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Ecosystem limits to food web fluxes and fisheries yields in the North Sea simulated with an end-to-end food web model.

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SUPPLEMENTARY MATERIAL

Technical description of the ecosystem model.

1. Physical structure

The model resolved 2 water column layers, and an underlying sediment layer in the vertical plane, because seasonal vertical layering has a defining influence on the food web fluxes of shelf seas (Tett, 1981). Fluxes of material across the internal interface between the water column layers were represented as being due to sinking, vertical advection and mixing, and also implicitly due to the activity of vertically migrating grazers. Vertical exchanges of dissolved inorganic components between the sediment layer and the overlying water layer were represented as a diffusive process, whilst the flux of particulate matter between the sediment and overlying water was due to sinking, predation on benthos by water-column living fauna, and filter-feeding by benthos.

2. The state variables

2.1. Primary producers

Phytoplankton were represented by a single guild which utilized both nitrate and ammonia but with different preferences. Nutrient uptake by phytoplankton guilds was constrained to the surface layer and formulated to depend on depth mean daily irradiance, and the mass of phytoplankton was subject to vertical exchange between layers by sinking, advection and mixing. Losses of phytoplankton were due to advection out of the model, predation by zooplankton, and a density-independent lysis rate. Phytoplankton biomass lost due to lysis was transferred to the suspended detritus state variable.

2.2. Zooplankton

Two guilds of zooplankton were represented. Herbivorous zooplankton (conceptually taxa ranging from micro-zooplankton to copepods) fed on phytoplankton and

suspended detritus. Carnivorous zooplankton (conceptually large predatory crustaceans and soft-bodied invertebrate predators) fed on herbivorous zooplankton and larval fish.

Both zooplankton guilds were represented as depth integrated populations, implying that their active migration behaviour outweighed any vertical exchanges due to physical advection and mixing. Herbivorous zooplankton distributed their feeding activity between the surface and deep layers in proportion to the vertical distribution of their prey. Both herbivorous and carnivorous zooplankton excreted to the surface and deep layer ammonia pools in proportion to layer thicknesses, but defecated material was transferred directly to the deep water detritus layer, reflecting the rapid sinking rate of zooplankton faecal particles.

2.3. Benthos

Benthic fauna were resolved into suspension/deposit feeding. and carnivorous/scavenge feeding guilds. The suspension/deposit feeders consumed suspended detritus and phytoplankton from that part of the water column assigned for them to filter, and sedimentary detritus. The carnivorous/scavenge guild fed on suspension/deposit feeders and the corpses of other guilds produced by densitydependent mortality (see later). In the model, both benthos guilds defecated detritus to the sediment layer and excreted ammonia to the deep layer of the water column. Both the suspension/deposit feeding and carnivorous/scavenge benthos guilds were potentially subject to harvesting by fishing.

2.4. Fish

Fish were resolved into pelagic and demersal guilds. Each guild had an internal demographic structure represented by an early life history stage (eggs and larvae), which for convenience is hereafter referred to here as "larvae", and a post-larval/mature stage which is referred to here as "adults". Adults were potentially subject to harvesting by fishing whilst larvae were not. Within a set interval of days each year, adult fish shed a percentage of their biomass per day which was transferred directly to larvae as a representation of spawning. Within a different set interval of days each year, a percentage of the biomass of larvae per day recruited to the adults.

Fish larvae (of both pelagic and demersal fish) fed on herbivorous zooplankton, and were preyed upon by carnivorous zooplankton and the adults of pelagic and demersal fish. Adult pelagic fish fed on herbivorous and carnivorous zooplankton, and larval fish. Adult demersal fish fed on carnivorous zooplankton, but not herbivorous zooplankton, all types of benthos, adult and larval fish, fishery discards and corpses (see later). Adult pelagic and demersal fish were preyed on by the top predator guild in the model.

Demersal fish excreted ammonia and defecated detritus only to the deep water column layer, whilst pelagic fish and all larval fish excreted to the surface layer and defecated to the deep water column layer.

2.5. Top predators

The top predators in the model were conceived as birds and mammals, and represented by a single demographically unstructured guild. The top-predator guild fed on adult pelagic and demersal fish, discards from the fisheries (see later), and corpses. Top predators excreted to the surface layer and defecated detritus to the deep layer.

2.6. Detritus and dissolved inorganic components

The model resolved ammonia and nitrate concentrations in the water column and sediment pore water layers, and various forms of organic detritus. Transformations between detritus and inorganic nitrogen in the real world are due to bacterial activity, but the model did not resolve the biomass of bacteria explicitly. To do so effectively, would require representation of, at least, carbon and oxygen dynamics in order to meaningfully articulate bacterial dynamics. The activities of bacteria with respect to nitrogen were therefore represented by three rates of exchange between the non-living components; 1) mineralization of detritus to ammonia, 2) nitrification of ammonia to nitrate, and 3) denitrification of nitrate to nitrogen gas. Denitrification was effectively a sink term for nitrogen in the model since there was no return process of nitrogen fixation.

Suspended detritus in the surface and deep layers originated from the defecation of zooplankton, fish and top predators, and the lysis of phytoplankton cells. Suspended detritus had a sinking rate expressed as a proportion per day transferring from the surface to deep layer, and from the deep layer to the sediment, and was also exchanged vertically by mixing and advection. For settlement from the deep layer to the sediment the proportion per day was also inversely related to the vertical mixing rate so that a smaller proportion settled to the sediment in more strongly mixed systems, as a caricature of the re-suspension of sediment in regions of strong tidal flow or during meteorological mixing events.

Detritus in the water column was consumed by bacterial mineralization and converted to ammonia, and grazed by herbivorous zooplankton. In the deep layer, suspension/deposit feeding benthos could also feed on suspended detritus in a layer of a given thickness above the seabed. Detritus was assumed to be uniformly distributed through the deep layer, so only a fraction of the deep layer suspended detritus was available to the benthos.

Sediment detritus was also consumed by the suspension/deposit feeding benthos guild, and mineralised by bacteria to ammonia. Ammonia produced in the seabed by mineralization and nitrate produced by nitrification of ammonia, contributed to dissolved pools in the pore-water layer. Exchange of ammonia and nitrate between the sediment pore-waters and the deep water column layer was then governed by the sediment-water diffusion coefficient acting on the concentration gradient across the interface.

Additional forms of detritus were included in the model to represent the corpses of the larger taxa in the food web (carnivorous benthos and plankton, fish, and birds/mammals). Fishery discards (see later) formed a food resource in the water column for birds/mammals and demersal fish, and were transformed at a fixed proportion per day to corpses. Corpses were also produced as a result of density-dependent mortality, and were consumed by carnivorous benthos, adult demersal fish and birds/mammals, and a temperature dependent proportion of their mass per day was converted to sediment detritus.

3. Biological rate processes

3.1. Bio-geochemical rates

Rates of mineralization, nitrification and denitrification were defined by proportions of substrate consumed per day. Temperature has a profound effect on bacterial processes, so these rate parameters were temperature dependent according to a Q_{10} relationship (see later).

3.2. Grazer uptake rates

The mass flux from prey to predator per unit time (Ω , mMN m⁻² d⁻¹) was given by a Michaelis-Menten relation.:

$$\Omega = \frac{predator . prey . pref_{prey-predator} .U_{max(predator)}}{prey + (h_{predator} .(T_l))}$$
(1)

The term *prey* referred to the abundance (mMN m⁻²) of a given prey guild in a depth layer of thickness T₁, whilst *predator* referred to the abundance (mMN m⁻²) of a predator guild. The half-saturation concentration $h_{predator}$ (mMN m⁻³) was considered to be independent of temperature, and the same for all prey of a given predator. The term $U_{max(predator)}$ (mMN. mMN⁻¹.d⁻¹) represented the maximum uptake rate of all prey classes combined by the predator guild, and was assumed be dependent on sea temperature according to a Q₁₀ function for all predators except birds/mammals.

The relative contributions of prey classes to uptake by a predator guild was set by the preference parameter $pref_{prey-predator}$. The value of the parameter represented the proportion of total uptake if all prey classes were present at equal concentration. Hence the sum of all prey preferences for a given predator was always unity. Note that this differs from formulations for representing weight-specific uptakes of multiple prey types by predators at a species level. When multiple prey classes are available to a species the effective concentration of prey against which the degree of saturation is judged, is the sum over all prey classes, with a preference term to scale the electivity of the predator of each prey class. Hence, a super-abundance of one prey class inhibits the uptake of others, for example:

$$\frac{\Omega}{predator} = \frac{prey. \ pref_{preyr} \ U_{\max(predator)}}{\sum (prey.pref_{prey}) + h_{predator}}.$$
(2)

In the model described here, however, the taxonomic range implicit in each guild was such that whilst a predator guild might rely on multiple prey guilds, there should be many species within the predator guild whose diets would not overlap. Hence, there was no *a priori* reason to suppose that uptake of one prey guild should markedly influence the uptake of others. For this reason, the uptake rates of different prey by a predator guild were represented as being independent and additive.

3.3. Autotrophic uptake functions

Primary production was represented by the light and concentration-dependent uptake rate of nutrient (nitrate or ammonia) by the phytoplankton guild (Ω , mMN.m⁻².d⁻¹). Exactly as for the uptake of prey by predators, the mass of nutrient taken up per unit time was represented by a Michaelis-Menten relation with no interaction between nutrients (Dortch, 1990). However, in addition, nutrient uptake was scaled by the depth mean daily irradiance, such that uptake was zero at zero irradiance and increasing lineally to a maximum rate at a saturating value of daily depth mean irradiance (L_{max}). Hence:

$$\Omega = Min \left\{ 1.0, \frac{L}{L_{\max}} \right\} \cdot \frac{phytoplankton \cdot nutrient \cdot pref_{nutrient - phytoplankton} \cdot U_{\max(phytoplankton)}}{nutrient + (h_{phytoplankton} \cdot T_l)}$$
(3)

As for the heterotrophic uptake processes, the parameter U_{max} (d⁻¹) was assumed to be temperature dependent and the half-saturation term h_{phytoplankton} was assumed to be independent of nutrient type. There is ample support from analyses of field data on depth integrated carbon and nitrogen assimilation for expressing biomass-specific uptake by coarse functional group of phytoplankton in terms of linear functions of depth averaged irradiance (Platt *et al.*, 1990; Forget et al., 2007; Lund-Hansen and Sorensen, 2009).

