ECOSYSTEMS

Habitat-Specific Effects of Fishing Disturbance on Benthic Species Richness in Marine Soft Sediments

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ABSTRACT

Around the globe, marine soft sediments on continental shelves are affected by bottom trawl fisheries. In this study, we explore the effect of this widespread anthropogenic disturbance on the species richness of a benthic ecosystem, along a gradient of bottom trawling intensities. We use data from 80 annually sampled benthic stations in the Dutch part of the North Sea, over a period of 6 years. Trawl disturbance intensity at each sampled location was reconstructed from satellite tracking of fishing vessels. Using a structural equation model, we studied how trawl disturbance intensity relates to benthic species richness, and how the relationship is mediated by total benthic biomass, primary productivity, water depth, and median sediment grain size. Our results show a negative relationship between trawling intensity and species richness. Richness is also negatively related to sediment grain size and primary productivity, and positively related to biomass. Further analysis of our data shows that the negative effects of trawling on richness are limited to relatively species-rich, deep areas with fine sediments. We find no effect of bottom trawling on species richness in shallow areas with coarse bottoms. These condition-dependent effects of trawling suggest that protection of benthic richness might best be achieved by reducing trawling intensity in a strategically chosen fraction of space.

Key words: benthic invertebrates; biomass; bottom trawling; trawl disturbance; marine soft-bottom environments; primary productivity; species richness.

INTRODUCTION

Identifying the factors that determine species richness has been central to community ecology. Much of the empirical and theoretical work has been dedicated to examine the relationships between species richness and both productivity (for review see Waide and others 1999) and disturbance (for review see Sousa 1984). The text-book prediction is that richness is highest at an intermediate level of productivity or disturbance (Grime 1973; Connel 1978). However, negative and positive monotonic,

U-shaped, and non-significant relationships have also regularly been observed (Mackey and Currie 2001; Mittelbach and others 2001; Hughes and others 2007; Adler and others 2011; Cusens and others 2012). The shape of the pattern has been suggested to depend on the scale of the observations (Moore and Keddy 1989), environmental heterogeneity (Guo and Berry 1998), or the combined effects of disturbance and productivity on communities (Huston 1979; Kondoh 2001).

Despite the persistence of the hump-shaped relationship in the literature, there is both limited empirical support for it, and the mechanistic underpinning of the pattern has repeatedly been challenged (Abrams 1995; Fox 2013). This has led some authors to call for the development of new, mechanistic explanations for the observed relationships between productivity, disturbance, and species richness (Adler and others 2011; Fox 2013).

In this study, we explore the effects of bottom trawl fishery disturbance and productivity on benthic richness in a soft-bottom habitat covering the Dutch part of the North Sea. This area is known to be intensively fished by beam trawlers, towing several tickler chains over the seafloor to chase their target species sole (*Solea solea*) and plaice (*Pleuronectus platessa*) (Rijnsdorp and others 2008). This type of fishery incurs severe physical disturbance on the seabed up to at least the first 6 cm (Bergman and Hup 1992), which may have major impacts on benthic organisms, processes, and functioning (Jennings and Kaiser 1998; Kaiser and others 2002). Some intensively fished areas in the North Sea are trawled more than 10 times per year (Rijnsdorp and others 1998; Piet and Hintzen 2012). The amount and timing of this trawl disturbance largely depend on the occurrence of commercial fish species, plaice, and sole, in the area (Rijnsdorp and others 2011). As these species feed on benthic invertebrate prey (Molinero and Flos 1992; Rijnsdorp and Vingerhoed 2001; Shucksmith and others 2006), both fish species and subsequently fishery may be attracted to areas of high benthic productivity. This may result in an interaction between trawl disturbance intensity and benthic productivity on large spatial and temporal scales and may affect species richness.

Many studies have examined the relationship between productivity or (trawl) disturbance and benthic richness in marine soft sediments (for example, Pearson and Rosenberg 1978; Collie and others 2000; Hall and others 2000; Huxham and others 2000; Hiddink and others 2006; Hinz and others 2009). This is often done on small spatial and temporal scale, to reduce the confounding effect of habitat heterogeneity. How habitat heterogeneity interacts with both disturbance and productivity and how all together affect species richness that is largely unknown. This is surprising, as marine soft-bottom habitats are the most common on earth and provide important ecosystem services, for example, contributing to biogeochemical cycles and food production (Snelgrove 1999). One reason for our lack of knowledge is the inaccessibility of the marine habitat, which restricts the possibilities to conduct underwater experiments, especially on large spatial and temporal scales (Thrush and others 1997). In some cases, large spatial and temporal scales are covered by benthic monitoring programs, usually constructed to acquire indications of ecosystems health. Although the data from such programs cannot replace the mechanistic knowledge obtained through manipulation experiments, it can be used to explore relationships between productivity and trawl disturbance and their combined effect on benthic communities.

