

**A food web model of  
invertebrate subtidal soft-  
bottom communities  
Part B: effects of fishery**

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## Samenvatting en beleidsrelevantie

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.

### *Voedselweb*

Verandering in visserijdruk, zoals sluiting, kan leiden tot onverwachte effecten, omdat allerlei secundaire effecten in het voedselweb kunnen optreden. Om een inschatting te maken van de mogelijke netto-effecten van sluiting en/of reducering van visserij (dus inclusief secundaire effecten) in deze gebieden analyseren we een model van het benthische voedselweb (van Kooten & Schellekens, 2014). 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 deze representatief is voor de Natura 2000-gebieden Noordzeekustzone en Vlakte van de Raan.

### *Benthos-sterfte door visserij*

Het hoofddoel van het VIBEG-akkoord is door middel van een ruimtelijke zonering bijdragen aan het behoud van de omvang en een toename in de kwaliteit van habitatype 1110B in de Natura 2000-gebieden Noordzeekustzone en Vlakte van de Raan. Bij het vormgeven van de zonering wordt stilzwijgend uitgegaan van het idee dat wanneer in een gebied de visserij-intensiteit afneemt, alle bodemfauna daar toeneemt. Dit is gebaseerd op de aanname dat alle visserij sterfte, of ten minste een ernstige verstoring veroorzaakt, voor alle in- en op de bodem levende fauna. In het geval van boomkorvisserij is experimenteel werk voorhanden (Bergman en Van Santbrink 2000), dat laat zien dat de variatie in directe sterfte door visserij tussen verschillende soorten zeer groot is. Veel van deze variatie wordt bepaald door de fysieke en ecologische eigenschappen van de soorten (Bolam et al. 2014). Voor de tuigen zoals in de garnalenvisserij gebruikt is er geen experimenteel onderzoek naar de directe sterfte.

### *Indirecte effecten*

Door zich te beperken tot de gemeten directe sterfte door visserij, wordt voorbijgegaan aan twee belangrijke andere aspecten van individuen, soorten en ecologische gemeenschappen. Ten eerste zijn sommige soorten van nature beter in staat te leven met de verstoring door visserij, bijvoorbeeld omdat ze snel reproduceren en goed zijn in het her-koloniseren van verstoorde bodems. Dit kan er toe leiden dat sommige soorten juist een voordeel hebben van visserij, omdat vanwege de hoge mate van verstoring er veel nieuw habitat vrijkomt, dat ze effectief kunnen benutten. Ten tweede het feit dat alle soorten die aan visserij worden blootgesteld, samen één ecosysteem vormen. Onderling hebben de individuen interacties als competitie en predatie. Visserij verandert het voorkomen van bepaalde soorten (door directe sterfte) en kan daardoor indirect ook het voorkomen van andere soorten beïnvloeden. Sommige soorten kunnen het extra moeilijk krijgen om dat bijvoorbeeld hun prooidieren worden gedood door het vistuig, terwijl anderen juist een voordeel hebben als hun voedselconcurrent harder wordt getroffen dan zij. Zulke indirecte voordelen kunnen in theorie zelfs groter zijn dan de nadelen, zodat soorten toenemen, ondanks dat zij zelf ook visserijsterfte ondervinden.

### *Resultaten*

In deze studie wordt onderzocht wat het netto-effect is van visserij op bodemdieren, wanneer de indirecte effecten van de meest in het oog springende ecologische interacties tussen soortgroepen worden meegenomen. De resultaten laten zeer duidelijk zien dat het meenemen van deze interacties tot wezenlijk andere effecten van visserij leidt, dan op basis van alleen de directe sterfte is te verwachten. Het duidelijkst is dit te zien aan de groep 'detritivoren' in het model. Onder alle onderzochte

omstandigheden en bij zowel garnalen- als boomkorvisserij zien we een positief verband tussen de talrijkheid van detritivoren en de visserij-intensiteit. Dit is ondanks het feit dat detritivoren wel directe sterfte ondervinden van beide typen visserij. Dit komt omdat detritivoren uitsluitend toegang hebben tot het voedsel dat overblijft na de consumptie door filter feeders en scavengers. Een visserij-geïnduceerde afname van de concurrentie (filter feeders en scavengers) en/of predatoren (scavengers), leidt dan ook tot een sterk positief effect, en een toename van de hoeveelheid detritivoren.

De dynamiek van schelpdieren (hier filter feeders) onder invloed van visserij is sterk afhankelijk van het type visserij. Garnalenvisserij heeft voornamelijk effect op scavengers, en leidt daardoor altijd tot een positief effect op filter feeders. Soms is dit effect geleidelijk, met oplopende visserij-intensiteit, maar het kan ook tot uiting komen als een plotselinge omslag bij een geringe verhoging van de visserij-intensiteit. Boomkorvisserij heeft echter juist voornamelijk effect op filter feeders (met name schelpdieren), waardoor over het algemeen een negatief verband bestaat tussen visserij-intensiteit en de hoeveelheid filter feeders in het model. Alleen bij voldoende productiviteit en in een sterk predatiegedreven systeem is de afnemende predatiedruk door scavengers op filter feeders zo sterk positief dat het sterk negatieve directe effect van visserij teniet wordt gedaan. Het resultaat is dat schelpdieren hier eerst iets toenemen en daarna licht afnemen met oplopende visserij-intensiteit.

Scavengers ondervinden altijd een negatief effect van garnalenvisserij, en deze vorm van visserij veroorzaakt een omslag in het systeem van predatiegedreven (scavengers als predatoren van filter feeders) naar competitie-gedreven (scavengers concurreren om voedsel met filter feeders). Ook bij boomkorvisserij nemen scavengers altijd af met toenemende visserijdruk als het systeem predatie-gedreven is. Alleen in een competitiegedreven systeem waar scavengers in lage dichtheden aanwezig zijn en sterke competitie ondervinden van filter feeders, kan een lichte mate van bevissing met boomkortuig leiden tot een toename van de hoeveelheid scavengers. De afnemende competitie met scavengers maakt in dit geval de directe sterfte voor scavengers meer dan goed.

