StrathE2E2 version 4.0.0: Overview of model concepts and design.

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Summary

- StrathE2E2 is a model of the 'big-picture', whole ecosystem effects of hydrodynamics, temperature, nutrient additions, and fishing on continental shelf marine food webs.

- StrathE2E2 has two linked parts - a fishing fleet model and an ecology model.

- The fishing model integrates harvesting, discarding and seabed disturbance rates across a range of gears and passes the results into the ecology model.

- The ecology model is a network of coupled ordinary differential equations representing the rates of change in organic detritus, dissolved inorganic nutrient, and coarse guilds of living biomass spanning microbes to megafauna. The equations include representations of feeding, metabolism, reproduction, active migrations, advection and mixing. Environmental driving data include temperature, irradiance, hydrodynamics, and nutrient inputs from rivers, atmosphere and ocean boundaries.

1 Introduction

The effects of anthropogenic or natural pressures applied to any part of an ecosystem are eventually felt everywhere to some extent through the phenomenon known as a 'trophic cascade' (Pace *et al*., 1999). Cascading effects are attenuated or amplified as they propagate through the food web, depending on the nature of the pressure and details of the ecology (Heath *et al.,* 2014). Diagnosing the type and magnitude of pressures that an ecosystem can sustain before being fundamentally altered requires simulation with mathematical models that aim to represent the key ecological components and processes which govern cascades.

StrathE2E2 models both bottom-up and top-down trophic cascades in shelf-sea ecosystems, spanning inorganic and organic nutrients through to birds and mammals. The model takes a highly macroscopic, view of ecology, aggregating over the many microscopic details of taxonomy, demography and spatial structure. The aim is to represent the gross dynamics with a tolerable parameter count so as to enable 'big-picture' strategic scenario analyses.

The model is supported by functions enabling computational parameter optimization, sensitivity analysis and estimation of credible intervals of model outputs. The scheme comprises a fishing fleet model and an ecology model with coupling between the two.

2 Ecology model general description

The ecology model is a network of mass conserving coupled ordinary differential equations (ODEs) describing spatially averaged rates of change in state variables representing organic detritus, dissolved inorganic nutrient, and living biomass. To simplify the description we can think of the variables as being divided between two coupled sub-networks: a predator-prey network - the food web - and a nutrient recycling network. Between the two, all marine life-forms are explicitly or implicitly accounted for, but aggregated into coarse groups or 'guilds' defined mainly by feeding characteristics and diet preferences (**Figure 1**). All state variables, except macrophytes, are expressed solely in terms of nitrogen mass, since this element is the most commonly limiting in temperate shelf seas. Macrophytes are expressed in terms of both nitrogen and carbon mass with dynamic stoichiometry since these organisms have an exceptional capacity to seasonally absorb and store nitrogen.

Each ODE comprises a set of rate-of-change terms representing a variety of biological and physical processes (**Box 1, Box 2** for macrophytes). Biological terms describe the balance between gains due to assimilation of food, and losses due to mortality and metabolism. Some components of the food web (planktivorous and demersal fish; suspension/deposit feeding and carnivore/scavenge feeding benthos) are resolved into life-stages and for these the equations also include the balance between gains due to recruitment and losses due to developmental progression or spawning. In addition, all components of the model are, in principle, replicated across homogeneous spatial compartments. To facilitate this each ODE also includes terms representing sinking, advection, mixing and migration flows through the system.