Our analysis of data from a North Sea benthic monitoring program shows that the effects of trawl disturbance and productivity on benthic richness are both negative, but are positively related to each other. Both explain a relatively small amount of the variation in species richness. Within two subsets of sediment grain size gradients, there is either a negative effect of trawl disturbance on species richness or no effect. These habitat-specific effects emphasize the importance of the choice of spatial scale to assess the impact of trawl disturbance on benthic communities.

METHODS

The effects of trawl disturbance and productivity on benthic species richness were examined using 6 years of data obtained from a benthic monitoring program in the Dutch part of the North Sea. Trawl disturbance intensity was estimated from Vessel Monitoring by Satellite (VMS) data (Hintzen and others 2010; Piet and Hintzen 2012). We used primary productivity, calculated from the ecosystem model ERSEM (Baretta and others 1995), as an approximation for benthic productivity and also included benthic biomass data, obtained from the monitoring program. Biomass has often been used to approximate productivity in terrestrial studies (Guo and Berry 1998; Mittelbach and others 2001) but will be decoupled from productivity when there is strong predation. Biomass has also been used to indicate the strengths of competitive interactions (Gough and others 1994). Finally, our analysis included both sediment grain size and water depth, which are seen as important factors to predict benthic richness in soft-bottom marine systems (Gray 2002) and hence help to prevent confounding effects.
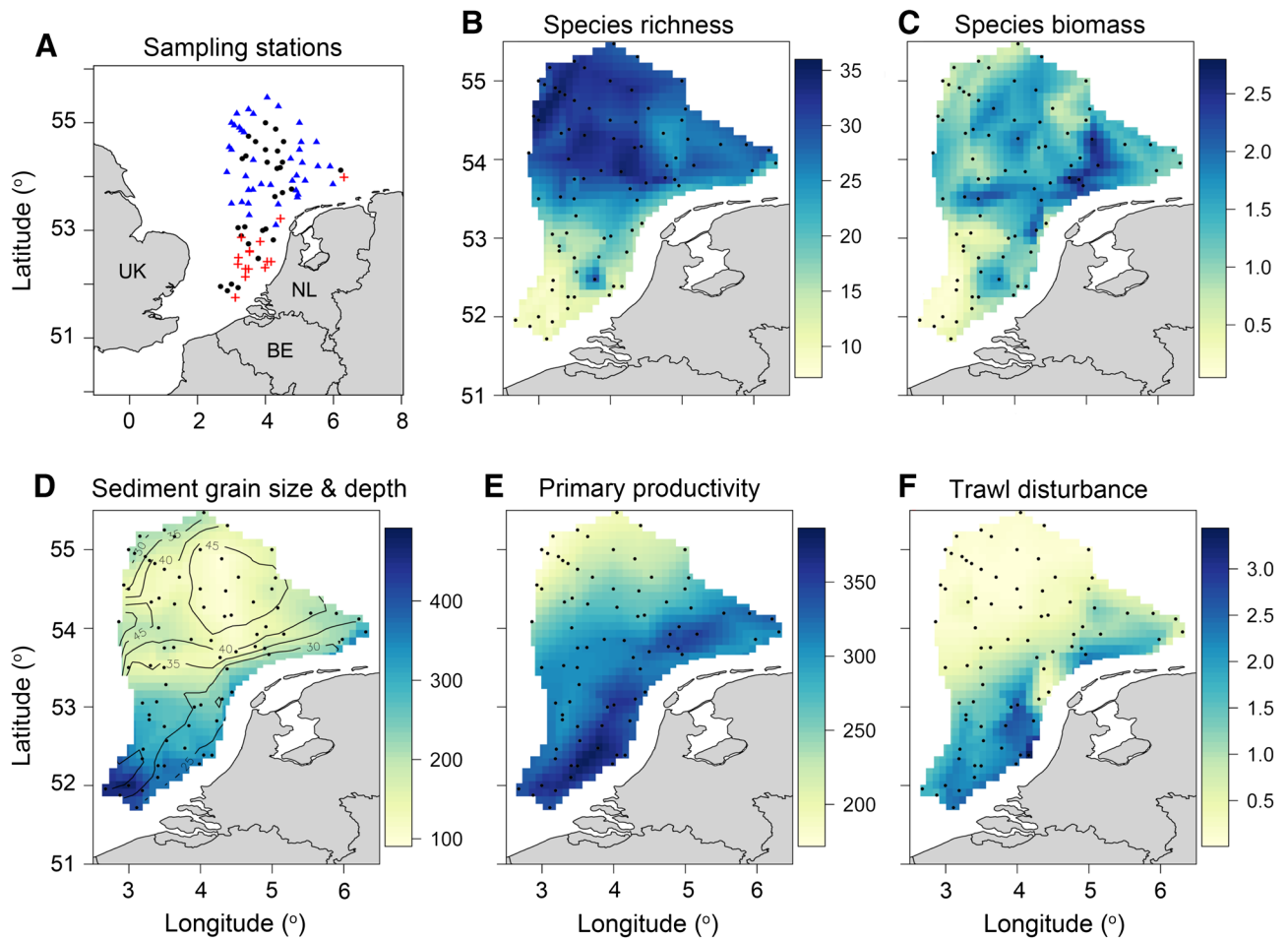
Figure 1. Maps of macrozoobenthos stations and the variables studied. **A** Macrozoobenthos stations sampled between 2002 and 2007 in the Dutch EEZ (all points). After exploration of the total data set, two subsets of the data with more homogenous sediment grain sizes were extracted, one with finer sediments, (125–235 μm, *triangles*) and one with coarser sediments (290–430 μm, *plus signs*). Subset selection is explained in the ''Method'' section. Panels **B–F** are created using point interpolation of the average of all years per station for species richness (**B**, *color scale*; number), species biomass (**C**, *color scale*; gram/sample), sediment grain size with depth contours (in meters) (**D**, *color scale*; μm), primary productivity (**E**, *color scale*; gr C/m^2/y), and trawl disturbance (**F**, *color scale*; average fraction of surface area trawled per year) (Color figure online).

