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Abstract: Chronic impact studies of bottom trawling aiming to reveal long term effects on benthic organisms are often hampered by the lack of comparable untrawled conditions and the difficulty to assess the spatial distribution of trawling intensity. We sampled soft sediment macrofauna over a precise trawling gradient in the Kattegat using hourly vessel monitoring systems and logbooks. The gradient accounted for the establishment of a marine protected area where trawling intensity declined sharply. Our results show shifts in the macrofauna assemblage and non-linear responses with decrease in number of species and diversity from low to medium trawling intensities. The benthic community was dominated by burrowing brittle stars, and one of the species *Amphiura chiajei* increased in abundance from low to medium trawling intensities. We interpret the positive response to increasing trawling intensities as a consequence of reduction in predation by benthivorous flatfish and *Nephrops norvegicus* that 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 benthivor 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

INTRODUCTION

Bottom trawls are designed to catch fish and shellfish that live on and close to the seabed and are therefore by design in contact with the seabed. As a result, bottom trawling can lead to disturbance of benthic habitats, and 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). Sensitivity 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 three-dimensional structures make up a significant component of the habitats (Fosså et al. 2002, Greathead et al. 2007, Jørgenssen 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 impact 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 in e.g. Collie et al. 2000, Løkkeborg 2005, Kaiser et al. 2006). The variation in outcomes of studies may relate to variations in fishing pressures as well 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. 2016a). Likewise, benthic communities are patchy due to the spatial heterogeneity of factors structuring the communities such as the sediment composition, depth, hydrodynamic regime and food availability (e.g. Rosenberg and 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 periodically are fished intensively, while other areas are fished in low intensities or not at all (Eigaard et al. 2016b, ICES 2016). These large spatial and temporal differences occur both on the wide scale between and within sea areas and on much finer scales of about 100 meters. 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 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 X 1 nm or larger (e.g. Hiddink et al. 2006, Reiss et al. 2009, Eigaard et al. 2016b, ICES 2016, Pommer et al. 2016). 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 have assessed the trawling intensity on 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 hypothesize that benthic macrofauna will be influenced by trawling intensity and evaluate 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 to the sites where the sampling was carried out. The stratification took into account the establishment of a marine protected area (MPA) where bottom trawling was stopped to ensure as far as possible the inclusion of comparable untrawled conditions. We also study the effect on the macrofauna following the enforcement of the MPA, and hypothesize that temporal changes in the assemblage within the MPA will deviate from changes outside the MPA where trawling continues.

MATERIAL AND METHODS

Study area

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 from the Baltic Sea by low saline surface waters creates a typical estuarine circulation pattern and strongly stratified water masses separated by a halocline that persists all year round at around 15 m depth but may extend down to 20 m (Granéli 1992). The outflow from the Baltic, 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 Skagerrak and the North Sea is more stable and marine conditions prevail with salinity conditions usually above 32 PSU (Andersson and 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 today dominated by brittle stars of the *Amphiura*-community (Gogina et al. 2016), but especially the south-eastern part was earlier dominated by amphipods of the *Haploops* community (Petersen 1913).

Fishing by bottom trawling in the Kattegat has been ongoing since early 1900 and target gadoid fish and flatfish in the south-eastern part of the Kattegat mainly using otter trawls (Bartolino et al. 2012). Off cod spawning season, and today all year round, the fishery is dominated by otter trawling targeting Norway lobster *Nephrops norvegicus* or *Nephrops* and a mixture of fish, mainly plaice *Pleuronectes platessa*, sole *Solea solea* and cod *Gadus morhua* (Hornborg et al. 2016). Denmark has the largest share (67%) of the Total Allowable Catch (TAC) of *Nephrops*, Sweden has the second largest share (31%), while Germany has the smallest share of demersal fish and *Nephrops* (ICES 2015).

In 2009 a large (653 km^2) marine protected area, (MPA), was closed for all fishing activities in the southeast Kattegat to protect spawning grounds for cod *G. morhua*. The MPA was one of the core spawning areas that was fished by otter trawls historically for about 100 years targeting aggregated cod during spawning season and *Nephrops* and mixture of fish the rest of the year (Vitale et al. 2008). Some illegal fishing activities was documented the first year after establishment of the MPA but seem 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 250m around the location benthic macrofauna were sampled. The method of using the Euclidian radial distance to a sampling station and interpolated trawl tracks has been shown to be consistent and accurate when compared to true distributions of trawl tracks for otter trawls (Lambert et al. 2012). The 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 in Eigaard et al. (2016a). VMS covers hourly updated GPS positions for vessels of 15 m length and larger over the period 2006 - 2011, and all vessels of 12 m length and larger 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 minutes' 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. 2016a). 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 months prior to the sampling date. The time scale of accumulating trawling over 32 months was chosen to achieve a wide gradient (0 – 15 yr^{-1}) of the bottom trawl history, accumulate the index to cover more than one 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 the analyses.

Benthic macrofauna sampling

Sampling of benthic macrofauna was carried out in May - June in 2009, 2010, 2011 and 2014 using a modified Smith-McIntyre grab (0.1 m^2) at 58 stations (Fig. 1). One sample was taken per station and sieved (1.0 mm mesh size) for macrofauna. Sediment properties mapped by Hallberg et al. (2010) was inspected by eye and fingers 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.

All statistical analyses on biomass were tested without large bodied species, i.e. the heart urchins *Brissopsis lyrifera* and *Echinocardium cordatum*, and the ocean quahog *Arctica islandica* that due to their individual weight in some samples may strongly influence 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 = 5.60, $df_1 = 3$, $df_2 = 228$, p = 0.0034). Removing these species thus improved the statistical results by reducing heterogeneity of biomass.

A total of 29864 specimens belonging to 261 different taxa of benthic fauna were present in the samples.