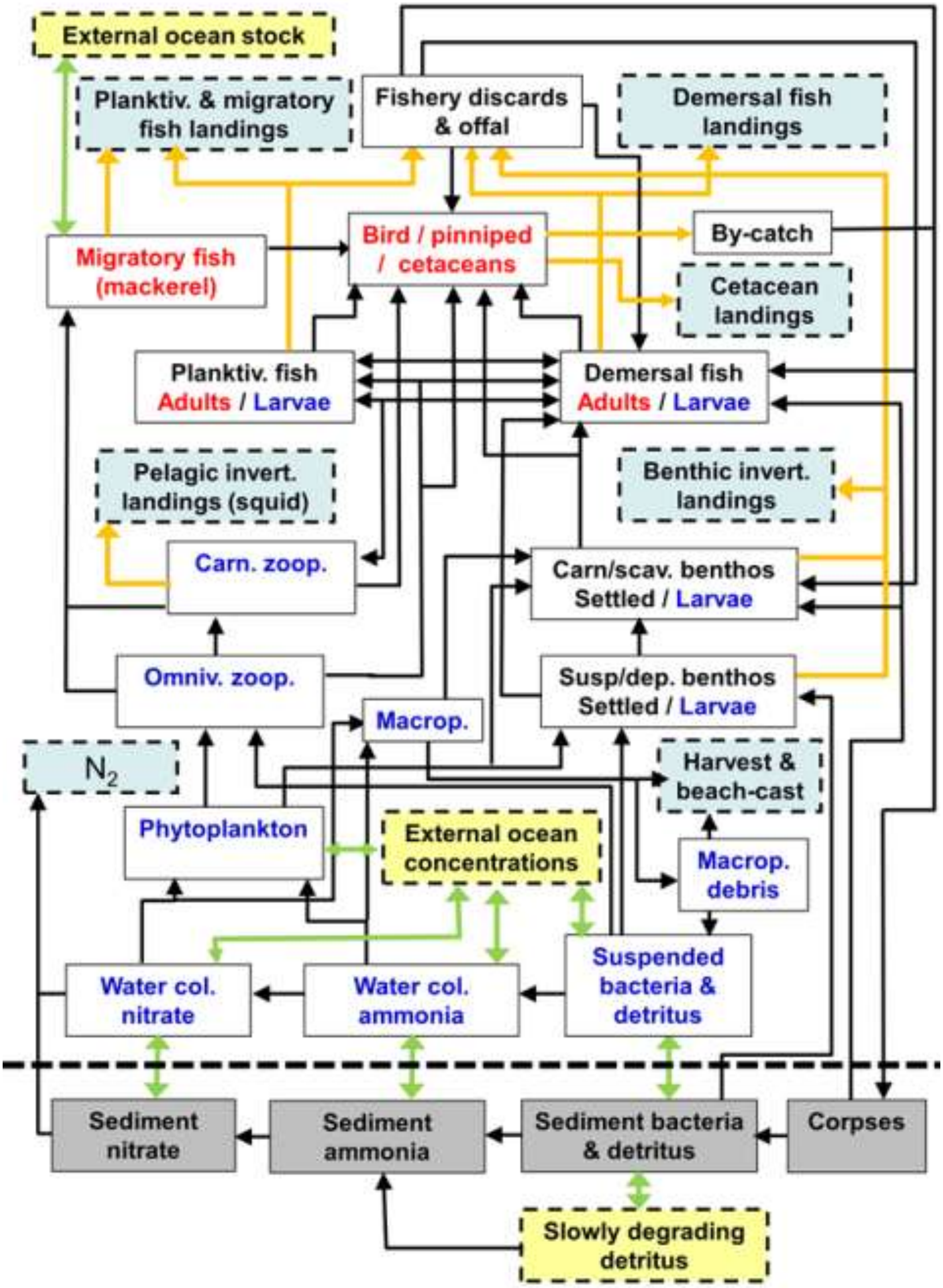

FIGURE 1. Schematic of the food web compartments of the StrathE2E2 model. Green arrows represent advection, mixing and migration; orange arrows represent fishery-related fluxes; black arrows represent biological fluxes. Red labelled components are active migrators whilst blue are subject to passive advection and mixing and black are anchored. Pale blue boxes represent quantities that are exported from the model whilst yellow are imported. The model also includes fluxes from living components to ammonia, detritus and corpses due to excretion, defecation and death but these are not shown for clarity. Also for clarity, birds, pinnipeds and cetaceans are combined as a single box but in the model are separate entities. The abbreviation "Macrop." is shorthand for macrophytes.

