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CONTRIBUTED PAPER

Long-term recovery and food web response of benthic macrofauna following cessation of bottom trawling in a marine protected area

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Abstract

The understanding of the depletion of species and communities and recovery following the reduction of pressures is fundamental in conservation biology. The impact of bottom trawl fisheries on benthic communities has been well studied, but there are few studies of the long-term recovery after the cessation of bottom trawling. Here we followed the recovery of the benthic macrofaunal community over 12 years in a large (426 km^2) no-take zone (NTZ) area in the south Kattegat after demersal trawling was stopped and compared it to a nearby area where trawling continued. Using multivariate analyses, we found shifts in the community composition. Two species of burrowing brittle stars, *Amphiura filiformis* and *Amphiura chiajei*, dominated abundance and biomass and decreased in the closed area (abundance effect size *A. filiformis* 48%; *A. chiajei* 45%). In parallel, there was an increase in benthivore flatfish. Stomach contents of the dominating flatfishes matched the availability of benthic prey taxa, and brittle stars were the staple food. Food web effects thus appear to override the decrease in mortality of the dominant macrofauna caused by the cessation of trawling in the NTZ. The recovery response in the species community in the NTZ correlated with the pattern in community composition along a chronic bottom trawling intensity gradient in the same area. This indicates that the recovery of the benthic community is not random but follows a successional pattern that can also be observed in chronic states of disturbance from bottom trawling. This is important information from the perspective of management efforts to restore marine ecosystems from the impact of bottom trawl fisheries, as it indicates that reduced effort may lead to predictable recovery.

KEYWORDS
benthic habitats, bottom trawling, cod, echinoderm, no-take zone, physical disturbance, stomach content

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1 | INTRODUCTION

The understanding of the depletion of species and communities due to disturbance and recovery following reduction of pressures is fundamental in conservation and restoration biology. Pressures on ecosystems are often multiple, and the response of organisms and communities is the cumulative result of mortality, recruitment, migration, and dispersal acting on organisms on different temporal and spatial scales. The release from pressures leads to the recovery of species and communities, and processes may follow a directional pattern, that is, succession, as more mature communities of species are established (Pearson & Rosenberg, 1978). However, restoration efforts of degraded communities may also produce inconsistent and unexpected results due to strong feedback between the physical environment and biotic factors (Suding et al., 2004).

Bottom trawling is a disturbance that selectively affects species within the benthic community due to their sensitivity to the reworking of the substrate and mortality induced by the gear, and that species are caught and removed (Kaiser et al., 2006). Theoretical studies have also incorporated food web effects to show how benthic communities are shaped by the interaction of the removal of fish and the removal of benthos due to bottom trawling (van Denderen et al., 2015; van de Wolfshaar et al., 2020). There are also studies indicating that invertebrate species targeted by fisheries benefit from the reduction of fish predators in bottom trawl fisheries (see review by Collie et al., 2016).

Fishing grounds that are repeatedly worked can be chronically disturbed and in transitional stages of succession. Such cases of fishing grounds with identified gradients in bottom trawling intensity have been used to study the impacts of bottom trawling (see reviews by Hiddink et al., 2017; Sciberras et al., 2018). Gradient studies have the advantage of being able to deliver results that are realistic, as important scale-dependent processes like dispersal and immigration will be included, and the results likely mirror the sum of depletion and recovery from disturbance (Hiddink et al., 2017). However, gradient studies are correlative observations, and other environmental factors shaping communities may vary along gradients, limiting the possibility to disentangle the effects of different factors. Experimental long-term studies of depletion or recovery from perturbations allow for hypothesis testing and can account for environmental variation. However, such control versus impact studies of depletion or recovery from bottom trawling are rare at realistic scales of large fishing grounds where trawling has been introduced in pristine areas or where trawled areas have been protected.

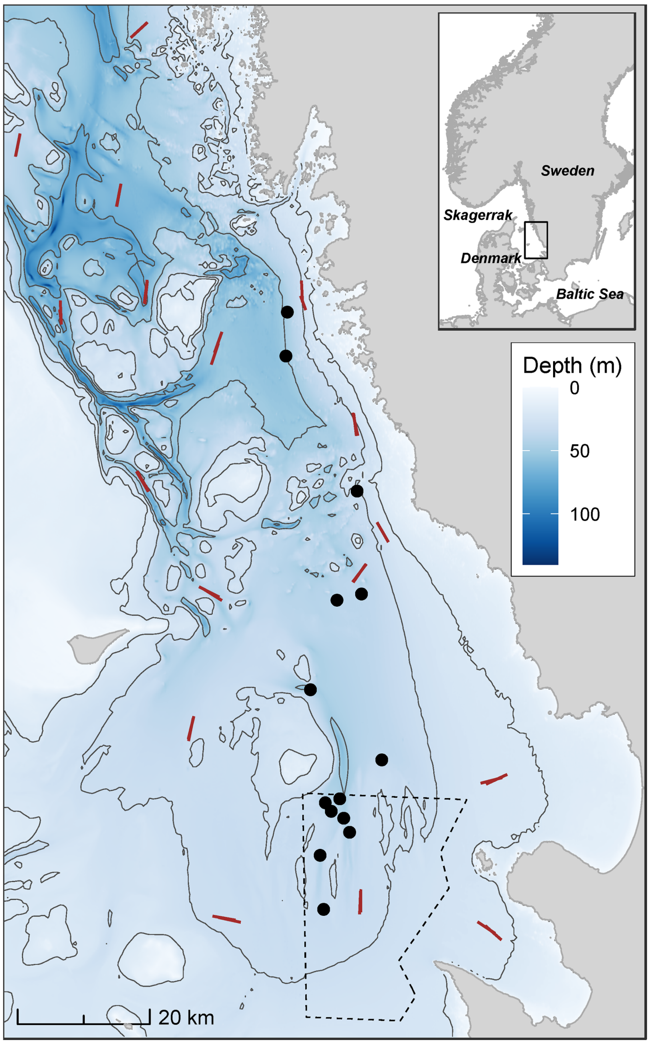

FIGURE 1 Map of the benthic macrofauna stations (black circles) sampled within and outside the NTZ (black dotted line), red lines show trawl hauls used for stomach content analysis. Depths from EMODnet Bathymetry (emodnet.ec.europa.eu/en/bathymetry) with 20, 30, 50, and 70 m depth contours.