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 was established inside and outside the MPA with the aim to cover a wide gradient in bottom trawling intensity (Fig. 1). The sampled stations were situated to cover the habitat and depths explored by the dominant demersal bottom trawl fisheries, and 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 expect 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 sampling station categorised into statistical quartiles ($<=0.4$, >0.4 $<=2.1$, >2.5 $<=4.6$, >4.6 yr^{-1}) as fixed factor. The categorisation was done to simplify interpretation of the results since two more factors was 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 a random factor nested in trawling intensity. Community composition were weighted both by abundance and biomass of species. Resemblance matrices were constructed using Bray-Curtis similarity and abundance and biomass data was fourth root transformed to reduce the influence of dominant species. Posthoc comparisons were done using pairwise PERMANOVA, and results were visualized with Canonical Analysis of Principal Coordinates (CAP). All data was evaluated for 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 and Göransson 2009, Pommer et al. 2016, Leonardsson 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 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 was 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 to model non-linear relationships without prior knowledge on their actual shape. The effect of trawling was tested by applying GAM on the following univariate response variables: number of species *Nspp*, total abundance *Nind*, total biomass *Biom*, abundance of the two dominant species *Amphiura filiform*is and *Amphiura chiajei*, Richness index *d* (Margalef 1958), Shannon diversity $H'(\log_2)$ (Shannon & Weaver 1949) and 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 model (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 one index. All the 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 performed accordingly. The models were formulated as follows:

$$Response_{(y,\rho,\varphi)} \sim \alpha_y + s\left(D_{(\rho,\varphi)}\right) + s\left(TI_{(y,\rho,\varphi)}\right) + s\left(Nind_{(y,\rho,\varphi)}\right) + \gamma_{(\rho,\varphi)} + e_{(y,\rho,\varphi)}$$

where α is the year specific intercept, s is a one-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 and Ripley 2002, Dormann et al. 2007), which was treated as a random effect (Pinheiro and Bates 2000), and a normally distributed error term (e). The total abundance (*Nind*) was included as a predictor only for the model using *Nspp* as a response variable to account for changes in the detection probability of new species as abundance increases. Model overfitting was controlled by constraining to 3 the maximum degrees of freedom on the depth variable. Inspection of models' residuals revealed no major departure from the model assumptions of normality and homogeneity of variance. The GAM models were fitted using R and the library *mgcv* (Wood 2011).

Effects of reduction in trawling intensity by the establishment of the marine protected area

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 continues. No benthic sampling was carried out prior to the establishment of the MPA in 2009. However, we assume that the macrofauna community status of 2009 sampled five months after the enforcement of the MPA can be considered as a reasonable baseline since the impact of previous years bottom trawling was likely to remain longer (i.e. > 1.9 years) for macrofauna (Hiddink et al. 2017).

Samples were collected at the same stations in 2009, 2010, 2011 and 2014. Stations sampled within the MPA prior to the establishment in 2009 and outside over all the years, 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 by the establishment of the MPA in 2009 was seen over time. However, trawling intensity was not reduced to zero at all stations inside the MPA indicating some noncompliance or misclassification of vessels on transit at slow speed (Fig. S2).

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 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 two most dominant species (*Amphiura filiformis* and *Amphiura chiajei*), and univariate total abundance, total biomass and number of species. As significant effects were detected for the dominant species these were as well 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 Welsch'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 range (median 2.1 yr^{-1}). The ranges and distributions of trawling intensity verified the stratification of the design and were stable over the four years sampled with the exception of the anticipated decrease at the 7 stations protected due to the establishment of the MPA from 2009 (Fig. S1 and S2, 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 two factors (p = 0.0749; Fig. 2). Pairwise comparisons of trawling intensity effect showed that the effect of trawling intensity categories differed between the overlapping two lower quartiles and the two highest overlapping quartiles. Similar statistical results as for abundance 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 two factors: p = 0.1045). Pairwise comparisons of trawling intensity categories again showed that the effect of trawling intensities differed between the overlapping two lower quartiles and the two highest overlapping quartiles (for details on statistics, see Supplement tables S1 on macrofauna abundance and table S2 on biomass). The multivariate PERMANOVA analysis thus 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 the gradient in trawling intensity, depth together with trawling intensity were evaluated as continuous predictors of community composition by Distance based Linear modelling (DistLM) and Distance based redundancy analysis (dbRDA). Since the year factor did not show interaction with trawling intensity in the foregoing PERMANOVA analysis, 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 Akaike’s Information Criterion with second order correction (AICc) both predictors were identified and explained together 7.4 % of the variation in the community composition. The Distance based redundancy analysis (dbRDA) visualise how the stations with differing trawling intensity and depth relates to the multivariate dbRDA axes 1 and 2 (Fig. 3). Trawling intensity correlated with dbRDA 1 (multiple partial correlation 0.52) that explained 6.4 % of the total variation and to dbRDA 2 (0.85) that explained 0.9 % of the total variation. Depth also correlated with both dbRDA 1 (multiple partial correlation 0.85) and dbRDA 2 (0.52). The testing procedure above was also done using biomass of species as dependent variable which showed the similar effects (log X+1 trawling intensity F=9.5, p = 0001 and square root depth F = 14.5, p = 0.0001) and correlations to the dbRDA axis 1 and 2 (multiple partial correlation 0.52 and 0.86 respectively) and overall contribution to the total variation 6.1 and 1 %. Depth also correlated with both dbRDA 1 (multiple partial correlation 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 abundance and trawling intensity showed agreement with the species that decreased along the axis for 58 % of the species that had the negative trends e.g. *Ampelisca tenuicornis* and *Phoronis muelleri*. For the species increasing 31 % showed conformity with the positive trend along e.g. *Amphiura chiajei* and *Labidoplax buskii* (Table 1).

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 (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 approx. 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 all the models 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 model of the number of species has a R^2 value of 0.34. In the other models the 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 *Amphiura filiformis* and *Amphiura chiajei*. Together these two species represented 50 % in 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 two species presented an opposite response to depth below 40 m, with *A. chiajei* increasing in deeper waters while *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 intensities and decreased only for trawling intensity levels above 5 yr^{-1}.

Effects of reduction in trawling intensity by the establishment of the marine protected area

To evaluate the potential recovery of the macrofauna within the MPA we hypothesized that the temporal development of the macrofauna within the MPA deviate from the area outside where trawling continued. Multivariate PERMANOVA tests of abundance and biomass and univariate tests with PERMANOVA number of species (Fig. 6a), total abundance (Fig. 6b) and total biomass (Fig. 6c) showed no interactions between the year and treatment (Table S3). However, abundance of the dominating species (*A. chiajei* and *A. filiformis*) showed a significant interaction between the factors treatment and year (Table S4 and 5). 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), however, 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, taking the establishment of a marine protected area (MPA) into account to ensure as far as possible 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 increases from low to medium levels i.e. below 5 yr^{-1}. Several taxa had a negative trend along the gradient of increasing trawling intensity while a few taxa increased. The dominant brittle star species showed different responses as *Amphiura chiajei* increased at low to medium trawling intensities and decreased only at trawling intensity above 5 yr^{-1}, while *Amphiura filiformis* showed no conclusive response. Effects along the trawling intensity gradient were non-linear and in general more evident at the lower range. 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, and 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 intensity to detect effects by bottom trawling on the benthic macrofauna. In another similar study of otter trawl disturbance at *N. norvegicus* soft sediment fishing 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 low ranges and untrawled comparable conditions in the MPA. The species decreasing with trawling intensity show some commonalities between the two studies for the following taxa: the Phoronida *Phoronis* sp., crustacean amphipods of the genus *Ampelisca* and the polychaete *Magelona alleni*, however, also contradicting results in that the dominating brittle star *A. filiformis* appears tolerant to bottom trawling in our study while 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 affected and depleted already at low trawling intensities, and the benthic fauna left 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 is evident mainly at the lower range of trawling intensity.

