movement of sandeels and their predators at each study site.

3.1 Evaluate chemical mass-marking techniques for release and retrieval of fish using a research vessel.
3.2 Develop acoustic methods for monitoring local-scale distribution and movement of sandeels.
3.3 Determine predator localized behaviour and residence time in response to sandeel density and distribution.

4 Establish feeding relationships between sandeels and their predators at each site.

4.1 Characterize sandeels and their predators in terms of fatty acid profiles and multiple stable isotope signatures (seal tissue analysis carried out in collaboration with SMRU).

5 Develop an ecosystem (Ecopath) model of the North Sea, with special application to sandeel.

5.1 Evaluate ecosystem consequences from various management scenarios.
5.2 Use the model's theoretical base and output for identifying ecosystem indicators

Appendix 2. Brief technical description of the management model

The multi-species model developed within this project is a radical departure from those previously used within Cefas and indeed in the wider ICES community, such as such as MSVPA (MultiSpecies Virtual Population Analysis).

MSVPA is an array based models which holds the numbers of individuals at a given age and all processes, including feeding, are age dependent. The underlying assumption behind this is that growth is constant and therefore feeding (in terms of energetic intake) is also constant. For species which feed exclusively on particular prey species, provided that these prey have a constant energy content, this assumption is valid, however for species with a wide dietary spectrum (i.e. cod) and where prey quality can vary, this assumption will be invalid. MSVPA assumes not only that all prey items are of equal energy content, but that individuals always eat enough to maintain their growth trajectory by making up any deficiencies in target prey with "otherfood". "Otherfood" is a limitless source of additional food items with the same energy content as the preferred prey. MSVPA is also for a single spatial area and there is the assumption that all individuals in the model have an equal probability of encountering each other individual. Diet composition is determined by "suitability" which is a fixed parameter for each combination age class of predator and prey, therefore a cod age 6 will have a set preference for whiting age 2. The parameterisation of this type of model is heavily data dependent and relies upon the ICES "Year of the Stomach" sampling programmes conducted in 1981 and 1991. Analysis of these data have shown that whilst the suitability parameters for some combinations of predator and prey remained constant between the two years, others varied considerably.

The modelling approach taken within this project is that of Individual Based Modelling (IBM). As the name suggests, the model tracks individual fish as they eat, migrate, grow and die. This type of model is significantly more flexible than array based models such as MSVPA and can mimic nature more closely. However this flexibility and realism comes at the expense of computational time which is vastly increased.

The model has been constructed using C++, an object orientated programming (OOP) language. OOP is ideal for individual based modelling as each individual is held in computer memory as a separate object. The model has a number of basic object types which are represented in Figure A2.1 and described below.

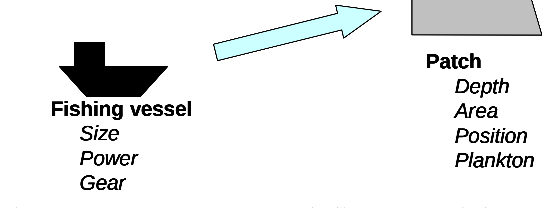

Figure A2.1. Conceptual diagram of the model objects, their attributes and linkages

Fish. These are the basis for the whole model and an implementation can generate as many fish objects as is required subject to the memory capacity of the computer. In order to conserve computer memory, the amount of information each fish carries with it must be kept to a minimum. Individual fish know what species they are, how old they are, what size they are and where they are.

Species. This object carries all the parameters that control the behaviour of the individual fish. These behaviours include spawning, growth, feeding and migration. Each species carries a list of prey types thus enabling the model a basic level of selectivity and restrict the dietary range of predators to that been observed in the field data.

Shoal. Fish can group together to form shoals of unlimited size. This allows the exploration of different shoaling behaviours that can potentially affect the feeding and fishing functions.

Otherfood. It is not anticipated that the full range of potential food items will be modelled, indeed for catholic predators such as cod it is physically impractical to model all individuals of all potential prey types. The model therefore utilises “otherfood” to generate “fish” objects to represent the biomass of all other potential prey. Fish of type “otherfood” are different in that they don’t die (so the availability of otherfood objects is constant) and they don’t migrate.

Patch. Although individual fish know their location in physical space, the environmental conditions for that space are held within this object. Such conditions include depth, temperature etc. Patches are also the spatial scale at which fishing and feeding occurs within each time-step of the model.

