Science Series
Technical Report no.142

An ecosystem model of the North Sea to support an ecosystem approach to fisheries management: description and parameterisation

S. Mackinson and G. Daskalov

Cefas

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Bill Mulligan	Kings College London	Economic and social analysis
Paul Eastwood	Cefas	Spatial data methods
Andrew South	Cefas	Spatial data preparation
Peter Robinson	Cefas	Data extraction
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Foreword

I am delighted to introduce this technical report that is an important product for a number of scientists and technicians both within, and outside of, Cefas. It represents the distillation of knowledge and ideas pertaining to the North Sea marine ecosystem contributed over the past six years from work undertaken both nationally and internationally.

This report describes the data sources, assumptions and analyses used in developing representational models of the North Sea ecosystem (defined by ICES area IV) for the years 1973 and 1991, and the simulations of changes over space and time. In doing so, it brings together in one source a vast range of data and scientific knowledge that will become a valuable resource to ecologists and modellers alike. The contributions of experts, reflected in the authorship of the individual sections, have been central to ensuring the relevance and high quality of this synthesis.

The models presented are just one of the tools needed to support the implementation of an ecosystem approach to fisheries management in the North Sea. While the reviews of biological knowledge for each functional group stand alone as useful contributions to knowledge on the North Sea, the added-value comes from the effort to render this information mutually compatible in the framework of an ecosystem model. The need to develop methods and approaches for exploring alternative hypotheses about ecosystem function and response to natural and human-induced change necessitates that such approaches be developed.

The models capture and quantify the trophic structure and energy flows in 68 functional groups including marine mammals, birds, fish, benthos, primary producers and categories of detritus. They also include the landings, discards, and economic and social data for appropriately defined fishing fleets. Hind caste predictions of changes in the North Sea during the recent past are 'calibrated' against time series data from assessments and scientific survey data.

Based on strong foundations, the models are useful tools for exploring dynamic change in ecosystems and macro-ecological patterns. The models may be further developed in their application to specific problems such as evaluating the relative influence of climate and fishing on ecosystem change, evaluating the effects of Marine Protected Areas (MPAs), predicting fish stock recovery and evaluating harvesting strategies.

This technical report is one of a comprehensive series, documenting the data sources and construction of ecosystem models of UK shelf seas. Previously published reports and models exist for the North Sea, Channel (combined for both Eastern and Western), Western Channel, Irish Sea, West of Scotland; with those of the Celtic Sea and Eastern Channel in the later stages of preparation.

Dr Carl M. O'Brien CStat FLS
Fisheries Division Director

Section A

A model representation of the North Sea ecosystem

1. Introduction

Authors: Steven Mackinson, Tom Howden and Bill Mulligan

1.1 Purpose and approach to modelling the North Sea

Investigating the effects of fishing on marine fauna and the environment has been an important impetus behind the proliferation of marine ecosystem models. More recently, it has been recognized that investigation of the effects of environmental changes (e.g., climate change and pollution) should also be undertaken in an ecosystem context. Together, fishing and environmental change influence the structure and function of marine ecosystems. Determining the relative importance of these controlling forces necessitates the development of ecosystem models that can be used to explore alternative hypotheses about ecosystem function and response to change. The knowledge is intended to help researchers, managers, and policy-makers answer the questions that will help to enable responsible resource management decisions to be made.

Although the potential questions that can be explored with an ecosystem model of the North Sea are broad, the immediate general purpose of constructing the model is to: (i) quantitatively describe the ecological and spatial structure of species assemblages of the North Sea ecosystem and (ii) calibrate the dynamic responses of the modeled system by comparison with observed historical changes. The model is developed using the Ecopath with Ecosim (EWE) approach (see section 1.4).

Four previous published Ecopath models exist for the North Sea. Based on 1981 year of the stomach data, Christensen (1995) constructed two models representing the 1981 period; a 24 box model and 29 box model including more detailed, size based plankton groups. Neither model includes fisheries data. Based on Christenson model, Beattie *et al.* (2002) developed a '1970' model, and used it for testing 'Ecoseed' predictions of size and placing of MPAs. The third was constructed by Mackinson (2002a) based on historical records. It gave a detailed representation of the North Sea in the 1880s, which included 49 functional boxes, with catch data from five different fishing fleets.

A review of the previous models for the North Sea highlighted a number of key topics that were considered to warrant more directed research effort before the models could be used (with any confidence) to investigate ecosystem responses to proposed management strategies. In particular, these included:

1. Improved resolution in the structure of the model and the trophic connections, with particular emphasis on the non-fish functional groups.
2. Improved detailed representation of fisheries and discards using best available data.
3. Calibration of dynamic simulations by tuning to observed time series data.
4. Spatial representation of functional groups and fleets.
5. Testing sensitivity.

Previous research has gone some way to improving our understanding of the importance of model structure and sensitivity to predator-prey interactions (Pinnegar *et al.*, 2005; Mackinson *et al.*, 2003). This knowledge has been used to guide the development of the structure of the North Sea model, so that it represents an unbiased ecological perspective of the system.

This report describes the data sources, analyses and assumptions used in construction of two new Ecopath models. A 1991 model and 1973 model (that uses the same structure). Both include detailed representation of the functional groups (68 groups including mammal groups, fish groups, benthic groups, primary producers and categories of detritus) and fishing fleets (12), together with their economics. Details of construction and parameterisation for time (Ecosim) and spatial dynamics (Ecospace) are also included. The development of these models has followed a strategic plan outlined in Figure 1.1 and has taken 6 years. A critical step has been to ensure quality control. Accordingly, we have invited experts in their field to review and contribute to the development of the model. Authorship of each section reflects this. A list of contributors is given in on page 3.

1991 was chosen as the ‘nominal’ year for which to construct the initial model the North Sea so that best use was made of the detailed information on fish diets (1991 “year of the stomach”) and catch and discards by specific fishing fleet segments (STCF, 1991 data). Another reason for choosing 1991 (and 1973) is that constructing a model in the past provides the opportunity to calibrate the model to changes that have been observed in the system since that time. (ie, survey and assessment data from 1973-2006).

1.2 Drivers behind ecosystem modelling research

With a growing body of evidence highlighting the parlous state of world fish stocks (eg Hutchings, 2000; FAO, 2002), new approaches to fisheries management that take account of how fishing and climate change affects ecosystem structure and function are being called for. Such principles are encapsulated in the ecosystem approach to fisheries

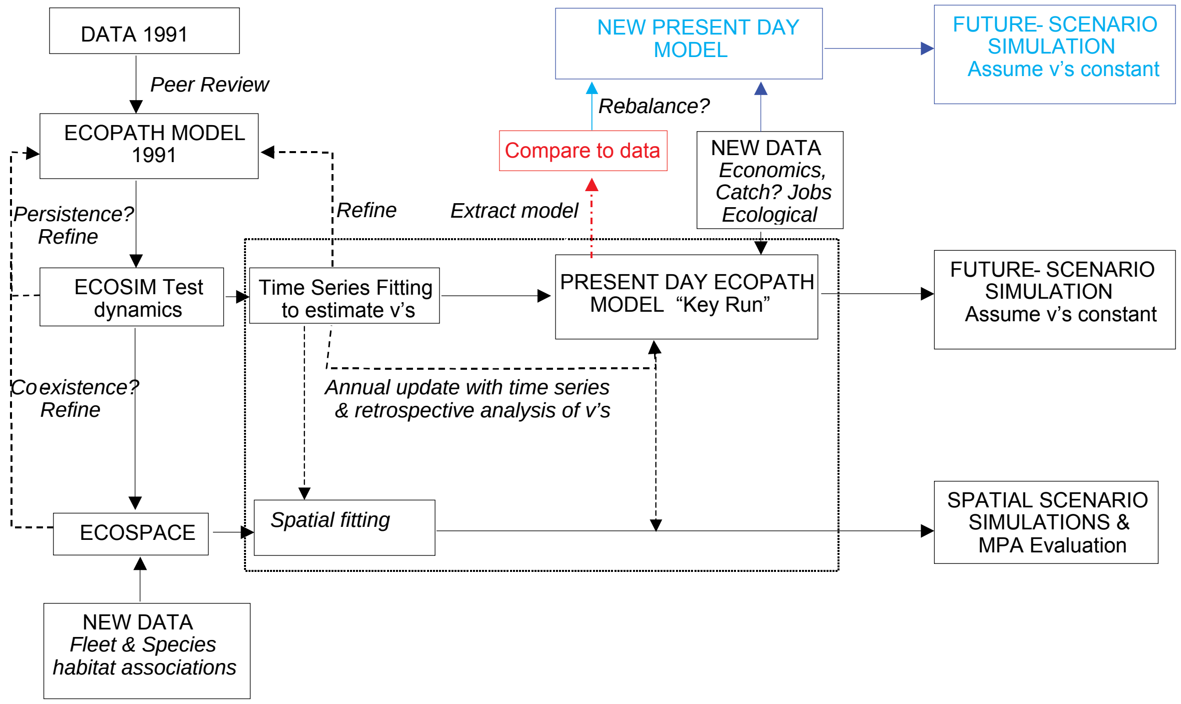


Figure 1.1. Strategic approach guiding construction testing and application of the North Sea model.

management (EAFM) (Botsford *et al.*, 1997, Christensen *et al.*, 1996; FAO, 2003). The EAFM aims to incorporate considerations about how fishing for one species affects other components of the ecosystem (see for example, Jennings and Kaiser, 1998; Kaiser and de Groot, 2000; Tegner and Dayton, 2000) and attempts to balance economic sustainability with maintaining ecosystem integrity and function. In doing so, the approach necessarily considers impacts of fishing on biodiversity, habitats, changes in the food web structure and productivity (Murawski, 2000). The evaluation of fishing impacts must be placed in the context of (and weighed against) natural changes arising from climate change.

The development of an EAFM has been driven by international initiatives such as the 1982 UN Convention on the Law of the Sea, the 1992 Convention on Biological Diversity, the 1995 Jakarta Mandate on Marine and Coastal Biological Diversity, the 1995 Kyoto Declaration on the Sustainable Contribution of Fisheries to Food Security, the 1995 FAO Code of Conduct for Responsible Fisheries and, more recently, the 2002 Johannesburg World Summit on Sustainable Development. In the United States, such high level committments are supported by legislation in the Magnusen–Stevens Fishery Conservation and Management Act (Public Law 94–265). In Europe, political and legislative support comes from the European Union Action Plan for Biodiversity in Fisheries, the Bergen Declaration, the Oslo and Paris (OSPAR) Biodiversity Strategy, the Common Fisheries Policy and the Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem. National policies and strategies provide further backing (eg, in the UK, 'Securing the Benefits' and Fisheries 2027 consultation).

The recently reformed Common Fisheries Policy (2003) contained substantial changes to the way EU fisheries are to be managed, with particular emphasis being placed on fishery managers adopting the precautionary and ecosystem approach to facilitate the long-term sustainability of fish stocks (EC Fisheries 2006). To help coordinate the provision of scientific advice on marine ecosystems, and research on the ecosystem effects of exploitation of marine resources in North Western Europe and the eastern Atlantic, the International Council for Exploration of the Sea (ICES), formed the Advisory Committee on Ecosystems (ACE) (eg, ICES, 2003).

It is with this background that ecosystem models of the UK shelf seas are being developed and used to explore the complexity of ecological interactions and possible consequences of management actions.

1.3 Single and multi-species/ecosystem approaches

Trying to account for the interdependencies between species and climate effects on the productivity of fisheries means an increase in the level of complexity for the fishery manager and an increase in the sophistication required to model it (Figure 1.2).

It is not unsurprising then that single species approaches to determining stock size and allowable catches still dominate fisheries management globally. Single species models represent the stock as self-determining with regards to recruitment. They do not include the interactions between the stock species and the rest of the ecosystem

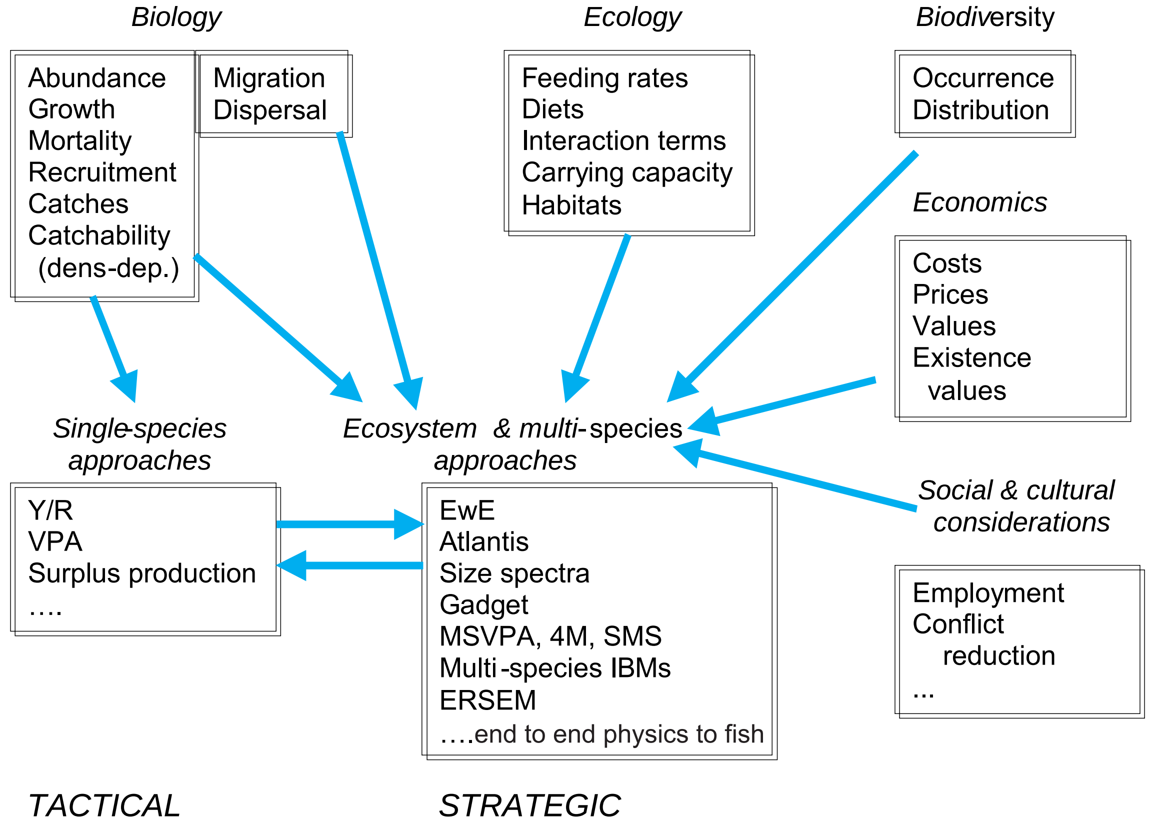


Figure 1.2. Information for fisheries modeling: from single-species to ecosystem approaches (Courtesy of Villy Christensen, adapted).

and thus management measures are based on information from a stock that is treated as disconnected from the ecosystem. *[NB: However, it must be recognised that the biological characteristics of any species stock is of course dependent upon and shaped over time by its interactions with other species in the ecosystem]*. The single species approach to management has a tendency to give priority to the short-term economic and social benefits over the longer-term sustainability of the stock. It is now generally accepted that the single species fishery management approach has failed to keep the fish stocks in Northwest Europe at a sustainable level. There is international consensus that there are major inadequacies in basing management objectives and decisions almost solely on short-term, single species stock assessments (Pitkitch *et al.*, 2004).

Because ecosystem-scale experiments are not possible, multi-species and ecosystem models are important tools for studying and predicting the possible effects of fisheries and climate change on the ecosystem. As such, they are anticipated as being helpful to guide strategic management decisions. It is fair to say nonetheless, that the risk of abandoning single species approaches is currently low, since few multi-species and ecosystem models (or applications thereof) have yet met the 'standards' that would be expected of them before being used routinely. Even though ill-informed scepticism often hinders development of ecosystem approaches, decisions to rely on single species approaches can be beneficial. This is because single species and ecosystem approaches are complementary; both provide information to improve understanding of the ecological processes and uncertainties that must be considered in management.

Multi-species models have helped to address food web complexities and, as our knowledge of trophic dynamics and energy flows within the marine system grows, multi-species stock assessments and simulation models (eg, SMS, 4M, multspec, Gadget, multi-species IBMs) are becoming increasingly more refined. Multi-Species Virtual Population Analysis (Anderson and Ursin, 1977; Sparre, 1991) which uses historic catches to reconstruct the (virtual) population structure, has been one of the cornerstones to such an approach. Typically centred on species of commercial interest however, these models fall short of assessing wider interactions among other species, habitat effects and responses to climate change, that may also be important to understanding ecosystem dynamics.

Ecosystem models (eg, Ecopath with Ecosim, Size spectra, Atlantis) try to represent all components of the ecosystem and their interconnected dependencies. Necessarily, there are trade-offs associated with the level of detail in accounting for processes in time and space. Few ecosystem models are being used to implement management decisions; most are currently being used in explorations of the impacts of fishing and environmental change on the structure and function of the ecosystem.

This report describes the construction and calibration of an ecosystem model of the North Sea using the Ecopath with Ecosim approach. Models of this type readily lend themselves to answering simple, ecosystem wide questions about the dynamics and the response of the ecosystem to anthropogenic changes. Thus, they can help design policies aimed at implementing ecosystem management principles, and can provide testable insights into changes that have occurred in the ecosystem over time. Moreover, they may provide new insights into marine ecosystems organization, functioning, stability and resilience.

1.4 The Ecopath with Ecosim approach to ecosystem modelling

The general logistical procedure for constructing an Ecopath model includes broad literature reviews, analysis of empirical data routinely collected by fisheries scientists and marine biologists and contributions by collaborations of experts. The Ecopath framework provides an accounting system where disparate information from various sources is standardized and rendered compatible. Thoroughness and thoughtfulness in representing an ecosystem are crucial, as the models produced are the foundation of subsequent analyses using the dynamic simulations tools. Like other models, Ecopath models should not be considered final because our knowledge about an ecosystem can never be complete (Okey *et al.*, 2002). Because they help identify knowledge and data gaps, even preliminary models can be useful, and indeed their usefulness increases, as the model is refined.

The fully integrated software package 'Ecopath with Ecosim' (EwE) is freely available at www.ecopath.org. With 2700+ registered users in 126+ countries and over 150+ primary publications arising from its application, it is the most widely used tool for systematically describing and analysing the properties of ecosystems and exploring the ecosystem effects of exploitation.

The EwE software tool is a common and flexible framework for the quantification of food webs and analysis of ecosystem dynamics (Pauly e*t al.*, 2000). The tool consists of three main components: Ecopath, Ecosim, Ecospace. An Ecopath model is a quantitative description of the average state of biomass organization and flows in a food web. The approach is founded on the static description of the energy flows in an ecosystem developed by Polovina (1984), and has since been refined considerably. Species are aggregated and represented in the model as ecologically functional groups connected as predators and prey through a diet composition matrix. All components of the defined ecosystem, from whales to bacteria, are represented by the user-defined functional groups (Polovina, 1993). In 1995, Carl Walters started working with Villy Christensen and Daniel Pauly and developed time and spatial dynamic modelling capability for exploring past and future impacts of fishing and environmental disturbances (Ecosim and Ecospace; Walters *et al.*, 1997, 2000). Ecosim also allows users to explore harvest strategies that trade-off social, economic and ecological goals (Pitcher and Cochrane, 2002). An additional routine, Ecotracer, can be used for tracing the fate on contaminants through the food web.

[Appendix 1 provides details of the formulations of the EWE].

General assumptions of the approach

In the Ecopath description,'mass-balance' or conservation of energy, is assumed for every identified component of the ecosystem, and the ecosystem as a whole. When biomass accumulation (recent trends in biomass) and migration factors are included, the Ecopath formulation is still mass-balanced, but the system not assumed to be in a 'steady state'.

Whilst it is recognised that production rates, consumption rates, and diet compositions vary among seasons and life history stages for many, if not most species, the biological components of the ecosystem are generally represented in Ecopath using average values, or other meaningful measures of central tendency in populations that take into account both annual (seasonal) changes and ontogenetic changes. It is possible however to explicitly include ontogenetic changes within particular groups of interest, by splitting the groups in to multi-stanza groups (at its simplest, adult and juvenile stages) that are linked through age structured growth and recruitment.

The assumptions of continuity and representation of species with central measures are extremely useful when parameterising models. By demanding that the energy flows in and out of each component and between connected components is reconciled, mass-balance, offers a powerful constraint to the parameterisation process. It allows the basic interaction and energy structure of a food web to be described, enables missing parameters to be estimated by the model, and provides starting points for dynamic simulations.

Because Ecopath models describe the trophic flows and interactions in a system, they are useful for describing the potential effects of disturbances that change the linkages in food-webs. Ecosim and Ecospace parameters from the mass balance Ecopath model to initilise dynamic simulations of changes in time and space. Physical forces are not explicitly included in the parameterization of Ecopath models, though they can be included (albeit crudely) in the Ecosim routine. The role of trophic forces, fishing and climate forces can be investigated during the process of fitting Ecosim prodictions to observed historical trends.

1.5 Ecosystem modelling of the UK shelf seas

Among other means, research on ecosystem dynamics at Cefas includes investigations using EwE. The approach provides a common platform for developing models of the UK shelf seas (Table 1.1), which enables comparative investigations of the structure and function of ecosystems and their response to change (Lees and Mackinson, 2007; Araujo *et al.*, 2007). Furthermore, it facilitates collaboration with researchers around the world on investigations of the dynamics of large marine ecosystems (eg Mackinson *et al.,* in prep).

Particular research areas include:

(i) The relative roles of fishing and climate change on species and ecosystem dynamics
(ii) Investigating the ecosystem impacts and trade-offs of alternative management strategies, including MPAs
(iv) The effects of fisheries upon non-target species and the environment
(v) Identifying and quantifying regime shifts
(vi) Critical evaluation of models – (eg the impacts of model structure and specification)
(vii) The ecology of species interactions (eg the functional responses, trophic cascades, roles of species)
(viii) The temporal and spatial dynamics of trophic interactions and fishing fleet dynamics (ie how both predators and the fishing fleet respond to shifts in abundance and distribution of prey/target species)

1.6 Disclaimer

This documentation has been a substantial piece of work, made possible by the contributions of many researchers. Every effort has been made to minimise any errors and ensure consistency throughout the document. Any remaining errors are solely the responsibility of the individual authors of each section.

Specific discussion of the useful and limitations of the model are provided in Section 6.

Table 1.1. UK shelf sea EwE models.

Region	Author
North Sea	Mackinson and Daskalov (this report)
Irish Sea	Lees and Mackinson 2007
English channel	Stanford and Pitcher 2004
Western English Channel	Araujo, Hart and Mackinson 2005
Eastern English Channel	Villanueva, Ernand and Mackinson (IFREMER/ Cefas report in prep)
Celtic Sea	Lauria, Mackinson and Pinnegar (in prep)
West of Scotland	Haggan, Morissette, Magil, Pitcher, Haggan, Ainsworth 2005 Being updated by S. Heymans (SAMS)

2. Characteristics of the North Sea ecosystem

Authors: Steven Mackinson, Tom Howden and Bill Mulligan

2.1 The physical and ecological setting

The North Sea is a mid-latitude, relatively shallow continental shelf covering approximately 570,000 km^2 (Jones, 1982) with an average depth of approximately 90 m, the deepest part in the Norwegian trench being approximately 400 m deep. It is bounded by the coasts of Norway, Denmark, Germany, the Netherlands, Belgium, France and Great Britain (Figure 2.1) and recognised as a Large Marine Ecosystem (McGlade, 2002). The continental coastal zone (mean depth 15 m) represents an area of about 60,000 km^2, under strong influence of terrigeneous inputs. The limits for this study are defined by ICES Area IV, divisions a,b,c.

The North Sea is influenced by the Atlantic Ocean, mainly by input from the north where the Atlantic current flows north along the edge of the continental shelf, but also, to a lesser extent, from the south via the English Channel. Two currents bring high salinity Atlantic water into the northern North Sea (Figure 2.2a). The first is an inflow through the Fair Isle channel off the north of Scotland, and the second, more significant inflow is along the western slope of the Norwegian Trench. There is a contrasting outflow along the eastern side of the Trench, northwards, carrying less saline water from fjords and rivers. This is called the Norwegian Coastal Current. Brown *et al.*, (1999) provided a synopsis of the surface currents of the North Sea, concluding that a large anti-clockwise gyre rotates around the basin affecting all areas (Figure 2.2b). Salinity ranges from approximately 29‰ in the south-eastern North Sea, where a large volume of fresh water runs off the continental land mass, to more than 35‰ in the north-west, where oceanic Atlantic water enters the North Sea.

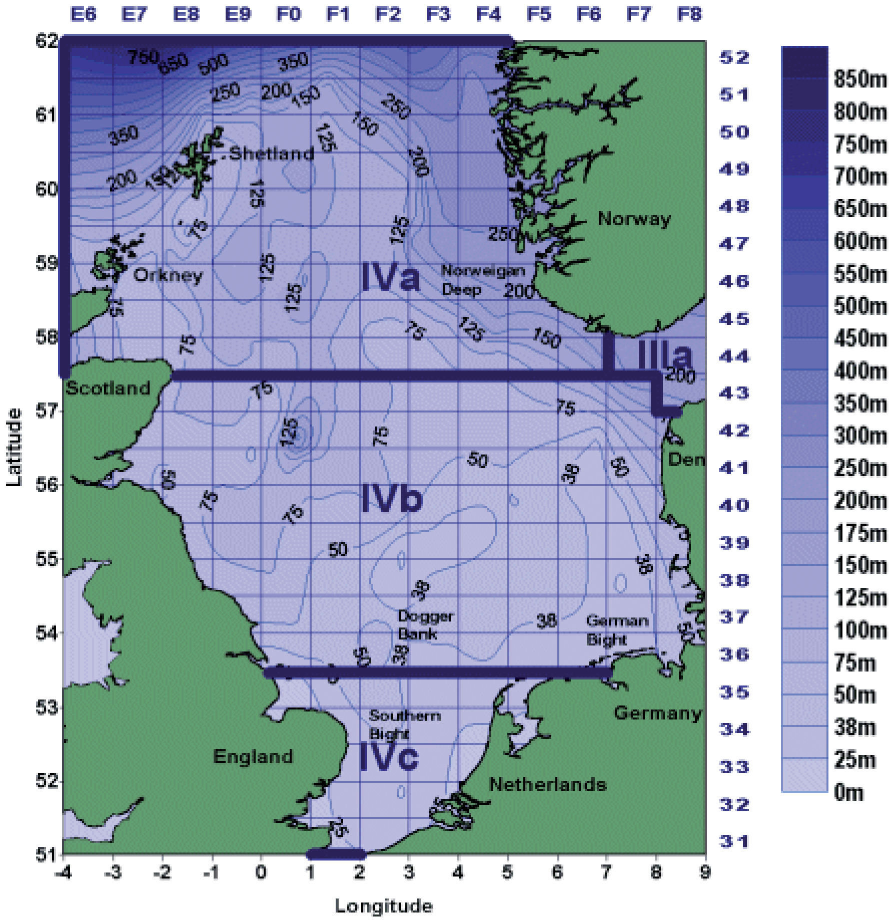


Figure 2.1. Location and bathymetry of the North Sea. ICES Divisions of the North Sea (Div IVa,b,c) and Skagerrak (Div IIIa) (Rijnsdorp *et al.*, 1991).

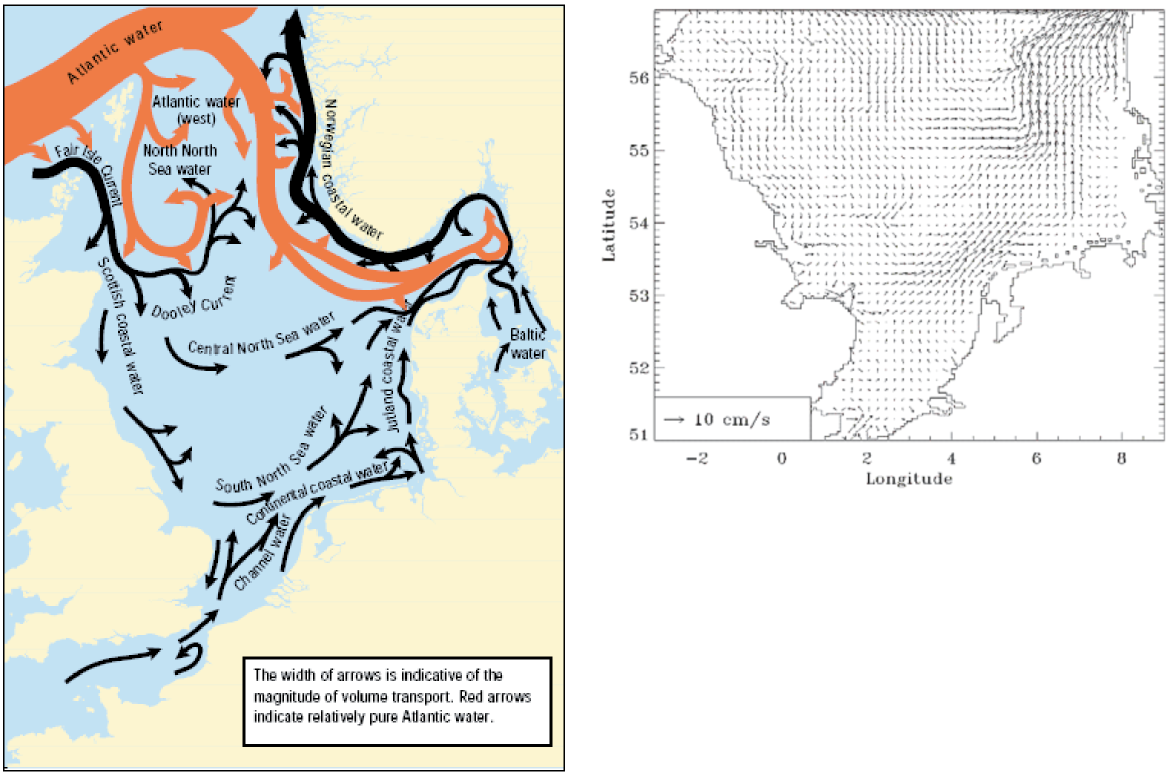


Figure 2.2. North Sea hydrography (a) Main flows (OSPAR, 2000) and (b) winter residual currents (Management Unit of the North Sea Mathematical Models (MUMM, 2002).

Although a number of classifications for the North Sea have been developed, the dominant physical division is between the north and the south. The northern part is comparatively deep, subject to strong oceanic influences, and characterised by seasonal stratification of the water column, whereby a thermocline develops resulting in a mixed layer depth of around 40 m during May and June (Figure 2.3). In these stratified waters the density boundary between the mixed and stable water (thermocline, halocline, pycnocline) divides the inorganic nutrient rich bottom water layer from the wind mixed upper layer where nutrients may be limiting. During summer months, algal concentrations track the thermocline, and 30–80% of the total production in the euphotic zone may occur in the thermocline (Reid *et al.*, 1990). Fronts typified by algal blooms are formed where the thermocline 'outcrops' at the surface. The southern North Sea is shallower (20–50 m) and remains mixed for most of the year, only developing a thermocline over deeper regions and where there are significant freshwater inputs such as from the River Thames (ICONA, 1992). The southern region is also influenced by inflowing waters from the English Channel, which generate strong tidal currents and an increased sediment load.

The level of nitrates and phosphates has increased over recent decades due to higher concentrations from rivers, coastal runoff and atmospheric inputs. The extensive inputs of these nutrients and the restricted nature of the North Sea circulation have led to an increase in eutrophication events, algal blooms and macroalgal mats.

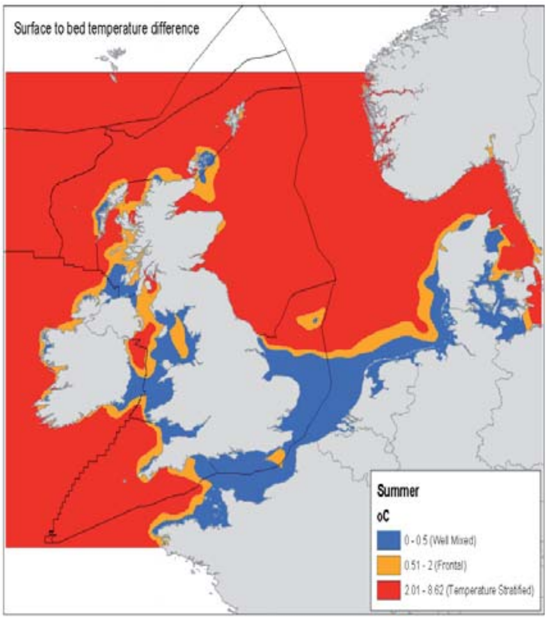
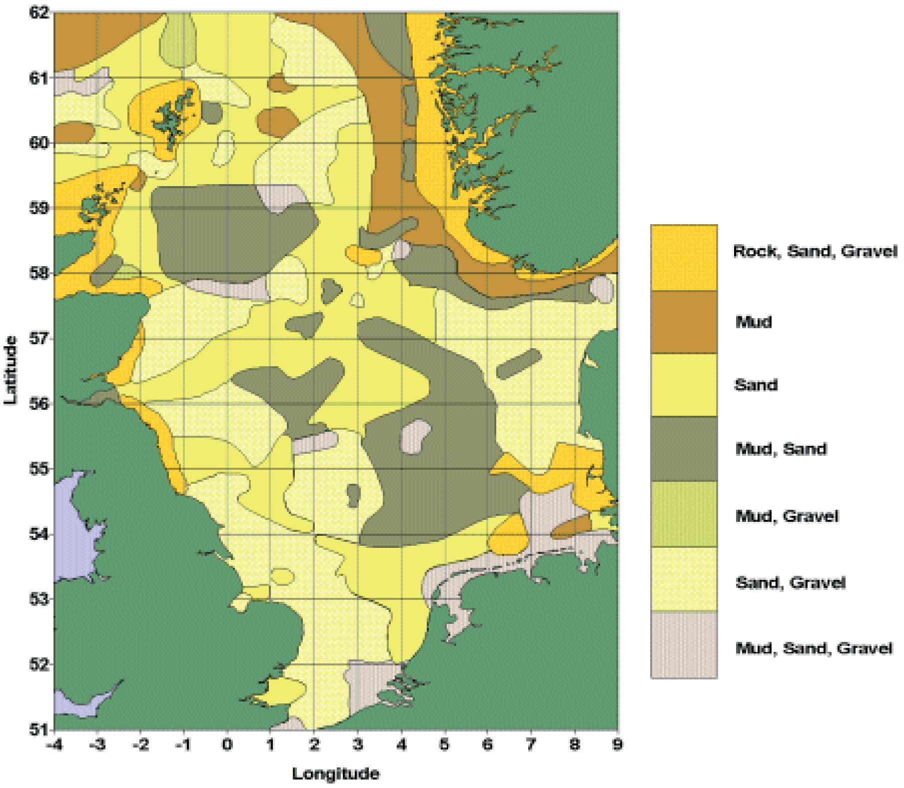


Figure 2.3. Stratified/mixed waters of the North Sea (from JNCC Review of Marine Nature Conservation).

The seafloor consists of mostly mixed sediments comprised of mud, sand, gravel and rock (Figure 2.4). In the north, the areas close to the Scottish and Norwegian coasts are rocky, with mud predominant in the other northerly areas. Coarser sands are dominant in the shallow

Figure 2.4. Seabed substrate classification. The seabed is similarly very variable, consisting of mud, sand, gravel or boulders. (Rijnsdorp *et al.*, 1991)



tidally active south. The patchwork distribution of the sediments is due to glacial deposition during the last ice age. Glaciers from Scotland and Scandinavia deposited large amounts of sand and gravel to the North Sea floor, creating features like the Dogger Bank.

The variation in the physical environment is reflected in the flora and fauna. The different sediment substrata support very diverse communities of bottom-living animals and, similarly, each water mass supports a different group of planktonic organisms. A total of 224 fish species have been recorded from the North Sea. These species originate from three zoogeographical regions: 66 species are of Boreal (northern) origin, 110 species are Lusitanian (southern) and 48 species are Atlantic. Knijn *et al.* (1993) provides a description of the abundance and distribution of many of them. Diversity is lower in the shallow southern North Sea and eastern Channel (Rogers *et al.*, 1998). Inshore, where there is more variation in sediment types and a higher level of spatial patchiness the species diversity is generally higher (Greenstreet and Hall, 1996).

There are 31 species of seabirds breeding along the coasts of the North Sea, with the major seabird colonies located on the rocky coasts in the northern part of the North Sea. Approximately 10 million seabirds are present at most times of the year, but seasonal shifts and migrations are distinct (OSPAR, 2000).

Two species of seal are regularly observed and breed in the North Sea, the grey seal (*Halichoerus grypus*) and the harbour seal (*Phoca vitulina,*). The grey seal is most abundant in exposed locations in the northwest, while the harbour seal is more widespread, preferring mud and sand flats.

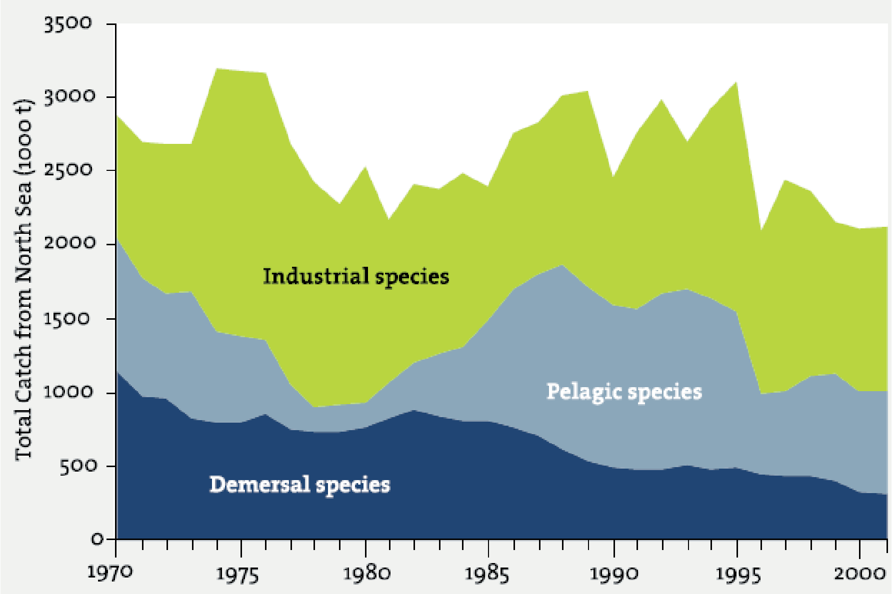
Sixteen species of cetacean commonly occur in the North Sea, the most frequently observed being the harbour porpoise (*Phocoena phocoena*). Other species of toothed cetacean that are sighted regularly include long-finned pilot whales (*Globicephala melas*), the common dolphin (*Delphinus delphis*), the whitesided dolphin (*Lagenorhynchus acutus*), Risso's dolphin (*Grampus griseus*) and the killer whale (*Orcinus orca*) (OSPAR, 2000).

2.2 Fisheries and fish stocks in the North Sea

Responsibilities for fisheries management in the North Sea lies both with neighbouring countries through Economic Exclusion Zones (EEZs) and also the European Commission (EC) by setting Total Allowable Catches (TACs) for countries, under the guidelines of the Common Fisheries Policy. Scientific advice on the state of the stocks and recommendations for TACs is undertaken by the International Council for Exploration of the Sea (ICES) and STECF.

Denmark, UK, Netherlands and Norway are the major fishing nations although Germany, Belgium and France all have vessels that operate in the North Sea (AER, 2005; Walday and Kroglund 2006). The main fisheries can be split into demersal, pelagic and industrial. Demersal fisheries target roundfish species such as cod (*Gadus morhua*), haddock (*Gadus aeglefinus*) and whiting (*Gadus merlangus*) in addition to flatfish species such as plaice (*Pleuronectes platessa*), sole (*Solea solea*) and a fishery for saithe (*Pollachius virens*). Pelagic fisheries target herring (*Clupea harenguss*) and mackerel (*Scomber scomber*) and

Figure 2.5. Total catch from the North Sea. (Source: ICES 2003).



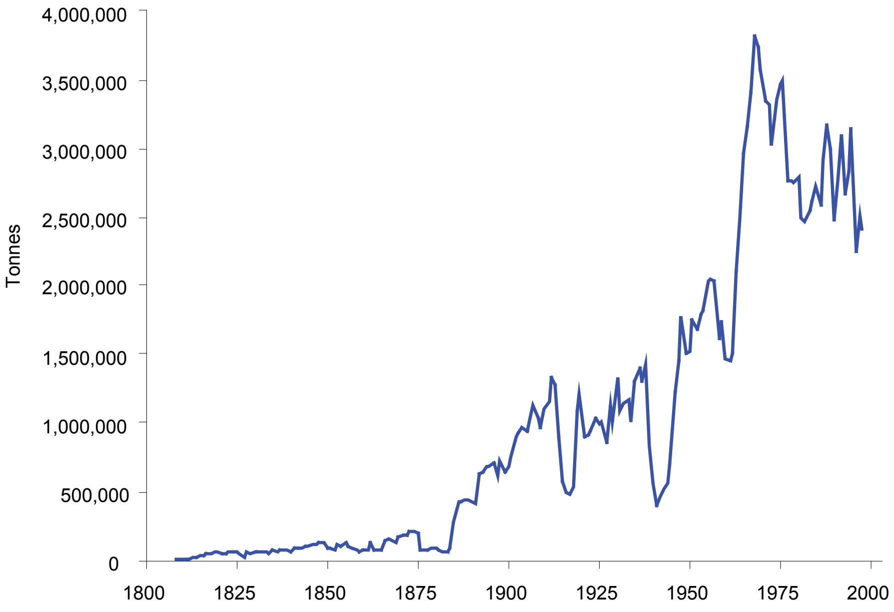
the industrial fisheries target sandeel (Ammodytes Spp), Norway pout (*Trisopterus esmarkii*) and sprat (*Sprattus sprattus*). There are also important crustacean fisheries for *Nephrops* (*Nephrops norvegicus*), pink shrimp (*Panadalus borealis*), brown shrimp (*Crangon crangon*) and brown crab (*Cancer pagurus*).

The North Sea supplies approximately two million tonnes of fish each year from the three main sectors (Figure 2.5). Industrial fisheries provide roughly one million tonnes of this, which is processed into fishmeal and fish oil, not for human consumption. The pelagic fishery is the next biggest proportion (approx 700,000 tonnes). The demersal fisheries accounts for approx. 300,000 tonnes but has been decreasing continuously since the early 1980s. Total catches of North Sea fish since 1800s provide the broader context for the declines seen over the last few decades (Figure 2.6).

Taken as a whole the pelagic stocks (herring and mackerel) have increased in the last two decades. Herring stocks are currently thought to be stable in the short term but the North Sea mackerel stock has all but disappeared. The mackerel caught in the North Sea come from a larger western group, which spawns outside the North Sea (ICES, 2003).

The economically important, smaller stocks of shrimps and *Nephrops* have also increased within the last two decades. *Nephrops* stocks within the North Sea are currently exploited at a sustainable level, while the shrimp stocks appear to be stable in some areas (Northern Scotland) but are uncertain in others (The Channel) (Walday and Kroglund, 2006).

Figure 2.6. Catches of North Sea fish compiled from historical data (Mackinson 2002), ICES Bulletin Statistique (later Statlant) and corrected catches reported by ICES WG for species included in MSVPA.



Demersal stocks (cod, haddock, whiting and plaice) have shown a decline during the last two decades. Many of the demersal stocks have been over exploited and are now depleted. The most highly publicised stock is that of the North Sea cod, which is at the lowest levels ever seen and subject to a recovery plan (ICES, 2006) EC Regulation #423, 2004). The haddock stock is considered within safe biological limits but it is the 1999-year class alone that supports the fishery (ICES, 2006). The current whiting stock status is unknown, but there have been declining landings and poor recruitment in recent years, so the stock is considered outside safe biological limits. Plaice is estimated to be near the lowest observed level for several decades and for sole the current fishing mortality levels are considered to be too high. The abundance of saithe has increased in recent years whilst fishing mortality has decreased, and the stock is considered to be within safe biological limits.

Sandeel stocks have fluctuated with recent recruitment being among the lowest recorded; as a result the status of the stocks is uncertain and is subject to in-year monitoring. The Norway Pout stock is thought to be within safe biological limits with the current fishing mortality. Sprat stocks are considered to be in good condition, with spawning biomass having increased in recent years (Walday and Kroglund, 2006).

3. The Ecopath model

Author: Steven Mackinson

3.1 Structure and basic input data

The present North Sea model is one of the most comprehensive Ecopath models constructed. The model structure was set to 68 functional groups including mammals (3), bird (1), fish (45), invertebrate (13), microbial (2), autotrophic (1), discards (1) and detritus groups (2). The commercially important target fish species were divided into juvenile and adult groups (e.g. cod, whiting, haddock, saithe, herring). Numerous fish species, which are also commercially and/or functionally important, were represented as single species or family groups (eg plaice, hake, dab, gurnards). The model is parameterised with estimates of biomass, production and consumption rates and diet composition compiled from survey data, stock assessments and literature sources and also contains information about landings and discards of various fishing gears grouped in 12 categories defined by the Data Collection Regulations. eg, demersal trawls, pelagic trawls, drift nets, etc. In-depth descriptions of the functional groups, their component species, data sources and analyses used in construction the model are presented in sections 7-15 and summarised below in table 3.1. data inputs, table 3.3. (model parameters), table 3.4. (diet composition), table 3.5. (catches and discards).

Author: Steven Mackinson

3.2 Data pedigree assignment

To capture uncertainties in parameter estimates for each functional group, a pedigree index was assigned to each parameter (Table 3.2). The pedigree index represents the quality or relative confidence of a parameter and is expressed as a coefficient of variation. Assigning pedigree values is important. It allows model developers to be explicit (even to some general degree) about the level of confidence in the data; it aids model balancing by guiding otherwise subjective choices about the prioritisation of, and degree to which parameters might be adjusted; it serves to inform other users of the uncertainties inherent in the model and thus points to areas that should be treated with caution. Assigning pedigree values to functional groups whose parameters are derived using combined estimates from many data sources of various quality is a particularly subjective task, but nonetheless instructive for the same reasons.

Author: Steven Mackinson

3.3 Balancing the North Sea model

3.3.1 The meaning of 'model balancing' and general strategies

If the total demand placed on a particular group by predation or fishing exceeds the production of that group, the group is commonly said to be out of balance. The degree of energy 'imbalance' of each functional group is determined in Ecopath by examining the ecotrophic efficiency (EE). A value of EE greater than one indicates that total energy demand exceeds total production. The EE is used as the basis for model balancing; changes in EE values being monitored as adjustments are made to input parameters. Due to the error inherent in estimating biological parameters for any identified group, imbalance is common and indeed, expected. During the balancing process the reliability and compatibility of parameters are questioned, thus serving as a vehicle for learning and refinement of knowledge about ecosystem structure.

Balancing of the North Sea model was undertaken manually. An even-handed and strategic approach was used to guide the stepwise process of making the production of each group compatible with the losses from predation and fishing.

The strategy consisted of the following elements (i) endeavouring to ensure that all parameters were kept within limits estimated from data, (ii) where outside the limits, being able to provide reasonable justification, (iii) using the data pedigree (quality and reliability) assignments (Table 3.2) as a guide to prioritising and justifying which parameters to change, (iv) ensuring that estimates of fishing mortality rates were consistent with best available estimates (this provided justification for maintaining (or changing) the biomass of groups since catches were never adjusted (NB: F=C/B)), (v) for those groups split in to adults and juveniles, the discards were assigned to the juvenile groups, reflecting the discard of undersized fish of that species, (vi) ensuring that parameters were internally consistent by complying with physiological and thermodynamic constraints (see note 1 below table 3.3.), (vii) specifying parameters for lower organisms (phytoplankton, microflora and zooplankton) such that model derived estimates of respiration and relative production and consumption rates were consistent with literature (vii) appling iterative process so that any changes made were revisited.

The importance of using an iteratative process was found to be critical in achieving a model balance that adhered closely to the data. During the convoluted process of balancing, embarking on a solution often ends up with the modeller finding out someway down the line that the real problem was something quite different than the symptoms that instigated the changes. Unfortunately changes may have already been committed to. At various stages of the balancing process, and in particular at the end when most of the oddities and glitches had been revealed, we reinstated the initial best estimates of input parameters derived from data. On most occasions the initial parameters values were found to be acceptable without modification.

A key part of the balancing procedure was determining which parameters were sensitive to change. Problems in the model balance were diagnosed through close inspection of the predation mortalities, total consumptions and fishing mortalities. For each group, Ecosim plots identifying the ranking of predation impacts and the proportions of prey in their diet were also used to rapidly screen and detect a number of diet oddities that were causing problems. Depending on the type of problem, they were resolved by making adjustments to the diet matrix, consumption and production rates and biomass. Diets were targeted first, because diet composition data tends have low reliability relative to other parameters since they provide only a snap shot of feeding habits. Although useful for identifying key interactions, diet data must be regarded as highly uncertain pictures of the 'average' feedings interactions within the system because of large biases associated with digestion and the ability to detect and subsequently identify food items.

During the balancing of any Ecopath model, there is a danger of employing an overly 'top-down' strategy, during which total biomasses of all groups can become unrealistically inflated if prey biomasses or production are increased in an attempt to meet the demands of higher predators. We specifically strived for an evenhanded approach. So that predator demands were met by realistic productivity of prey, when deemed necessary, predator biomass or consumption rates were reduced.

3.3.2 Changes made during balancing

Any adjustments made followed the strategy outlined above. Notes of any changes were made and the progress of the balancing process tracked by recording the reductions in Ecotrophic Efficiency (EE) at each step. Initial results of the Ecopath parameter estimation routine revealed several groups for which 'demand' was greater than 'supply', (ie, EE >1). Two main types of problems had to be resolved before the original parameters were reinstated and final adjustments made to ensure an acceptable parameterisation of the model, justifiable by the data and reasoned assumptions.

Problem 1. Predation mortality at the bottom of the food web too high.

Although large uncertainty exists in the initial parameterisation of meiofauna and microflora groups, the consumption from infaunal macrobenthos, small infauna and epifaunal macrobenthos was too high. Predation mortality was reduced through changes to the diet, consumption rates and finally biomass. We evaluated the impact of reducing the biomass of the main consumers after making reductions to the initial biomass in a stepwise manner.

Problem 2. Positive feedbacks resulting in overestimation of predation and having knock on effects through various groups.

Positive feedback effects and knock-on effects arise when one or more groups that consume one another, have their biomass estimated in the model. Any overestimation of biomass of a one group results in overestimation of the biomass of its prey. This cascades through the food chain and where the prey is also a consumer, the effect is a positive feedback on the biomass estimates.

The first of this type of problem was linked to problem 1 above. Overestimation of the bottom end of the food web had resulted in overestimating food available to zooplankton and fish. Very high consumption rates of carnivorous zooplankton by herring and Norway pout was resulting in a very high abundance of carnivorous zooplankton, which was causing knock on effects throughout the lower trophic levels. Assigning a larger proportion of herbivorous and omnivorous zooplankton in the diet of herring and Norway pout and reducing their Q/Bs reduced the predation impact and estimated biomass of carnivorous zooplankton. The reduction of predation pressure by carnivorous zooplankton alleviated the initial over-demands on several other groups.

Carnivorous zooplankton and other predatory invertebrate groups were also causing other problems for fish groups. In the initial diet matrix, fish comprised a tiny fraction (0.01 – 0.03%) of the diet of carnivorous zooplankton, but it resulted in a large impact because the overall consumption (estimated B and high Q/B) was so high. A similar problem was identified for squid and gelatinous zooplankton. The solution was to create a new group, 'Fish larvae food', representing larvae of fish destined only to be food. Their biomass is determined by consumption of predators and they feed on phytoplankton and zooplankton, thus accounting for their contribution to the food web dynamics. This is a pragmatic (and more realistic) solution that solves the problem of feeding the predatory invertebrates without them have large impacts on the dynamics of the adult fish groups in the model.

Problems caused throughout the model by over-consumption of ‘other gadoids’ and ‘small demersal fish’ were also symptomatic of the positive feedback problem. Key to solving several linked problems was identification of the most sensitive interactions. By examining changes in the predation mortalities on sensitive groups, these were found to be: other gadoids with small demersal fish (both estimated B so strong feedback interactions), mackerel and horse mackerel with other gadoids, Norway pout and herring with carnivorous zooplankton, flounder with small demersal fish, Long rough dab with shrimp, saithe with pelagic fish and dab with small infauna. Solutions to these problems were modification of diets (e.g. by removing diet on other gadoids and assigning it to particular gadoid species) and reducing cannibalism and reductions in consumption implemented through stepwise adjustments of biomass and consumption rates.

The sensitivities of changing input values on the estimated parameters within and among the groups in the model are detailed in section 3.5.2.

Table 3.3 reveals that even though the model balancing was a lengthy process, departures of final input parameters from the best estimates are reasonably small.

3.3.3 Warning! – key sensitive species

Top predatory species anglerfish, spurdog and large demersal fish that are not preyed upon and where fishing mortality is the largest proportion of total mortality, are very sensitive (respond strongly) to changes in fishing and the availability of their prey. The problem is that we simply do not know enough about the sources of mortality and so the natural dampening effects that might arise from predation effects. There are technical work-arounds that can be implemented to prevent unrealistic increases in biomass from occurring during model simulations, but this is generally a last resort since it is a poor way to address the lack of data and knowledge.

Table 3.1. Data derived best estimates for input parameters, with sources summarised.

	Group	Biomass (t km^2)	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Unassim	References
1	Baleen whales	0.067	0.02	9.9			0.2	Hammond *et al.*, 2002; Trites *et al.*, 1999; Olsen & Holst 2000
2	Toothed whales	0.017	0.02	17.63			0.2	Hammond *et al.*, 2002; Trites *et al.*, 1999, Santos, 1994, 1995, 2004
3	Seals	0.008	0.09	26.842			0.2	ICES, 2002; ICES WGMME, 2002, 2004; SCOS, 2002; Hall *et al.*, 1998; Hammond *et al.*, 1994,
4	Seabirds	0.003	0.28	216.56			0.2	ICES, 1996, 2002; Trites *et al.*, 1999
5	Juvenile sharks	0.001	0.5	2.5			0.2	This study; FishBase, 2004; Ellis *et al.*, 1996
6	Spurdog	0.013	0.48	2			0.2	This study; FishBase, 2004; Brett & Blackburn, 1978; Ellis *et al.*, 1996
7	Large piscivorous sharks	0.001	0.44	1.6			0.2	This study; FishBase, 2004; Ellis *et al.*, 1996
8	Small sharks	0.002	0.51	2.96			0.2	This study; FishBase, 2004; Ellis *et al.*, 1997
9	Juvenile rays	0.268	0.66	1.7			0.2	This study; FishBase, 2004; ICES, 2002; Daan *et al.*, 2003
10	Starry ray + others	0.109	0.66	1.7			0.2	This study; FishBase, 2004; ICES, 2002; Daan *et al.*, 2003
11	Thornback & Spotted ray	0.066	0.78	2.3			0.2	This study; FishBase, 2004; ICES, 2002; Daan *et al.*, 2003
12	Skate + Cuckoo ray	0.05	0.35	1.8			0.2	This study; FishBase, 2004; ICES, 2002; Daan *et al.*, 2003
13	Juvenile Cod (0-2, 0-40cm)	0.079	1.79	4.89			0.2	ICES, 2002; Hislop, 1997
14	Cod (adult)	0.161	1.19	2.17			0.2	ICES, 2002; Hislop, 1997
15	Juvenile Whiting (0-1, 0-20cm)	0.222	2.36	6.58			0.2	ICES, 2002; Hislop, 1997
16	Whiting (adult)	0.352	0.89	5.46			0.2	ICES, 2002; Hislop, 1997
17	Juvenile Haddock (0-1, 0-20cm)	0.284	2.54	4.16			0.2	ICES, 2002; Hislop, 1997
18	Haddock (adult)	0.104	1.14	2.35			0.2	ICES, 2002; Hislop, 1997
19	Juvenile Saithe (0-3, 0-40cm)	0.281	1	4.94			0.2	ICES, 2002; Hislop, 1997
20	Saithe (adult)	0.191	0.883	3.6			0.2	ICES, 2002; Hislop, 1997
21	Hake	0.014	0.82	2.2			0.2	This study; FishBase, 2004; Pauly, 1989; Du Buit 1996
22	Blue whiting	0.042	2.5	9.06			0.2	This study; FishBase, 2004; Bergstad, 1991
23	Norway pout	1.394	3.05	5.05			0.2	ICES, 2002; ICES, 2002; Greenstreet, 1996; Malyshev & Ostapenko, 1982
24	Other gadoids (large)	0.015	1.27	2.18			0.2	This study; FishBase, 2004; Hoines & Bergstad, 1999; Bergstad, 1991; Rae & Shelton, 1982
25	Other gadoids (small)	0.038	2.5	3.84			0.2	This study; FishBase, 2004; Albert, 1995; Armstrong, 1982
26	Monkfish	0.015	0.7	1.7			0.2	This study; FishBase, 2004; FishBase, 2004; Rae & Shelton, 1982
27	Gurnards	0.077	0.82	3.2			0.2	This study; FishBase, 2004; ICES, 2005
28	Herring (juvenile 0, 1)	0.63	1.31	5.63			0.2	ICES, 2002; Greenstreet, 1996; Last, 1989
29	Herring (adult)	1.966	0.8	4.34			0.2	ICES, 2002; Greenstreet, 1996; Last, 1989
30	Sprat	0.579	2.28	5.28			0.2	ICES, 2002; Greenstreet,1998; De Silva, 1973
31	Mackerel	1.72	0.6	1.73			0.2	ICES, 2002; Hislop, 1997
32	Horse mackerel	0.579	1.64	3.51			0.2	Rueckert *et al.*, 2002; ICES, 2002; Greenstreet, 1996

Table 3.1. continued: Data derived best estimates for input parameters, with sources summarised.

	Group	Biomass (t km^2)	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Unassim	References
33	Sandeels	3.122	2.28	5.24			0.2	ICES, 2002; Greenstreet, 1996; ICES, 2002; Reay, 1970
34	Plaice	0.703	0.85	3.42			0.2	ICES, 2002; AFCM, 2005; Greenstreet, 1996; De Clerck & Buseyne, 1989
35	Dab	4.634	0.672	4			0.2	This study; Greenstreet, 1996; De Clerck & Torreele, 1988
36	Long-rough dab	0.59	0.7	4			0.2	This study; FishBase, 2004; Ntiba & Harding, 1993
37	Flounder	0.453	1.1	3.2			0.2	This study; FishBase, 2004; Doornbos & Twisk, 1984
38	Sole	0.158	0.8	3.1			0.2	This study; AFCM, 2005; FishBase, 2004, ICES, 2002; Braber & Groot, 1973
39	Lemon sole	0.305	0.864	4.32			0.2	This study; FishBase, 2004; Greenstreet, 1996, Rae, 1956
40	Witch	0.082	0.9	3			0.2	This study; FishBase, 2004; Rae, 1969
41	Turbot and brill	0.054	0.86	2.1			0.2	This study; FishBase, 2004; Wetsteijn, 1981
42	Megrim	0.034	0.72	3.1			0.2	This study; FishBase, 2004; Du Buit,1984
43	Halibut	0.033	0.16	3.14			0.2	This study; FishBase, 2004; McIntyre, 1952
44	Dragonets	0.031	1.44	6.9			0.2	This study; FishBase, 2004; Gibson & Ezzi, 1987
45	Catfish (Wolf-fish)	0.01	0.48	1.7			0.2	This study, FishBase, 2004; Bowman *et al*., 2000
46	Large demersal fish	0.002	0.55	2.54			0.2	This study; FishBase, 2004; Bergstad *et al*., 2001, Bowman *et al*., 2000
47	Small demersal fish	0.089	1.42	3.73			0.2	This study; FishBase, 2004; Ebeling & Alshuth, 1989; Albert, 1993; Gibson & Robb, 1996
48	Miscellaneous filter feeding pelagic fish	0.013	4	10.19			0.2	This study; FishBase, 2004; Bowman *et al*., 2000
49	Cephalopods	0.0398	4	20			0.2	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 (food)	.	4	20	0.99		0.2	
51	Carnivorous zooplankton	0.6	2.5			0.3	0.2	Zooplankton: Lindley, 1980; Lindley, 1982; Williams & Lindley, 1980a; Lindley & Williams, 1980; Fransz *et al*., 1991b; Landry, 1981; Fransz & van Arkel, 1980; Fransz & Gieskes, 1984, Rae & Rees, 1947; Daan *et al*., 1988; Krause & Trahms, 1983; Williams & Lindley, 1980a; Williams & 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 & Franz, 1984; Nielsen & Richardson, 1989; Marshall & Orr, 1966; Checkley, 1980; Poulet,1973, 1974, 1976; Pepita *et al*., 1970; Anraku, 1964; Gaudy, 1974; Cowey & Corner, 1963; Daro & Gijsegem, 1984; Båmstedt, 1998; Cushing & Vucetic, 1963; Paffenhöfer, 1976; Huntley & Lopez, 1992; Sahfos, Reid. Clark, 2000; Clark *et al*., 2001
52	Herbivorous & Omnivorous zooplankton (copepods)	16.0	9.2	30		0.3	0.4	
53	Gelatinous zooplankton	0.1	2.9	0.181			0.2	Hay *et al*., 1990; Hansson *et al*., 2005; Martinussen & Båmstedt, 1995

Table 3.1. continued: Data derived best estimates for input parameters, with sources summarised.

	Group	Biomass ($t\ km^2$)	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Unassim	References
54	Large crabs	1.4	0.6			0.15	0.2	ICES SGCRAB, Lizárraga-Cubedo *et al.*, 2005
55	*Nephrops*	1.0	0.4			0.2	0.2	ICES WGNSSK, 2005; WGNEPH, 2004, North Sea Benthos Surveys, Brey, 2001
56	Epifaunal macrobenthos (mobile grazers)	158.0	0.4			0.15	0.2	For all Infaunal and Epifaunal benthos: Künitzer *et al.*, 1992; Craeymeersch *et al.*, 1997; Eleftheriou & Basford, 1989; Salzwedel *et al.*; 1985; Rumohr *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 & Craeymeersch, 1995
57	Infaunal macrobenthos	274.8	1.3			0.15	0.2	
58	Shrimp	0.3	3			0.3	0.2	ICES WGCRAN, 2005; ICES WGPAN, 2004, 2005; Hopkins, 1988; Shumway *et al.*, 1985; Brey, 2001; Hopkins *et al.*, 1993; Teming *et al.*, 1993; Oh & Hartnoll, Redant's review
59	Small mobile epifauna (swarming crustaceans)	23.9	1.4			0.3	0.2	
60	Small infauna (polychaetes)	256.0	0.9			0.2	0.2	
61	Sessile epifauna	210.6	0.3			0.15	0.2	
62	Meiofauna	1.8	10.8	206			0.2	Moens & Vincx, 1999; McIntyre, 1964, 1969, 1978; Heip *et al.*, 1995; Heip *et al.*, 1983; Gee, 1989; Heip & 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 & Vranken, 1988; Herman and Heip, 1983; Warwick,1984; Gee & Warwick, 1984; Vranken & Heip, 1986; Lasserre *et al.*, 1976; Faubel *et al.*, 1983; Wilde *et al.*, 1986; Carman & Frey, 2002; Donavaro *et al.*, 2002; Moens *et al.*, 1990; Moens & Vincx, 1999; Montagna, 1995; Decho & Lopez, 1992 in Moens and Vincx, 1999; Creed & Coull, 1984); Alkemade *et al.*, 1992; Riemann & Schrage, 1978
63	Benthic microflora (incl. Bacteria, protozoa))	0.0	9469.7			0.5	0.3	Microflora: Nielsen & 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 (incl. Bacteria, protozoa)	1.4	144.0			0.5	0.3	
65	Phytoplankton (autotrophs)	7.5	286.6666667					Reid *et al.*, 1990; Fransz & Gieskes, 1984; Lancelot *et al.*, 1988; Krause & Trahms, 1983; Hannon & Joires, 1989; Geider, 1988; Cadée, 1985; Linley *et al.*, 1983; Gieskes & Kraay, 1980; Lancelot & Mathot, 1987; Jones, 1984; Matthews & Heimdal, 1980
66	Detritus - DOM -water column	100						Fenchel, 1988; Hannon & Joires, 1989
67	Detritus - POM - sediment	100						
68	Discards	40						

Table 3.2. Pedigree index coefficient of variations assigned to input parameters in the model. Default values of CV were applied to the qualitative assigned indices.

Group	B	P/B	Q/B	Diet	Catch
Baleen whales	0	0.6	0.6	0.5	---
Toothed whales	0.4	0.6	0.6	0.5	---
Seals	0.7	0.6	0.6	0.5	---
Seabirds	0.7	0.6	0.6	0.5	---
Juvenile sharks	0.7	0.5	0.5	1	---
Spurdog	1	1	0.5	1	0.5
Large piscivorous sharks	0.4	0.5	0.5	1	0.5
Small sharks	0.7	0.5	0.5	1	0.5
Juvenile rays	0.7	0.5	0.5	1	---
Starry ray + others	1	1	0.5	1	0.5
Thornback & Spotted ray	1	1	0.5	1	
Skate	0.7	0.5	0.5	1	
Juvenile Cod(0–2, 0–40cm)	1	1	0.5	1	
Cod (adult)	1	1	0.5	1	0.5
Juvenile Whiting (0–1, 0–20cm)	1	1	0.5	1	
Whiting (adult)	1	1	0.5	1	0.5
Juvenile Haddock (0–1, 0–20cm)	1	1	0.5	1	
Haddock (adult)	1	1	0.5	1	0.5
Juvenile Saithe (0–3, 0–40cm)	1	1	0.5	1	
Saithe (adult)	1	1	0.5	1	0.5
Hake	0.7	0.5	0.5	1	0.5
Blue whiting	0.7	0.5	0.5	1	0.5
Norway pout	0.7	0.5	0.5	1	0.5
Other gadoids (large)	0.4	0.5	0.5	0.2	0.5
Other gadoids (small)	0.4	0.5	0.5	0.2	0.5
Monkfish	0.7	0.5	0.5	1	0.5
Gurnards	0.7	0.5	0.5	1	0.5
Herring (juvenile 0, 1)	1	1	0.5	1	
Herring (adult)	1	1	0.5	1	0.5
Sprat	0.7	0.5	0.5	1	0.5
Mackerel	0.7	0.5	0.5	1	0.5
Horse mackerel	0.7	0.5	0.5	1	0.5
Sandeels	0.7	0.5	0.5	1	0.5
Plaice	0.7	0.5	0.5	1	0.5
Dab	0.7	0.5	0.5	1	0.5
Long-rough dab	0.7	0.5	0.5	1	0.5
Flounder	0.7	0.5	0.5	1	0.5
Sole	0.7	0.5	0.5	1	0.5
Lemon sole	0.7	0.5	0.5	1	0.5
Witch	0.7	0.5	0.5	1	0.5
Turbot and brill	0.7	0.5	0.5	1	0.5
Megrim	0.7	0.5	0.5	1	0.5
Halibut	0.7	0.5	0.5	1	0.5
Dragonets	0.7	0.5	0.5	1	---
Catfish (Wolf-fish)	0.7	0.5	0.5	1	0.5
Large demersal fish	0.4	0.5	0.5	0.2	0.5
Small demersal fish	0.4	0.5	0.5	0.2	0.5
Miscellaneous filterfeeding pelagic fish	0.4	0.5	0.5	0.2	0.5
Squid & cuttlefish	0.7	0.1	0.1	0.2	0.5
Fish larvae	0	0.1	0.1	0	---
Carnivorous zooplankton	0.7	1	0.6	0.5	---
Herbivorous & Omnivorous zooplankton (copepods)	1	1	0.6	0.5	---

Table 3.2. continued: Pedigree index coefficient of variations assigned to input parameters in the model. Default values of CV were applied to the qualitative assigned indices.

Group	B	P/B	Q/B	Diet	Catch
Gelatinous zooplankton	0.4	0.1	0.5	0.2	---
Large crabs	0	0.5	0.5	0.2	0.5
Nephrops	0.7	0.5	0.5	0.2	0.5
Epifaunal macrobenthos (mobile grazers)	0.7	0.5	0.5	0.2	0.5
Infaunal macrobenthos	0.7	0.5	0.5	0.2	0.5
Shrimp	0.7	1	0.5	0.7	0.5
Small mobile epifauna (swarming crustaceans)	0.7	0.5	0.5	0.2	---
Small infauna (polychaetes)	0.7	0.5	0.5	0.2	---
Sessile epifauna	0.7	0.5	0.5	0.2	0.5
Meiofauna	0.7	0.5	0.5	0.5	---
Benthic microflora (incl. Bacteria, protozoa))	0.4	1	0.5	0.2	---
Planktonic microflora (incl. Bacteria, protozoa)	0.4	1	0.5	0.2	---
Phytoplankton	1	1	---	---	---

Table 3.3. Parameter values for the North Sea model. Where balanced model values differ from initial values derived from data, the closest estimate (or range) from data is given in brackets. Values in red are estimated by Ecopath.

Group		**Trophic level**	**Biomass (t km^2)**	**P/B y^{-1}**	**Q/B y^{-1}**	**EE**	**P/Q**	Unassim
1	Baleen whales	4.45	0.067	0.02	9.9	0	0.002	0.2
2	Toothed whales	4.78	0.017	0.02	17.63	0	0.0011	0.2
3	Seals	5	0.008	0.09	26.842	0	0.0034	0.2
4	Seabirds	3.5	0.003	0.28	216.56	0	0.0013	0.2
5	Juvenile sharks	4.29	0.001	0.5	2.5	0.3847	0.2	0.2
6	Spurdog	4.77	0.0167 (0.013)	0.6 (0.48)	2	0.95	0.3	0.2
7	Large piscivorous sharks	4.93	0.002 (0.001)	0.48 (0.44)	1.6	0.2833	0.3	0.2
8	Small sharks	4.34	0.002	0.51	2.96	0.4152	0.1723	0.2
9	Juvenile rays	4.23	0.268	0.66	1.7	0.0047	0.3882	0.2
10	Starry ray + others	4.49	0.109	0.66	1.7	0.0945	0.3882	0.2
11	Thornback & Spotted ray	4.49	0.066	0.78	2.3	0.1086	0.3391	0.2
12	Skate + cuckoo ray	4.44	0.05	0.35	1.8	0.0039	0.1944	0.2
13	Juvenile Cod(0-2, 0-40cm)	4.43	0.079	1.79	5.96 (4.89)	0.9359	0.3003	0.2
14	Cod (adult)	4.83	0.161	1.19	3.5 (2.17)	0.7498	0.34	0.2
15	Juvenile Whiting (0-1, 0-20cm)	4.27	0.222	2.36	6.58	0.8603	0.3587	0.2
16	Whiting (adult)	4.4	0.352	0.89	5.46	0.9322	0.163	0.2
17	Juvenile Haddock (0-1, 0-20cm)	4.06	0.284	2 (2.54)	5.39 (4.16)	0.4532	0.3711	0.2
18	Haddock (adult)	4.28	0.104	1.14	4.4 (2.35)	0.9717	0.2591	0.2
19	Juvenile Saithe (0-3, 0-40cm)	4.03	0.281	1	4.94	0.3149	0.2024	0.2
20	Saithe (adult)	4.36	0.22 (0.19)	0.95 (0.883)	3.6	0.621	0.2639	0.2
21	Hake	4.91	0.014	0.82	2.2	0.6422	0.3727	0.2
22	Blue whiting	4.1	0.08 (0.042)	2.5	9.06	0.8484	0.2759	0.2
23	Norway pout	3.59	1.394	2.2 (3.05)	5.05	0.7505	0.4356	0.2
24	Other gadoids (large)	4.53	0.0486 (0.015)	1.27	3.2 (2.18)	0.95	0.3969	0.2
25	Other gadoids (small)	3.83	0.1909 (0.038)	2.3 (2.5)	6 (3.84)	0.95	0.3833	0.2
26	Monkfish	4.85	0.042 (0.015)	0.7	1.9 (1.7)	0.848	0.3684	0.2
27	Gurnards	4.52	0.077	0.82	3.2	0.5772	0.2563	0.2
28	Herring (juvenile 0, 1)	3.42	0.63	1.31	5.63	0.6718	0.2327	0.2
29	Herring (adult)	3.44	1.966	0.8	4.34	0.6911	0.1843	0.2
30	Sprat	2.96	0.579	2.28	6 (5.28)	0.8059	0.38	0.2
31	Mackerel	3.9	1.72	0.6	1.73	0.6317	0.3468	0.2
32	Horse mackerel	4.33	0.579	1.2 (1.64)	3.51	0.356	0.3419	0.2
33	Sandeels	3.35	3.122	2.28	10.1 (5.24)	0.7851	0.2257	0.2
34	Plaice	3.99	0.703	0.85	3.42	0.6948	0.2485	0.2
35	Dab	4.01	3 (4.64)	0.672	3.36 (4)	0.2086	0.2	0.2
36	Long-rough dab	4.18	0.35 (0.59)	0.7	3.4 (4)	0.6055	0.2059	0.2
37	Flounder	4.38	0.25 (0.45)	1.1	3.2	0.2783	0.3438	0.2
38	Sole	4	0.158	0.8	3.1	0.894	0.2581	0.2
39	Lemon sole	3.94	0.305	0.864	4.32	0.2422	0.2	0.2
40	Witch	4.05	0.082	0.9	3	0.4206	0.3	0.2
41	Turbot and brill	4.62	0.054	0.86	2.3 (2.1)	0.1387	0.3739	0.2
42	Megrim	4.46	0.034	0.72	3.1	0.2425	0.2323	0.2
43	Halibut	4.85	0.033	0.16	3.14	0.2582	0.051	0.2
44	Dragonets	3.98	0.045 (0.031)	1.5 (1.44)	6 (6.9)	0.7545	0.25	0.2
45	Catfish (Wolf-fish)	4.27	0.014 (0.01)	0.48	1.7	0.7923	0.2824	0.2
46	Large demersal fish	4.21	0.017 (0.02)	0.55	2.54	0.9	0.2165	0.2
47	Small demersal fish	4.21	0.3431 (0.089)	1.42	3.7	0.98	0.3838	0.2

Table 3.3. continued: Parameter values for the North Sea model. Where balanced model values differ from initial values derived from data, the closest estimate (or range) from data is given in brackets. Values in red are estimated by Ecopath.

Group	Trophic level	Biomass (t km^2)	P/B y^{-1}	Q/B y^{-1}	EE	P/Q	Unassim
48 Miscellaneous filterfeeding pelagic fish	3.43	0.0298 (0.013)	4	10.19	0.98	0.3925	0.2
49 Squid & cuttlefish	3.86	0.08 (0.039)	4.5 (4)	20	0.8876	0.225	0.2
50 Fish larvae	2.85	0.3192	4	20	0.99	0.2	0.2
51 Carnivorous zooplankton	3.23	3.3453 (0.6)	4 (2.48)	12.5	0.99	0.32 (0.3)	0.2
52 Herbivorous & Omnivorous zooplankton (copepods)	2.06	16	9.2	30	0.4852	0.3067	0.38
53 Gelatinous zooplankton	3.58	0.066	2.858	0.18	0.7604	15.8778	0.2
54 Large crabs	3.71	1.354	0.5541	2.7704	0.9322	0.2 (0.15)	0.2
55 *Nephrops*	3.51	1.1 (0.98)	0.37 (0.35)	1.85	0.9937	0.2	0.2
56 Epifaunal macrobenthos (mobile grazers)	3.31	78 (157)	0.3884	1.942	0.4315	0.2 (0.15)	0.2
57 Infaunal macrobenthos	2.88	136 (274)	1 (1.26)	3.3333	0.2791	0.3 (0.15)	0.2
58 Shrimp	3.05	0.50 (0.32)	3	10	0.4486	0.3	0.2
59 Small mobile epifauna (swarming crustaceans)	2.91	30 (23.88)	1.9 (1.36)	5.4286	0.9249	0.35 (0.3)	0.2
60 Small infauna (polychaetes)	2.95	150 (255)	0.9	3	0.9079	0.3 (0.2)	0.2
61 Sessile epifauna	2.8	105 (210)	0.26	1.3	0.039	0.2 (0.15)	0.2
62 Meiofauna	3.03	4.1071 (1.81)	35 (10.8)	125 (206)	0.99	0.28	0.2
63 Benthic microflora (incl. Bacteria, protozoa))	2.24	0.105 (0.048)	9470	18940	0.9873	0.5	0.3
64 Planktonic microflora (incl. Bacteria, protozoa)	2.14	1.46 (1.44)	571 (144)	1142	0.7196	0.5	0.3
65 Phytoplankton	1	7.5	286	-	0.212	-	
66 Detritus - DOM -water column	1	25	-	-	0.9316	-	
67 Detritus - POM - sediment	1	25	-	-	0.9529	-	
68 Discards	1	50 (40)	-	-	0.7473	-	

Note 1. Internal consistency checks
Gross food conversion efficiency (production/consumption) typically ranges from 0.1 to 0.3, but can be higher for groups such as bacteria, fish larvae, and other small, fast growing organisms and coral reefs.
Respiration/Biomass ratio, should generally be in the range 1-10 year^{-1}for fish, but higher values are expected for faster turnover organisms such as zooplankton.
Respiration/Production ratio can take any positive value, but thermodynamic constraints limit the realised range to 0-1.
Empirically-derived GE (P/Q) estimates were available for some groups, and values were maintained at taxonomically reasonable levels within the above reference points for other groups.