#### *Conclusie*

Een belangrijke beheerdoelstelling van Natura 2000-gebied Noordzeekustzone is een verbetering van de functie als foerageergebied voor schelpdieretende vogels (zwarte zee-eend, topper en eidereend). Een aanname bij het ontwikkelen van het huidige beleid is geweest dat visserij een negatieve invloed heeft op de talrijkheid van schelpdieren. De resultaten van deze modelstudie laten zien dat dit voor garnalenvisserij niet hoeft te gelden. Wanneer predatie door garnalen op schelpdieren sterk genoeg is, kan het verwijderen van scavengers (zoals garnalen) juist leiden tot een verhoogde aanwezigheid van filter feeders, waartoe ook de prooi-soorten (Met name *Ensis sp.* en *Spisula subtruncata*) van schelpdieretende vogels behoren.

Een ander belangrijk doel van het beleid is het waarborgen van de van nature aanwezige variatie in bodemgesteldheid van de gebieden Noordzeekustzone en Vlakte van de Raan. Deze studie bevestigt dat visserij in sterke mate invloed heeft op niet alleen de organismen die het sterkst direct worden geraakt door visserij, maar ook de soorten en soortgroepen waarmee zij ecologische interactie vertonen. Vermindering van visserijdruk leidt dan dus niet alleen tot verandering in enkele soorten, maar tot veranderingen op het niveau van de gehele ecologische gemeenschap in en op de zeebodem.

## 1. Introduction

Along the Dutch coast multiple types of fishing occurs, from shrimp fishing 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 area 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 macro-benthic 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 food web model described here is a simplification of the macro-benthic community on a subtidal soft-bottom seafloor, such as commonly found in the North sea (van Kooten & Schellekens, 2014). It is designed to study the net effects of food web interactions on the dynamics and equilibria of the macro-benthic community such as found in the Dutch coastal zone. Here, we extend the model to incorporate the effects of bottom trawl fishing for fish and shrimp. We study the food web effects of these two types of fishing gear on the ecological community under different environmental circumstances (different levels of productivity and recruitment). The research questions we address with this model are: What are the potential effects of fishery in this food web? What are the consequences of a changing fishing intensity and to what extent are these effects dependent on environmental circumstances?

## 2. Methods

### Model formulation

The current analysis is based on the model developed in van Kooten & Schellekens (2014), which we extended to incorporate the effect of fishing. Fishing intensity is described by the parameter  $N$ , which was varied in order to study the effect of fishing intensity on the community structure and dynamics.

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  $\delta$  the turn-over rate and  $Z_{max}$  the maximum resource biomass. This resource infiltrates into a benthic food-source  $B$  at rate  $g$ :

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

In addition to inflow of biomass from  $Z$ , resource  $B$  receives biomass discarded from fisheries ( $e * N$ ), assuming discard fraction  $e$ . Resource  $B$  is consumed by scavengers ( $I_s * S$ ). Also, part of resource  $B$  ( $\theta$ ) trickles down to the resource only detritivores can feed on, detritus resource  $G$ :

$$G' = \theta * B - I_d * (J_d + A_d) - \Omega * G$$

Apart from being fed on by juvenile and adult detritivores ( $J_d$  and  $A_d$ ), this resource is remineralized by respiration at rate  $\Omega$ , 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  $\sigma$ ) before it is used for maintenance ( $T_i$ ). After assimilation and maintenance this energy is used for production of biomass ( $v_i$ ):

$$v_i = \sigma * I_i - T_i$$

We differentiate between juveniles and adults in both detritivores and filter feeders because of size-dependent predation of these groups by scavengers. 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. 2008) 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  $z$  (De Roos et al. 2008). 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.

Adults 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 ( $\rho_i$ ) 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:

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

$$dA_i/dt = y_i * J_i - m_{Ai} * A_i$$

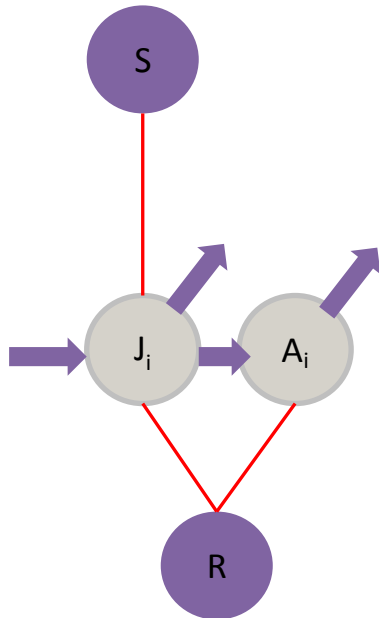


Figure 1: The processes governing changes in biomass abundance of juvenile (J) and adult (A) consumers (detritivores and filter feeders). Import-driven recruitment, resource-dependent growth, mortality (background and predation (by Scavengers)) and maturation. Detritivores and filter feeders feed on different resources, R. The population of detritivores and filter feeders increases in biomass by import of recruits ( $\rho_i$ ), and individual growth. Maturation forms the link between juveniles and adults, while the population decreases in biomass through mortality.

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

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

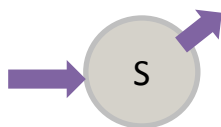


Figure 2: Interactions of scavengers. Import-driven biomass accumulation and mortality.

It decreases through mortality and increases through food dependent imports,  $\psi$ :

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

$\psi$  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  $\Psi$  by depletion of resources: once the food runs out, import stops.

