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The Mackinson-Daskalov North Sea EcoSpace model as a simulation tool for spatial planning scenarios

T. van Kooten & C. Klok

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The Netherlands Environmental Assessment Agency (PBL) developed several biodiversity models for the terrestrial environment to support policy making and evaluation. For the marine environment currently such modelling instruments are lacking. In 2009 an overview of modelling instruments was developed for marine biodiversity of its components. The objective of the current report is one of these modelling instruments, i.e. the Mackinson-Daskalov North Sea EcoSpace model. This model has been analysed in detail to assess its potential applicability for questions relevant for PBL. These questions are: (i) Can the model be used to assess the impact of primary production scenarios, (ii) can the model be used to develop output at a higher spatial resolution and (iii) can it generate output for biodiversity criteria.

Keywords: Ecosystem model, Fishery management, EcoPath with Ecosim, Mackinson-Daskalov North Sea model, biodiversity indicators

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Preface

The aim of the project reported in this document was to analyze the potential applicability of the EcoPath with Ecosim (EwE) model developed for the North Sea; the Mackinson and Daskalov North Sea (MDNS) model for specific questions raised by The Netherlands Environmental Assessment Agency (PBL). These questions were: (i) can the model be used to assess the impact of primary production scenarios, (ii) can the model be used to develop output at a higher spatial resolution and (iii) can it generate output for biodiversity criteria.

To study the potential applicability of the model we have chosen extreme scenarios, in the sense that they are expected to have substantial impact on the model ecosystem. This report therefore contains model simulations where fisheries is either completely banned in the North Sea, or where certain areas in the North Sea are closed to all or certain types of fishing activity. **The scenarios or the results in this report are in no way policy recommendations and cannot be used as arguments in a discussion about the merits or flaws of the design of closed areas.**

The conclusions from this report are of a technical nature, pertaining to the suitability of the model, not to the actual biological predictions obtained. Policy explorations on the basis of predictions of this model would have to be embedded in a much broader framework where the results are more rigorously tested against available data, scrutinized by experts in relevant ecological (sub)systems and stakeholders such as fishermen and NGOs.

The research leading up to this report has been kindly guided by Rick Wortelboer and Jaap Wiertz at the Netherlands Environmental Assessment Agency (PBL), and Rien Reijnen, Harm Houweling and Rogier Pouwels at WOT Nature & the Environment.

We would like to thank Steve Mackinson for making available the North Sea model and software and for providing valuable guidance during the entire process leading to this report.

Tobias van Kooten
Chris Klok

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Summary

The Netherlands Environmental Assessment Agency (PBL) seeks an instrument that can be used to explore the impact of spatially explicit changes in human use (e.g. fisheries, implementation of Marine Protected areas) or its consequences (e.g. eutrophication) on the biodiversity of the North Sea. The Mackinson-Daskalov North Sea (MDNS) Eco-space model has been selected by PBL as such an instrument with high potential. This model was developed by researchers at the Centre for Environment, Fisheries & Aquaculture Science (CEFAS) to explore the impact of changes in fishery especially on commercial fish species and some mammal species. The current model delivers spatial output at International ICES (Council for the Exploration of the Sea) rectangle scale.

In this report the MDNS model is analyzed on its potential applicability for specific questions raised by PBL regarding the use of the model to generate output at a finer spatial resolution, the opportunities to run eutrophication scenarios and the opportunities to generate output for biodiversity indicators selected by PBL.

Although in technical terms the model is able to generate output at a finer spatial scale this output is difficult to interpret on its ecological relevance since apart from more theoretical issues concerning the foraging arena concept, the model output cannot easily be validated since for most species groups used in the model information on biomass is not available at a finer scale of resolution than ICES quadrants. The model proved very useful for applications for which it is developed, to analyze the impact of fishery scenarios on commercial fish species and marine mammals. The model also showed representative biomass distributions for tested species under the reference scenario (business as usual) which further strengthens the conclusion that the model is a good instrument to assess the impact of fishery scenarios including absence of fishing in Marine Protected Areas.

The current model does not allow spatial analysis of primary production scenarios since in the current model EcoPath EcoSim calculations do not carry over to EcoSpace. Spatially specific output of primary production scenarios can be implemented in the MDNS model by adding nutrients as a specific functional group. Such a change results in a new model that must go through a round of calibration before it can be used. Future development of the MDNS model may allow such an extension. Given the above we restricted the analysis of the primary production scenarios on their consequences as calculated by EcoSim. These (non-spatial) results indicate that almost all groups in the model increase (decrease) in biomass with an increase (decrease) in nutrient load. There is no clear difference in response between groups.

It seems feasible to generate output with the MDNS model for biodiversity indicators (especially for fish and marine mammal species). However, it should be noted that the model only takes into account food web and fisheries effects. For many species, particularly non-fish species, abundance is not only set by the availability of food, but also the presence of other drivers such as temperature, ocean acidification, underwater noise, presence of ships, water transparency or pollution, the effects of which cannot be studied with this model framework.

1 Introduction

1.1 PBL questions and aim of this report

Biodiversity of the North Sea is currently under strong pressure resulting from expansion and intensification of traditional use e.g. shipping and fishing, but this also increasingly applies to less traditional forms of use such as tourism and offshore wind energy production.

Especially offshore wind energy will strongly develop in the coming years. In 2009 the Dutch cabinet agreed on a plan to realize a total of 6000 MW of wind energy on the Dutch Continental Shelf by 2020 (2009 National Water Plan draft, 2009-2019 North Sea Policy Memo) to reach the international objective of 20% sustainable energy by 2020. The planned 6000 MW of offshore wind energy can cover 10 to 15% of the Dutch energy needs sustainably. In January 2011 5% of the proposed 6000 MW is realized in two wind parks near the Dutch coast (Egmond aan Zee coast and Prinses Amalia), and another 15% is under construction. Spatial allocation of offshore wind parks is currently therefore an important issue, especially since they may be planned near to nature protection sites (Natura 2000) and impact on nature goals set for these sites.

Although various studies have been carried out on the impact of offshore windmill parks on ecological objectives (the most well studied being Horns Rev); still little is known on the potential impact of offshore windmill parks, partly also because basic ecological data on species abundance and distribution is missing. With the implementation of the last 80% of capacity in offshore windmill parks an extensive monitoring plan has been developed (Boon *et al.*, 2010) aiming at gaining more insight in this issue.

The Netherlands Environmental Assessment Agency (PBL) is a governmental institute that supports national and international policy makers by analyzing the environmental impact of policies and of trends in society. PBL provides independent integrated assessments on topics such as sustainable development, energy and climate change, biodiversity, transport, land use and air quality. The results of these assessments are available to the public. PBL functions as an interface between science and policy. To assess the impact of policies and societal development on biodiversity targets the Netherlands Environmental Assessment Agency (PBL) seeks to develop modeling instruments. Compared to terrestrial biodiversity, for which modeling instruments have been developed by PBL over the last decades, the impact of policies and societal development on marine biodiversity is difficult to estimate since modeling instruments for the marine environment are currently lacking.

The terrestrial modeling instruments used by PBL are based on local abiotic conditions that vary in space and that determine the habitats for species. Human activities strongly influence the spatial distribution of these habitats. Therefore, it is not surprising that in the models applied in the terrestrial environment the spatial constitution of habitat determines the viability of species (applying metapopulation theory Hanski, 1999). Given this importance of spatial distribution of habitat on the viability of species, spatial planning can be used to influence the last. Moreover, spatial planning has proven a very strong policy instrument.

In the marine environment, however, correlations between the abiotic environment and species occurrence are less clear-cut. In the sea living space for most organisms has three dimensions and particularly mobile marine species cannot so easily be pinpointed to specific two dimensional locations which can be represented on maps. Of course, such species are also limited by certain physical constraints (temperature, oxygen level, etc.). However, within these constraints aggregations of mobile or planktonic marine species often occur in ephemeral patches in locations where their food has high productivity. Such a patch disappears as soon as the food runs out.

Moreover, large parts of the North Sea have a sandy or silt bottom with relative few areas where hard substrate prevails, which results in larger areas with similar benthic communities, and on a two dimensional map similar habitats. The pelagic food chain of the North Sea is fuelled by phytoplankton of which the spatial position is to a major extent determined by currents and nutrient levels that can only to a certain extend be pinpointed to specific locations. Modeling the state of biodiversity in the North Sea therefore cannot be achieved by the same instruments as developed for the terrestrial area.

As a potential valuable model to describe changes in biodiversity in the North Sea PBL has selected the food web model instrument EcoPath with EcoSim (EwE) (www.EcoPath.org). More specifically the ecospace application for the North Sea developed by Mackinson and Daskalov (2008). The Mackinson and Daskalov North Sea (MDNS) model has been developed to assess the impact of changes in fisheries on the food web of the North Sea (among others commercial fish species and marine mammals). The current version of this model can deliver results of fishery scenarios on a resolution of ICES rectangles.

PBL would like to use this model to estimate the influence of scenarios on fishery, primary production (eutrophication) and the spatial allocation of marine protected areas and offshore wind parks on the biodiversity of the North Sea. Furthermore since the scale of operation of offshore wind parks is more at 10 x 10 km^2 scale than at ICES rectangle scale PBL needs instruments that can be used to assess the impacts at a higher resolution than ICES rectangles the MDNS model is currently providing.

The aim of this report therefore was to explore the MDNS model and assess the prospects to use this model to assess both fishery and primary production scenarios, develop model results that can be used to analyze the results of scenarios on biodiversity indicators and to seek the opportunities of application of the model output at a higher spatial resolution (e.g. 10 x 10 km^2).

1.2 Background on EcoSim (EwE)

The development of EcoPath with EcoSim (EwE) was started by Jeffrey Polovina in 1984 who used an EcoPath version to estimate the impact of fishery on non-target species in a coral reef system of the French Frigate Shoals (Polovina, 1984). This initiative was further developed and extended by Villy Christensen, Carl Walters, Daniel Pauly, and other fisheries scientists largely through case studies, where specific case based issues have resulted in addition of various capabilities to the software. The EcoPath II model appeared in the early 1990s (Christensen & Pauly, 1992), followed by the time-dynamic EcoSim model (Walters *et al.*, 1997, 2000), and the spatial-dynamic EcoSpace model (Walters *et al.*, 1999).

EwE has been developed to evaluate policy questions (especially in the field of fisheries) that cannot be answered by single species models. It can be used to assess the implications of direct and indirect ecological effects among species for fisheries management. For recent applications of comparison and optimization of policy scenarios see Ainsworth *et al.* (2008) and for evaluation of both ecological and socio-economical scenarios see Cheung & Sunauka (2008).

EwE provides user friendly tools for policy comparison. Policy scenarios in fishing policies, e.g. fishing rates can be 'sketched' over time (catches, economic performance indicators) which facilitates the comparison of policies. In EcoSim the user can define optimization routines on: Maximize fisheries rent; Maximize social benefits; Maximize mandated rebuilding of species; Maximize ecosystem structure or 'health', and can also develop a 'multi-criterion objective', represented as a weighted sum of these four objectives. By assigning alternative weights to these objectives tradeoff with one another in terms of policy choice can be visualized (www.EcoPath.org). It has been stated that EcoSpace (in version 6 of the EwE) has matured to the level where it can be seriously considered as a decision-support tool for use in ecosystem-based management, or multiple-objective marine spatial planning (Christensen *et al.*, 2009). A spatial planning optimization extension to EwE, similar to Marxan, has also been published recently (Christensen *et al.*, 2009) but this functionality is still in development and beyond the initial publication, no successful application is known (S. Mackinson, CEFAS-Lowestoft, UK, *personal communication)*.

Constructing an EwE model implies bringing together data, expertise and knowledge of different stakeholders such as governments, national and international research organizations, public interest groups and private sectors. Already the process of constructing an EcoPath model provides a valuable product in itself through explicit synthesis of work from many researchers. Such a synthesis can result in the creation of common goals between collaborating parties and the identification of data gaps that previously were hidden. In this way EwE creates a forum in which complex policy goals can be discussed given their implications at the ecosystem level. The EwE framework therefore strongly facilitates the interaction and cooperation between stakeholders and enables these interest groups to take ownership of the model that is derived in cooperation. This may result in policy choices that are supported by stakeholders and therefore have higher potential for successful implementation.

EwE has three main components:

- EcoPath – a static, mass-balanced snapshot of the system;
- EcoSim – a time dynamic simulation module for policy exploration;
- EcoSpace – a spatial and temporal dynamic module primarily designed for exploring impact and placement of protected areas.

In essence the EcoPath is a mass balance food web model in which nodes in the food web can be groups (e.g. feeding guilds) species or stages of species (e.g. juveniles and adults). For each node in the food web production and consumption are calculated:

- Production = catch + predation + net migration + biomass accumulation + other mortality;
- Consumption = production + respiration + unassimilated food.

EcoPath can work with energy - as well as with nutrient-related currencies (whereas EcoSim and EcoSpace only work with energy related currencies). If a nutrient based currency is used in EcoPath, the respiration term is excluded from the above equation, and the unassimilated food term is estimated as the difference between consumption and production (www.EcoPath.org).

Given the complexity of ecosystems and a limited amount of available input information EwE strives more to catch the basic features of these ecosystems than to mirror complex real ecosystems. Real ecosystems are obviously more complicated than the mass-balance fluxes of biomass in EcoPath, and have dynamics far more complex than represented in EcoSim.

Criticism on EwE is generally directed at its shortcomings in including detailed dynamics necessary for realistic single species model analysis. However, the objective of EwE is not to substitute single species models but to supply policy guidance to questions that single species models cannot provide. Single species models are still the dominant tools used worldwide to give scientific advice on the management of commercially valuable stocks (Plaganyi, 2007), and given their higher detail in relevant processes they are potentially better equipped to provide answers at the species level than ecosystem models. Therefore the developers of EwE advocate an iterative process where information is passed between single-species analysis and EwE (www.EcoPath.org).

Other criticism on EwE has been directed at handling uncertainty of data inputs and model structure (Plagányi & Butterworth, 2004), and the foraging arena concept in EcoSim (IWC 2004). The foraging arena concept (Walters *et al.*, 1997; Walters & Kitchell, 2001; Walters & Martell, 2004) is an original functional response representation that is supported to some extent by studies of fish populations. Its application results in more 'natural' predator prey behavior (it damps the large amplitude oscillations frequently predicted by multi-species models that apply a constant ration model). The basic idea of EwE's foraging arena theory is that marine species have limited access to prey resources because of spatial habitat-choice behaviors aimed at moderating their predation risk (Walters & Martell, 2004).

Moreover, satiation is rare in nature: “predators with full stomachs are not a common field observation” (Walters & Kitchell, 2001), and handling time effects are trivial in the field because if animals increased their rate of effective search to the extent where handling time became an issue, they would be exposed to additional risk of predation hence they avoid doing this (Walters *et al.*, 2000).

Although the user friendly software may suggest otherwise, setting up and EwE framework for a specific application remains a dedicated task. Shortcomings of EwE applications are in general caused by user misuse (or insufficient use) rather than by failure in model structure (www.EcoPath.org). Such shortcomings result from uncritical use of default parameter setting or applying the same constant vulnerability values (which regulate the extent to which oscillations are damped by the foraging arena concept) for all species. This may lead to over compensatory stock and recruitment relationships and thus incorrect conclusions. This implicates that despite the user friendly software, setting up an EwE application is not a modelers task alone but should be an interaction between modelers and ecologists of the different species /guild groups in the application. As agued above this interaction between different 'stakeholders' is also one of the great values of EwE.

Obviously as with all multi-species approaches, the major limitation in applying the EwE approach lies in the quality and quantity of available data.

2 Description of EwE as used in Mackinson-Daskalov North Sea model (v5.1)

2.1 Model scope, scale, structure and important assumptions

Below we describe briefly the basis of the EcoPath-EcoSim-EcoSpace approach to ecosystem modeling, with special reference to the MDNS model under study. We have no intention to write a complete documentation of either the approach or the specific model. The former can be found in the user guide which accompanies the EwE software (www.EcoPath.org), while the latter is documented in Mackinson & Daskalov (2008).

2.1.1 EcoPath

> *"One gathers all possible information about the components of an ecosystem, of their exploitation and interaction and passes them through the 'mass balance filter' of EcoPath. The result is a possible picture of the energetic flows, the biomasses and their utilization. The more information used in the process and the more reliable the information, the more constrained and realistic the outcome will be."*
>
> (Christensen *et al.*, 2005)

An EcoPath model of an ecosystem is, in essence, an internally consistent snapshot of an ecosystem representation simplified into an arbitrary number of 'groups'. The result of calculating an EcoPath model gives a quantitative picture of biomass abundances of all groups and the rates at which biomass is moving among groups. Internal consistency comes about because EcoPath relies on a balance approach, where biomass loss from one compartment necessarily ends up in another. The balance equation which is at the heart of the EcoPath approach is:

$$P_i = Y_i + B_i \cdot M_i + E_i + BA_i + P_i \cdot (1 - EE_i)$$

The subscript i indicates a specific functional group in the food web, where P is its productivity, Y the total fishery catch rate, M its total predation rate exerted by all predators on the group, B is its biomass, E its net migration rate (emigration-immigration), BA_i its biomass accumulation rate (which we disregard in the rest of this report, since it is unused in the studied model). EE is the ecotrophic efficiency, which is the fraction of production that is actual biomass, and $P \cdot (1-EE)$ is the mortality from other sources. The predation mortality term can be written more explicitly as:

$$B_i \cdot M_i = \sum_{j=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji}$$

Each predator consumes group i according to its biomass B_j times its consumption per unit biomass $(Q/B)_j$, multiplied by the fraction of prey type i in its diet, DC_{ji}. The total predation mortality rate on group i is then obtained by summing this quantity over all n groups in the ecosystem description. It is further assumed that production P equals biomass B times the production/biomass ratio (P/B).

While in general most values of *EE* are close to 1, meaning that most produced biomass from that stage is transferred up the food chain by predation, apex predators form an exception. They have no predators, and hence the bulk of their mortality is in the form of 'other mortality', which redirects biomass down the food web, into the detritus groups. Alternatively, they can be the target (or bycatch) of fishing.

For each group in the model, the user needs to supply EcoPath with estimates of at least 3 of the following variables:
- Biomass;
- Production/biomass;
- Consumption/biomass;
- Ecotrophic efficiency.

When not all four are provided, the following additional data must be supplied for EcoPath to close the mass balance equation:
- Catch data (landing and discard data);
- Net migration rate;
- Assimilation rate;
- Diet composition.

When all this data is provided, EcoPath solves the resulting set of linear equations to obtain estimates of the missing values. When too few variables are supplied (the model is under-determined), there are certain routines in the program that attempt to estimate sufficiently many terms such that the number of missing variables equals the number of equations, and the system can be solved. A model can also be over-determined, meaning that there are more equations than unknown variables. If the specified values are not consistent, no solution can be reached. The EcoPath software contains an algorithm that calculates least-squares estimates of consistent values and uses those to solve the system of equations.

The MDNS model under study consists of 68 groups, and the data come from a wide range of published sources, both in the peer-reviewed and grey literature (Mackinson & Daskalov 2008). For the majority of groups, good estimates of ecotrophic efficiency *EE* could not be obtained, and hence the value of this variable is left for EcoPath to solve. For a few groups, *EE* is estimated so that biomass can be solved for. These are mostly groups that consist of a large number of relatively rare species, for which it is difficult to obtain reliable biomass estimates.

In a second step, after the mass-balance described above has been closed for the whole system, an energy balance is formulated for each group in the model. This energy balance states that consumption equals the sum of production, respiration and unassimilated food. Again, any three of these quantities must be given as input, so that the 4th can be estimated.

Fishing fleets are handled in a similar way as biological groups in the model, but without an energy budget. They act as consumers, exerting mortality on their target species and discards. The mortalities are calculated from catch composition data, not unlike the diet composition data used to calculate feeding preferences of consumers. The target species are removed from the system, while the discards are a group of their own, where they are fed upon by for example seabirds, but also fuel the lower trophic levels as they are decomposed.

It is important to realize that while EcoPath relies on mass balance to construct the food web and interaction strengths, it does not assume 'equilibrium' in the ecological sense. The concept of time is not part of the EcoPath approach, so it cannot be used to predict any time trends. EcoSim (see next section) is a way to use the EcoPath model to parameterize a system of differential equations for time evolution of the system.

Lastly, we would like to stress that setting up an EcoPath model may sound like filling in a few forms and pushing a button, but this is not the case. In order to arrive at a balanced and plausible model, it is necessary to iteratively run the model and tune the input parameters based on the results. This process requires expert knowledge of the system under study and its outcome is dependent on the objectives of the modeling study.

2.1.2 EcoSim

Here we give a brief conceptual overview of the dynamic ecosystem simulation program 'EcoSim'. For a more in depth explanation, we refer the reader to the EwE documentation (www.EcoPath.org). We will not present any technical details, except when these are relevant to the objectives of this report.

General

EcoSim combines information from an EcoPath food web with additional information or assumptions pertaining to the functional form of feeding relationships, to parameterize a system of differential equations which can be used to study the evolution of the described system over time. Such a system can then be forced using time trends in for example fisheries effort data or nutrient input, to study the ecosystem response to such drivers. The EcoSim program also has a built-in routine which can fit the outcome of a simulation to independent time series data of groups, yielding a sum of squares value which gives a measure of how well the two fit. The data used in the fitting procedure can be time series of biomass, fishing mortality or catch per unit effort, and should all be expressed as relative to the EcoPath-fitted value.

At the heart of EcoSim is the differential equation which governs the rate of change of the biomass (B) in each model group i over time:

$$\frac{dB_i}{dt} = g_i \sum_j c_{ji}(B_i, B_j) - \sum_j c_{ij}(B_i, B_j) + I_i - (M_i + F_i + e_i) \cdot B_i$$

Where g_i is the net growth efficiency, which is the production/consumption ratio and can be derived from the EcoPath model. Multiplied by the sum of group *i*'s consumption from all other groups *j* (c_{ji}), this yields the rate of biomass increase by feeding. The second summation is the total biomass eaten from group *i* by all other groups *j* (c_{ij}) combined, the predation mortality term. *I* is the immigration rate, which is assumed independent of biomass abundance. *M*, *F* and *e* are the natural mortality, fishing mortality and emigration rates, respectively.

Primary producers form a special case in this respect, because they do not consume other groups in the model. Instead of the first term, primary producers have a saturating growth rate:

$$\frac{r_i B_i}{1 + h_i B_i}$$

where, r_i is the maximum production/biomass ratio when *B* approaches 0, and r_i/h_i is the maximum production at high B_i. In the EwE software, it is possible to apply a user-defined forcing function to the parameter r_i. Primary production and nutrient limitation is explained in more detail below.

A key aspect of changing from EcoPath to EcoSim is to go from the static diet composition Q to a functional relationship $c_{ij}(B_i,B_j)$, between consumption and the biomass of predator and prey. In EcoSim this is done using the foraging arena concept, which divides the prey biomass into a fraction which is vulnerable to predation, and an invulnerable fraction. The predator 'sees' only the vulnerable fraction. By assuming that the rate of exchange between the two states works on a relatively short time scale, the functional relationships for consumption can be derived (Christensen *et al.*, 2008) as:

$$c_{ij}(B_i, B_j) = \frac{a_{ij} \cdot v_{ij} \cdot S_{ij} \cdot T_i \cdot T_j \cdot B_i \cdot B_j / D_j}{v_{ij} + v_{ij} \cdot T_i + a_{ij} S_{ij} T_j B_j / D_j}$$

In this functional form, the following parameters are distinguished:

a_{ii}	Search rate of predator j for prey i
v_{ii}	Rate at which prey i becomes (in)vulnerable to predator j
S_{ii}	User-defined search rate forcing factor
T_i	Prey relative feeding time
T_i	Predator relative feeding time
D_i	Strength of predator handling time limitation

In the absence of forcing, and when v approaches 1, the function is similar to a type II functional response, and the consumption levels off at high predator abundance. When v is (much) larger than 1, the satiation occurs only at irrelevantly high values of B_j, meaning that a doubling in the biomass of predator j leads to an approximate doubling in predation mortality by j on prey i. S_{ij} is a user-defined forcing function which can be either long-term or seasonal.

These vulnerabilities can be used in an EcoSim model to tune the extent to which a group is controlled 'bottom up', that is, by the availability of its food, or 'top down', by the mortality imposed by its predators. A saturating functional response (low v) releases a group from top down control, as predation mortality becomes relatively independent of predator abundance, while a linear functional response (high v) imposes strong top-down control. The vulnerability parameters are among the most important parameters that users change to improve the agreement of the model's predictions with historical data. In the EwE user guide, the biological mechanisms behind the foraging arena approach are described as follows:

> *We know of at least four common mechanisms that can decrease the vulnerability parameters so as to create stabilizing and the appearance of 'ratio-dependent' or 'bottom-up' control of consumption rates:*
>
> 1. *Risk-sensitive prey behaviors: Prey may spend only a small proportion of their time in foraging arenas where they are subject to predation risk, otherwise taking refuge in schools, deep water, littoral refuge sites, etc.;*
> 2. *Risk-sensitive predator behaviors (the 'three to tango' argument): Especially if the predator is a small fish, it may severely restrict its own range relative to the range occupied by the prey, so that only a small proportion of the prey move or are mixed into the habitats used by it per unit time; in other words, its predators may drive it to behave in ways that make its own prey less vulnerable to it;*
> 3. *Size-dependent graduation effects: Typically a prey pool represents an aggregate of different prey sizes, and a predator can take only some limited range of sizes, limited vulnerability can represent a process of prey graduation into and out of the vulnerable size range due to growth. Size effects may of course be associated with distribution (predator-prey spatial overlap) shifts as well;*

4. *Passive, differential spatial depletion effects: Even if neither prey or predator shows active behaviors that create foraging arena patches, any physical or behavioral processes that create spatial variation in encounters between i and j will lead to local depletion of i in high risk areas and concentrations of i in partial predation 'refuges' represented by low risk areas. 'Flow' between low and high risk areas (vij) is then created by any processes that move organisms.*

> *These mechanisms are so ubiquitous that any reader with aquatic natural history experience might wonder why anyone would ever assume a mass-action, random encounter model (vulnerabilities = 100 in Vulnerabilities form) in the first place.*
> (Christensen *et al.*, 2005).

The effects of handling time as a limit to predation rate are given by the function:

$$D_j = \frac{h_j \cdot T_j}{1 + \sum_k a_{kj} B_k T_k}$$

Which is h_j, the predator handling time, multiplied by the prey mass encounter rate, to obtain the time spent handling prey.

A final adjustment to the consumption rates is made in EcoSim in the form of a foraging time-predation risk trade-off. Prey are assumed to change their time spent foraging according to:

$$T_{i,t} = T_{i,t-1}\left(1 - a + \frac{a \cdot c_{i,opt}}{c_{i,t} - 1}\right)$$

Where $T_{i,t}$ and $T_{i,t-1}$ are the time spent foraging in the current and previous time step, respectively. $c_{i,opt}$ is the feeding rate which optimizes feeding rate versus mortality risk, which is calculated internally by the program. $c_{i,t-1}$ is the consumption rate in the previous time step, while a is a user-defined rate which specifies how fast the optimum consumption rate is approached.

Although the actual intake of food depends on the search rate and the abundance of each potential prey group, it is worth noting that the diet composition data provided as part of from EcoPath to some extent restrict the diet of groups in EcoSim. If a predator-prey link between species *i* and *j* is not present in the EcoPath diet, this results in an estimate of zero for the search rate a_{ij} in EcoSim and hence such a link will never be established in EcoSim simulations. In other words, while quantitative changes in diet during an EcoSim or EcoSpace simulation are possible, qualitative changes (addition of new prey types) are not.

Primary productivity

Primary producers have in principle the same dynamics as other groups in an EcoSim/EcoSpace model. The only difference is that the input into the group by consumption is replaced by a primary production term. The production f depends on the biomass *B* of group *j* as:

$$f(B_j) = \frac{r_j B_j}{1 + h_j B_j}$$

The parameter *r* is the group's maximum rate of productivity, $(P/B)_{\max}$, which is reached at low biomass *B*. The parameter *h* is calculated as:

$$h_j = \frac{(r_j /(P/B)_E) - 1}{B_E}$$

Where $(P/B)_E$ and B_E are the EcoPath estimates of biomass and production per biomass.

The maximum rate of primary production r_j of group *j* depends on the availability of nutrients. During EcoPath initialization, the user is asked for an estimate of the ratio of the current productivity to maximum productivity. Using current productivity and current proportion of free nutrients, the maximum $r_{max,j}$ is calculated, which is reached when nutrient availability is very high. The parameter scales with the availability of free nutrients *Nf* according to a Michaelis-Menten relationship:

$$r_j = r_{\max,j} \frac{Nf}{(K_j + Nf)}.$$

The Michaelis constant K_j is set so that $PB_j = PB_{EcoPath,j}$ when *Nf* is at the initial concentration determined by $N_T - \sum_i n_i B_i$ when all B_i are at EcoPath base values.

Nf is that part of total nutrient availability (*NT*) which is not bound in biomass:

$$Nf = NT - \sum_i n_i B_i$$

The bound nutrient fraction is given by the sum over all groups of the nutrient density of each group times its density. The nutrient density of groups *n* is assumed constant.

Control over the strength of nutrient limitation in EcoSim is exerted through the use of the parameter *pf*, the base proportion of free nutrients. It defines a fixed fraction of *NT* which is assumed to be always in the form of free nutrients, so that

$$Nf = pf \cdot NT \text{ and hence, by definition, } NT = \frac{\sum_i n_i B_i}{(1 - pf)}$$

Because the parameter *pf* is given by the user, this last equation can be used at initialization of EcoSim to calculate the total nutrients in the system. By default, the parameter *pf* is set to almost unity, which means that the estimate of nutrients in the system approaches infinity. It furthermore means that the amount of free nutrients, *Nf*, is almost equal to *NT*, so that nutrient limitation by biomass accumulation is virtually switched off.

Fisheries

Effort dynamics over time can either be imposed by the user in the form of time series forcing functions, or can be modeled using a built-in model of effort and fleet dynamics.

This built in fleet & effort dynamics model assumes that effort is adapted on two different time scales: 1) A short time response to potential income from fishing, within the constraints imposed by current fleet size, and 2) A longer time investment/depreciation 'population dynamics' for capital capacity to fish (fleet size, vessel characteristics).

The short time response model is based on the current fleet-specific income per unit effort:

$$I_{g,t} = \sum_i q_{g,i} B_i P_{g,i}$$

Where $I_{g,t}$ is the income of fleet g at time t, which is the product of the biomass B_i of species/group i, its catchability $q_{g,i}$ and its relative value to fleet g, $P_{g,i}$. To predict the effort (E) by fleet g in the next time step $t+1$ in the next time step, the current value per unit effort is used in the sigmoid function

$$E_{g,t+1} = \frac{K_{g,t} I_{g,t}^p}{Ih_g^p + I_{g,t}^p}$$

Where $K_{g,t}$ is the current capacity of fleet g, and Ih_g is the half-saturation constant which determines the income at which effort is at 50% of capacity. The parameter p determines the steepness of the response to changes in income. When p is large, effort goes from 0 to K over a very narrow threshold range of I_g values, while when p is small, the process is more gradual.

The long-term response of the fishermen determines the dynamics of K_g, the capacity of fleet g, depending on the capital growth rate gf:

$$gf_{g,t+1} = \frac{K_{g,t}(r_{g,t} + \rho_g)}{PR_{g,t}} \quad .$$

Here $r_{g,t}$ and ρ_g are the capital growth and deprecation rates, respectively and $PR_{g,t}$ is the fleet's current profit. Capacity is updated annually according to

$$K_{g,t+1} = K_{g,t}(1 - \rho_g) + gf_{g,t+1} PR_{g,t}$$

Note that the index g,t to the capital growth rate r suggests that this parameter changes over time. It is currently unclear if and how this occurs, the equations are undocumented.

2.1.3 EcoSpace

General

EcoSpace is a way to project EcoSim dynamics onto a spatial grid of equally sized, homogeneous cells. EcoSpace links these cells through migration and fisheries effort allocation. It incorporates an advection model to incorporate water movement, and accounts for spatial variation in productivity and cost of fishing. Grid cells are characterized by their habitat type, which affects the dispersal, feeding and predation rates experienced by the organisms residing in them.

An EcoSpace model consists in essence of an EcoSim model for each grid cell, with global EcoPath and EcoSim parameters rescaled to reflect grid cell specific properties and scale differences. Each of these EcoSim models 'communicates' with neighboring grid cells through migration of biota (the parameters I and e in Section 2.1.2) and potentially through movement of water.

Going from an EcoSim to an EcoSpace environment requires specification of additional parameters. First and foremost, a 'basemap' needs to be defined, by setting its dimensions (number of cells) in the x and y direction and the size of the cells. Then, one or more habitats need to be defined. By assigning habitats to grid cells the user is able to implement spatial heterogeneity among grid cells. For each habitat type defined, the user needs to specify for each fishing fleet whether it can fish there. Furthermore, for every group in the model, the user needs to specify which habitats it prefers, and how strong the preference effects are. These preference effects are defined as an increased vulnerability to predators and a decreased feeding rate outside the preferred habitat. Last, it is necessary to specify dispersal parameters for each functional group. Movement is only possible to the 4 directly adjacent cells, diagonal movement is not possible. Dispersal to adjacent cells depends on a group's innate dispersal rate, which the user must specify. This dispersal rate (V_i) is used to calculate the rate at which individuals leave a grid cell, which equals

$$m_i = V_i / \pi L$$

Where L is the total grid cell side length (Martell *et al.*, 2005; Walters *et al.*, 1999) Furthermore, each group has a preference for its preferred habitat, which linearly reduces the movement rate out of cells of preferred habitat. The last major contributor to migration out of a certain grid cell is the 'risk ratio'

$$\frac{\sum_j c_{ij}}{\sum_j c_{ji}}$$

Which determines the ratio of feeding opportunity to predation risk for group I, and scales up migration out of a cell when consumption (the denominator) is low and/or predation (the numerator) is high. The details of these movement rules can be found in Walters *et al.* (1999).

Fisheries

To extend the EcoSim fleet & effort model to an EcoSpace context, several additional parameters are necessary. Most notably, the sailing cost should be specified separate from other variable costs. Additionally, in EwE v.5.x, the different fleets can be assigned 'ports', spatial home locations, and the sailing costs are calculated per grid cell as relative distances to these ports. This functionality seems to be absent in EwE v6.x.

Effort is distributed over space in EcoSpace in such a way that the proportion of total effort allocated to a certain cell is proportional to the relative profitability of fishing in that cell.