Sweden and Denmark established a large (426 km^2) no-take zone (NTZ) in the temperate sea Kattegat in 2009. The background for the regulations was that the cod *Gadus morhua* stock in the Kattegat had been overfished, with the spawning stock biomass being alarmingly low for several years (Cardinale & Svedäng, 2004; ICES, 2023; Sköld et al., 2022). This No-take zone therefore provides unique possibilities to study the recovery of soft sediment benthic fauna from an intense bottom trawl fishery.

The aim of this study is to evaluate the long-term recovery of benthic macrofauna following the enforcement of the Kattegat NTZ, using multi- and univariate approaches. We also use a previous study on the fish community and additional stomach content sampling of benthivore fish to assess the effects in the food web.

2 | MATERIALS AND METHODS

2.1 | Study area

The Kattegat is a shallow sea area (average depth 27 m) connected to the Baltic Sea via narrow straits in the south and to the North Sea in the north (Figure 1). Surface waters have low salinity from the freshwater-diluted Baltic Sea, creating a typical estuarine circulation pattern with stratified water masses separated by a halocline (Granéli, 1992). The marine water from the North Sea beneath the halocline has more stable marine conditions, with salinities usually above 32 PSU (Andersson & Rydberg, 1988). Surface tide and tidal currents are low, but deeper parts of the Kattegat channels may be swept with currents up to 35 cm s^{-1}, keeping the channels well oxygenated (Matthews et al., 1999). Seafloor habitats vary considerably, with shallow areas and offshore banks consisting of rocks, gravel, or sandy sediments, while the deeper areas are comprised of mixed sand, silt, and mud sediments (Hallberg et al., 2010).

The history of the fishery in the Kattegat is long, and industrial steam trawlers operated offshore as early as the 1900s (Bartolino et al., 2012). Today, the main fishery is demersal otter trawling, catching a mixture of fish and crustaceans, mainly plaice *Pleuronectes platessa*, sole *Solea solea*, cod *Gadus morhua*, and Norway lobster *Nephrops norvegicus* (ICES, 2022). The NTZ (Figure 1) covers parts of the cod spawning areas and was, before the closure, fished by otter trawlers targeting aggregated cod during the spawning season, and a mixture of *N. norvegicus* and demersal fish the rest of the year (Hornborg et al., 2016; Vitale et al., 2008).

2.2 | Benthic macrofauna

Macrofauna were sampled using a modified Smith–McIntyre grab (0.1 m^2) and sieved on a 1 mm sieve at 14 stations, 7 inside and 7 outside the NTZ where trawling continued, in May to early June in the years 2009 (i.e., the first year of enforcement of the NTZ), 2010, 2011, 2014, 2017, 2018, and 2020 (Figure 1). The seven replicate stations outside the NTZ are hereafter named "Trawled reference". With few exceptions, all taxa were identified to species level and were counted and weighed. Biomass was converted from wet weight to ash-free dry weight (AFDW) using conversion factors from Brey et al. (2010) and Gogina et al. (2022). Only AFDW was used as biomass values in the analyses.

2.3 | Benthivore fish

Benthivore fish biomass data was extracted from the joint Swedish and Danish survey for cod in the Kattegat for the same years as benthos was sampled (2009, 2010, 2011, 2014, 2017, 2018, and 2020) (Sköld et al., 2022). The survey is based on a stratified random design with 80 hauls distributed within a survey grid of 5 × 5 NM. The survey gear is a bottom trawl (door spread 70 m, wing spread 17 m, length 34 m) with 70 mm diamond mesh in the cod-end.

Fish for stomach content analysis was sampled during the International Bottom Trawl Survey (IBTS) in August 2020 in Kattegat (17 hauls, Figure 1) covering the same area as sampled for macrofauna using a standardized scientific GOV bottom trawl and protocols. For more details, see ICES, 2019 and the survey protocol by Bland and Börjesson (2020). The depth range of the trawl hauls was between 23 and 73 m. Three species of common benthivore flatfish were sampled: dab *Limanda limanda* ($n = 420$), long rough dab (a.k.a. American plaice) *Hippoglossoides platessoides* ($n = 306$), and plaice *Pleuronectes platessa* ($n = 217$). When available from the catch, stomachs were collected to represent the full size spectrum, that is, each 1 cm length class of fish length per trawl haul, and frozen immediately. From these specimens, stomachs were removed and frozen for later analysis. Fish showing signs of regurgitation, such as remains of prey in the mouth, were detected onboard and excluded. Analysis of prey in the stomachs was performed by the National Marine Fisheries Research Institute in Gdynia, Poland. Prey organisms were identified to the lowest taxonomic level possible, and the total weight of the prey taxa was noted per individual fish. Prey were later grouped into the following taxonomical groups that made up 75%–100% of the stomach content in the fish and size classes studied: Bivalvia, Decapoda, Ophiuroidea, Pisces, and Polychaeta.

2.4 | Experimental set-up and statistics

The experimental set-up for evaluating the effect of establishing the NTZ was to monitor the response by the macrofauna over time and compare that to similar areas where the fishery continues. The temporal development of the macrofauna community was evaluated in a stepwise procedure using PERMANOVA+ for PRIMER V7 (Anderson et al., 2008) and the effect of the closure was assessed through the interaction between the year of sampling and treatment. Dependent variables examined were taxa abundance or biomass. Results were further examined with canonical analysis of principal coordinates (CAP).