Autotrophic fixation of atmospheric nitrogen by cyanobacteria was disregard. In some ecosystems, direct nitrogen fixation can be a significant input to the nitrogen budget but the available evidence suggest that this is probably not important in the North Sea (Lipshultz and Owens, 1996).

3.4. Metabolism

Food ingested by heterotroph guilds was either assimilated or was passed to detritus and ammonia. The proportion assimilated was governed by a constant assimilation coefficient. Half of the non-assimilated food was assumed to be lost to detritus and half to ammonia. In addition to this feeding dependent ammonia excretion, all heterotroph guilds excreted a proportion of their biomass per day as ammonia, as a caricature of basal metabolism. The proportion excreted per day was assumed to be temperature dependent according to a Q_{10} function for all categories of heterotrophs except the top predators.

3.5. Density dependent mortality

Density-dependent mortality terms were included for carnivorous zooplankton, carnivorous/scavenge feeding benthos, larval and adult fish, and birds/mammals, and represented by quadratic functions defining a flux of biomass to corpses (flux of guild j to corpses = $z_j.j^2$). Hence the weight specific mortality rate increased linearly with guild biomass. Conceptually, the density-dependent mortality was regarded as a caricature of constraints on survival due to limitations of space (e.g. limited sheltering habitat for benthic fauna), or the attraction of predators to spatial aggregations of prey (e.g. attraction of piscivoious birds to schools of pelagic fish), or outbreaks of disease or parasitism at high population densities (e.g. high incidence of *Ichthyophonus hoferi* in herring during period of high stock density, Mellergaard and Spanggaard, 1997). In the model, the biomass killed by density dependent mortality was retained within the food web by allowing for scavenge feeding on corpses by carnivorous/scavenging benthos, adult demersal fish and birds/mammals.

3.6. Temperature dependency

For the uptake and metabolic parameters identified as being subject to temperature dependency, the response was represented by a Q_{10} function:

$$k = \exp\left(\frac{1}{10}(T - T_R) \log_e Q_{10} + \log_e k_{TR}\right)$$
(4)

where T_R was the reference temperature and k_{TR} was the value of the parameter k at the reference temperature. Parameters assumed to be sensitive to temperature were all uptake rates, background metabolism, and bacterial mineralization, nitrification and denitrification.

3.7. Fishing

Two key effects of fishing on the food web were represented in the model, in addition to the obvious mortality inflicted on fish and the removal of biomass from the system. Targeted catches of fish and benthos by four fishing 'fleets' were expressed as proportions of biomass captured per day (harvest rates). The four fleets were pelagic and demersal fisheries which targeted adult pelagic and demersal fish respectively, and two types of shellfish fisheries which targeted the suspension/deposit and carnivorous/scavenge feeding benthos. The two additional effects of fishing were bycatching and discarding. By-catch refers to the collateral mortality inflicted on nontarget guilds by a fishery, and was represented in the model as by-catch of benthos guilds by the demersal fishery. Discarding includes a) accidental or intentional (due to quota restrictions) spillage of marketable targeted catch from nets during gear recovery, b) throwing overboard of dead biomass of un-marketable species, and under-size or low value individuals of otherwise marketable species, and c) offal removed from the fish during gutting operations which is thrown overboard. In addition, though not normally regarded as a discard, fish which escape through net meshes but are damaged and do not survive, are functionally equivalent to discards. These components of the catch formed a potential food resource in the model for demersal fish, birds and mammals, and were also converted to corpses at a fixed daily rate representing settlement to the seabed.

There are few data on the collateral mortality rates inflicted on benthos fauna due to demersal fishing. As a rough estimate a collateral harvesting rate of 0.001-times the demersal fish harvesting rate was applied to both the suspension/deposit and carnivorous benthos guilds to represent by-catch. 100% of this by-catch was considered to be rejected at sea, so was retained in the model as discards. The by-catch in the model also functionally included fauna which are damaged and killed by the fishing gear but not actually retained by the net, which could be the case for many fragile benthic taxa.

Discarding of targeted guilds was represented as either a fixed or a variable proportion of catch. Fisheries for pelagic fish and benthos are generally highly targeted, that is, the catching process discriminates by virtue of location, fishing gear or technology (e.g. sonar) between species and, in the case of pelagic fish, sizes which are of marketable value. In addition, catches of pelagic fish are usually landed in bulk and not sorted or graded at sea. Hence, as a starting assumption the proportion of catch discarded from these fisheries was expected to be relatively low and constant. In contrast, fisheries for demersal fish are generally indiscriminate and the catch is intensively sorted and graded at sea. There is clear evidence that the proportion by weight of large fish in the North Sea demersal community has declined over time since the 1970's in parallel with stock abundances (Greenstreet et al. 2010). Hence, we would expect the proportion by weight of discardable fish (smaller than the

minimum landing size) to have increased in inverse relation to biomass. The discarded fraction of demersal fish catches ($disc_d$) was therefore parameterized as a function of adult demersal biomass:

$$disc_d = exp(-dfd.Fd)$$
⁽⁵⁾

where dfd was a constant (dfd<1) and Fd was the biomass of adult demersal fish.

Catch which was not discarded was referred to as 'landings' and was removed as an export flux from the model.

4. Physical exchanges

4.1. Vertical exchange across the interface between water column layers

<u>V</u>ertical exchanges between layers in the water column were represented as a simple diffusive process in the model. Diffusive processes produce net fluxes of material only when there is a concentration gradient across the interface between neighboring compartments, with the flux determined by a diffusion coefficient ($m^2 d^{-1}$). However, since the model only simulated the difference in concentration between the two layers, and not the gradient across the interface, the length term over which the gradient acted was specified as a separate time series parameter.

4.2. Vertical exchange across the sediment water interface

As for vertical exchanges in the water column,_the material flux of dissolved constituents across the sediment-water interface in the model was given by product of the concentration difference between sediment pore waters and the overlying water column layer, a diffusion coefficient, and an assumed length scale of action. Pore water concentrations were given by assuming that the mass of state variable in the sediment was uniformly distributed over the sediment layer which was of fixed thickness and uniform porosity (proportion by volume of water in the sediment).

4.3. Horizontal advection

Horizontal advection was represented by a volume inflow to the surface and deep layer (parameterised as a proportion of layer volume inflowing per day). To conserve volume, a balancing outflow was assumed from each layer. All horizontal inflow to the surface layer was assumed to exit via the surface layer. However, a proportion (between 0 and 1) of the inflow to the deep layer was potentially allowed to upwell vertically into the surface layer, augmenting the surface layer outflow. All components which were subject to vertical diffusion (nitrate, ammonia, suspended detritus, and phytoplankton) were also eligible to be advected vertically and horizontally. Ocean boundary concentrations (mM N.m⁻³) in inflows to the system were set as external values.

4.4. River inputs

Nutrient and detritus inputs from rivers were confined to the surface layer and represented by a volume inflow (proportion of surface layer volume per day) with given concentrations of nutrient load (mM N.m⁻³). The volume input from rivers

generated a corresponding outflow volume from the surface layer, which was added to that generated by horizontal advection.

4.5. Atmospheric input of nutrient

Deposition of nitrate and ammonia to the surface layer from the atmosphere was represented by an external driving dataset of fluxes (mM N.m⁻².d⁻¹)

5. References

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State variables and notations. Units of all variables are mMN.m⁻² in a given depth layer.

Term	Symbol
Surface detritus	Ds
Deep detritus	D _d
Sediment detritus	D _x
Fishery discards	D_{f}
Corpses	D _c
Surface ammonia	As
Deep ammonia	Ad
Sediment ammonia	A _x
Surface nitrate	Ns
Deep nitrate	N _d
Sediment nitrate	N _x
Surface phytoplankton	Ps
Deep phytoplankton	P _d
Mesozooplankton	Н
Carnivorous zooplankton	С
Suspension/deposit feeding benthos	Bs
Carnivorous/scavenge feeding benthos	Bc
Pelagic fish larvae	FLp
Demersal fish larvae	FLd
Pelagic fish adults	Fp
Demersal fish adults	Fd
Birds/mammals	J

Static physical setup parameters.

Parameter	Symbol	Description
Thicknesses of the surface	Ts	Vertical distance between the sea surface and
water column layer		the base of mixed layer
Thicknesses of the deep	T _d	Vertical distance between the base of mixed
water column layer		layer and the seabed
Thickness of benthic	T _{bl}	Bottom boundary layer (contained within the
feeding layer		deep layer) in which benthos have access to
		phytoplankton and suspended detritus (must
		be less than T _d).
Thickness of the sediment	T _x	Vertical depth over which sediment
layer		constituents are assumed to be well mixed
Thickness of the sediment-	T_{Vx}	Boundary layer thickness at the sediment-
water diffusion layer		water interface, over which the diffusion
		coefficient between deep water and sediment
		pore water is assumed to act
Sediment-water diffusivity	V _x	A constant coefficient governing the vertical
		flux between the sediment pore water and
		the deep water layer.
Sediment porosity	por _x	Proportion by volume of water in seabed
		sediment.

Time dependent external driving variables.

