

Effects of chronic bottom trawling on soft-seafloor macrofauna in the Kattegat

Mattias Sköld^{1,*}, Peter Göransson², Patrik Jonsson¹, Francois Bastardie³,
Mats Blomqvist⁴, Stefan Agrenius⁵, Jan Geert Hiddink⁶, Hans C. Nilsson¹,
Valerio Bartolino¹

¹Department of Aquatic Resources, Institute of Marine Research, Swedish University of Agricultural Sciences, 453 30 Lysekil, Sweden

²PAG Environmental Research, 252 70 Råå, Sweden

³National Institute of Aquatic Resources, DTU Aqua Technical University of Denmark, 2920 Charlottenlund, Denmark

⁴Hafok AB, 179 61 Stenhamra, Sweden

⁵Department of Marine Sciences Kristineberg, University of Gothenburg, 451 78 Fiskebäckskil, Sweden

⁶School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, UK

ABSTRACT: Impact studies of chronic bottom trawling aiming to reveal long-term effects on benthic organisms are often hampered by the lack of comparable untrawled conditions and the difficulty in assessing the spatial distribution of trawling intensity. We sampled soft-seafloor macrofauna over a precise trawling gradient in the Kattegat using hourly vessel monitoring systems and logbooks. The gradient included the establishment of a marine protected area (MPA), where trawling intensity declined sharply to zero. Our results show shifts in the macrofauna assemblage and non-linear responses, with decreases in the number and diversity of species at low to medium trawling intensities. The benthic community was dominated by burrowing brittle stars, of which one species, *Amphiura chiajei*, increased in abundance from low to medium trawling intensities. We interpret this positive response to increasing trawling intensities as a consequence of reduction in predation by benthivorous flatfish and Norway lobster *Nephrops norvegicus*, which are significant catches of the fishery. The response was supported by a corresponding trend towards lower abundance of the dominating brittle stars following enforcement of the MPA and presumably an increase in benthivore density and predation pressure within the MPA. We conclude that chronic bottom trawling reduces diversity and may boost the abundances of species resistant to bottom trawling. The results emphasize the need to consider food web effects when assessing the impact of bottom trawling.

KEY WORDS: Physical disturbance · *Amphiura filiformis* · Echinoderm · Otter trawling · Fishing impact · Food web · Benthic habitats · *Nephrops norvegicus* · Anti-predator defenses

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INTRODUCTION

Bottom trawls, which are used to catch fish and shellfish that live on or close to the seabed, are by design in contact with the seabed. As a result, bottom trawling can cause disturbance of benthic habitats, leading to changes in the abundance, biomass and

diversity of communities and species (Collie et al. 2000, Kaiser et al. 2006). Sensitivity of benthic habitats tends to be lower in shallow high-energy areas with high levels of natural disturbance than in deeper areas where physical disturbance by waves caused by wind-driven energy, i.e. storms, may not reach the seabed (van Denderen et al. 2015). Sensi-

tivity of the fauna also differs between species, depending on their biological traits and the mechanism of disturbance. Direct mortality of organisms and longer-term modification of habitats by mobile demersal fishing gear are most severe in vulnerable areas such as deep-water coral reefs and sponge communities where fragile species that build 3-dimensional structures make up a significant component of the habitats (Fosså et al. 2002, Greathead et al. 2007, Jørgensen et al. 2016). Other components of the fauna, like sediment-dwelling infauna, may be less sensitive to the direct physical impact because they are partly protected by burying in the substrate (Tillin et al. 2006). For such species, indirect effects such as changes in particle dynamics of the sediment (Dounas et al. 2007, Tjensvoll et al. 2013), or changes in the balance between predators and prey (Hiddink et al. 2016) and their interactions, or whether the abundance of benthos is top-down or bottom-up controlled (van Denderen et al. 2013), may have larger impacts.

The effects of bottom trawling on seafloor species, communities and habitats have been widely studied and, although some general patterns are emerging, there remains a lot of unexplained variation in the findings of individual studies (discussed by e.g. Collier et al. 2000, Løkkeborg 2005, Kaiser et al. 2006). The variation in outcomes of studies may relate to variations in fishing pressures as well as variations in the sensitivity of the system studied or other environmental factors that may interact with fishing. In a recent global analysis of depletion and recovery of benthic fauna based on gradient studies, only 5 of 24 studies included unfished conditions in their gradient of trawling (Hiddink et al. 2017). Observational studies that sample over existing gradients in trawling intensity may thus suffer from a lack of appropriate reference conditions, i.e. comparable sites without or with low bottom trawling intensity.

Fishing activities are patchy and concentrated on specific fishing grounds due to accumulated knowledge by the fishers on catchability of target species, and accessibility by the gears used (e.g. Bastardie et al. 2010, Eigaard et al. 2016). Likewise, benthic communities are patchy due to the spatial heterogeneity of factors structuring communities, such as sediment composition, depth, hydrodynamic regime and food availability (e.g. Rosenberg & Möller 1979, Gogina et al. 2016). With the introduction of satellite monitoring of fishing vessels and developed techniques to analyse and reconstruct fishing activities, it has been increasingly clear how certain areas and habitats are periodically fished with high intensity, while other areas are fished with low intensities or not at all (ICES

2016, Eigaard et al. 2017). These large spatial and temporal differences occur both at broad scales between and within sea areas and at much finer scales of about 100 m. It is crucial to assess the spatial distribution of bottom-trawling intensity at a fine resolution if the aim of impact studies is to cover long-term impacts and effects of direct disturbance of the seafloor. This is because relationships between trawling and responses might otherwise be confounded by misclassification of the pressure at the site where the impact is studied. A universal problem for observational studies of trawling gradients is that trawling intensity, for practical and data access reasons, is aggregated within grid cells much larger than the sampled site, usually 1 × 1 nautical miles or larger (e.g. Hiddink et al. 2006, Reiss et al. 2009, ICES 2016, Pommer et al. 2016, Eigaard et al. 2017). This may lead to unreliable estimations of the trawling intensity because large areas are likely to overestimate the trawling intensity in lightly trawled sites and underestimate the trawling intensity in heavily trawled sites. To our knowledge, no bottom-trawling gradient study of benthic fauna communities has assessed the trawling intensity at a fine scale directly on the sampled position using a Euclidian radial distance approach.

The aim of this study was to evaluate the effects of bottom trawling on benthic macrofaunal assemblages using fine-resolution trawling distribution data and untrawled reference conditions. We hypothesized that benthic macrofauna would be influenced by trawling intensity and evaluated this by stratifying a sampling programme in relation to a known bottom-trawling gradient in the Kattegat. The power to detect effects was maximized by precisely assessing the trawling pressure at the sites where the sampling was carried out. The stratification included a marine protected area (MPA), where bottom trawling had been stopped, to ensure the inclusion of comparable untrawled conditions. We also investigated the effect on the macrofauna following the enforcement of the MPA and the removal of trawling. We hypothesized that temporal changes in the assemblage within the MPA would deviate from changes outside the MPA where trawling continued.

MATERIALS AND METHODS

Study area

The Kattegat is a shallow (mean depth 27 m) sea area between Sweden and Denmark and connects to the Skagerrak in the north and to the Baltic Sea via

narrow straits in the south. The influence of low saline surface waters from the Baltic Sea creates a typical estuarine circulation pattern and strongly stratified water masses separated by a halocline, that persists year-round at around 15 m depth, but may extend down to 20 m (Granéli 1992). The outflow from the Baltic Sea, the so-called Baltic Current, is mostly concentrated along the Swedish coast where the halocline is deeper and stratification stronger than in the western parts. The water beneath the halocline, originating from the Skagerrak and the North Sea, is more stable, and marine conditions prevail, with salinity conditions usually above 32 PSU (Andersson & Rydberg 1988). Depths and substrate vary, with shallow areas with sandy sediments in the west and deeper soft-mud sediments in the east (Hallberg et al. 2010). Benthic fauna in the soft-mud habitats are currently dominated by brittle stars of the *Amphiura* community (Gogina et al. 2016), but especially the south-eastern part was previously dominated by amphipods of the *Haploops* community (Petersen 1913).