Table 3.4. Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	1	2	3	4	5	6	7	8	9	10	11	12
1	Baleen whales												
2	Toothed whales												
3	Seals												
4	Seabirds												
5	Juvenile sharks							0.060					
6	Spurdog					0.020		0.010					
7	Large piscivorous sharks												
8	Small sharks							0.050					
9	Juvenile rays							0.060			0.000		
10	Starry ray + others												
11	Thornback & Spotted ray												
12	Skate & cuckoo ray												
13	Juvenile Cod		0.020	0.030	0.003					0.002	0.027		
14	Cod (adult)			0.060									
15	Juvenile Whiting	0.024	0.196	0.049	0.009	0.005	0.028		0.001		0.032	0.018	0.015
16	Whiting (adult)		0.050	0.065		0.019	0.113		0.006		0.004		
17	Juvenile Haddock		0.026	0.006	0.011		0.006				0.013	0.003	0.006
18	Haddock (adult)		0.003	0.011			0.006						
19	Juvenile Saithe		0.044	0.003									
20	Saithe (adult)		0.010	0.030									
21	Hake		0.004										0.001
22	Blue whiting		0.002			0.004	0.020		0.074				0.002
23	Norway pout	0.005	0.176			0.072	0.094	0.100	0.021	0.011	0.106	0.001	0.047
24	Other gadoids (large)		0.011	0.066									
25	Other gadoids (small)		0.037	0.026	0.002	0.003	0.125	0.010	0.010	0.015	0.045	0.031	0.057
26	Monkfish			0.010									0.001
27	Gurnards							0.048	0.000		0.000		0.002
28	Juvenile Herring	0.011	0.011	0.000	0.020	0.006	0.020	0.011			0.003	0.037	0.139
29	Herring (adult)		0.003	0.006	0.015	0.062	0.178	0.101	0.005		0.008		
30	Sprat	0.010	0.082	0.003	0.034	0.023	0.039		0.014	0.000	0.000	0.018	
31	Mackerel	0.094	0.015		0.015	0.014	0.078	0.153	0.005				
32	Horse mackerel		0.010	0.012	0.007		0.018						
33	Sandeels	0.655	0.215	0.286	0.222	0.014	0.037		0.011	0.396	0.472	0.034	0.333
34	Plaice			0.058			0.045	0.061	0.002			0.009	
35	Dab			0.047		0.007	0.007	0.061	0.006	0.003	0.027		0.003
36	Long-rough dab		0.000	0.010					0.002	0.001	0.019		0.002
37	Flounder			0.011									
38	Sole			0.035					0.002		0.001	0.004	0.024
39	Lemon sole			0.023									
40	Witch			0.024			0.007				0.000		0.001
41	Turbot and brill			0.010									
42	Megrim			0.010									
43	Halibut										0.000		
44	Dragonets		0.000	0.010		0.001	0.026	0.054	0.017		0.005		0.069
45	Catfish (Wolf-fish)												

Table 3.4. continued: Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	1	2	3	4	5	6	7	8	9	10	11	12
46	Large demersal fish										0.000		0.002
47	Small demersal fish		0.000	0.098		0.010	0.010	0.011	0.003	0.001	0.009	0.066	0.011
48	Miscellaneous filterfeeding pelagic fish	0.025				0.004			0.004				
49	Squid & cuttlefish	0.025	0.086			0.012	0.022	0.203	0.026	0.001	0.002	0.005	0.008
50	Fish larvae												
51	Carnivorous zooplankton	0.150			0.047	0.020	0.005		0.001	0.008	0.000	0.002	0.003
52	Herbivorous & Omnivorous zooplankton				0.088								
53	Gelatinous zooplankton					0.027	0.036						
54	Large crabs					0.028	0.013		0.114	0.096	0.062	0.362	0.055
55	Nephrops					0.007	0.010		0.019				0.002
56	Epifaunal macrobenthos					0.331	0.009	0.007	0.303	0.066	0.045	0.195	0.018
57	Infaunal macrobenthos					0.059	0.008		0.182	0.003	0.002	0.002	0.001
58	Shrimp					0.077	0.019		0.037	0.053	0.010	0.110	0.084
59	Small mobile epifauna					0.068			0.041	0.239	0.078	0.091	0.074
60	Small infauna (polychaetes)					0.120	0.002		0.075	0.102	0.031	0.012	0.045
61	Sessile epifauna					0.009			0.009				
62	Meiofauna					0.001			0.010	0.004			
63	Benthic microflora												
64	Planktonic microflora												
65	Phytoplankton												
66	Detritus - DOM in water												
67	Detritus - POM in sediment												
68	Discards				0.203								
	Import				0.324								
	Sum	1	1	1	1	1	1	1	1	1	1	1	1

Table 3.4. continued: Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	13	14	15	16	17	18	19	20	21	22	23	24
1	Baleen whales												
2	Toothed whales												
3	Seals												
4	Seabirds												
5	Juvenile sharks												
6	Spurdog												
7	Large piscivorous sharks												
8	Small sharks												
9	Juvenile rays												
10	Starry ray + others												
11	Thornback & Spotted ray												
12	Skate & cuckoo ray												
13	Juvenile Cod	0.005	0.009	0.004	0.002		0.000						0.020
14	Cod (adult)		0.010										
15	Juvenile Whiting	0.023	0.047	0.007	0.049			0.007	0.004	0.030			0.040
16	Whiting (adult)		0.091		0.002				0.020				
17	Juvenile Haddock	0.024	0.020	0.009	0.015		0.011	0.002	0.016				0.003
18	Haddock (adult)		0.019						0.002				
19	Juvenile Saithe				0.000								
20	Saithe (adult)												0.020
21	Hake									0.007			
22	Blue whiting		0.019						0.034	0.309			0.030
23	Norway pout	0.121	0.067	0.135	0.183	0.010	0.089	0.237	0.322	0.103	0.094		0.080
24	Other gadoids (large)		0.011	0.066									
25	Other gadoids (small)		0.037	0.026	0.002	0.003	0.125	0.010	0.010	0.015	0.045	0.031	0.057
26	Monkfish												
27	Gurnards	0.002	0.006		0.000	0.000			0.000	0.003			
28	Juvenile Herring	0.004	0.024	0.003	0.052		0.015	0.000	0.047	0.026			0.258
29	Herring (adult)	0.002	0.056						0.190				0.113
30	Sprat	0.010	0.013	0.014	0.157		0.001	0.114	0.057	0.103	0.010		
31	Mackerel		0.012						0.004	0.164			
32	Horse mackerel	0.001	0.003	0.002	0.010					0.180			
33	Sandeels	0.136	0.049	0.303	0.324	0.129	0.288	0.009	0.020				0.277
34	Plaice	0.000	0.018				0.000						
35	Dab	0.006	0.170	0.000	0.000	0.021	0.003		0.001				
36	Long-rough dab	0.022	0.051	0.004	0.006				0.000				0.012
37	Flounder		0.003										
38	Sole	0.004	0.017	0.002	0.003	0.000	0.000						
39	Lemon sole												
40	Witch	0.000	0.001				0.000						
41	Turbot and brill												
42	Megrim												
43	Halibut												
44	Dragonets	0.005	0.014		0.000	0.000	0.001						
45	Catfish (Wolf-fish)												

Table 3.4. continued: Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	13	14	15	16	17	18	19	20	21	22	23	24
46	Large demersal fish		0.000		0.000		0.000		0.000				
47	Small demersal fish	0.043	0.015	0.027	0.013	0.002	0.001		0.000	0.016			0.005
48	Miscellaneous filterfeeding pelagic fish	0.000		0.001	0.003		0.000	0.011	0.010	0.011	0.010		
49	Squid & cuttlefish	0.004	0.002	0.021	0.008	0.013	0.002	0.006	0.002	0.001			0.037
50	Fish larvae												
51	Carnivorous zooplankton	0.150			0.047	0.020	0.005		0.001	0.008	0.000	0.002	0.003
52	Herbivorous & Omnivorous zooplankton				0.088								
53	Gelatinous zooplankton					0.027	0.036						
54	Large crabs					0.028	0.013		0.114	0.096	0.062	0.362	0.055
55	Nephrops					0.007	0.010		0.019				0.002
56	Epifaunal macrobenthos					0.331	0.009	0.007	0.303	0.066	0.045	0.195	0.018
57	Infaunal macrobenthos					0.059	0.008		0.182	0.003	0.002	0.002	0.001
58	Shrimp					0.077	0.019		0.037	0.053	0.010	0.110	0.084
59	Small mobile epifauna					0.068			0.041	0.239	0.078	0.091	0.074
60	Small infauna (polychaetes)					0.120	0.002		0.075	0.102	0.031	0.012	0.045
61	Sessile epifauna					0.009			0.009				
62	Meiofauna					0.001			0.010	0.004			
63	Benthic microflora												
64	Planktonic microflora												
65	Phytoplankton												
66	Detritus - DOM in water												
67	Detritus - POM in sediment												
68	Discards				0.203								
	Import				0.324								
	Sum	1	1	1	1	1	1	1	1	1	1	1	1

Table 3.4. continued: Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	25	26	27	28	29	30	31	32	33	34	35	36
1	Baleen whales												
2	Toothed whales												
3	Seals												
4	Seabirds												
5	Juvenile sharks												
6	Spurdog												
7	Large piscivorous sharks												
8	Small sharks												
9	Juvenile rays		0.006										
10	Starry ray + others												
11	Thornback & Spotted ray												
12	Skate & cuckoo ray												
13	Juvenile Cod		0.009	0.026				0.000	0.006				
14	Cod (adult)		0.009										
15	Juvenile Whiting	0.004	0.092	0.087				0.000	0.035				0.005
16	Whiting (adult)		0.092										
17	Juvenile Haddock		0.052	0.007					0.023				
18	Haddock (adult)		0.052										
19	Juvenile Saithe		0.003	0.000					0.001				
20	Saithe (adult)												
21	Hake		0.006										
22	Blue whiting			0.000				0.001	0.017				
23	Norway pout	0.000	0.103	0.065				0.009	0.229				0.005
24	Other gadoids (large)												
25	Other gadoids (small)	0.017		0.069				0.011	0.035				0.027
26	Monkfish		0.003										
27	Gurnards			0.000					0.005				
28	Juvenile Herring		0.093	0.001				0.011	0.049		0.003		
29	Herring (adult)		0.093										
30	Sprat	0.004	0.003	0.014				0.060	0.006				
31	Mackerel		0.053	0.001									
32	Horse mackerel			0.001				0.006					
33	Sandeels	0.001	0.133	0.412				0.263	0.043		0.008		0.023
34	Plaice		0.003	0.000									
35	Dab	0.005	0.024	0.009									0.038
36	Long-rough dab		0.035	0.015									
37	Flounder												
38	Sole										0.003		
39	Lemon sole		0.009										
40	Witch		0.003	0.000									
41	Turbot and brill												
42	Megrim		0.003										
43	Halibut												
44	Dragonets	0.005	0.003	0.021									
45	Catfish (Wolf-fish)												

Table 3.4. continued: Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	25	26	27	28	29	30	31	32	33	34	35	36
46	Large demersal fish												
47	Small demersal fish	0.014	0.032	0.017				0.000	0.007				0.037
48	Miscellaneous filterfeeding pelagic fish		0.003	0.000				0.000					
49	Squid & cuttlefish	0.001	0.071	0.015				0.017					0.003
50	Fish larvae				0.111	0.053	0.010			0.005			
51	Carnivorous zooplankton	0.100		0.010	0.221	0.292		0.170	0.447	0.063			
52	Herbivorous & Omnivorous zooplankton	0.299			0.620	0.636	0.792	0.113		0.607		0.013	
53	Gelatinous zooplankton										0.003		
54	Large crabs	0.016		0.062							0.016	0.010	0.042
55	Nephrops	0.068	0.006	0.001					0.034				0.014
56	Epifaunal macrobenthos	0.100	0.009	0.009				0.005		0.001	0.103	0.258	0.210
57	Infaunal macrobenthos	0.170		0.003				0.000	0.014	0.006	0.171	0.240	0.271
58	Shrimp	0.001		0.027				0.000			0.015	0.001	0.040
59	Small mobile epifauna	0.028		0.128	0.048	0.020		0.032		0.015	0.193	0.329	0.003
60	Small infauna (polychaetes)	0.169		0.000				0.119		0.187	0.469	0.138	0.282
61	Sessile epifauna							0.003			0.014	0.011	
62	Meiofauna									0.048	0.003	0.001	
63	Benthic microflora												
64	Planktonic microflora						0.099	0.180	0.049	0.047			
65	Phytoplankton						0.099			0.022			
66	Detritus - DOM in water												
67	Detritus - POM in sediment												
68	Discards												
	Import												
	Sum	1	1	1	1	1	1	1	1	1	1	1	1

Table 3.4. continued: Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	37	38	39	40	41	42	43	44	45	46	47	48
1	Baleen whales												
2	Toothed whales												
3	Seals												
4	Seabirds												
5	Juvenile sharks												
6	Spurdog												
7	Large piscivorous sharks												
8	Small sharks												
9	Juvenile rays												
10	Starry ray + others												
11	Thornback & Spotted ray												
12	Skate & cuckoo ray												
13	Juvenile Cod					0.051							
14	Cod (adult)												
15	Juvenile Whiting					0.119		0.301					
16	Whiting (adult)												
17	Juvenile Haddock							0.242					
18	Haddock (adult)												
19	Juvenile Saithe												
20	Saithe (adult)												
21	Hake												
22	Blue whiting						0.054				0.008		
23	Norway pout	0.044				0.100	0.240	0.100					
24	Other gadoids (large)												
25	Other gadoids (small)					0.030	0.227	0.015			0.026		
26	Monkfish												
27	Gurnards						0.006					0.010	
28	Juvenile Herring					0.015						0.000	
29	Herring (adult)												
30	Sprat					0.150	0.338	0.050			0.001	0.001	
31	Mackerel												
32	Horse mackerel										0.006		
33	Sandeels					0.159	0.018	0.201			0.000	0.329	
34	Plaice												
35	Dab	0.061				0.061					0.000	0.037	
36	Long-rough dab	0.044											
37	Flounder												
38	Sole											0.001	
39	Lemon sole	0.044											
40	Witch												
41	Turbot and brill												
42	Megrim												
43	Halibut												
44	Dragonets					0.063	0.031				0.001	0.005	
45	Catfish (Wolf-fish)												

Table 3.4. continued: Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	37	38	39	40	41	42	43	44	45	46	47	48
46	Large demersal fish										0.002		
47	Small demersal fish	0.010	0.013	0.007	0.008	0.100	0.006				0.066	0.037	
48	Miscellaneous filterfeeding pelagic fish						0.025				0.006		0.053
49	Squid & cuttlefish							0.040			0.000	0.026	0.006
50	Fish larvae												0.005
51	Carnivorous zooplankton	0.052								0.015	0.677	0.000	0.148
52	Herbivorous & Omnivorous zooplankton						0.003		0.005		0.077	0.091	0.691
53	Gelatinous zooplankton	0.071									0.001		0.033
54	Large crabs	0.049					0.028	0.049	0.008	0.051		0.050	
55	Nephrops	0.122											
56	Epifaunal macrobenthos	0.224	0.013	0.041	0.247	0.060	0.003	0.002	0.093	0.783	0.013	0.134	0.027
57	Infaunal macrobenthos	0.071	0.115	0.099	0.035	0.050			0.138	0.113	0.026	0.060	
58	Shrimp	0.007				0.044	0.021	0.001	0.081	0.037	0.062	0.020	0.014
59	Small mobile epifauna	0.153					0.001		0.221		0.004	0.131	0.012
60	Small infauna (polychaetes)		0.423	0.658	0.685				0.439	0.001	0.021	0.039	0.011
61	Sessile epifauna	0.049		0.195	0.024						0.005		
62	Meiofauna		0.436						0.018		0.001	0.029	
63	Benthic microflora												
64	Planktonic microflora												
65	Phytoplankton												
66	Detritus - DOM in water												
67	Detritus - POM in sediment												
68	Discards												
	Import												
	Sum	1	1	1	1	1	1	1	1	1	1	1	1

Table 3.4. continued: Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	49	50	51	52	53	54	55	56	57	58	59	60
1	Baleen whales												
2	Toothed whales												
3	Seals												
4	Seabirds												
5	Juvenile sharks												
6	Spurdog												
7	Large piscivorous sharks												
8	Small sharks												
9	Juvenile rays												
10	Starry ray + others												
11	Thornback & Spotted ray												
12	Skate & cuckoo ray												
13	Juvenile Cod	0.011											
14	Cod (adult)												
15	Juvenile Whiting	0.011											
16	Whiting (adult)												
17	Juvenile Haddock	0.011											
18	Haddock (adult)												
19	Juvenile Saithe	0.011											
20	Saithe (adult)												
21	Hake												
22	Blue whiting	0.010											
23	Norway pout	0.044				0.100	0.240	0.100					
24	Other gadoids (large)												
25	Other gadoids (small)					0.030	0.227	0.015			0.026		
26	Monkfish	0.010											
27	Gurnards												
28	Juvenile Herring												
29	Herring (adult)												
30	Sprat												
31	Mackerel	0.011											
32	Horse mackerel												
33	Sandeels	0.011											
34	Plaice												
35	Dab	0.011											
36	Long-rough dab	0.042											
37	Flounder	0.005											
38	Sole	0.005											
39	Lemon sole	0.005											
40	Witch	0.005											
41	Turbot and brill	0.005											
42	Megrim	0.005											
43	Halibut	0.005											
44	Dragonets												
45	Catfish (Wolf-fish)												

Table 3.4. continued: Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	49	50	51	52	53	54	55	56	57	58	59	60
46	Large demersal fish												
47	Small demersal fish												
48	Miscellaneous filterfeeding pelagic fish												
49	Squid & cuttlefish	0.005											
50	Fish larvae	0.213		0.052		0.257					0.050		
51	Carnivorous zooplankton												
52	Herbivorous & Omnivorous zooplankton	0.282	0.800	0.737		0.257					0.100		
53	Gelatinous zooplankton												
54	Large crabs						0.001						
55	Nephrops						0.020						
56	Epifaunal macrobenthos						0.287		0.050				
57	Infaunal macrobenthos						0.293	0.250	0.200				
58	Shrimp	0.020				0.064	0.001				0.010		
59	Small mobile epifauna	0.157		0.103		0.103	0.020	0.150	0.050	0.050	0.050	0.100	
60	Small infauna (polychaetes)	0.021					0.104	0.200	0.250	0.100	0.100		0.050
61	Sessile epifauna						0.049	0.100					
62	Meiofauna									0.050	0.100	0.150	0.150
63	Benthic microflora						0.049	0.100	0.100	0.300	0.150	0.200	0.400
64	Planktonic microflora			0.104	0.050	0.129	0.049	0.050	0.100	0.100	0.120	0.150	0.050
65	Phytoplankton	0.052	0.200		0.900	0.129		0.100	0.050				
66	Detritus - DOM in water				0.050			0.030	0.050	0.100	0.100	0.100	0.150
67	Detritus - POM in sediment							0.020	0.150	0.300	0.170	0.300	0.200
68	Discards						0.128				0.050		
	Import												
	Sum	1	1	1	1	1	1	1	1	1	1	1	1

Table 3.4. continued: Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	61	62	63	64	65	66	67	68
1	Baleen whales								
2	Toothed whales								
3	Seals								
4	Seabirds								
5	Juvenile sharks								
6	Spurdog								
7	Large piscivorous sharks								
8	Small sharks								
9	Juvenile rays								
10	Starry ray + others								
11	Thornback & Spotted ray								
12	Skate & cuckoo ray								
13	Juvenile Cod								
14	Cod (adult)								
15	Juvenile Whiting								
16	Whiting (adult)								
17	Juvenile Haddock								
18	Haddock (adult)								
19	Juvenile Saithe								
20	Saithe (adult)								
21	Hake								
22	Blue whiting								
23	Norway pout								
24	Other gadoids (large)								
25	Other gadoids (small)								
26	Monkfish								
27	Gurnards								
28	Juvenile Herring								
29	Herring (adult)								
30	Sprat								
31	Mackerel								
32	Horse mackerel								
33	Sandeels								
34	Plaice								
35	Dab								
36	Long-rough dab								
37	Flounder								
38	Sole								
39	Lemon sole								
40	Witch								
41	Turbot and brill								
42	Megrim								
43	Halibut								
44	Dragonets								
45	Catfish (Wolf-fish)								

Table 3.4. continued: Diet matrix showing proportions of each prey in the diet of predators.

Predator	Prey	61	62	63	64	65	66	67	68
46	Large demersal fish								
47	Small demersal fish								
48	Miscellaneous filterfeeding pelagic fish								
49	Squid & cuttlefish								
50	Fish larvae								
51	Carnivorous zooplankton								
52	Herbivorous & Omnivorous zooplankton								
53	Gelatinous zooplankton								
54	Large crabs								
55	Nephrops								
56	Epifaunal macrobenthos								
57	Infaunal macrobenthos								
58	Shrimp								
59	Small mobile epifauna								
60	Small infauna (polychaetes)								
61	Sessile epifauna								
62	Meiofauna		0.050						
63	Benthic microflora		0.750	0.100	0.020				
64	Planktonic microflora	0.700		0.100	0.100				
65	Phytoplankton	0.100							
66	Detritus - DOM in water			0.200	0.650				
67	Detritus - POM in sediment	0.200	0.200	0.600	0.230				
68	Discards								
	Import								
	Sum	1	1	1	1				

Table 3.5. Fisheries landings and discards for the 1991 model. (see section 14 for details)

Functional groups	Demersal trawl & seine	Beam trawl	Sandeel trawl	Pelagic trawl	Drift and fixed nets	*Nephrops* trawl	Hooks	Other	Total land-ings	Discards
1 Baleen whales	-	-	-	-	-	-	-	-	-	-
2 Toothed whales	-	-	-	-	-	-	-	-	-	-
3 Seals	-	-	-	-	-	-	-	-	-	-
4 Seabirds	-	-	-	-	-	-	-	-	-	-
5 Juvenile sharks	-	-	-	-	-	-	-	-	-	-
6 Spurdog	2,742	14	265	1,214	633	49	-	10	4,902	74
7 Large piscivorous sharks	4	0	-	-	11	-	140	-	171	-
8 Small sharks	92	6	1	-	43	-	9	-	171	-
9 Juvenile rays	-	-	-	-	-	-	-	-	-	-
10 Starry ray & others	3,870	-	-	-	-	-	-	-	3,876	0
11 Thornback & Spotted ray	707	93	3	11	548	-	-	1,642	3,021	181
12 Skate & cuckoo ray	39	-	-	-	-	-	-	-	57	0
13 Juvenile Cod	-	-	-	-	-	-	-	-	-	29,658
14 Cod (adult)	35,568	5,159	1,203	14,079	10,659	781	-	-	67,431	3,366
15 Juvenile Whiting	-	-	-	-	-	-	-	-	-	13,886
16 Whiting (adult)	25,251	1,887	31,863	22,458	91	1,180	-	1,294	84,018	19,416
17 Juvenile Haddock	-	-	-	-	-	-	-	-	-	35,992
18 Haddock (adult)	20,862	86	4,480	20,349	168	389	-	3,711	50,046	4,243
19 Juvenile Saithe	-	-	-	-	-	-	-	-	-	31,504
20 Saithe (adult)	52,782	8	1,402	12,312	300	76	-	-	66,861	0
21 Hake	1,066	12	166	426	667	5	-	10	2,337	662
22 Blue whiting	-	-	-	34,428	-	-	-	335	34,770	-
23 Norway pout	37	-	85,557	69,084	-	-	-	1,203	155,895	-
24 Other gadoids (large)	16,701	544	-	-	1,374	-	254	-	18,867	1,828
25 Other gadoids (small)	15,732	286	0	-	39	-	68	0	16,131	-
26 Monkfish	7,581	407	315	1,094	126	952	-	557	11,058	1,796
27 Gurnards	378	84	-	1	0	-	-	-	456	4,121
28 Juvenile Herring	-	-	-	-	-	-	-	-	-	86,214
29 Herring (adult)	54,093	2	120,840	211,014	403	-	-	101,574	487,920	1,854
30 Sprat	1,858	3	71,478	3,420	49	-	-	22,743	99,579	4,218
31 Mackerel	9,576	2	6,954	141,132	8	-	-	39,501	197,163	117,941
32 Horse mackerel	9,063	264	998	24,852	42	-	-	63,042	98,268	6
33 Sandeels	1	-	825,702	1,123	-	-	-	15,732	842,574	-
34 Plaice	23,313	107,673	76	1,590	3,893	159	-	20,748	157,434	59,737
35 Dab	1,556	243	11	308	120	33	-	129	2,394	76,055
36 Long-rough dab	-	-	-	-	3	-	-	-	-	-
37 Flounder	724	849	-	-	84	-	1	-	1,653	34,827
38 Sole	963	28,500	1	0	1,146	-	-	7,752	38,361	0
39 Lemon sole	3,933	328	12	1,294	72	76	-	207	5,928	2,450
40 Witch	1,773	541	-	0	0	-	16	-	2,337	6,975
41 Turbot and brill	392	587	6	0	827	-	-	214	2,052	407
42 Megrim	969	0	-	289	1	46	-	4	1,311	673
43 Halibut	713	36	-	-	1	-	8	-	741	-
44 Dragonets	-	-	-	-	-	-	-	-	-	-

Table 3.5. continued: Fisheries landings and discards for the 1991 model. (see section 14 for details)

Functional groups	Demersal trawl & seine	Beam trawl	Sandeel trawl	Pelagic trawl	Drift and fixed nets	*Nephrops* trawl	Hooks	Other	Total landings	Discards
45 Catfish (Wolf-fish)	2,713	282	-	0	11	-	30	-	3,021	-
46 Large demersal fish	3,124	58	0	20	174	-	18	2	3,420	703
47 Small demersal fish	13,509	1,106	26,334	4,497	44,403	-	0	6,669	96,501	-
48 filterfeeding pelagic fish	35	-	-	5,700	-	-	-	-	5,757	90
49 Squid & cuttlefish	952	48	-	-	0	-	-	2	1,026	227
50 Fish larvae	-	-	-	-	-	-	-	-	-	-
51 Carnivorous zooplankton	-	-	-	-	-	-	-	-	-	-
52 Omnivorous zooplankton	-	-	-	-	-	-	-	-	-	-
53 Gelatinous zooplankton	-	-	-	-	-	-	-	-	-	-
54 Large crabs	37	5	3,659	-	36	-	1	2,793	6,555	573
55 Nephrops	4,030	4	2	22	1	6,213	-	16	10,317	10
56 Epifaunal macrobenthos	661	11	307	-	12	-	0	2,787	3,762	-
57 Infaunal macrobenthos	-	-	-	-	-	-	-	51,756	51,756	28,443
58 Shrimp	707	22,287	328	5	0	-	-	1,411	24,738	-
59 Small mobile epifauna	-	-	-	-	-	-	-	-	-	-
60 Small infauna (polychaetes)	-	-	-	-	-	-	-	-	-	-
61 Sessile epifauna	-	-	-	-	-	-	-	120,270	120,270	-
TOTAL	318,107	171,414	1,181,963	570,723	65,945	9,959	547	466,113	2,784,906	568,131

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3.4 System analysis and characterisation

3.4.1 Ecosystem structure and biomass flows

After balancing, the model biomass estimates of the most important fish groups were compared to historical data (Daan *et al.*, 1990; Sparholt, 1990; Mackinson, 2002a a, Figures 4.1, 4.2). Total fish biomass in the North Sea was estimated ~26 million tonnes by the late 19th century (Mackinson, 2002 2002a a) and ~11 million tonnes in 1991 (this study). The biggest change (between 50 and 100%) was in exploited target species eg, gadoids (cod, haddock, saithe), herring and flatfish (Figure 3.1). There was also an important decrease in cetaceans, seabirds and elasmobranches and an increase in seals in 1991 compared to the 1880s. The biomass estimates in the 1880s model were based on scarce data and strong assumptions and should be interpreted with caution. The total biomass seems to stabilise at a level ~10-11 million tonnes in the 1980-1990s (Daan *et al.*, 1990; Sparholt, 1990), however there was a change in the relative importance of different stocks: sharks, gadoids, horse mackerel, and large demersal fish decreased between 1980s and 1991, but clupeids, gurnards, hake, some flat fish (dab, turbot, brill) and prey fishes (dragonets, small demersal fishes) increased in 1991 compared to 1980s (Figure 3.2). More than 100% increases in hake and turbot/brill must be regarded with caution. Although such changes have been previously reported (Hessen, 1996; Daan *et al.*, 1990), both 1980s and 1991 biomass estimates could be significantly biased due to problems in data or imprecision of the method, especially for the less abundant species (Sparholt, 1990). The changes were reflected in the relative biomass composition (Figure 3.3). The shares of elasmobranches, target commercial gadoids, flatfishes, clupeids significantly decreased and these of industrial and prey fish (sandeel, Norway pout) increased in the 1980s-1990s compared to 1880s. The target gadoids, Norway pout, mackerel/horse mackerel decreased, and clupeids and prey fish increased in 1991 compared to 1980s. These results confirm the trends in replacement of the valuable commercial species with smaller prey fish of low or no commercial value in the North Sea reported previously by other investigators (eg Greenstreet *et al.*, 1996 Jennings *et al.*, 1999).

Tables 3.5 and 3.6 summerise estimates of the fisheries catches, production, consumption, and the flow to detritus per functional group. Most of the catch as a quantity is taken by sandeel and pelagic trawls, followed by demersal and beam trawls. A considerable amount (17%) is taken by variety of smaller métiers (including pots, dredges, shrimp trawls). A considerable quantity (20%) of the total catch is discarded (Table 3.5). Sandeels are the highest percentage in the total catch, followed by clupeids, gadoids, and mackerel and horse mackerel (Figure 3.5). The largest flows to detritus are produced by plankton and small benthos (Table 3.6).

The relative importance of different groups in consumption is shown in Table 3.7. The most important consumers are small flatfishes (mainly dab), clupeids and sandeels related to their dominance as biomass (Table 3.7, Figure 3.3) and the most important food sources are zooplankton and small benthos (Table 3.6). The most important fish predator are the MSVPA gadoids (cod, whiting, haddock, and saithe), followed by mackerel and horse mackerel, and gurnards, but megrim, minke whales, and elasmobranchs (mainly rays) are also important (Table 3.7, Figure 3.4). On Figure 3.5 are presented the quantities of fish and invertebrates consumed by some of the main predators, and on Figure 3.6 are presented the quantities preyed and fished from the main prey groups. It is quite remarkable that our analyses give such an importance to minke whales (the only baleen whales for which we have more detailed information) which according to our data appear to consume about the same amount of fish as toothed whales, seals and seabirds together. It must be stressed however that the minke whale diet used in the model is based on only 15 stomach samples from only June–July 1999 taken in limited area in the central North Sea and containing only fish (mainly sandeel, Table 4.2, Olsen and Holst 2000). It might be that in other areas/time minke whales diet contains also zooplankton as it is observed in other areas (eg, Haug *et al.*, 1995; Folkow *et al.*, 1997) where minke whales appear to be rather opportunistic feeders. The most important fish preys are the gadoids, clupeids and sandeels (Table 3.7, Figure 3.4). The main predators of MSVPA gadoids are mackerel, porpoises (especially preying on juvenile whiting), gurnards (targeting juvenile whiting and cod), large flatfish – halibut and turbot/brill (juvenile whiting and haddock). Small gadoids are preyed mainly by predatory gadoids, mackerel/horse mackerel and other demersal predatory fish. The most important prey species is sandeel. Its dominant predators are: MSVPA gadoids, mackerel, gurnards, minke whales, followed by rays and seabirds (Table 3.7, Figure 3.4). Small flatfish and particularly dab is not as important as prey as it may seem, considering its importance in terms of biomass (Table 3.7, Figures 3.4, 3.6). Seabirds and seal are relatively moderate consumers of fish(only 2% of the consumption of fish, each of these groups consuming ~2% of the total quantity of fish consumed by all predators (Table 3.7).

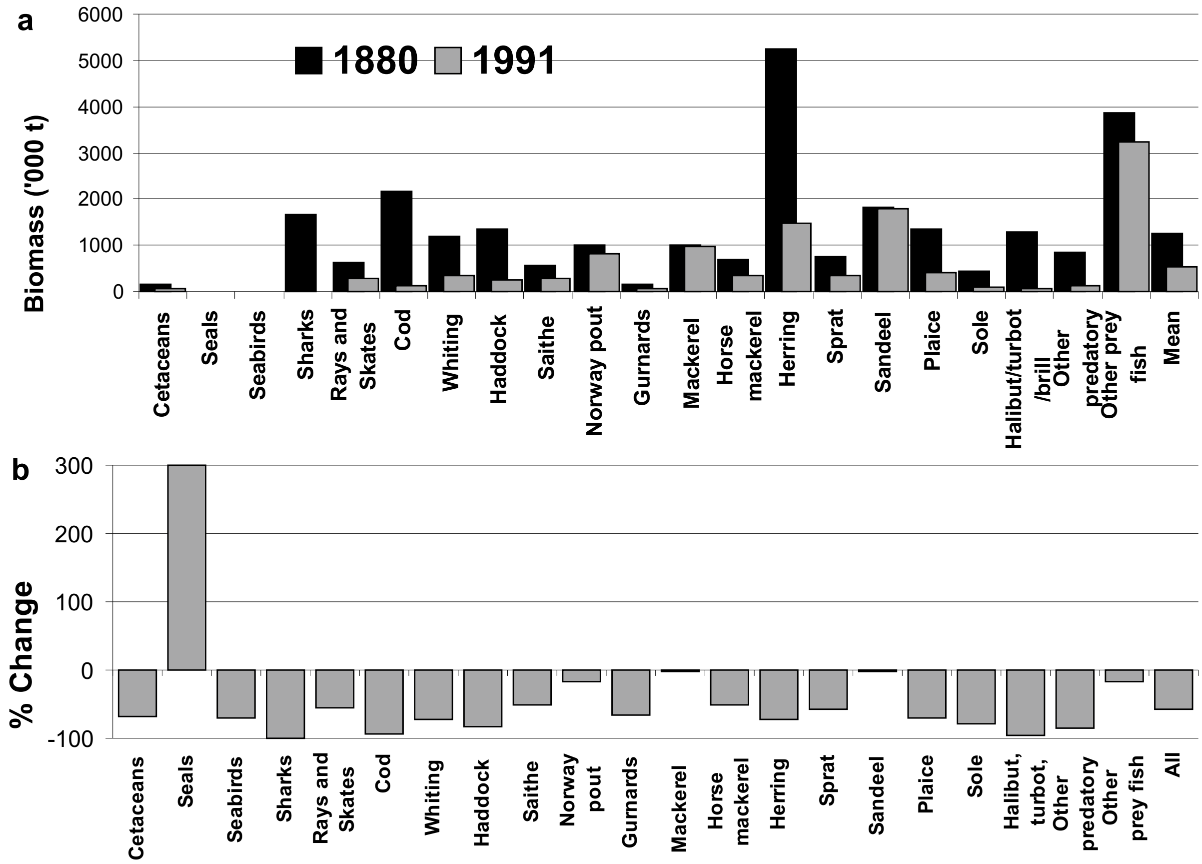


Figure 3.1. Fish biomass comparison between 1880 and 1991: (a) biomass, (b) % change between1880 and 1991.

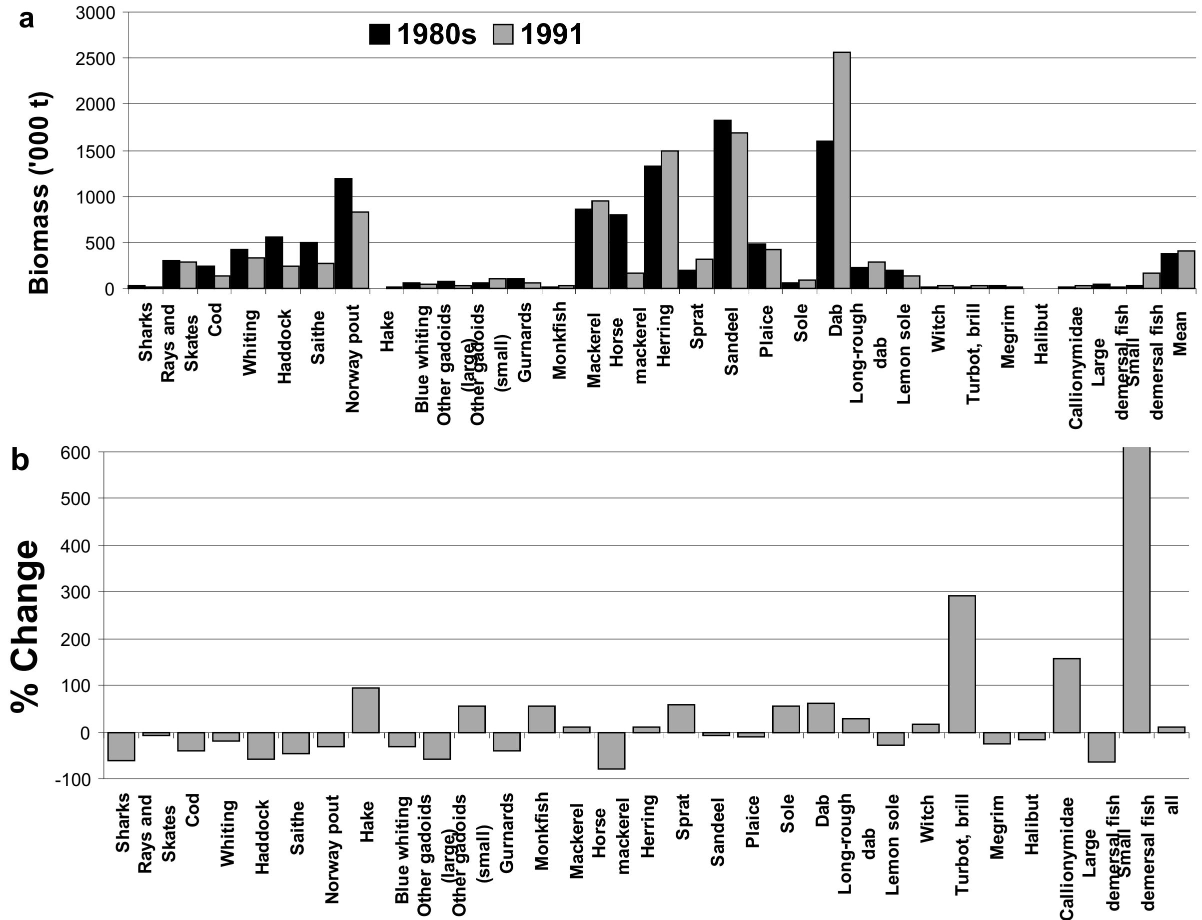
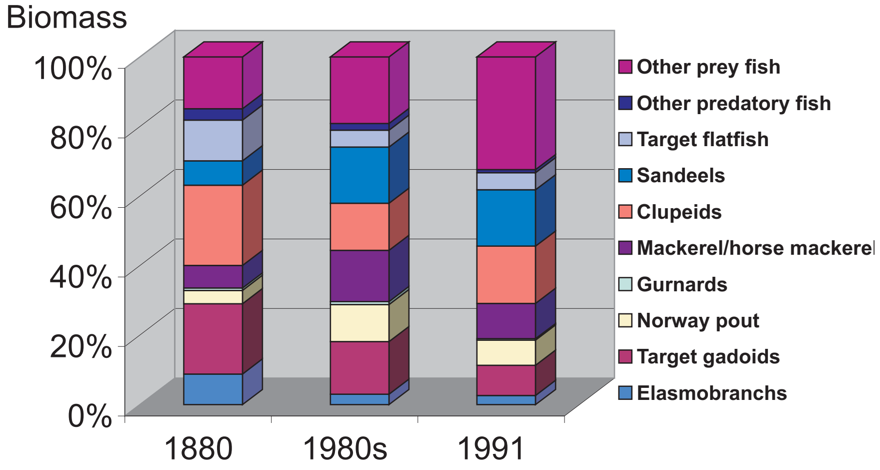


Figure 3.2. Fish biomass comparison between 1980s and 1991 (a) biomass, (b) % change between1980s and 1991.

Figure 3.3. Structure of fish biomass in 1880, 1980s and 1991.



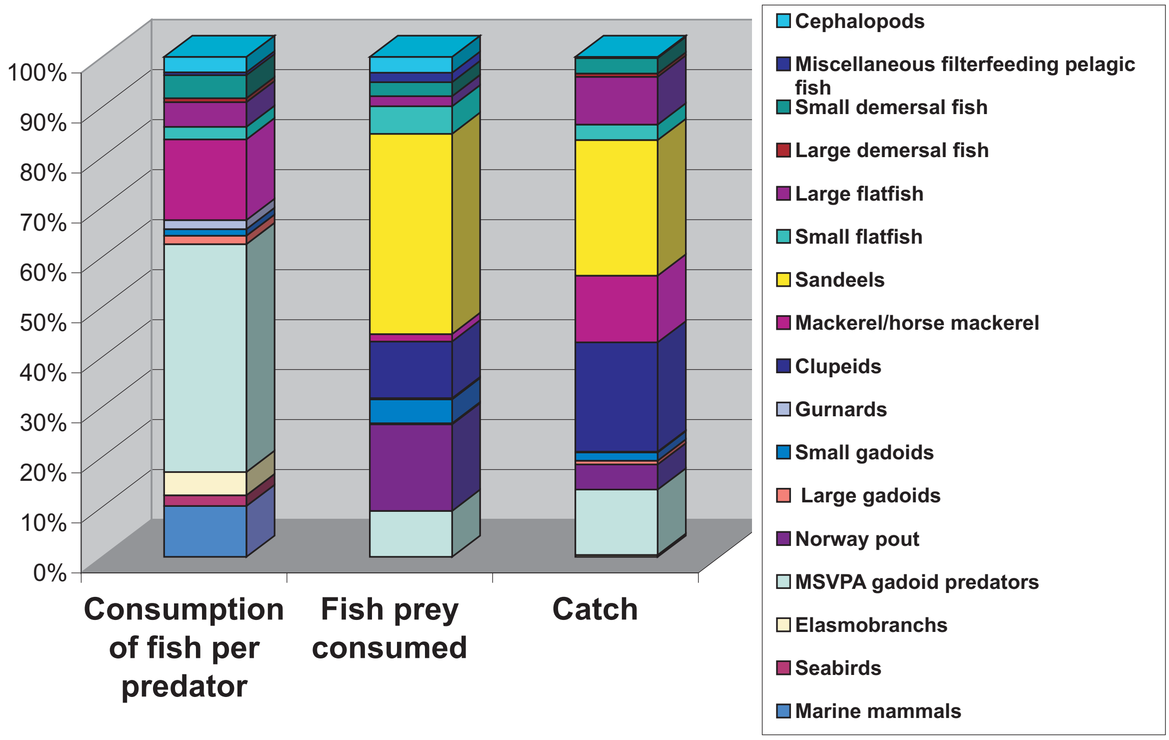


Figure 3.4. Structure of fish consumption and catch: 1st column is the % consumption of fish per predator groups; 2nd column is the % quantity of each fish group consumed by all predators; 3rd column is % quantity of each fish group in the catch.

Trophic levels

The concept of trophic levels (TL) was introduced by Lindeman (1942). Trophic levels describe the hierarchical architecture of the food web which could also be represented as a trophic pyramid (Clarke, 1946). In Ecopath, trophic levels are estimated as fractional quantities as suggested by Odum and Heald, 1975; Christensen *et al.*, 2005). Trophic level of 1 is assigned to producers and detritus and a trophic level of 1 + (the weighted average of the preys' trophic level) to consumers up in the trophic pyramid. Trophic levels of the FGs in the North Sea are sorted hierarchically on Figure 4.7. The lowest TL = 1 is by definition assigned to primary producers - phytoplankton, herbivores have TL>2, planktivorous fish and carnivorous zooplankton 2>TL>4, most of the benthivores 3>TL>4, and piscivores between 3>TL>5 depending on how much fish and invertebrates are in their diet (see also Figure 3.5). The dominant top-predators are seals (TL 5.01), large sharks levels(TL 4.93), spurdog, cod, monk, hake and halibut with TLs between 4.8 and 4.9 (Figure 3.7).

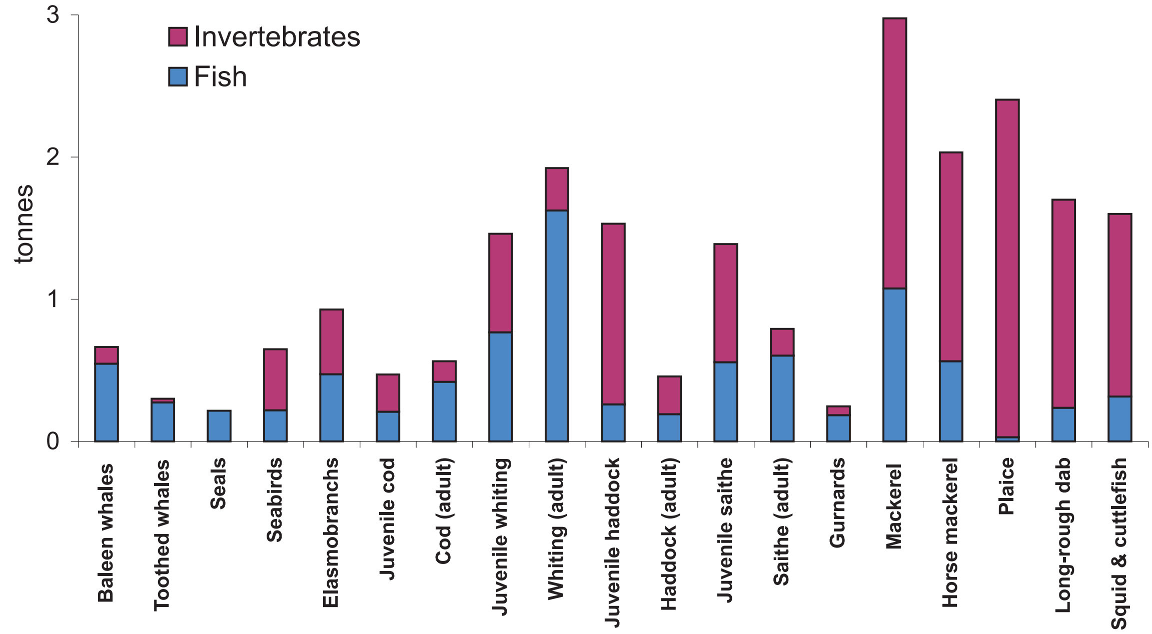


Figure 3.5. Consumption fish and invertebrates by the main predators.

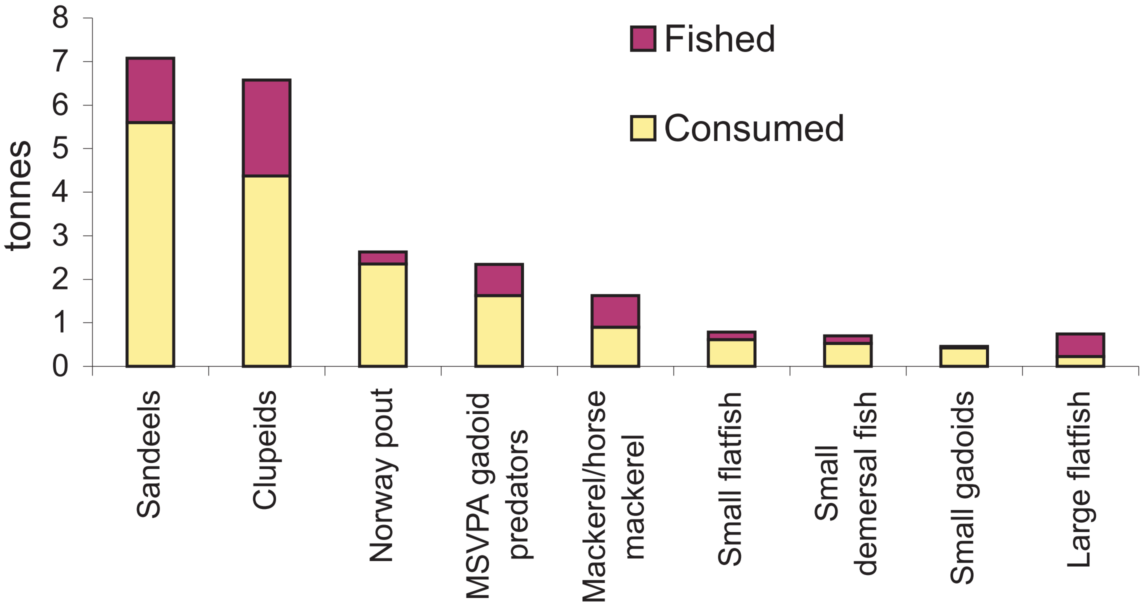


Figure 3.6. Quantity of fish consumed by predators and fished.

3.4.2 Food web interactions

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 their damage. The second is the indirect effect of decreasing fish biomass on ecosystem functioning (eg trophic cascade). We used various descriptive ecosystem indicators (eg as reviewed in Cury *et al.*, 2006) to evaluate the interactions between the different components, and of structural ecosystem changes resulting from exploitation.

Structure of mortality

The main prey groups in the system are sandeels, clupeids (sprat and herring), Norway pout, and juvenile gadoids fish (Figures 3.4, 3.6, 3.8, 3.9, 3.10). The highest predation is caused by commercial gadoids, mackerel and horse mackerel (Figures 3.8, 3.9, 3.10). Sandeels dominate in diets of marine mammals, elasmobranches, and other

Table 3.6. Main flows in the NS model.

Functional groups	Production t km^{-2} y^{-1}	Consumption t km^{-2} y^{-1}	Respiration t km^{-2} y^{-1}	Consumed as food t km^{-2} y^{-1}	Fisheries catch t km^{-2} y^{-1}	Flow to detritus t km^{-2} y^{-1}
1 Baleen whales	0.001	0.663	0.529	0.000	0.000	0.134
2 Toothed whales	0.000	0.300	0.239	0.000	0.000	0.060
3 Seals	0.000	0.223	0.171	0.000	0.000	0.044
4 Seabirds	0.001	0.648	0.518	0.000	0.000	0.130
5 Juvenile sharks	0.001	0.003	0.002	0.000	0.000	0.001
6 Spurdog	0.010	0.033	0.017	0.001	0.009	0.007
7 Large piscivorous sharks	0.001	0.003	0.002	0.000	0.000	0.001
8 Small sharks	0.001	0.006	0.004	0.000	0.000	0.002
9 Juvenile rays	0.177	0.456	0.188	0.001	0.000	0.267
10 Starry ray & others	0.072	0.185	0.076	0.000	0.007	0.102
11 Thornback & Spotted ray	0.051	0.152	0.070	0.000	0.006	0.076
12 Skate & cuckoo ray	0.018	0.090	0.055	0.000	0.000	0.035
13 Juvenile Cod	0.141	0.471	0.235	0.080	0.052	0.103
14 Cod (adult)	0.192	0.564	0.259	0.019	0.124	0.161
15 Juvenile Whiting	0.524	1.461	0.645	0.426	0.024	0.365
16 Whiting (adult)	0.313	1.922	1.224	0.111	0.181	0.406
17 Juvenile Haddock	0.568	1.531	0.657	0.194	0.063	0.617
18 Haddock (adult)	0.119	0.458	0.248	0.020	0.095	0.095
19 Juvenile Saithe	0.281	1.388	0.830	0.033	0.055	0.470
20 Saithe (adult)	0.209	0.792	0.425	0.012	0.117	0.238
21 Hake	0.011	0.031	0.013	0.002	0.005	0.010
22 Blue whiting	0.200	0.725	0.380	0.109	0.061	0.175
23 Norway pout	3.067	7.040	2.565	2.028	0.274	2.173
24 Other gadoids (large)	0.062	0.156	0.063	0.022	0.036	0.034
25 Other gadoids (small)	0.448	1.168	0.477	0.396	0.029	0.251
26 Monkfish	0.029	0.080	0.034	0.002	0.022	0.020
27 Gurnards	0.063	0.246	0.134	0.028	0.008	0.076
28 Juvenile Herring	0.825	3.547	2.012	0.403	0.151	0.980
29 Herring (adult)	1.573	8.532	5.253	0.228	0.859	2.192
30 Sprat	1.320	3.474	1.459	0.882	0.182	0.951
31 Mackerel	1.032	2.976	1.349	0.099	0.553	0.975
32 Horse mackerel	0.695	2.032	0.931	0.075	0.172	0.854
33 Sandeels	7.118	31.532	18.108	4.110	1.478	7.836
34 Plaice	0.598	2.404	1.326	0.034	0.381	0.663
35 Dab	2.016	10.080	6.048	0.283	0.138	3.612
36 Long-rough dab	0.245	1.190	0.707	0.148	0.000	0.335
37 Flounder	0.275	0.800	0.365	0.013	0.064	0.359
38 Sole	0.126	0.490	0.265	0.046	0.067	0.111
39 Lemon sole	0.264	1.318	0.791	0.049	0.015	0.463
40 Witch	0.074	0.246	0.123	0.015	0.016	0.092
41 Turbot and brill	0.046	0.124	0.053	0.002	0.004	0.065
42 Megrim	0.024	0.105	0.060	0.002	0.003	0.040
43 Halibut	0.005	0.104	0.078	0.000	0.001	0.025
44 Dragonets	0.068	0.270	0.149	0.051	0.000	0.071
45 Catfish (Wolf-fish)	0.007	0.024	0.012	0.000	0.005	0.006
46 Large demersal fish	0.009	0.043	0.025	0.001	0.007	0.010
47 Small demersal fish	0.489	1.275	0.528	0.309	0.170	0.264
48 filterfeeding pelagic fish	0.119	0.304	0.124	0.107	0.010	0.063

Table 3.6. Main flows in the NS model.

Functional groups	Production t km^{-2} y^{-1}	Consumption t km^{-2} y^{-1}	Respiration t km^{-2} y^{-1}	Consumed as food t km^{-2} y^{-1}	Fisheries catch t km^{-2} y^{-1}	Flow to detritus tkm^{-2} y^{-1}
49 Squid & cuttlefish	0.360	1.600	0.920	0.317	0.002	0.361
50 Fish larvae	1.270	5.080	3.831	1.006	0.000	1.290
51 Carnivorous zooplankton	13.148	41.086	20.072	13.016	0.000	8.497
52 Omnivorous zooplankton	147.200	480.000	150.400	71.422	0.000	258.177
53 Gelatinous zooplankton	0.189	0.012	-0.179	0.143	0.000	0.048
54 Large crabs	0.750	3.751	2.251	0.688	0.012	0.801
55 Nephrops	0.422	2.110	1.221	0.399	0.020	0.410
56 Epifaunal macrobenthos	30.295	151.476	90.884	13.065	0.008	47.517
57 Infaunal macrobenthos	136.000	453.329	226.667	37.862	0.095	188.712
58 Shrimp	0.795	2.650	1.325	0.556	0.093	0.676
59 Small mobile epifauna	58.161	166.177	73.286	53.790	0.000	36.854
60 Small infauna (polychaetes)	135.000	450.000	225.000	122.565	0.000	102.428
61 Sessile epifauna	27.300	136.500	81.900	0.851	0.210	53.534
62 Meiofauna	144.358	515.563	266.965	142.914	0.000	104.116
63 Benthic microflora	994.350	1988.700	397.740	981.765	0.000	609.195
64 Planktonic microflora	833.660	1667.320	333.464	599.897	0.000	733.959
65 Phytoplankton	2150.000			455.820	0.000	1694.180
66 Detritus - DOM in water				1642.507	0.000	0.000
67 Detritus - POM in sediment				2004.779	0.000	0.000
68 Discards				0.130	0.000	0.252
						3867.026

Table 3.7. Percentage of prey consumed by the main fish FGs.

Predator	Baleen whales	Toothed whales	Seals	Seabirds	Elasmobranchs	MSVPA gadoid predators	Large gadoids	Norway pout	Small gadoids	Mackerel/horse mackerel	Large flatfish	small flatfish	Gurnards	Large demersal fish	Small demersal fish	Clupeids	Sandeels	All
Prey																		
Consumption	0.8	0.3	0.2	0.6	1.1	10.1	0.2	8	0.7	8.2	11.6	20	1.9	0.1	0.6	17.2	18.6	100
Fish	5.1	2	1.7	2	3.7	37	1.1	0	0.4	29	5.4	1.9	8.8	0.5	1.3	0	0	100
MSVPA gadoid predators	0.1	1.4	0.4	0.1	0.2	2.9	0.1	0	0	11.6	0.9	0.1	1.5	0.2	0	0	0	19.5
large gadoids	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
Norway pout	0	0	0	0	0.3	9.8	0.1	0	0.3	0.2	0.7	0.1	0.8	0.1	0	0	0	12.4
Small gadoids	0	0	0	0	0.3	1.4	0.3	0	0	5.9	1.1	0.4	0.9	0	0	0	0	10.3
Mackerel/ horse mackerel	0.5	0.1	0	0.1	0.1	0.3	0.2	0	0	0.1	0	0	0	0	0	0	0	1.4
Clupeids	0.1	0	0	0.3	0.3	5.3	0.3	0	0	4.5	1.2	0	0.2	0.1	0	0	0	12.3
Sandeels	4.5	0.5	0.5	1.4	2.4	11.1	0.2	0	0	6.2	0.8	0.3	4.6	0.1	0.9	0	0	33.4
Large flatfish	0	0	0.3	0	0.1	1.2	0	0	0	0	0.2	0	0.1	0	0	0	0	1.8
Small flatfish	0	0	0.1	0	0.1	1.1	0	0	0	0	0	0.5	0.2	0	0.1	0	0	2.1
Gurnards	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0.2	0	0	0.5
Large demersal fish	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Small demersal fish	0	0	0.2	0	0.2	0.7	0	0	0.1	0.2	0.4	0.6	0.3	0	0.2	0	0	3

Table 3.8. Sensitivity of estimated EE or biomass of selected FGs of 50% change in input biomass or EE of other FGs - only sensitivities bigger than 10% are shown.

Group	Input parameter	Group	Estimated parameter	Change in input parameter	
				-50%	50%
Seals	Biomass	Other gadoids (large)	Biomass	-13%	13%
Seals	Biomass	Turbot and brill	EE	-17%	17%
Seals	Biomass	Megrim	EE	-19%	19%
Large piscivorous sharks	Biomass	Juvenile sharks	EE	-50%	50%
Large piscivorous sharks	Biomass	Coockoo ray/Skate	EE	-35%	35%
Whiting (adult)	Biomass	Juvenile herring	EE	-10%	10%
Whiting (adult)	Biomass	Sprat	EE	-11%	11%
Whiting (adult)	Biomass	Horse mackerel	EE	-11%	11%
Other gadoids (small)	EE	*Nephrops*	EE	28%	-9%
Monkfish	Biomass	Juvenile rays	EE	-34%	34%
Mackerel	Biomass	Horse mackerel	EE	-11%	11%
Horse mackerel	Biomass	Juvenile saithe	EE	-31%	31%
Horse mackerel	Biomass	Gurnards	EE	-14%	14%
Horse mackerel	Biomass	Juvenile herring	EE	-11%	11%
Flounder	Biomass	Long-rough dab	EE	-27%	27%
Flounder	Biomass	Lemon sole	EE	-23%	23%
Lemon sole	Biomass	Sessile epifauna	EE	-13%	13%
Small demersal fish	EE	Gurnards	EE	32%	-9%
Small demersal fish	EE	Dab	EE	12%	-4%
Small demersal fish	EE	Dragonets	EE	13%	-4%
Small demersal fish	EE	Squid & cuttlefish	EE	12%	-3%
Small demersal fish	EE	Large crabs	EE	11%	-3%
Miscellaneous filterfeeding fish	EE	Gelatinous zooplankton	EE	45%	-12%
Carnivorous zooplankton	EE	Juvenile cod	EE	44%	-11%
Carnivorous zooplankton	EE	Juvenile whiting	EE	12%	-3%
Carnivorous zooplankton	EE	Juvenile haddock	EE	58%	-14%
Carnivorous zooplankton	EE	Norway pout	EE	15%	-4%
Carnivorous zooplankton	EE	Juvenile herring	EE	13%	-3%
Carnivorous zooplankton	EE	Sprat	EE	24%	-6%
Carnivorous zooplankton	EE	Miscellaneous filterfeeding fish	Biomass	103%	-26%
Carnivorous zooplankton	EE	Herbivorous & Omnivorous zooplankton	EE	67%	-17%
Carnivorous zooplankton	EE	Gelatinous zooplankton	EE	33%	-8%
Carnivorous zooplankton	EE	Small mobile epifauna	EE	11%	-3%
Large crabs	Biomass	Witch	EE	-11%	11%
Large crabs	Biomass	*Nephrops*	EE	-13%	13%
Epifaunal macrobenthos	Biomass	Infaunal macrobenthos	EE	-40%	40%
Epifaunal macrobenthos	Biomass	Small infauna (polychaetes)	EE	-16%	16%
Infaunal macrobenthos	Biomass	Small mobile epifauna	EE	-20%	20%
Infaunal macrobenthos	Biomass	Small infauna (polychaetes)	EE	-19%	19%
Infaunal macrobenthos	Biomass	Benthic microflora	EE	-11%	11%
Small mobile epifauna	Biomass	Meiofauna	Biomass	-10%	10%
Small infauna (polychaetes)	Biomass	Meiofauna	Biomass	-29%	29%
Small infauna (polychaetes)	Biomass	Benthic microflora	EE	-21%	21%
Meiofauna	EE	Benthic microflora	EE	61%	-15%
Benthic microflora	Biomass	Planktonic microflora	EE	-17%	17%

Table 3.9. Comparison of selected system indicators of the North Sea model to other models of the British Seas.

Parameter	North Sea 1991	Irish Sea 2002	English Channel 1995	Western Channel 1994
Total biomass (excluding detritus) (t km^{-2})	554	377	227	198
Sum of all consumption (t km^{-2} y^{-1})	6157	11503	1361	1590
Calculated total net primary production (t km^{-2} y^{-1})	2607	1958	7547	2949
Sum of all production (t km^{-2} y^{-1})	4692	5505	7815	3424
Sum of all respiratory flows (t km^{-2} y^{-1})	2658	4223	716	796
Sum of all flows into detritus (t km^{-2} y^{-1})	3867	3889	7435	2683
Total catches (t km^{-2} y^{-1})	5.88	1.47	3.12	3.38
Total system throughput (t km^{-2} y^{-1})	12786	17630	16359	7223
Utilisation of primary production	0.33	0.99	0.07	0.26
Utilisation of detritus	0.95	0.99	0.08	0.20
Ascendency (%)	20.6	19.9	53.9	36.7
Total primary production/total respiration	0.98	0.46	10.54	3.71
Total primary production/total biomass	4.71	5.19	33.29	14.91
Total biomass/total throughput	0.04	0.02	0.01	0.03
Thermodynamic order (R/B)	4.80	11.20	3.16	4.02
Average organism size (B/P)	0.12	0.07	0.03	0.06
Mean trophic transfer efficiencies	30.2	25.4	12.6	11.7
Mean trophic level of the catch	3.6	3.57	2.57	2.44
Gross efficiency (catch/net p.p.)	0.00226	0.00075	0.00041	0.00115
Finn's cycling index (% of total throughput)	20.24	41.20	0.14	0.73
Finn's mean path length	4.63	7.88	2.02	2.01
Connectance Index	0.22	0.19	0.13	0.17
System Omnivory Index	0.23	0.36	0.17	0.14
mean PPR Catch % PP	5.88	7.99	2.78	11.61

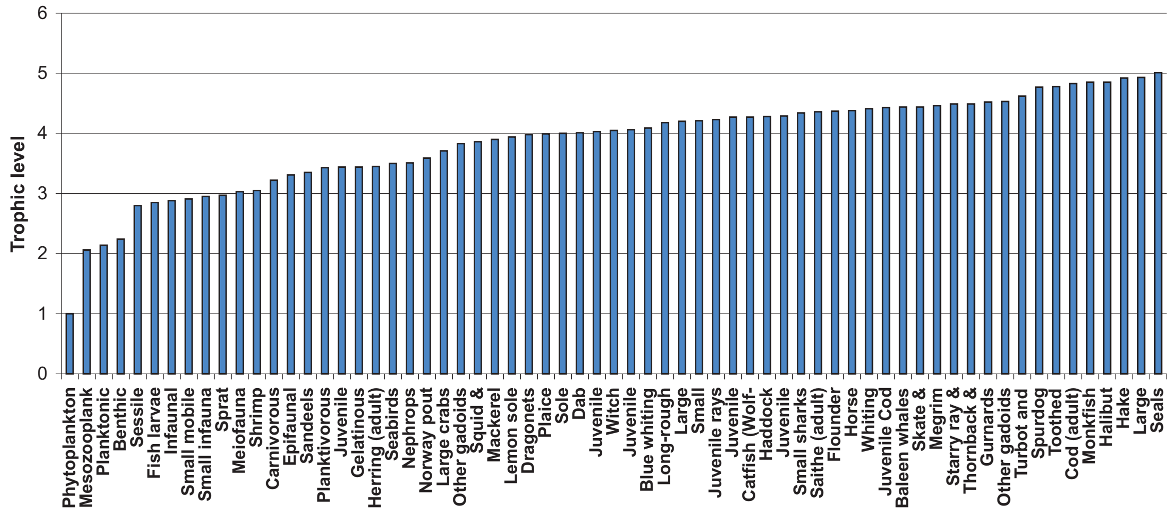


Figure 3.7. Trophic level.

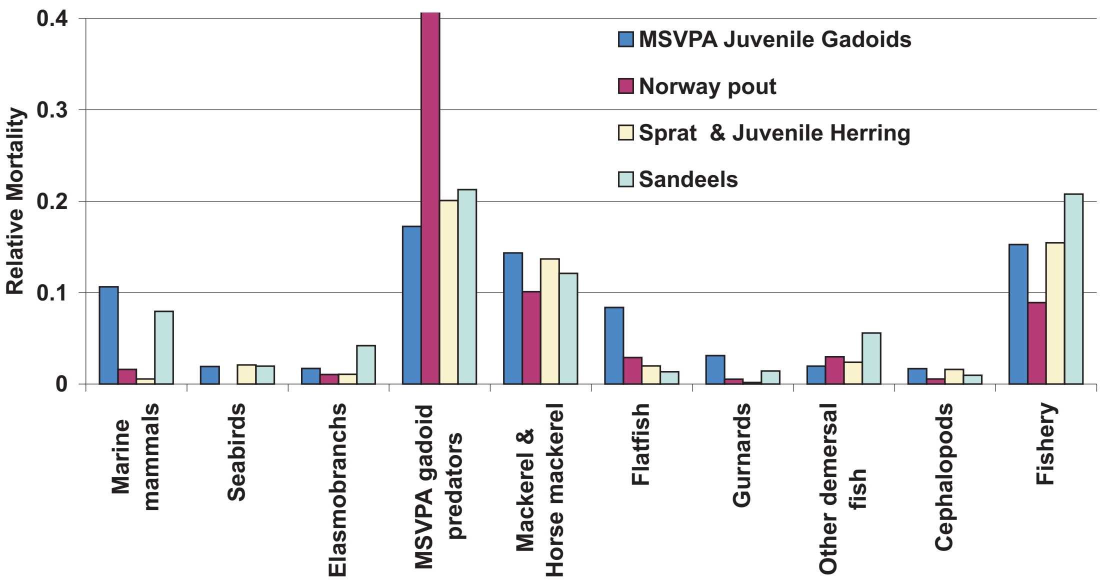


Figure 3.8. Mortality caused on fish groups by the main predator and the fisheries (shown on the x-axis). Columns are the main prey groups.

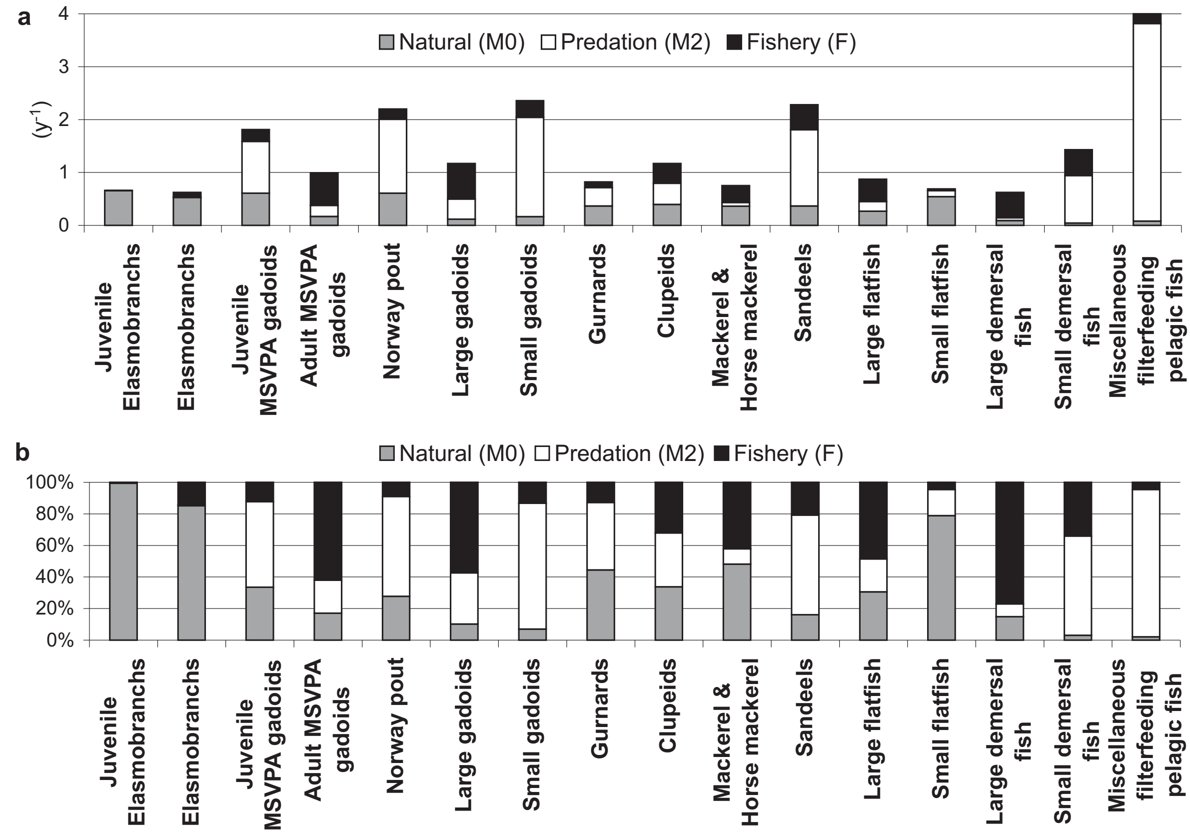


Figure 3.9. Structure of mortality: a. mortality , b. percentage of the total mortality.

demersal fish, and juvenile gadoids – in the diets of marine mammals, flatfish (plaice, turbot, halibut), and gurnards (Figures 3.8, 3.9, 3.10).

On Figure 3.11 mortality estimates in the 1991 model were compared to mortality in a earlier model constructed for the 1970s by Villy Christensen (Beattie *et al.*, 2002). Predation mortality decreased in 1991 compared to 1974 for the more abundant preys- sandeel, clupeids, juvenile gadoids (because of the decrease in predatory fish, Figure 3.11). Predation mortality increased for adult gadoids, plaice and sole, gurnards, and mackerel and horse mackerel (relative to the biomass decrease in these groups), and fishing mortality increased for mackerel and horse mackerel and sandeels Figure 3.11). For the whole system the fishing mortality increased and the predation mortality decreased in 1991 comparing to 1974 (Figure 3.12).

Selectivity index

The selectivity index describes a predator's preference for prey. It scales from -1 to 1; where -1 indicates total avoidance of a prey; 0 indicates that a prey is taken in proportion to its abundance in the ecosystem; and 1 indicates total preference for a prey. The selectivity index used is developed by Chesson (1983). This index is independent of prey availability. It is implemented in Ecopath to vary between -1 and 1, so that -1, 0 and 1 can be interpreted as for the Ivlev electivity index. (Christensen *et al.*, 2000). On Figure 3.13 are presented the selectivity indices of the four most consumed fish groups: sandeels, sprat, Norway pout and juvenile whiting. The main predators of sandeel are mackerel, whiting, baleen (minke) whales and small demersal fish (eg weevers). These predators are positively selective for sandeel as well as are the seabirds, rays, haddock and gurnard. Sandeel is not preferred by the sharks, saithe, small gadoids (eg pouting, poor cod), megrim, and large demersal fish. Norway pout is strongly preferred by commercial gadoids, spurdog and starry ray, and horse mackerel, and avoided by baleen whales, large sharks, thornback and spotted rays, and small gadoids. Sprat is preferred by seabrds, whiting, mackerel, and megrim, and avoided by seals, monkfish and small demersals; and juvenile whiting is a preferred prey of most of the predators including mammals and seabirds, commercial gadoids, monk, gurnards, turbot and halibut.

Niche overlap index

The niche overlap index (Pianka, 1973) can be used to describe trophic niche partitioning and food competition. Originally it has been derived from the competition coefficients of the Lotka-Volterra equations. A version of it (Christensen *et al.*, 2005) can be estimated for each couple of FGs within ecopath from the proportions of the resource used by each two FGs based to the diet matrix. The index is symmetrical and assumes values between 0 and 1. On Figure 3.14 are shown the niche overlap indices of the four dominant predators with their major competitors. It can be seen that mackerel compete for food with whiting, gurnards, rays, small demersal fish and gelatinous zooplankton;

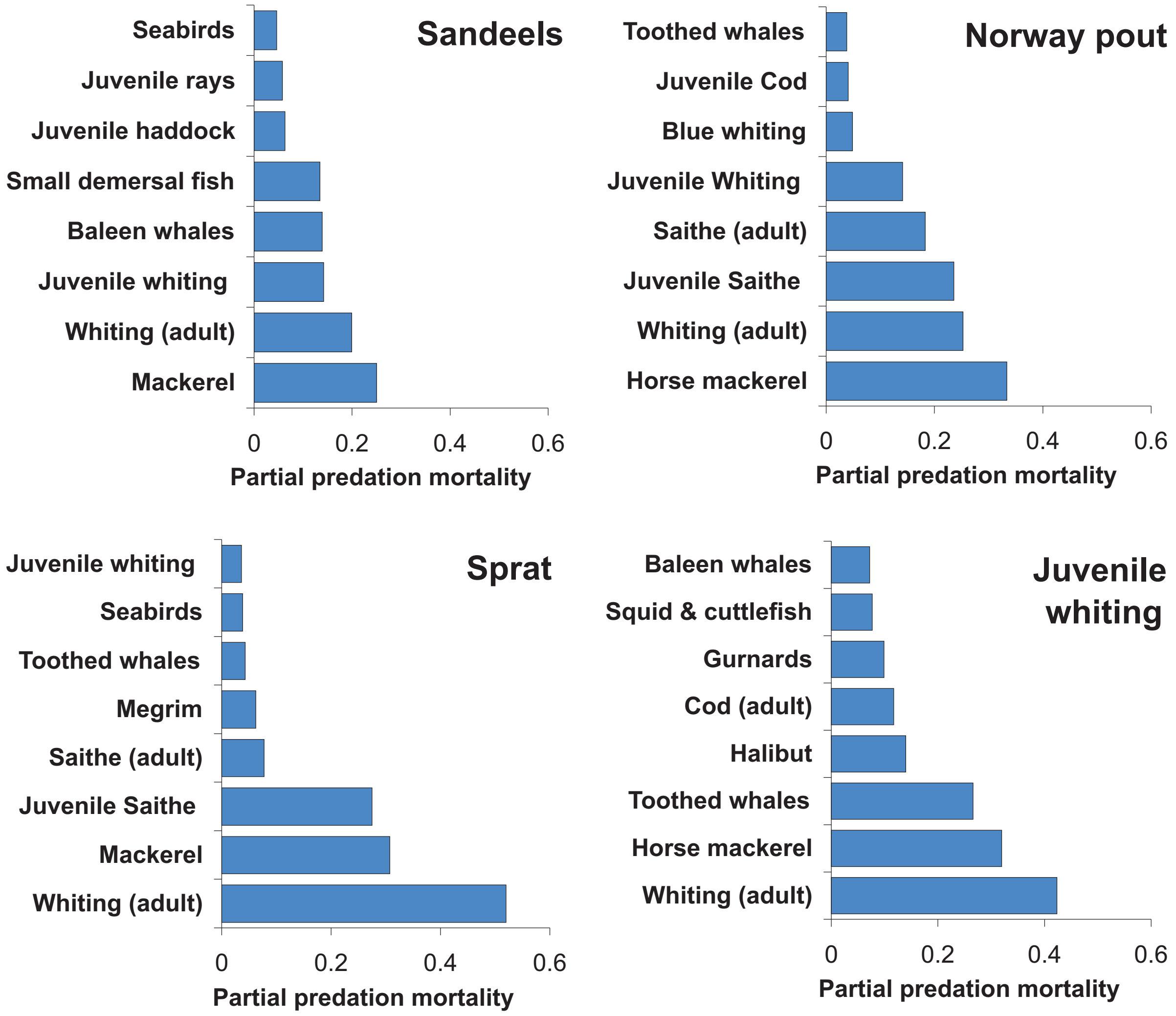


Figure 3.10. Partial predation mortality (M2) of the four heavily consumed fish preys by their most important predators.

whiting - with its own juveniles, gurnards, rays, seals and other gadoids; cod – elasmobranches, monk, turbot, seals, and other gadoids; and plaice – with dragonets, predatory macrobenthos, and other benthivore flatfish.

Mixed trophic impact

The mixed trophic impact (MTI) are indicators of the relative impact of a change in the biomass of one component on other components of the ecosystem (Ulanowicz and Puccia, 1990). They are calculated by multiplication of the matrix of the direct impacts which is compiled using the diet (positive direct impact) and consumption (negative direct impact) matrices (Ulanowicz and Puccia, 1990). The mixed impact is a sum of the direct and indirect impacts. The indirect impacts can be associated with intergroup competition and trophic cascades. MTI of some groups are shown on Figure 3.15. The estimation of the impacts shows that whiting, herring, mackerel, dab are affected negatively by their predators and competitors. MTI can also be used as indicator of direct and indirect effects of fishing (Figure 3.16). For instance strongest negative impacts of the demersal trawls and seines are on some elasmobranches (spurdog, starry ray), large gadoids (including cod and saithe), monk, megrim, catfish and large demersals; - of beam trawls on flatfish; pelagic trawls on sharks, gadoids, herring and mackerel. Fishing fleets exert some small positive indirect effects, due to increased growth of populations that compete with those, which are affected negatively.

3.4.3 Whole system indicators

The Ecopath model can be used is to assess the whole ecosystem state and to compare to other ecosystems. This provides an evaluation of the whole ecosystem in terms of productivity, complexity/connectance, trophic efficiency and ecosytem health.

Several system indices of ecosystem maturity have been identified (Christensen, 1995; Christensen and Pauly, 1998) that can be derived from a mass-balance model. According to Odum's theory of ecosystem development, control by trophic interactions in the mature system tends to dominate over control by environment, and provides a positive feedback leading to higher complexity and stability (Odum, 1969). The level of system's stability, complexity and

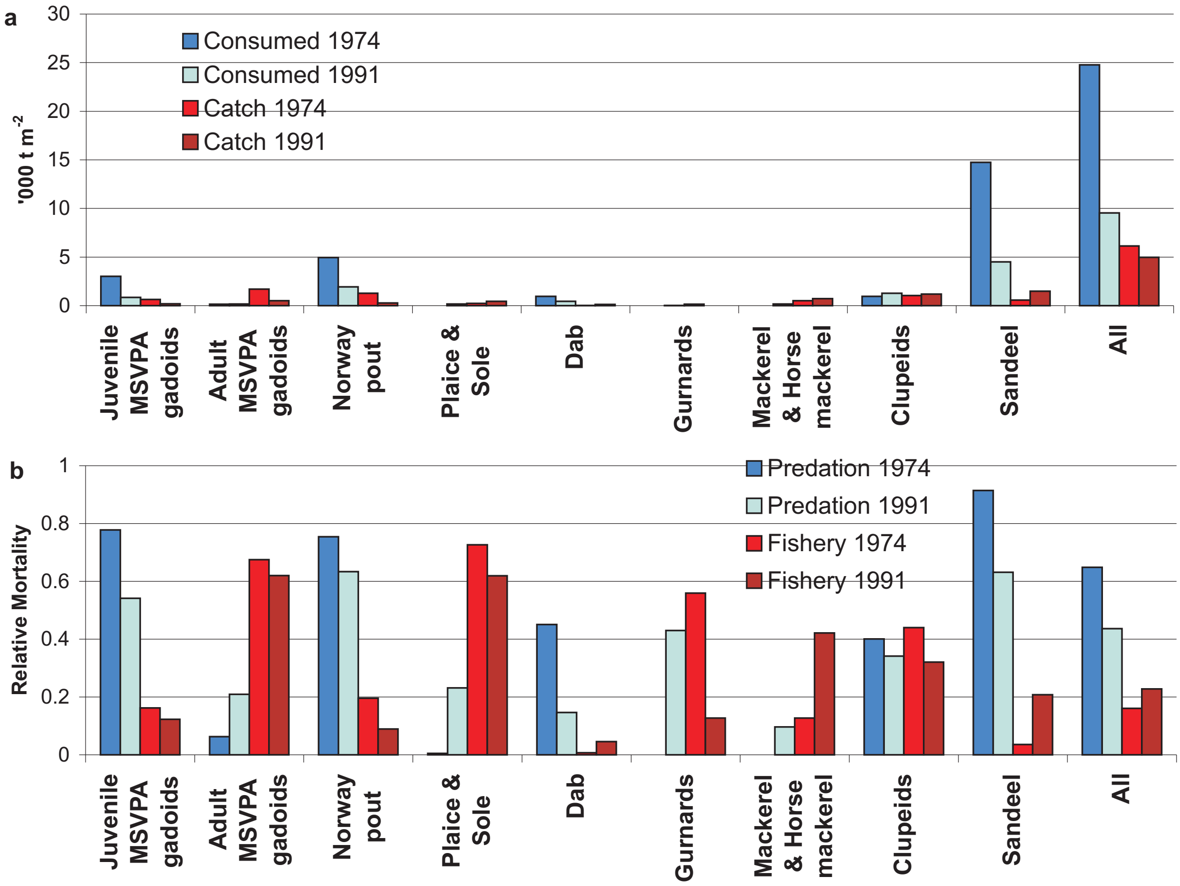
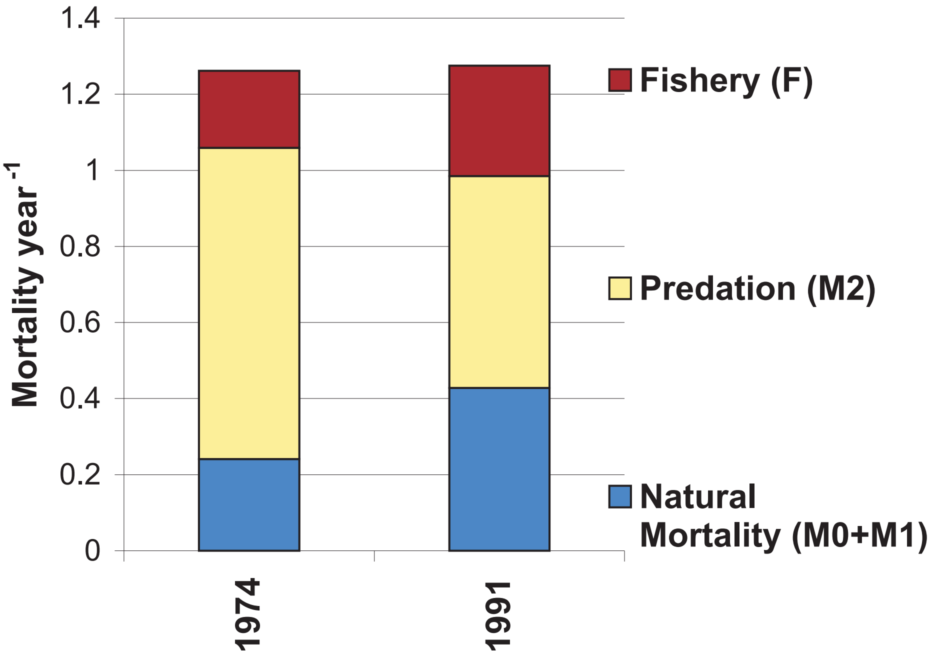


Figure 3.11. Comparison between predation and fishing: (a) consumed fish groups versus catch; (b) predation mortality versus fishing mortality in 1991 and 1974 model (Beattie *et al.*, 2002).

