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METHOD

ECOLOGICAL APPLICATIONS
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Bottom fishing assessment tool: An R package to model the effects of bottom trawling on the marine benthos

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Abstract

Bottom trawl fisheries are recognized to be a global threat to marine biodiversity and a dominant driver of sea floor ecosystem change. Although the mechanism of trawling impact on benthic life is more and more documented and empirically verified, there is still no standard toolbox that enables the prediction of impact in any area and that is soundly based on existing knowledge. We provide an R package ("Bfiat") endowed with functionalities that enable researchers as well as managers to assess the vulnerability of benthic organisms and associated ecosystem functions to trawling. The Bfiat package includes a deterministic modeling framework that predicts the state of benthic species following trawling disturbance as a fraction of pre-disturbance state. Benthic state is predicted according to the logistic population growth model combined with trawling parameters and organism functional traits. While trawling parameters determine the disturbance, functional traits express vulnerability through instantaneous sensitivity and longer term recoverability in the model response. We illustrate the potential of the package through a large-scale case study with species communities of contrasting functional compositions. Benthic response to trawling disturbance is exemplified from single species to entire community as well as from single station to larger spatial extent.

KEYWORDS
bottom trawling disturbance, deterministic modeling, fishery impact assessment, functional trait, marine benthos, marine ecosystem management, species vulnerability

INTRODUCTION

Terrestrial or aquatic, most ecosystems respond to physical disturbance. This has become especially conspicuous with the emergence of large-scale human activities and their effects on the entire biosphere. In the marine environment, bottom trawl fisheries represent a dominant driver of sea floor ecosystem change, especially due to their deleterious effects on benthic life (Jennings & Kaiser, 1998; Thrush & Dayton, 2002). In spite of the negative effects of this practice on ecosystem services, considerable social and economic issues are at stake when envisaging a reduction of fishing effort. Hence, fisheries stakeholders and managers are constrained in their decision leeway and must find optimal trade-offs between human and environmental costs.

A surge of ecological indicator development has taken place in the last 15 years to support marine ecosystem management (Beauchard et al., 2017; Miatta et al., 2021), especially in European waters under the impulse of the Marine Strategy Framework Directive (European Community, 2008). Nowadays, many benthic indicators enable some description of sea floor ecosystem state, but rare are those that directly relate state to pressure as part of the pressure-response-state framework (Bowen & Riley, 2003; OECD, 1993). What has been missing is a deterministic approach that returns benthic state as a direct function of pressure. Based on the logistic population growth model, Pitcher et al. (2016) introduced the relative benthic status (RBS) to assess variations in total benthic organism abundance as responses to bottom trawling disturbance: instantaneous depletion of the community followed by recovery toward carrying capacity. Hiddink et al. (2017) improved the RBS approach by considering trawling gear characteristics, whereby benthos mortality was shown to increase with gear penetration depth into the sediment. A further development was provided by the use of species life span as a proxy of the community recovery rate (Hiddink et al., 2019; Rijnsdorp et al., 2018). Now, these works are combined into an assessment framework established as part of the activities of the International Council for the Exploration of the Sea (ICES, 2019) and called the "PD method" (i.e., Population Dynamics). However, the PD method provides an assessment of benthic vulnerability only at the community level and does not decompose individual species response into two trait-specific phases: the instantaneous faunal depletion and the longer term recoverability.

To fill this gap, we provide an R package ("Bfiat") that enables predictions on the species level, with flexible applications. The method is a data-driven mechanistic model where species depletion during fishing depends on the overlap between the gear and species living space, while recovery between trawling events is based on the logistic growth formulation. Its parameters are derived from species abundance data combined with two types of trait information: age at maturity and the depth of occurrence in the sediment. The outcome of the model describes the trajectories of species abundances over time. As species modulate ecosystem functions, the Bfiat package also provides opportunities to assess sea floor functional vulnerability.

MECHANISTIC APPROACH TO TRAWLING DISTURBANCE

Logistic growth model

Trawling disturbance on the benthos can be modeled based on the logistic growth equation that describes how benthic faunal density (i.e., number of individual organisms or biomass per surface area) evolves when the sediment is undisturbed (i.e., between trawling events). The logistic growth model is mechanistic where density-limiting factors such as food limitation and predation are subsumed in the density that the species attains at equilibrium: the carrying capacity. The model reads

$$\frac{dD_i^t}{dt} = r_i \cdot D_i^t \cdot \left(1 - \frac{D_i^t}{K_i}\right). \quad (1)$$

D_i^t is the density of species i at time t, K_i is the carrying capacity and r_i is the logistic growth parameter (units [/time]). On the left-hand side, $\frac{dD_i^t}{dt}$ expresses how density D_i^t changes over time. The first part on the right-hand side $r_i \times D_i^t$ expresses how density increases in the absence of limitation, that is, when the density is far below the carrying capacity. Then, the term $\left(1 - \frac{D_i^t}{K_i}\right)$ evolves toward 0 as the density approaches the carrying capacity and causes the change in density over time to decrease and eventually disappear (when $D_i^t = K_i$). The parameters r_i and K_i are specific for species i; the carrying capacity K_i also depends on the site where the species is found (e.g., due to local resource availability, predation or competition).