However, our results differ from other studies (e.g. Hiddink et al. 2006, Hintz et al. 2009, Reiss et al. 2009, Hiddink et al. 2011, Johnson et al. 2015) in that we could not detect any shifts in total biomass. A possible explanation to this difference might be that in our study, one of the two dominant species *A. chiajei* increased along the trawling intensity gradient which may then mask the decrease in other less common species negatively affected. Reiss et al. (2009) in their study of beam trawling impact on macrofauna communities 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 penetrate the seafloor deeper than otter trawling (Eigaard et al. 2016), which might explain the different responses between our study and others where beam trawling is common (e.g. Hiddink et al. 2006, Reiss et al. 2009). However, all these other studies analysed the effect of trawling intensity using much coarser spatial resolutions (approximately 1 X 1 nm 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 the nations fishing in the area i.e. Sweden and Denmark, and was thus able to reconstruct with high precision the daily bottom trawling intensity at each station sampled for benthic macrofauna from 2006 to 2014. The VMS derived effort is considered to be an underestimate since vessels smaller than 15 m was not included in the gradient. However, we consider the gradient established 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 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 indicate only a decrease over time for the dominating brittle star species. Non-compliance during the two first year after enforcement of the MPA is evident as the VMS indicate rather high activity. This might explain the lacking 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 to capture and be able to ascertain the low-end part 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 by bottom trawling acting on macrofaunal assemblages, 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 by 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 resolution of 2 km by 2 km to 4 km by 4 km which represents a 20 - 80 times coarser cell resolutions than this study.

It should to be considered that even though our study included stations within the MPA that had not been trawled for 5 years, 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 two years 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 enforeced around year 2000. However, no reliable VMS data coupled to logbooks is available before 2005 to support this statement. Also, the Kattegat is a eutrophicated coastal sea area that had recurrent problems of oxygen deficiency mainly in the 1980's which resulted in large areas with mortality of benthic invertebrates (Rosenberg & Loo, 1988, Baden et al. 1990). The large number of stations sampled, however, allows historical comparison of the macrofauna community sampled in the early 1900's. Around this time, when industrial trawling started, Petersen (1913) made extensive quantitative benthic macrofauna mapping of the Kattegat that showed differences 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 beginning of the 1900's, 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 four of our samples within the historical main distribution area of these species. Petersen (1913), in contrast reported thousands of individuals per m^{-2} at the beginning of the century. Several other species were described to be associated to Petersens *Haploops* community, including the brittle star *Ophiura robusta*, the clams *Pseudamussium peslutrae* and *Limea loscombi*, the ostracod *Philomedes brenda*, the bivalves *Nuculana pernula* and *Nuculana minuta* and the brittle stars *Ophiura albida* and *Ophiocten affinis* (Petersen 1913, Göransson 2002, Göransson et al. 2010). Several of these species were noted at a few stations in our study between 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 has been put forward as possible explanations to the disappearance of *Haploops* and shift in species assemblages (Göransson 1999). Interestingly, in a study from the southern hemisphere in New Zealand, a similar shift in macrofaunal assemblages have 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 supports that bottom trawling contribute to the shift towards brittle star dominated communities since the two *Amphiura* species were tolerant to bottom trawling, and that *A. chiajei* increased in abundance at low to medium trawling intensities.

The *Amphiura* species dominate abundance and biomass over large areas in the Kattegat, Skagerrak and the North Sea with localized maxima of >1000 ind. m^{-2} (Duineveld et al. 1986, Gogina et al. 2016). Given that this distribution coincides with areas fished extensively by bottom trawls (Eigaard et al. 2016b, and this study), it is evident that these two species are resilient to trawling. Characteristic traits for these brittle stars are that they have planktonic larvae with great dispersal capability, are burrowed with their disc ca 5 cm in the sediments with their arms protruding above the sediment surface, and 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 differ considerably between the two species in that *A. filiformis* 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, comprised of adults and longevity has been estimated to more than 20 years (O'Connor et al. 1983). The frequency of sub-lethal predation can be assessed by counting scars on arms of brittle stars (Aronson 1989), and differences have been documented between species and among trawled versus untrawled areas, with lower incidence of scars of *A. filiformis* in trawled areas in the Skagerrak – Kattegat (Sköld & Rosenberg 1996). Mechanical damage of ophiuroid arms by trawling have 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 Norway lobster *Nephrops norvegicus* (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 by-catches of the above listed predators are significant (Hornborg et al. 2016). 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 one important mechanism behind the increase of *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 accordingly increased local predation pressure.

Several indirect effects of bottom fishing on fish and vice versa have been documented (Collie et al. 2016), and 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, *Amphiura* spp. being released from predation causes its population 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.

Conclusion

Our results show shifts in the macrofauna assemblage and a decrease in number of species and indices of diversity at low to medium trawling intensities. The dominant brittle stars *A.*

filiformis and *A. chiajei* are evidently resistant to trawling at low to intermediate intensities and *A. chiajei* showed positive response to increasing trawling intensity possibly caused by reduction in predation by demersal fish and the target species *N. norvegicus*. Furthermore, the study contributes to the understanding of how chronic bottom trawling contribute 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 for 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 cessation of bottom trawling.

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Figures and tables

Table 1. Linear trends of individual species abundance in relation to ordination along axis dbRDA 1 that best contributed to the total variation (6.4 %) and correlate with Trawling intensity (0.52). Correlations between species abundance and trawling intensity are given within brackets. Only significant correlations with the dbRDA axis 1 are shown i.e., Pearson correlation coefficient R > = 0.14, df = 252, p < 0.05.