Assuming that there are N cells representing water areas, each fleet g can cause a total fishing mortality rate NF_g. For each step in the simulation this rate is distributed among cells, c, in proportion to the weights G_{gc} based on:

$$G_{g,c} = O_{g,c} U_{g,c} \frac{\sum_i P_{g,i} q_{g,i} B_{i,c}}{C_{g,c}}$$

where $O_{g,c}$ is 1 if cell c is open to fishing by fleet g, and 0 if not; $U_{g,c}$ is 1 if the user has allowed fleet g to work in the habitat type to which cell c belongs, and 0 if not; $p_{g,i}$ is the relative price fleet g receives for fish group i, $q_{g,i}$ is the catchability of group i by fleet g (equal to the $F_{g,i}$ in the EcoPath model, because effort is assumed to be unity in the non-dynamic EcoPath model); $B_{i,c}$ is the biomass of group i in cell c; and $C_{g,c}$ is the cost for fleet g to operate in cell c. Based on the weights in $G_{g,c}$, the total mortality rate is distributed over cells according to

$$F_{g,c} = \frac{NF_g G_{g,c}}{\sum_c G_{g,c}}$$

while each group i in cell c is subject to total fishing mortality

$$F_{i,c} = \sum_{g} F_{g,c} q_{g,i} \ .$$

Note that the equation for $F_{g,c}$ contains the total fishing rate of fleet g, F_g. This is how the spatial model links to the fleet and effort dynamics model, since

$$F_g = E_g q_g$$

where q_g is the effective power of fleet g, a sort of innate, species-independent effectiveness.

2.2 The current Mackinson-Daskalov North Sea (MDNS) model

2.2.1 MDNS EcoPath model

The model distinguishes 68 functional groups, ranging from top predators like seals and sharks, to phytoplankton and dissolved organic matter. All functional groups and some key parameters are listed in Table 1. A thorough discussion on each group can be found in Mackinson & Daskalov (2008).

Table 1: List of functional groups (sorted by trophic level) and their key parameters estimated by EcoPath in the MDNS model.

Group	***Trophic Level***	***Biomass (t/km^2)***	***Production/Biomass (/year)***
Seals	4.80	0.01	0.09
Hake	4.77	0.01	0.82
Large piscivorous sharks	4.74	0.00	0.48
Monkfish	4.69	0.04	0.70
Halibut	4.67	0.03	0.16
Toothed whales	4.64	0.02	0.02
Spurdog	4.61	0.02	0.60
Cod (adult)	4.61	0.16	1.19
Turbot and brill	4.43	0.05	0.86
Other gadoids (large)	4.41	0.05	1.27
Gurnards	4.33	0.08	0.82
Megrim	4.32	0.03	0.72
Baleen whales	4.31	0.07	0.02
Starry ray + others	4.29	0.11	0.66
Whiting (adult)	4.26	0.35	0.89
Saithe (adult)	4.26	0.22	0.95
Skate + cuckoo ray	4.25	0.05	0.35
Thornback & Spotted ray	4.23	0.07	0.78
Juvenile Cod(0-2, 0-40cm)	4.21	0.08	1.79
Horse mackerel	4.19	0.58	1.20
Flounder	4.11	0.25	1.10
Juvenile Whiting (0-1, 0-20cm)	4.10	0.22	2.36
Small sharks	4.07	0.00	0.51
Large demersal fish	4.07	0.02	0.55
Juvenile sharks	4.05	0.00	0.50
Haddock (adult)	4.05	0.10	1.14

Group	***Trophic Level***	***Biomass (t/km^2)***	***Production/Biomass (/year)***
Juvenile rays	4.00	0.27	0.66
Catfish (Wolf-fish)	3.99	0.01	0.48
Small demersal fish	3.99	0.34	1.42
Blue whiting	3.98	0.08	2.50
Juvenile Saithe (0-3, 0-40cm)	3.94	0.28	1.00
Long-rough dab	3.88	0.35	0.70
Juvenile Haddock (0-1, 0-20cm)	3.81	0.28	2.00
Squid & cuttlefish	3.74	0.08	4.50
Dab	3.71	3.00	0.67
Witch	3.71	0.08	0.90
Mackerel	3.68	1.72	0.60
Plaice	3.67	0.70	0.85
Dragonets	3.66	0.05	1.50
Other gadoids (small)	3.63	0.19	2.30
Sole	3.61	0.16	0.80
Lemon sole	3.59	0.31	0.86
Norway pout	3.47	1.39	2.20
Gelatinous zooplankton	3.45	0.07	2.86
Seabirds	3.42	0.00	0.28
Large crabs	3.42	1.35	0.55
Herring (adult)	3.38	1.97	0.80
Miscellaneous filterfeeding pelagic fish	3.37	0.03	4.00
Herring (juvenile 0, 1)	3.36	0.63	1.31
Sandeels	3.20	3.12	2.28
Nephrops	3.20	1.10	0.37
Carnivorous zooplankton	3.12	3.38	4.00
Epifaunal macrobenthos (mobile grazers)	3.02	78.00	0.39
Sprat	2.89	0.58	2.28
Fish larvae	2.82	0.32	4.00
Shrimp	2.80	0.50	3.00
Small mobile epifauna (swarming crustaceans)	2.62	30.00	1.90
Small infauna (polychaetes)	2.60	150.00	0.90
Infaunal macrobenthos	2.57	136.00	1.00
Meiofauna	2.56	4.12	35.00
Sessile epifauna	2.43	105.00	0.26
Herbivorous & Omnivorous zooplankton (copepods)	2.03	16.00	9.20
Benthic microflora (incl. Bacteria, protozoa)	1.65	0.11	9470.00
Planktonic microflora (incl. Bacteria, protozoa)	1.62	1.46	571.00
Phytoplankton	1.00	7.50	286.67
Detritus - DOM -water column	1.00	25.00	na
Detritus - POM – sediment	1.00	25.00	na
Discards	1.00	50.00	na

In the MDNS model, fishing activity in the North Sea is simplified into 12 gear types (Table 2), each representing a fleet in the model. In an EcoPath model, each fleet is characterized by its catch, divided into landings and discards in biomass, specified per functional group in the model (in tons km^{-2}year^{-1}). Furthermore, each group is assigned a (relative) monetary value.

The values are fleet-specific because quality and hence price often differs more between than within fleet types.

The combination of species- and gear-specific value and landings is used to calculate the total value of the fleet. Other economic parameters of fleets are fixed costs, effort-dependent variable costs, and sailing costs (in case of an EcoSpace model). These parameters are all expressed as a percentage of value, so that the remaining fractions of value after all costs are accounted for equals the profits.

Table 2: Key properties and EcoPath estimates of the fishing fleets

Fleet	***Fixed cost (%)***	***Effort related cost (%)***	***Profit (%)***	***Total landings (t/km2/year)***	***Total discards (t/km2/year)***
Demersal trawl + dem seine	34.6	68.7	-3.3	0.56	0.23
Beam trawl	36	69.6	-5.6	0.30	0.22
Sandeel trawl	47.3	74.7	-22	2.07	0.00
Pelagic trawl	39.3	55.8	4.9	1.00	0.27
Drift and fixed nets	38.2	80	-18.2	0.12	0.01
Nephrops trawl	24.6	81.3	-5.9	0.02	0.02
Gears using hooks	38.2	80	-18.2	0.00	0.00
Shrimp trawlers	31.8	73.7	-5.5	0.00	0.00
Dredges	35.9	74.9	-10.8	0.26	0.00
Shellfish	38.2	80	-18.2	0.05	0.00
Pots	38.2	80	-18.2	0.01	0.00
Other	30.5	69.4	0.1	0.50	0.25

2.2.2 MDNS EcoSim model

General

The MDNS EcoSim model adds a time dimension to the EcoPath formulation. An important step from the EcoPath to the EcoSim formulation consists of parameterizing a functional response for each group (except the primary producers). The functional response framework used in EcoSim is described above (Section 2.1.2). Using the output of the EcoPath model, values for vulnerability and other EcoSim-specific parameters were chosen, based on different criteria. Initially, ecologically reasonable values were used, which were later adapted to iron out unlikely time trends which arose. This is a complex iterative process which ultimately led to a set of base parameters which gave stable dynamics and reasonable biomass estimates of all groups (Figure 1).

It is important to note that discards are parameterized from observer trips on board British vessels (Mackinson & Daskalov 2008). This means that certain species which are landed only by fleets of other nations may not have any fishing mortality imposed on them, while in reality they do. Furthermore, species which are currently very rare in the North Sea species may end up with zero fishing mortality, even though they are susceptible to fishing. This has consequences when one studies scenarios where such rare species substantially increase in abundance.

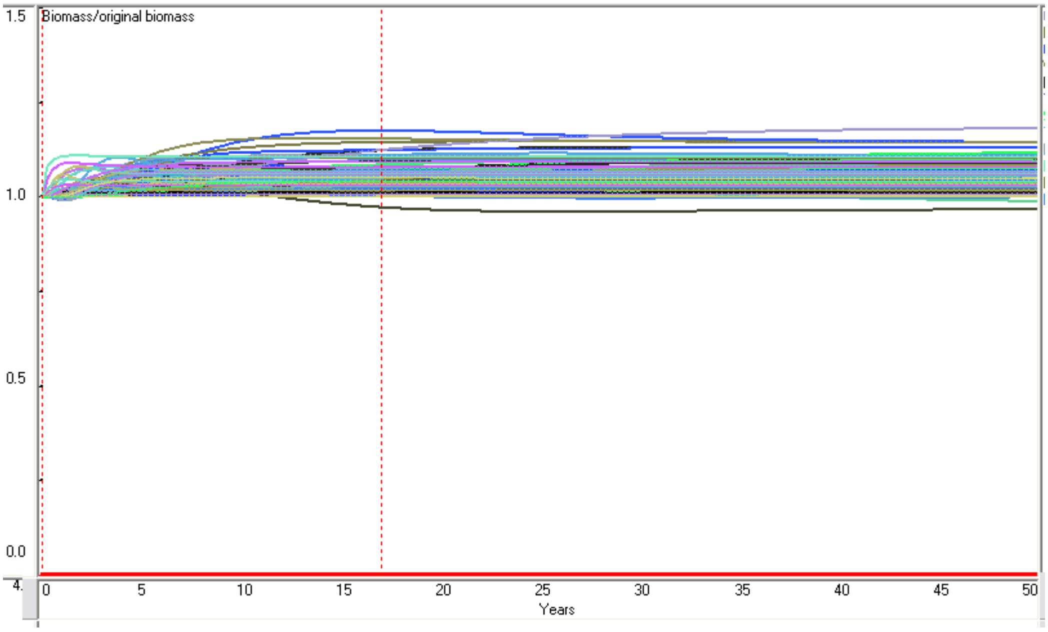


Figure 1: 50-year EcoSim test run of the MDNS EcoSim model. The x-axis shows time, the y-axis the biomass of all groups relative to the biomass at the start of the simulation. The final values of all biomasses stabilize within ~10% of their initial EcoPath-derived values after a transient period.

Time series fitting

The basic EcoSim model was used as a basis for a fitting procedure to optimize its potential to reproduce biomass patterns of key species during the period 1991-2003, using effort and climate time series to force the model. The species biomasses used to measure the goodness of fit were those used in the MSVPA 2005 key run by the ICES multispecies working group. These are:

- Cod (adult)
- Haddock (adult)
- Norway pout
- Saithe (adult)
- Whiting (adult)
- Herring (adult)
- Sandeels
- Sprat
- Mackerel
- Horse mackerel
- Plaice
- Sole
- Gurnards
- Starry ray + others

To improve the fit, the strength of the predation interaction between several consumers (juvenile cod, adult cod, juvenile whiting, juvenile saithe, horse mackerel and plaice) and all their prey species was forced using a 4-year running average of the North Atlantic Oscillation Index and/or a 2-year running average of temperature. This forcing function enters the functional response through the parameter S_{ij} in Section 2.1.2. Furthermore, the vulnerability parameters (v_{ij}) for selected species (those for which good time-series data existed) were fitted using the fitting procedure in the EwE software.

The fit to the time series data of the 14 groups listed above is shown in
Figure 2. It is obvious that the ability of the model to capture trends in the time series varies substantially with species and in time.

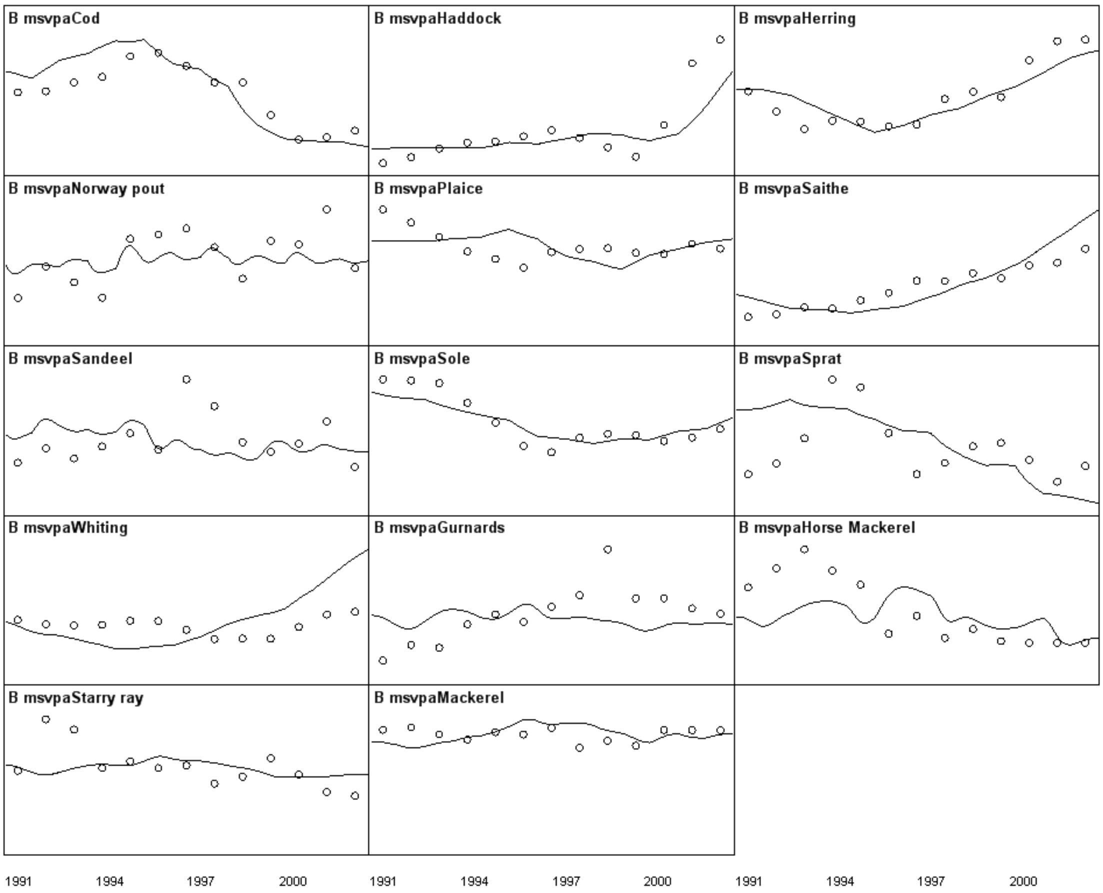


Figure 2: Best-fit model time series (drawn lines) to the MSVPA time series data (dots). Biomasses are scaled relative to the EcoPath-generated value.

Primary production

The MDNS model contains one primary producer group (phytoplankton), and two mixed groups (Benthic & planktonic microflora). These mixed groups contain a mixture of bacteria, flagellates, ciliates and protozoa, and together make up a simplified representation of the microbial loop (Figure 3). It is assumed that half of the production in these groups consists of primary production. These groups make use of organic carbon produced by phytoplankton, which is not otherwise transferred up the food chain.

It is important to note that nutrient limitation is not a part of the MDNS model. The parameter 'base proportion of free nutrients' (*Nf*) is set to 1.0, which sets nutrient availability at a static value (see Section 2.1.2) The temporal dynamics appear quite sensitive to this feature, but turning it on leads to an untested and unvalidated model.

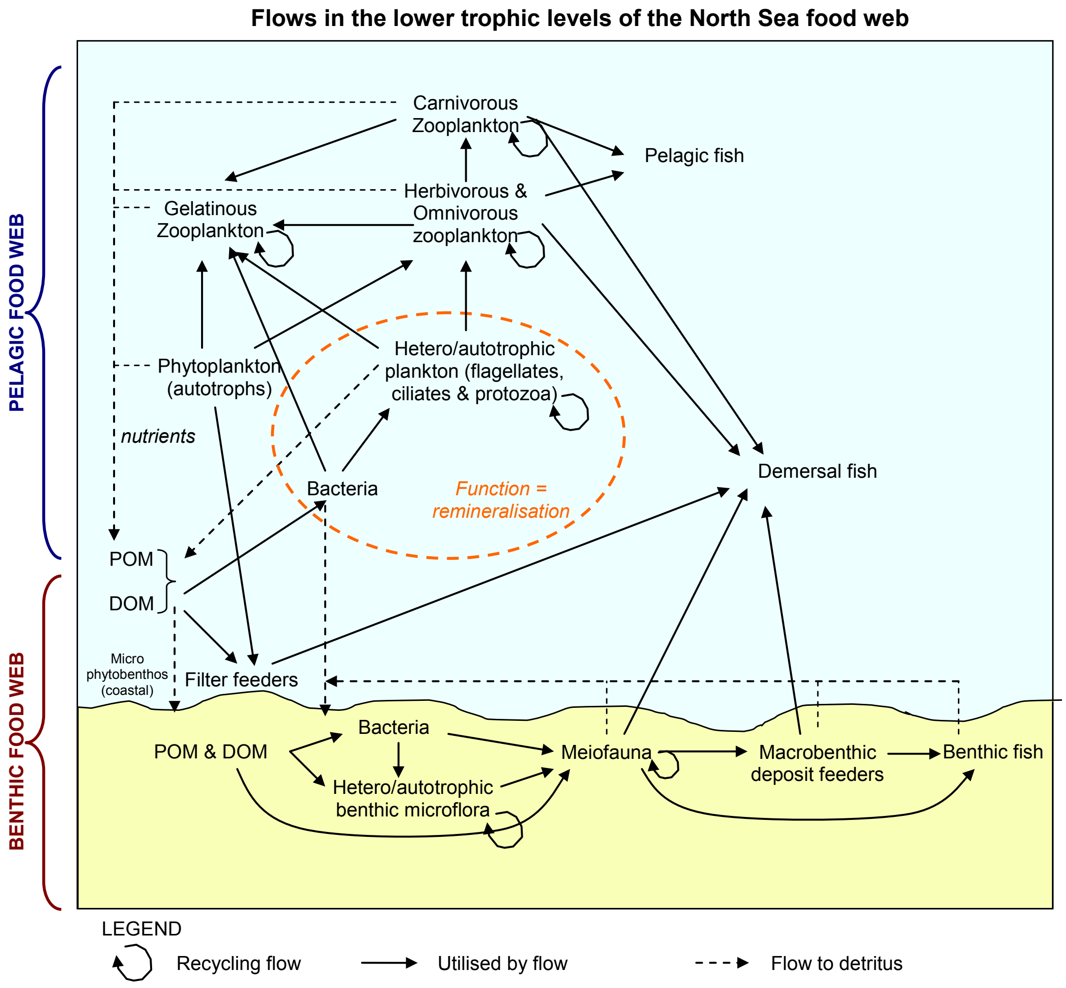


Figure 3: Flows in the lower trophic levels of the North Sea food web (figure from Mackinson & Daskalov, 2008)

Fisheries

Fishing effort for the fleets in the model was obtained from ICES stock assessments if available. This effort is made relative to the effort in the EcoPath-derived effort value, and can consequently be used to force the mortality of all groups susceptible to the activities of each fleet. If no ICES assessment data was available, fishing mortalities from MSVPA outputs were used instead.

It should be noted that all fishing fleets in the model only impose mortality on species which end up in the nets. An important aspect of many demersal fisheries, in particular beam trawling, is that they disturb bottom integrity and thereby impose mortality on epi- and infaunal benthos. These effects are not part of the MDNS model.

In the MDNS model, discards from fisheries are implemented as a separate detritus group. The biomass that ends up in this group depends on the fishing intensity which is applied. The proportion of discards per functional group per unit fishing effort per fleet are estimated from the discard mortality data (1991) which are used in the EcoPath model description and is assumed constant.

Stage-based representation of life history

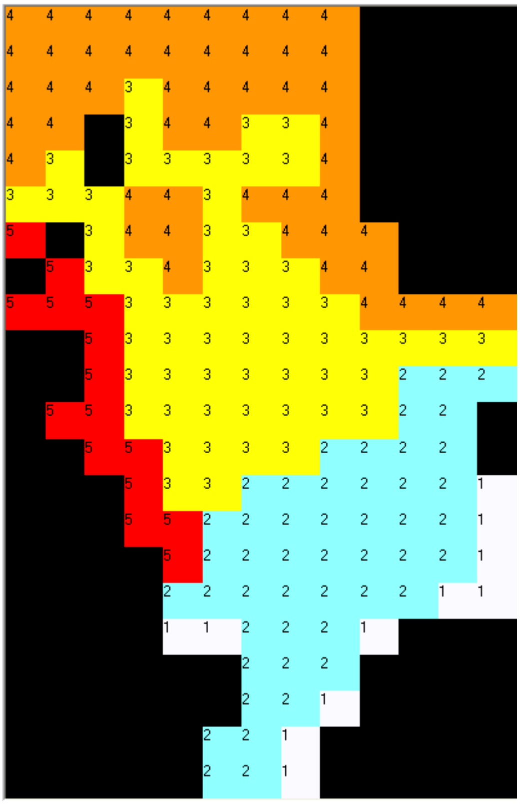
Several functional groups in the model, particularly commercially important species, are modeled as two separate functional groups, adults and juveniles. In the model used here, these life history stages are independent of each other, meaning that their dynamics are not coupled (other than through potential cannibalism). In other words, for example, the biomass of adult cod can in principle increase, while juvenile cod are extinct.

Feeding relationships

The diet data from which the feeding relationships are derived contain a large number of zeros, meaning that many species combinations have no predator-prey type interaction. This may constrain the outcome of the model results because the inclusion of new types of prey are impossible.

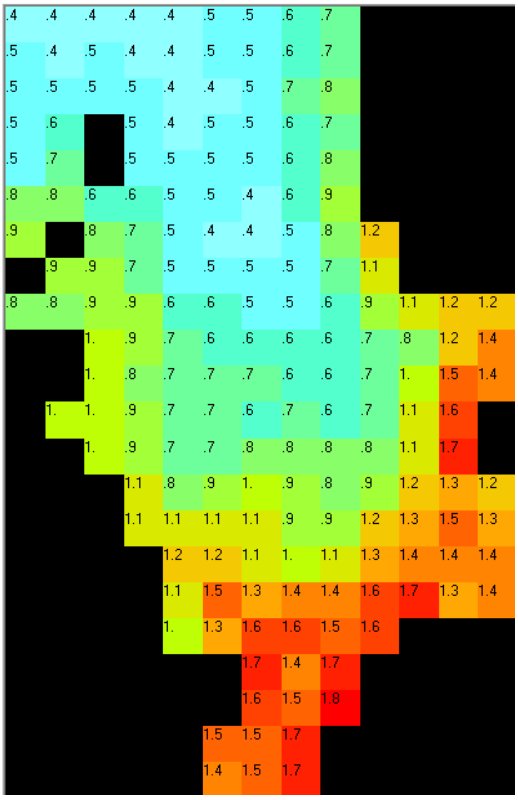
2.2.3 MDNS EcoSpace model

The current version of EwE incorporates the North Sea between -4°E and 9° E, and between 51 and 62° N. This is an area measuring 1222 km in the north-south direction. In the east-west direction, the spatial range differs because the distance between -4°E and 9° E varies with latitude. Hence, the Southern end of the area measures 910 km, while the Northern end is 680 km across. For simplicity, it is assumed that all cells in the EcoSpace formulation are of equal size.



4	4	4	4	4	4	4	4	4				
4	4	4	4	4	4	4	4	4				
4	4	4	3	4	4	4	4	4				
4	4		3	4	4	3	3	4				
4	3		3	3	3	3	3	4				
3	3	3	4	4	3	4	4	4				
5		3	4	4	3	3	4	4	4			
	5	3	3	4	3	3	3	4	4			
5	5	5	3	3	3	3	3	3	4	4	4	4
		5	3	3	3	3	3	3	3	3	3	3
		5	3	3	3	3	3	3	3	2	2	2
	5	5	3	3	3	3	3	3	3	2	2	
		5	5	3	3	3	3	2	2	2	2	
			5	3	3	2	2	2	2	2	2	1
			5	5	2	2	2	2	2	2	2	1
				5	2	2	2	2	2	2	2	1
				2	2	2	2	2	2	2	1	1
				1	1	2	2	2	1			
						2	2	2				
						2	2	1				
					2	2	1					
					2	2	1					

Figure 4: EcoSpace basemap with habitat types. 1=depth<22 m, 2= 22 m<depth<51 m, 3=51 m<depth<115 m, and 4=depth>115 m 5=coastal.



.4	.4	.4	.4	.4	.5	.5	.6	.7				
.5	.4	.5	.4	.4	.5	.5	.6	.7				
.5	.5	.5	.5	.4	.4	.5	.7	.8				
.5	.6		.5	.4	.5	.5	.6	.7				
.5	.7		.5	.5	.5	.5	.6	.8				
.8	.8	.6	.6	.5	.5	.4	.6	.9				
.9		.8	.7	.5	.4	.4	.5	.8	1.2			
	.9	.9	.7	.5	.5	.5	.5	.7	1.1			
.8	.8	.9	.9	.6	.6	.5	.5	.6	.9	1.1	1.2	1.2
		1.	.9	.7	.6	.6	.6	.6	.7	.8	1.2	1.4
		1.	.8	.7	.7	.7	.6	.6	.7	1.	1.5	1.4
	1.	1.	.9	.7	.7	.6	.7	.6	.7	1.1	1.6	
		1.	.9	.7	.7	.8	.8	.8	.8	1.1	1.7	
			1.1	.8	.9	1.	.9	.8	.9	1.2	1.3	1.2
			1.1	1.1	1.1	1.1	.9	.9	1.2	1.3	1.5	1.3
				1.2	1.2	1.1	1.	1.1	1.3	1.4	1.4	1.4
				1.1	1.5	1.3	1.4	1.4	1.6	1.7	1.3	1.4
				1.	1.3	1.6	1.6	1.5	1.6			
						1.7	1.4	1.7				
						1.6	1.5	1.8				
					1.5	1.5	1.7					
					1.4	1.5	1.7					

Figure 5: Spatial modifiers of primary productivity in the MDNS model. Colors indicate the numeric values, red indicating high-productivity regions, while green and blue are areas with lower productivity.

Each cell in the modeled geographical area consists of 1 of 5 habitat types: Coastal, depth <22m, 22m<depth<51m, 51m<depth<115m, and depth>115m (Figure 4). Based on spatially explicit production data, each cell on the map is assigned a modifier for the global productivity parameter (Figure 5). This data comes from the SeaWifs project (http://oceancolor.gsfc.nasa.gov/SeaWiFS/). The 4 depth-based habitats were derived from the distribution of species in the IBTS survey. The 'coastal' habitat was later added to obtain a better distribution of species (Mackinson & Daskalov, 2008).

The MDNS model as used in Mackinson & Daskalov uses a grid cell length of 10.25 km. This results in an incorrect scale for the North Sea (the correct value would be 55 km, S. Mackinson, CEFAS-Lowestoft, UK, *pers. comm.*). This was caused by an apparent bug in the EwE software. For the sake of comparability, we have kept this value at 10.25 km. The change from 10.25 to 55 km does affect the results and any application of this model for the exploration of spatial planning scenarios needs to consider this.

Habitat preference in the MDNS EcoSpace model

The distribution of species and functional groups across the map can be limited by setting habitat preferences for each group in the model. The habitat preferences for each group in the MDNS EcoSpace model are shown in Table 3. Outside preferred habitats, all groups in the model (with a few exceptions) in non-preferred habitats are assumed to have doubled vulnerability to predation, doubled dispersal rate has a maximum of only 5% of that in preferred habitats. This leads to that the spatial distribution of species is largely limited to their preferred habitats. Non-preferred habitats may hold some spillover population from nearby preferred habitats, but are likely to serve as a sink for such spillover biomass.

Table 3: Preferred habitat of all groups in the model. Plus signs indicate preference.

	Habitat				
Group	<22 m	22-51 m	52-115 m	>115 m	Coast
Seals	+	+	+		
Hake				+	
Large piscivorous sharks	+	+			
Monkfish			+	+	+
Halibut			+	+	
Toothed whales	+	+	+	+	+
Spurdog		+	+		
Cod (adult)			+	+	
Turbot and brill	+	+			
Other gadoids (large)				+	
Gurnards	+	+	+		
Megrim				+	
Baleen whales				+	
Starry ray + others			+	+	+
Saithe (adult)				+	
Whiting (adult)		+	+		+
Skate + cuckoo ray		+	+	+	+
Thornback & Spotted ray	+				
Juvenile Cod(0-2, 0-40cm)		+	+		
Horse mackerel	+	+			
Flounder	+	+			
Juvenile Whiting (0-1, 0-20cm)	+	+	+		+
Large demersal fish			+	+	
Small sharks		+	+		+
Haddock (adult)			+	+	+
Juvenile sharks	+	+	+	+	+
Juvenile rays	+	+			
Small demersal fish	+	+	+	+	
Catfish (Wolf-fish)			+	+	+
Blue whiting				+	
Juvenile Saithe (0-3, 0-40cm)				+	
Long-rough dab			+	+	+
Juvenile Haddock (0-1, 0-20cm)			+	+	+
Squid & cuttlefish		+	+	+	

	Habitat				
Group	<22 m	22-51 m	52-115 m	>115 m	Coast
Witch			+	+	
Dab	+	+			
Mackerel	+	+	+		
Plaice	+	+			
Dragonets	+	+			
Other gadoids (small)		+	+	+	
Sole	+	+			
Lemon sole			+		+
Norway pout			+	+	+
Gelatinous zooplankton	+	+	+	+	+
Seabirds	+	+	+	+	+
Large crabs	+	+	+		+
Herring (adult)		+	+	+	+
Miscellaneous filterfeeding pelagic fish		+	+	+	
Herring (juvenile 0, 1)	+	+	+		+
Sandeels		+			+
Nephrops				+	+
Carnivorous zooplankton	+	+	+	+	+
Epifaunal macrobenthos (mobile grazers)	+	+	+		+
Sprat	+	+			
Fish larvae	+	+	+	+	+
Shrimp	+				
Small mobile epifauna (swarming crustaceans)	+	+	+	+	+
Small infauna (polychaetes)	+	+	+	+	+
Infaunal macrobenthos	+	+	+		+
Meiofauna	+	+	+	+	+
Sessile epifauna	+	+	+	+	+
Herbivorous & Omnivorous zooplankton (copepods)	+	+	+	+	+
Benthic microflora (incl. Bacteria, protozoa))	+	+	+	+	+
Planktonic microflora (incl. Bacteria, protozoa)	+	+	+	+	+
Phytoplankton	+	+	+	+	+
Detritus - DOM -water column	+	+	+	+	+
Detritus - POM - sediment	+	+	+	+	+
Discards	+	+	+	+	+

Fisheries in the MDNS EcoSpace model

The basis for fisheries in any EcoSpace model is formed by a definition of which fleets can and cannot fish in which habitats (Table 4). Additionally, protected areas can be defined in which one or more fleets are not allowed to operate. Effort is distributed over available space in such a way that the proportion of total effort allocated to a certain cell is proportional to the relative profitability of fishing in that cell (see Section 2.1.2).

Table 4: Definition of fishable habitat per fleet

	Habitat				
Fleet	<22 m	22-51 m	52-115 m	>115 m	Coast
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	+	-	-	-	-

2.2.4 A note on EwE software versions

The EwE software used to calculate balanced EcoPath food webs, and simulate EcoSim and EcoSpace models is to a large extent built on a project basis. This means that much of the functionality is added to the software when users develop it or commission the EwE developers to add it. On first glance, it seems logical that version 6.x of the EwE software is newer and better than version 5.x. However, as a result of the development process, this is not the case. The two versions should largely be seen as parallel packages with differing functionality. Version 6.x for example can do calculations on larger maps than version 5.x, but version 5.x is able to connect to a database with relative productivity estimates from the SeaWifs project, located at the EwE developers home base at the University of British Columbia, Canada.

2.3 Model sensitivity, dependence on specific assumptions, input data

A model as parameter-rich as the MDNS model cannot be subjected to a systematic study of parameter sensitivity. However, several parameters can be identified to which the dynamics of the EcoSim and EcoSpace models are highly sensitive. In the MDNS model, nutrient dynamics are switched off by assuming that nutrients are never limiting and primary productivity is constant. Switching on the possibility of nutrient limitation (see Section 2.1.2) substantially reduces the stability of the EcoSim and EcoSpace formulations. The model is hence highly sensitive to the parameter 'Base proportion of free nutrients'. When this parameter equals 1, nutrients are constant, while a value of 0 indicates that all nutrients can potentially be bound in biomass of functional groups, so that free nutrients can become zero, halting primary production. Generally, values below 0.5 affect the model dynamics significantly.

Another set of key parameters related to model stability are the prey vulnerabilities. EcoSim and EcoSpace make use of the foraging arena concept (Walters *et al.* 1997) to model the predation interaction. This concept revolves around the notion that prey have two behavioral 'modes', one of which renders them sensitive to predation, while in the other predation risk is zero. The prey vulnerability parameters scale the change in the distribution of these states with predator abundance. A high value indicates a linear response, such that when predator abundance doubles, prey mortality (almost) doubles. A low value (close to 1) indicates that prey respond strongly to increases in predator abundance, switching to the protected behavioral mode, so that a doubling in predator abundance leads to (much) less than twice the prey mortality. Because no empirical observations exist of these vulnerability parameters, they are tuned to optimize model stability and equilibrium abundance of functional groups. Although testing the effects of changes in this parameters for individual groups is not feasible, it can be argued that high values of this parameter (linear responses) will in general work to destabilize the model in response to perturbations, while low values are expected to introduce stabilizing nonlinearities, which make sure that disturbances in one group are not carried over to the rest of the system.