Incorporating trawling disturbance

The effect of trawling on a benthic population is introduced as a succession of events that instantaneously deplete population abundance. Between these events, the population can recover to a certain proportion of its initial state. In this way, the model consists of two phases: an instantaneous depletion at the trawling time and a continuous logistic growth between trawling events (Figure 1). When a species community is trawled at times t_j, the density of each species i is instantaneously reduced according to

$$D_i^{t_j^+} = D_i^{t_j^-} \cdot p_i \quad (2)$$

where $D_i^{t_j^+}$ and $D_i^{t_j^-}$ are the densities immediately after and before trawling at time t_j, respectively, and p_i is the surviving fraction. Between trawling events, and starting from the initial condition $D_i^{t_j^+}$, the population recovers according to Equation (1) between t_j and t_{j+1}. Provided that r_i and K_i are constant over time, Equation (1) has an analytical solution that enables to calculate the density for each species (D_i) at each time point t between trawling events; analytical formula can be found in Appendix S1. The average time between trawling events (in years) can be estimated from the annual swept area

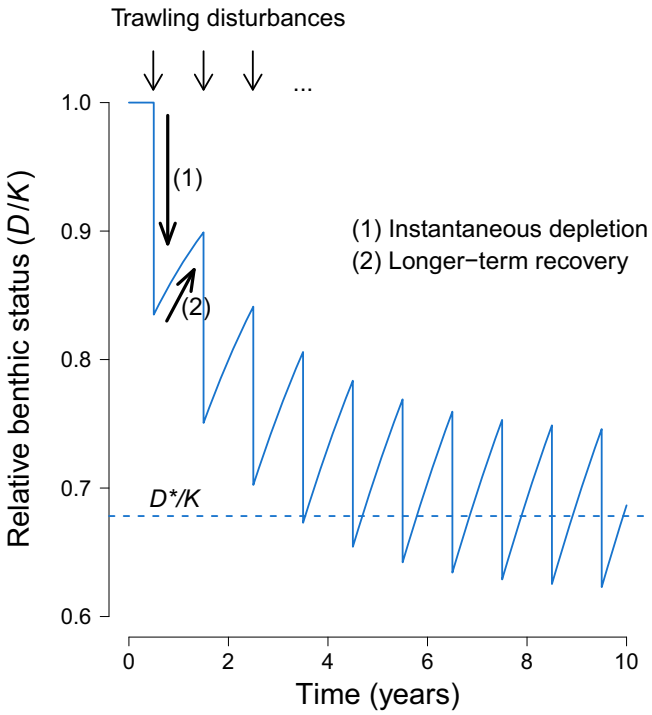

FIGURE 1 Illustration of logistic model-based trawling effect on a benthic organism population. *Y*-axis: faunal density *D* divided by carrying capacity *K*. Continuous blue line, faunal density undergoing a disturbance frequency of 1 trawling event per year. The effect of the trawling gear entails an instantaneous depletion (1); the recovery (at an intrinsic rate of natural increase *r*) operates until the next disturbance (2); see Equation (1) for *r* and *K* coefficients. As long as the recovery does not compensate for the depletion, the density decreases to a level at which the organisms represent the resilient or resistant fraction of the population (steady-state *D**, dashed blue line).

ratio S, as $1/S$. Thus, assuming that trawling occurs on regular intervals, the time at which fishing occurs is given by:

$$t_{j+1} = t_j + 1/S. \quad (3)$$

Specific depletion caused by trawling disturbance

The two phases of faunal response to trawling disturbance as shown in Figure 1 involve specific traits. Within a species community, the instantaneous depletion d_i of species i depends on organism sensitivity to physical damage. A trait that obviously determines organism exposure to trawling gear is sediment burying depth. To parameterize d_i, we assume that depletion depends on the overlap between gear penetration depth (p_G) and burying depth, which is parameterized as

$$d_i = \sum_{z=[z_u,\ z_l]} m_d \times \max(0, p_G - z_u) \cdot f_{i[z_u, z_l]} \quad (4)$$

with z_u and z_l, respectively, the upper and lower boundaries of the sediment layer, and f_i the fraction of the total community density in that layer. m_d is a linear coefficient that scales the depletion to the depth impacted by the gear per centimeter of sediment. The $\max(0, p_G - z_u)$ part ensures that $d_i = 0$ when the gear does not penetrate the layer. As d_i shows an asymptotic relationship with p_G in Hiddink et al. (2017), the depletion fraction of any species is limited to 0.42, the maximum in Hiddink et al. (2017):

$$d_i = \min(d_i, 0.42). \quad (5)$$

Based on this simple formulation, only the value of the mortality parameter m_d needs to be estimated. We estimate the parameter by fitting this function to data in Hiddink et al. (2017), who, based on a meta-analysis, quantified community depletion fraction as a function of gear penetration depth. A value for the mortality coefficient $m_d = 0.055\ \text{cm}^{-1}$ gives a good fit to the data (see *Contrasting species responses to trawling disturbance* below).