Species decreasing with trawling intensity and axis dbRDA 1	R		Species increasing with trawling intensity and axis dbRDA 1	R	
Ampelisca tenuicornis	-0.41	(-0.24)	*Amphiura chiajei*	0.50	(0.30)
Phoronis muelleri	-0.38	(-0.20)	*Ophiocten affinis*	0.26	(0.05)
Rhodine gracilior	-0.37	(-0.22)	*Labidoplax buskii*	0.25	(0.18)
Mysella bidentata	-0.34	(-0.21)	*Lipobranchius jeffreysii*	0.22	(0.13)
Nephtys hombergii	-0.33	(-0.19)	*Philomedes brenda*	0.22	(0.02)
Turritella communis	-0.29	(-0.17)	*Abyssoninoe hibernica*	0.22	(0.25)
Prionospio fallax	-0.29	(-0.25)	*Nuculana pernula*	0.21	(0.05)
Mysia undata	-0.28	(-0.16)	*Brada villosa*	0.21	(0.09)
Scoloplos armiger	-0.28	(-0.23)	*Ophiodromus flexuosus*	0.21	(0.23)
Praxillella praetermissa	-0.27	(-0.05)	*Panthalis oerstedi*	0.19	(0.10)
Pholoe baltica	-0.26	(-0.19)	*Leucon nasica*	0.18	(0.00)
Eudorella truncatula	-0.25	(-0.21)	*Photis longicaudata*	0.16	(0.00)

Aoridae	-0.25	(-0.17)	*Hyala vitrea*	0.15	(0.07)
Amphiura filiformis	-0.25	(-0.11)			
Chamelea striatula	-0.24	(-0.17)			
Trichobranchus roseus	-0.24	(-0.05)			
Pectinaria auricoma	-0.23	(-0.10)			
Nucula nitidosa	-0.21	(-0.14)			
Scalibregma inflatum	-0.21	(-0.11)			
Edwardsia spp.	-0.20	(-0.21)			
Terebellides stroemi	-0.20	(0.09)			
Sphaerodorum flavum	-0.19	(-0.11)			
Ampelisca brevicornis	-0.19	(-0.16)			
Dosinia lupines	-0.19	(-0.17)			
Abra nitida	-0.19	(0.09)			
Corbula gibba	-0.19	(0.00)			
Harpinia antennaria	-0.19	(-0.16)			
Notomastus latericeus	-0.17	(-0.11)			
Levinsenia gracilis	-0.17	(-0.01)			
Bela brachystoma	-0.17	(-0.14)			
Anobothrus gracilis	-0.17	(-0.09)			
Cylichna cylindracea	-0.17	(0.02)			
Spiophanes bombyx	-0.16	(-0.15)			

Gari fervensis	-0.16 (-0.11)
Magelona alleni	-0.16 (-0.15)
Chone fauveli	-0.15 (-0.12)
Spio filicornis	-0.14 (-0.16)
Arctica islandica	-0.14 (-0.20)
Virgularia mirabilis	-0.14 (-0.13)
Westwoodilla caecula	-0.14 (-0.05)

Table 2. Summary statistics of GAM of number of species (*Nspp*), total abundance (*Nind*), biomass (*Biom*), Richness according to Margalef (*d*), diversity according to Shannon (*H'*), Benthic Quality Index (BQI), and for the dominating *Amphiura* species by abundance. Equivalent degrees of freedom, is reported for the non-parametric predictors depth (D), trawling intensity (TI) and total abundance (Nind) and statistical significance (* $P < 0.05$, ** $P < 0.01$) for all terms. The family distribution adopted for each model and the R^2 are included.

Response	Predictor variable				R^2	Family
	a Year	s(D)	s(TI)	s(Nind)		
Nspp	**	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
Amphiura chiajei		1.95**	2.64**		0.283	Poisson
Amphiura filiformis		1.91**	1.00		0.132	Poisson

