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Food web feedbacks drive the response of benthic macrofauna to bottom trawling

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Abstract

Bottom trawl fisheries have significant effects on benthic habitats and communities, and these effects have been studied intensively in the last decades. Most of these studies have related the changes in benthic community composition to direct effect of trawl gears on benthos, through imposed mortality. This line of argumentation ignores the fact that benthic organisms themselves form a complex food web and that bottom trawling may trigger secondary effects through this food web. We studied the potential consequences of such food web effects using a model of benthic predators, filter feeders, deposit feeders and fish. Our analysis shows how inclusion of ecological interactions complicates the relationship between bottom trawling intensity and the state of the benthic community and causes a non-linear and non-monotonic response of the benthic community to trawling. This shows that indirect food web effects can fundamentally alter the response of a benthic ecosystem to bottom trawling, compared to the direct effects of mortality. In light of our results, we argue that indicators of fishing impact on benthos need to account for positive as well as negative effects of bottom trawling, in order to accurately quantify the impact. Our findings highlight that understanding the food web ecology of the benthic ecosystem is crucial for understanding and predicting the effects of trawling on the seafloor. Work that promotes such understanding of the food web ecology seems a more productive research strategy than conducting ever more empirical trawling effect measurements.

KEYWORDS
benthos, bottom fishing, food web model, trawling impact

1 | INTRODUCTION

It has long been acknowledged that bottom trawl fishing can strongly impact benthic habitats and the benthic ecosystem (Kaiser, 1998), something which was recently confirmed on a global scale (Hiddink et al., 2017). Bottom trawl gears physically disturb the seabed while catching demersal fish and benthic invertebrates. This causes resuspension of sediment, nutrients and organic material into the water column, modifies seabed habitats and imposes mortality on benthic organisms (Dayton, Thrush, Agardy, & Hofman, 1995; Jennings & Kaiser, 1998).

The effects induced by bottom trawl gears on benthos differ substantially among species (Bergman & van Santbrink, 2000). Individuals of large and sessile species are most vulnerable to the direct passing of a gear. When these species also have low reproduction rates, the population also recovers slowly after trawling has ceased (Kaiser et al., 2006). Faster population recovery is expected from mobile species or species that reproduce at an early age. These species are often found to dominate the benthic fauna in areas that are frequently trawled (van Denderen et al., 2015).

Experimental and empirical studies have reported a large range of effects of bottom trawling. A common observation is a reduction in filter feeder abundance at high trawling intensity (e.g. de Juan, Thrush, and Demestrem (2007), Tillin, Hiddink, Jennings, and Kaiser (2006), van Denderen et al. (2015)). In a comparative study, Lokkeborg (2005) finds higher deposit feeder (polychaete) biomass when trawling is increased. However, others do not find increased deposit feeder biomass in response to trawl disturbance (e.g. Jennings, Dinmore, Duplisea, Warr, and Lancaster (2001), Johnson, Gorelli, Jenkins, Hiddink, and Hinz (2015)). Mixed effects of trawling have also been found by McConnaughey, Mier, and Dew (2000), showing some infaunal bivalve species and motile species to increase while others decline. Such variable effects of trawling are supported by meta-analyses of bottom trawling effects showing high variability between studies (Kaiser et al., 2006; Sciberras et al., 2018). The large variation (and consequent lack of significant effects) in these studies is often attributed to inconsistencies in sampling design, data paucity or high background variation leading to low statistical power.

While the potential food web effects of fisheries have long been acknowledged (Jennings & Kaiser, 1998), theoretical studies focusing on the ecosystem effects of bottom trawling have generally interpreted their results as direct effects of the trawling gears (e.g. Mangano et al. (2014), Mangano et al. (2017), Rijnsdorp, de Haan, Smith, and Strietman (2016), Tillin et al. (2006)). A few theoretical studies did incorporate specific food web effects. Duplisea, Jennings, Warr, and Dinmore (2002) and Hiddink, Rijnsdorp, and Piet (2008) modelled the impact of trawling on competing invertebrate benthic species. van Denderen, van Kooten, and Rijnsdorp (2013) also included fish and showed how the combination of primary effects of trawling (removal of fish), the side effects of trawling (removal of benthos), the predation of fish on benthos and the competitive interactions between different benthos types interact to shape the net response of benthos to trawling. Our aim, rather than to provide an explanation for any particular empirical result, is to elucidate how food web effects may be behind some of the large variation observed among empirical studies relating bottom trawling to benthic ecosystem state (e.g. Collie, Hall, Kaiser, and Poiner (2000), Hiddink et al. (2017), Kaiser et al. (2006)).

The role of food web feedbacks in shaping observed effects of bottom trawling on the benthic ecosystem is relevant for management and policy. There is a global shift in fisheries management towards ecosystem-based fisheries management (EBFM; e.g. within the European Union's Common Fisheries Policy, the Australian Fisheries Management Authority and the Fisheries Ecosystem Plan

of the US Pacific Fishery Management Council). Understanding the interactions between fish, the ecosystem they are part of and the fishery is a necessary condition to successfully apply EBFM. The question is also relevant in relation to ecological risk assessments that are carried out globally, such as the EU's Marine Strategy Framework Directive or the Ecological risk management strategies for Commonwealth commercial fisheries (Australia), which use indicator-based management to achieve Good Environmental Status. Strong food web interactions can lead to interdependence of indicators (e.g. predator and prey abundance), which must be considered when determining threshold values for Good Environmental Status. Understanding the causes of variability between empirical results is also of importance for management and policymaking, because it will ensure that measures are appropriate, given the management objectives *and* the particular system they are applied to.