Specific recovery rate

The second phase of faunal response to trawling disturbance is a progressive faunal recovery toward the species carrying capacity, in the absence of new trawling disturbance. This phase is best expressed by the intrinsic rate of natural increase r as the per capita instantaneous rate of population increase for stable age distribution (Stearns, 1992), but it is missing for most species. r is proportional to inversed age at sexual maturity (Savage et al., 2004), itself a good correlate of life span. Considering that life span was more available than age at maturity, Hiddink et al. (2019) used life span ($T_{\max}$) to approximate r at the community level through community weighted mean correlation (CWM) whereby age categories were community-abundance weighted:

$$r = \frac{5.31}{T_{\max}}. \quad (6)$$

However, this relationship did not enable the back-calculation of carrying capacity for many observations (see Equation (8)), suggesting an underestimation of true r values. In addition, CWM is an unsuitable method that can provide unreliable regression coefficients as it ignores biological variations within communities (Peres-Neto et al., 2017). While age at maturity is sufficiently documented in the literature (Beauchard et al., 2021,

2022), we compiled r values for 56 marine macrozoobenthic species in order to determine r_i as a direct function of age maturity α_i:

$$r_i = \frac{2.26}{\alpha_i}. \quad (7)$$

We obtained a strongly significant relationship (Figure 2); data and related references are provided in Appendix S2.

The carrying capacity K_i is estimated assuming that the measured species density D^* is at equilibrium with the prevailing trawling intensity S. Then the carrying capacity can be estimated as follows:

$$K_i = \frac{D_i^*}{1 + \frac{S}{r_i}\ln(1-d_i)}. \quad (8)$$

If $\frac{S}{r_i}\ln(1-d_i) < -1$, the necessary condition $K_i/D_i^* > 0$ is violated; this implies that, non-exclusively, S is too high or r_i is too low. In such a case, the population is assumed to be extirpated since the population growth cannot compensate for the depletion.

Software

The trawling impact model runs in the open-source framework R (R Core Team, 2025) and has been implemented in the Bfiat R package (Beauchard & Soetaert, 2026b). Faunal composition and trait data are compiled in the R package Btrait that also contains functions to work on density and trait datasets (Soetaert & Beauchard, 2022). These packages can be found in Beauchard and Soetaert (2026a, 2026b) in Zenodo at https://doi.org/10.5281/zenodo.19861038. The major commands of the Bfiat package are listed in Table 1.

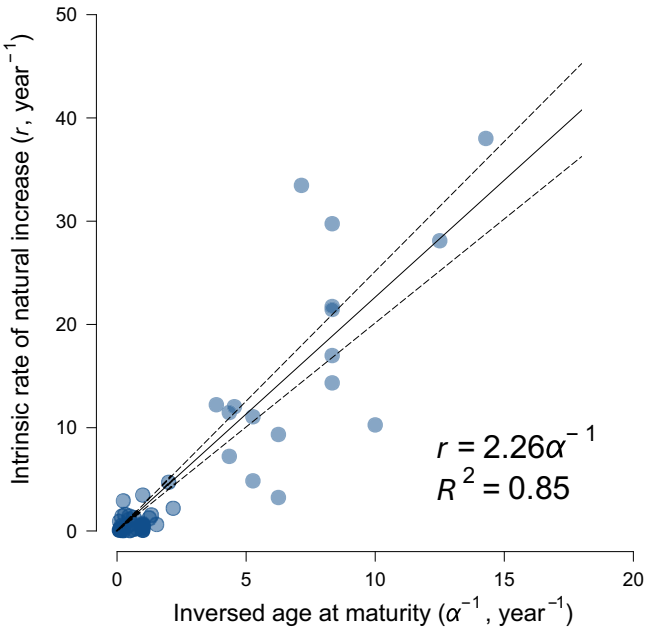

FIGURE 2 Relationship between intrinsic rate of natural increase and inversed age at maturity. Dashed lines, 95% CI of the slope (2.26 ± 0.24).

ILLUSTRATIVE CASE STUDY AND DISCUSSION

We illustrate the use of the Bfiat package with the benthic communities from the Dutch sector of the North Sea, an area with highly contrasting habitats and associated benthic faunas (Beauchard et al., 2022). The data are available in the Btrait R package (Beauchard & Soetaert, 2026b) and comprise the densities of more than 400 taxa in 103 stations (102 with non-null organism abundance since 2009). We considered the concomitant availability of faunal and trawling data from 2009 to 2018.

Contrasting species responses to trawling disturbance

The combination of two traits (age at maturity and burying depth) makes the model particularly comprehensive as it expresses the two phases detailed by Pitcher et al. (2016), namely sensitivity to trawling and recoverability after trawling according to former and later works (Beauchard et al., 2021; Bolam et al., 2014; Tyler-Walters et al., 2009). We selected four typical North Sea species exhibiting contrasting trait performances and ran a

TABLE 1 Major functions of the Bfiat R package, especially used in the case study.

Command	Description
par_r par_d par_K	Estimate model parameters for use in trawling disturbance models: "r," intrinsic rate of natural increase; "d," faunal depleted fraction; "K," carrying capacity.
density_perturb	Estimates faunal density at specific times in trawling disturbance models with successive disturbance events followed by instantaneous depletions.
steady_perturb	Estimates steady-state density for trawling disturbance models with successive disturbance events followed by instantaneous depletions.