BOX 1 Differential equations for the rate of change of living components in the model food web, apart from macrophytes. All mass in molar nitrogen units.

General equation for the rate of change of a food web component (*X*) given a set of *k* prey types (N_k) and a set of *j* predator types (Y_j), is:

$$\frac{dX}{dt} = A\sum_{k} U_{X(N_k)} - \sum_{j} U_{Y_j(X)} - \varepsilon(t)X - \delta X^2 + F_X - H(t)X - D(t)X + R_X$$

$Uv_1(v_2)$	Flux of ingestate to a predator (v_1) from prey (v_2). ($v_1, v_2 = X, N$ or $v_1, v_2 = Y, X$)
A	Assimilation efficiency. Ingestate not assimilated ($(1-A)\sum_k U_{X(N_k)}$) is divided equally between a flux to dissolved ammonia, and a flux to detritus.
ε(t)	Q_{10} temperature, and hence time-dependent basal metabolic rate coefficient (generates a flux from body mass to ammonia)
δ	Density dependent mortality coefficient (generates a flux from body mass to a detritus category)
F_X	Integral of all vertical and horizontal advection and diffusion fluxes affecting the food web component
H(t)	Harvest ratio (time-dependent rate of biomass capture by fisheries)
D(t)	Time-dependent developmental export rate for the food web component *X*. For *X* = adult stages, *D(t)X* represents the flux of spawning products to the egg, larval and juvenile (ELJ) stage. For *X* = ELJ stages, *D(t)X* represents the settlement flux to adults. For food web components lacking demographic structure, *D(t)* = 0
R_X	Recruitment flux to the food web component *X*. For *X* = adult stages, R_X is equal to the settlement flux from the ELJ stage. For *X* = ELJ stages R_X is equal to the flux of spawning products from the adults. For food web components lacking demographic structure, *Rx* = 0

General equation for the flux of ingestate to a predator (v_1) from prey (v_2) is:

$$U_{v_1(v_2)} = \frac{v_1.\, v_2.\, \rho_{v_1(v_2)}.\, Umax_{v_1}}{v_2 + h_{v_1}}$$

$\rho_{v_1(v_2)}$	Preference of the predator v_1 for the prey class v_2. For a given predator class, the sum of the preference coefficients over all prey classes = 1.
$Umax_{v_1}$	Q_{10} temperature, and hence time-dependent maximum uptake rate of the predator v_1
h_{v_1}	Half-saturation constant for uptake of prey by the predator v_1 (temperature independent)

For phytoplankton (v_1 = phytoplankton *(X = P)*), the assimilation efficiency *A* =1, temperature dependent basal metabolic rate coefficient *ε* = 0, and there is no demographic structure so *D(t)* = 0 (and hence R_X = 0). The uptake of prey (v_2 = dissolved nutrient N_k) has a light-dependent term:

$$U_{P(N_k)} = Min\left\{1, \frac{L(t)}{L_{max}}\right\} \frac{P.\, N_k.\, \rho_{P(N_k)}.\, Umax_P}{N_k + h_P}$$

L(t)	Time-dependent light intensity
L_{max}	Saturation light intensity for nutrient uptake

For the top-predators in the food web (birds, pinnipeds and cetaceans), uptake of prey follows the predator-density dependent Beddington-DeAngelis function (Beddington, 1975; DeAngelis *et al.,* 1975) rather than Michelis Menten, with an additional parameter γ:

$$U_{v_1(v_2)} = \frac{v_1.\, v_2.\, \rho_{v_1(v_2)}.\, Umax_{v_1}}{v_2 + \gamma v_1 + h_{v_1}}$$

BOX 2 Differential equations for the rate of change of macrophyte forest biomass. Macrophyte mass is resolved into molar nitrogen and carbon components (X_N and X_C).