Term	Symbol	Description
Sea surface irradiance	L(t)	A daily resolution time series cosine function
		varying between a winter minimum (L _w) on
		day 0 and 360, and a summer maximum (L_s)
TT T T T T T T T T 		on day 180
Vertical attenuation	Kvert(t)	A daily resolution time series of the log-e
(base a)		coefficient of vertical attenuation. The
(base e)		the mean light intensity in the surface layer
		is then derived from the integral of the light
		profile $(I_{x,y} = I_{z} e^{-kvert.depth})$ ie
		$(((1/kvert))^*e^{-kvert.0}) - ((1/kvert)^*e^{-kvert.thick_s})$
)/thick s
Temperature in each	TZ(t)	A daily resolution time series of sea
vertical layer of the model		temperatures for each model layer.
Vertical diffusion	V(t)	A daily resolution time series of either a
coefficient		constant value or a cosine function
		representing the seasonal variation of
		vertical diffusion coefficient.
Vertical diffusion length	$T_{Vsd}(t)$	The length scale over which vertical
scale		diffusion acts at the interface between water
		column layers – a derived function of the
	D (4)	magnitude of the diffusion rate.
Freshwater input to the	$\mathbf{K}(t)$	A daily resolution time series of the volume
surface layer from fivers		rivers as a proportion of surface layer
		volume per day
Horizontal advection	L(t)	A daily resolution time series or constant
inflow from the ocean to	3(-)	value of the inflow volume to the surface
the surface layer		layer as a proportion of surface layer volume
2		per day
Horizontal advection	I _d (t)	A daily resolution time series or constant
inflow from the ocean to		value of the inflow volume to the deep layer
the deep layer		as a proportion of deep layer volume per day
Proportion of deep inflow	p_{Id}	A daily resolution time series or constant
volume upwellng into the		value. The proportion of deep inflow which
surface later		is not upwelled, is treated as an outflow from
Harizantal autflaw valuma	O(t)	The deep layer Proportion of surface layer advacted
from the surface layer to	$O_{s}(t)$	horizontally out of the system each day =
the ocean		$I(t) + n_1 * (T_1 * I_1(t))/T_1 + R(t)$
External input of nitrogen	$[]_{A}(t)$	Mass of nitrate and ammonia introduced to
to the surface laver from		the system from the atmosphere (moles N m^{-2}
the atmosphere		d^{-1}) as a constant or time series
Concentrations of nitrogen	$[]_{R}(t)$	Nitrate and ammonia concentrations
in river waters flowing	/	(molesN m ⁻³) in river waters as a constant or
into the surface layer		time series

Ocean boundary	$[]_{bs}(t)$	Nitrate, ammonia, detritus, and
concentrations of	and	phytoplankton were susceptible to horizontal
horizontally advected	[] _{bd} (t)	advection and ocean boundary
components in the surface		concentrations (molesN m ⁻³) of each are
and deep layers		required as a constant or time series
Pelagic fish spawning	Pspn(t)	A daily resolution time series of the
pattern		proportion of adult pelagic fish biomass shed
		as eggs per day
Demersal fish spawning	Dspn(t)	A daily resolution time series of the
pattern		proportion of adult demersal fish biomass
		shed as eggs per day
Pelagic fish recruitment	Prec(t)	A daily resolution time series of the
pattern		proportion of larval pelagic fish biomass
		recruiting to the adult pelagic stock per day
Demersal fish recruitment	Drec(t)	A daily resolution time series of the
pattern		proportion of larval demersal fish biomass
		recruiting to the adult demersal stock per day
Fishery extraction rate	X_{Bs}	A daily resolution time sereies of the
from benthos		proportion of benthos suspension feeder
suspension/deposit feeders		biomass extracted per day
Fishery extraction rate	X_{Bc}	A daily resolution time sereies of the
from benthos carnivores		proportion of benthos carnivore biomass
		extracted per day
Fishery extraction rate	X_{Fp}	A daily resolution time sereies of the
from pelagic fish		proportion of pelagic fish biomass extracted
		per day
Fishery extraction rate	X_{Fd}	A daily resolution time sereies of the
from demersal fish		proportion of demersal fish biomass
		extracted per day

Static parameters of the model.

Parameter	Symbol
Preference of consumer guild (x) for resource guild (y)	pref _{y-x}
Temperature corrected weight specific maximum uptake rate (d ⁻¹) of	U _{max(x)}
resource guild (y) by consumer guild (x)	
Half-saturation concentration of resource for consumer guild (x)	h _x
Assimilation efficiency of heterotroph guild (x) (proportion of ingestate	a _x
converted into body mass)	
Temperature corrected background metabolic rate of heterotroph guild	e _x
(x) (proportion of nitrogen biomass which was converted to ammonia	
per day).	
I emperature corrected remineralisation of suspended detritus in the	m _s
surface water column layer to ammonia, expressed as the proportion of	
suspended detritus nitrogen converted to ammonia per day	
I emperature corrected remineralisation of suspended detritus in the	m _d
deep water column layer to ammonia, expressed as the proportion of	
Suspended detrifus mitrogen converted to ammonia per day	100
ammonia, expressed as the properties of sediment detritus nitrogen	Π_X
converted to ammonia per day	
Temperature corrected nitrification rate of ammonia to nitrate in the	n
surface layer of the water column expressed as the proportion of	Π_{S}
ammonia converted to nitrate per day	
Temperature corrected nitrification rate of ammonia to nitrate in the	na
deep layer of the water column, expressed as the proportion of ammonia	τ.u
converted to nitrate per day	
Temperature corrected nitrification rate of ammonia to nitrate in the	n _x
sediment pore waters, expressed as the proportion of ammonia	Α
converted to nitrate per day	
Temperature corrected denitrification rate of nitrate in the surface layer,	ds
expressed as the proportion of nitrate lost from the system to nitrogen	
gas per day	
Temperature corrected denitrification rate of nitrate in the deep layer,	d_d
expressed as the proportion of nitrate lost from the system to nitrogen	
_gas per day	
Temperature corrected denitrification rate of nitrate in the sediment pore	d_x
water layer, expressed as the proportion of nitrate lost from the system	
to nitrogen gas per day	
Death rate of phytoplankton in the surface layer, expressed as the	X _S
proportion of surface phytoplankton exported to detritus per day	
Death rate of phytoplankton in the deep layer, expressed as the	Xd
proportion of deep phytoplankton exported to detritus per day	
Density-dependent mortality rate of carnivorous zooplankton, expressed	ZC
as the proportion of biomass exported to seabed corpses, per unit	
Diomass, per day	
Density-dependent mortality rate of carnivorous benthos, expressed as	z_{Bc}
ine proportion of biomass exported to seabed corpses, per unit biomass,	

per day	
Density-dependent mortality rate of adult pelagic fish, expressed as the	\mathbf{z}_{Fp}
proportion of biomass exported to seabed corpses, per unit biomass, per	-
day	
Density-dependent mortality rate of adult demersal fish, expressed as	\mathbf{Z}_{Fd}
the proportion of biomass exported to seabed corpses, per unit biomass,	
per day	
Density-dependent mortality rate of birds/mammals, expressed as the	ZJ
proportion of biomass exported to seabed corpses, per unit biomass, per	
day	
Sinking rate of detritus in the surface layer, expressed as the proportion	X _{sink_s}
of surface layer detritus exported per day to the deep layer	
Sinking rate of detritus in the deep layer, expressed as the proportion of	X _{sink_d}
deep layer detritus exported per day to the sediment	_
Rate of conversion of fishery discards to seabed corpses	X _{disc corp}
Rate of conversion of seabed corpses to sediment detritus	X _{corp sed}
Fraction of pelagic fish catch which is discarded at sea	disc _p
Coefficient for biomass dependency of the fraction of demersal fish	dfd
catch which is discarded at sea	
Fraction of carnivorous benthos catch which is discarded at sea	disc _{Bc}
Fraction of suspension feeding benthos catch which is not landed	disc _{Bs}

Uptake equations of the model.