Figure3.12. Mortality in the whole fish community y.



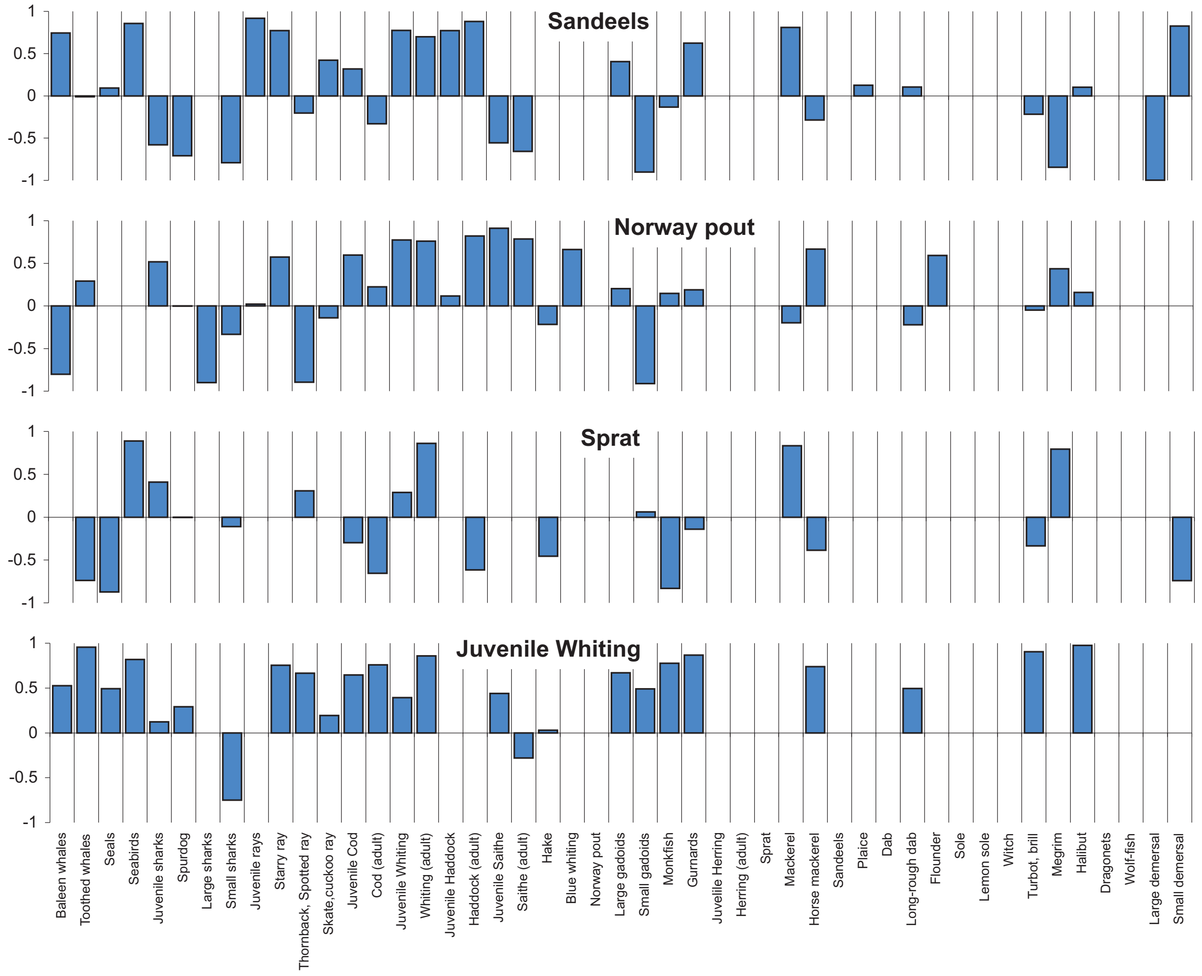
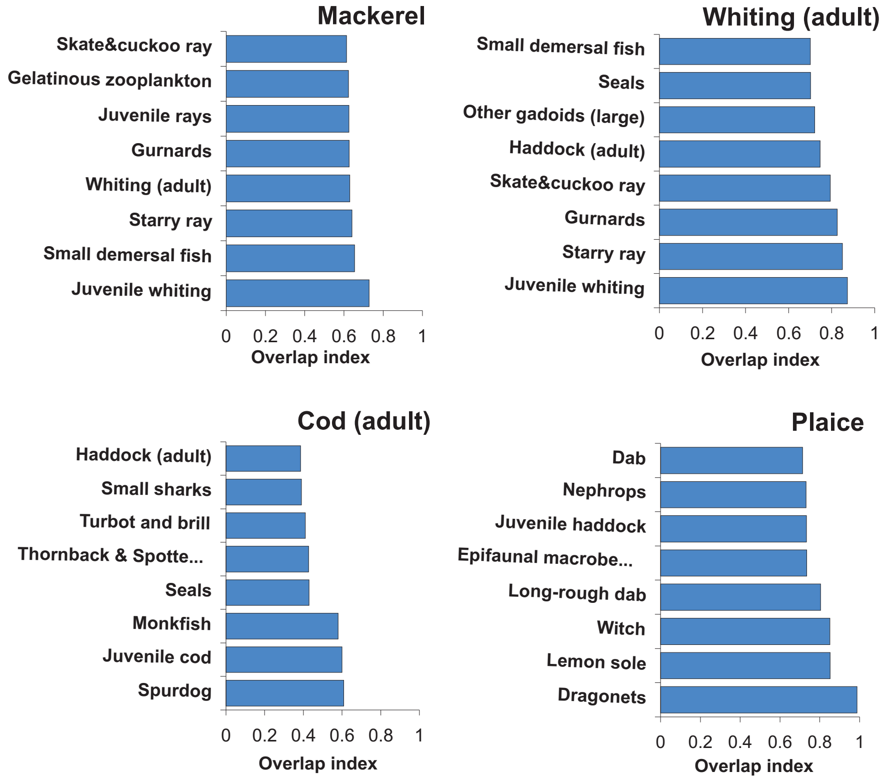


Figure 3.13. Selectivity index of the four heavily consumed fish preys.

Figure 3.14. Trophic niche overlap of some dominant predators.



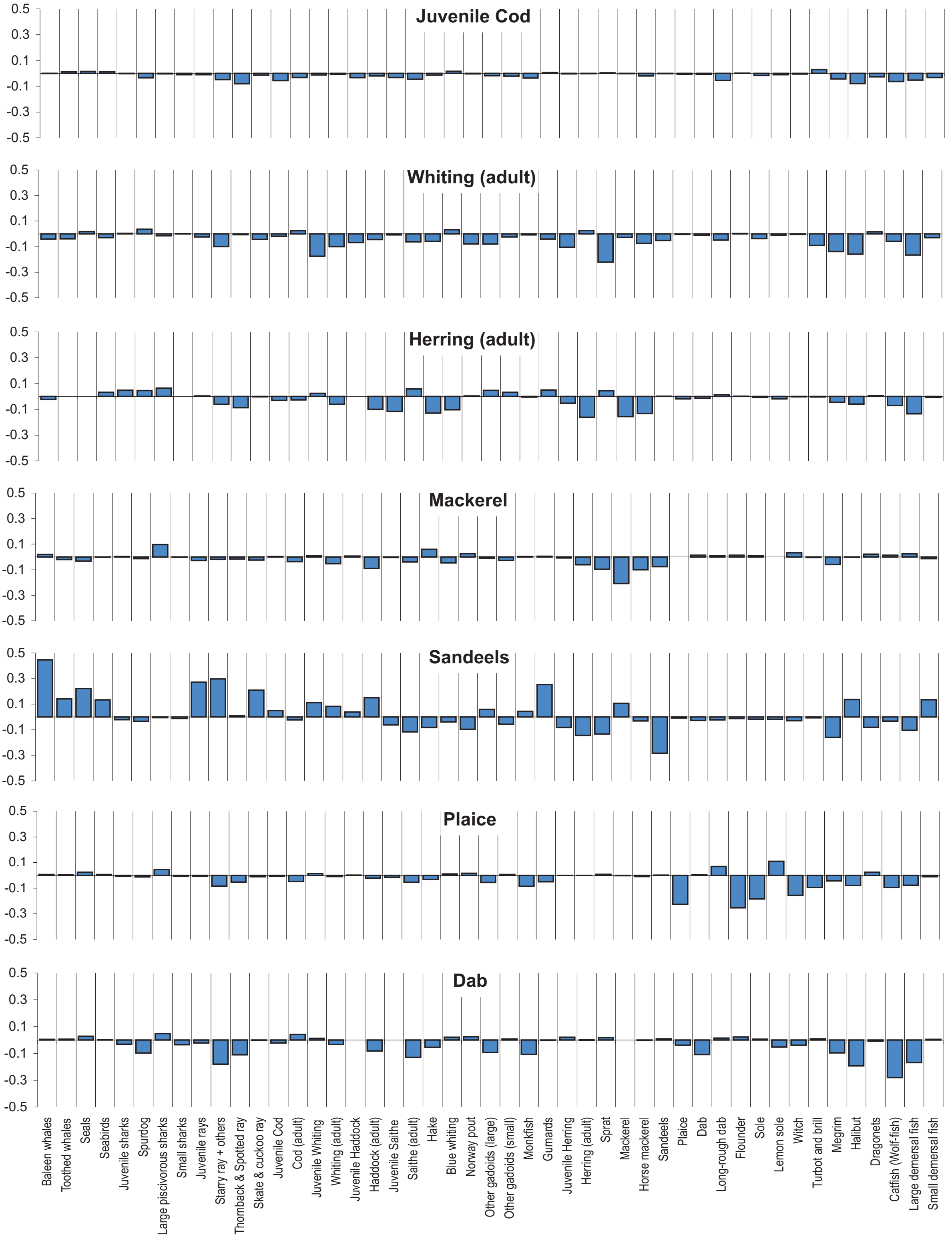


Figure. 3.15. Mixed trophic impacts of selected fish groups.

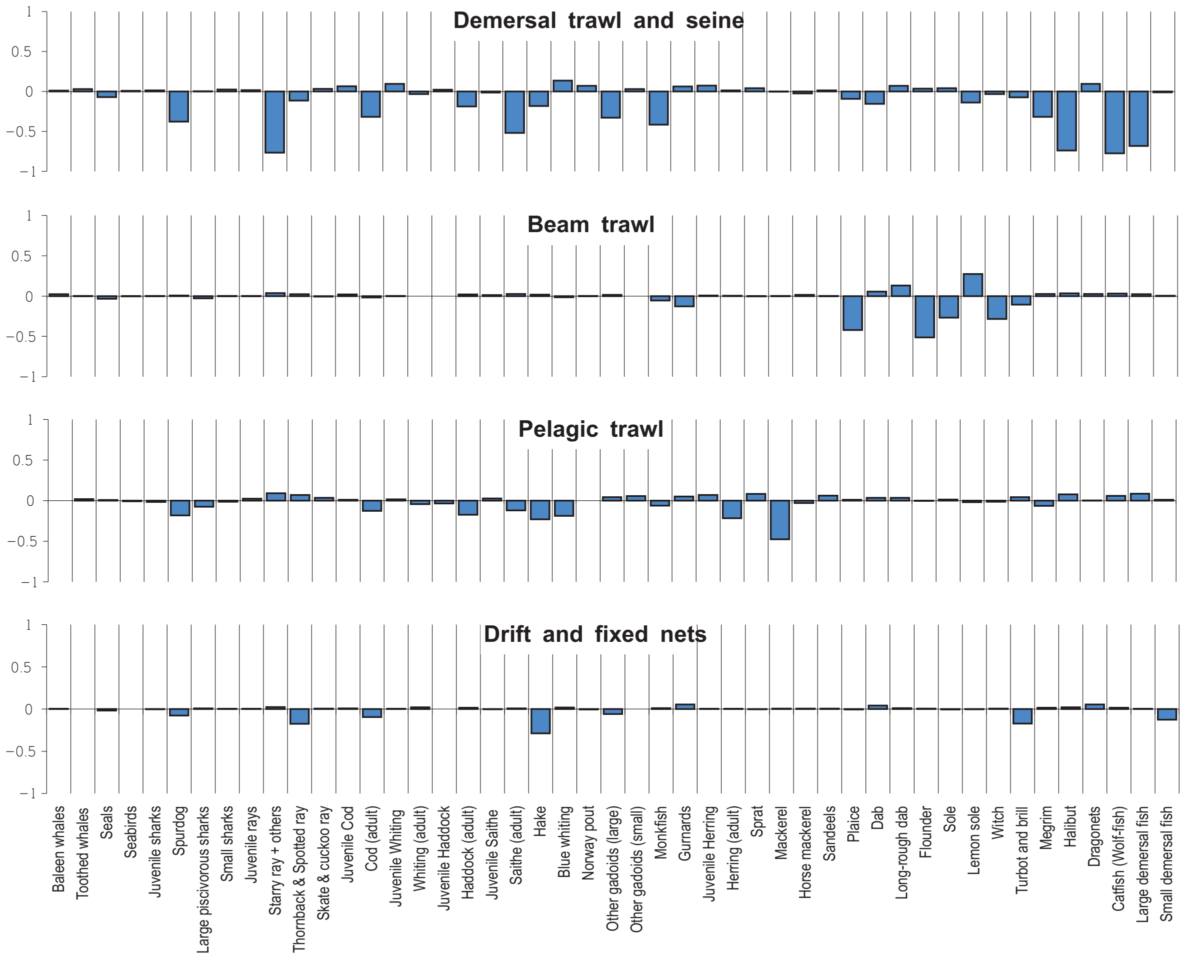


Figure. 3.16. Mixed trophic impacts of selected fishing gears.

maturity can be affected by fishing on different targets and resultant direct and indirect effects. Thus, system indices can be used to account for ecosystem effects of fisheries as well as effects of the environment (eg ocean climate).

Biomass (B) is probably the indicator most used in population and ecosystem science. It is an essential piece of information used in deriving many other indices such as consumption, production, assimilation, respiration and efficiencies estimated by ratios between them. Primary and secondary production (P), and fish production (recruitment) are influenced by bottom-up effects on productivity (eg enrichment, Bakun, 1996). Recruitment may also be controlled by predators or cannibalism. Indirect cultivation/depensation effects of predatory fish on their own offspring, by eliminating prey competing the same ecological niche, is reported by Walters and Kitchell (2001). Consumption (Q), assimilation (A) and respiration (R) are indicators of decomposition of organic matter. Sums of these indicators over the whole web can be used as system indicators e.g. $\sum B$, $\sum Q$, $\sum P$, $\sum R$. The total biomass is an index of ecosystem maturity according to Odum (1969) and is proportional to exergy defined as a measure of free energy of the system (Christensen, 1995). The total respiration is an index of activity of the system (Christensen *et al.*, 2001). Total flow to detritus is an index of cycling and maturity (Christensen *et al.*, 2001). It is high in immature and perturbed systems (dominance of bottom-up processes) and tends to be lower in mature systems. Throughput is the sum of all imports and exports, consumption, respiratory flows, and flows into detritus to and from each group – it is a measure of ecosystem size (Ulanowicz, 1986). Throughput and biomass are expected to increase as the system matures and grows. Utilization of primary production and detritus are measures of nutrient conservation, they are higher in mature systems (Christensen and Pauly, 1998). Fisheries' gross efficiency (catch/PP) is higher in systems fished low in the food web and low in systems fished higher in the food web (Christensen *et al.*, 2001). Primary production/respiration (Pp/R), and primary production/biomass (Pp/B) relate to the community energetic attributes of ecosystem maturity. In the early stages of ecosystem development primary production (Pp) is expected to exceed respiration (R) - Pp/R will be greater than 1. As the system matures the ratio is expected to move towards unity. Given that respiration is expected to be less than primary production in developing systems, it follows that biomass will accumulate as the system matures. Consequently, the

Pp/B ratio is expected to be high and diminish as the system matures. System trophic complexity also relates to ecosystem maturity. Odum (1969) postulated that ecosystems would develop from linear to complex food webs. The connectance index (CI) and system omnivory index (SOI) can be used as indicators of food web complexity. Connectance index measures the percentage of realized links over the number of possible links and the system omnivory is an index of trophic specialisation showing how feeding interactions are distributed between trophic levels (Christensen 1995; Christensen and Pauly 1998). Finn's cycling index - measured as a fraction of the system's throughput recycled, and path length - average number of groups that the flow passes through, are indces of ecosystem maturity, stability, resilience (Vasconcelollos *et al.*, 1997; Christensen 1995). Mean trophic level of catch is related to Odum's size and life cycles attributes of maturity. The catch/primary production (Y/P) ratio is a measure of gross fisheries efficiency, which is expected to increase as fishing is targeting lower down the food webs (Pauly *et al.*, 1998). Other system indicators of maturity are average size of organism (total biomass/total production, Christensen and Pauly, 1998) and Shrodinger ratio (total respiration/total biomass, Christensen and Pauly, 1998). Transfer efficiency between trophic levels is the ratio of the flow entering a trophic level that is subsequently transferred to the next level or harvested. It depends on changes in trophic control food quality and efficiency of feeding (Kozlovsky, 1968; Pauly and Christensen, 1995).

System's ascendancy is a product of throughput times information and accounts for both size and organization. It is a measure of ecosystem efficiency and by definition is higher in mature and complex systems (Ulanowicz, 1986; Vasconcellos *et al.*, 1997). Primary production required (PPR) is the energy to support consumption or catches. PPR is an index of the ecosystem efficiency similar to H. T. Odum's notion of ''emergy'' (Pauly and Christensen, 1995). Considerable uncertainty (consequently with heavy assumptions) still exists about the trophic structure of the lower part of most Ecopath models with implications for PPR estimates. More details on various ecosystem indicators and their application in fisheries management are given in Cury *et al.* (2006).

In Table 3.8 the system indicators from the North Sea model were compared to other UK marine ecosystems: English Channel (Stanford and Pitcher, 2000), Western English Channel model (Araujo *et al.*, 2005), and Irish Sea (Lees and Mackinson, 2007). The values of many 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 extent and dominance of predator groups. On the other hand the productivity indicators (eg, 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).

System indicators are heavily dependent on the model's structure and complexity. Throughput is affected by user defined detritus fate, model size, and complexity. 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. Primary production are dependent on model structure, eg, unlike the Irish Sea and Channel models, the North Sea model does not include primary production from seaweed and hence net Pp is considerably lower and ratio metrics using net Pp are not directly comparable. Indices of system trophic complexity are dependent on the detail and complexity of the diet matrix. Prior to making detailed between system comparison, Ecopath models should be calibrated in terms of structure (eg Moloney *et al.*, 2005).

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3.5 Sensitivity to impact

Sensitivity analysis in Ecopath (*sensu* Majkowski, 1982) works by altering basic input parameters: Biomass, P/B, Q/B, EE in steps from – 50% to + 50% to check what would be the effect on parameter estimated by Ecopath eg, EE, Biomass, P/B, or Q/B. The output is given as: (Estimated parameter - original parameter) / original parameter. An increase/decrease in either biomass or P/B of a group results in inverse change (decrease/increase), but increase/decrease in Q/B results in parallel change (increase/decrease) in the estimated parameter eg EE of the same group.

The sensitivity of estimated parameters of other groups to changes in the input parameters depends on the trophic linkages between those groups. Estimated parameters are more sensitive to changes in input parameters, where predation pressure is largely from a single group. The sensitivity analysis suggests that parameterisation of groups within the model is most sensitive to decreases in biomass and P/B estimates and that the impact of changes in the parameters of one group on another is influenced by the trophic dependency of the impacting on the impacted group.

Sensitivity analysis can be used to indicate food web interactions and as such is complimentary and comparable with other approaches used here such as mixed trophic impacts (MTI), niche overlap and selectivity indices. On Table 3.7 we show the highest sensitivity values of selected FGs corresponding to increase/decrease of an input parameter (biomass or EE) of 50% in different FGs. The changes observed in the estimated parameter (EE or biomass) can be interpreted as possible biotic (predation/competition) interactions between FGs. For instance, changes in biomass of whiting induce important changes in estimated EE of juvenile herring, sprat and horse mackerel, that can be interpreted as predatory effects; sensitivity of juvenile saithe, gurnards and juvenile herring - changes in biomass of horse mackerel – mostly competition effects (these species share their main food resources). Predation and competition for food could be the explanation of the high sensitivity of various dominantly planktivorous FGs such as juvenile gadoids, sprat and gelatinous plankton to changes in EE of FG 51 carnivorous zooplankton (Table 3.7).

4. Testing model stability using Ecosim

Author: Steven Mackinson

Ecosim parameterisation and evaluation of model dynamics

Ecosim is a dynamic trophic model structured from the mass-balance assessment carried out with Ecopath. Ecosim provides dynamic biomass predictions of each group as affected directly by fishing and predation, changes in available food, and indirectly by fishing or predation on other groups with which a group interacts (Walters *et al*., 1997; Christensen *et al*., 2000). (See Appendix 1 for further details).

Ecosim requires additional parameters to those already specified in Ecopath. These parameters define the linkages between juvenile and adult stages, the strength of predator-prey interactions (vulnerability), trophic mediations, time forcing functions and assumptions about changes in growth rates and how foraging time and time at risk to predation changes with feeding opportunities (see Christensen *et al*. 2000 for full descriptions)).

4.1 Ecosim parameterisation – stage 1: Adult-juveniles groups and stability testing

Ecosim parameters used to define linkages between adults and their respective juvenile groups are given in Table 4.1.

During basic testing of the model behaviour vulnerability was treated as a sensitivity parameter. Section 4.4 describes how vulnerability settings were parameterised through time series fitting.

Evaluation of basic model dynamics

Testing the basic dynamic behaviour of the North Sea model and refinement of Ecosim parameters was carried by evaluating the stability of the model when moved away from the equilibrium state described by Ecopath. As stated by Christensen *et al*. (2000), this type of parameterization of Ecosim aims at 'rescuing' the mass interaction model constructed in Ecopath by adding behaviour factors to the predator-prey relationships. In this process, parameter adjustments are made to adult-juvenile linkages, feeding time factors and prey vulnerabilities in order to eliminate four general types of instabilities commonly observed following model perturbations (Christensen *et al*., 2000): 1) predator-prey cycles and related multi-trophic level patterns; 2) system simplification (loss of biomass pools due to competition/predation effects); 3) stock-recruitment instabilities (cyclic or erratic changes in recruitment and stock size for split pool groups); 4) numerical 'chatter' in time solutions. Among the parameters described above, prey vulnerabilities have the most influence on overall model stability.

To examine the persistence of functional groups, we disturbed the system by applying a decrease in total fishing effort (Figure 4.1), examined how fast the system returned to an equilibrium state and checked if the response rates of groups were as might be expected. The system returned to equilibrium by year 45. Monkfish, adult saithe, other large gadoids, catfish and adult cod responded dramatically to the reduction in fishing. This is because fishing mortality accounts for a large proportion of the total mortality of these groups.

Closing all fisheries and running the simulation over a longer time period allowed us to investigate these responses in more detail (Figure 4.2). The recovery trajectories for many groups appeared qualitatively and quantitatively reasonable. For example, the recovery of Baleen whales was notably slow as we would expect. While the overall behaviour of the predicted responses was stable, for those groups where fishing mortality accounted for the majority of the explained mortality, the predicted increases in biomass appeared unrealistic. This prompted us to reconsider the P/B rates and sources of mortality for adult saithe, cod, monkfish, other large gadoids and catfish. From the data used to parameterise the diet matrix, we reconfirmed that adult saithe were only eaten by seals, monkfish eaten by themselves and skates and rays; cod only eaten by seal, itself and monkfish, and catfish only eaten by gurnards (probably as juveniles). Extending the scale of the plot (Figure 4.2(b)) we saw that the increase in adult cod was checked by predation from monkfish. The biomass trajectories of adult saithe and monkfish were still considered too far out; the problem being that they have high fishing mortality and very little other mortality (ie P/B nearly equals F). We consulted with other scientists regarding any evidence that might be used to better account for the total mortality. It was generally agreed that this behaviour was unreasonable but we had no other evidence to improve the parameters. It was decided that the best solution was to reduce the proportion of Z (P/B) accounted for by F. This was achieved by increasing the biomass of the groups in Ecopath, which resulted in F (C/B) decreasing. Increases in biomass were made only to the extent that they did not impact other groups and unbalance the model. The result was a less dramatic response to the fishery closure, but we still had some concerns about the fishing mortality of saithe being too high and the productivity being unrealistic. To prevent this, we assumed that small amounts of saithe are eaten by toothed whales, piscivorous sharks, themselves, seals and other large gadoids. The results are shown in Figure 4.2(c).

Table 4.1. Data for parameterising linked adult and juvenile groups in Ecosim. Values in bold are those used as initial input to Ecosim. Values in brackets are those set after testing. Data from MSVPA, 2005; Jennings *et al.*, 1997; Coull *et al.*, 1989.

	Cod	Whiting	Haddock	Saithe	Herring
Biological parameters					
Age at recruitment	2	2	2	3	2
W maturity (weight at recruitment) (kg)	1.03	0.18	0.27	0.89	0.12
L inf					
w inf (kg)	14.86	0.63	2.53	8.82	0.27
B adult (000t)	377	491	781	497	1022
Z adult	1.02	1.13	1.19	0.70	0.84
Z juvenile	1.27	1.53	1.96	0.25	0.90
QB adult	3.50	5.46	4.40	3.60	4.34
K	0.23	0.32	0.19	0.07	0.38
Lmaturity (cm)	69.7	20.2	33.5	55.4	24
Linf (cm)	123.1	42.4	68.3	177.1	30
a	0.0175	0.0093	0.0157	0.0238	0.00603
b	2.8571	2.9456	2.8268	2.7374	3.0904
Wmat (kg)	3.23	0.07	0.32	1.41	0.11
Winf (kg)	16.41	0.58	2.41	33.95	0.22
Wmat/Winf	0.20	0.11	0.13	0.04	0.50
Ecosim model parameters					
Min time as Juvenile	2	1	2	2	1
Max time as Juvenile	5	3	3	5	3
Min. time as juv. (rel. to orig. setting)	**0.40 [1]**	**0.33 [1]**	**0.67 [1]**	**0.40 [1]**	**0.33 [1]**
Max. time as juv. (rel. to orig. setting)	**2.50 [1.0001]**	**1.50 [1.0001]**	**1.50 [1.0001]**	**1.67 [1.0001]**	**1.50 [1.0001]**
Recruitment power parameter	1	1	1	1	1
Weight (g) at transition to adult group	1035	181	267	885	115
Age (year) at transition to adult group (tk)	2	2	2	3	2
Mean weight of adult (g)	6315	321	619	1820	183
Wavg / Wk (Av. adult weight / weight at transition)	**6.10**	**1.77**	**2.32**	**2.06**	**1.59**
K of the VBGF (/year)	**0.23**	**0.32**	**0.19**	**0.07**	**0.38**
Base fraction of food intake used for reproduction (default)	**0.5**	**0.5**	**0.5**	**0.5**	**0.5**
Fraction of increase in food intake used for growth (default)	**0.8**	**0.8**	**0.8**	**0.8**	**0.8**

Note: Base fraction of food intake used for reproduction is set as the default of 0.5. The fraction of increase in food intake used for growth' (default 0.8). These two parameters jointly determine how food intake is turned into reproductive products, as implied from the theory in Walters *et al.*, 1997. It has implications for the shape of SR relationship.

When we included feeding time factors and effects of predators on feeding time, and re-ran the simulation at different levels of vulnerability we found that at vulnerabilities above 3 the dynamics became unstable (Figure 4.3(a)). We investigated a combination of vulnerability and feeding time factor settings before finding a stable combination. Feeding time factors for top predators were set to 0.1 (predation mortality risks are probably very low for these groups, therefore feeding time ought to remain constant). All other piscivores and seabirds were assigned a feeding time factor of 0.5, and all mid and low trophic level fish, squids and mobile benthic invertebrates were assigned feeding time factors of 1. The assumption being made here is that these groups present strong behavioral mechanisms to decrease predation risks, which is represented in the model by allowing fast feeding time responses to changes in food availability. Planktonic and sessile organisms were assigned a feeding factor of 0. For predator effects on feeding time, the assumption was made that only when fish reach adults would they be prepared to give up feeding when faced with a direct threat from predators. Juveniles are unlikely to have this choice - feeding is critical when

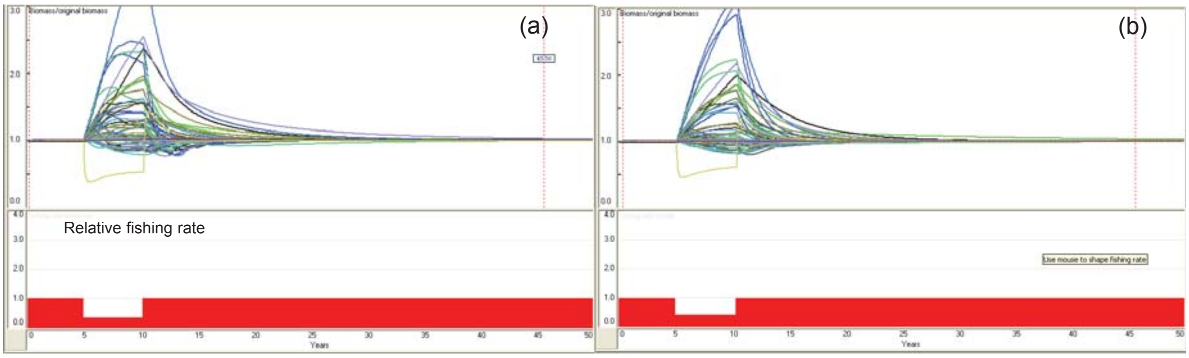
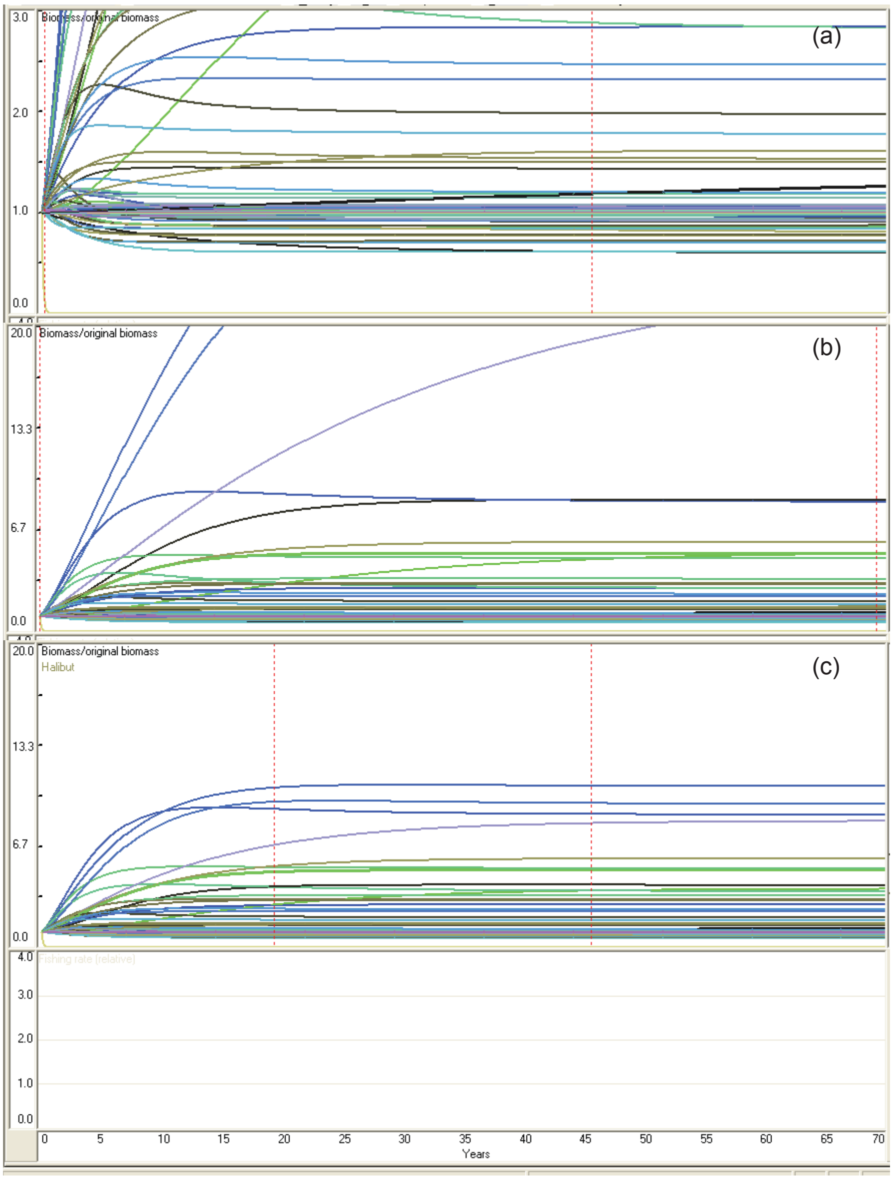


Figure 4.1. Impacts of small disturbance, default vulnerability = 2. (a) with adult linkages on (b) with adult linkages off.

Figure 4.2. Impact of stopping fishing for all gears, v=2 (a) vertical scale =3x, (b) vertical scale =20x, (c) with corrections made, 20 times scale.



survival depends on size. Predator swamping is a more common predation defence tactic used by larvae and juveniles. Top predators are assumed to feed independently of risk and so assigned a value of 0, otherwise adult fish = 1 and juvenile fish = 0 under the rationale that they are not afraid of predators and have to keep feeding. This also ensures compensatory responses were evident in stock-recruitment relationships. Other groups and benthos were assigned a value of 0.5.

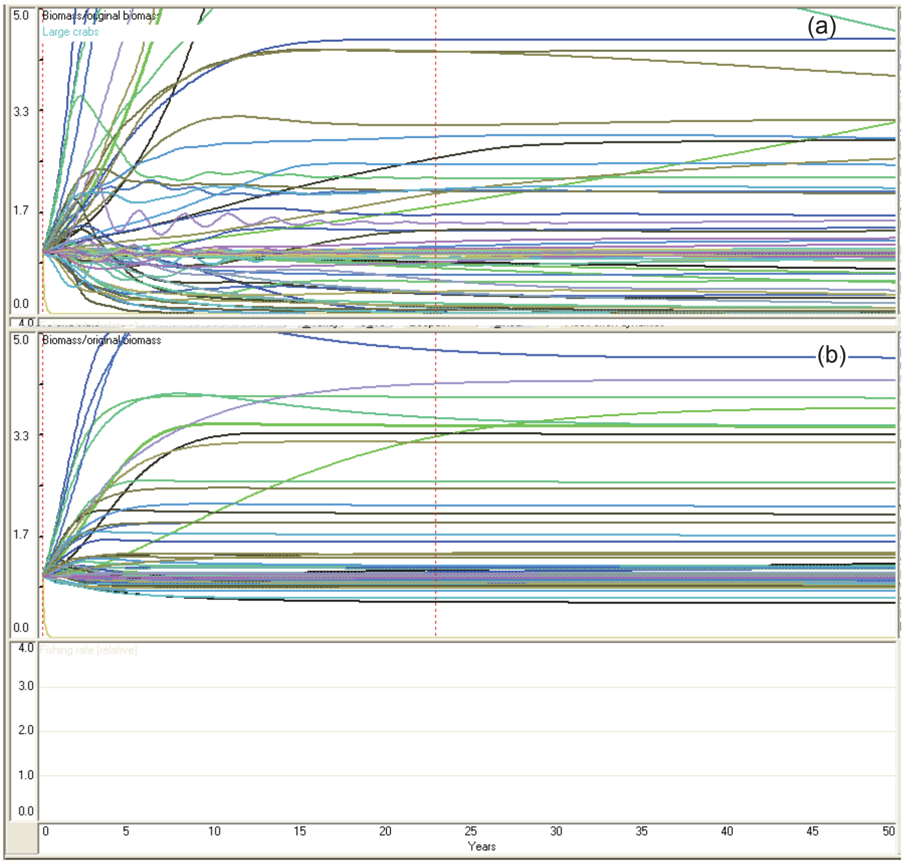
Adjustments were also made to the fraction of unexplained (other) mortality sensitive to changes in feeding time. It was assumed to be 1 for all except planktonic and sessile groups, whose values were set to 0. The result of these changes at v=2 are shown in Figure 4.3(b).

When the adult and juvenile links were turned back on, erratic cyclical behaviour indicative of stock-recruitment instabilities were detected (Figures 4.1(a) and 4.4). The inclusion of age structure dynamics in Ecosim requires users to think carefully about compensatory processes relating to the 'stock-recruitment' concept. Adult-juvenile linkage parameters need to be set so as to produce ‘emergent’ stock-recruitment (SR) relationships that are at least qualitatively similar to empirical data. In most cases, stock-recruitment relationships tend to 'flat' over a wide range of spawning stock sizes (Myers *et al.*, 1995; www.mscs.dal.ca/~myers/data.html; Walters and Martell, 2005), implying that in general there must be strong compensatory increases in juvenile survival rate as spawning stock declines (Christensen *et al.*, 2000). Stock-recruitment data derived from MSVPA, 2005 (key run) were plotted for the 5 adult-juvenile groups in the model (Figure 4.5). Plots of Beverton-Holt stock-recruit relationships highlight differences in the characteristics between species. An important attribute of the stock-recruitment plots that characterises the strength of compensation (ie at low stock sizes, how much recruitment increases for each unit of stock) is the steepness of the curve from the origin. For the MSVPA data presented here, the compensatory response of cod and herring would be expected to be lower than that of haddock, whiting and saithe.

Christensen *et al.* (2000), detail that at least two initial conditions are needed to eliminate stock-recruitment instabilities and define/create compensatory changes. The juvenile group must have a relatively high P/B rate (total mortality rate) or a relatively high EE (so that most mortality is accounted for as predation effects within the model), otherwise the user must specify a high (near 1.0) value in the Ecosim 'Group Info' Tab entry for the juvenile group’s ‘prop. of other mortality sensitive to changes in feeding time’ column. Both of these conditions were satisfied in the model. To parameterise stock recruitment relationships, we ran a simulation where fishing was switched off for 10 years, then increased gradually over a 60-year period (Figure 4.6(a)). By adjusting the predator effect on feeding time of juveniles to zero (assumes their feeding is not affected by predator presence – have to feed to get bigger) and changing the max and min time as juvenile, the parameters for the adult-juvenile split-groups (Table 4.2) were set so as to produce an 'emergent' Beverton-Holt type stock-recruitment relationships (Figure 4.6(b)). The result was that the instabilities were no longer present (Figure 4.6(c)). In these basic setup tests, we did not try to fine tune between species differences, but consideration of this would be important where the model is being applied to address specific questions.

Finally, we examined the effects of the vulnerability parameter values on model behaviour by simulating a decrease in fishing by all gears for a period of 5 years, followed by an increase back to the baseline fishing mortality (Figure 4.7). The key finding from this is that the high number of food-web connections cause dampening effects resulting in persistence of species and high stability of the responses even when vulnerabilities are set to high values.

Figure 4.3. Effects of including feeding time factors. (a) feeding time factor =1, v=4 (to magnify instabilities) (b) after correction, feeding time factors given in Table 4.2.



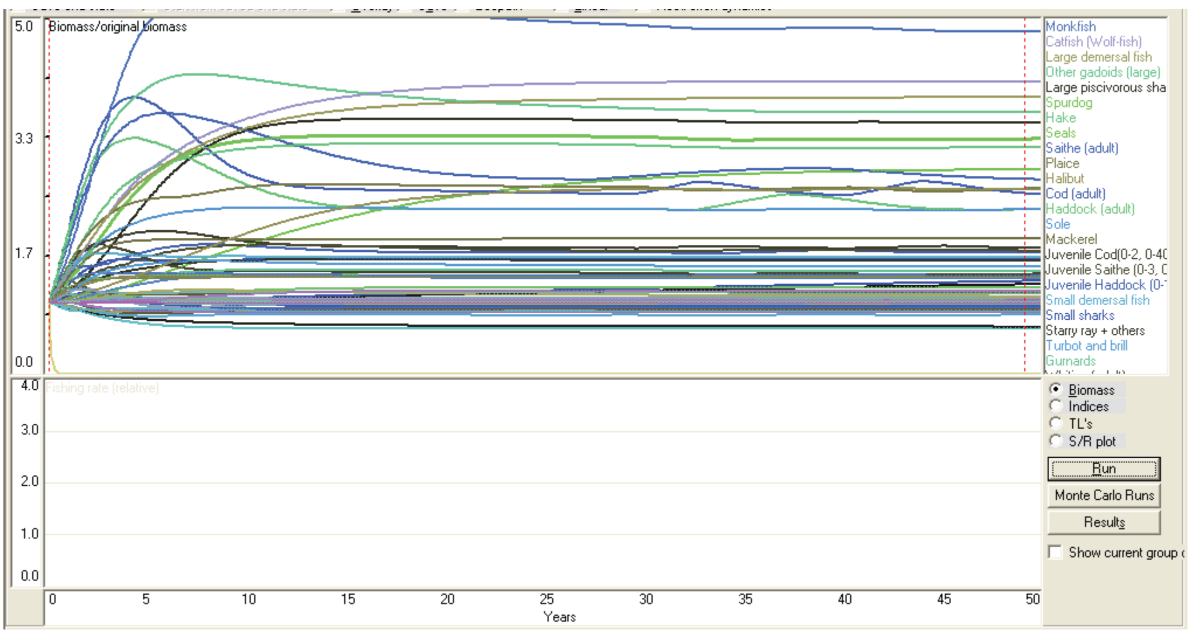


Figure 4.4. Stock-recruitment instabilities.

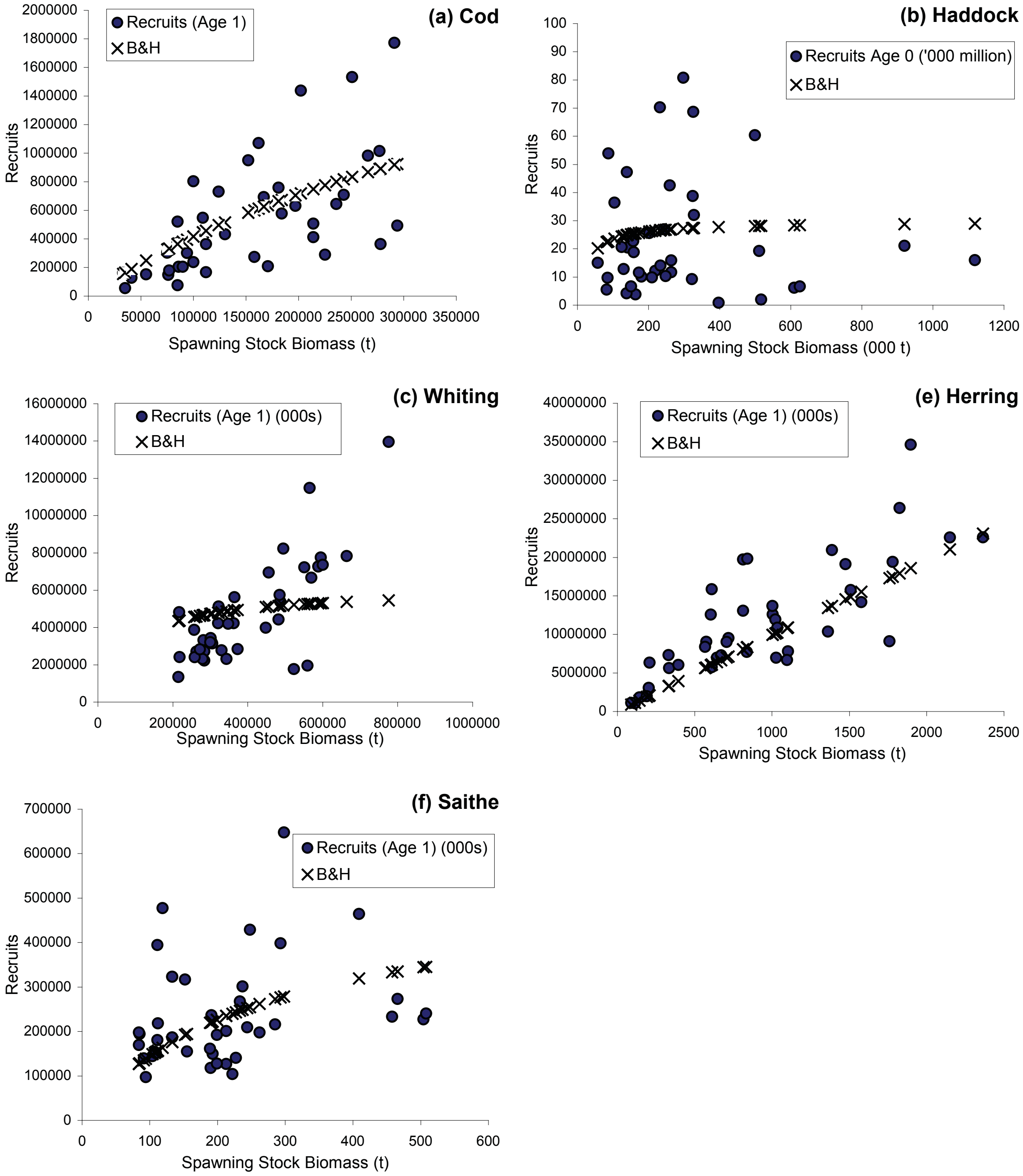


Figure 4.5. Stock-recruitment relationships derived from multi-species stock assessment 2003 for the North Sea.

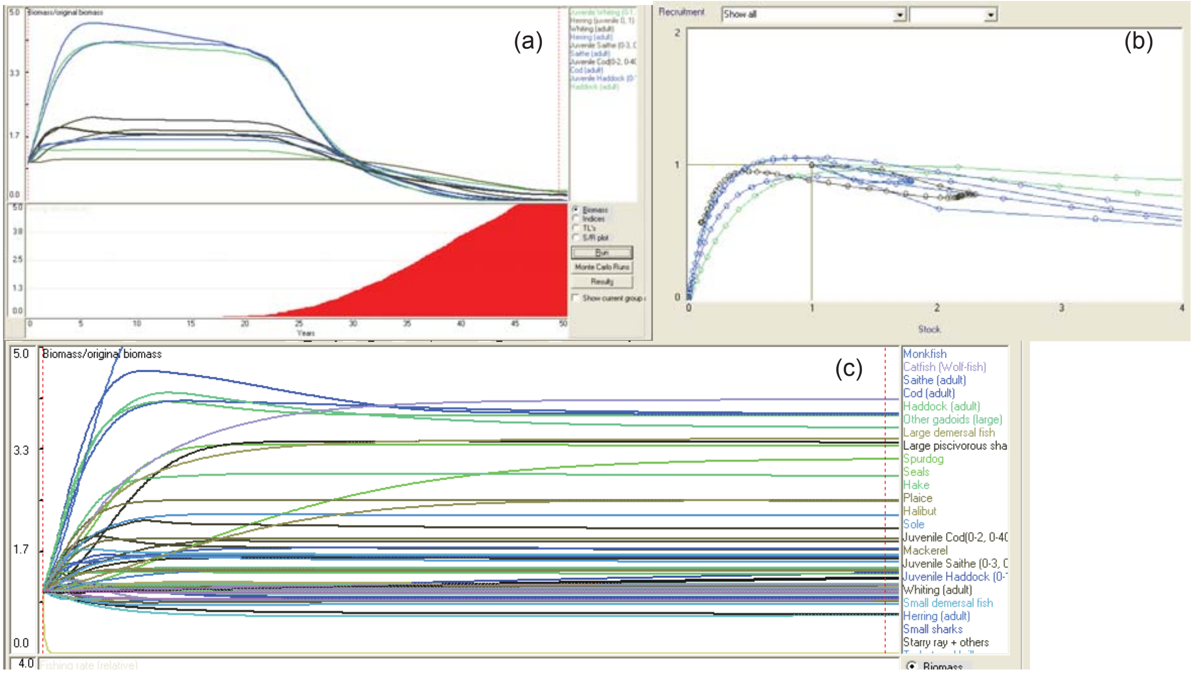


Figure 4.6. Stock-recruitment testing. (a) simulation setup to drive stocks from high to low (b) emergent stock-recruitment patterns (c) shape of response to no fishing scenario when stock-recruitment instabilities fixed.

Table 4.2. Group feeding parameters in ecosim (values used in fitted model).

Adjust rate [0,1]	Max rel. feeding time	Feeding time adjust rate [0,1]	Fraction of 'other' mortality sens. to changes in feeding time	Predator effect on feeding time [0,1]	Density-dep. catchability: Qmax/Qo [>=1]	QBmax/QBo (for handling time) [>1]
Baleen whales	2	0.1	1	0	1	1000
Toothed whales	2	0.1	1	0	1	1000
Seals	2	0.1	1	0	1	1000
Seabirds	2	0.5	1	0	1	1000
Juvenile sharks	2	0.5	1	0.5	1	1000
Spurdog	2	0.1	1	0	1	1000
Large piscivorous sharks	2	0.1	1	0	1	1000
Small sharks	2	0.5	1	1	1	1000
Juvenile rays	2	1	1	0.5	1	1000
Starry ray + others	2	0.1	1	1	1	1000
Thornback & Spotted ray	2	0.1	1	1	1	1000
Skate + cuckoo ray	2	0.1	1	1	1	1000
Juvenile Cod(0–2, 0–40 cm)	2	1	1	0	1	1000
Cod (adult)	2	0.1	1	0	1	1000
Juvenile Whiting (0–1, 0–20 cm)	2	0.2	1	0	1	1000
Whiting (adult)	2	0.5	1	1	1	1000
Juvenile Haddock (0–1, 0–20 cm)	2	0.2	1	0	1	1000
Haddock (adult)	2	0.5	1	1	1	1000
Juvenile Saithe (0–3, 0–40 cm)	2	1	1	0	1	1000
Saithe (adult)	2	0.1	1	0	1	1000
Hake	2	0.1	1	0	1	1000
Blue whiting	2	1	1	1	1	1000
Norway pout	2	1	1	1	1	1000
Other gadoids (large)	2	0.1	1	1	1	1000

Table 4.2. continued: Group feeding parameters in Ecosim (values used in fitted model)

Adjust rate [0,1]	Max rel. feeding time	Feeding time adjust rate [0,1]	Fraction of 'other' mortality sens. to changes in feeding time	Predator effect on feeding time [0,1]	Density-dep. catchability: Qmax/Qo [>=1]	QBmax/QBo (for handling time) [>1]
Other gadoids (small)	2	0.5	1	1	1	1000
Monkfish	2	0.1	1	0	1	1000
Gurnards	2	0.5	1	1	1	1000
Herring (juvenile 0, 1)	2	1	1	0.5	1	1000
Herring (adult)	2	1	1	1	1	1000
Sprat	2	1	1	1	1	1000
Mackerel	2	0.75	1	1	1	1000
Horse mackerel	2	0.75	1	1	1	1000
Sandeels	2	0.2	1	1	1	1000
Plaice	2	1	1	1	1	1000
Dab	2	1	1	1	1	1000
Long-rough dab	2	1	1	1	1	1000
Flounder	2	0.5	1	1	1	1000
Sole	2	1	1	1	1	1000
Lemon sole	2	1	1	1	1	1000
Witch	2	0.5	1	1	1	1000
Turbot and brill	2	0.1	1	0	1	1000
Megrim	2	0.5	1	1	1	1000
Halibut	2	0.1	1	0	1	1000
Dragonets	2	0.5	1	1	1	1000
Catfish (Wolf-fish)	2	0.1	1	0	1	1000
Large demersal fish	2	0.5	1	1	1	1000
Small demersal fish	2	1	1	1	1	1000
Miscellaneous filterfeeding pelagic fish	2	1	1	0.5	1	1000
Squid & cuttlefish	2	1	1	0.5	1	1000
Fish larvae	2	0.5	1	0	1	1000
Carnivorous zooplankton	2	1	1	0.5	1	1000
Herbivorous & Omnivorous zooplankton (copepods)	2	1	1	0.5	1	1000
Gelatinous zooplankton	2	1	1	0.5	1	1000
Large crabs	2	1	1	0.5	1	1000
Nephrops	2	1	1	0.5	1	1000
Epifaunal macrobenthos (mobile grazers)	2	1	1	0.5	1	1000
Infaunal macrobenthos	2	1	1	0.5	1	1000
Shrimp	2	1	1	0.5	1	1000
Small mobile epifauna (swarming crustaceans)	2	1	1	0.5	1	1000
Small infauna (polychaetes)	2	1	1	0.5	1	1000
Sessile epifauna	2	0	0	0	1	1000
Meiofauna	2	0	0	0	1	1000
Benthic microflora (incl. Bacteria, protozoa))	2	0	0	0	1	1000
Planktonic microflora (incl. Bacteria, protozoa)	2	0	0	0	1	1000

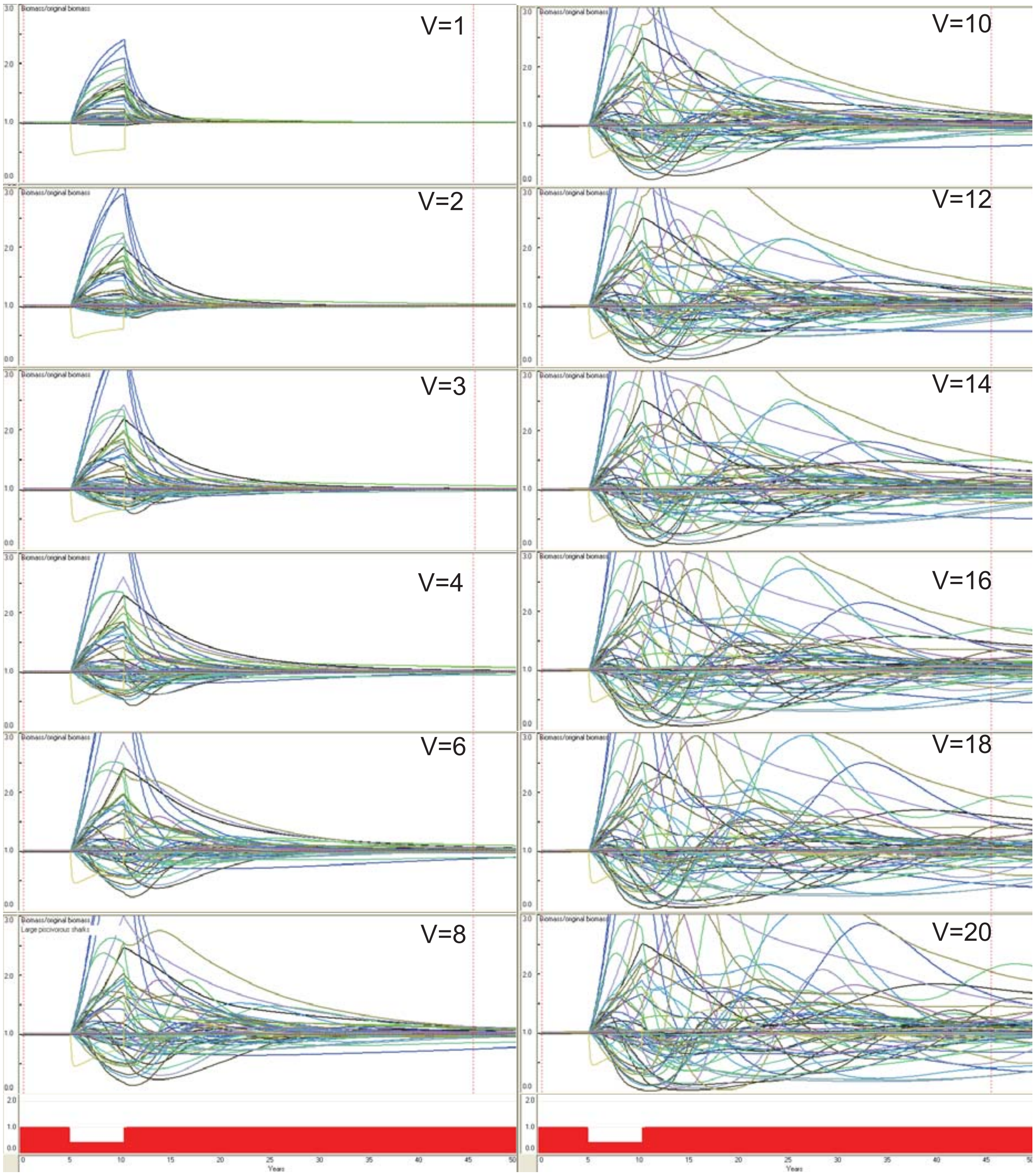


Figure 4.7. Examining the sensitivity to global vulnerability settings.

4.2 Ecosim paramterisation – stage 2: Estimating vuleenerbilities by time-series fitting

CAUTION. For the results presented here, the main source of time series data on the fishing mortality and relative biomasses groups are derived from MSVPA (2005 key run, WGMSNS, 2005), with the exception for fishing effort. This means that the model is being calibrated against another model. During subsequent refinements, the fitting process will be performed with single species assessment data and survey data from ICES International Bottom Trawl Surveys.

Time series fitting was used to estimate the vulnerability (v) of each prey species to its predators. The process is a lengthy iterative procedure that uses optimisation algorithms to improve the goodness of fit between model predictions and observed data by making adjustments to the vulnerability parameters.

Time series data – and its use in calibrating the model

During time series fitting, ‘observation’ data are used for two purposes (i) to drive the changes in the model, (ii) to provide a history of the changes in the biomass (absolute, or relative) against which the models predictions are compared for each parameterisation (Figure 4.8).

Data used to drive the North Sea model were of three types:

1. Fishing effort (made relative to the base year) from logbooks and fishing mortality time series derived from stock assessments. The fishing effort is applied to a fleet, which is translated in Ecosim to a partial F on each species by partitioning the total fishing mortality assigned to each species according to the catch composition of each fleet specified in Ecopath. Where direct information on the time series of F for a species is also available, this overwrites a relative F calculated from the fishing effort data. Time series data on effort were derived from ICES assessment working groups, whilst fishing mortalities were taken from MSVPA outputs. It is also possible to use catch forcing in model fitting, but this was not necessary because of the wealth of data on fishing effort and F.

2. Environmental data used to drive changes in the primary production. To identifying which environmental time series data best accounted for observed changes in production in the lower trophic levels in the North Sea model we collated environmental time series data on NAOI, GSI, temperature and phytoplankton colour index and examined the correlations with herbivorous and carnivorous zooplankton biomass (data from CPR, SAHFOS – uncorrected and corrected (Pitois and Fox, 2006) (Figure 4.9). The time series trends of herbivorous zooplankton were best explained by a 4 year running average of the NAOI for 1991-2003 and a 3 year running average of the Phytoplankton Colour Index for 1973-2003. There were strong cross correlations between parameters. Table 4.3 shows the results of correlation analysis and trends in relationships supporting the choice of environmental time series used in fitting the model. Where correlations are negative, inverse time series are used in the fitting procedure.

3. Biomass time series used to force changes in the biomass of functional groups. In the model we obtained biomass time series data for zooplankton groups from the CPR data. The time series trends were translated from relative to absolute biomass by scaling the time series to the biomass used in the Ecopath model. Direct biomass forcing was applied to herbivorous zooplankton and also on horse mackerel (on the basis that these enter the North Sea periodically from the South).

During model fitting we included a mediation function by jellyfish, which represented evidence that juvenile gadoids are protected from predators by aggregating under jellyfish umbrellas (Lynam and Brierly, 2007).

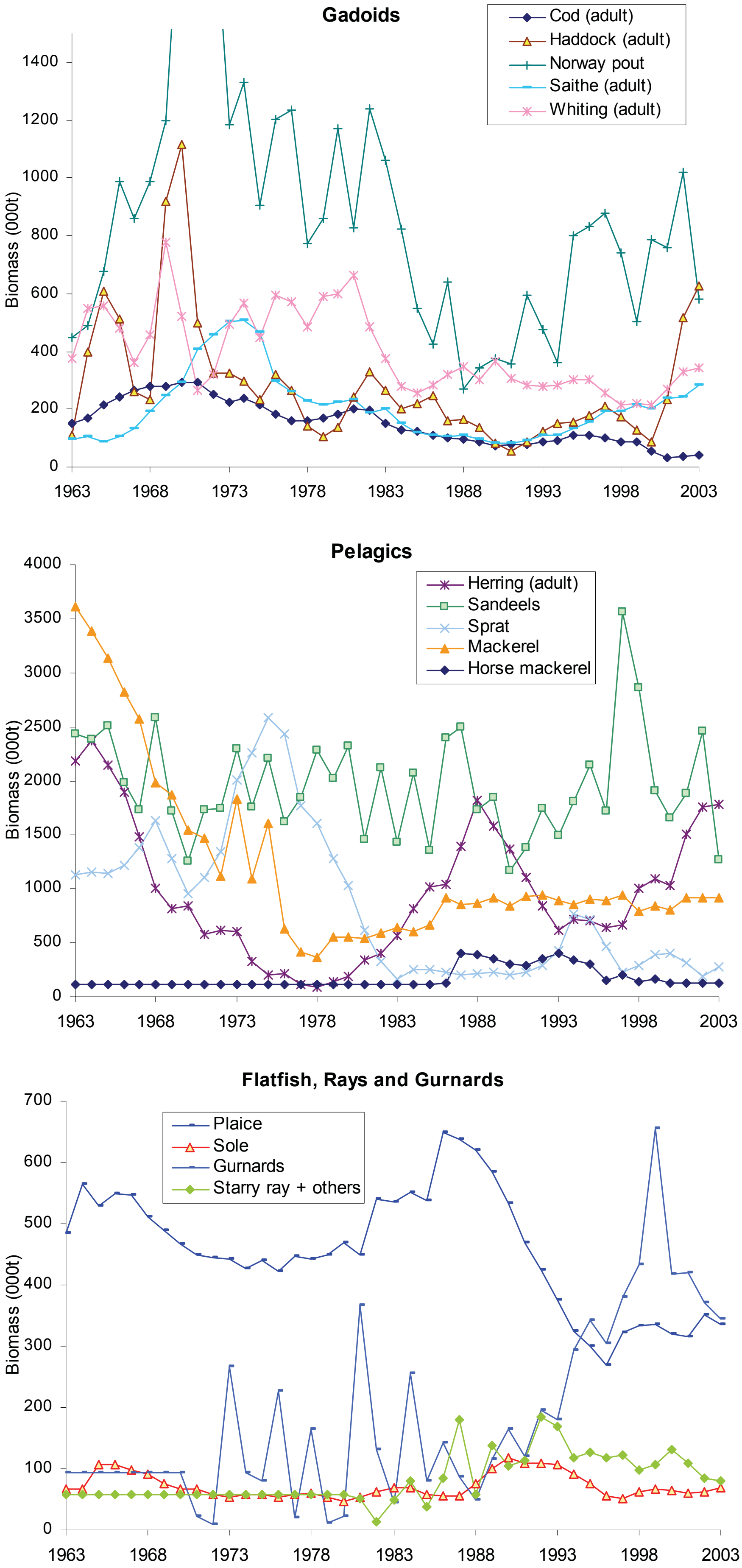
Strategy and procedure for fitting

We used the data and knowledge on long-term trends in abundance of fish stocks and the relationships between environmental parameters and phytoplankton and zooplankton to help guide our approach to model fitting. Initial values for vulnerabilities were assigned based on reasoning and information pertaining to:
(i) how far species were considered to be away from their carry capacity (by comparison of the recent biomass data with 1880s data, Figure 4.10), (ii) the relative contribution of fishing to their total mortality, (iii) how important they are as a consumer in the system and, (iv) their position in the food web in relation to how influential bottom-up changes in primary and secondary production might be expected to be on their dynamics. We reasoned that species whose biomass was far from carry capacity would be able to exert higher mortality on their prey (i.e. a higher v applied by predator), that juvenile fish, other zooplanktivores and invertebrates feeding at low trophic levels, ought to be more resource controlled (low v's), and intermediate groups would exhibit mixed control. As a first step we also ran the 'sensitivity to vulnerabilities' test to examine for which species, changes in vulnerability were mostly likely to have largest impacts on the goodness of fit. During the fitting procedure we used the optimisation routine to search for improved estimates of vulnerability for those species that we had good time series data for (i.e. mostly the MSVPA species) or were identified as being particularly sensitive. Vulnerabilities for other groups were left at the initial values.

Fitting the models

Fitting the 1973 and 1991 models was performed in a stepwise fashion so that we could investigate the relative influence of fishing and environmental factors on explaining past changes in relative abundance for each of the groups. This was a lengthy, iterative process. For both the models we found the best overall fits (to all groups, as opposed to the best for a single group) was derived by using a combination of fishing and environmental drivers (Figure 4.11, Table 4.4). Vulnerability matrices for the fitted models are given in Tables 5.5 and 5.6.

Figure 4.8. Fish biomass trends predicted by MSVPA 2005 key run.



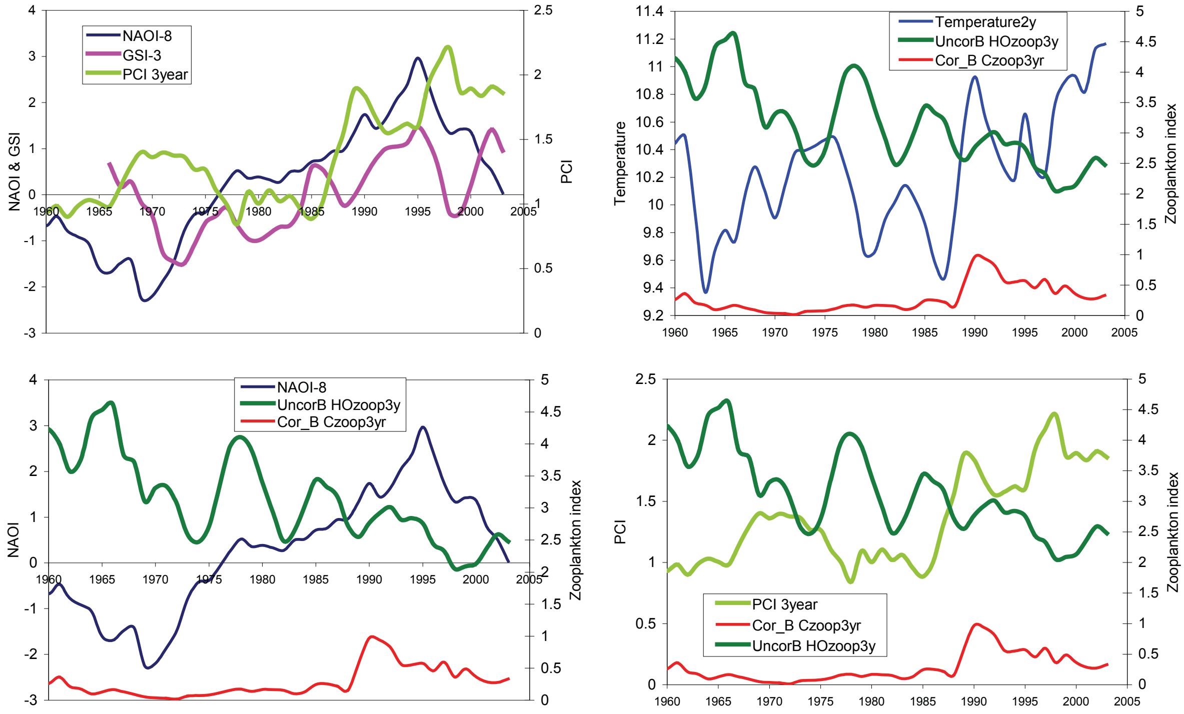


Figure 4.9. Selected time series of environmental parameters and trends in phytoplankton and zooplankton indices in the North Sea. Time series are smoothed using running averages UncorB HO zoop: Uncorrected biomass of herbivorous zooplankton. CorB Czoop: Corrected biomass of carnivorous zooplankton. Biomass corrected zooplankton data supplied by Pitois (Cefas).

Table 4.3. Correlation analysis of environmental parameters and phytoplankton and zooplankton indices. The information is used to help select parameters for time series fitting the 1991 and 1973 models. For brevity – only the best correlations are shown.

	NAOI-4	GSI-3	PCI 3year	Temperature2y	UncorB HOzoop3y	Cor_B Czoop3yr
Time series: 1991–2003						
NAOI-4	1					
GSI-3	0.62	1				
PCI 3year	-0.83	-0.57	1			
Temperature2y	-0.51	-0.19	0.25	1		
UncorB HOzoop3y	0.88	0.74	**-0.84**	-0.39	1	
Cor_B Czoop3yr	0.68	0.11	-0.54	-0.52	0.66	1
Time series 1973–2003						
NAOI-10	1					
GSI-9	0.85	1				
PCI 3year	0.72	0.88	1			
Temperature2y	0.34	0.59	0.69	1		
UncorB HOzoop3y	-0.43	-0.61	**-0.73**	**-0.6**	1	
Cor_B Czoop3yr	0.77	0.67	0.61	0.4	-0.23	1

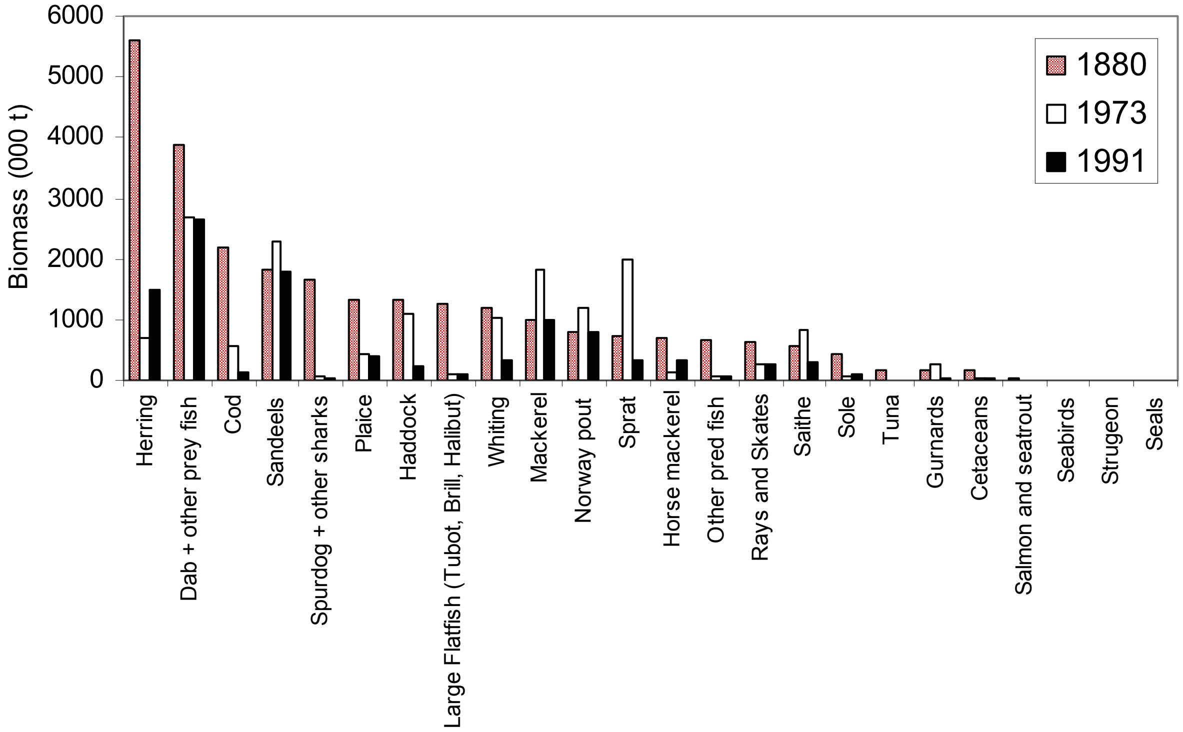


Figure 4.10. Comparison of historical biomasses with recent biomasses – used to help initialise starting vulnerablities.

Table 4.4. Model run set up for best fitting models 1991 and 1973.

1991 fitted model setup	1973 fitted model setup
Tuned vulnerabilities (see Table 5.5)	Tuned vulnerabilities (see Table 5.6)
Forcing function: NAOI 4yr average	Forcing function: inverse PCI 3yr average
Fishing mortalities from MSVPA and relative fishing effort data for fleets from ICES working groups	Fishing mortalities from MSVPA and relative fishing effort data for fleets from ICES working groups
Mediation with jelly fish negative slope applied across to juv whiting, cod, haddock, Norway pout	Mediation with jelly fish negative slope applied across to juv whiting, cod, haddock, Norway pout
Biomass forced horse mackerel	Biomass forced Carn zoops
Biomass forced Herb zoops	

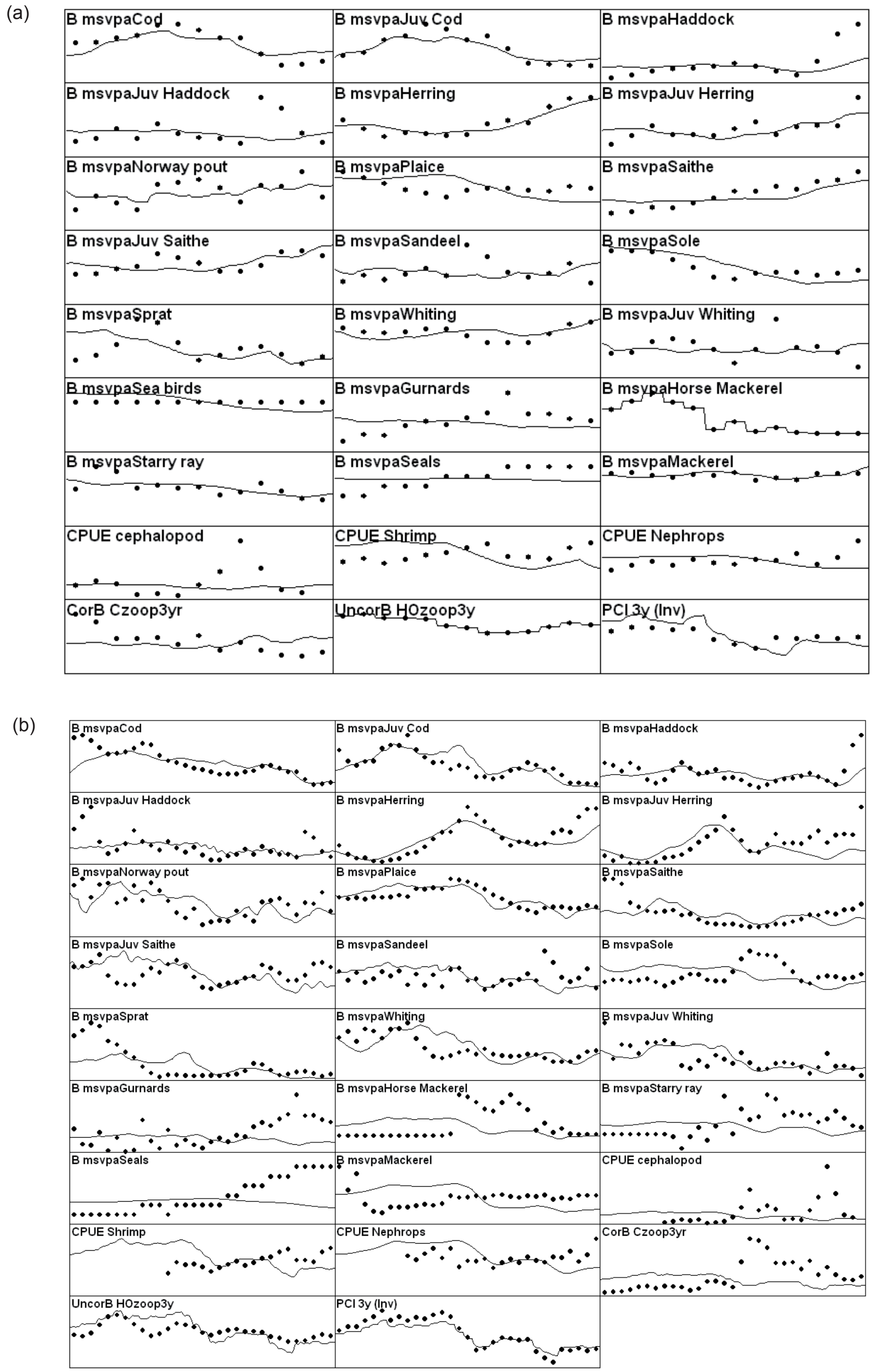


Figure 4.11. (a) North Sea 1991 model fit to time series data from MSVPA 2005 keyrun. Time axis covers period 1991-2003; (b) North Sea 1973 model fit to time series data from MSVPA 2005 keyrun. Time axis covers period 1973–2003.

Cautionary notes on fitting

The model fits produced here, present a global overall goodness of fit to the MSVPA time series data only. It will be important to fit the model to data from fisheries independent surveys and single species data. Trying to fit model predictions for many groups results in making compromises. If we were to fit the model to fewer groups, then the fits could be improved and thus we advise strongly that the model should be tailor fit to specific data depending on the purpose of the application. To enable a more satisfactory evaluation of the role that fishing and environmental forcing plays in explaining the fits, requires that the sums of squares for the fit of each groups is calculated and that consideration is given to how many parameters are estimated. One of the worrisome findings from our correlation analysis used to determine which environmental drivers to incorporate was that the nature of the correlations appears to have changed over time (See Table 4.3). This has important consequences for the choices and compromises that need to be made when fitting the model. It shows the importance of first conducting exploratory analyses of the relationships between drivers and biomass trends, and points clearly at the need to be cautious when developing scenarios for future simulations. We advise that when the model is fitted to alternative relative biomass data, the use of forcing functions to drive production of lower trophic levels should be guided by robust analysis of trends in environmental and biological data.