Equation for the rate of change of macrophyte forest nitrogen (X_N) given a set of k nitrogen nutrient types (N_k) and a set of j predator types (Y_j), is:

$$\frac{dX_N}{dt} = Q_N \sum_k U_{X_N(N_k)} - \sum_j U_{Y_j(X_N)} - \left(W(t)\, \zeta\, {X_C}^2\right) \frac{X_N}{X_C} - H(t) X_N$$

Equation for the rate of change of macrophyte forest carbon (X_C) given a set of j predator types (Y_j), is:

$$\frac{dX_C}{dt} = Q_C U_{X_C} - \sum_j U_{Y_j(X_N)} . \frac{X_C}{X_N} - \varepsilon(t) {X_C}^2 - \left(W(t)\, \zeta\, {X_C}^2\right) - H(t) X_C$$

$Uv_1(v_2)$	Flux of nitrogen to a predator (v_1) from prey (v_2). (v_1,v_2 = *macrophyte and nutrient* (X_N,N_k) or v_1,v_2 = *predator and macrophyte* (Y_j,X_N))
Ux_C	Flux of carbon to macrophyte (X_C)
Q_N	Carbon-dependent attenuation coefficient for nitrogen uptake
Q_C	Nitrogen-dependent attenuation coefficient for carbon uptake
$W(t)$	Time-dependent significant wave height
ζ	Coefficient for density dependent destruction of forest carbon by wave action. Creates a flux to the 'macrophyte debris' class of detritus.
$H(t)$	Harvest ratio (time-dependent rate of biomass harvesting)
$\varepsilon(t)$	Q_{10} temperature, and hence time-dependent coefficient for density dependent exudation loss of carbon as carbohydrate

Uptake flux of macrophyte by grazing predators ($U_{Y_j(X_N)}$) as in the general equations (Box 1)

Uptake flux of nutrient (k = nitrate or ammonia) into the macrophyte nitrogen pool is:

$$U_{XN,(N_k)} = \frac{X_C . N_k . \rho_{X_N(N_k)} . Umax_{X_N}}{N_k + h_{X_N}}$$

Note that nitrogen uptake is dependent on macrophyte carbon mass (X_C)

$\rho_{X_N(N_k)}$	Preference of the macrophyte for the nutrient N_k. The sum of the preference coefficients over all nutrient classes = 1.
$Umax_{X_N}$	Q_{10} temperature-dependent maximum uptake rate by the macrophyte X_N
h_{X_N}	Half-saturation constant for uptake of nutrient by the macrophyte X_N (temperature independent)

Uptake flux of carbon by the macrophyte is:

$$U_{X_C} = Min\left\{\left(X_C\, Umax_{X_C}\right), \left(X_C\, Umax_{X_C} \frac{L(t). e^{-X_C.S}}{L_{max}}\right)\right\}$$

$Umax_{X_C}$	Temperature-dependent maximum uptake rate of carbon by the macrophyte X_C
$L(t)$	Time-dependent light intensity
L_{max}	Saturation light intensity for carbon uptake
S	Self-shading coefficient

Carbon-dependent attenuation coefficient for nitrogen uptake

$$Q_N = \left\{0 \le \frac{1}{(\Phi_{max} - \Phi_{min})} \left(\Phi_{max} - \frac{X_N}{X_C}\right) \le 1\right\}$$

Nitrogen-dependent attenuation coefficient for carbon uptake

$$Q_C = \left\{0 \le \frac{1}{(\Phi_{max} - \Phi_{min})} \left(\frac{X_N}{X_C} - \Phi_{min}\right) \le 1\right\}$$

Φ_{max}	Maximum permitted ratio of macrophyte nitrogen : carbon ratio
Φ_{min}	Minimum permitted ratio of macrophyte nitrogen : carbon ratio