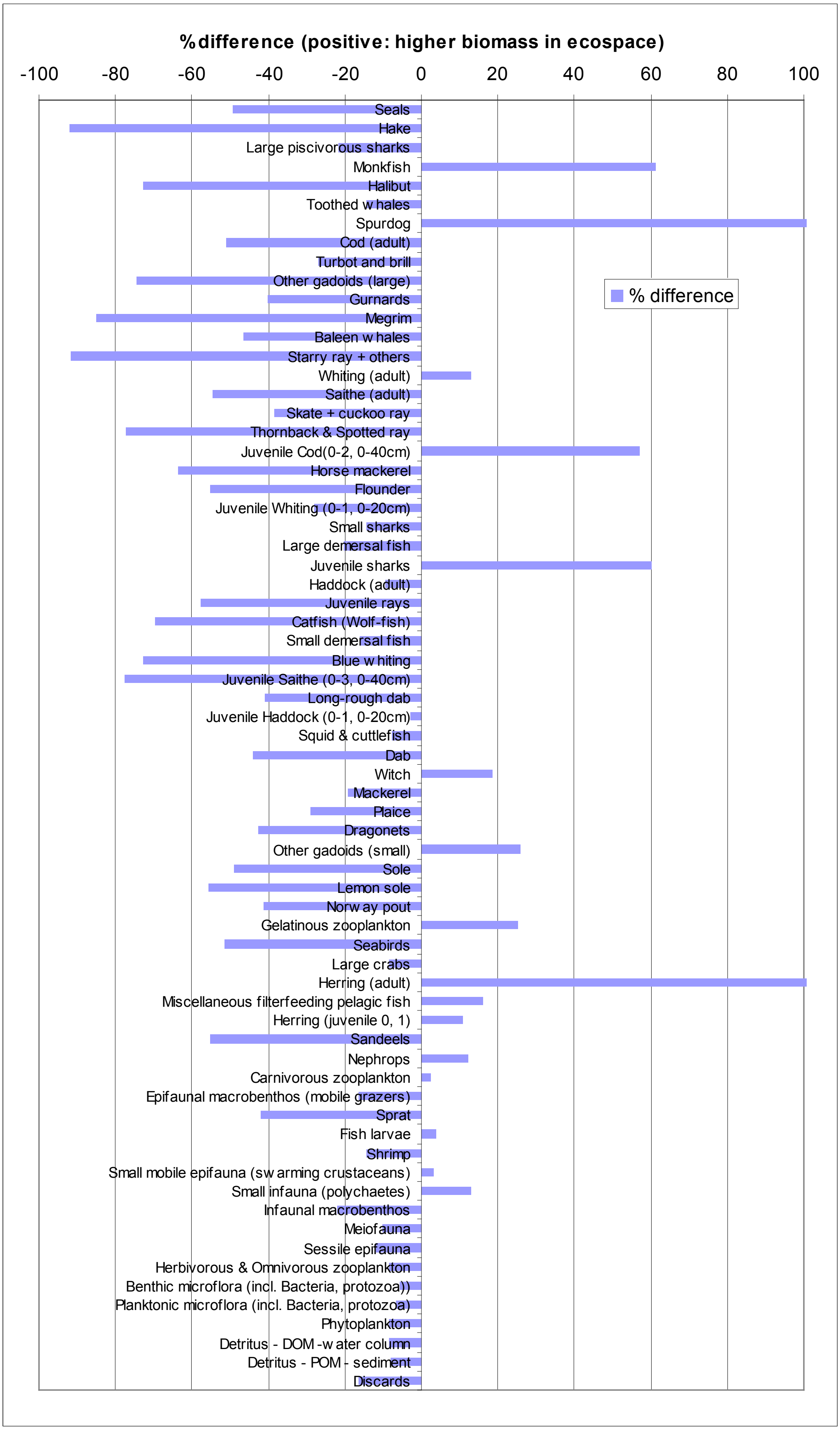
In relation to the Ecospace model, an important parameter set is the habitat preference of the functional group in the model. We find that with the setting used, individuals are at such a strong disadvantage when they are outside their preferred habitat, that they are effectively constrained to that habitat. While this is a way to correct the distributions of functional groups in space, it forms a potential problem for scenario studies. Adult cod, for example, is absent from the southern North Sea in the reference scenario (see below). This is a largely correct representation of the current situation, following years of overfishing. However, in the model, cod can never return to the southern North Sea, even if all fishing is banned in the entire North Sea. Such limitations of the model should be considered very carefully when using the model for policy explorations.

From EcoSim to EcoSpace

As a first test of the effects of going from an EcoSim to a spatially explicit EcoSpace approach, we compare the outcomes from the EcoSim and EcoSpace models directly by using the same EcoPath-derived starting biomasses to start both the spatial and non-spatial models. We use monthly time steps in EcoSpace, and compare the biomasses in groups at the end of these runs.

Table 5: Biomasses at the end of a simulation comparing the spatial and non-spatial models. Column 'EcoSim' lists final biomass of all groups in a non-spatial EcoSim run 50 years, column 'EcoSpace' lists them using the spatial model, at the end of an 18-year run.

	Biomass ($t\cdot km^{-2}$)			**Biomass ($t\cdot km^{-2}$)**	
Group	***EcoSim***	***EcoSpace***	***Group***	***EcoSim***	***EcoSpace***
Seals	0.0089	0.0045	Dab	3.3057	1.847
Hake	0.0148	0.0012	Witch	0.0937	0.111
Large piscivorous sharks	0.0023	0.0018	Mackerel	1.8066	1.4622
Monkfish	0.0439	0.0708	Plaice	0.8048	0.5709
Halibut	0.0357	0.0097	Dragonets	0.0474	0.0272
Toothed whales	0.0174	0.0149	Other gadoids (small)	0.1996	0.2512
Spurdog	0.0173	0.0407	Sole	0.1645	0.0842
Cod (adult)	0.1843	0.0904	Lemon sole	0.3377	0.1495
Turbot and brill	0.0599	0.0438	Norway pout	1.426	0.8398
Other gadoids (large)	0.0481	0.0122	Gelatinous zooplankton	0.0672	0.0841
Gurnards	0.0799	0.0478	Seabirds	0.0033	0.0016
Megrim	0.0363	5.50E-03	Large crabs	1.4316	1.3105
Baleen whales	0.0688	0.0369	Herring (adult)	1.965	4.0899
Starry ray + others	0.1198	0.01	Miscellaneous filterfeeding pelagic fish	0.03	0.0348
Whiting (adult)	0.3401	0.3844	Herring (juvenile 0, 1)	0.6444	0.7139
Saithe (adult)	0.2332	0.1062	Sandeels	3.2086	1.4387
Skate + cuckoo ray	0.0549	0.0337	Nephrops	1.166	1.3093
Thornback & Spotted ray	0.0745	0.017	Carnivorous zooplankton	3.4418	3.5261
Juvenile Cod(0-2, 0-40cm)	0.0842	0.1321	Epifaunal macrobenthos (mobile grazers)	83.5033	69.7578
Horse mackerel	0.5937	0.2159	Sprat	0.5983	0.3483
Flounder	0.2757	0.1232	Fish larvae	0.3254	0.3383
Juvenile Whiting (0-1, 0-20 cm)	0.2289	0.1647	Shrimp	0.5327	0.456
Small sharks	0.0021	0.0018	Small mobile epifauna (swarming crustaceans)	31.8575	32.9141
Large demersal fish	0.0184	0.0147	Small infauna (polychaetes)	159.2419	180.003
Juvenile sharks	0.001	0.0016	Infaunal macrobenthos	145.4816	113.23
Haddock (adult)	0.1067	0.0965	Meiofauna	4.262	3.8238
Juvenile rays	0.2883	0.1224	Sessile epifauna	114.6644	101.1355
Catfish (Wolf-fish)	0.0165	0.005	Herbivorous & Omnivorous zooplankton (copepods)	16.1363	14.7967
Small demersal fish	0.3595	0.3018	Benthic microflora (incl. Bacteria, protozoa))	0.1093	0.1031
Blue whiting	0.0811	0.0221	Planktonic microflora (incl. Bacteria, protozoa)	1.576	1.4714
Juvenile Saithe (0-3, 0-40 cm)	0.2909	0.0653	Phytoplankton	7.496	6.8641
Long-rough dab	0.379	0.2245	Detritus - DOM -water column	27.6761	25.3525
Juvenile Haddock (0-1, 0-20 cm)	0.2962	0.2881	Detritus - POM - sediment	25.7804	23.6782
Squid & cuttlefish	0.083	0.0766	Discards	52.4279	43.8123


%difference (positive: higher biomass in ecospace)
-100
-80
-60
-40
-20
0
20
40
60
80
100
% difference
Seals
Hake
Large piscivorous sharks
Monkfish
Halibut
Toothed w hales
Spurdog
Cod (adult)
Turbot and brill
Other gadoids (large)
Gurnards
Megrim
Baleen w hales
Starry ray + others
Whiting (adult)
Saithe (adult)
Skate + cuckoo ray
Thornback & Spotted ray
Juvenile Cod(0-2, 0-40cm)
Horse mackerel
Flounder
Juvenile Whiting (0-1, 0-20cm)
Small sharks
Large demersal fish
Juvenile sharks
Haddock (adult)
Juvenile rays
Catfish (Wolf-fish)
Small demersal fish
Blue w hiting
Juvenile Saithe (0-3, 0-40cm)
Long-rough dab
Juvenile Haddock (0-1, 0-20cm)
Squid & cuttlefish
Dab
Witch
Mackerel
Plaice
Dragonets
Other gadoids (small)
Sole
Lemon sole
Norw ay pout
Gelatinous zooplankton
Seabirds
Large crabs
Herring (adult)
Miscellaneous filterfeeding pelagic fish
Herring (juvenile 0, 1)
Sandeels
Nephrops
Carnivorous zooplankton
Epifaunal macrobenthos (mobile grazers)
Sprat
Fish larvae
Shrimp
Small mobile epifauna (sw arming crustaceans)
Small infauna (polychaetes)
Infaunal macrobenthos
Meiofauna
Sessile epifauna
Herbivorous & Omnivorous zooplankton
Benthic microflora (incl. Bacteria, protozoa))
Planktonic microflora (incl. Bacteria, protozoa)
Phytoplankton
Detritus - DOM -w ater column
Detritus - POM - sediment
Discards

← *Figure 6: Differences between EcoSim and EcoPath model results expressed as % difference in final group biomass between EcoSpace and EcoPath simulation (positive percentages indicate more biomass in the EcoSpace simulation). Bars for spurdog and adult herring are truncated, the percentages are 135 and 108 respectively. Constant EcoPath-derived fishing pressure was imposed.*

The comparison shows that there are substantial differences between the two (← Figure 6, Table 5). Most groups have a lower biomass in the EcoSpace model, while a few have substantially higher biomass in the EcoSpace model. The average difference between the two on a per group basis is 37%. Some of the groups with large differences are highly relevant to both fisheries (juvenile cod, adult herring, sole) and conservation (seals, toothed whales, baleen whales, thornback & spotted ray, seabirds).

This result clearly indicates that an EcoSpace model is not simply a spatially explicit version of an EcoSim model, it is truly a different model. This is not unexpected, given the spatial constraints imposed on species and fishing fleets in the EcoSpace model. A potential problem arises in that while the EcoSim model is well-founded in data, and yields results which correspond reasonably well with data, the EcoSpace model has gone through much less rigorous comparison with data, although such testing is underway (S. Mackinson, CEFAS-Lowestoft, UK, *personal communication*).

It is important to note that although the separation between temporal (EcoSim) and spatial (EcoSpace) dynamics makes it easy to build one from the other, the strict separation of the spatial and the temporal also imposes strict limitations: aspects of the model can be dynamic either in time or in space, but not both. For example, forcing functions for fishing effort of a specific fleet can vary in time, but the effort in each grid cell is a model result, and can not be directly modified, while the spatial modifiers of productivity on the EcoSpace basemap differ spatially but are fixed in time.

3 Scenario studies

3.1 Fisheries and closed area scenarios

3.1.1 Method

In order to assess the effects of different fishing regimes and different types of marine protected areas (MPAs), we have implemented a number of scenarios in the current EcoSpace model. These scenarios have been developed together with the Netherlands Environmental Assessment Agency (PBL).

The scenarios are:
1. A reference scenario, where all fisheries is allowed in all suitable habitat.
2. A baseline scenario where all fishery is prohibited.
3. A single large MPA in the southern North Sea (Figure 7a), where no fishing is allowed at all
4. The same MPA as under 3, but only bottom-disturbing fisheries (Beam trawlers, demersal trawlers & seiners and sandeel trawlers) are banned. Other fisheries continue as normal.
5. A number of small MPAs in a checkerboard pattern (Figure 7b), in the southern North Sea. Together these represent the same surface area as the large MPA used under 2 and 3. In this case, all fisheries is banned from the MPAs.
6. The same as 4, but with the MPA layout of 5.

In the closed-area scenarios, the total fishing effort in the entire North Sea is kept constant. Fishing intensity is hence more concentrated in the non-closed parts of the North Sea.

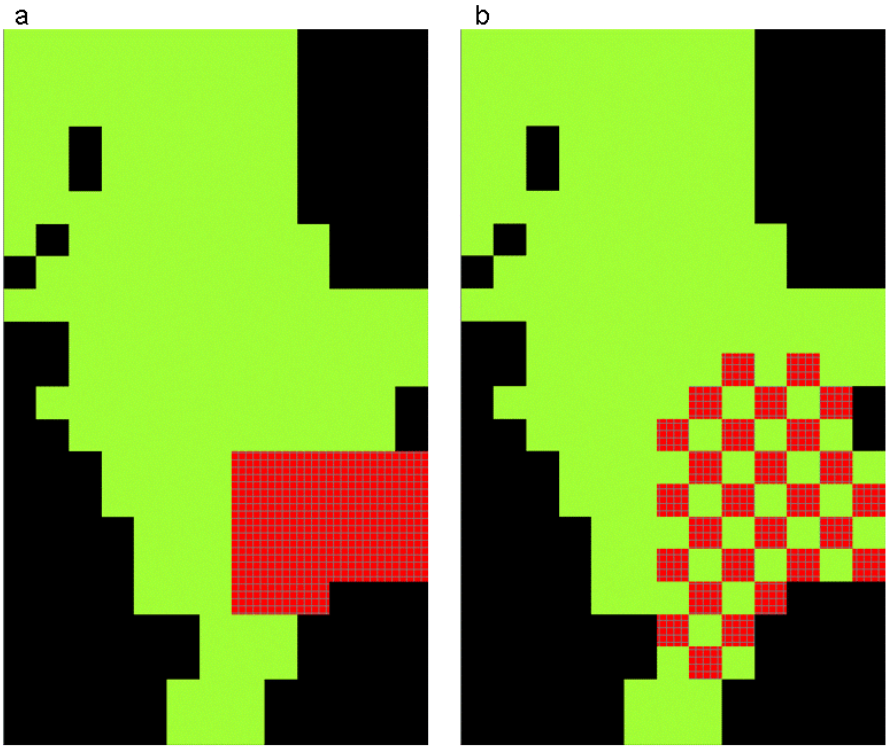


Figure 7: Shape of (a) the single large MPA (red, crosshatched area) used in scenarios 2 and 3, and (b) the collection of small MPAs used in scenarios 4 and 5.

We will use these scenarios to study the effects of MPA shape and type on global abundance effects on species and functional groups, on fishing yield on a species and fleet level, and on spatial distribution of species and functional groups. All simulations are performed using constant EcoPath-derived fishing intensity, so that the end states of the simulations reflect the long-term equilibrium state for the mid-1990's. We examine the total biomass in each group at the end of this run, as well as the spatial distributions at the end of the run. The local densities on the maps are color-coded as relative densities compared to the initial values. It should be noted that the MPA designs (single large or many small) differ implicitly also in the distribution of each habitat which is protected. This should be kept in mind when comparing the two spatial layouts. These scenarios do not reflect planned or desired policy options, but are merely designed to test model applicability to this type of marine spatial planning issues.

3.1.2 Results

Fisheries

Contrasting the basic fishing setup of the MDNS EcoSpace model with an 'extreme case' where no fishing is allowed at all immediately shows the scope of fishing effects on the North Sea ecosystem (Figure 8, Figure 9). The effect is clearly related to trophic level: Virtually all groups with high trophic position (from approximately 3.9, Long-rough dab) are increased in density in absence of fishery. The effects are strongest in groups in top predators for which virtually all mortality is fisheries-derived, such as large piscivorous sharks, spurdog and adult cod. Groups with low trophic level are generally not strongly affected by the presence of absence of a fishing fleet and no strong trophic cascade is observed. Note that the positive biomass in the group 'discards' (when there is no fishing) is left over from the initial biomass of discards at the end of 18 years. There are a few groups which show higher density in the presence of fishing (Figure 9). We expect that these are groups which either are not heavily targeted by fisheries themselves, but compete for food with species which are targeted, or their predators are heavily affected by fisheries. Fishing hence reduces either resource competition or predation mortality for these species.

The spatial distributions of species are fairly similar whether fishing is going on or not, but the overall density in the area where the fish occur appears to be lower. Compare for example the groups Seals and Spurdog between Figure 10 and Figure 12.

A total ban on fishing in the entire spatial domain leads to unrealistically low levels of mortality for groups at the top of the food web. In nature it is expected that, other processes such as disease, or emigration due to low food density may increase and compensate some of the mortality lost when fisheries are stopped. The model is not set up to include such possible compensation.

The absence of a clear trophic cascade and a extreme shift in the entire ecosystem may be a result of the strong non-linearity in the shape of the food web: the are many 'diagonal' links, and there is no single clear 'food chain' going up from primary producers to top predators. Such food webs are prone to harbor compensatory mechanisms like intraguild predation (Polis *et al.* 1989) and apparent competition (Holt, 1977), which can blur or prevent trophic cascades.

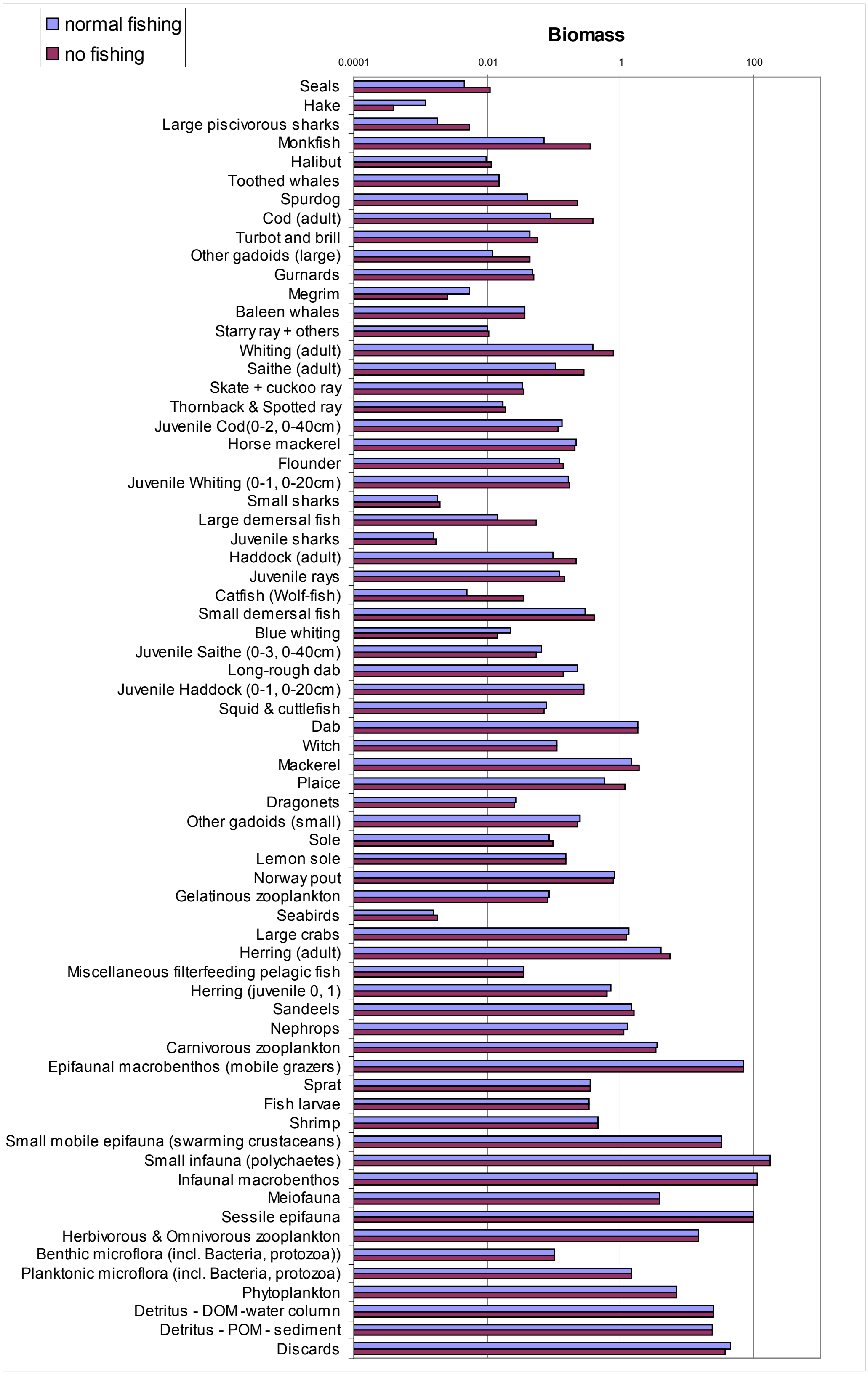


Figure 8: Biomass (t·km^{2}) of functional groups in the model with normal fishing (no MPAs) versus a total fishing ban (the entire North Sea as MPA for all fleets). Species sorted according to trophic level, with the highest on the top. Biomasses plotted are those found at the end of an 18-year run.

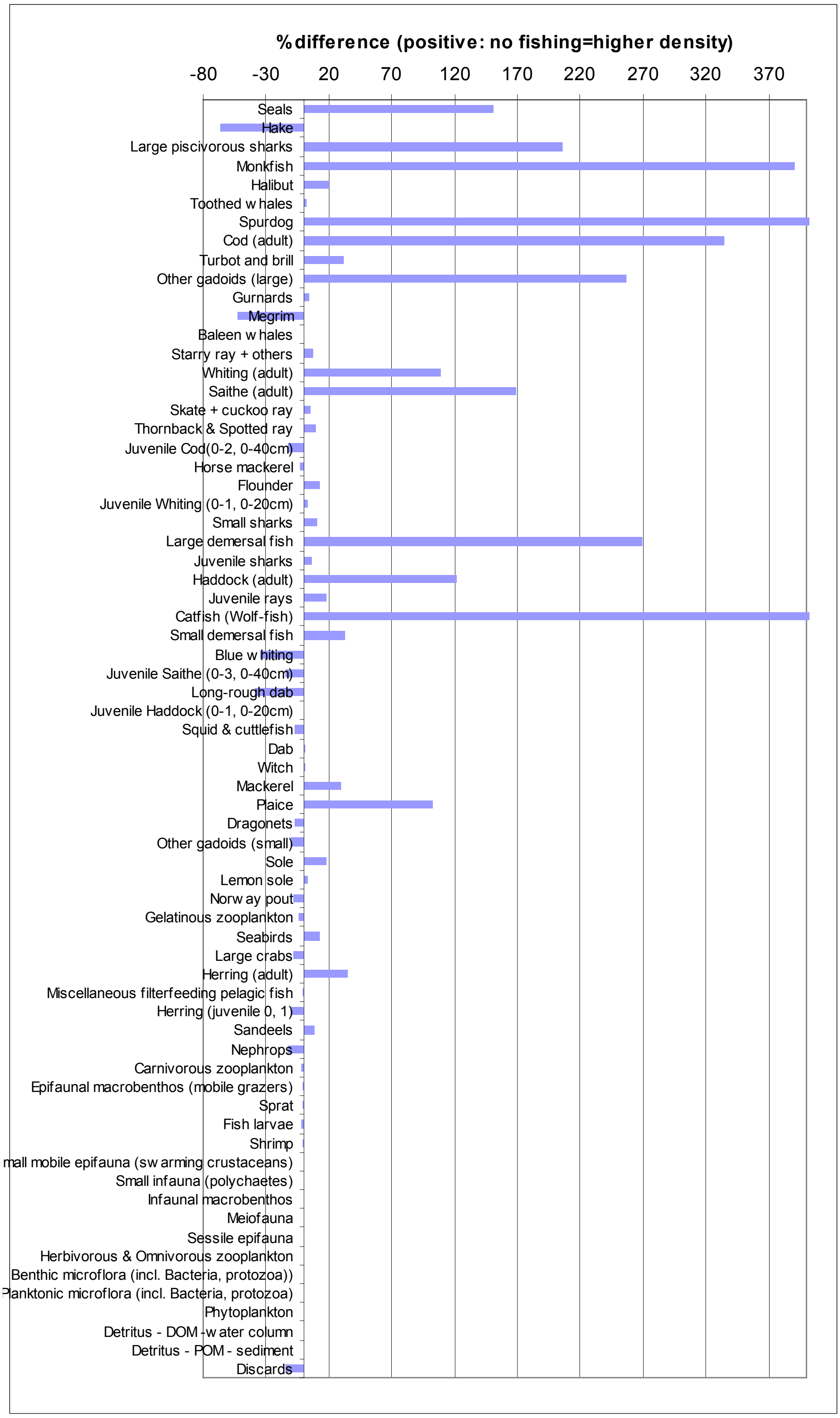


Figure 9 Percentage difference in biomass of functional groups in the model with normal fishing (no MPAs) versus a total fishing ban (the entire North Sea as MPA). Species sorted according to trophic level, with the highest on the top. Differences are calculated from biomasses found at the end of an 18-year run. Bars for groups Spurdog and Catfish (Wolf-fish) are truncated, percentages are 465 and 606, respectively.

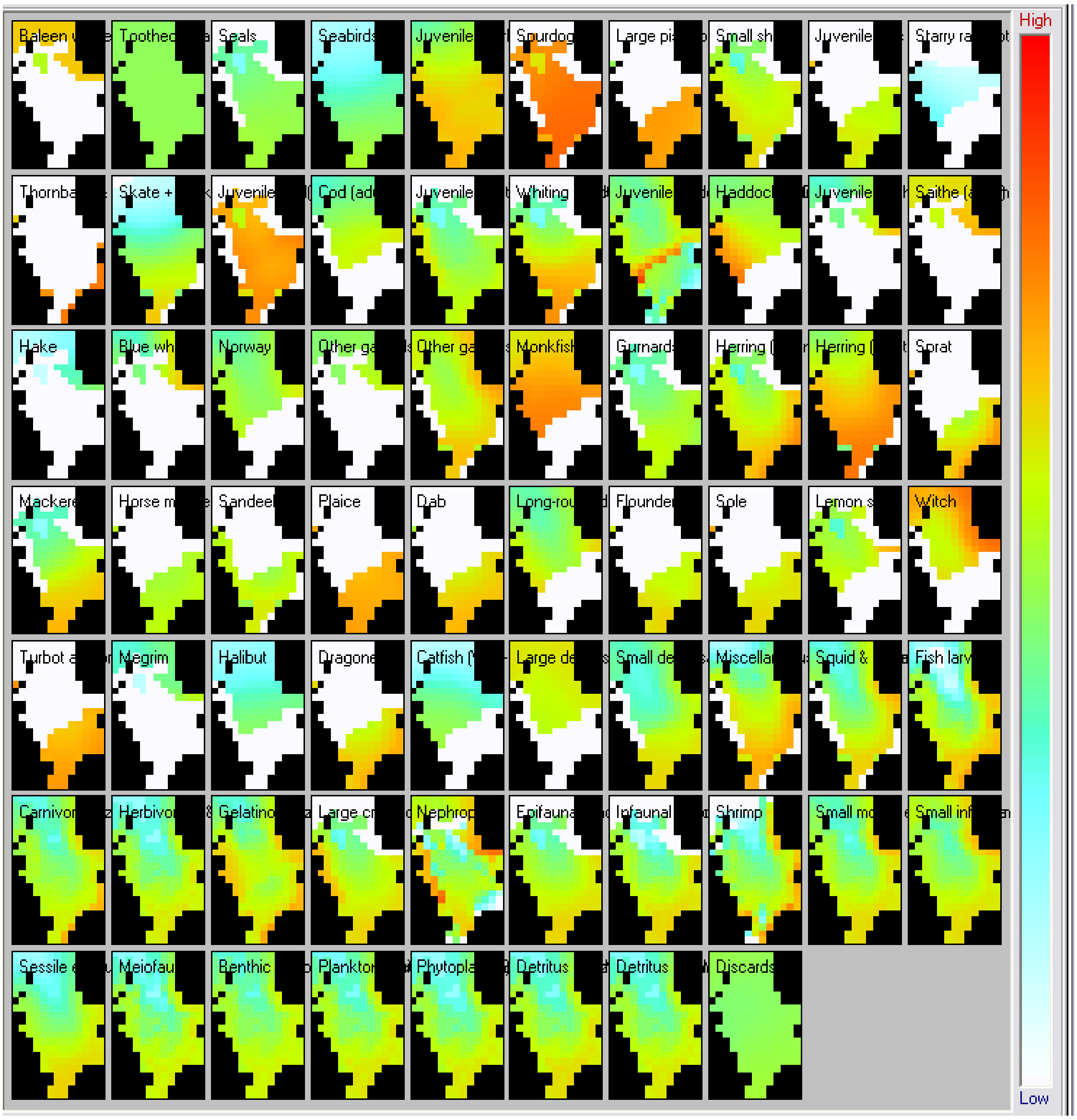


Figure 10: Relative distributions of biomass of groups in the model, after a run of 18 years using constant EcoPath-derived fishing effort. The bar on the right hand side of the figure indicates the color coding, densities are relative to EcoPath-derived initial values.

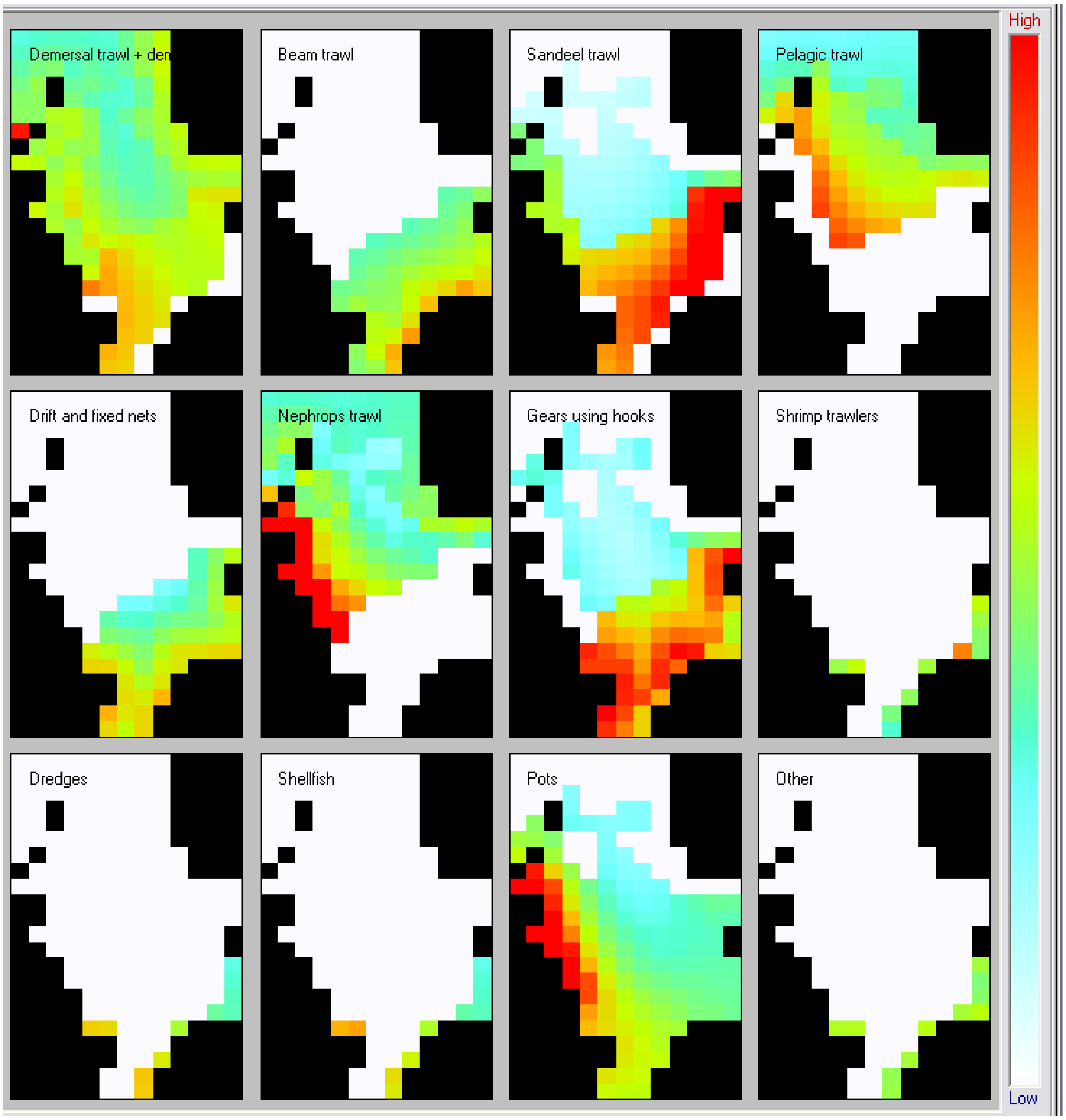


Figure 11: The distribution of fishing effort at the end of an 18-year EcoSpace run using constant EcoPath-derived fishing effort. The bar on the right hand side of the figure indicates the color coding; densities are relative to EcoPath-derived initial values.

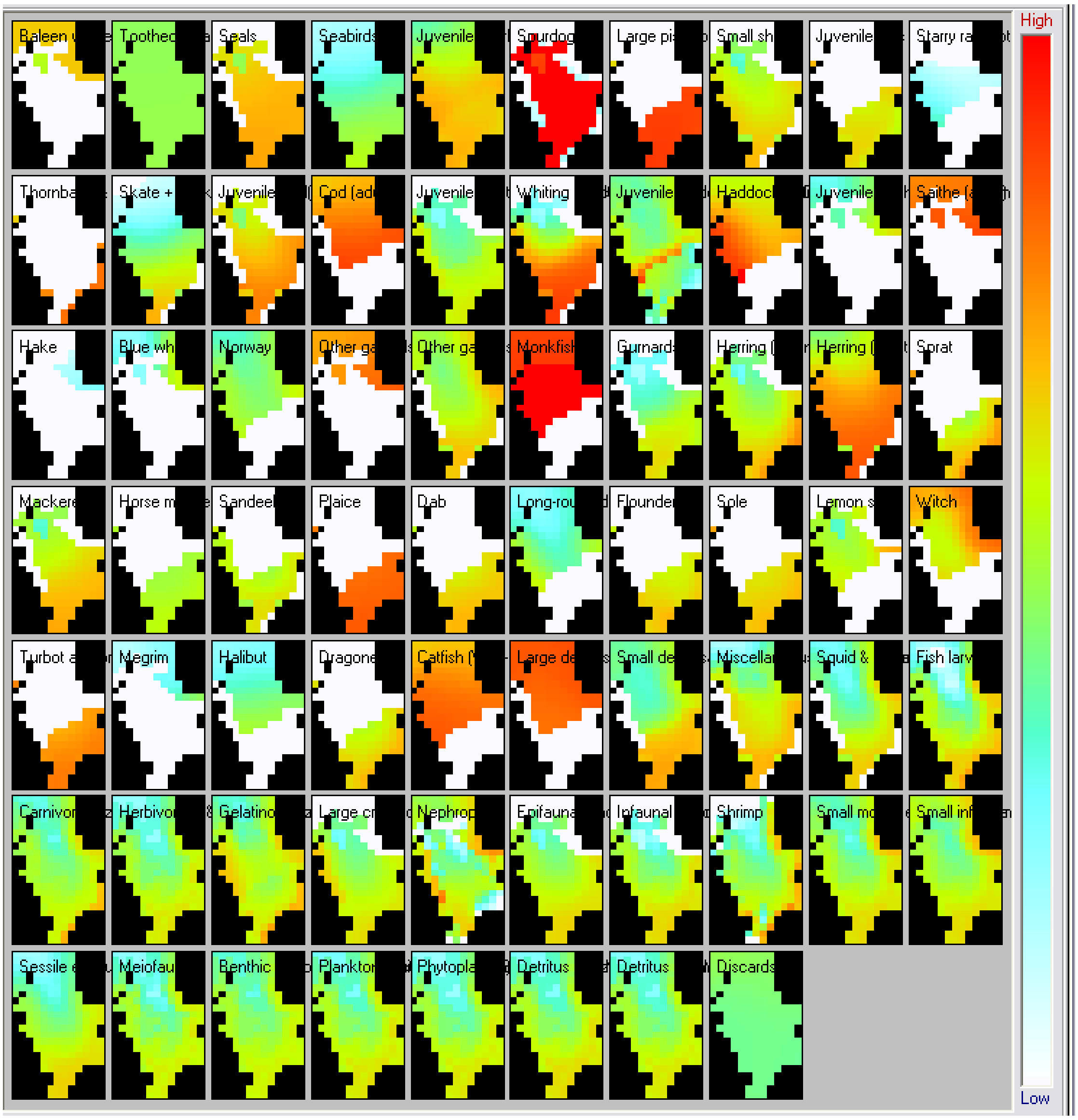


Figure 12: Relative distributions of biomass of groups in the model, after a run of 18 years when no fishing is allowed. The bar on the right hand side of the figure indicates the color coding; densities are relative to EcoPath-derived initial values.