Table 4.5. Vulnerability matrix for the fitted 1991 model.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Baleen whales	1																																		
Toothed whales	2																																		
Seals	3																																		
Seabirds	4																																		
Juvenile sharks	5							3																											
Spurdog	6						3	3							6																				
Large piscivorous sharks	7																																		
Small sharks	8							3																											
Juvenile rays	9							3			3				6												4	1.5							
Starry ray + others	10																																		
Thornback & Spotted ray	11																																		
Skate	12																																		
Juvenile Cod(0–2, 0–40cm)	13		2	3	3					2	3			4	6	1.1	3		6						3		4	1.5				1.5	1.2		
Cod (adult)	14			3											6												4								
Juvenile Whiting (0–1, 0–20cm)	15	2	2	3	3	2	3		2		3	3	3	4	6	1.1	3			2	6	3			3	2	4	1.5				1.5	1.2		
Whiting (adult)	16		2	3		2	3		2		3				6		3				6						4								
Juvenile Haddock (0–1, 0–20cm)	17		2	3	3		3				3	3	3	4	6	1.1	3		6	2	6				3		4	1.5					1.2		
Haddock (adult)	18		2	3			3								6						6						4								
Juvenile Saithe (0–3, 0–40cm)	19		2	3													3										4	1.5					1.2		
Saithe (adult)	20		2	3																					3										
Hake	21		2										3									3					4								
Blue whiting	22		2			2	3		2				3		6						6	3			3			1.5				1.5	1.2		
Norway pout	23	2	2			2	3	3	2	2	3	3	3	4	6	1.1	3	1	6	2	6	3	2		3	2	4	1.5				1.5	1.2		
Other gadoids (large)	24		2	3															6						3										
Other gadoids (small)	25		2	3	3	2	3	3	2	2	3	3	3	4	6	1.1	3	1	6	2	6	3			3	2		1.5				1.5	1.2		
Monkfish	26			3									3														4								
Gurnards	27							3	2		3		3	4	6		3	1			6	3						1.5					1.2		
Herring (juvenile 0, 1)	28	2	2	3	3	2	3	3			3	3	3	4	6	1.1	3		6	2	6	3			3		4	1.5				1.5	1.2		3
Herring (adult)	29		2	3	3	2	3	3	2		3			4	6						6				3		4								
Sprat	30	2	2	3	3	2	3		2	2	3	3		4	6	1.1	3		6	2	6	3	2			2	4	1.5				1.5	1.2		
Mackerel	31	2	2		3	2	3	3	2						6						6	3					4	1.5							
Horse mackerel	32		2	3	3		3							4	6	1.1	3					3						1.5				1.5			
Sandeels	33	2	2	3	3	2	3		2	2	3	3	3	4	6	1.1	3	1	6	2	6				3	2	4	1.5				1.5	1.2		3
Plaice	34			3			3	3	2			3		4	6				6								4	1.5							

Table 4.5. continued: Vulnerability matrix for the fitted 1991 model.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Dab	35			3		2	3	3	2	2	3		3	4	6	1.1	3		6		6					2	4	1.5							
Long-rough dab	36		2	3					2	2	3		3	4	6	1.1	3	1	6		6				3		4	1.5							
Flounder	37			3											6																				
Sole	38			3					2		3	3	3	4	6	1.1	3	1	6																3
Lemon sole	39			3																							4								
Witch	40			3			3				3		3	4	6				6								4	1.5							
Turbot and brill	41			3																															
Megrim	42			3																							4								
Halibut	43										3																								
Dragonets	44		2	3		2	3	3	2		3		3	4	6		3	1	6							2	4	1.5							
Catfish (Wolf-fish)	45																																		
Large demersal fish	46										3		3		6		3		6		6														
Small demersal fish	47		2	3		2	3	3	2	2	3	3	3	4	6	1.1	3	1	6		6	3			3	2	4	1.5				1.5	1.2		
Miscellaneous filterfeeding pelagic fish	48	2				2			2					4		1.1	3		6	2	6	3	2				4	1.5				1.5			
Squid & cuttlefish	49	2	2			2	3	3	2	2	3	3	3	4	6	1.1	3	1	6	2	6	3			3	2	4	1.5				1.5			
Fish Larvae	50																																1.2		
Carnivorous zooplankton	51	2			3	2	3		2	2	3	3	3	4	6	1.1	3	1	6	2	6		2	1.1	3	2		1.5	2.1	4		1.5	1.2	1.5	
Herbivorous & Omnivorous zooplankton (copepods)	52				3									4		1.1		1		2	6		2	1.1	3	2			2.1	4	2.2	1.5		1.5	
Gelatinous zooplankton	53	2				2	3								6																				3
Large crabs	54					2	3		2	2	3	3	3	4	6	1.1	3	1	6			3			3	2		1.5							3
Nephrops	55					2	3		2				3	4	6		3	1	6							2	4	1.5					1.2		
Epifaunal macrobenthos (mobile grazers)	56					2	3	3	2	2	3	3	3	4	6	1.1	3	1	6	2	6	3	2			2	4	1.5				1.5		1.5	3
Infaunal macrobenthos	57					2	3		2	2	3	3	3	4	6	1.1	3	1	6	2				1.1		2		1.5				1.5	1.2	1.5	3
Shrimp	58					2	3		2	2	3	3	3	4	6	1.1	3	1	6	2	6	3	2		3	2		1.5				1.5			3
Small mobile epifauna (swarming crustaceans)	59					2			2	2	3	3	3	4	6	1.1	3	1	6	2	6			1.1	3	2		1.5	2.1	4		1.5		1.5	3
Small infauna (polychaetes)	60					2	3		2	2	3	3	3	4	6	1.1	3	1	6	2	6		2		3	2		1.5				1.5		1.5	3
Sessile epifauna	61					2			2					4	6		3	1	6													1.5			3
Meiofauna	62					2			2	2								1	6															1.5	3
Benthic microflora (incl. Bacteria, protozoa))	63																																		
Planktonic microflora (incl. Bacteria, protozoa)	64																														2.2	1.5	1.2	1.5	
Phytoplankton	65																														2.2			1.5	
Detritus - DOM -water column	66																																		
Detritus - POM - sediment	67																																		
Discards	68				3																														

Table 4.5. continued: Vulnerability matrix for the fitted 1991 model.

		35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Baleen whales	1																														
Toothed whales	2																														
Seals	3																														
Seabirds	4																														
Juvenile sharks	5																														
Spurdog	6																														
Large piscivorous sharks	7																														
Small sharks	8																														
Juvenile rays	9																														
Starry ray + others	10																														
Thornback & Spotted ray	11																														
Skate	12																														
Juvenile Cod(0–2, 0–40cm)	13							3								2															
Cod (adult)	14																														
Juvenile Whiting (0–1, 0–20cm)	15		2					3		3						2															
Whiting (adult)	16																														
Juvenile Haddock (0–1, 0–20cm)	17									3						2															
Haddock (adult)	18																														
Juvenile Saithe (0–3, 0–40cm)	19															2															
Saithe (adult)	20																														
Hake	21																														
Blue whiting	22								3				3			2															
Norway pout	23		2	2				3	3	3						2															
Other gadoids (large)	24																														
Other gadoids (small)	25		2					3	3	3			3																		
Monkfish	26																														
Gurnards	27								3					2																	
Herring (juvenile 0, 1)	28							3						2		2															
Herring (adult)	29																														
Sprat	30							3	3	3			3	2		2															
Mackerel	31																														
Horse mackerel	32												3			2															
Sandeels	33		2					3	3	3			3	2		2															
Plaice	34															2															

Table 4.5. continued: Vulnerability matrix for the fitted 1991 model.

		35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
Dab	35		2	2				3					3	2		2															
Long-rough dab	36			2												2															
Flounder	37															2															
Sole	38													2		2															
Lemon sole	39			2												2															
Witch	40															2															
Turbot and brill	41																														
Megrim	42																														
Halibut	43																														
Dragonets	44							3	3				3	2																	
Catfish (Wolf-fish)	45																														
Large demersal fish	46												3																		
Small demersal fish	47		2	2	1.5	2	3	3	3				3	2		2															
Miscellaneous filterfeeding pelagic fish	48								3				3		2	2															
Squid & cuttlefish	49		2							3			3	2	2	2				1											
Fish Larvae	50															2		1		1											
Carnivorous zooplankton	51			2								3	3	2	2	2		1		1					1.5						
Herbivorous & Omnivorous zooplankton (copepods)	52	2							3		2		3	2	2	2	2	1		1					1.5						
Gelatinous zooplankton	53			2									3		2																
Large crabs	54	2	2	2					3	3	2	3		2							1.5										
Nephrops	55		2	2																	1.5										
Epifaunal macrobenthos (mobile grazers)	56	2	2	2	1.5	2	3	3	3	3	2	3	3	2	2						1.5		1.5								
Infaunal macrobenthos	57	2	2	2	1.5	2	3	3			2	3	3	2							1.5	1.5	1.5								
Shrimp	58	2	2	2				3	3	3	2	3	3	2	2	2				1	1.5				1.5						
Small mobile epifauna (swarming crustaceans)	59	2	2	2					3		2		3	2	2	2		1		1	1.5	1.5	1.5	1.5	1.5	1.5					
Small infauna (polychaetes)	60	2	2		1.5	2	3				2	3	3	2	2	2					1.5	1.5	1.5	1.5	1.5		1.5				
Sessile epifauna	61	2		2		2	3						3								1.5	1.5									
Meiofauna	62	2			1.5						2		3	2										1.5	1.5	1.5	1.5		1.5		
Benthic microflora (incl. Bacteria, protozoa))	63																				1.5	1.5	1.5	1.5	1.5	1.5	1.5		1.5	1.0	1.0
Planktonic microflora (incl. Bacteria, protozoa)	64																	1	1	1	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5		1.0	1.0
Phytoplankton	65															2	2		1	1		1.5	1.5					1.5			
Detritus - DOM -water column	66																		1			1.5	1.5	1.5	1.5	1.5	1.5			1.0	1.0
Detritus - POM - sediment	67																					1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.0	1.0
Discards	68																				1.5				1.5						

Table 4.6. Vulnerability matrix for the fitted 1973 model.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Baleen whales	1																																		
Toothed whales	2																																		
Seals	3																																		
Seabirds	4																																		
Juvenile sharks	5							2																											
Spurdog	6						2	2							6																				
Large piscivorous sharks	7																																		
Small sharks	8							2																											
Juvenile rays	9							2			1				6												5	1							
Starry ray + others	10																																		
Thornback & Spotted ray	11																																		
Skate + cuckoo ray	12																																		
Juvenile Cod(0–2, 0–40cm)	13		1.5	2	2					2	1			2.2	6	2.6	5		20		2.7				2		5	1				1.88	1		
Cod (adult)	14			2											6												5								
Juvenile Whiting (0–1, 0–20cm)	15	1.2	1.5	2	2	2	2		2		1	2	2	2.2	6	2.6	5			1	2.7	1.2			2	2	5	1				1.88	1		
Whiting (adult)	16		1.5	2		2	2		2		1				6		5				2.7						5								
Juvenile Haddock (0–1, 0–20cm)	17		1.5	2	2		2				1	2	2	2.2	6	2.6	5		20	1	2.7				2		5	1				1.88	1		
Haddock (adult)	18		1.5	2			2								6						2.7						5								
Juvenile Saithe (0–3, 0–40cm)	19		1.5	2													5										5	1					1		
Saithe (adult)	20		1.5	2																					2										
Hake	21		1.5										2									1.2					5								
Blue whiting	22		1.5			2	2		2				2		6						2.7	1.2			2			1				1.88	1		
Norway pout	23	1.2	1.5			2	2	2	2	2	1	2	2	2.2	6	2.6	5	1.01	20	1	2.7	1.2	1.2		2	2	5	1				1.88	1		
Other gadoids (large)	24		1.5	2															20						2										
Other gadoids (small)	25		1.5	2	2	2	2	2	2	2	1	2	2	2.2	6	2.6	5	1.01	20	1	2.7	1.2			2	2		1				1.88	1		
Monkfish	26			2									2														5								
Gurnards	27							2	2		1		2	2.2	6		5	1.01			2.7	1.2						1					1		
Herring (juvenile 0, 1)	28	1.2	1.5	2	2	2	2	2			1	2	2	2.2	6	2.6	5		20	1	2.7	1.2			2		5	1				1.88	1		1
Herring (adult)	29		1.5	2	2	2	2	2	2		1			2.2	6						2.7				2		5								
Sprat	30	1.2	1.5	2	2	2	2		2	2	1	2		2.2	6	2.6	5		20	1	2.7	1.2	1.2		2	2	5	1				1.88	1		
Mackerel	31	1.2	1.5		2	2	2	2	2						6						2.7	1.2			2		5	1							
Horse mackerel	32		1.5	2	2		2							2.2	6	2.6	5					1.2						1				1.88			
Sandeels	33	1.2	1.5	2	2	2	2		2	2	1	2	2	2.2	6	2.6	5	1.01	20	1	2.7				2	2	5	1				1.88	1		1
Plaice	34			2			2	2	2			2		2.2	6				20								5	1							

Table 4.6. continued: Vulnerability matrix for the fitted 1973 model.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Dab	35			2		2	2	2	2	2	1		2	2.2	6	2.6	5		20		2.7					2	5	1							
Long-rough dab	36		1.5	2					2	2	1		2	2.2	6	2.6	5	1.01	20		2.7				2		5	1							
Flounder	37			2											6																				
Sole	38			2					2		1	2	2	2.2	6	2.6	5	1.01	20																1
Lemon sole	39			2										2.2	6	2.6											5								
Witch	40			2			2				1		2	2.2	6				20								5	1							
Turbot and brill	41			2																															
Megrim	42			2																							5								
Halibut	43										1																								
Dragonets	44		1.5	2		2	2	2	2		1		2	2.2	6		5	1.01	20							2	5	1							
Catfish (Wolf-fish)	45																																		
Large demersal fish	46										1		2		6		5		20		2.7														
Small demersal fish	47		1.5	2		2	2	2	2	2	1	2	2	2.2	6	2.6	5	1.01	20		2.7	1.2			2	2	5	1				1.88	1		
Miscellaneous filterfeeding pelagic fish	48	1.2				2			2					2.2		2.6	5		20	1	2.7	1.2	1.2				5	1				1.88			
Squid & cuttlefish	49	1.2	1.5			2	2	2	2	2	1	2	2	2.2	6	2.6	5	1.01	20	1	2.7	1.2			2	2	5	1				1.88			
Fish larvae	50																																		
Carnivorous zooplankton	51	1.2			2	2	2		2	2	1	2	2	2.2	6	2.6	5	1.01	20	1	2.7		1.2	1.25	2	2		1	5	20		1.88	1	1	
Herbivorous & Omnivorous zooplankton (copepods)	52				2									2.2		2.6		1.01		1	2.7		1.2	1.25	2	2			5	20	1.7	1.88	1	1	
Gelatinous zooplankton	53	1.2				2	2								6																				1
Large crabs	54					2	2		2	2	1	2	2	2.2	6	2.6	5	1.01	20			1.2			2	2		1							1
Nephrops	55					2	2		2				2	2.2	6		5	1.01	20							2	5	1							
Epifaunal macrobenthos (mobile grazers)	56					2	2	2	2	2	1	2	2	2.2	6	2.6	5	1.01	20	1	2.7	1.2	1.2			2	5	1				1.88	1	1	1
Infaunal macrobenthos	57					2	2		2	2	1	2	2	2.2	6	2.6	5	1.01	20	1				1.25		2		1				1.88		1	1
Shrimp	58					2	2		2	2	1	2	2	2.2	6	2.6	5	1.01	20	1	2.7	1.2	1.2		2	2		1				1.88	1		1
Small mobile epifauna (swarming crustaceans)	59					2			2	2	1	2	2	2.2	6	2.6	5	1.01	20	1	2.7			1.25	2	2		1	5	20		1.88		1	1
Small infauna (polychaetes)	60					2	2		2	2	1	2	2	2.2	6	2.6	5	1.01	20	1	2.7		1.2		2	2		1				1.88		1	1
Sessile epifauna	61					2			2					2.2	6		5	1.01	20													1.88			1
Meiofauna	62					2			2	2								1.01	20															1	1
Benthic microflora (incl. Bacteria, protozoa))	63																																		
Planktonic microflora (incl. Bacteria, protozoa)	64																														1.7	1.88		1	
Phytoplankton	65																														1.7		1	1	
Detritus - DOM -water column	66																																		
Detritus - POM - sediment	67																																		
Discards	68				2																														

Table 4.6. continued: Vulnerability matrix for the fitted 1973 model.

		35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65
Baleen whales	1																															
Toothed whales	2																															
Seals	3																															
Seabirds	4																															
Juvenile sharks	5																															
Spurdog	6																															
Large piscivorous sharks	7																															
Small sharks	8																															
Juvenile rays	9																															
Starry ray + others	10																															
Thornback & Spotted ray	11																															
Skate + cuckoo ray	12																															
Juvenile Cod(0–2, 0–40cm)	13							3								1.2																
Cod (adult)	14																															
Juvenile Whiting (0–1, 0–20cm)	15		2					3		2						1.2																
Whiting (adult)	16																															
Juvenile Haddock (0–1, 0–20cm)	17			2						2						1.2																
Haddock (adult)	18																															
Juvenile Saithe (0–3, 0–40cm)	19			2												1.2																
Saithe (adult)	20																															
Hake	21																															
Blue whiting	22								2				2			1.2																
Norway pout	23		2	2				3	2	2						1.2																
Other gadoids (large)	24																															
Other gadoids (small)	25		2					3	2	2			2																			
Monkfish	26																															
Gurnards	27								2					2																		
Herring (juvenile 0, 1)	28							3						2		1.2																
Herring (adult)	29																															
Sprat	30							3	2	2			2	2		1.2																
Mackerel	31																															
Horse mackerel	32												2			1.2																
Sandeels	33		2					3	2	2			2	2		1.2																
Plaice	34															1.2																

Table 4.6. continued: Vulnerability matrix for the fitted 1973 model.

		35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65
Dab	35		2	2				3					2	2		1.2																
Long-rough dab	36			2												1.2																
Flounder	37															1.2																
Sole	38													2		1.2																
Lemon sole	39			2												1.2																
Witch	40															1.2																
Turbot and brill	41																															
Megrim	42																															
Halibut	43																															
Dragonets	44							3	2				2	2																		
Catfish (Wolf-fish)	45																															
Large demersal fish	46												2																			
Small demersal fish	47		2	2	1.01	2	2	3	2				2	2		1.2																
Miscellaneous filterfeeding pelagic fish	48								2				2		1.2	1.2																
Squid & cuttlefish	49		2							2			2	2	1.2	1.2				1.2												
Fish larvae	50															1.2		1		1.2												
Carnivorous zooplankton	51											2	2	2	1.2	1.2		1		1.2					1							
Herbivorous & Omnivorous zooplankton (copepods)	52	2		2					2		2		2	2	1.2	1.2	1.2	1		1.2					1							
Gelatinous zooplankton	53												2		1.2																	
Large crabs	54	2	2	2					2	2	2	2		2							1.2											
Nephrops	55		2	2																	1.2											
Epifaunal macrobenthos (mobile grazers)	56	2	2	2	1.01	2	2	3	2	2	2	2	2	2	1.2						1.2		1.2									
Infaunal macrobenthos	57	2	2	2	1.01	2	2	3			2	2	2	2							1.2	1	1.2									
Shrimp	58	2	2	2				3	2	2	2	2	2	2	1.2	1.2				1.2	1.2				1							
Small mobile epifauna (swarming crustaceans)	59	2	2	2					2		2		2	2	1.2	1.2		1		1.2	1.2	1	1.2	1.2	1	1.2						
Small infauna (polychaetes)	60	2	2	2	1.01	2	2				2	2	2	2	1.2	1.2					1.2	1	1.2	1.2	1		1.2					
Sessile epifauna	61	2				2	2						2								1.2	1										
Meiofauna	62	2		2	1.01						2		2	2										1.2	1	1.2	1.2	1.2				
Benthic microflora (incl. Bacteria, protozoa))	63																				1.2	1	1.2	1.2	1	1.2	1.2	1.2	1.2	1.2		
Planktonic microflora (incl. Bacteria, protozoa)	64																	1	1	1.2	1.2	1	1.2	1.2	1	1.2	1.2		1.2	1.2	1.2	
Phytoplankton	65															1.2	1.2		1	1.2		1	1.2								1.2	2
Detritus - DOM -water column	66																		1			1	1.2	1.2	1	1.2	1.2	1.2	1.2	1.2		
Detritus - POM - sediment	67																					1	1.2	1.2	1	1.2	1.2	1.2	1.2	1.2	1.2	1.2
Discards	68																				1.2				1							

5. Ecospace parameterisation

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Building on Ecopath with Ecosim, Ecospace (Walters et al.1998) is a spatially explicit model developed in response to the recognition that the major deficiency of the EwE approach was the assumption of homogenous distribution (Christensen et al. 2004). Essentially a spatial version of Ecosim, Ecospace was originally conceived as a device for predicting distributions of ecosystem components (Christensen et al. 2000) and for policy evaluation (Pauly et al. 2000).

While Ecospace relies on the Ecopath mass-balance approach for most of its parameterisation, it uses a cell-based format (cell size determined by the user) to describe the two-dimensional, spatial distribution of species under the influence of biotic and abiotic factors. Inputs include: (i) movement rates of fauna (used to calculate changes in species distribution) (ii) the vulnerability settings (top-down vs. bottom-up control) required for Ecosim (iii) habitat preferences (the influences of physical variables on spatial distribution of a species) (iv) spatial distribution of fishing effort and (v) vulnerability to predators in the various specified habitats (Walters et al. 1998).

Habitats in Ecospace are defined as sets of water cells sharing features affecting the movements, feeding rate and survival of the groups occurring therein (Christensen et al. 2000). Essentially they are habitat parameters linked to the distribution of the faunal groups included in the model. Such 'habitats' may include depth, temperature, sediment type, etc. These habitats from the Ecospace 'basemap', to which functional groups are assigned to habitats based on knowledge of requirements and observations of their main distribution areas.

5.1 Basemap and species habitat assignments

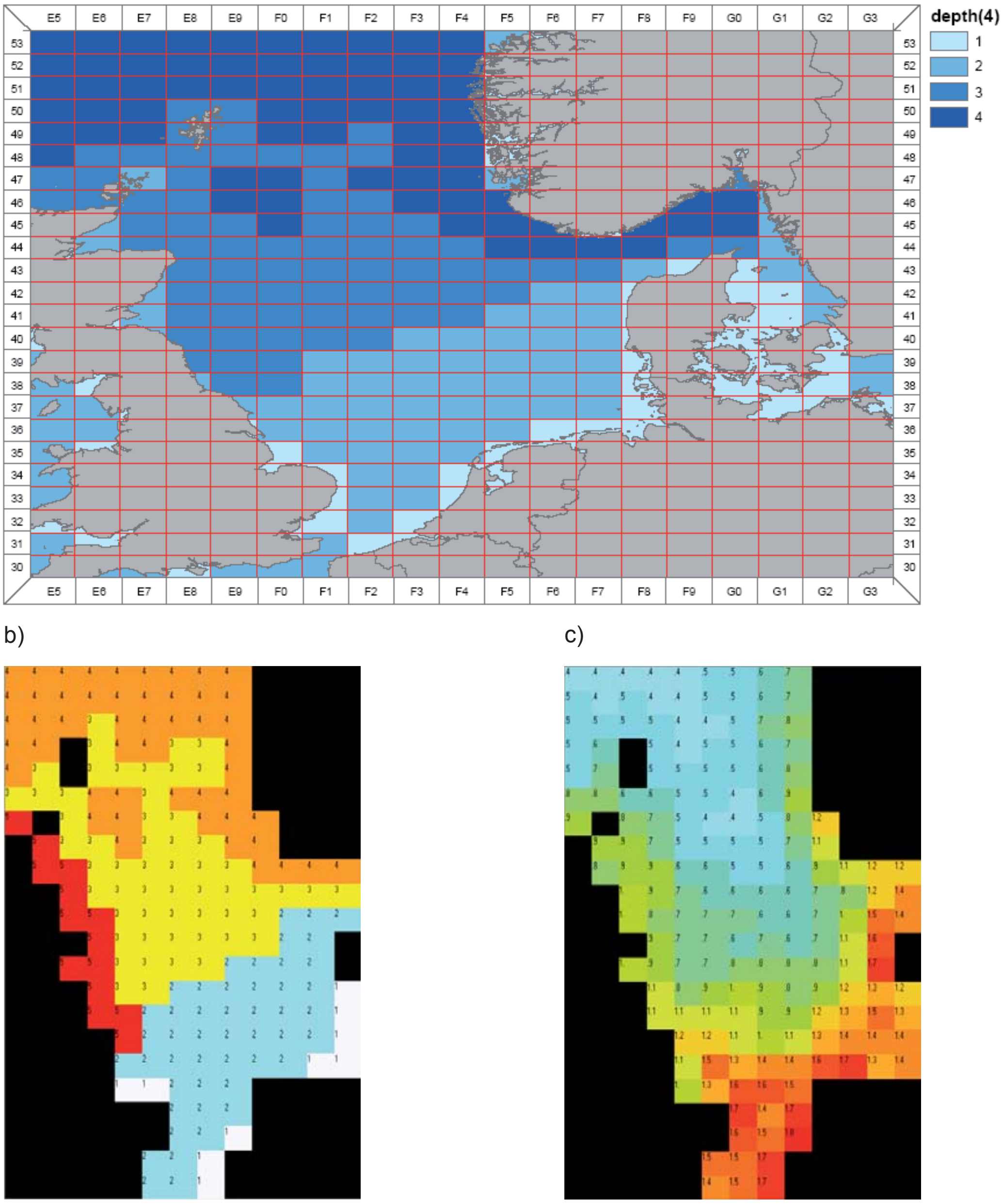
The basemap may either be imported (from a dedicated server), depending on its availability, or manually set up. Whilst the boundaries and resolution of an imported map are defined by lat-long co-ordinates and specifying a resolution (in minutes), those of a manually built map may be defined by entering the number of cells in rows and columns, followed by the cell length (in km). The cells in the North Sea Ecospace basemap were defined to match ICES rectangles (Figure 5.1a), because the empirical fish density from the IBTS was estimated at this resolution.

Once the area and resolution of a manually built map has been defined, the basemap is then used to show land and water areas further defining boundaries for modelling. The distinction between land and water cells also influences the movement of groups between areas, which needs considering since movements in Ecospace may only take place between cell boundaries and not across diagonals.

In the North Sea model, a range of habitat basemaps were developed using temperature, stratification, depth and sediment. Comparison of the habitat maps with the distribution of fish recorded from the IBTS surveyed indicated that the simplest division of habitat could be achieved using 4 depth categories only (Figure 5.1a). During model testing, it was later found to be necessary to create an additional coastal habitat (Figure 5.1b) to reflect the distribution of species in this particular area. The distribution of relative production was taken from SeaWifs data (Figure 5.1 c).

Figure 5.1 Representation of Ecospace 'habitats' defined by depth classes 1: 0-25m,
2: 25-50m,
3: 50-100m,
4: 100+).
A. Depth map with ICES rectangles, B. Basemap including 'habitats' and land areas in Ecospace.
C. Relative primary production based on SeaWifs data

a)



b)

c)

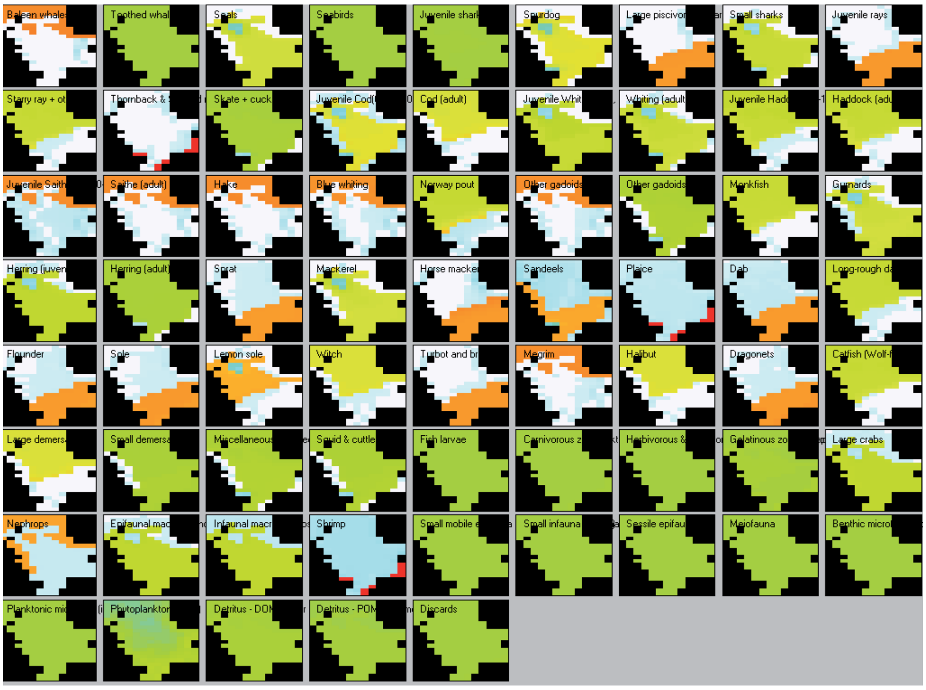
Table 5.1 Assigning functional groups to 'habitats'. Habitats are assigned simply by clicking on the relevant cells.

Group \ Habitat #	All habitats (e	‹22m	22-51m	52-115m	›115m	Coast
Baleen whales					+	
Toothed whales	+					
Seals		+	+	+		+
Seabirds	+					
Juvenile sharks	+					
Spurdog		+	+	+		
Large piscivorous sharks		+	+	+		
Small sharks		+	+	+		+
Juvenile rays		+	+			+
Starry ray + others			+	+	+	
Thornback & Spotted ray		+	+			+
Skate + cuckoo ray		+	+	+	+	+
Juvenile Cod(0-2, 0-40cm)			+	+		+
Cod (adult)		+	+	+	+	
Juvenile Whiting (0-1, 0-20cm)		+	+	+		+
Whiting (adult)			+	+		+
Juvenile Haddock (0-1, 0-20cm)				+	+	+
Haddock (adult)				+	+	+
Juvenile Saithe (0-3, 0-40cm)					+	
Saithe (adult)					+	
Hake					+	
Blue whiting					+	
Norway pout				+	+	+
Other gadoids (large)					+	
Other gadoids (small)			+	+	+	
Monkfish				+	+	+
Gurnards		+	+	+		
Herring (juvenile 0, 1)		+	+	+		+
Herring (adult)			+	+	+	+
Sprat		+	+			
Mackerel		+	+	+		
Horse mackerel		+	+			
Sandeels			+			+
Plaice		+				
Dab		+	+			
Long-rough dab				+	+	+
Flounder		+	+			
Sole		+	+			
Lemon sole				+		+
Witch				+	+	
Turbot and brill		+	+			
Megrim					+	
Halibut				+	+	
Dragonets		+	+			
Catfish (Wolf-fish)				+	+	+
Large demersal fish				+	+	
Small demersal fish		+	+	+	+	

Table 5.1 continued: Assigning functional groups to 'habitats'. Habitats are assigned simply by clicking on the relevant cells.

Group \ Habitat #	All habitats (e	‹22m	22-51m	52-115m	›115m	Coast
Miscellaneous filterfeeding pelagic fish			+	+	+	
Squid & cuttlefish			+	+	+	
Fish larvae	+					
Carnivorous zooplankton	+					
Herbivorous & Omnivorous zooplankton (copepods)	+					
Gelatinous zooplankton	+					
Large crabs		+	+	+		+
Nephrops					+	+
Epifaunal macrobenthos (mobile grazers)		+	+	+		+
Infaunal macrobenthos		+	+	+		+
Shrimp		+				
Small mobile epifauna (swarming crustaceans)	+					
Small infauna (polychaetes)	+					
Sessile epifauna	+					
Meiofauna	+					
Benthic microflora (incl. Bacteria, protozoa))	+					
Planktonic microflora (incl. Bacteria, protozoa)	+					
Phytoplankton	+					
Detritus - DOM -water column	+					
Detritus - POM - sediment	+					
Discards	+					

Figure 5.2 Distribution of the North Sea model functional groups before an Ecospace run (as assigned to habitats)



Once habitats have been defined and sketched onto the basemap, functional groups are assigned to their 'preferred' habitat (Table 5.1). 'Preferred' here means that the group in question will be adapted such that:

- its feeding rate and hence its growth rate as well are higher in that habitat than in others;
- its survival rate is higher in that habitat (because the predation rate is higher in non-preferred habitat);
- its movement rate is higher outside than within good habitat.

All three of these choices imply different mechanisms for defining what is good and bad habitat, and users can determine the relative strength of these mechanisms (see 5.2).

Relative densities of species recorded from the IBTS trawl survey data and North Sea benthos surveys were used to make initial assignments of the species to each habitat type. Minor modifications were made to these assignments during the process of parameterising the model so that the equilibrium distribution was broadly consistent with the 10 year average distribution of species (1985-1995) recorded from survey data. The distribution of the functional groups (as assigned to habitats) before the Ecospace run can be seen on Figure 5.2.

5.2 Dispersion from assigned habitat

In Ecospace, a fraction (B'i) of the biomass of each cell is always on the move. This is known as the base dispersal rate:

$$Bi = MBi$$

where M is the dispersal rate in *km / year*.

M is not a rate of directed migration, as occur seasonally in numerous fish populations, rather it should be regarded as dispersal and seen as the rate the organisms of given ecosystem would disperse as a result of random movements (Table 5.2).

Dispersal rate (Mi) can be estimated in association with data on fish swimming speed (Martell *et al*. 2005):

$$Mi = Si/\pi L$$

where Si is the swimming speed of different groups and L is the length of grid length side – 126km in the North Sea model. Dispersal rates in the North Sea model were estimated based on published fish movement rates (Aleyev, 1977).

Table 5.2 Dispersal parameters for the equilibrium scenario, representing the average distribution of species in the North Sea from 1985-1995.

Group	Base dispersal rate (km/ year)	Rel. dispersal in bad habitat	Rel. vul.to pred. in bad habitat (prod for pp)	Rel. feed.rate in bad habitat	Advected?
Baleen whales	652	2	2	0.05	
Toothed whales	975	2	2	0.05	
Seals	275	2	2	0.05	
Seabirds	275	2	2	0.05	
Juvenile sharks	79	2	2	0.05	
Spurdog	275	2	2	0.05	
Large piscivorous sharks	275	2	2	0.05	
Small sharks	79	2	2	0.05	
Juvenile rays	79	2	2	0.05	
Starry ray + others	157	2	2	0.05	
Thornback & Spotted ray	157	2	2	0.05	
Skate + cuckoo ray	157	2	2	0.05	
Juvenile Cod(0-2, 0-40cm)	110	2	2	0.05	
Cod (adult)	197	2	2	0.05	
Juvenile Whiting (0-1, 0-20cm)	110	2	2	0.05	
Whiting (adult)	157	2	2	0.05	
Juvenile Haddock (0-1, 0-20cm)	110	2	2	0.05	
Haddock (adult)	157	2	2	0.05	
Juvenile Saithe (0-3, 0-40cm)	110	2	2	0.05	
Saithe (adult)	197	2	2	0.05	
Hake	197	2	2	0.05	
Blue whiting	157	2	2	0.05	
Norway pout	500	2	2	0.05	
Other gadoids (large)	157	2	2	0.05	
Other gadoids (small)	157	2	2	0.05	
Monkfish	157	2	2	0.05	
Gurnards	157	2	2	0.05	
Herring (juvenile 0, 1)	110	2	2	0.05	
Herring (adult)	157	5	2	0.05	
Sprat	79	2	2	0.05	
Mackerel	236	2	2	0.05	
Horse mackerel	1000	2	2	0.05	
Sandeels	75	2	2	0.05	
Plaice	75	1.2	1	1	
Dab	75	1.2	1	1	
Long-rough dab	79	2	2	0.05	
Flounder	79	2	2	0.05	
Sole	79	2	2	0.05	
Lemon sole	79	2	2	0.05	
Witch	79	2	2	0.05	
Turbot and brill	79	2	2	0.05	
Megrim	79	2	2	0.05	
Halibut	79	2	2	0.05	
Dragonets	79	2	2	0.05	
Catfish (Wolf-fish)	157	2	2	0.05	
Large demersal fish	157	2	2	0.05	
Small demersal fish	79	2	2	0.05	
Miscellaneous filterfeeding pelagic fish	141	2	2	0.05	
Squid & cuttlefish	141	2	2	0.05	
Fish larvae	30	2	2	0.05	+
Carnivorous zooplankton	30	2	2	0.05	

Table 5.2 continued Dispersal parameters for the equilibrium scenario, representing the average distribution of species in the North Sea from 1985-1995.

Group	Base dispersal rate (km/year)	Rel. dispersal in bad habitat	Rel. vul.to pred. in bad habitat (prod for pp)	Rel. feed.rate in bad habitat	Advected?
Herbivorous & Omnivorous zooplankton (copepods)	30	2	2	0.05	
Gelatinous zooplankton	79	2	2	0.05	
Large crabs	20	2	2	0.05	
Nephrops	5	1.1	2	0.05	
Epifaunal macrobenthos (mobile grazers)	30	2	2	0.05	
Infaunal macrobenthos	5	5	2	0.05	
Shrimp	30	2	2	0.05	
Small mobile epifauna (swarming crustaceans)	30	2	2	0.05	
Small infauna (polychaetes)	30	2	2	0.05	
Sessile epifauna	30	2	2	0.05	
Meiofauna	30	2	2	0.05	
Benthic microflora (incl. Bacteria, protozoa))	30	2	2	0.05	+
Planktonic microflora (incl. Bacteria, protozoa)	30	2	2	0.05	+
Phytoplankton	30	2	2	0.05	+
Detritus - DOM -water column	30	2	2	0.05	+
Detritus - POM - sediment	30	2	2	0.05	+
Discards	10	2	2	0.05	

The Ecospace simulation is initiated by distributing all organisms evenly onto the basemap, at the density (Bi t km-2) defined by the underlying Ecopath model. Then all biomass pool start moving, as a function of their value of M, out of their cell and into adjacent cells, there consuming food, and being themselves consumed. Given differential food consumption and survival rates in preferred vs. non-preferred habitat (Table 5.2), this generates richly patterned distributions, wherein each cell includes different biomass of each of the groups in the system.

Dispersal rates differ between preferred and non-preferred habitats, with higher values of M within non-preferred habitats than in preferred habitats. Such assumption implies that organisms in non-preferred habitats will strive to leave these, and attempt to return as rapidly as possible to their preferred habitats. The multiplier of M is termed Relative dispersal in bad habitat The rate of dispersal can also be influenced by the changes in the vulnerability to predation and feeding success of organisms outside their 'preferred' habitat (Table 5.2). Advection and seasonal migration can also be parameterised in Ecospace (Christensen et al. 2000), but at this stage we did not use these options.

5.3 Spatial distribution of fishing fleets

The distribution of fishing fleet activity is specified in Ecospace by assigning fleets to habitats, (i.e. defining in which habitat(s) a fishing fleet may operate, Table 5.3), the costs of fishing based on distance from port (Figure 5.3) and whether a given fleet may operate within a restricted area. Fisheries restricted areas (e.g. MPAs) can be assigned by not allowing certain fleets to operate in them. During the simulation, the fishing mortality rates (F) of the fleets are distributed using a simple 'gravity model' where the proportion of the total effort allocated to each cell is assumed proportional to the sum over groups of the product of the biomass, the catchability, and the profitability of fishing the target groups (Caddy, 1975; Hilborn and Walters, 1987). Where costs or restricted areas are not prohibitive, the distribution of fishing fleets reflects the distribution of their target species.

In combination with adjustments to species habitat assignments, information of the distribution of fishing effort of North Sea beam and otter trawlers (Jennings et al. 1999) (Figure 5.3) and spatial effort data from UK logbook data (Fishing Activity Database), was used to help specification of fleet distribution variables such that the equilibrium distribution of effort most closely resembled that observed over a similar period (see next section).

Table 5.3 Defining fishery in Ecospace

Fleet \ Habitat use:	‹22m	22-51m	52-115m	›115m	Coast	MPA
Demersal trawl + dem seine		+	+	+	+	+
Beam trawl	+	+				+
Sandeel trawl		+	+		+	+
Pelagic trawl			+	+		+
Drift and fixed nets	+	+				+
Nephrops trawl			+	+	+	+
Gears using hooks	+	+	+			+
Shrimp trawlers	+					+
Dredges	+					+
Shellfish	+					+
Pots	+	+	+		+	+
Other	+					+

5.4 Equilibrium distribution of species and fishing activity

Determined only by food-web interactions, the spatial distribution of the biomass of each functional group took about 10 years to reach a state in which the biomass trajectories were stable. The resulting 'equilibrium' distributions (Figure 5.4) were compared to the average distribution of fish and benthos from 1985-1995 International Bottom Trawl (IBTS) and beam trawl surveys assembled and plotted by ICES rectangle (Figure 5.5). Comparison was also made between the resulting distribution of fishing effort (Figure 5.6) and those of Jennings et al. (1999) (Figure 5.7). Data matrices of data per ICES rectangle were created for most of the functional groups (subject to availability of data) annually for the period 1983-2005. Work is under progress to statistically compare empirical data to model predictions driven by changes in fishing effort from 1991-2005.

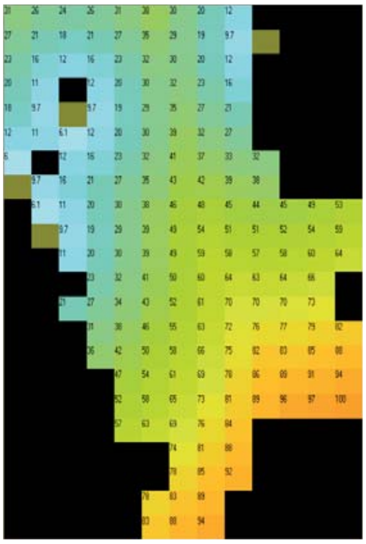
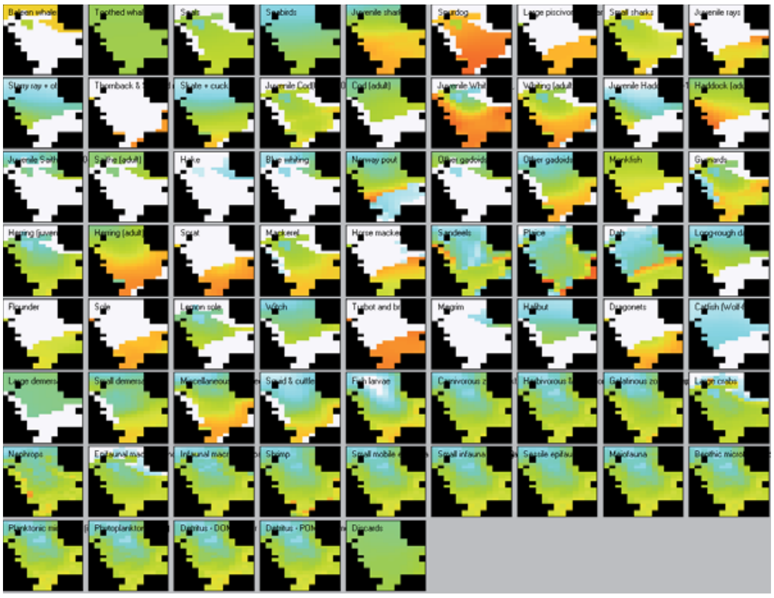


Figure 5.3 Variable costs of fishing based on distance from port (example for demersal trawlers)

Figure 5.4 Equilibrium distribution of selected functional groups after 15 years simulation with no fishing.



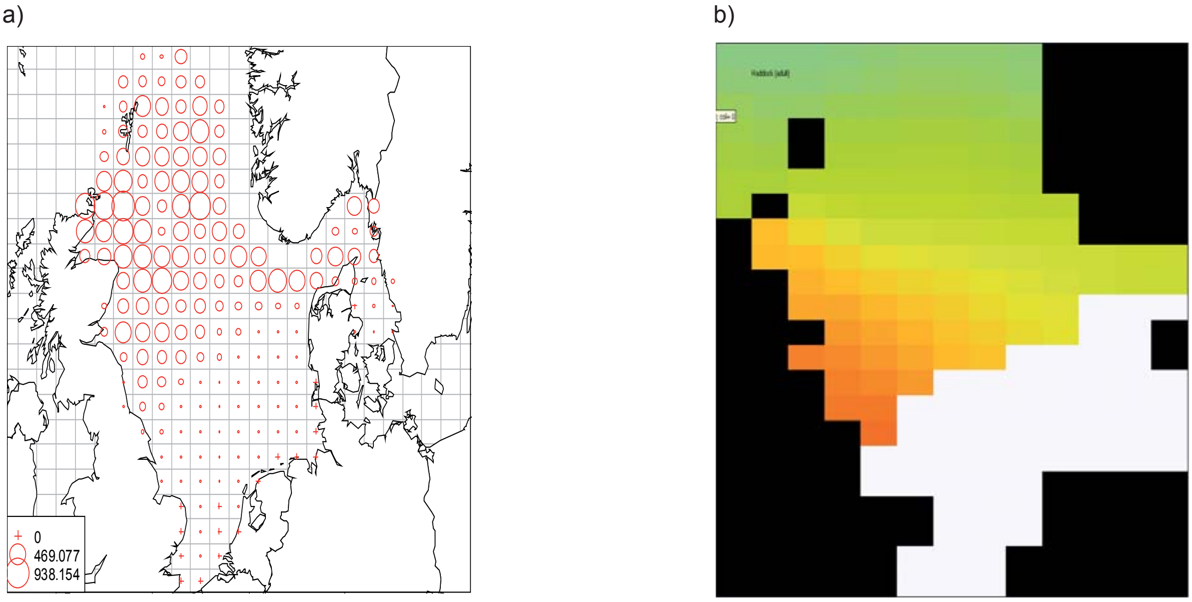


Figure 5.5 Comparison of the distribution of Haddock from (a) IBTS surveys (1985-1995) with (b) model equilibrium prediction for haddock.

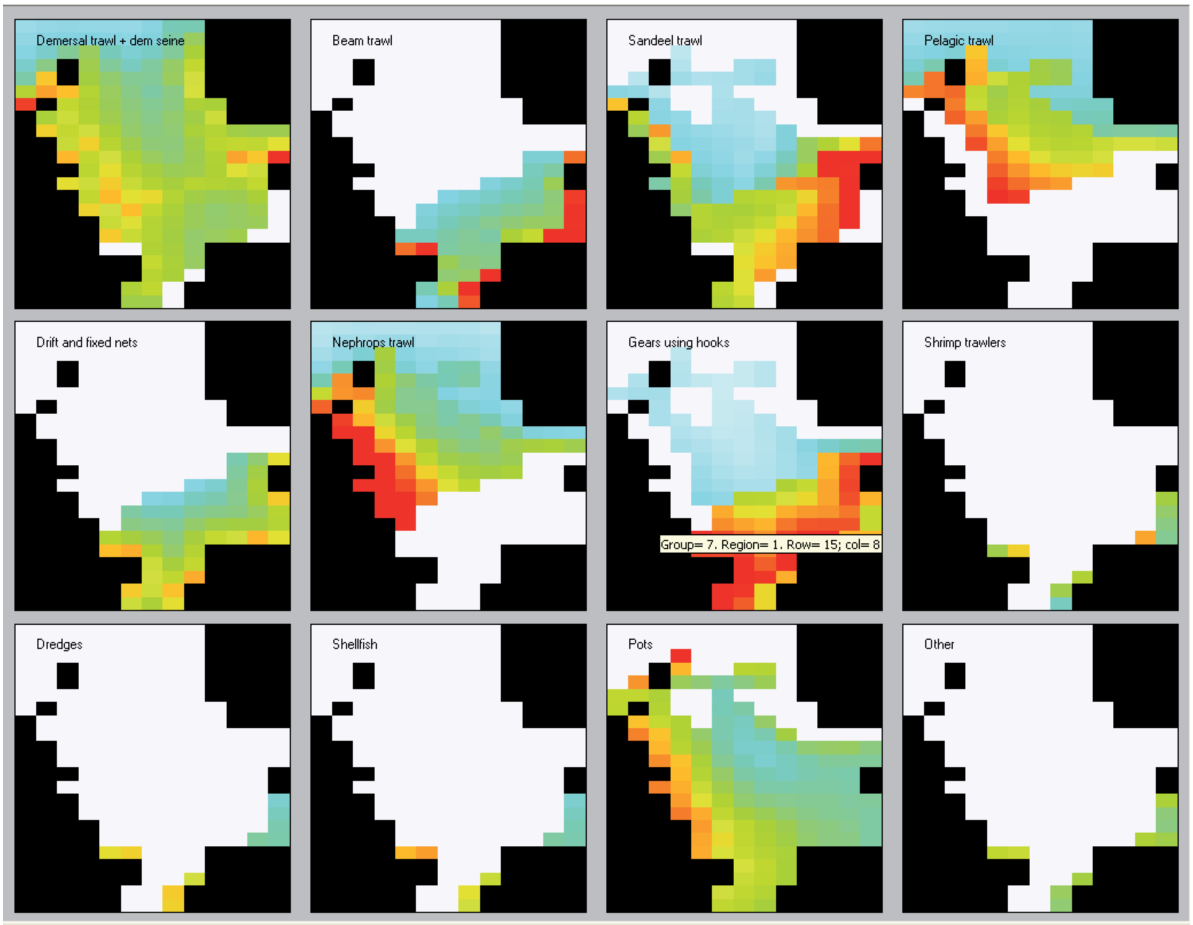
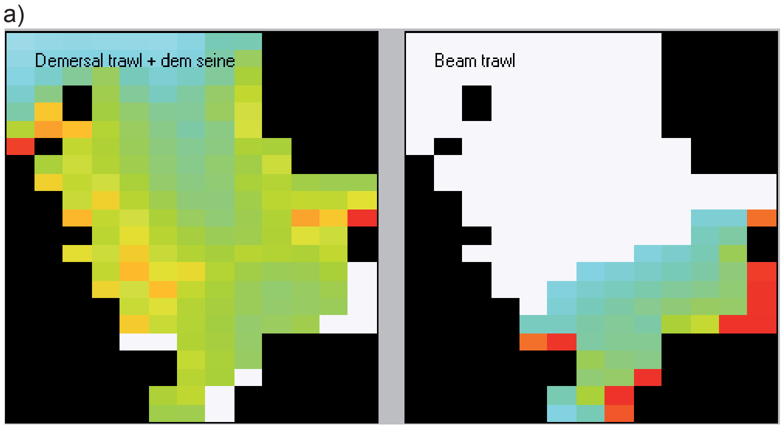


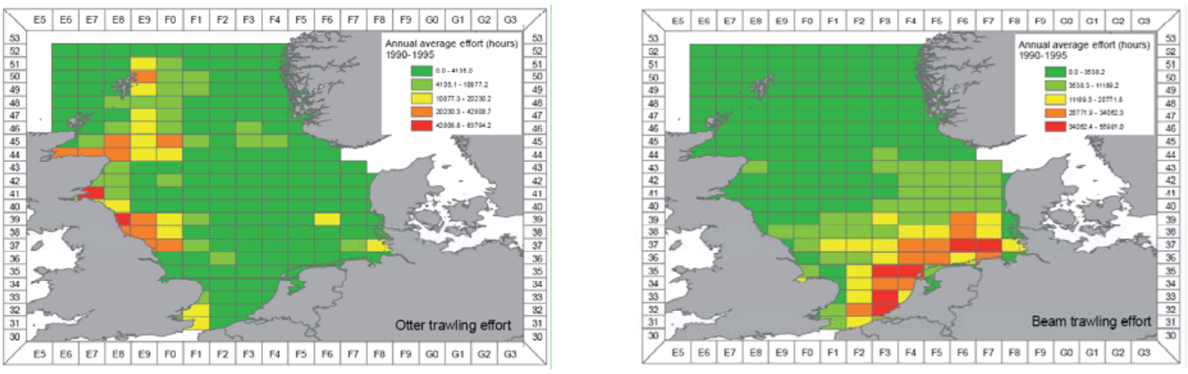
Figure 5.6 Distribution of fishing of various fleets representing the average distribution of fleets in the North Sea in the early 1990s.

Figure 5.7. Fishing fleet distribution equilibrium predictions (a) compared with (b) distribution of beam and otter trawl effort in the North Sea 1990-1995 (Jennings et al. 1999). Left hand side – Otter / demersal trawlers. Right hand side – beam trawlers.

a)



b)



5.5 Investigating MPA's

Ecospace has been designed to evaluate effects of Marine Protected Areas (MPA) on abundance and distribution of fish and associated fisheries and ecosystem changes (Walters et al. 1999, Beattie et al. 2002, Martell et al. 2005). Our preliminary investigations of the existing and proposed MPAs in the North Sea are currently underway as part of the EU framework 6 project 'INCOFISH'. (www.incofish.org).

The effects of an MPA are illustrated here by the simulations with the 'sandeel box' – an area along the Scottish coast where the sandeel fishery has been banned (Camphuysen, 2004). The fisheries closure in the 'sandeel box' in our simulations had a significant effect on sandeel, which biomass increased (Figure 5.8). The effects on sandeel also translated to its predators. Within the 'sandeel box' seabird biomass increased, but decreased else where. Within the 'sandeel box' many higher trophic level predators (especially whiting) also increased in biomass (Figure 5.9).

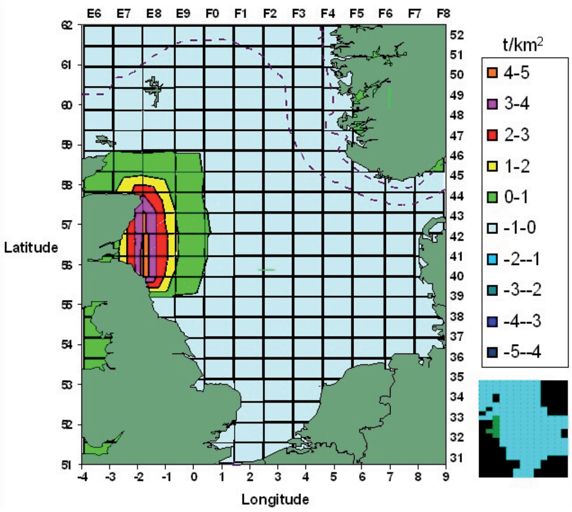


Figure 5.8 Change in biomass density (t/km2) of sandeel after 'closing' the fisheries in the 'sandeel box' within Ecospace: MPA 'sandeel box' shown on the embedded basemap in right lower corner

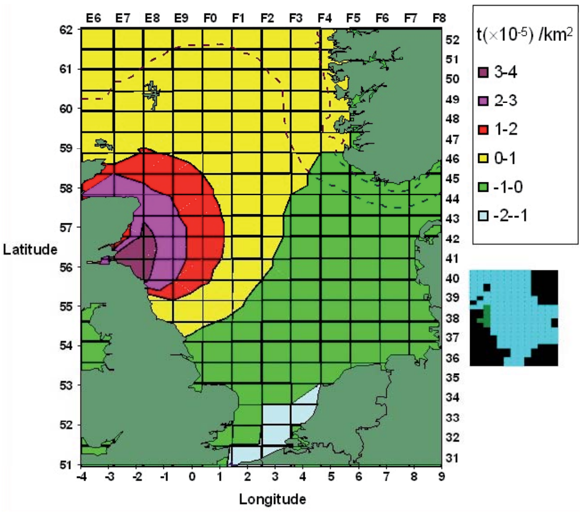


Figure 5.9 Change in biomass density (t/km2)of seabirds after 'closing' the fisheries in the 'sandeel box' within Ecospace: MPA 'sandeel box' shown on the embedded basemap in right lower corner

6. Notes on limitations and usefulness

Authors: Steven Mackinson

Some knowledge of the general EwE approach to ecosystem modelling is essential for understanding the limitations and usefulness of the North Sea model.

In undertaking an integrated and quantitative analysis of a whole ecosystem, the models 'building blocks' must represent relatively broad components or processes. Many of the uncertainties, simplifications, and assumptions of the EwE modeling approach relate to aggregation of species in to functional groups and representation as biomass units. Particular areas of caution include: the over or under estimation of fishing mortality, poor representation of the predation impacts on juvenile stages (when life history stanzas are not explicitly accounted for), overestimating effects of cannibalism, homogenizing of otherwise discrete spatial distributions. These issues have a bearing on analyses using Ecopath, Ecosim, and Ecospace.

Paucity and uncertainty of information about ecosystems influences the usefulness of ecosystem models. However, explicit recognition of the nature of uncertainties can guide us toward appropriate model application and interpretation of results. In addition to documenting derived ranges for input parameters, data uncertainties for the North Sea model were characterized during model construction using the 'data pedigree' approach (presented in Section 3.2).

A key element of our initial model testing (ongoing), whose importance cannot be understated, was the back and forth toggling between Ecopath, Ecosim, and Ecospace routines. Ecopath forms the foundation upon which Ecosim and Ecospace analyses are constructed, yet results from these analyses can in turn highlight weaknesses in the foundation; thus serving for refinement of the Ecopath model. Comparison of the analyses to independently-derived information about the system, is an important effective way to refine the model and continue to reduce uncertainty.

Detailed discussion of the capabilities, limitations, and major pitfalls of the Ecopath with Ecosim approach are discussed at length in Christensen and Walters (2000). Their discussion of how the following major pitfalls can be avoided, or accounted for, is particularly useful:

- Incorrect assessments of predation impacts for prey that are rare in predator diets
- Trophic mediation effects (e.g., trophic effects with a biological habitat effect)
- Underestimates of predation vulnerabilities
- Non-additivity in predation rates due to shared foraging arenas
- Temporal variation in species-specific habitat factors

The most important guideline for use of the North Sea model is for careful consideration of how a particular research question compares to the spatio-temporal scales of the model and the degree of aggregation of functional groups. The model is best designed to address questions regarding processes that occur over the whole North Sea and on time scales greater than one year. As such the model is designed to help address strategic long-term questions such as those relating to the long-term ecosystem effects of changes in fishing activity and climate. It is not useful for short-term tactical question regarding fisheries management. It is complementary to existing approaches; helping managers and policy makers by giving them a view of the possible surprising and counter-intuitive effects of particular management and policy options.

The structure of the model is also considered suitable to explore the effects of other disturbances, whether natural or anthropogenic. These could include any disturbance or source of stress with a known, or presumed, effect on some biotic component(s) of the system. Examples include examination of the effects of eutrophication and tracing the bioaccumulation of pollutants.

In this report, simple evaluations of model sensitivity to input data are provided. Any application of the model requires that a robust analysis of sensitivity to uncertain input data and model parameters is undertaken. The ecoranger and monte carlo routine in ecosim may be useful tools for this purpose.

Section B

Description of data sources, methods, and assumptions used in estimating parameters

7. Primary producers

Authors: Steven Mackinson and Steve Milligan

from (Fowler, 1912) (3) *Ceratium*

Phytoplankton (autotrophs – diatoms dinoflagellates, cryptomonads)

Phytoplankton is the major contributor to algal biomass and primary production in the North Sea although microphytobenthos dominates production in the coastal shallow tidal flat areas. Protozoans such as ciliates, acantharians and radiolarians that may have algae incorporated as symbionts, may at times also be important contributors to chlorophyll a levels. These producers are included in the microflora group.

The diverse phytoplankton flora ranges in size from 1 µm to 300 µm and is primarily composed of autochthonus meroplanktonic species present mostly in the water column or overwintering as cysts in the sediment. Oceanic forms seeded from the Atlantic also occur to a varying extent. During the spring bloom (April/May), diatoms are the dominant algae group, while later in the summer months (July/August), armoured dinoflagellates, particularly ceratium, dominate the sub-surface waters of the central and northern North Sea (Reid *et al.*, 1990; Geider, 1988).

Abundance and distribution is influenced by macronutients, turbidity, stratification, the location of frontal regions, suspended sediment characteristics, temperature, salinity and circulation. Data collected since 1932 during the Continuous Plankton Recorder Survey show regular spatial and temporal patterns of variation in the distribution and abundance of major taxonomic groups.

Production and biomass

Primary production refers to photosynethetic carbon fixation by phytoplankton cells. Net primary production (gross primary production minus respiration, i.e. phytoplankton growth) is that part available as food to higher trophic levels. Fransz and Gieskes, 1984 (p220, Table 1) provide estimates for the North Sea regions (Table 7.1), the average of which is 212 gC m^{-2} y^{-1}.

Phytoplankton growth models indicate an approximate 10 fold difference in growth rate between winter and spring (max) periods both in coastal and open sea, with simulations indicating that a mean growth yield of 40% (per day) should be considered for North Sea phytoplankton as a first approximation (Reid *et al.*, 1990).

Based on a critical examination of the primary production figures published in the literature and consideration of a physiological model of phytoplankton growth, Lancelot *et al.* (1988), evaluated the annual net particulate primary production in the continental coastal zone to be 170 gC m^{-2} y^{-1}. Extra cellular release (excretion) of organic compounds by phytoplankton was estimated at 20 gC m^{-2} y^{-1}. In the Central North Sea, net phytoplankton production is lower, amounting to around 45 gC m^{-2} (March–June) and excretion of organic components to 6 gC m^{-2}. Combining estimates, total primary production (av. March-June) from the coastal zone and central North Sea amounts to 2,150 g wet wt m^{-2} y^{-1} (based on 0.1 gC=0.2 g dry weight = 1 g wet weight (Mathews and Heimdal, 1980).

Krause and Trahms (1983) reported a maximum phytoplankton standing stock biomass during the Fladen ground experiment (FLEX) March-June 1976, of over 4000 mgC m^{-2}, with average phytoplankton standing stock biomass in March-June being approx 750 mgC m^{-2} (7.5 g wet wt m^{-2} using the above conversion). Hannon and Joires (1989) estimated the phytoplankton biomass in the southern North Sea the (microplankton) to be to 3.7 g C m^{-2} (or 43 g wet wt m^{-2}).

Using a biomass of 7.5 g wet wt m^{-2} and a productivity of 2,150 g wet wt m^{-2} y^{-1}, a P/B ratio of 286 y^{-1} was calculated. The value used for conversion of gC to g wet wt is an important source of uncertainty in

Table 7.1. Estimates of primary production mg C m-2 d-1, based on measurements from 1971-1981 (from Fransz and Gieskes 1984).

	January–February	March–May	June–September	October–December	Annual estimate gC m^{-2} y^{-1}
Southern Bight coast	100	1000	1000	100	200
Southern Bight offshore	100	1200	700	500	250
Central North Sea, 1981	100	1000	800	400	200–250
Northern North Sea (FLEX)	300	1000	-	-	>>100 (175)*

the calculations of phytoplankton productivity. A cursory comparison of alternative conversion factors provided productivity estimates (based on 170 gC m^{-2} y^{-1}) from 400 to 8000 g wet wt m^2 y^{-1}. Of these, the closest to the estimate used in the model is 2,480 g wet wt m^{-2} y^{-1}, based on the conversion factors used by Christensen (1995) (1 g C = 15 kcal; 1 g wet wt = 1.3 kcal; Jones 1984; ICES 1989, Figure 9.3.).

Predation and other mortality

Because of their large size, diatoms are a favoured food source of herbivorous zooplankton (mainly copepods). They may also be predated upon by dinoflagellates and protozoa. During summer, copepod grazing matches primary production in all areas of the North Sea. However, data from 1971 to 1981, show that during the spring and autumn bloom zooplankton grazing does not contribute significantly to the reduction of phytoplankton biomass (Fransz and Gieskes, 1984), suggesting perhaps that relationship between phytoplankton and zooplankton is one of resource control (ie, bottom-up). It is believed that much of the phytoplankton crop is either consumed directly by protozoa and bacteria in the water column or sinks to the bottom where it may be utilised in a similar benthic pathway. Sediment trap experiments indicate that 20–35% of the primary production deposits to the sediment during spring in the northern North Sea (Cadée, 1985). This evidence suggests that in the model we would expect the ecotrophic efficiency of phytoplankton to be relative low, with a considerable proportion of the production being made available through the microbial loop.

In addition to being eaten, phytoplankton mortality results from spontaneous or parasite induced cell lysis. Very little is known of the lysis although the process is very important in determining the supply of organic matter to microheterotrophs and bacterial consumers (labelled 'microflora' in the model). Calculations of carbon flow through the microheterotrophic consumer community suggest that approximately 20 to 60% of primary production, possibly representing the dissolved components leaching out of and lost from phytoplankton cells during zooplankton grazing, enters the microbial food chain (Linley *et al.*, 1983). Excretion of organic molecules by phytoplankton also provides an important food that can be used directly by bacteria. The percentage of extracellular release ranges from 0–10% in the open sea (Gieskes and Kraay, 1980) and 1–16% in coastal waters (Lancelot and Mathot, 1987).

8. Detritus

Author: Steven Mackinson

Seawater always contains suspended particulate detrital particles. Such particles originate from dissolved organic material through bacterial activity or from dead phytoplankton cells including diatom frustules, larvacean houses, or other remains of zooplankters, feacal pellets, and especially in coastal areas, debris of macroalgae or seagrasses or mineral grains. Often several such particles occur in small aggregates held together by microbial mucus secretions (Fenchel, 1988).

Gieskes and Kraay (1984) found the contribution of living phytoplankton to the total load of particulate organic carbon (POC) in the open North Sea to be between 25–65% in the vegetative season. In the model, 70% of the unutilised phytoplankton production goes to POM and 30% to DOM. Hagmier (1962), showed that, by weight, dead particular matter may exceed the contribution of plankton even in the central North Sea and spring bloom.

In the model, 'detritus' includes three groups of dead matter (discards, dissolved and particulate organic matter) that are eaten by the living groups in the model. Dissolved organic matter and particulate organic matter are consumed by microflora via planktonic and benthic pathways. Flow of material to the groups consists of excreted and unassimilated food, dead organisms etc. and is specified in the detritus fate and discard fate (see sections 19 and 15), the value of the biomass being nominal and not having influence over the balance of the model. Unutilised DOM flows to the POM pool of which any unitilised is exported.

The total biomass of POM and DOM applied in the model was taken as being 50 g wet wt m^{-2} based on the estimates of Hannon and Joires (1989) for the southern North Sea (4.3 gC m^{-2}) reported by Christensen (1995).

9. Microflora

Authors: Steven Mackinson, Melanie Sapp and Hans-Georg Happe

Planktonic and benthic auto/ heterotrophic protozoans – flagellates, ciliates and bacteria grazing on bacteria and particulate organic matter.

9.1 What the model needs to represent

It is now recognised that a large fraction of primary production flows through the pool of dissolved organic matter, either after excretion by phytoplankton or by lysis of ungrazed cells. This part of primary production is unavailable to herbivorous zooplankton for direct utilisation and is mainly utilised by bacteria and auto/ heterotrophic nanoflagellates that are able to take up dissolved organic substances. These organisms form a link between dissolved primary production and production at higher trophic levels (Billen *et al.*, 1990).

Heterotrophic microflora (bacteria and nanoflagellates) appear to utilise 5–50% of the primary production in planktonic marine ecosystems (van Es and Meyer–Reil, 1982). Thus, a substantial amount of primary production is converted to microflora biomass and made available to higher grazers by distribution to alternative food chains via the microbial loop (Azam *et al.*, 1983).

Complicating ecological interpretation of the role of microflora is that many unicells are not limited to one trophic role (Geider 1988). The micoflora group can be classified as the planktonic and benthic organisms that are smaller than phytoplankton (microplankton 20–200 µm). It comprises both producers (autotrophs) and consumers (heterotrophs) in the size ranges nano (2–20 µm) and picoplankton (0.2–2 µm) (Kirman, 2000). In the literature these most groups are often separated in to bacteria and unicellular flagellates and ciliates representing their functional distinction. In the mixed offshore waters of the North Sea, Van Duyl *et al.*, (1990) found that bacteria make up to 30–51% of the combined bacteria and nanoflagellate biomass, and in stratified waters heterotrophic flagellates were the most abundant.

9.2 How the ecology of microflora is represented in the model

Accounting for the role of auto/ heterotrophic nanoflagellates and bacteria in the ecology of the North Sea involves understanding, and representing how the organic matter produced from phytoplankton is partitioned between three concurrent pathways (i) direct grazing by zooplankters, (ii) incorporation into the microbial loop by uptake from mineralisation and direct uptake from microflora; (iii) sedimentation and incorporation into the benthic food chains (adapted from *Billen et al.*, 1990).

The representation of these pathways and the dynamics of microbial food web are simplified in the model by having heterotrophic flagellates (that prey on bacteria) and bacteria included in the same group. The group is allowed to feed on itself to represent the flagellate–bacteria dynamics. The most important point about the group is the role it serves in utilising the primary production of phytoplankton (from lysis and excretion) that is not consumed by zooplankton and higher trophic levels. It represents the processes of re-mineralisation where energy is fed back in to the system to sustain production of higher trophic levels through the microbial food web.

Furthermore, by having 'detritus' as two distinct groups, water column organic matter and sediment organic matter, the latter two pathways are represented in the model by allowing planktonic and benthic bacteria to utilise (principally but not exclusively) the respective sources of organic matter. In the planktonic pathway, phytoplankton derived organic matter is utilised by the planktonic microflora, which are in turn eaten by zooplankton. In the benthic pathway, dead ungrazed phytoplankton are utilised by benthic microflora that in turn are grazed predominantly by meiofauna and benthic macrofauna. The excretion from zooplankton and a fraction of the unutilised prodution from higher trophic levels (representing decay and mineralisation processes) is made available for itlisatio by microflora.

Splitting the benthic and pelagic pathways allows the model to capture (and represent albeit simply) the critical dynamics of the microscale processes that are pivotal in linking the pelagic and benthic systems and may have considerable bearing on production regimes in the marine environment. (Figure 9.1)

The text below summarises the key literature used in estimating parameters for this group. A summary of estimates is given in Table 9.3

Production and biomass (planktonic)

Bacteria and protists make up about half the total biomass of plankton in the marine environment [*20% in the model*] (Fenchel, 1988). Of the planktonic bacteria biomass, up to 10–20% may be attached to particles, the majority are free bacterioplankton (Azam *et al.* 1983).

Heterotrophic bacterial production forms a large component of total secondary production, being roughly

Table 9.1. Average biomass and production in planktonic groups. Summary of Nielson and Richardson, 1989, Table 8. Data averages over all sites sampled.

Means over all regions	Phytoplankton	Backterioplankton	Copepods
Biomass mgC m^{-3}	103.83	2.65	4.60
Production mgC m^{-3} d	33.55	1.08	0.12
P/B d^{-1}	0.39	0.40	0.02
After conversion			
Biomass g ww m^{-2}	93.44	1.45	4.94
Production g ww m^{-2} y^{-1}	11021.18	353.14	39.42
P/B y^{-1} (365 days)	144.14	144.37	8.33
P/B y^{-1} calculated	117.95	244.31	7.99

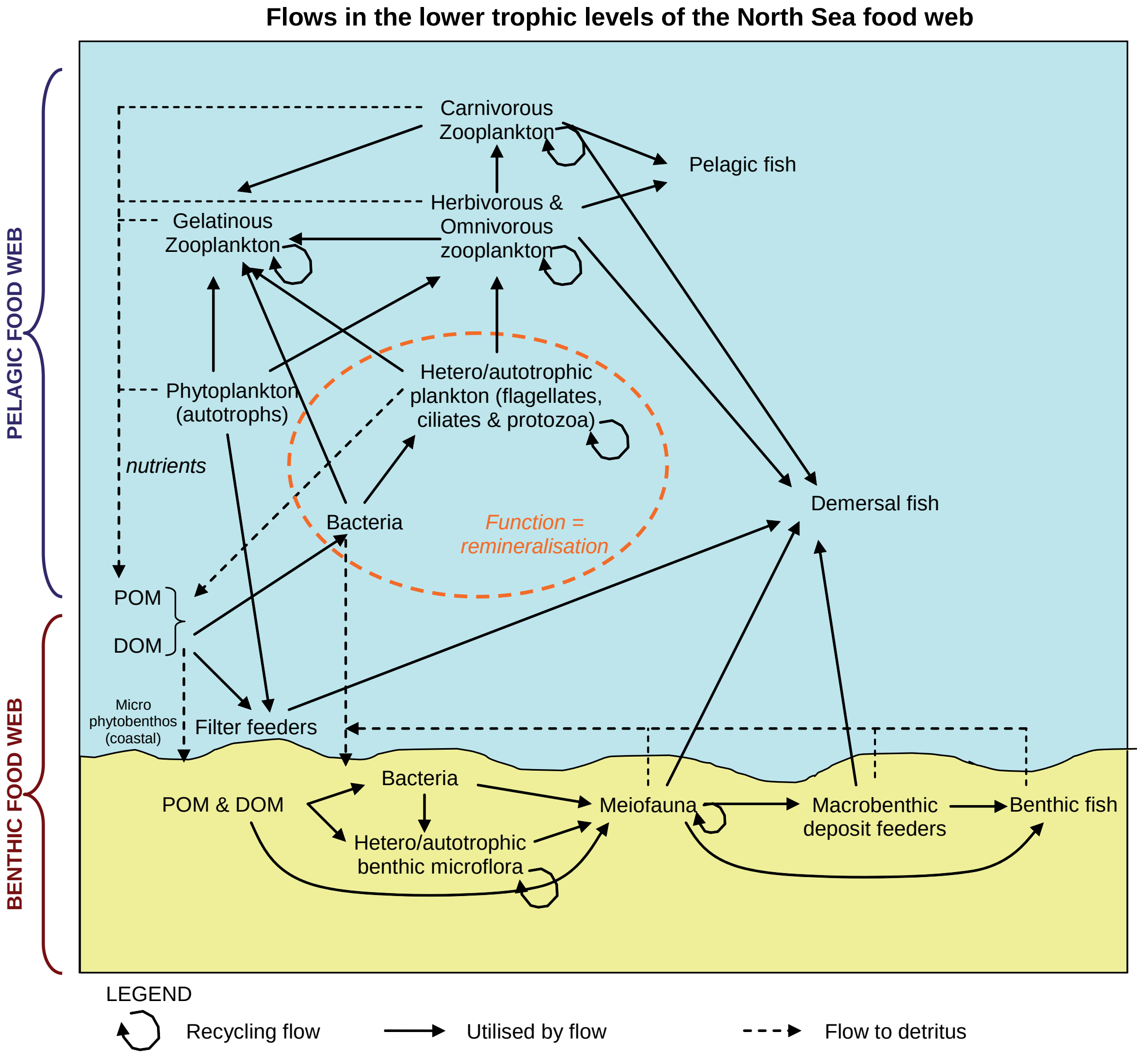


Figure 9.1 Model representation of flows in the lower trophic levels of the North Sea.

Table 9.2. Estimates of biomass of microflora (from van Duly *et al.* 1990, Table 4, p103. Average calculated assuming the '<1' are 0.1.

Biomass (mgC m^{-3})	Coastal zone to Central Oyster ground		Dogger Bank		Average (mgC m^{-3})	After conversion g ww m^{-2}
	min	max	min	max		
Autotrophic nanoflagellates (without phaeocystis)	0.1	94	0.1	175	67.3	36.71
Phaecystis like cells	0.1	16	0.1	6	5.55	3.03
Heterotrophic nanoflagellates	11	209	4	287	127.75	69.68
Bacteria	9	107	3	21	35	19.09

twice as large as the production of macrozooplankton (for a given level of primary production) (Cole *et al.*, 1989). Based on data from 70 studies in which production estimates of bacterial biomass (bacterial production) were reported for fresh and saltwater ecosystems, planktonic bacterial production averaged 20%–30% of total planktonic primary production. Van Duyl *et al.* (1990), found similar results from mixed and stratified in the North Sea, where bacterial production amounted to 3–31% of the primary production. [*In the model, planktonic microflora production (bacteria and flagellates) is 39% of primary production*].

Azam *et al.* (1983) reports that bacterial biomass is closely related to phytoplankton concentration with bacteria estimated to utilise 10 to 50% of carbon fixed by photsynthesis. Similarly, in the English Channel and Benguela, Linley *et al.* (1983) found numbers of bacteria are correlated with both the standing stocks of phytoplankton and heterotrophic microflagellates, which on average amounted to around 17% of bacterial standing stocks.

Nielsen and Richardson (1989) calculated the biovolume of planktonic heterotrophic nanoflagellates in Feb/March by assuming a spherical form and converting to biomass by multiplication of 0.12 µgC µm^{-3} (Fenchel, 1982c). Mean biomass over all stations was 0.14 µgC l^{-1}, which equates to 0.01235 g m^{-2} (with conversion 1 µg l^{-1}=0.015 g m^{-2} and wet mass to C mass conversion factor for protozoa of 0.125 from DeLaca, 1985 in Brey (2001)). They also reported that bacterial production ranged from 0.2 to 2.7 µgC l^{-1} d^{-1} at 3 m depth and virtually the same at 20 m depth, but much lower at 60 m. Assuming an average of 1.45 µgC l^{-1} d^{-1}, and using the same conversion factors as above, this equates to a production 481 g ww m^{-2} y^{-1}.

Nielsen and Richardson (1989, Table 8), compared carbon flows through phytoplankton, backterioplankton and copepods across various sites throughout the North Sea. Average volumetric values were converted to wet weight per unit area (using North Sea area of 575,000 km^{2}, average depth of 90 m and conversions factors for C to DM and WM specific to protozoa, copepods and phytoplankton (Brey, 2001, see Appendix 2). (Table 9.1)

Van Duyl *et al.* (1990) provide estimates of bacterial production and bacteria and flagellate biomass derived from samples taken from the coastal zone to central oyster bank and from the Dogger Bank (Table 1, p101, Table 4, p103). The authors note that the ranges recorded are the largest so far recorded in the literature, with bacterial production estimates ranging from 0.27 to 66 mgC m^{-3} d^{-1}. Using the average value of 18, and converting to wet weight (conversion for protozoa, WM–CM 0.165, De Laca, 1985 in Brey 2001) equates to bacterial production of 3755 g ww m^{-2} y^{-1}, nearly 2 times the estimated primary production in the North Sea. Biomass estimates also varied widely (Table 9.2), with average values yielding a total planktonic microflora biomass of 128 g ww m^{-2} (Table 9.3)

Van Duyl *et al.* (1990) compare their results to others. Linley *et al.*'s. (1983) estimates for flagellates are 6–18 times less than Van Duyl *et al.*'s, whilst Nielson and Richardsons max estimate of heterotrophic nanoflagellate biomass in the central North Sea (20 mg C m^{-3}) is around 14 times less. The authors also note that their estimate of maximum biomass (depth integrated) presented is 4–5 times higher (up to 14 gC m^{-2} north of the Dogger Bank) than the integrated values reported in other studies (3 gC m^{-2}, Holligan *et al.* 1984.). They comment that the wide range of conversion factors hampers comparisons. The same is true here and clearly it is difficult to synthesise reasonable estimates. However, because the estimates of Van Duyl *et al.* appear to be consistently high and most literature suggests that micoflora production should be roughly nearer to 30% of PP (rather than 200%), their estimates are not used and only taken as possible maximum values. It is noteworthy that such values are not necessarily unreasonable for inshore areas, where biomass far exceeds that found offshore. For example, Azam *et al.* (1983) provide biomass estimates of marine bacteria taken from Meyer-Reil (1982) and Es and Meyer-Reil (1982). Assuming a conversion factor of 10% from live mass to carbon equivalent, they found biomass in coastal waters ranged from 5–200 µgC l^{-1} (0.75–30 g ww m^{-2}), with offshore waters being 1–5 µgC l^{-1} (0.15–0.75 gww m^{-2}), with production rates of 2 to 250 µgC l^{-1} d^{-1} (Es and Meyer-Reil 1982).

Summary data on planktonic bacterial abundance and biomass in the upper layers of the North Sea presented by Billen *et al.* (1990) range from 0.15 to 9.4 x 10^{6} cells cm^{-3} and 2 to 140 µgC l^{-1} (Table 1, p269). They deduce from this that the average biomass of planktonic bacteria in the continental coastal zone is about 20 µgC l^{-1}, which is equivalent to about 0.3 gC m^{-2}, whilst planktonic bacterial production can be evaluated to about 20 gC m^{-2} y^{-1} (200 g ww m^{-2} y^{-1}) (p. 286). Billen *et al.* comment that his represents a mean growth and mortality rate of 0.0075 h^{-1}, in the middle of the range found experimentally. Furthermore, the estimated flux of 110 gC m^{-2} y^{-1} (20

Table 9.3. Summary table of parameter estimates for microflora. Shaded values are used are used as initial estimates in the model.

Source		Biomass (g m^{-2})	Production (g m^{-2} yr^{-1})	P/B y^{-1} (365 days)	P/B calc
Nielson and Ricardson, 1989	Heterotrophic nanoflagellates	0.0124			
	Backteriopplankton	1.45	481, 353	144	244
	Total planktonic microflora (used)	1.46	834		571
Van Duyl *et al.*, 1990	Auto and heterotrophic nanoflagellates	106.39			
	Planktonic bacteria	19.09	3755		196
	Total planktonic microflora	128.50			
Azam *et al.*, 1983	Planktonic bacteria – coastal	0.75–30	110–13688		7–890
	Planktonic bacteria – offshore	0.15–0.75	110–13688		243–30147
Billen *et al.*, 1990	Bacterioplankton – continental coastal zone	3	200		67
	Central North Sea Bacterioplankton	0.0375	22		586
McIntyre, 1978	Bentic bacteria/micoflora	0.048	455		9469

supplied by phytoplankton excretion, 90 from cell lysis) flowing through the bacterioplankton compartment in the continental coastal zone is in good agreement with the above estimation of 20 gC m^{-2} y^{-1} for bacterial production in the areas, as it implies a mean growth yield of 0.18, which they consider to be quite a reasonable figure when compared with experimental data. Kirman (2000) suggests a mean growth efficiency of around 0.26, with production about 10 x10^{-6} gC l^{-1} h^{-1} for backerioplankton whilst Fenchel (1988) cites values in the ranges 30%–50% to be realistic for microbial heterotrophs.

Production and biomass (Benthic)

Although though many studies have shown a correlation between bacterial abundance and organic matter content of the sediments (Billen *et al.*, 1990, Figure 18 and references on p. 280), much less reliable data are available for bacterial activity in the benthos, partly because of the specific difficulties arising from the attachment of bacteria to particles. Data on organic sedimentation indicate a flux of about 20–100 gC m^{-2} y^{-1} with large geographical variation, which can be inferred from mud and benthic organic matter disribution (see Eisma, 1981). The overall carbon flux in the benthic microflora (heterotrohic flagellates, bacteria) and meiofauna was estimated by Billen *et al.* (1990) to be about 10–40 gC m^{-2} y^{-1} in the Central North Sea and 50–100 gC m^{-2} y^{-1} in the continental coastal zone.

McIntyre (1978) estimated production of benthic bacteria/ microflora to be 75 gC m^{-2} y^{-1} (455 g ww m^{-2} y^{-1}, using DeLaca, 1985 in Brey, 2001 WM-C 0.165) and cites that in the German Bight, maximum wet weight biomass in the upper 2 mm of the sediment was calculated by Hickel and Gunkel (1968) to be 48 mg m^{-2}. This implies a P/B y^{-1} =9469 and is used in the model.