Fishing by bottom trawling in the Kattegat has been ongoing since the early 1900s (Bartolino et al. 2012). Currently, the fishery is dominated by otter trawling targeting a mixture of Norway lobster *Nephrops norvegicus* (hereafter *Nephrops*) and fishes, mainly plaice *Pleuronectes platessa*, sole *Solea solea* and cod *Gadus morhua* (Hornborg et al. 2017). Denmark has the largest share of total allowable catches (e.g. 67% of *Nephrops*), Sweden has the second-largest share (*Nephrops* 31%), and Germany has the smallest share of *Nephrops* and demersal fish (ICES 2015).

In 2009, a large (653 km²) MPA in the southeast Kattegat was established and closed to all fishing activities to protect spawning grounds for cod. The MPA was one of the core spawning areas that was fished by otter trawls historically for about 100 yr, targeting aggregated cod during the spawning season (Vitale et al. 2008). Some illegal fishing activities were documented during the first year after establishment of the MPA but appear to have decreased following actions taken by the Swedish and Danish enforcement agencies (Bergström et al. 2016).

Assessment of trawling intensity

Trawling intensity was estimated as precisely as possible for each sampling site in relation to the spatial resolution of the trawl path of the vessels within a radius of 250 m around the location where benthic macrofauna were sampled. The method of using the Euclidian radial distance to a sampling station and

interpolated trawl tracks is consistent and accurate when compared to true distributions of trawl tracks for otter trawls (Lambert et al. 2012). Swedish and Danish fleets equipped with vessel monitoring systems (VMS) were analysed using the VMStools R package (Hintzen et al. 2012) and protocols developed and described by Eigaard et al. (2016). The VMS data included hourly updated GPS positions for vessels of ≥ 15 m length over the period 2006–2011 and all vessels of ≥ 12 m length during 2012–2014. Based on logbook information of the total effort in the Kattegat, we estimated that the fleet coverage of vessels with VMS increased over the period studied from 50–60% in 2006–2011 to >75% in 2012–2014. The VMS data set was interpolated into positional data with 12 min temporal resolution (Hintzen et al. 2010). The spread between the trawl doors was estimated for each logbook trip based on the gear used and the vessel's engine power (Eigaard et al. 2016). This estimate was combined with interpolated VMS data to reconstruct individual trawl paths. Trawling intensity was then calculated around the sampled position for benthic fauna as the area swept by trawls within the 250 m radius at each station and summed over 32 mo prior to the sampling date. The time scale of accumulating trawling over 32 mo was chosen to achieve a wide gradient (trawling intensity of 0–15 yr⁻¹) of the bottom-trawl history, accumulate the index to cover more than 1 benthos recruitment event at a sampling station, and as a reasonable match to recovery time of the long-living and presumably more sensitive part of the macrofauna species. To ensure that the gradient was consistent and comparable over time, data on trawling intensity was standardised to vessels ≥ 15 m in all analyses.

Benthic macrofauna sampling

Sampling of benthic macrofauna was carried out in May and June in 2009, 2010, 2011 and 2014 using a modified Smith-McIntyre grab (0.1 m²) at 58 stations (Fig. 1). One sample was taken at each station and sieved (1.0 mm mesh size) for macrofauna. Sediment properties mapped by Hallberg et al. (2010) were inspected visually and manually for each sample and for all stations verified as soft-mud sediments sometimes mixed with fine sand–silt. Samples were stored in 4% borax-buffered formaldehyde prior to sorting, counting and weighing. With few exceptions, e.g. species belonging to the genus *Edwardsia* and the amphipod family Aoridae, all taxa were identified to species level. In total, 29 864 specimens belonging to

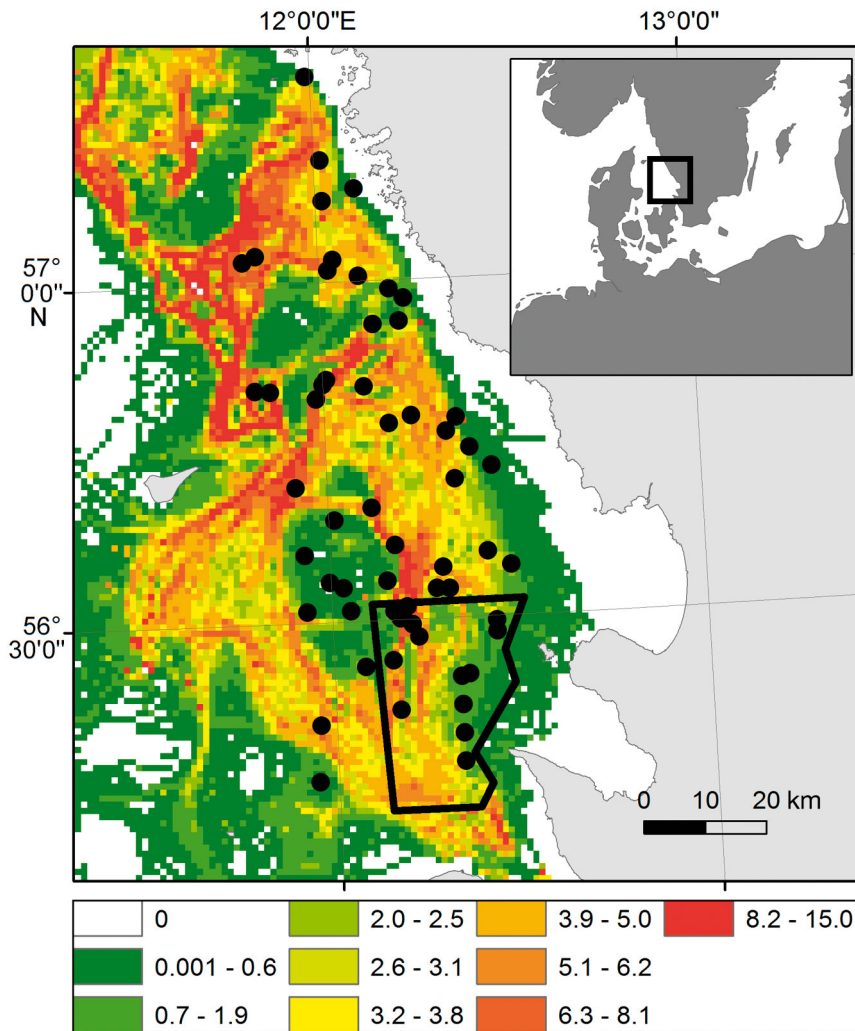


Fig. 1. Study area in the Kattegat. Colours indicate trawling intensity averaged per year for 2006–2008, i.e. the period before the marine protected area (MPA) was established in 2009. Trawling intensity was estimated from Danish and Swedish vessel monitoring system (VMS) and logbook data of bottom-trawl fleets as the total area swept yearly in grid cells of 1×1 km divided by grid cell size. Sampling stations for benthic macrofauna are indicated with black dots; the MPA is delineated

261 different taxa of benthic fauna were present in the samples.

All statistical analyses on biomass were tested without large-bodied species, i.e. the heart urchins *Brisopsis lyrifera* and *Echinocardium cordatum*, and the ocean quahog *Arctica islandica* that, due to their individual weight in some samples, may have strongly influenced the outcome of the results. The distance-based test for homogeneity of multivariate dispersions PERMDISP (for statistical methods, see below) was significant when including large-bodied species (group factor trawling intensity: $F_{3,228} = 5.60$, $p = 0.0034$). Removing these species thus improved the statistical results by reducing heterogeneity of biomass.