The spatial structure is highly stylised, consistent with the coarse guild-definitions of the living and chemical components of the system. Two horizontally distinct but interconnected bathymetric/hydrographic zones are distinguished - a shallow, vertically mixed zone mostly influenced by tides and freshwater inputs, and a deeper, potentially seasonally stratified zone mostly influenced by exchange with an external ocean (**Figure** 2). For convenience we refer to these as the inshore and offshore zones respectively, though there is no necessity for the inshore zone to be adjacent to the coast - in principle it could represent a shallow offshore bank. The water column in the offshore zone is divided vertically into two compartments or layers, whilst the inshore zone is represented by a single compartment. The offshore zone can optionally be configures to overhang over deep ocean, creating an additional external boundary from vertical exchange with the model.

Seabed habitats are represented by exposed rock and up to three compartments of different sediment properties in each zone, each defined by median grain size and natural disturbance rates. State variables are resolved hierarchically to spatial compartments with the largest (in terms of body size) and/or most mobile guilds being represented at the coarsest spatial resolution (**Table 1**). The nominal sea surface area of the model domain is 1m^2 sea surface area. Hence, the units of all the state variables (mM nitrogen) are also scaled to a domain of 1m^2.

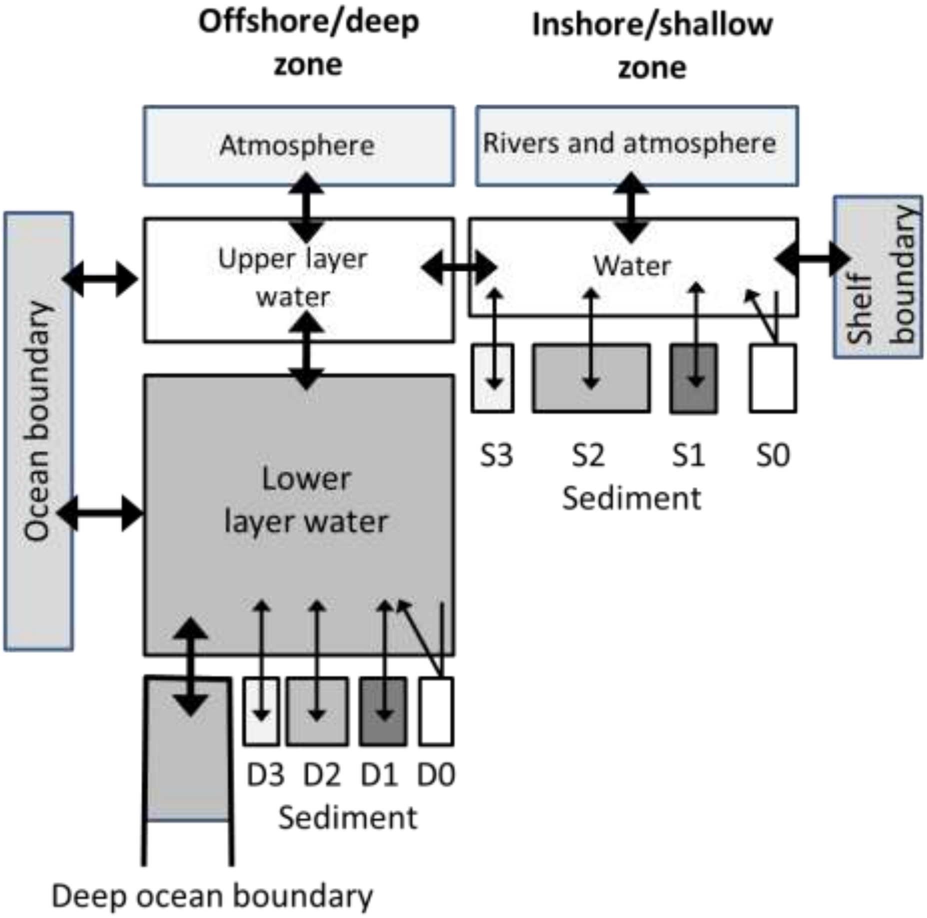

FIGURE 2. Schematic showing the horizontal and vertical spatial structure of the model. The compartments S0-S3 and D0-D3 refer to inshore/shallow and offshore/deep seabed sediment habitats respectively. S0 and D0 are rock habitats which reflect, rather than absorb, settling material back into the water column.