In shallow water benthic microalgae may contribute a significant part of the primary production, as for example on the tidal flats of the Wadden Sea where microflora annual autotrophic production of more than 100 gC m^{-2} has been measured (Cadée and Hegeman, 1974).

Respiration

Bacteria have growth efficiencies of around of about 50% (Cole 1982, in Cole *et al.*, 1989; Fenchel, 1988), with respiration averaging about 29% of primary production. [In the model PP = 2150 t y^{-1}, 29% is 623 t y^{-1}. Respiration for all microflora is 730 t y^{-1} , which seems very reasonable].

Consumption and Feeding

Data on production of planktonic micorflora reveal their prominent importance in the North Sea. Calculations of carbon flow through the microheterotrophic consumer community suggest that approximately 20 to 60% of primary production, representing the dissolved components leaching out of and lost from phytoplankton cells during lysis and zooplankton grazing, enters the microbial food chain (Linley *et al.*, 1983; Es and Meyer-Reil, 1982) via planktonic and benthic pathways. Es and Meyer-Reil (1982) point out that through mineralisation, bacteria provide the phytoplankton with nutrients that may be available in limiting amounts. In such cases, phytoplankton growth can be directly dependent upon bacterial activity.

Available evidence suggests that heterotrophic microflagellates control bacterial numbers with a lag of some 3 to 4 days between bacteria and flagellates peaks. Van Duyl *et al.* (1990) found that highest densities of nanoflagellates in mixed and frontal waters of the North Sea were accompanied by low bacterial abundances suggesting a regulation of bacterial numbers. Free-living bacteria in the water column can also be utilised to some extent by some larger animals such as sponges and bivalves, although bacteria are at the lower limit of efficient utilisation by macrofauna (Azam *et al.*, 1983). Acquisition of food particles by flagellates is a function of the velocity of the water currents produced by the single flagellum and the area of a ‘collector’ surface (Fenchel, 1982c). Consumption rates are influenced by the concentration of food particles and at high food concentrations by handling time, although typically they display a Type-I functional respsonse (Fenchel, 1982c). Flagellates may typically clear the entire water column of bacteria at rates ranging from 0.5 to 2 times per day (Fenchel, 1988). Consumption rate of microflagellates are in general 10 to 50 times higher than bactivorous ciliates, which suggests the importance of smaller protozoans as consumers of marine bacteria (Fenchel, 1982 b).

Bacteria also show patterns of seasonal abundance presumed linked directly to to dissolved organic matter released by phytoplankton (Azam *et al.*, 1983). In well mixed water of the northern North Sea peak abundance is generally observed in the spring, 7–10 days after the phytoplankton bloom, after which lower and less fluctuating values are observed (Billen *et al.*, 1990).

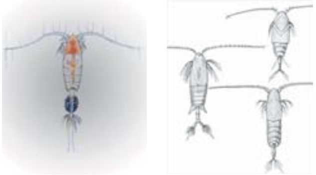
McIntyre (1978) affirms the role of microbenthos as an essential link in the food chain between benthos and fish. Microbenthos are ingested by macrobenthos when they take in sediment and detritus, and may indeed account for the main part of nutrition. Some individuals such as algae and larger protozoa are selectively preyed upon. However, it is not believed that the microbenthos constitute an important direct food for fish.

In the model representation, micorflora are assumed to get 80% of their uptake from particulate or dissolved organic matter and 20% from consumption of other microflora, to represent the consumption of bacteria by flagellates (Fenchel, 1982c; van Duyl *et al.*, 1990). Fenchel (1982b) calculated yields (gross growth efficiency) of two freshwater forms in terms of organic C were found to be 34 and 43%. Assuming a respiratory quotient of 1, net growth efficiencies are about 60% for both forms. Consequently, about 43 and 28% of the ingested bacterial food is egested (Fenchel, 1982b). Based on this and estimates bacterial growth efficiencies of around 50% (Cole, 1982, in Cole *et al.*, 1989; Fenchel, 1988; van Duyl *et al.*, 1990) and Fenchel's (1988) rule of thumb that phagotrophic micro-, nano-, and picoplankton incorporate about 40% of their uptake (be it in carbon, nitrogen or phosphorus), excrete about 30%, and mineralize or respire the remaining 30%, the gross growth efficiency (P/Q) was initially set to 0.45 and the fraction of unassimilated food (egested, excreted) to 30%).

10. Zooplankton

10.1. Herbivorous zooplankton (mainly copepods) and Omnivorous zooplankton (Microplankton)

Author: Steven Mackinson



Calanus finmarchicus

Based on evidence that cannibalism and carnivory/prey swithching is commonplace amongst copepods (Landry 1981; Daan *et al*., 1988), herbivous and omnivorous zooplankton were grouped into one functional group within the model.

With the onset of thermal stratification and the phytoplankton spring bloom, the biomass of copepods in the North sea increases rapidly, reaching as much as 80–90% of zooplankton biomass by May (Fransz *et al*., 1991b), with subadult copepodites typically accounting for more than 60% (Fransz and van Arkel, 1980). The bulk of the stock is comprised of only a few species, namely mention *Calanus finmarchicus, Psedocalanus elongates, Paracalnus parvus, Microcalanus pusillus, Acatia spp, Temora longicornis* (Krause and Trahms, 1983; Rae and Rees, 1947). Production in the northern North Sea is dominated by *Calanus finmarchicus* (Williams and Lindley, 1980a), whilst in the mixed and coastal areas, smaller species such as *Acartia tonsa* tend to dominate.

Production and biomass

It is challenging to provide an annual average estimate of the production and biomass of North Sea zooplankton, not least because of the large amount of work that it is necessary to review and compile, and particularly because the best available estimates vary considerably depending on what, where and when sampling was done and how the data have been treated. For this reason, this section provides information on the range of estimates readily available from literature. Fransz *et al.*'s (1991b) review of zooplankton in the North Sea is used extensively.

Copepods have a high growth rate. Fransz *et al*'s. (1991b) summary of information on the herbivorous and omnivorous zooplankton of the North Sea provides average daily production rates for May–September and P/B ratios for 3 common zooplankton (Table 10.1). Production was converted from g C to wet weight based using conversions factors for copepods given by Brey (2001) and summed giving a total estimate of 58.79 g ww m^{-2}. Using the average P/B of 9.2 y^{-1} for the three species over the same period, yields a biomass of 6.27 g ww m^{-2} (May–September). The estimate does not include information from *Calanus finmarchicus*, the most abundant and productive copepod in the northern North Sea. Fransz and Gieskes (1984) estimated total annual copepod production of 12.35 gC m^{-2} y^{-1} (147 g ww m^{-2} y^{-1}) for the whole North Sea using data from the Southern bight, Central North Sea and Northern North Sea. Applying Fransz *et al.*'s (1991b) estimate for P/B gives an estimate of total North Sea biomass of 16 g ww m^{-2}. This value was used in the model to achieve the production estimate of derived by Fransz and Gieskes (1984).

Production in the northern North Sea was studied intensively during FLEX (Fladen Ground Experiment 1976) and several authors have provided estimates from that data.

Combining information from Krause and Trahms (1983) on numbers of zooplankters March–June 1976 in the form of depth integrated time series (0–150 m) and mean weights from Broekheuizen *et al.* (1995) and Båmstedt (1998), standing stock biomass during summer peak was estimated to be 12.5 gC m^{-2} (roughly 125 g ww m^{-2}, assuming a 10:1 wet to carbon weight conversion). Table 10.2 and 10.3.

Table 10.1. Zooplankton production per day, per year (year = 153 days from May to September); Production/Biomass (P/B); g wet wt m^{-2} is the same as t km^{-2} (source data from Franz *et al.*,1991b, Table 5.1, p43).

Species	**Production per day g C m^{-2} d^{-1}**	**Production g wet wt m^{-2} y^{-1}**	**P/B yr^{-1}**	**Biomass g wet wt m^{-2}**
Temora longicornis	0.011933	21.76	8.667	2.511375
Acartia clause	0.006033	11.00	7.667	1.435333
Pseudocalanus elongates	0.014267	26.02	11.167	2.330241
		Total = 58.79	Average = 9.17	Total = 6.27

Table 10.2. Estimation of zooplankton biomass based on density per unit area and mean weights (g wet wt m^{-2} is the same as t km^{-2}).

Species	Average no. of individuals m^{-2} (0–150 m)[1]	Body weight (µg C)[2]	Biomass		
			(µg C m^{-2})	(g C m^{-2})	(g wet wt m^{-2})
Microcalanus pusillus	83,000	5.84	484720	0.48472	4.85
Oithona similis	222,000	1	222000	0.222	2.22
Paracalanus paracalanus	17,000	5.84	99280	0.09928	0.99
Calanus finmarchicus	167,000	67.2	11222400	11.2224	112.22
Pseudocalanus elongatus	42,000	5.84	245280	0.24528	2.45
Microsetella norvegica	11,000	5.84	64240	0.06424	0.64
Metridia lucens	11,000	5.84	64240	0.06424	0.64
Acartia claus	17,000	5.84	99280	0.09928	0.99
Total	570,000				125.61

[1] Based on Krause and Trahms (1983)

[2] Based on Broekheuizen *et al.* (1995; Table 31) and Båmstedt (1998; Table 1, p171)

Table 10.3. Individual weights used for converting numbers to biomass.

	Species	Body mass (µg C per individual)	
		Båmstedt (1998)	Broekheuizen *et al.* (1995)
Copepoda	*Calanus finmarchicus*	80	67.2
	Paracalanus parvus	5	
	Pseudocalanus	8	
	Acartia	4	
	Metridia longa	50	
	Temora longicornis	15	
	Centropages	10	
	Oithona similis	1	
	Harpacticoid copepod	2	
	Pareuchaeta		18
	Limacina retroversa		4.09
	Small copepods		5.84
Cladocera	*Evadne normanni*		1.01
	Evadne spinifera	1.01	
	Podon sp.	1	
	Unidentified	2	
Others	Ostracods	2	
	Barnacle nauplius	0.5	
	Metanauplius larvae	1	
	Zoea larvae	10	
	Calyptopis larvae	10	
	Foraminifera	5	
	Oikopleura sp.	1	
	Sagitta sp.	10	
	Pleurobranchia egg	0.4	
	Spionid larva	1	
	Euphasiids		1.58 mg C
	Tomopteris spp		200
	Hyperiid sp.		123
	Chaetognaths		24

The near coastal mixed areas of the North Sea have somewhat higher production than the northern and central regions with production estimated at around 5–20 gC m^{-2} y^{-1} (50–200 g ww m^{-2} y^{-1}) (Franz *et al*., 1991b).

Fransz *et al*. (1991b) provides other production estimates of abundant calanoid copepods in various regions of the North Sea given by Evans (1977), Martens (1980) and Roff *et al*. (1988):

- Evans (1977) multiplied the mean standing stock by the number of generations per year = 3.5 gC m^{-2} y^{-1} (7.74 g m^{-2} y^{-1}, 35 g wet wt m^{-2} y^{-1}).
- Martens (1980) summed peak maxima over the year for the Wadden Sea to give 0.4 gC m^{-2} y^{-1} (4 g wet wt m^{-2} y^{-1}). This estimate is considered too low by Fransz *et al.,* (1984).
- Roff *et al*. (1988) estimated production by multiplying mean biomass of copepods by instantaneous copepodite growth and the number of generation per year giving a mean of 16.5 gC m^{-2} y^{-1} (165 g wet wt m^{-2} y^{-1}). This value is considered by Fransz *et al*. (1984) as to high.

Other estimates of zooplankton production and biomass are found in the literature. Williams and Lindley (1980b) estimated zooplankton production of 14.5–27.8 g m^{-2} in May (0.5–0.9 gC m^{-2} d^{-1}). Fransz and van Arkel (1980) and Fransz (1980) estimated a daily production of 0.02–0.050 gC m^{-2} d^{-1} (0.2–0.5 g wet wt m^{-2} d^{-1}) during the peak of the phytoplankton biomass (end of April), when the population biomass was about 0.4 gC m^{-2}. In May the food level decreased but the *Calanus* biomass increased to 4 gC m^{-2} at the end of the month (equivalent to 40 g wet wt m^{-2}).

Nielsen and Richardson (1989) converted abundance of copepods to biomass using length–weight regressions taken from the literature (Table 1 in Nielson and Richardson 1989) and a conversion factor from dry weight to carbon of 45% (after Kiørboe *et al*., 1985). Total copepod biomass ranged from 2.5–8.8 mg C m^{-3} (approx. 2.7–9.5 g ww m^{-2} using Brey (2001) conversion for carbon to wet mass for copepods).

For comparison, Sherman *et al*. (1987) used P/B ratios from literature in estimating the production of macrozooplankton and microzooplankton on Georges Bank to be 17 gC m^{-2} y^{-1}, and 25 gC m^{-2} yr^{-1} respectively (in Mann, 2000, p252).

Consumption and Feeding

The energy transferred through the ecosystem by herbivorous and omnivorous zooplankton is not wholly derived through the direct consumption of living phytoplankton. There is now considerable evidence (Williams, 1981; Joiris *et al*., 1982; Sherr *et al*., 1986) that the zooplankton play an important part in the ‘recycling’ of energy, by their consumption of particulate organic material originating through heterotrophic processes. The packaging of particulate egesta into faecal pellets by many zooplankton is believed to be a highly important process in the rapid transport of food material to the seabed whereby it is made available to a benthic food-chain.

In 1974, Steele proposed that most primary production in the open sea was consumed by zooplankton but based on data from from 1971 to 1981, Fransz and Gieskes (1984) state that although copepod grazing matches primary production in all areas of the North Sea during the summer, zooplankton grazing during the spring and autumn bloom does not contribute significantly to the reduction of phytoplankton biomass. Much of the crop either sinks to the bottom or is consumed directly by protozoa and bacteria. Baars and Franz (1984, in Nielsen and Richardson, 1989) say that grazing by copepods in the central North Sea has been shown to be approximately 14, 9, and 3% of the primary production during the months of May, June and September. Overall, estimates of the percentage total primary production grazed by zooplankton in different areas of the North Sea vary from 35–100% (average 65%) (Fransz and Gieskes, 1984).

Copepods are the most important phytoplankton consumers but are also important in processing detritus as can be noted from the significance of detritus in the diets of several species. Cowey and Corner (1963) suggest that one of the reasons that detritus might be such an important food sources is that it appears to have an amino acid composition very similar to that of zooplankton. With increasing evidence, it is now generally accepted that adult stages of copepods are mixed food consumers (Pepita *et al*., 1970; Gaudy, 1974). *Calanus finamrchicus* feeds mainly of phytoplankton (Marshall and Orr, 1966) but is a capable of taking other (dead) material as well. It is armed with siliceous teeth that allow it to break diatomaceous shells. Landry (1981) conjectured that the sustained growth of *Calanus* after the diatom spring bloom might be a result of feeding on detrital remains or on animal food. Checkley (1980) stated that phytoplankton and dead particulate matter are used by *Paracalanus paracalanus*, but phytoplankton food is used for the production of eggs. Consuming mainly detritus *Microcalanus* is less dependent on phytoplankton food than other species. Poulet (1973, 1974, 1976) found that irrespective of season, non-living food formed the major part of the food ingested by *Pseudocalanus elongates*. Marshall and Orr

(1966) found that *Oithona similis* could eat only fairly large phytoplankton and very little of them. The small copepod feeds predominantly carnivorously. Pepita *et al.* (1970) characterised it as a mixed food consumer. Several authors noticed *Acartia clausi* feeding on phytoplankton (Anraku, 1964; Marshall and Orr, 1966). *Centropages typicus* fed almost equally well on animal and vegetable diets. *Temora stylifera* displayed a remarkable ability for predation.

Cannibalism is also known to be prevalent amongst zooplankton, particularly at times when food conditions for adults are poor. During an experimental study on population dynamics of copepods in the southern North Sea, Daan *et al.* (1988) showed that predation of nauplii by adults could be as high as 35% of the standing stock per day, although these rates were significantly depressed in the presence of alternative algal food.

Daro and Gijsegem (1984) estimated consumption rate by copepods stages II and IV to be around 4–5 µg C d^{-1} ind^{-1}. Assuming a mean weight of of a copepod to be 25.76 (µg C) (based on Båmstedt, 1998), gives and estimate of Q/B 0.19 d^{-1} or 30 y^{-1} (year May –Sept 153 days). Cushing and Vucetic (1963) suggested that the daily food intake of *Calanus* may be as much as 390% body weight, yielding a huge consumption rate estimate 262 (µgC d^{-1}) (where individual weight = 67.2 µg C after Broekheuizen *et al.*, 1995). The estimate based on Daro and Gijsegem (1984) appears to provide us with a reasonable estimate for these functional groups since total consumption compares favourably with that estimated by Paffenhöfer (1976). Paffenhöfer said that daily ingestions could be estimated at about 3–5 times daily production. In the model this implies a total consumption of around 450–750 g ww m^{-2} would be required. The value in the model is 480 g ww m^{-2}.

Daro and Gijsegem (1984) also report that daily net production efficiency versus ingestion was 20–30% for young copepod stages and perhaps even higher for adults. Based on this, the P/Q (gross efficiency) in the model is set to 30%. A value of 38% is used for the proportion of food unassimilated, which is close to an estimate of 33% for copepods given by Nielsen and Richardson (1989).

Environmental relationships

Information from the Continous Plankton Recorder has been used to investigate long term changes in the zooplankton community (Figure 10.1). Around 1980 a sudden decline of total biomass occurred followed by a recovery of biomass in the mid–late 1980s to early 1990s. These 2 events are visible for a majority of individual species as well and seem to affect smaller species more than larger ones as a result of the underlying structural shift in zooplankton communities, which have been widely reported and of a sufficiently large scale to be referred as a regime shift (Reid *et al.*, 1990; Beaugrand, 2004). The changes observed have been linked to changes in the flows of water masses and temperature (Clark, 2000; Clark *et al.*, 2001). Huntley and Lopez (1992) analyszed 181 instances of generation time and environmental temperature embracing 33 species of copepods and concluded that temperature alone accounts for more than 90% of the variation in growth, which might imply that copepods are seldom limited by food.

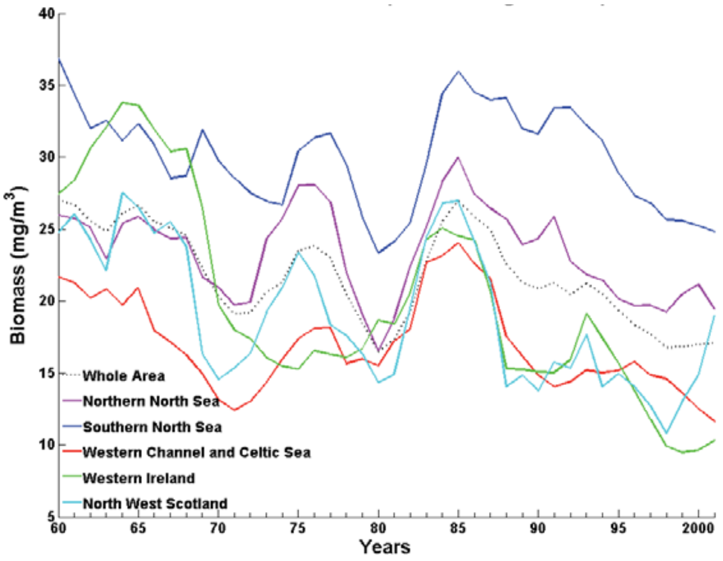


Figure 10.1. Evolution of annual average biomass concentration trend anomalies for the total 29 major species/taxa of copepods and cladocerans over the entire area and each of the five sub-areas. (figure courtesy of Dr. Clive Fox, data from SAHFOS).

10.2 Carnivorous zooplankton (Euphasiids, chaetognaths (arrow worms, eg sagitta), amphipods, mysiids, ichthyoplankton)

Author: Steven Mackinson

Euphausiid (Fowler, 1912)

Arrow worm

During March and April on the Fladen ground, Williams and Lindley (1980a) recorded large stocks of euphausiids which represented more than 90% of the standing stock of zooplankton biomass. Model parameter estimates for carnivorous zooplankton are based predominantly on Euphasiids, recognising that these form the major component of the biomass of this group.

Production and biomass

There are three dominant species of Euphausiacea in the North Sea, *Thysanoessa inermis* and *T. raschi* and *Meganyctiphanes norvegica*. *T. raschi* occurs almost exclusively over the continental shelf and is distribution is centred over shallower water than that of *T. inermis*, but their distributions overlap extensively. They mature in 1 year, no second year individuals have been found (Lindley and Williams, 1980).

Lindley (1980) gave estimates of production and biomass for the two *Thysanoessa* sp based on samples taken at 10 m deep from the Continous Plankton Recorder during 1966 and 1967 (Table 10.4). Using these and applying a conversion factor from wet to dry mass of 0.225 specific to euphasiids (Brey 2001) gives estimates of mean biomass equal to 0.78 g ww m^{-2} and production of 1.87 g ww m^{-2} y^{-1} and (represented over the entire North Sea), with a biomass weighted P/B ratio of 2.5 y^{-1} . Assuming (following Christensen 1995) that the third dominant Euphasiid species, *Meganyctiphanes norvegica*, adds 50% to the biomass, total North Sea euphasiid biomass and production can be estimated to be 1.17 g ww m^{-2} and 2.92 g ww m^{-2} y^{-1}.

In the model, a total biomass of carnivrous zooplankton of 3.4 g ww m^{-2} and production of 13.3 g ww m^{-2} y^{-1} are required to meet the consumption by higher trophic levels. Maximum biomass estimates for euphasiids from Lindleys data suggest a biomass 2.4 g ww m^{-2} and production of 5.4 g ww m^{-2} y^{-1}). Recognising that (i) euphassiids are often undersampled because they escape plankton nets, (ii) Lindley's calculations are based on biomass found at 10 m only and (ii) we do not have information on the biomass and production of other zooplankton to contributing to this group, the model estimates do not appear to be unreasonable.

Table 10.4. Annual production and biomass and P/B at 10 m depth estimated from CPR data in the North Sea area (adapted from Table 5, Lindley, 1980).

	1966			**1967**		
	Production (mg dry wt m^{-3} y^{-1})	**Biomass (mg dry wt m^{-3})**	**P/B y^{-1}**	**Production (mg dry wt m^{-3} y^{-1})**	**Biomass (mg dry wt m^{-3})**	**P/B y^{-1}**
T. inermis	2.5	1.47	1.7	3.25	2.37	1.37
B1	3.36	1.15	2.9	4.31	1.31	3.3
B2	1.69	0.69	2.46	2.13	0.75	2.84
C1	2.39	1.17	2.04	1.7	0.94	1.8
C2						
T.raschi						
C1	0.69	0.52	1.32	4.66	1.6	2.91
C2	1.36	0.45	3	1.3	0.31	4.14

Consumption and Feeding

Q/B is estimated in the model, assuming that ecotrophic efficiency = 0.95. In addition to Euphasiids, the arrow worm, *Sagitta* is known to be one of the major predators of copepods in the North Sea (Mann, 2000). Carnvirous zooplankton are fast swimming visual predators. In the model they prey mostly upon herbivorous and omnivorous zooplankton, with other small crustaceans, fish larvae and consumption through cannibalism being accounted for.

10.3. Gelatinous zooplankton

Authors: Georgi Daskalov, Steven Mackinson and Chris Lynam

The biomass estimate used in Ecopath B=0.066 t km^{-2} was based on Hay *et al.*'s (1990) report containing biomass estimates of *Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata* from North Sea trawl surveys in 1979, 1982, 1983. The jellyfish biomass was estimated in 4 sub-areas where jellyfishes are most abundant (East of Scotland, North of Scotland, East of Shetland, West of northern Denmark). Our estimate of the total biomass in the North Sea is a sum of the biomass from the 4 areas. The biomass originally given in carbon weight was converted back to wet weight using the relation ship 0.2% of wet weight = carbon weight, given in Hay *et al*. (1990). Hay *et al*. (1990) noted that their estimate may be substantially lower that the actual biomass because of the use of the poor of the gear used in the survey: International Young Gadoid Pelagic Trawl (IYGPT) so it can be assumed that the estimated value is the possible minimum of the actual gelatinous biomass in the sea. Other gelatinous organisms such as ctenophores are also not included, because of the lack of consistent information of their abundance.

Consumption rate was estimated using data on daily food ration (carbon) of 0.018 - 0.38 for *A. aurita* and 0.017 - 0.26 for *C. capillata* by Martinussen and Båmstedt (1995). We used the minimum estimates assuming that jellyfishes are food limited in nature. This yielded yearly Q/Bs of 6.48 and 6.12 of *A. aurita* and *C. capillata* respectively, which converted to wet weight and weighted by the respective biomass gave Q/B= 0.18 for the whole group.

The uncertainty of the biomass estimate makes even more important the setting of appropriate production/consumption rates. We estimated the production rates of *A. aurita* and *C. capillata* from their respective Q/Bs by multiplying with a P/Q coefficient 0.45. The resulting weighted group P/B is 2.858.

The diet composition of gelatinous plankton was compiled as an average from the diets of *A. aurita* and *C. capillata* reported by Martinussen and Båmstedt (1995) weighted by their respective consumption, and contained 90% zooplankton. During the balancing procedure it was modified due to instabilities in the model created by the original diet.

11. Benthic invertebrates (infauna and epifauna)

Author: Steven Mackinson

11.1 Data sources, treatment and approach

Data from synoptic surveys of the North Sea benthos (Figure 11.1) were compiled in to a single database and used to estimate the abundance, P/B ratio and production for over 1500 species of benthic invertebrates. Because of their particular importance in fisheries, additional information from from specific stock assessments, scientific papers and ICES working groups was used to estimate parameters for *Nephrops*, shrimp, large crabs and squid.

Infauna benthos survey

The North Sea Benthos (infauna) database contains 235 records from two sets of surveys (i) an international synpotic survey of macrobenthic infauna undertaken by the ICES Benthos Ecology Working Group (a group of ten laboratories from seven North Sea countries) in April 1986 using box corer's and sometimes van Veen Grab's covering 197 stations, and (ii) Data from the northern North Sea from 8 cruises (61 stations) in 1980 to 1985 (Eleftheriou and Basford (1989). The combined results are presented in various publications, syntheses of which are given in completeness by Künitzer *et al.* (1992) and the Atlas of the North Sea Bentic Infauna (Craeymeersch *et al.*, 1997) (VLIZ web page). Meiofauna samples (with replicates) were taken at 159 of the sites sampled in 1986. The mean of the replicates was used in the analyses done here. Macrofauna were recorded as numbers per m^2 and meiofauna as number per 10 cm^2.

The infauna benthos surveys counted the numbers of each species at each site, but pooled species in to taxonomic classes before weighing as g AFDW. Thus, without supplementary information on the mean weights of individual species the database cannot be used to calculate the biomass of each species. Conversion factors (Salzwedel *et al.*, 1985; Rumohr *et al.*, 1987) were used to convert the AFDW to wet weight. Weights of molluscs exclude shell, while echinoderm test and gut contents were weighed.

Epifaunal benthos surveys

Epibenthic fauna were sampled using a 2 m beam trawl during August 1999 and 2000 (total 511 stations) (Calloway *et al.*, 2002, Zühlke *et al.*, 2001). Sample abundances were standardized for trawl duration and speed to tows of 200 m, and represented as numbers per m^2. The numbers and weight of each species at each station was recorded, thus allowing the mean weight of each species and their biomass density at each station to be calculated. Bivalves and gasteropods were weighed with shells on, hermits crabs without shell, crabs with carapace, sea urchins and echinoderms with shell on (Calloway pers. comm.).

Approach to parameter estimation

The overarching strategy of the data analysis was to (i) maximise data by combining the two data sets, thereby filling information gaps and providing alternative estimates of parameters (i.e. getting a range) and (ii) work at the lowest possible resolution of the data so that the information is left in tact and can be used for other analyses and models that colleages may wish to undertake in the future. One of these opportunities has already been realised (Parker *et al.* in press) and another in progress.

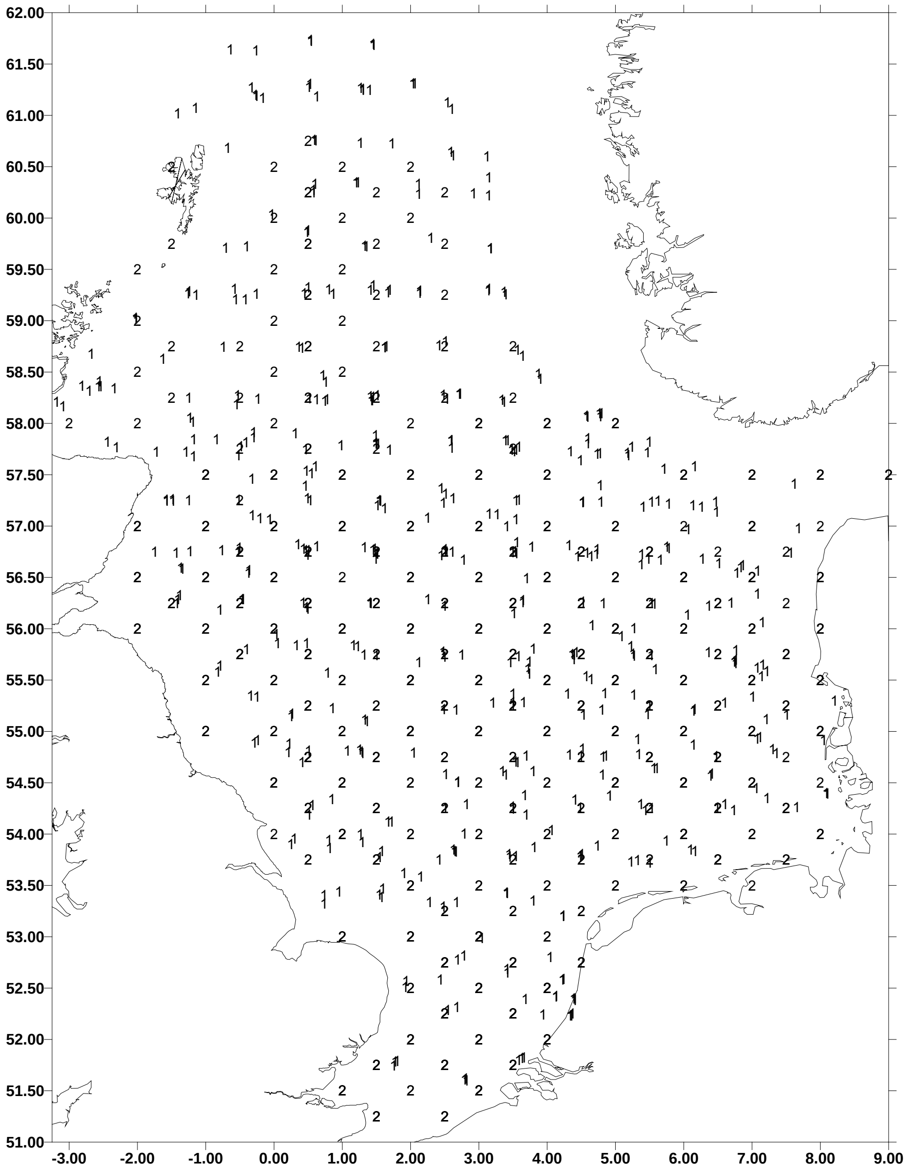
Because the infauna and epifauna surveys capture different information on the benthos by use of different samling devices, data sets were aggregated and complementary information from each survey was used to maximise the data opportunites of each individual data set. Under the assumption that sampling devices used in each survey give the best estimate of the relevant benthos components, epifauna surveys were used to estimate the species assigned to epifaunal functional groups and infauna suveys to estimate infauna and meiofauna functional groups (Table 11.2). Where gaps existed in the data for any species within a functional group, data from alternative surveys was used to fill these gaps whenever possible, thus allowing an estimate to be made for the majority of species. (ie, if they were not captured by one device, they probably were by the other). As an obvious example, the species classed as 'small mobile epifauna' were often not detected in the epifauna surveys, and so data from infauna surveys were used.

Estimates for all biomass, P/B ratios and production do not include the production of shell. Appropriate conversion factors taken from Dinmore (pers. comm.) and Brey (2001) were applied as necessary.

11.2 Estimating biomass from survey data

To calculate the biomass and P/B ratios, a mean weight of each species is required. Because the infauna survey did not record species weights, the mean weight had to be estimated for many species. These estimates are an important source of uncertaintly that translate through to biomass and production calculations. For this reason, it is necessary to describe in detail the methods and assumptions used in the estimation.

Figure 11.1. Epifauna (1) (1999 and 2000) and Infauna survey (2) (1986) sites.



11.2.1 Deriving mean weights for benthos

The method applied to derive mean weights for each of the 1500 species followed two main steps.

Step 1. Deriving mean weights from available data

1. Epifauna survey data was used to determine the mean weights for all species where numbers and sample weight were recorded.
2. The values obtained from the Epifauna data were assigned to each species sampled in the Infauna survey [note: Epifauna surveys generally catch larger individuals so this is likely a source so of overestimation of biomass and underestimation of P/B].
3. Species of the same genus, for which a mean was not available, were assigned an individual weight equivalent to the average of the species in the genus for which the mean weight was already assigned.
4. Data on the mean weight of 55 bivalves and 5 urchins collected from the North Sea for use in estimating Shell free wet weight : wet weight ratios (Dinmore, pers. comm. unpublished data) was applied to 11 bivalve species / genus.
5. Individual weights for 39 species, relating to samples from the North Sea only, were taken from Brey's database after applying the appropriate conversion from joules to grams.
6. Meiofaunal mean weights were taken from literature (Heip *et al.*, 1990; Huys *et al.*, 1992) and converted from dry to wet weight using a conversion of 0.25 (De Bovee, 1993 in Brey, 2001) (Table 11.1)

Table 11.1. Meiofauna mean weights of individuals.

	Mean ind. DW (µg)	Wet wt (g)
Nematodes	0.27	0.0000011
Harpacticoid copepods	2	0.0000080
Others	1.47	0.0000059

Step 2. Obtaining estimates for the remaining species.

Data on the mean weight individuals within a taxonomic classes, dervied seperately from Infauna surveys and epifauna surveys was used to estimate mean weights of the remaining species. Because the sampling method of each survey was better at sampling a particular component of the benthos, the information was used in two ways.

1. For infaunal functional groups (Table 11.2) (infaunal macrobenthos, small infauna and small mobile epifauna), the mean weight of the species taxonic class dervied from infauna surveys (Table 11.3) was applied to the relevant taxa within a functional group. The values from Eltheriuou and Basford (1989) were used. [note: for mullusca – this results in a higher estimate that Breys, an so overestimate biomass but underestimate P/B]
2. For epifauna groups (Epifaunal macrobenthos, large crabs, sessile epifauna sessile, shrimp, squid & cuttlefish, *Nephrops*) (Table 11.2), the mean weight of the species taxonic class dervied from the 1999 and 2000 epifauna surveys (Table 11.4) was applied to the relevant taxa within a functional group.

Table 11.2. Designation of the primary information sources used to estimate the biomass of each functional group.

Data source used	
Epifauna surveys	**Infauna survey**
Epifaunal macrobenthos	Infaunal macrobenthos
Sessile epifauna	Small infauna
Nephrops	Small mobile epifauna
Squid & cuttlefish	Meiofauna
Shrimp	
Lobsters & edible crabs (Large crabs)	

11.2.2 Biomass calculations

Data on biomass density calculated for the infauna and epifauna surveys were used to derive a 'best' estimate and range of total biomass of each species in the North Sea. The densities from the survey data considered most appropriate for the estimation of species within functional groups was taken as the the primary data source according

Table 11.3. Mean wet weights of individuals in a taxonmic class derived from infauna surveys data after conversion from AFDW to wet weight. Two conversion factors were tried and found to give broadly similar estimates. The values from Eltheriou and Basford were used*.

	Mean wt g wet weight Using Brey (2001) conversions	**Mean wt g wet weight Using Eleftheriou and Basford (1989) conversions**
Annelida	0.34	0.34
Bryozoa		
Cnidaria		
Crustacea	0.15	0.12
Echinodermata	0.52	0.55
Echiura		
Mollusca	0.48	0.76
Nemertea		
Phoronida		
Pycnogonida		
Tunicata		
Rest	0.43	0.23

* Eleftheriou and Basford (1989), Macrofauna wet weight to dry weight conversion factors: Polychaetes 15.50%, Crustaceans 22.50%, Echinoderms 8%, Molluscs 8.50%, Miscellaneous 15.50%.

Table 11.4. Mean wet weights of individuals in a taxonmic class derived from 1999 and 2000 ipifauna surveys data.

	Mean wt (g)
Annelida	9.74
Bryozoa	
Cnidaria	
Crustacea	5.16
Ctenophora	0.64
Echinodermata	10.80
Echiura	0.89
Mollusca	15.51
Nemertea	0.33
Phoronida	
Porifera	
Pycnogonida	0.65

Table 11.5. Brey's empirical model for estimating P/B.

log(P/B) =	7.947	Intercept	Variables
+	-2.294	* log(M)	M = Mean Indiv. Body Mass (kJ)
+	-2409.856	* 1/(T+273)	T = Bottom Water Temperature (°C)
+	0.168	* 1/D	D = Water Depth (m); Intertidal = 1m, Minimum = 1m
+	0.194	* SubT	Subtidal? Yes:1; No: 0
+	0.180	* In-Epi	Infauna =1 or Epifauna = 0
+	0.277	* MoEpi	Motile Epifauna? Yes:1; No: 0
+	0.174	* Taxon1	Annelida or Crustacea? Yes: 1; No: 0
+	-0.188	* Taxon2	Echinodermata? Yes: 1; No: 0
+	0.330	* Taxon3	Insecta? Yes: 1; No: 0
+	-0.062	* Habitat1	Habitat = Lake? Yes: 1; No: 0
+	582.851	* log(M)*1/(T+273)	Composite Variable log(M) * 1/T

to the designation in Table 11.2. Where no information from the primary survey existed, values were taken from the secondary data where available [in particular – small mobile epifauna, infaunal macrobenthos and small infauna were estimated using information from both surveys]. This approach provided us the opportunity to obtain a more complete estimation for each species and in many cases derive 2 or 3 estimates, from which best estimates and lower and upper limits could be defined.

Mutltiplying density estimates to total biomass

Both infauna and epifauna survey show excellent coverage throghout the North Sea (Figure 11.1), so the simplest calculation of total biomass is:

Biomass (t) = (Mean biomass density over all stations/ Efficiency factor) * Area of North Sea (Eq 1)

Grabs and cores used in the infauna surveys were assumed to take complete samples with an efficiency of 1. The beam trawl used in the epifauna surverys was assigned an efficiency of 0.35 based on estimates reported in Kaiser *et al*. (1994). Note: Reiss *et al*. (2006) give overall estimates for 2 m beam trawl 36–44%.

Meiofauna were samples less frequently and over a more restricted area than other infauna. An overall mean density was calculated as the mean densities from the stations at which each species was found multiplied by the proportion of stations sampled at which they were found (total 165 stations), total biomass being:

Biomass t = (average biomass density at stations found * proportion of stations found at/ efficiency factor) * Area of North Sea (Eq 2)

The epifauna survey data included information on the ICES rectangles from which samples were collected. This provided the opportunity to use approach to estimate biomass using an area based weighting, whereby the proportion of ICES rectangles that a species was found to occur was used to weight the average density of species. The total biomass of each species is:

Biomass t = (mean biomass density at station found at * proportion of ICES rectangle found at)/ efficiency factor * Area of North Sea (Eq 3)

For epifauna, the average of estimates derived from simple area based weighting (Eq 1) and rectangle weighting (Eq 3) was taken as the best estimate.

11.3 Estimating P/B

Information from Thomas Brey was used in deriving estimates for P/B.

Conversions for use in Brey sheet

Where available, P/B ratios for 39 North Sea species were taken from Breys database (kindly supplied by T. Brey). Brey's (2001) empirical model for estimating production of benthic invertebrates (version 4.04, Table 11.5) was then used to estimate a mean, upper and lower estimate for the P/B ratio for the remaining species (most). For quality control, Thomas Brey was consulted directly and kindly checked the calculations.

Note: Breys empiracle relationships spreadsheet has been shown to be a good estimator of P/B *ratios (Cartes et al. 2002), but it is particularly sensitive to the weight or the organism and so care must be taken to ensure a good estimate for the particlaur system. It is not advised to borrow a value for the same species from another system because the mean weight could be very different (Brey pers. comm.).*

After first converting to shell free weights, wet weight was converted to kilo joules using Breys conversion J/mgWM. Where possible, species specific conversions were obtained from Breys conversions database, otherwise the mean conversion factors were obtained from values reported for species within the same taxomic family, order, subclass, or class, which ever was the lowest resolution, with the number of records greater than 10 (under advice of T . Brey). These conversions were later applied backwards to calculate mean weights of 39 species sampled from the North Sea.

A mean annual bottom temperature of 10°C was used (Cefas Science Series Data Report No. 40) and mean water depth of 90 m was applied in the model.

11.4 Infaunal macrobenthos, Small infauna (polychaetes), Epifaunal macrobenthos (mobile grazers), Small mobile epifauna (swarming crustaceans), Sessile epifauna

Brittle star *Ophiura* (Fowler, 1912)

Excluding meiofauna (see section 11.7), five functional groups make up the major part of the biomass of benthic invertebrate sampled by the North Sea benthos surveys (Table 11.6). Consistent with the classifications used by benthic ecologists and the information available to estimate parameters for the groups, functional groups were designated on the basis of habitat (infaunal and epifauna) and size. These classifications bear relevance to the trophic interactions with predators of these groups whose feeding mode and selection is adapted to exploiting particular groups of prey species. The groups consist mainly of polychaetes, bivalve molluscs, echinoderms, and small crustaceans; organisms that make up an important part of the diet of main demersal fish (McIntyre, 1978).

Biomass, distribution and production

Infauna

North Sea infaunal macrobenthos can be characterised as consisting of northern species extending south to the northern margins of the Dogger Bank (50 m depth contour), and southern species extending north to the 100 m depth contour at 57–58°N. The central North Sea is an area of overlap especially around the 70 m depth contour (Künitzer *et al.*, 1992). Distributions and abundance are related to current patterns in the North Sea, sediment composition and chlorophyll a content, annual temperature variations and availability of food (Heip *et al.*, 1992; Heip and Craeymeersch, 1995) with some species being restricted to certain sediment types (Künitzer *et al.*, 1992). The northern region is typified by smaller body species, higher density and greater diversity, although total biomass and that of individual taxonomic groups is greater in the south (Figure 11.2). Overall average biomass of infaunal macrobenthos was estimated by Heip *et al.* (1992) to be around 7 g AFDW m^{-2} (SE=7.6) [see (copy) Figure 11.2 below]. Applying a conversion for wet weight to ash free dry weight 15:1 (Christensen, 1995, p. 26), this is 105 g WW m^{-2}. They caution that because sampling was undertaken in April, a time commonly assumed to be a moment of minimum biomass, before the onset of the main growing season it is likely to be an underestimation. Nonetheless, the value is twice as high as that previously estimated by Rachor (1982) (3.2 g AFDW m^{-2}).

Results of the analysis described in section 11.2 reveal that the bulk of the weight of the standing stock of infauna to be dominated by echinoderms, polychaetes and bivalve molluscs (Table 11.8). Five species, *Amphiura filiformis* (brittle star), *Aphrodita aculeata* (polychaete) *Myriochele* (polychaete), *Nephtys cirrosa* (polychaete) and *Arctica islandica* (bivalve) account for 50% of the infaunal biomass. Because of their small size, some of the species listed as indicator species by on the basis of their abundance Heip *et al.* (1992) (eg *Spiophanes bombyx*) , are notably absent from the biomass ranking (Table 11.7). Best estimates and ranges for the biomass and weighted P/B of functional groups are given in Table 11.9.

Epifauna

As for infauna, epibenthic species diversity is lower in the southern North Sea than in central and northern areas, and there are distinct boundaries between communities that relate to hydrodynamic conditions, particularly the boundary between mixed and stratified water masses. There is no clear latitudinal gradient in the biomass of epibenthic species in contrast to infauna. Bottom temperature, sediment characteristics parameters and beam trawling activity are also correlated with species richness and diversity. In the southern North Sea, free-living scavenging and predatory species predominate with species like echinoderms (asteroids and ophiuroids) making up most of the biomass, while north of the 50 m contour, filter-feeding sessile species (bryozoans, anthozoans) dominate the epibenthos (Callaway *et al.*, 2002).

Biomass estimates show the bulk of the weight of the standing stock of epifauna to be dominated by echinoderms, polychaetes and molluscs (Table 11.8). Four species *Euspira pulchellus* (formerly *Lunatia poliana)* (gastropod mollusc), *Philine quadrata* (gastropod mollusc), *Ophiura albida* (brittle star) and *Leptochiton asellus* (Chiton) account for 65% of the biomass of free-living species. The biomass of small mobile epifauna is dominated (20%) by the amphipod *Bathyporeia elegans* with numerous copepod species of great abundance. Some species that

Table 11.6. Description of functional groups used in the model.

Functional group	Description
Infaunal macrobenthos	Bivalves and gasteropods mostly larger than 2 mm, eg, cockles, cardium and buccinium. Filter feeders and grazers.
Small infauna	Mostly polychaetes (Sabella, Nereis, sipunculus, turbellaria, arenicola, sagitta and others) and small crustaceans that live in the sediment. Filter feeders and predators.
Epifaunal macrobenthos	Free-living surface living macrobenthos. Mostly echinodermes (brittle stars, sea urchins), small crabs, gasteropods, scallops.
Small mobile epifauna	Crustaceans, molluscs, and polychaetes that live on the benthic interface and mysids, gammarids and amphipods that swarm off the bottom.
Sessile epifauna	Suspension and filter feeders including anemones, sponges (dead-mans fingers), corals, tunicates, gorgonians, hydroids, anthozoans, pelecypods, barnacles (eg *Balanus*), bryozoans, attached bivalves (mussels), and crinoids, ascidians, oysters).

Table 11.7. Abundance and biomass of infaunal macrobenthos typically characteristic of the sourthern, central and northern North Sea. (after Künitzer *et al*., 1992, Table 5, p131).

	Southern			Central		Northern	
Indicator species	*Nephtys c.* *Echinocardium c.* *Urothoe p.*	*Aonides p.* *Phoxocephalus h.* *Pisione r.*	*Nocula n.* *Callianassa s.* *Eudorella t.*	*Ophelia borealis* *Nephtys longosetosa*		Minuspio c. *Thyasira sp.* *Aricidea c.* *Exogone v.*	Ophelia b. *Protodorvilla k.* *Exogone h.* *Spiophanes b.* *Polycirrus*
Sediment	<30 m coarser sediment	30–50, muddy fine sand		50–70, fine sand	70–100m	>100, fine sediment	<100 m coarser sediment
Species	27	29	44	43	54	51	44
Ind/m^2	805 (±728)	873 (±623)	1995 (±1499)	1093 (±686)	1224 (±1233)	2863 (±1844)	1775 (±1114)
Biomass (g AFDW/m^2)	9.5 (±9.9)	4.3 (±4.3)	12.6 (±7.5)	7.6 (±6.5)	7.4 (±7.0)	3.5 (±3.7)	3.8 (±2.2)

are know to be widely distributed (eg *Ophiura ophiura, Onchidoris bilamellata, Pagurus bernhardus, Astropecten irregularis, Anapagurus laevis, Pagurus pubescens, Luidia sarsi, Pagurus prideaux*) are notably absent from the biomass ranking. Sabellid fan worms are responsible for the vast majority of biomass in the sessile epifauna group. Best estimates and ranges for the biomass and weighted P/B of functional groups are given in Table 11.9.

It is noticeable from the figures in Calloway *et al.* (2002) that the numbers of demersal fish (caught in a 2 m beam trawl) is considerably higher in the southern North Sea and shows a distinct latitudinal gradient in the offshore waters. This pattern is consistent with the distribution of infaunal biomass suggesting that the biomass of available food is more important than the numbers of items. In contrast, the numbers of demersal fish caught with an otter trawl is distinctly higher in the northern North Sea, where the abundance of epibenthic species is higher. It is difficult to relate this to the distribution of benthos biomass since the epibenthos biomass distribution does not show a clear trend. It does however, relate more closely to the distribution of forage fish (Norway pout, herring, blue whiting, sandeel) that many of the larger demersal fish (cod, saithe) prey upon.

Consumption and feeding

The spectrum of feeding modes is exhited by benthic invertebrates. Duinelveld *et al.* (1991, Table 4, p 136–137) classified species according to 5 modes (i) suface deposit feeders, (ii) subsurface deposit feeders, (iii) carnivores, (iv) filter feeders, (vi) herbivores. The first three of these were the dominant types exhibited by North Sea fauna and were found to be closely related to the particle size and amount of organic carbon in the sediment. Subsurface deposit feeding occurred mainly in muddy sediments, predation by polychaetes in coarse sediments, and surface deposit feeding by polychaetes in fine sand level bottom areas.

Duinelveld *et al.* (1991) states that from a proposed average production figure and a realistic transfer efficiency of 20% (Gray, 1981) it follows that the potential food demand of the North Sea benthos amounts to an average of 50g AFDW m^{-2} or 20 g C m^{-2} yr^{-1}, and for the southern, central and northern North Sea, 40, 10 and 3 g C m^{-2} yr^{-1}, respectively (Table 4 in Duineveld *et al.*, 1991).

As Q/B is unknown, a gross conversion efficiency of 15% is assumed, leaving Q/B to be estimated in the model.

Environmental relationships

Major changes have occurred in the abundance and distribution of benthic fauna over the last half a century and are believed to be linked mainly to current patterns in the North Sea, annual temperature variations and availability of food (Kröncke, 1990; Heip and Craeymeersch, 1995).

Table 11.8. Table provides biomass (shell free), P/B and production (shell off) for main species in each functional groups for marine benthic invertebrates. The table shows the contributions of each species to the total benthos and to each functional group.

Functional Group	Species	Common/Phylum	Best estimate biomass (t)	P/B y^{-1}	Production g m^2 y (t km^2 y)	% of functional group	% of total benthos
Infaunal macrobenthos	*Amphiura filiformis*	Brittle star	59,284,123	1.97	204.55	38%	11%
Infaunal macrobenthos	*Arctica islandica*	Bivalve – Icelandic cyprine	19,680,382	0.32	11.05	13%	4%
Infaunal macrobenthos	*Aphrodita aculeata*	Polychaete	18,862,318	0.36	11.85	12%	3%
Infaunal macrobenthos	*Mysella bidentata*	Bivalve	10,230,285	0.71	12.79	7%	2%
Infaunal macrobenthos	NEMERTEA	Nemertea: ribbon worms	6,037,553	0.60	6.40	4%	1%
Infaunal macrobenthos	*Spisula subtruncata*	Bivalve	5,903,433	3.16	32.72	4%	1%
Infaunal macrobenthos	*Thyasira spp.*	Mollusca	3,051,671	0.81	4.33	2%	1%
Infaunal macrobenthos	*Chamelea gallina*	Bivalve – Striped Venus Clam	2,552,396	4.14	18.55	2%	0%
Infaunal macrobenthos	*Echinocardium cordatum*	Echinoderm – Sea Potato	2,314,220	0.44	1.80	1%	0%
Infaunal macrobenthos	*Abra prismatica*	Mollusca	1,791,534	2.64	8.30	1%	0%
Infaunal macrobenthos	*Gari fervensis*	Bivalve – Faroe sunset shell	1,766,421	0.38	1.17	1%	0%
Infaunal macrobenthos	*Echinocardium flavescens*	Echinoderm – heart urchin	1,730,580	0.46	1.40	1%	0%
Infaunal macrobenthos	*Dosinia lupinus*	Mollusca	1,607,864	0.47	1.32	1%	0%
Infaunal macrobenthos	*Antalis entalis*	Mollusc – Tusk shell	1,465,628	0.58	1.49	1%	0%
Infaunal macrobenthos	*Nicomache spp.*	Annelida	1,402,496	0.93	2.30	1%	0%
Infaunal macrobenthos	CAUDOFOVEATA	Mollusca	1,230,714	0.51	1.11	1%	0%
Infaunal macrobenthos	*Nuculoma tenuis*	Mollusca	1,025,121	0.69	1.24	1%	0%
Infaunal macrobenthos	*Phaxas pellucidus*	Bivalve – razor shell	919,438	0.60	0.97	1%	0%
Infaunal macrobenthos	PELECYPODA	Mollusca	910,928	0.66	1.06	1%	0%
Small infauna	*Myriochele spp.*	Annelida	25,411,578	0.93	41.61	17%	5%
Small infauna	*Nephtys cirrosa*	polychaete – catworm	12,173,138	0.62	13.22	8%	2%
Small infauna	*Ophelia borealis*	Polychaete	9,769,032	0.89	15.28	7%	2%
Small infauna	*Nephtys hombergii*	Polychaete – catworm	9,373,711	0.77	12.62	6%	2%
Small infauna	*Magelona spp.*	Annelida	9,153,197	0.93	14.99	6%	2%
Small infauna	*Pholoe spp.*	Annelida	7,758,503	0.93	12.70	5%	1%
Small infauna	*Phoronis spp.*	Phoronida	4,780,521	**1.30**	10.94	3%	1%
Small infauna	*Gattyana cirrosa*	Polychaete	4,310,655	0.52	3.97	3%	1%
Small infauna	*Minuspio cirrifera*	Annelida	3,544,541	0.93	5.80	2%	1%
Small infauna	*Nephtys longosetosa*	Polychaete – catworm	3,212,051	0.79	4.45	2%	1%
Small infauna	*Goniada maculata*	Polychaete	3,117,128	0.93	5.10	2%	1%
Small infauna	*Levinsenia gracilis*	Annelida	3,102,853	0.93	5.08	2%	1%
Small infauna	*Pisione remota*	Annelida	3,001,104	0.93	4.91	2%	1%
Small infauna	*Exogone verugera*	Annelida	2,513,936	0.93	4.12	2%	0%
Small infauna	*Amphictene auricoma*	Polychaete	2,047,433	0.93	3.35	1%	0%
Small infauna	*Spio filicornis*	Annelida	1,972,823	0.93	3.23	1%	0%
Small infauna	*Aonides paucibranchiata*	Annelida	1,965,104	0.93	3.22	1%	0%
Small infauna	*Owenia fusiformis*	Polychaete	1,884,708	1.30	4.29	1%	0%
Small infauna	*Exogone hebes*	Annelida	1,731,480	0.93	2.84	1%	0%
Small infauna	*Notomastus latericeus*	Annelida	1,696,706	0.93	2.78	1%	0%

Table 11.8. continued: Table provides biomass (shell free), P/B and production (shell off) for main species in each functional groups for marine benthic invertebrates. The table shows the contributions of each species to the total benthos and to each functional group.

Functional Group	Species	Common/Phylum	Best estimate biomass (t)	P/B y^{-1}	Production g m^2 y (t km^2 y)	% of functional group	% of total benthos
Small infauna	*Paramphinome jeffreysii*	Annelida	1,653,632	0.93	2.71	1%	0%
Small infauna	*Protodorvillea kefersteini*	Annelida	1,591,969	0.93	2.61	1%	0%
Small infauna	*Lumbrineris latreilli*	Annelida	1,332,201	0.93	2.18	1%	0%
Small infauna	*Caulleriella spp.*	Annelida	1,254,105	0.93	2.05	1%	0%
Small infauna	*Goniadella bobretzkii*	Annelida	1,161,153	0.93	1.90	1%	0%
Small infauna	*Diplocirrus glaucus*	Annelida	1,128,703	0.93	1.85	1%	0%
Small infauna	*Nephtys caeca*	Polychaete – catworm	1,099,251	0.77	1.48	1%	0%
Small infauna	*Prionospio malmgreni*	Annelida	1,065,960	0.93	1.75	1%	0%
Small infauna	*Pseudopolydora cf. pauchibranchiata*	Annelida	1,063,221	0.93	1.74	1%	0%
Small infauna	*Tharyx spp.*	Annelida	1,047,702	0.93	1.72	1%	0%
Small infauna	*Scalibregma inflatum*	Annelida	928,607	0.93	1.52	1%	0%
Small infauna	*Poecilochaetus serpens*	Annelida	826,443	0.93	1.35	1%	0%
Small infauna	*Anobothrus gracilis*	Annelida	813,330	0.93	1.33	1%	0%
Small infauna	*Nephtys paradoxa*	polychaete – catworm	809,476	0.73	1.04	1%	0%
Small infauna	*Glycinde nordmanni*	Annelida	783,618	0.99	1.36	1%	0%
Small infauna	*Sthenelais limicola*	Annelida	747,019	0.93	1.22	1%	0%
Small infauna	*Laonice sarsi*	Annelida	740,213	0.93	1.21	1%	0%
Small infauna	*Scoloplos armiger*	Annelida	736,499	1.67	2.16	1%	0%
Epifaunal macrobenthos	*Euspira pulchellus*	Mollusca	28,242,467	0.39	19.18	31%	5%
Epifaunal macrobenthos	*Leptochiton asellus*	Chitons	13,235,490	0.32	7.33	15%	2%
Epifaunal macrobenthos	*Philine quadrata*	Mollusca	8,256,192	0.39	5.61	9%	2%
Epifaunal macrobenthos	*Ophiura albida*	Brittle star	7,912,729	0.31	4.37	9%	1%
Epifaunal macrobenthos	OPHIUROIDEA	Echinodermata	6,813,422	0.53	6.34	8%	1%
Epifaunal macrobenthos	*Euspira montagui*	Mollusca	4,848,350	0.39	3.29	5%	1%
Epifaunal macrobenthos	*Hyala vitrea*	Mollusca	3,271,025	0.39	2.22	4%	1%
Epifaunal macrobenthos	*Ophiura affinis*	Brittle star	2,810,803	0.47	2.31	3%	1%
Epifaunal macrobenthos	*Anomia ephippium*	Bivalve – saddle oyster	1,642,671	0.42	1.21	2%	0%
Epifaunal macrobenthos	*Corystes cassivelaunus*	Crustacean – masked crab	1,563,156	0.54	1.48	2%	0%
Epifaunal macrobenthos	*Asterias rubens*	Asteroidea – Common starfish	1,328,595	0.23	0.55	1%	0%
Epifaunal macrobenthos	*Leptochiton*	Chitons	1,068,471	0.32	0.59	1%	0%
Small mobile epifauna	*Bathyporeia elegans*	Arthropoda	2,809,294	1.44	7.11	21%	1%
Small mobile epifauna	*Harpinia antennaria*	Arthropoda	1,146,257	1.44	2.90	1%	0%
Small mobile epifauna	*Urothoe poseidonis*	Arthropoda	976,727	1.44	2.47	1%	0%
Small mobile epifauna	*Eudorellopsis deformis*	Arthropoda	919,354	1.44	2.33	1%	0%
Small mobile epifauna	*Bathyporeia guilliamsoniana*	Arthropoda	764,209	1.44	1.93	1%	0%
Small mobile epifauna	*Philine scabra*	Mollusca	725,569	0.79	1.00	1%	0%
Small mobile epifauna	*Eudorella emarginata*	Arthropoda	554,876	1.44	1.40	1%	0%

Table 11.8. continued: Table provides biomass (shell free), P/B and production (shell off) for main species in each functional groups for marine benthic invertebrates. The table shows the contributions of each species to the total benthos and to each functional group.

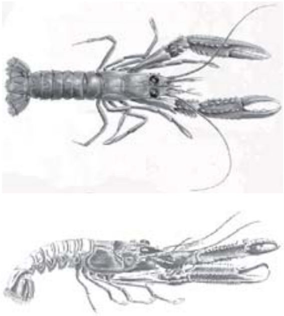
Functional Group	Species	Common/Phylum	Best estimate biomass (t)	P/B y^{-1}	Production g m^2 y (t km^2 y)	% of functional group	% of total benthos
Shrimp	*Crangon crangon*	Crustacean – brown shrimp	89,918	0.93	0.15	36%	0%
Shrimp	*Crangon allmanni*	Crustacean – shrimp	35,986	1.00	0.06	14%	0%
Shrimp	*Eualus pusiolus*	Crustacean	24,811	0.89	0.04	10%	0%
Shrimp	*Pandalus montagui*	Decapod	24,494	0.86	0.04	10%	0%
Shrimp	*Spirontocaris lilljeborgi*	Decapod	19,116	0.87	0.03	8%	0%
Shrimp	*Processa nouveli*	Decapod – processid shrimp sp.	14,390	1.10	0.03	6%	0%
Shrimp	*Pandalus borealis*	Decapod	11,068	0.80	0.02	4%	0%
Shrimp	*Pandalina spp.*	Decapod	10,395	0.57	0.01	4%	0%
Large crabs	*Liocarcinus holsatus*	Crustacean – flying crab	380,116	0.55	0.36	49%	0%
Large crabs	*Hyas coarctatus*	Crustacean – Lyre crab	125,792	0.64	0.14	16%	0%
Large crabs	*Cancer pagurus*	Crustacean – edible crab	70,986	0.28	0.04	9%	0%
Large crabs	*Liocarcinus marmoreus*	Crustacean – marbled swimming crab	48,291	0.54	0.05	6%	0%
Large crabs	*Pisidia longicornis*	Crustacean – squat lobster	36,460	0.94	0.06	5%	0%
Large crabs	*Lithodes maia*	Crustacean – northern stone crab	34,892	0.28	0.02	5%	0%
Sessile epifauna	Sabellidae	Annelida	84,232,955	0.28	41.55	70%	16%
Sessile epifauna	*Modiolus modiolus*	Bivalve – horse mussell	15,484,029	0.14	3.78	13%	3%
Sessile epifauna	*Chaetopterus variopedatus*	Annelida	10,625,359	0.28	5.24	9%	2%
Sessile epifauna	Serpulidae	Annelida	6,492,357	0.28	3.20	5%	1%
Sessile epifauna	*Musculus discors*	Bivalve – Green crenella	1,377,075	0.22	0.54	1%	0%
Sessile epifauna	*Modiolus barbatus*	Bivalve – bearded horse mussell	589,940	0.20	0.21	0%	0%
Sessile epifauna	*Musculus niger*	Mollusca	545,040	0.22	0.21	0%	0%
Sessile epifauna	*Pododesmus patelliformis*	Bivalve – ribbed saddle oyster	401,542	0.22	0.16	0%	0%
Sessile epifauna	*Modiolus spp.*	Mollusca	277,368	0.12	0.06	0%	0%
Sessile epifauna	*Serpula vermicularis*	Polychaete – Tube worm	40,149	0.28	0.02	0%	0%
Sessile epifauna	*Sabellaria spinulosa*	Polychaete – Ross worm	3,179	0.17	0.00	0%	0%
Meiofauna	NEMATODA	Nematoda	532,114	10.64	9.93	52%	0%
Meiofauna	COPEPODA	Arthropoda	141,194	11.26	2.79	14%	0%
Meiofauna	TURBELLARIA	Platyhelminthes	88,933	10.64	1.66	9%	0%
Meiofauna	GASTROTRICHA	Gastrotricha	32,880	10.64	0.61	3%	0%
Meiofauna	POLYCHAETA	Annelida	27,287	12.22	0.58	3%	0%
Meiofauna	OSTRACODA	Arthropoda	8,786	10.93	0.17	1%	0%

Table 11.9. Biomass ranges , P/B and production of functional groups. Group P/B is weighted by the biomass of species in the group.

Functional Group	Group biomass (t km^{-2}) (mean overall)	Group P/B	Production g m^2 y	MIN Group biomass (t km^{-2}) (mean overall)	MIN Group P/B	MIN Production g m^2 y	MAX Group biomass (t km^{-2}) (mean overall)	MAX Group P/B	Average P/B for fill ins
Infaunal macrobenthos	274.8041	1.262911	347.0530563	0.4253	0.367802	0.16	274.8041	1.3039	0.93
Nephrops	0.1393	0.350	0.048799555	0.1017	0.291	0.03	0.2131	0.421	
Small infauna	255.9500	0.9045401	231.5170445	0.1176	0.705703	0.0830044	255.9500	1.03052	1.60154
Epifaunal macrobenthos	157.9905	0.3884	61.36252985	7.8719	0.3209	2.5261873	6.7690	0.4539	0.625
Gelatinous zooplankton	0.0152	0.790	0.01202913	0.0085	0.696	0.0059004	0.0220	0.898	0.790
Large crabs	0.7948	0.5053076	0.401642622	0.5588	0.435693	0.2434597	1.3408	0.61106	
Sessile epifauna	210.6474	0.2609615	54.97085368	-	-	-	-	-	
Shrimp	0.4428	0.9113264	0.403573798	0.2453	0.778822	0.1910644	0.5671	1.03703	0.959
Small mobile epifauna	23.8811	1.3660235	32.62	0.0023	0.761171	0.00	0.0073	1.00322	1.72792
Squid & cuttlefish	0.0387	0.2658076	0.010276946	0.0184	0.240425	0.0044317	0.0589	0.30609	0.39203
Meiofauna	1.8090	10.818594	19.57126184	-	-	-	-	-	12.5633
Unclassified	21.0129	0.964987	20.27718324	-	-	-	-	-	1.43655

11.5 *Nephrops*

Authors: Steven Mackinson and Jon Elson



Nephrops norvegicus, the Norwegian Lobster forms burrows in distinct areas of suitable muddy sediment. Burrow emergence is known to vary with environmental (eg ambient light level, tidal strength) and biological factors (eg moult cycle, females reproductive condition).

Biomass and Production

Because catch rates depend heavily on burrow emergence, trawl catches may bear little resemblance to population abundance. Underwater TV surveys are used routinely by Scottish and English researchers to estimate *Nephrops* population abundance by averaging burrow densities of *Nephrops* and raising to stock area. Using all the available information from 1993–2004 TV surveys, mean burrow density for *Nephrops* was taken as 0.36 m^{-2} (Table 11.10). Weighted mean (based on area of each stock) = 0.25 m^{-2}.

Total abundance and biomass within the North Sea functional units (FU) was calculated by raising the mean survey density to the total area of the FUs (107,785 km^2) and converting weight, using a Length–Weight relationship based on 2003 *Nephrops* data (E. Bell, pers. comm.) $W(g) = 10^{(3.266*\log10\ \text{Length (mm)})} - 3.59$. Mean length of *Nephrops* in catches was calculated from data on FU 9,7,6 to be 28.46 mm, equating to a mean individual weight of 14.43 g. Total biomass within the North Sea FUs was estimated to be 557,310 t (392,884 t using weighted mean), which for application in the model translates to a mean density of 0.98 t km^{-2} (0.7 t km^{-2} using weighted mean density) across the entire of the North Sea.

Total mortality (Z) was used as the proxy for P/B y^{-1}, and was calculated by summing natural and fishing mortality. ICES (WGNNSK, 2005) assume a natural mortality rate of 0.3 for males and immature females, with a value of 0.2 for mature females. The lower value for mature females reflects the reduced burrow emergence while ovigerous, and hence an assumed reduction in predation (ICES WGNSSK, 2005). Accounting for the fact that roughly 35% of the catch is discarded, fishing mortality in 1991 (calculated as F=Landings+ estimated discards/biomass) is estimated to be 0.06, but can be considered low because there are concerns over the accuracy of landings (underreporting). A harvest control rule with F between 0.2 and 0.25 has been shown, for other species, to be sustainable while delivering a reasonably high yield (ICES WGNSSK, 2005). In the model an initial estimate of P/B of 0.35 y^{-1} is used based on M=0.25 and F=0.1.

Alternative calculations for biomass made using the 1999 and 2000 North Sea epifauna survey data and Brey's benthic invertebrate production model, provide very comparable estimates with an average biomass of 0.139 t km^{-2} and P/B ratio of 0.35 y^{-1} (Table 11.9).

Diet and Consumption

There was no quantitative information on the diet of *Nephrops*. Feeding mode was assumed to similar to crabs, mobile grazers feeding on small infauna and epifauna. Cod have been identified as a predator of *Nephrops* in some areas, and the generally low level of the cod stock is likely to have resulted in reduced predation.

Fishery and discards

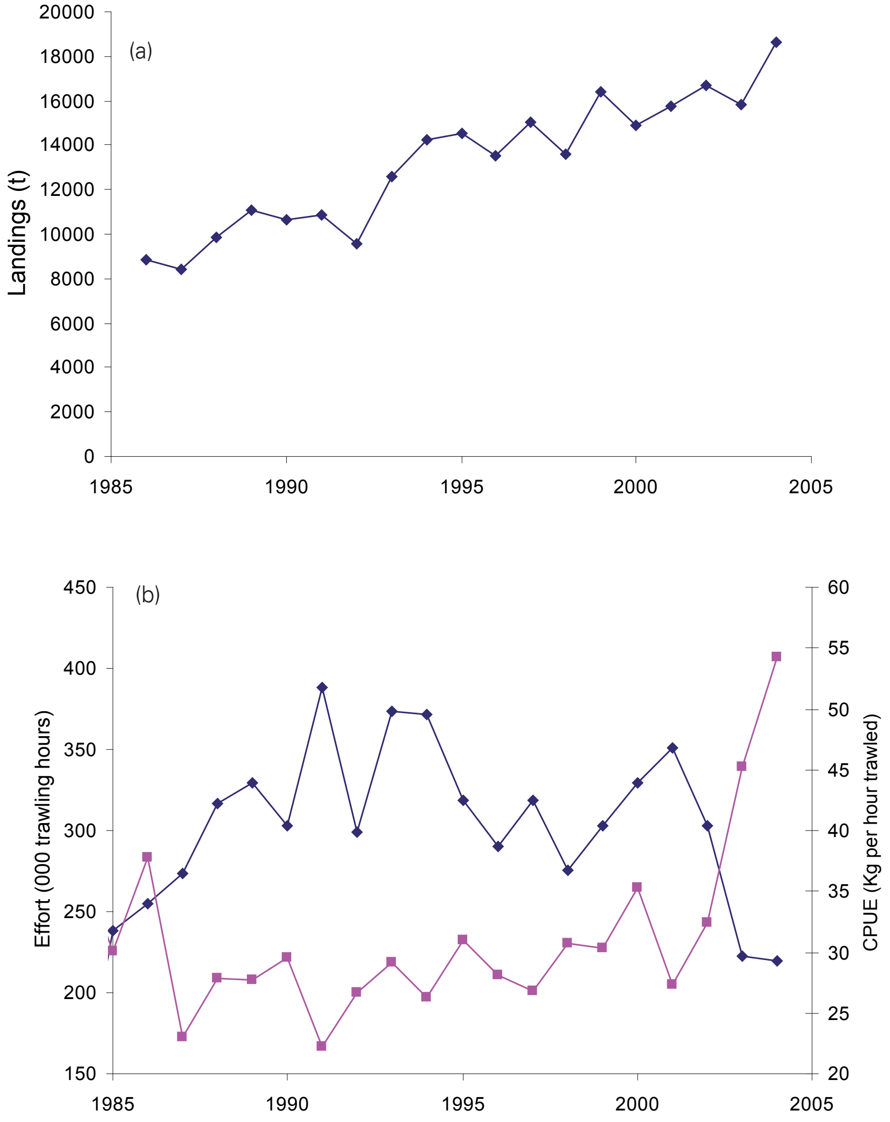
Management of North Sea *Nephrops* fisheries is applied at the TAC area level (ICES area IV). Eight distinct fisheries have been identified in the North Sea and for monitoring and assessment purposes these are defined by groups of ICES statistical rectangles (Functional units). Fisheries with similar characteristics have been grouped together into Management areas and these areas are the level at which ICES/ACFM management advice is given. (Table 11.11, Figure 11.2)

Nephrops stocks within the North Sea are generally thought to be exploited at sustainable levels, and may even be under-exploited in the northern North Sea. The majority of landings (approx 70%) are taken by the Scottish fleet using specific *Nephrops* trawls and other trawls. England and Wales and Denmark also have important *Nephrops* fleets. Recent more widespread use of flipup gears in twin rig *Nephrops* trawls will allow fleets to expand onto rougher ground, potentially exploiting new *Nephrops* areas (ICES WGNSSK, 2005). Landings in 1991 were approximately 11,000 t (ICES WGNSSK) and official ICES reported landings have shown and upward trend over the last 20 years (Figure 11.3a). Trends in effort and CPUE available from the ICES WG show a recent decline in effort and

Table 11.11. Management and functional units for North Sea *Nephrops* (source WGNEPH, 2004).

Management area	ICES rectangles	Functional unit	Region
F	IVa, rect. 44-48 E6-E7 + 44E8	9,10	Moray Firth,Noup
G	IVa, West of 2° E excl. MA F	7	Fladen ground
H	IVb,c, East of 1° E excl. rect. 43F5-F7	5,33	Botney Gut Off Horn Reef
I	IVb,c, West of 1° E	6,8	Farn Deeps, Firth of Forth
S	IVa, East of 2° E + rect. 43F5-F7	32	Norwegian Deep

Figure 11.3. ICES landings and effort and CPUE data for North Sea (div IV) *Nephrops* fisheries.



associated increase in CPUE (Figure 11.3b) although the data do not contain information from *Nephrops* fisheries in FU32, the Norwegian Deep. Historically, the Norwegian effort for *Nephrops* has been low, and the majority of the Norwegian *Nephrops* landings from FU 32 have largely been as by-catch from the *Pandalus* fishery. In recent years more boats have specifically targeted *Nephrops*. From 1999 to 2004, 159 to 185 vessels landed *Nephrops* from the Norwegian Deep (ICES WGNSSK, 2005).

The proportion of catches that are discarded was estimated as 35% using data from *Nephrops* fisheries in the Farn Deeps (FU 6) 1985–2004. (Table 14.36, ICES WGNSSK, 2005). However, we consider this figure to be relatively high in comparison to other North Sea fisheries. *Nephrops* fisheries have a bycatch of roundfish and flatfish.

Environmental trends/relationships

Although quantitative data are not available for all stocks, qualitative observations suggests *Nephrops* has increased in abundance throughout the North Sea in recent years and that this may be linked to environmental influence positively affecting recruitment (WGNSSK, 2005).

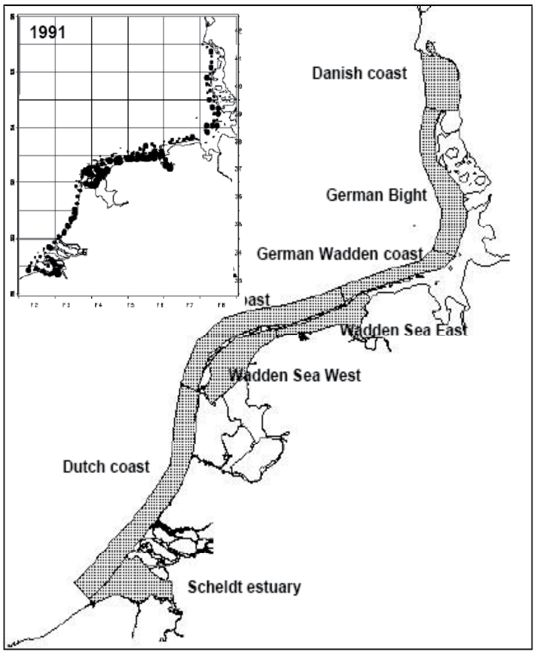


Figure 11.4. Main survey regions for brown shrimp. Inset shows distribution (all sizes) in 1991. Data from Dutch Demersal Fish Survey (DFS).

11.6 Shrimp

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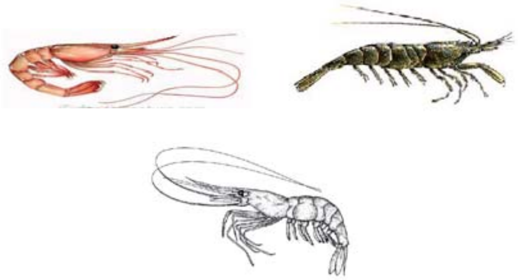


Pink shrimp (*Pandalus*), Brown shrimp (*Crangon*) and *Eualus pusiolus*

Biomass and Production

Calculations made from 1999 and 2000 North Sea epifauna survey data and North Sea 1986 Infauna survey data covering 30 species of shrimps give an average biomass of shrimps 0.443 t km^{-2}. Eight species of shrimp account for 90% of the biomass (Table 11.8). *Crangon* and *Pandalus*, the main commercial species make up 64% of the group, with *Eualus pusiolus* adding another 10%. The best estimate of total biomass from survey data is 0.44 t km^{-2}. ICES working groups provide detailed information and assessments for *Crangon* and *Pandalus*.

Crangon crangon (Brown shrimp)

Two annual surveys provide information on the distribution and abundance of *Crangon* in the eastern North Sea (see ICES WGCRAN, 2005). The Dutch Demersal Fish Survey carried out in September/October shows the distribution pattern to be similar throughout the period 1970–2003. (Figure 11.4). The German Demersal Young Fish Survey cover spring and autumn (although the spring series has terminated some time ago), providing information on the seasonal and interannual variability in density. The long term median density of *C. crangon* in the coastal zone of the German Bight during autumn is approximately 1400 shrimp per 1000 m^2, four times greater than the spring mean which reaches no more than 350 shrimp per 1000 m^2. Over the years, densities of shrimp in spring have varied by a factor 50 (ICES WGCRAN, 2005).

Using a mean density of 875 per 1000 m^2 for the areas where shrimp are caught (Figure 11.5) and mean weight of an individual *Crangon* taken from North Sea Infauna and Epifauna survey data = 0.58 g, the biomass over the area

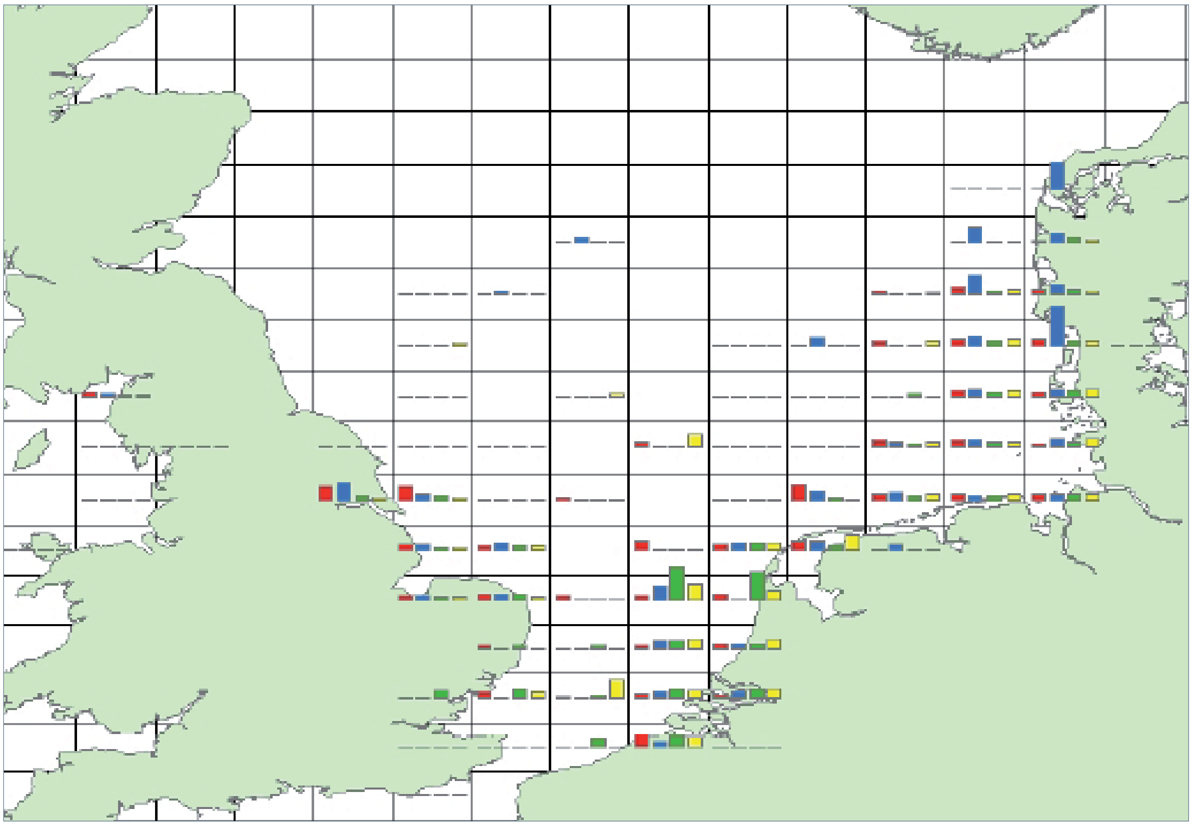


Figure 11.5. Distribution of landings of per unit effort (tonnes/hp-day) per quarter in 2000. Catches occur in 41 ICES rectangles whose total area is 149,598 km^2, 26% of the North Sea. Note that this graph does not include most of the Dutch catches, which is the largest fishery and the one with most fishing in deep waters in q1 and q4. Source W G Cran 2005

Table 11.12. Comparison and summary of parameters estimates for *Pandalus*.

