StrathE2E2 implementation for the North Sea.

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Introduction

This document describes the configuration of StrathE2E2 for the North Sea and its parameterization to enable stationary state fitting for two time periods; 1970-1999 and 2003-2013. These represent contrasting periods of environmental conditions and fishing intensity.

Volumetric and seabed habitat data define the physical configuration of the system, and we can regard these as being fixed in time. Similarly, we regard the physiological parameters of the ecology model as being fixed in time. Some of them are set from external data while the remainder are fitted as detailed here. Changes in the model performance between the different time periods are thus due only to the hydrodynamic, hydro-chemical and fishery driving data.

North Sea model domain, physical structure, and time-independent parameters

Model domain

The perimeter of the North Sea model domain is bounded to the west and east by the UK and continental European coastlines respectively, and by open-sea boundaries to the north between Scotland and Denmark, and to the south at the English Channel. The open boundary to the north separates the shelf west of Scotland from the northern North Sea along a transect across the gap between the Orkney and Shetland Islands and then tracks approximately along the 200m isobaths at the shelf edge (Figure 1). The internal boundary between the inshore/shallow and offshore/deep zones is defined as the 30m isobath, which roughly divides the region into the shallow southern North Sea (International Council for the Exploration of the Sea (ICES) area IVc, northern boundary at latitude 53° 30’N), and the deeper northern North Sea (ICES areas IVa and IVb).

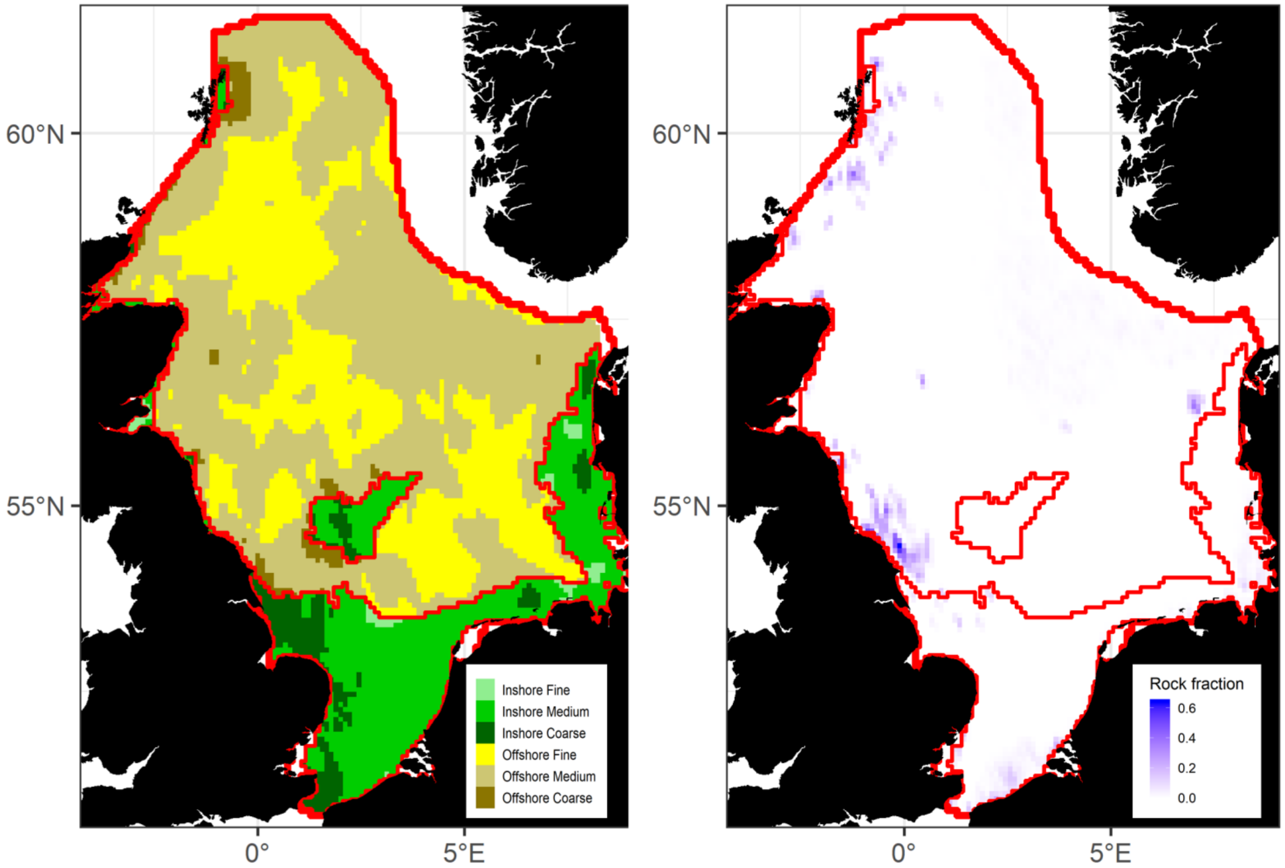

FIGURE 1 Maps of the StrathE2E2 model region. Within the North Sea the model resolves sub-area of seabed sediment habitat divided into inshore (shallower than 30m) and offshore (separated by the thin red line in each panel). Within each zone, three sediment classes are represented – fine (muddy), medium (sandy) and coarse (gravel) (left panel). Within each of the six sediment habitats a proportion of the seabed area may present as exposed bedrock (right panel) which has different geochemical properties and in the inshore zone supports the kelp forests which are included in the model food web. Sedimentary data are from Wilson *et al.* (2018).The sea surface area of the model domain was estimated to by 485,605 km^2.

Fixed physical configuration parameters

Background to the fixed area-proportions, volumetric and sediment property parameters of the model are shown in Tables 1 and 2.

TABLE 1. Description of the fixed (time-invariant) physical configuration parameters for the North Sea demonstration model.

Data	Description
Water column inshore/shallow and offshore/deep zone area proportions and layer thicknesses; seabed habitat area proportions and sediment properties.	Area proportions of depth zones and seabed habitats derived from 1/8 degree resolution atlas of seabed sediment properties (Wilson *et al*. 2018). The atlas provides gridded data sets of bathymetry, median grain size, mud, sand and gravel content, porosity, permeability, organic nitrogen and carbon content, and natural disturbance rates due to wave and current bed shear stress.
Parameters for relationship between median grain size, sediment porosity and permeability. Permeability is used as the basis for estimating hydraulic conductivity which is a parameter in the representation of sediment processes in the model.	Porosity (proportion by volume of interstitial water) and permeability of each sediment habitat were derived from median grain sizes using empirically-based relationships. $log_{10}(porosity) = p_3 + p_4\left(\frac{1}{1+e\left(\frac{-log_{10}(D_{50})-p_1}{p_2}\right)}\right)$ D_{50} = median grain size (mm); parameters p_1 = -1.227, p_2 = -0.270, p_3 = -0.436, p_4 = 0.366 (Heath *et al.* 2015) $permeability = 10^{p_5} . {D_{50}^{*}}^{p_6}$ where $D_{50}^{*} = 0.11 \leq D_{50} \leq 0.50$ p_5 = -9.213, p_6 = 4.615 (Heath *et al.* 2015) These relationships are coded into the StrathE2E2 R-package with the parameters in the csv setup file for the North Sea model. The parameters are probably a reasonable starting point for any future model of a new region. Derivation of the parameters is described in the following text.
Parameters for in-built relationship between sediment mud content, and slowly degrading (refractory) organic nitrogen content of seabed sediments (see description in this document).	Values for each sediment type derived from parameterised relationships between total organic nitrogen content of sediments (*TON%*, percent by weight), mud content (*mud%,* percent by weight) and median grain size (D_{50}, mm). $mud\% = 10^{p_7} . {D_{50}}^{p_8}$

	p_7 = 0.657, p_8 = -0.800 $TON\% = 10^{p_9} .mud\%^{p_{10}}$ p_9 = -1.965, p_{10} = 0.590 Proportion of *TON* estimated to be refractory = 0.9 These relationships are coded into the StrathE2E2 R-package with the parameters in the csv setup file for the North Sea model. The relationships and parameters are probably a reasonable starting point for any future model of a new region, though there are clear regional variations. Derivation of the parameters is described in the following text.

TABLE 2 Area-proportions of the inshore and offshore zones and the thicknesses of the water column layers. Sea surface area of the North Sea in the model domain was estimated to be 458,605 km^2.

Property	Inshore/shallow	Offshore/deep
Sea-surface area proportion	0.2496	0.7504
Upper layer thickness (m)	24.16	30
Lower layer thickness (m)	NA	50.04

Area-proportions of seabed-habitats

Derivation of the area-proportions of seabed habitat in the inshore and offshore zones of the model domain relied on the atlas of seabed sediment properties from Wilson *et al*. (2018). The atlas provides a range of seabed data for 1/8 degree cells over the NW European shelf, including the percentage of seabed area defined as rock (within 5cm of the seafloor), the percentage of mud, sand and gravel fractions in the sediments, the whole–sediment median grain size, and the natural disturbance rate by currents and waves. Within each zone, we ranked the spatial cells by median grain size, and assembled cumulative area-proportion curves (Figure 3). Cells were then assigned to fine, medium and coarse sediment habitats according to the 15th and 50th centiles of these curves. The actual area of each habitat was then the sum of the areas of each set of assigned cells, less the proportion of area in these cells defined as rock (Table 3).

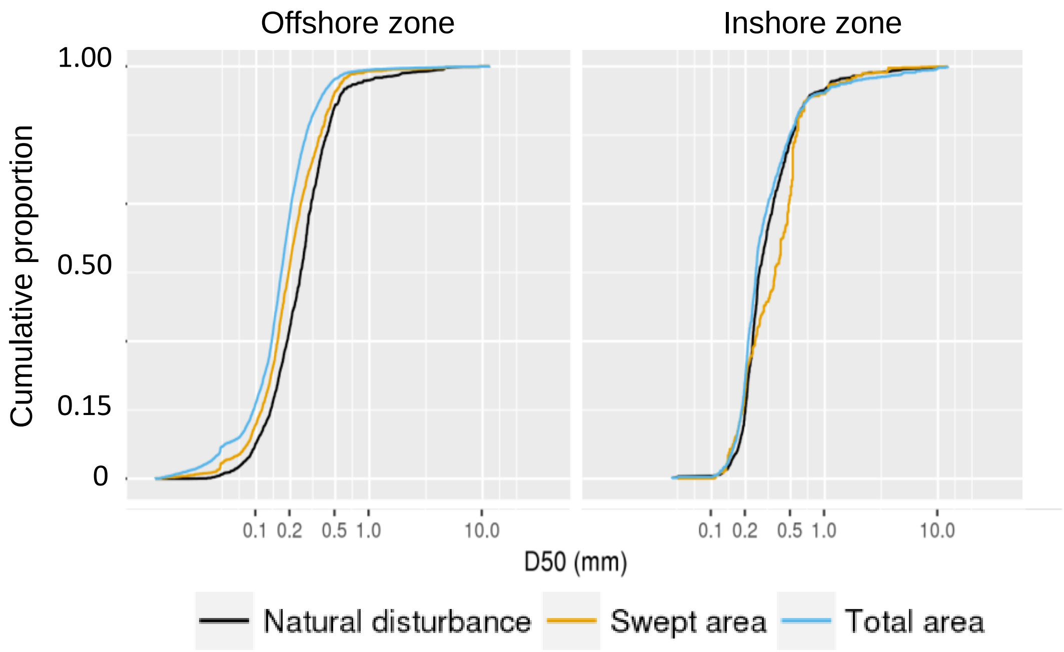

FIGURE 2 Cumulative proportion of area by whole-sediment median grain size (D50), for the inshore and offshore zones of the North Sea. Also shown is the cumulative proportion of natural disturbance due to currents and waves, and the cumulative proportion of seabed area swept by fishing gears (see later description), according to grain size.

TABLE 3 Area proportions of the 8 seabed habitat classes defined in the model by depth, rock or sediment type. Grey shaded cells indicate habitats in water deeper than 30m. The sea surface area of the model domain was estimated to by 485,605 km^2.

Sediment type and depth zone	**Inshore/ shallow rock**	**Inshore/ shallow muddy sediments**	**Inshore/ shallow sandy sediments**	**Inshore/ shallow gravels**	**Offshore/ deep rock**	**Offshore/ deep muddy sediments**	**Offshore/ deep sandy sediments**	**Offshore/ deep gravels**
Area proportions	0.0030	0.0110	0.1878	0.0478	0.0057	0.2665	0.4595	0.0187
Median grain size (mm)	NA	0.130	0.273	1.816	NA	0.114	0.231	0.928
Porosity	NA	0.441	0.391	0.367	NA	0.456	0.399	0.370
Permeability (m^2)	NA	5.00×10^{-14}	1.53×10^{-12}	2.50×10^{-11}	NA	2.68×10^{-14}	7.05×10^{-13}	2.50×10^{-11}
Refractory organic nitrogen content (%g.g^{-1})	NA	0.081	0.057	0.023	NA	0.064	0.046	0.024

Parameters linking median grain size to porosity, permeability and organic nitrogen content

Sediment porosity

Various authors have presented data on sediment porosity and grain size: Ruardij & Van Raaphorst (1995) and Lohse *et al.* (1993) for muds and sands from the southern North Sea; Serpetti (2012) and Serpetti *et al.* (2012) for coarse, mixed and fine grained sediments at 8 sites off the northeast coast of Scotland, repeated at monthly interval over an annual cycle. Wiesner *et al.* (1990), list data on grain size and water content (by weight) for a wide range of North Sea sediments. Water content can be converted to porosity assuming a solid material density of 2650 $kg.m^{-3}$ and a fluid density of 1027 $kg.m^{-3}$. Combining these data sets, log-transformed porosity showed a sigmoidal relationship with log_{10}(median grain size) (D, mm), to which we fitted a relationship of the logistic form using Nelder Mead optimization in the 'optim' package of R (Table 4, Figure 3):

$$log_{10}(porosity) = p_3 + p_4\left(\frac{1}{1+e^{\left(\frac{-log_{10}(D)-p_1}{p_2}\right)}}\right) \qquad \text{eqn 1}$$

TABLE 4 Fitted values and their standard error, of the four parameters for the function relating sediment porosity to median grain size.

Parameter	**Fitted value**	**Standard error**
p_1	-1.227	0.063
p_2	-0.270	0.046
p_3	-0.436	0.023
p_4	0.366	0.050

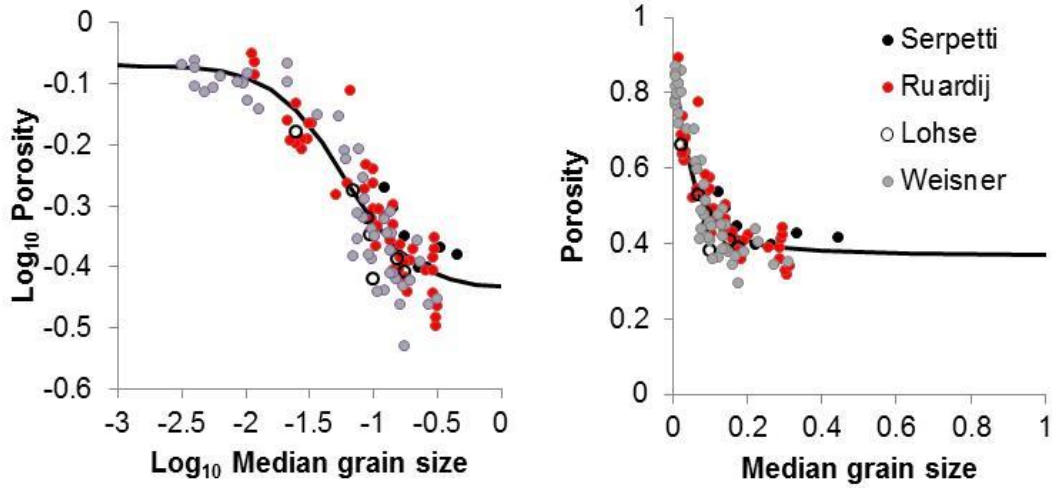

FIGURE 3 Assembled data on sediment porosity and median grain size, and the fitted relationship (solid line). Left panel, log-transformed data, right panel un-transformed data. black symbols: annual averaged data from Serpetti (2012) and Serpetti *et al*. (2012); red: Ruardij & van Raaphorst (1995); open: Lohse *et al*. (1993); grey: Weisner *et al.* (1990).

Hydraulic conductivity

Hydraulic conductivity (H, m.s^{-1}) represents the ease with which fluids flow through the particle grain matrix. The related term 'permeability' (m^{-2}) is a measure of the connectedness of the fluid filled void spaces between the particle grains. Permeability is a function only of the sediment matrix, whilst conductivity is a function of both the sediment and the permeating fluid, in particular the fluid viscosity and density.

Hydraulic conductivity is related to permeability by:

$$H = Permeability \cdot fluid\ density \cdot \frac{g}{dynamic\ viscosity} \qquad \text{eqn 2}$$

where: seawater density = 1027 kg.m^{-3} at salinity 35 and temperature 10°C; seawater dynamic viscosity = 1.48 x 10^{-3} kg.m^{-1}.s^{-1} at salinity 35 and temperature 10°C; g = acceleration due to gravity = 9.8 m.s^{-1}

Hence, $H = Permeability \cdot 6.8004 \times 10^6$ (m.s^{-1} at salinity 35 and temperature 10°C) eqn 3

One of the few available datasets on whole sediment permeability in relation to median grain size is that of Serpetti (2012) and Serpetti *et al.* (2012). These data cover muddy-sand, sand and mixed sediments in the median grain size range 0.11 to 0.45 mm median grain size, sampled approximately monthly over an annual cycle at 7 sites off the east coast of Scotland. Permeability and median grain size were measured on cores from the upper 5cm and upper 10cm of the seabed at each site. A power function of median grain size (D, mm) was found to explain the differences in annual average permeability (m^{-2}) between sites (r^2 = 0.999 for 10cm cores, r^2 = 0.966 for 5 cm cores) (Figure 4):

$Permeability = 10^{-8.675}.D^{4.958}$ (5 cm cores) eqn 4

$Permeability = 10^{-9.213}.D^{4.615}$ (10 cm cores) eqn 5

The relationship for 10cm cores was used in the model configuration to parameterise permeability given median grain size.

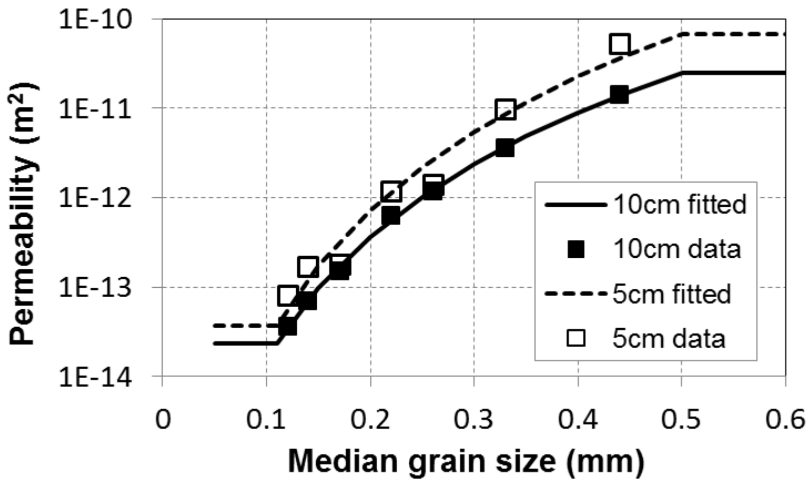

FIGURE 4 Annual average permeability (m^{-2}) of sediments from 7 sites off the north east coast of Scotland - data from Serpetti (2012) and Serpetti *et al.* (2012). Open symbols, permeability over the upper 5cm of sediment, filled symbols over the upper 10cm. We did not extrapolate the fitted permeability relationships to estimate values outside the median grain size range of the observations, but instead assumed that permeability was independent of grain size below 0.11mm and above 0.5mm. This constraint was based on unpublished field observations (M.Pace, pers. comm).

Refractory (non-dynamic) organic nitrogen content of sediments

The magnitude of the static organic nitrogen detritus pool in each sediment type is a required input to the model. The code includes an option to impute values from empirical relationships between total organic nitrogen (TON) and mud content, and between mud content and median grain size.

Comparison of sediment pigment content and total organic nitrogen (TON) content of sediments off northeast Scotland (Serpetti, 2012; Serpetti *et al.,* 2012) suggests that 90% may be refractory (assuming nitrogen:pigment ratios of labile material). This is borne out by the observation that although phytoplankton pigment contents of shelf sediments show strong seasonality, total organic nitrogen content as almost constant. Total organic nitrogen content is typically expressed as a dry-weight specific percentage ratio (TON%; percentage by weight, %g.g^{-1}). Using such data, the organic nitrogen mass (ONM, mMN) in each sediment habitat can be calculated depending on porosity and sediment layer area and thickness.

$$ONM = \frac{1}{14}(TON\% \, . \, 10^4 . \, \rho_{sediment} . area \, . thickness \, . (1 - porosity)) \qquad \text{eqn 6}$$

where $\rho_{sediment}$ is the density of particle grains in the sediment (quartz density = 2650 kg.m^{-3}), and the sediment layer area and thickness have units of m^2 and m respectively.

Empirical evidence shows that sediment TON% is strongly related to the mud content (% grain sizes <0.063mm). However, relating TON% to whole-sediment median grain size (which is the sediment-defining measure for imputing porosity and permeability) is more problematic since mixed and coarse grained sediments may have highly variable mud content, more or less independent of median grain size.

To derive parameters linking TON% and mud% content, we combined two sets of observations from the North Sea (Serpetti, 2012; Serpetti *et al.,* 2012; Stephens & Diesing, 2015; data for the latter being downloaded from the Cefas Data Hub (http://data.cefas.co.uk/#/Search/1/sediment). Together these sets provided 356 pairs of TON% and mud% values. The data from Serpetti (2012) and Serpetti *et al.* (2012) also included values for median grain size, but not the Cefas data. So, we also assembled data from the Cefas Data Hub on particle size distributions, measured according to the same protocol as followed by Serpetti (2012) and Serpetti *et al.* (2012), and from these computed percentage mud content and whole-sediment median grain size. Using the combined data sets we were able to compute an approximate relationship between median grain size and mud content (Table 5, Figure 4, 5).

$$mud\% = Min\{100 \, , \, 10^{tp1} . D^{tp2}\} \qquad \text{eqn 7}$$

$$TON\% = 10^{tp3} . (mud\%)^{tp4} \qquad \text{eqn 8}$$

TABLE 5 Fitted parameters for the relationships between mud content and whole-sediment median grajn size, and between Total Organic Nitrogen (TON; % dry weight) and mud content.

Relationship	Regression statistics	Parameter	Estimated value	Standard error
mud% vs median grain size	*R-squared: 0.6528*	*tp1*	0.65653	0.02263
	F-statistic: 577.2 on 1 and 307 DF	*tp2*	-0.80043	0.03332
TON% vs mud%	R-squared: 0.6576	*tp3*	-1.96546	0.03247
	F-statistic: 674.1 on 1 and 351 DF	*tp4*	0.58994	0.02272

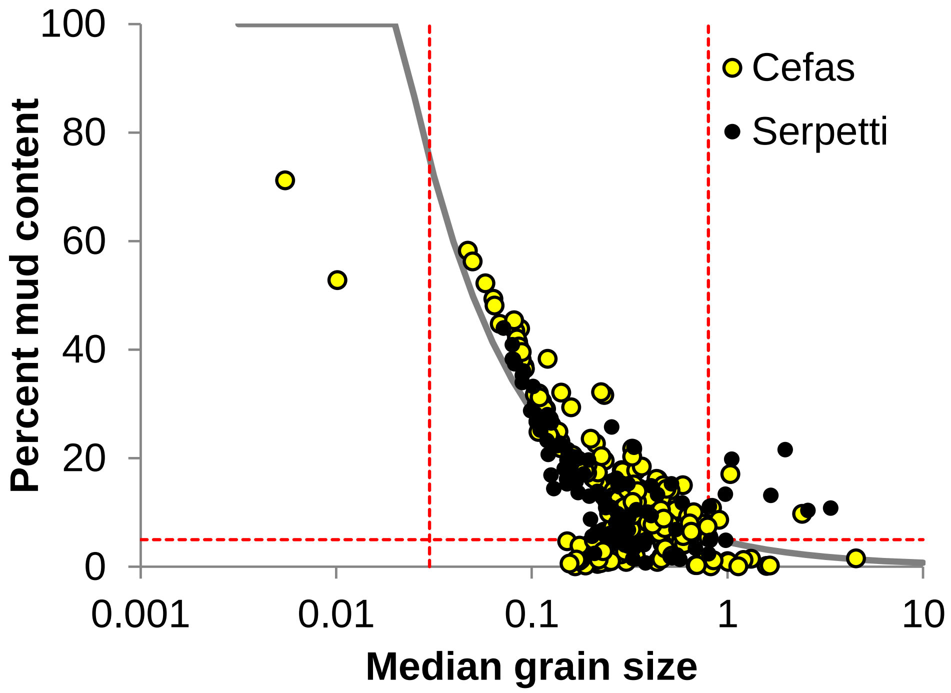

FIGURE 4 Data on mud content and corresponding whole-sediment median grain size from Serpetti (2012), Serpetti *et al.* (2012) and the Cefas Data Hub. As is to be expected given that many of the samples will have been from mixed sediment types, there is considerable scatter in these data, so we confined the dataset to points within the ranges defined by the red-dashed lines for the purpose of fitted the parameters for the curve shown by the grey line (Table 5).

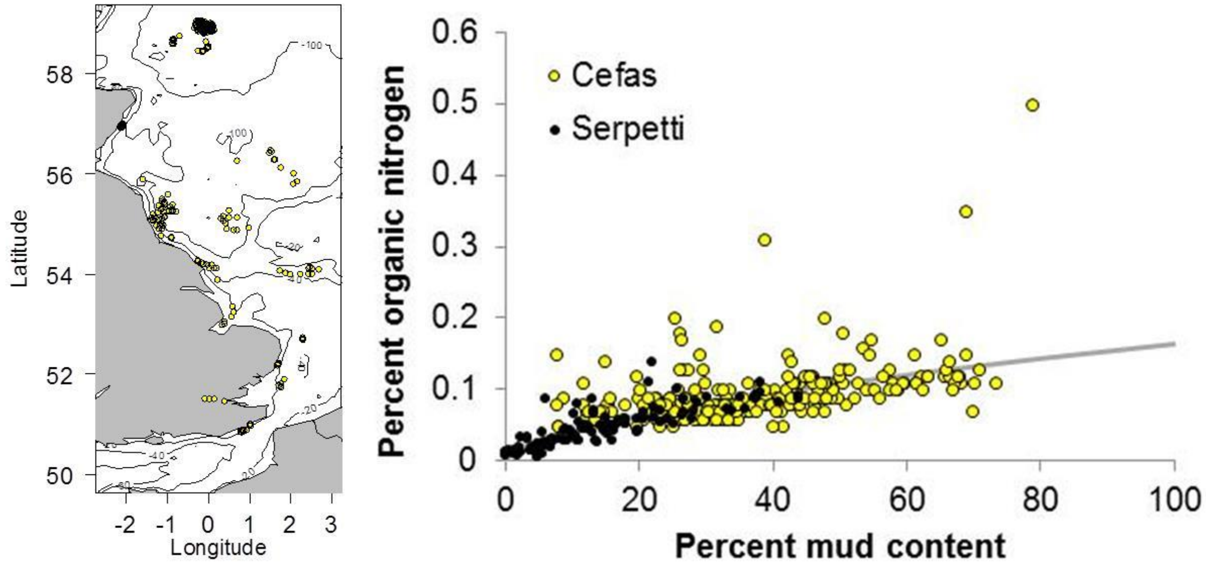

FIGURE 5 Left panel, sampling locations of sediments for Total Organic Nitrogen content (% dry weight) and mud content in Serpetti (2012), Serpetti *et al.* (2012) and the Cefas Data Hub. Right panel, scatter plot of the two data sets with the fitted relationship shown by the grey line (Table 5).

<u>Fixed biological configuration parameters which were not subject to fitting</u>

TABLE 6 Background to the fixed biological configuration parameters for the North Sea model which were not subject to fitting.

Data	**Description**
Assimilation efficiencies for each living guild in the model (Heath, 2012)	Fixed parameters defining the proportion of ingested mass of food that contributes to new body tissue, after subtracting defecation and the metabolic costs of digestion and synthesis.
Biomass loss rates due to	Proportion of biomass lost to ammonia per day due to non-feeding related metabolism at a given reference

temperature-dependent metabolism for each living resource guild	temperature. Rages for individual guilds broadly related to typical body mass of representative species. Temperature dependency following a Q_{10} function.
Q_{10} values for temperature dependent processes, and the Q_{10} reference temperature	Separate Q_{10} values for autotrophic uptake of nutrient, heterotrophic feeding, and heterotrophic metabolism based on literature data.
Light intensity required to saturate autotrophic nutrient uptake	Light saturation intensity for nutrient uptake cannot be treated as a fitted value since it is confounded with other uptake parameters. Value estimated from survey of laboratory experiments.
Annual weight specific fecundities of planktivorous and demersal fish guilds and the two benthos guilds in the model (suspension/deposit feeders and carnivore/scavenge feeders)	Guild-level values derived by surveying the literature
Harvestable biomass density threshold for each resource guild.	The living resource guilds in the model represent a mixture of harvestable and non-harvestable species, especially the invertebrate guilds. The density threshold parameter sets a limit for the guild biomass below which the harvestable species are assumed to be exhausted. Values set from analysis of trawl, plankton and benthos survey species biomass compositions.
Minimum inedible biomass of carnivorous zooplankton	The carnivorous zooplankton guild is a key component of the food web, predated on by all the fish and top-predators. However it represents an extremely diverse range of fauna many of which are not edible in significant quantities by the guild predators, e.g. scyphomedusae. A minimum edible threshold is set to ensure that the guild as a whole cannot be extirpated by predation. The value is a rough estimate of scyphomedusae biomass.

Biological event timing parameters

TABLE 7 Background to the biological event timing parameters for the North Sea model (not subject to fitting).

Data	**Description**
Spawning start and end dates for fish and benthos	For the fish guilds the dates were obtained from literature survey (Heath, 2012), and for the benthos guilds by reference to Continuous Plankton Recorder (CPR) data for the North Sea (Kirby *et al.,* 2008). The annual weight-specific fecundity is assumed to be shed uniformly between the start and end dates of spawning.

Recruitment start and end dates for fish and benthos	Obtained from literature survey (Heath, 2012). The annual cohort of larvae/juveniles of each fish and benthos guild is assumed to recruit to the settled stage at a uniform daily rate between the start and end dates.
Extra-domain stock biomass of migratory, and the proportion invading the domain each year. Start and end dates for the annual invasion, and start and end dates for the emigration. (see description below).	The main migratory fish species undertaking a seasonal transit of the North Sea is the Atlantic mackerel. Data on the North East Atlantic stock biomass, the proportion entering the North Sea and the timing of the migration, were derived from stock assessment literature (ICES, 2013a) and data on the spatial distribution of landings (Nøttestad *et al.,* 2016).

Migratory fish in the North Sea model are assumed to be Atlantic mackerel. The fishery for Atlantic mackerel is one of the most valuable in the northeast Atlantic. Spawning takes place off southwest Ireland in April, and post spawning fish migrating rapidly northwards along the continental shelf edge over several thousand km to feed in the Norwegian Sea or more recently off Iceland (Holst *et al.,* 2016; Nøttestad *et al.,* 2016). The return migration in autumn and winter is slower and a proportion of the stock travels south in shelf waters of the northern North Sea and west of Scotland where a proportion of the harvest is taken (ICES 2013a).

For the purposes of the model, we assume that there is no feedback between fishing and environmental conditions in the North Sea and the biomass and migrations patterns of the whole northeast Atlantic mackerel stock. Implementing such a feedback would be an interesting but separate research project. However, in this version of StrathE2E2 the timing of immigrations and emigrations, and the mass influx across the ocean boundary during the annual immigration phase are treated as period-specific external driving data.

Data on the 'global' stock of northeast Atlantic mackerel (wet biomass) are available from stock assessments (ICES, 2013a), and converted to molar nitrogen mass using appropriate conversion ratios (Greenstreet, 1996). The proportion of the migrating stock entering the North Sea, and the timing of the inward and outward migrations are estimated from monthly resolved data on the spatial distribution of fishery catches. A residual proportion of the peak abundance in the North Sea remaining as residents (if any) is estimated from summer trawl survey data. The model setup code calculates the parameters which are needed in the ecology model. These are the only fixed (i.e. non-fitted) ecology model parameters which are period-specific.

TABLE 8 Migratory fish data and parameters for the periods 1970-1999 and 2003-2013. The data are processed in the model setup to calculate the immigration flux parameters needed in the ecology model.

Migratory fish data and timing parameters	**1970-1999**	**2003-2013**
Migratory fish oceanic biomass (tonnes wet weight)	3190000	3800000
Migratory fish carbon to wet weight ($g.g^{-1}$)	0.184	0.184

Model domain sea surface area (for purposes of calculating immigration flux density (km^2)	485605	485605
Proportion of oceanic population entering the model domain each year	0.33	0.66
Immigration start day	210	210
Immigration end day	330	330
Proportion of peak population in the model domain which remains and does not emigrate	0.1	0.1
Emigration start day	15	15
Emigration end day	45	45

Time-varying physical and chemical driving data for the ecology model

Monthly resolution time-varying physical and chemical driving parameters for the model were derived from a variety of sources:

- Temperature, vertical mixing coefficients, volume fluxes, and boundary nutrient, detritus and chlorophyll concentrations from outputs of a NEMO-ERSEM, coupled hydro-geochemical model hindcast from 1980-2015 (Butenschön *et al.,* 2016)
- Bed shear stress due to tidal currents from a simulated climatological year with an FVCOM hydrodynamic model of the North Sea and waters west of the British Isles (Scottish Shelf Model; De Dominicis *et al.,* 2017)
- Remote sensing data products on Suspended Particulate Matter (SPM, ftp://cems-oc.isac.cnr.it/Core/OCEANCOLOUR GLO OPTICS L4 REP OBSERVATIONS 009 081/dataset-oc-glo-opt-multi-l4-spm 4km monthly-rep-v02)
- Wave height and period from the ERA-Interim reanalysis (Dee *et al*., 2011)
- Nitrate data from the NODC World Ocean Data Climatology 2013 (WOA13 V2; Garcia *et al.,* 2014)
- Ammonia data from the ICES Hydro-chemical Data Centre (http://www.ices.dk/marine-data/data-portals/Pages/ocean.aspx)
- Atmospheric deposition of nitrate and ammonia from the Co-operative Programme for Monitoring and Evaluation of the Long-range Transmission of Air pollutants in Europe (European Monitoring and Evaluation Programme; EMEP; Simpson *et al.*, 2003, Tarrasón, 2003)
- River nitrate and ammonia concentrations and freshwater volume outflows from a statistical reconstruction of European discharge data 1960-2005 (Heath, 2007a)

Details of how these data were processed are given in Table 9.

TABLE 9 Description of the time-varying (monthly resolution) physical, and chemical driving data for the North Sea model

Data	**Description**
Natural disturbance rate of each sediment habitat.	Monthly averaged area-proportions of each seabed sedimentary habitat type where the bed shear stress exceed the critical value for particle motion, were taken from the 1/8 degree resolution atlas of seabed sediment properties (Wilson *et al.,* 2018). The atlas of critical shear stress exceedance was based on a climatological year of high resolution hydrodynamic model outputs (FVCOM Scottish Shelf Model; De Dominicis *et al.,* 2017), and wave climatology from the ERA-Interim reanalysis (Dee *et al.,* 2011). Climatological annual cycle of data used for both 1970-1999 and 2003-2013 simulation periods.
Vertical mixing coefficients between the upper and lower layers of the deep zone.	Extracted as monthly averaged values from NEMO model output (Butenschön *et al.,* 2016). Period-specific climatological annual cycle of data used for 1970-1999 and 2003-2013 simulation periods.
Volume fluxes into the model domain across open sea boundaries, and from the upper layer of the offshore/deep zone into the inshore/shallow zone, expressed as proportions of the receiving layer volume per day	Monthly averaged daily inflow and outflow volume fluxes derived by integrating daily mean velocities directed perpendicular to the model domain boundary at grid points in each depth layer along transects through outputs from the NEMO hydrodynamic model (Butenschön *et al.,* 2016). Monthly averaged daily inflow volume fluxes then divided by the volume of the receiving layer in the model domain to estimate a daily flushing rate. Period-specific climatological annual cycles of data used for 1970-1999 and 2003-2013 simulation periods.
Monthly averaged temperatures for each water column layer.	Derived by monthly averaging values at grid points within the inshore and vertical layers of the offshore zones from the NEMO hydrodynamic model (Butenschön *et al.,* 2016). Period-specific climatological annual cycles of data used for 1970-1999 and 2003-2013 simulation periods.
Monthly averaged suspended particulate matter (SPM) concentrations ($mg.m^{-3}$) in the shallow zone and the deep zone upper layer	Monthly averaged of 4km, 8-day estimates of non-algal surface SPM ($g.m^{-3}$) from September 1997 to August 2017 from the Globcolour Project. These data are derived from satellite observations using the algorithm of Gohin (2011). Data were downloaded from the ftp server ftp://cems-oc.isac.cnr.it/Core/OCEANCOLOUR GLO OPTICS L4 REP OBSERVATIONS 009 081/dataset-oc-glo-opt-multi-l4-spm 4km monthly-rep-v02. Climatological annual cycle of data used for both 1970-1999 and 2003-2013 simulation periods.
Monthly average light attenuation coefficient for the inshore and offshore surface layers	Parameterised from a linear relationship between light attenuation coefficient and suspended particulate matter concentration (SPM) (Devlin *et al.*, 2008)
Monthly averaged daily integrated irradiance at the sea surface ($E.m^{-2}.d^{-1}$)	Derived from regional meteorology data. Climatological annual cycle of data used for both 1970-1999 and 2003-2013 simulation periods.