Uptake term	Description
Uptake of ammonia	$\Omega_{\text{As-Ps}} = \text{Min}\{1.0, L(t)/L_{\text{max}}\}.A_{\text{s}}.P_{\text{s}}.\text{ pref}_{\text{A-P}}.U_{\text{max}(\text{P})}/$
by phytoplankton	$(P_s+(h_p,T_s))$
Uptake of nitrate by	$\Omega_{\text{Ns-Ps}} = \text{Min}\{1.0, L(t)/L_{\text{max}}\}.N_{\text{s}}.P_{\text{s}}.\text{ pref}_{\text{N-P}}.U_{\text{max}(\text{P})}/$
phytoplankton	$(P_s+(h_p,T_s))$
Uptake of surface	$\Omega_{Ps-H} = P_s. H((pref_{P-H} . P_s + pref_{D-H} . D_s)/(pref_{P-H} . P_s + pref_{P-H})$
phytoplankton by	P_d + pref _{D-H} P_s + pref _{D-H} P_d)). pref _{P-H} $U_{max(H)} / (P_s + (h_H, T_s))$
herbivorous-	
zooplankton	
Uptake of deep	$\Omega_{Pd-H} = P_d. H((pref_{P-H}.P_d+pref_{D-H}.D_d)/(pref_{P-H}.P_s+pref_{P-H})$
phytoplankton by	P_d + pref _{D-H} P_s + pref _{D-H} P_d)). pref _{P-H} $U_{max(H)} / (P_d + (h_H, T_d))$
herbivorous-	
zooplankton	
Uptake of surface	$\Omega_{Ds-H} = D_s$. H((pref_{P-H}, P_s + pref_{D-H}, D_s)/(pref_{P-H}, P_s + pref_{P-H})
suspended detritus by	P_d + prei _{D-H} P_s + prei _{D-H} P_d)). prei _{D-H} $U_{max(H)} / (D_s + (n_H, I_s))$
nerorvorous-	
<u>Zoopialiktoli</u>	$O_{\rm D} = D_{\rm c} H(({\rm pref}_{\rm s.u.} {\rm P}_{\rm s.t.} {\rm pref}_{\rm s.u.} {\rm D}_{\rm s})/({\rm pref}_{\rm s.u.} {\rm P}_{\rm s.t.} {\rm pref}_{\rm s.u.} {\rm P}_{\rm s.t.} {\rm pref}_{\rm s.u.} {\rm P}_{\rm s.t.} {\rm P}_{\rm s.t.} {\rm pref}_{\rm s.u.} {\rm P}_{\rm s.t.} {\rm P}_{\rm s.$
nhytonlankton by	$22D_{d-H} = D_d$. II((prop-H .I. d + prop-H .D_d)/(prop-H .I. s + prop-H) P_+ pref_s y P_+ pref_s y P_1) pref_s y U m / (D_+(hy T_1))
suspension/deposit	H_{d} (H_{d})))
feeding benthos	
Untake of suspended	$\Omega_{\text{Dd},\text{Pc}} = D_{\text{d}} B_{\text{s}} \operatorname{pref}_{\text{Dd},\text{Pc}} U_{\text{max}(\text{Pc})} / (D_{\text{d}} + h_{\text{Pc}})$
detritus by	
suspension/deposit	
feeding benthos	
Uptake of sediment	$\Omega_{\text{Dx-Bs}} = D_{\text{x}}$. Bs. pref _{Dx-Bs} . $U_{\text{max(Bs)}} / (D_{\text{x}} + h_{\text{Bs}})$
detritus by	
suspension/deposit	
feeding benthos	
Uptake of fishery	$\Omega_{\text{Df-Fd}} = D_{\text{f.}} \text{ Fd. } \text{pref}_{\text{Df-Fd.}} U_{\text{max}(\text{Fd})} / (D_{\text{f}} + h_{\text{Fd.}}(T_{\text{s}} + T_{\text{d}}))$
discards by demersal	
tish	\mathbf{O} \mathbf{D} \mathbf{L} \mathbf{C} \mathbf{U} $(\mathbf{D} + \mathbf{I} / \mathbf{T} + \mathbf{T})$
Uptake of fishery	$\Omega_{\text{Df-J}} = D_{\text{f. J. } \text{pret}_{\text{Df-J}} \cup \text{max}(J) / (D_{\text{f}} + n_{\text{J.}} (1_{\text{s}} + 1_{\text{d}}))$
discards by birds and	
Untake of seabed	$O_{D-D} = D$ Ed preferre $U = \frac{1}{2} \left(D + h_{D} \left(T + T \right) \right)$
cornses by demersal	$22D_{c-Fd} = D_{c} \cdot I \cdot d \cdot prop_{c-Fd} \cdot O_{max(Fd)} / (D_{c} + n_{Fd} \cdot (I_{s} + I_{d}))$
fish	
Uptake of seabed	$\Omega_{\text{De Be}} = D_{\text{c}} B_{\text{c}} \text{ pref}_{\text{De Be}} U_{\text{max}(\text{Be})} / (D_{\text{c}} + h_{\text{Be}})$
corpses by	
carnivorous/scavenge	
feeding benthos	
Uptake of	$\Omega_{\text{Bs-Bc}} = \text{Bs. Bc. pref}_{\text{Bs-Bc}}.U_{\text{max(Bc)}} / (\text{Bs+h}_{\text{Bc}})$
suspension/deposit	- X / X ⁻
feeding benthos by	
carnivorous/scavenge	
feeding benthos	

Uptake of	$\Omega_{\text{H-C}} = \text{H. C. pref_{\text{H-C}}} U_{\text{max}(\text{C})} / (\text{H+h}_{\text{C}}(\text{T}_{\text{s}}+\text{T}_{\text{d}}))$
herbivorous-	
zooplankton by	
carnivorous	
zooplankton	
Uptake of pelagic	$\Omega_{FLp-C} = FLp. C. pref_{FLp-C} U_{max(C)} / (FLp+h_C(T_s+T_d))$
fish larvae by	
carnivorous	
zooplankton	
Uptake of demersal	$\Omega_{\text{FLd},C} = \text{FLd}_{C} C \text{ pref}_{\text{FLd},C} U_{\text{max}(C)} / (\text{FLd}+h_{C}(T_{s}+T_{d}))$
fish larvae by	
carnivorous	
zoonlankton	
Untake of	$O_{\text{HELE}} = H FL p \text{ prefuse} \left[\int_{-\infty}^{\infty} \int_{-\infty}$
herbivorous-	$22H-FLp$ II. I.D. proth-FLp. $O \max(FLp) / (II + IIFLp. (IS + Id))$
zoonlankton by	
pelagic fish larvae	
Untake of	$O_{\text{HP}} = H$ En prefue $II_{\text{HP}} / (H+h_{\text{P}} (T+T))$
berbivorous	$22_{H-Fp} = 11.1 \text{ p. } p101_{H-Fp} \cdot 0_{max}(Fp) / (11 + 11_{Fp} \cdot (1_{S} + 1_{d}))$
zoonlankton by	
zoopialikioli Uy	
Untalia of	$O = C E_{\mathbf{p}} \operatorname{prof} U / (C \pm \mathbf{h} (T \pm T))$
	$22_{C-Fp} = C. Fp. prer_{C-Fp} O_{max(Fp)} / (C + n_{Fp} (1_s + 1_d))$
callivolous	
zoopiankton by	
Untalia of malagia	O = EL = E = = = $(T + T)$
Cplake of pelagic	$\Omega_{FLp-Fp} - FLp. Fp. prel_{FLp-Fp} \cup_{max(Fp)} / (FLp+n_{Fp}(1_s+1_d))$
fish larvae by pelagic	
	$\mathbf{O} = \mathbf{\Gamma} [\mathbf{I} \mathbf{F}_{\mathbf{T}} + \mathbf{r}_{\mathbf{T}} \mathbf{F}_{\mathbf{T}}]$
Optake of demersal	$\Omega_{FLd-Fp} = FLd. Fp. preI_{FLd-Fp}. \bigcup_{max(Fp)} / (FLd+n_{Fp.}(1_s+1_d))$
fish larvae by pelagic	
	$\Omega_{\text{H-FLd}} = \text{H. FLd. pref_{\text{H-FLd}}} \cup_{\max(\text{FLd})} / (\text{H+n_{\text{FLd}}}(1_{s}+1_{d}))$
nerbivorous-	
zooplankton by	
demersal fish larvae	
Uptake of	$\Omega_{C-Fd} = C. Fd. pref_{C-Fd}. U_{max(Fd)} / (C+h_{Fd}.(1_s+1_d))$
carnivorous	
zooplankton by	
demersal fish	
Uptake of	$\Omega_{\text{Bs-Fd}} = \text{Bs. Fd. pref}_{\text{Bs-Fd.}} U_{\text{max}(\text{Fd})} / (\text{Bs+h}_{\text{Fd.}}(\text{T}_{\text{s}}+\text{T}_{\text{d}}))$
suspension/deposit	
feeding benthos by	
demersal fish	
Uptake of	$\Omega_{\text{Bc-Fd}} = \text{Bc. Fd. pref}_{\text{Bc-Fd.}} U_{\text{max}(\text{Fd})} / (\text{Bc+h}_{\text{Fd.}}(\text{T}_{s}+\text{T}_{d}))$
carnivorous/scavenge	
feeding benthos by	
demersal fish	
Uptake of pelagic	$\Omega_{FLp-Fd} = FLp. Fd. pref_{FLp-Fd.} U_{max(Fd)} / (FLp+h_{Fd.}(T_s+T_d))$
fish larvae by	
demersal fish	

Uptake of demersal	$\Omega_{\text{FLd-Fd}} = \text{FLd. Fd. pref}_{\text{FLd-Fd.}} U_{\text{max}(\text{Fd})} / (\text{FLd+h}_{\text{Fd.}}(\text{T}_{\text{s}}+\text{T}_{\text{d}}))$
fish larvae by	
demersal fish	
Uptake of pelagic	$\Omega_{\text{Fp-Fd}} = \text{Fp. Fd. pref}_{\text{Fp-Fd.}} U_{\text{max}(\text{Fd})} / (\text{Fp+h}_{\text{Fd.}}(\text{T}_{\text{s}}+\text{T}_{\text{d}}))$
fish by demersal fish	
Uptake of pelagic	$\Omega_{\text{Fp-J}} = \text{Fp. J. pref}_{\text{Fp-J}} U_{\text{max}(J)} / (\text{Fp+h}_J(T_s+T_d))$
fish by	• • •
birds/mammals	
Uptake of demersal	$\Omega_{\text{Fd-Fd}} = \text{Fd. Fd. pref}_{\text{Fd-Fd.}} U_{\text{max}(\text{Fd})} / (\text{Fd+h}_{\text{Fd.}}(\text{T}_{\text{s}}+\text{T}_{\text{d}}))$
fish by demersal fish	
Uptake of demersal	$\Omega_{\text{Fd-J}} = \text{Fd. J. pref}_{\text{Fd-J}} U_{\text{max}(J)} / (\text{Fd+h}_J(T_s+T_d))$
fish by	
birds/mammals	
Catch of	$\Omega_{\text{Bs-M}} = \text{Bs. } X_{\text{Bs}}$
suspension/deposit	
feeding benthos	
Catch of	$\Omega_{\text{Bc-M}} = \text{Bc. } X_{\text{Bc}}$
carnivorous/scavenge	
feeding benthos	
Catch of pelagic fish	$\Omega_{\rm Fp-M} = {\rm Fp.} \; {\rm X}_{\rm Fp}$
Catch of demersal	$\Omega_{\rm Fd-M} = \rm Fd. \ X_{\rm Fd}$
fish	

Balance equations for each state variable.