Multivariate analysis of macrofauna structure along the trawling intensity gradient

Taking into consideration that the bottom-trawling activities would be removed from the MPA, benthic fauna sampling stations were established inside and outside the MPA with the aim to cover a wide gradient in bottom-trawling intensity (Fig. 1). The sampling stations were situated to cover the habitat and depths explored by the dominant demersal bottom-trawl fisheries, and were thus chosen within the depth interval 23–65 m, where 95% of the trawled positions from the VMS of the dominant fisheries were located. Sampling stations were placed to reduce natural variation between habitats by limiting the stations to post-glacial soft-mud sediments according to sediment mapping of the Kattegat (Hallberg et al. 2010). In this design, we expected to identify macrofauna community shifts in the benthic community along the identified trawling intensity gradient.

All multivariate analyses were performed using the statistical package PERMANOVA+ for PRIMER (Anderson et al. 2008). The effect of trawling intensity on the macrofauna community was analysed with PERMANOVA, with trawling intensity at each sampling station categorised into statistical quartiles (≤ 0.4 , > 0.4 to ≤ 2.1 , > 2.5 to ≤ 4.6 , > 4.6 yr^{-1}) as fixed factors. The categorisation was done to simplify interpretation of the results, since 2 more factors were included in the design, and to standardise the trawling intensity gradient into informative statistical groups representing low to high intensities. Year of sampling was fixed, and sampling station was a random factor nested in trawling intensity. Community composition was weighted both by abundance and biomass of species. Resemblance matrices were constructed using Bray-Curtis similarity, and abundance and biomass data were fourth-root transformed to reduce the influence of dominant species. Post hoc comparisons were done using pairwise PERMA-

NOVA, and results were visualized with canonical analysis of principal coordinates (CAP). All data were evaluated with a distance-based test for homogeneity of multivariate dispersions using the function PERMDISP.

To further explore the effect of the gradient in trawling intensity and to account for the potential covariance of trawling intensity and depth-related environmental factors known to be important in the Kattegat (Petersen 1913, Rosenberg & Möller 1979, Rosenberg et al. 2000, Agrenius & Göransson 2009, Leonardsson et al. 2016, Pommer et al. 2016), we evaluated depth together with trawling intensity as predictors for community composition weighted by species abundance and biomass using distance-based linear modelling (DistLM) and distance-based redundancy analysis (dbRDA). The predictors were checked by draftsman plots, and trawling intensity was transformed by $\log(x + 1)$ and depth by square root to reduce skewness. Depth and trawling intensity were checked for collinearity, and a correlation of 0.64 was estimated for these variables. This is below the critical correlation level of 0.7 as suggested by Dormann et al. (2013). The best selection procedure was chosen together with the selection criteria modified Akaike's information criterion (AICc) for model selection, and only predictor variables that were significant in marginal tests were selected. Individual species contributing to the multivariate dbRDA model were evaluated using correlations (Pearson's R) between species abundance and the axis that explained most of the variation correlating with trawling intensity. In addition, correlations were done between species abundance and trawling intensity.

Univariate analysis of macrofauna metrics along the trawling intensity gradient

The effects of bottom trawling on macrofauna may be expected to depart from a linear relationship. For this reason, we analysed univariate response variables using generalized additive models (GAMs). GAMs use non-parametric functions which allow modelling non-linear relationships without prior knowledge of their actual shape. The effect of trawling was tested by applying GAMs on the following univariate response variables: number of species (Nsp), total abundance (Nind), total biomass (Biom), abundance of the 2 dominant species (*Amphiura filiformis* and *A. chiajei*), the richness index d (Margalef 1958), Shannon diversity $H'(\log_2)$ (Shannon & Weaver 1949) and

the benthic quality index (BQI). BQI was calculated according to Leonardsson et al. (2016) without the correction for depth, as depth is included in the GAM (see below). The BQI is used by Sweden for benthic quality assessments under the EU Water framework directive (2000/60/EC) and combines abundance-weighted species sensitivities with species diversity into 1 index. All variables were calculated at the level of individual sampling stations (i.e. for each year y and geographical location ρ, ϕ identified by longitude and latitude degrees), and the analysis was performed accordingly. The models were formulated as follows:

$$\text{Response}_{(y,\rho,\phi)} \sim \alpha_y + s(D_{(\rho,\phi)}) + s(TI_{(y,\rho,\phi)}) + s(Nind_{(y,\rho,\phi)}) + \gamma_{(\rho,\phi)} + e_{(y,\rho,\phi)} \quad (1)$$

where α is the year-specific intercept, and s is a 1-dimensional (Wood 2004) smoothing function on depth (D) and trawling intensity (TI). To account for dependency among sampling stations which are closer in space, the error part of the model was separated into a Gaussian spatially autocorrelated component (γ) (Venables & Ripley 2002, Dormann et al. 2007), which was treated as a random effect (Pineiro & Bates 2000), and a normally distributed error term (e). Nind was included as a predictor only for the model using Nsp as a response variable to account for changes in the detection probability of new species as abundance increases. Model overfitting was controlled by constraining the maximum degrees of freedom on the depth variable to 3. Inspection of model residuals revealed no major departure from the model assumptions of normality and homogeneity of variance. The GAMs were fitted using R and the library *mgcv* (Wood 2011).

Effects of reduction in trawling intensity through MPA enforcement

In the evaluation of the closure for trawling within the MPA, we expected potential temporal changes in the macrofauna assemblage within the MPA to deviate from changes outside the MPA where trawling continued. No benthic sampling was carried out prior to the establishment of the MPA in 2009. However, we assumed that the macrofauna community status of 2009 sampled 5 mo after the enforcement of the MPA could be considered a reasonable baseline since the impact of bottom trawling in previous years was likely to remain longer (i.e. >1.9 yr) for macrofauna (Hiddink et al. 2017).

Samples were collected at the same stations in 2009, 2010, 2011 and 2014. Stations sampled within the MPA and outside the MPA were defined as trawled if trawling intensities were above the median trawling intensity (≥ 2.5) estimated from all sampling stations and the whole study period. As expected, a reduction in trawling intensity in the MPA since its establishment in 2009 was seen over time. However, trawling intensity was not reduced to 0 at all stations inside the MPA, indicating some noncompliance or misclassification of vessels on transit at slow speed (see Fig. S2 in the Supplement at www.int-res.com/articles/suppl/m586p041_supp.pdf).

The experimental effect of the MPA on the temporal development of the species assemblage was evaluated using PERMANOVA, with year of sampling and treatment (i.e. closure versus continuously trawled) as fixed factors and station as a random factor nested in treatment. The effect of the closure on the macrofauna community will thus be the interaction between year of sampling and treatment (i.e. the 'closed' area versus the area outside the MPA that was continuously 'trawled'). Dependent variables examined were species composition weighted by abundance, biomass or abundance of the 2 most dominant species (*A. filiformis* and *A. chiajei*), and univariate total abundance, total biomass and number of species. As significant effects were detected for the dominant species, these were also examined by a factorial ANOVA with the same design. Dependent variables, i.e. abundances of the species, were transformed by $\log(x + 1)$ and tested for unequal variances by Welch's test. Univariate statistics were analysed using the statistical package JMP pro 12.0.1.

RESULTS

Multivariate analysis of macrofauna structure along the trawling intensity gradient

Trawling intensity, estimated as swept area ratio, ranged from 0–15 yr^{-1} and was heavily skewed towards the lower end of the range (median 2.1 yr^{-1}). The range and distribution of trawling intensity verified the stratification of the design and was stable over the 4 years sampled, with the exception of the anticipated decrease at the 7 stations protected due to the establishment of the MPA from 2009 (Figs. S1 & S2 in the Supplement).