Vessel. Fishing vessels are specified with size, operational speed, type and size of fishing gear. Fishing gears are specified with a mesh size so that the probability of capturing individual fish can be determined.

Logbook. For each time-period within the model a vessel will fill in a logbook object which records where it has been fishing and the numbers and tonnage of fish caught by species.

Within any given time-step the model implements the following actions, feeding, growth, migration and fishing which is does in a fixed pattern (Figure A2.2). At coarse temporal scales, changing the order of these events is highly likely to change the outcome of the model but given that the model has been implemented at weekly time steps (52 time steps per year) it is unlikely to be a significant factor. The temporal and spatial scales of the model have the potential to be fully flexible and can therefore operate on an annual scale and a single area, right down to daily time steps and thousands of patches. Care needs to be taken when defining the spatial and temporal scales as they need to match the foraging range of fishing vessels and predators alike such that a “patch” should be roughly equivalent to the area a typical fishing vessel would operate in for a given time-step.

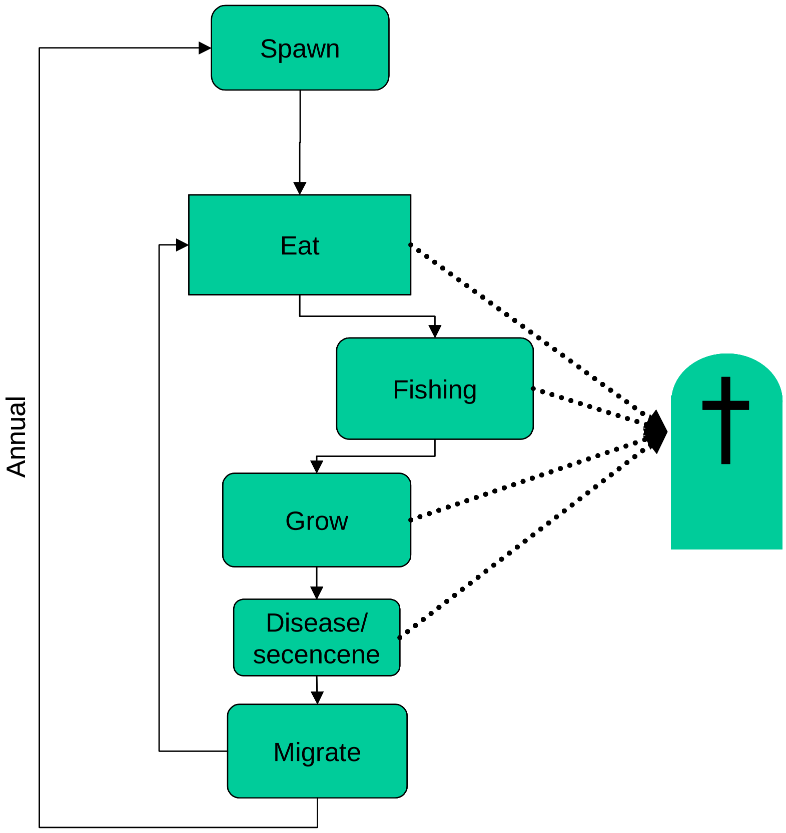

Figure A2.2. Implementation of the model routine.

The operational functions are as listed below.

Feeding. The model assumes that within a time step, all individuals residing within a patch have an equal chance of encounter and there is no chance of encounter with individuals from another patch. At each timestep and for each patch, all individuals within the patch are temporarily merged into one super-shoal. From this super-shoal all the fish that are currently hungry are identified and each of these hungry fish sequentially works through the super-shoal to identify which item to eat. As each predator encounters a new prey object the basic decision process is outlined in Figure A2.3.

