A food web model of invertebrate subtidal soft-bottom communities
Part A: model derivation and effects of productivity

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Nederlandse Samenvatting

Om visserij in de Natura-2000 gebieden Noordzeekustzone en Vlakte van de Raan zodanig te reguleren, dat zij het behalen van de geformuleerde beleidsdoelen niet in de weg staat, is het VIBEG-akkoord gesloten. Kern van de afspraken vormt een ruimtelijke zonering waarmee wordt bepaald welke visserijtechnieken in welke gebieden wel of niet zijn toegestaan.

Verandering in visserijdruk, zoals sluiting, kan leiden tot allerlei onverwachte effecten, omdat allerlei secundaire effecten in het voedselweb kunnen optreden. Om een inschatting te maken van de mogelijke netto-effecten van sluiting en reducering van visserij (dus inclusief secundaire effecten) in deze gebieden is het nodig inzicht te krijgen in het functioneren van het benthische voedselweb. In deze publicatie wordt een model van zo'n voedselweb van de benthische gemeenschap ontwikkeld en geanalyseerd. Het benthos wordt beschreven aan de hand van relevante soortgroepen (en dus niet op basis van specifieke soorten). De configuratie van het voedselweb is zodanig gekozen dat dit representatief is voor de Natura 2000-gebieden Noordzeekustzone en Vlakte van de Raan (Fig. 1). Het model beschrijft de situatie op een betrekkelijk kleine locatie, in de orde van grootte van de individuele deelgebieden in de zonering van de Noordzeekustzone. Door in het model de productiviteit te variëren, wordt het volledige spectrum van mogelijke dynamiek van het ecosysteem zichtbaar. Deze analyse vormt de basis voor een vervolgstudie, waarin zal worden gekeken hoe het model-ecosysteem reageert op bevissing met boomkor- en garnalentuig.

Het gemodelleerde systeem bestaat uit 3 functionele groepen benthos: scavengers, filter feeders en detritivoren.'Scavengers' zoeken de bodem af en eten wat ze maar te pakken kunnen krijgen, zowel levend als dood. 'Filter feeders' hebben een soort zeef-orgaan, waarmee ze algen en andere organische deeltjes uit het water filteren, en 'detritivoren' voeden zich met dood organisch materiaal (zoals afgestorven algen, vlokken bacteriën) op en in de bodem.

Analyse laat zien dat een viertal kwalitatief verschillende ecosysteem-toestanden zijn te onderscheiden, die zich voordoen bij toenemende productiviteit:

1. Uitsluitend detritivoren
2. Detritivoren en filter feeders
3. Detritivoren, filter feeders en lage dichtheid scavengers
4. Detritivoren, filter feeders en hoge dichtheid scavengers

Toestand 3 en 4 onderscheiden zich door de rol die scavengers innemen in het voedselweb. In toestand 3 zijn ze voornamelijk concurrenten van filter feeders, die bepalen hoeveel voedsel er voor de scavengers overblijft. In toestand 4 gedragen scavengers zich als top-predatoren, die in hoge dichtheid voorkomen en de dichtheid van alle andere groepen in het model laag houden door hun voedselconsumptie en predatie.

1. Introduction

Along the Dutch coast multiple types of fishing occurs, from shrimping with sumwings that hardly disturb the sediment to beam trawling for flatfish. These types of fisheries not only differ in the animals caught, but also differ in their physical disturbance of the sediment. Because of these differences, they could also have a different impact on benthic faunal communities. To regulate fisheries in the Natura-2000 areas along the Dutch coast the VIBEG-agreement was signed. The core of this agreement is a spatial zonation which restricts the use of different fishing gears to certain parts of the Natura 2000 areas in order to regulate the impact of fisheries on the benthic ecosystem. It is well-known that the response of benthic faunal communities to fishing gears is not straightforward. It can for example lead to increased resource availability, or create bare sediment available for colonization, and might be advantageous to species that can capitalize on these effects. Direct positive effects of reduced fishing intensity might therefore be offset by negative indirect effects. The balance between positive and negative effects eventually will determine whether a policy measure has the desired effect, no effect, or even backfires.