We analyse a model of a benthic food web consisting of invertebrate benthic predators, filter feeders and deposit feeders (Figure 1). These functional groups are present and dominant in abundance and biomass in the most, if not all, soft-bottom benthic ecosystems (Bolam, Coggan, Eggieton, Diesing, & Stephens, 2014; Mangano et al., 2014; Pearson, 2001) and are used to describe changes of food web functioning in relation to disturbance such as trawling (Rijnsdorp et al., 2016). The benthic predators feed on filter feeders and deposit feeders, while the latter two compete for resources. The benthic groups are preyed on by two fish groups, small and large fish, which are in turn a potential target for fisheries. The benthic groups differ in their vulnerability to

FIGURE 1 Schematic representation of the modelled food web. Orange (solid thick) arrows indicate foraging by the benthic groups. Red (small dash) arrows indicate resource degradation, and blue (large dash) arrows indicate foraging by fish. B and R are benthic and planktonic resources; *D, F* and *P* are deposit feeders, filter feeders and invertebrate predators, respectively. Subscripts a and j indicate adult and juvenile stages, respectively. L and S are large and small fish, drawn in square boxes to highlight that they are not modelled as dynamic variables. Figure appears in colour in the online version only
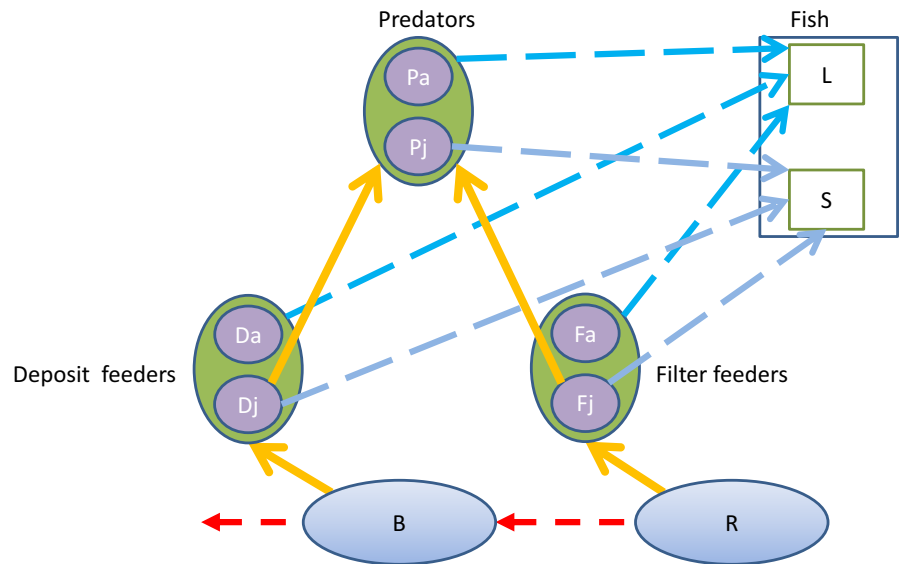
trawling (Sciberras et al., 2018). Using this model, we study how feedbacks through the food web can modify the effects of bottom trawling on long-term biomass abundance of functional groups in the benthos. Our model is tailored to study specifically the effects of feedbacks through the food web on the effects of bottom trawling, and ignores other important sources of complexity present in benthic ecosystems, such as spatial heterogeneity in abiotic factors, species distribution and trawling intensity. This reflects a deliberate choice to keep our model tractable and allows us to interpret our results as consequences of the implemented food web.

Our analysis focuses on otter trawls, a commonly used type of demersal fishing gear worldwide, but we also report results from other gears and study the consequences of using gears with reduced seafloor disturbance and benthic impact. To incorporate trawling-independent ecosystem variation, we also study the effects of trawling at different parameter values of productivity, competitive interactions between filter feeders and deposit feeders and mortality.

2 | METHODS

We use the stage-structured biomass model framework (De Roos et al., 2007, 2008) to model the benthic food web. The model consists of the three benthos groups filter feeders (*F*), deposit feeders (*D*) and predators (*P*), and two fish groups (Figure 1). Each of the functional benthic groups consists of juveniles *j* and adults *a* (Figure 1), to account for stage-specific predation of all groups.

2.1 | Resource dynamics

The model contains a phytoplankton resource (*R*), used by the filter feeders. This resource also precipitates onto the seafloor, where it is added to the detritus resource (*B*) and becomes available for the deposit feeders.

Phytoplankton (*R*) growth follows semichemostat dynamics and has a loss term representing the rate of deposition onto the seabed (Figure 1). The phytoplankton resource is hence described by

$$\frac{dR}{dt} = r\left(R_m - R\right) - pR - C_R \tag{1}$$

where *r* is the resource renewal rate and R_m is the maximum resource abundance in the absence of consumption and precipitation. We use semichemostat resource dynamics rather than the more common logistic growth, because we consider that only the near-bottom fraction of the water mass is available for phytoplankton consumption by filter feeders, whereas the bulk of phytoplankton production occurs in the upper water layers and reaches the *R* compartment by water mixing and particle sinking. Hence, phytoplankton production is positive even when *R* = 0. Phytoplankton precipitates to the seabed at constant rate *p*, and consumption by filter feeders is given by C_R. Consumption depends on *R* (see below), but this has been left out of the notation for simplicity.