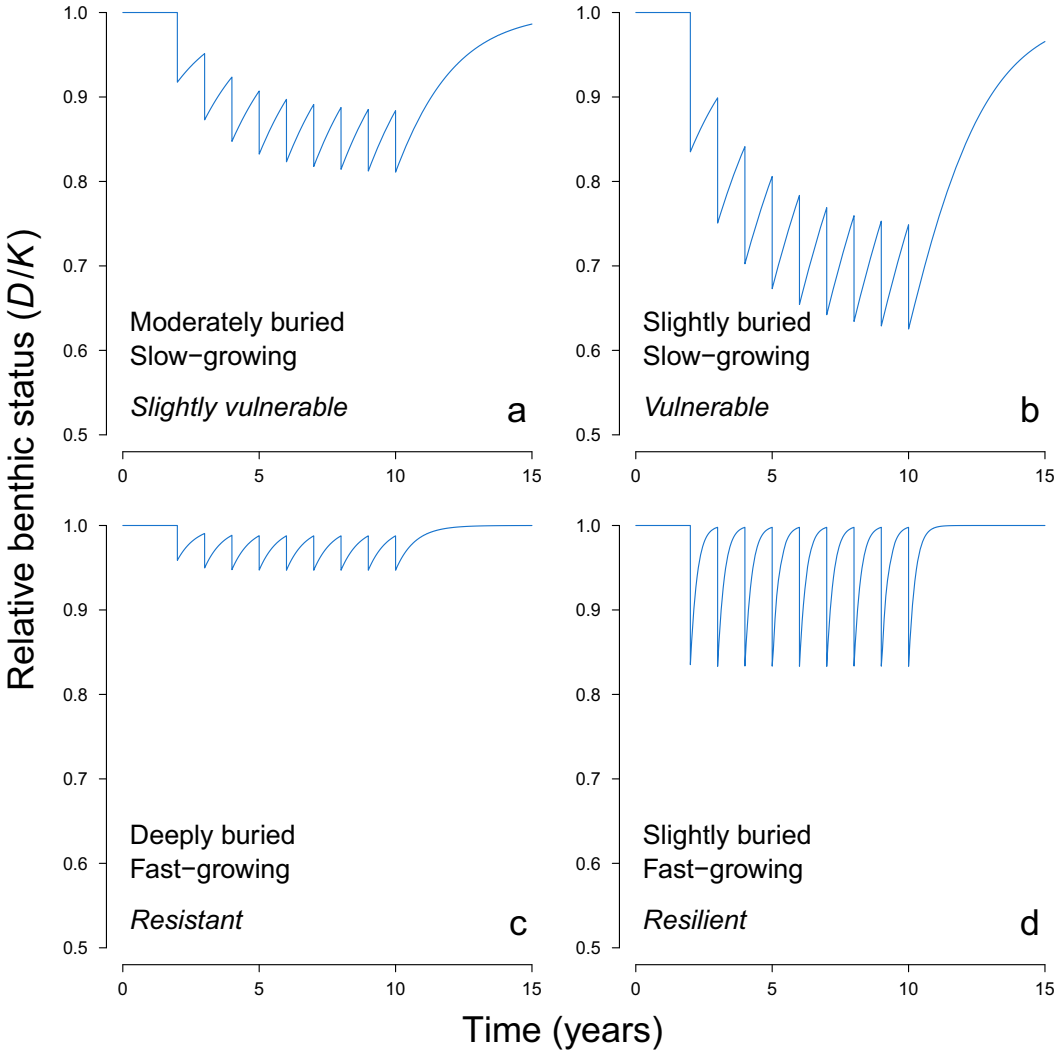

FIGURE 3 Simulation of species responses to trawling disturbance over time. Trawling frequency was fixed to one trawling events per year over 10 years, after which trawling was stopped over five additional years. Gear penetration depth was 3 cm. (a) *Echinocardium cordatum*; age at maturity 3 years; burying 5–15 cm deep. (b) *Amphiura filiformis*; age at maturity, 3 years; burying depth 3–5 cm. (c) *Callianassa subterranea*; age at maturity, 1–2 years; buried from 5 to more than 30 cm deep. (d) *Spio filicornis*; age at maturity, a few months; buried at 0–5 cm deep. Two components of species response are illustrated: from left to right: growing depletion (sensitivity); from top to bottom, growing intrinsic rate of natural increase (recoverability).

model simulation over a systematically disturbed period, followed by trawling exclusion (Figure 3). Sensitive species (Figure 3b,d) are those experiencing substantial decreases in abundance due to trawling (large value in parameter d), while species of high recoverability (large value in parameter r) are those that quickly recover to the carrying capacity (Figure 3c,d); an intermediate situation is found for small values in both parameters d and r (Figure 3a). Deeply buried species with higher growth rates are not depleted far from the carrying capacity and recover fast (resistant, Figure 3c), while shallow-living and slow-growing species have a higher probability to become extirpated (vulnerable, Figure 3b). Species with low depletion rates but low recoverability are slightly vulnerable (Figure 3a), while species with high depletion and high recoverability are resilient (Figure 3d).