Mortality of filter feeders and detritivores consists of background mortality and, for juvenile filter feeders and detritivores, predation by scavengers. To investigate the consequences of increasing fisheries mortality, total mortality is also dependent on fisheries intensity  $N$ , with a proportionality factor  $\kappa$  indicating what the proportional effect of fisheries mortality on a group is compared to others. Hence, the total mortality for detritivores and filter feeders is

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

$$m_{Ai} = \mu_i + \kappa_i * N$$

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

## Parameterization

Mortality among scavengers is composed of background mortality and fisheries mortality.

$$\mu_{totals} = \mu_s + \kappa_s * N$$

Table 1: scaled parameters of the model.

parameter	Default value	Units	Explanation
N	varied	/day	Fisheries mortality
$Z_{max}$	Varied	g/V	Maximum biomass Z
$Import_{max}$	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	-	Infiltration from Z to B
$\Theta$	0.5	-	Infiltration from B to G
$\Omega$	0.1	-	Degradation of G
E	0.1	-	Return of carrion from fisheries to B
$\rho_f$	0.001	g/day	Recruitment of F
$\rho_d$	0.001	g/day	Recruitment of D
$\alpha_d$	1		Proportionality constant D
$\alpha_f$	1		Proportionality constant F
$\alpha_s$	8		Proportionality constant S
$\Sigma$	0.1	/day	Turn-over rate Z
Z	0.01	-	mass at birth: mass at maturation
$\kappa_d$	0.1	-	Proportion of fisheries induced mortality in detritivores
$\kappa_f$	0.1 or 0.8	-	Proportion of fisheries induced mortality in filter feeders
$\kappa_s$	0.8 or 0.1	-	Proportion of fisheries induced mortality in scavengers

Maximum ingestion ( $I_{max}$ ), maintenance ( $T$ ) as well as the mortality parameter ( $\mu$ ) 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. The rates are multiplied to conform to the ratio 1:0.1:0.01 between these three rates (Peters 1983; Yodzis and Innes 1992; Gillooly et al. 2001) such that:

$$I_{max,i} = M_i^{-0.25}$$

$$T_i = 0.1 * M_i^{-0.25}$$

$$\mu_i = 0.01 * a_i * M_i^{-0.25}$$

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. To compensate for the difference in export, we assume the proportionality factor  $a$  higher 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 1983).

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 the dynamics of the system are 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). In the results section we present how the equilibria of the model respond to changes in productivity, import of scavengers and fisheries induced mortality.

## 3. Results

### The effect of fisheries

We will discuss results from analyses of two scenarios. One in which fisheries-induced mortality affects scavengers most and detritivores and filter feeders are only modestly affected (for instance shrimp fisheries). This leads to proportion  $\kappa_s = 0.8$  and  $\kappa_d$  and  $\kappa_f = 0.1$ .

The second scenario assumes filter feeders instead of scavengers are affected most by fisheries, leading to  $\kappa_s$  and  $\kappa_d = 0.1$ , and  $\kappa_f = 0.8$ . This scenario could represent fisheries with beam-trawls, where mechanical damage to sedentary benthic fauna is known to occur, while non-sedentary fauna, such as shrimp slip through the mazes of the net (Kaiser and Spencer 1996, Kaiser et al. 1998, Bergman and van Santbrink 2000).

*Shrimp fisheries ( $\kappa_s = 0.8$ ,  $\kappa_d$  and  $\kappa_f = 0.1$ )*

When maximum import rate of scavengers ( $\text{Import}_{\text{max}}$ ) is high, the ecosystem is predation-driven in absence of fishing. In such a predation-driven system, which is characterized by high abundance of scavengers, which keep all other groups in the model at low abundance (fig. 3), fishing ( $N$ ) reduces the dominance of scavengers and weakens their control of the ecosystem. This leads to a shift of the system from a predation-driven, to a competition-driven state. This shift, going from low to higher fishing intensity, starts out as a gradual decrease of scavenger abundance, accompanied by a gradual but accelerating increase in equilibrium abundance of filter feeders and detritivores, as scavengers are increasingly unable to control their abundance. This acceleration eventually results in a destabilization of the 'predation state', because there is a positive feedback in the system. As the abundance of scavengers is reduced by higher fishing intensity, filter feeder abundance increases. These filter feeders use up more and more of their resource ( $Z$ ), which limits the production of 'scavenger food' ( $B$ ), further limiting the scope for scavengers to persist. Beyond this destabilization, scavengers persist in very low density, and suffer from severe competition from filter feeders, of which they can only eat the juvenile stage. However, this consumption does still have a substantial effect on the food web: even in this competition-driven state, both detritivore and filter feeder biomass increase with increasing fishing intensity, indicating that the resulting reduction of predation by scavengers more than offsets the direct mortality these groups experience from fishing. There is a region of parameter space where both the competition-driven and predation-driven ecosystem state coexist, and an unstable equilibrium connects these states (fig. 3). At increasing fishing intensity, a threshold is eventually reached where scavengers, the target group of the fisheries, go extinct. Beyond this point the ecosystem is made up of only detritivores and filter feeders. Reducing fishing intensity from this high value reduces the mortality of detritivores and filter feeders, so that their equilibrium abundance increases, and eventually creates a scope for scavengers to invade (not shown?).

The presence of alternative stable states at high fishing intensity depends on the ecosystem productivity. At lower productivity (fig. 4), fishing still induces a shift from a predation- to a competition-driven ecosystem, but the shift is more gradual.

When maximum import rate of scavengers ( $\text{Import}_{\text{max}}$ ) is higher, scavengers are more resistant to fishing, because the population has a greater capacity to replenish biomass lost to fishing. As a result, the effect of fishing is dampened and the shift to a competition-driven system occurs at higher fishing intensity. At very high  $\text{Import}_{\text{max}}$ , the necessary fishing intensity becomes so high that the side-effects of fishing, the mortality on filter feeders and detritivores, prevents the increase of filter feeders and detritivores, even in absence of scavengers. As a result, the shift to a competition-driven system does not occur when  $\text{Import}_{\text{max}}$  is very high (fig. 5).