The PERMANOVA based on species abundance indicated significant effects of both year ($p = 0.0001$)

and trawling intensity ($p = 0.0001$) on the community composition of the macrofauna, but no interaction between these 2 factors ($p = 0.0749$; Fig. 2). Pairwise comparisons showed that the effect of trawling intensity categories differed between the 2 lower overlapping quartiles and the 2 highest overlapping quartiles. Similar statistical results were achieved using species biomass without large-bodied species (year: $p = 0.0001$; trawling intensity categorised into quartiles: $p = 0.0001$, and no interaction between these 2 factors: $p = 0.1045$). Pairwise comparisons of trawling intensity categories again showed that the effect of trawling intensities differed between the 2 lower overlapping quartiles and the 2 highest overlapping quartiles (for details on statistics, see Table S1 [macrofauna abundance] and Table S2 [biomass] in the Supplement). The multivariate PERMANOVA thus

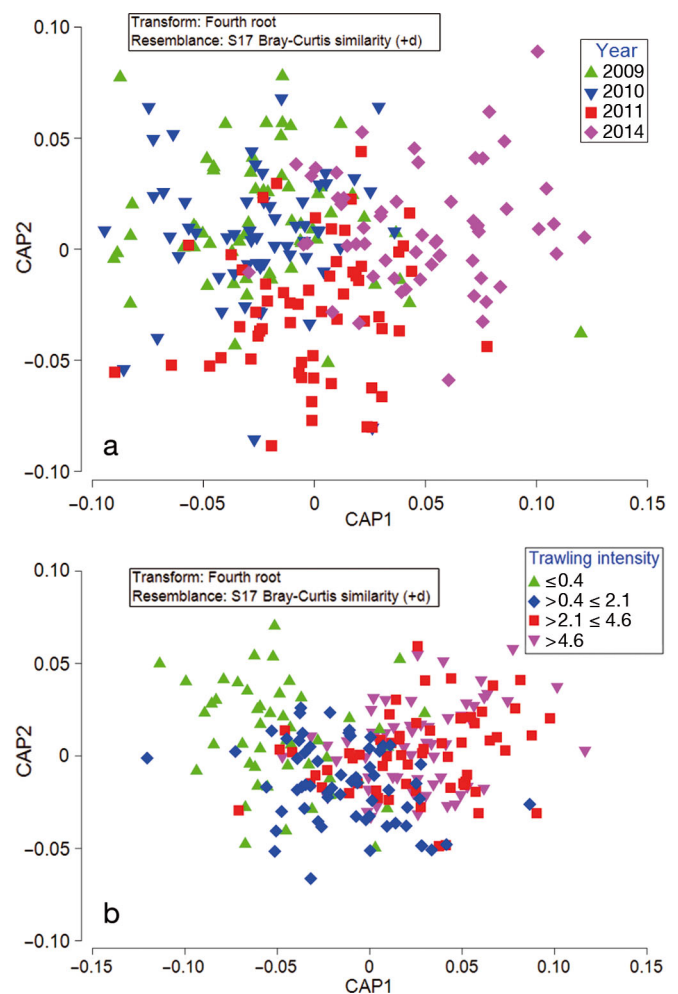


Fig. 2. Canonical analysis of principal coordinates (CAP) for visual presentation of macrofauna community composition (abundance of species) as shaped by (a) year and (b) trawling intensity (yr^{-1}) grouped into statistical quartiles as indicated in the legend

indicated that the macrofauna assemblage was structured differently over the years and along the trawling intensity gradient of the sampling stations, but that the effect of variation in trawling intensity did not change over time.

To further explore the effect of gradient in trawling intensity, depth together with trawling intensity were evaluated as continuous predictors of community composition by DistLM and dbRDA. Since the year factor did not show an interaction with trawling intensity in the foregoing PERMANOVA, data from all years were pooled to increase the generality of the tests. The marginal test showed both trawling intensity and depth to be significant predictors contributing to the model ($\log[x + 1]$ trawling intensity $F = 10.1$, $p = 0.0001$, and square-root depth $F = 15.3$, $p = 0.0001$). Using the best model selection procedure, i.e. all variable combinations, and AICc, both predictors were identified and together explained 7.4 % of the variation in community composition. The dbRDA visualizes how the stations with differing trawling intensity and depth relate to the multivariate dbRDA axes 1 and 2 (Fig. 3). Trawling intensity correlated with dbRDA 1 (multiple partial correlation 0.52), which explained 6.4 % of the total variation and with dbRDA 2 (0.85), which explained 0.9 % of the total variation. Depth also correlated with both dbRDA 1 (0.85) and dbRDA 2 (0.52). The testing procedure above was also done using biomass of species as the dependent variable, which showed similar effects ($\log[x + 1]$ trawling intensity $F = 9.5$, $p = 0.001$ and square-root depth $F = 14.5$, $p = 0.0001$) and correlations with dbRDA axes 1 and 2 (0.52 and 0.86, respectively), as well as overall contributions to the total variation of 6.1 and 1%. Depth also correlated with both dbRDA 1 (0.86) and dbRDA 2 (0.52).

Correlations between the multivariate ordination axis that explained most of the total variation and abundance of individual species indicated that 40 macrofauna species had a decreasing trend in abundance along the axis while 13 increased. Correlations between individual species abundances and trawling intensity showed agreement with the species that decreased along the axis for 58 % of the species that had negative trends, including *Ampelisca tenuicornis* and *Phoronis muelleri*. For the species that increased, 31 % showed conformity with a positive trend, including *Amphiura chiajei* and *Labidoplax buskii* (Table 1).

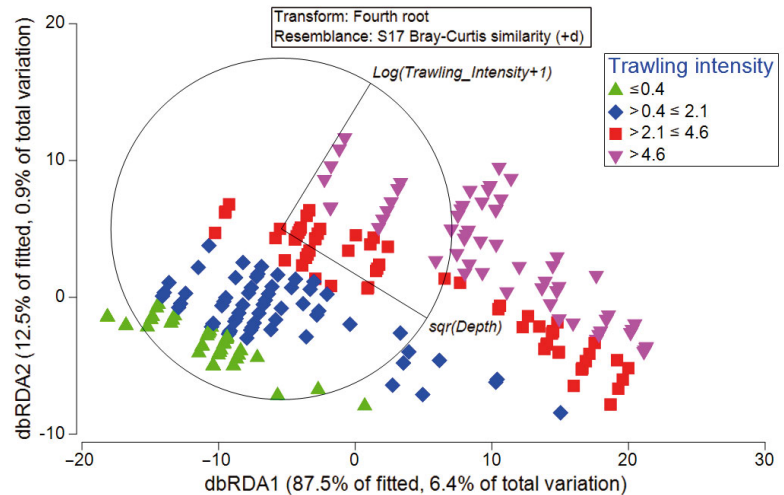


Fig. 3. Distance-based redundancy analysis (dbRDA) ordination of the fitted model of the macrofaunal community composition. The gradient in trawling intensity grouped into quartiles is illustrated by the sampling station colour according to the legend, and vectors of the predictor's trawling intensity and depth are indicated in the plot

Univariate analysis of macrofauna metrics along the trawling intensity gradient

Trawling intensity had a similar significant effect on the number of species, richness, diversity and the benthic habitat quality (measured by the BQI), while its effect was non-significant on the total biomass and abundance of benthos (Fig. 4). The effect of trawling intensity was negative for values below ca. 5 yr^{-1} , which include 64 % of the sampling stations, and the relationship became slightly positive for larger values. Depth had no significant effect in any model, with the exception of the benthos abundance which significantly decreased ($p < 0.01$) in response to increasing depth until approximately 40 m (Fig. 4). The GAM of the number of species had an R^2 value of 0.34. In the other models, R^2 ranged between 0.10 and 0.19, with the exception of the model on biomass, which had a value of 0.015 (Table 2).