MPAs with complete fishing ban

An MPA, be it a single large or a checkerboard pattern of small MPAs, in which no fleets are allowed to fish, has clear effects on the biomass abundance of the groups in the model (Table 6, Figure 13). For the majority of groups at higher trophic levels, MPAs increase abundance. The lower trophic levels suffer clear food web effects: their abundance generally declines in the presence of MPAs, as the abundance of their predators increases.

One particularly interesting case of indirect effects is adult cod, which shows a density reduction in response to either type of MPA. One explanation could be that by installing the MPAs, the fleets are redistributed to an area with more adult cod, which is reflected by an increase of cod biomass in the catches (Table 6). However, catches of adult cod are also reduced. Another explanation for the decrease of adult cod in the presence of MPAs can be some interaction with another group in the model. For example a competitive effect, where one or more of it's competitors are helped by the MPAs and hence put cod at a disadvantage, or one of its predators which becomes more abundant when MPAs are in place. The exact mechanism behind this result is very difficult to uncover due to the immense complexity of the food web and the vast number of possible indirect interactions. When the model is to be used to study spatial planning scenarios, the mechanisms behind surprising results such as this, must be fully understood so the results can either be disqualified as a model limitation or a realistic ecological effect to be taken into account in the decision making process.

Although for most groups, the direction of the effects of MPAs is independent of the configuration of the MPA, there are clear differences in the magnitude of the effects for many groups (Figure 13). Most often, the (positive or negative) effect of a single large MPA is stronger than that of a network of small MPAs, but several examples of the opposite also show in Figure 13.

Generally, the effects of an MPA become smaller at lower trophic levels. This could be different if effects of bottom disturbance of some of the fishing fleets would be accounted for in the model.

Spatially, the differences between a single large or many small MPAs are not generally very obvious (compare Figure 10 with 16 and 18) on the level of groups, with a few notable exceptions (Plaice, Turbot in the single large MPA scenario). The shapes of the MPAs are clearly discernible in the spatial distribution of the effort (compare Figure 17 with Figure 19).

Independent of the presence of MPAs, the majority of the harvested biomass is extracted by 4 fleets (Figure 14): 'Demersal trawl + dem seine', 'Beam trawl' and 'Sandeel trawl' and 'Pelagic trawl'. A single large MPA decreases the biomass harvested by all these fleets. A network of small MPAs slightly increases the harvested biomass for beam trawlers but decreases the harvest of the other 3, though to a lesser extent than a single large MPA. It is interesting that the beam trawl fleet is positively affected by the 'many small' MPAs, at least in terms of harvested biomass, since it typically operates strongly in the area where the MPAs are located and its spatial distribution is hence strongly affected (compare Figure 11 with Figures 17 and 19). The spatial effort allocation uses the value of the catch, rather than the total biomass, and despite the higher biomass in the catches, the total value of the catches of the beam trawl fleet is lower than that in absence of MPAs.

MPAs where no bottom-disturbing fisheries is allowed

To investigate the effects of specifically banning bottom-disturbing fisheries ('Demersal trawl+dem seine', 'Beam trawl' and 'Sandeel trawl'), we have repeated the two MPA scenarios, but now banned only these fleets from fishing in the MPA. Other fleets are allowed to fish in the MPAs unhindered, which most fleets actually do (Figure 24, Figure 26). The results are very similar to those for MPAs which are completely closed (compare Figure 13 to Figure 20). The similarity is not surprising given the fact that the 3 fleets for which the MPAs are off-limits, are responsible for the majority of the harvested biomass.

In its current form, the MDNS EcoSpace model is fully capable of simulating scenarios such as the above. The results are generally in line with what would be expected: Effects of a single large MPA are stronger than those of a network of many small MPAs. Some results are controversial or surprising, such as the large decrease in cod in the presence of MPAs. This result illustrates a common problem associated with highly complex models such as this: it becomes increasingly difficult to assess whether a specific result such as this should be attributed to a limitation of the model, or to a realistic food web effect. This illustrates the care that must be taken when interpreting the predictions of such a model.

Table 6: Biomass of functional groups in the model with normal fishing (no MPAs) versus a single large MPA versus a set of small MPAs (Figure 7) in which there is a complete fishing moratorium. Species sorted according to trophic level, with the highest on the top. Biomasses plotted are those found at the end of an 18-year run using constant fishing mortality estimated by EcoPath. Empty cells in the harvested biomass indicate groups not affected directly by fishing. Color coding indicates an at least 5% higher (green) or lower (red) biomass with the MPA compared to the non-MPA situation.

	Biomass (t/km2)			**Harvested biomass (t/km2)**		
Group name	**No MPA**	**Single large**	**Many small**	**No MPA**	**Single large**	**Many small**
Seals	0.0045	0.0048	0.0047			
Hake	0.0012	0.0018	0.0017	0.0002	0.0003	0.0003
Large piscivorous sharks	0.0018	0.0023	0.002	0.0004	0.0004	0.0004
Monkfish	0.0708	0.0502	0.057	0.029	0.0229	0.0253
Halibut	0.0097	0.0091	0.0094	0.0003	0.0004	0.0004
Toothed whales	0.0149	0.015	0.015			
Spurdog	0.0407	0.0597	0.0545	0.0181	0.0231	0.0219
Cod (adult)	0.0904	0.0674	0.0813	0.0504	0.0412	0.0481
Turbot and brill	0.0438	0.0466	0.045	0.0032	0.0027	0.0031
Other gadoids (large)	0.0122	0.0108	0.0107	0.0067	0.0066	0.0066
Gurnards	0.0478	0.0491	0.0488	0.0031	0.0031	0.0032
Megrim	0.0055	0.0061	0.0062	0.0005	0.0006	0.0006
Baleen whales	0.0369	0.0369	0.0369			
Starry ray + others	0.01	0.0086	0.0089	0.0006	0.0006	0.0006
Whiting (adult)	0.1062	0.0865	0.0837	0.0479	0.0429	0.0418
Saithe (adult)	0.3844	0.4839	0.4286	0.1771	0.182	0.1793
Skate + cuckoo ray	0.0337	0.0329	0.0337	0.0001	0	0
Thornback & Spotted ray	0.017	0.0173	0.0167	0.0011	0.001	0.0012
Juvenile Cod(0-2, 0-40cm)	0.1321	0.1357	0.1341	0.0084	0.0086	0.0083
Horse mackerel	0.2159	0.214	0.2132	0.0151	0.0131	0.0135
Flounder	0.1232	0.1216	0.1231	0.0314	0.0288	0.0312
Juvenile Whiting (0-1, 0-20cm)	0.1647	0.1651	0.1651	0.0123	0.0114	0.0117
Small sharks	0.0147	0.0104	0.0113	0.0051	0.0041	0.0044
Large demersal fish	0.0018	0.0018	0.0018	0.0002	0.0002	0.0002
Juvenile sharks	0.0965	0.0812	0.0797	0.0683	0.0626	0.06
Haddock (adult)	0.0016	0.0016	0.0016			
Juvenile rays	0.1224	0.1252	0.1257			
Catfish (Wolf-fish)	0.3018	0.3182	0.3116	0.0984	0.0826	0.0955
Small demersal fish	0.005	0.0026	0.0033	0.0016	0.001	0.0012
Blue whiting	0.0221	0.0242	0.024	0.0124	0.0136	0.0142
Juvenile Saithe (0-3, 0-40cm)	0.0653	0.0656	0.0659	0.001	0.001	0.0011
Long-rough dab	0.2245	0.2355	0.2311	0	0	0
Juvenile Haddock (0-1, 0-20cm)	0.2881	0.2881	0.289	0.0523	0.0542	0.0519
Squid & cuttlefish	0.0766	0.0766	0.0765	0.0021	0.0019	0.002
Dab	0.111	0.1103	0.1103	0.0038	0.0044	0.0043
Witch	1.847	1.8589	1.8544	0.0789	0.0582	0.062
Mackerel	1.4622	1.4817	1.4879	0.1827	0.1792	0.1748

	Biomass (t/km2)			Harvested biomass (t/km2)		
Group name	No MPA	Single large	Many small	No MPA	Single large	Many small
Plaice	0.5709	0.6174	0.5927	0.2804	0.1979	0.2678
Dragonets	0.0272	0.0268	0.0269			
Other gadoids (small)	0.2512	0.2534	0.2535	0.0372	0.0361	0.0363
Sole	0.0842	0.0815	0.0838	0.0295	0.0235	0.0286
Lemon sole	0.1495	0.1488	0.149	0.0062	0.007	0.0068
Norway pout	0.8398	0.842	0.845	0.0951	0.1105	0.107
Gelatinous zooplankton	0.0841	0.084	0.0838			
Seabirds	0.0016	0.0016	0.0016			
Large crabs	1.3105	1.3103	1.3092	0.0115	0.0116	0.0116
Herring (adult)	4.0899	4.2432	4.1865	1.0377	1.0113	1.0182
Miscellaneous filterfeeding pelagic fish	0.0348	0.0345	0.0346	0.0067	0.0067	0.0066
Herring (juvenile 0, 1)	0.7139	0.7052	0.7079	0.025	0.0209	0.0235
Sandeels	1.4387	1.4359	1.4562	1.0298	0.8617	0.9517
Nephrops	1.3093	1.3525	1.3395	0.0211	0.0224	0.0221
Carnivorous zooplankton	3.5261	3.5184	3.517			
Epifaunal macrobenthos (mobile grazers)	69.7578	69.7533	69.7257	0.0038	0.0036	0.0036
Sprat	0.3483	0.3373	0.3425	0.1112	0.0838	0.0925
Fish larvae	0.3383	0.338	0.3375			
Shrimp	0.456	0.4526	0.453	0.0453	0.0427	0.0465
Small mobile epifauna (swarming crustaceans)	32.9141	32.9088	32.9053			
Small infauna (polychaetes)	180.003	179.9951	179.9694			
Infaunal macrobenthos	113.23	113.2285	113.2161	0.009	0.0091	0.0091
Meiofauna	3.8238	3.8246	3.8247			
Sessile epifauna	101.1355	101.1416	101.1401	0.0216	0.0219	0.0217
Herbivorous & Omnivorous zooplankton (copepods)	14.7967	14.7967	14.7967			
Benthic microflora (incl. Bacteria, protozoa))	0.1031	0.1031	0.1031			
Planktonic microflora (incl. Bacteria, protozoa)	1.4714	1.4715	1.4715			
Phytoplankton	6.8641	6.8641	6.8641			
Detritus - DOM -water column	25.3525	25.3537	25.3537			
Detritus - POM - sediment	23.6782	23.6797	23.6797			
Discards	43.8123	43.045	43.4034			

Figure 13: Percentage differences in run outcomes between no MPA and a single large MPA and between no MPA and an array of small MPAs, as sketched in Figure 7. Simulation parameters as in Table 6. In the MPAs all fishing is banned. Bars for hake (50%), spurdog (47%) and catfish (wolf-fish) (single mpa: -48%, many small: 34%) are truncated.

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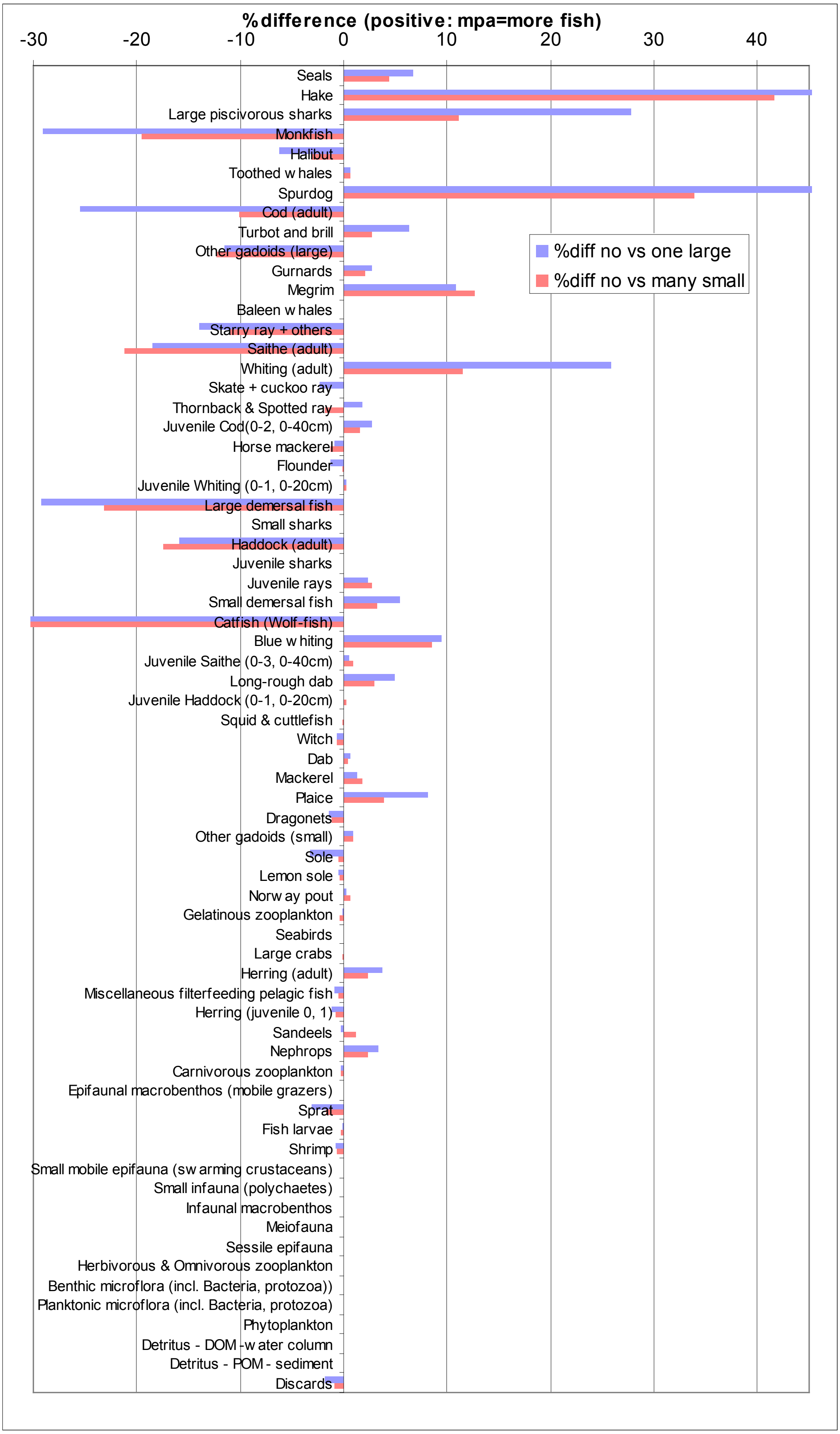
%difference (positive: mpa=more fish)
-30
-20
-10
0
10
20
30
40
%diff no vs one large
%diff no vs many small
Seals
Hake
Large piscivorous sharks
Monkfish
Halibut
Toothed w hales
Spurdog
Cod (adult)
Turbot and brill
Other gadoids (large)
Gurnards
Megrim
Baleen w hales
Starry ray + others
Saithe (adult)
Whiting (adult)
Skate + cuckoo ray
Thornback & Spotted ray
Juvenile Cod(0-2, 0-40cm)
Horse mackerel
Flounder
Juvenile Whiting (0-1, 0-20cm)
Large demersal fish
Small sharks
Haddock (adult)
Juvenile sharks
Juvenile rays
Small demersal fish
Catfish (Wolf-fish)
Blue w hiting
Juvenile Saithe (0-3, 0-40cm)
Long-rough dab
Juvenile Haddock (0-1, 0-20cm)
Squid & cuttlefish
Witch
Dab
Mackerel
Plaice
Dragonets
Other gadoids (small)
Sole
Lemon sole
Norw ay pout
Gelatinous zooplankton
Seabirds
Large crabs
Herring (adult)
Miscellaneous filterfeeding pelagic fish
Herring (juvenile 0, 1)
Sandeels
Nephrops
Carnivorous zooplankton
Epifaunal macrobenthos (mobile grazers)
Sprat
Fish larvae
Shrimp
Small mobile epifauna (sw arming crustaceans)
Small infauna (polychaetes)
Infaunal macrobenthos
Meiofauna
Sessile epifauna
Herbivorous & Omnivorous zooplankton
Benthic microflora (incl. Bacteria, protozoa))
Planktonic microflora (incl. Bacteria, protozoa)
Phytoplankton
Detritus - DOM -w ater column
Detritus - POM - sediment
Discards

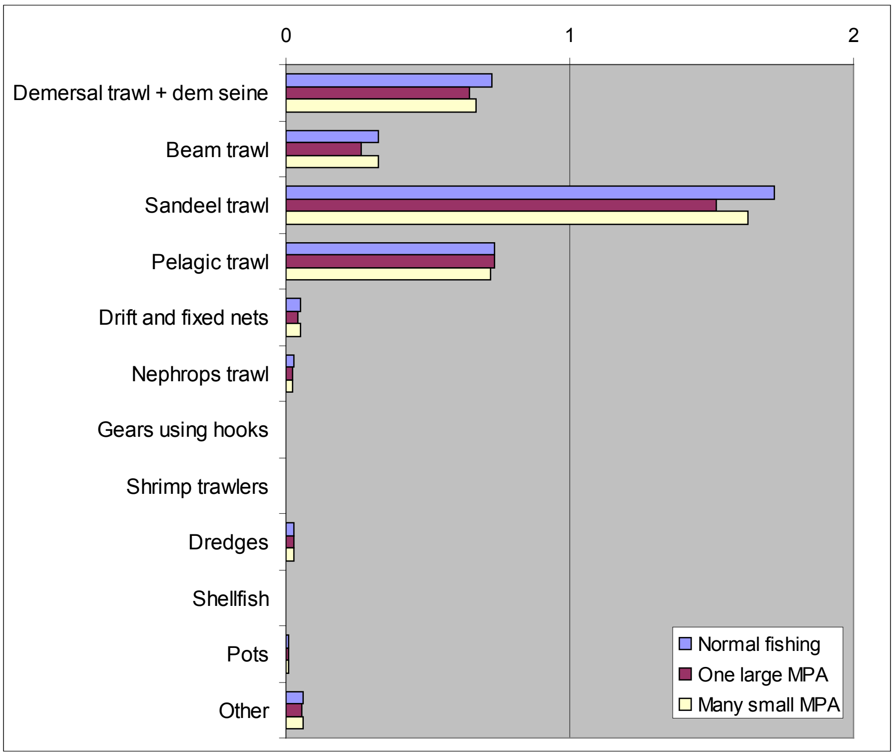

Figure 14: Biomass (t·km^2) harvested by the 12 fleets in the model groups in the model with normal fishing (no MPAs), a single large, or a patchwork of small MPAs (as sketched in Figure 7). All fishing is banned in the MPAs.

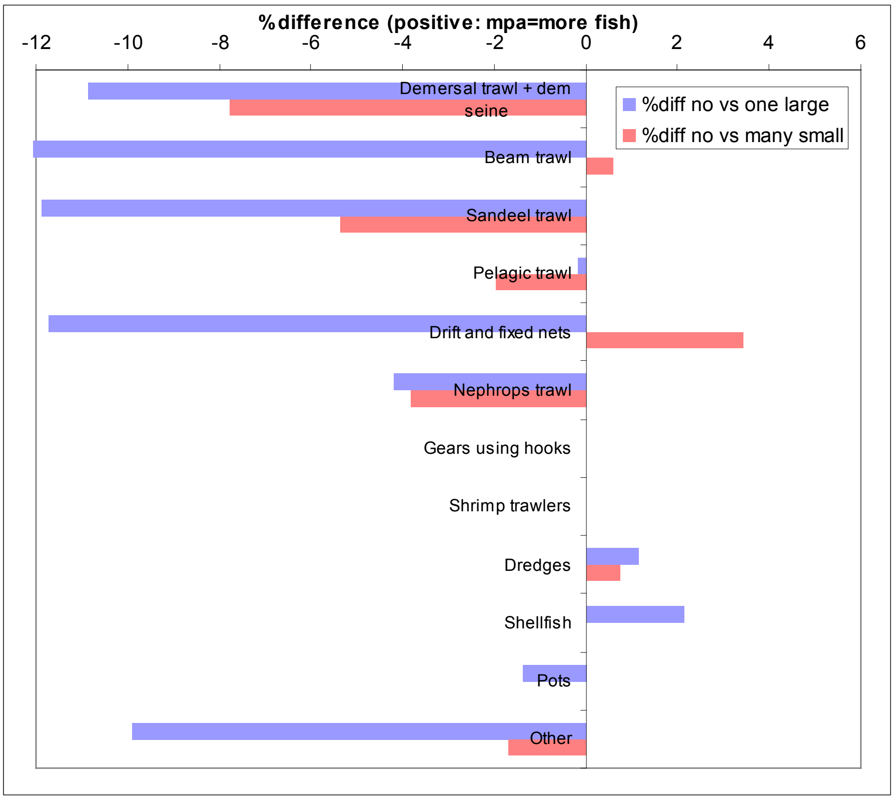

Figure 15: Percentage differences among each of the MPA scenarios versus no MPA, for the harvested biomasses given in Figure 14.

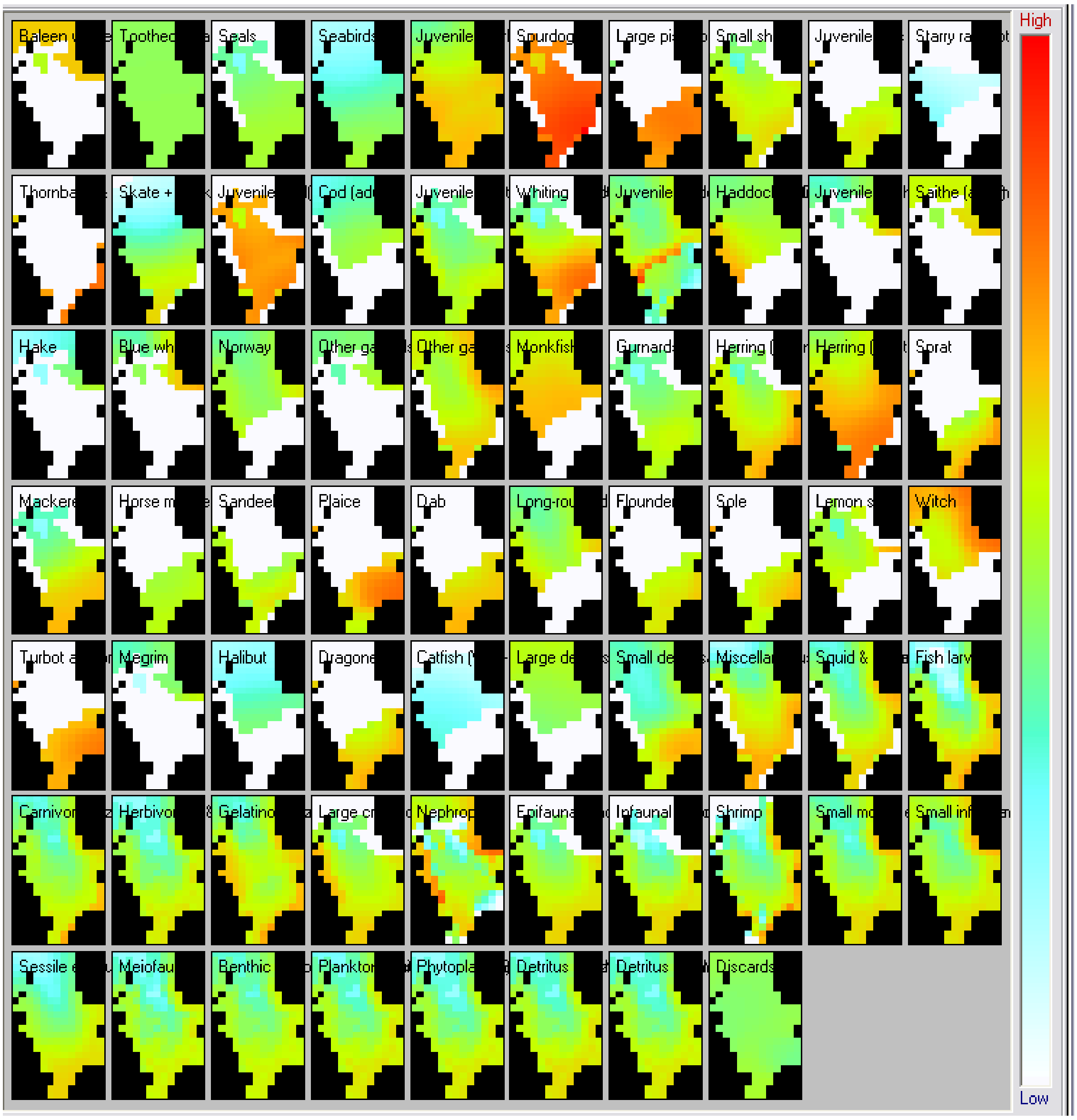

Figure 16: Relative distributions of biomass of groups in the model, after a run of 18 years. A single large MPA is put in place in which none of the fishing fleets operate (as in Figure 7a). The bar on the right hand side of the figure indicates the color coding; densities are relative to EcoPath-derived initial values.

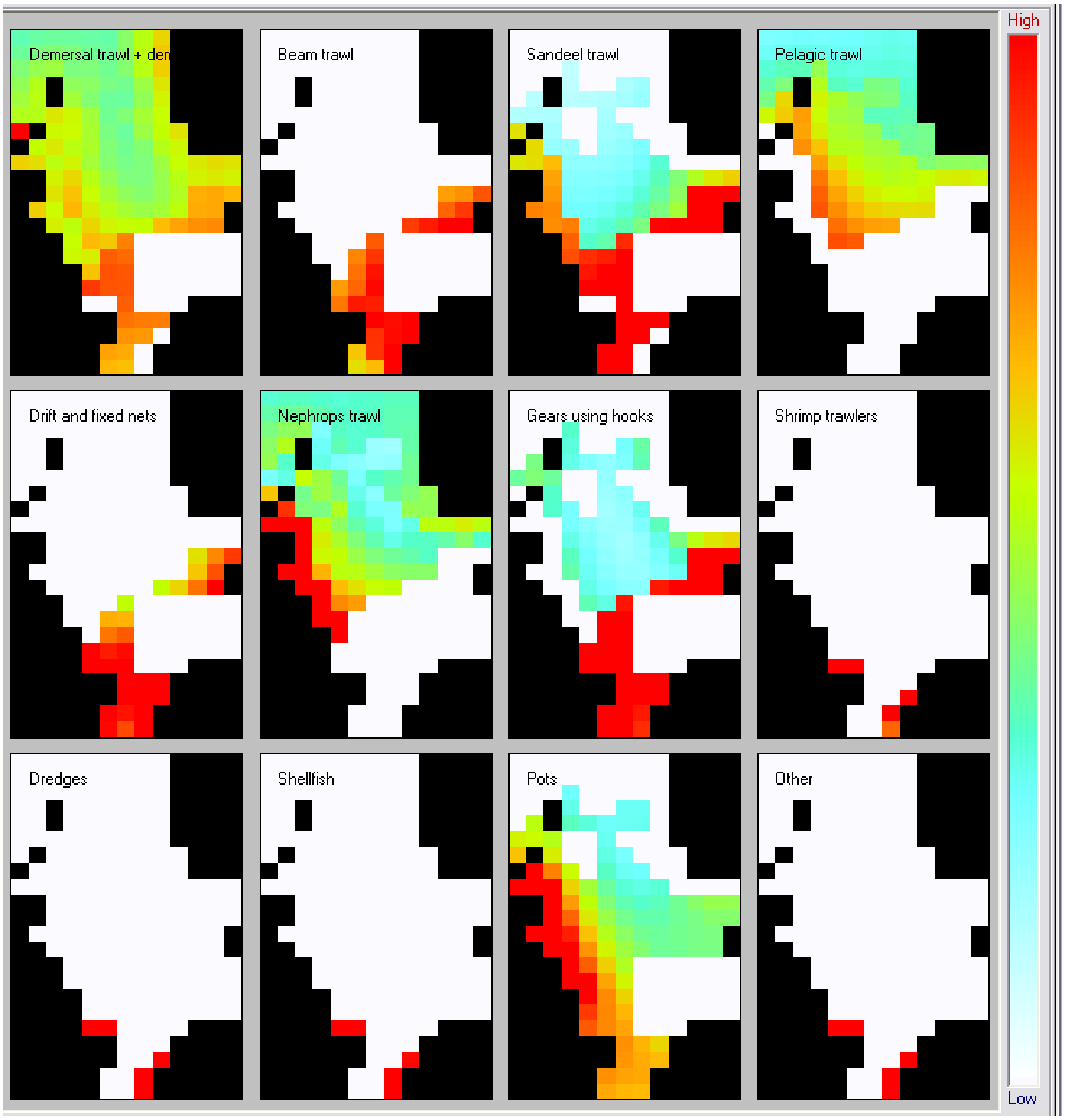

Figure 17: The distribution of fishing effort at the end of an 18-year EcoSpace run. A single large MPA is put in place in which none of the fishing fleets operate (as in Figure 7a). The bar on the right hand side of the figure indicates the color coding; densities are relative to EcoPath-derived initial values.

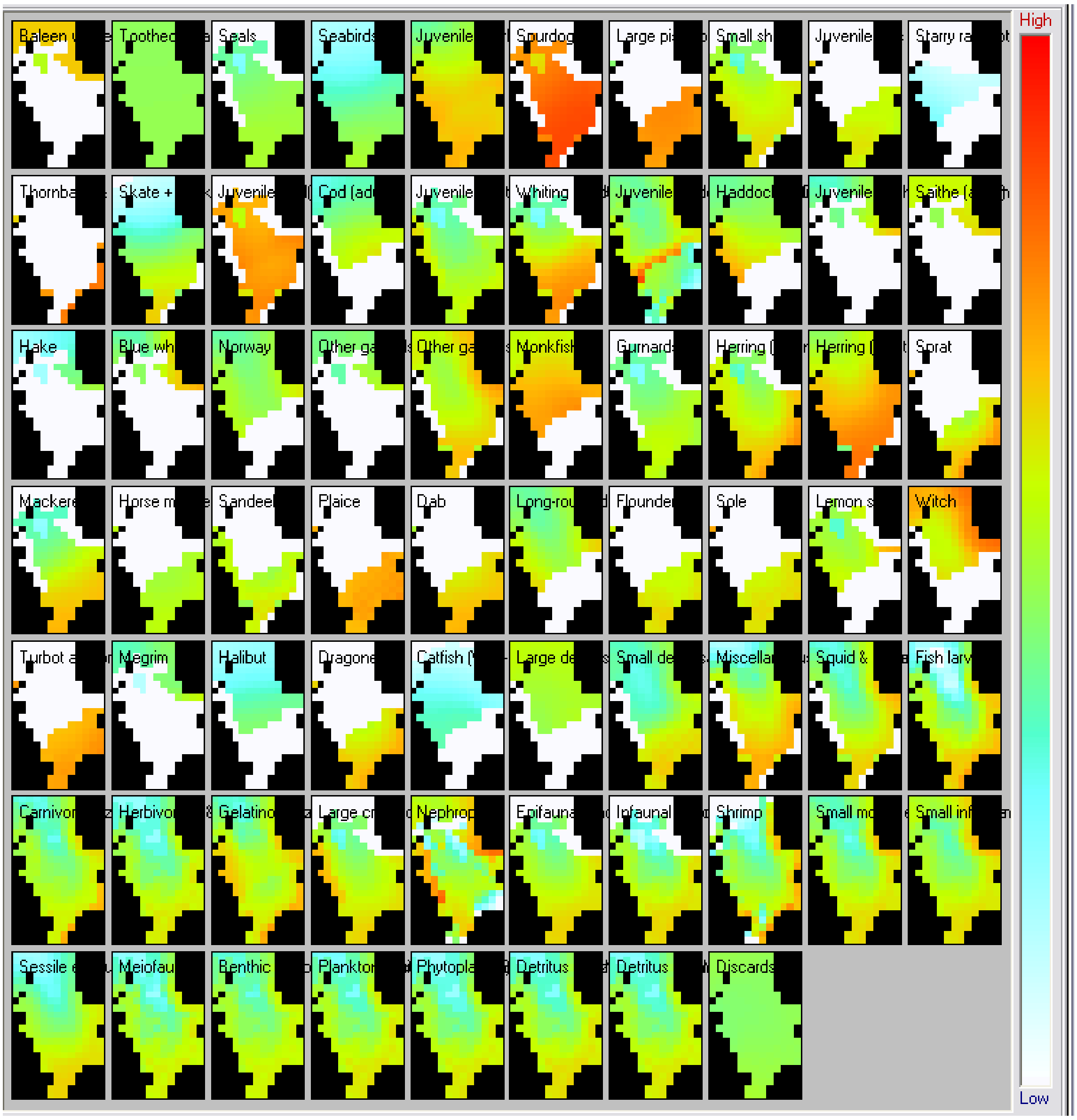

Figure 18: Relative distributions of biomass of groups in the model, after a run of 18. A checkerboard pattern of small MPAs is put in place in which none of the fishing fleets operate (as in Figure 7b). The bar on the right hand side of the figure indicates the color coding; densities are relative to EcoPath-derived initial values.