Monthly averaged daily atmospheric deposition rates of wet and dry, oxidised and reduced nitrogen onto the sea surface in the shallow and deep zones (mMN.m^{-2}.d^{-1})	Derived from 50 x 50 km^2 gridded data for the years 1980, 1985, 1990, 1995, and 2000 - 2015, available from the Co-operative Programme for Monitoring and Evaluation of the Long-range Transmission of Air pollutants in Europe (EMEP) Unified 50 x 50 km^2 grid model. Pre-2000 data available only as annual averages, from revision 1.7 of the model; Simpson *et al.*, 2003, Tarrasón, 2003; see https://www.emep.int/mscw/mscw_ydata.html#Foot2. Data previously downloaded from www.emep.int/Model_data/yearly_data.html in 2007 (Heath 2007a) and no longer available online. Data from 2000 onwards available as monthly averages from https://thredds.met.no/thredds/catalog/data/EMEP/2019_Reporting/catalog.html. Climatological annual cycles of monthly oxidised and reduced nitrogen deposition rates extracted for 2003-2013. Monthly rates relative to the annual mean were then used to generate a climatological seasonal cycle representative of the 1970-1999 period based on the annual mean deposition rates for 1980,1985,1990 and 1995.
Monthly averaged , freshwater river infow rates (expressed as a daily proportion o fthe receiving layer volume), and volume weighted concentrations of oxidised and reduced dissolved inorganic nitrogen in the inflowing river waters (mMN.m^{-3})	Derived from 1960-2005 monthly averaged nutrient flux and freshwater discharge fluxes into 1 longitude x 0.5 latitude cells around the entire northwest European coastline, originating from a synthesis of national monitoring data and statistical modelling based on rainfall data (Heath, 2007a). Period-specific climatological annual cycles of data used for 1970-1999 and 2003-2013 simulation periods.
Mean concentrations of nitrate, ammonia, phytoplankton and suspended detritus (mMN.m^{-3}), in adjacent ocean waters inflowing to the offshore/deep zone upper layer, adjacent ocean waters inflowing to the offshore/deep zone lower layer, and adjacent shelf waters inflowing to the inshore/shallow zone	Observational data on the boundary variables are of extremely variable resolution. However, simulated outputs of all four variables were available at high space-time resolution from a hind-cast run of the NEMO-ERSEM model (Butenschön *et al.,* 2016). Comparisons of the available observational data on nitrate, ammonia and chlorophyll with corresponding values in in the NEMO-ERSEM outputs (e.g. Ciavatta *et al.,* 2016 for chlorophyll) show sufficiently large space-time varying biases as to rule out driving the StrathE2E2 model with boundary data extracted directly from the NEMO-ERSEM outputs. To do so would mean that we were driving the model with data which were inconsistent with the other observational measurements on the state of the ecosystem against which the StrathE2E2 parameters were to be optimized. We therefore used a bias correction methodology (Maraun 2016) to generate monthly resolution 3-dimensional climatologies of nitrate, ammonia and phytoplankton concentrations from the NEMO-ERSEM outputs, and from these we extracted the required boundary concentrations for StrarhE2E.

	We used the same climatological boundary data for both the 1970-1999 and 2003-2013 StrathE2E2 simulation periods on the grounds that the magnitudes of the bias corrections were equivalent to or larger than inter-period differences in the ERSEM outputs. Nitrate A depth-resolved, 1 degree by 1-degree gridded monthly climatology of nitrate was available from the World Ocean Atlas 2013 Version 2 (WOA13 V2; Garcia *et al.,* 2014). These data alone were sufficient to have provided credible climatological boundary conditions for the offshore zone and layers of StrathE2E2, but not for the inshore zone. We therefore used the WOA13 climatology to bias-correct the monthly climatologies of nitrate predicted by NEMO-ERSEM over the period corresponding the years in which the majority of the WOA data were collected (1980-1999). We first calculated monthly 3-dimensional climatologies of NEMO-ERSEM nitrate data for the period 1980-1999. Then, for grid cells corresponding to the mid-points of WOA13 cells we calculated the relative bias or "change factor" ($Nitrate_{WOA}/Nitrate_{ERSEM}$), and interpolated these over the entire 3-dimensional grid using nearest neighbour. Finally, the interpolated monthly change factors grids were multiplied into the monthly ERSEM climatologies to generated a bias-corrected climatological annual cycle of 3-dimensional nitrate concentrations. Ammonia Observational ammonia data for the period 1980-2013 were downloaded from the ICES data portal (http://www.ices.dk/marine-data/data-portals/Pages/ocean.aspx). Each observation was resolved by time, longitude, latitude and depth of collection. However, the data set was extremely sparse with large spatio-temporal gaps. We first created an aggregated observational data set at a spatial resolution of 1 by 1 degrees per month, and for the surface and deep layers (surface defined as the top 30 m). This was an approximate climatology of ammonia, but with many gaps. We then followed the same procedure as for nitrate to create a bias-corrected climatological annual cycle of 3-dimensional ammonia concentrations. Phytoplankton There are no space-time gridded data produces of in-situ phytoplankton biomass. In addition, satellite chlorophyll products are almost universally based on algorithms fitted to global observational data and can therefore exhibit regional spatial and temporal bias. We therefore used

	the surface (top 5 m) chlorophyll climatology of Clarke *et al.* (2006) which was generated by a statistical methodology to blend satellite chlorophyll with in-situ water-bottle derived chlorophyll measurements from the North Atlantic. This surface climatology was first interpolated to the NEMO-ERSEM horizontal grid. We then calculated a comparable monthly climatology of surface chlorophyll from NEMO-ERSEM outputs. As with nitrate, we then calculated a change-factor (Chl_{Clarke}/Chl_{ERSEM}) for each surface grid cell and in each month and applied this across all NEMO-ERSEM chlorophyll predictions at each location in time and space. The change factors were applied uniformly across all depths on the assumption that NEMO-ERSEM reflected the true vertical distribution of chlorophyll. This resulted in a set of monthly 3-dimensional chlorophyll data sets where the surface chlorophyll climatology matched the observational data set of Clarke *et al.* (2006). Chlorophyll concentrations were then converted to nitrogen units assuming carbon:chlorophyll (weight ratio) of 20 and Redfield molar ratios of carbon:nitrogen. Suspended detritus Observational data on organic detritus are extremely sparse. Conditions for detritus nitrogen were therefore taken directly from NEMO-ERSEM without any bias correction. Boundary data extraction For each bias-corrected climatological data set we calculated monthly averages of values at grid cells located at vertical slices along each of the open inshore and offshore zone boundaries and depth layers of the StrathE2E2 model domain.

Inputs to the North Sea fishing fleet model

Background

The key configuration data for the fishing fleet model are the definitions of the gears in terms of their power with respect to each of the harvestable resource guilds, discarding rates, processing-at-sea rates, and their seabed abrasion rates. These can be regarded as static parameters for each gear.

An additional class of static parameters is the scaling coefficients between effort (activity x power) and the harvest ratio generated on each model resource guild. These parameters have to be derived by fitting.

Finally, there are parameters which we can consider as driving data since they would be expected to vary with time. These are the activity rates of each gear, and their spatial distributions across the habitat types.

Static gear-definition parameters in the fishing fleet model

TABLE 10 Description of static parameters for the fishing fleet model. These parameters would be expected to remain constant over time, so any changes invoked would imply a change in the design or operation of a gear type.

Data	**Description**
Definition of gear types, their catching power and discard rates for each resource guild	Data for 2003-2013 derived from EU Scientific, Technical and Economic Committee for Fisheries (STECF) reports (data filename: '2014_STECF 14-20 - Fishing Effort Regimes data tables.zip'; http://stecf.jrc.ec.europa.eu/data-reports). Full description in Heath *et al.,* 2015. Data for parameterising catching power of gears for small cetaceans derived from a variety of sources including the ICES Working Group on the Bycatch of Protected Species (ICES, 2015a,b)
Definition of the proportion of retained catch of each model resource guild which is processed (gutted) at sea by each gear type, and the proportion of live weight discarded as offal as a result of processing.	Proportion of live weight discarded by processing, from Coull *et al.* (1989). Proportion of retained catch processed at sea approximately estimated from the fish market sampling data.
Scaling parameters relating effort to harvest ratios applied to each model resource guild	Derived by fitting harvest ratios, as described later in this document..
Seabed abrasion rates of each gear type.	Data on the area of seabed disturbed per unit time of towing by different fishing gears obtained from published studies (Eigaard *et al.,* 2015).
Sediment penetration depth for seabed-contact fishing gears	Single penetration depth (5 cm) assumed across all seabed-contact gears, and independent of sediment type, based on data from Eigaard *et al.* (2015).
Damage mortality rates on benthos species caused by seabed-contact towed gears	Proportion of fauna killed per trawl pass assuming 5 cm penetration depth, obtained from literature meta-analysis (Hiddink *et al.,* 2017)
Parameters for an empirically-based	Relationship established from analysis of research vessel trawl survey catch per unit effort

relationship between demersal fish biomass in the model, and the proportion of annual catch weight made up of non-quota limited species (see this document for details).	data, and species landings data: $$\varphi_{NQ} = p_{11} \cdot e^{-p_{12}.B}$$ where φ_{NQ} is the proportion of annual commercial catch weight which comprises non-quota species, B is the demersal fish community biomass on 1 January, p_{11} and p_{12} are fitted parameters.
Parameters for empirically based relationships between demersal fish biomass in the model, and the proportion of annual catch which is undersize for landing or marketing. Separate relationships for quota-limited and non-quota species groups (see this document for details).	Relationship established from analysis of research vessel trawl survey catch per unit effort data, and species landings data: $$\varphi_{U,x} = p_{13,x} \cdot e^{-p_{14,x}.B}$$ where $\varphi_{U,x}$ (x = quota-limited/non-quota) is the proportion of catch weight which is undersize for legal landing (quota-limited group) or for marketing (non-quota group), B is the demersal fish community biomass on 1 January, $p_{13,x}$ and $p_{14,x}$ are fitted parameters.

Potentially time-varying parameters of the fishing fleet model

TABLE 11 Description of potentially time-varying driving data for the fishing fleet model.

Data	**Description**
Regional activity rates, of each gear type	Data for 2003-2013 derived from EU Scientific, Technical and Economic Committee for Fisheries (STECF) reports (data filename: '2014_STECF 14-20 - Fishing Effort Regimes data tables.zip'; http://stecf.jrc.ec.europa.eu/data-reports). Full description in Heath *et al.* (2015).
Spatial proportional distribution of activity by each gear	Proportion of domain-wide annual average activity rate over each seabed habitat type, derived by overlaying spatial distributions of activity from the EU Scientific, Technical and Economic Committee for Fisheries (STECF) reports, onto spatial distributions of seabed sediment types derived from the atlas of sediment properties (Wilson *et al.,* 2018).

Data processing to derive fish and invertebrate related parameters for the fleet model

Processing of Scientific, Technical and Economic Committee for Fisheries (STECF) and Norwegian landings data analysis

Data on the landings, discards, activity and economic performance of the fleet sectors of all EU member states are available for STECF (https://stecf.jrc.ec.europa.eu/dd/effort). From 2000 onwards, the landings and effort data are resolved by at least 1 longitude x ½ latitude cells (approximately 30 x 30 nautical miles). Discard data are available only at a more aggregated spatial resolution. The dataset for NW European water includes records on 101 different species covering mostly finfish. Invertebrates are under-represented in the records. We aggregated the species data into the coarse ‘functional’ categories defined in the StrathE2E2 model.

The data contain 32 different fishing gear designations. Some of which are local variants appropriate to particular countries or regions. We aggregated the STECF gear types up into 11 coarser groups for use in StrathE2E2. The aggregation rules are shown in Table 12

TABLE 12 Correspondence between raw STECF gear codes and gear categories in the analyses presented here.

STECF Code	**Gear description**	**StrathE2E2 model gear type**
PELAGIC TRAWLS	Pelagic trawls	Pelagic trawls & seines
PEL_TRAWL	Pelagic Trawl	
PEL_SEINE	Pelagic seine nets	
TR3	Bottom trawls and seines of mesh size equal to or larger than 16 mm and less than 32 mm – mostly targeting sprat.	Sandeel & sprat trawls
OTTER	Bottom trawls (for sandeel)	
LL (landings in a statistical rectangle >50% by weight mackerel)	Drifting longlines (for pelagic fish)	Longline mackerel
BT2	Beam trawls of mesh equal to or larger than 80 mm and less than 120 mm.	Beam trawl demersal
BT1	Beam trawls of mesh equal to or larger than 120 mm	
DEM_SEINE	Danish and Scottish seiners	Demersal seine
TR1	demersal trawls/seines with larger mesh sizes > 100MM	Demersal otter trawl (mainly TR1)
TR2 (landings in a statistical rectangle <30% by weight	Demersal trawls and seines with mesh 70-99mm	

Norway lobster)		
BOTTOM TRAWLS	Bottom trawls	
3A	Bottom trawler mesh size ≥ 32 mm)	
LL (landings in a statistical rectangle <50% by weight mackerel)	Set longlines (for demersal fish)	Longline & gillnets demersal
GN1	Gill nets, entangling nets.	
GILL	Drift and fixed Nets except Trammel Nets	
3B	Gillnet ≥60 mm	
TRAMMEL	Trammel nets	
GT1	Trammel nets	
BEAM	Beam trawl targeting shrimp (in the North Sea)	Beam trawl shrimp
TR2 (landings in a statistical rectangle >30% by weight Norway lobster)	Demersal trawls and seines with mesh 70-99mm	Nephrops trawl
POTS	Pots and traps	Creels and pots
DREDGE	Dredges (targeting scallops in the North Sea)	Mollusc dredges

There were some specific considerations involved in the gear aggregations, depending on the species targeted in particular areas.

Beam trawls: The STECF beam trawl categories BT1 and BT2 more or less exclusively target demersal finfish species in the North Sea. It is therefore reasonable to combine BT1 and BT2 into a single model gear. However, care must be taken with the BEAM class. In the North Sea, landings from BEAM gears are more or less exclusively common shrimp (98.7% of the total). Elsewhere, landings from BEAM are almost exclusively demersal fish. We therefore created a ‘Beam trawl shrimp’ gear in the North Sea.

TR2 trawls:_The TR2 category covers gears used in a variety of fisheries in the North Sea:

- A fishery for Nephrops, which has a significant bycatch of demersal fish
- Mixed fishery in the southern North Sea, with whiting and other finfish species as the main components

- Danish and Swedish fishery targeting demersal finfish in the Skagerrak.

Since the targeted Nephrops fishery operates exclusively in muddy areas and there are particular concerns about the seabed impact of this fishery we sought to disaggregate TR2 to identify the Nephrops trawl component. Country level landings data help us with the disaggregation. If the TR2 landings by an individual country from an individual ICES statistical rectangle comprised more than 30% Nephrops then we assigned that rectangle's TR2 landings and activity to the Nephrops gear. If it was less than 30% we assigned it to the demersal otter trawl category.

Longlines (LL): Longlines are extensively used in drifting, near-surface set mode for catching mainly mackerel and tuna, and in a near-seabed set mode for catching demersal fish such as cod and ling. Apart from the very different species-targeting of these two modes of operation, there are consequences for by-catch of non-target species. In particular, various seabird species are vulnerable to

Estimating Norwegian fishing activity from landings data

A shortcoming of the STECF data is that it only includes data from EU Member States. So, while effort and landings from EU activity in Norwegian and Faroese territorial waters are included, the equivalent data for Norwegian and Faeroese vessels are not. This is a problem for analysis of spatial and national shares of total yields and effort in the North Sea where Norway has a significant share of the total catch. The Faeroe Islands also have an access agreement with the EU, but their activities in the North Sea are relatively minor.

We made a request to the Norwegian Directorate of Fisheries, Statistics Department, who provided all the Norwegian annual landings data from the North Sea and west of Scotland regions, resolved by species and 1 longitude x ½ latitude cells for the years 2003-2016. We processed these data to conform with the STECF data, but still we lacked a breakdown of the landings by gear, or any record of the activity rates of Norwegian vessels to compare with the EU activity data. However, given that each of the STECF gears largely targets particular species (e.g. TR3 targets sandeels/sprats, etc), and assuming that the pattern of targeting and the selectivity of the gear types is the same in the EU and Norwegian fishery, we developed a scheme to impute the Norwegian gear activity and the distribution of Norwegian landings across gear types for a given year and geographic area (Figure 6). We carried out this procedure for the inshore and offshore zones separately.

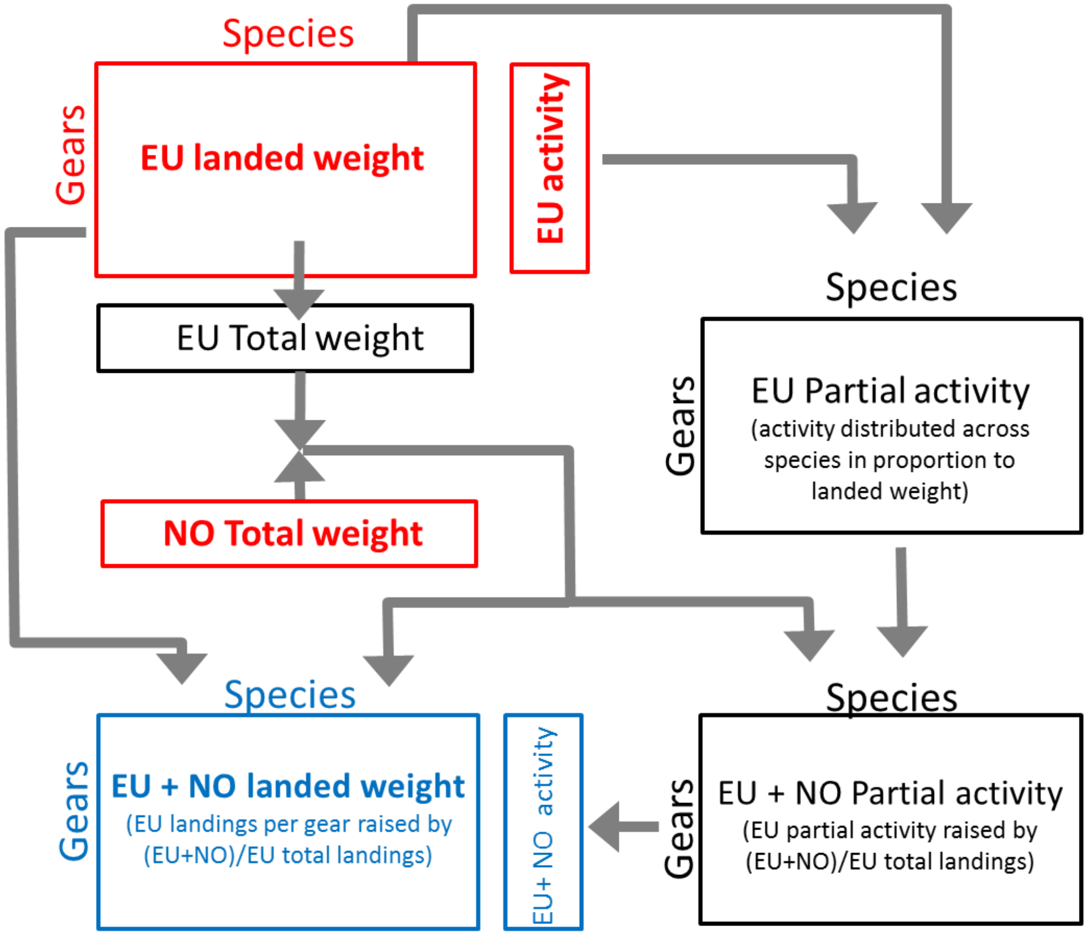

FIGURE 6 Workflow for imputing Norwegian effort per gear type, and the distribution of Norwegian landings across gear types in a given year and geographic area, given the STECF data and the Norwegian landings data obtained from the Directorate of Fisheries. Red cells indicate the input data that we have from STECF and the Norwegian Fisheries Directorate, blue cells indicate the data we wish to impute, grey cells represent intermediate data generated during the processing. EU = European Union fleet data, NO = Norwegian fleet data. Estimates of Norwegian effort and landings per gear alone, is simply the imputed total (EU+NO) minus the known EU component.

Impacts of different fishing gears on the seabed

Eigaard *et al.* (2015) evaluated seabed areas impacted per hour of trawling by a range of fishing gear fleets, including those listed by STECF. We mapped our gear classes on to those of Eigaard *et al.* and produced estimates of ploughed area per unit time, assuming a gear penetration depth of 5cm (Table 13).

TABLE 13. Seabed abrasion rates for fishing fleets in the North Sea (Eigaard *et al.,* 2015).

Gear category	**Seabed abrasion rate $m^2.s^{-1}$**
Pelagic trawls and seines	0
Sandeel and sprat trawls	8.8
Longline Mackerel	0
Beam trawl demersal	54.1
Demersal Seine	22.4
Demersal otter trawl	17.1
Longline & gillnets demersal	0
Beam trawl shrimp	13.5
Nephrops trawl	78.9
Creels & pots	0
Mollusc dredges	22.4
Norwegian whalers	0

Regional activity density of each gear category

For each of the StrathE2E2 gear types assembled from the STECF data (Table 12), we summed the inshore and offshore annual activity rates (seconds per year) of the StrathE2E2 gear groups, and the corresponding Norwegian activity, and divided by the area of the whole model domain to obtain an annual activity density. The inherent assumption in this process was that the STECF gears contributing to each StrathE2E2 gear group have equivalent power. Finally, we then averaged the annual values for each gear group over the duration of the STECF data period (2003-2013).

TABLE 14 2003-2013 annual average activity (hours per year within the StrathE2E2 model domain) by EU and Norwegian vessels for each of the gear aggregations in the fleet model.

StrathE2E2 gear group	Activity ($s.m^{-2}.d^{-1}$)
Pelagic Trawl & Seine	2.17E-06
Sandeel & sprat trawls (Otter30-70mm & TR3)	4.23E-06
Longline mackerel	1.68E-06
Beam Trawl demersal (BT1 & BT2)	1.15E-05
Demersal Seine	1.72E-08
Demersal Otter Trawl (TR1)	2.16E-05
Gill Nets & Longline demersal	7.92E-06
Beam Trawl shrimp	1.27E-05
Nephrops Trawl (TR2)	1.72E-05
Creels	2.40E-05
Mollusc Dredge	3.11E-06

Spatial distribution of fishing activity

The 2003-2013 average geographical distribution of EU gear activity, resolved by 1 degree longitude x 0.5 degree latitude statistical rectangles was derived from the STEFC database. Then, we overlaid the spatial distribution of the 8 seabed habitat classes in the model, and derived the proportion of total EU activity occurring within each habitat (Table 15). Finally, we assumed that Norwegian activity in each gear class was distributed in proportion to EU activity.

There are no data on the spatial distributions of gear activity during the 1970-1999 model fitting period, so we assumed that the proportional distribution of activity during 2003-2013 was also representative of this earlier period.

TABLE 15 2003-2013 average proportion of North Sea domain-wide activity by each gear category occurring over each seabed habitat, derived from STECF activity data and seabed sediment class data. The bottom row shows the area-proportions of each seabed habitat for comparison.

Gear category	Shallow rock	Shallow mud	Shallow sand	Shallow gravel	Deep rock	Deep mud	Deep sand	Deep gravel
Pelagic trawls & seines	0.0023	0.0223	0.1857	0.0566	0.0041	0.3618	0.3324	0.0349
Sandeel & sprat trawls	0.0016	0.0419	0.1885	0.0993	0.0033	0.2203	0.4222	0.0229
Longline Mackerel	0.0026	0.0192	0.1334	0.0046	0.0022	0.0481	0.7862	0.0037
Beam trawl demersal	0.0000	0.0103	0.5558	0.0516	0.0000	0.1579	0.2183	0.0061
Demersal seine	0.0108	0.0417	0.2481	0.0393	0.0157	0.2316	0.3695	0.0433
Demersal otter trawl	0.0038	0.0055	0.0791	0.0868	0.0096	0.3050	0.4735	0.0367
Longline & gillnets demersal	0.0176	0.0115	0.3819	0.3067	0.0097	0.0575	0.2055	0.0096
Beam trawl shrimp	0.0000	0.0414	0.8679	0.0612	0.0000	0.0190	0.0102	0.0003
Nephrops trawl	0.0000	0.1137	0.0000	0.0000	0.0000	0.8863	0.0000	0.0000
Creels & pots	0.0148	0.0484	0.1900	0.1670	0.0238	0.0503	0.4214	0.0845
Mollusc dredges	0.0000	0.0114	0.2565	0.0929	0.0000	0.0508	0.4915	0.0969
Habitat area proportion	0.0030	0.0110	0.1878	0.0478	0.0057	0.2665	0.4595	0.0187

Allocation of STECF fish and benthos landings and discards to gear classes

Full details of the procedures for a) allocating landed and discarded species to StrathE2E2 model guilds, b) allocating landings to gears, and c) allocating discards to gears and statistical rectangles, are described by Heath *et al.* (2015). Brief summaries of the essential results are presented here.

TABLE 16 2003-2013 average annual live weights landed (tonnes) of each StrathE2E2 fish and invertebrate resource category, by each gear in the fleet model, derived from the combined STECF and Norwegian data

Gear category	**Planktivorous fish**	**Demersal fish**	**Migratory fish**	**Suspension/ deposit feeding benthos**	**Carnivore/ scavenge feeding benthos**	**Carnivorous zooplankton**
Pelagic trawls & seines	349610	237	185311	0	1	0
Sandeel & sprat trawls	358202	571	13462	1	485	0
Longline Mackerel	2	11	1038	0	8	0
Beam trawl demersal	1	58239	51	3	687	0
DemersalSeine	0	25	16	0	0	6
Demersal otter trawl	1338	121323	3912	7	1875	1850
Longline & gillnets demersal	173	9177	28	2	50	0
Beam trawl shrimp	152	269	14	0	27124	0
Nephrops trawl	6	12005	133	1	16706	237
Creels & pots	1	66	80	8	7277	0
Mollusc dredges	32	11	2	4314	3	0
Totals	709516	201934	204046	4336	54216	2093

TABLE 17 2003-2013 average annual live weights discarded (tonnes) of each fish and invertebrate StrathE2E2 resource category, by each gear in the fleet model, derived from STECF

Gear category	Planktivorous fish	Demersal fish	Migratory fish	Suspension/ deposit feeding benthos	Carnivore/ scavenge feeding benthos	Carnivorous zooplankton
Pelagic trawls & seines	1031	30	10219	0	0	0
Sandeel & sprat trawls	42	664	118	0	101	0
Longline Mackerel	0	<1	0	0	0	0
Beam trawl demersal	0	69626	104	0	121	0
DemersalSeine	0	0	0	0	0	0
Demersal otter trawl	192	109270	13080	<1	852	0
Longline & gillnets demersal	0	260	9	0	49	0
Beam trawl shrimp	111	8770	8	0	36853	0
Nephrops trawl	4	26014	104	0	1070	0
Creels & pots	0	1	0	0	0	0
Mollusc dredges	0	10	0	24	0	0
Totals	1380	214644	23641	25	39048	**0**

Landings data required to be converted from live wet weight to nitrogen mass for use in the model. The wet weight to nitrogen conversion factors assumed as given in Table 18.

TABLE 18 Nitrogen content (mMN) per gram wet weight for living guilds which were assumed for converting landed live weights to nitrogen mass. Where necessary the values were estimated from quoted carbon mass data assuming Redfield molar ratios.

Guild	**Nitrogen mass per unit wet weight ($mMN.gWW^{-1}$)**	**Source**
Macrophytes	2.070	Black (1950), Sjøtun *et al*. (1996)
Carnivorous zooplankton	1.258	Greenstreet (1996)
Planktivorous fish	2.038	Greenstreet (1996)
Demersal fish	1.340	Greenstreet (1996)
Migratory fish	2.314	Greenstreet (1996)
Suspension/deposit feeding benthos	0.503	Greenstreet (1996), Ricciardi & Bourget (1998)
Carnivore/scavenge feeding benthos	1.006	Greenstreet (1996), Ricciardi & Bourget (1998)
Birds	2.518	Taylor & Konarzewski (1989), and assuming dry weight/wet weight = 0.440, carbon weight/dry weight = 0.455, and Redfield molar C:N ratio = 6.625.
Pinnipeds	2.518	Lavigne *et al.* (1986), and assuming dry weight/wet weight = 0.440, carbon weight/dry weight = 0.455, and Redfield molar C:N ratio = 6.625.
Cetaceans	2.518	Lavigne *et al.* (1986), and assuming dry weight/wet weight = 0.440, carbon weight/dry weight = 0.455, and Redfield molar C:N ratio = 6.625.

TABLE 19 Discard rates (proportion of catch discarded) by each gear with respect to each resource guild. Values calculated for the period 2003-2013.

Gear category	**Planktivorous fish**	**Demersal fish**	**Migratory fish**	**Suspension/ deposit feeding benthos**	**Carnivore/ scavenge feeding benthos**	**Carnivorous zooplankton**
Pelagic trawls & seines	0.003	0.112	0.052	0	0	0
Sandeel & sprat trawls	0	0.538	0.009	0	0.173	0
Longline Mackerel	0	0.005	0	0	0	0
Beam trawl demersal	0	0.545	0.671	0.014	0.150	0
DemersalSeine	0	0	0	0	0.000	0
Demersal otter	0.126	0.474	0.770	0.022	0.313	0

trawl						
Longline & gillnets demersal	0	0.027	0.231	0	0.498	0
Beam trawl shrimp	0.422	0.970	0.366	0	0.576	0
Nephrops trawl	0.380	0.684	0.439	0	0.060	0
Creels & pots	0.056	0.008	0.001	0	0	0
Mollusc dredges	0	0.477	0	0.006	0	0

TABLE 20 Catching power (mMN s^{-1}) of each gear with respect to each fish and invertebrate resource guild in the ecology model. Values calculated as the ratio of catch rate : activity rate for each gear, for the period 2003-2013.

Gear category	Planktivorous fish	Demersal fish	Migratory fish	Suspension/ deposit feeding benthos	Carnivore/ scavenge feeding benthos	Carnivorous zooplankton
Pelagic trawls & seines	1932.12	0.89	1077.41	0.00	0.00	0.00
Sandeel & sprat trawls	1013.87	2.12	38.43	0.00	0.77	0.00
Longline Mackerel	0.01	0.05	7.38	0.00	0.03	0.00
Beam trawl demersal	0.00	80.90	0.16	0.00	0.39	0.00
Demersal Seine	0.00	10.64	10.94	0.00	0.02	5.09
Demersal otter trawl	0.85	77.63	9.42	0.00	0.70	1.50
Longline & gillnets demersal	0.26	8.66	0.06	0.00	0.07	0.00
Beam trawl shrimp	0.25	5.18	0.02	0.00	27.91	0.00
Nephrops trawl	0.01	16.07	0.16	0.00	5.72	0.14
Creels & pots	0.00	0.02	0.04	0.00	1.68	0.00
Mollusc dredges	0.12	0.05	0.01	5.80	0.01	0.00

Processing of catch at sea and production of offal

The proportion of the catch of each resource guild which is processed at sea aboard each gear group was estimated roughly from market sampling data (proportion of landing as whole vs gutted fish) and expert knowledge (Table 21). The proportion of live weight discarded as offal as a result of processing was estimated to be 10%.

TABLE 21 Processing-at-sea proportions for each gear with respect to each fish and invertebrate resource guild in the ecology model.

Gear category	Planktivorous fish	Demersal fish	Migratory fish	Suspension/ deposit feeding benthos	Carnivore/ scavenge feeding benthos	Carnivorous zooplankton
Pelagic trawls & seines	0	0	0	0	0	0
Sandeel & sprat trawls	0	0	0	0	0	0
Longline Mackerel	0	0	0	0	0	0
Beam trawl demersal	0	0.5	0	0	0	0
Demersal Seine	0	0.5	0	0	0	0
Demersal otter trawl	0	0.5	0	0	0	0
Longline & gillnets demersal	0	0	0	0	0	0
Beam trawl shrimp	0	0	0	0	0	0
Nephrops trawl	0	0	0	0	0.8	0
Creels & pots	0	0	0	0	0	0
Mollusc dredges	0	0	0	0	0	0

Scaling parameters relating effort to harvest ratio for fish and invertebrate guilds in the model

The parameters linking effort (activity x power) of any gear in the fleet model to harvest ratios in the ecology model are key terms in the coupled system. To estimate these independently we need estimates of the integrated harvest ratios for each of the living resource guilds in the ecology model to compare with the integrated effort across all the gears in the fleet model.

Finfish harvest ratios

The approach to estimating fish harvest ratios was a refinement of that outlined by Heath (2012). Annual species-specific total stock biomass data from the analytical assessments conducted by the International Council for the Exploration of the Sea (ICES) were assembled for the period 1960-onwards where possible. For the North Sea these data are available for only the major commercial species but these constitute a high proportion of the community biomass of the guilds of fish in the model (planktivorous: herring, sandeel, Norway pout; demersal: cod, haddock, whiting, plaice, saithe, sole; migratory: mackerel). Assessments have commenced at different times for the various species, with plaice, cod, haddock and herring being the longest-running series. Data-gaps in the early years were filled by extrapolating back in time from the first assessed year using independent trawl survey data as an index of population biomass. In addition, the age at first inclusion in the assessment varied between 3 and 9 months depending on species, so a compensatory correction was applied to bring the biomasses of all species into line.

Annual catches of each of the assessed species were constructed from the sum of landings and discards as provided in the ICES stock assessment reports. Where discard data were absent, values were filled in from a statistical reconstruction of discard histories for the North Sea (Heath & Cook, 2015), or prior to 1980 by extrapolating the discard rate (proportion of catch discarded).

The whole-guild biomass of each guild was estimated by up-scaling the combined biomass of the assessed species, using a ratio of all-species to assessed species biomass derived from independent trawl surveys. Finally, the annual harvest ratios for each fish guild were determined from whole-guild biomasses and catches across all the species representing each guild;.

The estimated harvest ratios for both planktivorous and demersal fish increased from the 1960s to the 1970s and remained high during the 1990s. During the 2000s harvest ratios decreased towards low levels by 2010 (Figure 7). This pattern is entirely consistent with the changes in fishing mortality reported in the ICES Greater North Sea Eco-region review (ICES, 2016). ICES determined that fishing mortality rates during the period 1970-1999 were around 2-times F_{MSY} (the fishing mortality associated with maximum steady state catch) for demersal fish, and 1.0-1.3-times F_{MSY} for pelagic fish. The ratio F/F_{MSY} does not necessarily correspond to HR/HR_{MSY}, but we can be certain that average harvest ratios during this period (1970-1999) were in excess of HR_{MSY}, especially for demersal fish.

Benthic invertebrate harvest ratios

There are no stock assessments for invertebrates of comparable detail to those for finfish. This is partly due to the inability to reliably determine the age of individuals, so that there is a lack of data to support age-based population dynamics approaches. The most detailed assessments are for Norway lobster (*Nephrops norvegicus*) where television surveys are used to provide fishery-independent data on stock biomass. Some degree of assessment is available for Atlantic scallop and brown shrimp, but very little for other benthic crustaceans and molluscs, or for squids. Based on the time-series of Norway lobster stock and landings we estimated the harvest ratios for carnivorous/scavenge feeding benthic invertebrates (Figure 7), and assumed that these apply also to other invertebrates.

The ICES North Sea Eco-region review (ICES, 2016) determined that fishing mortality rates for invertebrates have risen steadily from around 0.3-times F_{MSY} to 1.25-times F_{MSY} between 1970 and 2010. This synopsis largely reflects the trend in landings over the period.

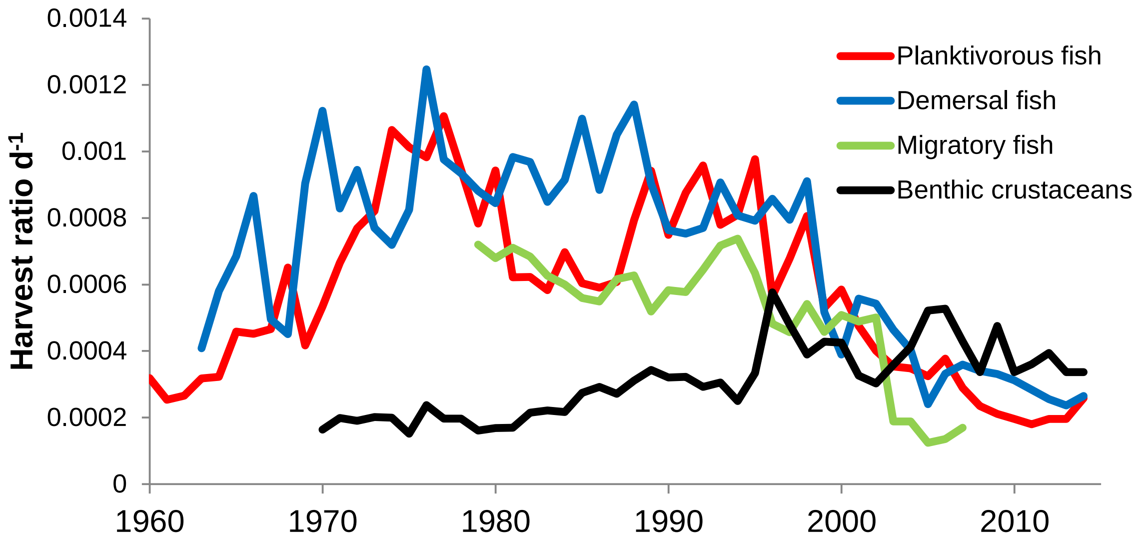

FIGURE 7 Time series of harvest ratio (proportion of biomass removed per day) for guilds of fish and benthic crustaceans in the North Sea. Data compiled from analyses of stock assessments, trawl survey data and with reference to ICES (2016).

Parameterisation of selectivity and harvest ratios for top predators.

In addition to the power parameters and the effort-harvest ratio scaling parameters defining the selectivity of each gear for fish and invertebrate guilds in the model, as outlined above, we also require equivalent parameters defining the unintended by-catch of the top-predator guilds (birds, pinnipeds, cetaceans) by these gears. There is no one simple source of data, equivalent to STECF, from which these parameters can be calculated, so we drew on data from a variety of sources:

First, we required data on the biomass of each top-predator guild in the North Sea, which we sourced from:

- Atlas of bird and cetacean species spatial abundances developed by statistical modelling of observer line-survey data on seabirds-at-sea and cetacean abundances (pers.comm, Dr James Waggitt & Dr Peter Evans, Bangor University; Waggitt *et al*., 2019)
- Periodic assessments of grey and common seal population numbers in UK and European waters (Sea Mammal Research Unit (SMRU) & Marine Scotland, 2017)

Data on by-catch rates were sourced as follows:

- Records of strandings of cetaceans around the UK including pathology data on the likely cause of death (Deaville & Jepson, 2011). These data were used to identify cetaceans which had died as a result of entanglement in ropes – which we assumed to be predominantly creel lines.
- Synthesis of data on numbers of cetaceans entangled in fishing gears from national returns to ICES (e.g. ICES, 2015a,b, 2018), and summaries by ASCOBANS (Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas, www.ascobans.org).
- Literature on cetacean by-catch (Bjorge *et al.,* 1994, 2013; Brown *et al.,* 2013; Dawson *et al.,* 2013; Evans & Hinter, 2013; Hammond *et al.*, 2002; Kaschner, 2003; Larsen & Eigaard, 2014; Morizur *et al.,* 1999; Northridge and Hammond, 1999; Northridge *et al.,* 2005, 2010; Pierce *et al.,* 2010; Read *et al.,* 2006; Ryan *et al.*, 2016; Vinther, 1995, 1999; Vinther and Larsen, 2004)
- Literature on seal by-catch (Cosgrove *et al.,* 2016)
- Literature on seabird by-catch (Anderson *et al.,* 2011; Genovart *et al.,* 2017; ICES, 2013b; Tasker *et al.,* 2000; Wiedenfeld *et al.,* 2012; Zydelis *et al.,* 2013)

Data on the activity rates of gears generating by-catch were as detailed in the preceding sections, based on the STECF database. The bird, pinniped and cetacean by-catch data to accompany these activity rates were assembled almost entirely from partial estimates for national fleet segments of particular gears, from a range of regions (not just the North Sea). For each ICES/FAO statistical region in the NE Atlantic where we were able to locate such data, we extracted the population biomass, the activity rate of the particular national fleet, and the corresponding species by-catch. From these data, we calculated a partial harvest ratio, and an activity density (activity per unit area) for the fleet segment. Finally, we combined all the individual records for a given species (partial harvest ratio and activity density) as a scatter-plot and fitted a linear regression forced through the origin (0,0). The slope of this regression represents the scaling coefficient between activity density and harvest ratio, which we assume to be fixed over time and regions. Finally, the individual species coefficients, harvest ratios and by-catch rates were aggregated up to guild-level, weighted by the estimates of species biomass in the North Sea (Tables 22-24). In effect, use of these activity-harvest ratio scaling parameters in the fishing fleet model assumes that each gear has a notional power of 1.0 for each vulnerable guild of top-predators.