The soft-mud macrofauna community in the area investigated was dominated by the burrowing brittle stars *A. filiformis* and *A. chiajei*. Together, these 2 species represented 50 % of the overall number of individuals and 58 % of the biomass. *A. filiformis* was present in 98 % and *A. chiajei* in 83 % of the samples. The 2 species presented an opposite response to depth below 40 m, with *A. chiajei* increasing in deeper waters and *A. filiformis* decreasing in abundance in the same depth range (Fig. 5). The response to trawling intensity was non-significant for *A. filiformis* but positive for *A. chiajei* at low to medium trawling intensi-

Table 1. Linear trends of individual species abundance in relation to ordination along axis 1 of the distance-based redundancy analysis (dbRDA 1) that best contributed to the total variation (6.4%) and correlated with trawling intensity (0.52). Correlations between species abundance and trawling intensity are in parentheses. Only significant correlations with dbRDA 1 are shown (i.e. Pearson correlation coefficient $R \geq 0.14$, $df = 252$, $p < 0.05$)

Species decreasing with trawling intensity and dbRDA 1	R
<i>Ampelisca tenuicornis</i>	-0.41 (-0.24)
<i>Phoronis muelleri</i>	-0.38 (-0.20)
<i>Rhodine gracilior</i>	-0.37 (-0.22)
<i>Mysella bidentata</i>	-0.34 (-0.21)
<i>Nephtys hombergii</i>	-0.33 (-0.19)
<i>Turritella communis</i>	-0.29 (-0.17)
<i>Prionospio fallax</i>	-0.29 (-0.25)
<i>Mysia undata</i>	-0.28 (-0.16)
<i>Scoloplos armiger</i>	-0.28 (-0.23)
<i>Praxillella praetermissa</i>	-0.27 (-0.05)
<i>Pholoe baltica</i>	-0.26 (-0.19)
<i>Eudorella truncatula</i>	-0.25 (-0.21)
Aoridae	-0.25 (-0.17)
<i>Amphiura filiformis</i>	-0.25 (-0.11)
<i>Chamelea striatula</i>	-0.24 (-0.17)
<i>Trichobranchus roseus</i>	-0.24 (-0.05)
<i>Pectinaria auricoma</i>	-0.23 (-0.10)
<i>Nucula nitidosa</i>	-0.21 (-0.14)
<i>Scalibregma inflatum</i>	-0.21 (-0.11)
<i>Edwardsia</i> spp.	-0.20 (-0.21)
<i>Terebellides stroemi</i>	-0.20 (0.09)
<i>Sphaerodorum flavum</i>	-0.19 (-0.11)
<i>Ampelisca brevicornis</i>	-0.19 (-0.16)
<i>Dosinia lupines</i>	-0.19 (-0.17)
<i>Abra nitida</i>	-0.19 (0.09)
<i>Corbula gibba</i>	-0.19 (0.00)
<i>Harpinia antennaria</i>	-0.19 (-0.16)
<i>Notomastus latericeus</i>	-0.17 (-0.11)
<i>Levinsenia gracilis</i>	-0.17 (-0.01)
<i>Bela brachystoma</i>	-0.17 (-0.14)
<i>Anobothrus gracilis</i>	-0.17 (-0.09)
<i>Cylichna cylindracea</i>	-0.17 (0.02)
<i>Spiophanes bombyx</i>	-0.16 (-0.15)
<i>Gari fervensis</i>	-0.16 (-0.11)
<i>Magelona alleni</i>	-0.16 (-0.15)
<i>Chone fauveli</i>	-0.15 (-0.12)
<i>Spio filicornis</i>	-0.14 (-0.16)
<i>Arctica islandica</i>	-0.14 (-0.20)
<i>Virgularia mirabilis</i>	-0.14 (-0.13)
<i>Westwoodilla caecula</i>	-0.14 (-0.05)
<i>Amphiura chiajei</i>	0.50 (0.30)
<i>Ophiocten affinis</i>	0.26 (0.05)
<i>Labidoplax buskii</i>	0.25 (0.18)
<i>Lipobranchius jeffreysii</i>	0.22 (0.13)
<i>Philomedes brenda</i>	0.22 (0.02)
<i>Abyssoninoe hibernica</i>	0.22 (0.25)
<i>Nuculana pernula</i>	0.21 (0.05)
<i>Brada villosa</i>	0.21 (0.09)
<i>Ophiodromus flexuosus</i>	0.21 (0.23)
<i>Panthalis oerstedii</i>	0.19 (0.10)
<i>Leucon nasica</i>	0.18 (0.00)
<i>Photis longicaudata</i>	0.16 (0.00)
<i>Hyalia vitrea</i>	0.15 (0.07)

ties and decreased only for trawling intensity levels above 5 yr^{-1} .

Effects of reduction in trawling intensity following MPA establishment

To evaluate the potential recovery of the macrofauna within the MPA, we hypothesized that the temporal development of the macrofauna within the MPA would deviate from the area outside where trawling continued. Multivariate PERMANOVA tests of abundance and biomass and univariate tests with PERMANOVA of number of species (Fig. 6a), total abundance (Fig. 6b) and total biomass (Fig. 6c) showed no interactions between year and treatment (Table S3). However, abundance of the dominant species (*A. chiajei* and *A. filiformis*) showed a significant interaction between the factors treatment and year (Tables S4 & S5 in the Supplement). Post hoc comparison with pairwise PERMANOVA indicated that the last year (2014) differed from the earlier years (2009–2011) within the closed area, while no difference between years occurred in the area where trawling continued. Examining the pattern with factorial ANOVA indicated the same interaction, with a decrease for both species within the closed area in 2014 compared to earlier years and no temporal trend within the trawled area (Fig. 7), albeit only at a significance level of $\alpha = 0.10$.

DISCUSSION

In this study, we found shifts in the structure of the macrofauna community in soft-mud substrate along a wide gradient in trawling intensity. We investigated this using a stratified sampling design covering a wide and precisely estimated gradient in bottom-trawling intensity, including an MPA established in 2009 to ensure that untrawled as well as intensively trawled sites were included in the gradient. Our results show small but significant shifts in community composition and a decrease in number of species and indices of diversity as trawling intensity increased from low to medium levels, i.e. below 5 yr^{-1} . Several taxa had a negative trend along the gradient of increasing trawling intensity, whereas a few taxa increased. The dominant brittle star species showed different responses: *Amphiura chiajei* increased at low to medium trawling intensities and decreased only at trawling intensities above 5 yr^{-1} , while *A. filiformis* showed no conclusive response. Effects