Biomass (t km^{-2}) (over all North Sea)		Swept area	Stock production model	Cohort analysis
	Min	0.0653	0.1017	
	Mean	0.1928	0.1766	
	Max	0.2975	0.2716	
F	Min		0.0860	
	Mean		0.1390	
	Max		0.1990	
M	Min		0.1840	
	Mean		0.3130	0.7500
	Max		0.4580	
Z	Min		0.2700	
	Mean		0.4520	
	Max		0.9490	

routinely caught is estimated as 76,273 t, which translates to a biomass density of 0.13 t km^{-2} over the whole North Sea.

Estimates of P/B for *Crangon* calculated using Brey's (2001) benthic invertebrate production model range from 0.81 to 1.07 y^{-1}.

Pandalus

Table 11.12 provides summary parameters for *Pandalus*.

The Norwegian trawl survey in the Skagerrak–Norwegian Deep has been conducted during October–November from 1984 to 2003. The swept area method is used to estimate the numbers of shrimp in each age group. The output is weight of shrimp "available to trawl" by stratum (see table 4.13, ICES WGPAN, 2004). To get an estimate of the total biomass in the surveyed area, a catch efficiency of 0.2 (= catchability coefficient) of the trawl is applied based on the work of Berenboim *et al.*, 1980. (ICES Table 4.14). Mean biomass (1985–2003) of shrimps over the total stock area of 56,799 km^2 was 109,887 t. In 1991, the biomass was 94,105 t. Calculated as an area density over the whole North Sea (570,000 km^2), this equates to 0.165 t km^{-2}. The fraction of North Sea in which the stock is found is roughly 10%. Over the period 1984–2004, biomass ranged from 0.0653 to max =0.2975 t km^{-2}.

Cohort analysis has also been used to assess the pandalus stock in div IIIa and IVa east from 1997 to 2000, although the assessements suffered from problems because several features characteristic to the shrimp stocks reduce the applicability of the XSA: few age groups in the stock, large uncertainties in the ageing of the older age groups, variable natural mortality exceeding the fishing mortality. More recent assessments have used a stock production model, which includes the effect of yearly recruitment and predation and is 'tuned' using the survey index. The model predicts a mean biomass (1985–2003) of 100,636 t. In 1991, the biomass was 57,985 t, which equivalent to a density over the whole North Sea of 0.101 t km^{-2}. The range of predictions is 0.101 to 0.271 t km^{-2}. The production model estimates that the exploitation (F= Yield/Biomass) has fluctuated between 0.086 and 0.199 with an average of 0.139. (Table 4.14 ICES WGPAN04).

Output from the stock production model estimates that since 1985 predation mortality (Consumption/Biomass) has varied between 0.184 and 0.458 with an average of 0.313 (Table 4.14 ICES WGPAN, 2004). In the cohort analyses, natural mortility is taken as being 0.75 on average and scaled to the abundance of predators (cod, haddock, whiting and saithe). Predators of *Pandalus* caught in the Norwegian surveys are: Blue whiting, saithe, cod, roundnose grendaier, rabbit fish, haddock, redfishes, velvet belly, skates, rays, long rough dab, hake, angler fish, witch, dogfish, whiting, blue ling, ling, fourbeard rockling, tusk, halibut, pollack, greater fork-beard.

The shrimp stock on Fladen has not been assessed since 1992, due to incomplete age data and the lack of separate, fishery independent data. Thus the most recent analytical assessment of this stock was presented in the 1992 Working Group Report (ICES, 1992).

Hopkins (1988) calculated P/B =1.7 y^{-1} for the deep-water prawn *Pandalus borealis* in Northern Norway. Freschette (1981) (in Shumway *et al.*, 1985) gave a mean total mortality of 1 with a range of 0.6 to 1.4 for populations of *P. borealis* in the Gulf of St. Lawrence. Other estimates given in Shumway are consistent with this range, as is the range 0.69–0.93 y^{-1} estimated using Brey's (2001) benthic invertebrate production model.

Combined 'best' estimates for *Crangon* and *Pandalus* for use in parameterisation of the shrimp group are given in Table 11.13 below.

Hopkins (1988) calculated P/B =1.7 y–1 for the deep-water prawn Pandalus borealis in Northern Norway. Freschette (1981) (in Shumway et al. 1985) gave a mean total mortality of 1 with a range of 0.6 to 1.4 for populations of P. borealis in the Gulf of St. Lawrence. Other estimates given in Shumway are consistent with this range, as is the range 0.69-0.93 y-1 estimated using Brey's (2001) benthic invertebrate production model. Temming (pers comm..)

Table 11.13. Biomass and production estimates for *Crangon* and *Pandalus* combined.

	Biomass					
	Min	Mean	Max	Min	Mean	Max
Crangon	0.05	0.13	0.21	0.81	4	9.3 Redant (1989)
Pandalus	0.1017	0.1928	0.2975	0.27	0.45	0.95
Sum	0.15	0.32	0.51			1.7 (Hopkins 1988)

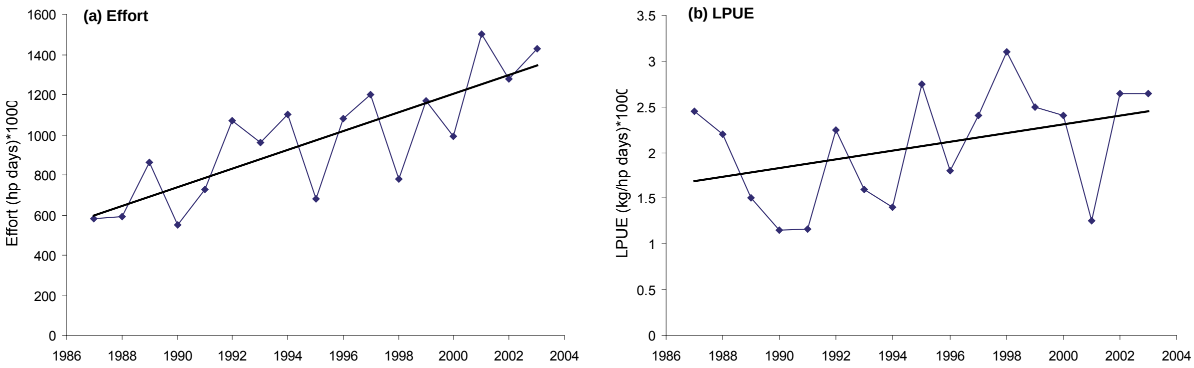


Figure 11.6. Brown shrimp effort and LPUE in the North Sea brown shrimp fishery (1987–2003) (a) Danish effort converted to hp-days at sea (b) Annual corrected LPUE From ICES WGCRAN, 2005.

Table 11.14. Vessels targeting shrimps as their main fishery. ICES WGPAN 05.

	Number
Danish	14
Norwegian	143
Swedish	52–75

considers these estimates far too low, suggesting adult brown shrimp (>45 mm) Z-values should range between 3 and 6 y-1- depending on the method and assumptions about growth. Temming refers to Oh et al. (1999) who cite P/B for crangon 3.96 y-1 and Redant (1989) who provides estimates ranging from 2-9.3y-1 for brown shrimp and values in the range 1.4 to 1.8 y-1 for other decapod shrimps.

Combined 'best' estimates for crangon and pandalus for use in parameterisation of the shrimp group are given in Table 11.13 below.

Fisheries and discards

Crangon

The main *Crangon* fisheries occur throughout the year in shallow coastal waters off Belgium, Netherlands and Denmark and the wash in the UK. Peak season of harvest vary between countries, but is mostly in autumn. In recent years, the Dutch fisheries have been the largest, followed by Germany and Denmark.

Pandalus

Norwegians, Swedish, Danish and UK are the main nationalities targeting *Pandalus* in the North Sea (Table 11.14), with catches dominated by shrimps of ages 1 and 2. The Danish fishery targets both the shrimp stock in the Sub-area IVa East and division IIIa and the one on Fladen Ground. Mainly the Danish and Scottish fisheries exploit the shrimp on Fladen. Denmark accounts for the majority of landings. Since 1991, only UK vessels have fished *Pandalus* in the Farn Deeps with landings low until

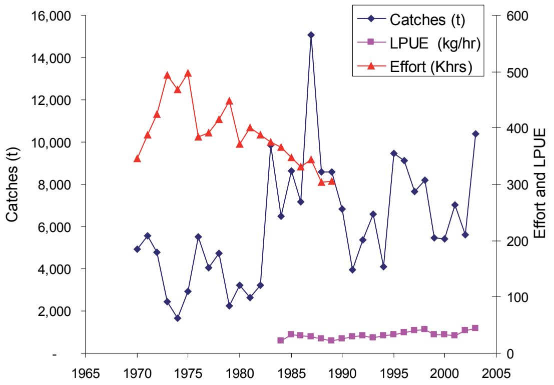


Figure 11.7. Catches (landings+discards) of *Pandalus* in North Sea (div IV), effort and LPUE (estimated by ICES WGPAN, 2005).

Table 11.15. By-catch proportions in the retained catch of Danish and Norwegian *Pandalus* fisheries.

Species	% of total catch
Blue whiting	0.3
Norway lobster	2.8
Pandalus	81.6
Angler fish	2.6
Whiting	0.1
Haddock	0.9
Hake	0.4
Ling	0.5
Saithe	3.2
Witch	0.3
Norway pout	0.4
Cod	4.4
Other market fish	1.6
Reduction fish	1.1

1996 (approx. 100 t) and nothing since. (see Table 6.1 in report). Total *Pandalus* catches in div IV were estimated by combining information from Tables 4.1. and 4.2 in the ICES WGPAN, 2004 report so that the official ICES landings in div IV could be multiplied up to account for the estimated discards (Figure 11.7). Total catches in 1991 are estimated by applying the formulas:

Discards / Landings = PropDL

(the discards as a proportion of landings.
From 1984–2002 data, table 4.2, PropDL=0.05)

Discards = L*PropDL

Catches = Landings + Discards

By-catch regulations for *Pandalus* fisheries restrict the amounts of by-catch, but nevertheless are several valuable fish species, eg cod, anglerfish, are taken and landed as by-catch. Recent by-catch data from Danish, Norwegian and Swedish *Pandalus* fisheries provide only qualitative information on the species caught because the records provide only information on the by-catch that is retained and not that which is discarded (Table 8.1 in ICES WGPAN, 2004). Table 11.15 summarizes the Danish and Norwegian data across both Norwegian deeps and Fladen Ground.

Diet and consumption

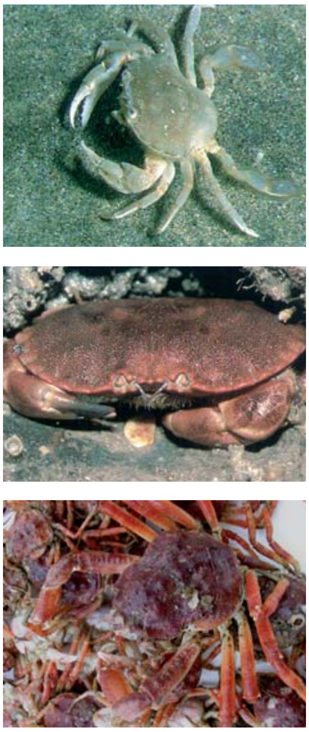
The diet of shrimps and prawns was based entirely on Northern shrimp, *Pandalus borealis*. Its feeding habitat is described as opportunistic omnivory, being both a predator and scavenger in the benthic and pelagic environments (Shumway *et al.*, 1985; Hopkins *et al.*, 1993), although predominantly benthic. The benthic diet is comprised mainly of detritus, phytoplankton and benthic microfauna, meiofauna, polychaetes, and molluscs, whilst the pelagic diet is contains mostly detritus, diatoms, small and large zooplankton (copepods and euphasiids) (see Tables 18 and 19 in Shumway *et al.*, 1985). Younger shrimp appear to spend more time actively migrating and feeding in the pelagic whilst older ones spend more time actively scavenging in the benthic region (Hopkins *et al.*, 1993). In the model, it was assumed that feeding is split 50:50 between benthic and pelgic environments, with the prey functional groups being meiofauna, small infauna, small mobile epifauna, detritus, benthic and planktonic microflora, herbivorous and omnivorous zooplankton and phytoplankton.

Environmental trends/relationships (from WGCRAN05)

German modelling studies suggests that nutrient levels (correlated to fluvial flows from the main rivers), water temperature and the abundance of whiting are the most important factors in determining shrimp productivity for the fishing seasons 1987 to 2002. Shrimp densities obtained from the German Young fish Survey showed that shrimp abundance over the Wadden Sea and was negatively related to winter NAO and water temperature in February but positively related to river run off in December. Shrimp densities for the North Frisian area were also positively related to river run off in December and negatively influenced by water temperature (March) and gadoid abundance. LPUE Data for The Wash (UK) support these findings, with oxidised nitrogen levels exerts a positive influence on shrimp abundance while temperature and predator abundance have a negative effects. Temperature appears rarely to be significant as a single effect.

11.7 Large crabs

Authors: Steven Mackinson and Derek Eaton



Liocarcinus holsatus (swimming crab), Cancer pagurus (edible crab) and Hyas coarctatus (Lyre crab)

The 'large crabs' functional group contains crabs (Brachyura) of modest size that are readily identified in the diet of fish and often taken in fisheries, as well as other large decapods such as European lobster (*Homarus gammarus*) and various squat lobsters. Commercially the most important species in the group are the edible (or brown) crab (*Cancer pagurus*), the common spider crab (*Maja brachydactyla*) and the velvet swimming crab (*Necora puber*). Other species in the group have only very limited commercial importance, as either food or bait.

Biomass and production

Whilst there are some local assessments of nationally important crab fisheries, currently there is no formal assessment of crab stocks by ICES. The Study Group on the Biology and Life History of Crabs (SGCRAB, meeting as the ICES Crab Working Group in 2007) are preparing for assessments of edible crab (*C. pagurus*) by addressing problems with stock identification and the reliability/paucity of data on the species. In particular there is a lack of accurate information on fishing effort in the major fisheries, but also on catch compositions and biological parameters (ICES SGCRAB, 2006).

Calculations made from 1999 and 2000 North Sea epifauna survey data and Brey's (2001) benthic invertebrate production model were used to provide biomass and P/B estimates for 27 species (Table 11.16) included in the functional group. Three species *Liocarcinus holsatus* (swimming crab), *C. pagurus* (edible crab) and *Hyas coarctatus* (Lyre crab) account for just over 75% of the total biomass of this functional group (Table 11.8). Total biomass and weighted P/B applied in the model were 1.3 t km^{-2} and 0.55 y^{-1}. These are close to the maximum values estimated from the data (Table 11.9).

Diet and consumption

Crabs are particulate feeders foraging on a range of benthos (eg bivalves, polychaetes) and fish, both alive and dead. They are important scavengers of discarded fish. A small allowance for cannibalism (1%) within the functional group was incorporated in the model to account for predation between species. No information could be found on consumption rates, so Q/B was estimated by the model assuming a gross efficiency (P/Q) = 0.15 (based on Christensen, 1995).

Fishery and discards

Edible crabs are found from the coastal fringe out to the edge of the continental shelf, wherever there is suitable habitat such as gravelly sands or shingle with patches of rock. Whilst both crabs and lobsters are caught in baited pots, lobsters and their fishery tend to be distributed closer inshore, often associated with a rocky bottom which offers more refuges. The main crab and lobster fisheries in the North Sea occur along the UK coast, from Norfolk northwards, and around the southern coast of Norway.

Prior to the introduction of the shellfish licensing scheme in 2006 in England and Wales there were difficulties in assessing the true landings of crabs and lobsters (*H. gammarus*), because of probable under-reporting by the <10 m fleet, operating mostly within jurisdictional limits (12 nm). Reported catches from the ICES database show a rapid increase in landings since 1990 (Figure 11.8), due mainly to the development of large, offshore fisheries for edible crab east of the Humber estuary and around the Shetland Isles. These are prosecuted by large, nomadic vessels fitted with refrigerated seawater tanks, allowing live crab to be landed after multi-day trips.

Table 11.16. Species included in the large crabs functional group with estimates of biomass derived from North Sea benthos survey data.

Species	Taxon/ vernacular name	Biomass (t)		
		Middle	Min	Max
Liocarcinus holsatus	Crustacean– flying swimming crab	228,145	184,548	380,116
Cancer pagurus	Crustacean – edible crab	70,986	39,552	102,420
Hyas coarctatus	Crustacean – Lyre crab	49,322	41,137	125,792
Lithodes maia	Crustacean – northern stone crab	34,892	18,549	51,235
Portunidae	Swimming crab species	23,868	10,938	36,798
Geryon trispinosus	Crustacean – deep sea crab	11,332	5,090	17,575
Munida rugosa	Crustacean – rugose squat lobster	7,553	4,421	10,686
Macropodia rostrata	Crustacean – longlegged spider crab	5,833	3,817	7,848
Carcinus maenas	Crustacean – shore crab	5,417	2,433	8,401
Liocarcinus marmoreus	Crustacean – marbled swimming crab	4,355	2,063	6,647
Hyas araneus	Crustacean – great spider crab	3,205	1,486	4,924
Inachus phalangium	Crustacea – Leach's spider crab	1,456	1,068	1,844
Inachus dorsettensis	Crustacean – Scorpion spider crab	1,111	661	1,561
Macropipus tuberculatus	Crustacean – a swimming crab	1,065	594	1,537
Munida sarsi	Crustacean – squat lobster spp.	943	424	1,463
Macropodia tenuirostris	Crustacean – slender spider crab	846	439	1,253
Macropodia deflexa	Crustacean – decoratored spider crab	566	286	846
Liocarcinus pusillus	Crustacean – dwarf swimming crab	443	176	710
Pisidia longicornis	Crustacean – squat lobster	431	226	635
Macropodia linaresi	Crustacean – a spider crab	386	173	599
*Liocarcinus depurator**	Crustacean – harbour swimming crab	316	142	490
Necora puber	Crustacean – velvet swimming crab	232	104	359
Inachus leptochirus	Crustacean – Slender-legged spider crab	212	95	329
Dorhynchus thomsoni	Crustacean – Deep sea spider crab	71	52	90
Liocarcinus arcuatus	Crustacean – arch fronted swimming crab	60	27	93
Pisa tetraodon	Crustacean – Four-horned spider crab	16	7	24

* may also be represented in Portunidaes

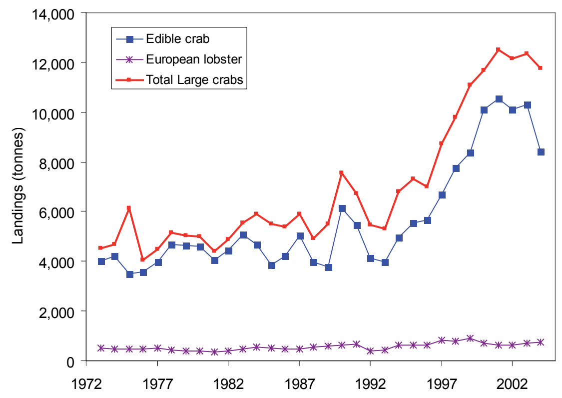


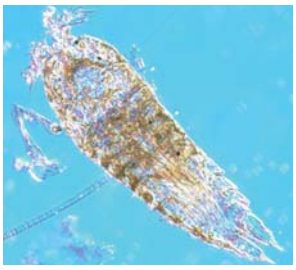
Figure 11.8. ICES official reported landings of edible crabs (*Cancer pagurus*), European lobster (*Homarus gammarus*) and total 'large crabs' in the North Sea. Total 'Large crabs' functional groups includes, Edible crab, European lobster, Green crab, King crabs Craylets, squat lobsters, Blue crab, marine crabs n.e.i., Portunid swimming crabs n.e.i., Red crab, Spinous spider crab, Stone king crab, Velvet swimming crab.

Environmental relationships

ICES SGCRAB provides relevant information in an ecosystem context, but mainly synthesized from the output of national research projects. Lizárraga-Cubedo *et al.* (2005) found that at locations in Southeast Scotland, catch rates of lobsters were related to SST.

11.8 Meiofauna

Authors: Steven Mackinson, Michaela Schratzberger and Tom Moens



A variety of phyla that are considered to live interstitially (eg nematodes, harpacticoid copepods, tubellarians polychaetes, oligochaetes, ostracods, tardigrades, isopods, gastrotrichs, kinorhynchs).

Operationally, meiofauna are defined as those benthic organisms which are retained on a 40 µm mesh sieve, but pass through a 1 mm sieve. They comprise the smaller metazoans with some larger protozoa often included (foraminifera and ciliata) (Moens and Vincx ,1996)

Over a general worldwide basis, Gerlach (1971, 1978) estimated the density of meiofauna in shallow waters is approx 1 x 10^6 m^{-2}, with a biomass of approximately 2 g ww m^{-2}, constituting up to 4% of the total macrofaunal biomass. With a high turnover rate, production may be high, yet its fate within the ecosystem is still relatively unknown.

In estuarine and shallow coastal environments, meiofauna are often present in densities ranging from 10^5 to 10^7 ind m^{-2}, corresponding to a biomass range of 0.01 to 10 g C m^{-2}, with average values approximating 1 gC m^{-2} (Heip *et al.*, 1995). The meiofauna community in the North Sea is overwhelmingly dominated by nematodes and copepods, with Turbellaria and Gastrotricha usually well represented (McIntyre, 1978). There is high species diversity with over 735 nematode species being reported for the North Sea (Heip *et al.*, 1983) and around a total of 1500 meiofauna species expected to occur (Heip and Craeymeersch, 1995). These are probably still underestimates, especially when we take into account that many morpho–species may in fact be complexes of cryptic species (see eg Derycke *et al.*, 2005, 2007)

Meiofauna have been demonstrated to play a potentially substantial role in the energy flows to higher trophic levels, both diretly through consumption by shrimps, other small crustaceans and surface dwelling fish (Gee, 1989 and references in Moens and Vincx, 1996) and indirectly through their role in the nutrient recycling process by means of grazing on bacteria (Montagna, 1995), bioturbation (Alkemade *et al.,* 1992) and mucus production (Riemann and Schrage, 1978).

Large variability and uncertainty exists in the estimates of biomass, production and consumption of meiofauna (as noted by Donavaro *et al.*, 2002). The following sections review the key literature in the North Sea and use the available information to derive a range of parameter estimates (Table 11.17)

Biomass, distribution and production

A large number of species new to science (40%) were recorded by the 1986 North Sea infaunal benthos synoptic survey (see Craeymeersch *et al.*, 1997). Nematodes were the most abundant group at virtually all stations, their densities ranging from 61 to 4167 individuals per 10 cm^2 (Mean = 759), with a tendency to increase toward the north. Only in the sandy sediments of the Southern Bight where nematode numbers were low, did harpacticoid copepods sometimes represent the dominant taxon. Copepod density and diversity was related to water depth and sediment type, with highest abundance recorded in the Southern Bight, due to the presence of many interstitial species. Overall, total meiobenthos density increased to the north (Huys *et al.*, 1992; Heip and Craeymeersch,1995).

Nematodes, copepods and tubellarians account for 75% of the estimated biomass of meiofauna, with biomass of nematodes being roughly 4 times higher than copepods, and 6 times higher than turbellarians (Table 11.6). Meiofauna constituted 1% of the total biomass of metazoan benthos calculated from North Sea benthos surveys. Total meiofaunal biomass was estimated to be approximately 1.8 g ww m^{-2} (approx 0.2 gC m^{-2}), which is close to the estimate of Gerlach (1971, 1978) and lower (as would be expected) than that estimated by Heip *et al.* (1995) for estuaries and shallow coastal environments.

Other estimates of meiofaunal biomass were determined from 2 sets of density data presented by McIntyre (1978). Assuming the average dry weight of nematodes to be 0.27 µg and copepod 1.8 µg (Heip *et al.*, 1984) and applying a conversion of dry mass to carbon mass of 0.463 (De Bovee and Labat, 1993; Sikora *et al.*, 1977 [*sensu* Heip *et al.*, 1985]), provides estimates of 21.1 g wet wt m^{-2} and 10.3 g wet wt m^{-2}. These are the highest estimates, which are based on sampling from coastal areas as opposed to offshore sites sampled during the North Sea benthos survey in 1986.

Total meiofaunal biomass used in the model was 4.1 g ww m^{-2}, two times higher than that estimated from surveys but close to McIntyre's (1978) estimate for the shelf region alone (4.4 g ww m^{-2}), and considerably lower than the high values expected in inshore waters. When

McIntyre's inshore water values are excluded the average of the biomass of meiofauna derived from various sources is 5.3 g ww m^{-2}.

Assuming values for production efficiency (Production/ Assimilated food, P/A) between 40–70%, and an assimilation efficiency (Assimilated food/Consumed food) of 20%, Heip *et al*. (1995) estimated production (and consumption, later) of nematodes from a sandbank with little organic input, where biomass was estimated to 0.07 gC m^{-2}, and respiration 1.06 gC m^{-2} y^{-1}. Production was estimated to be 0.71 gC m^{-2} y^{-1}, [implying a P/B = 10.1 y^{-1}] and 2.47 gC m^{-2}, (implying P/B = 35.3 y^{-1}) at 40 and 70% production efficiency respectively (see Heip *et al*., 1990, 1995). However, since all literature data on production efficiency are derived from fast growing bacterivores, the proposed range of production and assimilation efficiencies may not be quite representative of the whole group (Moens pers. comm.).

Heip *et al*. (1995) used the same approach to provide 'very rough' estimates of the production (and consumption, see later) of harpacticoid copepods in the North Sea. Assuming an average biomass of 20 µg dw cm^{-2}, and respiration rate of 3nl 0_2h^{-1} (µg dwt)$^{-1}$, (the lower end of the range described by Herman and Heip (1983) and the same order as found by Gee and Warwick (1984)) for interstitial species, respiration would amount to 0.21 gC m^{-2} yr^{-1}. With a production efficiency (P/A) of 40% (1 – see below), production is 0.14 gC m^{-2} yr^{-1} (P/B = 14 y^{-1}). Such estimates are likely to be highly temperate dependent.

An alternative (and equally uncertain) estimate of nematode P/B is obtained by Heip *et al*. (1990) using the equation of Vranken and Heip (1986) that scales P/B with body weight at sexual maturity. Using an average female size of 0.4 µg dwt (average individual size is 0.26 µg dwt) results in a yearly P/B of 16.6 which is in between the values above and near to the P/B=20 y^{-1} reported by Vranken *et al*. (1986) for an 'impoverished', stable sublittoral nematode community. The latter study by Vranken *et al*. also reports a P/B of 58 for a Sargassum community.

Gerlach (1971) gives a value for P/B = 9 y^{-1}, based on two components: a life cycle turnover rate of three and three generations per year. There is little discussion about the life cycle turnover rate, but huge uncertainty about the number of generations per year, which may range from less than 1 in some very large and probably slow-growing species, to 23 or more in fast-growing bacterivores like monhysterids (see Heip *et al*., 1985 and Vranken papers, 1986)

Herman *et al*., 1984b (in Heip *et al*., 1990) compared respiration and field production of three meiofaunal species (one ostracod and two harpacticoids) and found a constant value P/ (P+R) = 0.4 (approx).

Diet, consumption and predators

Many meiofauna are opportunistic feeders and may change feeding behaviour in relation to available food. They consume a wide variety of food including detritus, bacteria, diatoms and other small photoautotrophs, cyanophytes, ciliates and other meiofauna. Harpacticoids, nematodes and ostracods are thought to differentially exploit the food resource (Carman and Fry, 2002). Bacteria are an important part of their nutrition and it is estimated that meiofauna consume about 1% of bacterial and microalgal standing stock per hour Montagna (1995). Moens and Vincx (1996) point out that if on average microbial turnover times are about 4 days or less, meiofauna grazing would roughly be in equilibrium with microbial production suggesting a tight coupling of benthic meiofauna to benthic microbiota. According to Moens and Vincx (1996), it has not convincingly been shown that meiofauna are able to utilise DOM and are unlikely to be able to compete with bacteria. However because DOM is bound to bacteria and microalgae, it is inevitably consumed and may be utilised (Decho and Lopez, 1992 in Moens and Vincx, 1996). There are many carnivorous meiofauna such as *Turbellaria*, nematodes, halacarid mites and these may play an important role in the internal regulation of population biomass and composition (Gee, 1989).

A variety of estimates for consumption are given in Heip *et al*. (1990). Assuming values for production efficiency (Production/Assimilated food, P/A) between 40–70%, and an assimilation efficiency (Assimilated food/Consumed food) of 20%, Heip *et al*., (1995) estimated consumption (& production, see above) of nematode from a sandbank with little organic input, where biomass was estimated to 0.07 gC m^{-2}, and respiration 1.06 gC m^{-2} y^{-1}. Consumption was estimated to be 8.8 gC m^{-2} y^{-1} [implying a Q/B = 126 y^{-1}] and 17.7 gC m^{-2} [implying Q/B = 253 y^{-1}] at 40 and 70% production efficiency respectively. Admiraal *et al*. (1983) estimated that an individual nematode eats about double its own carbon content each day which equates to roughly 90 µg C per year [implying a Q/B =730 y^{-1}]. Using the same approach as above, Heip *et al*. (1990) estimated consumption of harpacticoid copepods to be 1.75 gC m^{-2} y^{-1} [implying a Q/B = 175 y^{-1}]. Such estimates depend strongly on environmental conditions, and may hold, or be even larger, at optimal temperature and feeding conditions, but may be much lower at low temperatures or low food availability. Hence, extrapolations of this sort of estimates to yearly estimates is very uncertain.

In an alternative estimation of meiofaunal consumption, Heip *et al*. (1990) assume consumption to be about 5 times production (P/Q=0.2), a biomass of 1–2 g dwt m^{-2} (for subtidal sediments) and a production of 8–20 g dwt m^{-2} y^{-1} (based on P/B 8–10 y^{-1}). Estimated consumption would be around 40–100 g dwt m^{-2} y^{-1}, which equates to a Q/B of 40–50 y^{-1}. They explicitly state that large uncertainties exist in such extrapolation.

Moens *et al*. (1999) estimated consumption rates of the bacterivorous rhabditid nematode *Pellioditis marina* to be between 26 and 4 times the body weight per day, depending on assumptions about gut passage time, and compared them with Tietjen's (1980) estimates for rhabditids of 3 to 8 times per day. However, due to a number of sources of errors in methods, Moens *et al*. (1999) warn that it may be an underestimation by as much as 15 times the actual consumption rate. Assuming these daily estimates of Q/B are sustained throughout the year, this implies annual Q/B rates in excess of 5000. It is likely that these are maximum consumption rates calculated under experimental conditions and that realised consumption rates would be considerably lower. Furthermore, the feeding behaviour of rhabditids is not representative of other, benthic nematodes: under conditions of food saturation, rhabditids continuously pump bacteria into their intestine at very high rates. Under these (and favourable temperature) conditions, they also have exceptionally short generation times and produce lots of progeny. Moreover, they tend to feed in bacterial biofilms on algal substrates, rather than in a sediment matrix. There is little doubt that most other nematodes have more selective feeding behaviours and feed at comparatively lower rates. Admiraal *et al*. (1983) observations on the ingestion rates of diatom-feeding nematodes suggest that nematodes with a very different feeding behaviour and food source from *P. marina* still ingest more than their own body mass per day.

Using indirect information based on respiration, body weight and life-history, Heip *et al*. (1990) estimated an energy consumption in the order of 10 gC m^{-2} y^{-1}. Heip *et al*. (1985) found meiofaunal consumption of bacteria and algae to be 14 to 60 µg C d^{-1} (5000–22,000 µg C y^{-1}, 365 days), although again such extrapolation heavily relies on the weak assumption that changing temperature and environmental conditions would not importantly affect feeding.

Key epibenthic predators of meiofauna are fish (Hicks and Coull, 1983), shrimps and prawns, crabs and mysids (see references in Gee, 1989). Meiofauna has been show to be an important food source for fish, particularly in inshore, littoral and sublittoral habitats (those most investigated by researchers). Typically, studies find strong predation on copepods but less on nematodes. However, this may be a bias resulting from the fact that hard-bodied copepods are more easily found in consumer guts than nematodes. Studies in Danish and UK waters revealed juvenile flatfish and gobies are active predators of meiofauna (Gee, 1989). Other known non-fish predators include shrimp, Nereis (polychaete) ragworm, crabs and predatory meiofauna mainly in the groups such as turbellarians and nematodes (see references in McIntyre, 1969).

Gerlach, 1978 in Gee, 1989 suggested that meiofauna could contribute about 20% of the food of deposit feeding macrofauna. By their very nature, non-selective deposit feeders such as polychaetes, echinoderms, holothurians and sipunculids cannot avoid ingesting meiofauna (Platt and Warwick, 1980 in Gee, 1989). Creed and Coull (1984) found evidence that the echinoderm *Mellila* and actinarian *Renilla* were feeding on meiofauna. Selective deposit feeders such as amphipods are known to eat large quantities of meiofauna (Elmgren, 1976 in Gee, 1989). Polychaetes are also known predatory macroinfauna (Sarvala, 1971 in Gee, 1989).

Table 11.17 Parameters for North Sea meiofauna.

	Individual sources	Nematodes	Harpacticoid copepods	Polychaetes	Turbellarians	Others/all	All meiofauna	Average of estimates
P/B y^{-1}	Warwick *et al.*, 1979	8.4	18	5	5	9.12	9.1	15.48
	Lasserre *et al.*, 1976	9.75	21	9.7	11.3		12.94	
	Heip *et al.*, 1990	10.1	14				12.07	
	Heip *et al.*, 1990	35.3					35.3	
	Heip *et al.*, 1984	8.9	7.2				8.0	
	McIntyre, 1964					10	10.0	
Production gC m^2 y^{-1}	McIntyre, 1964					3.15	3.15	2.73
	Heip *et al.*, 1983					9	9.00	
	Faubel *et al.*, 1983.					2.4	2.40	
	De Wilde *et al.*, 1986					1.1	1.10	
	De Wilde *et al.*, 1986					1.2	1.20	
	Heip *et al.*, 1990	0.71	0.14				0.85	
	Heip *et al.*, 1990	2.47					2.47	
	Heip *et al.*, 1984	1.6	0.086				1.69	
	Heip *et al.*, 1990						8.00	
Q g C m^2 y^{-1}	Heip *et al.*, 1990	8.80	1.75				10.55	14.13
	Heip *et al.*, 1990	17.70					17.70	
Biomass gC m^2	Survey estimate (my calc)						0.83	0.54
	McIntyre, 1978	0.28864512	0.067709107		0.091594	0.7506592	1.20	
	McIntyre, 1979 shelf only						0.51	
	Heip *et al.*, 1990	0.07	0.01				0.08	
	Heip *et al.*, 1990	0.07					0.07	
	Heip *et al.*, 1984	0.18	0.012				0.19	
	Heip *et al.*, 1990						0.88	
Q/B y^{-1}	Heip *et al.*, 1990	125.7	175				150.4	149.4
	Heip *et al.*, 1990	252.9					252.9	
	Heip *et al.*, 1990						45.0	
	Moens, 1990	5475.0						
Consumption gC m^{-2} y^{-1}	Heip *et al.*, 1990						30.0	20.0
	Heip *et al.*, 1990						10.0	
Mean ind.DW (µg)	Huys *et al.*, 1992		1.806				1.8	1.47
	Heip *et al.*, 1990	0.27	2				1.1	
Density mean ind. per 10 cm^2	Huys *et al.*, 1992	759					759.0	1224.5
	Heip *et al.*, 1984	1675	15				1690.0	
P/Q	Heip *et al.*, 1990						0.2	
Respiration gC m^{-2}	Heip *et al.*, 1984	1.81	0.32				2.1	2.1
	Heip *et al.*, 1985	1.06	0.21					

12. Squid and cuttlefish

Authors: Steven Mackinson and Graham Pierce

Veined Squid, *Loligo forbesi*

The veined squid, *Loligo forbesi* and European squid, *Loligo vulgaris,* are found throughout the North Sea and appear to be mainly demersal in distribution. *L. forbesi* is more common and the main cephalopod of commercial interest, being fished for mainly in the northern North Sea and west of Scotland where it is caught in demersal trawls to depths of 400 m (Pierce *et al.*, 1994a). However both species are important in the English channel. The most important species of cuttlefish is the common cuttlefish *Sepia officinalis*, which supports an important fishery in the English channel (Dunn, 1999) although its distribution probably does not extend into the northern North Sea. The little cuttlefish or bobtail squid is also common throughout the North Sea, and found mainly in the neritic zone (Collins *et al.*, 2002).

Biomass and Production

Standard swept area calculations were used to provide a first attempt to estimate the biomass density of *Loligo* in the North Sea using data from surveys made in February 1989–92 (Pierce *et al.*, 1998, Table 5). The calculations provide only a minimum estimate since they assume *Loligo* has a strictly demersal habit and there is no allowance for escapement from the trawls. Discounting data from 1990 when many small specimens were captured, the mean estimate is 0.0034 t km^{-2}, which equates to approximately 12 ind km^{-2}, with a mean weight of 312 g. Pierce *et al.* (1998) present the figures as a first assessment to be compared with alternative values.

Using data from 1989–1998, Young *et al.* (2004) estimated population size in ICES subdivision IVa (northern North Sea) and VIa (west Scotland) to be in the order of 10^{6} individuals. This gives a mean density of 1.8 ind km^{-2}. Monthly biological data collected between 1997–2000 provided a length–weight relationship of Weight (g) =0.00094 L(mm)$^{2.33295}$. Using length–frequency data supplied by Young (pers. comm.), a mean dorsal mantle length of 193 cm gives a mean weight of 202 g, which implies a biomass density of 0.0036 t km^{-2}. This must also regarded as a minimum value for the density of cephalopods in the North Sea recognising that it does not include biomass of *L. vulgaris, Sepia*, *Sepiola* and other less abundant species.

Calculations made from 1999 and 2000 North Sea epifauna survey data (Table 11.7), give an average biomass of 0.038 t km^{-2} for squid, octopus and cuttlefish. The majority of the biomass (96%) is represented by octopus (*Eledone cirrhosa*) and cuttle fish (*Sepia officinalis*, *Sepiola atlantica, Rossia macrosoma*) reflecting the bias inherent in the sampling gear.

Adding this to the biomass of *Loligo* provides a total minimum estimate of 0.0398 (0.04) t km^{2} for this functional group.

Using Brey's (2001) invertebrate production model, a P/B = 0.26 y^{-1} was estimated, but is known this is likely to be very low. A value of 4 is used initially in the model based on expert judgement (Roel, pers. comm.) and the instantaneous relative growth rate of 3.23 reported by Wood and O'Dor (2000).

Diet and Consumption

Daily food consumption of *Loligo forbesi* has been estimated at between 0.14% to 5.6% of body weight of body weight for *Loligo* (Pierce *et al.* 1994; Pierce and Santos, 1996). Assuming the weight of stomachs to equate to the weight of food eaten, provides an annual Q/B between 0.5 to 20 y^{-1}. Howard *et al.* (1987) (in Pierce *et al.*, 1994) recorded a mean weight of the stomach contents of *Loligo forbesi* of approx 2.5%, whilst (Segawa, 1990 in Pierce *et al.*, 1994) cites evidence that the daily food consumption is around 14%. These provide estimates of Q/B y^{-1} of 9 and 51 respectively. A value of 20 is used in the model.

Diet data is compiled from Pierce *et al.* (1994), Collins and Pierce (1996) and Johnson (2000). Main food items include fish (sandeels, gadoids, clupeids), crustaceans (euphasiids and copepods) and cephalopods.

Fishery and discards

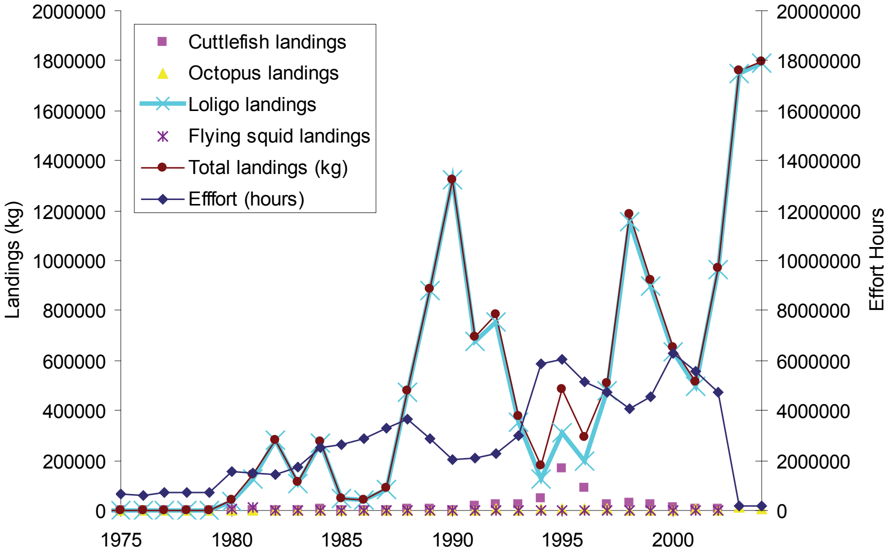
Squid in the North Sea are mainly caught as by-catch of whitefish and *Nephrops* trawling (Pierce *et al.* 1994a) although there has been some directed fishing in the northern North Sea since the early 2000s (Young *et al.*, 2006).

Discarding of squid appears to be only minor, with by-catch being mostly kept for sale. Young *et al.*, (2004) used data available from 1998, 1999 and 2000 to estimates of discards to be 1.38, 1.71 and 0.6% of landings weight. He showed that the effect on abundance estimates was shown to be so small such that it could be disregarded; implying LPUE can be treated as equivalent to CPUE. Pierce *et al.* (1998) found the average abundance for the February North Sea survey was to be a reasonable predictor of commercial CPUE in the autumn of the same year during the peak of the fishery.

Environmental trends/relationships

Loligo is patchily distributed in space and time with patterns in the North Sea during February strongly related to bottom temperature and to a lesser extent salinity (Pierce *et al.*, 1998).

Figure 12.1. Landings of squid and cuttlefish in the North Sea. (Data courtesy of G. Pierce).



13. Fishes

Authors: Georgi Daskalov

13.1 Functional groups (FGs)

Fish species were grouped into 44 functional groups (FG, Table 13.1). Different species either constitute single groups or are aggregations of species based on information on abundance, diet, and commercial or functional importance. The commercially important target fish species (cod, haddock, whiting, saithe, herring) were divided into juvenile and adult groups. Several non-target fish species, which are also commercially and/or functionally important were represented as single species or family groups (e.g. hake, dab, gurnards). Other species are included in aggregated groups based on similar taxonomic or functional characteristics eg, large and small gadoids, large and small demersals, pelagic fish (Table 13.1).

13.2 Biomass estimates

Biomasses of commercially important fishes (cod, haddock, whiting, saithe, Norway pout, herring, sprat, sandeel, plaice and sole) were taken from MSVPA results (ICES, 2002b).

The input parameters for the so-called non-target fish species were more difficult to obtain. Biomass of ~80 non-target fish species monitored by the IBTS, which are not subject to regular stock assessment, was estimated following the approach of Yang (1982) and Sparholt (1990), and also used by Daan *et al.* (1990) and Rueckert *et al.* (2002). The method consists in using reference (or "standard") species for which analytical assessments of abundance are available to estimate catchabilities (availabilities according to the terminology of Sparholt) in research trawl surveys. Catchabilities or availabilities are ratios between research vessel CPUE and abundance or biomass from assessments according to the relationship $CPUE = qB$ (q is catchability). The ratio estimates for reference species are then multiplied to CPUE of the rest of the species caught which are assumed to have similar catchability/availability to some of the reference species. Biomass estimates of the MSVPA species were used as reference to estimate catchability/availability in IBTS CPUE data from 1991. Four groups are formulated: group 1, with reference species cod, haddock, whiting and saithe – mean quarterly q of these species is then used to estimate B of the "other" species of non-target demersal round fish (such as dogfish, hake and other gadoids) from IBTS CPUE; group 2, with reference species Norway pout to estimate B of deep water demersal and benthoplelagic species, such as *Chimaera sp., Argentina sp.*, blue whiting, etc.; group 3, with reference species herring and sprat to estimate B of non-target pelagic fishes; group 4, with reference species plaice to estimate B of other flat fish, skates, and small demersal fishes. Estimated biomass densities (from data) that are presented in (Table 3.1) referred to "this study". Scientists previously using this the method accepted its deficiency based on assumptions about equality of catchabilities/availabities of reference species and other species. Nevertheless, unless better abundance estimates are available this is an useful approximation.

13.3 Production

Production rate (P/B) in Ecopath is assumed to be equal to total mortality Z (Allen, 1971), which can be estimated as $Z= F+M2+M0$ where Z is total moratlity, F – fishing mortality, M2 – natural mortality due to predation, and M0 – natural mortality due to old age, deceases, etc. For commercial species assessed by the ICES working groups, mortality estimates (Z, F, and M) were compiled from stock assessment reports.

Natural mortality rate (M) of fish was estimated from empirical relationship linking M, the parameters of the von Bertalanffy Growth Function (VBGF) and mean environmental temperature (Pauly, 1980).

$$M = K^{0.65} \cdot L_{\infty} -0.279 \cdot T_c^{\ 0.463}$$

where M is the natural mortality (/year), K is the curvature parameter of the VBGF (/year), L_{∞} is the asymptotic length in cm, T_c is the mean ambient temperature, in °C.

A life-history routine (FishBase - Froese and Pauly, 2003 http://www.fishbase.org) was used to estimate M and Z, L_{∞} being assumed to equal L_{max}. Coull *et al.* (1989) have reported size and growth parameter of North Atlantic fishes and their data of the maximum length L_{max} were used as a proxy of L_{∞}. K was determined using known relationships between L_{∞} and K within the FishBase life-history routine. Ambient temperature was assumed to be the average temperature of the North Sea = 10°C. Fishing mortality (F) was estimated from the catches (C) and biomass (B): $F = C/B$. In cases when no catches were recorded natural mortality was assumed to equal Z.

When functional groups are composed of several species, the group P/B is estimated as a weighted mean (weighted by each species biomass B) of the species P/Bs.

13.4 Consumption

Consumption rates (Q/B) of commercial species were estimated from mean daily rations by quarters and quarterly abundance for 1991 from MSVPA (ICES 2002b). Other published sources were used to derive plausible estimates of consumption rates (Table 3.1).

For species which there is no published information on feeding, empirical formulae implemented in the life-history routine of FishBase (Froese and Pauly, 2003 http://www.fishbase.org) were used. Two such formulae were derived by Palomares and Pauly (1998):

$$\text{Log(Q/B.y-1)=5.847+0.280LogZ-0.152*logW}\infty\text{-1.360*T'+0.062*A+0.510*h+0.390*d}$$

where *Z* is total mortality, *W∞* is the asymptotic weight (g), *T′* is the mean annual temperature (expressed using *T′* = 1000/Kelvin (Kelvin = °C + 273.15), A is the aspect ratio (height^2(cm)/surface area (cm) of the caudal fin), *h* is a dummy variable expressing food type (1 for herbivores, and 0 for detritivores and carnivores), and *d* is a dummy variable also expressing food type (1 for detritivores, and 0 for herbivores and carnivores). For cases where *Z* is not available, the following relation may be used:

$$\text{Log (Q/B.y-1)=7.964-0.204*LogW}\infty\text{-1.965*T'+0.083*A+0.532*h+0.398*d}$$

.

13.5 Diet

The diet matrix of commercial species was compiled using data from the 1991 year of stomachs (Hislop 1997). Unpublished data from the 1991 Year of the Stomach for grey gurnard and four skate species were kindly provided by Niels Daan (Niels Daan IMARES, Netherlands, personal communication). Diets of other species were compiled based on literature sources (Table 3.4).

In aggregated FGs species diet matrices are aggregated as each percentage in the aggregated diet is a weighted mean (weighted by each species consumption Q) of the respective percentages from the species diets.

13.6 Elasmobranchs

Biomass of elasmobranchs were estimated using the method of Sparholt (1990) with reference species cod, haddock, whiting, and saithe for all shark species and plaice for skates (Table 3.1).

Spurdog is an important market fish for human consumption and, although abundance is decreasing in recent years, it is targeted by some fisheries e.g. using longline and gillnet, as well as being caught as a by-catch with demersal trawls (ICES 2006). Demersal elasmobranchs are caught as bycatch in the mixed demersal fisheries. Skates are targeted inshore with tangle nets and long-line. Thornback ray *Raja clavata*, is probably the most important skate for the commercial fisheries. Elasmobranchs are also important target species in some recreational and charter boat fisheries. In 2005 ICES provided advice that target fisheries for common skate *Dipturus batis* and thornback ray *R. clavata* should not be permitted, and bycatch in mixed fisheries should be reduced to the lowest possible level. Moreover, ICES advised that if the fisheries for skates and rays continue to be managed with a common TAC for all species, this TAC should be set at zero for 2006. In Sweden a number of demersal and deep-water elasmobranchs are contained in the Swedish Red List: velvet belly *Etmopterus spinax*, Greenland shark *Somniosus microcephalus*, *D. batis*, and rabbit fish *Chimaera monstrosa*. Furthermore, fishing for and landing of lesser spotted dogfish, *R. clavata* and *D. batis* is prohibited. OSPAR have listed several species as threatened and declining.

13.7 Juvenile sharks (5)

This group mainly consists of young spurdog *Squalus acanthias* as well as juveniles of other shark species smaller than 40 cm. Total biomass is 0.6 thousand tonnes and biomass density is 0.001 t.km2 (Table T1). P/B= 0.5, Q/B=2.5 were estimated using empirical formulae in FishBase and the diet was taken from Ellis *et al.* (1996), and Bergstad *et al.* (2001) and aggregated accordingly. Juvenile sharks feed on fish and invertebrates and the trophic level is 4.29 (Table 3.3).

13.8 Spurdog (6)

Veined Squid, *Loligo forbesi*

This group consist of adult spurdog *Squalus acanthias* (>40cm). Total biomass is 7.4 thousand tonnes and biomass density is 0.013 t.km^2 (Table T1). P/B= 0.048 was estimated using the empirical formula in FishBase, Q/B=2 based on the report by Brett & Blackburn (1978), and the diet was taken from Ellis *et al.* (1996). Adult spurdog is mainly piscivorous with addition of some larger invertebrates such as cephalopods, large crabs, *Nephrops* and shrimp; trophic level is 4.77 (Table 3.5).

13.9 Large piscivorous sharks (7)

This group mainly consist of tope, *Galeorhinus galeus*. Other large piscivorous sharks such as porbeagle *Lamna nasus* and thresher sharks *Aloplas vulpinus (*Ellis, 2004) also should be included here but these were not recorded in the IBTS catches in 1991. Total biomass is 0.6 thousand tonnes and biomass density is 0.001 t.km^2 (Table 3.5); P/B =0.44, and Q/B =1.6 were estimated using empirical formulae in FishBase and the diet was taken from Ellis *et al.* (1996). They feed on various fish and cephalopods and have the highest trophic level 4.93 of fish groups (Table 3.5). In the North Sea large sharks are not commercially important mainly because of their low abundance, although these have been targeted fisheries for porbeagle.

13.10 Small sharks (8)

This group aggregates four species: lesser-spotted dogfish *Scyliorhinus canicua*, smooth hounds Mustelus spp., and velvet-belly *Etmopterus spinax*. Their biomass estimated using the method of Sparholt (1990) is 1.14 thousand tonnes and biomass density is 0.002 t.km^2 (Table 3.5). Each species production and consumption rates were estimated using empirical formulae in FishBase and then weighted mean calculated for the FG: P/B =0.51, and Q/B =2.96. The diets of spotted dogfish and smooth hound were taken from Ellis *et al.* (1996), and velvet-belly – from Bergstad *et al.* (2001) and aggregated accordingly. The diet of this group consist of various fish and invertebrate and trophic level is 4.34 (Tables 3.3, 3.4).

Skates were grouped in four functional groups according to their trophic requirements. Biomasses of all were estimated using the method of Sparholt (1990) with plaice as a reference species (Table). P/Bs were estimated using empirical formulae in FishBase. Diet information for the ray species was taken from the 1991YoS database of the Year stomachs provided by Daan and colleagues (Daan *et al.* 1993, Niels Daan personal communication)

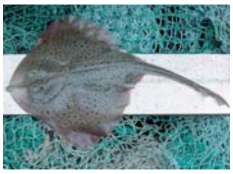
13.11 Juvenile skates and rays (9)

Consists of all skates smaller than 30 cm. Biomass is 152.8 thousand tonnes and biomass density is 0.268 t.km^2, P/B =0.66 and Q/B =1.7, and diets were estimated as weighted means of all species (Tables 3.3, 3.4),. Diet is dominated by sandeels and benthos, trophic level is 4.23.

13.12 Starry ray and others (10)

This group consists of starry ray *Amblyraja radiata* and unidenfied rajiid skates. Biomass is 62.1 thousand tonnes and biomass density is 0.109 t.km^2, P/B=0.66 was estimated using empirical formulae in FishBase; Q/B =1.7 was estimated from consumption data in MSVPA report (ICES 2002); diet is from Daan *et al.* (1993). Diet of starry ray is dominated by fish, but benthos also makes a considerable part of it. Trophic level is 4.49 (Tables 3.3, 3.4).

13.13 Thornback and Spotted ray (11)



The thornback ray *Raja clavata* and the spotted ray *Raja montagui* are aggregated into one group due to similarities in their diets (Ellis *et al.* 1996). Biomass is 37.6 thousand tonnes and biomass density is 0.066 t.km^2, P/B=0.78 and Q/B=2.3 were estimated using empirical formulae in FishBase, and diets - from Daan *et al.* (1993) were averaged accordingly. Aggregate diet of this group is dominated by fish, but benthos also makes a considerable part of it. Trophic level is 4.49 (Tables 3.3, 3.4).

13.14 Common skate and cuckoo ray (12)

Common skate *Dipturus batis* and cuckoo ray *Leucoraja naevus* were combined into one group due to similarities in their diets. Biomass is 28.5 thousand tonnes and biomass density is 0.05 t.km^2, P/B=0.35 and Q/B=1.8 were estimated using empirical formulae in FishBase, and diets from Daan *et al.* (1993) were averaged accordingly. Aggregate diet of this group is dominated is dominated by fish, and mobile benthos such as crabs, nephrops and shrimps. Trophic level is 4.44 (Tables 3.3, 3.4).

The input parameters of the main commercial gadoids: cod, whiting, haddock and saithe were taken from ICES MSVPA working group (SGMSNS, ICES 2002b). All species were split into juvenile and adult FGs. Biomasses of juveniles and adult fishes were calculated separately. Production rates (P/B) were calculated from *Z=F+M0+M2*, consumption rates (Q/B) from consumption at age in MSVPA (Table T1, ICES 2002b), and diets are taken from the 1991 year of stomachs database (Table T3.4, Hislop 1997).

13.15 Juvenile cod (13) and Adult cod (14)

Cod *Gadus morhua* is an important species in the North Sea. They are targeted mainly by otter trawl, longline and gillnet vessels. The fishery is year-round, although some fleets exhibit seasonal fishing patterns. Trawlers usually catch cod as part of a mixed fishery with haddock and whiting. Gillnet vessels are better able to target their effort towards cod alone. Cod is also taken as a by-catch in the beam trawl fisheries targeting plaice and sole and in the otter trawl fisheries targeting *Nephrops*.

Juvenile cod was defined as cod of 0-2 years of age and <40 cm of length. Cod of age 3 and more years and bigger than 40 cm was presented in the FG 14 Adult cod. Biomass of juvenile cod (FG 13) is 45.03 thousand tonnes and biomass density is 0.079 t.km^2, P/B=1.79, and Q/B=4.89; and for adult cod (FG 14) – biomass is 91.8 thousand tonnes and biomass density is 0.161 t.km2, P/B=1.19, and Q/B=2.17. One of the top predators, during their first six months, cod are pelagic and feed mainly on copepods. At a size of approximately 7 cm they adopt a demersal way of life. Food is initially dominated by crustaceans, but as they grow bigger fish become more and more important as prey. Trophic levels of juvenile and adult cod are 4.43 and 4.83, respectively.

13.16 Juvenile whiting (15) and Adult whiting (16)

North Sea whiting *Merlangius merlangus* are caught throughout the North Sea especially in the northwestern North Sea, off the northeast coast of England and off the coast of Denmark, Germany and the Netherlands. The majority of landings are from the mixed demersal fishery in the northern North Sea mostly by Scottish light trawlers and seiners and off the northeast coast of England. By-catches are taken by trawlers targeting *Nephrops*, beam-trawlers targeting flatfish and by vessels fishing for industrial species. In the eastern English Channel, whiting are caught mainly by bottom trawlers as a by-catch in a mixed demersal fishery, but a seasonal fishery targets whiting using midwater trawls. A high proportion of the whiting catch is discarded at sea.

Juvenile whiting was defined as whiting of 0-1 years of age and <20 cm length. Whiting aged 2 or more years and bigger than 20 cm was presented in the FG 16 Adult whiting. Biomass of juvenile whiting (FG 15) is 126.5 thousand tonnes and biomass density is 0.222 t.km^2, P/B=2.36, and Q/B=6.58; and for adult whiting (FG 16) - biomass is 200.6 thousand tonnes and biomass density is 0.352 t.km^2, P/B=0.89, and Q/B=5.46. Whiting is dominantly piscivorous, but targets mainly smaller prey such as sandeels, sprats and Norway pout (also depending on the smaller size of whiting compared to cod); benthos is also an important share of the ration especially for younger/smaller fish. Trophic levels of juvenile and adult whiting are 4.27 and 4.41, respectively.

13.17 Juvenile haddock (17) and Adult haddock (18)

North Sea haddock *Melanogrammus aeglefinus* are caught in the mixed demersal fishery, mainly by Scottish light trawlers, seiners and pair trawlers. Smaller quantities are taken by *Nephrops* trawlers as by-catch in the mixed demersal fishery and the small mesh industrial fishery, in the Skagerrak. They are caught throughout the year, especially in the northwestern North Sea but they are largely absent from the southern North Sea (ICES Division IVc). A high proportion of the haddock catch is discarded at sea because they are smaller than legal size.

Juvenile haddock was defined as haddock of 0-1 years of age and <20 cm length. Haddock aged 2 or more years and bigger than 20 cm was presented in the FG 18 Adult haddock. Biomass of juvenile haddock (FG 17) is 161.9 thousand tonnes and biomass density is 0.284 t.km^2, P/B=2.54, and Q/B=4.16; and for adult haddock (FG 18) biomass is 59.3 thousand tonnes and biomass density is 0.104 t.km^2, P/B=1.14, and Q/B=2.35. Juvenile haddock is dominantly benthivorous, but also feeds on small fish such as sandeels and dab. Adult haddock feeds on various fish and benthic species (Table). Trophic levels of juvenile and adult haddock are 4.06 and 4.28, respectively.

13.18 Juvenile saithe (19) and Adult saithe (20)

Saithe *Pollachius virens* are mainly targeted by French, German and Norwegian otter-trawlers but some UK vessels also particpate in the fishery. Catches occur year-round in the northern North Sea, to the west and north of Shetland and on the southern and western limits of the Norwegian Trench (Rhinne) usually in depths greater than 150 m.

Juvenile saithe were defined as saithe of 0-3 years of age and <40 cm length. Saithe aged 4 and more years and bigger than 40 cm was presented in the FG 20 Adult saithe. Biomass of juvenile saithe (FG 19) is 160.2 thousand tonnes and biomass density is 0.281 t.km^2, P/B=1, and Q/B=4.94; and for adult saithe (FG 20) – biomass is 10.8 thousand tonnes and biomass density is 0.19 t.km^2, P/B=0.88, and Q/B=3.6. Juveniles, feed mainly on Norway pout, sprat, euphasiids, and zooplankton, while adult saithe is mainly piscivorous (Table 3.4). Trophic levels are 4.03 for juvenile - and 4.36 for adult saithe.

13.19 Hake (21)

Hake *Merluccius merluccius* is an important commercial species caught in the North Sea mainly as by-catch. Biomass of hake was estimated using the method of Sparholt (1990) with cod, whiting, haddock, and saithe as reference species. P/B and Q/B were estimated using empirical formulae in FishBase. Biomass of hake (FG 21) is 8 thousand tonnes and biomass density is 0.014 t.km^2, P/B= 0.82, and Q/B= 2.2. The diet was reported by Du Buit (1996). Hake is preferentially piscivorous with trophic level - 4.92.

13.20 Blue whiting (22)

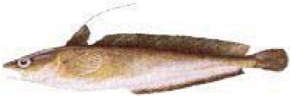
Blue whiting *Micromesistius poutassou* is a bathypelagic fish living mainly in mid water over the edge of the continental shelf at 100-300 m. It is an important target for industrial fisheries for production of fish meal. It is also a prey for larger fish and dolphins.

Biomass of blue whiting was estimated using the method of Sparholt (1990) with Norway pout as reference species. P/B and Q/B were estimated using empirical formulae in FishBase. Biomass of blue whiting (FG 22) is 23.9 thousand tonnes and biomass density is 0.08 t.km^2, P/B= 2.5, and Q/B= 9.06. The diet was reported by Bergstad (1991). Blue whiting feeds dominantly on euphasiids, and zooplankton, but fish (Norway pout and sprat) and shrimp are also essential parts of its diet. Trophic level is 4.09.

13.21 Norway pout (23)

Distributed in the northern North Sea, Norway pout *Trisopterus esmarkii* has a benthopelagic to pelagic mode of life, living in shoals in the open sea, mostly in waters between 100 and 200 m depth. A target species for the industrial fishery. Because of large by-catches of juvenile haddock, an area in the northern North Sea has been closed to the fishery (Norway pout box). Biomass and P/B=*Z* were based on MSVPA results (ICES 2002b). Consumption rate was taken from Greenstreet (1996) and diet data – from Malyshev & Ostapenko (1982). Biomass of Norway pout (FG 23) is 794.6 thousand tonnes and biomass density is 1.394 t.km^2, P/B=3.05, and Q/B= 5.05. Norway pout is zooplanktivorous with trophic level 3.59 (Tables 3.3, 3.4). Norway pout is one of the dominant prey fish species in the North Sea.

13.22 Other gadoids (large, 24)



Other large gadoids with lower population abundances and importance for the fisheries were aggregated in FG 24. The group consists of pollack *Pollachius pollachius*, tusk *Brosme brosme*, ling *Molva molva* , greater forkbeard *Phycis blennoides*. Though not directly targeted (except in northern areas) these fishes are commercially important, as well as for the recreational fishery. They are also important for the ecosystem as predators. Their respective biomasses were estimated using the method of Sparholt (1990) with cod, whiting, haddock and saithe as reference species. Combined biomass of FG 24 was estimated as 8.6 thousand tonnes. Each species production and consumption rates were estimated using empirical formulae in FishBase and then used to calculate weighted mean for the FG: P/B =1.27, and Q/B =2.18. The diets of large gadoids were taken from published studies (Hoines & Bergstad 1999, Bergstad 1991, Rae & Shelton 1982) and aggregated for the FG by weighting diets by consumption. Dietary preferences are mainly fish and larger invertebrates such as squid and shrimp resulting in quite high aggregate trophic level of 4.53 (Table 3.4).

13.23 Other gadoids (small, 25)

This group consists of different species which biomass was estimated using the method of Sparholt (1990): four-bearded rockling *Rhinonemus cimbrius*, five-bearded rockling *Ciliata mustela*, three-bearded rockling *Gaidropsarus vulgaris*, shore rockling *Gaidropsarus mediterraneus*, were estimated with cod, whiting, haddock and saithe as reference species, and. poor cod *Trisopterus minutus*, bib *Trisopterus luscus*, and silvery pout *Gadiculus argenteus*, with Norway pout as a reference species. Combined biomass of FG 25 was estimated as 21.7 thousand tonnes. Each species production and consumption rates were estimated using empirical formulae in FishBase and then used to calculate weighted mean for the FG: P/B =2.5, and Q/B =3.84. The aggregate diet was compiled based on published studies of the diets of poor-cod and bib from Armstrong (1982), and four-bearded rockling and silvery pout from Albert (1993). Diets mainly consist of invertebrates, trophic level is 3.83 (Table 3.3). The species in this group are mainly prey fishes being quite important part of the diet of almost all top-predators such as dolphins, seals, elasmobranchs and cod (Table 3.4)

13.24 Anglerfish (monkfish) (26)

Monkfish Lophius piscatorius is an important commercial species although caught mostly as by-catch in the North Sea. Biomass of monkfish was estimated using the method of Sparholt (1990) with cod, whiting, haddock and saithe as reference species. P/B and Q/B were estimated using empirical formulae in FishBase. Biomass of monkfish (FG 26) is 8.6 thousand tonnes and biomass density is 0.042 t.km2, P/B= 0.7, and Q/B= 1.7.The diet was reported by Rae & Shelton (1982). Anglerfish feed on a wide range of fish species and size-classes and legitimately has one of the highest trophic level from all FGs - 4.85.

13.25 Gurnards (27)

Grey Gurnard *Eutrigla gurnardus* is an abundant demersal species. In winter it forms dense aggregations locally to the northwest of the Dogger Bank, in summer it is more widespread.

Its importance for the fisheries is as a by-catch species in demersal fisheries for which only a small market exists. Catches are largely discarded.

Biomass of gurnards *Trigla* sp, *Eutrigla* sp. and *Aspitrigla* was estimated using the method of Sparholt (1990) with cod, whiting, haddock, saite as reference species. P/B was estimated using empirical formulae in FishBase and Q/B was based on consumption of the grey gurnard *Eutrigla gurnardus*, which is the dominant species, reported by the MSVPA working group (ICES 2002b). Biomass of gurnards (FG 27) is 43.9 thousand tonnes and biomass density is 0.077 t.km2, P/B= 0.82, and Q/B= 3.2. The diet was based on the 1991 year of stomachs data for grey gurnard as reported by Gee & Kikkert (1993). Gurnards are key predators in the North Sea which importance increased in the last years (Floeter *et al*. 2005). Juveniles feed on a variety of crustaceans. The diet of older specimens consists mainly of juvenile fish. (Table 3.4). Trophic level is 4.52.

13.26 Juvenile herring (28) and Adult herring (29)

North Sea herring *Clupea harengus* stocks have shown enormous fluctuation in the past. There was a rapid stock decline in the late 1970's due to the overfishing and recruitment failure. This was followed by a four year closure of the fishery and then another decline in the mid 1990's mainly due to high by catch of juveniles in the industrial fishery. This led to the implementation of a recovery plan in 1997, which was successful. Two fisheries exploit the autumn spawning herring: the directed herring fisheries with purse seiners and trawlers in the North Sea and ICES Division IIIa (Skagerrak and Kattegat) and the one where herring is taken as a by-catch in the industrial small-mesh fisheries which operate in the same areas.

Herring biomass and P/B=Z were based on MSVPA results (ICES 2002b). Herring was split to juvenile ages 0-1, length <20 cm (FG 28) and adult (FG 29). Consumption rate of both FGs were taken from Greenstreet (1996) and diets – from Last (1989). Biomass of juvenile herring (FG 28) is 359.1 thousand tonnes and biomass density is 0.63 t.km^2, P/B=1.31, and Q/B= 5.63; and for adult herring (FG 29) – biomass is 1.1 million tonnes and biomass density is 1.966 t.km^2, P/B=0.8, and Q/B= 4.34. Herring is zooplanktivorous with trophic level 3.44 for juveniles and 3.45 for adults.

13.27 Sprat (30)

Sprats *Sprattus sprattus* are caught by trawl, midwater trawl, pair trawl and seine net, and are often preserved by smoking. Juvenile sprats are marketed as whitebait. However, the larger part of the international catch is used in the fishmeal industry. Sprat is an important prey species for most of the North Sea predators.

Sprat biomass and P/B=Z were based on MSVPA results (ICES 2002b). Consumption rate was taken from Greenstreet (1996) and diet – from De Silva (1973). Biomass of sprat (FG 30) is 330 thousand tonnes and biomass density is 0.579 t.km^2, P/B=2.28, and Q/B= 5.28. Sprat is zooplanktivorous with trophic level 2.97.

13.28 Mackerel (31)

There are two components to the mackerel Scomber scomberstocks in the North Sea, a resident population called North Sea mackerel and a migratory population called Western mackerel (ICES 1997). Historically the resident population has been very large (c.a. 2.5 million tonnes, Hamre (1978)), but since the 1970's it has decreased (36 – 110 thousand tonnes SSB, ICES (2002a)). It is not possible to distinguish between the two stock components in the catches, however due to the differing time of residency, ICES working groups treat the two stocks components differently. Mackerel are mainly exploited in a directed fishery for human consumption, which tends to target bigger fish, potentially causing smaller, less marketable fish to be discarded (high-grading).

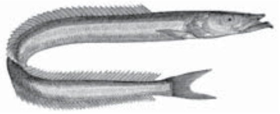
The biomass of the North Sea stock component was estimated by MSVPA to be 57 thousand tonnes in 1991 (ICES 1997). Abundance of the Western mackerel was estimated as 923.4 thousand tonnes in 1991 by the Study Group on Multispecies assessment in the North Sea (SGMSNS) based on assessment of the whole Western stock (ICES 2002a) and fractions migrating into the North Sea (ICES 2002b). P/B assumed as equal to Z is 0.793 for the North Sea mackerel (ICES 1997) and 0.38 for the Western mackerel (ICES 2002a). Q/B=1.73 was based on consumption rates used in MSVPA (ICES 2002b) and the diet composition was taken from the 1991 year of stomachs database (Hislop 1997). North Sea and Western mackerel are practically undistinguishable and they were aggregated into a single mackerel group with biomass 980.4 thousand tonnes and biomass density - 1.72 t.km^2, P/B=0.6. Mackerel feeds on both pelagic and benthic organisms: fish (sprats, sandeel), euphasiids, copepods, as well as polychaetes, mysids and other benthos. Trophic level is 3.9.

13.29 Horse mackerel (32)

Traditionally, most horse mackerel *Trachurus trachurus* were landed in small-mesh industrial fisheries, though there has been an increase in targeted fisheries landing larger fish for human consumption.

In the North Sea horse mackerel is considered as two stocks (ICES 2002a). The North Sea stock spawns in the southern North Sea and migrates partly westwards through the English Channel in winter. The western stock spawns off the western slope of the European shelf and migrates partly into the North Sea in the autumn. Analytical assessment is done for the Western Stock, while catch figures only are available for the North Sea Stock. Rueckert *et al*. (2002) estimated horse mackerel abundance applying the approach of Sparholt (1990) and using International Bottom Trawl Survey (IBTS) data using whiting as a reference species. Mean biomass in the North Sea in 1991 was 96.16 thousand tons (Rueckert *et al*. 2002). However these authors warranted that their estimate of the Western stock component "should be regarded as significant underestimate" (Rueckert *et al*. 2002) possibly for two reasons: 1. It is concentrated in a limited area on the north of ICES area IV; 2. Schools are distributed in deeper waters over the shelf break where they are less accessible to the bottom trawl used by IBTS. The multispecies study group SGMSNS uses another figure: 329.75 in MSVPA. It is based on single species assessment (ICES 2002a) and proportion of the horse mackerel stock migrating in the North Sea. This estimate however is subject to many assumptions and also does not seem very reliable. Here we used the SGMSNS estimates of biomass 330 thousand tonnes and biomass density 0.579 t.km2 (ICES 2002b) for reasons of consistency with other commercial species estimates also based on MSVPA. The P/B =1.64 was estimated with FishBase and the Q/B=3.51 from the SGMSNS report (ICES 2002b). The diet composition was based on quarterly estimate of Greenstreet (1996) who used the original data of Dahl and Kirkegaard (1987). In the North Sea horse mackerel is mainly piscivorous (gadoids, herring, sandeel), but also eat nephrops and some benthos. As a result trophic level is relatively high 4.38.

13.30 Sandeels (33)



Sandeels (Ammodytidae) are caught in large quantities by specialized industrial fisheries. Sandeel biomass and P/B=Z were based on MSVPA results (ICES 2002b). Consumption rate was taken from Greenstreet (1996) and diet – from Reay (1970) Biomass of sandeel (FG 33) is 1.8 million tonnes and biomass density is 3.122 t.km^{-2}, P/B=2.28, and Q/B= 5.24. Feeding of sandeels reflects their bentho-pelagic mode of life: diet is dominated by zooplanktoon, but polychaetes, meiofauna and other small benthos have also an important role, trophic level is 3.35. Sandeels are one of the dominant prey fish in the North Sea (Figure 3.6).

13.31 Plaice (34)

English vessels have traditionally caught plaice *Pleuronectes platessa* in a directed beam-trawl fishery using 120 mm mesh north of 56°N, and in a mixed fishery with sole, using 80 mm mesh in the southern North Sea. Plaice are also a by-catch in inshore and offshore otter-trawl fisheries. Historically the main English ports were Lowestoft and Grimsby, but with the decline of the English beam trawl fleet, plaice is mainly landed into Grimsby, Hartlepool and abroad. In 2005, international landings amounted to 55 700 t compared with a peak of 170 000 t in 1989. About 40% of the total international landings were reported by Dutch vessels, the UK accounted for 23%, Danish landings for 20%, while Belgium, Germany, France and other countries landed the remaining 17%.

Biomass and P/B=Z of plaice were based on MSVPA results (ICES 2002b). Biomass of plaice (FG 34) is 400.7 thousand tonnes and biomass density is 0.703 t.km-2, P/B=0.85, and Q/B= 3.42. Consumption rate was taken from Greenstreet (1996) and diet – from De Clerck & Buseyne (1989). Plaice is dominantly benthivorous, although larger specimens also feed on small demersal fish trophic, level is 3.99.

13.32 Dab (35)

Dab *Limanda limanda* is one of the most frequent and abundant species in the North Sea at present. It has a growing importance as a by-catch and obviously an important role in the food web as both consumer and prey, mainly because of its great abundance. Biomass of dab was estimated using the method of Sparholt (1990) with plaice as reference species. P/B was estimated using the empirical formula in FishBase and Q/B was based on consumption reported by Greenstreet (1996). Biomass of dab (FG 35) is 2.6 million tonnes and biomass density is 4.64 t.km^{-2}, *B*= t km^2, P/B= 0.672, and Q/B= 4. The diet was reported by De Clerck & Torreele (1988). Dab is dominantly benthivorous, although larger specimens occasionally feed on small demersal fish, trophic level is 4.01.

13.33 Long-rough dab (36)

Long-rough dab *Hippoglossoides platessoides* has some commercial importance as a by-catch and mainly ecological importance as a consumer and prey. Biomass of was estimated using the method of Sparholt (1990) with plaice as a reference species. P/B and Q/B were estimated using empirical formulae in FishBase. Biomass of long-rough dab (FG 36) is 336 thousand tonnes and biomass density is 0.59 t.km^{-2}, P/B= 0.7, and Q/B= 4. The diet was reported by Ntiba & Harding (1993). Long-rough dab is predominantly benthivorous, but unlike dab, fish is found in a greater proportion in the stomachs of the long-rough dab (Table 3.4). Trophic level is 4.18.

13.34 Flounder (37)

Flounder *Platichthys flessus* is caught as a by-catch by beam trawls in shallow areas and has some commercial importance. Biomass was estimated using the method of Sparholt (1990) with plaice as reference species. P/B and Q/B were estimated using empirical formulae in FishBase and diet was reported by Doornbos & Twisk (1984). Biomass of flounder (FG 37) is 256 thousand tonnes and biomass density is 0.45 t.km^{-2}, P/B= 1.1, and Q/B= 3.2. Flounder feeds mainly on benthos but small demersal fish also makes an important part of its diet (~20% Table). Trophic level is 4.37.

13.35 Sole (38)

Sole *Solea solea* is mainly caught by Dutch beam-trawlers in a mixed fishery with plaice in the southern North Sea using 80 mm mesh south of 56° N. There is also a directed gillnet fishery around the Danish coast, mainly in the second quarter of the year. In the English fishery, the high value of sole makes it one of the most important species targeted by inshore vessels using trawls, and fixed and draft trammel nets. The main fishery is from March to October. Sole is also taken as a target and by-catch species by offshore beam- and otter-trawlers and gillnetters. In 2005 the Netherlands reported about 67% of the total landings of sole in ICES Division IV, Belgium accounted for 8% and France, Germany, the UK and Denmark made up the remaining 18%. Landings during the period 1990-1995 were dominated by two strong year-classes, 1987 and 1991, and averaged about 32 000 t. Since then, reported landings decreased to 16 355 t in 2005.

Biomass and P/B=Z of sole *Solea solea* were based on MSVPA results (ICES 2002b). Consumption rate was taken from Greenstreet (1996) and diet – from Braber & Groot (1973). Biomass of sole (FG 38) is 90.1 thousand tonnes and biomass density is 0.158 t.km-2, P/B=0.8, and Q/B= 3.1. Sole's main preys are polychaetes and meiofauna, but large specimens also eat small fish such as gobies and dragonets. Trophic level is 4.0.

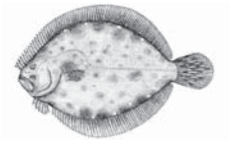
13.36 Lemon sole (39)

Lemon sole *Microstomus kitt* is a valuable market species usually caught as a by-catch. Biomass was estimated using the method of Sparholt (1990) with plaice as a reference species. P/B was estimated using the empirical formula in FishBase and Q/B was based on consumption reported by Greenstreet (1996). The diet, as reported by Rae (1956), is dominated by small benthos e.g. polychaetes, meiofauna (Table). Trophic level is 3.94. Biomass of lemon sole (FG 39) is 173.8 thousand tonnes and biomass density is 0.305 t.km^{-2}, P/B= 0.864, and Q/B= 4.32.

13.37 Witch (40)

Witch *Glyptocephalus cynoglossus* is mainly distributed on mud grounds in the northern North Sea. It is caught as a by-catch and has a limited market importance. Biomass was estimated using the method of Sparholt (1990) with plaice as a reference species. P/B and Q/B were estimated using empirical formulae in FishBase. Biomass of witch (FG 40) is 46.7 thousand tonnes and biomass density is 0.082 t.km-2, P/B= 0.9, and Q/B= 3. The diet as reported by Rae (1956) is dominated by small benthos e.g. polychaetes (Table). Trophic level is 4.05.

13.38 Turbot and brill (41)



Turbot *PSetta maxima* and brill *Scopthalmus rhombus* are valuable market species usually caught as a by-catch in trawls and gillnets (Table 3.5). They were aggregated in one group because of their taxonomic and ecological similarity. Biomass was estimated using the method of Sparholt (1990) with plaice as areference species. P/B and Q/B were estimated using empirical formulae in FishBase. Biomass of turbot and brill is 30.8 thousand tonnes and biomass density is 0.054 t.km^{-2}, P/B= 0.86, and Q/B= 2.1 (Table 3.5). The diets (reported by Wetsteijn, 1981) were aggregated weighted by each species consumption. Turbot and brill are dominantly piscivorous feeding on different (mainly) demersal fish species (Table 3.4). Aggeregate trophic level is 4.62.

13.39 Megrim (42)

Megrim *Lepidorhombus whiffiagonis* is caught as a by-catch with beam trawls mainly in the northern Noth Sea. It was presented as a separate FG mainly because of its importance as a fish predator. Commercially it is of moderate importance (although more important in western waters). Biomass was estimated using the method of Sparholt (1990) with plaice as a reference species. P/B and Q/B were estimated using empirical formulae in FishBase. Biomass of megrim is 19.4 thousand tonnes and biomass density is 0.034 t.km^{-2}, P/B= 0.72, and Q/B= 3.1. The diet as reported by Du Buit (1984) is dominated by fish (Table 3.4). Trophic level is 4.46.

13.40 Halibut (43)

The halibut *Hippoglossus hippoglossus* is an important commercial species although its abundance is in decline. Biomass of halibut was estimated using the method of Sparholt (1990) with plaice as reference species. P/B and Q/B were estimated using empirical formulae in FishBase. Biomass of halibut is 18.8 thousand tonnes and biomass density is 0.033 t.km^{-2} is B=0.033 t km^{2}, P/B= 0.16, and Q/B= 3.14.The diet was reported by McIntyre (1952). Halibut is a voracious predator preying on gadoids, sandeel, sprat, cephalopods and crabs (Table 3.4). Trophic level is 4.85.

13.41 Dragonets (44)

Dragonets genus *Callionymus* are quite common in the North Sea mostly in shallower water, and are mainly important as a prey of predatory demersal fish. Biomass of dragonets was estimated using the method of Sparholt (1990) with plaice as a reference species. P/B and Q/B were estimated using empirical formulae in FishBase. Biomass of dragonets is 17.7 thousand tonnes and biomass density is 0.031 t.km^{-2},P/B= 1.4, and Q/B= 6.9. The diet was reported by Gibson & Ezzi (1987) and mainly consists of benthic invertebrates (e.g. polychaetes) and trophic level is 3.98 (Tables 3.3, 3.4).