TABLE 22 Fishing gears for which there are quantitative data on by-catch weights of particular species of top-predators, together with North Sea guild-aggregated scaling parameters linking regionally averaged activity density ($sec.m^{-2}.d^{-1}$) and regional harvest ratio (d^{-1}).

Gear	Vulnerable seabird species	Vulnerable pinniped species	Vulnerable cetacean species	Seabird guild scaling parameter	Pinniped guild scaling parameter	Cetacean guild scaling parameter
Demersal gillnets	Guillemot, razorbill, fulmar, gannet	Grey seal	Common dolphin, striped dolphin, harbour porpoise	0.011	0.750	1.812
Pelagic trawl and seine	Gannet		Common dolphin, bottlenose dolphin, striped dolphin, pilot whale	0.175		0.351
Pelagic longlines	Fulmar			0.085		
Creels & pots			Fin whale, Minke whale			0.033

TABLE 23 2003-2013 annual average partial harvest ratio (d^{-1}), of the three top-predator guilds in the North Sea by each of the relevant fishing gear groups in the model.

Gear	Seabird harvest ratio	Pinniped harvest ratio	Cetacean harvest ratio
Demersal gillnets	7.07×10^{-8}	4.97×10^{-6}	1.20×10^{-5}
Pelagic trawl & seine	4.02×10^{-7}		8.40×10^{-8}
Pelagic longlines	1.21×10^{-7}		
Creels & pots			8.33×10^{-7}

TABLE 24 2003-2013 annual by-catch rates ($mMN.m^{-2}.y^{-1}$) of the three top-predator guilds in the North Sea by all fishing gears combined.

Seabird by-catch	Pinniped by-catch	Cetacean by-catch
6.25×10^{-7}	2.74×10^{-5}	2.75×10^{-4}

Clearly, the methodology outlined above is an approximation since, for example, it disregards the relative spatial distributions of animals and fishing gear activity within the North Sea and how this many vary seasonally. Also, the national by-catch data are almost certainly partial. However, we do not regard the results as a definitive study, merely a pragmatic approach which is sufficient for the purposes of parameterising the coarse-scale StrathE2E2 model.

Directed whaling catch in the North Sea

In addition to the unintended by-catch of cetaceans by fishing gears, there is a small-scale targeted catch of Minke whales in the Norwegian sector of the region under objection to the International Whaling Commission zero catch limits. We obtained spatially resolved (1° longitude x ½° latitude) annual catch weights during 2003-2013 from the Norwegian Directorate of Fisheries and, using the Minke whale population biomass data as outlined above in the description of by-catch estimation, we estimated the annual harvest ratio. In order to represent this whaling activity in the model, we designated an additional fishing gear “Norwegian whalers”, which has no interaction with any other aspect of the ecosystem except the cetacean guild. This meant that we could assign this fleet a notional activity density during 2003-2013 and a power or 1.0, and derive the scaling parameter linking activity density of the whalers to the harvest ratio (Table 25).

TABLE 25 2003-2013 annual average Minke whale by-catch rate in the North Sea, harvest ratio, and the derived parameter linking activity density of “Norwegian whalers” to harvest ratio assuming a notional activity density of 1000 hours per year.

2003-2013 annual average Minke whale catch	67 tonnes = 8.38×10^{-5} mMN.$m^{-2}.y^{-1}$
Harvest ratio (d^{-1})	4.17×10^{-6}
Scaling parameter linking activity density (s.$m^{-2}.d^{-1}$) to harvest ratio (d^{-1})	210.31

We did not have access to annual Minke whale catch data prior to 2003, so we roughly estimated the catches in earlier years by assuming that North Sea catches have varied in proportion to the total Norwegian catch in the NE Atlantic (1986-onwards data compiled from the IWC www.iwc.int/table_objection). On this basis, the 1986-1999 average catch in the North Sea was estimated to be 32 tonnes per year.

Parameterisation of quota-limited/non-quota species composition of demersal fish catches

For the North Sea, the empirical evidence for density dependent relationships describing catch and discard composition comes from analysis of catch per unit effort data in research vessel trawl surveys carried out in quarter 1 of each year since 1980, and the corresponding species composition of annual commercial landings and discards (Heath & Cook, 2015). The analysis shows that at the scale of the whole North Sea the proportion of non-quota demersal fish species in the commercial catch has been indirectly related to the community biomass (Figure 8). There may be a number of explanations for this, but most likely is that depletion of the community biomass reflects the selective targeting of the valuable quota-limited species by the fisheries. In the model, we represent this relationship by a negative exponential function.

$$p_{(non\text{-}quota)} = a_{pnq} \cdot exp(-b_{pnq} \cdot N_{dem.fish}) \qquad \text{eqn 9}$$

where b_{pnq} is a scaling parameter, and ($N_{dem.fish}$) is the survey-based demersal fish biomass per unit swept area (mMN.m^{-2}), as measured on 1st January. The survey data were converted to nitrogen units by applying species-specific wet-weight to length relationships to the individual species number density-at-length data, and summing over all demersal species (Heath & Cook, 2015). Then, we assumed a nominal catching efficiency for the survey gear of 20% (Fraser *et al.,* 2007), and a wet-weight to nitrogen conversion of 1.34 mMN.g-WW^{-1}

Capture efficiency of the survey trawl is only approximately known, so to facilitate incorporation of this relationship in the model we included a proportionality constant (φ) to relate survey catch per unit swept area to nitrogen mass per unit sea surface area ($M_{dem.fish}$) as simulated in the model:

$$p_{(non\text{-}quota)} = a_{pnq} \,.\, exp(-b_{pnq} \,.\, \varphi . M_{dem.fish}) \qquad \text{eqn 10}$$

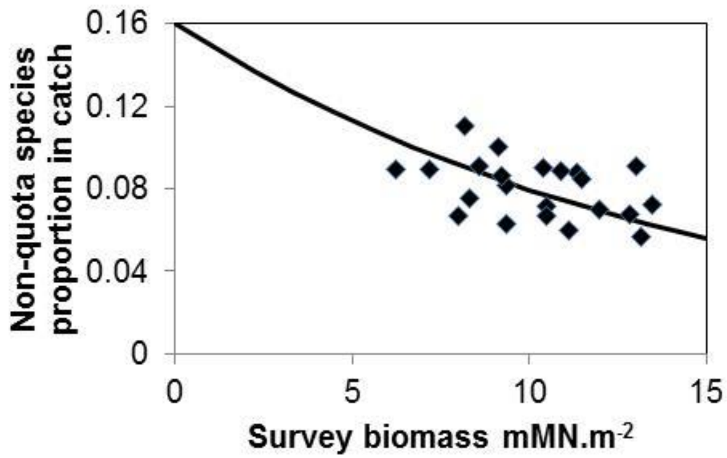

FIGURE 8 Proportion by weight of non-quota species in commercial catches from the North Sea, 1989-2010, in relation to the total biomass density of the demersal fish community as estimated in the corresponding year by the ICES IBTS quarter 1 surveys. Fitted equation: $p_{(non\text{-}quota)} = a_{pnq} \,.\, exp(-b_{pnq} \,.\, N_{dem.fish})$, $a_{pnq} = 0.16$, $b_{pnq} = 0.07$; $p<0.05$.

Parameterisation of the proportion of demersal fish catch which is smaller than the legal or *de-facto* marketable landing size.

The prototype version of StrathE2E2 included an empirically parameterised relationship between the proportion of demersal fish in commercial catches which were discarded on account of being undersize, and the biomass of demersal fish in the sea. The relationship expressed an exponentially declining discard rate with increasing biomass:

$$p_{(discarded)} = a_{disc} \cdot exp(-b_{disc} \cdot M_{dem.fish}) \qquad \text{eqn 11}$$

The general form of this relationship is retained in the new version of the model, but separate parameters are needed for the quota-limited and non-quota fractions of the demersal fish catch.

Technically, there is no minimum legal landing size for non-quota species. However, there is a de-facto minimum marketable size, below which there is no incentive to land the fish. Combined analysis of the 1980-2010 North Sea survey, landings and discards data (Heath & Cook, 2015) has shown that the average proportion by weight of non-quota species in the commercial catches which is below the marketable size, is approximately double the corresponding proportion of quota-limited species smaller than the minimum legal landing size. In addition, for both groups, these proportions have varied in inverse relation to demersal fish community biomass (Figure 9). The explanation for these density dependent relationships lies in the observed decrease in mean body size of demersal fish with declining community biomass. This is typically summarised for ecosystem assessment purposes by the Large Fish Indicator (LFI) which, in the North Sea, is defined as the proportion by weight of fish in the community which are larger than 40cm in length (Greenstreet *et al.,* 2011; Modica *et al.,* 2014).

The data from the North Sea showed that the exponents, or slopes, of the negative exponential relationships defining the proportion by weight of fish smaller than the minimum landing size (corresponding roughly to the historic discard rates) were not significantly different between the quota-limited and non-quota groups. However, the intercept term is substantially higher for the non-quota group.

$$p_{(undersize)Q} = a_{undersizeQ} \cdot exp(-b_{undersizeQ} \cdot N_{dem.fish}) \text{ (for quota limited catch)} \qquad \text{eqn 12}$$

$$p_{(undersize)NQ} = a_{undersizeNQ} \cdot exp(-b_{undersizeNQ} \cdot N_{dem.fish}) \text{ (for non-quota limited catch)} \qquad \text{eqn 13}$$

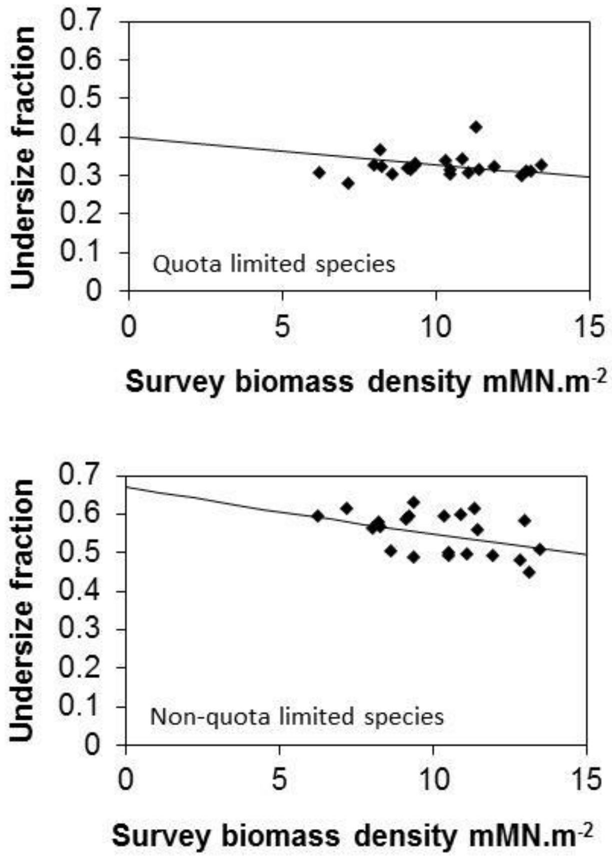

FIGURE 9 Proportions by weight of under minimum or marketable landing size demersal fish in the commercial catch from the North Sea, 1989-2010, in relation to the total biomass density of the demersal fish community as estimated in the corresponding year by the ICES IBTS quarter 1 surveys. Upper panel, quota-limited species, lower panel, non-quota species. Fitted equations of the form: $p_{(undersize)} = a_{undersize} \cdot exp(-b_{undersize} \cdot N_{dem.fish})$. Separate fits for the quota and non-quota species showed that the coefficients $b_{undersize}$ were not significantly different ($p<0.05$). Refitting assuming a common value for this parameter resulted in, for quota-limited species, $a_{(undersize)Q} = 0.40$, $b_{(undersize)Q} = 0.02$; and for non-quota species, $a_{(undersize)NQ} = 0.67$, $b_{(undersize)NQ} = 0.02$.

As for the imputation of non-quota fraction in the catch, we include the same scaling coefficient linking the survey catch per unit swept area and the biomass density in the model

$$N_{dem.fish} = \varphi . M_{dem.fish} \qquad \text{eqn 14}$$

Observational data for model fitting

Observational data on conditions in the North Sea during the periods 1970-1999 and 2003-2013 were assembled from a range of literature and data analyses (Table 26, 27). The data assembly by Mackinson & Daskalov (2007) was a key source of information for 1970-1999. In each case the information was such that an equivalent measure could be derived for comparison from the final year of a run to stationary state of the model.

TABLE 26 Observational data on the conditions in the North Sea relevant to the period 1970-1999, or a general value where no period-specific data were available. The standard deviation of the observed data was in some cases based on an actual analysis of multi-year data (e.g. in the case of fishery landings). In other case the standard deviation was a rough estimate based on very few data, or just a scaled value relative to the mean to assign a weighting to a particular measure in the likelihood calculation.

Description	**Sources**	**Mean value**	**s.d. of value**	**Units**	**Notes**
Annual total primary production	Skogen & Moll (2005)	1522	150.94	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual new production from drawdown of depth integrated nitrate plus summer river and atmospheric nitrate inputs	Heath & Beare (2008)	624.4	66.4	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual within forest net production of kelp	Burrows *et al.* (2018)	600	100	$gC.m^{-2}.y^{-1}$	General value
Annual omnivorous zooplankton gross production	Heath (2005); Mackinson & Daskalov (2007)	339.6	25.16	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual carnivorous zooplankton gross production	Heath (2005); Mackinson & Daskalov (2007)	44.35	2.516	$mMN.m^{-2}.y^{-1}$	Period-specific

Annual planktivorous fish gross production	Heath (2005)	29.97	3.509	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual demersal fish gross production	Heath (2005)	11.5	2.277	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual suspension/deposit feeding benthos gross production	Eleftheriou & Basford (1989); Greenstreet *et al.* (2007); Heip & Craeymeersch (1995); Heip *et al.* (1984, 1989,1992); Kiinitzer *et al.* (1992); Mackinson & Daskalov (2007)	1248	449	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual carnivore/scavenge feeding benthos gross production	Eleftheriou & Basford (1989); Greenstreet *et al.* (2007); Heip & Craeymeersch (1995); Heip *et al.* (1984, 1989,1992); Kiinitzer *et al.* (1992); Mackinson & Daskalov (2007)	21.1	7.6	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual net production of birds	Mackinson & Daskalov (2007)	8.452E-04	2.00E-04	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual net production of pinnipeds	Mackinson & Daskalov (2007)	7.245E-04	3.50e-04	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual net production of cetaceans	Mackinson & Daskalov (2007)	1.691E-03	8.00E-04	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual monthly max concentration of benthos suspension/deposit feeder larvae	Lindley & Kirby (2007); Analysis of Continuous Plankton Recorder data	1.185	0.4421	$mMN.m^{-3}$	Period-specific
Annual monthly max concentration of benthos carnivore/scavenge feeder larvae	Lindley & Kirby (2007); Analysis of Continuous Plankton Recorder data	0.334	0.1013	$mMN.m^{-3}$	Period-specific
Annual consumption of planktivorous fish by fish	Heath (2005); Mackinson & Daskalov (2007)	23.48	9.057	$mMN.m^{-2}.y^{-1}$	Period-specific

Annual consumption of demersal fish by fish	Heath (2005); Mackinson & Daskalov (2007)	2.138	0.503	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual consumption of omnivorous zooplankton by fish and fish larvae	Heath (2005, 2007b); Mackinson & Daskalov (2007)	92.28	13.019	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual consumption of omnivorous zooplankton by carnivorous zooplankton	Heath (2005); Mackinson & Daskalov (2007)	60.38	25.157	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual consumption of benthos by fish	Heath (2005); Mackinson & Daskalov (2007)	12.58	6.289	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual food consumption by birds	Bryant & Doyle (1992); Mackinson & Daskalov (2007)	0.6538	0.325	$mMN.m^{-2}.y^{-1}$	Period-specific
Proportion planktivorous fish in diet of birds	Bryant & Doyle (1992); Mackinson & Daskalov (2007)	0.6	0.2	dimensionless	Period-specific
Proportion demersal fish in diet of birds	Bryant & Doyle (1992); Mackinson & Daskalov (2007)	0.1	0.05	dimensionless	Period-specific
Proportion migratory fish in diet of birds	Bryant & Doyle (1992); Mackinson & Daskalov (2007)	0.05	0.015	dimensionless	Period-specific
Proportion discards in diet of birds	Bryant & Doyle (1992); Mackinson & Daskalov (2007)	0.05	0.02	dimensionless	Period-specific
Annual food consumption by pinnipeds	Mackinson & Daskalov (2007)	0.2161	0.105	$mMN.m^{-2}.y^{-1}$	Period-specific
Proportion pelagic fish in diet of pinnipeds	Mackinson & Daskalov (2007)	0.2910	0.0728	dimensionless	Period-specific
Proportion demersal fish in diet of pinnipeds	Mackinson & Daskalov (2007)	0.6969	0.1742	dimensionless	Period-specific
Proportion migratory fish in diet of pinnipeds	Mackinson & Daskalov (2007)	0.01208	0.0030	dimensionless	Period-specific
Annual food consumption by cetaceans	Mackinson & Daskalov (2007)	0.9691	0.48	$mMN.m^{-2}.y^{-1}$	Period-specific

Proportion pelagic fish in diet of cetaceans	Mackinson & Daskalov (2007); Olsen & Holst (2001)	0.6632	0.1658	dimensionless	Period-specific
Proportion demersal fish in diet of cetaceans	Mackinson & Daskalov (2007); Olsen & Holst (2001)	0.0995	0.04	dimensionless	Period-specific
Proportion migratory fish in diet of cetaceans	Mackinson & Daskalov (2007); Olsen & Holst (2001)	0.08014	0.035	dimensionless	Period-specific
Annual planktivorous fish landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.,* 2012)	5.555	0.2	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual demersal fish landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.,* 2012)	1.735	0.08	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual migratory fish landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.,* 2012)	0.775	0.308	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual suspension/deposit feeding benthos landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.,* 2012)	0.0953	0.0382	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual carnivore/scavenge feeding benthos landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.,* 2012)	0.0829	0.0169	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual carnivorous zooplankton landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.,* 2012)	0.00147	9.32E-04	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual kelp landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.,* 2012)	0	0	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual carbon gross PB ratio of kelp	Brady-Campbell *et al.* (1984)	2	0.5	y^{-1}	General value
Annual gross PB ratio larvae of suspension/deposit feeding benthos	Mackinson & Daskalov (2007)	10	5	y^{-1}	General value
Annual gross PB ratio larvae of carnivore/scavenge feeding benthos	Mackinson & Daskalov (2007)	10	5	y^{-1}	General value

Annual gross PB ratio suspension/deposit feeding benthos	Mackinson & Daskalov (2007)	10	3	y^{-1}	General value
Annual gross PB ratio carnivore/scavenge feeding benthos	Mackinson & Daskalov (2007)	1.2	1	y^{-1}	General value
Annual gross PB ratio omnivorous zooplankton	Mackinson & Daskalov (2007)	20	10	y^{-1}	General value
Annual gross PB ratio carnivorous zooplankton	Mackinson & Daskalov (2007)	5	1.315	y^{-1}	General value
Annual gross PB ratio larvae of planktivorous fish	Mackinson & Daskalov (2007)	4	2	y^{-1}	General value
Annual gross PB ratio larvae of demersal fish	Mackinson & Daskalov (2007)	4	2	y^{-1}	General value
Annual gross PB ratio planktivorous fish	Mackinson & Daskalov (2007)	1.72	0.86	y^{-1}	General value
Annual gross PB ratio demersal fish	Mackinson & Daskalov (2007)	0.88	0.44	y^{-1}	General value
Annual gross PB ratio migratory fish	Mackinson & Daskalov (2007)	1.3	0.6	y^{-1}	General value
Annual net PB ratio birds	Mackinson & Daskalov (2007)	0.28	0.14	y^{-1}	General value
Annual net PB ratio pinnipeds	Mackinson and Daskalov 2007	0.09	0.045	y^{-1}	General value
Annual net PB ratio cetaceans	Mackinson & Daskalov (2007)	0.02	0.01	y^{-1}	General value
Annual average proportion of kelp C uptake which is exuded	Abdullah & Fredriksen (2004)	0.3	0.1	dimensionless	General value
Annual average molar NC ratio of kelp	Broch & Slagstad (2012); Sjotun *et al.* (1996)	0.12	0.2	dimensionless	General value
Annual denitrification	Brion *et al.* (2004)	129	42	$mMN.m^{-2}.y^{-1}$	Period-specific
Proportion of demersal fish catch discarded	Heath & Cook (2015)	0.37	0.075	dimensionless	Period-specific
Annual average ammonia concentration in porewater of sand grain size 0.25mm	Serpetti (2012); Serpetti *et al.* (2016)	19.24	9	$mMN.m^{-3}$	General value

Annual average ammonia concentration in porewater of mud grain size 0.12mm	Serpetti (2012); Serpetti *et al.* (2016)	63.45	22	$mMN.m^{-3}$	General value
Annual average nitrate concentration in porewater of sand grain size 0.25mm	Serpetti (2012); Serpetti *et al.* (2016)	4.15	2	$mMN.m^{-3}$	General value
Annual average nitrate concentration in porewater of mud grain size 0.12mm	Serpetti (2012); Serpetti *et al.* (2016)	2.34	1	$mMN.m^{-3}$	General value
Annual average organic N content of sand grain size 0.25mm (0.19-0.43mm)	Serpetti (2012); Serpetti *et al.* (2016)	0.05152	0.02441	%N (gN.(g dry sed)$^{-1}$)	General value
Annual average organic N content of mud grain size 0.12mm (0.03-0.07mm)	Serpetti (2012); Serpetti *et al.* (2016)	0.07357	0.0343	%N (gN.(g dry sed)$^{-1}$)	General value
Average winter (Nov-Feb) nitrate concentration shallow layer	Analysis of ICES hydro-chemical data	9.998	2.135	$mMN.m^{-3}$	Period-specific
Average summer (May-Aug) nitrate concentration shallow layer	Analysis of ICES hydro-chemical data	2.161	1.089	$mMN.m^{-3}$	Period-specific
Average winter (Nov-Feb) nitrate concentration deep layer	Analysis of ICES hydro-chemical data	6.995	0.836	$mMN.m^{-3}$	Period-specific
Average summer (May-Aug) nitrate concentration deep layer	Analysis of ICES hydro-chemical data	2.837	0.917	$mMN.m^{-3}$	Period-specific
Average winter (Nov-Feb) ammonia concentration shallow layer	Analysis of ICES hydro-chemical data	2.367	0.774	$mMN.m^{-3}$	Period-specific
Average summer (May-Aug) ammonia concentration shallow layer	Analysis of ICES hydro-chemical data	1.737	0.669	$mMN.m^{-3}$	Period-specific
Average winter (Nov-Feb) ammonia concentration deep layer	Analysis of ICES hydro-chemical data	0.853	0.32	$mMN.m^{-3}$	Period-specific
Average summer (May-Aug) ammonia concentration deep	Analysis of ICES hydro-chemical data	1.338	0.708	$mMN.m^{-3}$	Period-specific

layer					
Inshore offshore ratio of annual mean carnivorous zooplankton depth averaged concentration	Analysis of Continuous Plankton Recorder data	0.9041	0.2	dimensionless	Period-specific
Inshore offshore ratio of annual mean omnivorous zooplankton depth averaged concentration	Analysis of Continuous Plankton Recorder data	1.676	0.2715	dimensionless	Period-specific
Inshore offshore ratio of annual mean phytoplankton surface layer concentration	Analysis of ICES hydro-chemical data	3.744	1	dimensionless	Period-specific
Inshore offshore ratio of annual mean nitrate surface layer concentration	Analysis of ICES hydro-chemical data	3.000	1	dimensionless	Period-specific
Inshore offshore ratio of annual mean ammonia surface layer concentration	Analysis of ICES hydro-chemical data	2.4294	0.9	dimensionless	Period-specific
Inshore offshore ratio of annual mean planktivorous fish density (m^{-2})	Analysis of ICES International Bottom Trawl Survey data and Stock Assessment Working Group reports	0.67	0.49	dimensionless	Period-specific
Inshore offshore ratio of annual mean demersal fish density (m^{-2})	Analysis of ICES International Bottom Trawl Survey data and Stock Assessment Working Group reports	0.39	0.31	dimensionless	Period-specific
Annual bycatch of birds	Insufficient data available	NA	NA	$mMN.m^{-2}.y^{-1}$	NA
Annual bycatch of pinnipeds	Insufficient data available	NA	NA	$mMN.m^{-2}.y^{-1}$	NA
Annual bycatch of cetaceans	Insufficient data available	NA	NA	$mMN.m^{-2}.y^{-1}$	NA
Proportion of kelp annual nitrogen uptake exported as beach-cast	Zemke-White *et al.* (2005)	0.15	0.05	dimensionless	General value
Cetacean (Minke whale) catch	Analysis of data from Norwegian Directorate of Fisheries and	4.05E-05	2.00E-05	$mMN.m^{-2}.y^{-1}$	Period-specific

	International Whaling Commission				

TABLE 27 Observational data on the conditions in the North Sea relevant to the period 2003-2013, or a general value where no period-specific data were available. The standard deviation of the observed data was in some cases based on an actual analysis of multi-year data (e.g. in the case of fishery landings). In other case the standard deviation was a rough estimate based on very few data, or just a scaled value relative to the mean to assign a weighting to a particular measure in the likelihood calculation. For many fields, no period specific data were available for 2003-2013 or have not yet been processed for use in the model.

Description	Sources	Mean value	s.d. of value	Units	Notes
Annual total primary production	Skogen & Moll (2005)	1522	150.94	$mMN.m^{-2}.y^{-1}$	General value
Annual new production from drawdown of depth integrated nitrat, plus summer river and atmospheric nitrate inputs	Heath & Beare (2008)	672.8	73.0	$mMN.m^{-2}.y^{-1}$	Period-specific (partial)
Annual within forest net production of kelp	Burrows *et al.* (2018)	600	100	$gC.m^{-2}.y^{-1}$	General value
Annual omnivorous zooplankton gross production	Heath (2005); Mackinson & Daskalov (2007)	339.6	25.157	$mMN.m^{-2}.y^{-1}$	Period-specific (partial)
Annual carnivorous zooplankton gross production	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual planktivorous fish gross production	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual demersal fish gross production	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual suspension/deposit feeding benthos gross production	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual carnivore/scavenge feeding benthos gross production	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual net production of birds	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual net production of pinnipeds	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data

Annual net production of cetaceans	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual monthly max concentration of benthos suspension/deposit feeder larvae	NA	NA	NA	$mMN.m^{-3}$	Insufficient data
Annual monthly max concentration of benthos carnivore/scavenge feeder larvae	NA	NA	NA	$mMN.m^{-3}$	Insufficient data
Annual consumption of planktivorous fish by fish	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual consumption of demersal fish by fish	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual consumption of omnivorous zooplankton by fish and fish larvae	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual consumption of omnivorous zooplankton by carnivorous zooplankton	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual consumption of benthos by fish	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Annual food consumption by birds	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Proportion planktivorous fish in diet of birds	NA	NA	NA	dimensionless	Insufficient data
Proportion demersal fish in diet of birds	NA	NA	NA	dimensionless	Insufficient data
Proportion migratory fish in diet of birds	NA	NA	NA	dimensionless	Insufficient data
Proportion discards in diet of birds	NA	NA	NA	dimensionless	Insufficient data
Annual food consumption by pinnipeds	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Proportion pelagic fish in diet of pinnipeds	NA	NA	NA	dimensionless	Insufficient data

Proportion demersal fish in diet of pinnipeds	NA	NA	NA	dimensionless	Insufficient data
Proportion migratory fish in diet of pinnipeds	NA	NA	NA	dimensionless	Insufficient data
Annual food consumption by cetaceans	NA	NA	NA	$mMN.m^{-2}.y^{-1}$	Insufficient data
Proportion pelagic fish in diet of cetaceans	NA	NA	NA	dimensionless	Insufficient data
Proportion demersal fish in diet of cetaceans	NA	NA	NA	dimensionless	Insufficient data
Proportion migratory fish in diet of cetaceans	NA	NA	NA	dimensionless	Insufficient data
Annual planktivorous fish landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.*, 2012)	2.928	0.6	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual demersal fish landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.*, 2012)	0.6408	0.3	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual migratory fish landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.*, 2012)	0.9925	0.25	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual suspension/deposit feeding benthos landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.*, 2012)	0.07444	0.028	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual carnivore/scavenge feeding benthos landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.*, 2012)	0.12801	0.05	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual carnivorous zooplankton landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.*, 2012)	0.006976	0.004	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual kelp landings (live weight)	Analysis of EuroSTAT ICES landings data (Lassen *et al.*, 2012)	0	0	$mMN.m^{-2}.y^{-1}$	Period-specific
Annual carbon gross PB ratio of kelp	Brady-Campbell *et al.* (1984)	2	0.5	y^{-1}	General value
Annual gross PB ratio larvae of suspension/deposit feeding	Mackinson & Daskalov (2007)	10	5	y^{-1}	General value

benthos					
Annual gross PB ratio larvae of carnivore/scavenge feeding benthos	Mackinson & Daskalov (2007)	10	5	y^{-1}	General value
Annual gross PB ratio suspension /deposit feeding benthos	Mackinson & Daskalov (2007)	10	3	y^{-1}	General value
Annual gross PB ratio carnivore/scavenge feeding benthos	Mackinson & Daskalov (2007)	1.2	1	y^{-1}	General value
Annual gross PB ratio omnivorous zooplankton	Mackinson & Daskalov (2007)	20	10	y^{-1}	General value
Annual gross PB ratio carnivorous zooplankton	Mackinson & Daskalov (2007)	5	1.315	y^{-1}	General value
Annual gross PB ratio larvae of planktivorous fish	Mackinson & Daskalov (2007)	4	2	y^{-1}	General value
Annual gross PB ratio larvae of demersal fish	Mackinson & Daskalov (2007)	4	2	y^{-1}	General value
Annual gross PB ratio planktivorous fish	Mackinson & Daskalov (2007)	1.72	0.86	y^{-1}	General value
Annual gross PB ratio demersal fish	Mackinson & Daskalov (2007)	0.88	0.44	y^{-1}	General value
Annual gross PB ratio migratory fish	Mackinson & Daskalov (2007)	1.3	0.6	y^{-1}	General value
Annual net PB ratio birds	Mackinson & Daskalov (2007)	0.28	0.14	y^{-1}	General value
Annual net PB ratio pinnipeds	Mackinson & Daskalov (2007)	0.09	0.045	y^{-1}	General value
Annual net PB ratio cetaceans	Mackinson & Daskalov (2007)	0.02	0.01	y^{-1}	General value
Annual average proportion of kelp C uptake which is exuded	Abdullah & Fredriksen (2004)	0.3	0.1	dimensionless	General value
Annual average molar NC ratio of kelp	Broch & Slagstad (2012); Sjotun *et al.* (1996)	0.12	0.2	dimensionless	General value
Annual denitrification	Brion *et al.* (2004)	129	42	$mMN.m^{-2}.y^{-1}$	Period-specific
Proportion of demersal fish catch discarded	Heath & Cook (2015)	0.51	0.1	dimensionless	Period-specific

Annual average ammonia concentration in porewater of sand grain size 0.25mm	Serpetti (2012); Serpetti *et al.* (2016)	19.24	9	$mMN.m^{-3}$	General value
Annual average ammonia concentration in porewater of mud grain size 0.12mm	Serpetti (2012); Serpetti *et al.* (2016)	63.45	22	$mMN.m^{-3}$	General value
Annual average nitrate concentration in porewater of sand grain size 0.25mm	Serpetti (2012); Serpetti *et al.* (2016)	4.15	2	$mMN.m^{-3}$	General value
Annual average nitrate concentration in porewater of mud grain size 0.12mm	Serpetti (2012); Serpetti *et al.* (2016)	2.34	1	$mMN.m^{-3}$	General value
Annual average organic N content of sand grain size 0.25mm (0.19-0.43mm)	Serpetti (2012); Serpetti *et al.* (2016)	0.051515	0.02441	%N (gN.(g dry sed)$^{-1}$)	General value
Annual average organic N content of mud grain size 0.12mm (0.03-0.07mm)	Serpetti (2012); Serpetti *et al.* (2016)	0.07357	0.0343	%N (gN.(g dry sed)$^{-1}$)	General value
Average winter (Nov-Feb) nitrate concentration shallow layer	NA	NA	NA	$mMN.m^{-3}$	Insufficient data
Average summer (May-Aug) nitrate concentration shallow layer	NA	NA	NA	$mMN.m^{-3}$	Insufficient data
Average winter (Nov-Feb) nitrate concentration deep layer	NA	NA	NA	$mMN.m^{-3}$	Insufficient data
Average summer (May-Aug) nitrate concentration deep layer	NA	NA	NA	$mMN.m^{-3}$	Insufficient data
Average winter (Nov-Feb) ammonia concentration shallow layer	NA	NA	NA	$mMN.m^{-3}$	Insufficient data
Average summer (May-Aug) ammonia concentration shallow layer	NA	NA	NA	$mMN.m^{-3}$	Insufficient data
Average winter (Nov-Feb) ammonia concentration deep	NA	NA	NA	$mMN.m^{-3}$	Insufficient data

layer					
Average summer (May-Aug) ammonia concentration deep layer	NA	NA	NA	$mMN.m^{-3}$	Insufficient data
Inshore offshore ratio of annual mean carnivorous zooplankton depth averaged concentration	Analysis of Continuous Plankton Recorder data	0.904055	0.2	dimensionless	Period-specific
Inshore offshore ratio of annual mean omnivorous zooplankton depth averaged concentration	Analysis of Continuous Plankton Recorder data	1.675727	0.271539	dimensionless	Period-specific
Inshore offshore ratio of annual mean phytoplankton surface layer concentration	Analysis of ICES hydro-chemical data	3.744403	1	dimensionless	Period-specific
Inshore offshore ratio of annual mean nitrate surface layer concentration	Analysis of ICES hydro-chemical data	3.000139	1	dimensionless	Period-specific
Inshore offshore ratio of annual mean ammonia surface layer concentration	Analysis of ICES hydro-chemical data	2.429353	0.9	dimensionless	Period-specific
Inshore offshore ratio of annual mean planktivorous fish density (m^{-2})	Analysis of ICES International Bottom Trawl Survey data and Stock Assessment Working Group reports	0.67	0.49	dimensionless	Period-specific
Inshore offshore ratio of annual mean demersal fish density (m^{-2})	Analysis of ICES International Bottom Trawl Survey data and Stock Assessment Working Group reports	0.39	0.31	dimensionless	Period-specific
Annual bycatch of birds	Insufficient data available	6.25E-07	3.00E-07	$mMN.m^{-2}.y^{-1}$	NA
Annual bycatch of pinnipeds	Insufficient data available	2.74E-05	5.00E-05	$mMN.m^{-2}.y^{-1}$	NA
Annual bycatch of cetaceans	Insufficient data available	0.000275	1.00E-04	$mMN.m^{-2}.y^{-1}$	NA
Proportion of kelp annual nitrogen uptake exported as beach-cast	Zemke-White *et al.* (2005)	0.15	0.05	dimensionless	General value

Cetacean (Minke whale) catch	Analysis of data from Norwegian Directorate of Fisheries and International Whaling Commission	8.38E-05	4.00E-05	$mMN.m^{-2}.y^{-1}$	Period-specific

Model fitting

The major unknown parameters of the model system are within ecology model, especially those related to the temperature-dependent physiological and behavioural functioning of the guilds and geochemical cycling processes. We expect these parameters to remain constant over time unless there have been extensive changes in species composition of the guilds. Since there is no realistic prospect of independently estimating most of these parameters we require to estimate them by fitting the stationary model to target data on the observed state of the system in a given time period. Constraining the ecology model parameters is clearly dependent on the diversity and quality of the target data, but also conditional on the quality of the information on environmental drivers and fishing fleet parameters

Among the fishing fleet parameters that are required, we can assume that the power parameters and seabed impact properties of the fishing gears remain constant over time. These are defining feature of each of the gear types which determine selectivity with respect to the harvestable guilds and seabed disturbance. Of course, it is likely that in reality there have been some changes in these gear properties, but we can assume that at the coarse taxonomic resolution of the model guilds these are likely to be small. Realistic changes in selectivity and seabed impact are probably at the scale of the species within each guild and hence not resolved by this model. Changes in selectivity and seabed impact at the scale of the model guilds would more likely justify the definition of different gear types.

Similarly, the scaling parameters linking effort to harvest ratios of each guild must be assumed to remain constant over time. To assume otherwise would risk confounding the translation of changes in fishing gear activity and distribution into changes in harvest ratio.

The remaining drivers and properties of the model which define the conditions that make one time period different from another, are the environmental conditions, fishing gear activity, distribution and discard rates, and the seasonal immigration flux of migratory fish from outside the system.

Unfortunately the data required to independently determine the defining properties of the fishing fleet model are not uniformly available over time in the North Sea (Table 28). Full data requirements were not satisfied for either of the time periods 1970-1999 and 2003-2013. As a result, we had to develop an iterative process to arrive at a parameter set which provided a credible fit to the observed target data for both time periods.

TABLE 28 Quality of key datasets needed for fitting of StrathE2E2 in the North Sea.