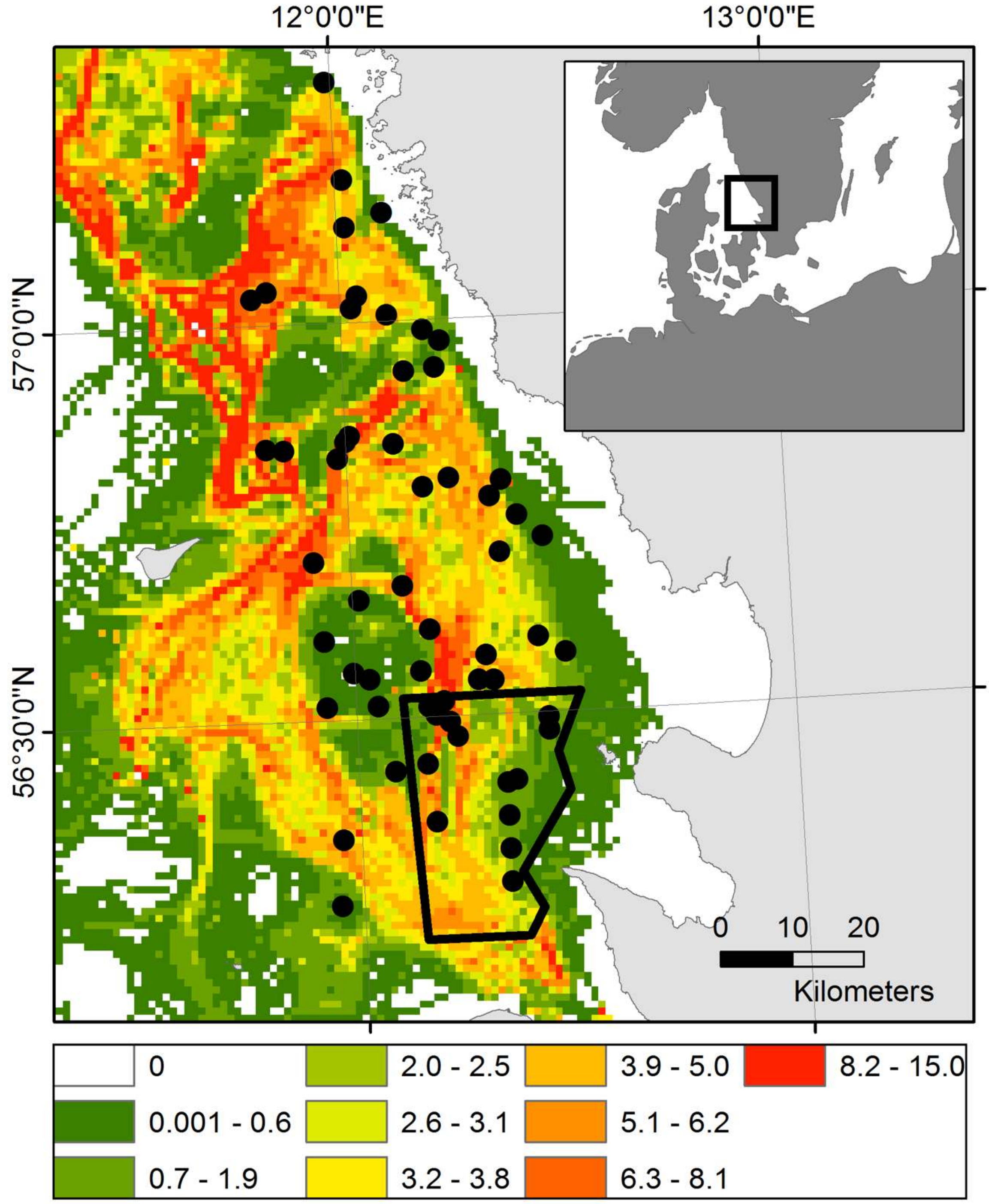
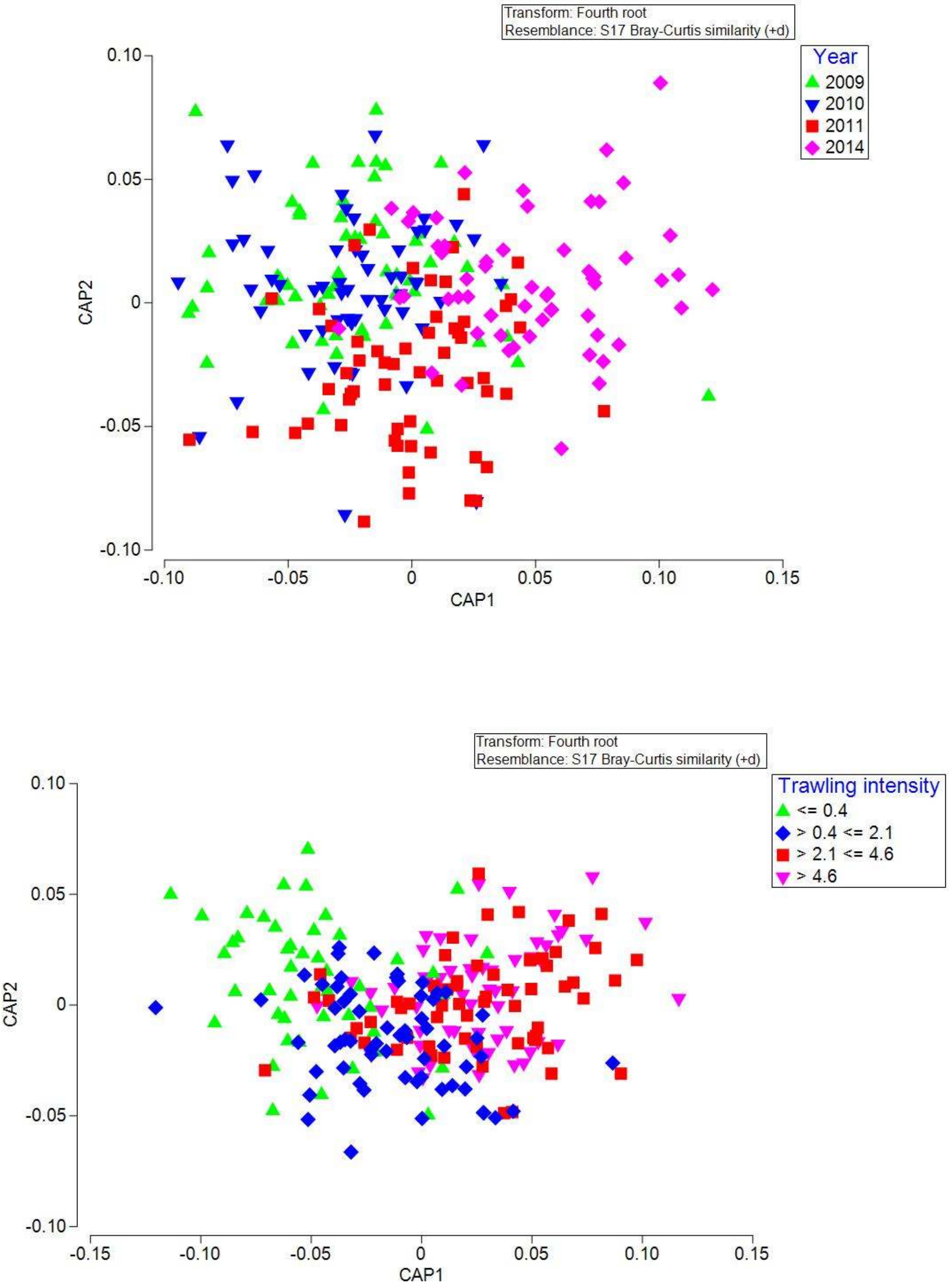


Fig. 1. Map of the study area in Kattegat. Colours indicate yearly averaged trawling intensity averaged per year for 2006-2008, i.e. the period before the MPA was established in 2009. Trawling intensity is estimated from Danish and Swedish VMS and logbook data of bottom trawl fleets as the total area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



a.

b.

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.

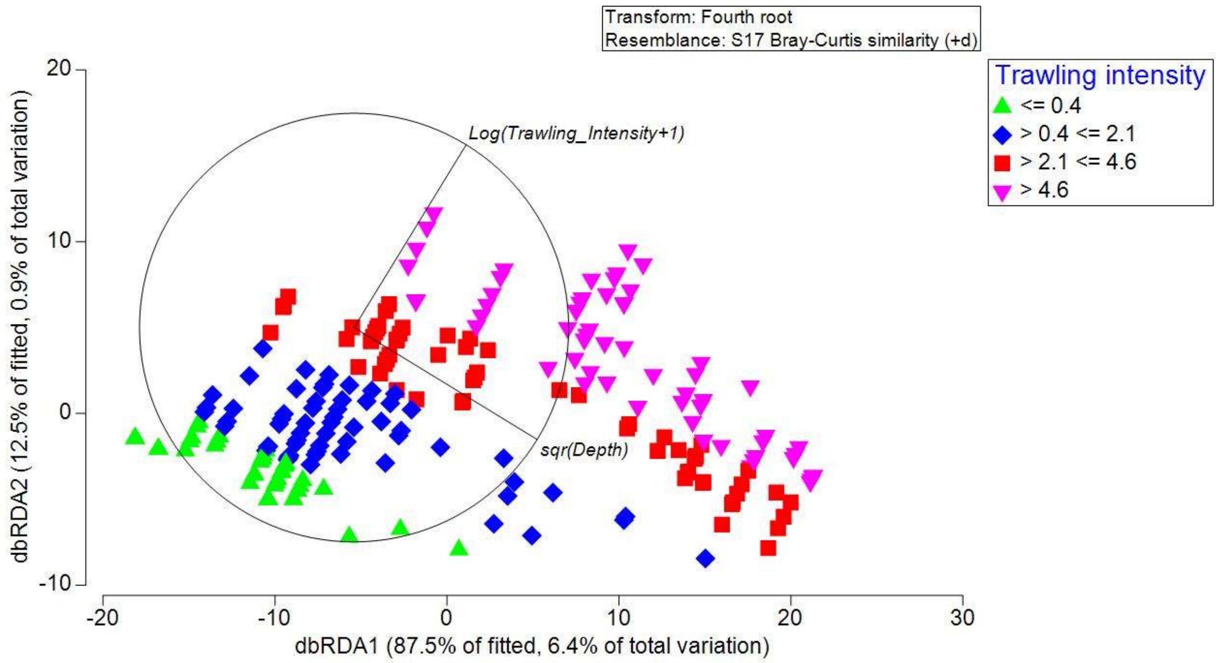


Fig. 3. Distance based redundancy analysis (dbRDA)ordination of the fitted model of the macrofaunal community composition. The gradient in trawling intensity grouped into quartiles is illustrated by the sampling stations colour according to the legend and vectors of the predictors trawling intensity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