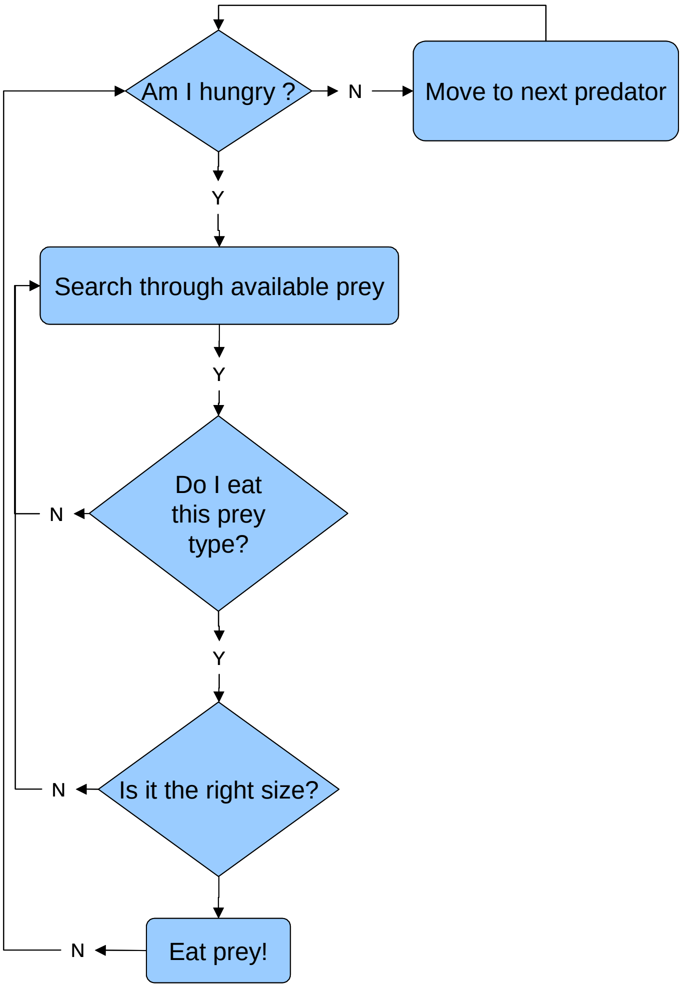

Figure A2.3 Feeding decision-making process

The size function has been parameterised from field data (section 4.2) and assumes that a predator of given size will have a range of preferred prey sizes. The model has been constructed such that predators can carry a number of prey-size functions so that where data are sufficient to parameterise a prey-selection curve for a particular predator-prey pairing this can be used and for other prey types a more generic prey selection curve can be used. At each predation event, the total energy content of the prey is passed to the stomach of the predator with 100% efficiency. Assimilation efficiency and energy requirements for respiration and growth are dealt with by the growth function.

Feeding ceases once the predator is full. This is controlled by the maximum energy requirements of the fish are determined using parameters taken from published sources(Corma ????).

Growth. Growth has been implemented as a bioenergetic function and uses the energy contained within the stomach to fuel metabolism and growth. All parameters for this routine were taken from Corma (????) Energy is transferred to from the stomach to the individual with a user-specified transfer efficiency. For the purposes of this exercise a standard figure of 0.45 has been used. The energy requirements for basic metabolism and locomotion are then deducted from the assimilated energy. Any remaining energy is therefore available for somatic growth, for the purposes of this model we have ignored the portion of energy which goes into reproduction, but this could be added at a later date. Growth occurs in both weight and length of individuals, however if there is insufficient energy to supply the basic metabolic requirements of the predator then its weight will decrease whilst the length will remain constant.

Migration. Migration has been implemented as a function of Lewy flight. This describes the probability of an individual moving a number of body lengths in a given time period. Three parameters control the shape of this function and determine the speed and probability of movement. For most individuals and short time steps there is a high probability that it will only move a short distance and a low probability that it will move a long distance. Different migration patterns have been constructed for different species, life stages and seasonality's. Adult cod, for instance, will undergo directional migration in order to spawn, reverse the migration path to return to the feeding grounds and then undergo short-scale random migrations as they move about to feed. By contrast, juvenile cod undergo random movement with little dispersion all year round. Adult sandeels however will only undergo very short scale random migrations and always remain within a given patch.

Fishing. Fishing works on a swept area basis. Within a time-step, a fishing vessel will operate for a number of hours (determined from satellite data), towing gear with a known door-spread. From this we determine the swept area within the time step and divide this by the total surface area of the patch the vessel is currently operating in. This gives a probability of covering any particular point within the patch (point probability). We assume that shoals have a random uniform distribution within the patch and therefore the probability of encounter between vessel and shoal is the same as the point probability. The shoal is then filtered using the size selectivity parameters of the specified gear. The model can be adapted to include information on the spatial pattern of aggregation of sandeel shoals (see objective 2), which is likely to influence the probability of encounter for fishing vessels.

Spawning.