To study the potential indirect effects triggered by fishing, under a range of (a-)biotic conditions, a food-web model is developed to represent the macrobenthic community on a subtidal soft-bottom seafloor as found along the Dutch coastal zone. The model aims to mechanistically describe the interactions between components of the community and effects of fisheries on them. The food web does not consist of species, but of guilds and the model is not spatially explicit, but represents a community at a given location.

A model is, by definition, a simplified representation of reality. For any given ecosystem, many different food web models can be constructed, each with different simplifying assumptions. Each possible model representation is relevant in relation to certain research questions, and irrelevant in relation to others. When constructing a model, certain aspects may be incorporated in a relatively complex way, while others are more strongly simplified. Such choices reflect the purpose of the model. As an analogy: When designing a new airplane, an engineer may construct a scale model to study the aerodynamic properties, but the same scale model would be of no use for studying the required capacity of the plane's air-conditioning.

The model developed here is designed to study the effects of bottom trawl fishing for fish and shrimp on the ecological community under different environmental circumstances (different levels of productivity and recruitment). In the current study, we put together the model and study its basic dynamics in relation to the productivity of the environment. In a follow up to this publication, we study the effects of different kinds of fisheries on the modeled ecosystem.

2. Model description

Macrobenthos feeding types

We have divided the macrobenthos in our model into 3 feeding types: filter feeders, detritivores and scavengers. These are commonly used feeding types in the classification of marine soft-bottom macroinvertebrates (Bremner et al. 2003, Oug et al. 2012).

Filter feeders

These are organisms that feed by capturing organic matter from the water column. For simplicity, there is no distinction between active filter feeders (those that, like many bivalves, pump water through a filtering apparatus) and passive filter feeders (like anemones, which capture particles from the ambient water flow), and there is no distinction between those that feed on live- or dead organic material. This group represents in particular filter feeding bivalve species, including species of special conservation concern such as *Spisula subtruncata* and *Ensis sp.*

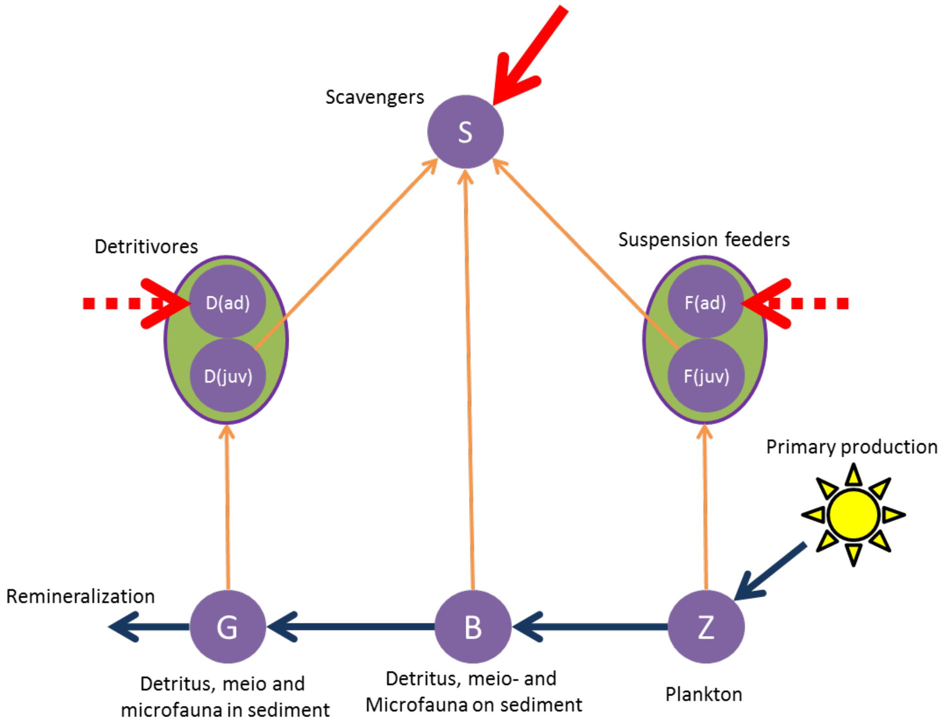

Figure 1: Graphical representation of the modelled food web. Red arrows indicate mortality as a result of shrimp fishing (drawn line) and beam trawling (dotted line). See main text for further details.