Rate term	Description
Rate of change of	$dD_s/dt = x_s.P_s - \Omega_{Ds-H} - m_s.D_s - x_{sink_s}.D_s + V(t).((D_d/T_d)-$
surface detritus (formed	$(D_s/T_s))/T_{Vsd}(t) + I_s(t)*T_s*[D]_{bs}(t) + p_{Id}*I_d(t)*D_d -$
from death of surface	$(I_{s}(t)*T_{s}+p_{Id}*I_{d}(t)*T_{d}+R(t))*D_{s}/T_{s}$
phytoplankton).	
Rate of change in deep	$dD_d/dt = ((1-a_H)/2). (\Omega_{Ps-H} + \Omega_{Pd-H} + \Omega_{Ds-H} + \Omega_{Dd-H})$
detritus (formed from	+ $((1-a_C)/2) \cdot (\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C})$
death of deep	$+((1-a_{FL,p})/2).(\Omega_{H-FL,p})$
phytoplankton, sinking	$+((1-a_{FLd})/2).(\Omega_{H-FLd})$
of detritus from the	+ $((1-a_{F_{p}})/2)$. $(\Omega_{H-F_{p}} + \Omega_{C-F_{p}} + \Omega_{FL,p-F_{p}} + \Omega_{FL,d-F_{p}})$
surface layer, and the	+ ((1- a_{Fd})/2). (Ω_{C-Fd} + $\Omega_{FL,p-Fd}$ + $\Omega_{FL,d-Fd}$ + Ω_{Fp-Fd} + Ω_{Bs-Fd} +
faeces of zooplankton	$\Omega_{\text{Bc-Fd}} + \Omega_{\text{Fd-Fd}} + \Omega_{\text{Df-Fd}} + \Omega_{\text{Dc-Fd}})$
fish and	+ $((1-a_I)/2)$. $(\Omega_{Fp-I} + \Omega_{Fd-I} + \Omega_{Df-I})$
birds/mammals).	$+ x_d.U_d + x_d.P_d + x_{sink}.D_s - m_d.D_d - x_{sink}.d.D_d$
,	$-\Omega_{\text{Dd-Bs}} - \Omega_{\text{Dd-H}} - V(t).((D_d/T_d)-(D_s/T_s)) / T_{\text{Vsd}}(t) +$
	$I_d(t) * T_d * [D]_{bd}(t) - I_d(t) * D_d$
Rate of change in	$\frac{dD_v}{dt} = \frac{dU_v}{dt} = \frac{dU_v}{dt}$
sediment detritus	$+ ((1-a_{Bs})/2) (\Omega_{Dd-Bs} + \Omega_{Pd-Bs} + \Omega_{Dv-Bs})$
(formed from the	$+((1-a_{B_{0}})/2)(\Omega_{B_{0}} a_{0} + \Omega_{D_{0}} a_{0})$
settlement of deep	$+ X_{sink} d D_d$
suspended detritus	$+ X_{corp, sed} D_c$
faeces of benthos and	$- m_v D_v - Q_{Dv} P_c$
corpses)	
Rate of change in	$dD_{e}/dt =$
fishery discards	$+ \operatorname{disc}_{\mathrm{P}} \Omega_{\mathrm{Fr}} M$
nonery abourds.	$+ \exp(-dfd Fd) O_{EdM}$
	$+ \operatorname{disc}_{\mathbf{P}_{-}} O_{\mathbf{P}_{-}} M$
	$+ \operatorname{disc}_{D_{2}} \Omega_{D_{2}} M$
	- X disc som Df
	- Opera
	$- O_{\rm Def}$
Rate of change in	$\frac{dD}{dt} =$
seabed corpses	$dD_0 dt$
seabed corpses.	$-\mathbf{x}$
	$z_{corp-sed}$, z_{c} , $C^{2} + z_{p}$, $Bc^{2} + z_{p}$, $En^{2} + z_{p}$, $Ed^{2} + z_{r}$, I^{2}
	$+2C_{C}C_{F}+2B_{C}DC_{F}+2F_{B}D_{F}+2F_{d}D_{C}+2J_{F}$
	$- \Omega_{\rm DC-Fd}$
Rate of change in	$\frac{d\Delta}{dt} = m D$
surface ammonia	$dA_{s}/dt = M_{s}.D_{s}$ + $(T/(T+T))(e_{x}H + e_{z}C + e_{x}FIn + e_{x}FId + e_{z}Fn)$
surface annihoma.	+ $(T_{s}(T_{s}+T_{d})(c_{H},H+c_{C},C+c_{FLp},H_{Lp}+c_{FLd},H_{Ld}+c_{Fp},H_{p})$ + $(T_{s}/(T_{s}+T_{d})(((1-2\pi))/2)(O_{V,P}+O_{P,P}+O_{P,P}+O_{P,P})$
	$(1_{S}(1_{S}+1_{d})(((1-a_{Fp})/2))(22_{H-Fp}+22_{C-Fp}+22_{FLp-Fp}+22_{FLd}))$
	$(T_{1})^{(1)} + (T_{1})^{(1)} ((1_{2})^{(1)})^{(2)} (\Omega_{1})^{(2)}$
	+ $(T_{1})((T_{1}-a_{FL})/(2)(2+FL))$ + $(T_{1})(((T_{2}-a_{FL})/2)(0,, .))$
	+ $(T_{s}(1_{s}+1_{d})(((1_{a}+1_{d})/2)(2_{a}+1_{c}+1_{c})))$ + $(T_{s}(1_{s}+1_{d})(((1_{a}+1_{c})/2)(0_{c}+1_{c}+0_{c}+1_{c}+0_{c})))$
	+ $(1_{2})^{1_{5}+1_{d}}((1_{-\alpha_{c}})^{2})(2_{H-C} + 2_{FLp-C} + 2_{FLd-C})$ + $((1_{-2})^{2}(O_{p})^{2} + O_{p}^{2})(0_{p})$
	+ $((1 - a_H)/2).((3 - a_H + 3 - a_H))$ + $((1 - a_H)/2).((O_H - a_H + O_{H - A_H} + O_{H - A_H}))$
	$+ ((1-a_J)/2). (S2F_{p-J} + S2F_{d-J} + S2D_{f-J})$