Macrobenthic Data Collection

Data on macrobenthic richness and biomass were obtained from the Dutch monitoring program MWTL in the Dutch Exclusive Economic Zone (EEZ) (www.waterbase.nl). Benthos data were collected from 81 stations (2002–2005) and then from 79 (2006–2007) (Figure 1). All selected stations were located outside the 12-mile zone, as these areas are less affected by coastal fisheries and natural disturbances. At all stations, samples were collected between March and June using a 0.078 m^2 Reineck box corer and sieved over a 1 mm mesh sieve (Daan and Mulder 2009). In the retained fraction of the sample, biota were manually separated from sediment and other material and identified to species level. When unknown (3 % of the total biomass), biota were determined to higher taxonomic groupings (genus, family, order, class, or phylum) and counted, when belonging to the same taxonomic grouping, as a single species in the calculation of species richness.

Total biomass per station per year was the sum of all individuals collected in grams ash-free dry weight. Some individuals had biomass larger than the rest of the sample combined. These individuals, mostly large bivalves, are not effectively sampled with a Reineck box corer and were hence classified as outliers and removed. This occurred for 10 observations, sampled in 10 different stations and 5 different years. Finally, a sorting error in the data from 2006 made a portion of the observations unusable (pers. comm. Dutch Waterbase), this did not affect the outcome of the analysis for 2006 compared to the other years.

Primary Productivity Estimation

Primary productivity was obtained through predictions from GETM-ERSEM (General Estuarine Transport Model—European Regional Seas Ecosystem Model) (Baretta and others 1995). GETM-ERSEM describes the temporal and spatial patterns of the biogeochemistry of the water column and sediment using two coupled hydrodynamic models. These models predicted total production of new phytoplankton biomass for each year (g $C/m^2/y$) per sampled macrobenthic station on a 10×10 km spatial scale. Total production was estimated for each area over a period of one year prior to the sampling date. These modeled productivities approximate measured primary productivity (Ebenhoh and others 1997).

Trawl Disturbance

Trawl disturbance at the sampled locations was estimated from the VMS data. VMS data provided information for each fishing vessel on its position, speed, and heading approximately every 2 h. The VMS data were linked per fishing trip to vessel logbook data with information on vessel and gear characteristics (Hintzen and others 2012). Only VMS data from vessels with beam trawl gear and large engine power (>349 kW) were included in the analysis, as these dominated the study area (Rijnsdorp and others 2008). We checked the activity of low-power vessels and confirmed that it was present at negligible intensity for all stations (results not shown). From this selected dataset, trawl disturbance was estimated on a fine spatial grid, 0.001° latitude by 0.001° longitude (approximating an area of 110 by 70 meter), to have the best approximation of disturbance at each sampling station using the method described in Hintzen and others (2010) and Piet and Hintzen (2012). Trawl disturbance was expressed as the fraction of cumulative surface area trawled in each grid cell over a period of one year prior to the sampling date. This annual trawl disturbance estimation might not cover all benthic responses, as we know that recovery for benthic species following trawling disturbance may last more than one year (Kaiser and others 2006). Some of these effects are indirectly picked up, because there is a clear correlation between disturbance at a station in one year and the year before (mean correlation coefficient = 0.89 using Pearson product–moment correlation).