Spawning occurs at the beginning of the year for all species, but the individuals produced do not enter the system immediately, but at a species-specific date specified in the set-up files. It was unrealistic to model the first 6 months of life due to not only the massive computational load, but also the lack of data for these life stages.

Appendix 3. Stomachs sampled by CEFAS research cruises in 2004, 2005 and 2006

Species	Species Code	Research Cruise Name						Total
		Cory-04/2004	Cory-09/2004	CEnd-07/2005	CEnd-16/2005	CEnd-11/2006	CEnd-17/2006	
Brill	BLL	0	0	1	5	0	3	9
Bullrout	BRT	0	0	6	0	4	3	13
Cod	COD	34	58	1	34	42	9	178
Cuckoo Ray	CUR	0	0	0	1	0	0	1
Dragonet	CTD	1	0	0	0	0	0	1
Dab	DAB	9	102	0	82	51	29	273
Flounder	FLE	1	0	2	0	1	0	4
5 - b'd rockling	FVR	0	0	0	0	1	1	2
Greater Sandeel	GSE	2	41	73	1	23	34	174
Spurdog	DGS	0	0	0	5	0	9	14
Grey Gurnard	GUG	568	1527	829	1018	588	628	5158
Red Gurnard	GUR	0	0	1	1	0	0	2
Haddock	HAD	199	172	111	61	134	50	727
Herring	HER	1	0	0	1	0	4	6
Horse Mackerel	HOM	0	9	1	2	0	2	14
John Dory	JOD	0	0	1	2	1	1	5
Lemon Sole	LEM	1	0	0	71	38	46	156
LS-Dogfish	LSD	0	0	0	0	0	1	1
Mackerel	MAC	1	44	137	57	50	165	454
Red Mullet	MUR	0	28	0	12	4	3	47
LR-Dab	PLA	0	0	2	0	4	17	23
Plaice	PLE	180	580	226	234	129	161	1510
Poor-cod	POD	3	15	0	0	26	0	44
Scaldfish	SDF	1	0	0	0	0	0	1
Smoothound	SMH	0	0	0	1	0	0	1
Sprat	SPR	1	0	0	0	0	0	1
Tub Gurnard	TUB	0	0	1	0	0	1	2
Sole	SOL	0	0	0	0	1	1	2
Solenette	SOT	0	0	0	0	2	0	2
LS-Scorpionfish	SSN	0	0	0	0	1	0	1
Stary Ray	SYN	0	0	0	0	2	0	2
Turbot	TUR	0	0	0	2	1	1	4
Lesser Weever	WEL	4	636	470	356	322	253	2041
Whiting	WHG	755	385	826	486	691	283	3426
Grand Total	**34 spp**	**1781**	**3612**	**2688**	**2432**	**2133**	**1705**	**14351**

Appendix 4. Basic parameter values for the North Sea 1991 Ecopath model.