	$-n_s.A_s - \Omega_{As-Us} - \Omega_{As-Ps} + V(t).((A_d/T_d)-(A_s/T_s)) / T_{Vsd}(t)$
	+ $I_s(t) T_s [A]_{bs}(t) + p_{Id} I_d(t) A_d + R(t) T_s [N]_R(t)$
	$+ [N]_{A}(t)$
	$-(I_{s}(t)*T_{s}+p_{Id}*I_{d}(t)*T_{d}+R(t))*A_{s}/T_{s}$
Rate of change in deep	$dA_d/dt = m_d.D_d$
ammonia.	$+ (T_d/(T_s+T_d)(e_H.H + e_C.C + e_{Fp}.Fp)$
	$+ e_{Bs}.Bs + e_{Bc}.Bc + e_{Fd}.Fd$
	+ $(T_d/(T_s+T_d))(((1-a_{FLp})/2).(\Omega_{H-FLp}))$
	+ $(T_d/(T_s+T_d))(((1-a_{FLd})/2).(\Omega_{H-FLd}))$
	+ $(T_d/(T_s+T_d)(((1-a_{Fp})/2)).(\Omega_{H-Fp}+\Omega_{C-Fp}+\Omega_{Fd-Fp}))$
	+ (((1- a_{Fd})/2). (Ω_{C-Fd} + Ω_{FLp-Fd} + Ω_{FLd-Fd} + Ω_{Fp-Fd} + Ω_{Bs-Fd} +
	$\Omega_{\text{Bd-Fd}} + \Omega_{\text{Bc-Fd}+} + \Omega_{\text{Fd-Fd}+} + \Omega_{\text{Df-Fd}} + \Omega_{\text{Dc-Fd}}))$
	+ $(T_d/(T_s+T_d)(((1-a_C)/2).(\Omega_{H-C}+\Omega_{FLp-C}+\Omega_{FLd-C}))$
	+ $((1-a_{\rm H})/2).(\Omega_{\rm Dd-H} + \Omega_{\rm Pd-H})$
	+ $((1-a_{Bs})/2)$. $(\Omega_{Dd-Bs} + \Omega_{Dx-Bs} + \Omega_{Pd-Bs})$
	+ ((1- a_{Bc})/2). (Ω_{Bs-Bc} + Ω_{Dc-Bc})
	+ $V_x.((A_x/(T_x.por_x)) - (A_d/T_d)) / T_{V_x}$
	$-n_{d}A_{d} - V(t).((A_{d}/T_{d})-(A_{s}/T_{s})) / T_{Vsd}(t)$
	$+ I_d(t) * T_d * [A]_{bd}(t) - I_d(t) * A_d$
Rate of change in	$dA_x/dt = m_x.D_x - n_x.A_x - V_x.((A_x/(T_x.por_x)) - (A_d/T_d)) / T_{Vx}$
sediment ammonia.	
Rate of change in	$dN_s/dt = n_s.A_s - \Omega_{Ns-Ps} - \Omega_{Ns-Us} - d_s.N_s + V(t).((N_d/T_d)-$
surface nitrate	$(N_s/T_s)) / T_{Vsd}(t) + R(t) *T_s *[N]_R(t) + [N]_A(t)$
	$+ I_{s}(t) T_{s}^{*}[N]_{bs}(t) + p_{Id} I_{d}(t) N_{d}$
	$-(I_{s}(t)*T_{s}+p_{Id}*I_{d}(t)*T_{d}+R(t))*N_{s}/T_{s}$
Rate of change in deep	$dN_d/dt = n_d.A_d - d_d.N_d - V(t).((N_d/T_d)-(N_s/T_s)) / T_{Vsd}(t)$
nitrate.	+ $V_x.((N_x/(T_x.por_x)) - (N_d/T_d)) / T_{V_x}$
	$+ I_{d}(t) T_{d} [N]_{bd}(t) - I_{d}(t) N_{d}$
Rate of change in	$dN_x/dt = n_x.A_x - d_x.N_x - V_x.((N_x/(T_x.por_x)) - (N_d/T_d)) / T_{Vx}$
sediment nitrate.	
Rate of change in	$dP_s/dt = \Omega_{As-Ps} + \Omega_{Ns-Ps} - x_s P_s - \Omega_{Ps-H} + V(t) \cdot ((P_d/T_d) - $
surface phytoplankton.	$(P_s/T_s)) / T_{Vsd}(t)$
	$+ I_{s}(t) T_{s}^{*}[P]_{bs}(t) + p_{Id}^{*}I_{d}(t) P_{d}$
	$-(I(t)*T + n_1*I(t)*T + P(t))*P/T$
\mathbf{D} $(1$ 1	$(1_{s}(t) + 1_{s} + \mathbf{p}_{ld} + 1_{d}(t) + 1_{d} + \mathbf{N}(t) + 1_{s} + 1_{s}$
Rate of change in deep	$\frac{dP_{s}/dt = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / C_{s}/T_{s}}{dP_{s}/dt = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / C_{s}/T_{s}}$
Rate of change in deep phytoplankton.	$\frac{(I_{s}(t) - I_{s} + P_{Id} - I_{d}(t) - I_{d} + R(t)) - I_{s} + I_{s}}{dP_{s}/dt = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / T_{Vsd}(t) + I_{d}(t)^{*}T_{d}^{*}[P]_{bd}(t) - I_{d}(t)^{*}P_{d}$
Rate of change in deep phytoplankton. Rate of change in	$ \frac{(I_{s}(t) - I_{s} + P_{Id} - I_{d}(t) - I_{d} + R(t)) - I_{s} + I_{s}}{dP_{s}/dt = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / T_{Vsd}(t) + I_{d}(t)*T_{d}*[P]_{bd}(t) - I_{d}(t)*P_{d} $ $ \frac{dH}{dt} = a_{H}. (\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H}.H - \Omega_{H-C} - C $
Rate of change in deep phytoplankton. Rate of change in herbivorous	$ \frac{(I_{s}(t) - I_{s} + P_{Id} - I_{d}(t) - I_{d} + R(t)) - I_{s} + I_{s}}{dP_{s}/dt = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / T_{Vsd}(t) + I_{d}(t)^{*}T_{d}^{*}[P]_{bd}(t) - I_{d}(t)^{*}P_{d} $ $ \frac{dH}{dt} = a_{H}. (\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H}.H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp} $
Rate of change in deep phytoplankton. Rate of change in herbivorous zooplankton.	$\frac{(I_{s}(t) - I_{s} + P_{Hd} - I_{d}(t) - I_{d} + R(t)) - I_{s} + I_{s}}{dP_{s}/dt = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d}) - (P_{s}/T_{s})) / \frac{T_{Vsd}(t) + I_{d}(t) + T_{d} + [P]_{bd}(t) - I_{d}(t) + P_{d}}{dH/dt = a_{H}.(\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H}.H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp}$
Rate of change in deep phytoplankton. Rate of change in herbivorous zooplankton. Rate of change in	$\frac{dP_{s}(t) - r_{s} + p_{Id} - I_{d}(t) - r_{d} + R(t) - r_{s} + r_{s}}{dP_{s}/dt = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / \frac{T_{Vsd}(t) + I_{d}(t)*T_{d}*[P]_{bd}(t) - I_{d}(t)*P_{d}}{dH/dt = a_{H}.(\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H}.H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp}}$ $\frac{dC/dt}{dt} = a_{C}.(\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C}) - e_{C}.C - \Omega_{C-Fd} - \Omega_{C-Fp} - \frac{e_{C}}{2}$
Rate of change in deep phytoplankton. Rate of change in herbivorous zooplankton. Rate of change in carnivorous	$\frac{(I_{s}(t) - I_{s} + P_{Id} - I_{d}(t) - I_{d} + R(t)) - I_{s} + I_{s}}{dP_{s}/dt = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / T_{Vsd}(t) + I_{d}(t)*T_{d}*[P]_{bd}(t) - I_{d}(t)*P_{d}$ $\frac{dH}{dt} = a_{H}. (\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H}.H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp}$ $\frac{dC}{dt} = a_{C}. (\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C}) - e_{C}.C - \Omega_{C-Fd} - \Omega_{C-Fp} - z_{C}.C^{2}$
Rate of change in deep phytoplankton. Rate of change in herbivorous zooplankton. Rate of change in carnivorous zooplankton.	$\frac{(I_{s}(t) - I_{s} + P_{Id} - I_{d}(t) - I_{d} + R(t)) - I_{s} + I_{s}}{dP_{s}/dt = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / T_{Vsd}(t) + I_{d}(t)*T_{d}*[P]_{bd}(t) - I_{d}(t)*P_{d}$ $\frac{dH}{dt} = a_{H}. (\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H}.H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp}$ $\frac{dC}{dt} = a_{C}. (\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C}) - e_{C}.C - \Omega_{C-Fd} - \Omega_{C-Fp} - z_{C}.C^{2}$
Rate of change in deep phytoplankton. Rate of change in herbivorous zooplankton. Rate of change in carnivorous zooplankton. Rate of change in	$\frac{dP_{s}(t) - r_{s} + p_{Id} - I_{d}(t) - r_{d} + R(t) - r_{s} + r_{s}}{dP_{s}/dt = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / \frac{T_{Vsd}(t) + I_{d}(t)*T_{d}*[P]_{bd}(t) - I_{d}(t)*P_{d}}{dH/dt = a_{H}.(\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H}.H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp}}$ $\frac{dC/dt = a_{C}.(\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C}) - e_{C}.C - \Omega_{C-Fd} - \Omega_{C-Fp} - z_{C}.C^{2}}{dBs/dt = a_{Bs}.(\Omega_{Pd-Bs} + \Omega_{Dd-Bs} + \Omega_{Ds-Bs}) - e_{Bs}.Bs - \Omega_{Bs-Bc} - \frac{1}{2}$
Rate of change in deep phytoplankton. Rate of change in herbivorous zooplankton. Rate of change in carnivorous zooplankton. Rate of change in suspension/deposit	$\frac{(I_{s}(t) - I_{s} + P_{Id} - I_{d}(t) - I_{d} + R(t)) - I_{s} + I_{s}}{dP_{s}/dt} = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / \frac{1}{T_{Vsd}(t) + I_{d}(t) + T_{d}}[P_{bd}(t) - I_{d}(t) + P_{d}}{dH/dt} = a_{H}.(\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H}.H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp}$ $\frac{dC/dt}{dt} = a_{C}.(\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C}) - e_{C}.C - \Omega_{C-Fd} - \Omega_{C-Fp} - z_{C}.C^{2}$ $\frac{dBs/dt}{dt} = a_{Bs}.(\Omega_{Pd-Bs} + \Omega_{Dd-Bs} + \Omega_{Dx-Bs}) - e_{Bs}.Bs - \Omega_{Bs-Bc} - \Omega_{Bs-Fd} - \Omega_{Bs-M}$
Rate of change in deep phytoplankton. Rate of change in herbivorous zooplankton. Rate of change in carnivorous zooplankton. Rate of change in suspension/deposit feeding benthos.	$\frac{(I_{s}(t) - I_{s} + P_{Id} - I_{d}(t) - I_{d} + R(t)) - I_{s} + I_{s}}{dP_{s}/dt} = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / \frac{1}{T_{Vsd}(t) + I_{d}(t)*T_{d}*[P]_{bd}(t) - I_{d}(t)*P_{d}}{dH/dt} = a_{H}.(\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H}.H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp}$ $\frac{dC/dt}{dt} = a_{C}.(\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C}) - e_{C}.C - \Omega_{C-Fd} - \Omega_{C-Fp} - z_{C}.C^{2}$ $\frac{dBs/dt}{dt} = a_{Bs}.(\Omega_{Pd-Bs} + \Omega_{Dd-Bs} + \Omega_{Dx-Bs}) - e_{Bs}.Bs - \Omega_{Bs-Bc} - \Omega_{Bs-Fd} - \Omega_{Bs-M}$
Rate of change in deep phytoplankton. Rate of change in herbivorous zooplankton. Rate of change in carnivorous zooplankton. Rate of change in suspension/deposit feeding benthos. Rate of change in	$\frac{dP_{s}(d) = -x_{d}P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d}) - (P_{s}/T_{s})) / T_{Vsd}(t) + I_{d}(t)*T_{d}*[P]_{bd}(t) - I_{d}(t)*P_{d}$ $\frac{dH/dt = a_{H.} (\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H.}H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp}$ $\frac{dC/dt = a_{C.} (\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C}) - e_{C.}C - \Omega_{C-Fd} - \Omega_{C-Fp} - z_{C.}C^{2}$ $\frac{dBs/dt = a_{Bs.} (\Omega_{Pd-Bs} + \Omega_{Dd-Bs} + \Omega_{Dx-Bs}) - e_{Bs.}Bs - \Omega_{Bs-Bc} - \Omega_{Bs-Fd} - \Omega_{Bs-M}$
Rate of change in deep phytoplankton. Rate of change in herbivorous zooplankton. Rate of change in carnivorous zooplankton. Rate of change in suspension/deposit feeding benthos. Rate of change in carnivore/scavenge	$\frac{dP_s(t) - T_s + PId^{-1}d(t) - T_d + R(t)) - T_{s'} T_s}{dP_s(t) = -x_d.P_d - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_d/T_d) - (P_s/T_s)) / T_{Vsd}(t) + I_d(t) * T_d * [P]_{bd}(t) - I_d(t) * P_d}$ $\frac{dH/dt = a_{H.} (\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H.}H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp}$ $\frac{dC/dt}{dt} = a_{C.} (\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C}) - e_{C.}C - \Omega_{C-Fd} - \Omega_{C-Fp} - z_{C.}C^2$ $\frac{dBs/dt}{dBs/dt} = a_{Bs.} (\Omega_{Pd-Bs} + \Omega_{Dd-Bs} + \Omega_{Dx-Bs}) - e_{Bs.}Bs - \Omega_{Bs-Bc} - \Omega_{Bs-Fd} - \Omega_{Bs-M}$ $\frac{dBc/dt}{dBc/dt} = a_{Bc.} (\Omega_{Bs-Bc} + \Omega_{Dc-Bc}) - e_{Bc.}Bc - \Omega_{Bc-Fd} - \Omega_{Bc-M} - z_{Bc.}Bc^2$
Rate of change in deep phytoplankton. Rate of change in herbivorous zooplankton. Rate of change in carnivorous zooplankton. Rate of change in suspension/deposit feeding benthos. Rate of change in carnivore/scavenge feeding benthos.	$\frac{(I_{s}(t) - I_{s} + p_{Id} - I_{d}(t) - I_{d} + R(t)) - I_{s} + I_{s}}{dP_{s}/dt} = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / \frac{1}{T_{Vsd}(t) + I_{d}(t)*T_{d}*[P]_{bd}(t) - I_{d}(t)*P_{d}}{dH/dt} = a_{H}.(\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H}.H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp}$ $\frac{dC/dt}{dt} = a_{C}.(\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C}) - e_{C}.C - \Omega_{C-Fd} - \Omega_{C-Fp} - z_{C}.C^{2}$ $\frac{dBs/dt}{dBs/dt} = a_{Bs}.(\Omega_{Pd-Bs} + \Omega_{Dd-Bs} + \Omega_{Dx-Bs}) - e_{Bs}.Bs - \Omega_{Bs-Bc} - \Omega_{Bs-Fd} - \Omega_{Bs-M}$ $\frac{dBc/dt}{dBc/dt} = a_{Bc}.(\Omega_{Bs-Bc} + \Omega_{Dc-Bc}) - e_{Bc}.Bc - \Omega_{Bc-Fd} - \Omega_{Bc-M} - z_{Bc}.Bc^{2}$
Rate of change in deep phytoplankton. Rate of change in herbivorous zooplankton. Rate of change in carnivorous zooplankton. Rate of change in suspension/deposit feeding benthos. Rate of change in carnivore/scavenge feeding benthos. Rate of change in	$\frac{(I_{s}(t) - I_{s} + p_{Id} - I_{d}(t) - I_{d} + R(t)) - I_{s} + I_{s}}{dP_{s}/dt} = -x_{d}.P_{d} - \Omega_{Pd-H} - \Omega_{Pd-Bs} - V(t).((P_{d}/T_{d})-(P_{s}/T_{s})) / \frac{T_{Vsd}(t) + I_{d}(t)*T_{d}*[P]_{bd}(t) - I_{d}(t)*P_{d}}{dH/dt} = a_{H}.(\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H}) - e_{H}.H - \Omega_{H-C} - \Omega_{H-FLp} - \Omega_{H-FLd} - \Omega_{H-Fp}$ $\frac{dC/dt}{dt} = a_{C}.(\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C}) - e_{C}.C - \Omega_{C-Fd} - \Omega_{C-Fp} - z_{C}.C^{2}$ $\frac{dBs/dt}{dBs/dt} = a_{Bs}.(\Omega_{Pd-Bs} + \Omega_{Dd-Bs} + \Omega_{Dx-Bs}) - e_{Bs}.Bs - \Omega_{Bs-Bc} - \Omega_{Bs-Fd} - \Omega_{Bs-M}$ $\frac{dBc/dt}{dEc} = a_{Bc}.(\Omega_{Bs-Bc} + \Omega_{Dc-Bc}) - e_{Bc}.Bc - \Omega_{Bc-Fd} - \Omega_{Bc-M} - z_{Bc}.Bc^{2}$