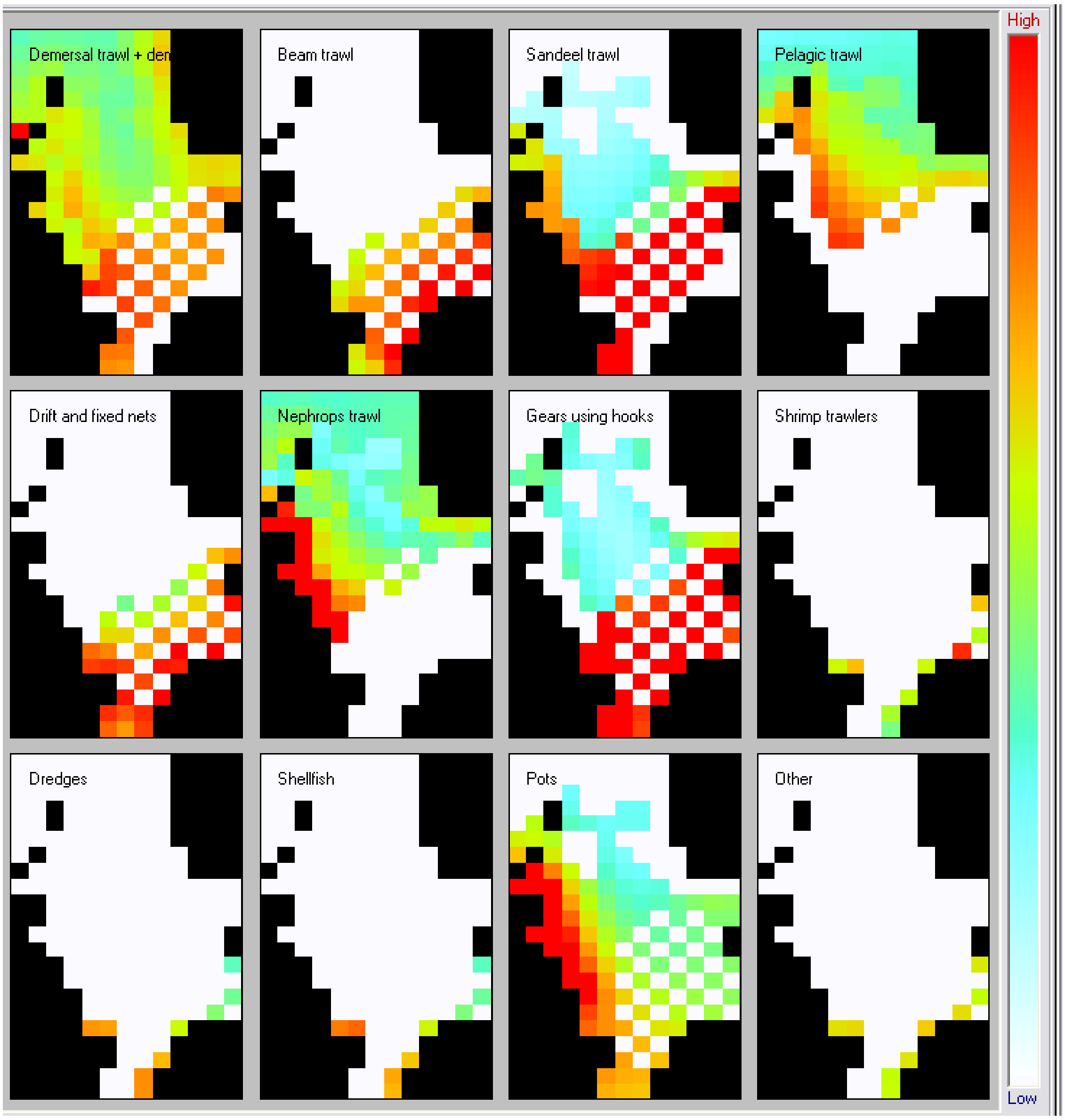

Figure 19: The distribution of fishing effort at the end of an 18-year EcoSpace run. A checkerboard pattern of small MPAs is put in place in which none of the fishing fleets operate (as in Figure 7b). The bar on the right hand side of the figure indicates the color coding; densities are relative to EcoPath-derived initial values.

Table 7 Biomass of functional groups in the model with normal fishing (no MPAs) versus a single large MPA versus a set of small MPAs (Figure 7) in which fishing activities causing bottom disturbance (Fleets 'Demersal trawl + dem seine', 'Beam trawl' and 'Sandeel trawl') are banned. Species sorted according to trophic level, with the highest on the top. Biomasses plotted are those found at the end of an 18-year using constant fishing mortality estimated by EcoPath. Empty cells in the harvested biomass indicate groups not caught by any fishing fleets. Color coding indicates an at least 5% higher (green) or lower (red) biomass with the MPA compared to the non-MPA situation.

	Biomass (t/km2)			**Harvested biomass (t/km2)**		
Group name	**No MPA**	**Single large**	**Many small**	**No MPA**	**Single large**	**Many small**
Seals	0.0045	0.0048	0.0047			
Hake	0.0012	0.0018	0.0017	0.0002	0.0003	0.0003
Large piscivorous sharks	0.0018	0.002	0.0019	0.0004	0.0004	0.0004
Monkfish	0.0708	0.0503	0.0564	0.029	0.0229	0.0251
Halibut	0.0097	0.0091	0.0094	0.0003	0.0004	0.0004
Toothed whales	0.0149	0.015	0.015			
Spurdog	0.0407	0.0585	0.0533	0.0181	0.023	0.0218
Cod (adult)	0.0904	0.0677	0.078	0.0504	0.0413	0.0464
Turbot and brill	0.0438	0.0456	0.0449	0.0032	0.003	0.0031
Other gadoids (large)	0.0122	0.0108	0.0107	0.0067	0.0066	0.0066
Gurnards	0.0478	0.049	0.0489	0.0031	0.003	0.0032
Megrim	0.0055	0.0061	0.0061	0.0005	0.0006	0.0006
Baleen whales	0.0369	0.0369	0.0369			
Starry ray + others	0.01	0.0086	0.009	0.0006	0.0006	0.0006
Whiting (adult)	0.1062	0.0866	0.0853	0.1771	0.1823	0.1817
Saithe (adult)	0.3844	0.4835	0.4311	0.0479	0.0429	0.0425
Skate + cuckoo ray	0.0337	0.0331	0.0337	0.0001	0	0
Thornback & Spotted ray	0.017	0.017	0.0168	0.0011	0.0011	0.0012
Juvenile Cod(0-2, 0-40cm)	0.1321	0.1356	0.1345	0.0084	0.0083	0.0082
Horse mackerel	0.2159	0.2132	0.2131	0.0151	0.0132	0.0135
Flounder	0.1232	0.1213	0.1231	0.0314	0.0288	0.0311
Juvenile Whiting (0-1, 0-20cm)	0.1647	0.1649	0.1649	0.0123	0.0114	0.0117
Small sharks	0.0147	0.0104	0.0113	0.0002	0.0002	0.0002
Large demersal fish	0.0018	0.0019	0.0018	0.0051	0.0041	0.0044
Juvenile sharks	0.0965	0.0811	0.079			
Haddock (adult)	0.0016	0.0016	0.0016	0.0683	0.0625	0.0599
Juvenile rays	0.1224	0.1251	0.1258			
Catfish (Wolf-fish)	0.3018	0.3147	0.3104	0.0016	0.001	0.0012
Small demersal fish	0.005	0.0026	0.0034	0.0984	0.0946	0.0967
Blue whiting	0.0221	0.0242	0.0241	0.0124	0.0136	0.0136
Juvenile Saithe (0-3, 0-40cm)	0.0653	0.0656	0.0656	0.001	0.001	0.0011
Long-rough dab	0.2245	0.2356	0.2321	0	0	0
Juvenile Haddock (0-1, 0-20cm)	0.2881	0.2882	0.2888	0.0523	0.0542	0.0527
Squid & cuttlefish	0.0766	0.0766	0.0765	0.0021	0.0019	0.002
Dab	0.111	0.1103	0.1104	0.0789	0.0583	0.062
Witch	1.847	1.8584	1.8544	0.0038	0.0044	0.0043
Mackerel	1.4622	1.4858	1.4791	0.1827	0.1796	0.1809
Plaice	0.5709	0.6074	0.5944	0.2804	0.205	0.2686
Dragonets	0.0272	0.0268	0.0269			
Other gadoids (small)	0.2512	0.2532	0.2533	0.0372	0.0362	0.0363

	Biomass (t/km2)			Harvested biomass (t/km2)		
Group name	**No MPA**	**Single large**	**Many small**	**No MPA**	**Single large**	**Many small**
Sole	0.0842	0.0811	0.0839	0.0295	0.0248	0.0287
Lemon sole	0.1495	0.1488	0.149	0.0062	0.007	0.0068
Norway pout	0.8398	0.8419	0.8435	0.0951	0.1105	0.1068
Gelatinous zooplankton	0.0841	0.0841	0.0838			
Seabirds	0.0016	0.0016	0.0016			
Large crabs	1.3105	1.3103	1.3103	0.0115	0.0116	0.0115
Herring (adult)	4.0899	4.2445	4.1814	1.0377	1.0109	1.0236
Miscellaneous filterfeeding pelagic fish	0.0348	0.0346	0.0346	0.0067	0.0067	0.0067
Herring (juvenile 0, 1)	0.7139	0.7022	0.7061	0.025	0.0241	0.0244
Sandeels	1.4387	1.4354	1.4564	1.0298	0.8595	0.9518
Nephrops	1.3093	1.3525	1.3432	0.0211	0.0224	0.022
Carnivorous zooplankton	3.5261	3.5228	3.5188			
Epifaunal macrobenthos (mobile grazers)	69.7578	69.7522	69.7237	0.0038	0.0037	0.0037
Sprat	0.3483	0.3381	0.3428	0.1112	0.0846	0.0927
Fish larvae	0.3383	0.338	0.3375			
Shrimp	0.456	0.4527	0.453	0.0453	0.0426	0.0452
Small mobile epifauna (swarming crustaceans)	32.9141	32.9085	32.9049			
Small infauna (polychaetes)	180.003	179.994	179.9671			
Infaunal macrobenthos	113.23	113.2277	113.2141	0.009	0.009	0.009
Meiofauna	3.8238	3.8246	3.8247			
Sessile epifauna	101.1355	101.1405	101.1395	0.0216	0.0216	0.0216
Herbivorous & Omnivorous zooplankton (copepods)	14.7967	14.7967	14.7967			
Benthic microflora (incl. Bacteria, protozoa))	0.1031	0.1031	0.1031			
Planktonic microflora (incl. Bacteria, protozoa)	1.4714	1.4715	1.4715			
Phytoplankton	6.8641	6.8641	6.8641			
Detritus - DOM -water column	25.3525	25.3536	25.3536			
Detritus - POM - sediment	23.6782	23.6796	23.6797			
Discards	43.8123	43.0969	43.4621			

Figure 20: Percentage differences in run outcomes between no MPA and a single large MPA and between no MPA and an array of small MPAs, as sketched in Figure 7. Simulation parameters as in Table 7. The fleets 'Demersal trawl + dem seine', 'Beam trawl' and 'Sandeel trawl' are banned from the MPAs, but other fleets can operate inside the MPAs unrestrictedly. Bar for hake (50%) is truncated.

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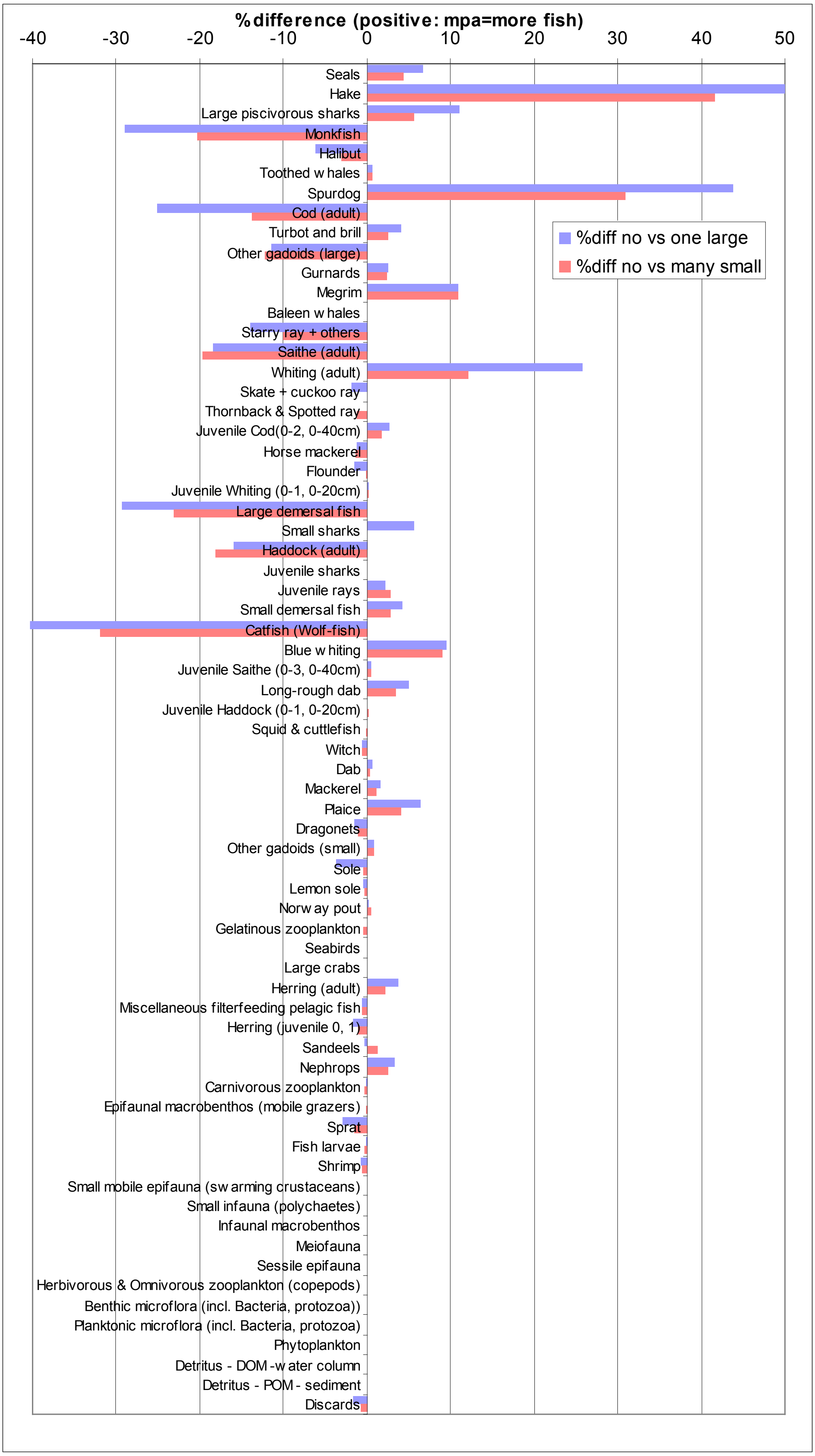
%difference (positive: mpa=more fish)
-40
-30
-20
-10
0
10
20
30
40
50
Seals
Hake
Large piscivorous sharks
Monkfish
Halibut
Toothed w hales
Spurdog
Cod (adult)
Turbot and brill
Other gadoids (large)
Gurnards
Megrim
Baleen w hales
Starry ray + others
Saithe (adult)
Whiting (adult)
Skate + cuckoo ray
Thornback & Spotted ray
Juvenile Cod(0-2, 0-40cm)
Horse mackerel
Flounder
Juvenile Whiting (0-1, 0-20cm)
Large demersal fish
Small sharks
Haddock (adult)
Juvenile sharks
Juvenile rays
Small demersal fish
Catfish (Wolf-fish)
Blue w hiting
Juvenile Saithe (0-3, 0-40cm)
Long-rough dab
Juvenile Haddock (0-1, 0-20cm)
Squid & cuttlefish
Witch
Dab
Mackerel
Plaice
Dragonets
Other gadoids (small)
Sole
Lemon sole
Norw ay pout
Gelatinous zooplankton
Seabirds
Large crabs
Herring (adult)
Miscellaneous filterfeeding pelagic fish
Herring (juvenile 0, 1)
Sandeels
Nephrops
Carnivorous zooplankton
Epifaunal macrobenthos (mobile grazers)
Sprat
Fish larvae
Shrimp
Small mobile epifauna (sw arming crustaceans)
Small infauna (polychaetes)
Infaunal macrobenthos
Meiofauna
Sessile epifauna
Herbivorous & Omnivorous zooplankton (copepods)
Benthic microflora (incl. Bacteria, protozoa))
Planktonic microflora (incl. Bacteria, protozoa)
Phytoplankton
Detritus - DOM -w ater column
Detritus - POM - sediment
Discards
%diff no vs one large
%diff no vs many small

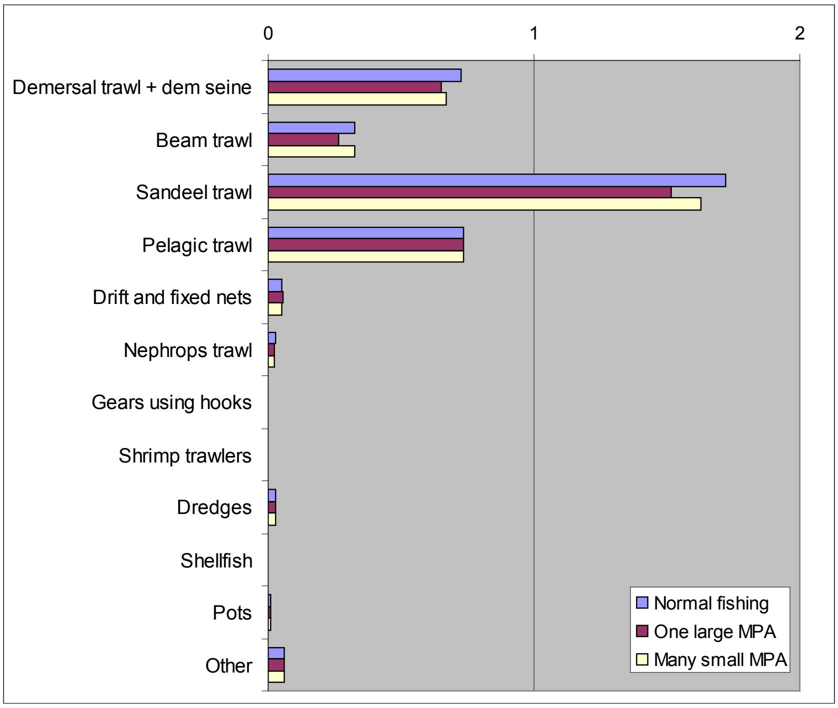

Figure 21: Biomass (t·km^{2}) harvested by the 12 fleets in the model groups in the model with normal fishing (no MPAs), a single large, or a patchwork of small MPAs (as sketched in Figure 7). The fleets 'Demersal trawl + dem seine', 'Beam trawl' and 'Sandeel trawl' are banned from the MPAs, but other fleets can operate inside the MPAs unrestrictedly.

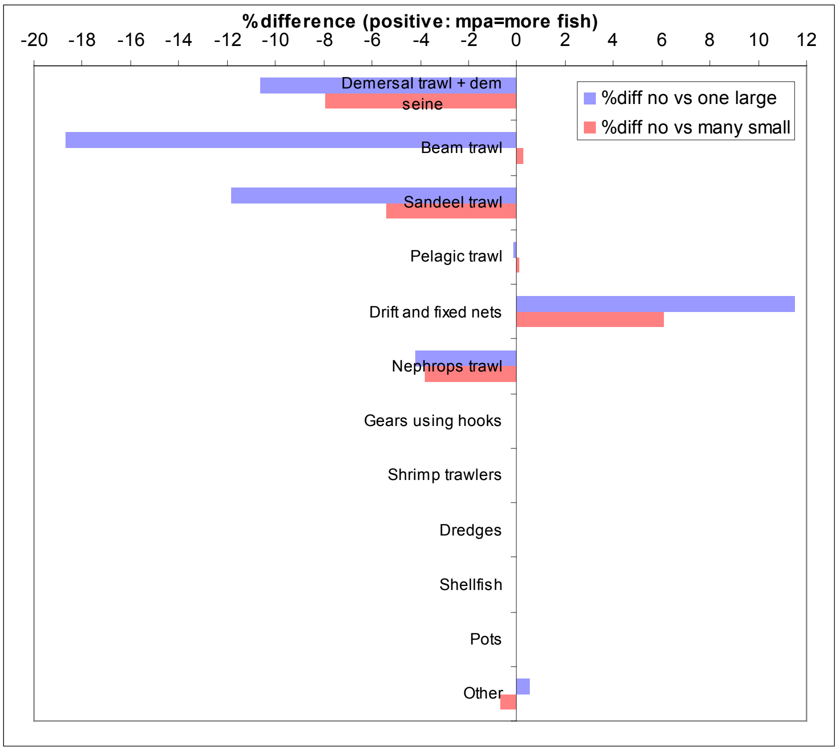

Figure 22: Percentage differences among the 3 scenarios for the harvested biomasses given in Figure 21. The fleets 'Demersal trawl + dem seine', 'Beam trawl' and 'Sandeel trawl' are banned from the MPAs, but other fleets can operate inside the MPAs unrestrictedly.

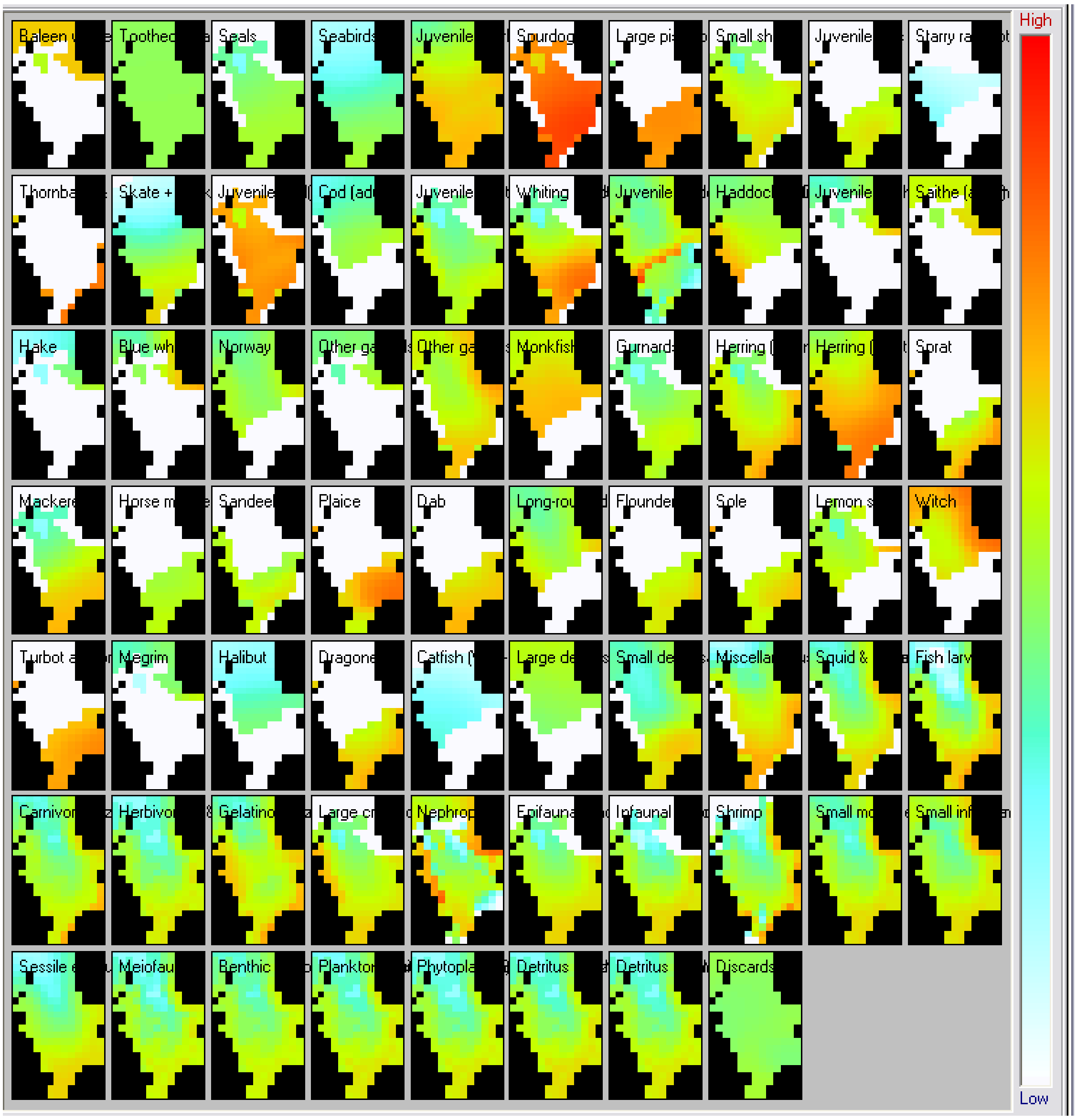

Figure 23: Relative distributions of biomass of groups in the model, after a run of 18 years. A single large MPA is put in place (as in Figure 7a). The fleets 'Demersal trawl + dem seine', 'Beam trawl' and 'Sandeel trawl' are banned from the MPAs, but other fleets can operate inside the MPAs unrestrictedly. The bar on the right hand side of the figure indicates the color coding, densities are relative to EcoPath-derived initial values.

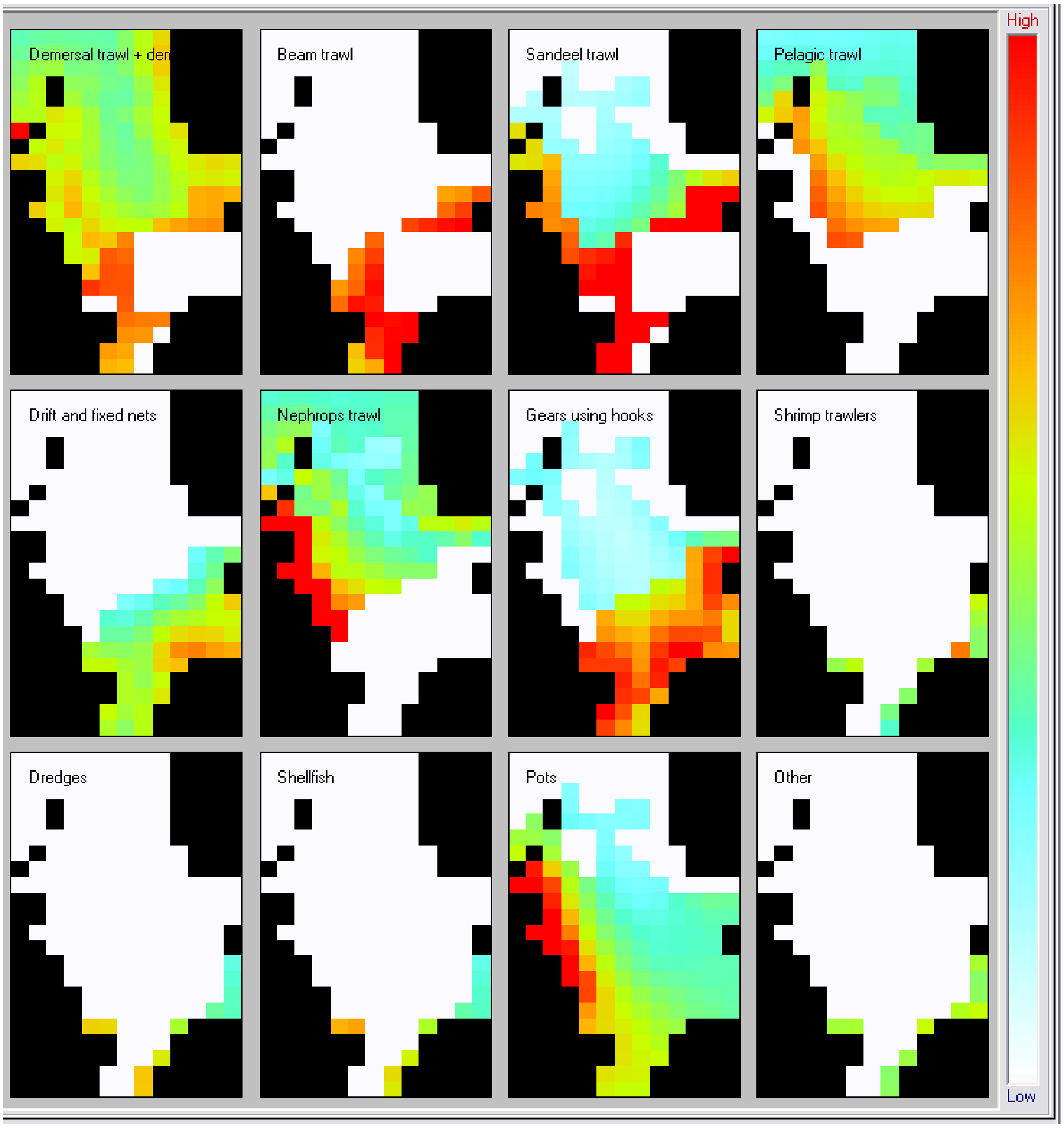

Figure 24: The distribution of fishing effort at the end of an 18-year EcoSpace run. A single large MPA is put in (as in Figure 7a). The fleets 'Demersal trawl + dem seine', 'Beam trawl' and 'Sandeel trawl' are banned from the MPAs, but other fleets can operate inside the MPAs unrestrictedly. The bar on the right hand side of the figure indicates the color coding, densities are relative to EcoPath-derived initial values.

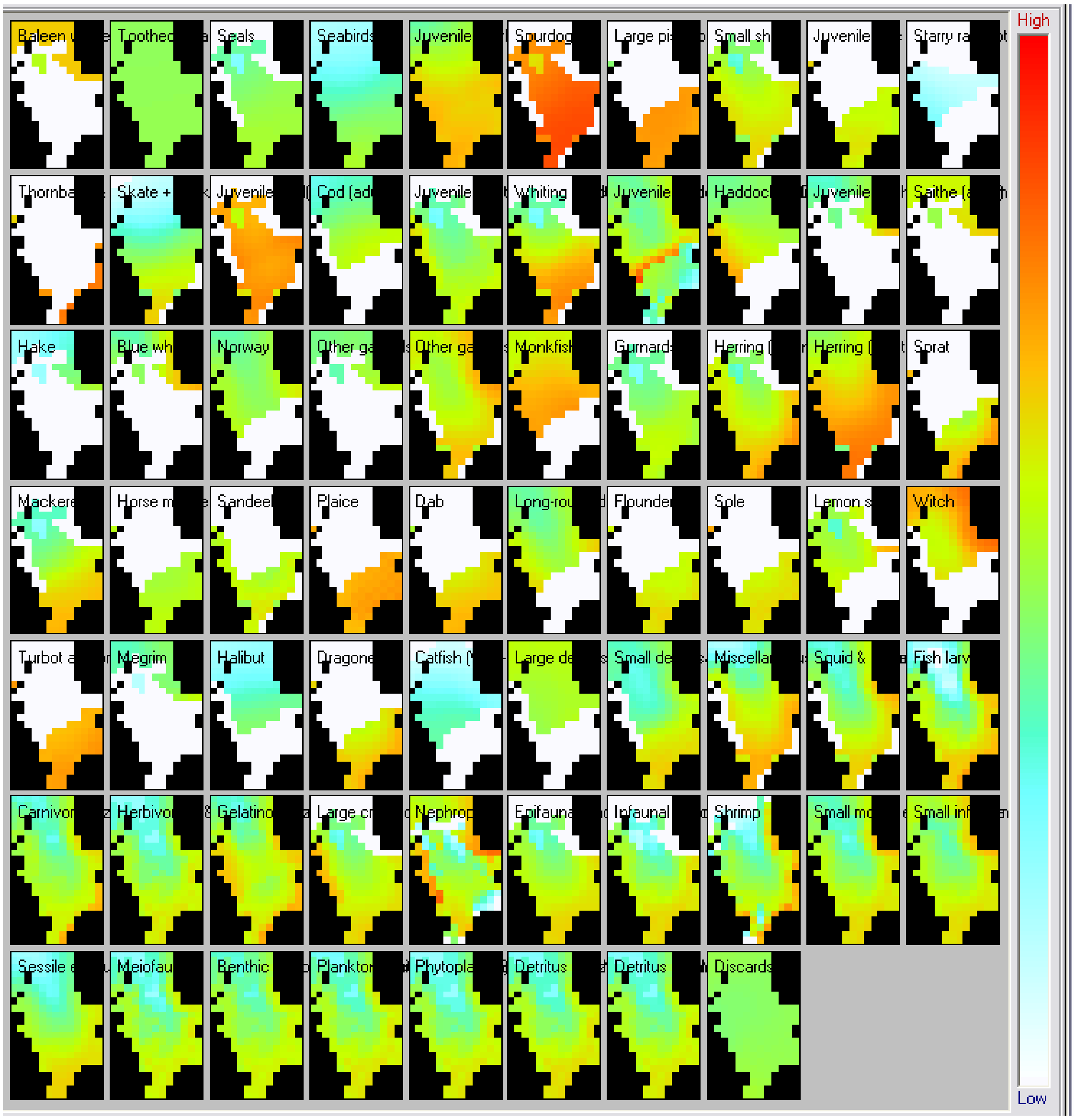

Figure 25: Relative distributions of biomass of groups in the model, after a run of 18 years. A checkerboard pattern of small MPAs is put in place (as in Figure 7b). The fleets 'Demersal trawl + dem seine', 'Beam trawl' and 'Sandeel trawl' are banned from the MPAs, but other fleets can operate inside the MPAs unrestrictedly. The bar on the right hand side of the figure indicates the color coding, densities are relative to EcoPath-derived initial values.