Model calibration

We used the data from Hiddink et al. (2017) to calibrate the depletion fraction parameter m_d in the model (Figure 4). For each benthic species in all stations, we back-calculated the carrying capacity K (Equation (8)) to define an untrawled state and estimated the depletion fraction using Equation (5) for disturbances with a growing gear penetration into the sediment. From the species-depletion rates, the community depletion for each station

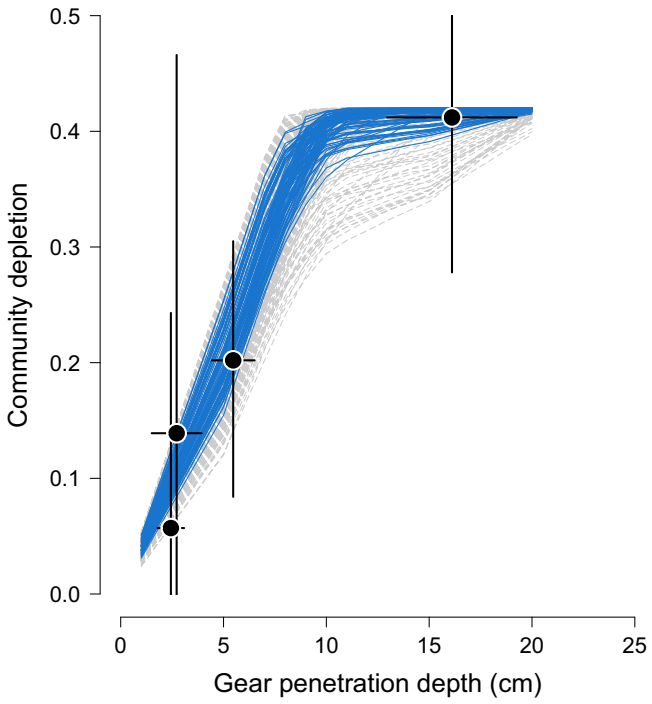

FIGURE 4 Community depletion as a fraction of the total community individual density. Each blue line represents the summed response of the species in each of the 102 stations, to increased penetration depth into the sediment; gray dashed lines, lower 2.5 and upper 97.5% limits of CIs; the four black dots represent data from Hiddink et al. (2017), provided in Pitcher et al. (2022), representing mean ± 95% propagated CI; from left to right: otter trawl, beam trawl, towed dredge, and hydraulic dredge.

was estimated and compared to the data. The results, using a depletion parameter $m_d = 0.055\ \text{cm}^{-1}$, accurately followed the experimental measurements compiled in Hiddink et al. (2017). For each station, we ran the procedure through 1000 resampling with replacement of the faunal occurrences in order to derive a 95% CI.

Impact assessment over space and across habitats

A habitat can host several dominant species that are similarly adapted to the same environmental constraints such as storm disturbance or tidal stress. Bottom trawling can mimic these natural forces in an exacerbating way, so where natural disturbances are prominent, trawling will have minor effects on species. Therefore, bottom trawling can differently impact species communities depending on the habitat (Beauchard et al., 2021; van Denderen et al., 2015). We exemplify trawling effects in the southern North Sea with different physical regimes (Beauchard et al., 2022; Figure 5a). The model was applied on individual densities; species carrying capacities were first estimated, after which each community was disturbed according to the current trawling regime (trawling frequency and gear penetration depth for the period 2009–2017).

Highest trawling intensities led to the highest community depletions, with a clearly perceptible habitat effect (Figure 5b). The greatest depletions were observed in the low dynamics habitat where they could reach one third of the carrying capacity. The low-stress environments are composed of twice as many organisms with late maturity (>3 years; Beauchard et al., 2022) and are therefore generally more impacted by bottom trawling (Figure 6a).

We sorted out the degree of species vulnerability among short- and longer term responses to trawling disturbance (Figure 6b). Model outputs show largest depletions for species having both low intrinsic rate of natural increase and surficial living depth (vulnerable); deep burying can reduce depletion by two (slightly vulnerable). Similarly, taxa with a greater intrinsic rate of natural increase can be substantially depleted when more exposed to trawling gear (resilient), while they stay close to the carrying capacity when buried deeper (resistant).

Uncertainty in model parameters

Since our model considers solely trawling gear exposition and intrinsic rate of natural increase, its outputs, paced by trawling events, may return an oversimplified image of reality. This is due to our limited knowledge and ability to predict subtle processes from depletion to recovery. These involve many ecological parameters for which the simultaneous measurements in the many existing habitats are unrealistic. Therefore, the predictive ability of the model may be subject to some degree of uncertainty.

Burying depth is an important aspect to consider regarding the effect of bottom trawling on the benthos, as shown in trait analyses, with deeper burrowing ability toward finer sediment types (Beauchard et al., 2022; Beauchard, Thompson, et al., 2023). This may explain the interaction between gear and sediment types observed by Pitcher et al. (2022), depletion increasing less in finer sediment with deeper gear penetration. In spite of the absence of burying depth in assessments of in situ depletion rates, our estimates consistently lie within CIs of meta-analytical observations (Figure 4). Previous North Sea observations already underlined the importance of burying depth when assessing gear effects on the benthos. Bergman and Hup (1992) evidenced substantial effects on the burrowing urchin *Echinocardium* sp., but stronger for juveniles, more abundant in the surface sediment layer (0–6 cm deep) than for adults (6–14 cm).