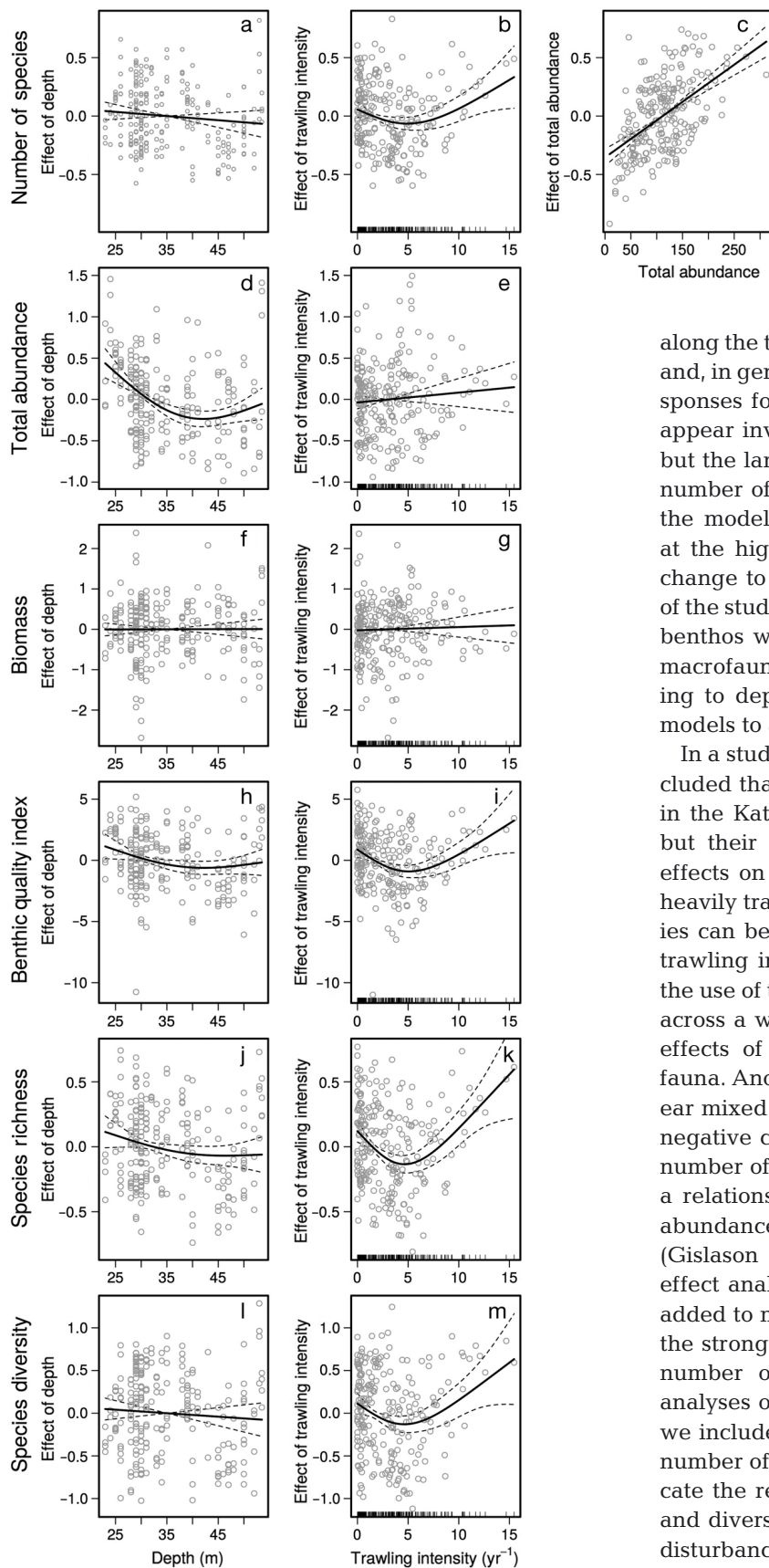


Fig. 4. Effect of different predictors on (a–c) the number of species, (d,e) total abundance, (f,g) biomass, (h,i) benthic quality index, (j,k) species richness according to Margalef and (l,m) species diversity according to Shannon as estimated from generalized additive models with 95 % confidence interval (dotted lines) and partial residuals (grey dots)

along the trawling intensity gradient were non-linear and, in general, more evident at lower intensities. Responses for number of species and diversity indices appear inverted at high levels of trawling intensity, but the large confidence intervals related to the low number of observations suggest high uncertainty of the model to explain the effect of fishing intensity at the high end of the range. There was temporal change to the benthic community over the duration of the study, but the effect of trawling intensity on the benthos was consistent over time. As expected, the macrofauna community was also structured according to depth, which was included in the statistical models to avoid confounding effects.

In a study similar to ours, Pommer et al. (2016) concluded that nearly 100 % of the habitats below 22 m in the Kattegat were impacted by bottom trawling, but their analysis could not discriminate between effects on the macrofauna in lightly trawled versus heavily trawled areas. Differences between the studies can be explained by higher spatial resolution of trawling intensity in our study in combination with the use of the MPA to ensure that sampling was done across a wide range of trawling intensities to detect effects of bottom trawling on the benthic macrofauna. Another recent study in the Kattegat using linear mixed modelling found similarly to our results a negative correlation between trawling intensity and number of species as well as the BQI index, but also a relationship between trawling intensity and total abundance per sample that differs from our results (Gislason et al. 2017). An important complicating effect analysed by Gislason et al (2017) is the noise added to multimetric indicators for macrobenthos by the strong correlation between total abundance and number of species per sample, that complicates analyses of changes in species density. In our study, we included total abundance in the GAM model for number of species, but the correlation might complicate the results for the other indicators i.e. richness and diversity. In another similar study of otter trawl disturbance at *N. norvegicus* soft sediment fishing

Table 2. Summary statistics of the generalized additive model of the number of species (Nsp), total abundance (Nind), biomass, richness according to Margalef (d), diversity according to Shannon (H') and the benthic quality index (BQI), and for the dominant *Amphiura* species by abundance. Equivalent degrees of freedom are reported for the non-parametric predictors depth (D), trawling intensity (TI) and Nind and statistical significance ($*p < 0.05$, $**p < 0.01$) is given for all terms. The family distribution adopted for each model and the R^2 are included

Response	— Predictor variable —			R^2	Family
	s(D)	s(TI)	s(Nind)		
Nsp	1.00	2.29**	1.00**	0.344	Poisson
Nind	1.93**	1.00		0.130	Poisson
ln(biomass)	1.00	1.00		0.015	Gaussian
\sqrt{d}	1.57	2.64**		0.177	Gaussian
H'	1.00	2.36**		0.103	Gaussian
BQI	1.76	2.54**		0.187	Gaussian
<i>A. chiajei</i>	1.95**	2.64**		0.283	Poisson
<i>A. filiformis</i>	1.91**	1.00		0.132	Poisson

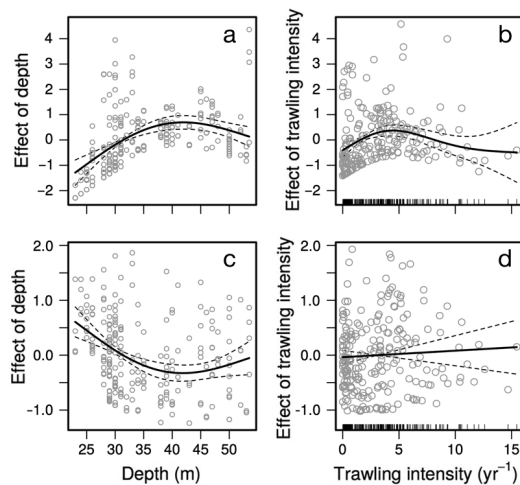


Fig. 5. Effect of different predictors on the abundance of (a,b) *Amphiura chiajei* and (c,d) *A. filiformis* as estimated from generalized additive models with 95% confidence interval (dotted lines) and partial residuals (grey dots)

grounds in the Irish Sea, Hinz et al. (2009) found negative effects of trawling intensity on macrofauna abundance, number of species and total biomass. Similar ranges of trawling intensities were observed by Hinz et al. (2009) and in our study (maximum 18.2 in the Irish Sea and 15.8 yr^{-1} in our study); however, in the Irish Sea, comparable stations with trawling intensity below 1.3 yr^{-1} could not be identified while our study included lower trawling intensity and untrawled comparable conditions in the MPA. The species decreasing with trawling intensity showed some commonalities between the 2 studies for the following taxa: the Phoronida *Phoronis* sp., crustacean

amphipods of the genus *Ampelisca* and the polychaete *Magelona allenii*; however, we also found contradicting results in that the dominating brittle star *A. filiformis* appeared tolerant to bottom trawling in our study but decreased in response to trawling in the Irish Sea. In explaining the differences, we emphasize the need to consider non-linear effects, detailed spatial estimates of trawling intensity and again the necessity of including untrawled and lightly trawled conditions in gradient studies, as effects are most prominent at low levels of the gradient. The most sensitive species are likely already affected and depleted at low trawling intensities, and the benthic fauna that remain are the more resilient species (National Research Council 2002). Our results support this pattern of response, as the macrofauna composition and the decrease in number of species and indices of diversity were evident mainly at lower trawling intensities.