The general pattern when fisheries-induced mortality  $N$  affects scavengers  $S$  more than filter feeders  $F$  and detritivores  $D$  is that  $S$  is affected directly and therefore decreases, while  $F$  and  $D$  both increase as long as the system remains predation-driven. This is because for them, the positive effects of reduced scavenger predation outweigh the negative effects of fishing mortality. In the competition-driven state, filter feeders control food availability for both detritivores and scavengers. Increasing  $N$  therefore causes a stronger increase in filter feeders than detritivores, and a stronger increase of filter feeders in the competition-driven state than in the predation-driven state. Hence, in the competition-driven state,  $D$  and  $S$  suffer more from filter feeders  $F$  with increasing  $N$ , because filter feeders  $F$  increase in biomass (fig. 3).

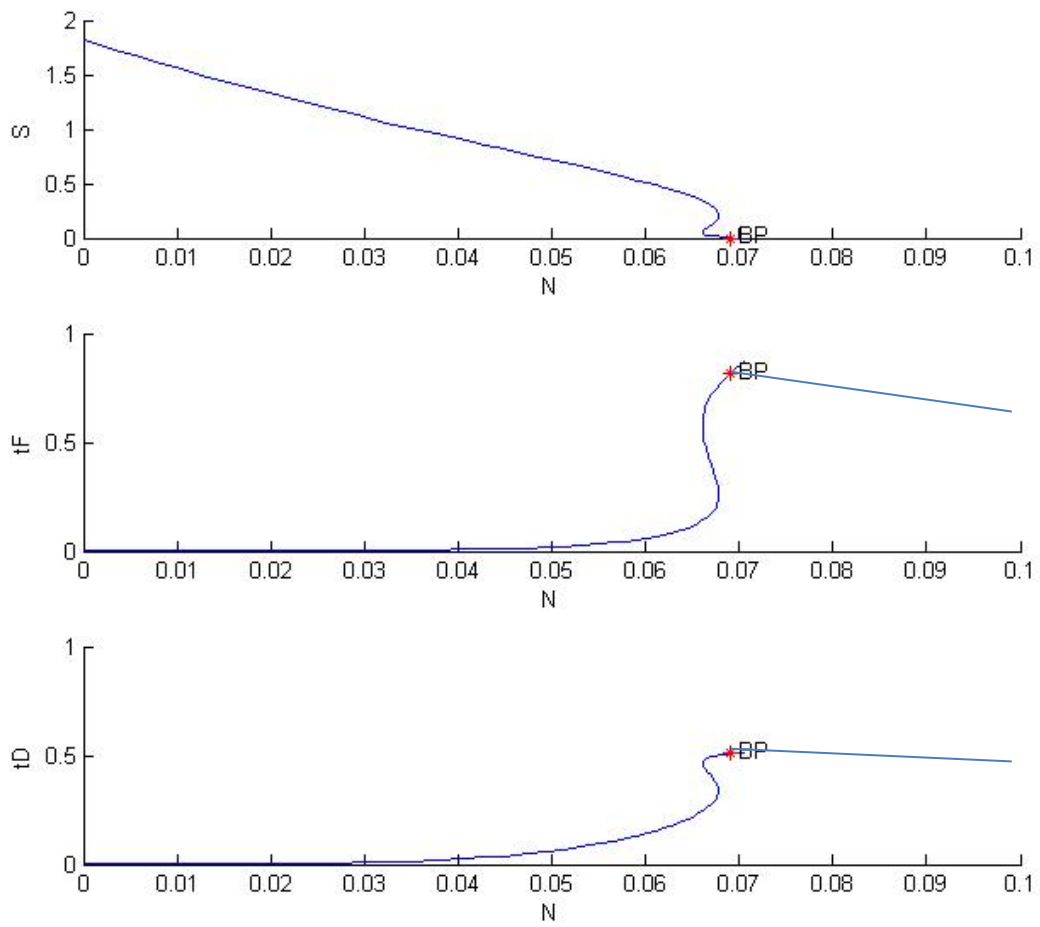


Figure 3: Shrimp-fisheries. Bistability between predation- and competition-dominated system. Biomass of scavengers  $S$  (top), filter feeders  $tF$  ( $J_f + A_f$ , middle) and detrivores  $tD$  ( $J_d + A_d$ ) over  $N$ .  $Z_{max}=10$ ,  $import_{max}=0.3$ .