	Functional groups	Trophic level	Biomass	Production/ biomass	Consumption/ biomass	Ecotrophic efficiency	Production/ consumption	Reference
1	Baleen whales	4.44	0.067	0.020	9.900	0.000	0.002	Hammond et al 2002,Trites et al. 1999,Olsen & Holst 2000
2	Toothed whales	4.78	0.017	0.020	17.630	0.000	0.001	Hammond et al 2002, Trites et al. 1999, Santos et al. 1994, 1995, 2004
3	Seals	5.01	0.008	0.090	26.842	0.000	0.003	ICES 2002, Hall et al 1998, Hammond et al 1994,
4	Seabirds	3.5	0.003	0.280	216.000	0.000	0.001	ICES 2002, ICES 1996
5	Juvenile sharks	4.29	0.001	0.500	2.500	0.385	0.200	This study, Ellis et al. 1996
6	Spurdog	4.77	0.017	0.600	2.000	0.950	0.300	This study, FishBase 2004, Brett & Blackburn 1978, Ellis et al. 1996
7	Large piscivorous sharks	4.93	0.002	0.480	1.600	0.283	0.300	This study, FishBase 2004, Ellis et al. 1996
8	Small sharks	4.34	0.002	0.510	2.960	0.415	0.172	This study, FishBase 2004, Ellis et al. 1997
9	Juvenile rays	4.23	0.268	0.660	1.700	0.005	0.388	This study, FishBase 2004, ICES 2002, Daan et al 2003
10	Starry ray + others	4.49	0.109	0.660	1.700	0.095	0.388	This study, FishBase 2004, ICES 2002, Daan et al 2003
11	Thornback & Spotted ray	4.49	0.066	0.780	2.300	0.109	0.339	This study, FishBase 2004, ICES 2002, Daan et al 2003
12	Skate & cuckoo ray	4.44	0.050	0.350	1.800	0.004	0.194	This study, FishBase 2004, ICES 2002, Daan et al 2003
13	Juvenile Cod	4.43	0.079	1.790	5.960	0.945	0.300	ICES 2002, Hislop 1996
14	Cod (adult)	4.83	0.161	1.190	3.500	0.750	0.340	ICES 2002, Hislop 1996
15	Juvenile Whiting	4.27	0.222	2.360	6.580	0.875	0.359	ICES 2002, Hislop 1996
16	Whiting (adult)	4.41	0.352	0.890	5.460	0.932	0.163	ICES 2002, Hislop 1996
17	Juvenile Haddock	4.06	0.284	2.000	5.390	0.462	0.371	ICES 2002, Hislop 1996
18	Haddock (adult)	4.28	0.104	1.140	4.400	0.972	0.259	ICES 2002, Hislop 1996
19	Juvenile Saithe	4.03	0.281	1.000	4.940	0.316	0.202	ICES 2002, Hislop 1996
20	Saithe (adult)	4.36	0.220	0.950	3.600	0.621	0.264	ICES 2002, Hislop 1996
21	Hake	4.92	0.014	0.820	2.200	0.642	0.373	This study, FishBase 2004, Pauly 1989, Du Buit 1996
22	Blue whiting	4.09	0.080	2.500	9.060	0.868	0.276	This study, FishBase 2004, FishBase 2004, Bergstad 1991
23	Norway pout	3.59	1.394	2.200	5.050	0.767	0.436	ICES 2002, ICES 2002, Greenstreet 1996, Malyshev & Ostapenko 1982
24	Other gadoids (large)	4.53	0.049	1.270	3.200	0.950	0.397	This study, FishBase 2004, Hoines & Bergstad 1999, Bergstad 1991,Rae&Shelton 1982

25	Other gadoids (small)	3.83	0.195	2.300	6.000	0.950	0.383	This study, FishBase 2004, Albert 1995, Armstrong 1982
26	Monkfish	4.85	0.042	0.700	1.900	0.848	0.368	This study, FishBase 2004, FishBase 2004, Rae & Shelton 1982
27	Gurnards	4.52	0.077	0.820	3.200	0.596	0.256	This study, FishBase 2004, ICES 2005, Mickleburgh 2003
28	Juvenile Herring	3.44	0.630	1.310	5.630	0.685	0.233	ICES 2002, Greenstreet 1996, Last 1989
29	Herring (adult)	3.45	1.966	0.800	4.340	0.691	0.184	ICES 2002, Greenstreet 1996, Last 1989
30	Sprat	2.97	0.579	2.280	6.000	0.807	0.380	ICES 2002, Greenstreet 1998, De Silva 1973
31	Mackerel	3.9	1.720	0.600	1.730	0.632	0.347	ICES 2002,
32	Horse mackerel	4.38	0.579	1.200	3.510	0.356	0.342	Rueckert et al 2002, ICES 2002, Greenstreet 1996
33	Sandeels	3.35	3.122	2.280	10.100	0.787	0.226	ICES 2002, Greenstreet 1996, ICES 2002, Reay 1970
34	Plaice	3.99	0.703	0.850	3.420	0.695	0.249	ICES 2002, AFCM 2005, Greenstreet 1996, De Clerck & Buseyne 1989
35	Dab	4.01	3.000	0.672	3.360	0.209	0.200	This study, Greenstreet 1996, De Clerck & Torreele 1988
36	Long-rough dab	4.18	0.350	0.700	3.400	0.606	0.206	This study, FishBase 2004, Ntiba & Harding 1993
37	Flounder	4.37	0.250	1.100	3.200	0.278	0.344	This study, FishBase 2004, Doornbos & Twisk 1984
38	Sole	4	0.158	0.800	3.100	0.894	0.258	This study, AFCM 2005, FishBase 2004, ICES 2002, Braber & Groot 1973
39	Lemon sole	3.94	0.305	0.864	4.320	0.242	0.200	This study, FishBase 2004, Greenstreet 1996, Rae 1956
40	Witch	4.05	0.082	0.900	3.000	0.421	0.300	This study, FishBase 2004, Rae 1969
41	Turbot and brill	4.62	0.054	0.860	2.300	0.139	0.374	This study, FishBase 2004, Wetsteijn 1981
42	Megrim	4.46	0.034	0.720	3.100	0.243	0.232	This study, FishBase 2004, Du Buit 1984
43	Halibut	4.85	0.033	0.160	3.140	0.258	0.051	This study, FishBase 2004, McIntyre 1952
44	Dragonets	3.98	0.045	1.500	6.000	0.757	0.250	This study, FishBase 2004, Gibson & Ezzi 1987
45	Catfish (Wolf-fish)	4.27	0.014	0.480	1.700	0.792	0.282	This study, FishBase 2004, Bowman et al 2000
46	Large demersal fish	4.2	0.017	0.550	2.540	0.900	0.217	This study, FishBase 2004, Bergstad et al 2001, Bowman et al 2000
47	Small demersal fish	4.21	0.345	1.420	3.700	0.980	0.384	This study, FishBase 2004, Ebeling & Alshuth 1989, Albert 1993, Gibson&Robb 1996
48	Miscellaneous filterfeeding pelagic fish	3.43	0.030	4.000	10.190	0.980	0.393	This study, FishBase 2004, Bowman et al 2000
49	Squid & cuttlefish	3.86	0.080	4.500	20.000	0.888	0.225	Pierce et al., 1994a, Collins et al. 2002, Pierce et al. 1998, Young et al. (2004), Wood and O’Dor (2000), Pierce et al. 1994, Johnson (2000).
50	Fish larvae	2.85	0.254	5.000	20.000	0.990	0.250	