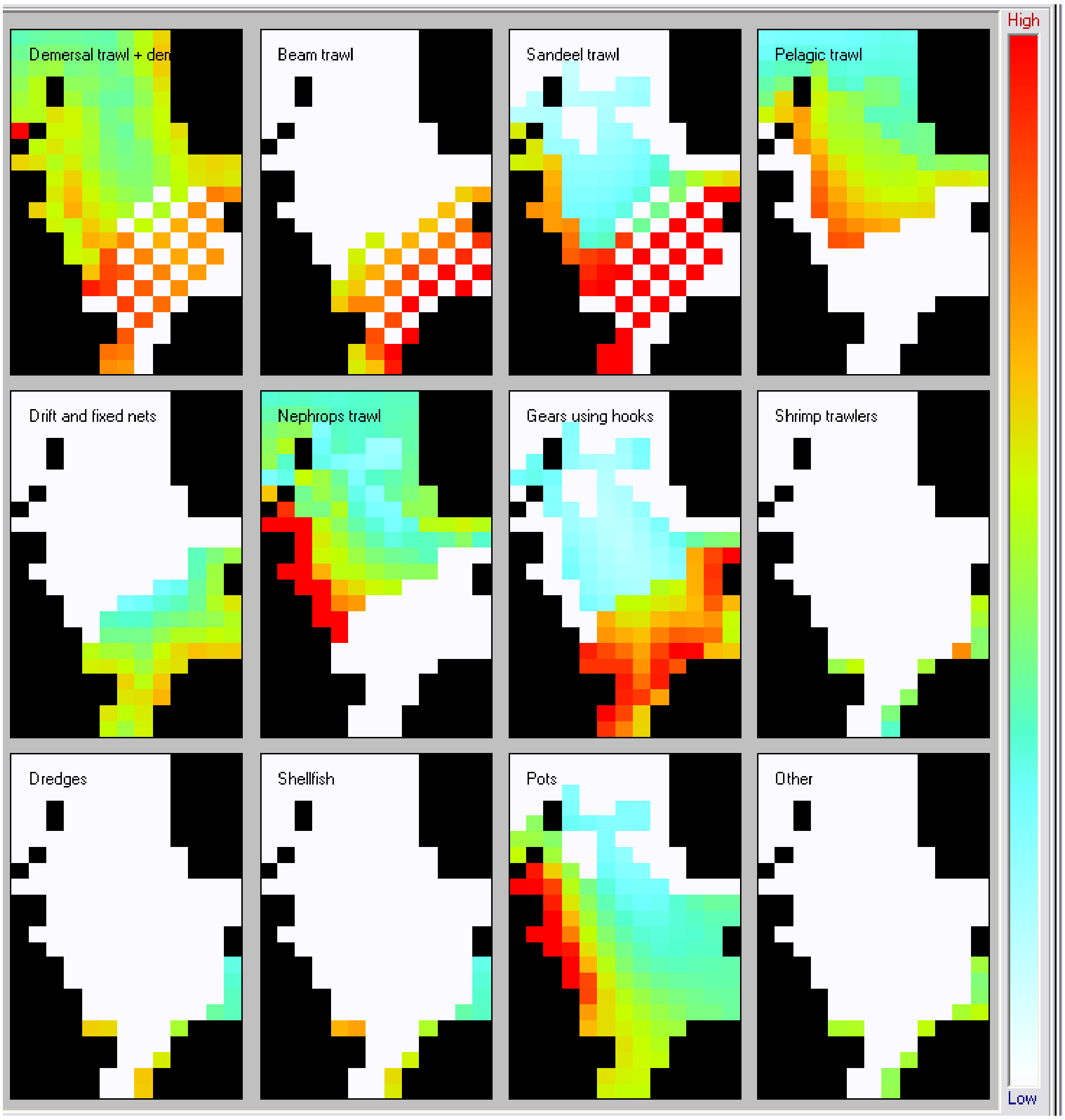

Figure 26: The distribution of fishing effort at the end of an 18-year EcoSpace run. A checkerboard pattern of small MPAs is put in place (as in Figure 7b). The fleets 'Demersal trawl + dem seine', 'Beam trawl' and 'Sandeel trawl' are banned from the MPAs, but other fleets can operate inside the MPAs unrestrictedly. The bar on the right hand side of the figure indicates the color coding, densities are relative to EcoPath-derived initial values.

3.2 Primary production scenarios

3.2.1 Method

The following primary production modification scenarios have been formulated by PBL:

1. a 50% increase in primary productivity;
2. a reference scenario with unmodified primary productivity;
3. a 25% decrease in primary productivity;
4. a 50% reduction in primary productivity.

The primary productivity forcing which can be used to modify primary productivity in EcoSim does not carry over to EcoSpace (S. Mackinson, CEFAS-Lowestoft, UK, *personal communication*). The only other way to change global primary productivity is to change the production/biomass ratio in the EcoPath model. However, even a small change in these values leads to an unbalanced model with ecotrophic efficiencies >1, meaning that the biomass production in the model is smaller than biomass lost through mortality. Such an unbalanced model cannot serve as a starting point for EcoSim or EcoSpace, because not all biomass flow is accounted for.

Studying eutrophication scenarios is only possible by substantially adapting the existing model. An example of how this can be done can be found in Libralato & Solidoro (2009). For the study of such scenarios it is necessary to add nutrients as a functional group in the model. This group then functions as food for the primary producers, but is not reduced by their consumption. This requires a recalibration of the model.

In order to explore the consequences of the eutrophication scenarios as far as possible with the current model, we have studied them using the EcoSim MDNS model. We produced runs of 50 year starting with the EcoPath-derived food web, and using a forcing function to modify the rate of primary production according to the scenarios above.

3.2.2 Results

When the rate of primary production is increased to 150% of the original EcoPath-derived value, we see an increase in biomass in virtually all groups in the model (Figure 27). Many groups stay at an increased level throughout the simulation, but a few return to a value close to the start value. The rate at which groups change is very variable, with some groups reaching the new equilibrium value in a fraction of the simulation duration, while others are still increasing gradually at the end of the simulation.

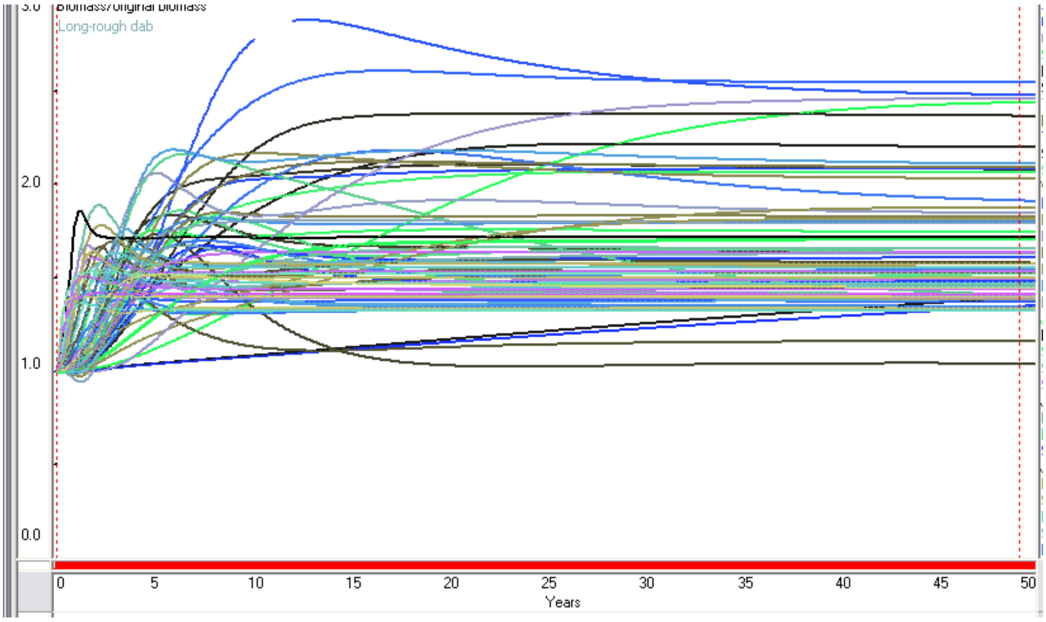

Figure 27: Ecosim output for 50 years using the ecopath-derived values as starting point, and increasing the rate of primary production to 150% of that value. Colored lines represent groups in the model.

When rate of primary production is unchanged, biomass of all groups rapidly stabilizes and settles on values within ~10% of their initial EcoPath-derived value (see Figure 1).

A clear negative trend can be observed in the general development of the biomass in the different groups when the rate of primary production is reduced by 25% (Figure 28). The majority of groups eventually stabilizes at values higher than 0, but almost all are lower than the initial values. Notable exceptions are adult Whiting and Haddock.

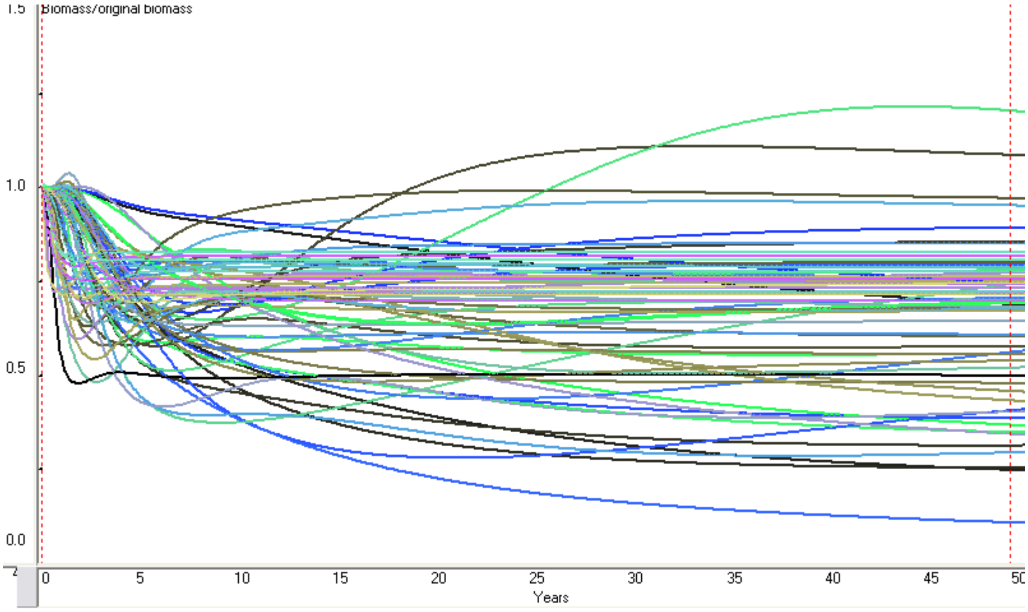

Figure 28: Ecosim output for 50 years using the ecopath-derived values as starting point, and decreasing the rate of primary production to 75% of that value. Colored lines represent groups in the model.

The effects of a 50% decrease in rate of primary production are substantially more severe than those of the 25% reduction (Figure 29). A large number of groups declines to very low levels within 10 years of the start of the simulation. A few groups eventually come back to levels close to their ecopath-derived value, but the bulk remains at values less than half that.

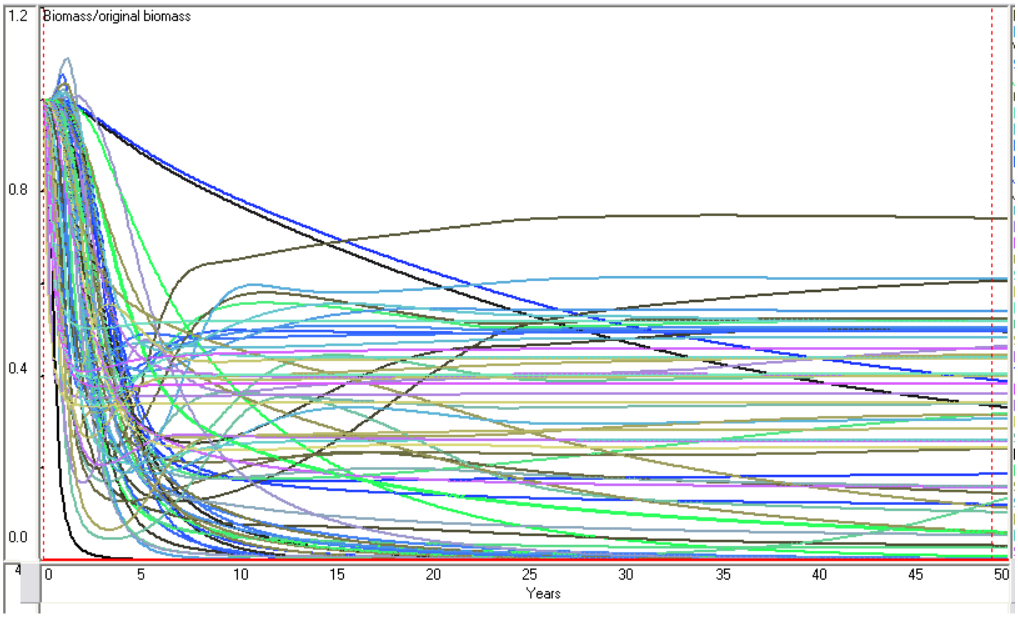

Figure 29: Ecosim output for 50 years using the ecopath-derived values as starting point, and decreasing the rate of primary production to 50% of that value. Colored lines represent groups in the model.

As Table 8 clearly shows, in the nutrient increase scenario (150%), the biomass of all groups is increased by between 7.7% (adult whiting) and 140% (adult saithe). In both nutrient depletion scenarios, all groups in the model are reduced in biomass, but in the relatively mild scenario no groups are lost completely and the majority of groups are within 50% of their reference density. In more severe nutrient depletion scenario, where rate of primary production is halved, a total of 14 groups completely disappear from the model system (a percentage change of 100%), while the vast majority is brought down to less than half their reference biomass density. There is no clear trophic level pattern in the effects of both the in- and the decreased rate of primary production scenarios. This indicates that the effects of changes at the bottom of the food web are transferred throughout the food web.

A linear regression between results of the 50% and 75% reduction in the rate of primary productivity explains a substantial fraction of the difference between the two (Figure 30). This indicates that the effects of the strong reduction are qualitatively similar to those at less reduction in the rate of primary production, but of a larger magnitude.

Table 8: Final biomass values of model groups in the reference and modified rate of primary production scenarios. The colors indicate an in- (green) or decrease (red) relative to the reference scenario at the end of a 50-year ecosim simulation. The percentages (% change) give the percentage change in final density compared to the reference scenario.

	Final biomass				**% change**		
Group name	**Reference**	**150%**	**75%**	**50%**	**150%**	**75%**	**50%**
Seals	0.0089	0.0195	0.0029	0.0001	119.1	-67.4	-98.9
Hake	0.0148	0.0228	0.0098	0.0004	54.1	-33.8	-97.3
Large piscivorous sharks	0.0023	0.0047	0.0005	0	104.3	-78.3	-100.0
Monkfish	0.0439	0.0803	0.0237	0	82.9	-46.0	-100.0
Halibut	0.0357	0.0619	0.0151	0.002	73.4	-57.7	-94.4
Toothed whales	0.0174	0.0229	0.0127	0.0067	31.6	-27.0	-61.5
Spurdog	0.0173	0.0286	0.0116	0.001	65.3	-32.9	-94.2
Cod (adult)	0.1843	0.3988	0.0659	0	116.4	-64.2	-100.0
Turbot and brill	0.0599	0.1139	0.016	0	90.2	-73.3	-100.0
Other gadoids (large)	0.0481	0.0684	0.0364	0.006	42.2	-24.3	-87.5
Gurnards	0.0799	0.1087	0.0578	0.0309	36.0	-27.7	-61.3
Megrim	0.0363	0.0628	0.0138	0	73.0	-62.0	-100.0
Baleen whales	0.0688	0.0933	0.0461	0.0225	35.6	-33.0	-67.3
Starry ray + others	0.1198	0.2266	0.0342	0	89.1	-71.5	-100.0
Whiting (adult)	0.3401	0.3664	0.3823	0.213	7.7	12.4	-37.4
Saithe (adult)	0.2332	0.5597	0.0237	0	140.0	-89.8	-100.0
Skate + cuckoo ray	0.0549	0.1031	0.0174	0	87.8	-68.3	-100.0
Thornback & Spotted ray	0.0745	0.1374	0.0255	0	84.4	-65.8	-100.0
Juvenile Cod(0-2, 0-40cm)	0.0842	0.1291	0.0676	0.0392	53.3	-19.7	-53.4
Horse mackerel	0.5937	0.7797	0.4428	0.2929	31.3	-25.4	-50.7
Flounder	0.2757	0.4567	0.1388	0	65.7	-49.7	-100.0
Juvenile Whiting (0-1, 0-20cm)	0.2289	0.2943	0.1732	0.1161	28.6	-24.3	-49.3
Small sharks	0.0021	0.0032	0.0016	0.0002	52.4	-23.8	-90.5
Large demersal fish	0.0184	0.0308	0.0073	0.002	67.4	-60.3	-89.1
Juvenile sharks	0.001	0.0015	0.0009	0.0002	50.0	-10.0	-80.0
Haddock (adult)	0.1067	0.1583	0.125	0.0329	48.4	17.2	-69.2
Juvenile rays	0.2883	0.467	0.1495	0.0007	62.0	-48.1	-99.8
Catfish (Wolf-fish)	0.0165	0.0344	0.0048	0	108.5	-70.9	-100.0
Small demersal fish	0.3595	0.5327	0.2334	0.1049	48.2	-35.1	-70.8
Blue whiting	0.0811	0.0929	0.0777	0.0594	14.5	-4.2	-26.8

	Final biomass				% change		
Group name	**Reference**	**150%**	**75%**	**50%**	**150%**	**75%**	**50%**
Juvenile Saithe (0-3, 0-40cm)	0.2909	0.4435	0.1625	0.0088	52.5	-44.1	-97.0
Long-rough dab	0.379	0.5711	0.2386	0.0558	50.7	-37.0	-85.3
Juvenile Haddock (0-1, 0-20cm)	0.2962	0.3899	0.2253	0.1412	31.6	-23.9	-52.3
Squid & cuttlefish	0.083	0.1243	0.0538	0.0253	49.8	-35.2	-69.5
Dab	3.3057	5.3932	1.8245	0.0063	63.1	-44.8	-99.8
Witch	0.0937	0.1665	0.0442	0	77.7	-52.8	-100.0
Mackerel	1.8066	2.6109	1.1747	0.4151	44.5	-35.0	-77.0
Plaice	0.8048	1.47	0.3375	0.0006	82.7	-58.1	-99.9
Dragonets	0.0474	0.0622	0.0428	0.0275	31.2	-9.7	-42.0
Other gadoids (small)	0.1996	0.2759	0.1532	0.0999	38.2	-23.2	-49.9
Sole	0.1645	0.2111	0.1344	0.0854	28.3	-18.3	-48.1
Lemon sole	0.3377	0.5469	0.1964	0.0164	61.9	-41.8	-95.1
Norway pout	1.426	1.8454	1.1006	0.6969	29.4	-22.8	-51.1
Gelatinous zooplankton	0.0672	0.0914	0.0496	0.0294	36.0	-26.2	-56.3
Seabirds	0.0033	0.0066	0.0007	0	100.0	-78.8	-100.0
Large crabs	1.4316	1.9664	1.0686	0.7012	37.4	-25.4	-51.0
Herring (adult)	1.965	3.0432	1.3867	0.006	54.9	-29.4	-99.7
Miscellaneous filterfeeding pelagic fish	0.03	0.0417	0.023	0.0138	39.0	-23.3	-54.0
Herring (juvenile 0, 1)	0.6444	0.9623	0.3804	0.0918	49.3	-41.0	-85.8
Sandeels	3.2086	4.56	2.1919	1.0566	42.1	-31.7	-67.1
Nephrops	1.166	1.6388	0.8177	0.4383	40.5	-29.9	-62.4
Carnivorous zooplankton	3.4418	4.5016	2.66	1.6344	30.8	-22.7	-52.5
Epifaunal macrobenthos (mobile grazers)	83.5033	122.6721	56.1229	22.1471	46.9	-32.8	-73.5
Sprat	0.5983	0.9593	0.3017	0.0605	60.3	-49.6	-89.9
Fish larvae	0.3254	0.5519	0.161	0	69.6	-50.5	-100.0
Shrimp	0.5327	0.7668	0.359	0.1292	43.9	-32.6	-75.7
Small mobile epifauna (swarming crustaceans)	31.8575	44.9107	22.8995	11.9609	41.0	-28.1	-62.5
Small infauna (polychaetes)	159.2419	221.3411	116.743	65.9995	39.0	-26.7	-58.6
Infaunal macrobenthos	145.4816	211.172	98.423	35.4079	45.2	-32.3	-75.7
Meiofauna	4.262	5.4963	3.3223	1.7987	29.0	-22.0	-57.8
Sessile epifauna	114.6644	171.8243	73.2637	16.6411	49.8	-36.1	-85.5
Herbivorous & Omnivorous zooplankton (copepods)	16.1363	22.2972	11.7203	5.7696	38.2	-27.4	-64.2
Benthic microflora (incl. Bacteria, protozoa))	0.1093	0.1393	0.0869	0.0546	27.4	-20.5	-50.0
Planktonic microflora (incl. Bacteria, protozoa)	1.576	2.0981	1.1961	0.6705	33.1	-24.1	-57.5
Phytoplankton	7.496	10.4711	5.3756	2.5628	39.7	-28.3	-65.8
Detritus - DOM -water column	27.6761	38.022	20.2125	10.0813	37.4	-27.0	-63.6
Detritus - POM - sediment	25.7804	35.2181	18.9456	9.6032	36.6	-26.5	-62.7
Discards	52.4279	72.3649	37.3317	12.1854	38.0	-28.8	-76.8

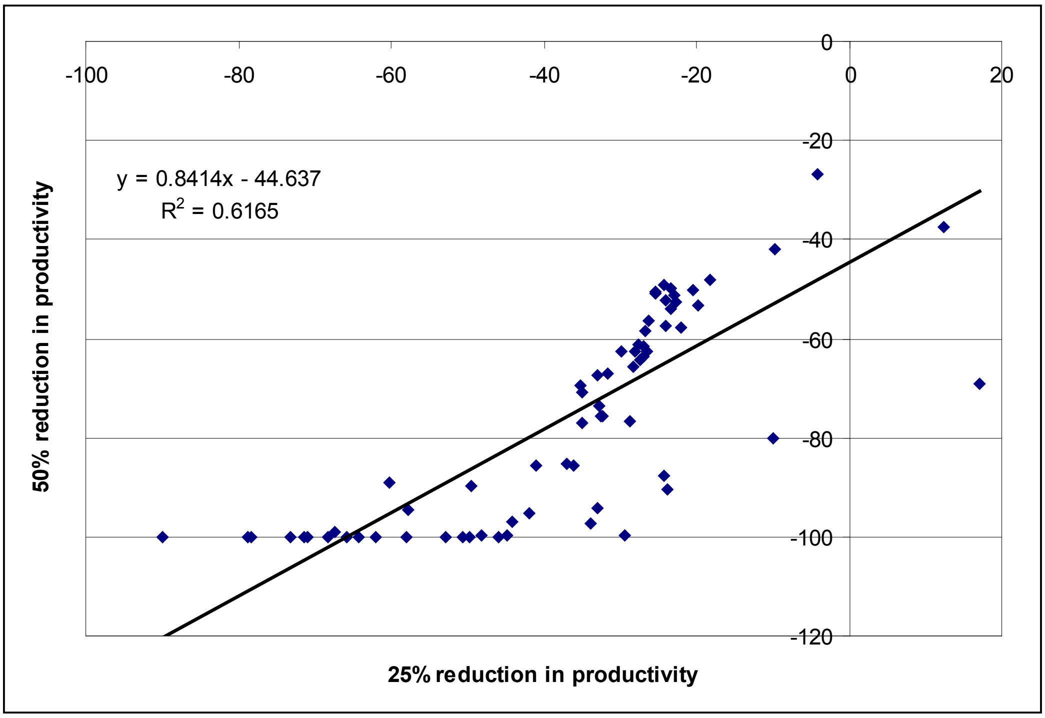

Figure 30: Consistency check between effects of 25 and 50% reduction in productivity. Plotted are the percentages change relative to the reference scenario (last two columns in Table 7) for all groups. The line is a linear regression, the equation and R^2-value are shown in the plot.

4 Biodiversity indicators in the MDNS model

The MDNS model delivers output for a large number of (to be specific 68) groups (functional, species and sub-species) and detritus and discards. Some of these directly link with the biodiversity indicators used to quantify nature quality (Wortelboer, 2009), some can be linked to the MDNS model output through their prey, and some are absent and have no link in the MDNS model. Table 6 shows the link of the biodiversity indicators given in the Nature Balance (Wortelboer, 2009) with the output of the MDNS model.

Table 6. Indicator species of Nature Balance and their appearance in the MDNS model.

Taxonomic group	Species/groups	Included in MDNS	Prey included in MDNS
Phytoplankton	Chlorophyll-a	no	no
	Phaeocystis	no	no
	Dinophysis acuminata	no	no
Macrobenthos	*Macoma balthica* Baltic macoma	no	no
	Arctica islandica	no	no
	Crangon crangon Brown shrimp	yes[0]	
Fish	Acipenser sturio European sea sturgeon	no	no
	Raya clavata Thornback ray	yes	
	Cupea harengus Herring	yes[1]	
	Gadus morhua Cod	yes[1]	
	Pleuronectes platessa Plaice	yes	
Birds	*Uria aalge* Common murre	yes[2]	
	Somateria mollissima Common eider	no	no
	Charadius alexandrinus Keltish plover	no	no
	Arenaria interpres Ruddy turnstone	no	no
	Sterna sandvicensis Sandwich tern	yes[2]	
	Sterna hirundo Common tern	yes[2]	
	Sterna albifrons Little tern	yes[2]	
	Fulmarcus glacialis Nothern fulmar	yes[2]	

Taxonomic group	Species/groups	Included in MDNS	Prey included in MDNS
Marine mammals	*Phocoena phocoena* Harbour porpoise	yes[3]	
	Balaenoptera acutorostrata Mink whale	yes[4]	
	Globicephala melas Long-finned pilot whale	no	yes
	Tursiops trucatus Bottlenose dolphin	no	yes
	Lagenorhynchus albirostris White-beaked dolphin	yes[3]	
	Phoca vitulina Harbour seal	yes[5]	
	Halichoerus grypus Grey seal	yes[5]	

0- in group shrimps; 1- in two size classes; 2- in group birds; 3- in group toothed whales; 4- in group of baleen whales
5- in group seals

Based on Table 6 we conclude that there is a good link between the indicators used by Nature Balance and MDNS (with the exception of phytoplankton, macrobenthos (except the commercially exploited brown shrimp), the commercially not exploited European sturgeon, and the non-fish eating bird species common eider, keltish plover and ruddy turnstone) which implies that the output of MDNS can be reformulated to study the impact of fishery scenarios on these indicators.

We estimated the impact of the different fishery (and primary production) scenarios for the Nature Quality indicators by taking the direct result from the MDNS model for the species included in the model (Figures 31- 33). For those species that are included in the MDNS model as part of a group instead of a single species we took the output of that group as a representative for the indicator species. For fish species that are divided into juvenile and adult stages in the MDNS model we used the output generated for the adults (in long lived species adult mortality in general has a much higher influence on the population viability than juveniles or reproduction) to represent the impact on the indicator species.

The Pilot whale and bottlenose dolphin belong to the group of toothed whales. These species are not included in the MDNS model. For the bottlenose dolphin this is motivated by its low occurrence in the North Sea and absence of data on its abundance (Mackinson & Daskalov, 2008).

Pilot whales are opportunistic feeders that may exploit any locally abundant prey, but they are primarily consumers of squid. The squid species *Illex illecebrosus* and *Loligo peulei* dominate the diet of pilot whales in the Northwest Atlantic, but they also eat Atlantic mackerel (*Scomber scombrus*) and Atlantic herring (*Clupea harengus*) (Mercer 1975; Gannon *et al*., 1997a,1997b).

Little is known of the feeding habits of the Bottlenose dolphin but in general squid, small schooling and non-schooling fish and crustaceans are the most important diet components. Diet composition may vary with season, geographical location, age and sex and, in females, reproductive status (Kastelein *et al*., 2002). Based on stomach contents of 25 animals stranded on the coast of Normandy De Pierrepont *et al*., (2008) found mainly gadoid fish (*Trisopterus* sp.), gobies and mackerel (*Scomber scombrus*), but almost no cephalopods occurred in the diet and commercially important species like cuttlefish and common squid were very scarce. Blue whiting (*Micromesistius poutassou*) and hake (*Merluccius merluccius*) were the most important food species found in stomachs of animals stranded on the north Spanish coastline (82 individuals Santos *et al.*, 2007).

For the Pilot whale and Bottllenose dolphin, the food species are included in the MDNS model. For these two species we present the impact of scenarios as if they were a member of the group of toothed whales and give an index based on how well their food species are doing. Obviously such an index has limited value, since we only have information on how well the food species are doing. For extreme responses in food species (such as their disappearance) such an index is informative (no food implying very bad conditions for the indicator species), for all the intermediate responses in food species, the impact on the indicator species is difficult to assess without more direct information on the density of the indicator species, its food needs per time etc.

We estimated the impact of the different scenarios on the index for the pilot whale assuming a diet of 90% squid and 10% fish and for the Bottlenose dolphin based on a diet of 10% squid, 80% fish and 10% crustaceans (shrimps and small mobile epifauna).

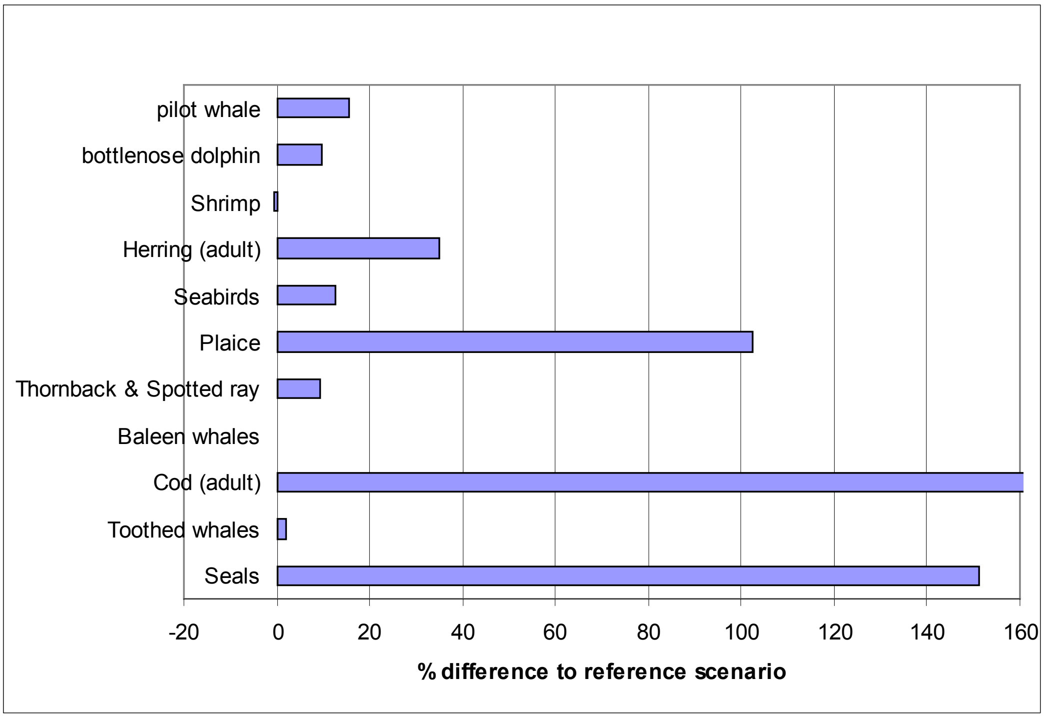

Figure 31: The relative effects of a total fishing ban on biodiversity indicator species as used in the 'Nature Balance'. The category 'pilot whale' was calculated as the sum of its main food sources squid & cuttlefish, herring and mackerel. The x-axis is cut off at 160% for clarity, but cod increases up to 334% in absence of fishing.

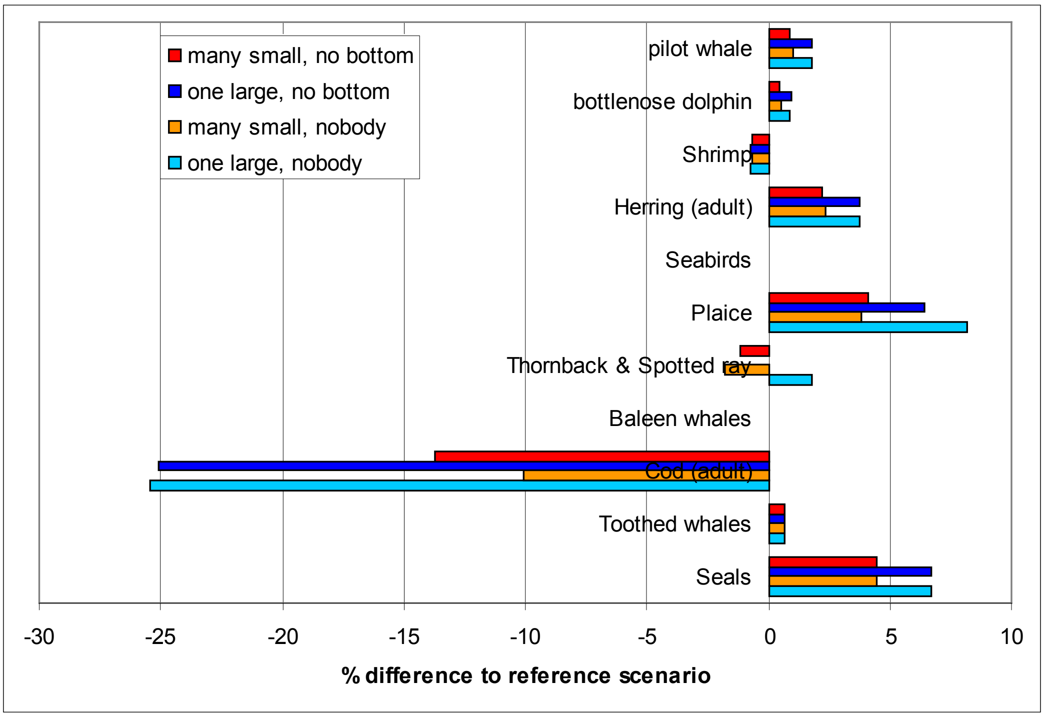

Figure 32: The relative effects of the 4 different MPA scenarios on biodiversity indicator species as used in the 'Nature Balance'. The category 'pilot whale' was calculated as the sum of its main food sources squid & cuttlefish, herring and mackerel.

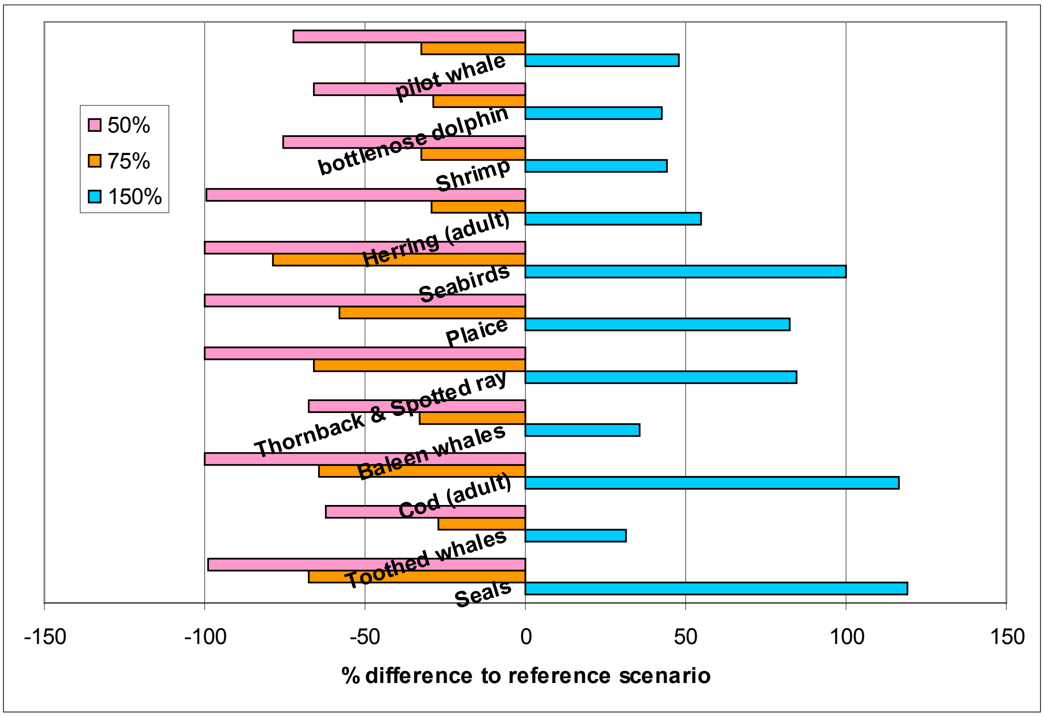

Figure 33: Relative effects of the 3 modified primary production scenarios for the indicator species used in the Nature Balance.