Detritivores

Detritivores are organisms that feed on organic matter in and/or on the seafloor. We assume that these species are indiscriminate feeders targeting both live meio- and microfauna and dead organic material. They include in particular the polychaete species which form an important food source for several species of flatfish. In the model, it is assumed that they feed only on detritus which is bound to or incorporated into the sediment, to distinguish them from scavengers which feed on organic deposit lying on the seabed.

Scavengers

Scavengers are organisms with a wide range of food items. They feed on dead organic material and micro- and meiofauna on the seabed, but also on the smaller stages of filter feeders and detritivores. This group is especially tailored to represent brown shrimp (*Crangon crangon*), but also includes other generalist feeders such as the swimming crab *Liocarcinus holsatus,* and common starfish (*Asterias rubens*). Brown shrimp (*Crangon crangon)* has been shown to be an efficient predator of small bivalves (Andresen and van der Meer 2010), but polychaete worms (detritivores, in our model) are also an important food source (Delnortecampos and Temming 1994). Similarly, *Asterias rubens* is an important predator of mussel seed (Aguera et al. 2012).

Another common property of this group is that they are able to actively move around.

Resources

Three resources are used in the model: Plankton, organic matter on the surface and organic matter in the sediment. Plankton (P) are all small organic particles suspended in the water, both living and dead, and both auto-, mixo- and heterotrophic. Organic matter on the seafloor (B) is all plankton which settles on the seafloor surface, plus all associated meio- and microfauna (hereafter: surface resource). This compartment contains many of the small seafloor fauna (such as nematodes, foraminifera, etc.) which do not fall into any of the other categories. The last resource compartment is organic matter in the sediment, which, analogous to the surface resource, includes both detritus, and all associated meio- and microfauna (hereafter: sediment resource).

Plankton is the only source of new biomass in the model. In each transfer of matter from one stage to another, a fraction of the biomass is lost (transfer efficiency is <1). The abundance of plankton is fueled by processes in the pelagic food web, and eventually by photosynthesis of algae, which is outside the scope of our model. The rate at which plankton grows in our model is the inflow of new biomass into the benthic ecosystem.

Spatial domain

The model is tailored to capture the processes that govern food web dynamics on a spatial scale small enough that all populations are open, in the sense that the reproductive output from the local population is not coupled to the inflow of newborns (Roughgarden et al. 1985). Reproductive output is modeled as a biomass loss term, with the implicit assumption that this contributes to a larger pool of reproduction. Similarly, newborn biomass is modeled as an immigration term, assumed to be a small fraction of this larger pool of reproductive biomass. The two are not explicitly coupled. On the other hand, the spatial domain that the model encompasses is large enough that the dynamics are not completely governed by immigration and emigration, and growth and mortality do also affect population dynamics.

Size structure and life history

Detritivores and filter feeders are represented in the model by separate juvenile and adult life stages, while for other groups we do not make such a distinction. The reason for the stage separation is that many scavengers are important predators on the small juvenile filter feeders and detritivores, while the larger, adult individuals are generally better protected, buried in the sediment, and/or are too large to be eaten by the scavengers. We know from general ecological theory that such size-dependent predation is an important source of emergent food web responses (van Kooten et al. 2005, De Roos et al. 2008a).

For detritivores and filter feeders, we assume that reproduction occurs via a (pelagic) larval stage outside the modeled habitat, which is produced by a much larger adult population than that included in the model. Hence, the populations are open with regards to reproduction. This means that we model reproduction as an immigration term which occurs at a fixed rate and energy invested in reproduction as a loss of biomass from the modelled population.

For the scavengers, we model only the larger individuals in the population and assume that the smaller live in habitats which are not covered by our model. We assume that these smaller individuals undergo an ontogenetic habitat shift at a certain size, at which point a fraction of them migrate into the area covered by the model. The total scavenger biomass migrating in to the modelled spatial domain depends on the food availability. The reproductive process of scavengers is not modelled explicitly. This formulation reflects a balance between the inclusion of enough biological realism relevant to this study, and keeping the model mathematically tractable.

Fish and fisheries

The model described here does not include fish. Although various fish species are important predators of a number of benthic invertebrates, in this model we focus only on the invertebrate dynamics and not on the complex feedbacks introduced by the addition of fish predation (Blanchard et al. 2009, van Denderen et al. 2013). However, an extension of this model with fish predation on macrobenthos would be a logical next step in its development.