To analyze if the outcome of the CAP analysis could be related to patterns in community composition along a trawling intensity gradient in the same area (Sköld et al., 2018) we made a simple correlation between the correlation coefficients (r) for contributing taxa to the CAP analysis and the corresponding r for taxa to the distance-based redundancy analysis (dbRDA) composition along the trawl gradient (table 1 in Sköld et al., 2018).

The temporal development of abundance, biomass, and of the dominant brittle stars *Amphiura filiformis* and *Amphiura chiajei* was examined using a mixed model ANOVA.

To test if there was a correlation between the dominating benthivore flatfish and the dominating food, that is, brittle stars, the yearly benthivore fish biomass was tested against the brittle star biomass using a one-sided Pearson correlation, assuming a negative effect due to predation.

For more details on the experimental set-up and statistics, see Appendix S1.

3 | RESULTS

The premise for the evaluation of the NTZ is that changes in the macrofauna community composition over time within the NTZ deviate from changes in the Trawled reference area. We analyzed this in a stepwise procedure, and significant differences were found for the interaction term Treatment × Year using both macrofauna community abundance (pseudo $F_{6,\,72} = 1.46$, $p = .0016$) and biomass (pseudo $F_{6,\,72} = 1.36$, $p = .0103$) as dependent variables. In the second step, comparisons using pairwise PERMANOVA showed, for both abundance and biomass, that the later years (2017, 2018, and 2020) differed from the earlier years (2009–2011) within the NTZ, while fewer and less clear differences occurred between years in the Trawled reference area. The overall multivariate analysis thus indicated more consistent changes over time in species composition within the NTZ. In the third step, we attempted to resolve this shift in community composition over periods using canonical analysis of principal coordinates (CAP). The CAP allowed us to further disentangle how individual taxa correlated to the shift in the macrofauna community along CAP axes shaped by the Treatment × Periods (early 2009–2011 vs. late 2017, 2018, and 2020) interaction. Year 2014 was omitted in the CAP as being intermediate in the time series and did not show significant effects in step 2. The first two canonical correlations were both reasonably large (for abundance CAP 1 = 0.82 and CAP 2 = 0.68, For biomass CAP 1 = 0.83 and CAP 2 = 0.71) and indicated different separations between the periods for the reference and NTZ stations (Figure 2). The species matrix included 162 taxa, of which correlations with $r > 0.4$ or < -0.4 to one or both CAP axes were found for abundance (12 taxa) and biomass (15 taxa), and among these, 8 taxa were common (Table 1).

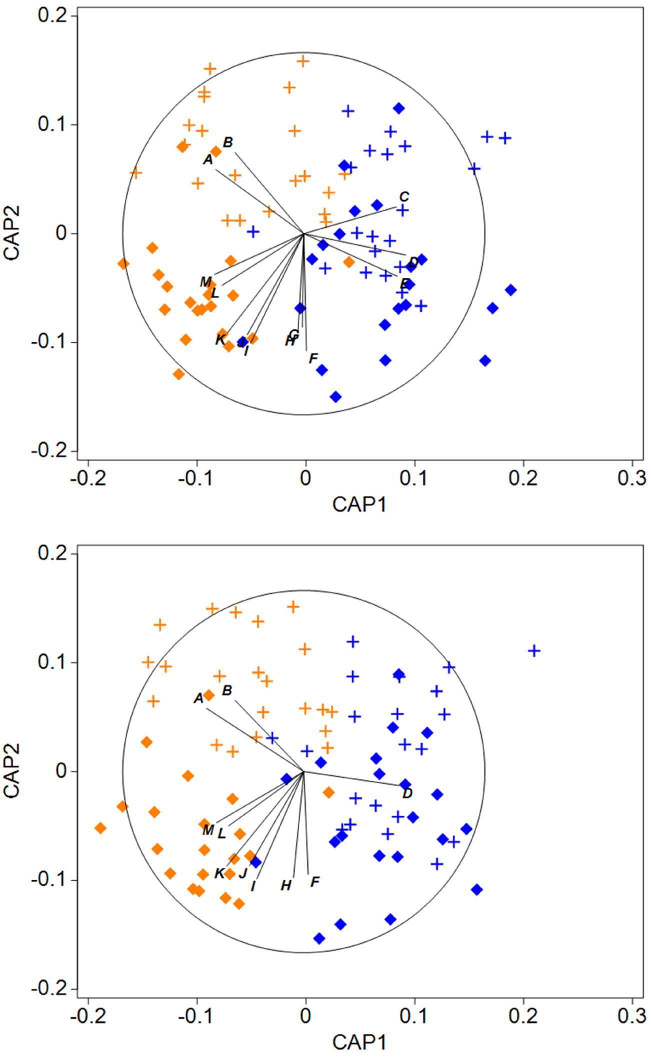

FIGURE 2 Canonical analysis of principal coordinates (CAP) plot for macrofauna community composition of abundance (top) and biomass (bottom) of species by the interaction term Treatment × Periods of sampling. Taxa that correlate with $r > 0.5$ to one or both CAP axes are overlaid on the plot. A = *Maldane sarsi*, B = *Oxydromus flexuosus*, C = *Hyala vitrea*, D = *Eudorella emarginata*, E = *Nucula nitidosa*, F = *Praxillella praetermissa*, G = *Prionospio fallax*, H = *Ampelisca tenuicornis*, I = *Ennucula tenuis*, J = *Phoronis muelleri*, K = *Abra nitida*, L = *Anobothrus gracilis*, M = *Kurtiella bidentata*. See Table 1 for further details.

To explore if the detected recovery pattern in the CAP analysis of species within the NTZ was related to patterns in species composition along a trawling intensity gradient in the same area (Sköld et al., 2018) we made a simple correlation between the r of the CAP analysis for each taxa and the corresponding r of the distance-based redundancy analysis of the gradient. In total, 154 species were common to both datasets. The pattern in the community shift for the interaction term Treatment × Year

TABLE 1 Correlation of species with principal coordinates of canonical analysis (CAP) of the two most explanatory CAP axes in Figure 2.