5 Discussion

5.1 Match of current MDNS model reference scenario with field data

While the EcoSim MDNS model corresponds fairly well to time series from the multi-species VPA performed by the ICES multispecies working group, the spatial results from the EcoSpace MDNS model have not been compared to real data as rigorously. Here we compare the spatial output from this model for all species in the ICES fishmap which correspond to functional groups in the model. We have used data from the IBTS survey. The data points are averages for the period 1991-2004.

Herring

In the IBTS data, herring is found nearly everywhere in the North Sea (Figure 34), with an increasing gradient towards the southeast. If we add up juvenile and adult herring, this same pattern is found in the model output (Figure 10). The model accurately captures the pattern in the data.

Plaice

The model predicts a sharp drop in the plaice abundance along a diagonal between northern Denmark and central England (Figure 10), with high densities to the south and lower densities to the north. This division is not present in our data, which indicates some plaice throughout the surveyed area (Figure 35). In the data, a strong concentration of plaice can be found along the southeastern coast. In the model this coastal increased abundance is not observed.

Cod

In our data (Figure 36) cod is found throughout the North Sea. In the model, large adult cod does not occur in the Southern North sea, but juvenile cod does except for a small area in the German Bight (Figure 10). We find a high concentration of cod in exactly this area in the data.

Thornback ray

Thornback rays are in the IBTS data concentrated along the British east coast close to the channel (*Figure 37*). The model correctly predicts their (virtual) absence from the majority of the North Sea (Figure 10), but does predict a substantial population along the entire Belgian, Dutch, German and Danish coastal area, which is not supported by the data.

Grey gurnard

In the model, the group 'Gurnards', which includes the grey gurnard, occur throughout the Sourthern North Sea (Figure 38), but are constrained away from the coastal areas in more northerly latitudes (Figure 10). In the data we see that they indeed occur through the southern North sea but the non-coastal pattern in the north is absent for the British coast. We have no data for the Scandinavian coast because the IBTS does not sample there.

Mackerel

Mackerel in the model are concentrated in the southern North Sea and extend to the north only in the deeper central waters (Figure 10). We do see a concentration in the south in the data (*Figure 39*) but we do not find the coastal/noncoastal pattern from the model in the data.

Whiting

In the model (Figure 10) whiting shows a clear gradient, decreasing from south to north, to complete absence in the far north. Remarkably, there are some coastal ‘gaps’ in the whiting distribution along the German and Danish coast. The north-south gradient is clearly present in the data (***Figure 40***), but there is no evidence for the southern ‘gaps’.

Spurdog

With the exception of the far north, spurdog occur in all offshore waters in the model (Figure 10). In the data we see that the distribution is more concentrated in the north than the model predicts, almost no spurdog is found in the southern North Sea (***Figure 41***).

Saithe

Saithe (both adults and juveniles) are constrained to the northern North Sea in both model and data. The distributions match well (Figure 10, ***Figure 42***).

Sole

In both model and data, sole is clearly a southern species (Figure 10, ***Figure 43***). The distributions generally match well.

Sprat

In the model (Figure 10) sprat is confined to the southern North Sea. Although the sprat stock is clearly concentrated in the south, substantial numbers are found further north (***Figure 44***), which is not captured in the model.

Haddock

Adult haddock are confined to the northern North sea in the model, while juveniles occur throughout the North sea (Figure 10). In the data we find no haddock in the southern North Sea (***Figure 45***). It is not clear whether this is because the survey does not catch juvenile haddock, or the model distribution misses the pattern in the data. The east-west density gradient in adult haddock is not found in the data.

Horse mackerel

In the model, horse mackerel do not occur in the northern half of the North Sea (Figure 10). Although in the data the highest concentration is found in the southern North Sea (***Figure 46***), horse mackerel is found throughout the North Sea. The elevated catches around the Shetland Islands are not present in the model.

Norway pout

The distribution of Norway pout is accurately captured in the model. In both model (Figure 10) and data (***Figure 47***), Norway pout is constrained to the northern North Sea.

Comparison of the distributions of the above species highlights that there are substantial differences between the distributions found in the model runs and those we observe in data. Species with wide spatial distributions such as herring, plaice and cod are, at least qualitatively, predicted well by the model. Spatial distribution of rare species may be less accurately captured by the model, as indicated by the distribution of thornback ray and spurdog.

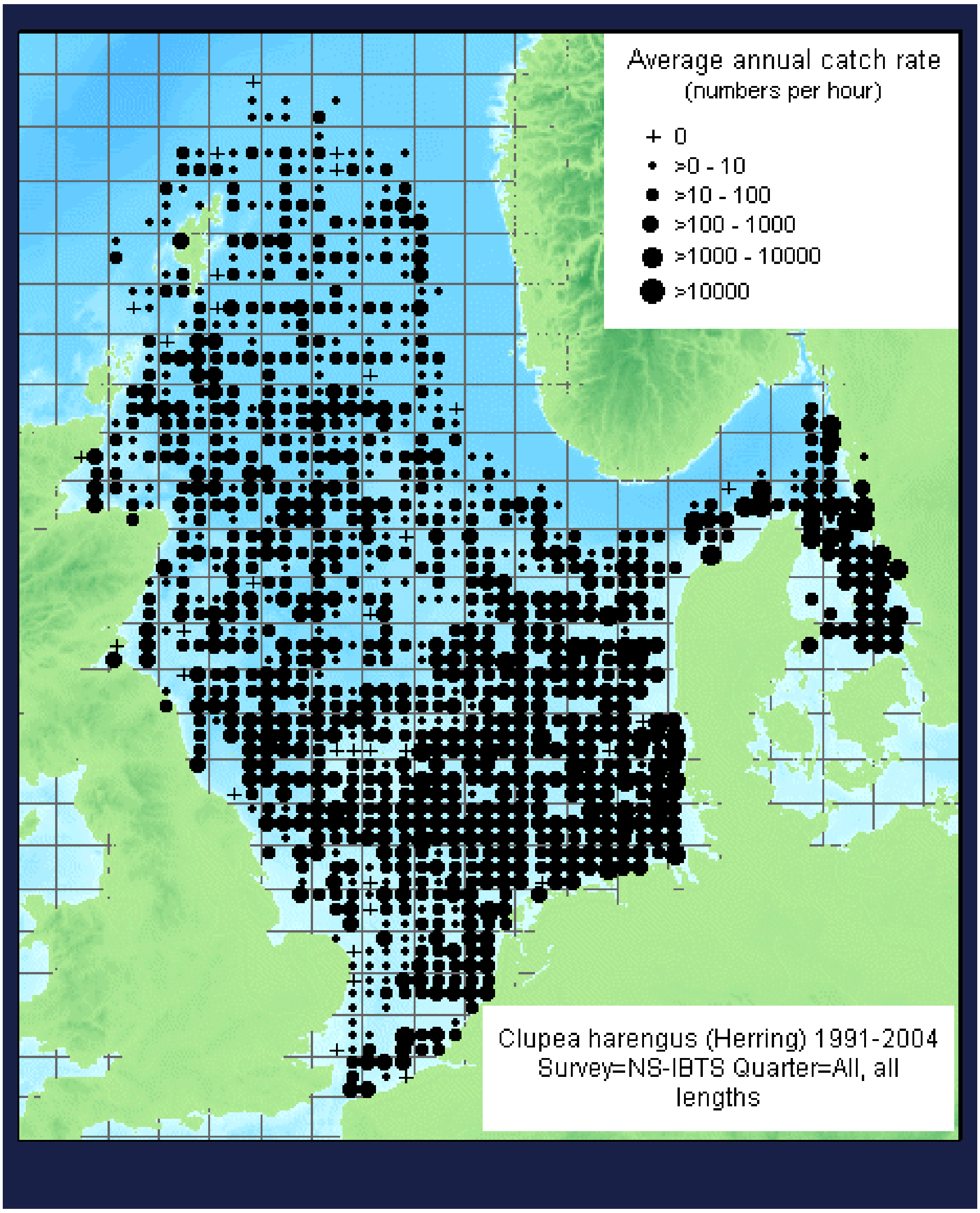

Figure 34: Herring catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

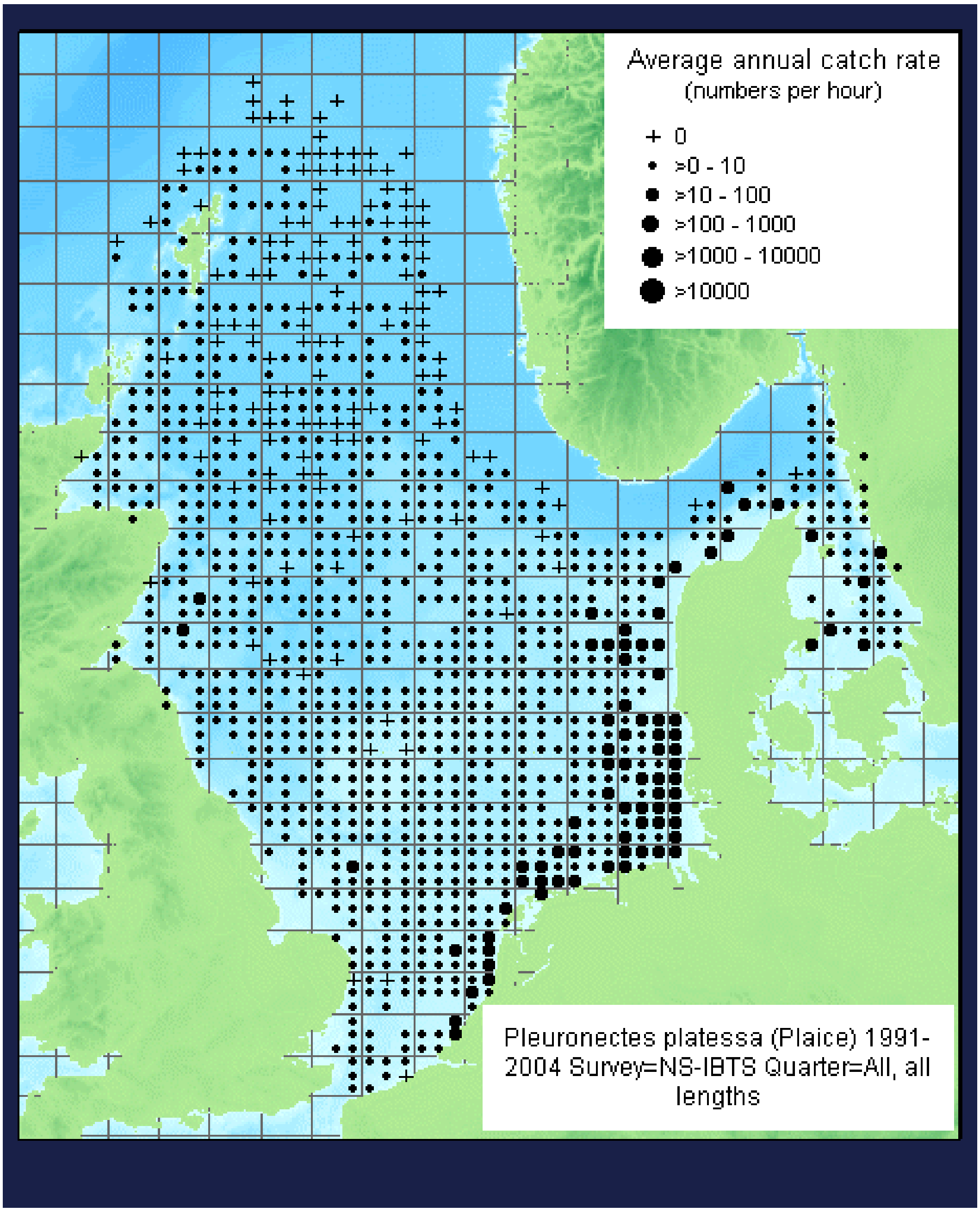

Figure 35: Plaice catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

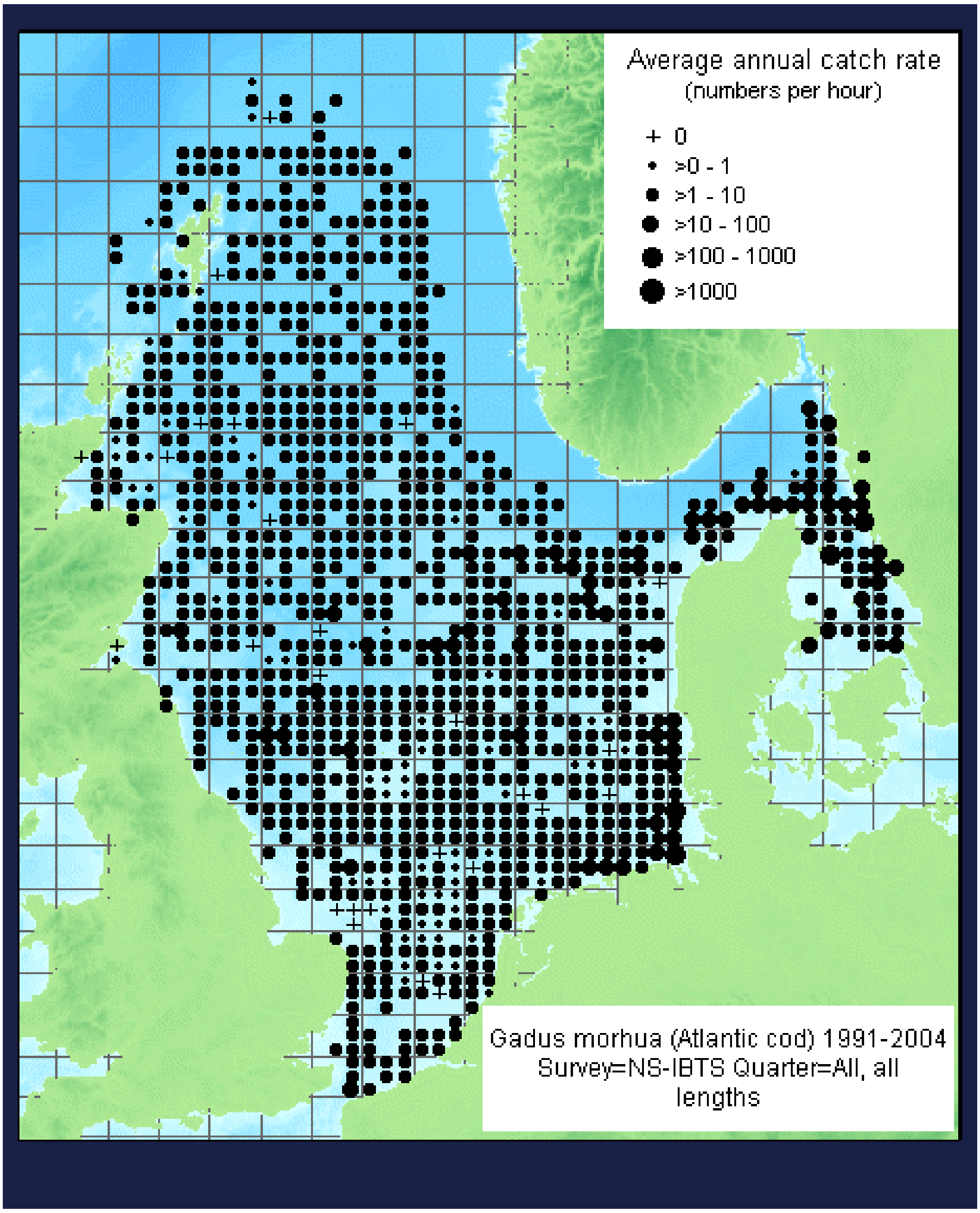

Figure 36: Cod catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

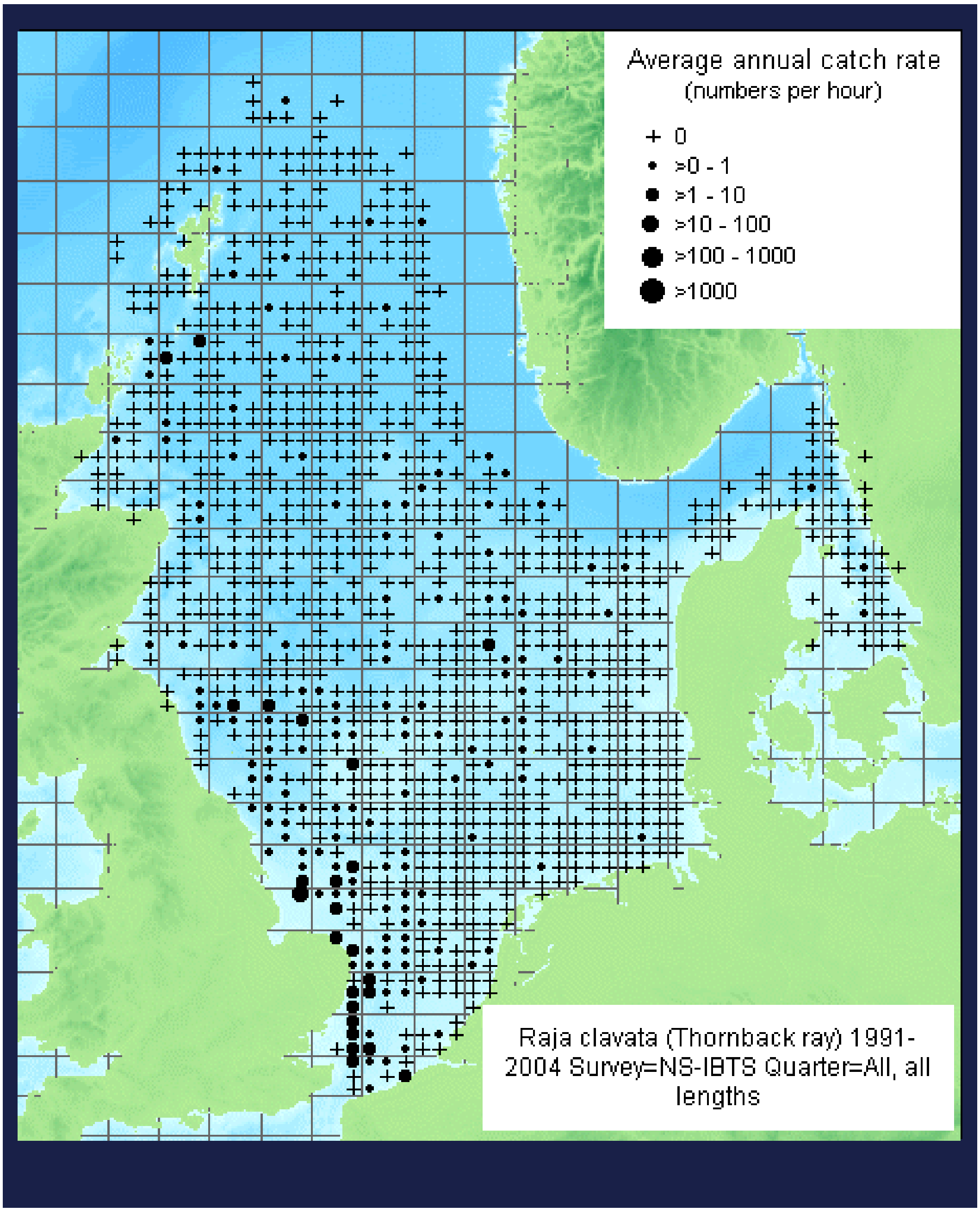

Figure 37: Thornback ray catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