Fishery is represented in the model as a constant mortality on a number of groups in the model. Which groups, and how the mortalities of these groups relate to one another, depends on which type of fisheries is simulated. We focus on beam trawl fisheries using tickler chains, and on shrimp trawling. Shrimp trawling affects mostly the scavengers, which include the target group of this fishery (*Crangon crangon*), and to a lesser extent the large filter feeders and detritivores. Beam trawling affects most strongly the large filter feeders, and to a lesser extent the detritivores and scavengers (Bergman and van Santbrink 2000).

3. Methods

Model formulation

We assume that in absence of consumption I_f by juvenile and adult filter feeders (J_f and A_f) the basal pelagic resource Z follows semi-chemostat dynamics:

$$dZ/dt=\delta*(Z_{max}-Z) - I_f*(J_f+A_f) - g*Z$$

$\delta*Z_{max}$ determines the productivity of this resource, with δ the turn-over rate and Z_{max} the maximum resource biomass. A part of this resource (g) infiltrates into a benthic food-source, B:

$$dB/dt=g*Z - S*(I_{max,S}*B)/(Dj+Fj+B+H) - \theta*B$$

Resource B is consumed by scavengers (I_s*S). Also, part of resource B (θ) trickles down to the resource only detritivores can feed on, detritus resource G:

$$dG/dt= \theta*B - I_d*(J_d+A_d) - \Omega*G$$

Apart from being fed on by juvenile and adult detritivores (J_d and A_d), this resource is remineralized by respiration at rate Ω, and is lost to the benthic food web.
Consumption of resources takes place following type 2 functional responses (Holling 1959), with consumption of resource j by consumer i:

$$I_{i,j}=(I_{max,i}*j)/(j+H)$$

Where $I_{max,i}$ is the maximum ingestion rate of a consumer and H the half-saturation constant. Filter feeders feed on resource Z, zooplankton, while detritivores feed on resource G, detritus.
Scavengers feed on multiple resources (J_d, J_f and B) with equal efficiency, assuming completely complementary resources *sensu* (Tilman 1984). The consumption of scavengers is hence described by the following equation:
$I_S=(I_{max,S}*(Dj+Fj+B))/(Dj+Fj+B+H)$.

In detritivores and filter feeders, ingested food is first assimilated (with efficiency σ) before it is used for maintenance (T_i). After assimilation and maintenance this energy is used for production of biomass (v_i):

$v_i=\sigma*I_i-T_i$

The biomass produced in the juvenile detritivore and filter feeder stages is used by individuals to grow and mature into adulthood.
The mass-specific maturation rate is derived in (De Roos et al. 2008b) and given by:

$$\gamma_i = \frac{v_i - m_{Ji}}{1 - z^{1 - m_{Ji}/v_i}}$$

Maturation depends on net biomass production of juveniles, v_i, juvenile mortality m_{Ji} and the ratio of body size at birth and at maturation, represented by the parameter z. This definition of maturation captures the flow of biomass of the juvenile into the adult stage in such a way that the stage-structured biomass model in equilibrium is exactly identical to a physiologically structured population model accounting for a continuous size-distribution of juveniles.
Adult detritivores and filter feeders spend all their biomass production on reproduction, which is assumed not to affect the local recruitment. Adults therefore do not grow.
All consumer populations (scavengers, detritivores and filter feeders) are assumed to be open, in the sense that imports of biomass (ρ_i) determine the growth of populations, opposed to a closed system where reproduction by adults drives recruitment.

The populations of detritivores and filter feeders each consist of a juvenile and adult size class and are described by the following equations:

$dJ_i/dt = \rho_i + (v_i - y_i)*J_i - m_{Ji}*J_i$
$dA_i/dt = y_i*Ji - m_{Ai} * A_i$

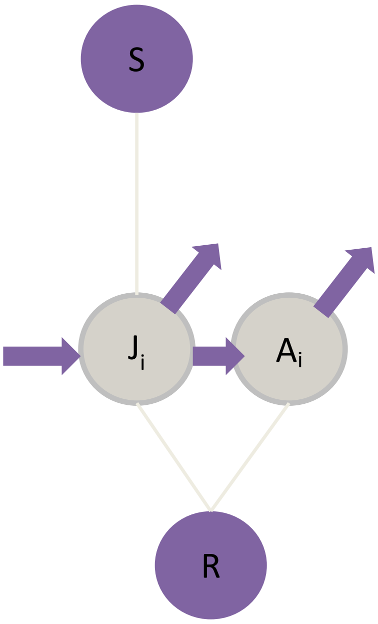

Figure 2:The processes governing changes in biomass abundance of juvenile (J) and adult (A) consumers (detritivores and filter feeders). Import-driven recruitment, resource-dependent growth, mortality (background and predation (by Scavengers)) and maturation.