Data type	**1970-1999**	**2003-2013**
Target data to which the model can be fitted	Comprehensive coverage of data fields as a consequence of large research programmes during the period	Many missing fields in the target data
Gear activity rates and spatial distributions	Unknown	Well known
Discard rates for each gear	Unknown	Well known
Power parameters for each gear	Unknown	Well known
Harvest ratios for ecology model guilds	Reasonably well known for fish based on long-standing stock assessments (ICES 2016). Less certain for invertebrates and top predators.	Reasonably well known based on long-standing stock assessments (ICES 2016), by-catch and strandings data.
Environmental driving data	Well known from NEMO-ERSEM outputs and World Ocean Atlas (Butenschön *et al.* 2016, Garcia *et al.* 2014)	Well known from NEMO-ERSEM outputs and World Ocean Atlas (Butenschön *et al.* 2016, Garcia *et al.* 2014)

The starting point for the iterative scheme (Figure 10) relied on four ‘solid’ sets of information:
1) the environmental driving data for the two periods derived from the NEMO-ERSEM model outputs,
2) the 1970-1999 and 2003-2013 guild-level harvest ratios for fish and invertebrates,
3) the 2003-2013 gear activity and discard rate data derived from the STECF database,
4) the comprehensive assemblage of 1970-1999 target data on the ecological state of the system.

Gear activity rates for 1970-1999 were not available, so we estimated approximate values by up-scaling the well-established values for 2003-2013. The basis for the up-scaling was the synthesis of 60-year changes in functional guild aggregated fishing mortality rates in the North Sea compiled for the ICES Greater North Sea Eco-region review (ICES, 2016). The digitised data show that 1970-1999 averaged mortality rates for pelagic fish stocks were 1.513-times higher than during 2003-2013, demersal fish rates 1.616-times higher. On the other hand, mortality rates of benthic invertebrates were lower during 1970-1999 than in the more recent period, by a factor of 0.401. We therefore scaled the 2003-2013 activity densities of the pelagic-fish-targeting gears (pelagic trawls and seine, and mackerel longlines) by a factor of 1.513; the demersal-fish-targeting gears (demersal beam trawl, seine, otter trawl, longlines and gillnets) by 1.616; and the benthos-targeting gears (shrimp trawl, Nephrops trawl, creels and pots, and mollusc dredges) by 0.401. We adopted the proportional spatial distribution of activity by each gear from 2003-2013. This provided enough information to calculate initial values for the scaling parameters linking effort to harvest ratios using the function **e2e_calculate_hrscale()**.

The patterns of inshore and offshore harvest ratios for each of the ecology model guilds, given these parameters, represents an element of known driving data for the model. Based on these data we then obtained a first set of ecology model parameters by fitting to the target data, using the function **e2e_optimize_eco()**.

The next step was to focus on the 2003-2013 period. This time, we adopted the ecology model parameters from the previous step, the known activity, spatial distribution and discard rate data from STECF, and instead estimate the effort – harvest ratio scaling parameters required to produce the best fit to the 2003-2013 target data using the function **e2e_optimize_hr()**.

Stage 3 returned to the 1970-1999 period. This time we adopted the newly estimated effort – harvest ratio scaling parameters from stage 2, and focussed on finding the gear activity rates required to reproduce the harvest ratios for each ecology model guild which were independently derived prior to stage 1. This is not a trivial task since the gears had overlapping selectivity patterns for the model resource guilds. The process involved using the function **e2e_optimize_act()** to optimize the gear activity rates (but not their spatial distributions) so as to maximise the likelihood of the expected harvest ratios given the other parameters of the fishing fleet model. Some groups of gears were constrained to vary in concert to a degree, rather than completely independently. For example the subset of gears targeting demersal fish (demersal seine, demersal otter trawl, demersal gill nets and long-lines) were linked so that changes in their activities at each iteration of the annealing process were proportional to each other plus or minus some random variation.

Stage 4 was a repeat of stage 1 but using the gear activity rates from stage 3 and the effort – harvest ratio scaling parameters from stage 2. A further cycle through the loop of fitting stages produced minimal changes in the ecology model parameters, the effort – harvest ratio scaling parameters, or the estimates of 1970-1999 activity rates.

In the case of the whaling fleet in the North Sea, there were no data on activity rates, so a notional value was assigned for 2003-2013 when the whaling catch is known, and the effort – harvest ratio scaling parameter manually adjusted to achieve the target catch of cetaceans. This was entirely justified since the whaler catch is confined to cetaceans with no by-catch of other guilds.

For the 1970-1999 model the annealing process converged to a robust set of ecology model parameters within 11,000 iterations, with each iteration entailing a 50 year run for each proposed parameter set (stages 1, 4, 7 in the fitting scheme). Convergence was deemed to be attained when the system completed 200 iterations without finding any improvement in the likelihood. At convergence, the overall likelihood of the observed data given the parameters, driving data and the model structure was 0.379. For the 2003-2013 period the overall likelihood with the same ecology model parameters and effort – harvest ratio scaling values was 0.510 (but note that there were fewer target data available for the 2003-2013 period). All of the observed data values, the maximum likelihood model value, and the corresponding partial likelihoods, are given in Tables 31 and 32. Convergence of the fitting process for effort – harvest ratio scaling values (stages 2, 5) and 1970-1999 gear activity rates (stages 3, 6) was within 1000 iteration since far fewer parameters were involved in the process.

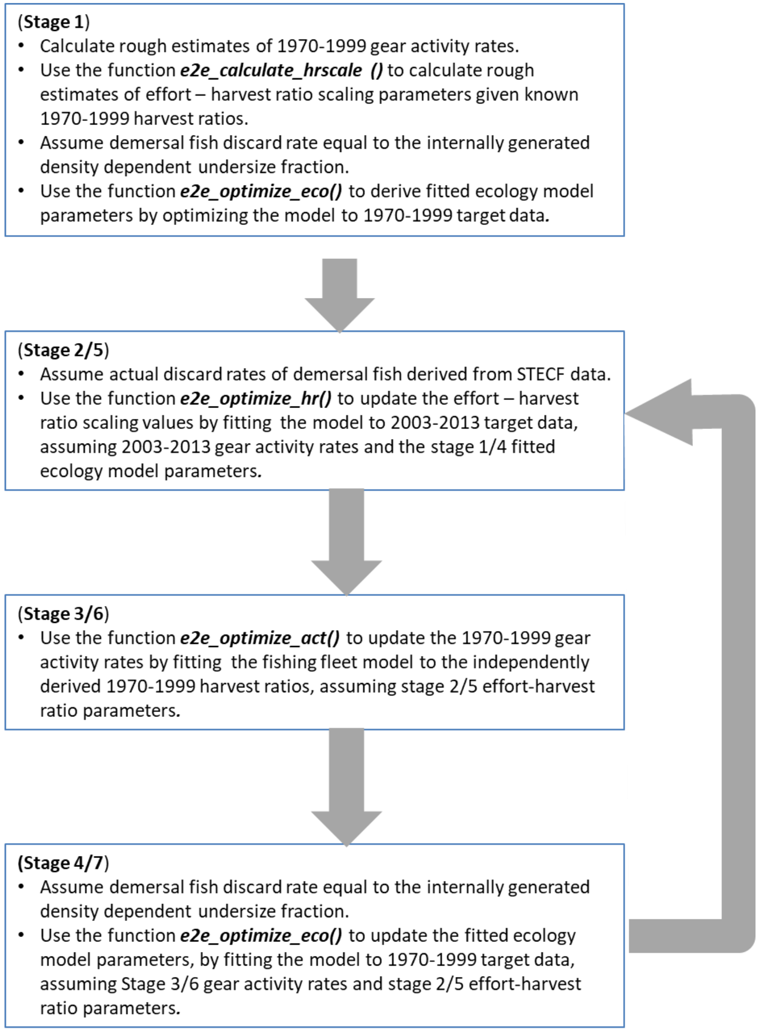

FIGURE 10 Workflow diagram for the scheme devised to fit the combined fleet and ecology model to the target data available for the two periods 1970-1999 and 2003-2013.

Results of the model fitting procedure

TABLE 29. North Sea domain-wide activity rates ($s.m^{-2}.d^{-1}$) for each gear during 2003-2013 derived from the STECF data, and estimates for 1970-1999 derived by fitting the combined fishing fleet and ecology model to the observed ecosystem data.

Gear category	STECF activity 2003-2013	Estimated activity 1970-1999
Pelagic trawls & seines	2.170E-06	4.462E-06
Sandeel & sprat trawl (Otter30-70mm+TR3)	4.230E-06	3.334E-06
Longline mackerel	1.680E-06	3.899E-06
Beam trawls for demersal fish (BT1+BT2)	1.150E-05	5.932E-05
Demersal seine	1.720E-08	9.118E-08
Demersal otter trawl (TR1)	2.160E-05	1.181E-04
Gill nets & longlines for demersal fish	7.920E-06	5.345E-05
Beam trawl for shrimp	1.270E-05	9.456E-06
Nephrops trawl (TR2)	1.720E-05	6.313E-06
Creels	2.400E-05	3.539E-06
Mollusc dredge	3.110E-06	3.805E-06
Whaling vessels	1.980E-08	1.316E-08

TABLE 30 Harvest ratios in the two periods (1970-1999 and 2003-2013) and scaling coefficients for each ecology model resource guild on conclusion of the fitting procedure.

Ecology model resource guild	1970-1999 inshore harvest ratio	1970-1999 offshore harvest ratio	2003-2013 inshore harvest ratio	2003-2013 offshore harvest ratio	Effort to harvest ratio scaling coefficient
Planktivorous fish	9.640E-04	8.053E-04	7.116E-04	5.534E-04	0.06971
Demersal fish	1.502E-03	9.684E-04	3.075E-04	2.025E-04	0.07548
Migratory fish	2.272E-03	2.245E-03	1.063E-03	9.875E-04	0.36956
Suspension/deposit feeding benthos	4.094E-04	2.411E-04	3.320E-04	1.956E-04	12.66203

Carnivore/scavenge feeding benthos	7.448E-04	1.033E-04	9.568E-04	1.155E-04	0.63005
Carnivorous zooplankton	1.967E-03	3.077E-03	3.756E-04	6.034E-04	15.71639
Birds	7.301E-06	3.668E-06	2.013E-06	1.531E-06	2.71791
Pinnipeds	3.206E-04	4.195E-05	4.751E-05	6.216E-06	2.78155
Cetaceans	1.649E-03	2.369E-04	2.552E-04	5.946E-05	5.87927
Macrophytes	0	0	0	0	1

TABLE 31 Observational indices of the1970-1999 state of the North Sea ecosystem to which the model was fitted using 1970-1999 environmental drivers and fishing fleet inputs, Indices include fluxes between guilds, and annual ratios, and their standard deviations. For each index (*i*) the partial likelihood between observed and modelled values with parameter set θ, obtained from the simulated annealing scheme, was calculated as $exp(-\chi_{\theta i}^2)$, where $\chi_{\theta i}^2 = \frac{(observed_i - model_{\theta,i})^2}{2\sigma_i^2}$ (σ_i is the standard deviation of observed index *i*), and the overall likelihood is given by $exp(-(mean(\chi_\theta^2))$. The results are shown graphically in Figure 11.

Description	Observational value	s.d. of observational value	Units	Maximum likelihood model value	Partial likelihood
Annual total primary production	1522	150.94	$mMN.m^{-2}.y^{-1}$	1221.358	0.137569
Annual new production from depth integrated nitrate	624.4	66.4	$mMN.m^{-2}.y^{-1}$	493.8495	0.144695
Annual within forest net production of kelp	600	100	$gC.m^{-2}.y^{-1}$	597.5808	0.999707
Annual omnivorous zooplankton gross production	339.6	25.16	$mMN.m^{-2}.y^{-1}$	321.0715	0.762443
Annual carnivorous zooplankton gross production	44.35	2.516	$mMN.m^{-2}.y^{-1}$	39.54958	0.161931
Annual planktivorous fish gross production	29.97	3.509	$mMN.m^{-2}.y^{-1}$	23.03797	0.142089
Annual demersal fish gross production	11.5	2.277	$mMN.m^{-2}.y^{-1}$	7.217124	0.170512
Annual suspension /deposit feeding benthos gross production	1248	449	$mMN.m^{-2}.y^{-1}$	596.1756	0.348627
Annual carnivore/scavenge feeding benthos gross production	21.1	7.6	$mMN.m^{-2}.y^{-1}$	23.38592	0.955774
Annual net production of birds	8.452E-04	2.00E-04	$mMN.m^{-2}.y^{-1}$	0.001167	0.274825
Annual net production of pinnipeds	7.245E-04	3.50e-04	$mMN.m^{-2}.y^{-1}$	0.000864	0.923399

Annual net production of cetaceans	1.691E-03	8.00E-04	$mMN.m^{-2}.y^{-1}$	0.002557	0.5562
Annual monthly max concentration of benthos suspension /deposit feeder larvae	1.185	0.4421	$mMN.m^{-3}$	0.620904	0.443074
Annual monthly max concentration of benthos carnivore/scavenge feeder larvae	0.334	0.1013	$mMN.m^{-3}$	0.322068	0.993087
Annual consumption of planktivorous fish by fish	23.48	9.057	$mMN.m^{-2}.y^{-1}$	2.784971	0.073494
Annual consumption of demersal fish by fish	2.138	0.503	$mMN.m^{-2}.y^{-1}$	1.058454	0.099947
Annual consumption of omnivorous zooplankton by fish and fish larvae	92.28	13.019	$mMN.m^{-2}.y^{-1}$	77.53647	0.526641
Annual consumption of omnivorous zooplankton by carnivorous zooplankton	60.38	25.157	$mMN.m^{-2}.y^{-1}$	108.8008	0.156836
Annual consumption of benthos by fish	12.58	6.289	$mMN.m^{-2}.y^{-1}$	7.210685	0.694669
Annual food consumption by birds	0.6538	0.325	$mMN.m^{-2}.y^{-1}$	0.113519	0.251128
Proportion planktivorous fish in diet of birds	0.6	0.2	Dimensionless	0.527197	0.935893
Proportion demersal fish in diet of birds	0.1	0.05	Dimensionless	0.212134	0.080879
Proportion migratory fish in diet of birds	0.05	0.015	Dimensionless	0.044799	0.941665
Proportion discards in diet of birds	0.05	0.02	Dimensionless	0.006342	0.092317
Annual food consumption by pinnipeds	0.2161	0.105	$mMN.m^{-2}.y^{-1}$	0.146009	0.800343
Proportion pelagic fish in diet of pinnipeds	0.2910	0.0728	Dimensionless	0.396866	0.347221
Proportion demersal fish in diet of pinnipeds	0.6969	0.1742	Dimensionless	0.555861	0.720666
Proportion migratory fish in diet of pinnipeds	0.01208	0.0030	Dimensionless	0.010016	0.790961
Annual food consumption by cetaceans	0.9691	0.48	$mMN.m^{-2}.y^{-1}$	0.723972	0.877777
Proportion pelagic fish in diet of cetaceans	0.6632	0.1658	Dimensionless	0.696303	0.980197
Proportion demersal fish in diet of cetaceans	0.0995	0.04	Dimensionless	0.156068	0.36794
Proportion migratory fish in diet of cetaceans	0.08014	0.035	Dimensionless	0.092003	0.944145
Annual planktivorous fish landings (live weight)	5.555	0.2	$mMN.m^{-2}.y^{-1}$	5.548956	0.999544
Annual demersal fish landings (live weight)	1.735	0.08	$mMN.m^{-2}.y^{-1}$	1.717724	0.976952
Annual migratory fish landings (live weight)	0.775	0.308	$mMN.m^{-2}.y^{-1}$	0.775707	0.999997
Annual suspension /deposit feeding benthos landings (live weight)	0.0953	0.0382	$mMN.m^{-2}.y^{-1}$	0.094569	0.999817
Annual carnivore/scavenge feeding benthos landings (live weight)	0.0829	0.0169	$mMN.m^{-2}.y^{-1}$	0.069949	0.745548
Annual carnivorous zooplankton landings (live weight)	0.00147	9.32E-04	$mMN.m^{-2}.y^{-1}$	0.003266	0.1561

Annual kelp landings (live weight)	0	0	$mMN.m^{-2}.y^{-1}$	0	NA
Annual carbon gross PB ratio of kelp	2	0.5	y^{-1}	1.319421	0.395986
Annual gross PB ratio larvae of suspension/deposit feeding benthos	10	5	y^{-1}	15.32578	0.567067
Annual gross PB ratio larvae of carnivore/scavenge feeding benthos	10	5	y^{-1}	15.69397	0.522868
Annual gross PB ratio suspension/deposit feeding benthos	10	3	y^{-1}	11.87641	0.822336
Annual gross PB ratio carnivore/scavenge feeding benthos	1.2	1	y^{-1}	1.938912	0.761096
Annual gross PB ratio omnivorous zooplankton	20	10	y^{-1}	10.52631	0.638423
Annual gross PB ratio carnivorous zooplankton	5	1.315	y^{-1}	3.731479	0.62796
Annual gross PB ratio larvae of planktivorous fish	4	2	y^{-1}	0.650482	0.246004
Annual gross PB ratio larvae of demersal fish	4	2	y^{-1}	6.37257	0.494783
Annual gross PB ratio planktivorous fish	1.72	0.86	y^{-1}	1.025134	0.721503
Annual gross PB ratio demersal fish	0.88	0.44	y^{-1}	0.301225	0.420995
Annual gross PB ratio migratory fish	1.3	0.6	y^{-1}	0.185064	0.177905
Annual net PB ratio birds	0.28	0.14	y^{-1}	0.148116	0.641651
Annual net PB ratio pinnipeds	0.09	0.045	y^{-1}	0.042047	0.566789
Annual net PB ratio cetaceans	0.02	0.01	y^{-1}	0.044199	0.053512
Annual average proportion of kelp C uptake which is exuded	0.3	0.1	Dimensionless	0.297361	0.999652
Annual average molar NC ratio of kelp	0.12	0.2	Dimensionless	0.123468	0.99985
Annual denitrification	129	42	$mMN.m^{-2}.y^{-1}$	208.4928	0.166771
Proportion of demersal fish catch discarded	0.37	0.075	Dimensionless	0.362514	0.995031
Annual average ammonia concentration in porewater of sand grain size 0.25mm	19.24	9	$mMN.m^{-3}$	4.728422	0.272556
Annual average ammonia concentration in porewater of mud grain size 0.12mm	63.45	22	$mMN.m^{-3}$	52.65414	0.886563
Annual average nitrate concentration in porewater of sand grain size 0.25mm	4.15	2	$mMN.m^{-3}$	5.171709	0.877669
Annual average nitrate concentration in porewater of mud grain size 0.12mm	2.34	1	$mMN.m^{-3}$	3.11393	0.741201
Annual average organic N content of sand grain size 0.25mm (0.19-0.43mm)	0.05152	0.02441	%N (gN.(g dry sed)$^{-1}$)	0.049978	0.998019

Annual average organic N content of mud grain size 0.12mm (0.03-0.07mm)	0.07357	0.0343	%N (gN.(g dry sed)$^{-1}$)	0.066279	0.977661
Average winter (Nov-Feb) nitrate concentration shallow layer	9.998	2.135	mMN.m^{-3}	9.427078	0.964877
Average summer (May-Aug) nitrate concentration shallow layer	2.161	1.089	mMN.m^{-3}	3.24313	0.610357
Average winter (Nov-Feb) nitrate concentration deep layer	6.995	0.836	mMN.m^{-3}	9.521078	0.010409
Average summer (May-Aug) nitrate concentration deep layer	2.837	0.917	mMN.m^{-3}	5.717038	0.007212
Average winter (Nov-Feb) ammonia concentration shallow layer	2.367	0.774	mMN.m^{-3}	1.789509	0.757038
Average summer (May-Aug) ammonia concentration shallow layer	1.737	0.669	mMN.m^{-3}	3.203024	0.090624
Average winter (Nov-Feb) ammonia concentration deep layer	0.853	0.32	mMN.m^{-3}	1.576997	0.077349
Average summer (May-Aug) ammonia concentration deep layer	1.338	0.708	mMN.m^{-3}	2.854398	0.100896
Inshore:offshore ratio of annual mean carnivorous zooplankton depth averaged concentration	0.904055	0.385	Dimensionless	1.435149	0.386176
Inshore:offshore ratio of annual mean omnivorous zooplankton depth averaged concentration	1.676	0.2715	Dimensionless	1.408752	0.616726
Inshore:offshore ratio of annual mean phytoplankton surface layer concentration	3.744	1	Dimensionless	0.991064	0.022586
Inshore:offshore ratio of annual mean nitrate surface layer concentration	3.000	1	Dimensionless	0.878729	0.105379
Inshore:offshore ratio of annual mean ammonia surface layer concentration	2.4294	0.9	Dimensionless	1.596371	0.651611
Inshore:offshore ratio of annual mean planktivorous fish density (m^{-2})	0.67	0.49	Dimensionless	0.418337	0.876437
Inshore:offshore ratio of annual mean demersal fish density (m^{-2})	0.39	0.31	Dimensionless	0.880957	0.285331
Annual bycatch of birds	NA	NA	mMN.m^{-2}.y^{-1}	1.11E-06	NA
Annual bycatch of pinnipeds	NA	NA	mMN.m^{-2}.y^{-1}	6.42E-05	NA
Annual bycatch of cetaceans	NA	NA	mMN.m^{-2}.y^{-1}	0.000788	NA
Proportion of kelp annual nitrogen uptake exported as beach-cast	0.15	0.05	Dimensionless	0.085577	0.436021

Annual cetacean catch	4.05E-05	2.00E-05	$mMN.m^{-2}.y^{-1}$	4.05E-05	1
Overall model					0.382664

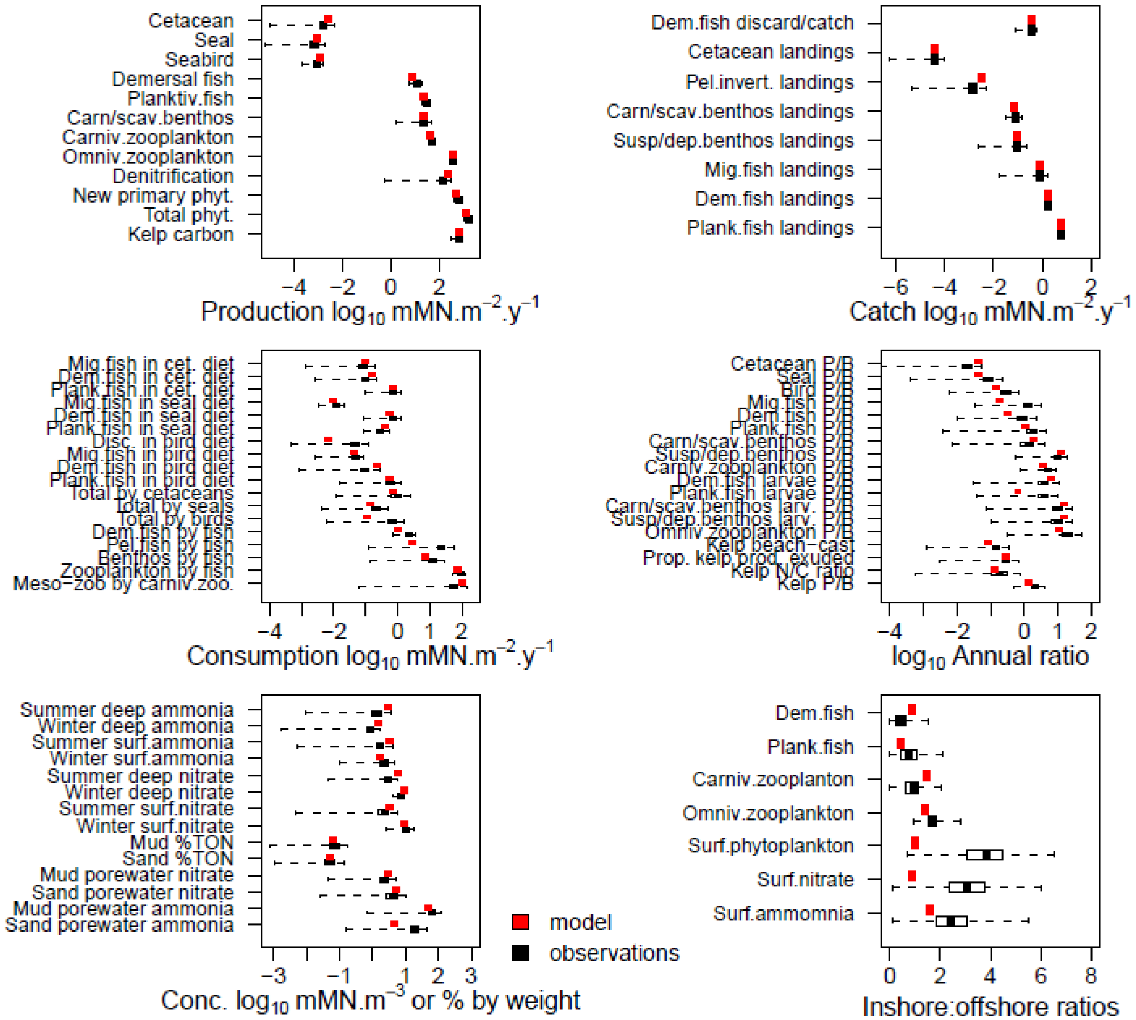

FIGURE 11 Annual integrated or averaged results from the best-fit 1970-1999 stationary model and the corresponding observed data from the North Sea. Red boxes and whiskers show the 0.5, 25, 50, 75 and 99.5 centiles of the likelihood distribution of model results given the uncertainty in fitted parameter values. Black boxes and whiskers show the equivalent variability in measurements from the North Sea aggregated over the period 1970-1999. Drawn with the function e2e_compare_obs(,,selection="ANNUAL").

TABLE 32 Observational indices of the 2003-2013 state of the North Sea ecosystem to which the model was fitted using 2003-2013 environmental drivers and fishing fleet inputs, Indices include fluxes between guilds, and annual ratios, and their standard deviations. For each index (*i*) the partial likelihood between observed and modelled values with parameter set *θ*, obtained from the simulated annealing scheme, was calculated as $exp(-\chi_{\theta i}^2)$, where $\chi_{\theta i}^2 = \frac{(observed_i - model_{\theta,i})^2}{2\sigma_i^2}$ (σ_i is the standard deviation of observed index *i*), and the overall likelihood is given by $exp(-(mean(\chi_\theta^2))$. The results are shown graphically in Figure 12.

Description	Observational value	s.d. of observational value	Units	Maximum likelihood model value	Partial likelihood
Annual total primary production	1522	150.94	$mMN.m^{-2}.y^{-1}$	1234.36	0.162712
Annual new production from depth integrated nitrate	672.8	73.00	$mMN.m^{-2}.y^{-1}$	482.8477	0.033912
Annual within forest net production of kelp	600	100	$gC.m^{-2}.y^{-1}$	599.6151	0.999993
Annual omnivorous zooplankton gross production	339.6	25.157	$mMN.m^{-2}.y^{-1}$	318.1539	0.695329
Annual carnivorous zooplankton gross production	NA	NA	$mMN.m^{-2}.y^{-1}$	47.09973	NA
Annual planktivorous fish gross production	NA	NA	$mMN.m^{-2}.y^{-1}$	12.39101	NA
Annual demersal fish gross production	NA	NA	$mMN.m^{-2}.y^{-1}$	19.49517	NA
Annual suspension /deposit feeding benthos gross production	NA	NA	$mMN.m^{-2}.y^{-1}$	604.4848	NA
Annual carnivore/scavenge feeding benthos gross production	NA	NA	$mMN.m^{-2}.y^{-1}$	30.44384	NA
Annual net production of birds	NA	NA	$mMN.m^{-2}.y^{-1}$	0.002314	NA
Annual net production of pinnipeds	NA	NA	$mMN.m^{-2}.y^{-1}$	0.005919	NA
Annual net production of cetaceans	NA	NA	$mMN.m^{-2}.y^{-1}$	0.002698	NA
Annual monthly max concentration of benthos suspension /deposit feeder larvae	NA	NA	$mMN.m^{-3}$	0.607045	NA
Annual monthly max concentration of benthos carnivore/scavenge feeder larvae	NA	NA	$mMN.m^{-3}$	0.463617	NA
Annual consumption of planktivorous fish by fish	NA	NA	$mMN.m^{-2}.y^{-1}$	3.10436	NA
Annual consumption of demersal fish by fish	NA	NA	$mMN.m^{-2}.y^{-1}$	2.201847	NA
Annual consumption of omnivorous zooplankton by fish and fish larvae	NA	NA	$mMN.m^{-2}.y^{-1}$	67.38016	NA

Annual consumption of omnivorous zooplankton by carnivorous zooplankton	NA	NA	mMN.m^{-2}.y^{-1}	127.7885	NA
Annual consumption of benthos by fish	NA	NA	mMN.m^{-2}.y^{-1}	22.04659	NA
Annual food consumption by birds	NA	NA	mMN.m^{-2}.y^{-1}	0.163818	NA
Proportion planktivorous fish in diet of birds	NA	NA	Dimensionless	0.243056	NA
Proportion demersal fish in diet of birds	NA	NA	Dimensionless	0.46929	NA
Proportion migratory fish in diet of birds	NA	NA	Dimensionless	0.089837	NA
Proportion discards in diet of birds	NA	NA	Dimensionless	0.00422	NA
Annual food consumption by pinnipeds	NA	NA	mMN.m^{-2}.y^{-1}	0.41985	NA
Proportion pelagic fish in diet of pinnipeds	NA	NA	Dimensionless	0.121256	NA
Proportion demersal fish in diet of pinnipeds	NA	NA	Dimensionless	0.845798	NA
Proportion migratory fish in diet of pinnipeds	NA	NA	Dimensionless	0.013862	NA
Annual food consumption by cetaceans	NA	NA	mMN.m^{-2}.y^{-1}	0.843069	NA
Proportion pelagic fish in diet of cetaceans	NA	NA	Dimensionless	0.366895	NA
Proportion demersal fish in diet of cetaceans	NA	NA	Dimensionless	0.374638	NA
Proportion migratory fish in diet of cetaceans	NA	NA	Dimensionless	0.204947	NA
Annual planktivorous fish landings (live weight)	2.928	0.6	mMN.m^{-2}.y^{-1}	2.050946	0.343569
Annual demersal fish landings (live weight)	0.6408	0.3	mMN.m^{-2}.y^{-1}	0.821286	0.834457
Annual migratory fish landings (live weight)	0.9925	0.25	mMN.m^{-2}.y^{-1}	1.001251	0.999387
Annual suspension /deposit feeding benthos landings (live weight)	0.07444	0.028	mMN.m^{-2}.y^{-1}	0.075677	0.999025
Annual carnivore/scavenge feeding benthos landings (live weight)	0.12801	0.05	mMN.m^{-2}.y^{-1}	0.131877	0.997014
Annual carnivorous zooplankton landings (live weight)	0.006976	0.004	mMN.m^{-2}.y^{-1}	0.006926	0.999921
Annual kelp landings (live weight)	0	0	mMN.m^{-2}.y^{-1}	0	NA
Annual carbon gross PB ratio of kelp	2	0.5	y^{-1}	1.332569	0.410274
Annual gross PB ratio larvae of suspension /deposit feeding benthos	10	5	y^{-1}	15.5282	0.542688
Annual gross PB ratio larvae of carnivore/scavenge feeding benthos	10	5	y^{-1}	15.6402	0.529281
Annual gross PB ratio suspension /deposit feeding benthos	10	3	y^{-1}	12.22606	0.759346
Annual gross PB ratio carnivore/scavenge feeding	1.2	1	y^{-1}	1.974316	0.740979

benthos					
Annual gross PB ratio omnivorous zooplankton	20	10	y^{-1}	11.59643	0.702507
Annual gross PB ratio carnivorous zooplankton	5	1.315	y^{-1}	3.580513	0.558436
Annual gross PB ratio larvae of planktivorous fish	4	2	y^{-1}	0.630788	0.241968
Annual gross PB ratio larvae of demersal fish	4	2	y^{-1}	5.523025	0.748301
Annual gross PB ratio planktivorous fish	1.72	0.86	y^{-1}	1.028998	0.724119
Annual gross PB ratio demersal fish	0.88	0.44	y^{-1}	0.299865	0.419284
Annual gross PB ratio migratory fish	1.3	0.6	y^{-1}	0.178485	0.174307
Annual net PB ratio birds	0.28	0.14	y^{-1}	0.206734	0.872025
Annual net PB ratio pinnipeds	0.09	0.045	y^{-1}	0.10475	0.9477
Annual net PB ratio cetaceans	0.02	0.01	y^{-1}	0.039502	0.149313
Annual average proportion of kelp C uptake which is exuded	0.3	0.1	Dimensionless	0.297738	0.999744
Annual average molar NC ratio of kelp	0.12	0.2	Dimensionless	0.122238	0.999937
Annual denitrification	129	42	$mMN.m^{-2}.y^{-1}$	205.2756	0.192226
Proportion of demersal fish catch discarded	0.51	0.1	Dimensionless	0.514943	0.998779
Annual average ammonia concentration in porewater of sand grain size 0.25mm	19.24	9	$mMN.m^{-3}$	4.800768	0.276102
Annual average ammonia concentration in porewater of mud grain size 0.12mm	63.45	22	$mMN.m^{-3}$	53.67874	0.906075
Annual average nitrate concentration in porewater of sand grain size 0.25mm	4.15	2	$mMN.m^{-3}$	5.049986	0.90371
Annual average nitrate concentration in porewater of mud grain size 0.12mm	2.34	1	$mMN.m^{-3}$	3.043604	0.780727
Annual average organic N content of sand grain size 0.25mm (0.19-0.43mm)	0.051515	0.02441	%N (gN.(g dry sed)$^{-1}$)	0.049979	0.998021
Annual average organic N content of mud grain size 0.12mm (0.03-0.07mm)	0.07357	0.0343	%N (gN.(g dry sed)$^{-1}$)	0.066287	0.977708
Average winter (Nov-Feb) nitrate concentration shallow layer	NA	NA	$mMN.m^{-3}$	9.333873	NA
Average summer (May-Aug) nitrate concentration shallow layer	NA	NA	$mMN.m^{-3}$	2.925153	NA
Average winter (Nov-Feb) nitrate concentration deep layer	NA	NA	$mMN.m^{-3}$	9.425888	NA
Average summer (May-Aug) nitrate concentration	NA	NA	$mMN.m^{-3}$	5.610742	NA

deep layer					
Average winter (Nov-Feb) ammonia concentration shallow layer	NA	NA	$mMN.m^{-3}$	1.817435	NA
Average summer (May-Aug) ammonia concentration shallow layer	NA	NA	$mMN.m^{-3}$	3.237119	NA
Average winter (Nov-Feb) ammonia concentration deep layer	NA	NA	$mMN.m^{-3}$	1.599315	NA
Average summer (May-Aug) ammonia concentration deep layer	NA	NA	$mMN.m^{-3}$	2.906644	NA
Inshore:offshore ratio of annual mean carnivorous zooplankton depth averaged concentration	0.904055	0.2	Dimensionless	1.396254	0.0484
Inshore:offshore ratio of annual mean omnivorous zooplankton depth averaged concentration	1.675727	0.271539	Dimensionless	1.278118	0.342304
Inshore:offshore ratio of annual mean phytoplankton surface layer concentration	3.744403	1	Dimensionless	1.001465	0.023241
Inshore:offshore ratio of annual mean nitrate surface layer concentration	3.000139	1	Dimensionless	0.879379	0.105525
Inshore:offshore ratio of annual mean ammonia surface layer concentration	2.429353	0.9	Dimensionless	1.607346	0.658958
Inshore:offshore ratio of annual mean planktivorous fish density (m^{-2})	0.67	0.49	dimensionless	0.363762	0.822591
Inshore:offshore ratio of annual mean demersal fish density (m^{-2})	0.39	0.31	Dimensionless	0.937668	0.210018
Annual bycatch of birds	6.25E-07	3.00E-07	$mMN.m^{-2}.y^{-1}$	6.18E-07	0.999721
Annual bycatch of pinnipeds	2.74E-05	5.00E-05	$mMN.m^{-2}.y^{-1}$	3.11E-05	0.997315
Annual bycatch of cetaceans	0.000275	1.00E-04	$mMN.m^{-2}.y^{-1}$	0.000239	0.935773
Proportion of kelp annual nitrogen uptake exported as beach-cast	0.15	0.05	Dimensionless	0.083794	0.416181
Cetacean catch	8.38E-05	4.00E-05	$mMN.m^{-2}.y^{-1}$	7.92E-05	0.993339
Overall model					0.486621

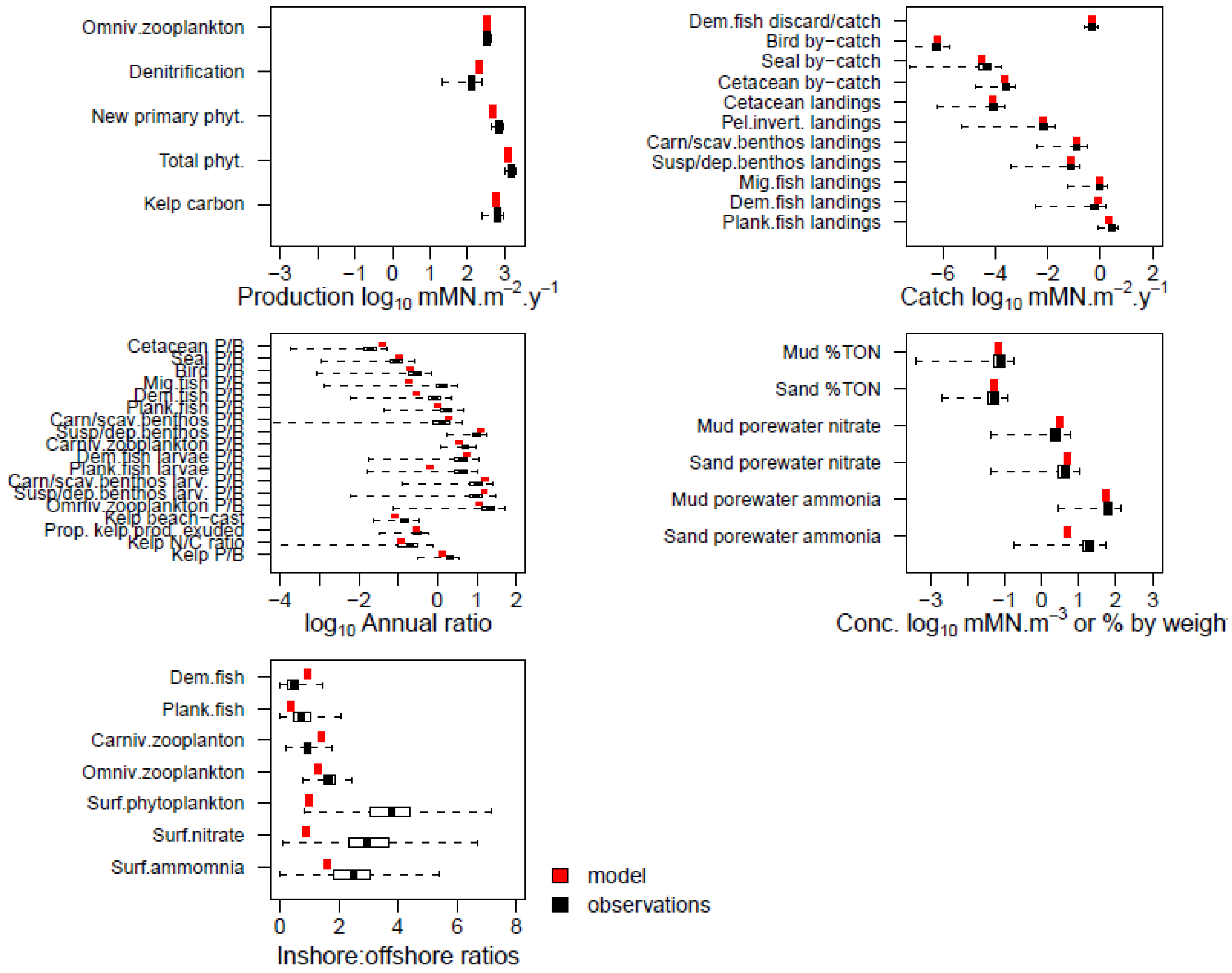

FIGURE 12 Annual integrated or averaged results from the best-fit 2003-2013 stationary model and the corresponding observed data from the North Sea. Red boxes and whiskers show the 0.5, 25, 50, 75 and 99.5 centiles of the likelihood distribution of model results given the uncertainty in fitted parameter values. Black boxes and whiskers show the equivalent variability in measurements from the North Sea aggregated over the period 2003-2013. Drawn with the function e2e_compare_obs(,,selection="ANNUAL").