51	Carnivorous zooplankton	3.22	3.287	4.000	12.500	0.990	0.320	Zooplankton: Lindley 1980, Lindley 1982, Williams and Lindley (1980a), Lindley and Williams (1980), Fransz et al., 1991b, Landry 1981, , Fransz and van Arkel 1980, Fransz and Gieskes 1984, Rae and Rees 1947), Daan et al. 1988, Krause and Trahms 1983, Williams and Lindley, 1980a, Williams and Lindley (1980b) , Broekheuizen et al. (1995), Evans (1977), Martens (1980), Roff et al. (1988), Fransz et al. (1984), Fransz (1980), Sherman et al. (1987), Williams, 1981, Joiris et al., 1982, Sherr et al., 1986, Baars and Franz 1984, Nielsen and Richardson 1989, Marshall and Orr 1966, Checkley 1980, Poulet (1973, 1974, 1976), Pepita et al. 1970, Anraku, 1964, Gaudy 1974, Cowey and Corner 1963, Daro and Gijsegem 1984, Båmstedt 1998, Cushing and Vucetic (1963), Paffenhöfer 1976, Huntley and Lopez 1992, Sahfos, Reid. Clark 2000, Clark et al. 2001
52	Herbivorous & Omnivorous zooplankton	2.06	16.000	9.200	30.000	0.474	0.307	
53	Gelatinous zooplankton	3.44	0.066	2.858	0.180	0.760	15.878	
54	Large crabs	3.71	1.354	0.554	2.770	0.933	0.200	ICES SGCRAB, Lizárraga-Cubedo et al. (2005)
55	Nephrops	3.51	1.140	0.370	1.850	0.980	0.200	ICES WGNSSK 2005, WGNEPH 2004, North Sea Benthos Surveys, Brey (2001),
56	Epifaunal macrobenthos	3.31	78.000	0.388	1.942	0.432	0.200	For all Infaunal and Epifaunal benthos: Künitzer et al. (1992), Craeymeersch et al. 1997, Eleftheriou and Basford (1989), Salzwedel et al. 1985; Romohr et al. 1987, Calloway et al. 2002, Calloway..report, Brey (2001), Kaiser et al. (1994), Reiss et al (2006, McIntyre, 1978, Heip et al. 1992, Rachor (1982), Duineveld et al. (1991) , Gray (1981), Kröncke 1990, Heip and Craeymeersch 1995.
57	Infaunal macrobenthos	2.88	136.000	1.000	3.333	0.279	0.300	
59	Small mobile epifauna	2.91	30.611	1.900	5.429	0.990	0.350	
60	Small infauna (polychaetes)	2.95	150.000	0.900	3.000	0.874	0.300	
61	Sessile epifauna	2.8	105.000	0.260	1.300	0.039	0.200	
58	Shrimp	3.05	0.530	1.500	5.000	0.817	0.300	ICES WGCRAN 2005, ICES WGPAN 2004, 2005, Hopkins 1988, Shumway et al. 1985., Brey 2001. Hopkins et al. 1993.
62	Meiofauna	3.03	4.125	35.000	125.000	0.990	0.280	Moens and Vincx (1999), McIntyre (1964, 1969, 1978),