Benthic detritus resource *B* increases by deposition of phytoplankton *R* and decreases by deposit feeder consumption (C_B), and the combined effect of microbial respiration and loss to biologically inactive deep sediments where the carbon is excluded from the food web (at rate *L*):

$$\frac{dB}{dt} = pR - LB - C_B \tag{2}$$

2.2 | Consumer and predator dynamics

The key aspects of the structured biomass community framework are the equations for biomass accumulation governing growth and reproduction, and the equation for maturation. The biomass accumulation is based on the net biomass from feeding.

$$v_i = \sigma I_i - T_i \tag{3}$$

(where $i \in \{D_j, D_a, F_j, F_a, P_j, P_a\}$). Here I_i is the mass-specific intake rate, T_i is the mass-specific maintenance rate, and σ is the conversion efficiency of resource to consumer biomass. Transfer from juvenile to adult biomass through maturation (γ) is governed by

$$\gamma_k = \frac{\nu_{k_j} - \mu_{k_j}}{\left(1 - z_k^{1 - \frac{\mu_{k_j}}{\nu_{k_j}}}\right)} \tag{4}$$

(where $k \in \{D, F, S\}$). This function is derived in such a way that it corresponds exactly to a model with continuous size structure under equilibrium dynamics, and approximates it otherwise (De Roos et al., 2008). Maturation is a function of ν, the net biomass production rate, the mortality rate μ, and z, which is the ratio between the size at birth and the size at maturation.

The equations for ν and γ above are the basis of the dynamics of filter feeders (F_j and F_a), deposit feeders (D_j and D_a) and predators (P_j and P_a), where the index indicates the juvenile (j) or adult (a) stage:

$$\frac{dD_j}{dt} = \nu_{D_a}^+ \left(I_{D_a}\right) D_a + \nu_{D_j} \left(I_{D_j}\right) D_j - \gamma_{D_j}^+ \left(I_{D_j}\right) D_j - \mu_{D_j} D_j \tag{5}$$

$$\frac{dD_a}{dt} = \gamma_{D_j}^+ \left(I_{D_j}\right) D_j + \nu_{D_a} \left(I_{D_a}\right) D_a - \nu_{D_a}^+ \left(I_{D_a}\right) D_a - \mu_{D_a} D_a \tag{6}$$

$$\frac{dF_j}{dt} = \nu_{F_a}^+ \left(I_{F_a}\right) F_a + \nu_{F_j} \left(I_{F_j}\right) F_j - \gamma_{F_j}^+ \left(I_{F_j}\right) F_j - \mu_{F_j} F_j \tag{7}$$

$$\frac{dF_a}{dt} = \gamma_{F_j}^+ \left(I_{F_j}\right) F_j + \nu_{F_a} \left(I_{F_a}\right) F_a - \nu_{F_a}^+ \left(I_{F_a}\right) F_a - \mu_{F_a} F_a \tag{8}$$

$$\frac{dP_j}{dt} = \nu_{P_a}^+ \left(I_{P_a}\right) P_a + \nu_{P_j} \left(I_{P_j}\right) P_j - \gamma_{P_j}^+ \left(I_{P_j}\right) P_j - \mu_{P_j} P_j \tag{9}$$

$$\frac{dP_a}{dt} = \gamma_{P_j}^+ \left(I_{P_j}\right) P_j + \nu_{P_a} \left(I_{P_a}\right) P_a - \nu_{P_a}^+ \left(I_{P_a}\right) P_a - \mu_{P_a} P_a \tag{10}$$

In these equations, terms superscripted "+" are restricted to non-negative values, for example $\nu_{P_a}^+ = max\left(0, \nu_{P_a}\right)$. This is necessary to ensure that biomass flows from juveniles to adults by maturation and from adults to juveniles through reproduction do not reverse under adverse food conditions. This formulation ensures that the adult stages lose biomass under starvation. Under sufficient food, adults are assumed to convert all biomass gains into offspring, and do not grow. This is an assumption inherent to this modelling framework (De Roos et al., 2008). The final term in each differential equation is mortality, determined by the mortality rates μ.

2.3 | Ingestion, consumption and mortality

The feeding relationships between the groups in the model are summarized in Figure 1. All consumption follows a type II functional

response, with full complementarity of resources (sensu Tilman and Sterner (1984)). Intake rates for each consumer group in the model are limited by their biomass-specific maximum intake rate M and half-saturation constant H. Deposit feeders and filter feeders feed only on a single resource compartment, and hence their intake is given by

$$I_{D_j} = M_{D_j} \frac{B}{H + B} \tag{11}$$

$$I_{D_a} = M_{D_a} \frac{B}{H + B} \tag{12}$$

$$I_{F_j} = M_{F_j} \frac{R}{H + R} \tag{13}$$

and

$$I_{F_a} = M_{F_a} \frac{R}{H + R} \tag{14}$$

Consequently, the grazing of resources R and B is given by

$$C_R = I_{F_j} F_j + I_{F_a} F_a \tag{15}$$

and

$$C_B = I_{D_j} D_j + I_{D_a} D_a \tag{16}$$

respectively. Predators feed on juvenile filter feeders and deposit feeders, and hence their intake is given by

$$I_{P_j} = M_{P_j} \frac{F_j + D_j}{H + F_j + D_j} \tag{17}$$

and
for juveniles and adults, respectively.

$$I_{P_a} = M_{P_a} \frac{F_j + D_j}{H + F_j + D_j} \tag{18}$$

Mortality of filter feeders, deposit feeders and predators consists of a constant stage-specific background mortality, mortality from trawling and predation mortality from fish. Furthermore, juvenile filter feeders and deposit feeders also suffer mortality from predation by invertebrate predators.