Benthic fauna NTZ versus trawled reference					
Abundance			**Biomass**		
Taxa	**CAP1**	**CAP2**	**Taxa**	**CAP1**	**CAP2**
Abra nitida	−0.42	−0.55	*Abra nitida*	−0.43	−0.52
Ampelisca tenuicornis	−0.03	−0.55	*Abyssoninoe hibernica*	0.25	0.41
Amphiura chiajei	−0.18	0.41	*Ampelisca tenuicornis*	−0.06	−0.59
Anobothrus gracilis	−0.45	−0.29	*Anobothrus gracilis*	−0.41	−0.30
Ennucula tenuis	−0.29	−0.61	*Ennucula tenuis*	−0.26	−0.59
Kurtiella bidentata	−0.49	−0.23	*Eudorella emarginata*	0.53	−0.08
Maldane sarsi	−0.49	0.35	*Hyala vitrea*	0.44	0.13
Notomastus latericeus	−0.05	−0.42	*Kurtiella bidentata*	−0.48	−0.28
Oxydromus flexuosus	−0.38	0.45	*Maldane sarsi*	−0.54	0.35
Phoronis muelleri	−0.31	−0.56	*Notomastus latericeus*	−0.03	−0.43
Prionospio fallax	−0.01	−0.52	*Nucula nitidosa*	0.42	−0.20
Turritella communis	−0.11	−0.43	*Pholoe pallida*	0.44	0.10
			Phoronis muelleri	−0.30	−0.52
			Polyphysia crassa	−0.11	0.44
			Praxillella praetermissa	0.02	−0.57
			Prionospio fallax	−0.03	−0.49

Note: Species that correlate with $r > 0.4$ or < -0.4 to one or both CAP axes are included.

correlated with the community changes (r from dbRDA) over the gradient in trawling intensity ($r = -0.66$, $p < .001$, Figure 3) using CAP axis 2 and abundance data. No correlation was found between CAP axis 1 and the gradient in trawling intensity.

The two overall dominant species in the NTZ and the trawled reference areas were the brittle stars *A. filiformis* and *A. chiajei*, both in abundance (60%) and biomass (69%). Only 12 out of the 162 taxa in the matrix had average abundances >1, and except for the two *Amphiura* species, all of these had heterogeneous variances, being zero-inflated and did not allow for univariate testing of the interaction term Treatment × Year. For the two *Amphiura* species, the mixed model ANOVA indicated an interaction, with a decrease in abundance of *A. filiformis* within the NTZ over time relative to the Trawled reference, albeit at a significance level of $\alpha = 0.10$ but not for biomass ($F_{6,\ 72} = 2.16$, $p = .057$; Biomass $F_{6,\ 72} = 1.704$, $p = .132$). A similar pattern was shown for *A. chiajei*, with differences for both abundance and biomass with $\alpha = 0.10$ (Abundance $F_{6,\ 72} = 1.96$, $p = .081$; Biomass $F_{6,\ 53} = 2.07$, $p = .073$, Figure 4). Effect sizes in abundance in the NTZ were estimated between early and late periods, that is, 2009–2011 versus 2014–2020, to a reduction of 48% for *A. filiformis* and 45% for *A. chiajei*.

Total abundance and biomass of the macrofauna community mirrored the interactions for the dominating brittle stars and showed a significant interaction between treatment and year in the univariate analyses for abundance ($F_{6,\ 58} = 2.199$, $p = .056$) at a significance level of $\alpha = 0.10$ but not for biomass ($F_{6,\ 55} = 0.282$, $p = .943$). Univariate analysis of total abundance and biomass for the community without the two dominant *Amphiura* species showed no significant interaction (Abundance $F_{6,\ 72} = 1.60$, $p = .158$; Biomass $F_{6,\ 57} = 0.285$, $p = .942$).

Stomach content of the three flatfish species investigated showed a dominance in biomass of ophiuroids in all three species and in all size classes (42%–100% of stomach content). Ophiuroid content was composed of both discs and arms and was not possible to identify to species level due to degradation and separation of arms from the disc body. However, the ophiuroid content was most likely dominated by *Amphiura* spp., since the presence of other species of brittle stars is comparatively low in the area as revealed from the macrofauna samples. Other main taxa contributing to the stomach contents biomass were, in decreasing order of importance, decapods, bivalves, fish, and polychaetes. Larger dab and, in particular, long rough dab had a higher proportion of decapods, mainly swimming crabs (Portunidae) and shrimps (Caridea), and fish (Gobidae and Pleuronectidae) in their stomachs in comparison to plaice, which mainly had ophiuroids, bivalves, and polychaetes in their stomachs (Figure 5).