								Heip et al. 1995, Heip et al. 1983, Gee 1989, Heip and Craeymeersch (1995), Huys et al. (1992). Heip et al. 1990, Huys et al. 1992, De Bovee 1993 in Brey 2001. Gerlach 1971, 1978, Admiraal et al 1983, Heip et al. 1985., Herman and Vranken 1988, Herman and Heip 1983, Warwick 1984, Gee and Warwick 1984, Vranken and Heip (1986), Lasserre et al. 1976, Faubel et al. 1983, Wilde et al. 1986, Carman and Frey (2002), Donavaro et al. 2002, Moens et al. 1990, Moens and Vincx 1999. Montagna 1995, Decho and Lopez 1992 in Moens and Vincx 1999. Creed and Coull (1984).
63	Benthic microflora	2.24	0.105	9470.000	18940.000	0.990	0.500	Microflora: Nielsen and Richardson 1989, , Linley et al. 1983, Cole et al. 1989, Fenchel 1982a,b,c, Fenchel 1988, Van Duyl et al. 1990, Billen et al. 1990, Azam et al. 1983, McIntyre 1978, Geider 1988, Rheinheimer 1984, deLaca 1985, Brey 2001, Holligan et al. 1984, Meyer-Reil (1982) and Es and Meyer-Reil (1982); Kirman (2000).
64	Planktonic microflora	2.14	1.460	571.000	1142.000	0.720	0.500	
65	Phytoplankton	1	7.500	286.667	-	0.212	-	Reid et al. 1990, Fransz and Gieskes 1984, Lancelot et al. 1988, Krause and Trahms 1983, Hannon and Joires 1989, Geider 1988, Cadée 1985, Linley et al. 1983, Gieskes and Kraay 1980, Lancelot and Mathot 1987, Jones 1984, Matthews and Heimdal 1980..
66	Detritus - DOM in water	1	25.000	-	-	0.932	-	Fenchel 1988, Hannon and Joires 1989
67	Detritus - POM in sediment	1	25.000	-	-	0.953	-	
68	Discards	1	50.000	-	-	0.747	-	