We model fish as a generalist predator that forages elsewhere when the modelled prey availability is low (i.e. following a type 3 functional response), and whose maximum density (N_s^m and N_l^m) is asymptotically reduced to zero by trawling intensity E. Hence, fish density is described by

$$N_s = N_s^m e^{-EQ_{N_s}} \tag{19}$$

and

$$N_l = N_l^m e^{-EQ_{N_l}} \qquad (20)$$

This choice corresponds to a quasi-steady-state assumption for fish, which reflects the relatively high mobility of fish compared to benthic invertebrates. Small fish N_s feed on the juvenile stages P_j, D_j and F_j, while large fish N_l feed on both the adult and juvenile stages. Fish consumption of filter feeders, deposit feeders and predators hence follows

$$C_x = N_s M_{N_s} \frac{x}{H + (F_j + D_j + P_j)^2} + N_l M_{N_l} \frac{x}{H + (F_j + D_j + P_j + F_a + D_a + P_a)^2} \qquad (21)$$

with $x \in \{D_j, F_j, P_j\}$, for the juvenile deposit feeders, filter feeders and predators. Fish maximum intake rate is M, and half-saturation density is H. Adults of all benthic groups are only fed on by large fish, so that the consumption equation of benthic adults simplifies to

$$C_y = N_l M_{N_l} \frac{y}{H + (F_j + D_j + P_j + F_a + D_a + P_a)^2} \qquad (22)$$

with $y \in \{D_a, F_a, P_a\}$.

We can now derive total benthic mortality, which for the juvenile filter feeders and deposit feeders equals.

$$\mu_{D_j} = \mu_{D_j}^B + \rho E Q_{D_j} + M_{P_j} \frac{P_j}{H + F_j + D_j} + M_{P_a} \frac{P_a}{H + F_j + D_j} + C_{D_j} \qquad (23)$$

and

$$\mu_{F_j} = \mu_{F_j}^B + \rho E Q_{F_j} + M_{P_j} \frac{P_j}{H + F_j + D_j} + M_{P_a} \frac{P_a}{H + F_j + D_j} + C_{F_j} \qquad (24)$$

where μ^B is a stage-specific constant background mortality rate, ρ is the scalar of gear damage, and Q_x is the stage-specific relative vulnerability of each benthic group/stage x, to trawling, of which E denotes the intensity. The next two terms are the predation mortality imposed by juvenile and adult predators, and finally the consumption by fish. For the remaining benthic groups, mortality equals.

$$\mu_u = \mu_u^B + \rho E Q_u + C_u \qquad (25)$$

(where $u \in \{D_a, F_a, P_j, P_a\}$).

2.4 | Parameter values

Parameter values used to model the benthic food web are presented in Table 1. Because we model biomass in each model compartment, rather than number of individuals, all rate parameters (those expressed per unit time) are mass-specific. The parameters for the functional groups in our model are chosen such that they represent "typical members" of the group they represent. Rather than modelling specific species, we use averages for a large number of species and general allometric scaling laws to derive representative parameter values.

The values for maximum intake rate M and maintenance rate T are assumed to be inversely proportional to the quarter power of adult body mass (for which we use body mass at maturation in the model) (Appendix S1B). We furthermore assume that mass-specific maintenance rate is generally in the order of 10% of the mass-specific maximum intake rate (Gillooly, Brown, West, Savage, & Charnov, 2001; Peters & Wassenberg, 1983; Yodzis & Innes, 1992). Hence, we assume that

$$M = W_{mat}^{-0.25} \text{ and } T = 0.1 W_{mat}^{-0.25}$$

We used an extensive data set of benthic invertebrate samples from the Dutch Continental Shelf area in the North Sea (van Denderen, Hintzen, Rijnsdorp, Ruardij, & van Kooten, 2014) to derive the average weight (W) of individuals in each benthic functional group (F, D and P) (Appendix S1B). Using a biological trait database (Bolam et al., 2014), we used trait information on feeding mode and maximum size to estimate the average size for each of the benthos functional groups in the model. Similarly, we used trait information on longevity to calculate group-specific values for the background mortality (μ^B) (Appendix S1B). These data were collected using a Reineck box-corer (Daan & Mulder, 2009). However, this device is not particularly suitable for sampling the generally larger, mobile (epi-) benthic predators. For these, data from the ICES Beam Trawl Survey (using an 8 m beam trawl with a 40 mm cod end mesh size in the North Sea) were used (Appendix S1A).

The maximum resource density R_m and half-saturation density H are expressed as biomass per unit volume and therefore the only parameters containing the unit volume. H can be set to 1 without loss of generality, since this merely implies a scaling of the units of the total system volume (Van Leeuwen, De Roos, & Persson, 2008). Maximum resource density R_m is then expressed as multiples of the half-saturation density. A conversion efficiency (σ) of 0.5 is used for conversion of both resource and consumer biomass (Peters & Wassenberg, 1983).