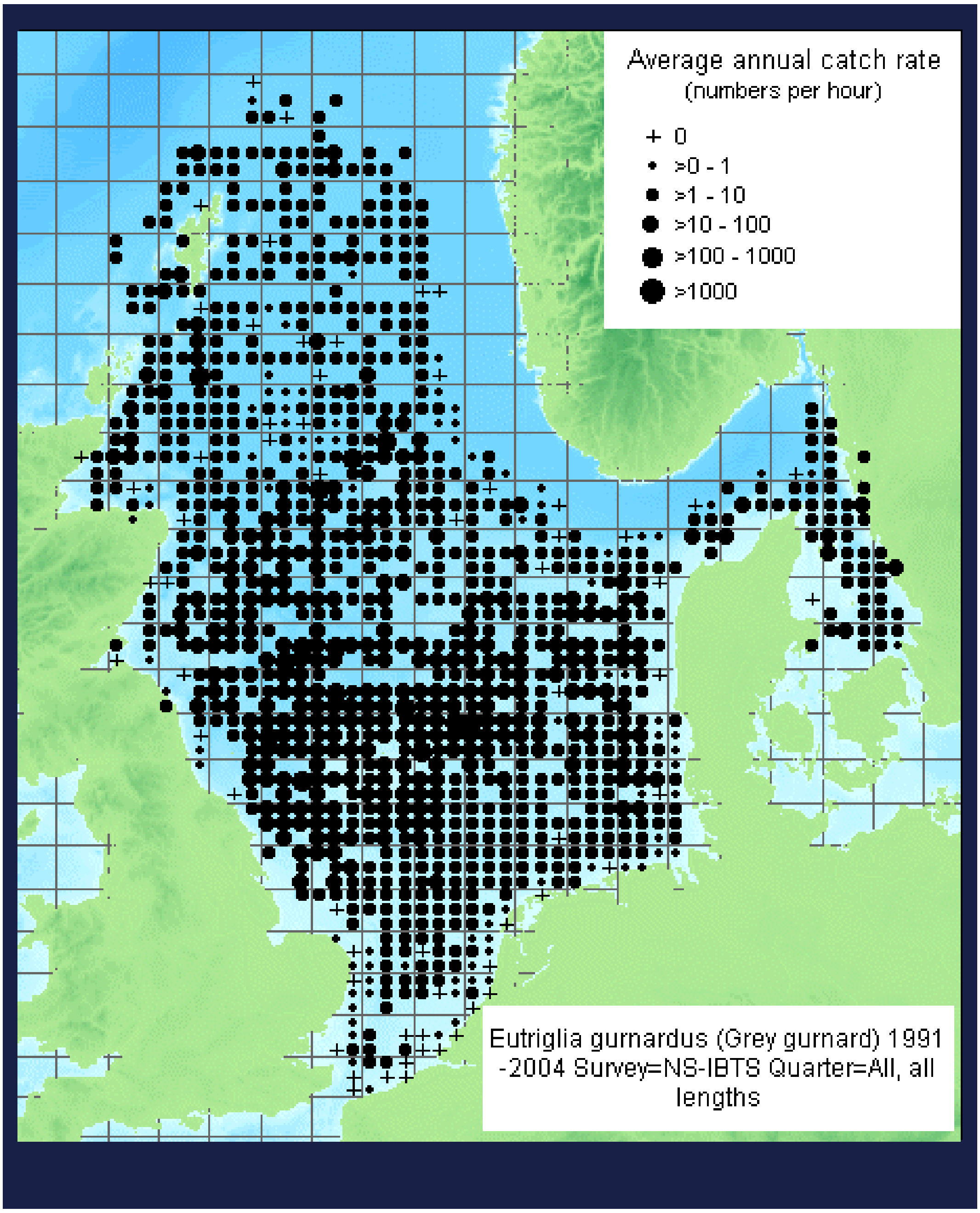

Figure 38: Grey gurnard catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

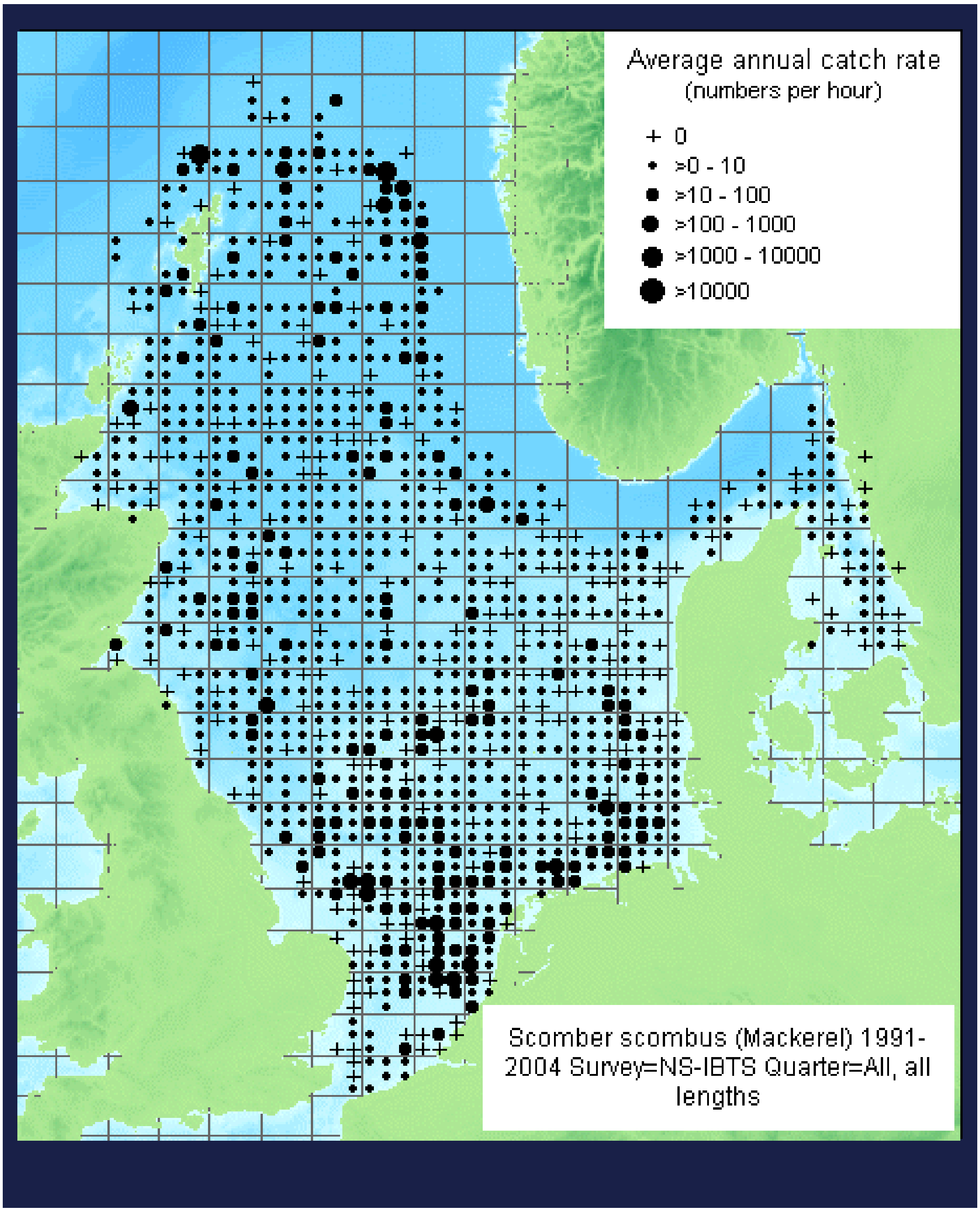

Figure 39: Mackerel catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

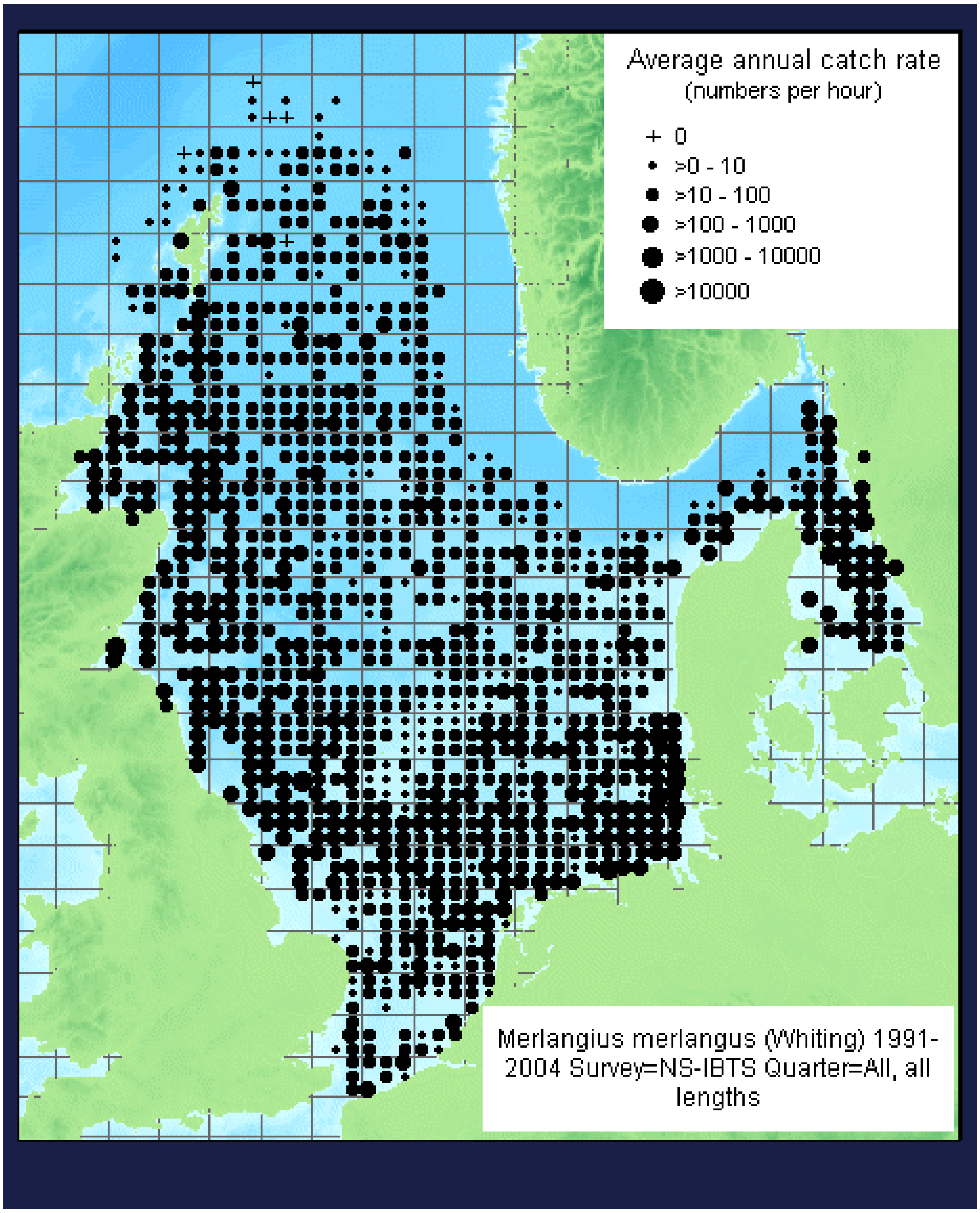

Figure 40: Whiting catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

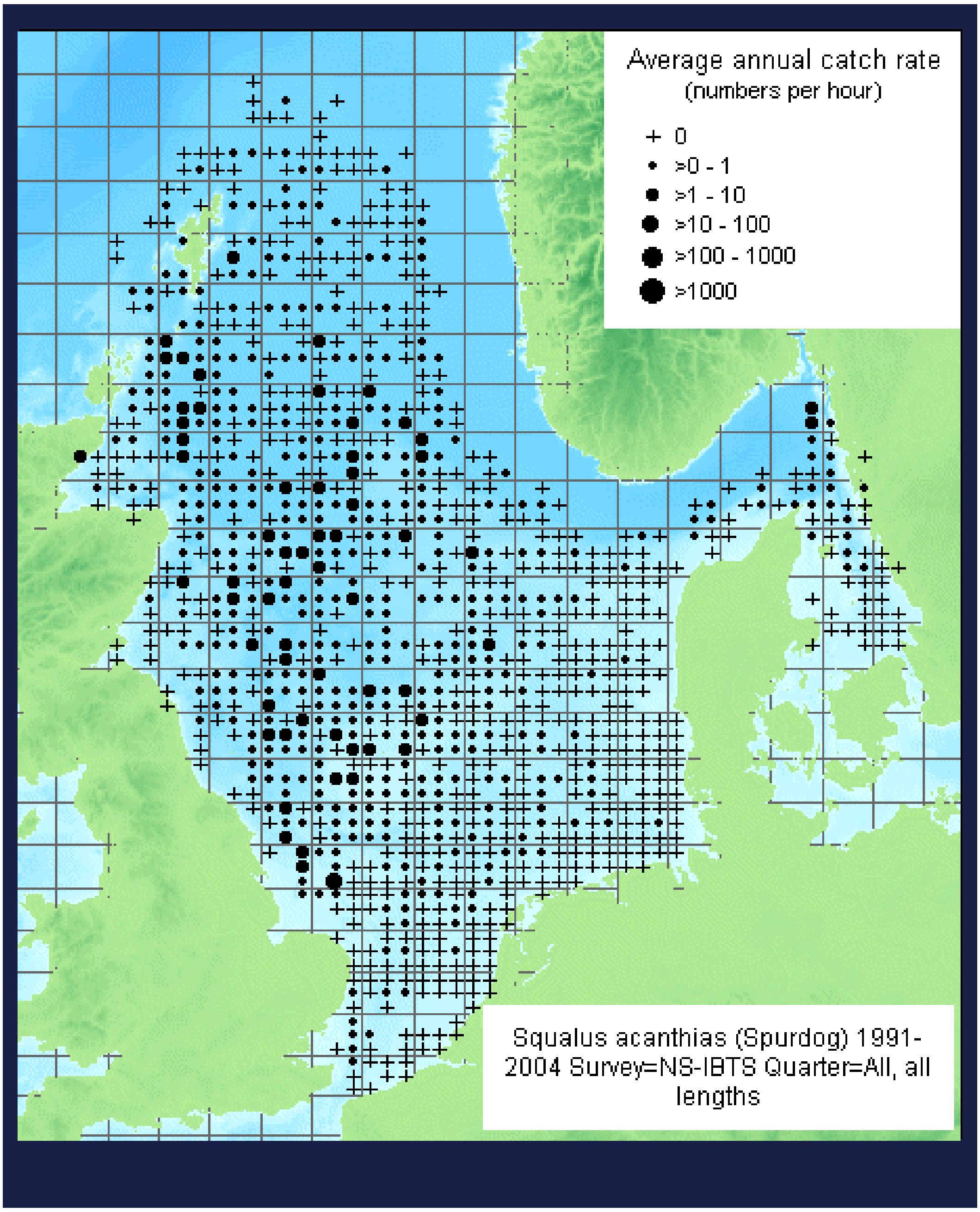

Figure 41: Spurdog catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

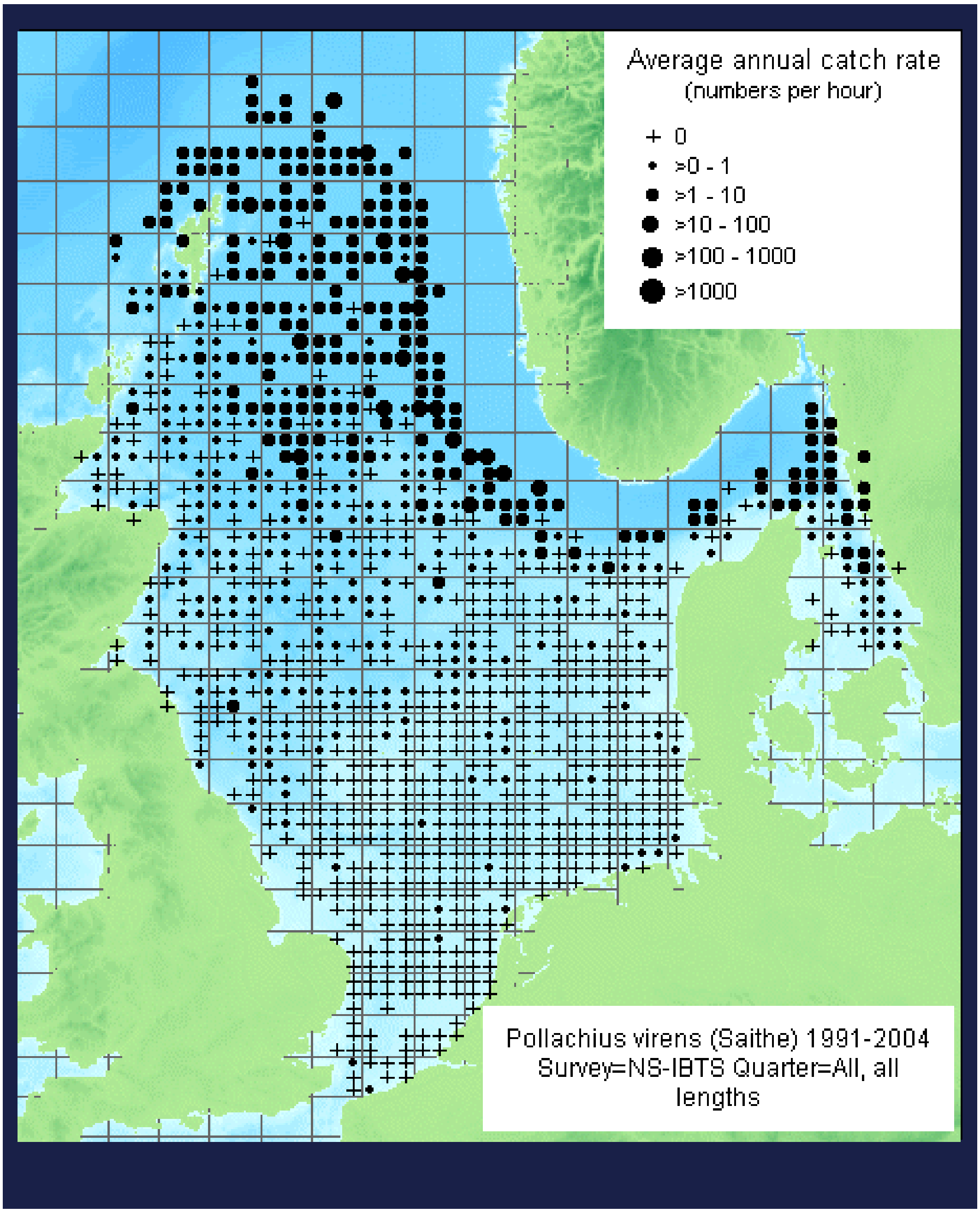

Figure 42: Saithe catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

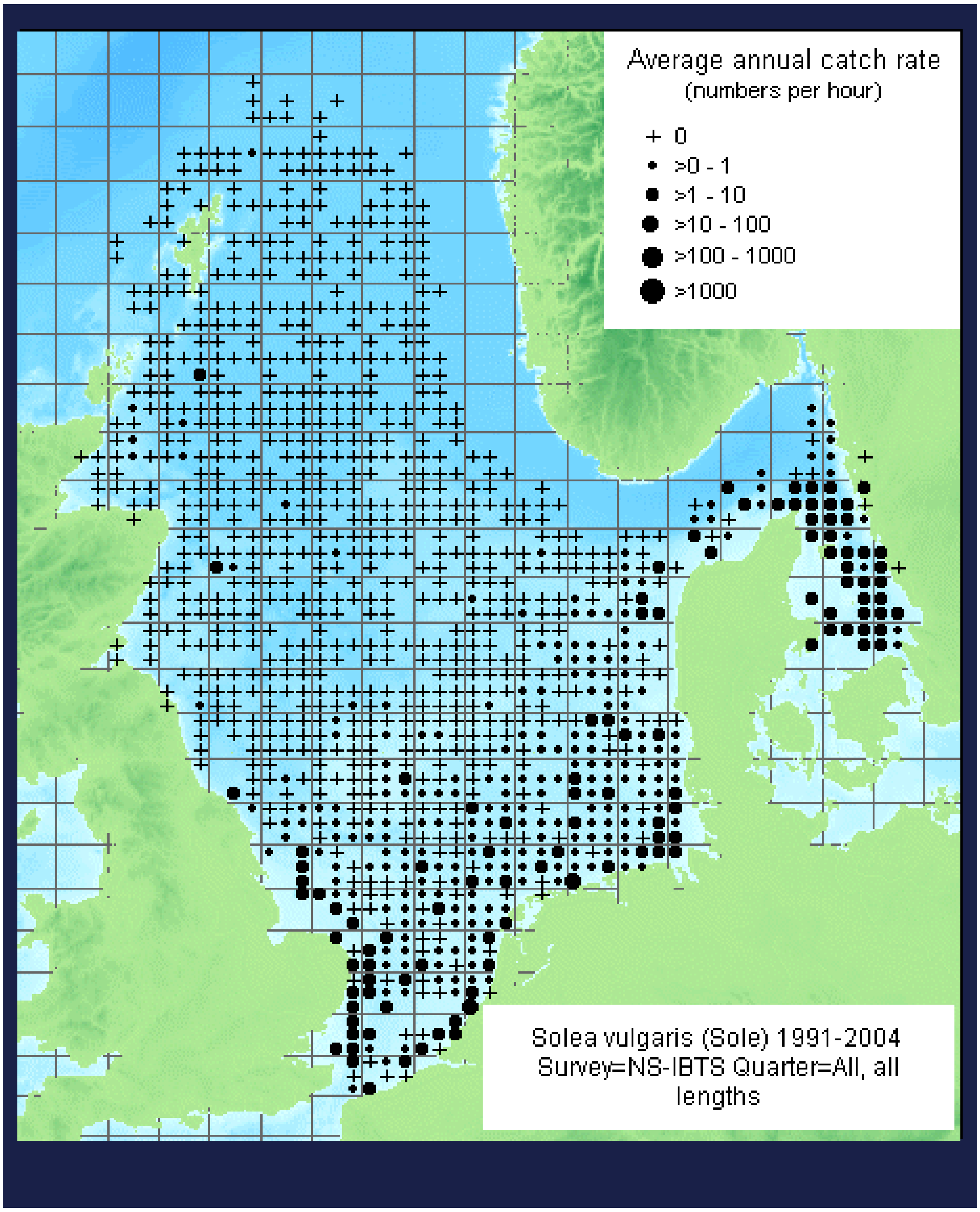

Figure 43: Sole catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

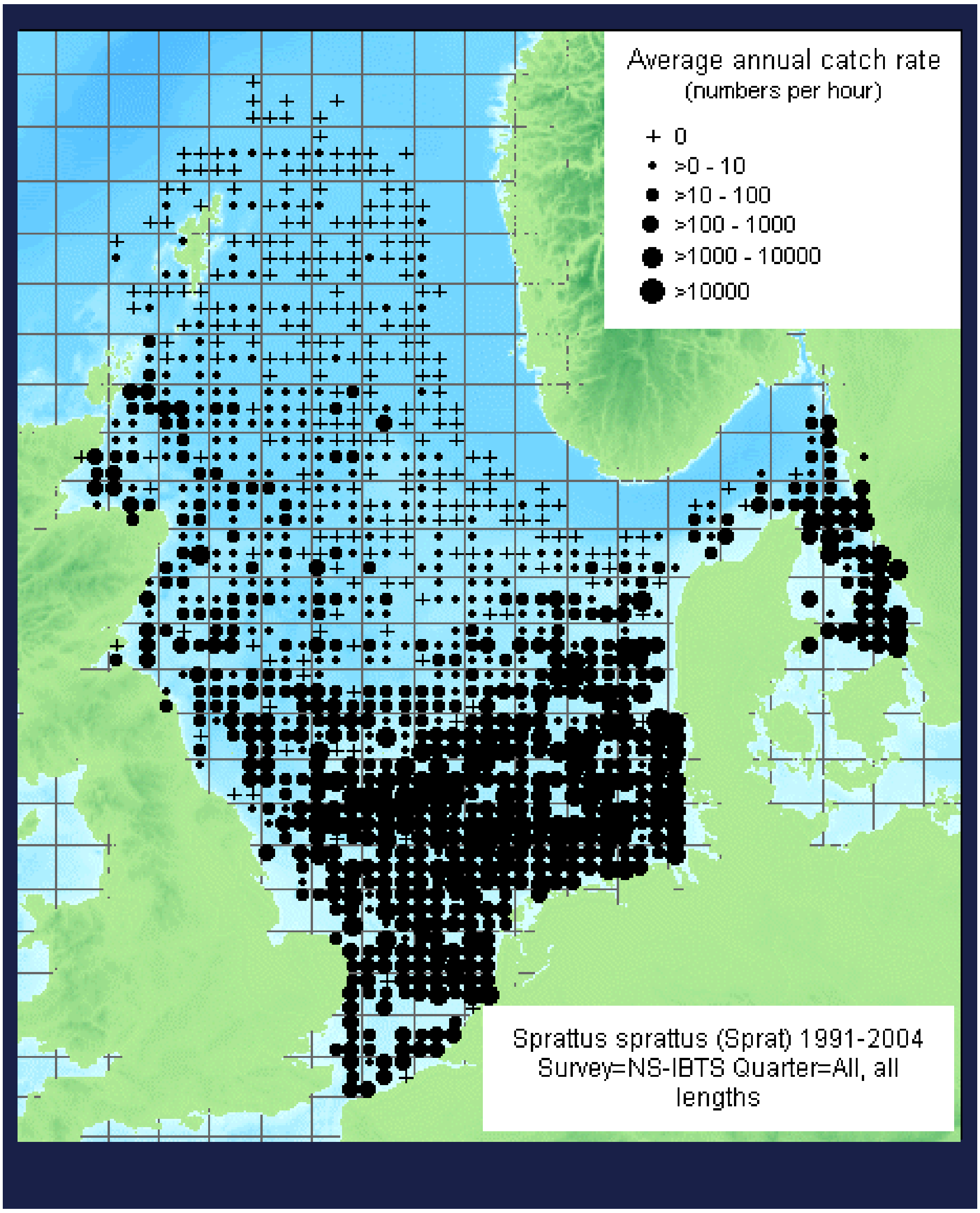

Figure 44: Sprat catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

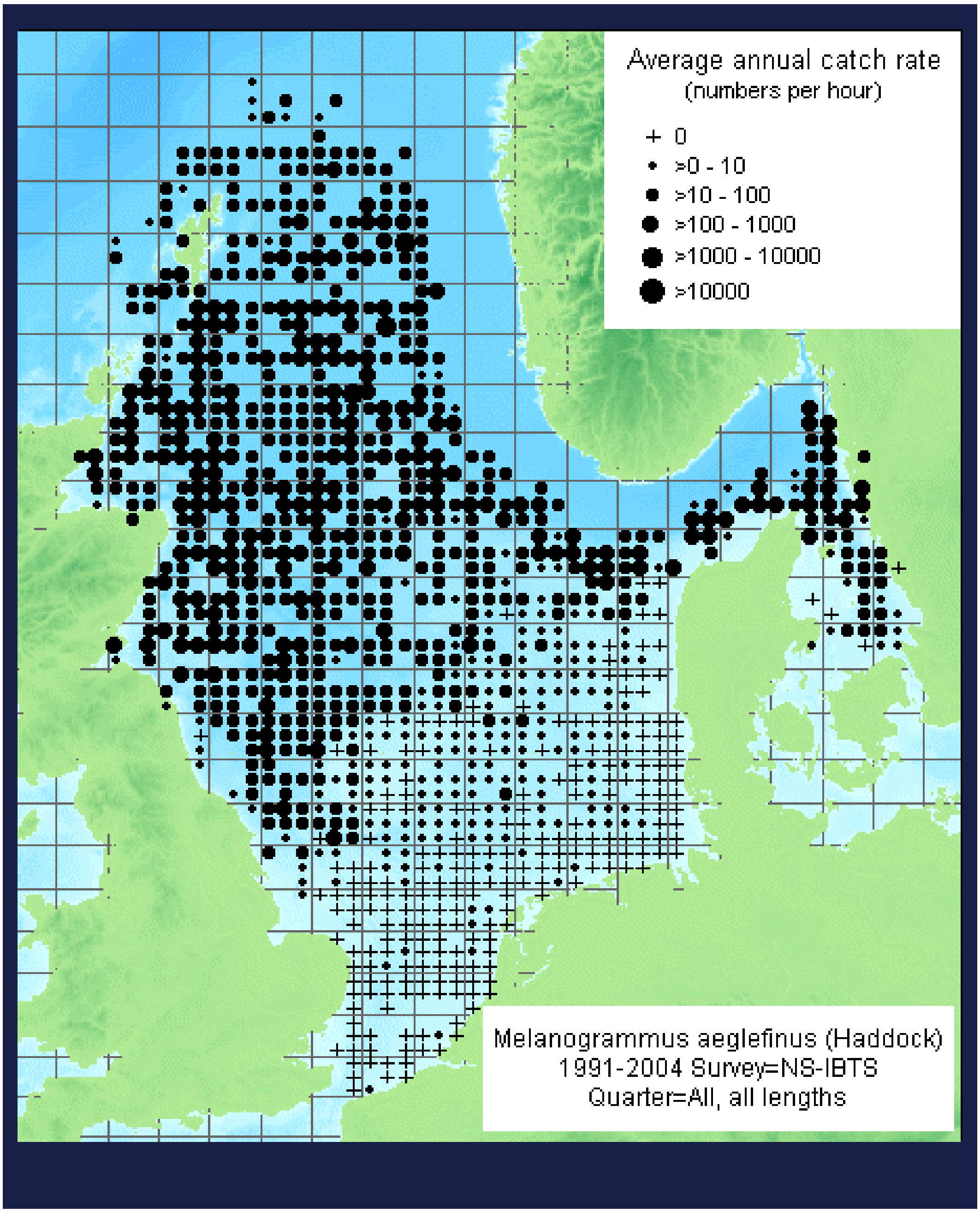

Figure 45: Haddock catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

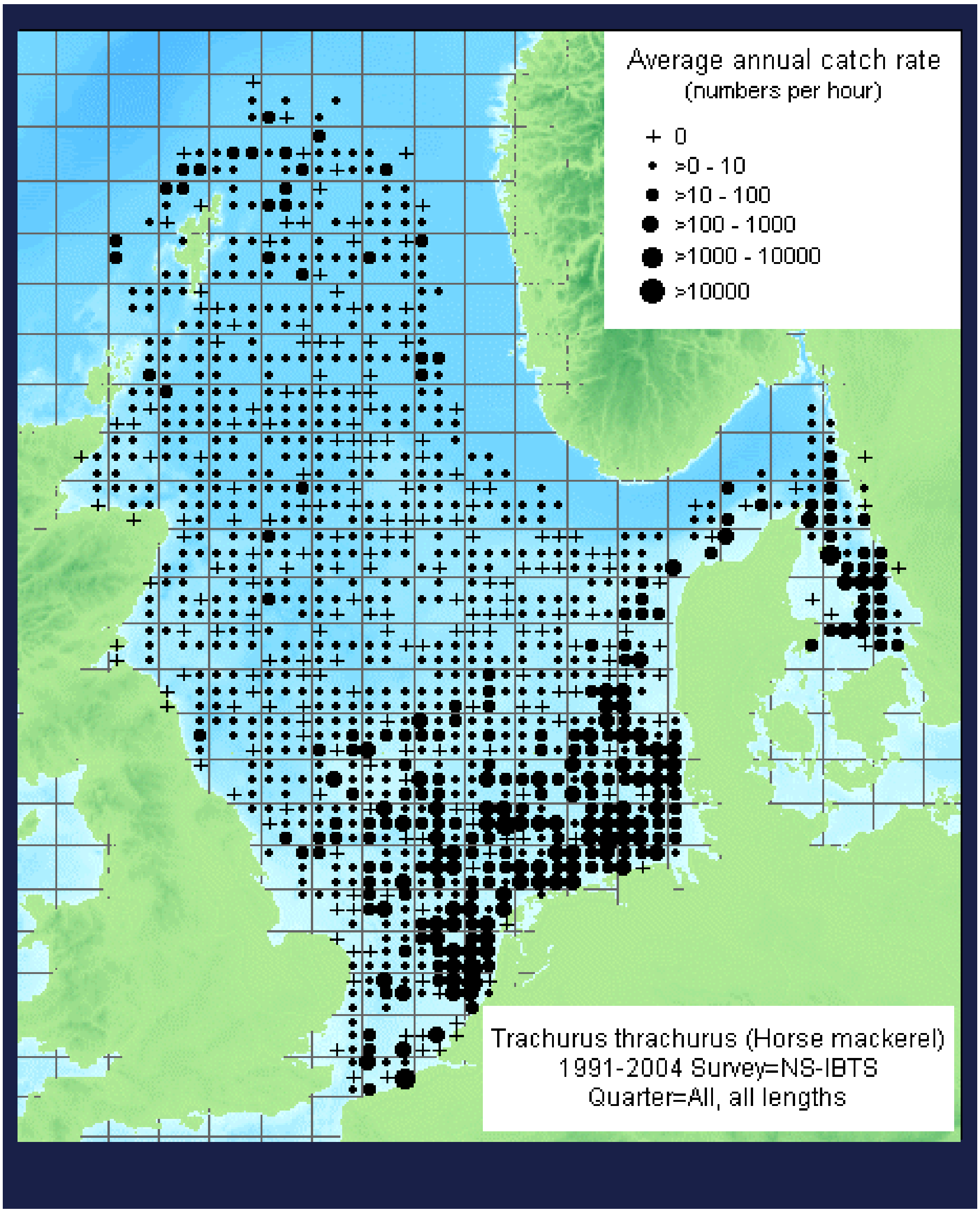

Figure 46: Horse mackerel catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

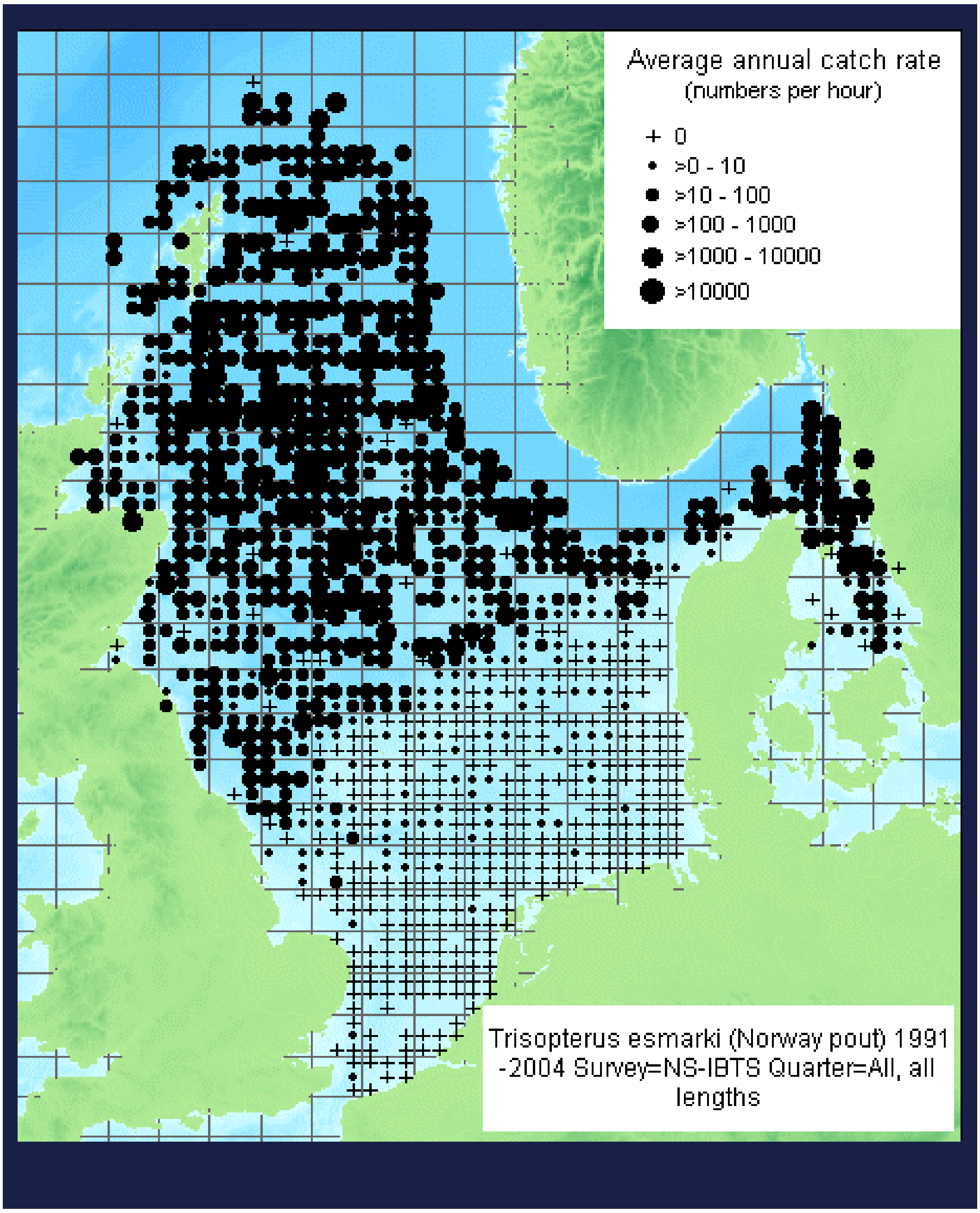

Figure 47: Norway pout catch rates per 1/9th ICES rectangle as calculated from IBTS data (ICES FishMap. http://www.ices.dk/marineworld/fishmap/ices/)

5.2 Applicability of current MDNS model to develop output of scenarios for biodiversity indicators

In principle the MDNS model can deliver output for 14 of the 26 indicators used in the Nature Balance (Wortelboer, 2009). For fish species (Thornback ray, Herring, Cod and Plaice) the match with the MDSN output is straightforward, these species are modeled as single species in the MDNS model. Given the fact that the MDNS model is currently the best fish based ecosystem model in use for the North Sea, is based on relevant food chain relations, and has been fully parameterized and thoroughly tested, one can have confidence in the scenario outputs for these species. Especially the direction (positive or negative) and relative difference between scenarios and the baseline are informative.

The results on birds and marine mammals are less straightforward since these species are modeled as groups in the MDNS model. The scenario results are therefore not informative for the individual species but give interesting responses at the group level. An interesting result is that seabirds, as a group, show no response to the implementation of MPAs, which suggests that in the model MPAs do not result in a higher availability of food for seabirds. Seals, on the other hand show a large positive response to the implementation of MPAs, especially when this is one large unfished area. This suggests that this species group profits from higher food availability. Both the group of baleen whales and toothed whales profit from the implementation of MPAs, this profit is independent of the spatial distribution of MPAs. Given the large body size and swimming capacity of these species this result seems logical, improved food conditions in a single MPA or a constellation of small MPAs within swimming distance may work out similarly. As shown in Figure 28 and the discussion above the results of the MDNS model for a selection of indicator species of the Nature Balance correspond. However, it should be noted that the model only takes into account food web and fisheries effects. For many species, particularly non-fish species, abundance is not only set by the availability of food, but also by other drivers such as temperature, acidification, underwater noise, presence of ships, water transparency or pollution.

5.3 Applicability of current MDNS model to apply primary production scenarios

Due to software limitations, it has so far been impossible to simulate the suggested increased/decreased productivity scenarios in the MDNS EcoSpace model. We have instead performed these simulations using the EcoSim model (Section 3.2.2). The results of this are logical and consistent. Reduced productivity leads to reduced density of all groups (with the exception of adult whiting and haddock in the 25% reduction scenario). The effect is rapidly distributed throughout the food web, independent of trophic level. It is interesting that a 25% reduction in productivity does not lead to the extinction of functional groups, while a 50% reduction does cause a number of groups to decline to zero biomass. Despite this seemingly stepwise effect, more than 60% of the difference between the 25 and 50% reduction scenarios is explained by a linear trend (Figure 30).

Increasing productivity by 50% leads to an increase in all functional groups but the magnitude of the effect differs almost 20-fold among groups in the model. It appears that certain groups are highly sensitive to changes in productivity (examples: adult saithe, adult cod, catfish, seals, large piscivorous sharks and seabirds), while others seem much less vulnerable (such as juvenile and adult whiting, blue whiting, toothed & baleen whales, sole, dragonets and other gadoids). The consistency in the (in)sensitivity of particular species to changes in productivity indicate that the model itself is internally consistent and suitable for analyzing alternative productivity scenarios. It should be noted however that in models in general ‘extinct’ usually translates to ‘very low density’ in the field.

5.4 Applicability of current MDNS to develop output at a higher spatial resolution

Because of the strict separation of temporal and spatial aspects, it is technically relatively simple to implement the model on a finer spatial scale. EcoSpace basemaps are essentially matrices of numbers, which can be pasted into the EwE software in the proper format from for example Microsoft Excel. Alternatively, EwE 5.x, contains functionality to download maps from the SeaWifs project website (www.seawifs.org). These maps contain measures of depth and relative productivity. According to the percentage water measured on the satellite imagery, each cell is assigned the status ‘land’ or ‘water. As a result of this methodology, areas with substantial inland waters are qualified as water, while for our marine purpose they should be qualified as ‘land’, since they are not ‘sea’. This can however be fixed by overlaying GIS maps of the North Sea coastline. The depth values obtained from the SeaWifs project can be reworked into the depth-based habitats which the MDNS EcoSpace model uses. The only problem here is the ‘coastal’ habitat in the MDNS model, which is not depth-based (it exists in parallel to the <22 m depth-based habitat) and has to be estimated in another way.

5.4.1 Spatial scale of ecological interactions

The maps used in EcoSpace are translated linearly from latitude-longitude to equally sized grid cells. This simple conversion from the curved surface of a sphere to a flat rectangle might lead to problems when the grid cells become small. As the number of cells increases, while the total surface stays the same, the number of migrations across grid cells will increase. The rate at which this migration occurs depends strongly on the length of the borders of the cell. It is assumed that these lengths are equal for all cells in an EcoSpace model. When cells are large, and processes within cells are important relative to exchange of biomass between cells (migration and random drift), the inaccuracy can be ignored. However, when cells become small, so that migration becomes highly important, this could potentially cause a misrepresentation of the spatial dynamics.

Each ecological process plays out on a characteristic spatial scale (Levin, 1992). In spatially explicit models, the choice of which processes are mechanistically incorporated and which processes are ignored or approximated depends strongly on the spatial scale chosen, which in turn depends on the questions the model is designed to investigate (Dieckmann *et al.* 2000). EcoSpace models are limited in this respect by the processes which are incorporated into the non-spatial EcoSim model, combined with the rules for immigration and emigration that are added when an EcoSim model is expanded into an EcoSpace model. When we increase the spatial resolution (i.e. make the grid cells smaller and more numerous), the degree of mismatch between the modelled processes and those that are relevant to the local dynamics potentially increases. The EwE software has built-in functionality to deal with some of the issues that arise, but this requires extensive detailed parametrization, and for many functional groups such parameters are not known.

Software issues

We furthermore have run into a more practical problem. The MDNS model runs under version number 5.1 of the EwE software, which is unable to deal with the map size which is necessary when the whole North Sea is implemented on for example a 10x10km grid cell size.

5.4.2 Availability of input data

As stated above, under Section 2.3, all data that goes into the MDNS model is either time- or space invariant. The data either applies to specific grid cells but is constant in time, or is variable in time but applies to all grid cells in the same way. Anything in a model simulation that changes in a spatio-temporal way is a model result, and not input data. This leads to that for example fisheries effort time series need not be spatially resolved to be used in the model. The habitats in the MDNS EcoSpace model are defined by the water depth (with one exception). A change in the spatial scale would require higher resolution depth data of the modeled area, but such data is available. The modifiers of productivity (Figure 5) used in the ecospace basemap would also have to be obtained in higher resolution. Currently, these values are obtained from the SeaWifs project, and higher resolution data appears to be available from that source. Required input data to develop a version of the MDNS EcoSpace model with a higher spatial resolution is available and we foresee no problems regarding input data for such an exercise.

5.4.3 Availability of finer-scale output data

Data on the abundance of higher trophic levels, particularly fish, is often only available, at least on a North Sea wide scale, from ICES stock assessment working groups. These stock assessments use a combination of landing data, logbook data, and survey data to reconstruct the abundance of different fish species. Higher resolution data is simply not available. It is possible to interpolate between ICES rectangles and subsequently discretize space into a finer spatial grid, but this produces a spatial smoothing effect which is entirely due to the data manipulation and has no basis in actual observations.

Data on seabirds and marine mammals and certain benthos species may be available at higher resolution for the Dutch Continental Shelf. Other countries may have similar data for their continental waters, and such data could be combined to obtain higher resolution data for a larger part of the North Sea.

High resolution location data for certain fishing fleets (e.g. the Dutch beam trawl fleet) is available for recent years from the Vessel Monitoring System. It is difficult to obtain a consistent international set of this data, because its use can be subject to strong privacy regulations and different countries have different VMS protocols. However, it is likely that at least for a few fleets in the MDNS EcoSpace model, such datasets can be obtained.

5.4.4 Towards a higher resolution

In principle it is possible to keep everything in the model as it is, but increase only the spatial resolution. This is ecologically questionable, but technically possible. A problem then arises in that the output of such a model can, with few exceptions, only be compared with existing data on ICES quadrant scale. Higher-resolution data is simply not available, and interpolation is a largely cosmetic operation, which does nothing to increase the ecological relevance of the data. The same conclusion was reached by the group of Steve Mackinson at CEFAS, where an attempt was made to scale the MDNS EcoSpace model to quarter ICES rectangle scale (S. Mackinson, CEFAS-Lowestoft, UK, *personal communication*)

A first step towards resolving these technical issues would be to port the existing MDNS model to work correctly under version 6 of the EwE software. Given the complexity of the model, this can realistically only be undertaken by the developers of the model (i.e. the group of dr. S. Mackinson at CEFAS, Lowestoft, UK) in collaboration with the makers of the EwE software (The groups of Christensen, Pauly & Walters at UBC, Vancouver).

The problem outlined above, the lack of fine-scale spatial data, is furthermore aggravated by the fact that ecological processes are scale-dependent and hence a change in scale requires a reconsideration of the processes incorporated in the model. The necessary reconsideration on a process level means that a re-validation step after changing the spatial scale is absolutely necessary.

Despite the issues outlined above, it is still technically possible to increase the spatial resolution of the map, and validate by comparing ICES-rectangle scale data with model output re-aggregated to match the data scale. This would only ensure correspondence between the current EcoSpace model and the finer scale model, is in fact a validation on the currently existing scale and the result is a model which has a finer spatial scale purely for cosmetic purposes: it is unvalidated at the finer spatial resolution and hence should not be used to draw conclusions on realistic spatial planning scenarios at finer than ICES rectangle resolution.

Another alternative, which is common practice in terrestrial spatial modeling (R. Wortelboer, PBL-Bilthoven, *pers. comm.*), would be to interpolate the existing data so that it can be used at a finer spatial scale. On land, the distribution of certain species is often strongly tied to specific immobile habitat traits, such as the availability of water, hiding places, the right kind and quantity of vegetation. This allows for the development of a statistical distribution model based on these features, which can be used to interpolate the spatial distribution of species. In the marine realm, this association between relatively stationary features and the presence of certain species is much less tight, especially for non-sedentary species such as plankton, fish, birds and mammals. Use of a sophisticated statistical distribution model seems hence not feasible for the available data.

6 Conclusions & recommendations

The MDNS EcoSim/EcoSpace model is a valuable instrument to estimate the impact of fishing scenarios on the biomass of fish species (especially commercially exploited species), and mammals, within the limitations of the modeling framework. The spatial MDNS EcoSpace model has not been as thoroughly validated as the non-spatial MDNS EcoSim model, but this process is ongoing and results at ICES scale appear reasonable for key species. The scenarios we have simulated are designed to analyze the suitability of the modeling framework for exploration of spatial planning options. We clearly state that the reported results of the scenarios should not be used for such advice. For the results to be used in such a way requires more careful study of variations and uncertainty in outcomes and interpretation of results.

One issue that should be specifically taken care with when interpreting spatial results from policy exploration using EcoSpace is the constraining effect of the preferred habitat setting. With the currently used severe 'punishment' of living outside one's preferred habitat, groups are effectively constrained by the imposed habitat preference. This means that no matter what policy scenario is studied, one will not likely find viable populations of groups outside their preferred habitats. This causes for example the absence of adult cod from the southern North Sea even long after a complete fishing ban has been imposed.

It seems reasonable to use the MDNS model output (both EcoSim and EcoSpace) for a selection of the indicator species used in the Nature Balance to assess the impact of fishery scenarios on these species (groups). However, such scenarios should always be contrasted with existing data and literature, and should be scrutinized by relevant expert ecologists.

The above holds true also with regards to the MDNS EcoSim model and its application to study the effects of global changes in productivity. The model appears capable of consistently simulating such scenarios, but results should always be contrasted with existing data and literature, and should be scrutinized by relevant expert ecologists. If the EcoSpace model becomes available in a version which can vary global productivity, we expect it can also be used for such scenarios, but a round of testing will be necessary to confirm this.

With regards to implementing the MDNS EcoSpace model at a higher spatial resolution, there is a data problem; spatially resolved data on a finer than ICES-rectangle scale is scarce if not absent. Although technically the model can be implemented on a finer spatial scale, the absence of data to compare to model output, can only result in an unvalidated model. It should furthermore be noted that although it is technically possible, implementation of a higher spatial resolution in the model requires some hereto unsolved issues with the EwE software.

Coming back to the specific questions posed in Chapter 3:
1. Can we use the model to analyze primary production scenarios?
2. How can the model results of the MDNS model be related to the PBL-selected biodiversity indicators used in the Nature Balance (Wortelboer, 2009)?
3. What are the possibilities to use the current MDNS model to deliver output at a finer scale aiming to explore the impact of e.g. small offshore windmill parks?

1. The non-spatial EcoSim model can be used to analyze the effects of changes in global primary productivity. The results of the scenarios produced with the MDNS EcoSim model are

consistent with expectations and we find the model suitable for computing such scenarios. Unfortunately, due to software issues, it is currently not possible to perform a similar exercise using the MDNS EcoSpace model. If this becomes possible, testing will be needed.

2: We have done this in Section 3.2. It is feasible. Other biodiversity indicators can be calculated from the model output using information on the species content of each functional group in the model.

3. Although there are some complicating software issues, there are no fundamental technical barriers to the implementation of a higher spatial resolution. However, such an excercise would largely be cosmetic given the lack of reference data to validate model output on the appropriate spatial scale. Such an unvalidated model would not be suited to study the effects of spatial alterations in the North Sea on a smaller scale than can be studied using the current EcoSpace MDNS model.

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