The population of detritivores and filter feeders increases in biomass by import of recruits (ρ_i), and individual growth, while the population decreases in biomass through mortality. Maturation forms the link between juveniles and adults.

The population of scavengers is considered to be unstructured and is described by the following equation:

$$dS/dt = \Psi * S - m_s * S$$

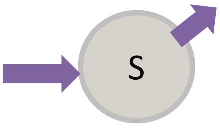

Figure 3: Interactions of scavengers. Import-driven biomass accumulation and mortality.

It decreases through mortality and increases through food dependent imports, Ψ:

$$\Psi = import_{max} * I_{max,\,s} * (B+J_d+J_f)/(B+J_d+J_f+H)$$

Ψ follows a saturating function over food-availability, with the maximum import ($import_{max}$) possible at a saturating amount of food. The underlying assumption of the immigration process is that local reproduction and recruitment are not driving the biomass of S. Instead, we assume that the local biomass of S is determined by local food availability and local mortality; Upon reaching a certain size, scavengers migrate into the modeled area, and the total scavenger biomass that settles there depends on food availability. Consequently, the scavengers in the modeled population control their own import Ψ by depletion of resources: once the food runs out, import stops.

Mortality of filter feeders and detritivores consists of background mortality and predation by scavengers for juveniles J_i. Both detritivores and filter feeders undergo similar types of mortality in adults and juveniles:

$$m_{Ji} = \mu_i + I_{max,s} * S * J_i/(B+J_d+J_f+H)$$
$$m_{Ai} = \mu_i$$

For scavengers, total mortality follows the adult equation, as there is no predation term. We assume scavengers only cause mortality among juvenile detritivores and filter feeders.

Parameterization

Maximum ingestion (I_{max}), maintenance (T) as well as the mortality parameter (μ) are all mass-specific rates (expressed in unit biomass per unit biomass per unit time).
Default values for these rates are taken inversely proportional to the quarter power of adult body size, with proportionality constants α_i for maximum ingestion, maintenance and background mortality to conform to the ratio 1:0.1:0.01 (Peters 1983a, Yodzis and Innes 1992, Gillooly et al. 2001) such that:

$$I_{max,i} = \alpha_i * M_i^{-0.25}$$
$$T_i = 0.1 * \alpha_i * M_i^{-0.25}$$
$$\mu_i = 0.01 * \alpha_i * M_i^{-0.25}$$

Background mortality of scavengers is assumed to include both natural mortality and natural export of scavengers from the system, so that $m_s = \mu_s$. Filter feeders and detritivores are assumed to be sessile after their planktonic larval phase, so that there is no export. Hence, α is lower for scavengers than for filter feeders and detritivores (see table 1).

The maximum resource density Z_{max} and half-saturation density H are expressed as gram biomass per unit volume and therefore the only parameters containing the unit of volume. H can be set to 1 without loss of generality, as this merely implies a scaling of the unit of the total system volume. Maximum resource density Z_{max} is then expressed as multiples of the half-saturation density. A conversion efficiency of 0.5 is used for conversion of both resource and consumer biomass (Peters 1983b).

Table 1: parameters of the model.

parameter	**Default value**	**Units**	**Explanation**
Z_{max}	Varied	g/V	Maximum biomass Z
H	1	g/V	Half-saturation constant
$Import_{max}$	Varied	g/day	Maximum import S
M_d	0.1	g	Individual body-mass of adult D
M_f	0.1	g	Individual body-mass of adult F
M_s	1	g	Individual body-mass of adult S
g	0.5	/day	Infiltration rate from Z to B
Θ	0.5	/day	Infiltration rate from B to G
Ω	0.1	/day	Respiration rate of G
ρ_f	0.001	g/day	Recruitment of F
ρ_d	0.001	g/day	Recruitment of D
α_d	0.01	-	Proportionality constant D
α_f	0.01	-	Proportionality constant F
α_s	0.08	-	Proportionality constant S
Σ	0.1	/day	Turn-over rate Z
Z	0.01	-	mass at birth: mass at maturation for D and F