2.5 | Trawling

The proportionality constants (Q_i) for the direct mortality per unit trawling intensity E (for otter trawls) were taken from a recent meta-analysis (Sciberras et al., 2018). The constants were scaled by setting the highest value (the effect on predators) to 1 (Table 1). The value for fish was based on the assumption that these are affected more than any of the benthic groups. This approach means that trawling intensity E should be interpreted as a relative measure only.

TABLE 1 Model parameters and default values

Parameter	Default value	Units	Explanation
E	Varied	d^{-1}	Trawling intensity
R_m	Varied	g	Scaled maximum phytoplankton biomass density
r	0.1	d^{-1}	Phytoplankton turnover rate
N_s^m, N_l^m	0.1	g	Fish maximum density
W_d	4	g	Individual body mass of adult deposit feeders
W_f	9	g	Individual body mass of adult filter feeders
W_p	11	g	Individual body mass of adult predators
$T_P, T_F T_D$	0.055, 0.058, 0.071	d^{-1}	Mass-specific maintenance rate of predators, filter feeders and deposit feeders
M_P, M_F, M_D	0.55, 0.58, 0.71	d^{-1}	Mass-specific intake rate of predators, filter feeders and deposit feeders
H	1	g	Half-saturation constant
σ	0.5	-	Conversion efficiency
p	0.5	d^{-1}	Deposition rate of R to B
L	0.5	d^{-1}	Loss rate from B
ρ	1	-	Coefficient of trawling effect on benthos
μ_{bD_j}, μ_{bD_a}	0.009	d^{-1}	Background mortality deposit feeders
μ_{bF_j}, μ_{bF_a}	0.005	d^{-1}	Background mortality filter feeders
μ_{bP_j}, μ_{bP_a}	0.012	d^{-1}	Background mortality predators
z	0.01	-	Ratio of mass at birth to mass at maturation
Q_p	1	-	Trawling mortality scaling coefficient for predators
Q_d	0.09	-	Trawling mortality scaling coefficient for deposit feeders
Q_f	0.38	-	Trawling mortality scaling coefficient for filter feeders
Q_N	2	-	Trawling mortality scaling coefficient for small and large fish

2.6 | Analysis

To determine an appropriate starting point for the analysis of trawling effects, we first studied the effects of changes in plankton resource carrying capacity on stable coexistence of the three benthic functional groups (Appendix S1C). From these results, we chose a plankton carrying capacity value such that all three benthic groups are present, and used this as a starting point for further analysis. In this system, the filter feeders are competitively superior to the deposit feeders as a constant fraction of the pelagic resource becomes available for the deposit feeders. For a given plankton resource carrying capacity, filter feeder consumption determines the food availability of the deposit feeders; that is, the deposit feeders get the left overs. We study the effects of trawling on the benthic food web dynamics by varying trawling intensity (E), starting out in a system without fish. Thereafter, the interplay of plankton carrying capacity and trawling intensity on coexistence is studied in a system with and without fish. All analyses were conducted using Content (Kuznetsov, Levitin, & Skovoroda, 1996), a software package for numerical analysis of dynamical systems.

3 | RESULTS

3.1 | Biomass changes over time and an instantaneous increase in trawling intensity

Under the chosen parameter values (Table 1), but without fish or trawling, we find a stable equilibrium with a relatively low filter feeder biomass, higher levels of deposit feeder biomass and highest predator biomass. Filter feeders and deposit feeders compete for resource in the sense that a constant fraction of the pelagic resource precipitates to the seafloor where it becomes available as benthic detritus resource for the deposit feeders. Precipitated pelagic resource is no longer available for filter feeders. With little filter feeder biomass, there is plenty pelagic resource that trickles down to the sea floor to support high deposit feeder biomass. An instantaneous increase in trawling intensity (at time = 200, E increased from 0 to 0.05) leads to a period of transient dynamics, after which the system converges to a new equilibrium state, with fewer predators (the group with highest direct mortality per unit trawling) and strongly increased biomass of deposit and filter feeders (Figure 2). Despite the increased mortality from trawling on deposit and filter feeders, these groups have higher equilibrium abundance with trawling. This is because trawling also decreases predator abundance, which leads to a reduction in predation mortality. The reduction of predation mortality outweighs the increase of trawling mortality. As a result, total benthic biomass in the system increases when a trawler has passed. This is due to the lower trophic position of these groups compared to predators, so that system-level losses to conversion are lower.

3.2 | Biomass changes with an constant increase in trawling intensity

When studying the equilibrium biomass of the food web, we find that the equilibrium abundance of predators, preying on both filter
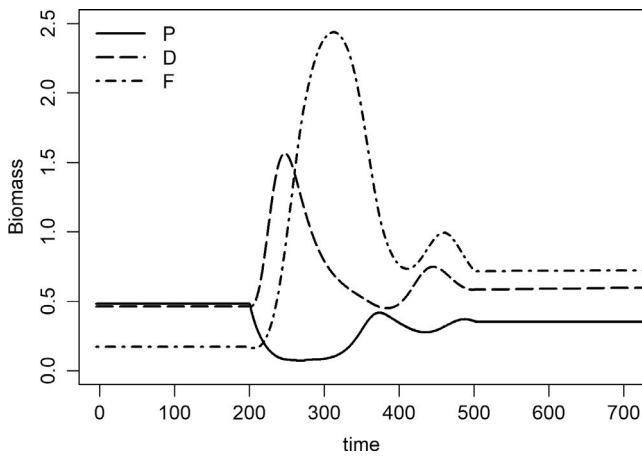
FIGURE 2 Temporal dynamics of filter feeder (*F*), deposit feeder (*D*) and predator (*P*) biomass. At time 200, trawling intensity is increased from 0 to 0.05. *Rm = 7* and $N_s^m = N_l^m = 0$, so that fish are absent. Other parameters at default values