Habitat Characteristic Parameters

Median sediment grain size for each macrobenthic station per year was obtained from particle size analysis of sediments directly taken from the benthic monitoring program (www.waterbase.nl). Depth was extracted from bathymetric data on the North Sea for all sampled stations on a 1×1 km spatial scale (based on bathymetric data from (www.helpdeskwater.nl) and verified with bathymetric data from Deltares 2011).

Statistical Procedure

A structural equation model (SEM), a multivariate analysis of networks of causal relationships (Grace 2006), was used to examine the combined effects of productivity, disturbance, biomass, sediment grain size, and depth on species richness. All the factors included in the model were expected to interact both directly and indirectly. In the SEM, depth was the exogenous variable, that is, connected with all others (see for terminology of SEM: Grace and others 2012). It was assumed that in addition to depth, both productivity and sediment grain size might explain variations in trawl disturbance, as we expect that these together might explain the spatial distribution of the target species in the area. The model connected the four variables (sediment grain size, depth, primary productivity, and trawl disturbance) with biomass, and it was expected that these variables explained variation in species richness. The SEM had a double arrow between sediment grain size and productivity to represent a joint factor not included in the analysis (see ''Discussion'' section). The constructed SEM had as many pathways between the variables as there were degrees of freedom, which means that we started with a saturated model. The model was tested for each year separately to obtain indications of temporal variability for the different model pathways. When pathways were non-significant (P value >0.05) in 6 out of 6 years, they were removed, leading to a revised model for which we reviewed the distributional properties of the residuals at each node. After certain nodes were improved by transformation, that is, a log-transformation for grain size and richness and a $\log(x + 1)$ transformation for biomass, the final model was tested for overall model fit using a Chi square test. SEM analyses were performed using the package Lavaan in R (Rosseel 2012). SEM outcome per year is shown in Table S1, S2, and S3 in Appendix S1.