TABLE 33 Maximum likelihood preference parameters $pref_{resource\text{-}consumer}$ for all resource-consumer links in the model, estimated using the simulated annealing scheme to fit the 1970-1999 model to the observed data on ecosystem state. Preferences for each consumer guild (columns) sum to 1.0. Values shown are constrained to 3 decimal places   Note that the preference parameters are inputs to the model, and do not represent proportions in the diet, Diet composition is an emergent output of the model.

		Consumers															
Resources	ID	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Water column ammonia	1	0.271	0.271														
Water column nitrate	2	0.729	0.729														
Suspended detritus	3			0.001							0.976	0.312	0.295				
Sediment detritus	4												0.478				
Macrophyte debris	5													0.007			
Corpses	6									0.010				0.420	0.100	0.057	
Fishery discards	7									0.097					0.220	0.065	0.119
Macrophytes	8													0.013			
Phytoplankton	9			0.906							0.024	0.688	0.227				
Omnivorous zooplankton	10				0.653	0.147	0.947	0.361	0.366								0.010
Carnivorous zooplankton	11							0.152	0.014	0.075					0.100	0.000	0.020
Larvae of planktivorous fish	12				0.017			0.128	0.050	0.116							
Larvae of demersal fish	13				0.041			0.179	0.058	0.111							
Planktivorous fish	14									0.106					0.200	0.184	0.292
Migratory fish	15									0.018					0.180	0.052	0.392
Demersal fish	16									0.006					0.200	0.641	0.162
Larvae of suspension/deposit feeding benthos	17			0.002	0.192	0.588	0.043	0.088	0.285								
Larvae of carnivorous/scavenge feeding benthos	18			0.092	0.096	0.265	0.010	0.092	0.227								
Suspension/deposit feeding benthos	19									0.390				0.561	0.000	0.000	0.000
Carnivorous/scavenge feeding benthos	20									0.072					0.000	0.000	0.000
Birds	21															0.000	0.000
Pinnipeds	22																0.005
Cetaceans	23																

TABLE 34 Fitted uptake, mortality, migration and exploitable fraction parameters for the maximum likelihood model, estimated using the simulated annealing scheme. Maximum uptake rates are given at the Q_{10} reference temperature.

Consumer guild	Maximum carbon uptake rate	Carbon exudation rate	Maximum nitrogen uptake rate	Nitrogen uptake half-saturation coefficient	Beddington-DeAngelis parameter	Density dependent mortality coefficient	Active migration coefficient	Maximum exploitable fraction of the stock
Macrophytes	0.026	1.811E-08	0.009	18.272		3.099E-08		0.041
Phytoplankton – shallow			2.876	4.302		5.142E-02		
Phytoplankton – deep						6.328E-02		
Omnivorous zooplankton			2.156	3.390		3.346E-05		
Carnivorous zooplankton			0.154	1.086		2.090E-04		0.004
Larvae of planktivorous fish			0.315	6.408		4.101E-06		
Larvae of demersal fish			0.233	2.036		5.787E-07		
Planktivorous fish			0.134	2.127		1.906E-05	1.579E-03	0.874
Migratory fish			0.033	2.264		1.691E-06	3.545E-05	0.684
Demersal fish			0.011	0.526		3.760E-05	2.205E-03	0.900
Larvae of suspension/deposit feeding benthos			0.334	1.033		9.633E-06		
Larvae of carnivorous/scavenge feeding benthos			0.993	2.371		2.540E-07		
Suspension/deposit feeding benthos			0.910	1.722		3.674E-04		0.030
Carnivorous/scavenge feeding benthos			0.027	9.016		3.979E-04		0.155
Birds			0.794	1.000	9415.521	4.971E-02	9.759E-03	0.100
Pinnipeds			0.416	1.583	4056.226	5.063E-03	9.837E-03	0.099
Cetaceans			0.500	0.520	1281.383	1.303E-03	9.985E-03	0.313

TABLE 35 Fitted values for parameters of microbiological rates at the Q_{10} reference temperature, and other related parameters, for the maximum likelihood model, estimated using the simulated annealing scheme.

Description	Value
Water column detritus mineralisation rate	1.676E-05
Upper layer water column nitrification rate	1.187E-07
Upper layer water column denitrification rate	2.380E-09
Lower layer water column nitrification rate	3.052E-02
Lower layer water column denitrification rate	4.873E-07
Formation rate parameter for refractory detritus	4.962E-01
Mineralisation rate scaling parameter for refractory detritus	1.627E-04
Proportion of refractory detritus digestible by benthos	2.614E-02
Sediment detritus mineralisation rate	1.485E-02
Grain size sensitivity for sediment detritus mineralisation rate	-1.598E-08
Sediment nitrification rate	6.276E-05
Grain size sensitivity for sediment nitrification rate	-2.645E-06
Sediment denitrification rate	5.281E-01
Grain size sensitivity for sediment denitrification rate	1.537E-07
Conversion rate of discards to corpses	1.837E-02
Conversion rate of corpses to sediment detritus	2.233E-01
Detritus sinking rate in the upper layers	2.669E-02
Detritus sinking rate in the lower layer	9.813E-02
Density dependent self-shading parameter for macrophytes	3.580E-06
Wave-dependent beach-cast rate for macrophyte debris	4.422E-05
Fitting parameter for undersize demersal fish function	1.481E-03

TABLE 36 Fixed assimilation, metabolism, fecundity, and exploitation threshold parameters which were not subject to fitting. The only parameter which differed between the 1970-1999 and 2003-2013 simulation periods was the threshold for zero remaining exploitable biomass of carnivorous zooplankton. The value was set to 14 $mMN.m^{-2}$ as shown here for 1970-1999, and 4 $mMN.m^{-2}$ for 2003-2013 to reflect an observed trend in squid abundance and landings in the North Sea (Pierce *et al.,* 1998**;** van der Kooij *et al.,* 2016)

Consumer guild	**Assimilation efficiency**	**Background metabolic rate at Q_{10} reference temperature (d^{-1})**	**Annual weight-specific fecundity**	**Threshold for zero exploitable biomass remaining ($mMN.m^{-2}$)**	**Minimum inedible biomass ($mMN.m^{-2}$)**
Macrophytes				1	
Phytoplankton					
Omnivorous zooplankton	0.34	1.000E-02			
Carnivorous zooplankton	0.34	5.000E-03		14	1
Larvae of planktivorous fish	0.34	5.000E-05			
Larvae of demersal fish	0.34	5.000E-05			
Planktivorous fish	0.275	1.400E-03	0.25	0.1	
Migratory fish	0.25	4.000E-04		0.1	
Demersal fish	0.25	8.200E-04	0.25	0.1	
Larvae of suspension/deposit feeding benthos	0.34	1.000E-02			
Larvae of carnivorous/scavenge feeding benthos	0.34	1.000E-02			
Suspension/deposit feeding benthos	0.34	1.000E-02	0.10	20	
Carnivorous/scavenge feeding benthos	0.34	1.000E-03	0.40	1	
Birds	0.15	5.500E-03		0.0006	
Pinnipeds	0.15	2.800E-03		0.002	
Cetaceans	0.15	5.000E-03		0.03	

TABLE 37. Other fixed parameters which were not subject to fitting.

Description	**Value**
Irradiance at maximum carbon uptake by macrophytes ($E.m^{-2}.d^{-1}$)	3
Minimum nitrogen:carbon molar ratio for macrophytes	0.02
Maximum nitrogen:carbon molar ratio for macrophytes	0.15
Irradiance at maximum nitrogen uptake by phytoplankton ($E.m^{-2}.d^{-1}$)	4
Autotroph Q_{10} value	1.20
Heterotroph uptake Q_{10} value	1.32
Metabolic and bacterial Q_{10} value	1.44
Q_{10} reference temperature	10

Sensitivity analysis

The sensitivity analysis (e2e_run_sens()) tested the influence of individual parameters and the fishing and environmental drivers on the overall likelihood of the observational target data given the 1970-1999 model. The analysis was conducted on the basis of the factorial sampling scheme (Morris, 1991) as implemented in the StrathE2E2 package with 16 trajectories of the model (randomised parameter sets). For each trajectory, multiple model runs were executed, with a different single internal parameter being varied in each successive run, drawn from a symmetrical random uniform distribution. With a total of 453 parameters and drivers being included in the analysis therefore required a total of 7264 model runs each of 100 years.

The analysis included the fixed and fitted parameters of the ecology model, fishing fleet model parameters, harvest ratios on each model guild, environmental and biological event drivers, and the physical configuration parameters (layer thicknesses, inshore/offshore areas, sediment properties).

For the ecology model component, the number of parameters in the sensitivity analysis was greater than the number of input parameters for the model. This was because within the model each prey-predator pair is represented by a discrete uptake function defined by a maximum uptake rate and half-saturation coefficient. These are derived by the combination of the preference matrix and, for each predator, the single values of maximum uptake rate and half-saturation coefficient which are the input parameters to the model.

Of the 453 parameters in the analysis, 72 emerged as having significant sensitivity with respect to overall model fit to the observed data (95% probability that the distributions of elementary effects were non-zero). Of these 67% were ecology model parameters (38% fitted, 29% fixed). Physical configuration parameters made up 14% of the significantly sensitive set; harvest ratios only 3%. This does not mean that model was insensitive to harvest ratios; just that compared to many of the other parameters in the model the harvest ratios were not among the most sensitive for the overall fit given the range of variations imposed in the analysis (Table 38, Figure 13).

The parameter class with the highest proportion of significantly sensitive terms was the fixed ecology model group (21 out of 52; 40%). The standard deviations of the significantly sensitive parameters indicated that they all had strong interactions with other parameters. 30% of the physical configuration parameters had significant sensitivity.

The main conclusions from the sensitivity analysis were:

1) assimilation efficiencies and maximum uptake rates of mid-trophic level guilds were the most sensitive parameters for the overall model. This implies that the food web as a whole was potentially sensitive to processes that might change the community-level feeding responses of these guilds, such as species invasions and replacements, and physiological effects not represented in the model such as ocean acidification (temperature effects are included in the model already and the Q_{10} for heterotrophic uptake rates emerge as having significant sensitivity).

2) The high proportion of significantly sensitive ecology model parameters (44%) were independently fixed and not included in the simulated annealing fitting process. This indicates that the fixed parameters were well chosen. Given that the model as a whole was somewhat under-constrained by the observed fitting data, the selection of high-sensitivity parameters for independent constraint was a sound choice.

Parameter sensitivity analysis of the 1970-1999 maximum likelihood model

TABLE 38 One-at-a-time factorial sampling scheme sensitivity analysis results based on 16 trajectories, measuring the sensitivity of the overall likelihood of the 1970-1999 model to each of the parameters and drivers. The mean elemental effect (EE_mean) is a measure of the sensitivity of the model to each individual parameter. The corresponding standard deviation of the elemental effect (EE_sd) is a measure of the susceptibility of each parameter to interactions with other parameters. The results are ranked by decreasing values of the absolute value of EE_mean, so the model is most sensitive to the first parameters in the list. The column labelled 'Signif' indicates whether the value of EE_mean was significantly different from zero ($p<0.05$). Significant parameters are highlighted by grey-shaded cells. Parameters with EE_mean and EE_sd = NA were set to zero in the baseline model or not included in the sensitivity analysis.

Parameter class	Parameter description	Model guild or feature	EE_mean	EE_sd	Signif.
Ecology model fitted	Maximum uptake rate	Omnivorous zooplankton by carnivorous zooplankton	-3.1576	1.5359	sig
Ecology model fixed	Assimilation efficiency	Planktivorous fish	-3.0831	1.0094	sig
Ecology model fixed	Assimilation efficiency	Carnivorous zooplankton	-2.8390	1.5590	sig
Ecology model fixed	Assimilation efficiency	Demersal fish lavae	-2.5736	1.3599	sig
Ecology model fitted	Maximum uptake rate	Omnivorous zooplankton by planktivorous fish	-2.3868	1.0885	sig
Ecology model fitted	Maximum uptake rate	Omnivorous zooplankton by demersal fish larvae	-2.3589	1.3555	sig
Ecology model fixed	Assimilation efficiency	Omnivorous zooplankton	-2.3478	1.1739	sig
Ecology model fitted	Maximum uptake rate	Phytoplankton by omnivorous zooplankton	-2.2313	1.3448	sig
Ecology model fitted	Uptake half saturation coefficient	Omnivorous zooplankton by carnivorous zooplankton	-2.1505	1.1742	sig
Ecology model fitted	Uptake half saturation coefficient	Phytoplankton by omnivorous zooplankton	-1.8623	1.5599	sig
Ecology model fitted	Uptake half saturation coefficient	Omnivorous zooplankton by planktivorous fish	-1.7450	1.0172	sig
Ecology model fitted	Uptake half saturation coefficient	Omnivorous zooplankton by demersal fish larvae	-1.5664	1.4946	sig
Ecology model fixed	Background metabolic rate coefficient	Planktivorous fish	-1.3390	0.8908	sig
Ecology model fixed	Background metabolic rate coefficient	Carnivorous zooplankton	-1.2975	1.0932	sig
Ecology model fitted	Maximum uptake rate	Nitrate by phytoplankton	-0.8142	0.5902	sig

Biological event driver	Spawning rate	Demersal fish	-0.6305	0.8458	sig
Ecology model fixed	Annual fecundity	Demersal fish	-0.6305	0.8458	sig
Environmental driver	Boundary concentration	Lower layer nitrate	-0.6281	0.3928	sig
Ecology model fitted	Maximum uptake rate	Carnivorous zooplankton by planktivorous fish	-0.5517	0.6302	sig
Ecology model fixed	Assimilation efficiency	Demersal fish	-0.4812	0.7260	sig
Physical configuration	Vertical thickness	Offshore zone lower layer	-0.4522	0.5630	sig
Ecology model fitted	Density dependent mortality coefficient	Carnivorous zooplankton	-0.4512	0.6580	sig
Physical configuration	Vertical thickness	Offshore zone upper layer	-0.3460	0.8995	ns
Ecology model fitted	Uptake half saturation coefficient	Carnivorous zooplankton by planktivorous fish	-0.3185	0.7201	ns
Ecology model fitted	Density dependent mortality coefficient	Phytoplankton upper layer	-0.3143	0.8392	ns
Ecology model fitted	Uptake half saturation coefficient	Demersal fish larvae by planktivorous fish	-0.3127	0.5745	sig
Ecology model fixed	Maximum exploitable fraction of stock	Planktivorous fish	-0.2882	0.4202	sig
Environmental driver	Sea surface irradiance	Inshore and offshore zones	-0.2820	0.3885	sig
Ecology model fitted	Maximum uptake rate	Suspension/deposit feeding benthos by demersal fish	-0.2768	0.5353	sig
Ecology model fixed	Maximum exploitable fraction of stock	Demersal fish	-0.2455	0.6674	ns
Ecology model fixed	Background metabolic rate coefficient	Demersal fish	-0.2383	0.7594	ns
Harvest ratio	Harvest ratio offshore	Planktivorous fish	-0.2030	0.3422	sig
Ecology model fixed	Saturation light intensity for uptake	Nutrient by phytoplankton	-0.1877	0.4417	ns
Ecology model fitted	Uptake half saturation coefficient	Nitrate by phytoplankton	-0.1652	0.3921	ns
Fishing fleet model	Discard rate offshore	Cetaceans	-0.1565	0.0606	sig
Ecology model fitted	Density dependent mortality coefficient	Planktivorous fish	-0.1539	0.3228	ns
Ecology model fitted	Maximum uptake rate	Demersal fish larvae by planktivorous fish	-0.1512	0.6352	ns
Ecology model fixed	Background metabolic rate coefficient	Omnivorous fish	-0.1432	0.5724	ns
Ecology model fixed	Assimilation efficiency	Carnivore/scavenge feeding benthos larvae	-0.1374	0.2896	ns
Ecology model fixed	Assimilation efficiency	Suspension/deposit feeding benthos	-0.1354	0.3077	ns
Ecology model fixed	Q10	Autotrophic uptake	-0.1324	0.5500	ns
Ecology model fixed	Q10	Heterotrophic uptake	-0.1261	0.6258	ns
Ecology model fixed	Assimilation efficiency	Birds	-0.1245	0.1072	sig
Ecology model fitted	Maximum uptake rate	Suspended detritus by suspension/deposit feeding benthos	-0.1171	0.2909	ns

Environmental driver	Temperature	Offshore zone upper layer	-0.1128	0.2390	ns
Ecology model fixed	Q10	Metabolism and microbial rates	-0.1067	0.2929	ns
Ecology model fitted	Maximum uptake rate	Ammonia by phytoplankton	-0.1044	0.2410	ns
Harvest ratio	Harvest ratio offshore	Demersal fish	-0.0922	0.4594	ns
Ecology model fixed	Assimilation efficiency	Cetaceans	-0.0886	0.1227	sig
Ecology model fixed	Q10 reference temperature	All temperature dependent processes	-0.0782	0.5721	ns
Ecology model fitted	Maximum uptake rate	Carnivore/scavenge feeding benthos larvae by omnivorous zooplankton	-0.0781	0.2155	ns
Ecology model fitted	Maximum uptake rate	Planktivorous fish by demersal fish	-0.0742	0.2196	ns
Environmental driver	Boundary concentration	Upper layer offshore nitrate	-0.0676	0.1609	ns
Ecology model fitted	Maximum uptake rate	Planktivorous fish by cetaceans	-0.0537	0.0890	sig
Environmental driver	Temperature	Inshore zone	-0.0536	0.1747	ns
Ecology model fitted	Maximum uptake rate	Suspended detritus by carnivore/scavenge feeding benthos larvae	-0.0523	0.1661	ns
Ecology model fitted	Uptake half saturation coefficient	Phytoplankton by carnivore/scavenge feeding benthos larvae	-0.0508	0.1693	ns
Environmental driver	Boundary volume inflow rate	Lower layer offshore	-0.0507	0.0945	sig
Fishing fleet model	Discard rate all areas	Demersal fish all areas	-0.0507	0.1473	ns
Physical configuration	Coefficient	Light attenuation coefficient vs SPM	-0.0504	0.2980	ns
Biological event driver	Recruitment rate	Demersal fish	-0.0486	0.4548	ns
Physical configuration	Vertical thickness	Benthic boundary feeding layer	-0.0482	0.1496	ns
Ecology model fitted	Maximum uptake rate	Planktivorous fish by birds	-0.0426	0.0407	sig
Ecology model fitted	Uptake half saturation coefficient	Suspension/deposit feeding benthos larvae by carnivorous zooplankton	-0.0359	0.1222	ns
Ecology model fitted	Uptake half saturation coefficient	Demersal fish larvae by carnivorous zooplankton	-0.0302	0.1166	ns
Ecology model fitted	Maximum uptake rate	Suspended detritus by suspension/deposit feeding benthos larvae	-0.0287	0.1948	ns
Ecology model fitted	Maximum uptake rate	Demersal fish by birds	-0.0285	0.0522	sig
Ecology model fitted	Uptake half saturation coefficient	Phytoplankton by suspension/deposit feeding benthos	-0.0285	0.0989	ns
Ecology model fixed	Assimilation efficiency	Suspension/deposit feeding benthos larvae	-0.0280	0.2451	ns
Environmental driver	Boundary concentration	Inshore nitrate	-0.0246	0.0955	ns
Physical configuration	Intercept	Light attenuation coefficient vs SPM	-0.0242	0.1534	ns
Ecology model fitted	Uptake half saturation coefficient	Suspended detritus by carnivore/scavenge feeding	-0.0240	0.0955	ns

		benthos larvae			
Environmental driver	River volume inflow rate	Inshore zone	-0.0208	0.0919	ns
Ecology model fitted	Maximum uptake rate	Carnivorous zooplankton by demersal fish	-0.0208	0.0845	ns
Ecology model fitted	Maximum uptake rate	Sediment detritus by suspension/deposit feeding benthos	-0.0203	0.0668	ns
Ecology model fixed	Assimilation efficiency	Pinnipeds	-0.0185	0.0229	sig
Environmental driver	Boundary concentration	River nitrate	-0.0178	0.0822	ns
Biological event driver	Recruitment rate	Suspension/deposit feeding benthos	-0.0176	0.0836	ns
Ecology model fitted	Remobilisation parameter	Refractory to labile sediment detritus	-0.0174	0.0584	ns
Ecology model fitted	Density dependent mortality coefficient	Carnivore/scavenge feeding benthos	-0.0169	0.0614	ns
Ecology model fitted	Maximum uptake rate	Suspension/deposit feeding benthos larvae by demersal fish larvae	-0.0168	0.0798	ns
Environmental driver	Boundary concentration	Lower layer ammonia	-0.0164	0.0295	sig
Environmental driver	Suspended particulate matter	Offshore zone	-0.0161	0.2115	ns
Ecology model fitted	Uptake half saturation coefficient	Ammonia by phytoplankton	-0.0159	0.1652	ns
Ecology model fitted	Uptake half saturation coefficient	Suspended detritus by suspension/deposit feeding benthos larvae	-0.0157	0.0797	ns
Ecology model fitted	Density dependent mortality coefficient	Cetaceans	-0.0152	0.0298	sig
Ecology model fixed	Background metabolic rate coefficient	Birds	-0.0150	0.1303	ns
Ecology model fitted	Maximum uptake rate	Demersal fish by cetaceans	-0.0147	0.0533	ns
Ecology model fitted	Maximum uptake rate	Planktivorous fish by pinnipeds	-0.0144	0.0333	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Carnivorous zooplankton offshore	-0.0144	0.1896	ns
Ecology model fitted	Maximum uptake rate	Phytoplankton by carnivore/scavenge feeding benthos larvae	-0.0140	0.2027	ns
Ecology model fitted	Density dependent mortality coefficient	Birds	-0.0138	0.0209	sig
Harvest ratio	Harvest ratio inshore	Planktivorous fish	-0.0136	0.0780	ns
Ecology model fixed	Assimilation efficiency	Carnivore/scavenge feeding benthos	-0.0136	0.0510	ns
Ecology model fitted	Maximum uptake rate	Planktivorous fish larvae by planktivorous fish	-0.0128	0.0853	ns
Environmental driver	Vertical diffusion rate	Offshore zone	0.0124	0.1352	ns
Ecology model fitted	Uptake half saturation coefficient	Suspension/deposit feeding benthos larvae by planktivorous fish	-0.0122	0.0857	ns
Ecology model fitted	Density dependent mortality coefficient	Phytoplankton lower layer	-0.0120	0.3328	ns

Ecology model fitted	Maximum uptake rate	Demersal fish larvae by carnivorous zooplankton	0.0119	0.1237	ns
Ecology model fitted	Coefficient	Macrophyte self shading	-0.0118	0.0105	sig
Environmental driver	Boundary concentration	Lower layer detritus	-0.0118	0.0375	ns
Environmental driver	Boundary volume inflow rate	Inshore zone	-0.0118	0.0568	ns
Ecology model fitted	Maximum uptake rate	Suspension/deposit feeding benthos larvae by carnivorous zooplankton	0.0115	0.1732	ns
Ecology model fitted	Maximum uptake rate	Suspension/deposit feeding benthos larvae by planktivorous fish	-0.0114	0.1047	ns
Ecology model fitted	Uptake half saturation coefficient	Carnivore/scavenge feeding benthos larvae by carnivorous zooplankton	-0.0112	0.0470	ns
Ecology model fixed	Background metabolic rate coefficient	Pinnipeds	-0.0110	0.0215	sig
Ecology model fixed	Background metabolic rate coefficient	Carnivore/scavenge feeding benthos larvae	-0.0109	0.0523	ns
Ecology model fitted	Density dependent mortality coefficient	Demersal fish	0.0106	0.3095	ns
Ecology model fitted	Uptake half saturation coefficient	Carnivorous zooplankton by demersal fish	0.0105	0.0646	ns
Ecology model fixed	Background metabolic rate coefficient	Suspension/deposit feeding benthos larvae	-0.0101	0.0463	ns
Harvest ratio	Harvest ratio offshore	Carnivorous zooplankton	-0.0098	0.0448	ns
Ecology model fixed	Maximum exploitable fraction of stock	Carnivorous zooplankton	-0.0098	0.0448	ns
Ecology model fitted	Maximum uptake rate	Carnivore/scavenge feeding benthos by demersal fish	-0.0097	0.0508	ns
Ecology model fitted	Bedding DeAngelis parameter	Cetaceans	0.0096	0.0923	ns
Fishing fleet model	Discard rate offshore	Demersal fish	0.0092	0.1057	ns
Ecology model fitted	Uptake half saturation coefficient	Demersal fish by birds	0.0091	0.0228	ns
Environmental driver	Temperature	Lower layer offshore	0.0089	0.0687	ns
Fishing fleet model	Coefficient	Demersal fish quota-limited undersize vs nitrogen mass	0.0088	0.1325	ns
Ecology model fitted	Uptake half saturation coefficient	Suspension/deposit feeding benthos larvae by demersal fish larvae	0.0084	0.0661	ns
Ecology model fixed	Background metabolic rate coefficient	Cetaceans	0.0079	0.1323	ns
Ecology model fitted	Nitrification rate coefficient	Lower layer ammonia	-0.0078	0.0548	ns
Ecology model fixed	Maximum exploitable fraction of stock	Cetaceans	-0.0077	0.0134	sig
Ecology model fitted	Maximum uptake rate	Carnivore/scavenge feeding benthos larvae by carnivorous zooplankton	0.0077	0.0574	ns
Ecology model fitted	Uptake half saturation coefficient	demersal fish larvae by demersal fish	-0.0075	0.0326	ns
Ecology model fitted	Sinking rate coefficient	Upper layer suspended detritus	-0.0073	0.0445	ns
Ecology model fitted	Uptake half saturation coefficient	Planktivorous fish larvae by planktivorous fish	-0.0073	0.0830	ns

Ecology model fitted	Uptake half saturation coefficient	Omnivorous zooplankton by planktivorous fish larvae	-0.0072	0.0532	ns
Ecology model fitted	Maximum uptake rate	Carnivorous zooplankton by birds	-0.0072	0.0108	sig
Ecology model fitted	Bedding DeAngelis parameter	Birds	0.0072	0.0615	ns
Ecology model fitted	Maximum uptake rate	demersal fish larvae by demersal fish	0.0071	0.0364	ns
Harvest ratio	Harvest ratio offshore	Cetaceans	-0.0069	0.0119	sig
Fishing fleet model	Discard rate inshore	Demersal fish	0.0064	0.0476	ns
Ecology model fitted	Uptake half saturation coefficient	Carnivore/scavenge feeding benthos larvae by planktivorous fish	-0.0064	0.0598	ns
Ecology model fitted	Uptake half saturation coefficient	Demersal fish by pinnipeds	-0.0061	0.0119	sig
Ecology model fitted	Scaling parameter	Linking demersal fish survey and model abundance	0.0060	0.0296	ns
Environmental driver	Boundary concentration	Upper layer offshore phytoplankton	-0.0060	0.0276	ns
Environmental driver	Volume outflow rate	Inshore zone	-0.0059	0.0262	ns
Ecology model fitted	Uptake half saturation coefficient	Planktivorous fish by cetaceans	0.0059	0.0251	ns
Ecology model fitted	Maximum uptake rate	Migratory fish by cetaceans	-0.0054	0.0115	ns
Environmental driver	Boundary concentration	Upper layer offshore detritus	-0.0054	0.0183	ns
Environmental driver	Boundary concentration	Inshore phytoplankton	-0.0052	0.0273	ns
Fishing fleet model	Exponent	Demersal fish quota-limited undersize vs nitrogen mass	-0.0052	0.0214	ns
Ecology model fitted	Density dependent mortality coefficient	Suspension/deposit feeding benthos	0.0052	0.1595	ns
Ecology model fitted	Uptake half saturation coefficient	Carnivore/scavenge feeding benthos by demersal fish	0.0051	0.0370	ns
Biological event driver	Immigration rate	Migratory fish	-0.0050	0.0075	sig
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Cetaceans inshore	0.0047	0.0189	ns
Environmental driver	Boundary concentration	Upper layer offshore ammonia	-0.0047	0.0106	ns
Ecology model fitted	Bedding DeAngelis parameter	Pinnipeds	-0.0046	0.0129	ns
Ecology model fitted	Uptake half saturation coefficient	Planktivorous fish by birds	0.0045	0.0184	ns
Physical configuration	Hydraulic conductivity	Offshore muddy sediments	-0.0045	0.0100	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Cetaceans offshore	0.0045	0.0101	ns
Ecology model fitted	Conversion rate coefficient	Labile to refractory sediment detritus	0.0044	0.0942	ns
Ecology model fitted	Maximum uptake rate	Suspension/deposit feeding benthos by carnivore/scavenge feeding benthos	-0.0044	0.0859	ns
Ecology model fitted	Uptake half saturation coefficient	Suspension/deposit feeding benthos by demersal fish	0.0044	0.2188	ns

Ecology model fitted	Uptake half saturation coefficient	Suspended detritus by suspension/deposit feeding benthos	0.0043	0.1376	ns
Ecology model fitted	Maximum uptake rate	Carnivore/scavenge feeding benthos larvae by planktivorous fish	-0.0043	0.0675	ns
Ecology model fitted	Maximum uptake rate	Planktivorous fish larvae by demersal fish	-0.0042	0.0259	ns
Ecology model fitted	Maximum uptake rate	Phytoplankton by suspension/deposit feeding benthos	-0.0041	0.1161	ns
Biological event driver	Spawning rate	Suspension/deposit feeding benthos	0.0039	0.0529	ns
Ecology model fixed	Annual fecundity	Suspension/deposit feeding benthos	0.0039	0.0529	ns
Environmental driver	Boundary concentration	Inshore detritus	-0.0036	0.0149	ns
Ecology model fitted	Maximum uptake rate	Corpses by birds	-0.0036	0.0064	sig
Ecology model fitted	Uptake half saturation coefficient	Planktivorous fish by pinnipeds	0.0035	0.0176	ns
Physical configuration	Proportion of depth range occupied	Phytoplankton inshore	0.0033	0.0904	ns
Ecology model fitted	Density dependent mortality coefficient	Suspension/deposit feeding benthos larvae	-0.0032	0.0166	ns
Ecology model fitted	Uptake half saturation coefficient	Suspension/deposit feeding benthos by carnivore/scavenge feeding benthos	-0.0031	0.0194	ns
Fishing fleet model	Coefficient	Demersal fish non-quota undersize vs nitrogen mass	0.0030	0.0223	ns
Ecology model fitted	Disintigration rate	Macrophyte debris to detritus	-0.0030	0.0078	ns
Environmental driver	Significant wave height	Inshore zone	0.0029	0.0157	ns
Biological event driver	Spawning rate	Carnivore/scavenge feeding benthos	-0.0029	0.0523	ns
Ecology model fixed	Annual fecundity	Carnivore/scavenge feeding benthos	-0.0029	0.0523	ns
Fishing fleet model	Discard rate inshore	Carnivore/scavenge feeding benthos	-0.0028	0.0051	sig
Ecology model fitted	Conversion rate	Macrophyte debris to beach-cast	0.0028	0.0079	ns
Ecology model fitted	Uptake half saturation coefficient	Migratory fish by pinnipeds	-0.0027	0.0044	sig
Physical configuration	Sediment porosity	Offshore sandy sediments	-0.0027	0.0274	ns
Environmental driver	Boundary concentration	Lower layer phytoplankton	-0.0027	0.0152	ns
Ecology model fitted	Uptake half saturation coefficient	Planktivorous fish larvae by demersal fish	0.0026	0.0240	ns
Environmental driver	Boundary concentration	River ammonia	-0.0026	0.0134	ns
Ecology model fitted	Uptake half saturation coefficient	Demersal fish by cetaceans	0.0025	0.0154	ns
Environmental driver	Suspended particulate matter	Inshore zone	0.0025	0.0850	ns
Ecology model fixed	Inedible biomass inshore	Carnivorous zooplankton	0.0025	0.0207	ns
Ecology model fixed	Saturation light intensity for uptake	Nutrient by macrophytes	-0.0024	0.0046	sig

Ecology model fixed	Maximum exploitable fraction of stock	Carnivore/scavenge feeding benthos	0.0024	0.0122	ns
Fishing fleet model	Discard rate inshore	Cetaceans	-0.0024	0.0035	sig
Ecology model fitted	Maximum uptake rate	Migratory fish by pinnipeds	0.0023	0.0083	ns
Biological event driver	Emigration rate	Migratory fish	-0.0023	0.0066	ns
Ecology model fitted	Denitrification rate coefficient	Sediment porewater nitrate	-0.0023	0.0654	ns
Environmental driver	Volume exchange rate	Offshore to inshore zone	-0.0021	0.0108	ns
Harvest ratio	Harvest ratio offshore	Carnivore/scavenge feeding benthos	0.0021	0.0073	ns
Ecology model fitted	Uptake half saturation coefficient	Carnivorous zooplankton by birds&mammala	0.0021	0.0049	ns
Ecology model fitted	Mineralistation rate scaling parameter	Refractory sediment detritus	-0.0020	0.0079	ns
Ecology model fitted	Maximum uptake rate	Demersal fish by demersal fish	0.0020	0.0090	ns
Ecology model fitted	Conversion rate coefficient	Corpses to labile sediment detritus	0.0019	0.0079	ns
Ecology model fitted	Density dependent mortality coefficient	Pinnipeds	-0.0019	0.0066	ns
Physical configuration	Proportion of depth range occupied	Macrophytes inshore	-0.0018	0.0039	ns
Ecology model fixed	Background metabolic rate coefficient	Carnivore/scavenge feeding benthos	-0.0018	0.0107	ns
Ecology model fixed	Assimilation efficiency	Planktivorous fish larvae	-0.0017	0.0839	ns
Environmental driver	Boundary concentration	Inshore ammonia	-0.0017	0.0087	ns
Ecology model fitted	Uptake half saturation coefficient	Omnivorous zooplankton by migratory fish	-0.0017	0.0049	ns
Ecology model fitted	Maximum uptake rate	Migratory fish by birds	-0.0017	0.0014	sig
Fishing fleet model	Damage mortality rate by fishing gears	Suspension/deposit feeding benthos offshore	0.0017	0.0105	ns
Ecology model fitted	Maximum uptake rate	Omnivorous zooplankton by planktivorous fish larvae	0.0017	0.0595	ns
Ecology model fitted	Maximum uptake rate	Carnivore/scavenge feeding benthos larvae by demersal fish larvae	-0.0016	0.0104	ns
Ecology model fitted	Maximum uptake rate	Omnivorous zooplankton by migratory fish	0.0016	0.0047	ns
Harvest ratio	Harvest ratio inshore	Carnivore/scavenge feeding benthos	0.0016	0.0046	ns
Ecology model fitted	Mineralisation rate coefficient	Labile sediment detritus	0.0015	0.0175	ns
Ecology model fitted	Maximum uptake rate	Planktivorous fish larvae by carnivorous zooplankton	-0.0015	0.0222	ns
Ecology model fitted	Uptake half saturation coefficient	Carnivore/scavenge feeding benthos larvae by demersal fish larvae	0.0015	0.0094	ns
Fishing fleet model	Damage mortality rate by fishing gears	Carnivore/scavenge feeding benthos offshore	-0.0014	0.0097	ns
Physical configuration	Vertical thickness	Inshore zone	-0.0014	0.2522	ns
Ecology model fitted	Uptake half saturation coefficient	Demersal fish by demersal fish	-0.0014	0.0066	ns

Ecology model fixed	Background metabolic rate coefficient	Demersal fish larvae	0.0014	0.0087	ns
Ecology model fitted	Active migration coefficient	Planktivorous fish	-0.0014	0.0122	ns
Environmental driver	Boundary volume inflow rate	Inshore zone	-0.0014	0.0130	ns
Fishing fleet model	Coefficient	Demersal fish non-quota proportion in catch vs nitrogen mass	0.0013	0.0090	ns
Ecology model fitted	Uptake half saturation coefficient	Migratory fish by cetaceans	0.0012	0.0040	ns
Ecology model fitted	Uptake half saturation coefficient	Corpses by birds	0.0012	0.0029	ns
Ecology model fitted	Maximum uptake rate	Carnivorous zooplankton by cetaceans	-0.0011	0.0020	sig
Ecology model fitted	Maximum uptake rate	Omnivorous zooplankton by cetaceans	-0.0011	0.0028	ns
Biological event driver	Recruitment rate	Carnivore/scavenge feeding benthos	-0.0011	0.0097	ns
Fishing fleet model	Discard rate offshore	Carnivore/scavenge feeding benthos	-0.0011	0.0022	ns
Ecology model fitted	Maximum uptake rate	Suspension/deposit feeding benthos larvae by planktivorous fish larvae	0.0010	0.0174	ns
Ecology model fitted	Uptake half saturation coefficient	Suspension/deposit feeding benthos larvae by planktivorous fish larvae	-0.0010	0.0163	ns
Physical configuration	Hydraulic conductivity	Offshore sandy sediments	-0.0010	0.0104	ns
Ecology model fitted	Maximum uptake rate	Suspension/deposit feeding benthos larvae by omnivorous zooplankton	-0.0010	0.0051	ns
Ecology model fixed	Inedible biomass offshore	Carnivorous zooplankton	0.0010	0.0078	ns
Environmental driver	Atmospheric deposition rate	Inshore nitrate	-0.0009	0.0069	ns
Fishing fleet model	Exponent	Demersal fish non-quota proportion in catch vs nitrogen mass	-0.0009	0.0047	ns
Ecology model fitted	Uptake half saturation coefficient	Planktivorous fish larvae by carnivorous zooplankton	-0.0009	0.0217	ns
Environmental driver	Atmospheric deposition rate	Offshore nitrate	-0.0009	0.0057	ns
Ecology model fitted	Maximum uptake rate	Phytoplankton by suspension/deposit feeding benthos larvae	0.0009	0.0055	ns
Ecology model fixed	Assimilation efficiency	Migratory fish	0.0009	0.0019	ns
Ecology model fitted	Uptake half saturation coefficient	Suspension/deposit feeding benthos larvae by omnivorous zooplankton	0.0009	0.0046	ns
Biological event driver	Spawning rate	Planktivorous fish	-0.0009	0.0555	ns
Ecology model fixed	Annual fecundity	Planktivorous fish	-0.0009	0.0555	ns
Ecology model fixed	N:C molar ratio maximum	Macrophytes	-0.0009	0.0022	ns
Environmental driver	Atmospheric deposition rate	Inshore ammonia	-0.0009	0.0045	ns
Ecology model fitted	Active migration coefficient	Demersal fish	-0.0008	0.0035	ns