feeders and deposit feeders, decreases with increasing trawling intensity. The equilibrium biomass of filter feeders in first instance decreases with increasing trawling intensity, but quickly starts to increase strongly with increasing intensity (Figure 3a), because the reduced predation mortality increasingly outweighs the mortality imposed by the trawling gear. Deposit feeders show a different pattern, because their equilibrium biomass initially increases due to reduced predation mortality *and* reduced competition from filter feeders. However, at somewhat higher trawling intensity (*E* > 0.045, Figure 3a), the highly abundant filter feeders reduce the plankton resource to such an extent that very little reaches the benthic resource. This causes a decline in benthic resource availability and a decrease in deposit feeder biomass. The release of filter feeders from predation causes deposit feeder equilibrium biomass to decrease with further increasing trawling intensity.

Predator equilibrium biomass declines with trawling intensity at an accelerating rate since they suffer most from trawling mortality. The initial lag in the decrease is a result of the increased food abundance represented by the increasing availability of deposit feeders with increasing trawling intensity. At trawling intensity ~0.07 (Figure 3a), predators go extinct, and a system with only deposit feeders and filter feeders remains. With a further increase of trawling intensity, the filter feeders and eventually the deposit feeders go extinct due to fishing mortality (not shown).

At a higher value of plankton carrying capacity (Figure 3b), the patterns in biomass differ. Without trawling, high predator abundance prevents filter feeders from being present in the system. Filter feeders only appear in the system at higher trawling intensity (*E* > 0.034). For the deposit feeders, the increased inflow of food to the benthic resource more than compensates for the losses to predation. In fact, the high deposit feeder biomass promotes predator biomass and hence indirectly amplifies the predation pressure on filter feeders.
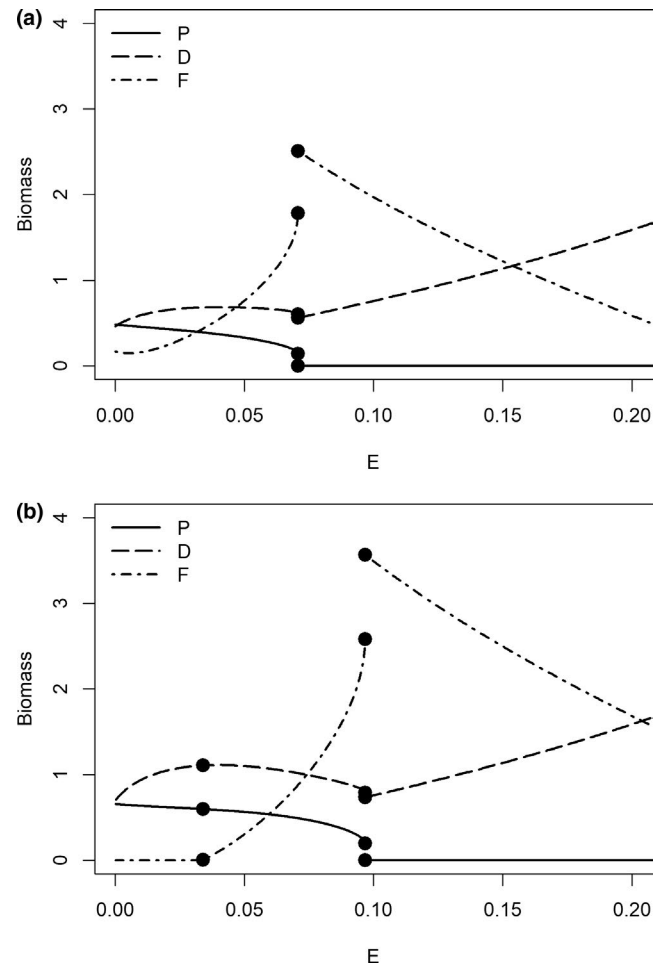
FIGURE 3 Equilibrium biomass of predator (P), filter feeder (F) and deposit feeder (D) biomass (juvenile and adult summed) as a function of trawling intensity (E). (a): Rm = 7. The dots indicate the trawling intensity at which predators go extinct. (b): Rm = 10. The dots on the left-hand side (E ~ 0.35) mark the trawling intensity above which filter feeders can persist in the system. The dots on the right-hand side (E ~ 0.95) mark the trawling intensity above which predators are extinct. At higher trawling intensity, deposit feeders and filter feeders coexist until (at E » 0.2) first the filter feeders and then the deposit feeders go extinct

3.3 | The interplay between carrying capacity and mortality

The persistence boundaries of the three benthos groups as a function of plankton carrying capacity and trawling intensity (Figure 4) show that changes in the two have similar effects, though in opposite direction: an increase in trawling intensity has a qualitatively similar effect as a decrease in carrying capacity. For example, the pattern of invasion of filter feeders, followed by extinction of predators with increasing trawling intensity (Figure 3b), is also obtained when carrying capacity is reduced from high values (e.g. following a horizontal cross section of Figure 4 at *E* = 0.05).