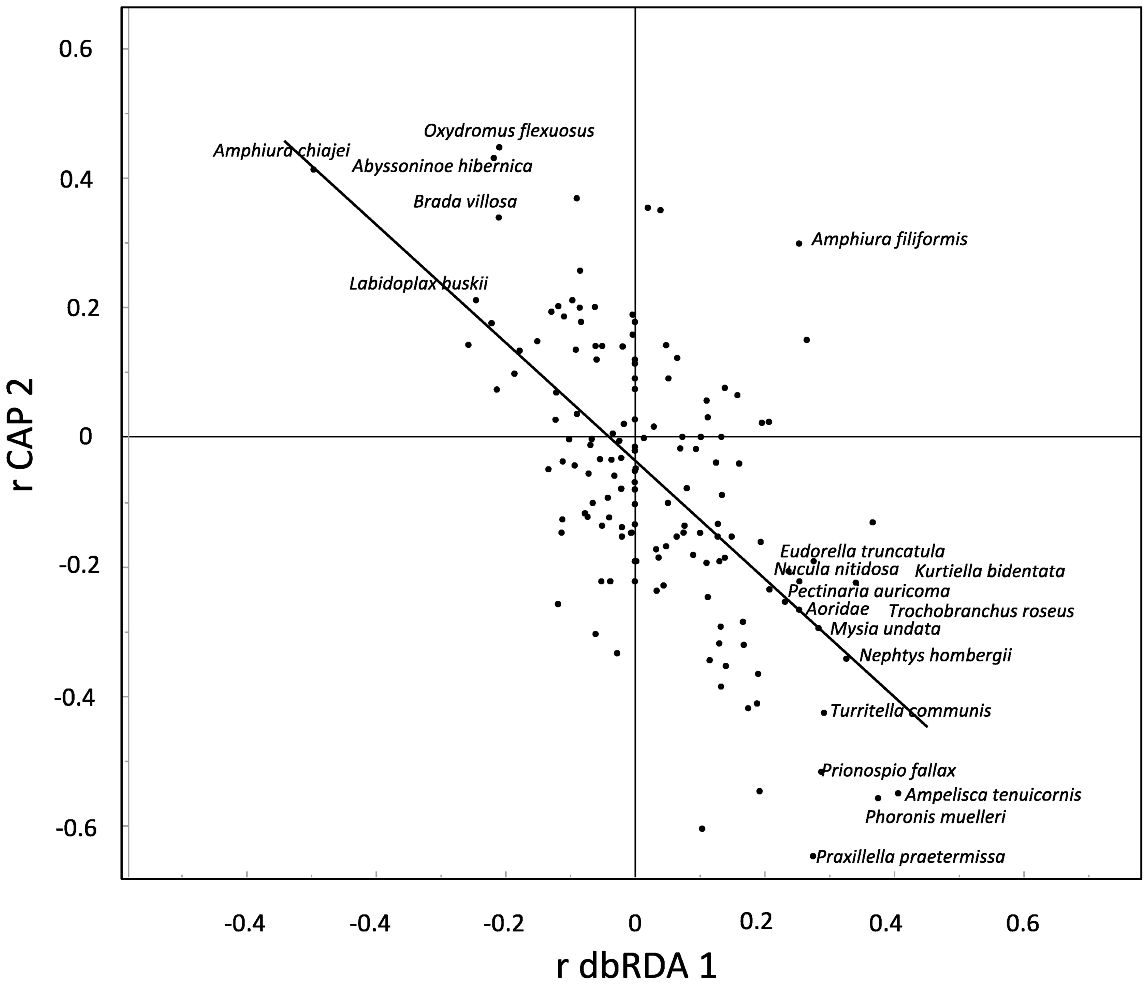

FIGURE 3 Correlation ($r = -0.66$, $p < .001$) between r for species in distance-based redundancy analysis (dbRDA) axis 1 ordination of the fitted model of the macrofaunal community composition (weighted by abundance) responding to the gradient in trawling intensity (x-axis, see Sköld et al., 2018), and r of species in the canonical analysis of principal coordinates (CAP) axis 2, this study. Species with names indicated have r values >0.2 and <−0.2 (both the dbRDA and the CAP axes).

The yearly benthivore fish biomass tested with one-sided Pearson against the brittle star biomass indicated a significant negative correlation ($r = -0.74$, $p = .029$) in the NTZ, but no correlation was observed in the Trawled reference (Figure 6).

4 | DISCUSSION

Our results indicate significant shifts in the macrofauna community within the NTZ over the 12 years following its closure to fishing, suggesting a long-term recovery trend towards a non-trawled state due to the cessation of bottom trawling. Total abundance of the macrofauna community mirrored the interactions for the dominating brittle stars that decreased in the NTZ. However, total biomass of the community showed no significant interaction due to large variability. This corroborates other studies in the Kattegat that total macrofauna biomass is highly variable and may not be a sensitive indicator of bottom trawling, showing no or only slight relationship along gradients of trawling (McLaverty et al., 2020; Sköld et al., 2018). An obvious explanation based on results in our study is also that dominating species may respond to protection from trawling by increasing, thus masking effects of decreasing sensitive taxa.

Food web effects likely explain the decrease in abundance and biomass of the dominating taxa, that is, the burrowing brittle stars in the NTZ, as the increase in benthivore flatfish correlates with the decrease of the brittle stars following closure for fishing within the NTZ. Brittle stars are important organisms in benthic ecosystems, and in particular, burrowing brittle stars of the family Amphiuridae are globally abundant, the most diverse ophiuroid family with 467 described species (Stöhr et al., 2012) and may dominate macrofauna