Ecology model fitted	Maximum uptake rate	Discards by birds	0.0008	0.0023	ns
Environmental driver	Atmospheric deposition rate	Offshore ammonia	-0.0008	0.0024	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Demersal fish offshore	-0.0008	0.0065	ns
Ecology model fitted	Uptake half saturation coefficient	Phytoplankton by suspension/deposit feeding benthos larvae	-0.0008	0.0044	ns
Physical configuration	Sediment porosity	Offshore muddy sediments	-0.0008	0.0010	sig
Harvest ratio	Harvest ratio inshore	Cetaceans	-0.0008	0.0016	ns
Ecology model fixed	Maximum exploitable fraction of stock	Migratory fish	-0.0008	0.0019	ns
Ecology model fixed	Background metabolic rate coefficient	Suspension/deposit feeding benthos	0.0007	0.1025	ns
Harvest ratio	Harvest ratio offshore	Migratory fish	-0.0007	0.0019	ns
Ecology model fitted	Maximum uptake rate	Demersal fish by pinnipeds	0.0007	0.0246	ns
Ecology model fitted	Uptake half saturation coefficient	Suspended detritus by omnivorous zooplankton	0.0007	0.0035	ns
Ecology model fixed	Maximum exploitable fraction of stock	Suspension/deposit feeding benthos	-0.0007	0.0007	sig
Physical configuration	Sediment porosity	Inshore sandy sediments	0.0007	0.0298	ns
Environmental driver	Natural disturbance rate	Offshore muddy sediments	-0.0007	0.0019	ns
Physical configuration	Physical disturbance depth	Offshore muddy sediments	-0.0007	0.0019	ns
Fishing fleet model	Exponent	Demersal fish non-quota undersize vs nitrogen mass	-0.0006	0.0034	ns
Harvest ratio	Harvest ratio inshore	Demersal fish	-0.0006	0.2241	ns
Biological event driver	Recruitment rate	Planktivorous fish	-0.0006	0.0029	ns
Ecology model fitted	Maximum uptake rate	Corpses by demersal fish	-0.0006	0.0035	ns
Ecology model fitted	Uptake half saturation coefficient	Corpses by carnivore/scavenge feeding benthos	-0.0005	0.0072	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Demersal fish inshore	-0.0005	0.0035	ns
Ecology model fitted	Uptake half saturation coefficient	Corpses by demersal fish	0.0005	0.0028	ns
Environmental driver	Natural disturbance rate	Offshore sandy sediments	-0.0005	0.0025	ns
Ecology model fitted	Carbon exudation rate	Macrophytes	0.0005	0.0029	ns
Physical configuration	Physical disturbance depth	Offshore sandy sediments	-0.0005	0.0025	ns
Ecology model fitted	Uptake half saturation coefficient	Planktivorous fish by demersal fish	-0.0004	0.1338	ns
Ecology model fitted	Uptake half saturation coefficient	Discards by demersal fish	0.0004	0.0018	ns
Ecology model fitted	Uptake half saturation coefficient	Carnivore/scavenge feeding benthos larvae by omnivorous zooplankton	-0.0004	0.2045	ns

Ecology model fitted	Maximum uptake rate	Discards by demersal fish	-0.0004	0.0019	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Carnivore/scavenge feeding benthos inshore	-0.0004	0.0008	ns
Ecology model fitted	Uptake half saturation coefficient	Migratory fish by demersal fish	0.0004	0.0020	ns
Physical configuration	Sediment porosity	Inshore coarse sediments	0.0003	0.0108	ns
Ecology model fitted	Maximum uptake rate	Suspended detritus by omnivorous zooplankton	-0.0003	0.0023	ns
Ecology model fitted	Maximum uptake rate	Corpses by carnivore/scavenge feeding benthos	-0.0003	0.0113	ns
Ecology model fitted	Maximum uptake rate	Carbon by macrophytes	-0.0003	0.0053	ns
Ecology model fitted	Maximum uptake rate	Migratory fish by demersal fish	-0.0003	0.0021	ns
Ecology model fitted	Uptake half saturation coefficient	Carnivorous zooplankton by cetaceans	0.0003	0.0006	sig
Ecology model fitted	Uptake half saturation coefficient	Discards by birds	-0.0003	0.0010	ns
Ecology model fitted	Uptake half saturation coefficient	Carnivorous zooplankton by migratory fish	0.0003	0.0017	ns
Ecology model fitted	Maximum uptake rate	Carnivorous zooplankton by migratory fish	-0.0003	0.0018	ns
Ecology model fitted	Uptake half saturation coefficient	Migratory fish by birds	-0.0003	0.0006	ns
Ecology model fitted	Maximum uptake rate	Carnivore/scavenge feeding benthos larvae by planktivorous fish larvae	0.0003	0.0035	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Carnivore/scavenge feeding benthos offshore	-0.0002	0.0006	ns
Ecology model fitted	Uptake half saturation coefficient	Omnivorous zooplankton by cetaceans	0.0002	0.0007	ns
Harvest ratio	Harvest ratio offshore	Suspension/deposit feeding benthos	-0.0002	0.0004	sig
Ecology model fitted	Conversion rate coefficient	Discards to corpses	-0.0002	0.0028	ns
Fishing fleet model	Damage mortality rate by fishing gears	Carnivore/scavenge feeding benthos inshore	-0.0002	0.0093	ns
Fishing fleet model	Abrasion rate by fishing gears	Offshore muddy sediments	-0.0002	0.0006	ns
Ecology model fitted	Density dependent mortality coefficient	Omnivorous zooplankton	-0.0002	0.0273	ns
Fishing fleet model	Penetration depth by fishing gears	Offshore muddy sediments	-0.0002	0.0005	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Suspension/deposit feeding benthos offshore	-0.0002	0.0002	sig
Ecology model fitted	Active migration coefficient	Cetaceans	0.0002	0.0004	ns
Physical configuration	Physical disturbance depth	Inshore sandy sediments	-0.0002	0.0005	ns
Environmental driver	Natural disturbance rate	Inshore sandy sediments	-0.0002	0.0005	ns
Ecology model fitted	Maximum uptake rate	Demersal fish larvae by migratory fish	0.0002	0.0008	ns
Ecology model fixed	Background metabolic rate coefficient	Planktivorous fish larvae	-0.0001	0.0023	ns

Ecology model fitted	Maximum uptake rate	Discards by cetaceans	-0.0001	0.0003	ns
Ecology model fitted	Uptake half saturation coefficient	Demersal fish larvae by migratory fish	-0.0001	0.0008	ns
Ecology model fitted	Uptake half saturation coefficient	Carnivore/scavenge feeding benthos larvae by planktivorous fish larvae	-0.0001	0.0033	ns
Ecology model fitted	Density dependent mortality coefficient	Demersal fish larvae	0.0001	0.0005	ns
Ecology model fitted	Wave height dependent conversion rate	Macrophytes to macrophyte debris	0.0001	0.0078	ns
Physical configuration	Sediment porosity	Offshore coarse sediments	-0.0001	0.0024	ns
Physical configuration	Hydraulic conductivity	Inshore muddy sediments	-0.0001	0.0004	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Planktivorous fish offshore	0.0001	0.0014	ns
Fishing fleet model	Damage mortality rate by fishing gears	Suspension/deposit feeding benthos inshore	0.0001	0.0029	ns
Ecology model fitted	Maximum uptake rate	Planktivorous fish larvae by migratory fish	-0.0001	0.0016	ns
Ecology model fitted	Uptake half saturation coefficient	Nitrate by macrophytes	-0.0001	0.0008	ns
Ecology model fixed	Maximum exploitable fraction of stock	Pinnipeds	-0.0001	0.0005	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Suspension/deposit feeding benthos inshore	-0.0001	0.0001	sig
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Planktivorous fish inshore	0.0001	0.0008	ns
Ecology model fitted	Maximum uptake rate	Nitate by macrophytes	0.0001	0.0010	ns
Physical configuration	Hydraulic conductivity	Inshore sandy sediments	0.0001	0.0054	ns
Physical configuration	Hydraulic conductivity	Inshore coarse sediments	0.0001	0.0007	ns
Ecology model fitted	Uptake half saturation coefficient	Planktivorous fish larvae by migratory fish	0.0001	0.0016	ns
Fishing fleet model	Penetration depth by fishing gears	Offshore sandy sediments	-0.0001	0.0003	ns
Fishing fleet model	Abrasion rate by fishing gears	Offshore sandy sediments	-0.0001	0.0002	ns
Ecology model fitted	Maximum uptake rate	Ammonia by macrophytes	5.02E-05	4.29E-04	ns
Ecology model fitted	Active migration coefficient	Birds	-4.98E-05	1.53E-04	ns
Harvest ratio	Harvest ratio inshore	Pinnipeds	-4.96E-05	3.39E-04	ns
Ecology model fixed	Background metabolic rate coefficient	Migratory fish	-4.59E-05	4.07E-04	ns
Ecology model fitted	Density dependent mortality coefficient	Planktivorous fish larvae	-4.50E-05	1.19E-03	ns
Ecology model fitted	Uptake half saturation coefficient	Ammonia by macrophytes	-4.24E-05	3.59E-04	ns
Ecology model fitted	Uptake half saturation coefficient	Discards by cetaceans	3.93E-05	1.10E-04	ns
Ecology model fitted	Maximum uptake rate	Corpses by pinnipeds	3.55E-05	7.03E-04	ns

Ecology model fixed	N:C molar ratio minimum	Macrophytes	-3.41E-05	1.10E-04	ns
Ecology model fitted	Density dependent mortality coefficient	Carnivore/scavenge feeding benthos larvae	-2.77E-05	3.11E-04	ns
Fishing fleet model	Processing at sea rate offshore	Demersal fish	2.68E-05	1.07E-04	ns
Harvest ratio	Harvest ratio offshore	Pinnipeds	-2.67E-05	1.72E-04	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Birds inshore	2.37E-05	3.22E-05	sig
Ecology model fitted	Density dependent mortality coefficient	Migratory fish	2.35E-05	3.07E-05	sig
Fishing fleet model	Offal as proportion of live weight	All guilds	2.31E-05	1.75E-04	ns
Ecology model fitted	Maximum uptake rate	Carnivore/scavenge feeding benthos larvae by migratory fish	2.02E-05	8.65E-05	ns
Ecology model fitted	Active migration coefficient	Migratory fish	-2.00E-05	1.25E-04	ns
Harvest ratio	Harvest ratio inshore	Migratory fish	1.99E-05	5.28E-05	ns
Ecology model fitted	Maximum uptake rate	Suspension/deposit feeding benthos larvae by migratory fish	1.94E-05	1.45E-04	ns
Physical configuration	Physical disturbance depth	Offshore coarse sediments	1.91E-05	3.28E-05	sig
Fishing fleet model	Processing at sea rate offshore	Carnivore/scavenge feeding benthos	1.90E-05	4.57E-05	ns
Physical configuration	Bioturbation depth	Offshore coarse sediments	1.81E-05	3.83E-05	ns
Fishing fleet model	Penetration depth by fishing gears	Inshore muddy sediments	1.73E-05	3.83E-05	ns
Ecology model fitted	Nitrification rate coefficient	Upper layer ammonia	1.66E-05	4.60E-05	ns
Fishing fleet model	Discard rate offshore	Birds	1.65E-05	3.64E-05	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Migratory fish inshore	1.58E-05	3.64E-05	ns
Ecology model fitted	Uptake half saturation coefficient	Corpses by pinnipeds	-1.54E-05	3.74E-04	ns
Ecology model fitted	Mineralisation rate coefficient	Suspended detritus	-1.52E-05	7.56E-05	ns
Fishing fleet model	Discard rate inshore	Migratory fish	1.49E-05	4.18E-05	ns
Ecology model fitted	Uptake half saturation coefficient	Sediment detritus by suspension/deposit feeding benthos	1.44E-05	3.66E-05	ns
Fishing fleet model	Processing at sea rate inshore	Carnivore/scavenge feeding benthos	1.43E-05	4.35E-05	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Pinnipeds inshore	1.42E-05	8.27E-05	ns
Physical configuration	Bioturbation depth	Inshore sandy sediments	1.42E-05	5.27E-05	ns
Physical configuration	Bioturbation depth	Offshore sandy sediments	1.38E-05	3.93E-05	ns
Fishing fleet model	Penetration depth by fishing gears	Inshore sandy sediments	-1.37E-05	5.57E-05	ns

Fishing fleet model	Penetration depth by fishing gears	Inshore coarse sediments	1.34E-05	3.66E-05	ns
Physical configuration	Physical disturbance depth	Inshore coarse sediments	1.33E-05	5.51E-05	ns
Fishing fleet model	Discard rate inshore	Planktivorous fish	1.32E-05	7.01E-05	ns
Harvest ratio	Harvest ratio inshore	Suspension/deposit feeding benthos	-1.30E-05	2.37E-04	ns
Fishing fleet model	Discard rate inshore	Pinnipeds	1.26E-05	5.34E-05	ns
Ecology model fitted	Mineralisation rate sensitivity to grain size	Labile sediment detritus	1.18E-05	4.13E-05	ns
Ecology model fixed	Maximum exploitable fraction of stock	Birds	-1.18E-05	3.82E-05	ns
Fishing fleet model	Abrasion rate by fishing gears	Inshore sandy sediments	-1.14E-05	4.56E-05	ns
Ecology model fitted	Uptake half saturation coefficient	Pinnipeds by cetaceans	1.11E-05	4.35E-05	ns
Fishing fleet model	Discard rate offshore	Suspension/deposit feeding benthos	1.11E-05	4.38E-05	ns
Fishing fleet model	Discard rate offshore	Pinnipeds	1.09E-05	4.25E-05	ns
Ecology model fitted	Uptake half saturation coefficient	Macrophyte debris by carnivorous/scavenge feeding benthos	9.76E-06	4.15E-05	ns
Harvest ratio	Harvest ratio offshore	Birds	-9.69E-06	5.88E-05	ns
Physical configuration	Bioturbation depth	Inshore muddy sediments	9.57E-06	3.69E-05	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Pinnipeds offshore	8.64E-06	4.99E-05	ns
Physical configuration	Hydraulic conductivity	Offshore coarse sediments	8.61E-06	1.85E-04	ns
Fishing fleet model	Discard rate inshore	Suspension/deposit feeding benthos	8.55E-06	4.50E-05	ns
Ecology model fitted	Denitrification rate coefficient	Lower layer nitrate	8.42E-06	5.55E-05	ns
Fishing fleet model	Abrasion rate by fishing gears	Offshore rock	7.86E-06	3.60E-05	ns
Physical configuration	Bioturbation depth	Inshore coarse sediments	7.25E-06	3.17E-05	ns
Physical configuration	Physical disturbance depth	Inshore muddy sediments	7.00E-06	5.78E-05	ns
Environmental driver	Natural disturbance rate	Offshore coarse sediments	6.99E-06	4.29E-05	ns
Ecology model fitted	Maximum uptake rate	Macrophytes by carnivorous/scavenge feeding benthos	6.92E-06	5.06E-05	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Migratory fish offshore	6.89E-06	1.14E-04	ns
Ecology model fitted	Sinking rate coefficient	Lower layer suspended detritus	6.89E-06	3.02E-05	ns
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Birds offshore	6.51E-06	3.34E-05	ns
Physical configuration	Hydraulic conductivity	Reference value for sediment-dependent processes	6.48E-06	5.84E-05	ns
Ecology model fitted	Maximum uptake rate	Discards by pinnipeds	6.25E-06	5.45E-05	ns

Ecology model fitted	Uptake half saturation coefficient	Carnivore/scavenge feeding benthos larvae by migratory fish	5.88E-06	1.21E-04	ns
Fishing fleet model	Processing at sea rate inshore	Demersal fish	5.69E-06	8.41E-05	ns
Fishing fleet model	Abrasion rate by fishing gears	Inshore coarse sediments	5.62E-06	5.55E-05	ns
Physical configuration	Bioturbation depth	Offshore muddy sediments	-5.61E-06	4.40E-05	ns
Fishing fleet model	Discard rate offshore	Migratory fish	5.33E-06	3.73E-04	ns
Ecology model fitted	Maximum uptake rate	Macrophyte debris by carnivorous/scavenge feeding benthos	5.18E-06	4.34E-05	ns
Ecology model fitted	Maximum uptake rate	Pinnipeds by cetaceans	5.09E-06	9.28E-05	ns
Fishing fleet model	Abrasion rate by fishing gears	Inshore rock	4.97E-06	4.93E-05	ns
Environmental driver	Natural disturbance rate	Inshore muddy sediments	4.80E-06	5.55E-05	ns
Harvest ratio	Harvest ratio inshore	Birds	-4.45E-06	5.67E-05	ns
Ecology model fitted	Denitrification rate coefficient	Upper layer nitrate	3.77E-06	3.55E-05	ns
Ecology model fitted	Uptake half saturation coefficient	Macrophytes by carnivorous/scavenge feeding benthos	2.91E-06	4.44E-05	ns
Ecology model fitted	Uptake half saturation coefficient	Discards by pinnipeds	2.08E-06	3.02E-05	ns
Fishing fleet model	Discard rate inshore	Birds	2.03E-06	3.25E-05	ns
Physical configuration	Sediment porosity	Inshore muddy sediments	-2.03E-06	2.41E-04	ns
Fishing fleet model	Penetration depth by fishing gears	Offshore coarse sediments	1.87E-06	4.57E-05	ns
Ecology model fitted	Nitrification rate coefficient	Sediment porewater ammonia	1.82E-06	3.52E-05	ns
Ecology model fitted	Active migration coefficient	Pinnipeds	-1.78E-06	6.08E-05	ns
Fishing fleet model	Discard rate offshore	Planktivorous fish	1.67E-06	5.53E-04	ns
Fishing fleet model	Abrasion rate by fishing gears	Inshore muddy sediments	1.57E-06	3.47E-05	ns
Fishing fleet model	Abrasion rate by fishing gears	Offshore coarse sediments	-1.52E-06	5.79E-05	ns
Ecology model fitted	Uptake half saturation coefficient	Suspension/deposit feeding benthos larvae by migratory fish	-1.37E-06	1.57E-04	ns
Ecology model fitted	Nitrification rate sensitivity to grain size	Sediment porewater ammonia	1.30E-06	3.39E-05	ns
Ecology model fitted	Denitrification rate sensitivity to grain size	Sediment porewater nitrate	-1.25E-06	5.42E-05	ns
Environmental driver	Natural disturbance rate	Inshore coarse sediments	2.63E-07	3.11E-05	ns
Environmental driver	Volume outflow rate	Offshore surface	NA	NA	NA
Environmental driver	Volume outflow rate	Lower layer offshore	NA	NA	NA
Environmental driver	Volume exchange rate	Inshore to offshore zone	NA	NA	NA

Environmental driver	Upwelling rate	Offshore zone	NA	NA	NA
Environmental driver	Boundary concentration	River detritus	NA	NA	NA
Harvest ratio	Harvest ratio inshore	Carnivorous zooplankton	NA	NA	NA
Harvest ratio	Harvest ratio inshore	Macrophytes	NA	NA	NA
Harvest ratio	Harvest ratio offshore	Macrophytes	NA	NA	NA
Fishing fleet model	Discard rate inshore	Carnivorous zooplankton	NA	NA	NA
Fishing fleet model	Discard rate offshore	Carnivorous zooplankton	NA	NA	NA
Fishing fleet model	Discard rate inshore	Macrophytes	NA	NA	NA
Fishing fleet model	Discard rate offshore	Macrophytes	NA	NA	NA
Fishing fleet model	Processing at sea rate inshore	Planktivorous fish	NA	NA	NA
Fishing fleet model	Processing at sea rate offshore	Planktivorous fish	NA	NA	NA
Fishing fleet model	Processing at sea rate inshore	Migratory fish	NA	NA	NA
Fishing fleet model	Processing at sea rate offshore	Migratory fish	NA	NA	NA
Fishing fleet model	Processing at sea rate inshore	Suspension/deposit feeding benthos	NA	NA	NA
Fishing fleet model	Processing at sea rate offshore	Suspension/deposit feeding benthos	NA	NA	NA
Fishing fleet model	Processing at sea rate inshore	Carnivorous zooplankton	NA	NA	NA
Fishing fleet model	Processing at sea rate offshore	Carnivorous zooplankton	NA	NA	NA
Fishing fleet model	Processing at sea rate inshore	Birds	NA	NA	NA
Fishing fleet model	Processing at sea rate offshore	Birds	NA	NA	NA
Fishing fleet model	Processing at sea rate inshore	Pinnipeds	NA	NA	NA
Fishing fleet model	Processing at sea rate offshore	Pinnipeds	NA	NA	NA
Fishing fleet model	Processing at sea rate inshore	Cetaceans	NA	NA	NA
Fishing fleet model	Processing at sea rate offshore	Cetaceans	NA	NA	NA
Fishing fleet model	Processing at sea rate inshore	Macrophytes	NA	NA	NA
Fishing fleet model	Processing at sea rate offshore	Macrophytes	NA	NA	NA
Fishing fleet model	Penetration depth by fishing gears	Inshore rock	NA	NA	NA
Fishing fleet model	Penetration depth by fishing gears	Offshore rock	NA	NA	NA
Ecology model fitted	Maximum uptake rate	Suspension/deposit feeding benthos by birds	NA	NA	NA
Ecology model fitted	Uptake half saturation coefficient	Suspension/deposit feeding benthos by birds	NA	NA	NA
Ecology model fitted	Maximum uptake rate	Carnivore/scavenge feeding benthos by birds	NA	NA	NA

Ecology model fitted	Uptake half saturation coefficient	Carnivore/scavenge feeding benthos by birds	NA	NA	NA
Ecology model fitted	Maximum uptake rate	Carnivorous zooplankton by pinnipeds	NA	NA	NA
Ecology model fitted	Uptake half saturation coefficient	Carnivorous zooplankton by pinnipeds	NA	NA	NA
Ecology model fitted	Maximum uptake rate	Suspension/deposit feeding benthos by pinnipeds	NA	NA	NA
Ecology model fitted	Uptake half saturation coefficient	Suspension/deposit feeding benthos by pinnipeds	NA	NA	NA
Ecology model fitted	Maximum uptake rate	Carnivore/scavenge feeding benthos by pinnipeds	NA	NA	NA
Ecology model fitted	Uptake half saturation coefficient	Carnivore/scavenge feeding benthos by pinnipeds	NA	NA	NA
Ecology model fitted	Maximum uptake rate	Birds by pinnipeds	NA	NA	NA
Ecology model fitted	Uptake half saturation coefficient	Birds by pinnipeds	NA	NA	NA
Ecology model fitted	Maximum uptake rate	Suspension/deposit feeding benthos by cetaceans	NA	NA	NA
Ecology model fitted	Uptake half saturation coefficient	Suspension/deposit feeding benthos by cetaceans	NA	NA	NA
Ecology model fitted	Maximum uptake rate	Carnivore/scavenge feeding benthos by cetaceans	NA	NA	NA
Ecology model fitted	Uptake half saturation coefficient	Carnivore/scavenge feeding benthos by cetaceans	NA	NA	NA
Ecology model fitted	Maximum uptake rate	Birds by cetaceans	NA	NA	NA
Ecology model fitted	Uptake half saturation coefficient	Birds by cetaceans	NA	NA	NA
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Carnivorous zooplankton inshore	NA	NA	NA
Ecology model fitted	Threshold biomass for zero exploitable stock remaining	Macrophytes inshore	NA	NA	NA
Ecology model fixed	Maximum exploitable fraction of stock	Macrophytes	NA	NA	NA

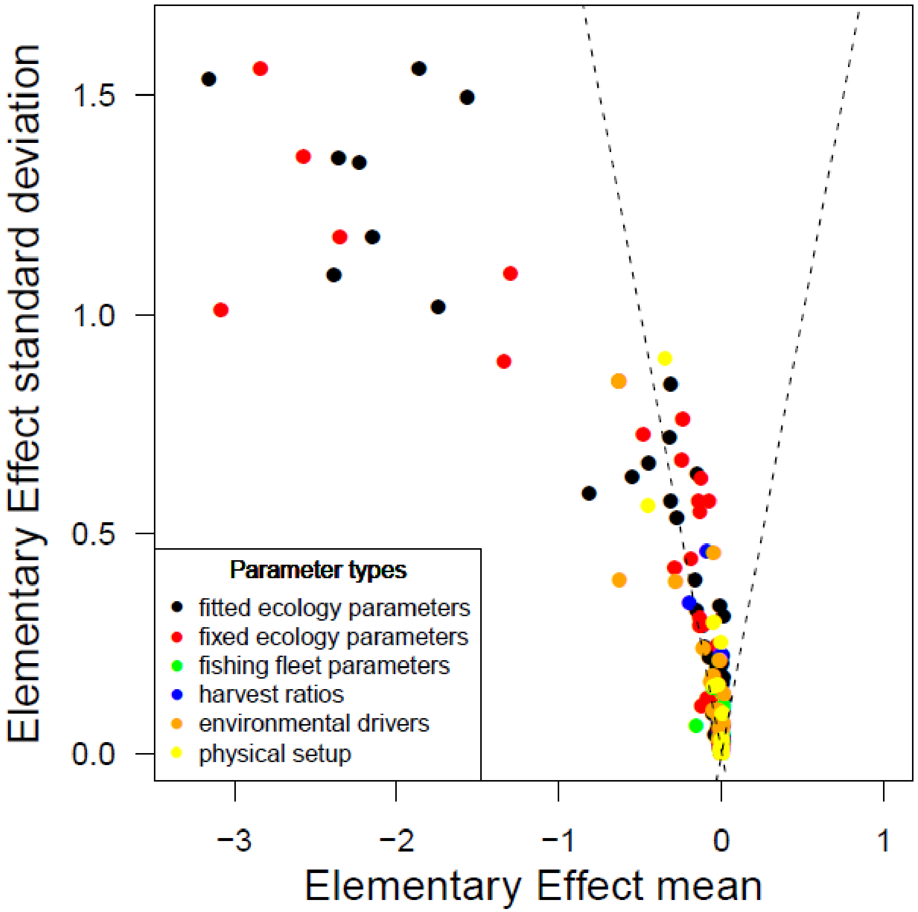

FIGURE 13 Means (EE_mean) and standard deviations (EE_sd) of the distributions of elementary effects of parameters in the sensitivity analysis of the 1970-1999 North Sea model. Black symbols indicate ecology model parameters which were optimized by simulated annealing; red symbols indicate the fixed parameters which were not optimized; green symbols indicate fishing fleet model parameters; blue symbols indicate harvest ratios; orange symbols indicate environmental and biological event drivers; yellow symbols indicate the physical setup parameters. The wedge formed by the two dashed lines corresponds to ±2 standard errors of the mean, so for points falling outside of the wedge there is a significant expectation that the distribution of elementary effects is non-zero. Drawn with the function e2e_plot_sens_mc().

Performance of the maximum likelihood fitted model

The data required to derive credible intervals around the maximum likelihood fitted model were generated by 1000 runs of the 1970-1999 model, each of 50 years. The parameters values for each run were drawn from symmetrical random uniform distributions around the maximum likelihood values with a bandwidth of ±15%.

Annual average biomass density in the model (mMN.m-2) varied by around 5 orders of magnitude across the guilds. Biomass density was higher in the offshore zone than the inshore for all guilds. In general, the uncertainty in annual average biomass increased with the trophic level of guilds (Figure 14).

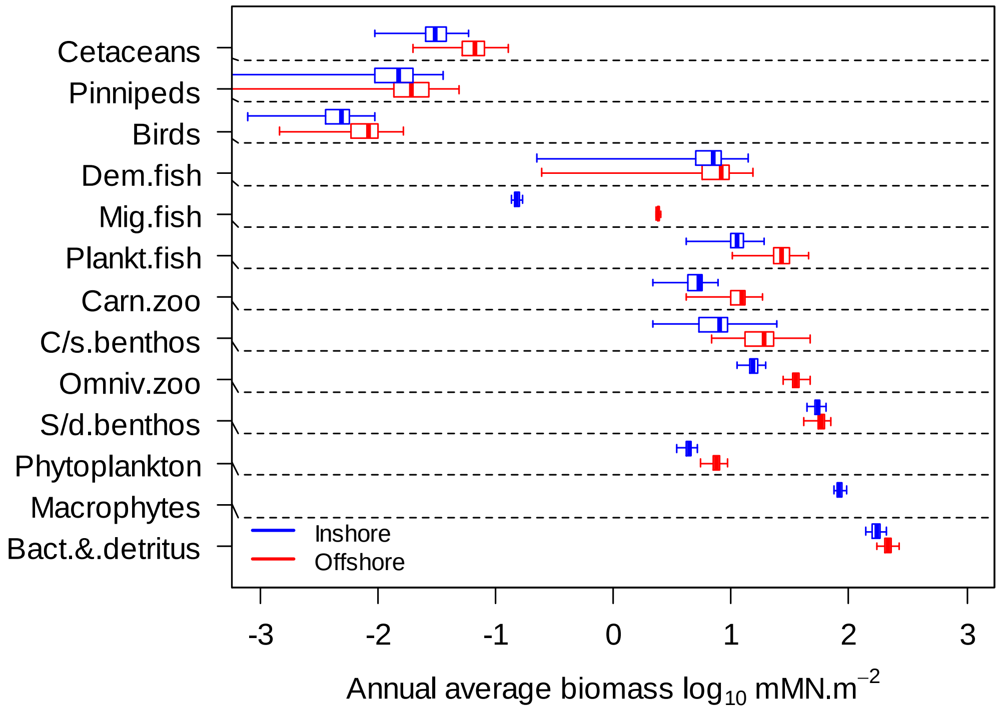

FIGURE 14 Credible intervals of the annual averaged values of living state variables in the model. X-axis shows $\log_{10}$ values of the average biomass density (mMN m^{-2}) over a stationary annual cycle for the 1970-1999 fitted model. Blue box-and-whisker plots refer to the

inshore/shallow zone, red to the offshore/deep zone. Whiskers span the 99% likelihood interval, boxes span 50%, and the central tick-mark indicates the median value. Drawn with the function e2e_plot_biomass().

Stationary annual cycles of the each of the model state variables and their credible intervals, with the maximum likelihood fitted parameter set, fixed parameters, and driving data corresponding to the 1970-1999 period, are shown in Figures 15-22.

The annual cycles of the fish and the birds & mammals guilds in the model show the effects of the dynamic, food-motivated active migrations (Figure 23). The primary driver for the feeding migrations is the timing of seasonal peaks of omnivorous and carnivorous zooplankton concentrations, which higher in the inshore zone than offshore during summer, and conversely higher offshore in winter. These gradients drive an inshore movement of fish in the spring and an offshore movement in winter. This in turn drives an inshore spring immigration of especially birds, and offshore winter movement.

For some of the nutrient and plankton variables in the model we have corresponding monthly averaged observational data from various sources, aggregated up to the scale of the whole model domain (i.e. combining both the inshore and offshore sub-domains). Comparison of the observed and modelled monthly averaged data is shown in Figure 24. This represents an independent qualitative test of the model performance. The results show some under-prediction of the biomass of omnivorous zooplankton and meroplankton (larvae of benthic taxa). However the overall agreement is good, particularly with respect to the timing of peaks in abundance.

Data generated by the NetIndices package showed that the certainty of mean trophic level of the living state variables in the whole domain was relatively high (i.e. narrow credible intervals), except for the birds guild. However, the omnivory index was more uncertain for all guilds especially the birds (Figure 25).

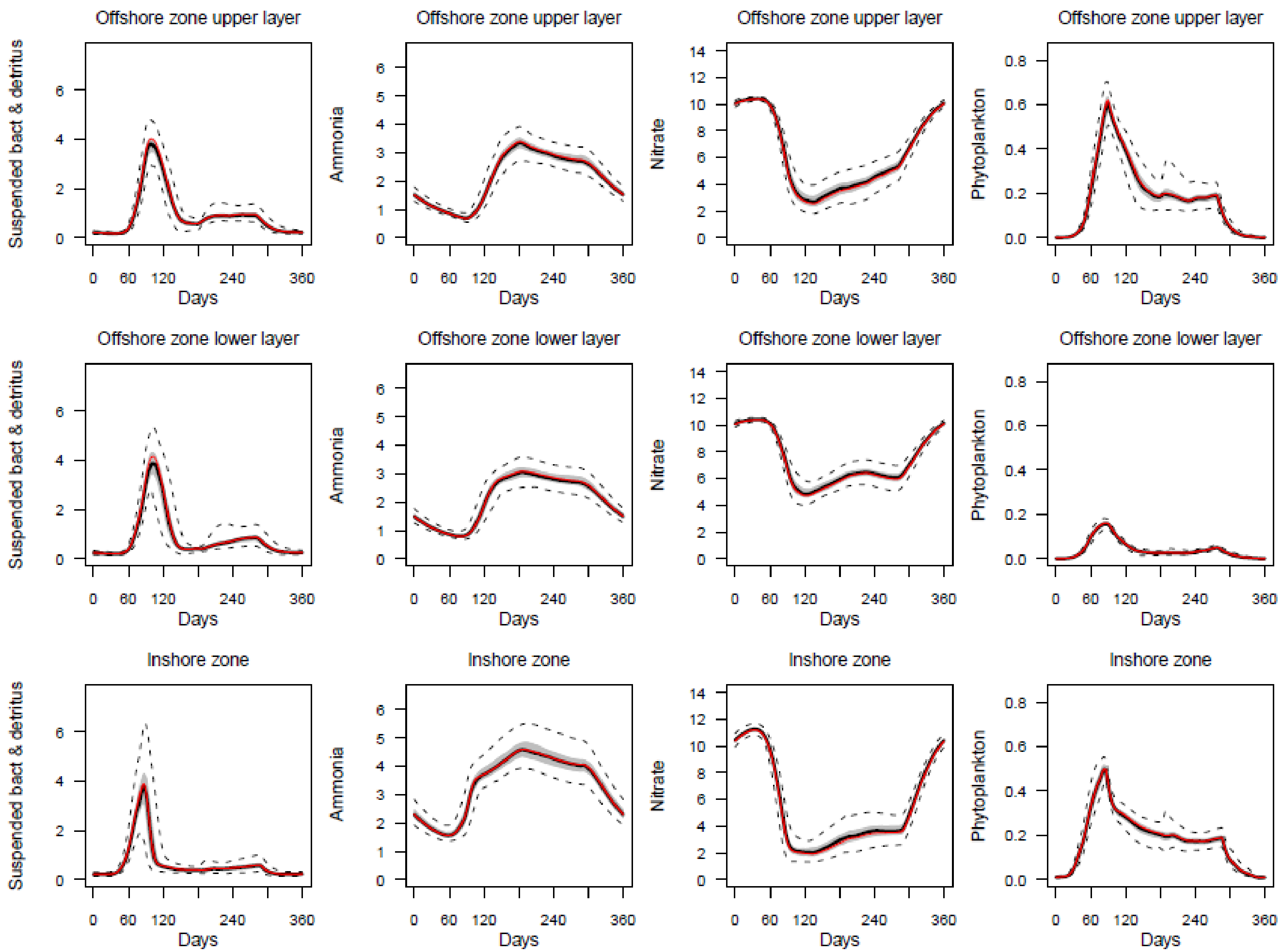

FIGURE 15 Stationary annual cycles of water column suspended detritus (implicitly including bacteria), dissolved nutrients, and phytoplankton for the 1970-1999 fitted model. Dashed lines span the 99% likelihood interval of model outputs given the observed indices of the state of the North Sea during this period. Grey shading spans the 50% likelihood interval. Solid black line is the median of the likelihood distribution and the red line is the maximum likelihood model. In this case the grey shading and black and ted lines are almost coincident for all variables. Columns of panels are different variables output from the model, rows are different spatial compartments. Units for all variables: mMN m^{-3}.

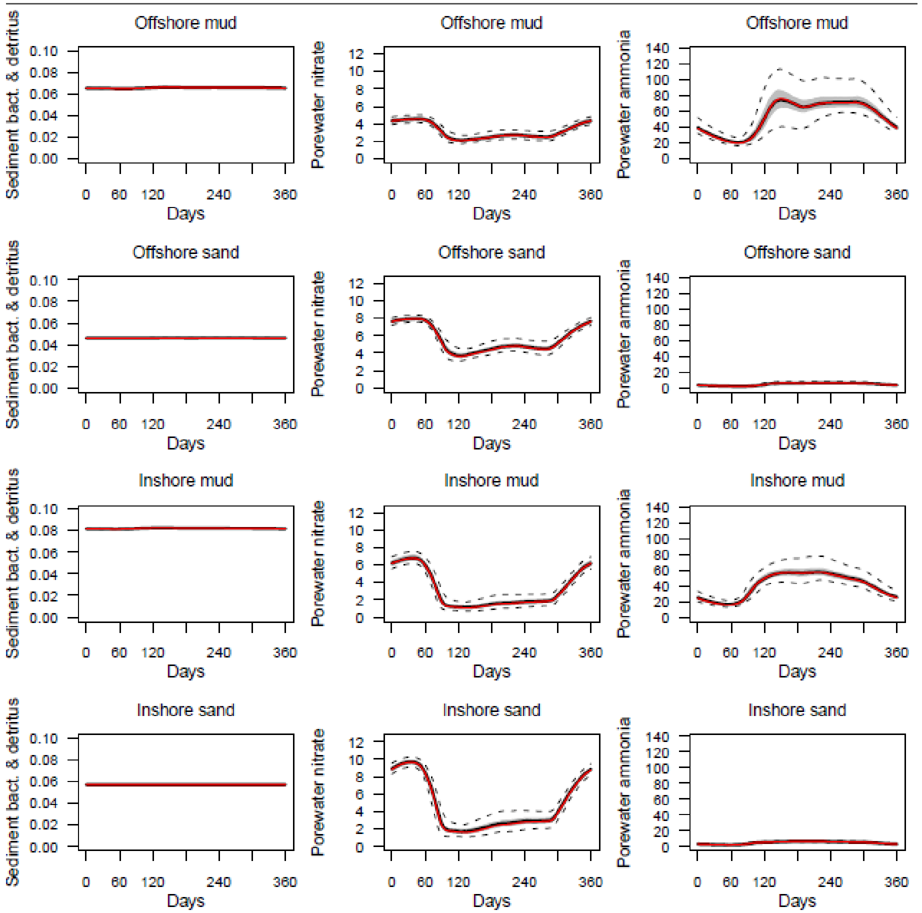

FIGURE 16 Stationary annual cycles of sediment detritus (implicitly including bacteria) and porewater nutrients for the 1970-1999 fitted model. Dashed lines span the 99% likelihood interval of model outputs given the observed indices of the state of the North Sea during this period. Grey shading spans the 50% likelihood interval. Solid black line is the median of the likelihood distribution and the red line is the maximum likelihood model. In this case the grey shading and black and ted lines are almost coincident for all variables. Columns of panels are different variables output from the model, rows are different spatial compartments. Units: detritus %N by weight, dissolved nutrients mMN m^{-3}.