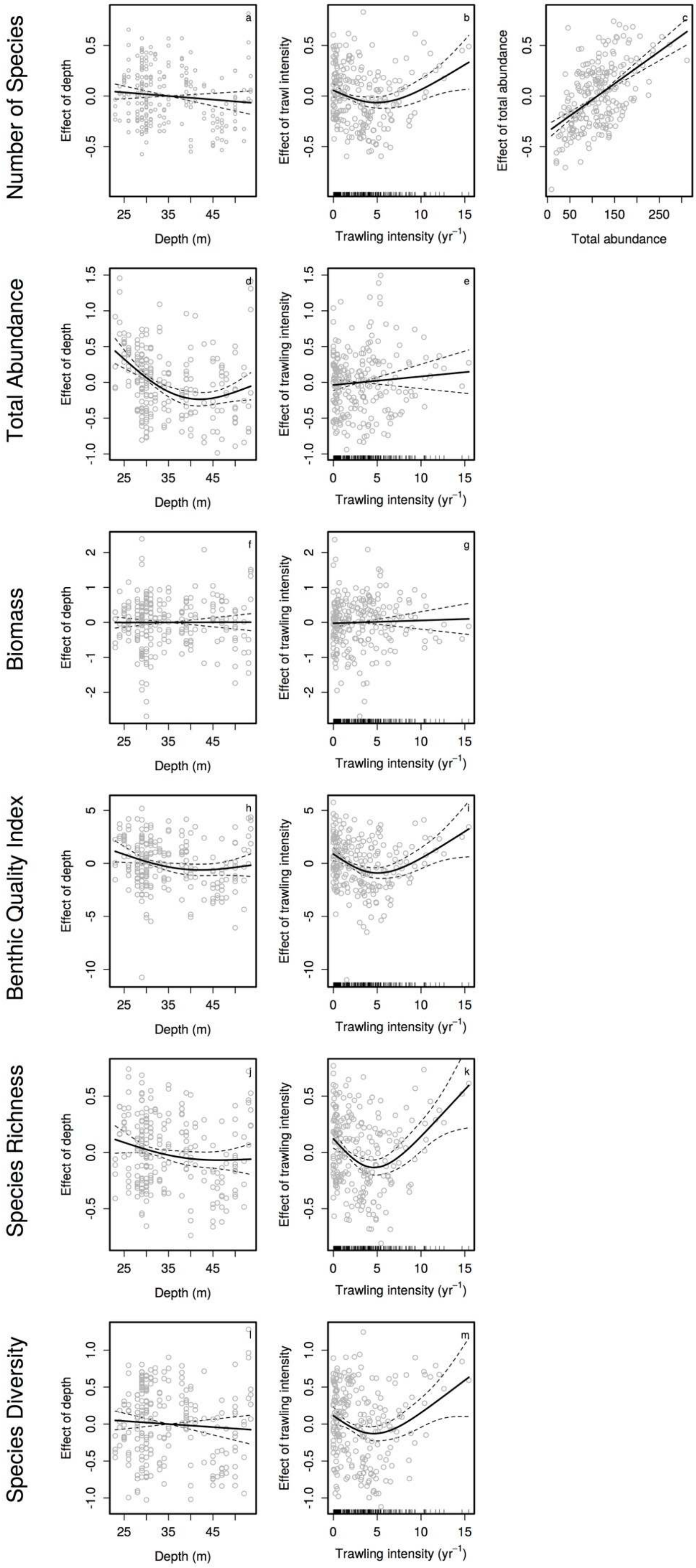

Number of Species
Total Abundance
Biomass
Benthic Quality Index
Species Richness
Species Diversity
a
b
c
d
e
f
g
h
i
j
k
l
m
Effect of depth
Effect of trawl intensity
Effect of total abundance
Effect of trawling intensity
Depth (m)
Trawling intensity (yr^{-1})
Total abundance
25
35
45
0
5
10
15
50
150
250
-0.5
0.0
0.5
1.0
1.5
-1.0
-2
-1
2
-10
-5

Fig. 4. Effect of different predictors on the number of species *Nspp* (a-c), total abundance *Nind* (d-e), biomass (f-g), Benthic Quality Index (*BQI*, h-i*)* Richness according to Margalef (*d*, j-k), diversity according to Shannon (*H'*, l-m) as estimated from GAMs with 95% confidence interval (dotted lines) and partial residuals (grey dots).