13.42 Catfish (wolf-fish, 45)

Catfish (wolf-fish) *Anarrhichas lupus* is a commercially important species caught mainly with otter trawls in the northern North Sea. Biomass was estimated using the method of Sparholt (1990) with cod, whiting, haddock and saithe as reference species. P/B and Q/B were estimated using empirical formulae in FishBase. Biomass of catfish (FG 45) is 5.7 thousand tonnes and biomass density is 0.01 t.km^{-2}, P/B= 0.48, and Q/B= 1.7. The diet was reported by Bowman *et al.* (2000). Catfish feed mainly on hard-shelled molluscs, crabs, lobsters, sea urchins and other echinoderms. Trophic level is 4.27.

Demersal fish not included in previous FGs were grouped in two residual groups FG 46 Large demersal fish and FG 47 Small demersal fish

13.43 Large demersal fish (46)

This group consists of various larger demersal and benthopelagic fish having been caught with the surveys such as chimera *Chimaera monstrosa*, John Dory *Zeus faber*, seatrout *Salmo trutta*, Norway haddock *Sebastes viviparous*, bluemouth redfish *Helicolenus dactylopterus*, and roundnose grenadier *Coryphaenoides rupestris*. Their respective biomasses were estimated using the method of Sparholt (1990) to be on overall ~1 thousand tonnes. Each species production and consumption rates were estimated using empirical formulae in FishBase and then aggregated as weighted means to P/B =0.55, and Q/B =2.54. The diets of large gadoids were taken from published studies (e.g. Bergstad *et al.*, 2001, Bowman *et al.*, 2000) and aggregated as weighted means weighted by each species consumption. Aggregate trophic level is 4.2 (Table 3.3).

13.44 Small demersal fish (47)

This group consists of the rest of the unspecified demersal fish found in the samples such as viviparous eelpout *Zoarces viviparous*, bullrout *Myoxocephalus scorpius*, Vahl's eelpout *Lycodes vahlii*, sea scorpion *Taurulus bubalis*, pogge *Agonus cataphractus*, sea-snail *Liparis liparis*, greater weever *Trachinus draco*, lesser weever *Echiichthys vipera*, snake blenny *Lumpenus lampretaeformis*, red mullet *Mullus surmuletus*, solenette *Buglossidium luteum*, thickback sole *Microchirus variegatus*, scaldfish *Arnoglossus laterna* and argentine *Argentina* sp.. Their respective biomasses were estimated using the method of Sparholt (1990) with plaice as a reference species. Initial biomass estimates were 50 thousand tonnes. This and other aggregate groups such as FGs 24 and 25 other gadoids, FG 46 large demersal fish and FG 48 miscellaneous filter feeding pelagic fish, were used as buffers for balancing consumption of the rest of the groups where more precise data were available so their biomasses may possibly be overestimated. Each species production and consumption rates were estimated using empirical formulae in FishBase and then aggregated as weighted means to P/B =1.42, and Q/B =3.7. The diet was compiled based on published studies (e.g. Bergstad *et al.*, 2001, Bowman *et al.,* 2000) and aggregated as weighted means weighted by each species consumption. Aggregate trophic level is 4.21 (Table 3.3).

13.45 Miscellaneous filter feeding pelagic fish (48)

This group consists of different planktivorous species: shad *Alosa sp.*, anchovy *Engraulis encrasicolus*, and sardine *Sardina pilchardus* were estimated using the method of Sparholt (1990) with herring and sprat as reference species and that of lanternfish *Maurolicus muelleri* – with Norway pout as a wreference species. Initial biomass estimates were 7.4 thousand tonnes. Each species production and consumption rates were estimated using empirical formulae in FishBase and then aggregated as weighted means to P/B =4, and Q/B =10.19. The aggregate diet was compiled based on Bowman *et al* (2000). Diet mainly consists of zooplankton, trophic level is 3.43 (Table 3.4).

14. Fisheries landings, discards, economic and social metrics

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The following section documents the sources and ranges of data used to define the fishing fleets and estimate landings, discards and economic and employment parameters. The preparation of the data revealed that no one data source is able to provide the required information in sufficient completeness. Thus, it is necessary to make assumptions when weaving together the various sources of data and information. Primary data sources were the STCF 1991 database, ICES STATLANT, Cefas discards database (Trio), the UK fishing activity database (FAD) and STECF Annual Economic Report.

14.1 Database descriptions

Five databases/sources were used which collect and summarise the landings, by-catch, discards and economics information used in the model.

Scientific and Technical Committee for Fisheries (STCF) database 1991

The STCF North Sea database contains port landings data and some economic data for the top 27 commercially important species in the North Sea. Data come from eight countries and are divided into 58 fleets (Lewy *et al.*, 1992; Vinther and Thomsen, 1992). Discard values are already included for five species: cod, haddock, whiting, plaice and sole.

STATLANT 27A

Nominal landings of fish and shellfish obtained from port sampling are officially submitted to ICES by 19 member countries on an annual basis. The Co-ordinating Working Party on Fishery Statistics (CWP) organises the collection of these statistics under the STATLANT programme. ICES have published these data in the *Bulletin Statistique des Pêches Maritimes* from 1903 to 1987, and from 1988 onwards in ICES *Fisheries Statistics*, and from 1973 onwards collated the data in the STATLANT database. The database provides a comprehensive catalogue of reported landings for 223 North Sea species. Unfortunately they are not broken down in to gear types. Annual catches for each species in ICES divisions IVa, IVb and IVc were downloaded from the website www.ices.dk and abstracted for the period 1973-2005 using the Fishstat 2.3 programme (Food and Agriculture Organisation (FAO)) query tool.

UK Fishing Activity Database (FAD)

Developed by Cefas to hold the official British landings statistics, the UK Fishing Activity Database System holds information on fishing catch and effort by gear type for all recorded commercial landings into England, Wales and Northern Ireland. It provides information needed by the Defra HQ divisions to allocate, monitor and control uptake of fishing quotas; it is used by the Sea Fisheries Inspectorate (SFI) to aid the enforcement of the Common Fisheries Policy; it supports the fish stock assessment work at Cefas.

Discards database (TRIO)

Discards were obtained from the Cefas discards database, Trio. Table 14.1 provides a summary of information contained in the database. At the time of extraction, Trio contained records from 274 observer trips from a wide range of vessels from 1994 to present. For safety reasons, trips were confined to vessels less than 12 metres registered length. Although this leaves out a considerable proportion of the fleets, it is only a relatively small proportion of the effort and catches. This is because many of the smaller vessels only trawl part-time. Details on this and sampling practices are described by Cotter *et al.* (2002).

Annual Economic Report (AER) of the STECF

The 2005 STECF Annual Economic Report contains data from all EU Member States with marine fisheries (except France) in addition to the non-EU countries Norway, Iceland and the Faeroe Islands. The economic performance of eighty-nine different fishing segments from 2004 is discussed and a time series covering the years 1999–2004 presented. This was the document that all economic data used in this project was sourced from. It represents the most up to date source available for economic data on the marine fisheries of the EU. The report covers approximately 60% of the total value of the EU fisheries sector, 70% of the landings and 40% of the employment.

Table 14.1. Summary of data stored on the Cefas Trio discards database.

Name of database	Project name (Code)	Period of data collection	Sea area	Notes on vessel selection	Fish species studied	Benthos data collected	Commercial shellfish data collected
Rawdata	Historic MAFF data	January 1994 – April 1997	North Sea	Co-operative 'ships of opportunity' restricted to vessels using towed nets, sailing from ports on the NE coast of England.	Cod, haddock, whiting	No	No
	EC 95/094 (UEA)	May 1997 – November 1998	North Sea	Vessels equal to or greater than 12 m reg. length using towed nets and sailing from ports on the NE coast of England. (Includes visiting Scottish vessels) PPSsampling scheme.	Cod, haddock, whiting	No	No
	C0272	December 1998 – March 1999	North Sea	As 'EC 95/094 (UEA)' above.	Cod, haddock, whiting	No	No
Beamdata	Beam trial	February 1998	North Sea	The first trial of sampling discards on a beam trawler, using a ship of opportunity.	All	No	No
RD C0739	C0739 (EC98/097	August 1999 – September 2001	North Sea	E&W reg. vessels equal to or greater than 12 m reg. length using towed nets, sailing from UK or foreign ports. Random draw sampling scheme	All	Yes	No
Combined new database	M0150	October 2001 – March 2002	North Sea	E&W reg. vessels equal to or greater than 10 m reg. length using all gear types in all sea areas. This study was conducted as support for the incoming EU regulation on data collection, whilst collecting data relevant to the Cod and Hake recovery plans. Random draw sampling scheme.	All	Yes	No
Combined new database	MD001	April 2002 – present	North Sea	E&W reg. vessels equal to or greater than 10 m reg. length using all gear types in all sea areas. This project is being conducted to fulfil the UK's commitment to EU regulation 1639/2001 on fisheries data collection. Random sampling scheme stratified by gear and area.	All	Yes	Yes
TRIO – all Databases Combined	TRIO – A combination of all the above databases.						

The STECF designations for gears and fleets

The STECF AER contains the various fleets used by each member state. The member states are responsible for classifying their fleets and passing the information on to the STECF. This results in different classifications being used by different member states. The majority of the fleets are segmented by the activity they practice (eg pelagic and demersal trawlers) but there are also the gears used (eg Gillnetters and Beam trawlers), the length of the vessels (eg Beam trawlers > 24 m and Beam trawlers < 24 m) and the areas fished (eg North Sea trawlers and Baltic trawlers).

The origin of the AER data used by the STECF

In order to use the data from the AER report it was necessary to understand the methodology that was used in the preparation of the document. The STECF AER 2005 is the last of the Concerted Action (CA) reports, a total of three published between 1996 and 2004 (AER, 2000).

The CA reports were a development of the Multi Annual Guidance Programmes (MAGP) that were initiated to reduce the size of the member states fleets in order to reduce the overcapacity of the total EU fleet. To reduce the number of fishing vessels in the EU it was essential to know how many there were. The creation of the Community vessel register was proposed and the associated EC legislation was approved. The EC regulation 2090/98 concerns the forming of a community vessel register and designates codes for the type of fishing gear being used and states that the member states when forming their vessel registers should use these codes and classifications (EC Regulation 2091/98). The community fleet register gear codes are based on the FAO document the International Statistical Standards Classification of Fishing Gears (ISSCFG) (EC Codifications standards 2006). The regulations concerning the community fleet register have been updated several times with amendments to the older EC regulations, in order to incorporate the changing nature of vessel classifications and data requirements.

From the origin of the community fleet register, 'fleet segments' were created and used to define the different member states fleets; from there it has gone through a convoluted process as member states continue to update the community fleet register according to the updated EU legislation on the definition of fleet segments. The outcome is that the fleets within the STECF AER are given to the STECF by the member states themselves, and aggregated by the member states. Therefore they are all slightly different to each other but follow the basic principals laid down by the community fleet register and the ISSCFG.

The aggregation and collection of data from different member states is a complicated one, exacerbated by the lack of collaboration between the organisations that deal with the biological and economic data in each member state. For the constructive use of the large amounts of fisheries data that is available throughout the EU a standardised method of collecting and sharing data was needed. This was the driver behind implementation of the recent Data Collection Regulation (DCR, EC Regulation 1639/2001).

The DCR deals with the collection and distribution of fishery data (biological and economic) and aims to unify the disjuncture between member states and their individual collection methods and codification schemes. It places the STECF at the head of the data dissemination in the form of the Annual Economic Reports. Classifications for the Fleets of the European Union (EU) contained in the 2005 STECF AER are the template for classification under the new DCR. Thus, the DCR gear codes are based on the ISSCFG, however there are more detailed levels relating to the length, power and capacity of vessels.

The STECF 2005 AER did not use the DCR gear codification scheme for the member states fleets. The first data to be collected inline with the DCR should be in 2006 although this will vary by country. All fisheries data, economic and biological, should be collected using the codification schemes laid down in the DCR from 2006 onwards. This will facilitate the unification and relevance of cohesive data between member states and their collection programmes.

14.2 Matching fleet and species definitions used in databases

Traditionally there has been little unification of biological and economical fisheries data. The two have remained distinct and the various bodies charged with retrieving and making sense of the information have developed different ways of classifying and aggregating data about the same fisheries.

Deriving information on the landings and economic information for each fleet required matching with one another, the fishing gear classifications used in each database. This was an involved and lengthy procedure. Part way through the process, the decision was made to update the models original 16 fleet descriptions (based on the STCF 1991 database) and make them consistent with the new DCR fleet categories (DCR Codification standards and definitions 2006) to facilitate future updating of the model. The mapping of the AER to the DCR classifications has already been done by the STECF on their website (STECF, SGECA, 2006) for the purpose of facilitating the process of change and providing for the member states an example of the differences between the classification schemes.

The level detail used in the lowest level of the DCR codification scheme is too fine to use in model, and so level 2 of the DCR codification was chosen (Codification Standards and definition of Standard Outputs for EC 1639/2001data. http://datacollection.jrc.cec.eu.int/documents/Codes-Standard-Outputsv3.pdf).

By choice, certain data were kept separate from some of the groups classified by DCR categories. This was data pertaining to specific fleets that are of interest, notably sandeel, shrimp and *Nephrops* trawlers. This resulted in a total of 12 gear groups being defined for the model (Table 14.2), that were subsequently matched to the STECF AER, STCF 1991 and FAD databases (Table 14.3, 14.4, 14.5)

We also had to match up the fish and invertebrate names used in each database before we could accurately assign the fish landings and discards to the functional group categories used in the model (Table 14.6). After doing so we were able to perform analyses with any dataset, with knowledge that it could be easily translated across to a different database using other definitions.

14.3 Manipulation of data and assumptions used

To compliment the main text, a flow chart provides an overview of data collection and manipulation for landings and discards (Figure 14.1).

Landings data

The STCF data provides information on the landings, by gear, for the top 27 commercial species, comprising approximately 90% of the total landings in the North Sea in 1991 (2,811,819 tonnes). For the species representing the remaining 10% of landings, we used the total landings from the ICES Statlant database and allocated this to each gear type by assuming the that the proportion of the species caught by each gear types was the same as that calculated from the UK FAD. This was a pragmatic solution to a rather awkward problem. Data for other countries was not available (the information was requested via correspondence from the ICES working group members from each member country, yet only the British data was provided). This problem should be remedied by the introduction of the new data collection regulations. These regulations will require landings to be reported for each gear type in a consistent manner for each country.

The species landings were then assigned to the model functional groups. Two landing recordings could not be allocated to functional groups due to ambiguity as to what species the groups consisted of. The two groups were: unspecified finfishes and unspecified marine fishes. These groups accounted for only 0.57% of the total landings in the North Sea in 1991.

Discards data

Note: Discard values for cod, haddock, whiting, plaice and sole are already included in the STCF database so we did not have to do this for them. These values were used directly.

Using the Trio database, we queried 342,510 discard records in order to obtain the discarding practices for the British vessels in the North Sea and calculate the proportion of the catch discarded by each gear type. In lieu of better data we assumed that the discarding practices of the UK fleet would be broadly reflected in the fleets of other countries and so the North Sea fleet as a whole. This was a crude, but necessary assumption to try and estimate a ball-park figure for North Sea discards.

For the UK vessels we calculated the fraction of the landings that the discards represented. We then used this fraction to raise the total landings by fleet to the total catch. Discard values were collated for finfishes and benthic species from the trio database.

The proportion of the total catch which are discarded was calculated using the formulae:

Discards =
Catch x Proportion of the catch that is discarded

This can be written as:

$$D = C \times D_{pc} \qquad \text{(Equation 1)}$$

Similarly,

Landings =
Catch x Proportion of catch that is landed (L_{pc})

$$L = C \times L_{pc} \qquad \text{(Equation 2)}$$

or,

$$C = \frac{L}{L_{pc}} \qquad \text{(Equation 3)}$$

We do not know the value of C, but, D_{pc} and L_{pc} are known from the Trio Database and the value of L is known from STATLANT.

Substituting equation 3 into Equation 1:

$$D = \frac{L}{L_{pc}} \times D_{pc} \qquad \text{(Equation 4)}$$

Where:

$$L_{pc} = 1 - D_{pc}$$

These formula were applied to each species by gear type in order to calculate the discards in tonnes. There is however a flaw in the utilisation of this method. The formula works on the basis that discards can be calculated as a proportion of the landings. This breaks down when 100% of a particular species are discarded, as there will be no landings recorded. In effect when landings equal zero, the discards will also equal zero. We implemented rules in our spreadsheet formulas to prevent this from occurring, and thus when all landings were discarded, we were able to assign them directly to discards for that gear type.

Input values for landings and discards used in the model are given in Tables 14.7 and 14.8.

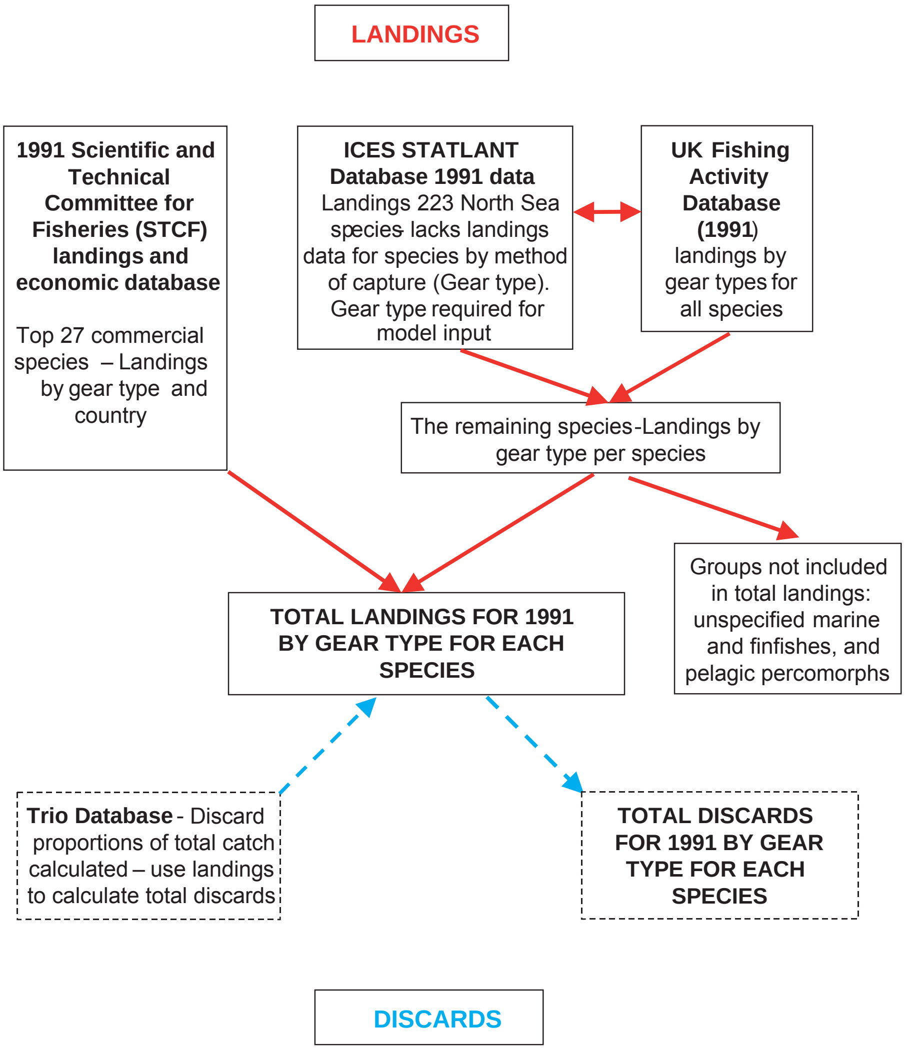

Figure 14.1. Flow chart of the collection of landings and discards data for 1991.

Economic and social data

Economic and social data required by the model include fixed costs, effort related costs (variable costs), market price (of fish), non-market price (intrinsic value), employment. With the exception of non-market price, information was taken directly from the 2005 STECF AER (see Table 14.9 for example) and aggregated to the gear and functional groups used in the model (see for example Table 14.10).

Costs were calculated as:

Variable costs =
Fuel costs + Other running costs + Crew share
Fixed costs = Vessel costs+Depreciation+Interest

Net profit is expressed as a percentage, using the market price and landings values to calculate the total profit, minus the fixed and variable costs.

Market price for each species/functional group as gear type was derived by dividing the landings value by volume data, giving a price in thousand Euros per tonne for each of the species by gear group.

Input values for costs and prices used in the model are given in Tables 14.11 and 14.12.

For each gear group used in the model, the number of jobs relative to the amount landed by that gear group is used as an index of the social value of the gear group (Table 4.13). Crew sizes for each gear type were taken from the AER.

Non-market price is assumed to be a function of the longevity of the species and B/P ratio is assumed to reflect this. This means that larger slower growing species are assumed to have more intrinsic value.

Table 14.2. Gear classifications from Fleet Register, DCR and model. Note that gear groups used in the model follow the DCR definitions. Fleet register gear types formed from EU regs. (1998) concerning the fishing vessel register of the community. EC No 2090/98 and EC No 2091/98.

Fleet register	Data Collection Regs	Ecopath model fleet
Gillnets (set)	Drift and fixed nets	Drift & fixed nets
Pots	Pots and traps	Pots
Longlines (set)	Gears using hooks	Gears using hooks
Hand-line and pole-line operated	Gears using hooks	Gears using hooks
Dredges	Dredges	Dredges
Trammel net	Drift and fixed nets	Drift & fixed nets
Beam trawls	Beam trawl	Beam trawls
Bottom otter trawls	Demersal trawl and demersal seiner	Demersal trawl & demersal seiner
Longlines (drifting)	Gears using hooks	Gears using hooks
Bottom pair trawls	Demersal trawl and demersal seiner	Demersal trawl & demersal seiner
Danish seines (anchor)	Demersal trawl and demersal seiner	Demersal trawl & demersal seiner
Mid-water otter trawls	Pelagic trawl and seiners	Pelagic trawls & seine
Mid-water pair trawls	Pelagic trawl and seiners	Pelagic trawls & seine
Gillnets (drift)	Drift and fixed nets	Drift & fixed nets
otter twin-trawl	Demersal trawl and demersal seiner	Demersal trawl & demersal seiner
Combined gillnets-trammel nets	Drift and fixed nets	Drift & fixed nets
Scottish seines (fly-dragging)	Demersal trawl and demersal seiner	Demersal trawl & demersal seiner
mechanised dredges	Dredges	Dredges
Pair seines	Demersal trawl and demersal seiner	Demersal trawl & demersal seiner
Encircling gillnets	Drift and fixed nets	Drift & fixed nets
Trolling lines	Gears using hooks	Gears using hooks
Hand dredges	Dredges	Dredges
Unknown gear	NA	Other methods
Boat-operated lift nets	NA	Other methods
Handlines and pole-lines (mechanised)	Gears using hooks	Gears using hooks
		Nephrops trawlers
		Shrimp trawlers
		Shellfish picking
		Sandeel trawlers

Table 14.3. Employment and values for each fleet.

flag.state	DCR group	Client segments(from STECF AER)	Ecopath model fleet
BE	Beam trawl	Beam trawlers < 24 m	Beam trawls
BE	Beam trawl	Beam trawlers > 24 m	Beam trawls
BE	Beam trawl	Shrimp beam trawlers	Shrimp trawlers
DK	Pelagic trawl and seiners	Purse seiners and trawlers >= 40 m	Pelagic trawls & seine
DK	Demersal trawl and demersal seiner	Trawlers 24 - < 40 m	Demersal trawl & demersal seiner
DK	Demersal trawl and demersal seiner	Trawlers < 24 m	Demersal trawl & demersal seiner
DK	Drift and fixed nets	Gillnetters	Drift & fixed nets
DK	Demersal trawl and demersal seiner	Danish seiners	Demersal trawl & demersal seiner
GE		Demersal freezer trawlers	Demersal trawl & demersal seiner
GE	Beam trawl	Shrimp beam trawlers	Shrimp trawlers
GE		Pelagic freezer trawlers	Pelagic trawls & seine
GE	Beam trawl	Baltic trawlers	Beam trawls
GE	Demersal trawl and demersal seiner	North sea trawlers	Demersal trawl & demersal seiner
GE		Baltic coastal vessels	Other methods
NL	Beam trawl	Shrimp beam trawlers < 24 m	Shrimp trawlers
NL	Beam trawl	Beam trawlers <= 24 m	Beam trawls
NL	Beam trawl	Beam trawlers > 24 m	Beam trawls
NL	Demersal trawl and demersal seiner	Trawlers > 24 m	Demersal trawl & demersal seiner
NL	Pelagic trawl and seiners	Pelagic freezer trawlers	Pelagic trawls & seine
UK	Demersal trawl and demersal seiner	Scottish demersal trawlers > 24 m	Demersal trawl & demersal seiner
UK	Demersal trawl and demersal seiner	Scottish demersal trawlers < 24 m	Demersal trawl & demersal seiner
UK	Demersal trawl and demersal seiner	Scottish seiners	Demersal trawl & demersal seiner
UK	Beam trawl	Beam trawlers	Beam trawls
UK	Demersal trawl and demersal seiner	Northern Irish *Nephrops* trawlers	*Nephrops* trawlers
UK	Demersal trawl and demersal seiner	Scottish *Nephrops* trawlers	*Nephrops* trawlers
UK	Dredges	Scallop trawlers	Dredges
NO	Polyvalent	Coastal vessels	Other methods
NO	Demersal trawl and demersal seiner	Trawlers	Demersal trawl & demersal seiner
NO	Pelagic trawl and seiners	Trawlers/purse seiners	Pelagic trawls & seine
NO	Pelagic trawl and seiners	Pelagic trawlers	Pelagic trawls & seine

Table 14.4. Gear classifications from STCF 1991 database and the model.

Country	Fleet code	County	Fleet code	Stcf fleet description	Gear type	Ecopath model fleet
Bel	1	Bel	1	Beamtrawl > 300 hp	Trawl	Beam trawls
	2	Bel	2	Beamtrawl < 300 hp	Trawl	Beam trawls
	3	Bel	3	Otter trawl	Trawl	Demersal trawl & demersal seiner
	5	Bel	5	Pair trawl	Trawl	Demersal trawl & demersal seiner
Den	A	Den	A	Gill-net	Gill-net	Drift & fixed nets
	B	Den	B	Danish seine	Danish seine	Demersal trawl & demersal seiner
	C	Den	C	Ind. Trawl sin. 0- 50 Grt	Trawl	Sandeel trawl
	D	Den	D	Ind. Trawl sin.51-100 Grt	Trawl	Sandeel trawl
	E	Den	E	Ind. Trawl sin. > 100 Grt	Trawl	Sandeel trawl
	F	Den	F	Con. Trawl sin. 0- 50 Grt	Trawl	Demersal trawl & demersal seiner
	G	Den	G	Con. Trawl sin.51-100 Grt	Trawl	Demersal trawl & demersal seiner
	H	Den	H	Con. Trawl sin. > 100 Grt	Trawl	Demersal trawl & demersal seiner
	I	Den	I	Ind. Trawl pair 0- 50 grt	Trawl	Sandeel trawl
	J	Den	J	Ind. Trawl pair51-100 grt	Trawl	Sandeel trawl
	K	Den	K	Ind. Trawl pair > 100 grt	Trawl	Sandeel trawl
	L	Den	L	Con. Trawl pair 0- 50 grt	Trawl	Demersal trawl & demersal seiner

Table 14.4. continued: Gear classifications from STCF 1991 database and the model.

Country	Fleet code	County	Fleet code	Stcf fleet description	Gear type	Ecopath model fleet
	M	Den	M	Con. Trawl pair51-100 grt	Trawl	Demersal trawl & demersal seiner
	N	Den	N	Con. Trawl pair > 100 grt	Trawl	Demersal trawl & demersal seiner
	O	Den	O	Purse seine	Purse seine	Pelagic trawls & seine
	P	Den	P	Other	Other	Other methods
Eng	1	Eng	1	Beam trawls	All beam trawls	Beam trawls
	2	Eng	2	Otter trawls	All otter trawls	Demersal trawl & demersal seiner
	3	Eng	3	Pair trawls	All pair trawls	Demersal trawl & demersal seiner
	4	Eng	4	Seine nets	Anchor,fly,beach	Demersal trawl & demersal seiner
	5	Eng	5	Other	Gill nets,lines,pots	Drift & fixed nets
Fra	A	Fra	A	Very big trawlers bottom	Bottom otter trawl	Demersal trawl & demersal seiner
	B	Fra	B	Very big trawlers pelagic	Pelagic trawl	Pelagic trawls & seine
	C	Fra	C	Freezer trawlers bottom	Bottom otter trawl	Demersal trawl & demersal seiner
	D	Fra	D	Freezer trawlers pelagic	Pelagic trawl	Pelagic trawls & seine
	E	Fra	E	High sea trawlers bottom	Bottom otter trawl	Demersal trawl & demersal seiner
	F	Fra	F	High sea trawlers pelagic	Pelagic trawl	Pelagic trawls & seine
	G	Fra	G	Coastal trawlers bottom	Bottom otter trawl	Demersal trawl & demersal seiner
	H	Fra	H	Coastal trawlers pelagic	Pelagic trawl	Pelagic trawls & seine
	I	Fra	I	Coastal trawlers beam	Beam trawl	Beam trawls
	J	Fra	J	Coastal vessels fix	Various fixed gears	Drift & fixed nets
Gfr	A	Gfr	A	All cod		Demersal trawl & demersal seiner
Ned	A	Ned	A	Beam trawl >300hp	Beam trawl	Beam trawls
	B	Ned	B	Beam trawl <300hp	Beam trawl	Beam trawls
	O	Ned	O	Otter trawlers	Otter trawl	Demersal trawl & demersal seiner
	P	Ned	P	Pair trawlers	Pair trawl	Demersal trawl & demersal seiner
Nor	F	Nor	F	Trawlers >250 grt consump	Otter trawl	Demersal trawl & demersal seiner
	K	Nor	K	Trawlers <250 grt consump	Otter trawl	Demersal trawl & demersal seiner
	O	Nor	O	Industr. Trawl targ. Nop	Otter trawl	Pelagic trawls & seine
	P	Nor	P	Purse seiners	Purse seine	Pelagic trawls & seine
	T	Nor	T	Industr. Trawl targ. San	Otter trawl	Sandeel trawl
	X	Nor	X	Non-trawlers fishing pok	Various	Other methods
Oth	1	Oth	1	Reported landings	Unknown	Other methods
	2	Oth	2	Not reported landings	Unknown	Other methods
	4	Oth	4	Mackerel, not reportet	Unknown	Other methods
Sco	A	Oth	A	Trawl		Demersal trawl & demersal seiner
	B	Sco	B	Light trawl		Demersal trawl & demersal seiner
	C	Sco	C	*Nephrops* trawl		Nephrops trawlers
	D	Sco	D	Seine net		Pelagic trawls & seine
	E	Sco	E	Pair trawl demersal		Demersal trawl & demersal seiner
	F	Sco	F	Pair trawl herring		Pelagic trawls & seine
	G	Sco	G	Pair trawl mackerel		Pelagic trawls & seine
	I	Sco	I	Purse seine herring		Pelagic trawls & seine
	J	Sco	J	Purse seine mackerel		Pelagic trawls & seine
	K	Sco	K	Single trawl pelagic		Pelagic trawls & seine
	L	Sco	L	Industrial trawl		Other methods
	M	Sco	M	Other		Other methods
						Shrimp trawlers

Table 14.5. Gear classifications from UK FAD database and those used in the model.

UK FAD	Ecopath model fleet
Heavy otter trawl	Demersal trawl & demersal seiner
Light otter trawl	Demersal trawl & demersal seiner
Twin otter trawl	Demersal trawl & demersal seiner
Triple otter trawl	Demersal trawl & demersal seiner
Unspecified otter trawl	Demersal trawl & demersal seiner
Scottish fly seine	Demersal trawl & demersal seiner
Pair fly seine	Demersal trawl & demersal seiner
Bottom pair trawl	Demersal trawl & demersal seiner
Danish seine	Demersal trawl & demersal seiner
Any other trawls	Demersal trawl & demersal seiner
Midwater trawl	Pelagic trawls & seine
Midwater pair trawl	Pelagic trawls & seine
Purse seine	Pelagic trawls & seine
Beam trawl	Beam trawls
Gill net (not 52 or 53)	Drift & fixed nets
Gill net (trammel)	Drift & fixed nets
Gill net (tangle)	Drift & fixed nets
Fyke net	Drift & fixed nets
Unspecified gill net	Drift & fixed nets
Stake net	Drift & fixed nets
Fixed net	Drift & fixed nets
Drift net	Drift & fixed nets
Other nets	Drift & fixed nets
Shank nets	Drift & fixed nets
Hand pushed nets	Drift & fixed nets
Long lines	Gears using hooks
Hand lines (inc gurdy	Gears using hooks
Top opening pots	Pots
Side opening pots	Pots
Parlour pots	Pots
Other or mixed pots	Pots
Surface picking	Shellfish picking
Hand dredge	Dredges
Power dredge	Dredges
Suction dredge	Dredges
Unspecified dredge	Dredges
Danish anchor seine	Demersal trawl & demersal seiner
Gill net (danish)	Drift & fixed nets
Nephrops otter trawl	*Nephrops* trawlers
Twin *Nephrops* otter trawl	*Nephrops* trawlers
Gill net (unspecified)	Drift & fixed nets
	Other methods
	Sandeel trawl
	Shrimp trawlers

Table 14.6. Matching fish and invertebrate names with functional groups used in the model.

UK FAD	ICES Statlant	STCF 1991	STEFC AER	Functional Group in model	Species	sp. code
	Aesop shrimp			Shrimp		
Long Roungh Dabs	Amer. plaice(=Long rough dab)			Long-rough dab		
Monks/Anglers	Angler(=Monk)	Monk	Anglerfish	Monkfish	*Lophius piscatorius*	MON
Monks/Anglers	Anglerfishes nei	Monk		Monkfish	*Lophius piscatorius*	MON
	Argentines		Argentines	Other gadoids (small)	*ARGENTINIDAE*	ARG
Cod	Atlantic cod	Cod	Cod	Cod (adult)	*Gadus morhua*	COD
Halibut	Atlantic halibut			Halibut	*Hippoglossus hippoglossus*	HAL
Herring	Atlantic herring	Herring	Herring	Herring (adult)	*Clupea harengus*	HER
Horse Mackerel	Atlantic horse mackerel	Horse Mackerel		Horse mackerel	*Trachurus trachurus*	HOM
Mackerel	Atlantic mackerel	Mackerel	Mackerel	Mackerel	*Scomber scomber*	MAC
Red Fishes	Atlantic redfishes nei		Redfish	Large demersal fish	*SEBASTES SPP*	RED
	Atlantic Salmon		Salmon	Large demersal fish	*SALMO SALAR*	SAL
Catfish	Atlantic wolffish			Catfish (Wolf-fish)	*Anarrhichas lupus*	CAA
	Baird's slickhead			Small demersal fish		
	Basking shark			Baleen whales	*CETORHINUS MAXIMUS*	BSK
	Black scabbardfish		Black scabbard	Large demersal fish	*APHANOPUS CARBO*	BSF
Sea Breams	Black seabream			Large demersal fish	*SPARIDAE*	SBZ
	Blackbelly rosefish			Large demersal fish	*Spondyliosoma cantharus*	BKS
Blue Ling	Blue ling			Other gadoids (large)	*M.dypterygia*	0
Mussel	Blue mussel			Sessile epifauna		
	Blue shark			Large piscivorous sharks	*PRIONACE GLAUCA*	BSH
	Blue skate			Skate + Cuckoo ray	*Dipterus batis and Raja naevus*	SKT
	Blue whiting(=Poutassou)	Blue whiting	Blue whiting	Blue whiting	*Micromesistius poutassou*	WHB
Brill	Brill	Brill		Turbot and brill	*Scopthalmus rhombus*	BLL
	Clupeoids nei			Sprat		
	Common cuttlefish			Cephalopods	*SEPIA OFFICINALIS*	CTC
Dabs	Common dab	Dab	Dab	Dab	*Limanda limanda*	DAB
Cockles	Common edible cockle			Infaunal macrobenthos		
Brown Shrimps	Common shrimp			Shrimp		
Sole	Common sole	Sole	Sole	Sole	*Solea solea*	SOL
Squid	Common squids nei			Cephalopods	*LOLIGO VULGARIS*	LLV
	Crangon shrimps nei			Shrimp		
	Cuckoo ray			Skate + Cuckoo ray	*Raja naevus*	CUR
	Cuttlefish,bobtail squids nei			Cephalopods		
	Demersal percomorphs nei			Small demersal fish		

Table 14.6. continued: Matching fish and invertebrate names with functional groups used in the model.

UK FAD	ICES Statlant	STCF 1991	STEFC AER	Functional Group in model	Species	sp. code
Unidentified Dogfish	Dogfish sharks nei			Small sharks		
Spurdog	Dogfishes and hounds nei			Small sharks		
Unidentified Dogfish	Dogfishes nei			Small sharks		
Crabs (mixed sexes)	Edible crab		Crab	Large crabs	*CANCER PAGURUS*	CRE
Conger Eels	European conger			Large demersal fish	*CONGRIDAE*	COX
Eels	European eel		Eel	Large demersal fish	*ANGUILLIDAE*	EEL
Native Oysters	European flat oyster			Sessile epifauna	*OSTREA EDULIS*	OYF
Flounder or Flukes	European flounder		Flounder	Flounder	*Platichthys flessus*	FLE
Hake	European hake	Hake	Hake	Hake	*Merluccius merluccius*	HKE
Lobsters	European lobster			Large crabs	*HOMARUS GAMMARUS*	LBE
	European perch			Small demersal fish	*PERCA FLUVIATILIS*	FPE
	European pilchard(=Sardine)	Pilchard		Miscellaneous filter feeding pelagic fish	*Sardina pilchardus*	PIL
Plaice	European plaice	Plaice	Plaice	Plaice	*Pleuronectes platessa*	PLE
Bass	European seabass			Large demersal fish	*DICENTRARCHUS (MORONE) LABRAX*	ESB
	European smelt			Large demersal fish		
Sprats	European sprat	Sprat	Sprat	Sprat	*Sprattus sprattus*	SPR
	European whitefish			Miscellaneous filter feeding pelagic fish		
	European whitefish			Other gadoids (large)		
	Finfishes nei			Other gadoids (small)		
	Flatfishes nei			Small demersal fish		
	Freshwater breams nei			Small demersal fish		
	Gadiformes nei			Other gadoids (large)		
Garfish	Garfish			Large demersal fish	*Belone belone*	0
	Golden redfish			Large demersal fish		
	Great Atlantic scallop			Epifaunal macrobenthos (mobile grazers)		
	Greater argentine			Other gadoids (small)	*A.silus*	0
Greater Forked Beard	Greater forkbeard			Other gadoids (large)		
	Green crab			Large crabs		
Mock Halibut	Greenland halibut		Gr. halibut	Halibut	*REINHARDTIUS HIPPOGLOSSOIDES*	GLH
	Grey gurnard	Gurnards		Gurnards	*Eutrigula gurnardus*	GUG
	Groundfishes nei			Small demersal fish		
	Groundfishes nei			Small demersal fish		
Gurnard and Latchet	Gurnard and Latchet	Gurnards		Gurnards	*Triglidae*	GUX

Table 14.6. continued: Matching fish and invertebrate names with functional groups used in the model.

UK FAD	ICES Statlant	STCF 1991	STEFC AER	Functional Group in model	Species	sp. code
Gurnard and Latchet	Gurnards, searobins nei			Gurnards	*Triglidae*	GUX
Haddock	Haddock	Haddock	Haddock	Haddock (adult)	*Gadus aeglefinus*	HAD
	Jack and horse mackerels nei	Horse Mackerel	Horse mackerel	Horse mackerel	*Trachurus trachurus*	HOM
Lemon Sole	Lemon Sole	Lemon sole	Lemon sole	Lemon Sole	*Microstomus kitt*	LEM
Ling	Ling		Ling	Other gadoids (large)	*Molva molva*	LIN
	Longnosed skate			Skate + Cuckoo ray		
	Lophius Piscatorus			Monkfish		
Lumpfish	Lumpfish(=Lumpsucker)			Small demersal fish		
Mixed Crabs	Marine crabs nei			Epifaunal macrobenthos (mobile grazers)		
	Marine fishes nei			Small demersal fish		
	Marine molluscs nei			Infaunal macrobenthos		
Megrim	Megrim	Megrim	Megrim	Megrim	*Lepidorhombus whiffiagonis*	MEG
Megrim	Megrims nei	Megrim		Megrim	*Lepidorhombus whiffiagonis*	MEG
Grey Mullet	Mullets nei			Small demersal fish	*MUGIL CEPHALUS*	MTG
Nephrops	Nephrops	Nephrops		Nephrops	*Nephrops norvegicus*	NEP
	Northern pike			unclassified		
	Northern prawn		Northern prawn	Shrimp		
Nephrops	Norway lobster	Nephrops	Norway lobster	Nephrops	*Nephrops norvegicus*	NEP
	Norway Pout	Norway pout		Norway pout	*Trisopterus esmarkii*	NOP
	Nursehound			Small sharks		
Octopus	Octopuses nei			Cephalopods	*OCTOPUS VULGARIS*	OCV
	Octopuses, etc. nei			Cephalopods		
	Orange roughy			Small demersal fish		
	OTH			Small demersal fish		
Pacific Oysters	Pacific cupped oyster			Sessile epifauna		
Deep Sea Shrimps	Pandalus spp.	Pandalid shrimp	Shrimp	Shrimp	*Pandalus spp.*	PAN
	Pelagic percomorphs nei			Miscellaneous filter feeding pelagic fish		
	Periwinkles nei			Epifaunal macrobenthos (mobile grazers)		
	Picked dogfish			Spurdog	*Squalus acanthias*	
	Pike-perch		Pike-perch	unclassified		

Table 14.6. continued: Matching fish and invertebrate names with functional groups used in the model.

UK FAD	ICES Statlant	STCF 1991	STEFC AER	Functional Group in model	Species	sp. code
Pollack	Pollack		Pollack	Other gadoids (large)	*Pollachius pollachius*	POL
	Porbeagle			Large piscivorous sharks		
	Portunus swimcrabs nei			Large crabs		
Pout	Pouting(=Bib)			Other gadoids (small)		
Queen Scallops	Queen scallop		Queen scallops	Epifaunal macrobenthos (mobile grazers)	*CHLAMYS OPERCULARIS*	QSC
	Raja rays nei			Starry ray + others		
	Red gurnard			Gurnards	*Aspitrigla cuclus*	GUR
Red Mullet	Red mullet			Large demersal fish	*Mullus surmuletus*	MUR
	Roach			unclassified	*RUTILUS RUTILUS*	FRO
	Roundnose grenadier			Large demersal fish	*CORYPHAENOIDES RUPESTRIS*	RNG
Saithe	Saithe(=Pollock)	Saithe	Saithe	Saithe (adult)	*Pollachius virens*	POK
Sand Sole	Sand sole			Small demersal fish	*Solea lascaris*	SOS
	Sandeels(=Sandlances) nei	Sandeel	Sandeel	Sandeels	*AMMODYTES SPP*	SAN
Scallops	Scallops nei		Scallop	Epifaunal macrobenthos (mobile grazers)		
Sea Trout	Sea trout			Large demersal fish	*Salmo trutta trutta*	0
	Seabasses nei			Large demersal fish		
	Shagreen ray			Starry ray + others	*RAJA FULLONICA*	SHR
	Skate and Rays			Starry ray + others	*Raja spp.*	SKA
Lesser Spotted Dog	Small-spotted catshark			Small sharks		
Spider Crabs	Spinous spider crab			Large crabs	*MAJIDAE*	MJX
Spur Dog	Spurdog	Spurdog		Spurdog	*Squalus acanthias*	DGS
Skates and Rays	Thornback ray	Skates and Rays	Skates and rays	Thornback & Spotted ray	*Raja clavata and Raja montagui*	THR and SDR
Tope	Tope shark			Large piscivorous sharks	*Galeorhinus galeus*	GAG
	Tub gurnard			Gurnards	*Trigla lucerna*	TUB
Turbot	Turbot	Turbot	Turbot	Turbot and brill	*Scopthalmus maximus*	TUR
Torsk (Tusk)	Tusk(=Cusk)			Other gadoids (large)		
	Various sharks nei			Small sharks		
	Various squids nei			Cephalopods	*LOLIGO SPP*	SQC
Whelks	Whelk		Whelk	Epifaunal macrobenthos (mobile grazers)	*BUCCINIDAE*	WHZ
Whiting	Whiting	Whiting	Whiting	Whiting (adult)	*Gadus merlangus*	WHG
Witch	Witch flounder		Witch flounder	Witch	*Glyptocephalus cynoglossus*	WIT

Table 14.6. continued: Matching fish and invertebrate names with functional groups used in the model.

UK FAD	ICES Statlant	STCF 1991	STEFC AER	Functional Group in model	Species	sp. code
Catfish	Wolffishes(=Catfishes) nei			Catfish (Wolf-fish)		
Ballan Wrasse				Small demersal fish	*Labrus bergylta*	BNW
Cuttlefish				Cephalopods		
English Prawns				Shrimp		
Greater Spotted Dog				Small sharks		
Greater Weever				Small demersal fish		
John Dory				Large demersal fish	*Zeus faber*	JOD
Mixed Demersal				Small demersal fish		
Pink Shrimps				Shrimp		
Sharks				Large piscivorous sharks		
Silver Smelt				Miscellaneous filter feeding pelagic fish		
Sturgeon				Large demersal fish		
White Bait				Miscellaneous filter feeding pelagic fish		
Wrasses				Small demersal fish	*LABRIDAE*	WRA
		Other	Other fish	Small demersal fish	*Other*	OTH
			Baltic herring	Miscellaneous filter feeding pelagic fish		
			Capelin	Miscellaneous filter feeding pelagic fish		
			Crustacea and molluscs	Large crabs		
			Industrial fishery	Sandeels		
			King scallops	Epifaunal macrobenthos (mobile grazers)		
			Marine crustaceans	Large crabs		
			Other income	unclassified		
			Other pelagic fish	Miscellaneous filter feeding pelagic fish		
			Tunas	Large demersal fish		

Table 14.7. North Sea landings in tonnes (1991).

Group #	Functional group	Demersal trawl & demersal seiner	Beam trawls	Sandeel trawl	Pelagic trawls & seine	Drift & fixed nets	*Nephrops* trawlers
1	Baleen whales	-	-	-	-	-	-
2	Toothed whales	-	-	-	-	-	-
3	Seals	-	-	-	-	-	-
4	Seabirds	-	-	-	-	-	-
5	Juvenile sharks	-	-	-	-	-	-
6	Spurdog	2,742	14	265	1,214	633	49
7	Large piscivorous sharks	4	0	-	-	11	-
8	Small sharks	92	6	1	-	43	-
9	Juvenile rays	-	-	-	-	-	-
10	Starry ray + others	3,870	-	-	-	-	-
11	Thornback & Spotted ray	707	93	3	11	548	-
12	Skate + Cuckoo ray	39	-	-	-	-	-
13	Juvenile Cod(0-2, 0-40 cm)	-	-	-	-	-	-
14	Cod (adult)	35,568	5,159	1,203	14,079	10,659	781
15	Juvenile Whiting (0-1, 0-20 cm)	-	-	-	-	-	-
16	Whiting (adult)	25,251	1,887	31,863	22,458	91	1,180
17	Juvenile Haddock (0-1, 0-20 cm)	-	-	-	-	-	-
18	Haddock (adult)	20,862	86	4,480	20,349	168	389
19	Juvenile Saithe (0-3, 0-40 cm)	-	-	-	-	-	-
20	Saithe (adult)	52,782	8	1,402	12,312	300	76
21	Hake	1,066	12	166	426	667	5
22	Blue whiting	-	-	-	34,428	-	-
23	Norway pout	37	-	85,557	69,084	-	-
24	Other gadoids (large)	16,701	544	-	-	1,374	-
25	Other gadoids (small)	15,732	286	0	-	39	-
26	Monkfish	7,581	407	315	1,094	126	952
27	Gurnards	378	84	-	1	0	-
28	Herring (juvenile 0, 1)	-	-	-	-	-	-
29	Herring (adult)	54,093	2	120,840	211,014	403	-
30	Sprat	1,858	3	71,478	3,420	49	-
31	Mackerel	9,576	2	6,954	141,132	8	-
32	Horse mackerel	9,050	264	995	24,843	42	-
33	Sandeels	1	-	825,702	1,123	-	-
34	Plaice	23,313	107,673	76	1,590	3,893	159

Table 14.7. continued: North Sea landings in tonnes (1991).

Group #	Functional group	Demersal trawl & demersal seiner	Beam trawls	Sandeel trawl	Pelagic trawls & seine	Drift & fixed nets	*Nephrops* trawlers
35	Dab	1,556	243	11	308	120	33
36	Long-rough dab	-	-	-	-	3	-
37	Flounder	724	849	-	-	84	-
38	Sole	963	28,500	1	0	1,146	-
39	Lemon sole	3,933	328	12	1,294	72	76
40	Witch	1,773	541	-	0	0	-
41	Turbot and brill	392	587	6	0	827	-
42	Megrim	969	0	-	289	1	46
43	Halibut	713	36	-	-	1	-
44	Dragonets	-	-	-	-	-	-
45	Catfish (Wolf-fish)	2,713	282	-	0	11	-
46	Large demersal fish	3,124	58	0	20	174	-
47	Small demersal fish	13,509	1,106	26,334	4,497	44,403	-
48	Miscellaneous filter feeding pelagic fish	35	-	-	5,700	-	-
49	Cephalopods	952	48	-	-	0	-
50	Fish Larvae (food)	-	-	-	-	-	-
51	Carnivorous zooplankton	-	-	-	-	-	-
52	Herbivorous & Omnivorous zooplankton (copepods)	-	-	-	-	-	-
53	Gelatinous zooplankton	-	-	-	-	-	-
54	Large crabs	37	5	3,659	-	36	-
55	*Nephrops*	4,030	4	2	22	1	6,213
56	Epifaunal macrobenthos (mobile grazers)	661	11	307	-	12	-
57	Infaunal macrobenthos	-	-	-	-	-	-
58	Shrimp	707	22,287	328	5	0	-
59	Small mobile epifauna (swarming crustaceans)	-	-	-	-	-	-
60	Small infauna (polychaetes)	-	-	-	-	-	-
61	Sessile epifauna	-	-	-	-	-	-

Table 14.7. continued: North Sea Landings in tonnes (1991).

Group #	Functional group	Gears using hooks	Shrimp trawlers	Dredges	Shellfish picking	Pots	Other methods	Total
1	Baleen whales	-	-	-	-	-	-	-
2	Toothed whales	-	-	-	-	-	-	-
3	Seals	-	-	-	-	-	-	-
4	Seabirds	-	-	-	-	-	-	-
5	Juvenile sharks	-	-	-	-	-	-	-
6	Spurdog	-	-	-	-	-	10	4,927
7	Large piscivorous sharks	140	-	-	-	-	-	155
8	Small sharks	9	-	-	-	-	-	150
9	Juvenile rays	-	-	-	-	-	-	-
10	Starry ray + others	-	-	-	-	-	-	3,870
11	Thornback & Spotted ray	-	-	-	-	-	1,642	3,004
12	Skate + Cuckoo ray	-	-	-	-	-	-	39
13	Juvenile Cod(0-2, 0-40cm)	-	-	-	-	-	-	-
14	Cod (adult)	-	-	-	-	-	-	67,448
15	Juvenile Whiting (0-1, 0-20cm)	-	-	-	-	-	-	-
16	Whiting (adult)	-	-	-	-	-	1,294	84,023
17	Juvenile Haddock (0-1, 0-20cm)	-	-	-	-	-	-	-
18	Haddock (adult)	-	-	-	-	-	3,711	50,044
19	Juvenile Saithe (0-3, 0-40cm)	-	-	-	-	-	-	-
20	Saithe (adult)	-	-	-	-	-	-	66,880
21	Hake	-	-	-	-	-	10	2,352
22	Blue whiting	-	-	-	-	-	335	34,763
23	Norway pout	-	-	-	-	-	1,203	155,881
24	Other gadoids (large)	254	-	-	-	-	-	18,873
25	Other gadoids (small)	68	-	-	0	-	-	16,126
26	Monkfish	-	-	-	-	-	557	11,032
27	Gurnards	-	-	-	-	-	-	463
28	Herring (juvenile 0, 1)	-	-	-	-	-	-	-
29	Herring (adult)	-	-	-	-	-	101,574	487,926
30	Sprat	-	-	-	-	-	22,743	99,551
31	Mackerel	-	-	-	-	-	39,501	197,172
32	Horse mackerel	-	-	-	-	-	63,031	98,225
33	Sandeels	-	-	-	-	-	15,732	842,558

Table 14.7. continued: North Sea Landings in tonnes (1991).

Group #	Functional group	Gears using hooks	Shrimp trawlers	Dredges	Shellfish picking	Pots	Other methods	Total
34	Plaice	-	-	-	-	-	20,748	157,452
35	Dab	-	-	-	-	-	129	2,400
36	Long-rough dab	-	-	-	-	-	-	3
37	Flounder	1	-	-	-	-	-	1,659
38	Sole	-	-	-	-	-	7,752	38,362
39	Lemon sole	-	-	-	-	-	207	5,923
40	Witch	16	-	-	-	-	-	2,331
41	Turbot and brill	-	-	-	-	-	214	2,025
42	Megrim	-	-	-	-	-	4	1,310
43	Halibut	8	-	-	-	-	-	757
44	Dragonets	-	-	-	-	-	-	-
45	Catfish (Wolf-fish)	30	-	-	-	-	-	3,036
46	Large demersal fish	18	-	-	2	0	-	3,396
47	Small demersal fish	0	-	-	-	-	6,669	96,518
48	Miscellaneous filter feeding pelagic fish	-	-	-	-	-	-	5,735
49	Cephalopods	-	-	2	-	-	-	1,001
50	Fish Larvae (food)	-	-	-	-	-	-	-
51	Carnivorous zooplankton	-	-	-	-	-	-	-
52	Herbivorous & Omnivorous zooplankton (copepods)	-	-	-	-	-	-	-
53	Gelatinous zooplankton	-	-	-	-	-	-	-
54	Large crabs	1	-	-	-	2,793	-	6,533
55	*Nephrops*	-	-	-	-	-	16	10,289
56	Epifaunal macrobenthos (mobile grazers)	0	-	1,562	-	1,226	-	3,779
57	Infaunal macrobenthos	-	-	40,869	10,887	-	-	51,756
58	Shrimp	-	1,408	3	-	-	-	24,738
59	Small mobile epifauna (swarming crustaceans)	-	-	-	-	-	-	-
60	Small infauna (polychaetes)	-	-	-	-	-	-	-
61	Sessile epifauna	-	-	104,481	15,789	-	-	120,270

Table 14.8. North Sea discards (tonnes) used in the model.

Group #	Functional group	2 Demersal trawl & demersal seiner	1 Beam trawls	10 Sandeel trawl	8 Pelagic trawls & seine	4 Drift & fixed nets	6 *Nephrops* trawlers
1	Baleen whales	-	-	-	-	-	-
2	Toothed whales	-	-	-	-	-	-
3	Seals	-	-	-	-	-	-
4	Seabirds	-	-	-	-	-	-
5	Juvenile sharks	-	-	-	-	-	-
6	Spurdog	0.1	12.3	-	-	45.2	16.1
7	Large piscivorous sharks	-	-	-	-	-	-
8	Small sharks	-	-	-	-	-	-
9	Juvenile rays	-	-	-	-	-	-
10	Starry ray + others	0.0	-	-	-	-	-
11	Thornback & Spotted ray	0.0	180.7	-	-	0.0	-
12	Skate + Cuckoo ray	0.0	-	-	-	-	-
13	Juvenile Cod(0-2, 0-40 cm)	1,140.0	464.6	-	1,470.6	0.2	77.5
14	Cod (adult)	1,350.9	464.6	-	1,470.6	0.2	77.5
15	Juvenile Whiting (0-1, 0-20 cm)	5,700.0	570.0	171.0	5,700.0	31.7	1,305.3
16	Whiting (adult)	10,659.0	883.5	200.1	5,928.0	31.7	1,305.3
17	Juvenile Haddock (0-1, 0-20 cm)	19,665.0	43.0	77.5	13,224.0	75.8	1,259.7
18	Haddock (adult)	570.0	43.0	77.5	570.0	75.8	1,259.7
19	Juvenile Saithe (0-3, 0-40 cm)	1,094.4	19.3	-	1,812.6	23.9	53.3
20	Saithe (adult)	-	-	-	-	-	-
21	Hake	0.0	18.0	-	0.0	644.1	0.0
22	Blue whiting	-	-	-	-	-	-
23	Norway pout	-	-	-	-	-	-
24	Other gadoids (large)	0.0	15.2	-	-	1,812.6	-
25	Other gadoids (small)	-	-	-	-	-	-
26	Monkfish	661.2	1,100.1	-	-	8.4	26.0
27	Gurnards	0.1	4,121.1	-	-	-	0.1
28	Herring (juvenile 0, 1)	0.1	47.0	-	1,806.9	-	0.0
29	Herring (adult)	0.1	47.0	-	1,806.9	-	0.0
30	Sprat	0.4	4,218.0	-	-	0.0	0.0
31	Mackerel	0.0	0.3	-	117,933.0	7.8	0.0
32	Horse mackerel	0.4	0.7	-	4.8	0.0	0.0
33	Sandeels	-	-	-	-	-	-
34	Plaice	18,354.0	41,211.0	-	-	0.0	172.1

Table 14.8. continued: North Sea discards (tonnes) used in the model.

Group #	Functional group	2 **Demersal trawl & demersal seiner**	1 **Beam trawls**	10 **Sandeel trawl**	8 **Pelagic trawls & seine**	4 **Drift & fixed nets**	6 ***Nephrops* trawlers**
35	Dab	70,110.0	1,613.1	-	-	0.0	4,332.0
36	Long-rough dab	-	-	-	-	-	-
37	Flounder	0.0	34,827.0	-	-	-	0.5
38	Sole	-	-	-	-	0.0	-
39	Lemon sole	2,257.2	132.8	-	-	0.0	60.4
40	Witch	20.0	6,954.0	-	0.7	0.2	-
41	Turbot and brill	128.8	210.9	-	-	67.3	-
42	Megrim	672.6	0.0	-	-	0.2	-
43	Halibut	-	-	-	-	-	-
44	Dragonets	-	-	-	-	-	-
45	Catfish (Wolf-fish)	-	-	-	-	-	-
46	Large demersal fish	666.9	12.4	-	2.5	21.3	-
47	Small demersal fish	-	-	-	-	-	-
48	Miscellaneous filter feeding pelagic fish	0.0	-	-	90.1	0.0	-
49	Cephalopods	212.0	14.4	-	0.1	-	0.0
50	Fish Larvae (food)	-	-	-	-	-	-
51	Carnivorous zooplankton	-	-	-	-	-	-
52	Herbivorous & Omnivorous zooplankton (copepods)	-	-	-	-	-	-
53	Gelatinous zooplankton	-	-	-	-	-	-
54	Large crabs	-	-	-	-	-	-
55	*Nephrops*	121.4	-	-	-	-	451.4
56	Epifaunal macrobenthos (mobile grazers)	-	9.9	-	-	-	-
57	Infaunal macrobenthos	-	-	-	-	-	-
58	Shrimp	-	28,443.0	-	-	-	-
59	Small mobile epifauna (swarming crustaceans)	-	-	-	-	-	-
60	Small infauna (polychaetes)	-	-	-	-	-	-
61	Sessile epifauna	-	-	-	-	-	-

Table 145.8. continued: North Sea discards (tonnes) used in the model.

Group #	Functional group	5 Gears using hooks	12 Shrimp trawlers	3 Dredges	11 Shellfish picking	9 Pots	7 Other methods	Total
1	Baleen whales	-	-	-	-	-	-	-
2	Toothed whales	-	-	-	-	-	-	-
3	Seals	-	-	-	-	-	-	-
4	Seabirds	-	-	-	-	-	-	-
5	Juvenile sharks	-	-	-	-	-	-	-
6	Spurdog	0.0	-	-	-	-	-	73.7
7	Large piscivorous sharks	-	-	-	-	-	-	-
8	Small sharks	-	-	-	-	-	-	-
9	Juvenile rays	-	-	-	-	-	-	-
10	Starry ray + others	-	-	-	-	-	-	0.0
11	Thornback & Spotted ray	-	-	-	-	-	-	180.7
12	Skate + Cuckoo ray	-	-	-	-	-	-	0.0
13	Juvenile Cod(0-2, 0-40 cm)	-	-	-	-	-	26,505.0	29,657.9
14	Cod (adult)	-	-	-	-	-	2.6	3,366.3
15	Juvenile Whiting (0-1, 0-20 cm)	-	-	-	-	-	408.1	13,886.2
16	Whiting (adult)	-	-	-	-	-	408.1	19,415.7
17	Juvenile Haddock (0-1, 0-20 cm)	-	-	-	-	-	1,647.3	35,992.3
18	Haddock (adult)	-	-	-	-	-	1,647.3	4,243.3
19	Juvenile Saithe (0-3, 0-40 cm)	0.1	-	-	-	-	28,500.0	31,503.6
20	Saithe (adult)	0.1	-	-	-	-	-	0.1
21	Hake	-	-	-	-	-	-	662.1
22	Blue whiting	-	-	-	-	-	-	-
23	Norway pout	-	-	-	-	-	-	-
24	Other gadoids (large)	-	-	-	-	-	-	1,827.8
25	Other gadoids (small)	-	-	-	-	-	-	-
26	Monkfish	-	-	-	-	-	-	1,795.8
27	Gurnards	-	-	-	-	-	-	4,121.3
28	Herring (juvenile 0, 1)	-	-	-	-	-	84,360.0	86,214.1
29	Herring (adult)	-	-	-	-	-	-	1,854.1
30	Sprat	-	-	-	-	-	-	4,218.4
31	Mackerel	-	-	-	-	-	-	117,941.1
32	Horse mackerel	-	-	-	-	-	-	5.9
33	Sandeels	-	-	-	-	-	-	-
34	Plaice	-	-	-	-	-	-	59,737.1

Table 14.8. continued: North Sea discards (tonnes) used in the model.

Group #	Functional group	5 Gears using hooks	12 Shrimp trawlers	3 Dredges	11 Shellfish picking	9 Pots	7 Other methods	Total
35	Dab	0.0	-	0.0	-	-	-	76,055.1
36	Long-rough dab	-	-	-	-	-	-	-
37	Flounder	-	-	-	-	-	-	34,827.5
38	Sole	-	-	-	-	-	-	0.0
39	Lemon sole	-	-	-	-	-	-	2,450.4
40	Witch	0.0	-	-	-	-	-	6,974.9
41	Turbot and brill	0.0	-	-	-	-	-	407.0
42	Megrim	-	-	-	-	-	-	672.8
43	Halibut	-	-	-	-	-	-	-
44	Dragonets	-	-	-	-	-	-	-
45	Catfish (Wolf-fish)	-	-	-	-	-	-	-
46	Large demersal fish	-	-	0.0	-	-	-	703.1
47	Small demersal fish	-	-	-	-	-	-	-
48	Miscellaneous filter feeding pelagic fish	-	-	-	-	-	-	90.1
49	Cephalopods	-	-	0.0	-	-	-	226.6
50	Fish Larvae (food)	-	-	-	-	-	-	-
51	Carnivorous zooplankton	-	-	-	-	-	-	-
52	Herbivorous & Omnivorous zooplankton (copepods)	-	-	-	-	-	-	-
53	Gelatinous zooplankton	-	-	-	-	-	-	-
54	Large crabs	-	-	-	-	-	-	-
55	*Nephrops*	-	-	-	-	-	-	572.9
56	Epifaunal macrobenthos (mobile grazers)	-	-	-	-	-	-	9.9
57	Infaunal macrobenthos	-	-	-	-	-	-	-
58	Shrimp	-	-	-	-	-	-	28,443.0
59	Small mobile epifauna (swarming crustaceans)	-	-	-	-	-	-	-
60	Small infauna (polychaetes)	-	-	-	-	-	-	-
61	Sessile epifauna	-	-	-	-	-	-	-

Table 14.9. Example economic data used in the AER. Data for Belgian beam trawlers.

Economic indicators (mEUR)	1999	2000	2001	2002	2003	2004
Value of landings	15	12	14.4	14.8	15.1	12
Fuel costs	2	2	2.5	2.5	2.5	2.4
Other running costs	3	2	2.6	3.1	3.1	1.6
Vessel costs	1	1	1.3	1.5	1.6	2.4
Crew share	5	4	4.5	4.5	4.6	4.2
Gross cash flow	4.2	2.1	3.5	3.2	3.3	1.4
Depreciation	2	2	1.9	1.8	1.7	1.8
Interest	1	1	0.6	0.8	0.3	0.8
Net profit	1	-1	1	0.6	1.3	-1.2
Gross value added	9	6	8.1	7.7	7.9	5.6
Other economic indicators						
Employment on board (FTE)	100	100	100	100	100	118
Invested capital (mEUR)	20	20	21	19	16.5	23.4
Effort (1000 days at sea)	6	6	6	6	6	5.5
Capacity indicators						
Volume of landings (1000 t)	3	3	3.1	3.4	3.3	3.3
Fleet – number of vessels	31	30	33	32	32	35
Fleet – total GRT (1000)						
Fleet – total GT (1000)	3	3	3	3	3	3
Fleet – total kW (1000)	7	7	7	7.1	7.1	7.5
Composition of landings (Value (mEUR))						
Major species						
Sole	3.7	4.9	6.3	6	7	6.7
Plaice	1.4	1.1	1.4	1.4	1.6	1.2
Cod	1.6	1.1	0.4	0.7	0.3	0.2
Other fish	8.3	4.9	6.3	6.7	6.2	3.9
Total	15	12	14.4	14.8	15.1	12
Composition of landings (Volume (1000 t))						
Sole	0.5	0.6	0.7	0.7	0.8	0.8
Plaice	0.7	0.7	0.8	0.8	0.8	0.7
Cod	0.6	0.4	0.1	0.3	0.1	0.1
Other fish	1.4	1.6	1.5	1.6	1.6	1.7
Total	3.2	3.3	3.1	3.4	3.3	3.3

Table 14.10. Economic data for gear groups used in the model.

Ecopath gears	Economic indicators (mEUR)					
	Year	Value of landings	Fuel costs	Other running costs	Vessel costs	Crew share
Beam trawls	2004	12	2.4	1.6	2.4	4.2
Beam trawls	2004	66.7	18	7.8	12	23
Shrimp trawlers	2004	2.5	0.6	0.3	0.8	0.8
Pelagic trawls and seine	2004	82.4	12.3	8.2	17.8	23.5
Demersal trawl and seine	2004	74.5	15.9	11.5	16.2	27.1
Demersal trawl and seine	2004	81.2	12.6	10.3	17	42
Drift and fixed nets	2004	42.9	2.5	5.7	8.3	26.1
Demersal trawl and seine	2004	14	0.9	2.1	3.3	7.7

Table 14.11. Relative costs for each gear type used in the model.

Name of fleet	Fixed cost (%)	Effort related cost (%)	Profit (%)	Total value (%)
Demersal trawl + demersal seine	34.6	68.7	-3.3	100
Beam trawl	36.0	69.6	-5.6	100
Sandeel trawl	47.3	74.7	-22	100
Pelagic trawl	39.3	55.8	4.9	100
Drift and fixed nets	38.2	80.0	-18.2	100
Nephrops trawl	24.6	81.3	-5.9	100
Gears using hooks	38.2	80.0	-18.2	100
Shrimp trawlers	31.8	73.7	-5.5	100
Dredges	35.9	74.9	-10.8	100
Shellfish	38.2	80.0	-18.2	100
Pots	38.2	80.0	-18.2	100
Other	30.5	69.4	0.1	100

Table 145.12. Relative prices for each species by gear used in the model.

Group Name	Demersal trawl + dem seine	Beam trawl	Sandeel trawl	Pelagic trawl	Drift and fixed nets	*Nephrops* trawl	Gears using hooks	Shrimp trawlers	Dredges	Shellfish	Pots	Other
Baleen whales	1	1	1	1	1	1	1	1	1	1	1	1
Toothed whales	1	1	1	1	1	1	1	1	1	1	1	1
Seals	1	1	1	1	1	1	1	1	1	1	1	1
Seabirds	1	1	1	1	1	1	1	1	1	1	1	1
Juvenile sharks	1	1	1	1	1	1	1	1	1	1	1	1
Spurdog	1	1	1	1	1	1	1	1	1	1	1	1
Large piscivorous sharks	1	1	1	1	1	1	1	1	1	1	1	1
Small sharks	1	1	1	1	1	1	1	1	1	1	1	1
Juvenile rays	1	1	1	1	1	1	1	1	1	1	1	1
Starry ray + others	1	1	1	1	1	1	1	1	1	1	1	1
Thornback & Spotted ray	1	1	1	1	1	1	1	1	1	1	1	1
Skate	1	1	1	1	1	1	1	1	1	1	1	1
Juvenile Cod(0-2, 0-40cm)	1	1	1	1	1	1	1	1	1	1	1	1
Cod (adult)	2.42	3.58	3.07	1.47	2.92	1	1.26	2.83	1	1	1	2.35
Juvenile Whiting (0-1, 0-20cm)	1	1	1	1	1	1	1	1	1	1	1	1
Whiting (adult)	1.96	2.44	1.34	1.26	2.29	1	1.05	1	1	1	1	1
Juvenile Haddock (0-1, 0-20cm)	1	1	1	1	1	1	1	1	1	1	1	1
Haddock (adult)	1.45	2.3	1.97	1.2	2	1	1.19	1	1	1	1	1.74
Juvenile Saithe (0-3, 0-40cm)	1	1	1	1	1	1	1	1	1	1	1	1
Saithe (adult)	1.55	1.54	1.53	1.09	2	1	1.23	1	1	1	1	1.44
Hake	1	1	1	1	1	1	1	1	1	1	1	1
Blue whiting	1	1	1.09	1.17	1	1	1	1	1	1	1	1
Norway pout	1.01	1	1.06	1.01	1	1	1.01	1	1	1	1	1
Other gadoids (large)	1	1	2	1	4	1	1	1	1	1	1	1
Other gadoids (small)	1	1	1	1.34	1	1	1	1	1	1	1	1
Monkfish	1	1	5.04	1	4	1	1	1	1	1	1	3.78
Gurnards	1	1	1	1	1	1	1	1	1	1	1	1
Herring (juvenile 0, 1)	1	1	1	1	1	1	1	1	1	1	1	1
Herring (adult)	1.37	1.26	1.25	1.32	1.5	1.15	1.01	1	1	1	1	1
Sprat	1.03	1.14	1.08	1.02	1.11	1	1.01	1	1	1	1	1
Mackerel	1.26	1.33	1.21	1.24	1.86	1	1.01	1	1	1	1	1
Horse mackerel	1.33	1	1	1.38	1	1	1	1	1	1	1	1
Sandeels	1.01	1	1.1	1.1	1	1	1.01	1	1	1	1	1
Plaice	2.66	2.49	2.72	1.35	2.74	1	1.27	2.34	1	1	1	1

Table 14.12. Relative prices for each species by gear used in the model.

Group Name	Demersal trawl + dem seine	Beam trawl	Sandeel trawl	Pelagic trawl	Drift and fixed nets	*Nephrops* trawl	Gears using hooks	Shrimp trawlers	Dredges	Shellfish	Pots	Other
Dab	1.86	1	1.9	1	2	1	1	1	1	1	1	1
Long-rough dab	1	1	1	1	1	1	1	1	1	1	1	1
Flounder	1	1	1	1	1	1	1	1	1	1	1	1
Sole	4.76	8.31	9.67	2.33	10.43	1	1.96	9.5	1	1	1	1
Lemon sole	5	1	4.5	1	6	1	1	1	1	1	1	1
Witch	3.5	1	3.52	1	1	1	1	1	1	1	1	1
Turbot and brill	1	14	7.25	1	8.25	1	1	1.17	1	1	1	1
Megrim	1	1	1	1	1	1	1	1	1	1	1	1
Halibut	3.37	1	1	1	1	1	1	1	1	1	1	1
Dragonets	1	1	1	1	1	1	1	1	1	1	1	1
Catfish (Wolf-fish)	1	1	1	1	1	1	1	1	1	1	1	1
Large demersal fish	1.88	2.33	2.5	1	2	1	1	1	1	1	1	1
Small demersal fish	1.76	2.69	1.62	1.14	2.82	1	1	2.38	1	1	1	2.02
Miscellaneous filterfeeding pelagic fish	1	1	1	1	1	1	1	1	1	1	1	1
Squid & cuttlefish	1	1	1	1	1	1	1	1	1	1	1	1
Carnivorous zooplankton	0	0	0	0	0	0	0	0	0	0	0	0
Herbivorous & Omnivorous zooplankton (copepods)	1	1	1	1	1	1	1	1	1	1	1	1
Gelatinous zooplankton	1	1	1	1	1	1	1	1	1	1	1	1
Large crabs	1	1	1	1	1	1	1	1	1	1	1	1
Nephrops	1	1	4	1	1	1	1	1	1	1	1	3.75
Epifaunal macrobenthos (mobile grazers)	1	1	7.82	1	1	1	1	1	1	1	1	1
Infaunal macrobenthos	1	1	1	1	1	1	1	1	2	1	1	1
Shrimp	1	1	1	1	1	1	1	1	1	1	1	1
Small mobile epifauna (swarming crustaceans)	2.41	3.52	3.15	1	1	1	1	3.34	1	1	1	1
Small infauna (polychaetes)	1	1	1	1	1	1	1	1	1	1	1	1
Sessile epifauna	1	1	1	1	1	1	1	1	1	1	1	1
Meiofauna	1	1	1	1	1	1	1	1	1	1	1	1
Benthic microflora (incl. Bacteria, protozoa))	1	1	1	1	1	1	1	1	1	1	1	1
Planktonic microflora (incl. Bacteria, protozoa)	1	1	1	1	1	1	1	1	1	1	1	1
Phytoplankton	1	1	1	1	1	1	1	1	1	1	1	1
Detritus - DOM -water column	1	1	1	1	1	1	1	1	1	1	1	1
Detritus - POM - sediment	1	1	1	1	1	1	1	1	1	1	1	1
Discards	1	1	1	1	1	1	1	1	1	1	1	1

Name of fleet	Value of landings (mill euro)	Employment on board (FTE)	Value/jobs
Beam trawl	389.2	2836	7.3
Demersal trawl + dem seine	322.3	2688.1	8.3
Dredges	64.6	536	8.3
Drift and fixed nets	42.9	592.5	13.8
Nephrops trawl	66.3	961	14.5
Other methods	112.9	2250.2	19.9
Pelagic trawl	497.4	2020.1	4.1
Sandeel trawl	201.6	2003.5	9.9
Shrimp trawlers	51.3	787	15.3
Gears using hooks	-	-	-
Shellfish	-	-	-
Pots	-	-	-

15. Mammals and Birds

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15.1 Baleen whales

Minke whales (*Balenoptera acutorostrata*) are the most commonly and regularly occuring baleen whales in the North Sea, which are generally more abundant in the western North Sea (ICES WGMME, 2004). Abundance estimates are available from SCANS (Small Cetacean Abundance in the North Sea survey, Hammond *et al.*, 2002) which uses a combination of shipboard and aerial survey methodology. Abundance in the summer of 1994 was estimated to 7250 individuals which multiplied by average individual weight 5251 kg (Trites *et al.*, 1999) resulted in total biomass 38.07 thousand tonnes or biomass density of B= 0.067 t km^{-2} (Table 3.1). We used the production rate (P/B) of 0.02 used by Trites *et al.*, 1999. Q/B= 9.9 was estimated from mean daily ration (R) as a function of individual weight (w) (Trites *et al.*, 1999):

$$R = 0.1w^{0.8}$$

The diet data are from 15 samples from minke whale stomachs in taken in June-July 1999 in the central North Sea (Olsen and Holst, 2000). The diet is dominated by fish: mostly sandeel (66%), but also herring, mackerel and gadoids (whiting, haddock, Norway pout, Table T3.4). No invertebrates were found in the samples in contrast with Barents Sea where minke whale diets are dominated by krill (eg Folkow *et al.*, 1997). Herring has been the dominant prey in May-June 1999-2000 in the Norwegian Sea (Olsen and Holst, 2000). Minke whales appear to be euryphagous according to Haug *et al.* (1995), who studied diets in several regions in the Norwegian and Barents Seas. Whilst the results of Olsen and Holst (2000) are limited, we assume them to be representative of the area. Trophic level is 4.44.

Other baleen whales (eg sei whale, fin whale) possibly appear at the border of the model area: Faroe shelf and Shetland-Faroe channel (Reid *et al.*, 2003)., but no data of their abundance have been reported.

15.2 Toothed whales

Harbour porpoise *Phocoena phocoena*, white-beaked dolphin *Lagenorhynchus albirostris* and Atlantic white-sided dolphin *Lagenorhynchus acutus* are included in the toothed whales group. Abundance estimates are taken from the SCANS survey (Hammond *et al.*, 2002). Poirpoises are most abundant and widely distributed in Northern and central North Sea (Reid *et al.*, 2003; ICES WGMME, 2004). White-beaked dolphin is mostly distributed in the western part of the North Sea and the Atlantic white-sided dolphin - in the northern North Sea (Reid *et al.*, 2003). Seasonal distribution and movements are rarely studied and not well known (Reid *et al.*, 2003). Biomasses were estimated from numeric abundance reported by Hammond *et al.*, (2002) multiplied by average individual weight from Trites *et al.* (1999). Total biomass of the 3 species is 9.9 thousand tonnes and biomass density is B= 0.017 t km^{-2}. P/B and Q/B were estimated for each species following Trites *et al.* (1999) and then weighted means were estimated for the whole group: P/B = 0.02 Q/B = 17.63.

The aggregate diet of the 3 species was compiled based on data from Santos *et al.* (1994, 1995, 2004) from Scottish waters. Whiting and sandeel are the two dominant species in the diet of porpoise, whilst whiting and cephalopods dominate the diets of *Lagenorhynchus* spp. Trophic level is 4.78.

Limited occurrence have been reported in the area of bottlenose dolphin, killer whale, Risso's dolphin, and sperm whale (ICES WGMME, 2004), but data on abundance are not available.

15.3 Seals

Two species were included: the grey seal *Halichoerus grypus* and harbour seal *Phoca vitulina*. Grey seals are included in the MSVPA assessment as fish predators and their biomass (3000 t) and consumption rate were taken from the SGMNS (ICES, 2002). Abundance of harbour seals in different areas in the North Sea was reported by the Special Committee on Seals (SCOS, 2002) and the ICES WGMME (2002, 2004). Total abundance on 24 000 specimens was multiplied by average individual weight of 63 kg from Trites *et al.* (1999) and added to the biomass of the grey seal. Total estimated biomass is 4400 t or 0.008 t km^{-2}. The maximum rate of population growth rate for pinnipeds is believed to be about 12% yr^{-1} (Small and DeMaster, 1995). The P/B ratio was therefore set at 6%, half of the maximum as used by Trites *et al. (*1999). Consumption rates of 26.84 of grey seals (ICES, 2002) and 30 – for harbour seal estimated using Trites *et al.* formula (1999) were aggregated giving the FG Q/B = 27.87.

Diet of seals was compiled from 3 sources. The diet of seals (FG 3) was estimated as a weighted mean from the diets of grey seals and harbour seals from around the British Isles reported by Hammond *et al.* (1994) and Hall *et al.* (1998) respectively (Table T3.4). Grey seals feed mostly on sandeels (~40%), but diet of harbour seal is more variable, with relatively high proportions of gadoids, flatfish and coastal demersal fish (gobies, bullrout, dragonets). The SGMNS (ICES 2002) provide the proportions of the MSVPA species of different age in the diet of grey seal. This information was used to determine the proportion of juvenile and adults cod, haddock, whiting, saithe, and herring, in the seal diet. Trophic level is 5.01, the highest of all FGs. This is explained by the relatively high proportion of predatory fish, such as cod, hake and monkfish, in the diet.