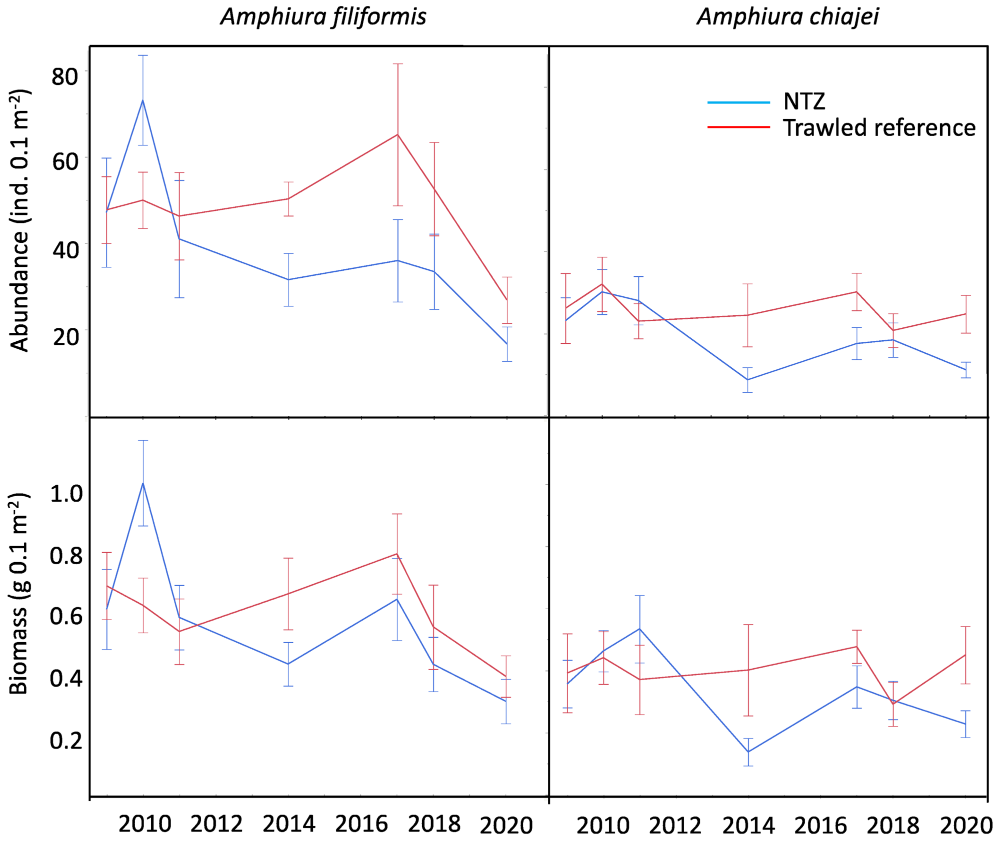

FIGURE 4 Average abundance (top) and ash-free dry weight biomass (bottom) ± standard error of *Amphiura filiformis* (left) and *Amphiura chiajei* (right) in the NTZ (blue line, $n = 7$) and trawled reference (red line, $n = 7$).

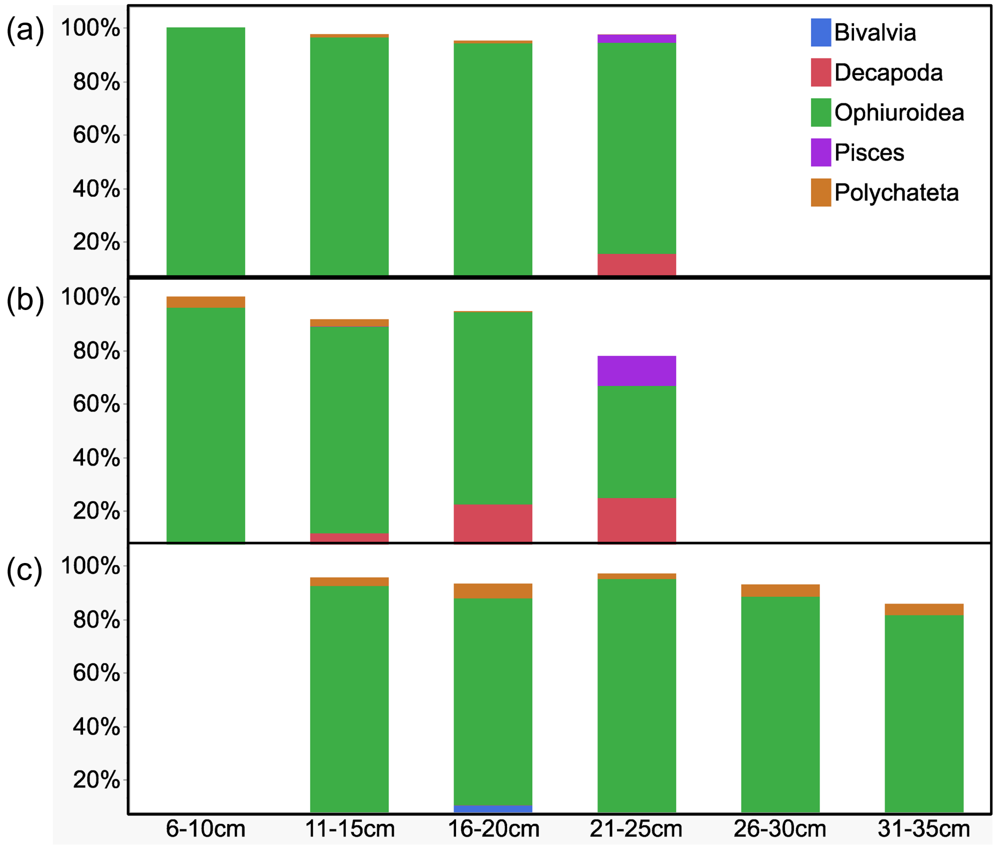

FIGURE 5 Proportion of stomach content by wet weight in 5 cm size classes of (a) dab *Limanda limanda*, (b) long rough dab *Hippoglossoides platessoides* and (c) plaice *Pleuronectes platessa*.