However, our results differ from other studies (e.g. Hiddink et al. 2006, 2011, Hinz et al. 2009, Reiss et al. 2009, Johnson et al. 2015) in that we could not detect any shifts in total biomass. A possible explanation for this difference might be that, in our study, 1 of the 2 dominant species, namely *A. chiajei*, increased along the trawling intensity gradient, which may then have masked the decrease in other less common species that were negatively affected. In their study of beam trawling impact on macrofauna communities, Reiss et al. (2009) found that, even in areas of high trawling disturbance, further increase still caused additional damage to the faunal communities in terms of biomass and number of species. The ground-gear used in beam trawling penetrates the seafloor deeper than otter trawling (Eigaard et al. 2016), which might explain the different responses between our study and others where beam trawling was common (e.g. Hiddink et al. 2006, Reiss et al. 2009). However, all of these other studies analysed the effect of trawling intensity using much coarser spatial resolutions (approximately 1×1 nautical mile or larger) compared to our analysis, making the studies difficult to compare.

It is crucial to assess the spatial distribution of bottom-trawling intensity at a fine resolution if the aim of impact studies is to cover long-term impact and effects of direct disturbance on the seafloor. This is because relationships between trawling and responses might otherwise be confounded by misclassification of the pressure at the site where the impact is monitored. Our study had access to reliable raw VMS data and logbooks from all nations fishing in the area, i.e. Sweden and Denmark and was thus able to reconstruct the daily bottom trawling inten-

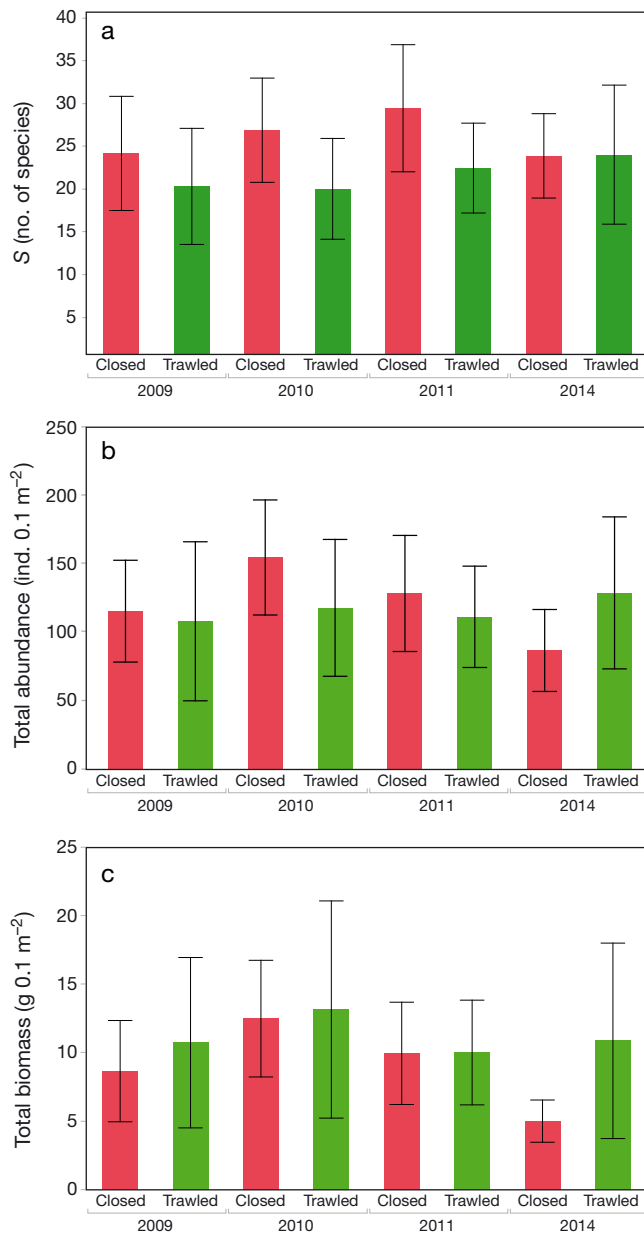


Fig. 6. (a) Number of species, (b) total abundance and (c) total biomass of macrofauna excluding large-bodied species across years in the marine protected area (red, $n = 7$) and continuously trawled area (green, $n = 7$). Error bars are 95% confidence intervals

sity at each station sampled for benthic macrofauna from 2006 to 2014 with high precision. The VMS-derived effort is considered to be an underestimate since vessels <15 m were not included in the gradient. However, we consider the established gradient to be reliable since the main fishing grounds for trawlers in the Kattegat are expected to be similar for large and small vessels without VMS due to the large coverage of the soft-mud habitat, and that the

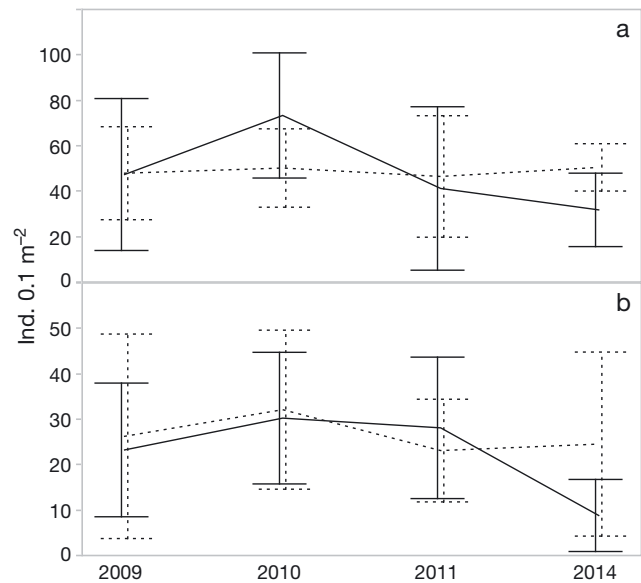


Fig. 7. Mean \pm SD abundance of (a) *Amphiura filiformis* and (b) *A. chiajei* across years in the closed marine protected area (solid line, $n = 7$) and continuously trawled area (dotted line, $n = 7$)

smaller trawlers target the same species composition as the larger fleet. Differences in compliance between small and large vessels, however, may have introduced bias in the estimates of trawling intensity within the MPA due to the lack of VMS monitoring of smaller vessels. The examination of the trend over time within the closed area indicates only a decrease over time for the dominant brittle star species. Non-compliance during the 2 first yr after enforcement of the MPA is evident, as the VMS indicate rather high activity. This might explain the lack of a response over time for the macrofauna community over the relatively short period studied following the closure.

The choice of grid cell and resolution will always be a trade-off with the risk of mismatch between the direct impact at each sampling location and the patchiness of the trawling pressure. In this study, we used a fine-scale search radius to the stations studied as we prioritized the ability to capture and to ascertain the lower end of the trawling intensity gradient, i.e. lightly or untrawled areas within the Kattegat *Nephrops* fishing ground. However, it is unclear whether the indirect ecological disturbance of macrofaunal assemblages through bottom trawling e.g. due to shifts in predator-prey relationships (van Denderen et al. 2013, Hiddink et al. 2016), will be larger than the direct localized physical disturbance through a single trawl path. Response curves to trawling intensity from indirect effects may further differ both

in shape and trigger levels, as these impacts might act on larger temporal and spatial scales. Impacts might reflect how the communities connect to each other and how fast animals can recolonize an impacted site either by migration or recruitment of new animals, as discussed by Lambert et al. (2012), who found the most significant relationships between spatial resolutions of 2×2 km and 4×4 km, which represent a 20–80 times coarser cell resolution than used in our study.