Growth of detritivores and filter feeders from juvenile to adult is food-dependent (which is driven by primary production), but biomass production of adults does not lead to local spat/brood fall. Instead, spat fall for these groups is dependent on (constant) external import. For scavengers however, import is a saturating function of food-availability. The consequence is that dynamics of the system is primarily driven by the balance between imports, mortality and primary production. These parameters have been varied to discern their effects on the ecosystem.

Model analysis

For the analysis of the model we used Matcont, an extension module for Matlab for numerical bifurcation analysis and continuation of equilibria (Dhooge et al. 2003). We analyze how the equilibria of the model change with varying productivity, which reveals a number of qualitatively different emergent ecosystem states.

4. Results

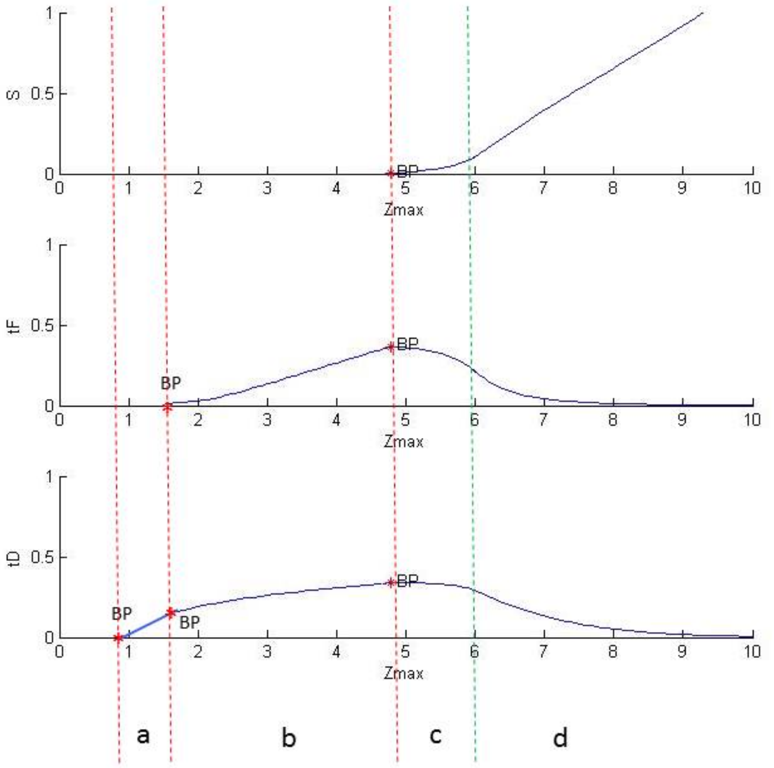

*Figure 4: Biomass of Scavenger (S; top), adult and juvenile Filter feeders (tF; middle) and adult and juvenile Detritivores over resource productivity Zmax. *BP denotes a Branching Point; a persistence boundary of a population, the value of Zmax at which a population goes extinct. Vertical lines delineate regions of resource productivity with qualitatively different community composition; a: detritivore-only system, b: coexistence between filter feeders and detritivores, c and d: coexistence between scavengers detritivores and filter feeders. The community systems in regions c and d differ in the dominant interaction between scavengers and filter feeders; c: a competition-driven system, and d: a predation-driven system. At values of Zmax lower than region a, productivity is too low for any of the consumers and the system consists only of resources. Import*$_{max}$*=0.25, values of other parameters as listed in table 1.*

Increasing productivity from zero reveals the emergence of four qualitatively different ecosystem states (figure 4 and 5), not counting the trivial state at very low productivity, with resource populations only. At low resource productivity, only detritivores are present (figure 4 region a). This is because the rate at which the detritivore resource (G) is remineralized is assumed to be lower than the rate at which the resources B and Z are transferred to G, leading to a build-up of resource availability for detritivores. As a result, they can persist in the system at low productivity, while filter feeders, despite having identical ingestion, maintenance and mortality rates, cannot. When resource productivity is increased further, the abundance of suspended resource Z increases to the extent that it can support a population of filter feeders (figure 4 region b and figure 5, left panel). The filter feeders (F) have ‘first access’ to the resource Z, before it becomes accessible to the detritivores as G. As a result, the increase of detritivores with productivity is less steep in the presence of filter feeders (figure 4, region b) than in their absence (figure 4 region a).