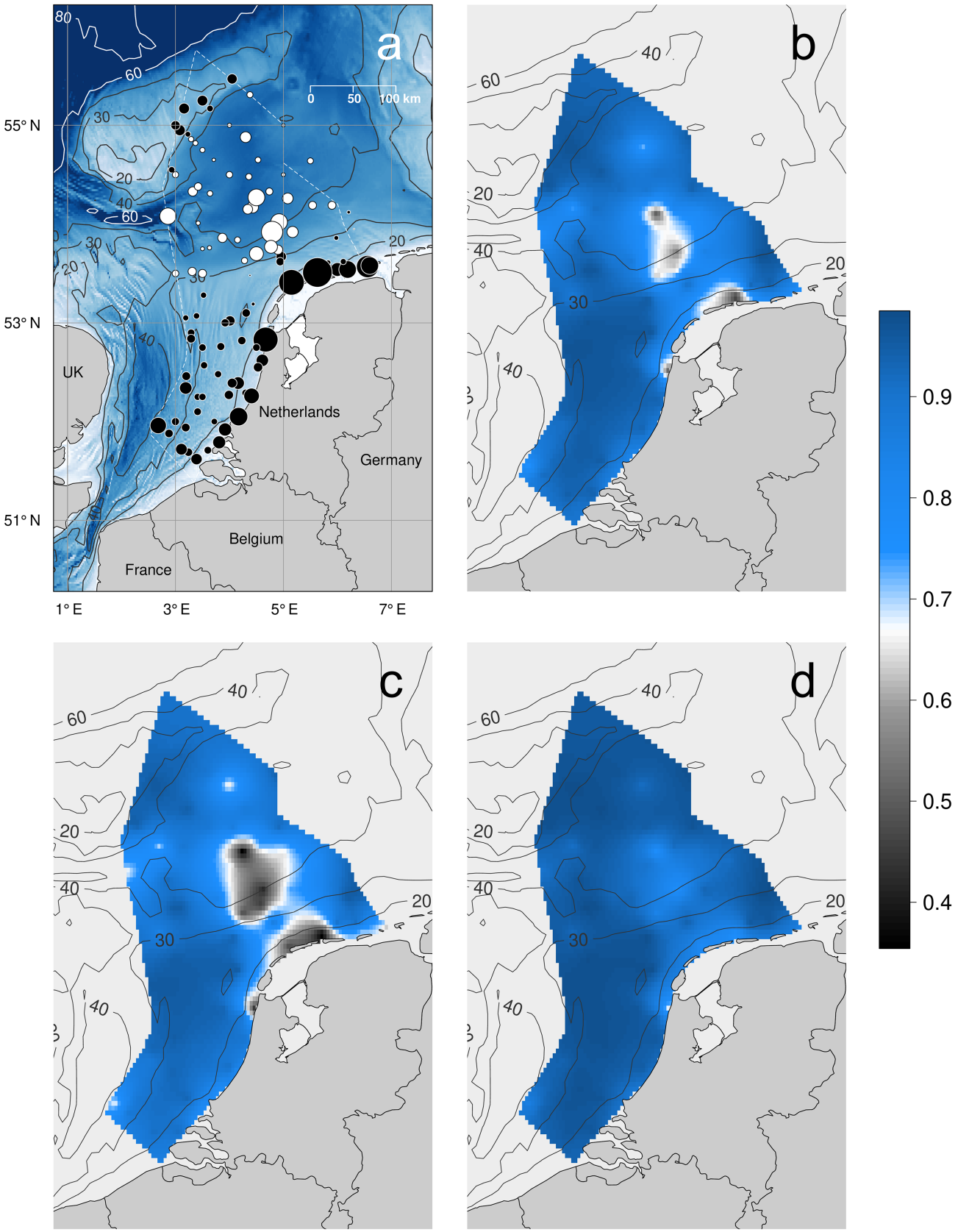

FIGURE 5 Model applications to the Dutch sector of the North Sea (a); dots, sampling stations; black, high hydrodynamics habitat; white, low hydrodynamics habitat; see Beauchard et al. (2022) for more details. Dot size proportional to trawling intensity (min = 0.09; max = 11.82 year^{-1}). (b) Relative benthic status (D/K): interpolated total faunal densities as fraction of summed back-calculated species carrying capacities. (c) Lower 2.5% CI limit. (d) Upper 97.5% CI limit.