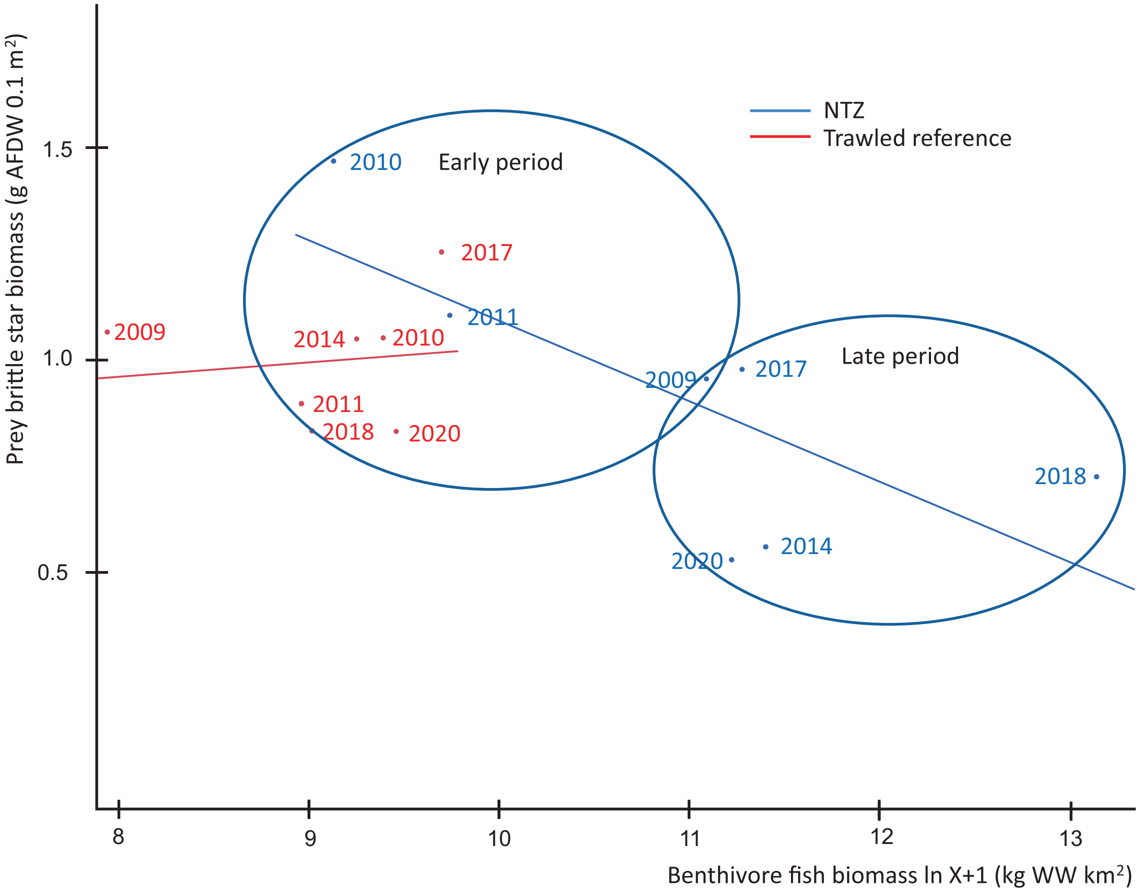

FIGURE 6 Benthivore fish biomass (sum of yearly average biomass of *P. platessa*, *L. limanda* and *H. platessoides*) versus brittle star prey biomass (sum of yearly average biomass of *A. filiformis* and *A. chiajei*) in the NTZ (blue) and the Trawled reference (red). One-sided negative Pearson correlation is significant for the NTZ ($r = -0.74$, $p = .029$).

abundance and biomass in soft seafloors. In the silt-mud bottoms of the Northeast Atlantic, for example, in the North Sea, the Celtic Sea, and the Kattegat, densities may reach >1000 individuals per m^2 (O'Connor et al., 1983; Duineveld & Noort, 1986; this study). The resilience to bottom trawling (Sköld et al., 2018) and the decrease of the brittle stars in the community in this study in response to protection from bottom trawling, are in some aspects contradictory to prevailing conclusions that soft-bottom habitats impacted by bottom trawling have reduced production and biomass (Queiros et al., 2006; Hiddink et al., 2017), that suspension feeders are particularly sensitive (e.g., Tillin et al., 2006; de Juan et al., 2007), and that longevity is a trait that generally is sensitive to bottom trawling (Hiddink et al., 2019). The two brittle stars characteristic for, and dominating, in these communities (Gogina et al., 2016) have long lifespans, up to 25 years (O'Connor et al., 1983) and grow slowly and mature around 4 years of age (Muus, 1981). *A. chiajei* has significantly slower somatic growth than *A. filiformis* (Sköld & Gunnarsson, 1996). Both species deposit feed, but *A. filiformis* is also a facultative suspension feeder, protruding its arms in the water column above the sediment (Buchanan, 1964; Loo et al., 1996). The brittle stars are resistant to trawling and have, in different studies, shown both a positive response along gradients in trawling in the Kattegat or stable densities (McLaverty et al., 2020; Sköld et al., 2018). However, bottom trawl gradient studies have also shown opposing results for *A. filiformis*, and observations from the Irish Sea and the North Sea have indicated this species to be sensitive to trawling (Hinz et al., 2009; Queirós et al., 2006; Tinlin-Mackenzie et al., 2023).

The species *Ampelisca tenuicornis*, *Phoronis muelleri*, and *Kurtiella bidentata* correlated to the CAP analysis and indicated sensitivity by decreasing along the trawl gradient (Figure 3). According to Josefson et al. (2018), small tube-building crustaceans of the genus *Ampelisca* spp. have in recent years been found to a larger extent in shallower untrawled areas in the Kattegat in comparison to the 1880s. *Ampelisca* spp. also decreased along a trawl gradient in the Irish Sea (Hinz et al., 2009). Tube-building phoronids *Phoronis* spp. showed a decrease with bottom trawling both in the Irish Sea and the Kattegat along trawling gradients, and the small bivalve *Kurtiella bidentata* in the Danish Kattegat and the North Sea (Hinz et al., 2009; McLaverty et al., 2020; Tinlin-Mackenzie et al., 2023). A general pattern also identified by Josefson et al. (2018) in the Kattegat was a shallower distribution in recent times of abrasion-sensitive species compared to the 1880s, which they attributed to adverse large-scale effects of bottom trawling in the deeper areas.

Studies on the recovery of benthic fauna from bottom trawl closures are rare using conclusive control–impact comparisons. However, megafaunal production by scallops, sea urchins, and tube-building polychaetes in gravel pavement fishing grounds (47–62 m depth) at Georges bank showed a 5–10-fold increase after a 5-year period without trawling (Hermsen et al., 2003). Bradshaw et al. (2001) found that scallop *Pecten maximus* in the Irish Sea increased and had 50% higher abundance within compared to outside a closed area after 11 years of protection. In the same closed area, after 14 years, abundance had further increased about 5 times in comparison to the fished area with a significant shift in the age and size structure of *P. maximus* (Beukers-Stewart et al., 2005). No effects on soft bottom fauna were detected in the North Sea following the closure from bottom trawling in an area where offshore wind farms were established following 5 years after closure (Bergman et al., 2015). However, this area in the southern North Sea is relatively shallow (12–20 m) with high tidal-bed shear stress, and in such areas, the disturbance effects from bottom trawling are difficult to detect since similar impacts occur due to natural disturbance (van Denderen et al., 2015).