TABLE 1. Ecology model state variables and spatial hierarchy.

Differentiated by horizontal zone and sediment habitat	**Differentiated by horizontal zone and water column layer**	**Differentiated by horizontal zone with modelled vertical distribution**	**Differentiated by horizontal zone only**
Sediment bacteria and labile detritus	Water column nitrate	Omnivorous zooplankton	Suspension/deposit feeding benthos
Refractory sediment detritus	Water column ammonia	Carnivorous zooplankton	Carnivore/scavenge feeding benthos
Pore-water nitrate	Suspended bacteria and detritus	Larvae of suspension/deposit feeding benthos	Planktivorous fish
Pore-water ammonia	Phytoplankton	Larvae of carnivore/scavenge feeding benthos	Demersal fish (divided into fishery quota-limited and non-quota components)
Fishery discards		Larvae of planktivorous fish	Migratory fish
Corpses		Larvae of demersal fish	Pinnipeds
Macrophytes (confined to inshore rock habitat)			Seabirds
			Cetaceans

2.1 Predator-prey connections, demography and mortality

Ingestion of prey by a predator is governed by a preference matrix and a standard type II response in which per-unit-biomass predator consumption rates increase asymptotically towards a Q_{10} temperature-dependent maximum with increasing prey concentration (**Box 1**). A proportion of ingested food becomes new body mass in the predator. The remainder is divided equally between fluxes to organic detritus and ammonia, to represent defecation of undigested material and food-dependent metabolism. Background (non-feeding) metabolism increases with temperature but with a higher Q_{10} than maximum uptake rates, so the net result is that productivity, i.e. production rate per unit biomass, will exhibit a dome-shaped response to temperature.

2.2 Nutrient recycling network

Six forms of organic detritus are represented in the recycling network: suspended material, labile and refractory sediment material, 'macrophyte debris', 'corpses', and 'discards'. Both the suspended and sediment fractions implicitly include dissolved and particulate organic matter and associated bacterial flora, and are formed in the living food web by defecation and density-dependent mortality fluxes from plankton and the larval stages of fish and benthos. Corpses are produced by density-dependent mortality of fish, benthos and top predators, and the decay of discards. The latter are a short-lived, special form of detritus generated as a by-product of fishery harvesting. Macrophyte debris is created by wave and density-dependent destruction of living macrophyte forest biomass. All forms of detritus are regarded as a potential food source for detritivorous and scavenge feeding guilds of living organisms.

The dynamics of each detritus and dissolved nutrient category are governed by an ODE in which the rate-of-change terms correspond to the production and consumption rates elsewhere in the food web, plus physical flows between spatial compartments. Q_{10} temperature-dependent coefficients govern transformations between different forms of detritus, conversions of detritus into ammonia (mineralisation); ammonia to nitrate (nitrification), and nitrate to nitrogen gas (denitrification). To complete the biogeochemical cycle, nitrate and ammonia are re-absorbed into the food web by phytoplankton and macrophytes, governed by light and temperature-dependent uptake responses.

2.3 Interior and boundary fluxes: sinking, advection, mixing and migration terms

Passive transport (sinking, advection, and mixing) and, where appropriate, active migration terms in each ODE form the links between the vertical and horizontal spatial compartments of the model, and connections to the world outside the model domain.