At low carrying capacity, filter feeder and deposit feeder equilibrium biomasses are low and there is not enough food for invertebrate predators to persist (Figure 4). With increasing productivity, predators persist and stable coexistence of all three benthic groups is possible. The predator abundance is primarily set by the abundance of deposit feeders, which feed on resource leftovers from filter feeders. At even higher productivity, the increase in predator biomass, and hence predation mortality with increasing productivity, increasingly removes filter feeders from the system. Deposit feeders profit from the removal of filter feeders because more food is left for them to grow on, increasing the biomass of predators and the removal of filter feeders further. Eventually this positive feedback loop leads to the extinction of the filter feeders from the system. Bottom trawling allows filter feeders to persist at high carrying capacity, because the effect of trawling on predators is stronger than that on filter feeders, and this indirect positive effect for filter feeders outweighs the direct trawling mortality. Changes in background mortality for the benthic groups (results not shown) are similar to changes in trawling intensity and similarly lead to opposite effects compared to those of changes in carrying capacity. An increase in background mortality has an effect qualitatively similar to a decrease in carrying capacity.

3.4 | The role of fish

The addition of fish to the system adds another source of mortality for all benthic groups, the strength of which is negatively related to trawling intensity that reduces fish abundance. Fish presence hence causes the benthos mortality to be high even at low trawling intensity. The only quantitative effect of adding fish to the model system is that the persistence boundary of filter feeders shifts to
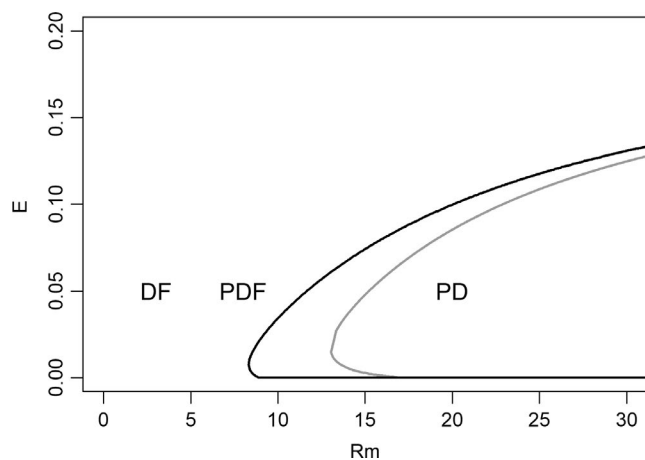
FIGURE 4 Extinction boundaries of filter feeders (drawn black and grey lines) and predators (dashed line) as a function of plankton carrying capacity (Rm) and trawling intensity (E). Predators can persist below and to the right of the dashed line (areas indicated as PDF and PD). Filter feeders can persist above and to the left of the drawn lines (areas indicated DF and PDF), and the black line is the filter feeder extinction boundary in the absence of fish and the grey line in the presence of fish

higher productivity and lower trawling intensity (Figure 4, grey line). This occurs because fish effectively reduce abundance of predators at low trawling intensity, and this indirect reduction of predation mortality for filter feeders outweighs the direct mortality from fish predation.

3.5 | The role of predator prey preference

When predators prefer deposit feeders over filter feeders, filter feeders may persist at low trawling intensities, even at higher carrying capacity values (the solid line in Figure 4, denoting the persistence of F, will move to higher values of Rm; results not shown). When deposit feeders are the preferred prey, the initial decrease in filter feeder biomass with increasing trawling effort becomes more pronounced at high levels of carrying capacity (Appendix S1D).

3.6 | Other trawl gears

We have used relative gear impact scaling for otter trawl gears, but we found similar results for other gears (beam trawl and scallop dredge, Appendix S1E). However, in case of the dredge the deposit feeders go extinct instead of the predators because they suffer most from direct gear mortality.

3.7 | Trawl gears with reduced benthic impact

Trawl gears with reduced benthic impact (a lower value of ρ) do not qualitatively change the pattern of equilibrium abundances with either trawling intensity or resource productivity (results not shown). With a reduced gear impact on benthos, predators can persist at increasing trawling intensity, since the direct mortality on both predators and their prey is reduced. The reduction of fish predation with increasing trawling intensity remains, causing a net reduction of mortality for the benthic groups. A reduced trawling impact on the benthos furthermore weakens the indirect positive effect of trawling on filter feeders, because their release from benthic predators is also weakened. The net result is that at low carrying capacity, reduced benthic gear impact means higher trawling intensity is required before filter feeders can persist (the trawling intensity E, at which filter feeders invade in Figure 3b, shifts to a higher value).

4 | DISCUSSION

The results presented here highlight how ecological interactions may affect the response of the benthic food web to bottom trawling. The change in benthos in response to trawling is usually predicted to vary among species, habitats and types of trawl gear (Collie et al., 2000; Kaiser et al., 2006), and these differences are generally attributed to species-specific variation in sensitivity to trawling. Our

results indicate that ecological interactions in the benthic food web may be important determinants of the effects of bottom trawling on benthos, and that these indirect feedback effects could in some cases even reverse the direct effect of trawling, leading to strong increases in some functional groups.