Rate of change in	$dFLd/dt = a_{FLd.}(\Omega_{H-FLd}) - e_{FLd.}FLd - \Omega_{FLd-C} - \Omega_{FLd-Fp} -$
demersal fish larvae.	Ω_{FLd-Fd} + Dspn(t) * F _d - Drec(t) * FL _d
Rate of change in	$dFp/dt = a_{Fp} (\Omega_{C-Fp} + \Omega_{H-Fp} + \Omega_{FLp-Fp} + \Omega_{FLd-Fp}) - e_{Fp} Fp$ -
pelagic fish.	$\Omega_{\text{Fp-Fd}} - \Omega_{\text{Fp-M}} - \Omega_{\text{Fp-J}} - z_{\text{Fp}} \cdot Fp^2 - Pspn(t) * F_p + Prec(t) *$
	FLp
Rate of change in	$dFd/dt = a_{Fd}$.($\Omega_{Bs-Fd} + \Omega_{Bd-Fd} + \Omega_{Bc-Fd} + \Omega_{C-Fd} + \Omega_{FLp-Fd} +$
demersal fish.	$\Omega_{FLd-Fd} + \Omega_{Fp-Fd} + \Omega_{Fd-Fd} + \Omega_{Df-Fd} + \Omega_{Dc-Fd}) - e_{Fd}Fd - \Omega_{Fd-M} - \Theta_{Fd-M} - \Theta_$
	$\Omega_{\text{Fd-J}} - z_{\text{Fd}} \cdot Fd^2$ - Dspn(t).F _d + Drec(t).FL _d
Rate of change in	$dJ/dt = aJ. (\Omega_{Fp-J} + \Omega_{Fd-J} + \Omega_{Df-J}) - e_J.J - z_J.J^2$
birds/mammals.	-

Table S7Derived properties of the model.

Property	Description
Total annual primary production	$T = \sum_{day0}^{day360} \left(\Omega_{As-Ps} + \Omega_{Ns-Ps} \right)$
Annual MMP	$\tau = \max_{day0}^{day360} (N_s + N_d) - \min_{day0}^{day360} (N_s + N_d)$
Annual PNP	$\tau p_N = \sum_{day0}^{day360} \left(\Omega_{Ns-Ps} + d.N_s - n.A_s \right)$
Annual MMIP	$\pi i_{N} = \tau + \sum_{day 90}^{day 270} \left(R(t) + I_{s}(t) * T_{s} * ([N]_{bs} + [A]_{bs}) + I_{d}(t) * (N_{d} + A_{d}) \right)$
Annual vertical nitrate flux	$Vf_{N} = \sum_{day 0}^{day 360} (V(t).((N_{d}/T_{d}) - (N_{s}/T_{s}))/T_{Vsd(t}) + I_{d}(t) * N_{d})$
Annual horizontal nitrate flux in the surface layer	$Hf_{N} = \sum_{day0}^{day360} ((I_{s}(t) * T_{s} * [N]_{bs}) - (I_{s}(t) * T_{s} + I_{d}(t) * T_{d}) * N_{s}/T_{s})$
Total annual nitrate uptake	$T_N = \sum_{day0}^{day360} \left(\Omega_{Ns-Ps} \right)$
Annual f-ratio	$f = \tau p / T$
Annual mesozooplankton gross production	$\gamma = \sum_{day0}^{day360} \left(a_{\mathrm{H}} \cdot \left(\Omega_{Ds-H} + \Omega_{Ps-H} + \Omega_{Dd-H} + \Omega_{Pd-H} \right) \right)$

Annual	$\chi = \sum_{L}^{day 360} \left(a_{C} \cdot \left(\Omega_{H-C} + \Omega_{FLp-C} + \Omega_{FLd-C} \right) \right)$
zoonlankton	day 0
gross production	
Annual benthos gross production	$\beta = \sum_{day0}^{day360} \left(\mathbf{a}_{B} \cdot \left(\Omega_{Pd-Bs} + \Omega_{Dd-Bs} + \Omega_{Dx-Bs} + \Omega_{Bs-Bc} \right) \right)$
Annual demersal fish gross production	$\phi d = \sum_{day0}^{day360} \left(a_{Fd} \left(\Omega_{C-Fd} + \Omega_{Bs-Fd} + \Omega_{Bc-Fd} + \Omega_{Fp-Fd} + \Omega_{FLp-Fd} + \Omega_{FLd-Fd} + \Omega_{Fd-Fd} + \Omega_{Df-Fd} + \Omega_{DcFd} \right) \right)$
Annual pelagic fish gross production	$\phi p = \sum_{day0}^{day360} \left(a_{Fp} \left(\Omega_{H-Fp} + \Omega_{C-Fp} + \Omega_{FLp-Fp} + \Omega_{FLd-Fp} \right) \right)$
Annual demersal fish larvae gross production	$\phi Ld = \sum_{day 0}^{day 360} (a_{FLd} (\Omega_{H-FLd}))$
Annual pelagic fish larvae gross production	$\phi Lp = \sum_{day0}^{day360} \left(a_{FLp} \left(\Omega_{H-FLp} \right) \right)$
Annual bird/mammal gross production	$\Pi = \sum_{day 0}^{day 360} \left(a_J \left(\Omega_{Fp-J} + \Omega_{Fd-J} + \Omega_{Df-J} \right) \right)$
Pelagic fish annual egg production	$\sum_{day 0}^{day 360} (Pspn(t) . Fp)$
Pelagic fish annual recruitment	$\sum_{day0}^{day360} (\operatorname{Prec}(t) FLp)$