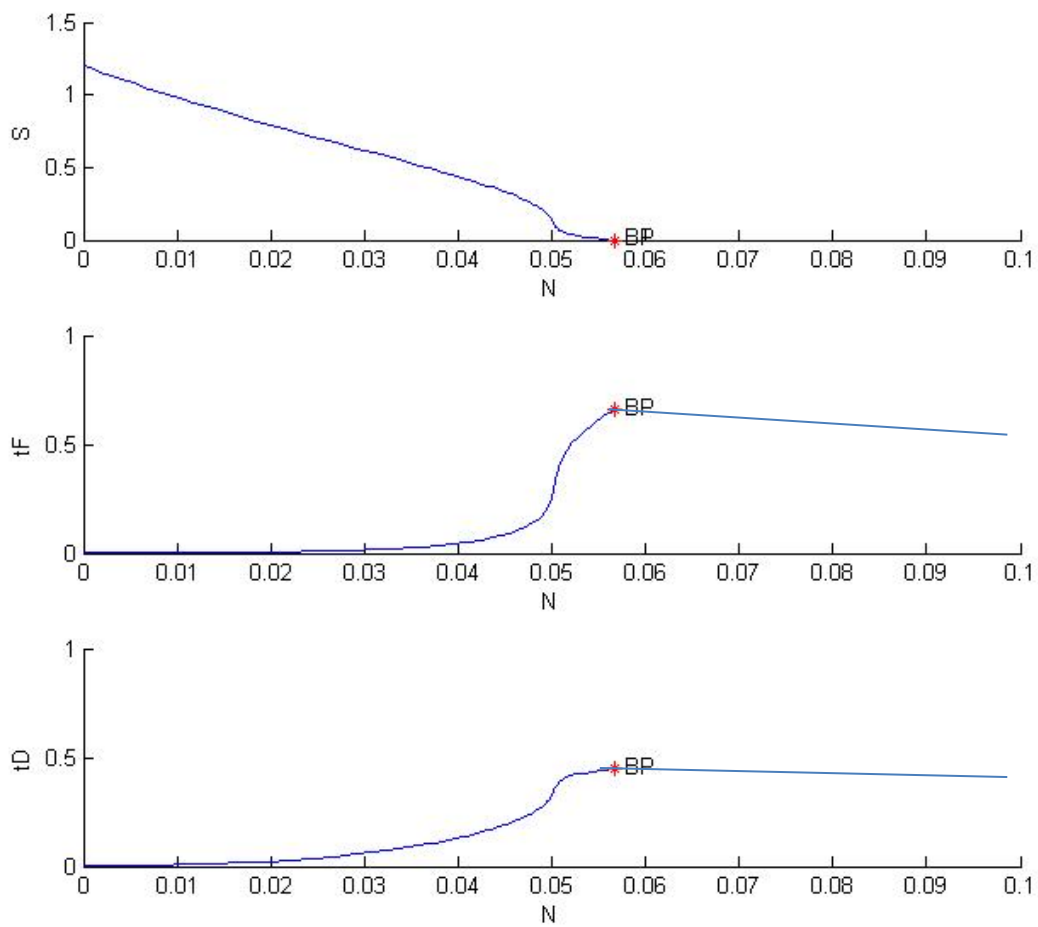


Figure 4: Shrimp-fisheries. Lowered productivity; gradual shift between predation- and competition-driven system over  $N$ . Biomass of  $S$  (top),  $tF$  ( $J_f + A_r$ , middle) and  $tD$  ( $J_d + A_d$ ) over  $N$ .  $Z_{max}=8$ ,  $import_{max}=0.3$ .

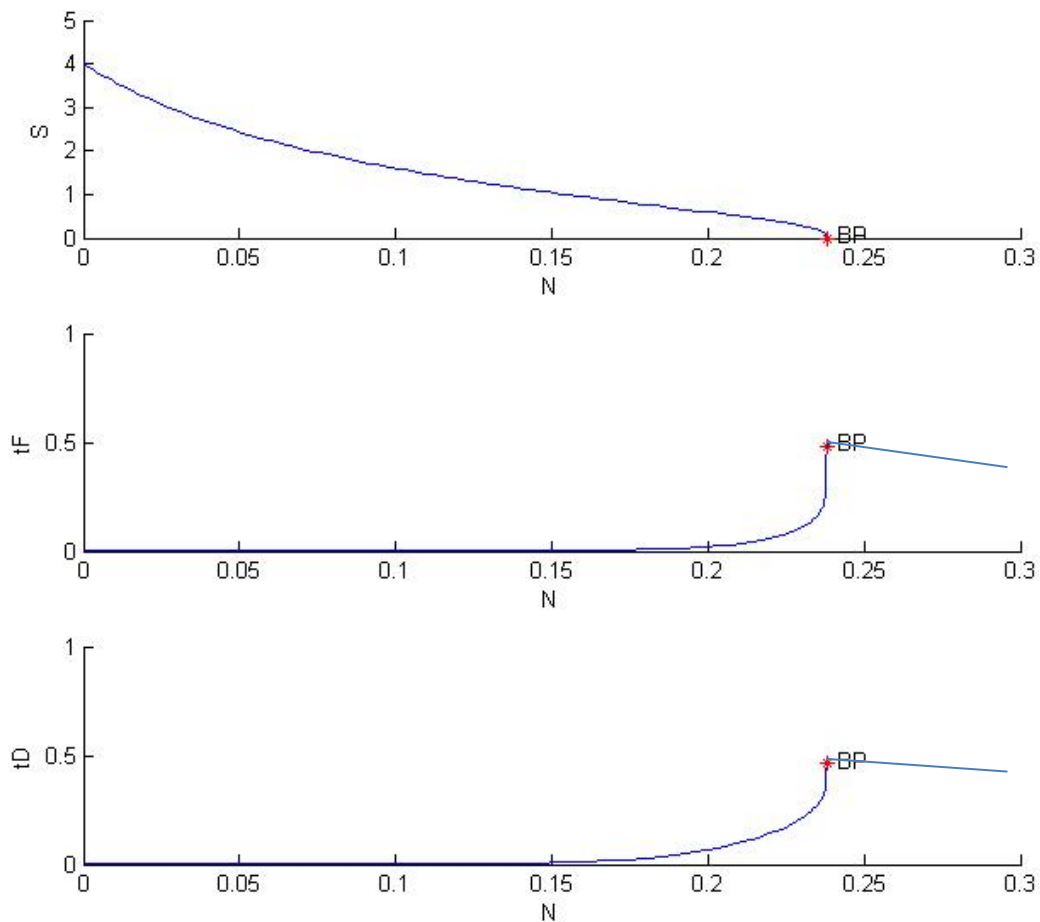


Figure 5: Shrimp-fisheries. Increased import; predation driven throughout. Biomass of  $S$  (top),  $tF$  ( $J_f + A_f$ , middle) and  $tD$  ( $J_d + A_d$ ) over  $N$ .  $Z_{max}=9$ ,  $import_{max}=0.55$ .

#### Beam-trawling ( $\kappa_s$ and $\kappa_d = 0.1$ , $\kappa_f = 0.8$ )

When fisheries induced mortality  $N$  mainly affects filter feeders instead of scavengers, bistability between predation- and competition-driven systems occurs only for a very limited range of fishing intensity  $N$  and resource productivity ( $Z_{max}$ ). Both states generally exist, but the shift from one to the other is gradual. In absence of fishing intensity, the system can be in a competition-driven (fig. 6) or a predation driven state (figs. 7, 8), depending on the resource productivity and the maximum import of scavengers.