Passive fluxes between water column compartments within the model domain are the product of the dynamic differences in concentrations between vertical or horizontal spatial compartments, scaled by hydrodynamic mixing coefficients supplied as time-varying parameters. Active vertical and horizontal migration fluxes of zooplankton, fish and top-predators between spatial compartments are modelled as if motivated by food - migration is directed up gradients in the ratio of preference-weighted prey:predator concentrations.

Differences in nutrient concentrations between sediment pore waters and the overlying water column generate a diffusion flux with the rate coefficient defined by sediment permeability. Disturbance also generates a nutrient flux, and is modelled as an instantaneous equilibration of pore-water and water column concentrations in the disturbed volume-fraction of each sediment layer. Three types of sediment disturbance are represented - bioturbation by deposit feeding benthos, natural erosion by bed shear stress, and fishing-related abrasion. Disturbance also generates a resuspension flux of labile sediment detritus to suspended detritus. Conversely, deposition of suspended detritus to become labile sediment material is regarded as a first-order rate process.

Influxes of material to the model domain from the world outside are defined by driving data-sets. These comprise hydrodynamic flows of dissolved nutrient, suspended detritus and phytoplankton from adjacent sea-regions, dry and wet deposition of atmospheric nutrient to the sea surface, nutrient inputs from river discharges and other unspecified sources (e.g. aquaculture), and the active immigration flux of migratory species. Boundary export fluxes, which are dynamic and computed by the model, comprise hydrodynamic losses of nutrient, suspended detritus and phytoplankton to adjacent sea-regions assuming conservation of fluid volume within the model domain, loss of gaseous nitrogen generated by denitrification, burial of refractory organic nitrogen in the sediments, emigration of migratory species, beach-cast of macrophyte debris, and extraction of biomass by fishing.

The inputs to, and outputs from, the ecology model are summarised in **Table 2**.

TABLE 2 Ecology model parameters, input and outputs

Static configuration data
Model domain sea surface area; area-proportions of bathymetric zones and water column layer thicknesses; area-proportions of seabed habitats and median grain sizes of sediments
Parameters for deriving sediment porosity, permeability and organic nitrogen content in each seabed habitat from median grain size, and light attenuation coefficients from suspended particulate matter (SPM) concentration
Ocean biomass of migratory fish stock and the annual proportion entering the model domain

Monthly resolution internal driving data
Proportion of each seabed habitat sediment layer volume disturbed by natural bed shear stress per unit time.
Vertical mixing and horizontal advection rates between compartments within the model
Temperature and suspended particulate matter concentrations in water column layers, sea surface irradiance in each depth zone, significant wave height adjacent to the coast
Monthly resolution external boundary influxes of nutrient
Volume inflows across the external ocean boundaries of the model and from rivers, and concentrations of nutrient, phytoplankton and suspended detritus in the inflows
Atmospheric deposition of nutrient to the sea surface
Other nutrient discharges into the model domain (assumed to enter the inshore zone)
Inputs from the fishing fleet model
Inshore and offshore zone harvest ratios, proportions of catch rejected (discarded) and proportions of retained catch processed at sea for each resource guild
Area-proportion of each seabed habitat abraded by trawling per unit time
Proportion of discards and offal deposited over each seabed habitat
Biological parameters (* indicates fitted parameters)
*Prey preference parameters for each predator-prey pairing
*Maximum uptake rate and prey half saturation concentration for each consumer guild
*First-order rate coefficients for microbial processes
*Density dependent mortality coefficients
*Coefficients for active horizontal migration rates of fish and top-predators
*Sinking rates for detritus
*Parameters for the exploitable fraction of biomass for each guild subjected to fishing.
Saturating irradiances for nutrient uptake by phytoplankton, and carbon uptake by macrophytes
Assimilation efficiency for each consumer guild
Maximum and minimum nitrogen:carbon ratios for macrophytes
Food-independent metabolic rates for each consumer guild, and density-dependent carbohydrate excretion rate for macrophytes
Q_{10} temperature dependency coefficients for autotropic and heterotrophic maximum uptake rates, metabolic rates and microbial processes
Annual weight-specific fecundities for fish and benthos guilds; start and end dates for egg production, and for recruitment of larval stages to the settled stocks
Start and end dates for immigration and emigration of migratory fish
Parameters for relationship between demersal fish biomass and a) proportion of non-quota demersal fish and b) proportion of undersize quota-limited and non-quota fish in the catches
Model outputs (all at daily intervals)
Mass of each state variable
Model import and export fluxes (transport, atmospheric deposition, river inflows, denitrification, fishery landings)
Derived internal fluxes: consumption flux for each prey-predator pair, consumption and production fluxes of nitrate and ammonia in each depth zone and layer, fishery discards and offal