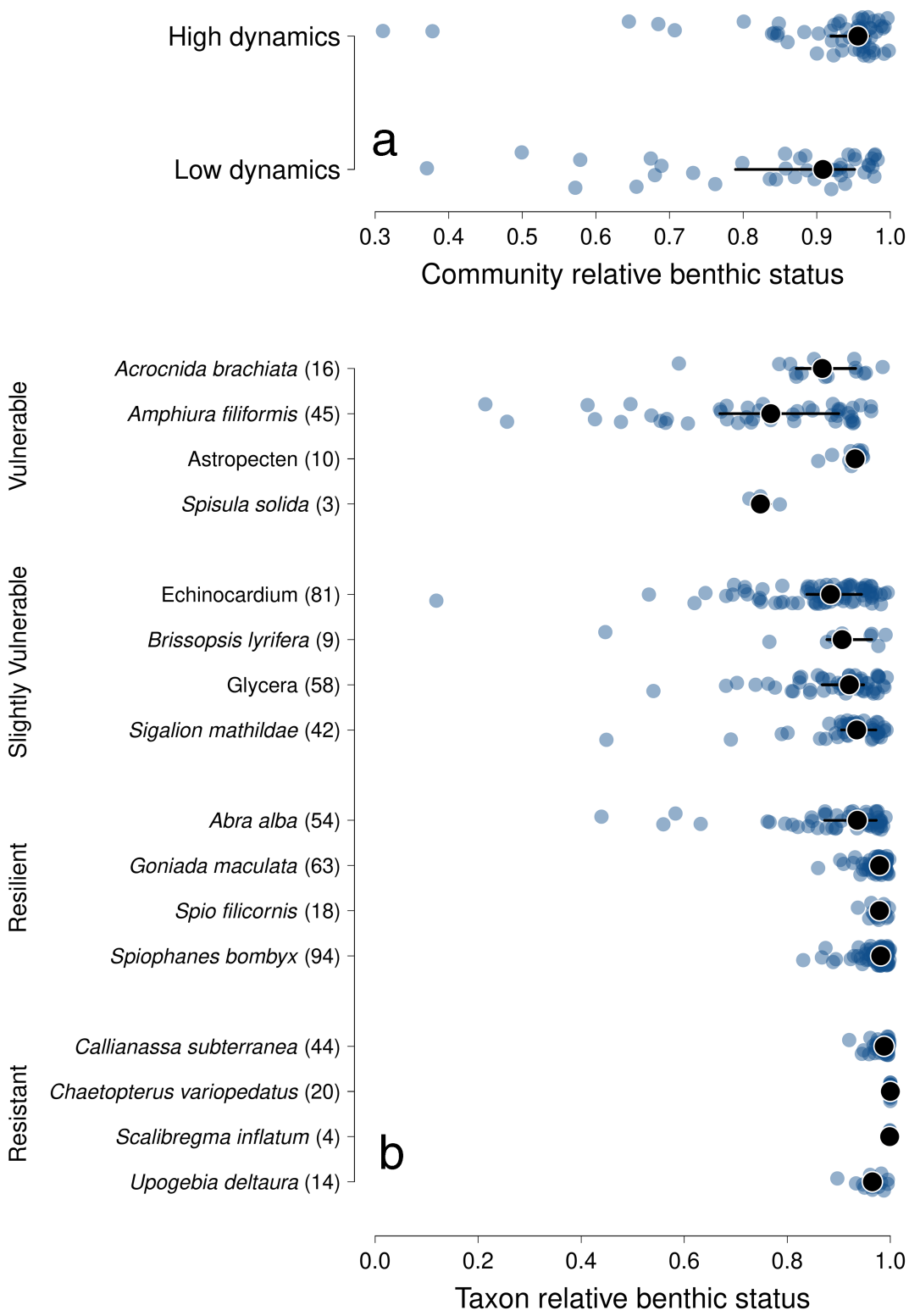

FIGURE 6 (a) Habitat effect on trawling impact; blue dots, total faunal densities as a fraction of summed species carrying capacities; black dots, median response; bars, range between 25th and 75th percentiles. (b) Individual taxon responses; blue dots, D/K for stations where the taxon was encountered (values within parentheses, counts). The taxa were selected as representative of the four categories exemplified in Figure 3.

These authors also suggested that the adult population might have been strongly impacted when reaching the sediment surface to spawn. Similarly, Tiano et al. (2020) showed a low effect on the deep burrowing mudshrimp *Callianassa subterranea*, but strong trawling effects on the juveniles of several other species. Species vertical

distribution is not always easy to incorporate in trait analysis due to organism vertical mobility, but a multiple case study evidenced the resistance of deepest burrowing functional groups to highest trawling frequencies (Beauchard, Bradshaw, et al., 2023). Hence, the incorporation of burying depth in the model soundly prevents an overestimation of the depletion parameter *d*, though the model may underestimate the true number of impacted organisms given the general higher vulnerability of juvenile or newly settled offspring.

Recovery, represented by parameter *r*, only considers individual organism ability to reach the reproductive stage, while, in the marine benthos, a long life span in slow-growing species compensates for rare successful reproductions (Beukema, 1989; Hedgecock & Pudovkin, 2011; Powell & Cummins, 1985) that are conditioned by many environmental aspects such as water circulation, temperature, and predation on propagules (Beukema & Dekker, 2014; Siegel et al., 2008). A more stochastic pattern might better depict the reality through alternations of more limited and irregular recovery phases between trawling events due to variable reproductive propagule survival and settlement. Our *r* estimations returned faster recoveries than previously estimated by Hiddink et al. (2019). For instance, 3 years is in general a late age for maturing, and many such species have a life span >15 years. In this case, following Hiddink et al. (2019), $r = 0.4$ based on life span while $r = 0.8$ following our estimation based on age at maturity. According to our relationship ($r = 2.26 \times 1/\alpha$), the lower α, the stronger the influence on the slope, especially when $\alpha < 1$ year. Most of the trend was thus determined by very short-lived species (i.e., early maturing), whereas a large part of communities is usually represented by species for which $\alpha \geq 1$ year. Assessing the relationship within the interval [0; 1] of $1/\alpha$ was not realistic since available values may have not always been the maximum *r* estimates, and the trend being driven by outliers. However, we are confident when using the overall dataset, especially for $1/\alpha \geq 1$ since the relationship, without excessive uncertainty, was derived from phylogenetically distant taxa (e.g., bivalves, cephalopods, annelids, arthropods). By ignoring offspring dynamics and settlement success, our model may not correctly estimate recovery rates. Also, in mobile species, recovery should be complemented by adult recolonization, what the model does not include.