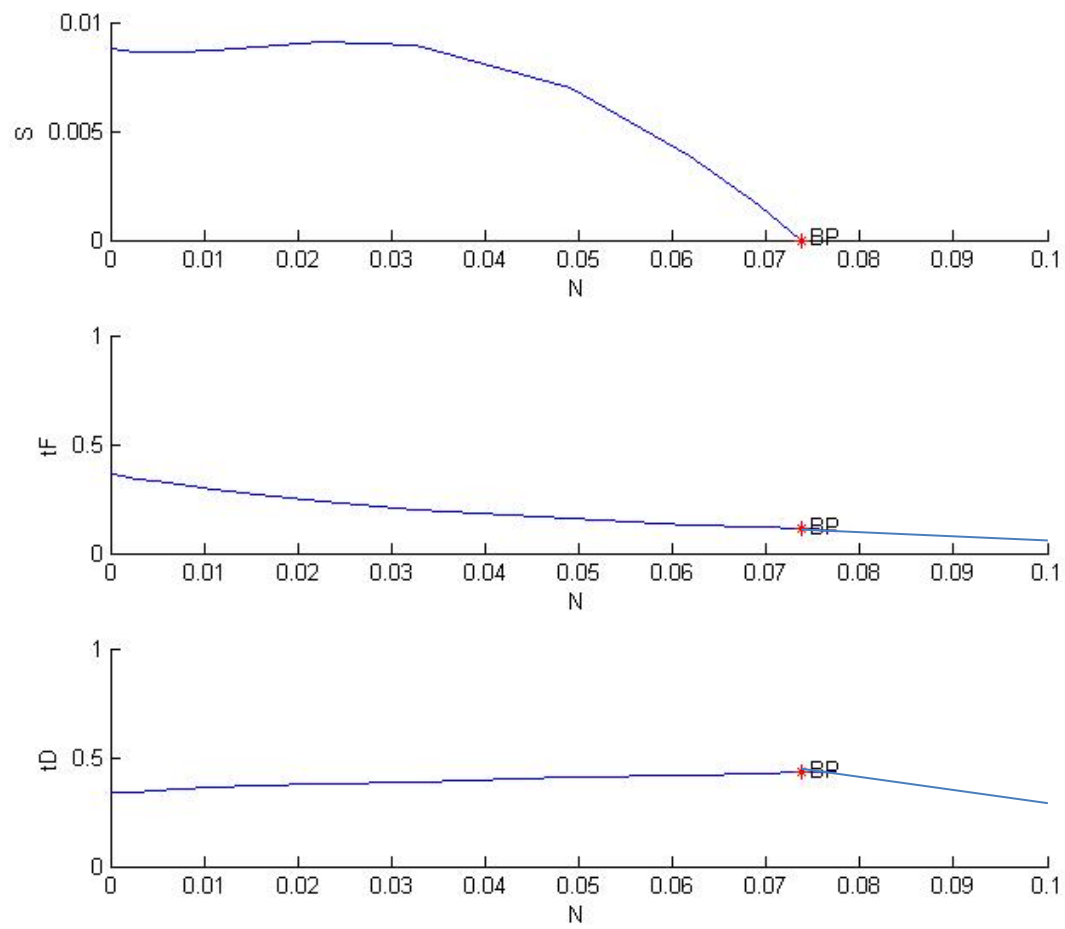


Figure 6: Beam-trawling. Low import, low productivity. Competition driven system over  $N$ . Biomass of  $S$  (top),  $tF$  ( $J_f + A_f$ , middle) and  $tD$  ( $J_d + A_d$ ) over  $N$ .  $Z_{max}=6$ ,  $import_{max}=0.25$ .