Appendix 5: Dynamic coupled size spectrum model equations and descriptions

Model Equations	Description
Subcript 0 = predators; 1 = detritivores	
$\frac{\partial N_0}{\partial t}(x,t) = \frac{-\partial(g_0 N_0)}{\partial x} - m_0 N_0$ $\frac{\partial N_1}{\partial t}(x,t) = \frac{-\partial(g_1 N_1)}{\partial x} - m_1 N_1$	**State variables:** The numerical density (m^{-3}) of predators = N_0 and detritivores = N_1. The rates of change are a functions of x (ln body mass in grams) and time t due the fluxes (t^{-1}) of growth (g) and mortality (*m*).
$\frac{dB_D}{dt} = \mathrm{det}_{in} - \mathrm{det}_{out}$	B_D = biomass density (g.m-3) of detritus. Rate of change through time is due to flux in (det_{in}) from faeces produced in the predator spectrum and flux out (det_{out}) determined by the consumption by detritivores.
where the growth and mortality equations for each size spectrum are: $g_0(x,t) = \omega K_0 A_0 e^{\alpha_0 x} \int_0^\infty \varphi(q)\ N_0(t,x-q)\ e^{-q}\ dq + (1-\omega) K_1 A_0 e^{\alpha_0 x} \int_0^\infty \varphi(q)\ N_1(t,x-q)\ e^{-q}\ dq$	**Parameters:** The dimensionless weighting factor ω determines the relative preference of food that is ingested from each size spectrum. Gross growth conversion efficiency, *K* (dimensionless) determines the fraction of the food ingested that is assimilated and then converted into growth.
$\mu_0(x,t) = \omega A_0 e^{\alpha_0 x} \int_0^\infty \varphi(q) N_0(t,x+q)\ e^{\alpha_0 q}\ dq + m_0 N_0(x,t)$ $g_1(x,t) = \frac{1}{e^x} K_1 A_1 e^{\alpha_1 x} N_D$	Allometric relationship for the volume of water encountered that would be required for individuals of size *x* (dimensions: $m^3\ t^{-1}$) to meet their metabolic demands is given by $A_0 e^{\alpha_0 x}$ and $A_1 e^{\alpha_1 x}$ for predators and detritivores, respectively. The probability of a predator of size y eating a predator of size x, where y -x = q (the logarithmic ratio of predator to prey size) is described by the function: $\varphi(q)=e^n (q/q0)e^{-nq/q0}$ if *q* is greater than or equal to 0 and $\varphi(q) = 0$ otherwise.
$\mu_1(x,t) = (1-\omega) A_0 e^{\alpha_0 x} \int_0^\infty \varphi(q)\ N_0(t,x+q)\ e^{\alpha_0 q} dq + m_1 N_1(x,t)$	Other sources of mortality ($m,\ t^{-1}$) include instrinsic non-predation mortality plus sensescence and fishing mortality.
and fluxes into and out of the detritus pool are modelled as: $\mathrm{det}_{in} = \int_0^\infty D\ (A_0 e^{\alpha_0 x} \int_0^\infty \varphi(q)\ N_0(t,x-q)\ e^{-q}\ dq + A_0 e^{\alpha_0 x} \int_0^\infty \varphi(q)\ N_1(t,x-q) e^{-q} dq)\, dx$	The flux into the detritus pool (det_{in}, g t^{-1}) is determined by the fraction of the biomass density of food ingested per unit time that is defecated (*D,* dimensioneless) by all predators.
$\mathrm{det}_{out} = \int_0^\infty (A\ e^{\alpha_1 x}\ B_D N_1)\ dx$	The flux out of the detritus pool (det_{out},g t-1) is the biomass density per unit time consumed by all detritivores.

Appendix 6: Symbol definitions, parameter values and units for the dynamic coupled spectrum model (from Blanchard et al. in prep)

Symbol	**Definition**	**Parameter Values**	**Unit**	**Source**
1.$[x_{min}, x_1)$ 2.$[x_1, x_{max}]$ 3.$[x_2, x_{max}]$	Size ranges of *x*, logarithm of the mass (g), for each component community: 1.plankton (model input) 2.fish predators 3.benthic detritivores	x_{min}=-6 x_1=-2 x_2=-2 x_{max}=6		Boudreau and Dickie (1992)
dt	Timestep	dt=0.00274 (1 day)	yr-1	
$B_D(t=0)$	Initial biomass density of detritus material	0.2 g m-3	g.m^{-3}	
Ω	Weighting [0,1] for relative preference of feeding on the two size spectra.	0.5 (equal feeding on benthic and fish communities)		
e^q	Predator-prey mass ratio (PPMR), where q is simply x_{pred} - x_{prey} and e^{q0} represents the modal PPMR	100		Daan, 1973; Ware, 1978; Silvert and Platt, 1980; Borgman, 1982; Cohen et al., 1993; Thiebaux and Dickie, 1993; Kerr and Dickie, 2001
A	Volume of water required to meet metabolic demands by unit mass	640 64	m^{-3} yr^{-1}	Ware, 1978; Peters, 1983
α	Exponent of mass in volume of water required	-0.82 -0.75		Ware, 1978; Peters, 1983
n	Measure of the width of the PPMR distribution	3.0		Daan, 1973; Cohen et al., 1993
K	Gross growth conversion efficiency	0.2 (high quality prey) 0.1 (low quality prey)		Paloheimo and Dickie, 1966; Ware, 1978; Borgman, 1982; Gurney et al., 1990; Buckel et al., 1995; Cauffope and Heymans, 2005
E,	Egestion efficency	0.3 (high quality prey) 0.4 (low quality prey)		Peters, 1983
R	Fraction of assimilated food allocated to reproduction	0.2		Peters, 1983
M	Fraction of assimilated food lost as respiration	0.3		Peters, 1983
m	Intrinsic non-predation natural mortality rate	0.20	yr^{-1}	Gislason and Helgason, 1985; Gislason, 1999; Andersen and Ursin, 1977