Demersal fish annual egg production	$\sum_{day0}^{day360} (\text{Dspn}(t) . \text{Fd})$
Demersal fish annual recruitment	$\sum_{day 0}^{day 360} (\text{Drec}(t) \cdot \text{FLd})$
Total export from secondary producers	$\sum_{day0}^{day360} \left(\Omega_{\text{H-C}} + \Omega_{\text{H-FLp}} + \Omega_{\text{H-Fld}} + \Omega_{\text{H-Fp}} + \Omega_{\text{Bs-Bc}} + \Omega_{\text{Bs-Fd}} \right)$
Total animal production	$\Psi + \gamma + \chi + \beta + \phi L p + \phi L d + \phi p + \phi d + \Pi$
Fishery landings	$\sum_{day 0}^{day 360} \left(\left(1 - disc_{Fp}\right) \Omega_{Fp-M} + \left(1 - \exp(-dfd.Fd)\right) \Omega_{Fd-M} + \left(1 - disc_{Bs}\right) \Omega_{Bs-M} + \left(1 - disc_{Bc}\right) \Omega_{Bc-M} \right) \right)$
Total annual water column mineralization flux	$\sum_{day0}^{day360} \left(m_{s}.D_{s} + m_{d}.D_{d} \right)$
Total annual sediment mineralization flux	$\sum_{day0}^{day360} m_x . D_x$
Total annual denitrification flux	$\sum_{day0}^{day360} \left(\mathbf{d}_{s} \cdot \mathbf{N}_{s} + \mathbf{d}_{d} \cdot \mathbf{N}_{d} \right)$
Total annual nitrification flux	$\sum_{day0}^{day360} (n_{s}.A_{s} + n_{d}.A_{d} + n_{x}.A_{x})$

Total annual sediment-water ammonia flux	$\sum_{day0}^{day360} \left(V_{x.}T_{Vx}.((A_{x}/(T_{x}.por_{x})) - (A_{d}/T_{d})) \right) + \sum_{day0}^{day360} (((1 - a_{Bs})/2).(\Omega_{Dd-Bs} + \Omega_{Dx-Bs} + \Omega_{Pd-Bs})) + $
	$\sum_{day0}^{day360} (((1 - a_{Bc})/2).(\Omega_{Bs-Bc} + \Omega_{Dc-Bc}))$
Total annual sediment-water nitrate flux	$\sum_{day0}^{day360} (V_{x}T_{vx}.((N_{x}/(T_{x}.por_{x})) - (N_{d}/T_{d}))))$
Total annual particulate flux from water column to the sediment	$\sum_{day0}^{day360} \left(\Omega_{Pd-Bs} + \Omega_{Dd-Bs} + x_{disc-corp}.D_f + x_{\sin k_d}.D_d\right)$
Total annual flux of fishery discards to the sediment	$\sum_{day0}^{day360} \left(\mathbf{x}_{disc\text{-corp}} \cdot \mathbf{D}_{f} \right)$
Total mass of nitrogen	$\begin{array}{l} D_s+D_d+D_x+D_f+D_c+A_s+A_d+N_s+N_d+P_s+P_d+H+C+Bs+Bc+FLp+FLd+Fp\\ +Fd+J \end{array}$

Metabolic parameters for all living components of the model. These parameters were fixed and not subject to fitting by the simulated annealing process.

		Durantian of	Background proportion of	
		Proportion of	biomass excreted	O for
		uplake	d ⁻¹) at reference	Q ₁₀ IOI
			d) at reference	Dackground
	Q_{10} for	biomass (a_x ,	temperature of	excretion
Predator	uptake rates	d ⁻¹)	10°C	rates
Phytoplankton	2.0	0.34	n/a	n/a
Herbivorous	2.2	0.34	0.01	2.4
zooplankton				
Carnivorous	2.2	0.34	0.005	2.4
zooplankton				
Suspension/deposit	2.2	0.34	0.01	2.4
feeding benthos				
Carnivorous/scavenging	2.2	0.34	0.0075	2.4
benthos				
Pelagic fish larvae	2.2	0.34	0.00005	2.4
Pelagic fish adults	2.2	0.275	0.001	2.4
Demersal fish larvae	2.2	0.34	0.00005	2.4
Demersal fish adults	2.2	0.25	0.001	2.4
Birds/mammals	2.2	0.15	0.0005	2.4

Miscellaneous biological parameters of the model which were fixed and not subject to fitting by the simulated annealing process.

Parameter	Value	Units
Irradiance at maximum nutrient uptake by	5	$E.m^{-2}.d^{-1}$
phytoplankton		
Pelagic fish: date of onset of spawning	100	Day of the year
Pelagic fish: duration of spawning	250	d
Pelagic fish: date of onset of recruitment	1	Day of the year
Pelagic fish: duration of recruitment	150	d
Pelagic fish: annual potential fecundity	0.25	g.g ⁻¹
Demersal fish: date of onset of spawning	60	Day of the year
Demersal fish: duration of spawning	90	d
Demersal fish: date of onset of recruitment	200	Day of the year
Demersal fish: duration of recruitment	150	d
Demersal fish: annual potential fecundity	0.4	g.g ⁻¹
Q_{10} for mineralization, nitrification and	2.4	°C-1
denitrification (same in all water column layers		
and sediment)		

Table S10

Maximum likelihood uptake rate parameters $U_{max(consumer)}$ (d⁻¹) at the reference temperature of 10°C, and half-saturation constants $h_{(consumer)}$. Units of the half-saturation constants are mMN.m⁻³, except for the benthos guilds (suspension/deposit, and carnivorous/scavenging benthos) where the units are mMN.m⁻².

Consumer	$U_{max(consumer)}$	$h_{(consumer)}$	Density
			dependent
			mortality
			coefficient
Phytoplankton	2.791	16.464	n/a
Herbivorous zooplankton	1.147	4.675	n/a
Carnivorous zooplankton	0.322	1.769	8.175E-04
Suspension/deposit feeding			n/a
benthos	2.838	148.637	
Carnivorous/scavening benthos	0.060	6.702	6.193E-04
Pelagic fish larvae	0.534	5.801	1.990E-06
Pelagic fish adults	0.058	1.176	5.260E-05
Demersal fish larvae	0.209	2.818	1.140E-06
Demersal fish adults	0.015	0.365	4.770E-05
Birds/mammals	0.137	1.433	7.384E-03

Maximum likelihood preference parameters $pref_{resource-consumer}$ for all resource-consumer links in the model. Preferences for each consumer guild (columns) sum to 1.0

						Cor	nsumers				
											Birds/
Resource	ID	7	8	9	10	11	12	13	14	15	mammals
Ammonia	1	0.614									
Nitrate	2	0.386									
Suspended detritus	3		0.053		0.675						
Sediment detritus	4				0.014						
Corpses	5					0.512				0.025	0.205
Fishery discards	6									0.091	0.641
Phytoplankton	7		0.947		0.311						
Herbivorous											
zooplankton	8			0.840			1.000	0.712	1.000		
Carnivorous											
zooplankton	9							0.222		0.017	
Suspension/deposit											
feeding benthos	10					0.488				0.421	
Carnivorous/scavenging											
benthos	11									0.032	
Pelagic fish larvae	12			0.120				0.050		0.119	
Pelagic fish adults	13									0.132	0.116
Demersal fish larvae	14			0.040				0.016		0.048	
Demersal fish adults	15									0.115	0.038

Table S12Maximum liklelihood values of biogeochemical and fishery discarding parameters.

Parameter	Surface	Deep layer	Sediment
Lysis rate of phytoplankton d ⁻¹	0.0321	0.0501	n/a
Sinking rate of detritus d ⁻¹	0.128	$0.266 \text{ at } \log_{10} \text{ vertical}$ diffusion (V(t)) = -6 $0.049 \text{ at } \log_{10} \text{ vertical}$ diffusion (V(t)) = -3.4	n/a -
Coefficient for biomass dependency of demersal fish discard rate	0.089	n/a	n/a
Conversion rate of fishery discards to corpses d ⁻¹	n/a	0.414	n/a
Conversion rate of seabed corpses to sediment detritus d ⁻¹	n/a	n/a	0.0946
Mineralization rate of detritus at the reference temperature of 10°C, d ⁻¹	0.0082	0.0082	0.0077
Nitrification rate of ammonia at the reference temperature of 10°C, d ⁻¹	0.0041	0.0427	0.0358
Denitrification rate of nitrate at the reference temperature of 10°C, d ⁻¹	0.0000405	0.0000621	0.2638

Stationary time series of dissolved inorganic nutrient state variables in the water column layers and sediment pore water of the model, over the final year of an 80 year run with the maximum likelihood parameter vector and 1970-1999 climatological average physical and chemical driving data. Units for all dissolved nutrient variables: mMN.m⁻³.



Stationary time series of dead organic state variables in the model, over the final year of an 80 year run with the maximum likelihood parameter vector and 1970-1999 climatological average physical and chemical driving data. Units for water column detritus variables: mMN.m⁻³. Units for fishery discards and corpses: mMN.m⁻².



Stationary time series of phytoplankton and zooplankton state variables in the water column layers of the model, over the final year of an 80 year run with the maximum likelihood parameter vector and 1970-1999 climatological average physical and chemical driving data. Units for all plankton variables: mMN.m⁻³.



Stationary time series of larval and adult fish state variables in the model, over the final year of an 80 year run with the maximum likelihood parameter vector and 1970-1999 climatological average physical and chemical driving data. Units for all fish variables: mMN.m⁻³.



Stationary time series of filter & deposit feeding benthos, carnivorous & scavenge feeding benthos, and bird/mammal state variables in the model, over the final year of an 80 year run with the maximum likelihood parameter vector and 1970-1999 climatological average physical and chemical driving data. Units for benthos and birdm/ammal variables: mMN.m⁻².