2.4 Representation of fishing in the ecology model

Living biomass guilds considered vulnerable to targeted capture or incidental by-catch by fishing gears are the top-predators (birds, pinnipeds and cetaceans); planktivorous, demersal and migratory fish; carnivorous/scavenge and suspension/deposit feeding benthos, carnivorous zooplankton, and macrophytes. In each case, the fishing process is represented in the ODE for each guild by a 'harvest ratio' (proportion of instantaneous biomass captured per unit time). Then, a proportion of the catch is directed to the discards class, comprising whole-animal rejects and viscera arising from at-sea processing of the remaining catch. Only the residual fraction of the catch weight is exported from the model to represent landings.

In addition to the direct capture process, three collateral effects of fishing activity are represented in the ecology model - release of pore-water nutrients, resuspension of sediment detritus, and damage mortality of benthos, due to sea-bed abrasion by bottom-contact mobile fishing gears. These processes are driven by the area-proportion of each seabed sediment habitat abraded per unit time by fishing gears.

3 Fishing fleet model description

The fishing fleet model is a static, matrix-based scheme which integrates across up to 12 different types of fishing gears to assemble the data on harvest ratios and discard rates for each guild and abrasion rates for each seabed habitat that are required as inputs to the ecology model. Key inputs are, for each gear type, the spatial distribution of activity density, catching power, selectivity, discard and at-sea processing rates for each ecology model guild, and contact rate with the seabed (**Table 3**). Activity density is defined as the deployment duration of a given gear per unit sea surface area in a given time interval, integrated across all vessels (units: m^{-2}). The power of a gear is a measure of its efficiency at catching biomass of a given resource guild. The product of activity density and power is a quantity that we refer to as fishing effort. For a given resource guild, effort is proportional to the harvest ratio and so can be summed across gears.

TABLE 3 Fishing fleet model inputs and outputs

Input data for each gear type (maximum 12 types)
Annual model domain averaged fleet activity density (number of boats x time spent fishing per boat, per day, per unit area)
Proportion of annual activity over each model seabed habitat
Selectivity (catching power) for each ecology model resource guild
Rejection (discard) rate for each ecology model resource guild
Proportion of each catch guild processed (gutted) at sea
Seabed area abraded per unit activity
Gear-independent parameters
Parameters for scaling effort (activity x power) to harvest ratio for each ecology model resource guild
Seabed sediment penetration depth (common value across all gears)
Damage-related mortality rate of benthos per bottom-contact gear pass (common value across all gears)
Proportion by weight of viscera for catch guilds processed at sea
Model outputs
Bathymetric zone harvest ratios and processing-at-sea and discard rates for each ecology

model resource guild due to all gears combined (required for input to the ecology model)
Area-proportion of each seabed habitat abraded per unit time by all gears combined (required for input to the ecology model)
Proportion of discards (rejects and offal) from all gears combined, which are deposited over each seabed habitat (required for input to the ecology model)
For each horizontal zone separately, proportion of total effort directed at each ecology model resource guild which is attributable to each gear (required for disaggregating simulated landings and discards to individual gears from ecology model output)

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