The back-calculation of the carrying capacity (*K*), another key aspect in the model, ignores biotic interactions that might limit *K*. However, unlike in hard substratum communities that are strongly regulated by competition for space and predation (Dayton, 1971; Paine & Levin, 1981; Sousa, 1979), biotic interactions in soft sediments seem generally less determinant in community composition and structure than abiotic forces (Gerwing et al., 2016; Osman & Whitlatch, 2004; Rosenberg, 1977; Seitz, 1998; Wilson, 1991). Also, competition for space is usually considered to be low, mainly due to the tri-dimensional nature of the sediment matrix (Wilson, 1991). Under minor physical constraints, community structure can be regulated by predation (Peterson, 1979), especially for young and vulnerable organisms such as those newly settled (Ólafsson et al., 1994), but such organisms may not be systematically considered in impact assessments.

To summarize, the back-calculated carrying capacity *K* might overestimate reality in some cases. The depletion *d* may slightly underestimate instantaneous mortality while *r* is more uncertain due to complex and unquantifiable processes during recovery. Besides, estimated *r*, possibly higher than reality, may be partly compensated by the absence of consideration in the model for adult organism recolonization in mobile species. Otherwise, a net overestimation of *r* may limit the model predictability with increasing trawling frequency whereby recolonization through reproductive propagule becomes less likely.

Comparative methodological context

An untrawled benthic state represents an ideal reference to find faunal carrying capacity in impact assessment studies such as experiment, or along a gradient of trawling intensity. However, there are critical issues with trawling gradients. From a so-called untrawled state, minimum trawling intensities are considered to have already substantial impacts on historical assemblages. For a long time, there has been a large consensus among benthic biologists who consider that the current states of the shelves with a long fishing history are far from their preindustrial states (Auster et al., 1996; Callaway et al., 2007; de Groot, 1984; Frid et al., 2000; Houziaux et al., 2011; Jones, 1992; Kaiser et al., 2000; Kerby et al., 2012; Robinson & Frid, 2008; Thurstan et al., 2010, 2014). Hence, in most areas where bottom trawling occurs, there is no appropriate reference benthic state. Also, trawling gradients that are substantially variable to meet experimental relevance (i.e., heavily fished/not fished for the same habitat) usually extend over different habitats that host functionally dissimilar communities. This creates confounding effects between habitat descriptors and trawling disturbance which can prevent the identification of likely impacts (Beauchard et al., 2021; Beauchard, Bradshaw, et al., 2023). As a consequence, a same assemblage undergoes a too narrow range of trawling frequencies to offer relevant experimental opportunities.

The main advantage of the deterministic model is that it is based on a causal mechanism universally valid and statistically and spatially unconstraint since it estimates trawling effect for the local species response. Other approaches use statistical modeling and are critically constrained by regression methods and spatial scales. Especially when using trait data to express vulnerability, all statistical frameworks that aggregate trait values per sample are penalized by excessively inflated type I error (Miller et al., 2019; Peres-Neto et al., 2017; ter Braak et al., 2017) and, similarly, fail in correctly representing vulnerability patterns over space (Hawkins et al., 2017). Even with appropriate methods, the problem of scale is particularly constraining in trait statistical modeling due to the phenomenon of spatial contingency in species assemblages (Peres-Neto et al., 2012): Two similar species pools can find different solutions in habitat occupancy due to different levels of environmental heterogeneity. As shown in the marine benthos, this seems to restrict trait predictability at smaller scales (Beauchard et al., 2022). Therefore, deterministic modeling may be more suitable to provide a universal method free of such constraints to assess bottom trawling impact, particularly at the large-scale.

PERSPECTIVES AND APPLICATIONS

The Bfiat package provides useful tools for managers and fisheries ecologists when assessing the effects of fishing activities on the sea floor. By taking burying depth into account, the model marks an advancement from existing frameworks that may overestimate instantaneous mortality induced by trawling gear (ICES, 2019). Applications should gain greater feasibility with the increased availability of biological trait data at the continental scale (Beauchard, Thompson, et al., 2023). While we illustrated the impact of bottom trawling on benthic faunal abundance, such depletion represents a loss of ecosystem function (e.g., food availability for upper trophic levels) or a loss of ecosystem engineering such as biodeposition and bioturbation (biomixing and bioirrigation; Kristensen et al., 2012). Hence, the Bfiat package also offers great research potential for more fundamental purposes in the field of functional ecology.

AUTHOR CONTRIBUTIONS

The two authors conceptualized the modeling procedure, and both authors contributed and approved the final version of the manuscript. Karline Soetaert wrote the R package Btrait.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Beauchard & Soetaert, 2026a, 2026b) are available in Zenodo at https://doi.org/10.5281/zenodo.19861038 and https://doi.org/10.5281/zenodo.20743033, respectively.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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