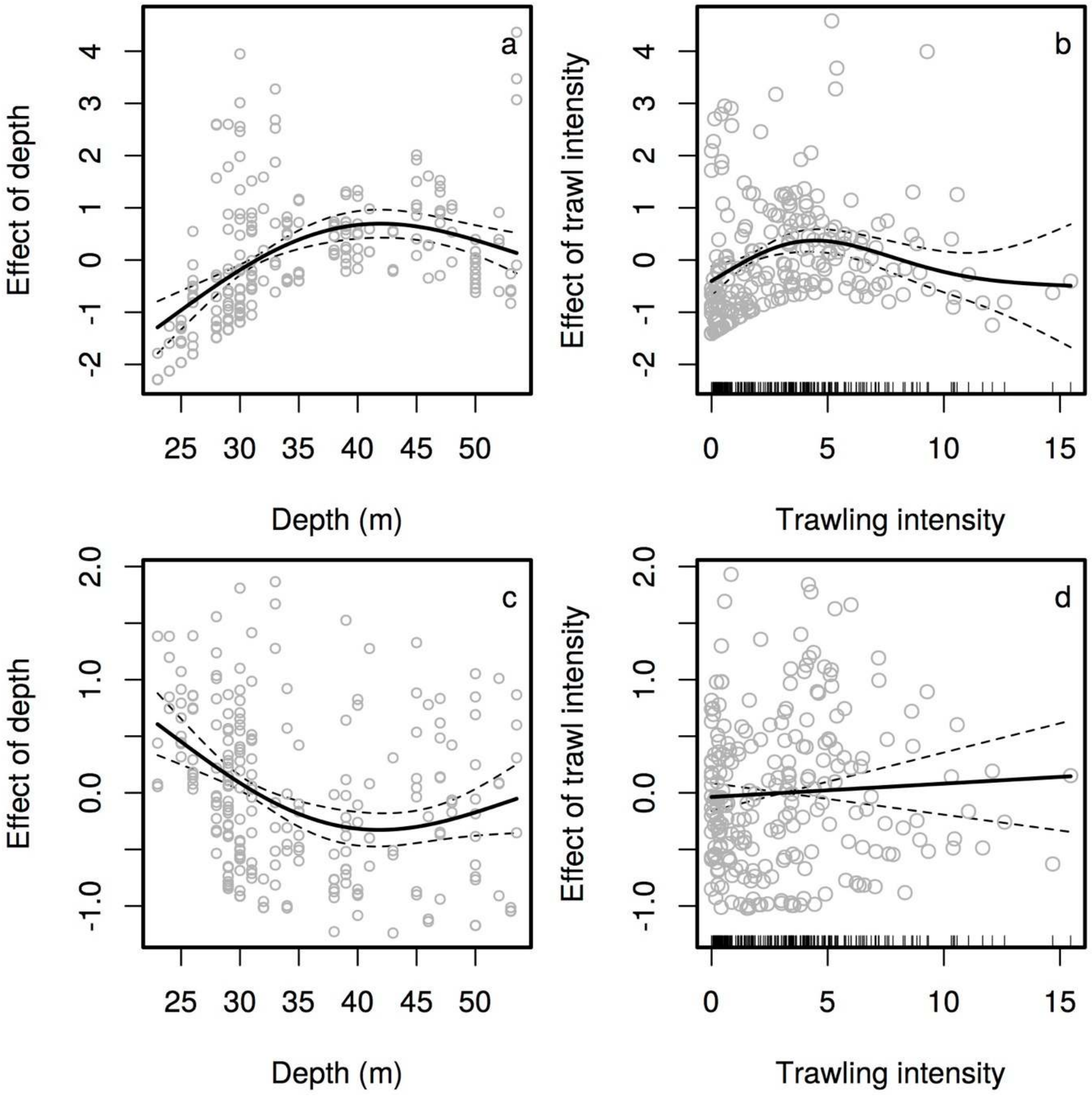
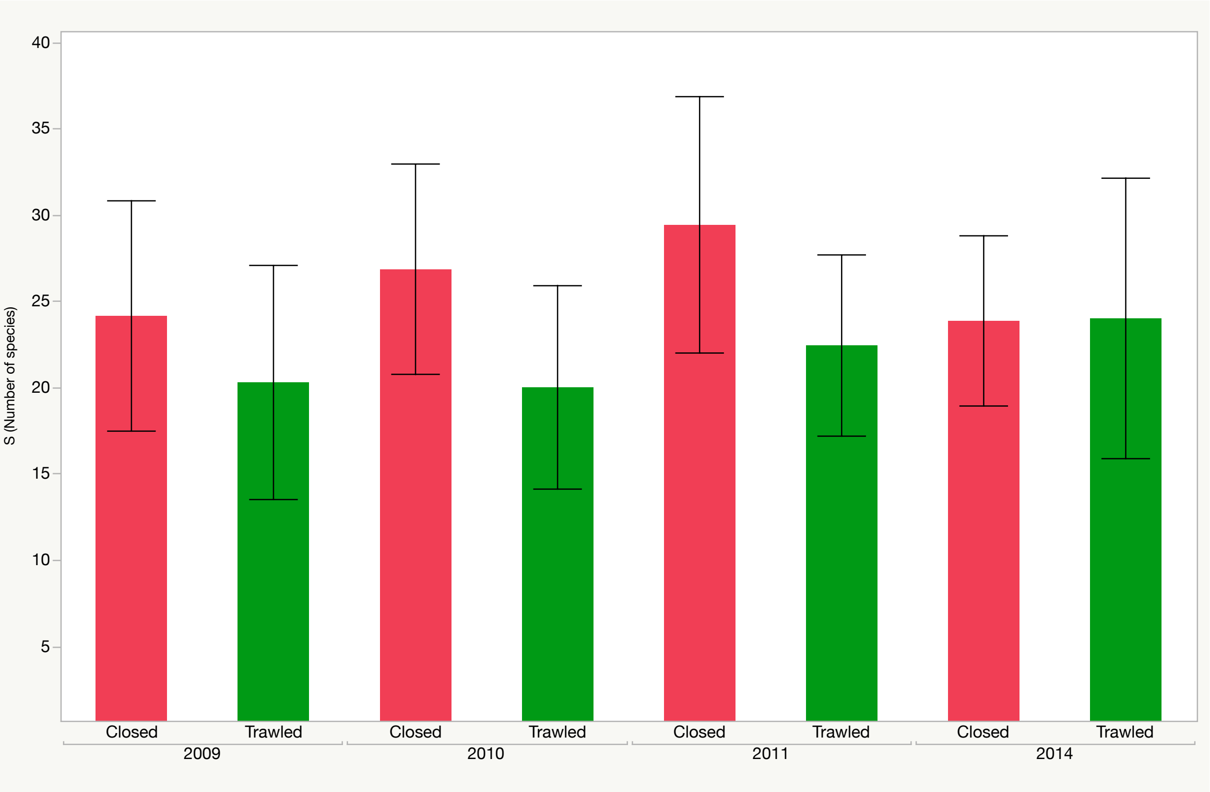