Because the results of the final SEM pointed toward examining the effects of the variables on richness and biomass according to different sediment grain sizes, rather than across a gradient, we divided the data according to grain size into two
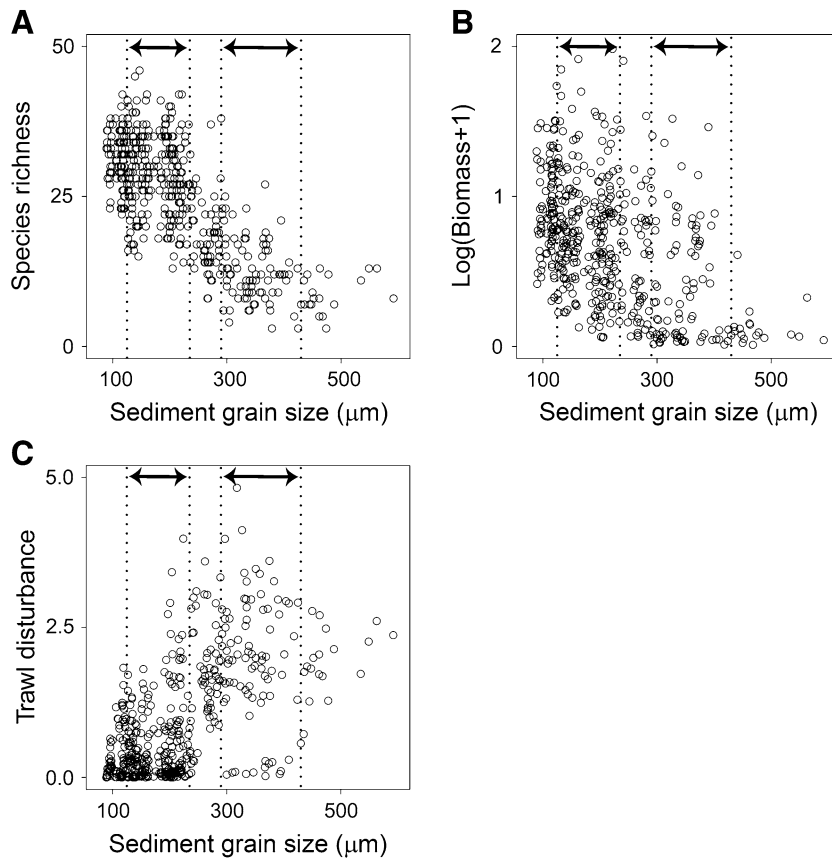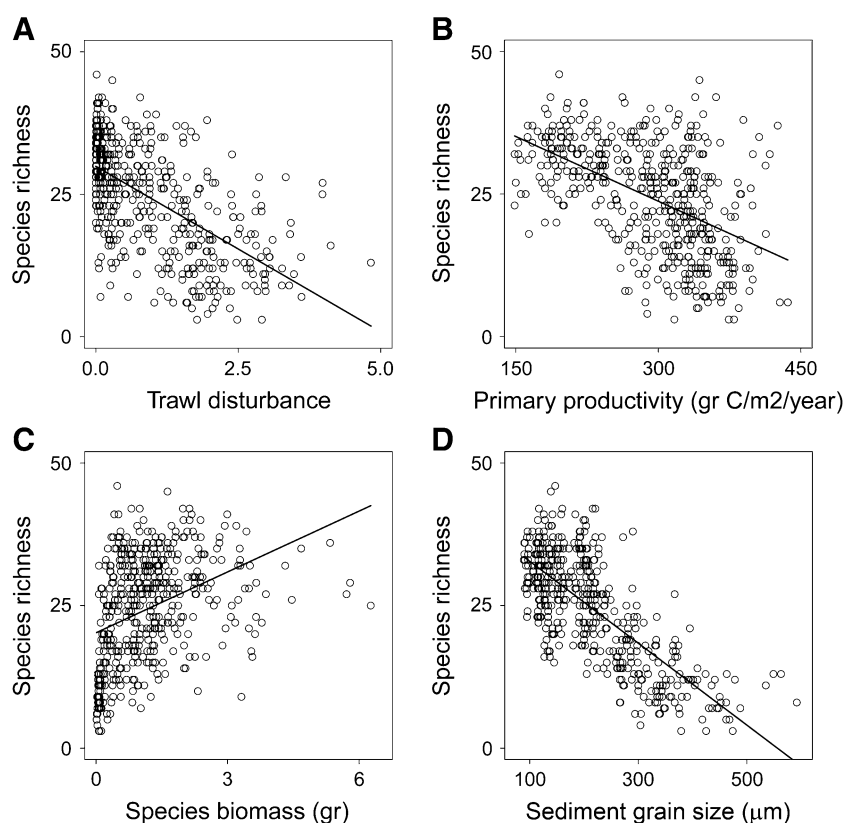
Figiure 3. Bivariate correlations between species richness and trawl disturbance (**A**), primary productivity (**B**), species biomass (**C**), and sediment grain size (**D**). See Table 1 for correlation coefficient and significance values. The *lines* in the bivariate plots were constructed using linear regression.

We examined linear relationships in all statistical procedures. Because unimodal patterns have been predicted for some of the variables studied here (between richness and disturbance and richness and productivity), we verified by testing model residuals that there were no clear unimodal relationships.

RESULTS

Bivariate correlations show that most variables strongly correlate with each other except between biomass and primary productivity, and biomass and trawl disturbance (Table 1). Correlations between richness and trawl disturbance (Figure 3A, $r^2 = 0.36$), primary productivity (Figure 3B, $r^2 = 0.25$), and sediment grain size (Figure 3D, $r^2 = 0.55$) are negative, while biomass (Figure 3C, $r^2 = 0.14$) and depth ($r^2 = 0.23$) correlate positively with richness. Whether the changes observed in richness are direct effects of the gradient in the predictor variable or indirect effects governed by other predictor variables (affecting them together) are examined with a SEM, which allow us to study the relative strengths of the different factors in combination.

We started with a saturated SEM (see ''Method'' section) and tested whether pathways were non-significant in 6 out of 6 years. This was true for the

pathways between trawl disturbance and biomass, which is unsurprising as there is no strong bivariate correlation (Table 1); it was also true for the pathway between depth and species richness, which is unexpected as these are strongly correlated (Table 1). Hence, depth only has an indirect effect on richness, passed on through the other endogenous variables (grain size, primary productivity, trawl disturbance, and biomass).