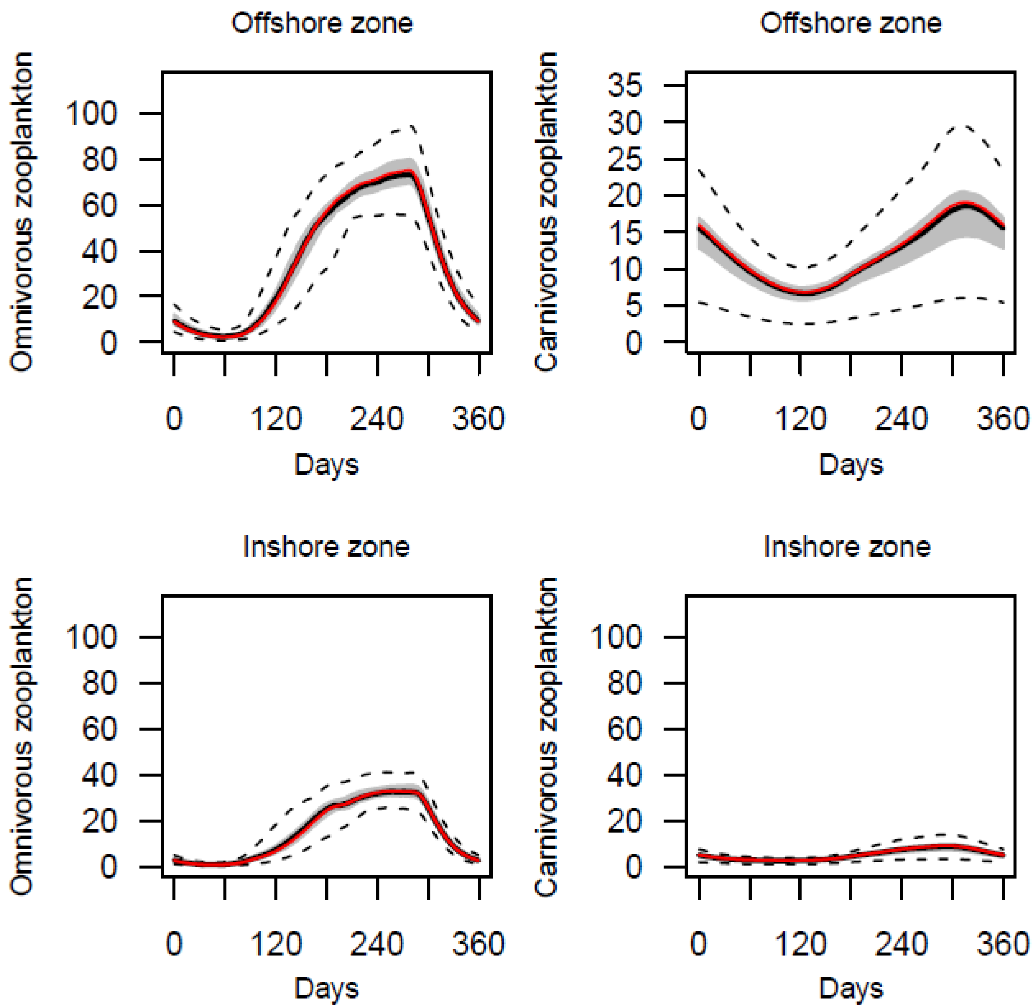

FIGURE 17 Stationary annual cycles of zooplankton guilds for the 1970-1999 fitted model. Dashed lines span the 99% likelihood interval of model outputs given the observed indices of the state of the North Sea during this period. Grey shading spans the 50% likelihood interval. Solid black line is the median of the likelihood distribution and the red line is the maximum likelihood model. Columns of panels are different variables output from the model, rows are different spatial compartments. Units for all variables: mMN m^{-2}.

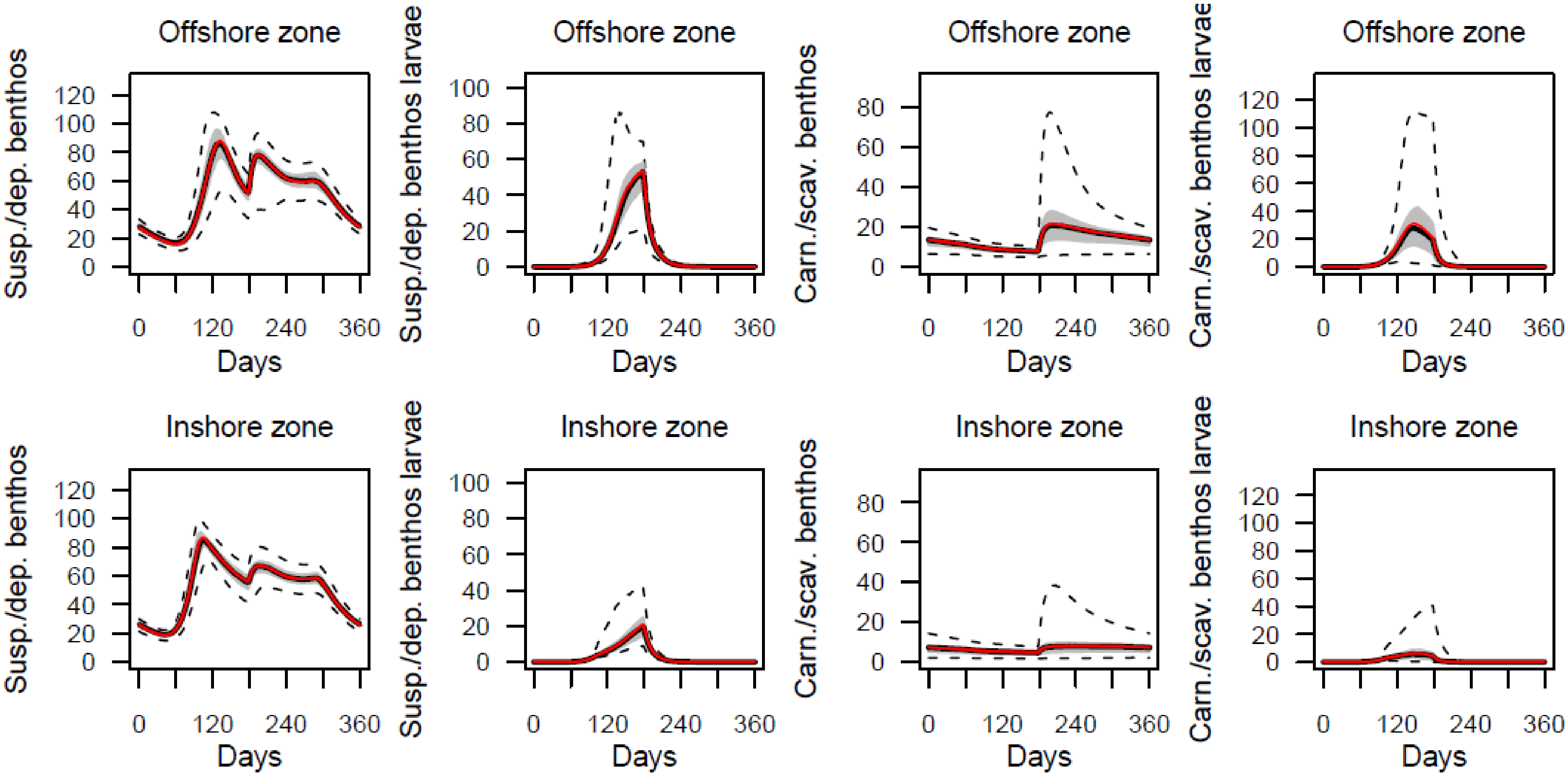

FIGURE 18 Stationary annual cycles of benthos guilds and their larval stages for the 1970-1999 fitted model. Dashed lines span the 99% likelihood interval of model outputs given the observed indices of the state of the North Sea during this period. Grey shading spans the 50% likelihood interval. Solid black line is the median of the likelihood distribution and the red line is the maximum likelihood model. Columns of panels are different variables output from the model, rows are different spatial compartments. Units for all variables: mMN m^{-2}.

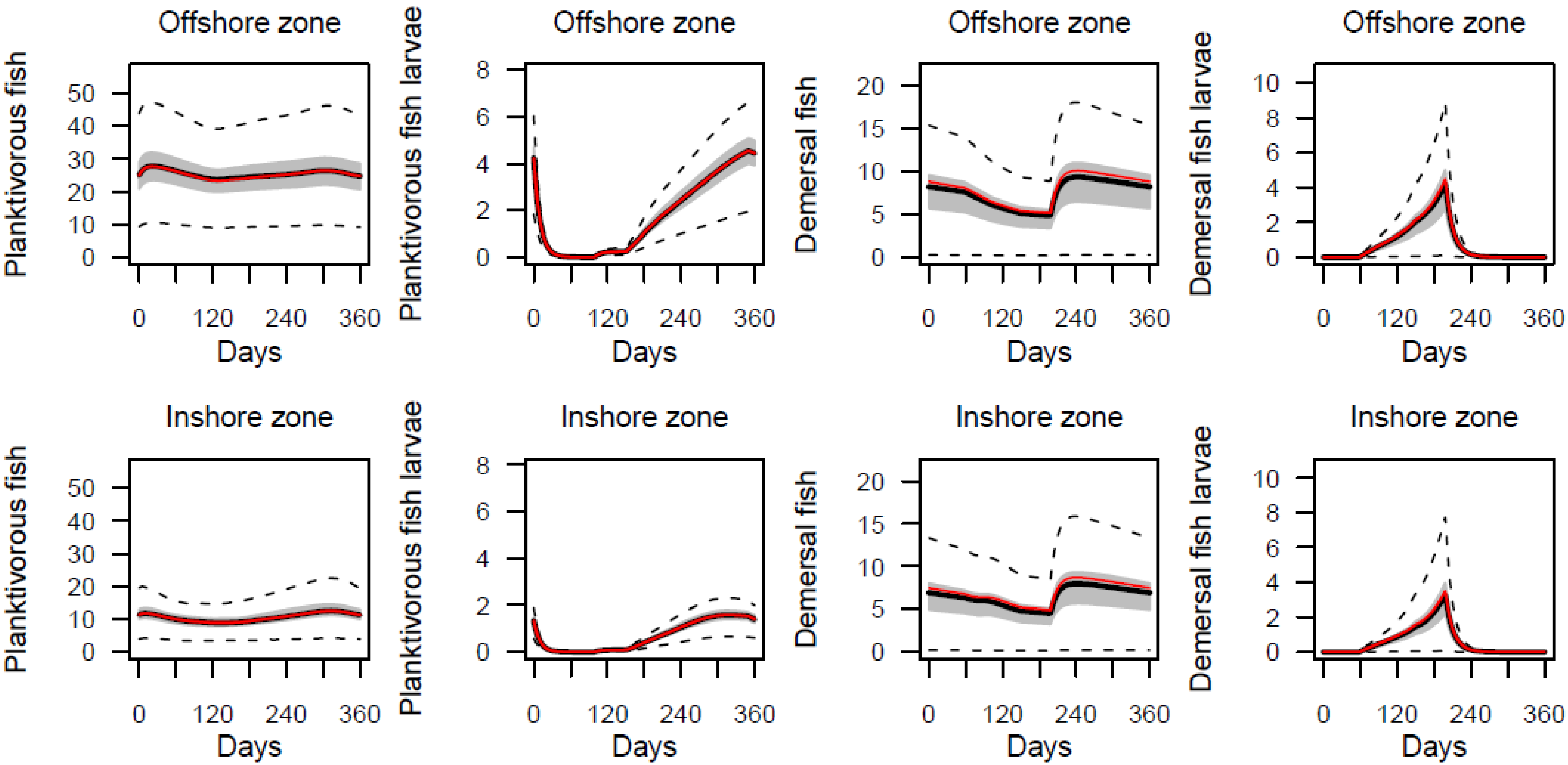

FIGURE 19 Stationary annual cycles of planktivorous and demersal fish guilds and their larval stages for the 1970-1999 fitted model. Dashed lines span the 99% likelihood interval of model outputs given the observed indices of the state of the North Sea during this period. Grey shading spans the 50% likelihood interval. Solid black line is the median of the likelihood distribution and the red line is the maximum likelihood model. Columns of panels are different variables output from the model, rows are different spatial compartments. Units for all variables: mMN m^{-2}.

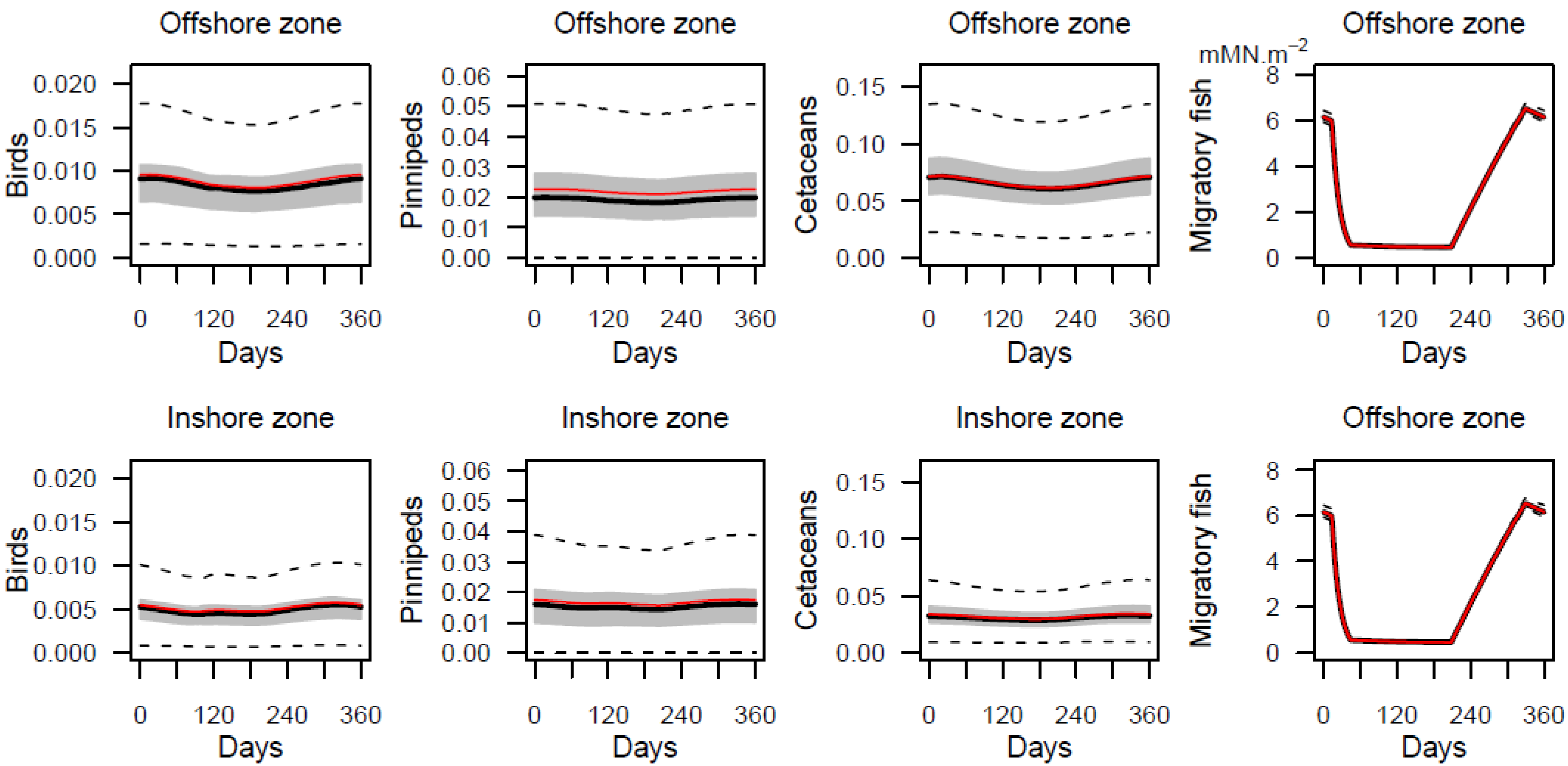

FIGURE 20 Stationary annual cycles of the birds & mammals guilds, migratory fish, and dead corpses for the 1970-1999 fitted model. Dashed lines span the 99% likelihood interval of model outputs given the observed indices of the state of the North Sea during this period. Grey shading spans the 50% likelihood interval. Solid black line is the median of the likelihood distribution and the red line is the maximum likelihood model. Columns of panels are different variables output from the model, rows are different spatial compartments. Units for all variables: mMN m^{-2}.

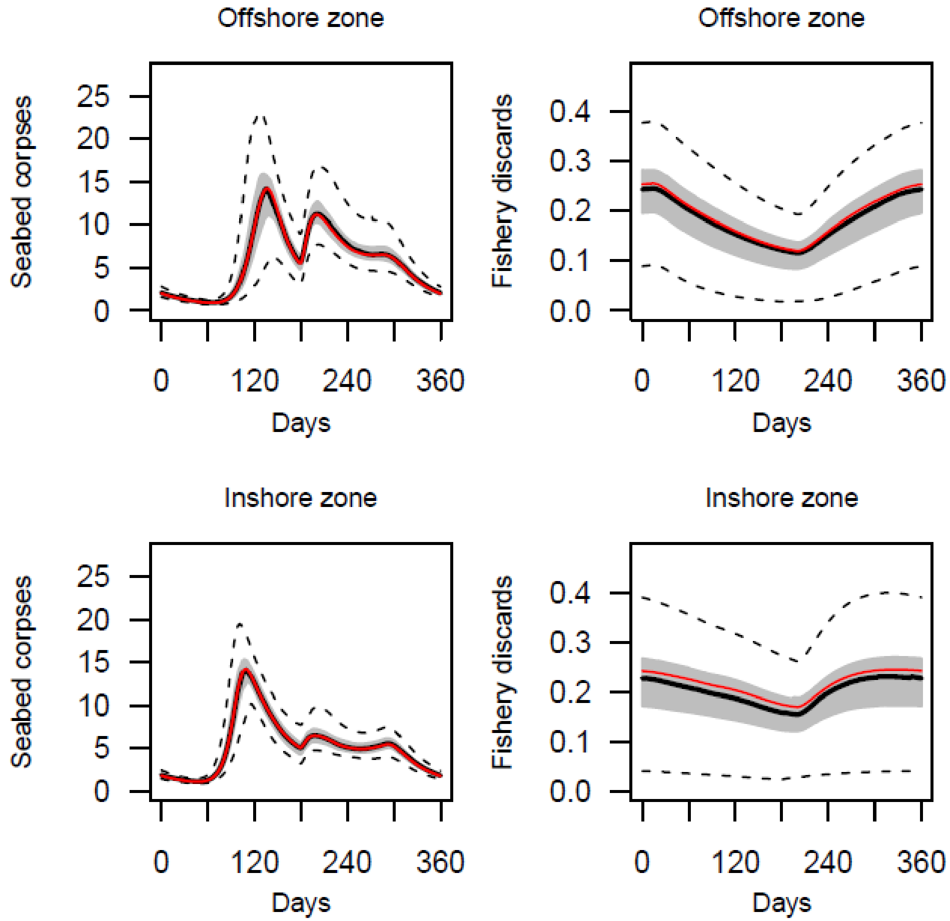

FIGURE 21 Stationary annual cycles of seabed corpses and fishery discards for the 1970-1999 fitted model. Dashed lines span the 99% likelihood interval of model outputs given the observed indices of the state of the North Sea during this period. Grey shading spans the 50% likelihood interval. Solid black line is the median of the likelihood distribution and the red line is the maximum likelihood model. Columns of panels are different variables output from the model, rows are different spatial compartments. Units for all variables: mMN m^{-2}.

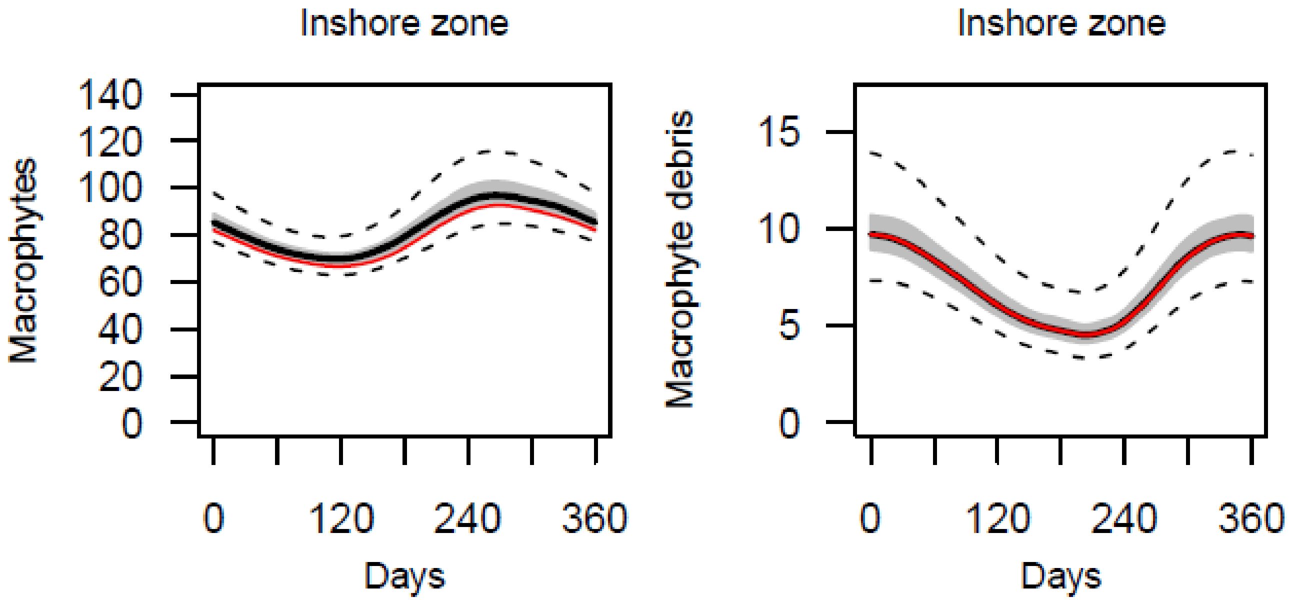

FIGURE 22 Stationary annual cycles of macrophytes and macrophyte debris in the inshore zone for the 1970-1999 fitted model. Dashed lines span the 99% likelihood interval of model outputs given the observed indices of the state of the North Sea during this period. Grey shading spans the 50% likelihood interval. Solid black line is the median of the likelihood distribution and the red line is the maximum likelihood model. Macrophytes are absent from the offshore zone. Units for all variables: mMN m^{-2}.

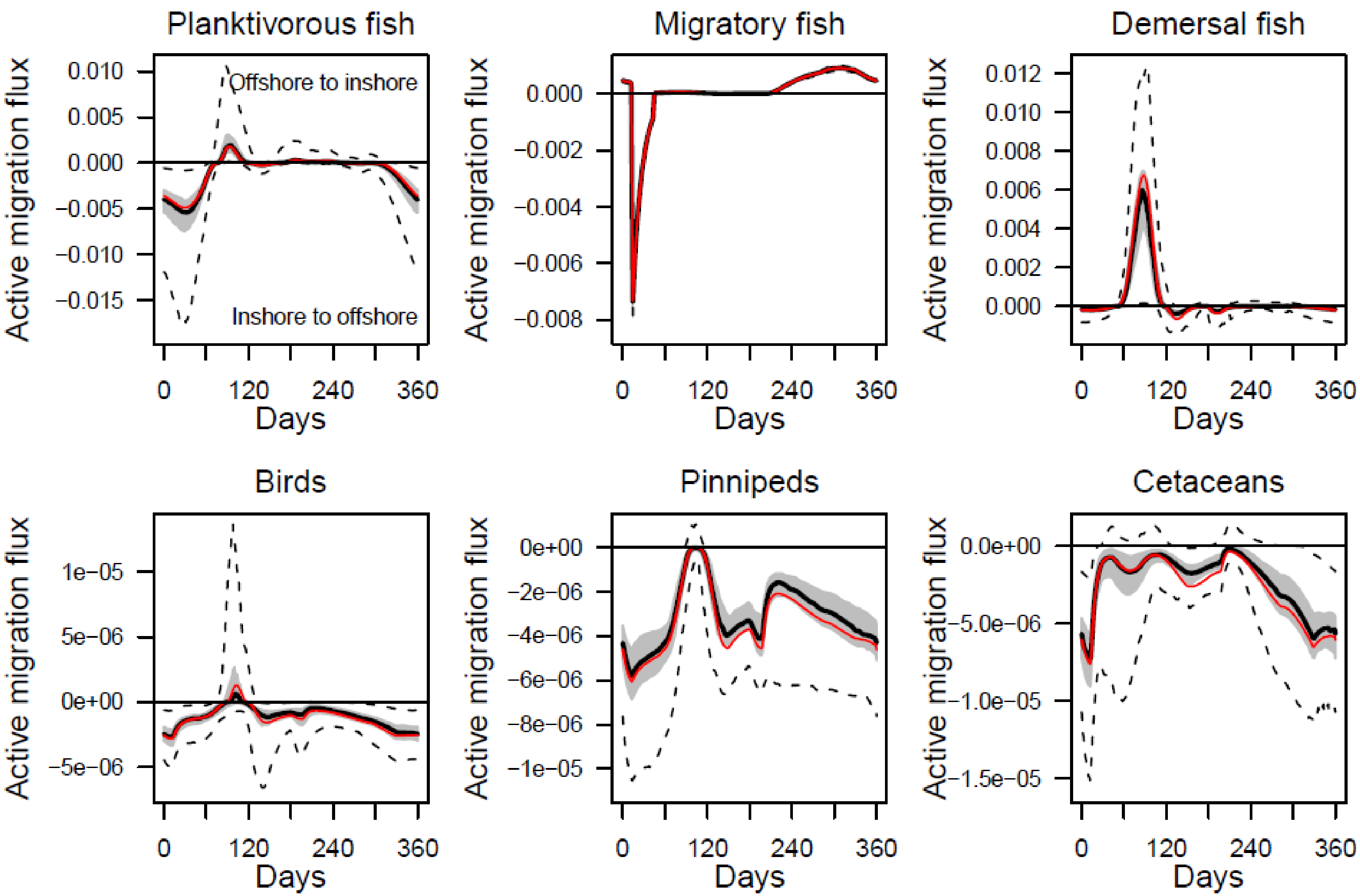

FIGURE 23 Stationary annual cycles of net active migration fluxes (mMN.m^{-2}.d^{-1}) of biomass between the offshore and inshore zones for the 1970-1999 fitted model. Positive values indicate net flux from offshore to inshore, and vice-versa for negative values. Dashed lines span the 99% likelihood interval of model outputs given the observed indices of the state of the North Sea during this period. Grey shading spans the 50% likelihood interval. Solid black line is the median of the likelihood distribution and the red line is the maximum likelihood model.

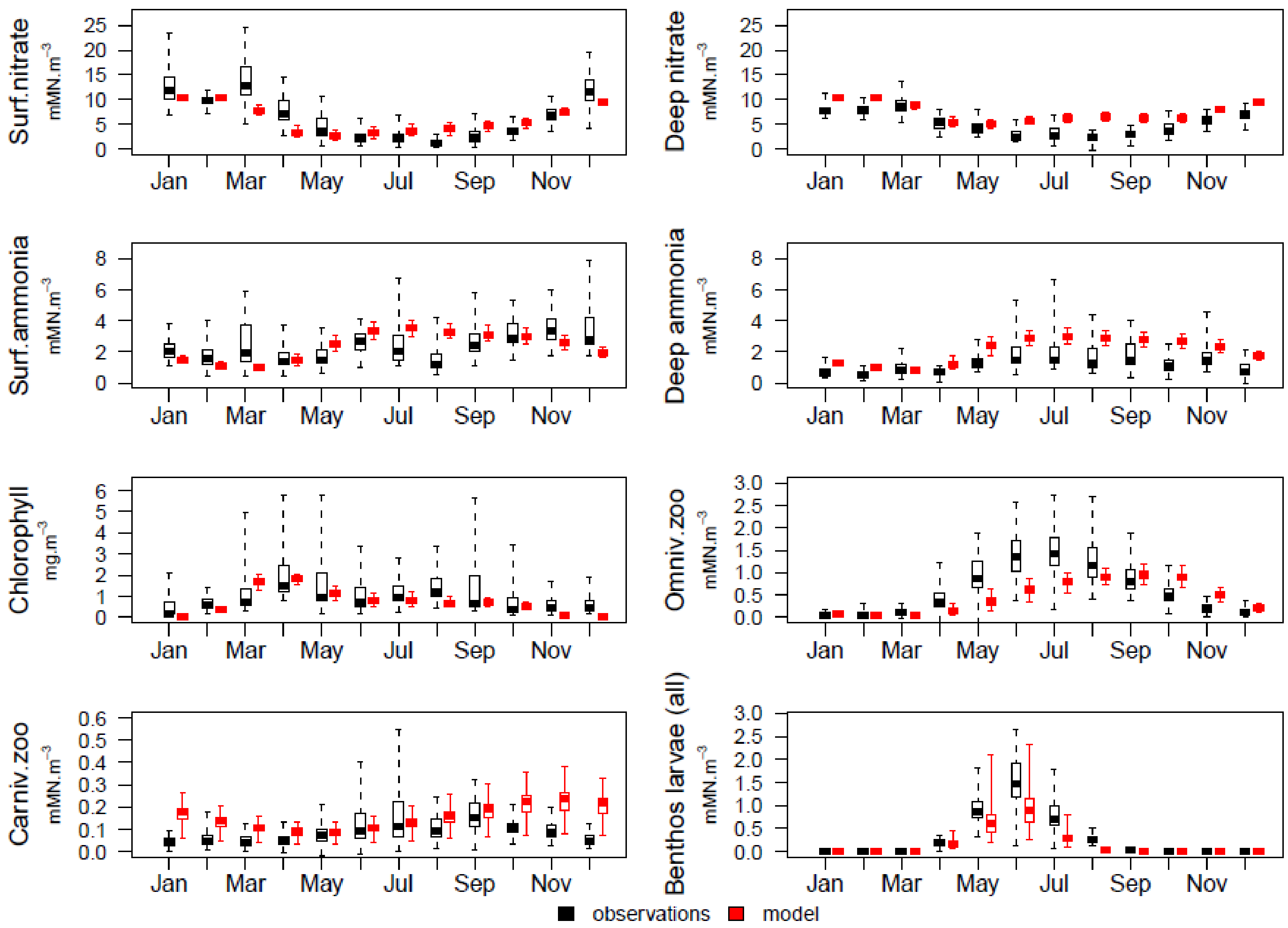

FIGURE 24 Monthly averages of the 1970-1999 stationary annual cycle daily resolution output for the whole model domain (red) and observed monthly averaged data from the North Sea (black). Box and whiskers for the model data show the 0.5, 25, 50, 75 and 99.5 centiles of the likelihood distribution of results given the uncertainty in fitted parameter values. For the observed data the box and whiskers show the equivalent variability in measurements form the North Sea aggregated over the period 1970-1999. Note that the model was not fitted to these observed data so the comparison represents a validation of the fitted model.

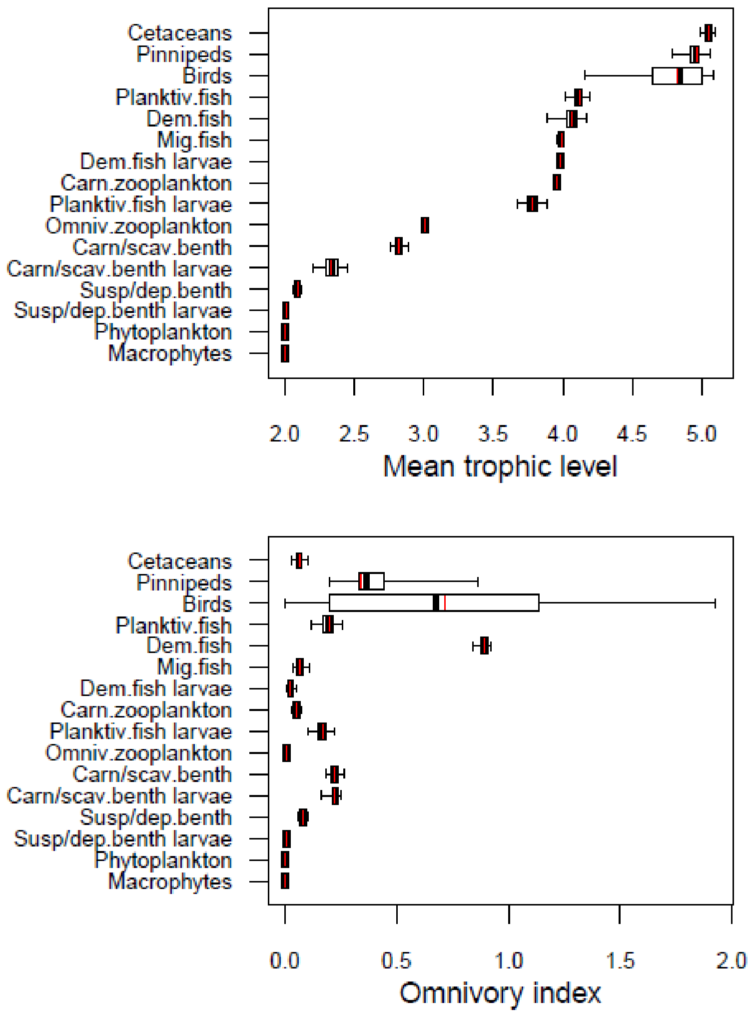

FIGURE 25 Credible intervals of the annual mean trophic level (upper panel) and omnivory index (lower panel) for the stationary 1970-1999 model. Black boxes span 50% of the likelihood interval, whiskers span 99%, thick black bar represents the median likelihood. The red bar in each case indicates the maximum likelihood model. Guilds (rows) in each panel are ranked by the mean trophic level in the maximum likelihood model.

Annual integrated mass fluxes in the maximum likelihood fitted model

At stationary state, 1970-1999 fishery landings represented 0.3 - 0.4% of annual gross primary production (GPP); sediment burial fluxes 15 - 17% of GPP, and denitrification was 130% of the combined atmospheric and riverine dissolved nutrient input (Figure 26). Overall, the model was a net importer of nitrogen from across the ocean boundaries, with exports due to advection and migrations equivalent to 91% of imports. A detailed breakdown of the mass balance fluxes is provided in Tables 39 and 40.

Burial of organic nitrogen in the seabed sediments emerges as a significant export flux from the model (17% of gross primary production in the inshore zone, 15% offshore) although the confidence intervals are wide (Tables 39 and 40). It is not at all clear whether this is a realistic figure or not. There seem to be few if any empirical estimates of nitrogen burial. Empirical estimates of carbon burial in the North Sea are also scarce and highly variable (de Haas *et al.,* 2002), but given the model assumption of constant Redfield stoichiometry (which may be particularly suspect in the context of sediment geochemistry) a 10% burial flux seems feasible though on the high-side of empirical evidence. Hence, the realism of the simulated burial fluxes remains an unresolved issue.

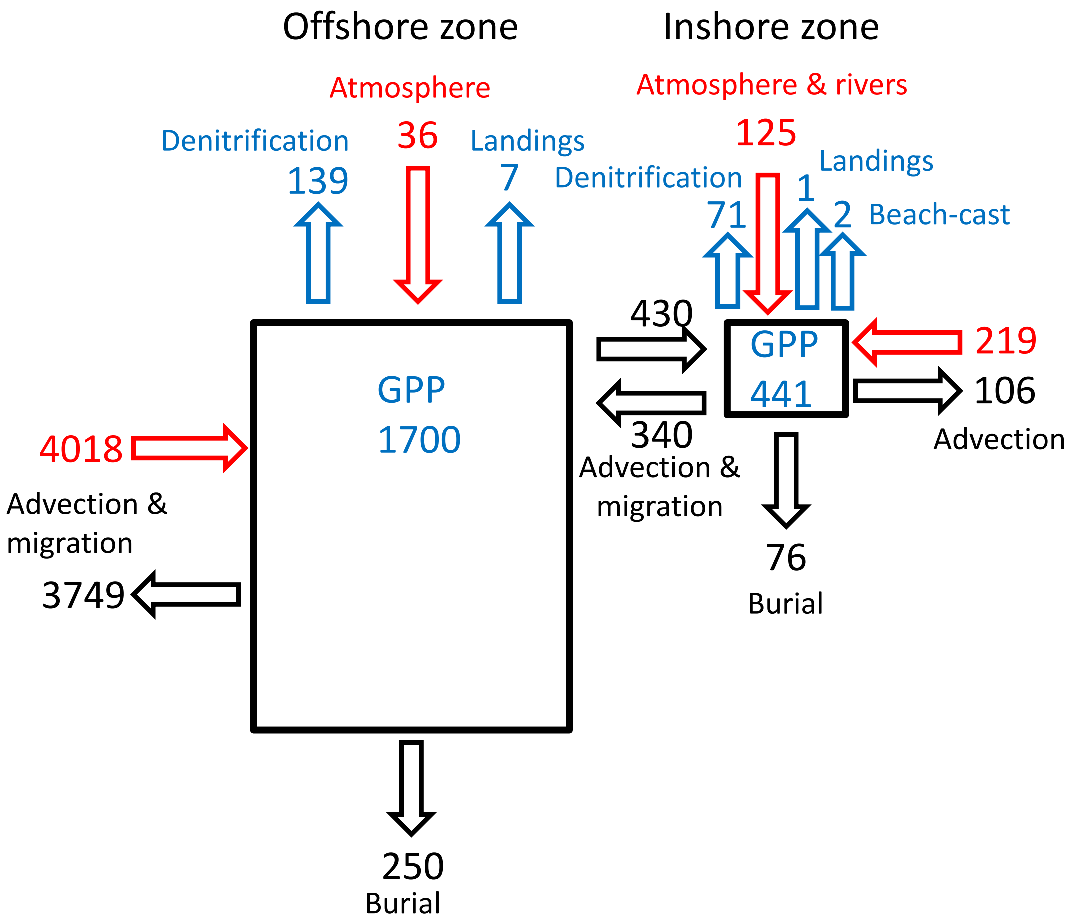

FIGURE 26 Stationary state nitrogen mass fluxes for the 1970-1999 model. Flux units: $mMN.y^{-1}$ scaled to a model domain sea surface area of $1m^2$. Red arrows: fluxes defined by external driving data; blue arrows: modelled fluxes included in the target data set for fitting the model; black arrows: modelled fluxes not in the target data set. GPP indicates gross annual primary production.