It should be considered that, even though our study included stations within the MPA that had not been trawled for 5 yr, stations with pristine conditions were not represented. We could not find any trend in the macrofauna community indicating recovery within the closed area, possibly due to the short period of time since the MPA was established and the lack of compliance by the fleet during the first 2 yr following enforcement of the MPA. Taking a longer historical perspective, the trawl fishery in the Kattegat was likely more widespread when the fishery targeted cod *Gadus morhua* before quotas were severely enforced around the year 2000. However, no reliable VMS data coupled to logbooks are available before 2005 to support this statement. Also, the Kattegat is a eutrophic coastal sea area that had recurrent problems with oxygen deficiency mainly in the 1980s, which resulted in large areas with high mortality of benthic invertebrates (Rosenberg & Loo 1988, Baden et al. 1990). The large number of stations sampled, however, allows historical comparisons to the macrofauna community sampled in the early 1900s. Around this time, when industrial trawling started, Petersen (1913) made extensive quantitative benthic macrofauna mapping of the Kattegat that showed differences between, but also large similarities with, the assemblages observed today, e.g. large areas dominated by the brittle stars *Amphiura* spp. Pearson et al. (1985) re-assessed Petersen's stations in the Kattegat and found generally higher abundances and biomass, and that *A. filiformis* had increased in dominance at over 70% of the stations compared. Also, in the early 1900s, a large area in the south-eastern Kattegat was dominated by amphipods, i.e. the *Haploops* community which has not been found again in the area following revisits (Göransson 1999). Only 15 specimens of *Haploops* spp. were noted in 4 of our samples within the historical main distribution area of these species. In contrast, Petersen (1913) reported 1000s of individuals per m^2 at the beginning of the century. Several other species were described to be associated with Petersen's *Haploops* community, including the brittle star *Ophiura*

robusta, the clams *Pseudamussium peslutrae* and *Limea loscombi*, the ostracod *Philomedes brenda*, the bivalves *Nuculana pernula* and *N. minuta* and the brittle stars *O. albida* and *Ophiosten affinis* (Petersen 1913, Göransson 2002, Göransson et al. 2010). Several of these species were noted at a few stations in our study but in comparably low numbers, and the species *O. robusta*, *P. peslutrae* and *L. loscombi* were not found at all in the investigated area. Oxygen deficiency and bottom trawling have been proposed as possible explanations for the disappearance of *Haploops* and the shift in species assemblages (Göransson 1999). Interestingly, in a study from the southern hemisphere in New Zealand, a similar shift in macrofaunal assemblages has been described (Handley et al. 2014). In that study, amphipods, ostracods and bivalves numerically dominated soft-mud communities within a relatively pristine untrawled protected area, while nearby trawled comparable mud habitats were dominated by burrowing brittle stars (*Amphiura* sp.) and polychaetes. In summary, our results confirm the disappearance of dense *Haploops*-dominated communities in the Kattegat and support that bottom trawling contributes to the shift towards brittle star-dominated communities since the 2 *Amphiura* species were tolerant to bottom trawling, and *A. chiajei* increased in abundance at low to medium trawling intensities.

The 2 *Amphiura* species dominate in abundance and biomass over large areas in the Kattegat, Skagerrak and the North Sea, with localized maxima of >1000 ind. m^{-2} (Duineveld & Van Noort 1986, Gogina et al. 2016). Given that this distribution coincides with areas fished extensively by bottom trawls (Eigaard et al. 2017, this study), it is evident that these 2 species are resilient to trawling. Characteristic traits for these brittle stars are that they have planktonic larvae with great dispersal capability, they burrow with their disc ca. 5 cm in the sediment with their arms protruding above the sediment surface, and they frequently autotomize their arms, or even discs in *A. filiformis*, as a response to attacks from predators (Sköld et al. 1994). Their arm regeneration potential is great but differs considerably between the 2 species in that *A. filiformis* can regenerate an arm about 5 times faster than *A. chiajei* (Sköld & Gunnarsson 1996). Both species are deposit feeders, and *A. filiformis* is also a facultative suspension feeder (Loo et al. 1996, Solan & Kennedy 2002). Populations are often stable and are comprised of adults, and longevity has been estimated to more than 20 yr (O'Connor et al. 1983). The frequency of sub-lethal predation can be assessed by counting

scars on the arms of brittle stars (Aronson 1989), and differences have been documented between species and among trawled versus untrawled areas, with a lower incidence of scars on *A. filiformis* in trawled areas in the Skagerrak–Kattegat (Sköld & Rosenberg 1996). Mechanical damage of ophiuroid arms by trawling has not been investigated; however, storms do not appear to cause arm damage in brittlestar populations on tropical reefs, and predation is considered to be the prime source of arm injuries (Aronson 1991). Important predators of *Amphiura* spp. are demersal fish species and crustaceans, e.g. haddock *Melanogrammus aeglefinus*, dab *Limanda limanda*, American plaice *Hippoglossoides platessoides*, plaice *Pleuronectes platessa* and *Nephrops* (Duineveld & Van Noort 1986, Baden et al. 1990, Mattson 1992, Pihl 1994, Kaiser & Ramsey 1997, Hiddink et al. 2016). Fishing effort is intense and stable in the fishing grounds examined, and targeted as well as bycatches of the above listed predators are significant (Hornborg et al. 2017). In addition, some of these predators are stationary, in particular *N. norvegicus* in its adult stages. We thus conclude that reduced predation pressure due to local depletion of these predators at fished stations may be an important mechanism behind the increase in *A. chiajei* along the trawling intensity gradient. The examination of the trend over time within the closed area supports this conclusion, as the dominating species, i.e. both *Amphiura* species, indicate a decrease over time which could be due to increased abundance of fish and *Nephrops* following cessation of the fishery and subsequent increased local predation pressure.

Several indirect effects of mobile bottom fishing gears on fish have been documented (Collie et al. 2017). Studies from the Irish sea (Hiddink et al. 2011, Johnson et al. 2015) and the Kattegat (Hiddink et al. 2016) at soft-seafloor otter trawl fishing grounds link the chronic trawling effects to the condition of predators and explain the results as responses to the ratio of prey to predator biomass and dietary shifts. Our study emphasizes the complex interplay between predators, their benthic prey and the interaction with bottom trawling. *Amphiura* spp. have their arms protruding above the sediment surface when feeding, and arms are frequently preyed on by fish and *Nephrops*. As these heavily fished predators are locally removed by trawling, the release from predation causes populations of *Amphiura* spp. to grow. That is, if predators are more strongly affected than their prey by bottom trawling, prey may increase with bottom trawling until trawling becomes so intense that the prey is also affected.

CONCLUSIONS

Our results show shifts in the macrofauna assemblage and a decrease in the number of species and indices of diversity at low to medium trawling intensities. The dominant brittle stars *Amphiura filiformis* and *A. chiajei* are evidently resistant to trawling at low to intermediate intensities, and *A. chiajei* showed a positive response to increasing trawling intensity, possibly as a result of reduced predation by demersal fish and the target species *Nephrops norvegicus*. Furthermore, this study contributes to our understanding of how chronic bottom trawling contributes to the documented historical shifts in benthic macrofauna assemblages of soft seafloors by reducing diversity and benefitting resistant species like brittle stars. The Kattegat is representative of similar soft-seafloor coastal and shelf areas exploited by bottom otter trawl fisheries for fish and crustaceans. The large MPA provides a unique potential for further studies of recovery of the benthic fauna following the cessation of bottom trawling.

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