With further increasing productivity, scavengers can eventually enter the system (figure 4 region c and figure 5 middle panel). Just like detritivores, scavengers are subjected to highly asymmetrical resource competition with filter feeders, who have ‘first access’ to the newly produced resource. However, unlike detritivores, scavengers can feed directly on the juvenile stage of the filter feeders and the detritivores. As a result, the addition of scavengers to the food web causes a decline in the equilibrium abundance of both detritivores and filter feeders, while the scavenger abundance increases with productivity. It is important to note that the adult stages of filter feeders and detritivores form a ‘size refuge’ from predation by scavengers, which limits the impact of scavengers on filter feeders and detritivores.

At the lower end of the productivity range where all groups are present in the community (figure 4 region c and figure 5 middle panel), the dynamics of the system are driven by competition between filter feeders, scavengers and detritivores. An implication of this is that although with increasing productivity, filter feeders and detritivores decline in equilibrium abundance, this decline is not very steep. It is faster in filter feeders than in detritivores because although scavengers feed on their juveniles, detritivores also benefit from the additional resources which reach them as scavengers reduce the abundance of filter feeders. We refer to this as the ‘competition driven state’.

With further increasing productivity, we find a marked change in the rate of increase of scavenger equilibrium abundance with productivity. This is because the gradual shift in balance between scavengers and filter feeders triggers a positive feedback mechanism when the predation mortality inflicted by scavengers starts to lead to a significant reduction of filter feeder equilibrium abundance. When that occurs, scavengers get a double advantage from feeding on filter feeders: it not only provides a source of food, but also ‘eliminates the competition’, inducing a higher flow of resource Z into the scavenger resource compartment B. This increase in food availability of resource B amplifies the increase in scavenger biomass even further through the food dependent immigration. This causes a change to a new ecosystem state, where scavengers act as top predators, controlling the density of detritivores and filter feeders (figure 4, region d and figure 5 right panel). Any further increase in productivity leads to an asymptotic decline in the ‘prey species’ (filter feeders and detritivores), and a linear increase in the equilibrium abundance of the predators, scavengers.

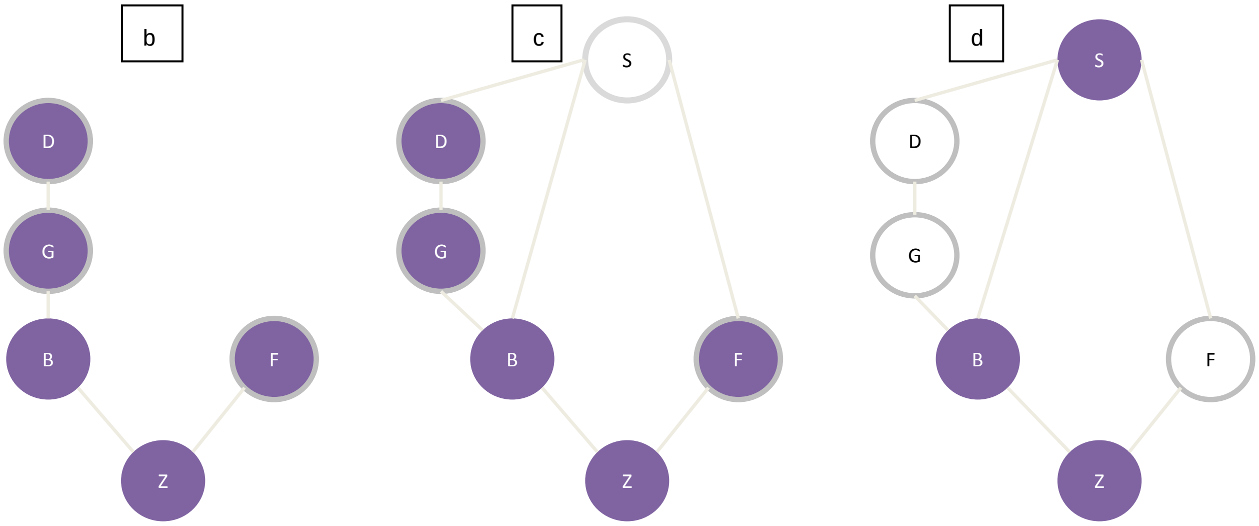

Figure 5: Ecosystem state with increasing resource productivity with corresponding parameter regions of figure 4.