We show that, when food web effects are taken into account, the response of benthos functional groups to trawling is highly complex, non-monotonic with trawling intensity and depends on external factors such as system productivity and biotic relationships in the food web. The interplay of productivity and trawling intensity affects not only the magnitude, but also the direction of the effect. Moreover, factors such as prey preference, mortality and gear effects can enhance or dampen the effects of trawling. These results add a new dimension to the interpretation of the literature on this subject. Experimental and empirical studies have reported a large range of effects of bottom trawling. Such variable effects of trawling are reflected in meta-analyses of bottom trawling effects where the variability between studies prevented significant effects for many gear/habitat combinations, particularly on longer time scales (Collie et al., 2000; Kaiser et al., 2006). A more recent meta-analysis indicated that on the level of feeding types (corresponding roughly to the groups in our model), the variation between studies is similarly large (Sciberras et al., 2018). The large variation (and consequent lack of significant effects) in these studies is often attributed to inconsistencies in sampling design, data paucity or high background variation leading to low statistical power.

Our results show that the non-linear responses of benthic functional groups to trawling, resulting from food web interactions, provide alternative explanations and a potential mechanistic underpinning of the lack of consensus regarding the observed effects of bottom trawling on benthic macroinvertebrates. This finding has important strategic consequences for future work. Instinctively, the "wide error bars" in meta-analyses, such as Collie et al. (2000), Kaiser et al. (2006) or Sciberras et al. (2018), seem like a strong argument for conducting more trawling effect studies, in the hope of obtaining statistically robust results in the face of measurement error, stochasticity and environmental variability. However, if the food web feedbacks we study here are important determinants shaping the effects of trawling, a higher degree of replication may not lead to converging results and consensus at all. In this case, it would be more productive to focus research effort on the differences in food web dynamics between individual studies, and on understanding the consequences of these differences, which we have shown can lead to qualitatively different effects of bottom trawling.

Our results are also relevant in relation to estimating the conservation status of seafloor habitat, such as under the Marine Strategy Framework Directive in EU waters. Here, sensitivity of benthic species is often inferred from direct estimates of mortality after trawling to determine sensitivity, and sampling at a later date to determine recovery (Hiddink et al., 2017; Kaiser et al., 2006; Mazor et al., 2017; Pitcher et al., 2017). Although our analysis relies on equilibrium states, and hence cannot be used to draw conclusions regarding

recovery following individual trawl events, it is likely that the recovery time following a trawl will be highly context-specific, even for a single species. Furthermore, these approaches assume that the effects of trawling are always negative, while we show that if ecological feedbacks are as important as we have here assumed them to be, the net effect may be an increase in biomass. In frameworks based on community means such as longevity (Rijnsdorp et al., 2016), positive effects on biomass could even cancel out negative effects on biomass. This creates the risk that simultaneous strong positive and strong negative effects of bottom trawling would lead to an indicator falsely showing "no effect." These large potential consequences warrant further consideration of ecological feedbacks in developing management indicators.

It is important to note that we have chosen to ignore spatial variation in abiotic factors, benthic groups, fish and trawling intensity in our study. While this choice facilitates mechanistic understanding of our results, spatial heterogeneity is an ubiquitous feature of benthic ecosystems, which can modify food web interactions. It may lead to reduced interaction strengths and hence reduced relevance of food web feedbacks. However, it can also lead to more complex modifications of food web interactions, driven by spatial pattern formation. This aspect of our work requires further consideration before our results can be implemented in operational indicators.

Currently, many initiatives are under way for technical gear adaptations to reduce impact on the seafloor (Catchpole, Revill, Innes, & Pascoe, 2008; Depestele et al., 2016; Soetaert, Decostere, Polet, Verschueren, & Chiers, 2015; Valdermalsen, Jorgensen, & Engas, 2007). Such low-impact gears are viewed as an important factor in operationalizing ecosystem-based management of bottom trawl fisheries (Pikitch et al., 2004). Although such gear modifications can clearly reduce the direct effects on benthos, our results show that in the presence of strong food web feedbacks, they may actually result in stronger net negative effects of trawling on the biomass of filter-feeding organisms, when mediation of predation mortality (through trawling-induced removal of their invertebrate predators) is no longer present. Indirect effects on benthos can also affect the availability of fish food, potentially leading to a "cultivation effect," where trawling stimulates the production of fish food, and a collapse of this effect when low-impact gears are used (van Denderen et al., 2013).

Our study focused on the dynamics of the benthic food web in response to both fish and trawling mortality. We did not study how changes in the benthic food web in response to bottom trawling may affect fish diet and production. Fish can be added as dynamical variables to the model, allowing an even more integral effect of bottom trawling on the benthic community to be studied. This would also provide important insights into how benthic food web feedbacks affect fisheries yield and efficiency. The benthic food web model developed here provides a relatively simple model framework that can be parametrized and applied to specific regions to predict the effects of various gears in relation to benthic community composition. The functional grouping into predators, filter feeders and deposit feeders holds for many if not all regions,

including the north-east Atlantic and Mediterranean (Sciberras et al., 2018), but other groups may be added if the ecosystem or research questions require them.

In conclusion, our work shows that food web effects can alter the response of a benthic ecosystem to bottom trawling. This may lead to that low-impact fishing gears may have totally unexpected effects since they can alter the strength of ecological interactions in the food web. In light of our results, indicators of fishing impact need to be able to properly account for positive components of net effects of bottom trawling on biomass, in order to accurately quantify the degree of impact. Furthermore, our findings highlight that understanding the food web ecology of the benthic ecosystem is crucial to understand and predict the net effects of bottom trawling on the sea floor. Work that promotes such an understanding of the food web ecology seems a more productive research strategy than conducting ever more empirical trawling effect measurements.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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