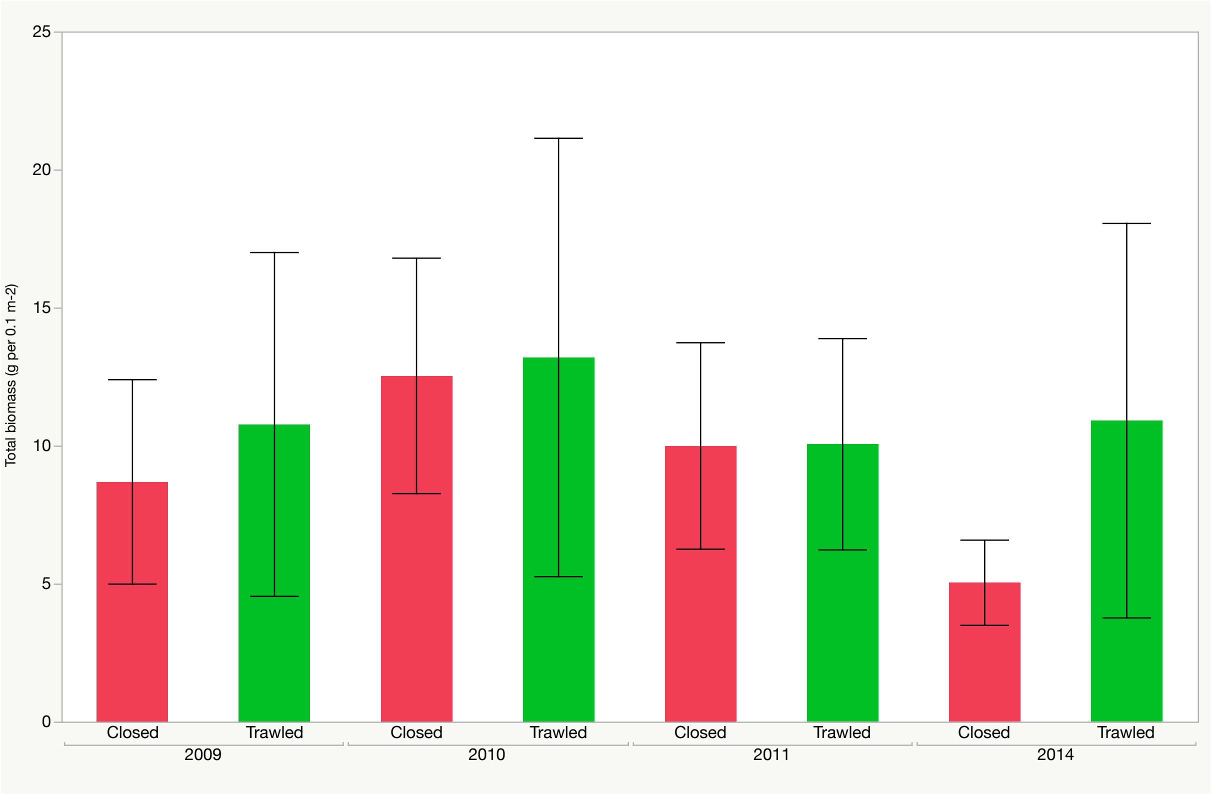
Fig. 5. Effect of different predictors on abundance of *Amphiura chiajei* (a-b) and *Amphiura filiformis* (c-d) as estimated from GAMs with 95% confidence interval (dotted lines) and partial residuals (grey dots).


S (Number of species)
40
35
30
25
20
15
10
5
Closed
Trawled
Closed
Trawled
Closed
Trawled
Closed
Trawled
2009
2010
2011
2014

a)


Total abundance (individuals per 0.1 m-2)
250
200
150
100
50
0
Closed
Trawled
Closed
Trawled
Closed
Trawled
Closed
Trawled
2009
2010
2011
2014

b)



c)

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

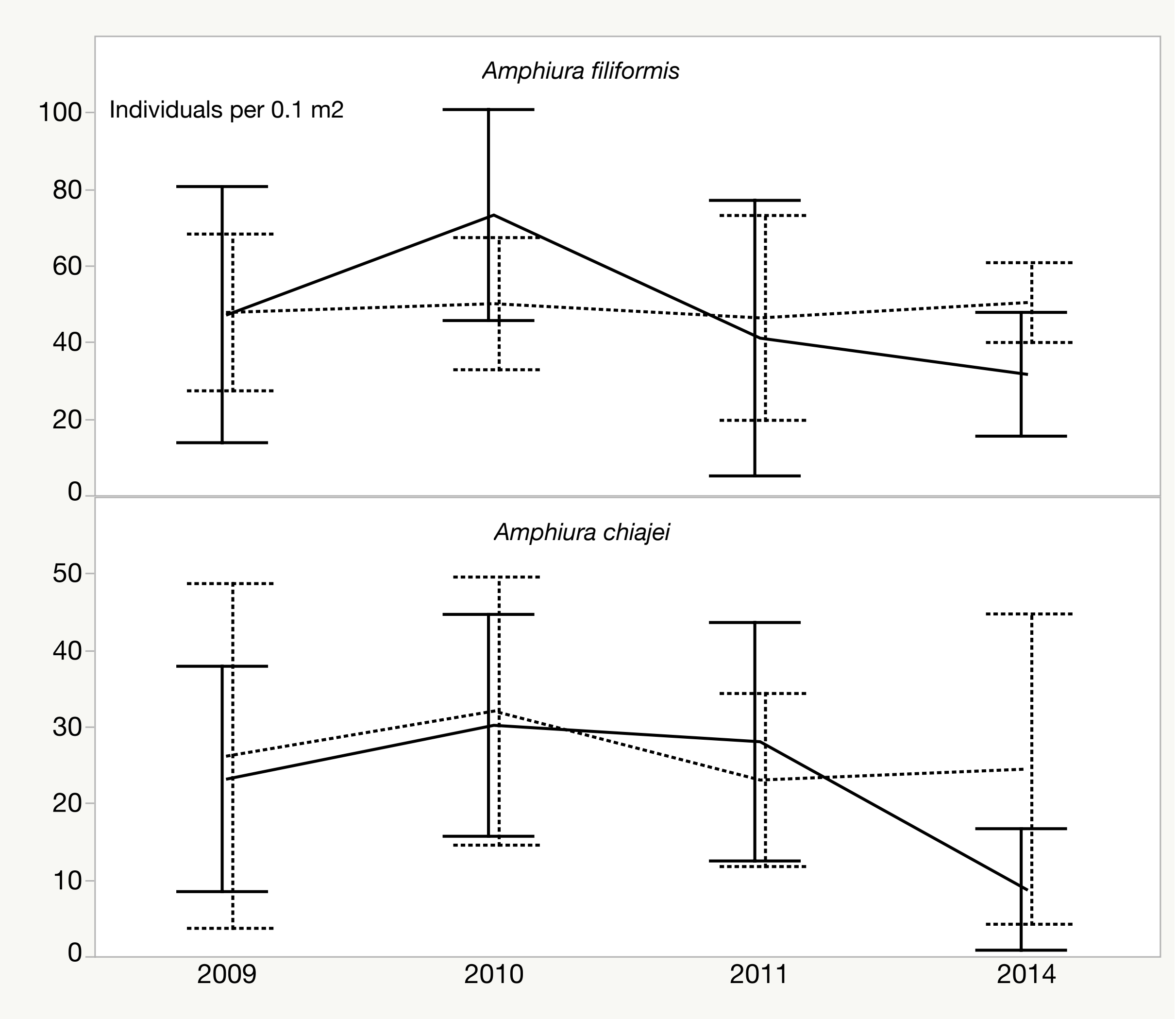


Fig. 7. Abundance of *Amphiura filiformis* (upper panel) and *Amphiura chiajei* (lower panel) across years in the closed MPA (solid line, n=7) and continuously trawled area (dotted line, n=7). Error bars are standard deviation of the mean