15.4. Birds

The most abundant species of seabirds in the North Sea are fulmar (*Fulmarus glacialis*), gannet (*Sula bassana*), shag (*Phalacrocorax aristotelis*), herring gull (*Larus argentatus*), great black backed gull (*Larus marinus*), lesser black backed gull (*Larus fuscus*), kittiwake (*Larus tridactyla*), terns (Sternidae), guillemot (*Uria aalge*), razorbill (*Alca torda*), puffin (*Fratercula arctica*), great skua (*Catharacta skua*). The estimation methods for abundance and consumption are described in ICES, 1996. Biomass and consumption rate (Q/B) were taken from information used in the MSVPA analyses (ICES, 2002): B= 0.003 t km^{-2} Q/B = 216. Production rate P/B = 0.4 was taken from Trites *et al.* (1999). Diet of seabirds was compiled based on ICES 1996. Seabirds consume mainly fish (eg sandeels), some zooplankton, discards and offal from fishing vessels (ICES 1996, Table 3.4). Trophic level is 3.5, but this is incorrect because an important proportion of the diet are discards (offal) for which a trophic level 1 is assigned even if they may originate from organisms of higher trophic level (TL 3 or 4).

16. References

Admiraal, W., Bouwman, L.A., Hoekstra, L. and Romeyn, K., 1983. Qualitative and quantitative interactions between microphyobenthos and herbivorous meiofauna on a brackish water intertidal mudflat. Int. Revue ges. Hydobiolo. 68:175-191.

Albert, O.T., 1993. Distribution, population structure and diet of silvery pout (*Gadiculus argenteus thori* J. Schmidt), poor cod (*Trisopterus minutus minutus* (L.)), four-bearded rockling (*Rhinonemus cimbrius* (L.)), and Vahl's eelpout (*Lycodes vahlii gracilis* Reinhardt) in the Norwegian Deep SO. Sarsia, 78(2): 141-154.

Aleyev Yu. A. 1977. Nekton. Dr. W. Junk b.v. Publishers, The Hague, pp 435.

Alkemade, R. A., Wielemaker, and Hemminga, M.A., 1992. Stimulation of decomposition of Spartina anglica leaves by the bactivorous nematode *Diplolaimelloides bruciei* (Monhysteridae), J. Exp. Mar. Biol. Ecol. 159: 267-278.

Andersen, K.P. and Ursin, E., 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. Meddelelser, 7: 319-435.

Annual Economic Report, 2000. STECF, Economic performance of selected European fishing Fleets Downloaded at http://stecf.jrc.cec.eu.int/ (Accessed 12 June 2006).

Annual Economic Report, 2005 STECF, Economic performance of selected European fishing Fleets Downloaded at http://stecf.jrc.cec.eu.int/ (Accessed 12 June 2006)

Anon., 2004. Report of the Working Group on Nephrops Stocks. ICES CM 2004/ACFM:19

Anon., 1997. Report of the working group on elasmobranchs. ICES Demersal Fish Committe. CM 1997/G:2. 123 pp.

Anon., 1999b. Study group on elasmobranch fishes (SGEF). ICES CM 1999/G:11. 18 pp.

Anon., 1999c. Working group on marine mammal population dynamics and trophic interactions (WGMMPD). ICES CM 1999/G:3. 26 pp.

Anon. 1999d. Working group on the assessment of mackerel, horse mackerel, sardine and anchovy (WGMHSA). ICES CM 1999/ACFM:6. 468 pp.

Araújo, J., Mackinson, S. and Hart, P.J.B., 2007. Exploring long-term fisheries strategies for the western English Channel using an ecosystem model.

Araújo, J., Mackinson, S., Ellis, J. and Hart, P.J.B. 2005. An Ecopath model of the Western English Channel ecosystem with an exploration of its dynamic properties. 2005. Cefas tech rep 125, 45 p.

Armstrong, M.J., 1982 The predator-prey relationships of Irish Sea poor-cod (*Trisopterus minutus*), pouting (*Trisopterus luscus*) and Cod (*Gadus morhua*) J. Cons Int. Explor. Mer. 40: 135-152.

Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L-A. and Thingstad, F., 1983. The ecological role of water column microbes in the sea. Mar. Ecol. Prog. Ser., 10: 257-263.

Baars and Franz, 1984 in Nielsen and Richardson, 1989.

Bakun, A. 1996. Patterns in the Ocean: Ocean Processes and Marine Population Dynamics. California Sea Grant Coll. Syst.

Baden, S.P., 1986. Recent changes in the Kattegat and Skagerrak ecosystem and their possible interdependence. - Nat. Swedish Envir. Prot. Bd. Rep., 3157: 91pp.

Båmstedt, U., 1998. Trophodynamics of *Pleurobranchia pileus* (Ctenophora) and ctenophora summer occurrence off the Norwegian Northwest coast. Sarsia, 83:169-181.

Båmstedt, U., Martinussen, M.B., Matsakis, S., 1994. Trophodynamics of the two scyphomedusae *Aurelia aurita* and *Cyanea capillata*, in western Norway. ICES J. Mar. Sci., 51: 369-382.

Basford, D.J., Eleftheriou, S., and Raffaelli, D., 1990. The infauna and epifauna of the North Sea. Neth. J. Sea. Res., 25: 165-173.

Beattie, A., Sumailia, U.R., Christensen, V., and Pauly, D. 2002. A model for the bioeconomic evaluation of marine protected area size and placement in the North Sea. Nat. Resour. Model. 15: 413–437.

Beaugrand, G., 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog.Oceanogr., 60: 245–262.

Bergstad, O.A., 1991. Distribution and trophic ecology of some gadoid fish of the Norwegian Deep. 1. Accounts of individual species. Sarsia 75: 269-313.

Beukers-Stewart, B.D., Jenkins, S.R., Brand, A.R., 2001. The efficiency and selectivity of spring-toothed scallop dredges: A comparison of direct and indirect methods of assessment. J. Shell. Res., 20(1): 121-126.

Billen, G., Joiris, C., Meyer-Reil, L., and Lindeboom, H., 1990. Role of bacteria in the North Sea ecosystem. Neth. J. Sea Res., 26(2-4): 265-293.

Botsford, L.W., Castilla, J.C. and Petersen, C.H., 1997. The management of fisheries and marine ecosystems. Science, 277: 509-515.

Bowman, R.E., Stillwell, C.E., Michaels, W.L. and Grosslein, M.D., 2000. Food of northwest Atlantic fishes and two common species of squid.. NOAA Tech. Memo. NMFS-NE, 155: 138pp

Braber, L. and de Groot, S.J., 1973. Neth. J. Sea Res., 6: 163-172. The food of five flatfish species (Pleuronectiformes) in the southern north sea. Neth. J. Sea Res. 6: 163-172.

Brey, T. 2001. Population dynamics in benthic invertebrates. A virtual handbook. The Virtual Handbook http://www.thomas-brey/science/virtualhandbook

Broekheuizen, N., Heath, M.R., Hay, S.J., and Gurney, W.S.C., 1995. Modelling the dynamics of the North Sea's Mesozooplankton. Neth. J. Sea Res., 33(3/4): 381-406.

Brown, J., Hill, A., Fernand, L. and Horsburgh, K., 1999. Observations of a seasonal jet-like circulation at the central North Sea cold pool margin. Est. Cstl. Shelf Sci., 44: 343-355.

Cadée, G. S., and Hegeman, J., 1974. Primary production of the benthic microflora living on tidal falts in the Dutch Waddensea. Neth. J. Sea Res., 8(2-3): 260-291.

Cadée, G.C., 1985. Macroaggregates of Emiliana Huxley in sediment traps. Mar. Ecol. Prog. Ser., 24: 193-196.

Calloway, R., Alsvåg, J., de Boois, I., Cotter, J., Ford, A., Hinz, H., Jennings, S., Kröncke, I., Lancasterm J., Piet, G., Prince, P. and Ehrich, S., 2002. Diversity and community structure of epibenthic invertebrates and fish in the North Sea. ICES J. Mar. Sci., 59: 1199-1214.

Camphuysen, C.J.e., 2004. Understanding marine foodweb processes: an ecosystem approach to sustainable sandeel fisheries in the North Sea, Interactions between the Marine environment, PREdators, and prey: implications for Sustainable Sandeel fisheries (IMPRESS). Royal Netherlands Institute for Sea Research, Texel, The Netherlands.

Carman, K.R and Fry, B., 2002. Small-sample methods for δ13C and δ15N analysis of the diets of marsh meiofaunal species using natural abundance and tracer additional isotope techniques. Mar. Ecol. Prog. Ser., 240: 85-92.

Cartes, J.E., Brey, T., Sorbe, J.C. and Maynou, F., 2002. Comparing production-biomass ratios of benthos and suprabenthos in macrofaunal marine crustaceans. Can. J. fish. Aquat. Sci., 59:1616-1625.

Charnock, K., Dyer, R., Huthnance, J.M., Liss, P.S., Simpson, J.H. and Tett, P.B., 1994. Understanding the North Sea system. Chapman and Hall for the Royal Society. 222p.

Checkley, D.M. Jr., 1980. The egg production of marine plankton copepod in relation to its food: Laboratory studies. Limonol. Oceanogr., 25: 430-446.

Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D'Antonio, C. Francis, R., McMahon, J.F., Noss, R.F., Parsons, D.J., Peterson, C.H., Turner, M.G. and Woomansee, R.G., 1996. The Report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. Ecol. App., 6(3): 665-691.

Christensen, V., 1995. A model of trophic interactions in the North Sea in 1981, the year of the stomach. Dana, 11(1): 1-28.

Christensen, V. and Walters, C.J., 2000. Ecopath with Ecosim: methods, capabilities and limitations. pp79-105. In: (D. Pauly. and T.J. Pitcher (eds.)). Methods for assessing the impact of fisheries on marine ecosystems of the North Atlantic. Fisheries Centre Research Reports 8(2): 195pp.

Christensen, V., Walters, C., and Pauly, D., 2000. Ecopath with Ecosim: a users guide. October 2000 edition. Fisheries Centre, University of British Columbia, Vancouver, Cananda and ICLARM, Penang, Malaysia. 130pp.

Clark, R.A., Frid, C.L.J. and Batten, S., 2001. A critical comparison of two long term zooplankton time series from the central-west North Sea. J. Plankt. Res., 23: 27–39.

Clark, R.A., 2000. Long term changes in the North Sea ecosystem. PhD thesis. University of Newcastle-upon-Tyne. 273pp

Cole, J.J., Finlay, S., and Pace, M.L., 1989. Bacterial production in fresh and saltwater ecosystems: a cross system overview. Mar. Ecol. Prog. Ser., 43: 1-10.

Collins, M.A. and Pierce, G.J., 1996. Size selectivity in the diet of *Loligo forbesi* (Cephalopoda: Loliginidae). J. Mar. Biol. Ass. UK, 76: 1081-1090.

Collins, M.A., Yau, C., Boyle, P.R., Friese, D. and Piatkowski, U., 2002. Distribution of cephalopods from plankton surveys around the British Isles. Bull. Mar. Sci., 71(1): 239-254

Cotter, J., Course, G., Buckland, S., and Garrod, C., 2002. A PPS sample survey of English fishing vessels to estimate discarding and retention of North Sea cod, haddock, and whiting. Fish. Res., 55(1-3): 25-35.

Coull, B.C. 1990. Are members of the meiofauna food for higher trophic levels? Trans. Am. Microsc. Soc., 109(3): 233-246.

Coull, J.R., 1972. The Fisheries of Europe. An Economic Geography. G.Bell and Sons Ltd., London. 240 pp.

Coull, K.A., Jermyn, A.S., Newton, A.W., Henderson, G.I., and Hall, W.B., 1989. Length/weight relationships for 88 species of fish encountered in the North Atlantic. Scot. Fish. Res. Rep., 43: 80pp.

Cowey, C.B. and Corner, E.D.S., 1961. On the nutrition and metabolism of zooplankton. II. The realtionship betweenthe marine copepod *Calanus helgolandicus* and particulate materials in Plymouth seawater in terms of amino acids composition. J. Mar. Biol. Ass. UK, 43: 495-511.

Craeymeersch, J.A., Heip, C.H.R. and Buijs, J., 1997. Atlas of the North Sea Benthic Infauna. ICES Coop. Res. Rep., 218: 86pp.

Creed, E.L. and Coull, B.C., 1984. Sand dollar, *Mellita quniquiesperforata* and Sea Pansy, *Renilla remiformis* effects on meiofaunal abundance. J. Exp. Mar. Biol. Ecol., 84:225-134.

Creutzberg, F., and Duineveld., G.C.A., 1986. The role of the lesser weaver *Trachinus vipera* and the dab *Limanda limanda* in the benthic system of the southern North Sea. ICES CM 1986/L:4. 10pp.

Crisp, D. J. 1975. Secondary productivity in the sea. - Productivity of world ecosystems, pp.71-89. National Academy of Sciences, Washington, DC.

Cury, P and Christensen, V. 2006. Quantitative Ecosystem Indicators for Fisheries Management. 2006. ICES Journal of Marine Science, 62: 307-310 (2005).

Cushing, D.H. 1973. Productivity in the North Sea. pp 249-266. *In:* G.D. Goldberg. North Sea Science. MIT press, Cambridge, MA.

Cushing, D.H., 1988. The Provident Sea. Cambridge University Press, Cambridge. 329 pp.

Cushing, D.H. and Vucetic, T., 1963. Studies on a *Calanus* patch. III. The quantity of food eaten by *Calanus finmnarchicus*. J. Mar. Biol. Ass. UK, 43: 349-371.

Daan, N., 1978. Changes in cod stocks and cod fisheries in the North Sea. Rapp. P.-V. Réun. Cons. Int. Explor. Mer, 172: 39-57.

Daan, R., Gonzalez, S.R. and Klein Breteler, W.C.M., 1988. Cannibalism in omnivorous calanoid copepods. Mar. Ecol. Prog. Ser., 47: 45-54.

Daan, N., Bromley, P.J., Hislop, J.R.G. and Nielsen, N.A., 1990. Ecology of North Sea fish. Neth. J. Sea Res., 26: 343-386.

Daan, N., Johnson, B., Larsen, J.R. and Sparholt, H., 1993. Analysis of the ray (*Raja* spec.) samples collected during the 1991 international stomach sampling project ICES CM 1993/G:15. 17p.

Dahl, K. and Kirkegaard, E.,1987].The diet and consumption of Horse Mackerel (*Trachurus trachurus*) in the Eastern North Sea, ICES CM 1987/H43.

Dare, P.J., Key, D., and Connor, P.M., 1993. The efficiency of spring-loaded dredges used in the Western English Channel fishery for scallops, *Pecten maximus*. ICES CM 1993/B:15.

Daro, M.H. and B. van Gijsegem., 1984. Ecological factors affecting weight, feeding, and production of five dominant copepods in the Southern Bight of the North Sea. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, 183: 226-233.

DCR Codification Standards and definition of Standard Outputs for EC1639/2001 data, Available at http://datacollection.jrc.cec.eu.int/documents/Codes-Standard-Outputsv3.pdf (Accessed on 28 June 2006).

De Bovee, 1993 (in Brey) or Debovee and Labat 1993.

De Bovee, F. and Labat, J.P., 1993. A simulation-model of a deep meiobenthic compartment - a preliminary approach Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I, 14(2): 159-173.

Decho, A.W. and Lopez, G.R., 1992. Exopolymer microenvironments of microbial flora; Multiple and interactive effects on trophic relationships. Limnol. Oceanogr., 38: 1633-1645.

De Clerck R & Buseyne D 1989. On the feeding of plaice (*Pleuronectes platessa* L.) in the Southern North Sea. ICES-CM-1989/G:23, 21 p.

De Silva, S.S., 1973. Food and feeding habits of the herring *Clupea harengus* and the sprat *C. sprattus* in inshore waters of the west coast of Scotland. Mar. Biol., 20: 282-290.

DeLaca, 1985, in Brey 2001.

Deree, H.L., 1998. Age and growth, dietary habits and parasitism of the fourbeard rockling, *Enchelyopus cimbrius*, from the Gulf of Maine. Fish. Bull., 97: 39-52.

Derycke, S., Remerie, T., Vierstraete, A., Backeljau, T., Vanfleteren, J., Vincx, M. and Moens, T., 2005. Mitochondrial DNA variation and cryptic speciation within the free-living marine nematode Pellioditis marina. Mar. Ecol. Prog. Ser., 300: 91-103.

Derycke, S., Backeljau, T., Vlaeminck, C., Vierstraete, A., Vanfleteren, J., Vincx, M. and Moens, T., 2007. Spatiotemporal analysis of population genetic structure in *Geomonhystera disjuncta* (Nematoda, Monhysteridae) reveals high levels of molecular diversity. Mar. Biol. in press.

Donavaro, R., Gambi, C. and Mirto, S., 2002. Meiofaunal production and energy transfer effeiciency in a seagrass bed in the western Mediterranean. Mar. Ecol. Prog. Ser., 234: 95-104.

Du Buit, M-H., 1984. Prédation de la cardine (*Lepidorhombus whiffiagonis* W.) au nord et à l'ouest de l'Ecosse. J. Cons. Int. Explor. Mer, 41: 194-198.

Duineveld, G.C.A., Kunitzer, A., Niermann, U., de Wilde, P. A.W.J., and Gray, J.S., 1991. The macrobenthos of the North Sea. Neth. J. Sea Res., 28(1/2): 53-65.

Ebeling, E. and Alshuth, S., 1989. Food preferences and diseases of *Myoxocephalus scorpius* in the German Bight. ICES-CM-1989/G:48. 6pp.

Eisma, D., 1981. Supply and deposition of suspended matter in the North Sea. – Spec publs. Int. Ass. Sediment 5: 415-428.

Eleftheriou, A. and Basford, D.J., 1989. The macrobenthic infauna of the offshore northern North Sea. J. Mar. Biol. Ass. UK, 69:123-143.

Ellis, J.R., Pawson, M.G. & Shackley S.E., 1996. The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the north-east Atlantic. J. Mar. Biol. Ass. UK, 76(1): 89-106.

ES, F.B. van. and Meyer-Reil, L-A., 1982. Biomass and metabolic activity of heterotrophic marine bacteria. *In* K.C. Marshall. Adv. Microb. Ecol., 6: 111-170.

European Commission Regulation (EC) No. 1639/2001 of 25 July 2001 establishing the minimum and extended Community programmes for the collection of data in the fisheries sector and laying down detailed rules for the application of Council Regulation (EC) No 1543/2000.

European Commission Regulation (EC) No 2090/98 of 30 September 1998 concerning the fishing vessel register of the Community.

European Commission Regulation EU Data Collection Regulation No. 1543/2000, Establishing a Community Framework for the Collection and Management of Data Needed to Conduct the CFP.

European Council Regulation No 423/2004. Establishing measures for the recovery of cod stocks. 26 February 2004.

Evans, F., 1977. Season density and production estimates of the commoner planktonic copepods of Northumberland coastal waters. Est. Cstl. Mar. Sci., 5: 233-241.

FAO, 2002. The State of World Fisheries and Aquaculture. www.fao.org

FAO, 2003. FAO technical Guidelines for Responsible Fisheries 4(2). www.fao.org

Fasham, M.J.R. 1984. Flows of energy and materials in marine ecosystems. Theory and practice. (NATO conference series IV). Marine Sciences, Vol. 13. Plenum, New York: 733pp.

Faubel *et al.*, 1983. In Heip *et al.*, 1990

Fenchel, T., 1982a. Ecology of heterotrophic microflagellates, 1. Some important forms and their functional morphology. Ecol. Prog. Ser., 8: 211-223.

Fenchel, T., 1982b. Ecology of heterotrophic microflagellates, 2. Bioenergetics and growth. Ecol. Prog. Ser., 8: 225-231.

Fenchel, T., 1982c. Ecology of heterotrophic microflagellates, 4. Quantitative occurrence and importance as bacterial consumers. Mar. Ecol. Prog. Ser., 9: 35-42.

Fenchel, T., 1988. Marine plankton food chains. Ann. Rev. Ecol. Syst., 19: 19-38.

Floeter, J., Kempf, A., Vinther, M., Schrum, C. and Temming A., 2005. Grey gurnard (*Eutrigla gurnadus*) in the North Sea: an emerging key predator? Can. J. Fish. Aquat. Sci., 62: 1853-1864.

Folkow, L.P., Haug, T., Nilssen, K.T. and Nordøy, E.S., 2000. Estimated food consumption of minke whales *Balaenoptera acutorostrata* in Northeast Atlantic waters in 1992-1995. NAMMCO Sci. Publ. 2: 65-80.

Fowler, H., 1912. Science of the Sea. John Murray, London. 453pp.

Fransz, H.G., 1980. Computation of secondary production of *Calanus finmarchicus* using multiple regression method. Proc. Final ICES/JONIS workshop on JONSDAP '76. ICES CM 1980/C:3, 99-108.

Fransz, H. G., and Gieskes, W.W.C., 1984. The unbalance of phytoplankton and copepods in the North Sea. Rapp. P.-v. Réun. Cons. Int. Explor. Mer., 183: 218-225.

Fransz, H.G., and van Arkel, W.G., 1980. Zooplankton activity during and after the phytoplankton spring bloom at the central station in the FLEX box, northern North Sea, with special reference to the calanoid copepod *Calanus finmarchicus* (Gunn). 'Meteor' Forsch. Ergebnisse A, 22: 113-121.

Fransz, H.G., Miquel, J.C., and Gonzalez, S.R., 1984. Mesozooplankton composition, biomass and vertical distribution, and copepod production in the stratified central North Sea. Neth.J. Sea Res.,18: 218-225.

Fransz, H. G., Mommaerts, J. P., and Radach, G., 1991a. Ecological modelling of the North Sea. Neth.J. Sea Res., 28(1/2): 67-140.

Fransz, H. G., Colebrook, J. M., Gamble, J. C., and Krause, M., 1991b. The zooplankton of the North Sea. Neth.J. Sea Res., 28(1/2): 1-52.

Froese, R. and Pauly, D. (eds)., 2004. FishBase. World Wide Web electronic publication. www.fishbase.org,

Gaedke, U., 1995. A comparison of whole-community and ecosystem approaches (biomass size distributions, food web analysis, network analysis, simulation models) to study the structure, function and regulation of pelagic food webs. J. Plank. Res., 17: 1273-1305.

Gaudy, R., 1974. Feeding in four species of pelagic copepods under experimental conditions. Marine Biology, 25: 125-141.

Gee, J.M., 1989. An ecological economic review of meiofauna as food for fish. Zool. J. Linn. Soc., 96: 243-261.

Gee, de A. and Kikkert, A.H., 1993 Analysis of the grey gurnard (*Eutrigla gurnardus*) samples collected during the 1991 international stomach sampling project ICES CM 1993/G:14, 25pp

Geider, R.J., 1988. Abundances of autotrophic and heterotrophic nanoplankton and the size distribution of microbial biomass in the southwestern North Sea in October 1986. – J. Exp. Mar. Biol. Ecol., 123: 127-145.

Gerlach, S.S., 1971. On the importance of marine meiofauna for benthos communities. Oecologia 6:176-190.

Gibson and Ezzi, 1987. Feeding relationships of a demersal fish assemblage on the west coast of Scotland. J. Fish. Biol., 31: 55-69.

Gieskes, W.W.C. and Kraay, G.W., 1980. Primary productivity and phytoplankton pigment measurements in the Northern North Sea during FLEX 76. Meteor Forsch. Erg., A22: 105-112.

Gieskes, W.W.C. and Kraay, G.W., 1984. Phytoplankton, its pigments and primary production at a central North Sea station in May, July and September 1981. Neth. J. Sea. Res. 18:51-70.

Gray, 1981 in Duineveld *et al.,* 1991,

Greenstreet, S.P.R., 1996 Estimation of the daily consumption of food by fish in the North Sea in each quarter of the year. Scottish fisheries research report. Scott. Fish. Res. Rep., 55: 16pp.

Greenstreet, S.P.R. and Hall, S.J., 1996. Fishing and the ground-fish assemblage structure in the north-western North Sea: An analysis of long-term and spatial trends, J. Animal Ecol., 65: 577-98.

Guénette, S. 1996. Macrobenthos. pp65-67. *In:* Mass balance models of North-eastern Pacific ecosystems. University of British Columbia, Fisheries Centre Research Reports, Vol. 1 no. 4.

Haggan, N and Pitcher, T. (eds), 2005. Ecosystem simulation models of Scotlands west coast and sea lochs. Fish. Centre Res. Rep., 13(4): 67p.

Hagmier, E. 1962. Das seston und seine Komponenten. Kieler Meeresforsch. 18:189-197.

Hall, A.J., Watkins, J. and Hammond, P.S., 1998. Seasonal variation in the diet of harbour seals in the south-western North Sea. Mar. Ecol. Prog. Ser., 170: 269-281.

Hammond, P.S., Hall, A.J. and Prime, J.H., 1994. The diet of grey seals around Orkney and other island and mainland sites in north-eastern Scotland. J. Appl. Ecol., 31: 340-350.

Hammond, P.S., Berggren, P., Benke, H., Borchers, D.L., Collet, A., Heide-Joergensen, M.P., Heimlich, S., Hiby, A.R., Leopold, M.F. and Oeien, N., 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. J. Appl. Ecol., 39(2): 361-376.

Hannon, B., and Joiris, C. 1989. A seasonal analysis of the southern North Sea ecosystem. Ecology, 70: 1916-1934.

Hansson, L.J. Moeslund, O., Kiørboe, T. and Riisgård, H.U., 2005. Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). Mar. Ecol. Prog. Ser., 304: 117–131.

Hatch, S.A., Byrd, G.V., Irons, D.B., and Hunt, G.L. Jr., 1993. Status and ecology of kittiwakes (*Rissa tridactyla* and *R. brevirostris*) in the North Pacific. pp140-153. *In:* K. Vermeer, K.T. Briggs, K.H. Morgan, and D. Siegel-Causey (Eds.). The Status, Ecology, and Conservation of Marine Birds of the North Pacific. Canadian Wildlife Service Special Publication, Ottawa.

Haug, T., 1990. Biology of the Atlantic halibut, *Hippoglossus hippoglossus* (L. 1758). Adv. Ma. Biol., 26: 2-63.

Haug, T., Gjosaeter, H., Lindstrom, U. and Nilssen, K.T., 1995. Diet and food availability for north-east Atlantic minke whales (*Bulaenoptera acutorostrata*), during the summer of 1992. ICES J. Mar. Sci., 52: 77-86.

Hay, S.J., Hislop, J.R.G. and Shanks, A.M., 1990. North-Sea scyphomedusae - summer distribution, estimated biomass and significance particularly for O-group gadoid fish. Neth. J. Sea Res., 25: 113-130.

Heessen, H.J.L., 1996. Time-series data for aselection of forty fish species caught during the International Bottom trawl Survey. ICES J Mar. Sci, 53: 1079-1078.

Heip, C. and Craeymeersch, J.A., 1995. Benthic community structures in the North Sea. Helgoland Mar. Res., 49: 313-328.

Heip, C., Herman, R., and Vincx, M. 1983. Subtidal meiofauna of the North Sea: a review. Biolo. Jb. Dodonaea., 51: 116-170.

Heip, C., Herman, R. and Vincx, M., 1984. Variability and productivity of the meiobenthos in the Southern Bight of the North Sea. Rapp. P.-v. Réun. Cons. Int. Explor. Mer., 183 :51-56.

Heip, C., Huys, R., Vincx, M., Vanreusel, A., Smol, N., Herman, R., and Herman, P.M.J., 1990. Composition, distribution, biomass and production of North Sea Meiofauna. Neth. J. Sea Res., 26(2-4): 333-342.

Heip, C., Basford, D., Craeymeersch, J.A., Dewarumez, J.M., Dörjes, J., de Wilde, P.A.J., Duineveld, G.C.A., Eleftheriou, A., Herman, P.M. Niermann, U., Kingston, P., Künitzer, A, Rachor, E., Rumohr, H., Soetaert, K., and Soltwedel, T., 1992. Trends in biomass, density and diversity of North Sea macrofauna. distribution and assemblages. ICES J. Mar. Sci., 49: 13-22.

Heip, C.H., Goosen, N.K., Herman, P.M.J., Kromkamp, J., Middleburg, J.J. and Soetaert, K., 1995. production and consumption of biological particles in temperate tidal estuaries. Oceanogr. Mar. Biol. Annu. Rev., 33: 1-150.

Herman, P.M.J. and Vranken, G., 1988. Studies of the life history and energetics of marine and brackish water nematodes. II. Production, respiration and food uptake by *Monhystera disjuncta*. Oecologia, 77: 457-463.

Hickel, W., and Gunkel, W., 1968. Untersuchungen uber die Haufigheit der bakterien in dr obersten sedimentschicht der Deutschen Bucht in beziehung su den substrateigenschafen. Helgolander wiss. Meeresunters, 18: 213-231.

Hislop, J. (ed), 1997. Database report of the Stomach Samplinmg Project 1991. ICES Coop. Res. Rep., 219: 422pp

Holligan *et al.*, 1984 in van Duyl *et al.*, 1990.

Hopkins, C.C.E. 1998. Energy content and production of the deepwater prawn Pandalus borealis, as a function of body size/age and season. ICES CM1988/K24 Ref G.

Hopkins, C.C.E., Sargent, J.R. and Nilssen, E.M., 1993. total lipid content and lipid an fatty acid composition of the deepwater prawn Pandalus borealis for Blasfjord, northern Norway: growth and feeding relationships. Mar. Ecol. Prog. Ser., 96: 217-228.

Huntley, M.E. and Lopez, M.D.G., 1992. Temperature-dependent production of marine copepods: a global synthesis. Am. Nat., 140: 201-242.

Hutchings, J.A., 2000. Collapse and recovery of marine fishes. Nature, 406: 882-885

Huys, R., Herman, P.M.J., Heip, C.H.R. and Soetaert, K., 1992. The meiobenthos of the North Sea: density, biomass trends and distribution of copepod communities. ICES J. Mar. Sci. 49:23-44.

ICES WGCRAN. 2005. Report of the Working Group on Crangon Fisheries and Life History (WGCRAN), 4–9 October 2004, Copenhagen, Denmark. ICES CM 2005/. 89 pp.

ICES WGPAN 2005. Report on the Pandalus Assessment Working Group. ICES Advisory Committee on Fishery Management ICES CM 2005/ACFM:05.

ICES, 1989. Report of the Multispecies Assessment Working Group, 7-16 June 1989, Copenhagen. ICES Counc. Meet. 1989/Assess:20, 125pp.

ICES, 1997. Report of the Multispecies Assessment Working Group ICES CM 1997/Assess: 16.

ICES, 2001. Report of the WGMHSA ICES CM 2001/ACFM:06.

ICES, 2002. Report of the WGMHSA ICES CM 2002/ACFM:06.

ICES, 2002. Report of the workshop on MSVPA in the North Sea. Charlottenlund, Denmark, 8th-12th April 2002. ICES CM 2002/D:04

ICES, 2003. ICES CM 2003/D:09

ICES 2003. Report of WGMME. ICES CM 2003/ACE:03 Ref E, G http://www.ices.dk/reports/ACE/2003/WGMME03.pdf

ICES, 2003. Environmental status of the European seas, Prepared for the German Ministry for the Environment, Nature Conservation and Nuclear Safety.

ICES, 2003. Report of the Advisory Committee on Ecosystems, 2003. ICES Cooperative Research Report, 262. 229pp

ICES, 2004. Report of WGMME. ICES CM 2004/ACE:02 Ref E, G http://www.ices.dk/reports/ACE/2004/WGMME04.pdf

ICES, 2005. SGCRAB 2005.

ICES, 2005. Working Group on the Assessment of Demersal Stocks in the North Sea.

ICES 2006. Report of the Working Group on Elasmobranch Fishes (WGEF) ICES CM 2006/ACFM:31.

ICES, 2006. Cod stock latest information and advice, available at http://www.ices.dk/committe/acfm/comwork/report/asp/advice.asp (Accessed on 20 August 2006).

ICES Fisheries Statistics, 2000. CD Rom for use with FAO FISHSTAT database.

ICONA, 2002. North Sea Atlas for Netherlands Policy and Management. Stadsuitgeverij, Amsterdam, The Netherlands, 96pp.

Jennings, S. and Kaiser, M., 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol., 34: 201-352.

Jennings, S., Reynolds, J.D., and Mills, S.C., 1997. Life history correlates of responses to fisheries exploitation. Proc. Royal Soc. London Ser. B, 265: 333-339.

Jennings, S. Alvsvag, J., Cotter, J., Ehrich, S., Greenstreet, S., Jarre- Teichmann, A., Mergardt, N., Rijnsdorp, A. and Smedstad, O., 1999. Fishing effects in north-east Atlantic shelf seas: patterns in fishing effort, diversity and community structure. I. Introduction. Fish. Res., 40: 103-106.

Johnson, N., 2000. Does prey size of Loloigo Forbesi vary with squid size. Thesis report, University of Aberdeen.

Joint, I.R., and Pomroy, A.J., 1987. Activity of heterotrophic bacteria in the euphotic zone of the Celtic Sea. Mar. Ecol. Prog. Ser., 41: 155-165.

Joiris, C., Billen, G., Lancelot, C., Daro, M.H., Mommaerts, J.P., Bertels, A., Bossicart, M., Nijs, J., and Heco, J.H. 1982. A budget of carbon cycling in the Belgian coastal zone: Relative roles of zooplankton and benthos in the utilisation of primary production. Neth. J. Sea Res., 16: 260-275.

Jones, B.C., and Green, G.H., 1977. Food and feeding of the spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Bd. Fish (Canada), 34: 2067-2078.

Jones, R., 1982. Species interactions in the North Sea. pp48-63. *In*: (M. C. Mercer (Ed.)) Multispecies Approaches to Fisheries Management Advice, Canadian Special Publication of Fisheries and Aquatic Science no. 59. 169 pp.

Jones, R., 1984. Some observations on energy transfer through the North Sea and Georges Bank food webs. Rap p. P.-v. Reun. Cons. int. Explor. Mer, 183: 204-217.

Jones, R., and Hislop, J.R.G. 1975. Changes in the North Sea haddock and whiting. ICES Symposium on the Changes in the North Sea Fish stocks and their Causes, 25: 32.

Kaiser, M.J., Rogers, S.I., and McCandless, D.T., 1994. Improving quantitative surveys of epibenthic communities using a modified 2 m beam trawl. Mar. Ecol. Prog. Ser., 106: 131-138.

Kaiser, M.J. and de Groot, S.J. (eds), 2000. Effects of Fishing on Non-Target Species and Habitats: Biological, conservation and socio-economic issues. pp105-117. Blackwell Science Ltd, Oxford, UK 399pp.

Karpov, K.A., and Cailliet, G.M., 1978. Feeding dynamics of Loligo opalescens. pp45-66. *In*: (C.W. Reckseik and H.W. Frey (Eds.)). Biological, Oceanographic, and Acoustic aspects of the market squid, *Loligo opalescens*, California Department of Fish and Game, Fish Bulletin no. 169.

Kiørboe, T., Møhlenberg, f., and Hamburger, K., 1985. Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration and composition of specific dynamic action. Mar. Ecol. Prog. Ser., 26: 85-97.

Kirman, D.L., 2000. Micorbial ecology of the oceans. Wiley-Liss, NY.

Klein and Breteler *et al.*, 1982 in Fransz and Gieskes 1984.

Knijn, R.J., Boon, T.W., Heessen, H.J.L. and Hislop, J.R.G., 1993. Atlas of North Sea fishes, based on bottom-trawl survey data for the years 1985-1987. ICES Coop. Res. Rep., 194: 268pp.

Knust, R., 1990. Food and condition of dab, *Limanda limanda* (L.) from the Dogger Bank and the German Bight. ICES CM 1990/G:62. 7pp.

Krause, M. and Trahms, J., 1983. Zooplankton dynamics during FLEX' 76. pp632-661. In: (J.W. Lenz (Ed.)). North Sea Dynamics Sündermann, Springer-Verlag, Berlin.

Kröncke, I., 1990. Macrofauna standing stock of the Dogger bank. A comparison: II. 1951-1952 versus 1985-1987. Are the changes in the norheastern part of the Dogger bank due to environmental changes? Neth. J. Sea Res., 25: 189-198.

Kuipers, B.R., Gaedke, U. Enserink, L. and White, H., 1990. Effect of ctenophore predation on mesozooplankton during a spring outburst of *Pleurobrachia pileus*. Neth. J. Sea Res., 26(1): 111-124.

Künitzer, A., 1990. The infauna and epifauna of the central North Sea. Meeresforschung, 33: 23-37.

Künitzer, A, Basford, D., Craeymeersch, J.A., Duineveld, G.C.A., Dewarumez, J.M., Niermann, U., Rachor, E., Rumohr, H., and de Wilde, P.A.J., 1992. The benthic infauna of the North Sea: species distribution and assemblages. ICES J. Mar. Sci., 49: 127-143.

Lancelot, C and Mathot, S., 1987. Dynamics of phaeocystis dominated spring bloom in Belgian coastal waters. I. Phytoplankton activities and related parameters. Mar. Ecol. Prog. Ser., 37: 239-248.

Lancelot, C., Billen, G. and Mathot, S., 1988. Ecophysiology of the phyto- and bacterioplankton growth in the Pryds Bay area during austral summer 1987. Part I. Modelling phytoplankton growth. pp116-132. *In*: Proceedings of the Belgian National Colloquiums on Antarctic research, October 20, 1987, Prime Ministers Service -Science Policy Office, Brussels.

Landry, M.R., 1981. Switching between herbivory and carnivory by the planktonic marine copepod Calanus pacificus. Marine Biol., 65(1): 77-82.

Lasserre *et al.*, 1976 in Heip *et al.*, 1990.

Last, J.M., 1987. The food of immature sprat (*Sprattus sprattus* (L.)) and herring (*Clupea harengus* L.) in coastal waters of the North Sea. J. Cons. Int. Explor. Mer, 44: 73-79.

Lee, S. and Fuhrman, J.A. 1987. Relationships between biovolume and biomass of naturally derived backetrioplankton. Appl. Environ. Microbiol., 53: 1298-1303.

Lees, K. and Mackinson, S., 2007. An ecopath model of the Irish Sea: ecosystem properties and sensitivity analysis. Sci. Ser. Tech Rep. Cefas Lowestoft, 138: 49pp.

Lees, K. and Mackinson, S., 2008. An Irish Sea Regime Shift: Evidence and drivers from empirical data and model predictions. Submitted.

Lewy, P., Vinther, M. and Thomsen, L., 1992. Description of the STCF North Sea database system and the prediction model ABC, assessments of bio-economic consequences of technical measures. ICES CM1992/D:17.

Lindley, J.A. 1980. Population dynamics and production of euphasiids. Part II. *Thyanoessa inermis* and *T. raschi* in the North Sea and American coastal waters. Mar. Biol., 59: 225-234.

Lindley, J.A. 1982. Continuous plankton records: Geographical variations in numerical abundance, biomass and production of euphasiids in the North Atlantic Ocean and the North Sea. Mar. Biol., 71: 7-10.

Linley, E.A.S, Newell, R.C. and Lucas, M.I., 1983. Quantitative relationships between phytoplankton, bacteria and heterotrophic microflagellates in shelf waters. Mar. Ecol. Prog. Ser., 12:77-89.

Lizárraga-Cubedo, H.A., Tuck, I., Bailey, N., Pierce, G.J., Zuur, A.F., 2005. Common trends in two populations of the European lobster, *Homarus gammarus*, in Scottish waters. ICES CM 2005/O:12.

Lourdes, M., Palomares, D., and Pauly, D., 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salininty. Mar. Fswtr. Res., 49: 447-53.

Lynam, C and Brierly, A., 2007. Enhanced survival of 0-group gadoid fish under jellyfish umbrellas. Mar. Biol., 150(6): 1397-1401.

McGlade J., 2002. The North Sea Large Marine Ecosystem p339-412. *In*: (Sherman, K. and Skjoldal HR (Eds.)). Large Marine Ecosystems of the North East Atlantic: changing states and sustainability. Elsevier, Amsterdam, The Netherlands.

McIntyre, A. D., 1952. The food of the halibut from North Atlantic fishing grounds. Scottish Home Department. Marine Research, Edinburgh, HMSO, 3: 19 pp.

McIntyre, A.D. 1964. Meiobenthos of sublittoral muds. J. Mar. Biol. Assoc. UK. 44:665-674.

McIntyre, A.D. 1969. Ecology of Marine meiobenthos. Biol. Rev. 44 :245-290.

McIntyre, A.D. 1978. The Benthos of the western North Sea. Rapp. P-v. Réun. Cons. Int. Explor. Mer, 172: 405-417.

MacIntyre, H.L., Geider, R.J. and D.C. Miller. 1996. Microphytobenthos: The ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. Estuaries, 19(2A): 186-201.

MacLeod, C.D., Santos, M.B. and Pierce, G.J., 2003. Review of data on diets of beaked whales: evidence of niche separation and geographic segregation. Journal of the J. Mar. Biol. Assoc. UK, 83(3): 651-665.

Mackinson, S. 1995. System definition and primary production in the Georgia Strait. pp63-64. *In:* Mass balance models of North-eastern Pacific ecosystems, University of British Columbia, Fisheries Centre Research Reports, Vol. 1 no. 4.

Mackinson, S., 2002a. Representing trophic interaction in the North Sea in the 1880s using the Ecopath mass-balance approach. p35-98. *In:* (S. Guénette, V. Christensen, D. Pauly. (Eds.)). Fisheries impacts on North Atlantic ecosystems: models and analyses. Fisheries Centre Research Reports 9(4).

Mackinson, S., 2002b. Simulating management options for the North Sea in the 1880s. pp73-83. *In:* (T.J. Pitcherand K. Cochrane, K. (eds)). The use of ecosystem models to investigate multi-species management strategies for capture fisheries. Workshop 17th-20th July 2000, Vancouver. Fisheries Centre Research Reports, 2002, 10(2): 156pp.

Mackinson, S., Blanchard, J., Pinnegar, J. and Scott, R., 2003. Consequences of alternative functional response formulations in models exploring whale-fishery interactions. Mar. Mamm. Sci., 19(4): 661-681.

Mackinson, S., *et al.*, in prep. Which forcing factors fit? The relative influence of climate and fishing.

Macpherson, 1979. Estudio sobre el regimen alimentario de algunos peces en el Mediterraneo occidental. Misc. Zool., 5: 93-107.

Majkowski, J. 1982. Usefulness and applicability of sensitivity analysis in a multispecies approach to fisheries management. In Pauly, D; Murphy, GI (eds). ICLARM/CSIRO Workshop on the Theory and Management of Tropical Multispecies Stocks, Cronulla (Australia), 12 Jan 1981.

Malyshev, V.I. and Ostapenko, A.T., 1982 Tr. ATLANTNIRO, Kaliningrad: 24-30.

Mann, K., 2000. Ecology of coastal waters with implications for managements. 2nd Ed. Blackwell Science. Oxford, England. 406p.

Mann, K.H., 1988. Towards predictive models for coastal marine ecosystems, pp291-316. *In*: (L.R. Pomeroy and J.J. Alberts (Eds.)). Concepts of Ecosystem Ecology, Ecological Studies 67, Springer, New York.

Marshall, S.M., and Orr, A.P., 1966. Respiration and feeding in some small copepods. J. Ma. Biol. Ass. UK, 46: 513-530.

Martell, S. J. D., T. Essington, B. Lessard, J. F. Kitchell, C. J. Walters and C. H. Boggs. 2005. Interactions of productivity, predation risk and fishing effort in the efficacy of marine protected areas for the central Pacific. Can. J. Fish. Aquat. Sci. 62:1320-1336.

Martens, P., 1980. Contributors to the Mesozooplankton of the northern Wadden Sea of Sylt, German Bight, North Sea. Helgol. Meeres., 34: 41-45.

Martinussen, M.B. and Båmstedt, U., 1995. Diet, estimated daily food ration and predator impact by the scyphozoan jellyfishes *Aurelia aurita* and *Cyanea capillata*. pp127-145. *In*: (H.R. Skjoldal, C. Hopkins, K.E. Erikstad and H.P. Leinaas (eds.)). Ecology of fjords and coastal waters. Elsevier Science B.V.

Matthews, J.B.L., and Heimdal, B.R. 1980. Pelagic productivity and food chains in fjord systems. NATO Conference series, Series 4. Mar. Sci., 4: 377-398.

Mattson, S., 1981 The food of *Galeus melastomus*, *Gadiculus argenteus thori*, *Trisopterus esmarkii*, *Rhinonemus cimbrius*, and *Glyptocephalus cynoglossus* (Pisces) caught during the day with shrimp trawl in a West-Norwegian Fjord. Sarsia, 66(2): 109-127.

Meyer-Reil, L.A. 1982. Bacterial biomass and heterotrophic activity in sediments and overlying waters. *In*: (Hobbie, J. Leb, E., Williams, P.J. (Eds.)). Heterotrophic activity in the sea. Plenum press, New York.

Mickleburgh, P., 2003. Fisheries landings and discards of the North Sea in 1991: contribution to an ecosystem model. MSc thesis, King's College, London 53p.

Moens, T. and Vincx, M., 1996. Do meiofauna consume primary production? About many questions and how to answer them. *In*: (J. Baeyens, F. Dehairs and L. Goeyens (Eds.)). Integrated Marine System Analysis. European Network for Integrated Marine System Analysis. Nationaal Fonds voor Wetenschappelijk Onderzoek. Minutes of the first network meeting, Brugge, 29 February-2 March 1996: 188-202.

Moens, T., Verbeeck, L. and Vincx, M., 1999. Preservation and incubation time-induced bias in tracer-aided grazing studies on meiofauna. Mar. Biol., 133(1): 69-77.

Moloney, C.L., Jarre, A., Arancibia, H., Bozec, Y-M., Neira, S., Roux, J-P. and Shannon, L.J., 2005. Comparing the Benguela and Humboldt marine upwelling ecosystems with indicators derived from inter-calibrated models. e ICES J. Mar. Sci., 62: 493-502.

Montagna, P.A. 1995. Rates of metazoan meiofaunal microbivory: a review. Vie et Milieu, 45: 1-9.

Morte, Redon, Sanz-Brau 1999. Feeding habits of trachinus draco off the eastern coast of Spain (western Mediterranean). Vie et Milieu, 49(4): 287-291.

MUMM 2002. Management Unit of the North Sea Mathematical Models http://www.mumm.ac.be

Murawski, S., 1992. The challenges of finding solutions in multispecies fisheries. *In*: (R. Schoning, R. Jacobson, D. Alverson, T. Gentle and J. Auyong (Eds.)). Proceedings of the National Industry Bycatch Workshop, February 4-6, 1992, Newport, Oregon. Natural Resources Consultants, Inc., Seattle, WA 98199.

Murawski, S., 2000. Definitions of overfishing from an ecosystem perspective. ICES J. Mar. Sci., 57(3): 649-658.

Myers, R.A., Bridson, J., and Barrowman, N.J. 1995. Summary of worldwide stock and recruitment data. Can. Tech. Rep. Fish. Aquat. Sci. 2024: 274 pp.

Nielsen, T.G. and Richardson, K., 1989. Food chain structure of the North Sea plankton communities: seasonal variations of the role of the microbial loop. Mar. Ecol. Prog Ser., 56: 75-87.

Ntiba, M.J. and Harding D., 1993. The food and the feeding habits of the long rough dab, *Hippoglossoides platessoides* (fabricius 1780) in the north sea. Neth. J. Sea Res 31: 189-199.

Oh, C.-W., Hartnoll, R.G. and Nash, R.D.M., 1999. Population dynamics of the common shrimp, *Crangon crangon* (L.)in Port Erin Bay, Isle of Man, Irish Sea. ICES J. Mar. Sci., 56(5): 718-733.

Okey, T., Vargo, G., Mackinson, S., Vasconcellos, M., Mahmoudi, B. and Meyer, C., 2002. Simulating community effects of sea floor shading by plankton blooms over the West Florida shelf. pp55-56. *In:* (V. Christensen, G. Reck and J.L. Maclean (Eds.)). Proceedings of the INCO-DC Conference Placing Fisheries in their Ecosystem Context, Galápagos Islands, Ecuador, 4-8 December 2000. ACP-EU. Fish. Res. Rep., (12).

Olsen, E. and Holst, J.C., 2001. A note on common minke whale (*Balaenoptera acutorostrata*) diets in the Norwegian Sea and North Sea. J. Cetacean Res. Manag., 3: 179-183.

OSPAR, 2000. Quality Status Report 2000, Region II - Greater North Sea.

Otto, L. J., Zimmerman,T. F., Furnes, G. K., Mork, M., Saetre, R., and Becker, G., 1990. Review of the physical oceanography of the North Sea. Neth. J. Sea Res., 26: 161-238.

Paffenhöfer, G.A., 1976. Feeding, growth and food conversion of the marine planktonic copepod *Calanus helgolandicus*. Limnol. Oceanogr., 21(1): 39-50.

Pahl-Wostl, C.,1993. Food webs and ecological networks across temporal and spatial scales. Oikos, 66: 415-432

Paloheimo, J. E., and Dickie, L. M., 1966. Food and growth of fishes. Part III. Relations among food, body size, and growth efficiency. J. Fish. Res. Bd. Can., 23(8): 1209-1248.

Palomares D. and Pauly D., 1989. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Mar. Freshwater Res., 49: 447-53.

Parker, R. *et al.*, paper on infauna and sediment turnover.

Pauly, D., 1989. Food consumption by tropical and temperate marine fishes: Some generalizations. J. Fish Biol., Suppl. A: 11-20.

Pauly, D. (ed.) 1998. Use of Ecopath with Ecosim to evaluate strategies for sustainable exploitation of multi-species resources. Fisheries Centre Research Reports, 6(2). 49pp.

Pauly, D., Christensen, V. and Walters, C., 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci., 57: 697-706

Pepita, T.S., Pavlova, E.V., and Mironov, G.N., 1970. The food web structure, utilization and transport of energy by trophic levels in the planktonic communities. pp142-167. *In*: (J.H. Steele (Ed.)). Marine Food Chains. Oliver and Boyd, Edinburgh.

Pianka, E. R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4: 53-74.

Pierce G.J., Bailey N., Stratoudakis Y. and Newton, A., 1998. Distribution and abundance of the fished population of Loligo forbesi in Scottish waters: analysis of research cruise data. ICES J. Mar. Sci., 55: 14-33.

Pierce, G.J. and Santos, M.B., 1996. Trophic interactions of squid in Scottish waters. pp. 58-64. *In*: (S.P.R. Greenstreet, S.P.R. and M.L. Tasker (Eds.). Aquatic Predators and their Prey, Fishing News Books, Oxford.

Pierce, G.J., Boyle, P.R, Hastie, L.C, Shanks, A.M., 1994a. Distribution and abundance of the fished population of *Loligo forbesi* in UK waters: analysis of fishery data. Fish. Res., 21(1-2): 193-216

Pierce, G.J., Boyle, P.R., Hastie, L.C. and Santos, M,B. 1994. Diets of squid *Loligo forbesi* and *Loligo vulgaris* in the north east Atlantic. Fish. Res., 21: 149-163.

Pinnegar, J., Blanchard, J. Mackinson, S., Scott, R. and Duplisea, D., 2005. Affects of aggregation and removing weak links in food web models on predictions of system stability and resilience. Ecol. Model., 184: 229-248.

Pitcher, T.J. and Cochrane, K. (eds), 2002. The use of ecosystem models to investigate multi-species management strategies for capture fisheries. Workshop 17th-20th July 2000, Vancouver. FCRR 2002, Vol. 10(2): 156pp.

Pitkitch, E.K., Dantora, C.S., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A. Mangel, M., McAllister, M.K. Pope, J. and Sainsbury, K.J., 2004. Ecosystem-based fishery management. Science, 305: 346-7.

Pitois, S. and Fox, C.J., 2006. Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data. ICES J. Mar. Sci., 63: 785-798.

Polovina J.J., 1984. Model of a coral reef ecosystem I. The ECOPATH model and its applications to French Frigate Shoals. Coral Reefs, 3: 1-11.

POLOVINA, J.J., 1993. The first Ecopath. pp7-8. *In*: V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

POSTMA, H., 1978., The nutrient contents of the North Sea water: Changes in recent years, particularly in the southern bight. Rapp P.-v. Réun. Cons. Int. Explor. Mer, 172: 350-357.

POULET, S.A., 1973. Grazing of *Pseudocalanus minutus* on naturally occuring particulate matter. Limnological Oceanography, 18: 564-573.

POULET, S.A., 1974. Seasonal grazing of *Pseudocalanus minutus* on particles. Mar. Biol., 25: 109-123.

POULET, S.A., 1976. Feeding of *Pseudocalanus minutus* on living and non living particles. Mar. Biol., 34: 117-125.

PURCELL, J.E., 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata, Cyanea capillata and Aequorea aequorea*, in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser., 246: 137-152.

RACHOR, E., 1982. Biomass distribution and production estimates of macro-endofauna in the North Sea. ICES CM 1982/L2: 1-10.

Rae, K.M. and Rees, C.B. 1947. Continuous plankton records: the copepoda of the North Sea. 1938-39. Hull Bull. Mar. Ecol. 2:84-87.

RAE AND REES, 1947 [in Franz *et al.*, 1991b]

RAE, B.B. AND SHELTON R.G.J., 1982. Notes on the food of nine species of elasmobranch (part 1) and nine species of demersal teleost (part 2) fishes from Scottish waters. ICES-CM-1982/G:56 24pp.

RAE, B.B., 1965. Fishing News Books, London. 106pp.

REAY, P.J., 1970. Synopsis of biological data on North Atlantic sand eels of the genus Ammodytes. Fish. Synop. 82.

REDANT, F., 1989. Productivity of epibenthic species: a review. ICES CM1999/L2. Shellfish Committee. 33pp.

REID, J.B., EVANS, P.G.H. AND NORTHRIDGE, S.P. (EDS.), 2003. Atlas of cetacean distribution in north-west European waters. Joint Nature Conservation Committee, Peterborough.

REID, P. 1987. The importance of the planktonic ecosystem of the North Sea in the context of oil and gas development. Phil. Trans. R. Soc. Lond. B, 316: 587-602.

REID, P.C., LANCELOT, C., GIESKES, W.W.C., HAGMEIER, E., AND WEICHART, G., 1990. Phytoplankton of the North Sea and its dynamics, a review. Neth. J. Sea Res., 3: 28pp.

REID, P.C., BORGES, M.F. AND SVENDSEN, E., 2001a. A regime shift in the North Sea circa 1990. Fish. Res., 50: 163-171.

REILLY, S. B., AND BARLOW, J., 1986. Rates of increase in dolphin population size. Fish. Bull., 84: 527-533.

REISS, H., KRONCKE, I AND EHRICH, S., 2006. Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments. ICES J. Mar. Sci., 63: 1453-1464.

RIEMANN, F AND SCHRAGE, M., 1978. The mucus trap hypothesis on feeding aquatic nematodes and implications for biodegradation and sediment texture. Oecologia. 34: 75-88.

RIJNSDORP, A.D., DAAN, N., BEEK, F.A. VAN, AND HEESEN, H.J.L., 1991. Reproductive variability in North Sea plaice, sole and cod. J. Cons. Int. Explor. Mer, 47: 352-375

RIJNSDORP, A.D., DAAN, N., BEEK, F.A. VAN, AND HEESEN, H.J.L., 1991. Reproductive variability in North Sea plaice, sole and cod. J. Conseil Int. pour l'Expl. Mer, 47: 352-375.

RIJNSDORP, A.D., VAN LEEUWEN, P., DAAN, N., HEESEN, H., 1996. Changes in abundance of demersal fish species in the North Sea between 1906-1909 and 1990-1995. ICES J. Mar. Sci., 53: 1054-1062.

ROFF, C. J., MIDDLEBROOK, K., AND EVANS, F., 1988. Long term variability in the North Sea zooplankton off the Northumberland coast: Productivity of small copepods and analysis of trophic interactions. J. Mar. Biol. Ass. UK, 68: 143-164.

ROGERS, S.I., RIJNSDORP, A.D., DAMM, U. AND VANHEE, W., 1998. Demersal fish populations in the coastal waters of the UK and continental NW Europe from beam trawl survey data collected from 1990 to 1995, J. Sea Res., 39: 79-102.

Rumohr, H., Brey, T., and Ankar, S., 1987. A compilation of biometric conversion factors for benthic invertebrates in the Baltic Sea. Baltic Mar. Biol. Pub., 9: 1-56.

Rueckert, C., Floeter, J. and Temming, A., 2002. An estimate of horse mackerel biomass in the North Sea 1991-1997. ICES J. Mar. Sci., 59(1): 120-130.

Sahrhage, D. and Wagner, G., 1978. On the fluctuations in the haddock population in the North Sea. Rapp P.-v.Réun. Cons. Int. Explor. Mer, 172: 72-85.

Sahrhage, D., and Lundbeck, J., 1992. A History of Fishing. Springer-Verlag, Berlin.

Salzwedel, H., Rachor, E., and Gerdes, D., 1985. Benthic macrofauna communities in the German Bight. Veräffent-lichungen des Instituto für Meeresforschung, Bremerhaven, 20: 199-267.

Santos, M.B., Pierce, G.J., Ross, H.M., Reid, R.J. and Wilson, B., 1994. Diets of small cetaceans from the Scottish coast ICES CM 1994/N:11. 16pp.

Santos, M.B., Pierce, G.J., Wijnsma, G., Ross, H.M. and Reid, R.J. 1995. Diets of small cetaceans stranded in Scotland 1993-1995. ICES CM 1995/N:6. 8pp.

Santos., M.B Pierce, G.J., Lopez, A., Barreiro, A. and Guerra, A., 1996. Diets of small cetaceans stranded NW Spain 1994-95 ICES-CM-1996/N:11, 4p.

Santos, M.B., Pierce, G.J., Boyle, P.R., Reid, R.J., Ross, H.M., Patterson, I.A.P., Kinze, C.C., Tougaard, S., Lick, R. et al., 1999. Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990-1996. Mar. Ecol. Prog. Ser., 183: 281-294.

Santos, M.B., Pierce, G.J., Reid, R.J., Patterson, I.A.P., Ross, H.M. and Mente, E., 2001. Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. J. Mar. Biol. Assoc. UK, 81(5): 873-878.

Santos, M.B., Pierce, G.J., Smeenk, C., Addink, M.J., Kinze, C.C., Tougaard, S. and Herman, J., 2001. Stomach contents of northern bottlenose whales *Hyperoodon ampullatus* stranded in the North Sea. J. Mar. Biol. Assoc. UK, 81(1): 143-150.

Santos, M.B., Pierce, G.J., Learmonth, J.A., Reid, R.J., Ross, H.M., Patterson, I.A.P., Reid, D.G. and Beare, D., 2004. Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992-2003. Mar. Mamm. Sci., 20(1): 1-27.

Santos, M.B., Pierce, G.J., Gibson, R.N. and Atkinson, R.J.A. The diet of harbour porpoise (*Phocoena phocoena*) in the northeast Atlantic. Oceanography and Marine Biology: An Annual review. Oceanography and marine biology: an annual review. Oceanogr. Mar. Biol. Annu. Rev., 41: 355-390.

SCOS [Special Committee on Seals], 2002. Scientific advice on matters related to the management of seal populations http://smub.st-and.ac.uk/pdfs/SCOS%2002_A.pdf 57 pp

SCOS [Special Committee on Seals], 2003. Scientific advice on matters related to the management of seal populations (http://smub.st-and.ac.uk/pdfs/SCOS%2003_v7.pdf) 75 pp.

SGEEMI, 2001. Study group to evaluate the effects of multispecies interactions. ICES CM 2001/D:03.

Sherman, K., Smith, W.G., Green, J.R., Cohen, E.B., Berman, M.S., Marti, K.A. and Goulet, J.P., 1987. Zooplankton production and fisheries of the Northeastern Shelf. pp 268-282. *In:* (R.H. Backus and D.W. Bourne (eds.)). Georges Bank. Cambridge, MA : MIT press.

Sherr, E.B., Sherr, B.F., and Paffenhöfer, G.A., 1986. Phagotrophic protzoa as food for metazoans: A missing trophic link in marine pelgic food webs? Mar. Microbiol. Food Webs, 1: 61-80.

Shumaway, S.E., Perkins, H.C., Schick, D.F. and Stickney, A.P., 1985. Synopsis of the biological data on the pink shrimp, *Pandalus borealis*, Kroyer, 1838. NOAA Tech. Rep. NMFS 30 FAO Fish. Synop., 144: 57pp.

Shushkina, E.A., Musaeva, E.I., Anokhina, L.L. and Lukasheva, T. A., 2000. The role of gelatinous macroplankton, jellyfish *Aurelia*, and ctenophores *Mnemiopsis* and *Beroe* in the planktonic communities of the Black Sea. Oceanology, Moscow 40: 809-816. In Russian.

Skagerrak (WGNSSK), 6-15 September 2005, ICES Headquaters Copenhagen. ICES CM.

Small, R. J. and DeMaster, D., 1995. Alaska marine mammal population assessments. US Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-57. 93 pp.

Sparholt, H., 1990. An estimate of the total biomass of fish in the North Sea. J. Cons. Int. Explor. Mer, 46: 200-210.

Sparre, P., 1991. Introduction to multispecies virtual population analysis. ICES Mar. Sci. Symp., 193: 12-21.

Stanford, R. J., Pitcher T. J., 2004. Ecosystem simulations of the English Channel: climate and trade-offs. Fisheries Centre Research Reports 12(3). The University of British Columbia, Vancouver.

STECF, SGECA, 2006 http://stecf.jrc.cec.eu.int/meetings/sgeca/0602/fleet.php (Accessed 1 July 2006).

Steele, J.H., 1974. The structure of marine ecosystems. Blackwell scientific publications, Oxford. 127 pp.

Stillwell, C.E. and Kohler, N.E., 1982. Food, feeding habits and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the northwest Atlantic. Can. J. Fish.Aquat. Sci., 39: 407-414.

Summers, C.F., 1978. Changes in the seal populations of the North Sea. Rapp P.-v. Réun. Cons. Int. Explor. Mer., 172: 278-285.

Tegner, M.Y. and Dayton, P.K., 2000. Ecosystem effects of fishing in kelp forest communities. ICES J. Mar. Sci., 57: 579-589.

Temming, A., Damm, U. and Neudecker, T., 1993. Trends in the size composition of commercial catches of brown shrimp (*Crangon crangon*) along the German coast. ICES CM/K:53.

Tietjen, J.H., 1980. Microbial-meiofauna interactions: a review. pp335-338. *In:* (R.R. Colwell, and J. Foster (Eds.)). Aquatic microbial ecology. University of Maryland Press, College Park.

Trites, A.W., Livingston, P., Vasconcellos, M.C., Mackinson, S., Springer, A.M., and Pauly, D., 1999. Ecosystem change and the decline of marine mammals in the Eastern Bering Sea: Testing the ecosystem shift and commercial whaling hypotheses. Fish. Ctre. Res. Rep., 7: 106pp.

Trites, A., and Pauly, D., 1998. Estimating mean body masses of marine mammals from maximum body lengths. Can. J. Zool., 76: 886-896.

Ulanowicz, R.E. and C.J. Puccia. 1990. Mixed trophic impacts in ecosystems. Coenoses 5:7-16.

van Duyl, F.C., Bak, R.P.M., Kop, A.J. and Nieuwland, G. 1990. Bacteria, auto- and heterotrophic nanoflagellates, and their relations in mixed frontal and stratified waters of the North Sea. Neth. J. Sea. Res. 26(1): 97-109.

Vinther, M. and Thomsen, L., 1992. The North Sea STCF database system, STCFBASE users guide. Danmarks Fiskeri – og Havundersøglelser.

Vranken *et al.*, 1986 in Donavaro, 2002

Walday, M. and Kroglund, T., 2006. European Environment Agency, Europe’s biodiversity - biogeographical regions and seas, North Sea region, Norwegian Institute for Water Research (NIVA)

Walker, P. A., Witte, J. I. J. and van Steenbergen, H., 2000. Growth and maturation of ray species in the North Sea: A comparative study. (in prep.)

Walters, C.J., Christensen, V. and Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev. Fish Biol. Fisheries, 7: 139-172

Walters, C.J., Kitchell, J.F. , Christensen, V. and Pauly, D., 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: Ecosim II. Ecosyst, 3: 70-83.

Walters, C.J. and Martell, S. 2004. Fisheries ecology and management, Princeton University Press, Princeton, New Jersey.

Walters, C., Pauly, D., and Christensen, V. 1999. Ecospace: predictions of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with empahsis on the impacts of marine protected areas. Ecosystems, 2: 539–554.

Warwick, R.M. Joint, I.R. and Radford, P.J., 1979. Secondary production of the benthos in an estuarine environment. pp429-450. *In*: (R.L. Jeffries and A.J. Davey (eds)).

Ecological processes in coastal environments. Blackwell Scientific Publications, Oxford,

Warwick, R.M., 1989. The role of meiofauna in the marine ecosystem: evolutionary considerations. Zool. J. Linn. Soc., 96: 229-241.

Wetsteijn, B., 1981 Feeding of North Sea Tubot and Brill. ICES CM1981/G:74. 18pp

Wilde, P.A.W.J., Berghuis, E.M., and Kok, A., 1986. Biomass and activity of benthic fauna on the Fladen ground (northern North Sea). Neth. J. Sea Res., 20: 313-323.

Williams, 1984 in van Duyl *et al.*, 1990

Williams, P.J. le B., 1981. Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. Kiel. Meeresforsch. Son-derh, 5: 1-28.

Williams, R., and Lindley, J.A., 1980a. Plankton of the Fladen ground during FLEX '76. Part I. Spring development of the plankton community. Mar. Biol., 57: 73-78.

Williams, R. and Lindley, J.A., 1980b. Plankton of the Fladen ground during FLEX '76. Part III. Vertical distribution, population dynamics and production of *Calanus finmarchicus* (Crustacea: Copepoda). Mar. Biol., 60: 47-56.

Wood, C.C., Ketchen, K.S. and Beamish, R.J., 1979. Population dynamics of spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Bd. Can. Fish, 36: 647-656.

Wood, J.B. and O'Dor, R.K., 2000. Do larger cephalopods live longer? Effects of temperature.

Yang, J., 1982. An estimate of fish biomass in the North Sea. J. Cons. Int. Explor. Mer, 40: 161-172.

Young, I.A.G., Pierce, G.J., Daly, H.I., Santos, M.B., Key, L.N., Bailey, N., Robin, J.-P., Bishop, A.J., Stowasser, G., Nyegaard, M., Cho, S.K., Rasero, M. and Pereira, J.M.F., 2004. Application of depletion methods to estimate stock size in the squid *Loligo forbesi* in Scottish waters (UK). Fish. Res., 69, 211-227.

Zühlke, R., Cotter, J., Piet, G., do Boois, I., Krönke, I., Hinz, H., Jarre-Teichmann, A., Prince, P., Alvsvåg, J., 2001. Monitoring Biodiversity of Epibenthos and Demersal Fish in the North Sea and Skagerrak. EC Project 98/021. Report of the European Commission.

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Ifremer: Cod, haddock, dab, flounder, herring, lemon sole, sole, long Rough Dab, plaice, megrim, red Mullet, dogfish, thornback ray, witch, whiting.

Martin Lilley: Gannets flying

Michaela Schratzberger: Meiofauna

Jim Ellis: Spotted Ray, Skate

Fishery Group: www.fisherygroup.lt: Blue whiting, catfish

Appendix 1. Ecopath with Ecosim formulation

ECOPATH - mass-balance ecosystem model

Ecopath is based on a set of simultaneous linear equations (one for each group i in the system (Christensen and Pauly 1995). The master equation simply states that at equilibrium, for all i: Production by (i) utilized within the system - catches of (i) - consumption of (i) by its predators – net migration – biomass change = 0

This can also be put as:

$$0 = B_i \cdot (P/B)_i \cdot EE_i - F_i \cdot B_i - M_0 B_i - \sum_{j=1}^{k} Q_{ij} - NM_i - BA_i \qquad (1)$$

where; B_i is the biomass of i during the period in question; P/B_i the production to biomass rate of i, equal to the total mortality rate (Z) under the assumption of equilibrium (Allen, 1971); EE is the ecotrophic efficiency, ie, the fraction of the production ($P = B_i \cdot P/B_i$) that is consumed within the system; F is the fishing mortality on i; M_0 is the mortality rate not accounted for by consumption within the system; Q_{ij} is the amount of i consumed by j, NM_i is net migration and BA_i is biomass accumulation.

Groups are linked through predators consuming prey, where *Consumption = production +un-assimilated food + respiration.* (2) The implication of these two relationships is that the system or model is mass-balanced, ie, mass is 'conserved', or accounted for. This principle provides rigorous framework - formalized by a system of linear equations, through which the biomasses of different consumer groups within an ecosystem can be estimated, along with the trophic fluxes among them (Christensen and Pauly, 1995).

The main input parameters required as part of the model are biomass, relative production (P/B), consumption: biomass ratio (Q/B) and ecotrophic efficiency (EE) of all the groups; if one of the parameters is unknown for a group, then the model can estimate it by solving the set of simultaneous equations. Additionally, catches, assimilation, migration and biomass accumulation rates, as well as diet composition for all groups are required as inputs. Other inputs include discards and economic information on the fishing fleets. The "detritus" groups are formed as a model output from the "flows to detritus" of all living groups, consisting of the non-assimilated fraction of the food and the losses due to "other mortality".

The result is a food web model of the ecosystem in which the sources of mortality and energy flows are quantified.

ECOSIM - dynamic mass-balance approach for ecosystem simulation

Ecosim is a dynamic trophic model structured from the mass-balance assessment carried with Ecopath. In Ecosim, the system of linear equations of Ecopath is re-expressed as differential equations suitable for simulating the effects of varying fishing mortality and changes in primary production on the biomass of each group in the system. The model provides dynamic biomass predictions of each group as affected directly by fishing and predation, changes in available food, and indirectly by fishing or predation on other groups with which a group interacts (Walters *et al.*, 1997, Christensen *et al.*, 2000). Constructing a dynamic model from the mass-balance equations involves two important changes: a) providing a functional relationship to predict changes in P/B with biomass and consumption; and b) providing a functional relationship to predict how the consumption will change with changes in the biomasses of preys and predators. Generalizing for both equilibrium and non equilibrium situations in Ecosim, the Ecopath master equation is re-expressed (Walters *et al.*, 1997):

$$\frac{dB_i}{dt} = f(B_i) - M.B_i - F_i.B_i - \sum_{j=1}^{n} c_{ij}(B_i.B_j) \qquad (2)$$

where $f(B_i)$ is a function of B_i if (i) is a primary producer (a simple saturating production relationship is used) or $f(B_i) = g_i \sum C_{ji}(B_i, B_j)$ if (i) is a consumer, where g_i is the net growth efficiency, and $C_{ij}(B_i, B_j)$ is the function used to predict consumption rates from B_i to B_j. In its simplest form, Ecosim uses a function for C_{ij} derived from assuming possible spatial/behavioral limitations in predation rates:

$$C_{ij} = \frac{v_{ij} a_{ij} B_i B_j}{v_{ij} + v'_{ij} + a_{ij} B_j} \qquad (3)$$

where:

C_{ij} is the trophic flow, biomass per time, between prey (i) and predator (j) pools;

B_i and B_j are the biomasses of prey and predators, respectively;

a_{ij} is the rate of effective search for prey i by predator j; and

v_{ij} and v'_{ij} are prey vulnerability parameters, with default setting $v_{ij} = v'_{ij}$.

Parameters v_{ij} and v'_{ij} (or prey vulnerabilities) represent the rate of exchange (flow control) of biomass between two prey behavioural states: a state vulnerable to predation and a state invulnerable to predation. The rationale of this representation is that at a given moment in time not all prey biomass is vulnerable to predators; predator-prey relationships in nature are often limited by behavioural and physical mechanisms, such as schooling behaviour and diel vertical migration patterns in clupeid fish, and spatial refuges used by many reef fish that considerably limit exposure to predation (Walters and Martell, 2004). The model is designed so that the user can specify the type of trophic control in the food web by hypothesizing the maximum consumption rate that a predator can exert on prey through by specifying indirectly the rate of exchange of biomass v_{ij} using the flow control (vulnerability) setting. For low predator biomass or high prey vulnerability (v_{ij}) the functional relationship approximates a mass-action flow, or Lotka-Volterra type of model $C_{ij} = aB_iB_j$, implying a strong 'top-down' effect. High vulnerability (over 28) means that if a predator biomass is doubled, predation mortality exerted on it prey will be doubled i.e. totally top-down (Christensen *et al.*, 2005). For high predator biomass or low prey vulnerabilities (close to one) the functional relationship approaches a donor-controlled (bottom-up) flow rate ($C_{ij} = v_{ij}B_i$), so v_{ij} can be interpreted as the maximum possible instantaneous mortality rate that a predator can cause on a prey (see Walters *et al.*, 1997). The relationship between the vulnerability parameter value and 'Vulnerability' in the model is largely a theoretical concept, and direct estimates of this parameter are not available from the literature. Model simulations are particularly sensitive to this parameter. It is currently the convention that this parameter is adjusted in fitting model predictions to time series observations, and/ or adjusted so as to allow groups that are far from carrying capacity, the scope to increase consumption and recover to former biomass levels. The default value of 2 indicates 'mixed control'.

In addition to the prey vulnerabilities, Ecosim requires a set of input parameters that will define linkages between split pool pairs (juvenile and adult stages). During simulations, a Deriso-Schnute delay-difference model is used to keep account of the numbers that recruit from the juvenile to the adult stages and the number at age/ size in the adult group. Recruitment to the adult group is a function of the adult numbers, biomass and food consumption. Recent developments now allow for more explicit representation of life history stages through the inclusion of multi-stanza groups whose parameterisation is specified in the Ecopath model.

Other additional parameters are included to specify trophic mediations, time forcing functions, and the representation of hypotheses about changes in growth rates, and how foraging time and time at risk to predation changes with feeding opportunities (see Christensen *et al.*, 2000 for full descriptions). The effects of these additional parameters are implemented through modification of the basic consumption equation (see Christensen *et al*. 2000).

ECOSPACE – spatial dynamic ecosystem simulations

Ecospace is a spatially explicit model for policy evaluation that relies on the Ecopath mass-balance approach for most of its parameterization. Ecospace requires additional parameters representing: i) movement rates of organisms between spatial grid cells; ii) habitat preferences for each of the functional groups; and iii) the spatial dynamics of fishing mortality, such as associations between fishing gears and habitats, marine protected areas, and the relative cost/attractiveness of fishing in each spatial cell by each fishing gear (Walters *et al.*, 1999).

Ecospace represents biomass dynamic patterns over two-dimensional space grid (of cells) as well as time through incorporating co-ordinates *u* and *v* to the Ecosim equation (1) Foraging, avoidance of predation, and intrinsic dispersal rates linked to specified habitats drive biomass movements through the cells using a Eulerian approach. This approach treats movement as 'flows' of organisms among fixed spatial reference cells, without retaining information about the history of the organisms present at any point at any moment. Instantaneous emigration rates for any organism are calculated from simple input information on average movement that includes dispersal, advection and diffusion speeds Vi (mean distance moved per time for organism type i). For trophic interaction, harvesting and movement calculations, biomass densities are treated as homogeneous within each cell (Walters *et al.*, 1998).

Ecospace represents spatial distribution of fishing mortality using a relatively simple "gravity model" (Caddy, 1975; Hilborn and Walters, 1987); a model in which the fisheries (specific gears) act to maximize their catches (profits) depending on the attractiveness and the costs of the access to the cells (fishing grounds). Each biomass pool in each cell (i) is subject to a total fishing mortality rate equal to:

$$F_{ic} = \Sigma_k F_{kc}\, q_{ki} \qquad (4)$$

where q_{ki} is catchability of type i organism by gear k, F_{kc} is the total mortality by gear k in cell c, by all gears together (Σ_k).

The program interface allows the user to load in or 'sketch' base-maps showing topographic features (shorelines, islands, areas of high primary productivity habitat types and preferences), gear type associations, prices and cost fields of diverse fisheries and, policy options such as location, size or shape of MPAs. The resultant biomass patterns predicted over time are shown as color-coded density maps but also as relative biomass values to the original started biomass. Validation of the equilibrium distribution maps is achieved through visual or statistical comparison with maps of observed distributions recorded from routine surveys. This is an ongoing area of development.

Ecospace can generate decadal time scale predictions of spatial biomass patterns for several hundred grid cells, for biomass/species pools ranging from phytoplankton to marine mammals. It does not explicitly represent the full variety of physical transport and migratory processes that may be critical in the spatial organization of ecosystems, but all these mechanisms can be implicitly integrated into the food, refuge, and movement variables. This approach can provide some insights about the likely efficacy of alternative MPA policies in relation to questions, for example, about 'drainage' of large predators from such areas due to impacts on their prey within, and their dispersal out of an MPA, while accounting for the distribution of fishing effort on predators and prey.

Ecospace should be seen not as a tool for making detailed quantitative predictions, but rather as a 'policy screening' method for finding policy alternatives using indicators of the *direction* of predicted change (Walters *et al*. 1988).

Appendix 2. Conversion factors

Conversion	Ratio	Source
Phytoplankton		
Chlorophyll a to Carbon (Phytoplankton)	1 to 44.9	Durban & Durban 1998
Carbon to dry organic matter (Phytoplankton)	1 to 5.4	Durban & Durban 1998
Carbon (g) to Wet weight (g) (Phytoplankton)	1 to 10	based on 0.1gC=0.2g dry weight = 1 g wet weight (Mathews and Heimdal 1980- from Mackinson 1995).
Protozoa and bacteria		
Wet Mass to Organic carbon (protozoa)	1 to 0.165	DeLaca 1985
Ug/L to g/m2 (Bacteria)	1 to 0.015	Billen et al. 1991
Numbers to biomass (Bacteria)	0.22*10^{-12} gC.um-3	van Duyl et al. 1990 - biovolume (after Bratbak and Dundas 1984)
Numbers to biomass (Nanoflagellates)	0.20*10^{-12} gC.um^{-3}	an intermediate value of Fenchel 1982b and Børsheim and Bratbak 1987)
Meiofauna		
Carbon to dry organic matter (Meiobenthos)	1 to 2.5	Warwick (Plymouth marine laboratory; pers. comm. 12 June 2000)
WM -> DM	1 to 0.25	De Bovee 1993 (in Brey 2001)
nlVol -> µgWM	1 to 1.13	Wieser 1960 (in Brey 2001)
WM -> DM	1 to 0.25	De Bovee 1993 (in Brey 2001)
DM -> Corg	1to 0.463	De Bovee 1993, Sikora et al. 1977 (sensu Heip et al. 1985) (in Brey 2001)
WM -> Corg	1 to 0.116	De Bovee 1993 (in Brey 2001)
AFDM -> Corg	1 to 0.42	Sikora et al. 1977 (sensu Heip et al. 1985) (in Brey 2001)
Zooplankton		
Wet mass to Dry Mass (Copepods)	1 to 0.186	Brey 2001
Dry Mass to Wet Mass (Copepods)	1 to 0.451	Brey 2001
Wet mass to Dry Mass (Euphasiids)	1 to 0.225	Brey 2001
General		
Chlorophyll a to Carbon	1 to 25	Parsons et al. 1977 in Browder 1993
Carbon to dry organic matter	1 to 2.5	Parsons et al. 1977 in Browder 1993
Dry to wet organic matter	1 to 5	Parsons et al. 1977 in Browder 1993

Conversion	Ratio	Source
Benthos		
Carbon to dry organic matter (Benthic macrofauna)	1 to 10	Rowe and Menzel (1971) ("5 to 15 times")
Dry to wet weight (Benthic primary producers)	1 to 7.7	Arreguín-Sánchez et al. 1993
Dry to wet weight (Benthic macrofauna)	1 to 7.5	Rowe and Menzel (1971) ("5 to 10 times")
Carbon to dry organic matter (Crustaceans)	1 to 2.5	Bougis 1979 in Cushing 1984
Dry to wet weight (Shrimp)	1 to 7.7	Bougis 1979 in Cushing 1984
Carbon to wet weight (Shrimp)	1 to 19.2	Cushing 1984
Wet weight to dry weight (Polychaetes)	15.50%	Eleftheriou and Basford. 1989
Wet weight to dry weight (Crustaceans)	22.50%	Eleftheriou and Basford. 1989
Wet weight to dry weight (Echinoderms)	8%	Eleftheriou and Basford. 1989
Wet weight to dry weight (Molluscs)	8.50%	Eleftheriou and Basford. 1989
Wet weight to dry weight (Miscellaneuos)	15.50%	Eleftheriou and Basford. 1989

Units

Area
1cm2 = 100mm2
1m2 = 10000cm2
1km2 = 1000000m2

Volume
1cm3 =1000mm3
1m3 = 1000000cm3
1km3 = 1000000000m3
1 litre = 1000cm3
1000cm3 = 100cm2 x 10
1 litre (1000cm3)/10 = 100cm2

Weight
1mg=0.001g
1g=1000000ug
1g=1000mg

North Sea
Area = 570,000 km2
Mean depth = 90m

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