All other pathways were at least two times significant in the six years tested and were retained in the final SEM (Figure 4). The final model has a mean χ^2 of 3.58 (standard error $\chi^2 = 0.60$), 2 degrees of freedom, and p-values ranging between 0.06 and 0.36, which suggests that model structure supports the data. Based on the final model structure, we obtained the following results: (1) variation in benthic richness is reasonably well explained (mean $r^2 = 0.69$), but variation in biomass much less so (mean $r^2 = 0.30$); (2) sediment grain size, as the standardized coefficients show, has the strongest effect on both benthic richness and biomass; (3) trawl disturbance has a negative effect on richness and no effect on biomass; (4) biomass and primary productivity show a positive relationship, and have opposing relationships with richness (richness is positively correlated with biomass and negatively with primary productivity);
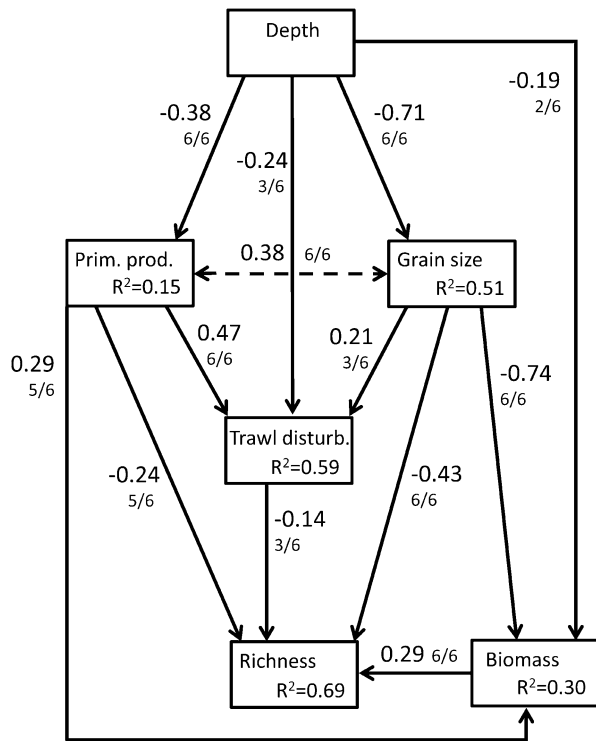
Figure 4. Final structural equation model (SEM) that fitted the data between 2002 and 2007 best (average $\chi^2 = 3.58$, standard error $\chi^2 = 0.604$, $df = 2$ and 6/6 times P value > 0.06). *Boxes* represent our variables. The numbers next to the *arrows* are the mean standardized coefficients (based on these 6 years) and number of times that this pathway had a P value lower than 0.05. The *dashed line with arrows* on both sides shows strong correlation but direction is unknown (see ''Discussion'' section). Model selection procedure and data transformations are explained in the main text.

and (5) variation in trawl disturbance is largely explained by depth, primary productivity, and sediment grain size (mean $r^2 = 0.59$).

The final structure of the SEM allowed us to examine the direction of the effect between richness and biomass in 5 of the 6 years (2003 did not meet the requirements to test the reciprocal interaction because depth had no effect on biomass and trawl disturbance had no effect on richness, see Table S3 in Appendix S1). In 3 of these 5 years, we observed a positive effect of biomass on richness (all P values < 0.04), whereas we found no effect of richness on biomass.

Given the strong effect of grain size on richness and biomass, we analyzed whether the results of the SEM would still hold within subsets of the range of sediment grain size in our data. The subset with relatively small grain sizes (125–235 µm) covers almost the entire range of variability in all

other variables, except for trawl disturbance which ranges between 0.0 and 4.0, as opposed to 4.8 (Table S4 in Appendix S2). Analyzing this subset with a linear mixed model gives a similar outcome as the SEM for explaining variation in species richness (Figure 4). Richness is best described by the combined effects of trawl disturbance (negatively correlated), primary productivity (negatively correlated), and species biomass (positively correlated) (Table 2). Variation in biomass is best described by the combined effect of primary productivity and trawl disturbance (both positively correlated) (Table 2). This differs from the SEM results, where trawl disturbance had no effect on biomass.

The subset with larger sediment grain size (290–430 µm) has smaller gradients in depth, primary productivity, and biomass compared to the total data set, but covers the entire range of trawl disturbance intensity (Table S4 in Appendix S2). Analyzing this subset gives a different outcome than the SEM for explaining variation in species richness. Richness is positively correlated with biomass but none of the other variables add any explanatory value. This is true even for the model that includes trawl disturbance (which only reduces the AIC with 1.9). Variation in biomass is best described by depth (Table 2).

DISCUSSION

Our analysis demonstrates how a combination of direct and indirect effects in this soft-bottom marine habitat shapes benthic species richness. Richness is mostly determined by the gradient in sediment grain size, and is negatively related to both primary productivity and trawl disturbance. The effects of disturbance on richness and biomass diverge within subsets of our data with a relatively homogenous grain size. These habitat-dependent effects have important implications for the conservation and restoration of marine benthic habitats.