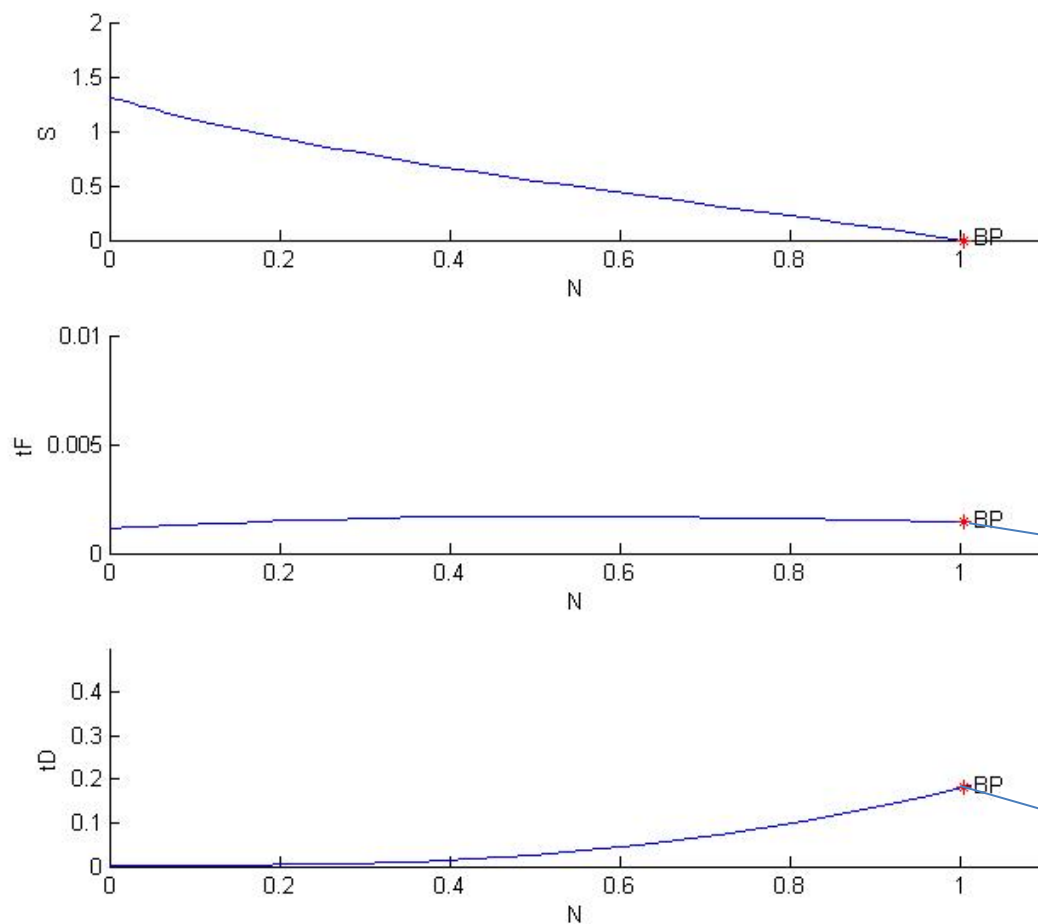


Figure 7: Beam-trawling. Higher import, low productivity. Predation driven system over  $N$ . Biomass of  $S$  (top),  $tF$  ( $J_f + A_f$ , middle) and  $tD$  ( $J_d + A_d$ ) over  $N$ .  $Z_{max}=6$ ,  $import_{tmax}=0.4$ .

Beam trawl fishing has the strongest negative effects on filter feeders ( $F$ ). In a system which is competition-driven in absence of fishing (low productivity, low maximum import of  $S$ ), this means that the equilibrium abundance of  $F$  always declines with increasing fishing intensity (fig. 6). The resulting reduction in consumption of  $Z$  leads to a higher production of the resources  $B$  and  $G$  and consequently, detritivores ( $D$ ) show a marked increase in response to beam trawling. The dynamics of scavengers ( $S$ ) is driven in part by their immigration, which depends on their food availability (juvenile filter feeders and detritivores, and resource  $B$ ). The effects of beam trawl fishing on  $S$  are hence the net result of the complex response of the food of  $S$  and the direct mortality caused by fishing, leading to multiple up- and downswings in the equilibrium curve of  $S$  with fishing intensity ( $N$ ).

At high productivity and/or high maximum import of  $S$ , the system is predation-driven in absence of fishing, with high biomass of  $S$  and low biomass of  $F$  (fig 7 and 8). When the predation-driven state is caused by high import of  $S$  (fig. 7), there is a strong compensatory effect of increased fishing which at low fishing intensity causes  $F$  to increase with higher  $N$ . The higher mortality of  $F$  leads to more per capita resource availability, and hence faster development to maturity. As a consequence, at higher fishing intensity, a higher fraction of  $F$  is hence in the adult state ( $A_f$ ), where it is immune to predation



from scavengers. At low fishing intensity, this predation reduction more than compensates for the biomass loss through fishing, and leads to a positive response of  $F$  to increasing fishing intensity. The reduced abundance of  $J_F$  and (to a lesser extent)  $J_D$  also lead to a reduction in import- and hence equilibrium abundance of  $S$  with increasing fishing intensity, despite an increase in  $B$ , their other food source.

When the predation-driven state in absence of fishing is the result of high productivity ( $Z_{max}$ ), a large fraction of  $F$  and  $D$  biomass is already in the adult state, so that the compensation of fishing mortality by reduced predation is less pronounced, and  $F$  always declines with increasing fishing (fig. 8). Detritivores and scavengers show roughly the same pattern as with high import, although high import allows scavengers to remain in the system up to much higher fishing intensity (compare upper panels of figs 7 and 8).

A general result, true in all considered parameter combinations in this scenario ( $\kappa_s$  and  $\kappa_d = 0.1$ ,  $\kappa_f = 0.8$ ), is that when fishing intensity increases, the system changes to one which is dominated by detritivores. When  $F$  and  $S$  decrease, more of the resource produced in  $Z$  flows to  $G$ , supporting a higher abundance of detritivores.