5. Discussion

The system we have studied strongly resembles a number of archetype food webs of which the dynamics have widely been studied. This similarity in its topology is also clearly visible in the observed equilibrium patterns in response to increasing productivity. The sequential addition of higher trophic levels with increasing productivity corresponds to classical linear food chain models (Oksanen et al. 1981). The decrease of the prey (filter feeders and detritivores) abundance after the addition of the top predator (scavengers) is commonly found in intraguild predation (IGP) systems (Diehl and Feissel 2000, Mylius et al. 2001, Hin et al. 2011). In fact, if scavengers would feed directly on the suspended resource Z, the interaction between scavengers and filter feeders in our system would be identical to that studied in (Mylius et al. 2001). Th separate but sequential resource use for the intraguild predator in the model presented here means that no resource competition is experienced by the intraguild prey from the intraguild predator. Consequently, this ‘softens’ the transition from an intraguild prey- to a predator-dominated system as productivity goes up.

The majority of food web models for which the effects of enrichment have been studied are closed systems, in the sense that reproduction of the present population fully determines the production of newborns. We study an open population, with active immigration and passive import of biomass. The addition of juvenile detritivores and filter feeders is modeled as constant import into the area modeled, whereas immigration of scavengers depends on their food availability.

We find that a stronger immigration response (maximum import rate) of scavengers extends the range of productivity for which there is coexistence (of scavengers, filter feeders and detritivores) to lower productivity, but limits this range at high productivity. When the maximum immigration rate of scavengers into the system is low, we find that our system tends to stay in the competition-dominated state (fig 5, middle panel), where an increase in productivity benefits filter feeders, corresponding to general theory for parallel food chains (Wollrab et al. 2012). At higher import, the system acts as a ‘looped’ food web *sensu* (Wollrab et al. 2012), the system is dominated by scavengers, and predation of detritivores and filter feeders by scavengers is the driving interaction. In that case, changing productivity mostly affects the abundance of scavengers.

Higher import of filter feeders enhances the capacity of these filter feeders to monopolize their resource and also allows them to persist up to a higher level of predation. Hence, both the productivity at which scavengers enter the system and the productivity at which filter feeders are lost from the system shift to higher values with increasing filter feeder import.
Detritivores have a peculiar role in the food web. They are ‘last in line’ for resources. They can survive at the lowest productivity, because the remineralization of their resource is relatively slow (see table 1). Consequently, in absence of other consumers, resource G accumulates to high density. At high productivity, in the presence of other model groups, their abundance is negatively affected because fewer resources reach them and their juveniles are eaten by scavengers. The dominance of detritivores at low productivity occurs irrespective of their feeding efficiency or the diet preference of scavengers. It is simply the configuration of the food web which determines that detritivores are last in line for resources, so that whenever another group establishes itself, detritivores are negatively affected. Mechanisms leading to higher flow of resources to detritivores, even at high productivity, could be reduced inflow/immigration or increased mortality of other model groups. Fisheries could be a source of such mortality, which may hence induce a shift from one ecosystem state to another.

6. Quality Assurance

The authors have, among them, 20 years’ experience in formulating and analyzing food web models such as developed here, and 10 years’ experience applying these models to marine ecosystems. Both have a PhD and have published extensively in internationally leading scientific journals on the subject.

IMARES utilises an ISO 9001:2008 certified quality management system (certificate number: 124296-2012-AQ-NLD-RvA). This certificate is valid until 15 December 2015. The organization has been certified since 27 February 2001. The certification was issued by DNV Certification B.V. Furthermore, the chemical laboratory of the Fish Division has NEN-EN-ISO/IEC 17025:2005 accreditation for test laboratories with number L097. This accreditation is valid until 1th of April 2017 and was first issued on 27 March 1997. Accreditation was granted by the Council for Accreditation.

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Justification

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The scientific quality of this report has been peer reviewed by the a colleague scientist and the head of the department of IMARES.

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