We observed a negative relationship between productivity and richness in the SEM. This negative relationship could be the declining part of a hump-shaped pattern. Although the mechanisms behind this declining phase continue to be debated, two predicted mechanisms have received most attention in plant communities (Waide and others 1999; Adler and others 2011). The first mechanism implies that high productivity reduces the heterogeneity of limiting resources and that this results in a situation in which only the dominant competitors persist (Tilman and Pacala 1993). If so, competitive exclusion would show up in the data as a decline in

Table 2. Model Selection for Richness and Biomass in the Data Subsets

	Best model fits:	P value	Estimated intercept	AIC	Δ AIC
Sediment grain size between 125 and 235 μm (n = 230 for 6 years)					
Richness ~	Trawl disturbance + primary productivity	$P1 = 0.004;$ $P2 = 0.002$	$Y = 36.3 - 2.0$ $* x1 - 0.02 * x2$	1,489.1	9.3
	Trawl disturbance + primary productivity + biomass	$P1 = 0.001;$ $P2 < 0.000;$ $P3 = 0.001$	$Y = 35.4 - 2.4$ $* x2 + 3.8 * x3$	1,479.8	0.0*
Biomass ~	Trawl disturbance	$P1 < 0.000$	$Y = 0.65 + 0.187 * x1$	188.7	13.4
	Primary productivity	$P1 < 0.000$	$Y = 0.14 + 0.002 * x1$	179.1	3.8
	Trawl disturbance + primary productivity	$P1 = 0.017;$ $P2 < 0.000$	$Y = 0.24 + 0.099 * x1$ $+ 0.002 * x2$	175.3	0.0*
Sediment grain size between 290 and 430 μm (n = 84 for 6 years)					
Richness ~	Biomass	$P1 < 0.000$	$Y = 10.3 + 5.9 * x1$	494.2	1.9*
	Trawl disturbance + biomass	$P1 = 0.054;$ $P2 < 0.000$	$Y = 11.9 - 0.9$ $* x1 + 6.1 * x2$	492.3	0.0
Biomass ~	Depth	$P1 < 0.000$	$Y = 1.41 - 0.03 * x1$	79.9	0.0*
	Depth + trawl disturbance	$P1 < 0.000;$ $P2 = 0.689$	$Y = 1.47 - 0.04$ $* x1 - 0.02 * x2$	81.7	1.8
	Depth + primary productivity	$P1 < 0.000;$ $P2 = 0.585$	$Y = 1.72 - 0.04$ $* x1 - 0.0007 * x2$	81.6	1.7

*Model selection was based on AIC. The two or three models that fitted data best are shown (Δ AIC shows best candidate model by *). The names P1 and x1 refer to the first predictor variable in the same row, P2 and x2 to the second, etcetera. We used a linear mixed model with year as random factor. Biomass is log(x + 1) transformed.*

species richness as biomass increases. However, in our data, a positive relationship exists between richness and biomass. The second hypothesized mechanism requires the inclusion of disturbance (Huston 1979; Kondoh 2001). A negative relationship between productivity and richness may typically be observed at low disturbance (Kondoh 2001). It is unlikely that this is the underlying explanation in our area, as our results show a positive relationship between productivity and trawl disturbance.

In contrast to the negative relationship between productivity and richness, a positive relationship between biomass and richness was observed. The directionality of this effect was tested in our SEM (by including a reciprocal interaction between richness and biomass) (Grace 2006) and this showed that biomass affects richness, but not vice versa. One suggested explanation for the opposing responses of productivity and biomass on richness is the omnipresent impact of predation in soft-bottom habitats (for a review, see Wilson 1991 and Seitz 1998), because predation may decouple the strong correlation between productivity and biomass (Oksanen and others 1981).

Within the subset of the data with larger grain sizes, no effect was found between productivity and benthic richness. This subset started at higher

productivities compared to the other subset where a negative relationship with benthic richness was found. One possible explanation could be that the effect of productivity on richness is limited to low and intermediate productivity, while other factors determine richness at higher productivity.

In this study, we used primary productivity as the best approximation of benthic productivity. However, benthic production depends not only on the amount but also on the quality of organic matter that is available as food for benthos (Dauwe and others 1998). Variation in quality could thus decouple this relationship. This decoupling seems to have limited effects, as we still find a strong relationship in the SEM between trawl disturbance and primary productivity. This relationship was expected when areas with high productivity produce large quantities of fish food, to which the fish are attracted.

We observed a negative relationship between trawl disturbance and species richness in the SEM (Figure 4). These negative effects have most commonly been described in areas with gradients of human disturbance (Mackey and Currie 2001). They are also observed in studies specifically examining the impact of bottom trawling on benthic richness (Collie and others 2000; Hiddink and others 2006; Hinz and others 2009). However, the

effects of disturbance on richness diverge within subsets of our data with a relatively coarse or fine grain size.