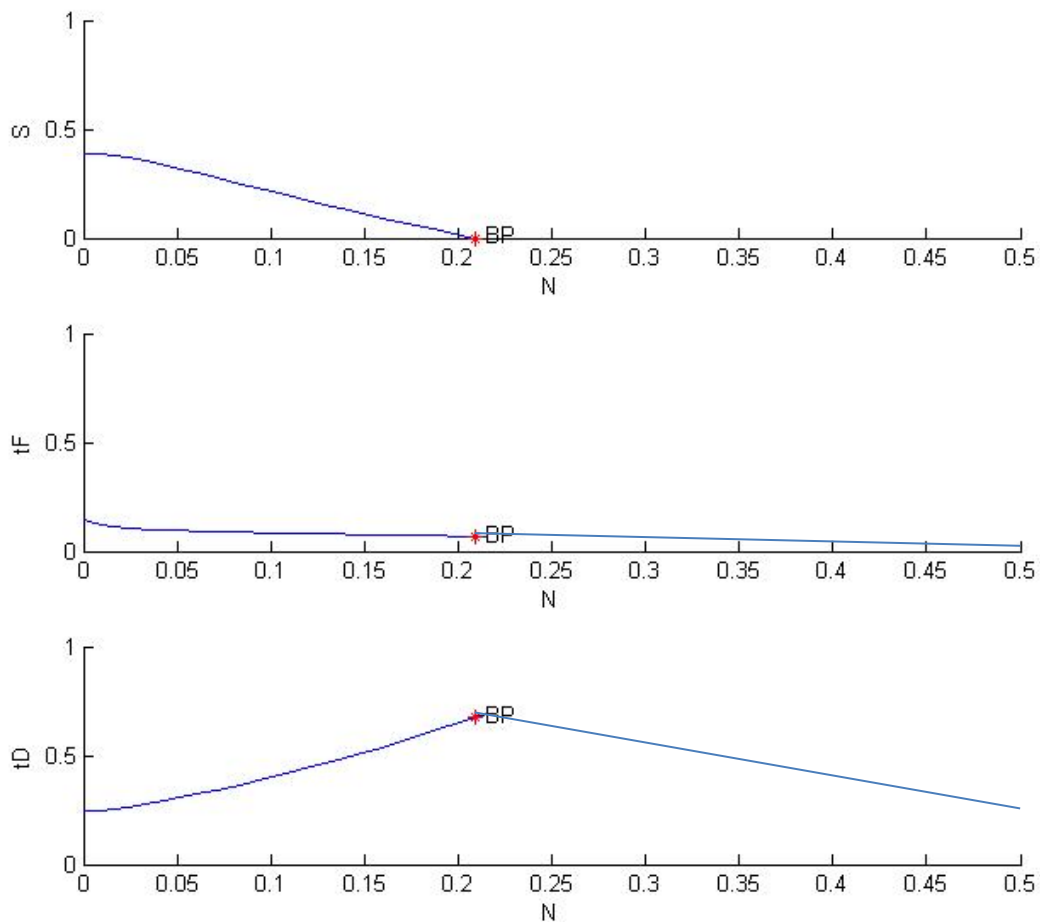


Figure 8: Beam-trawling. Low import, higher productivity; predation-driven system. Biomass of  $S$  (top),  $tF$  ( $J_f + A_f$ , middle) and  $tD$  ( $J_d + A_d$ ) over  $N$ .  $Z_{max}=10.5$ ,  $import_{max}=0.2$ .

## 4. Discussion

We have studied the consequences of two types of fishery on a modeled functional benthic food web. The aim of this work was to study if and how feedback mechanisms in the food web change the generally encountered (though naive) view that fishing has a negative effect on all benthic organisms it affects, and a reduction in fishing will hence lead to recovery of all those organisms. Our results show clearly that food web interactions do substantially alter the effects of fishing on the ecosystem, away from a simple negative effect. Such feedbacks can both strengthen and weaken the effects of direct mortality, depending on the type of fishing and the properties of the ecosystem. In fact, our analysis shows that when food web interactions are considered, the strongest effects of fishing are often not on the groups most strongly/directly affected by fishing mortality.

We find two striking results which are independent of the type of fishery and the productivity of the ecosystem. First, scavengers, (which assume the role of predators) are always the first group to go extinct at high fishing intensity, even when they are not the primary target of fishing (in the case of beam trawl fishing). Second, detritivores, which are at the end of the 'resource chain', always increase as a result of fishing, even though we assume some direct mortality of fishing on them. Only after both scavengers and filter feeders are lost from the system will detritivores negatively respond to fishing intensity (results not shown).

In a previous study (van Kooten & Schellekens 2014), we have shown that depending on ecosystem productivity, a number of food web states are possible. These states are also important in relation to our shrimp trawling scenario, where fishing predominantly targets scavengers, which act as the top predators in our food web. The effect of such fishing is similar to the effect of productivity: an increase in fishing intensity moves the system towards a competition-driven state, in the same way that a reduction in productivity does.

All components of the food web we study here can exhibit either an increase or a decrease in equilibrium biomass abundance, depending on a number of other factors. We have shown that this response depends on system productivity, import of biomass from outside the model, the initial fishing intensity and the type of fishing. Any answer to the ultimate question of which types of taxa would benefit (i.e. increase in equilibrium biomass) from reduced fishing intensity is hence dependent on these factors. Notwithstanding this strong context-dependence, a number of general principles emerge from our analysis. First, in a competition-driven system, fishing always negatively affects the primary target, and benefits its competitors, as they have more resources available. Second, in a predation-driven system, fishery which primarily targets the predator (scavengers) leads to reduced predator abundance and increased abundance of both of its prey groups (filter feeders and detritivores).

In general, low productivity means that competition is the dominant interaction and predation is not an important process shaping the community state. Fishing in a competition-driven system generally reduces the equilibrium abundance of the most-harmed group, which leads to an increased density of all its competitors. For shrimp trawling, this means that filter feeders and detritivores profit, while for beam trawling, detritivores increase. In the latter scenario, one could expect scavengers to also increase, but this occurs only under a very limited range of conditions. Scavenger abundance would increase in response to a decrease in filter feeder abundance, but this decrease is actually very limited. In a competition-driven system, filter feeders are strongly resource limited, meaning that their biomass growth is far below the maximum. Biomass production speeds up when fishing increases filter feeder mortality, largely compensating for the negative effect of fishing on filter feeder equilibrium biomass. This lack of a negative response in filter feeders limits the positive effect on scavengers.

At higher productivity, predation by scavengers on filter feeders becomes a more important interaction, and the system becomes predation-driven. However, the predation-driven state can only be attained when scavenger maximum import is high enough, so that they can profit from the increasing food availability. Fishing mortality on scavengers (shrimp trawling) can keep the system in a competition-dominated state, even at higher productivity.

The maximum import of scavengers also limits the extent to which they can act as a dominant predator, because it determines the extent to which their abundance can increase in response to higher food availability at higher productivity. Increased fishing mortality on filter feeders (beam trawling) facilitates a shift towards a predation-dominated system, because it reduces competitive dominance of filter feeders, while maintaining high food availability for scavengers. In this case, essentially the fishery is helping the scavengers to impose mortality on its competitors, the filter feeders.

Detritivores are at the end of the 'resource conveyor belt' formed by compartments Z, B and G. As a result, they generally increase when other consumers (F and S) decrease. As a consequence, a detritivore-dominated system only occurs when other groups experience severe mortality, such as from fishing. As a potential consequence, predators of detritivores, such as flatfish, could potentially have more food when filter feeders and/or scavengers are subjected to fishing mortality. In a similar system, it has been shown that this can stimulate fish production and eventually, increase harvestable biomass (van Denderen et al. 2013).

## **5. 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 uses 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

Report: C131/15  
Project number: 4316810004

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

Approved: Dr. K.E. van de Wolfshaar  
Scientist

Signature:



Date: 15 September 2015

Approved: Drs. J.H.M Schobben  
Head of Fish Department

Signature:



Date: 15 September 2015