TABLE 39 Stationary annual mass fluxes of nitrogen (mMN.y^{-1}) into and out of the offshore zone of the 1970-1999 model domain (surface area 0.735 m^2). Figures in brackets are 99% credible intervals. DIN refers to dissolved inorganic nitrogen (nitrate + ammonia). In this case the fisheries landings are the processed weigh, not the live weight landed.

		Inputs	**Outputs**		
		Transport & migration	**Transport & migration**	**Geochemistry**	**Fisheries**
Ocean boundary	DIN	3635.2	3400.4 (3277.8-3590.2)		
	Plankton & detritus	378.0	345.2 (238.7-459.7)		
	Active migrations	5.1	4.1 (4.0-4.3)		
Inshore/offshore boundary (net flux)	DIN	357.9 (326.3-404.0)	267.7 (247.8-292.8)		
	Plankton & detritus	72.4 (52.5-104.4)	72.5 (55.8-89.2)		
	Active migrations	0.49 (0.14–1.60)	0.36 (0.10-1.14)		
Land and atmosphere	Atmospheric DIN deposition	36.9			
	River DIN discharges	0			
	Water column denitrification			0.04 (0.04-0.05)	
	Sediment denitrification			138.7 (116.2-161.2)	
	Macrophyte beach-cast		0		
Seabed sediments	Net burial			249.8 (121.1-358.3)	
Human extraction	Planktivous fish landings				4.76 (1.76-7.79)
	Demersal fish landings				1.12 (0.02-2.13)
	Migratory fish landings				0.77 (0.67-0.87)
	Susp/deposit benthos landings				0.060 (0.033-0.085)
	Carn/scav benthos landings				0.041 (0.017-0.078)
	Pelagic invert. Landings				0.003 (<0.001-0.015)
	Cetacean landings				3.6E-05 (0-10.8E-05)
TOTAL		4485.9	4090.2	388.5	6.8
TOTAL GAS				138.5	
TOTAL DIN IN/OUT		4030.0	3668.1		
TOTAL PON IN/OUT		456.0	422.1	249.8	6.8
Net primary production		972.6 (750.1-1170.2)			
Gross primary production		1699.8.0 (1207.3-2154.9)			

TABLE 40 Stationary annual mass fluxes of nitrogen ($mMN.y^{-1}$) into and out of the inshore zone of the 1970-1999 model domain (surface area 0.265 m^2). Figures in brackets are 99% credible intervals. DIN refers to dissolved inorganic nitrogen (nitrate + ammonia). In this case the fisheries landings are the processed weigh, not the live weight landed.

		Inputs	Outputs		
		Transport & migration	**Transport & migration**	**Geochemistry**	**Fisheries**
Ocean boundary	DIN	147.2	96.5 (90.3-106.8)		
	Plankton & detritus	71.7	9.3 (5.9-13.9)		
	Active migrations	0	0		
Inshore/offshore boundary	DIN	267.7 (247.8-292.8)	357.9 (326.3-404.0)		
	Plankton & detritus	72.5 (55.8-89.2)	72.4 (52.5-104.4)		
	Active migrations	0.36 (0.10-1.14)	0.49 (0.14–1.60)		
Land and atmosphere	Atmospheric DIN deposition	18.2			
	River DIN discharges	107.5			
	Water column denitrification			0.006 (0.004-0.008)	
	Sediment denitrification			70.6 (54.3-89.2)	
	Macrophyte beach-cast		1.60 (1.13-2.31)		
Seabed sediments	Net burial			75.9 (35.3-104.1)	
Human extraction	Planktivous fish landings				0.79 (0.27-1.33)
	Demersal fish landings				0.51 (0.01-0.97)
	Migratory fish landings				0.009 (0.007-0.011)
	Susp/deposit benthos landings				0.035 (0.024-0.047)
	Carn/scav benthos landings				0.028 (0.005-0.070)
	Pelagic invert. Landings				0.0
	Cetacean landings				0.0
TOTAL		685.2	538.2	146.5	1.37
TOTAL GAS				70.5	
TOTAL DIN IN/OUT		540.6	454.4		
TOTAL PON IN/OUT		144.6	83.8	75.9	1.37
Net primary production		248.8 (203.1-307.0)			
Gross primary production		440.7 (342.7-547.9)			

Disaggregation of catch into landings and discards by each fishing gear

The raw output from the ecology model includes the total landings and discards of each guild from the inshore and offshore zones by the combined actions of all the fishing gears. Output from the fleet model is then used to disaggregate the annual integrated landings and discards between the gears (see model documentation). These results are illustrated in Figure 27 for a stationary year of the 1970-1999 model.

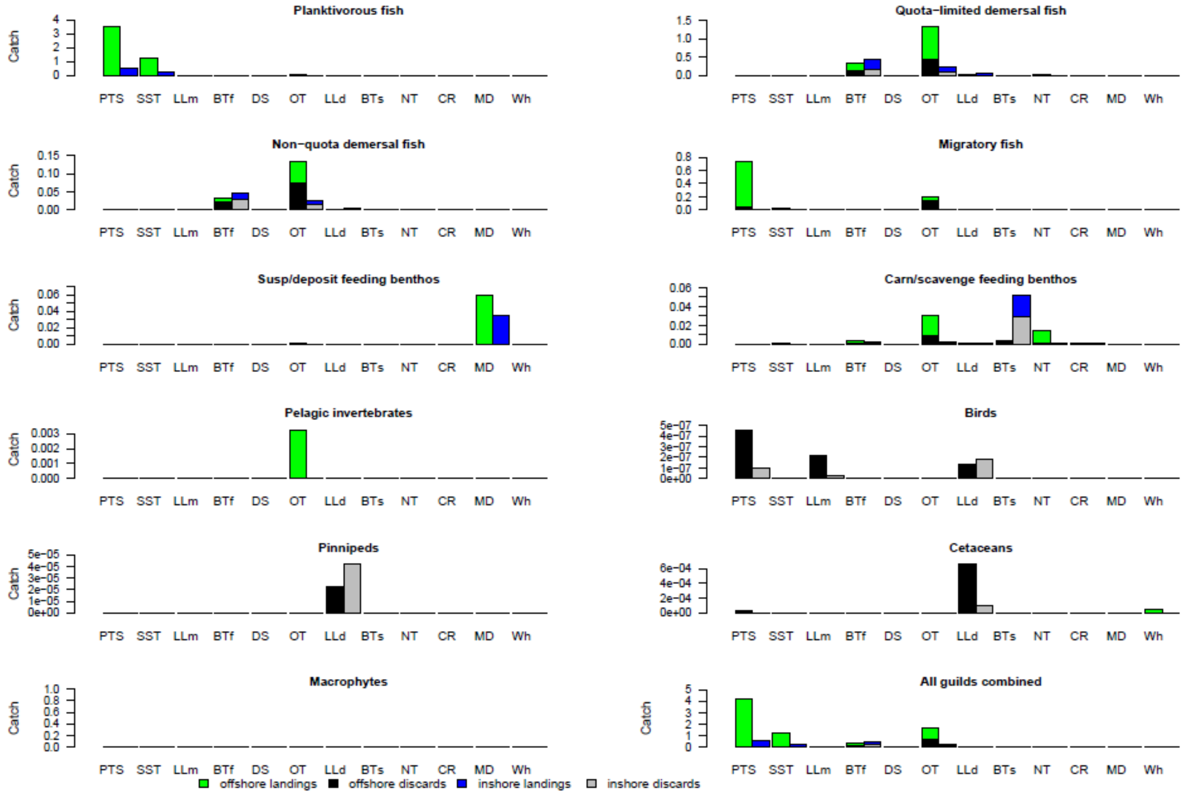

FIGURE 27 Distribution of 1970-1999 fishery catch across gears for each resource guild in the ecology model. Black and green bars represent discards and landings respectively from the offshore zone of the model. Grey and blue represent discards and landings from the inshore zone. The different fishing gear fleets are indicated along the x-axis by the codes: PT = Pelagic trawls and seines; SST = sandeel/sprat trawls; LLm = long-line for mackerel; BTf = fish beam trawl; DS = demersal seine; OT = demersal otter trawl; LLd = demersal long-lines and gill net; BTs = shrimp beam trawl; NT = Nephrops trawl; CR = creels; MD = mollusc dredges; Wh = Norwegian whaler.

Sensitivity to variations in pelagic and demersal harvesting at the scale of the whole model domain.

Sensitivity of the stationary state of the 1979-1999 model to bi-variate changes in pelagic and demersal fishfish harvest ratios was carried out by replicating the approach taken by Heath (2012). The model was run to a stationary state for each of 49 combinations of pelagic and demersal fish harvest ratios, forming a 7 x 7 matrix of values, with each harvest rate varying between 0 and 3-times the baseline 1970-1999 rate, in intervals of 0.5. Hence, the baseline model was represented by matrix cell coordinates 3,3 (pelagic and demersal harvest ratios 1.0 and 1.0-times the baseline respectively). The term ‘pelagic’ harvest ratio here refers to the harvest ratios of both planktivorous and migratory fish which were varied in synchrony.

Practically, the structured variations in harvest ratio were achieved by alterations to the harvest ratio multiplier values for the planktivorous, migratory and demersal fish guilds in the parameter file ‘harvest_ratio_multiplier.csv’. This means that while the harvest ratios were varied, the activity rates of the fishing gears were not. So, other consequences of fishing such as seabed abrasion rates and harvest ratios on other resources guilds were unaffected. Essentially, the variations in pelagic and demersal harvesting were implicitly achieved by systematic changes in the selectivity patterns and catching power of each gear. Discard and processing at sea rates from all guilds except demersal fish were constant across all the model runs. In the case of demersal fish, discard rates were set to vary according the in-built density dependent relationship with demersal fish biomass within the model.

At the end of each run, the annual averaged biomasses of model components were calculated for the final year of the simulation, together with annual integrals of production rates, dietary fluxes, landings and discards. In addition, a range of network information indices were derived from the annual integrated flow matrix for the final year, using the R package NetIndices (Soetaert & Kones 2014).

On conclusion of all 49 model runs, the data on each individual model output (e.g. planktivorous fish landings) was assembled across all runs into a 7 x 7 matrix and visualised as contoured and colour-shaded maps (Figures 28-33)

The maps of planktivorous and demersal fish landings (Figure 28) both show a characteristic ridge of peak values running through the two-dimension parameter space defining pelagic and demersal harvest ratios. The ‘height’ of the crest of each ridge represents the maximum sustainable yield (MSY; in terms of landings) for each resource guild, which is a key criterion in fisheries management. The combination of harvest ratios defining the trajectory of MSY through the harvest ratio space (HR_{MSY}) represents the fishing conditions which deliver MSY – equivalent to the term F_{MSY} in the fisheries management context. These results are some of the most important outputs from the model – they show that MSY and HR_{MSY} for planktivorous and demersal fish are inter-independent. This interaction between the two fishing sectors arises as a result of the direct predator-prey relationship between the two guilds (demersal fish eat planktivorous fish and larvae; planktivorous fish each demersal fish larvae), and also from indirect food web interactions via zooplankton and the predators on the fish guilds. The magnitude of MSY for planktivorous fish is highly sensitive to the demersal fish harvest rate (i.e. planktivorous MSY is strongly depressed at low demersal harvest ratio (high demersal fish biomass), and conversely high at high demersal harvest ratio (low demersal biomass). On the other hand, demersal fish MSY is relatively insensitive to pelagic harvesting. The clear implication is that demersal fish exert a strong top-down effect on planktivorous fish productivity, but planktivorous fish have only a weak bottom-up effect on demersal fish. These are key elements of guidance for the strategic management of fisheries.

For the demersal fish guild, the pattern of discard quantity across the pelagic and demersal harvest ratio space is not exactly proportional to the pattern of landings, because of the effects of the density-dependent discard rate which was implemented in the simulations. Demersal fish discard rate is indirectly related to demersal fish biomass in the model, mimicking the empirically observed response of average fish size to variations in stock biomass.

The landings map for migratory fish does not show the same distribution with respect to harvest ratios as the planktivorous fish despite the ratios for the two guilds being varied in concert, because the biomass of migratory fish in the system is sustained by external immigration. In the model, the immigration rate is independent of the intensity of harvesting within the model domain – the assumption is that harvesting within the North Sea is a minor component of the overall harvesting rate of the whole northeast Atlantic stock. Parameterising a feedback between the local harvest rate within the model domain and the magnitude of the external ocean stock of migratory fish, and potentially its migration pattern (i.e. the proportion entering the model each year) is a topic for future development.

The top-down effects of harvesting on the model food web are clearly visible in the maps of annual averaged masses of zooplankton, benthos, phytoplankton and nutrient within the two-dimensional harvest ratio space. Similarly, the bottom-up effects of harvesting on the annual average biomass of birds, pinnipeds and cetaceans (Figure 29). The response patterns are complex, but a clear feature is that the top-down effects generate only small variations in nutrient and plankton generate across the harvest-ratio space, whereas the bottom-up effects generate large variations on the top-predators with near-extinction in some parts of the space. Similarly, the top-down effects of harvesting caused only small variability in annual mean trophic level and omnivory indices of the zooplankton and benthos guilds, but the bottom-up effects on top-predator groups were considerably larger (Figure 34). The variations in omnivory indices were reflected in the emergent diet compositions of the top-predator groups which were mainly linked to the availability of planktivorous fish which are the main preferred food type of birds, pinnipeds and cetaceans (Figure 32).

The maps of network indices generated by the model simulations show clear patterns, but have not yet been subject to serious consideration (Figure 33). They are included here to illustrate the responses generated by the model. Possibly of significance are the maps of system ascendency, and the ratio of ascendency:capacity (AC ratio). Ascendency is a measure of the degree of organisation of the network, or the extent to which the capacity is being utilised. The AC ratio has been proposed as a useful index of the 'maturity' of a network (Allesina & Ulanowicz, 2004). In these simulations, the AC ratio is clearly correlated with top-down driven variations in primary production, whilst the distribution of ascendency appears to be loosely correlated with distribution of planktivorous fish landings.

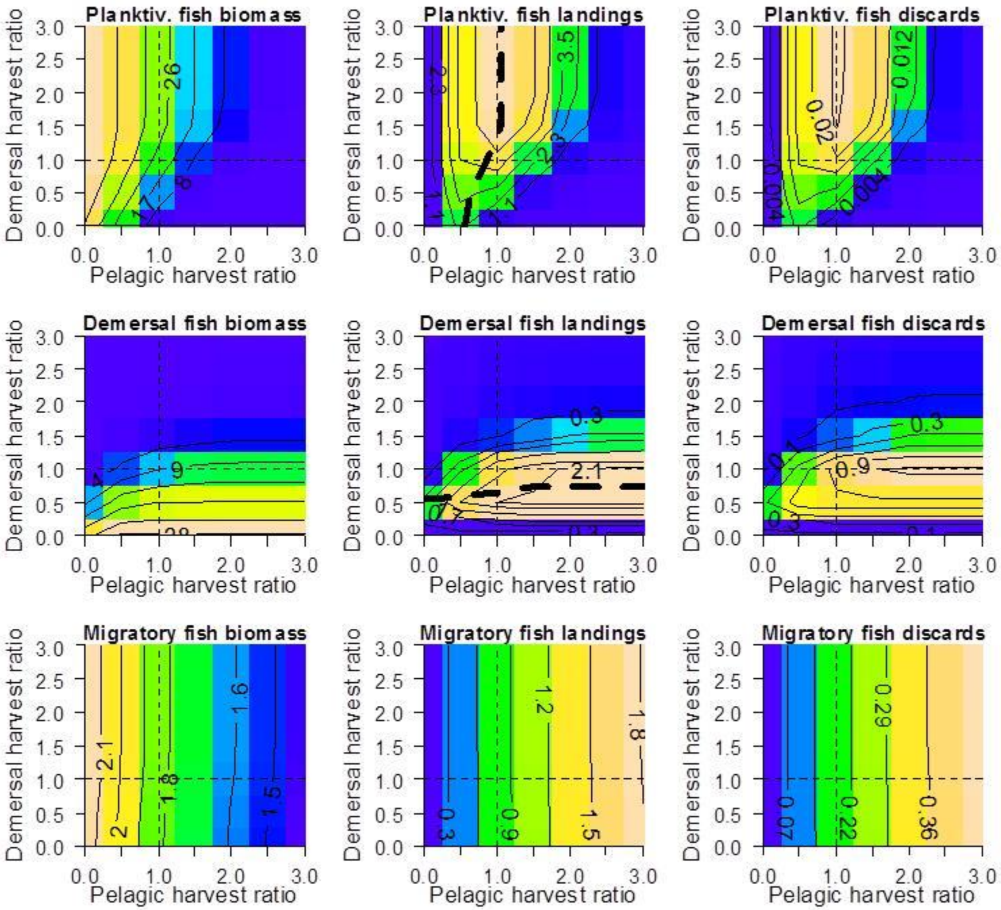

FIGURE 28 Variations in stationary annual mean biomass ($mMN.m^{-2}$), annual integrated landings ($mMN.m^{-2}.y^{-1}$), and annual integrated discards ($mMN.m^{-2}.y^{-1}$) for each guild of the three finfish in the 1970-1999 model, in relation to pelagic and demersal harvest ratios. The x and y-axis scales show the multipliers applied to the baseline 1970-1999 harvest ratios, so coordinates 1,1 (indicated by the thin dashed 'cross-wires') correspond to the baseline model. Harvest ratios for migratory and planktivorous fish were varied in simultaneously. The heavy black dashed line in the landings panel for planktivorous fish and demersal indicates the trajectory of harvest ratios generating maximum sustainable landings.

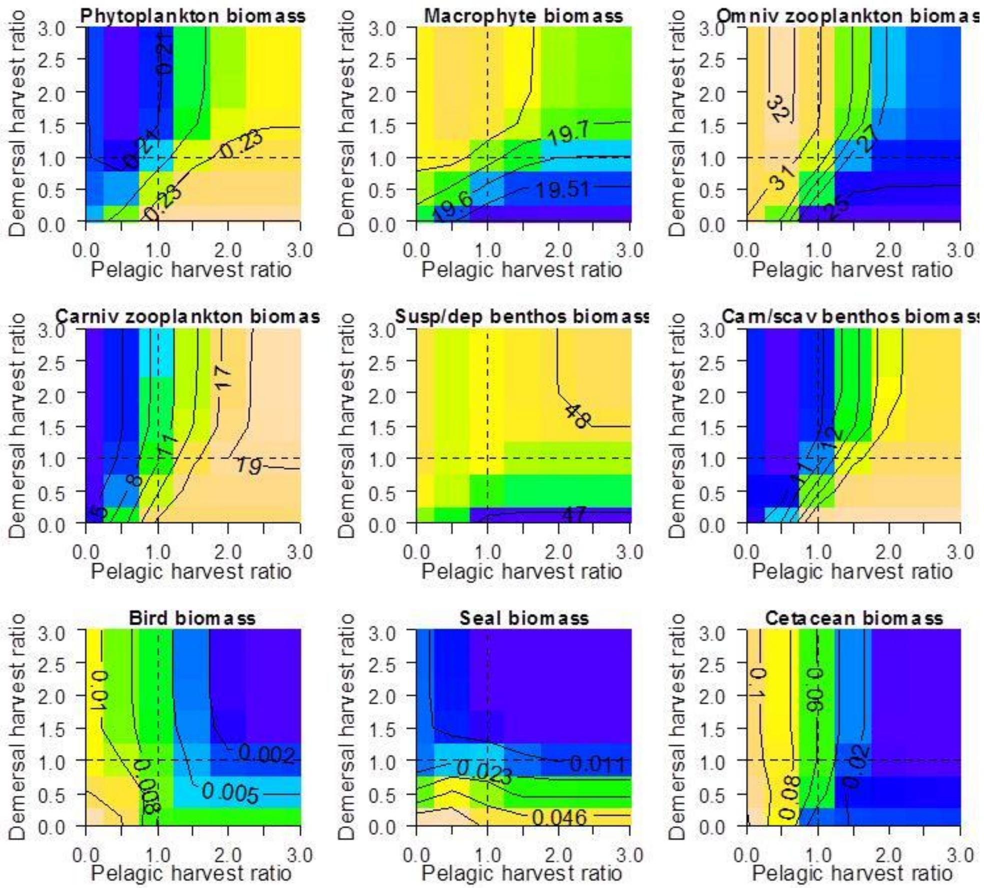

FIGURE 29 Variations in stationary annual mean biomass (mMN.m^{-2}) of each living guild other than finfish in the 1970-1999 model, in relation to pelagic and demersal harvest ratios. The x and y-axis scales show the multipliers applied to the baseline 1970-1999 harvest ratios, so coordinates 1,1 (indicated by the thin dashed 'cross-wires') correspond to the baseline model. Harvest ratios for migratory and planktivorous fish were varied in simultaneously.

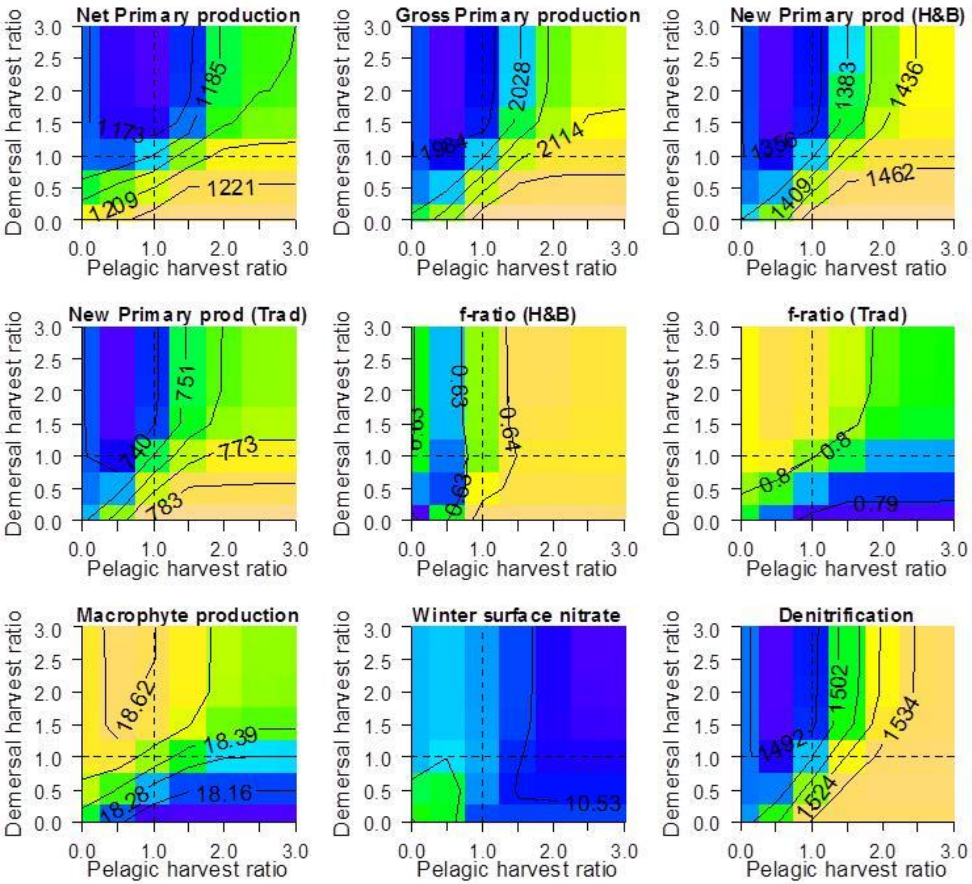

FIGURE 30 Variations in annual integrated primary production and denitrification fluxes (mMN.m^{-2}.y^{-1}), in the 1970-1999 model, in relation to pelagic and demersal harvest ratios. The x and y-axis scales show the multipliers applied to the baseline 1970-1999 harvest ratios, so coordinates 1,1 (indicated by the thin dashed ‘cross-wires’) correspond to the baseline model. Harvest ratios for migratory and planktivorous fish were varied in simultaneously. Net primary production is the net of gross production (annual integrated nutrient assimilation) and annual integrated non-grazing mortality an metabolic losses. Two versions of new primary production are shown (traditional: annual integrated nitrate assimilation, and H&B: annual draw-down of depth-integrated nitrate between winter and summer (Heath and Beare 2008)). The f-ratio is the ratio of new production to gross primary production.

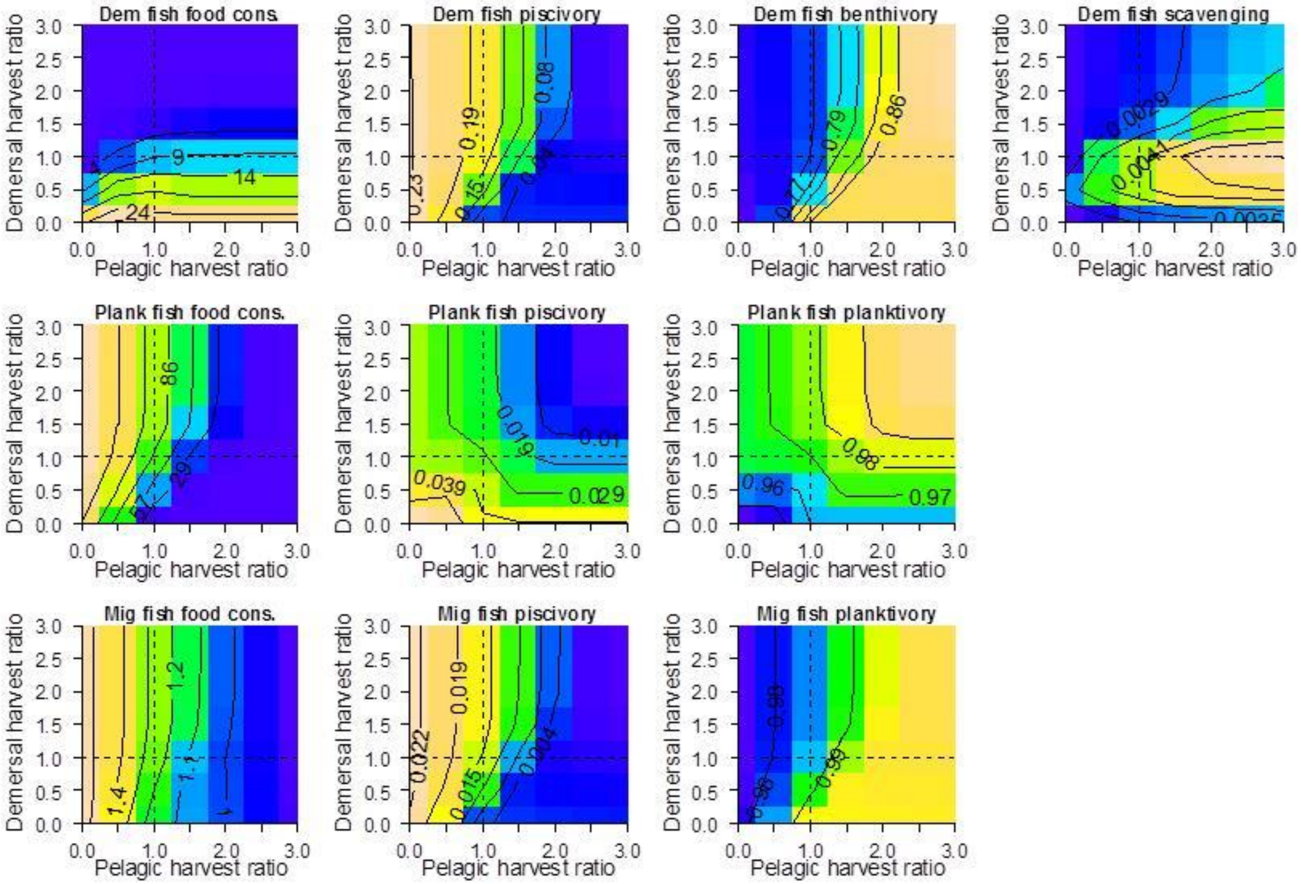

FIGURE 31 Variations in annual integrated food consumption and diet composition for each of the three finfish guilds in the 1970-1999 model, in relation to pelagic and demersal harvest ratios. The x and y-axis scales show the multipliers applied to the baseline 1970-1999 harvest ratios, so coordinates 1,1 (indicated by the thin dashed 'cross-wires') correspond to the baseline model. Harvest ratios for migratory and planktivorous fish were varied simultaneously. Left-hand column; food consumption ($mMN.m^{-2}.y^{-1}$), Second column: proportion of annual integrated food consumption made up of fish (piscivory). Third column: proportion of annual integrated food consumption made up of benthos or zooplankton (benthivory or planktivory). Final column (demersal fish only): proportion of annual integrated food consumption made up of corpses and discards (scavenging).

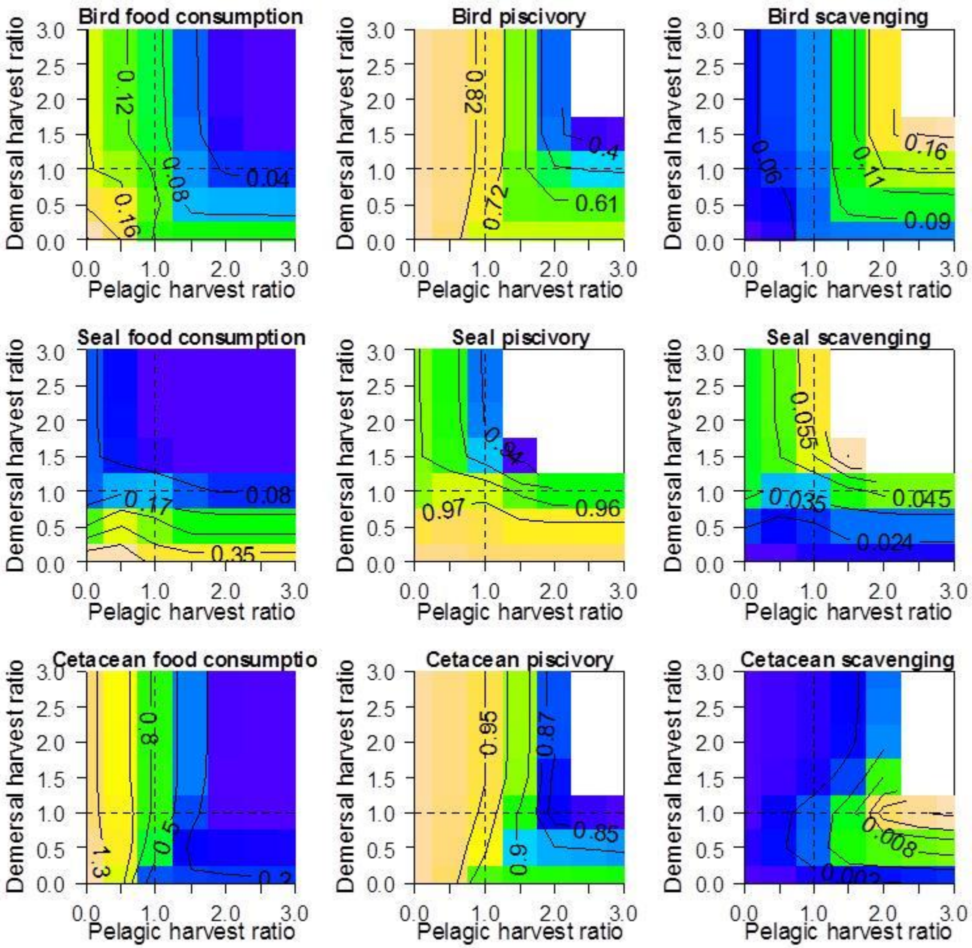

FIGURE 32 Variations in annual integrated food consumption and diet composition for each of the three top-predator guilds in the 1970-1999 model, in relation to pelagic and demersal harvest ratios. The x and y-axis scales show the multipliers applied to the baseline 1970-1999 harvest ratios, so coordinates 1,1 (indicated by the thin dashed 'cross-wires') correspond to the baseline model. Harvest ratios for migratory and planktivorous fish were varied in simultaneously. Left-hand column; food consumption (mMN.m^{-2}.y^{-1}), Second column: proportion of annual integrated food consumption made up of fish (piscivory). Third column: proportion of annual integrated food consumption made up of corpses and discards (scavenging). White areas indicate harvest ratio combinations where the diet proportion was undefined due the consumer mass being extremely small or zero.

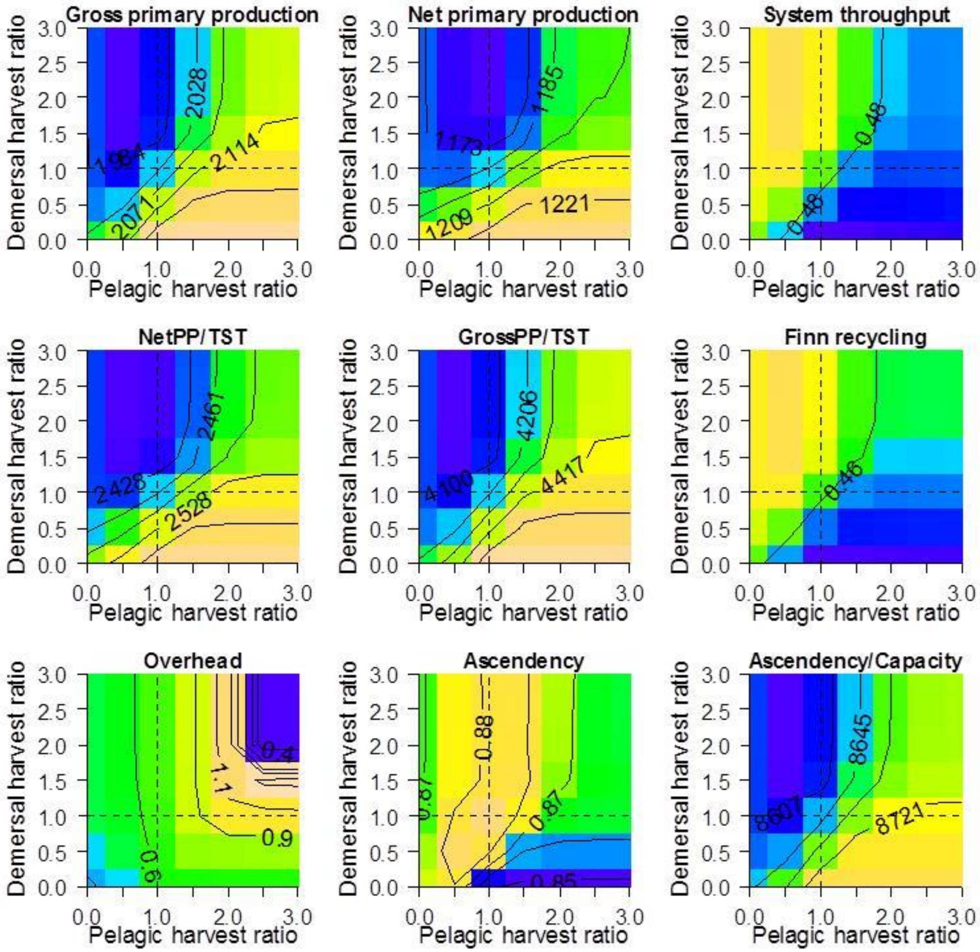

FIGURE 33 Variations in annual network information indices generated by the NetIndices package for the 1970-1999 model, in relation to pelagic and demersal harvest ratios. The x and y-axis scales show the multipliers applied to the baseline 1970-1999 harvest ratios, so coordinates 1,1 (indicated by the thin dashed 'cross-wires') correspond to the baseline model. Harvest ratios for migratory and planktivorous fish were varied in simultaneously.

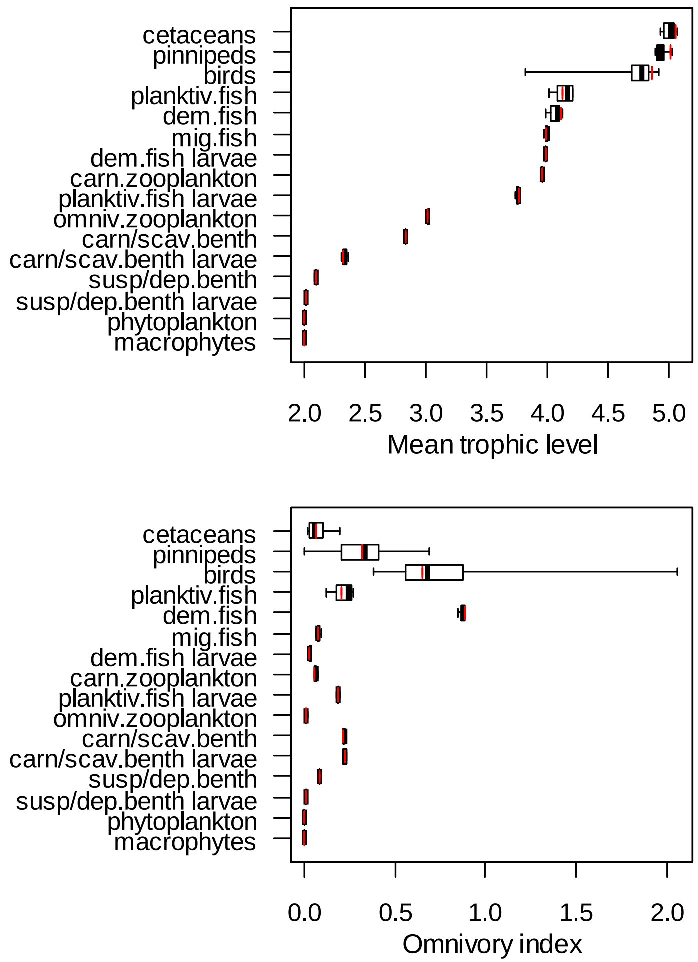

FIGURE 34 Variations in the stationary state annual mean trophic level (upper panel) and omnivory index (lower panel) of the living guilds within the bi-dimensional space of pelagic and demersal harvest ratio for the 1970-1999 model. Each harvest ratio was varied by factors of 0 to 3-times the 1970-1999 baseline value in intervals of 0.5-times. Black boxes span 50% of the distribution of values, whiskers the span full range, thick black bar represents the median value. The red bar in each case indicates the 1970-1999 baseline model. Guilds (rows) in each panel are ranked by the mean trophic level in the baseline model.

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