Within the subset of the data with coarser grain sizes, no effect was found between trawl disturbance and species richness, which was surprising as this subset had a large trawl disturbance gradient. This gradient ranged from two locations in a protected area (the Plaice Box), where beam trawl effort decreased by more than 90% after the establishment of the protected zone in 1989 (Beare and others 2013), to different locations where trawl disturbance was estimated to be the highest in the entire data set. These findings lead to the question of whether fishing occurs predominantly in low diversity areas, where its effects matter least, or whether the benthic ecosystem in heavily fished areas adapts accordingly (and for the stations in the Plaice Box remains in this state). The former scenario suggests that there is limited need to protect benthic richness from trawl disturbance in this habitat. In contrast, the latter scenario suggests that the absence of trawl disturbance in the protected area has (so far) not induced benthos recovery. The opposing scenarios clearly show the limits to the use of species richness as an indicator to examine effects of trawl disturbance on ecosystem health. Richness points only at one aspect of ecosystem health and a further exploration of trawl disturbance should look into possible changes in community structure or functioning, for example, using a trait-based approach (Bremner 2008).

At finer sediment grain sizes, we observed a stronger negative relationship between disturbance and richness. This suggests that marine protected areas may work to protect benthic richness when placed in these habitats. Interestingly, we also saw a positive relationship between disturbance and biomass in these finer sediments. An increase in biomass in response to trawling was also observed with the model result by van Denderen and others (2013). Based on the model, such an increase may be expected in a top–down controlled system where trawling reduces fish abundance and its predation impact on benthic prey, or in a bottom-up controlled system where trawling increases productivity of the area.

Patterns in benthic richness in our data are best explained by a complex structure of interacting variables. The high degree of interaction is clearly visible for the trawl disturbance gradient, which is largely related to (and explained by) habitat characteristics. To disentangle the relative strengths of the interacting variables on richness, we used a SEM that included an unknown relationship between sediment grain size and primary productivity. The variables covaried, although there is no clear causal link between them. Both are high/large near the coast and low/small further away from the coast and this correlation is probably due to a third, confounding factor. This may also apply to other pathways in our SEM, although most were based on a better understanding of the causal mechanisms involved.

Assessing the strength of the different predictor variables in the SEM showed that sediment grain size had the strongest effect on benthic richness. Sediment grain size, it should be noted, is measured directly at the sampling locations together with the biological samples, and therefore may have higher accuracy than the estimates used for the other predictor variables. This may have influenced the statistical model outcome. For example, some variables might have had more importance if the measurement errors had been lower. Besides the variables studied here, there are two others that likely interact with the other predictor variables to affect benthic richness: natural disturbance and fish abundance. Natural disturbance is expected to covary with depth and for that reason we also removed the number of points at very shallow sampling locations which are likely outliers in terms of natural disturbance (see ''Method'' section). As some have proposed, frequent natural disturbance may lower the relative impact of trawling on the benthic habitat (Hall 1994; Kaiser and Spencer 1996; Kaiser 1998; Diesing and others 2013). Natural disturbance may thus interact with trawl disturbance and could be one of the reasons that we found no effect of trawl disturbance in the subset of the data with the largest grain size. The inclusion of fish (especially plaice and sole) and their predation impact on benthic prey could have an even more profound effect on benthic richness (and biomass). These effects on richness and biomass have been observed in many predator–prey studies (for example, Paine 1966; Oksanen and others 1981; Shurin and others 2002).

In this study, we explored how different factors interact and together affect species richness in a marine soft-bottom environment. Although the monitoring data do not allow us to determine the mechanisms behind these observed patterns, our results provide insight into the potential processes. Although part of our results, in particular, the negative relationship between disturbance and richness, corroborate earlier findings, other (combinations of) results were unexpected. This is especially the case for the negative relationship between richness and primary productivity and the

positive relationship between richness and biomass. Another important result of our work is the habitat-specific response of trawl disturbance on benthic richness. This suggests a multivariate, non-linear relationship between these factors and hence indicates habitat-dependent effects of bottom trawl fisheries. Such a multivariate response has been suggested by others (for example, Kaiser and others 2006), but it has, to the best of our knowledge, never been shown to occur in one dataset, under the influence of a single type of fishing.

Our outcome emphasizes the importance of the choice of spatial scale to assess the impact of trawl disturbance on the benthic community. It suggests that the right spatial scale depends on the heterogeneity of the habitat and the combined effects of trawl disturbance and productivity on the benthic community. A clearer understanding of the processes and patterns associated with benthic richness and biomass in these habitats is a requirement for the conservation of these systems and the management of their exploitation.

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