Gradient studies have the advantage of being able to deliver results that are realistic as important scale-dependent processes like dispersal and immigration are included, and the results likely mirror the sum of depletion and recovery from disturbance (Hiddink et al., 2017). However, gradient studies are correlative observations, and other environmental factors shaping communities often vary along trawl gradients, limiting the possibility to disentangle effects. Gradient studies may also be severely limited by the difficulties in identifying comparable untrawled areas and habitats. By combining the present recovery study with the detailed bottom trawl gradient study of Sköld et al. (2018) in the Kattegat, we found that the two dominating brittle stars appear to respond differently to bottom trawling. *A. chiajei* benefits from increased trawling likely due to reduced predation and a decrease in the NTZ along with an increase in benthivore predators. *A. filiformis* abundance is stable or indicates a slight decrease along the trawling gradient and a decrease in the NTZ as predation increases. The difference in exposure to predators related to feeding mode between these closely related and visually almost identical species may explain the deviating responses to bottom trawling. In addition, the slow growth of *A. chiajei* may explain why this species benefits from bottom trawling as predators are reduced along with the intensity in fishing. Minor differences in traits for apparently comparable species may thus have a profound effect on the sensitivity of benthic macrofauna to disturbances and response to measures. Regardless of hypothesizing, our results emphasize the importance of long-term experimental approaches of depletion and recovery at the species level to support observations along gradients in impact studies.

The results from the present long-term study show that the abundance and biomass of the brittle stars in the NTZ initially decrease and remain lowered after 12 years. This provides support for food web effects as it correlates with the increase of consumers of the brittle stars. Several fish species and crustaceans are predators of brittle stars. We found indications of ontogenetic shifts in prey preferences in long rough dab and dab with elevated proportions of decapods and fish in the stomach contents of larger size classes, but not in plaice. However, arms and discs of brittle stars were still the bulk of the stomach contents in all three species and size classes, accounting for more than 50% in weight. The economically most important species for the bottom trawl fishery in Kattegat is the Norway lobster, *Nephrops norvegicus*, and, like benthivore flatfish, it has increased following the closure of the NTZ (Sköld et al., 2022). The Norway lobster is omnivorous and capable of suspension feeding in its burrows (Santana et al., 2020), but it also consumes benthic invertebrates, including brittle stars (Baden et al., 1990; Johnson et al., 2013).

The indicated food web effect with increased abundance and biomass of *Amphiura* spp. at increased levels of trawling is an alternative explanation to earlier suggestions that the long-term (>70 years) historical shift in the Kattegat with increasing dominance of the brittle star *A. filiformis* is due to a general eutrophication of the area (Pearson et al., 1985). This shift parallels the evolution in intensity of the bottom trawl fisheries in the 1900's in the Kattegat and the North Sea which, according to our study, might explain the increase in biomass and abundance of these brittle stars. However, Göransson (2002) also found a long-term increase in *A. filiformis* in the non-trawled but still intensively fished neighboring area Öresund, in parallel to increased nutrient load and oxygen deficiency. Both eutrophication and trawling may thus have contributed to the historical increase in *A. filiformis* in the Kattegat. Bottom trawling causes negative physical impacts, including mortality and a reduction in biomass, on the benthic community, particularly affecting sensitive species (Hiddink et al., 2017; Kaiser et al., 2006). This is consistent with the findings of this study. However, if fish and invertebrate predators are reduced by fishing, the resulting decrease in predation mortality on dominant species may outweigh the increase in trawling-induced mortality. Such an effect could limit the utility of using traits, such as longevity composition, as sensitivity metrics for benthic invertebrates, as suggested by Rijnsdorp et al. (2018) and Hiddink et al. (2019), to estimate impact indicators for bottom trawling.

Succession refers to change in species and habitat composition over time following a disturbance. The shift in species composition and the contribution by individual taxa in this study of long-term recovery of the macrofaunal community correlate with how the same species contributed to explain the species composition along a trawling intensity gradient in the same area (Figure 3). The otter trawl effort targeting demersal fish and crustaceans is usually aggregated on core fishing grounds (ICES, 2022), and the results of our study then imply that the trawled areas might be locked in chronic states of disturbance. Correspondingly, the pattern in recovery is not random, and community shifts found along gradients of bottom trawling may be used as a proxy for expected recovery. This is important information from the perspective of management efforts to restore marine ecosystems from the impact of bottom trawl fisheries, as it indicates that reduced effort may lead to predictable recovery.

5 | CONCLUSION

We have followed the recovery of the benthic macrofaunal community over 12 years in a large NTZ in the south Kattegat after demersal trawling was stopped and compared it to a nearby area where trawling continued. Using multivariate analyses, we found significant shifts in the community composition within the NTZ. The recovery response in the benthic macrofauna community correlates with shifts in the community composition along a chronic bottom trawling intensity gradient in the same area. This indicates that the recovery of the benthic community follows a successional pattern that also can be observed in different chronic states of disturbance from bottom trawling. Two species of burrowing brittle stars dominated abundance and biomass and decreased in the closed area. In parallel, benthivore flatfish and Norway lobster increased. Stomach contents of the dominating flatfishes matched the availability of benthic prey taxa, and brittle stars were the staple food. Food web effects with predator release of the dominant macrofauna species in the trawled areas thus appear to override the decrease in trawling-induced mortality of dominant macrofauna in the NTZ.

AUTHOR CONTRIBUTIONS

MS, PG, and HW contributed to the conception of the paper. PG sampled and analyzed macrofauna. MS, PB, and MB designed and conducted the data analysis. All authors contributed to the interpretation of results. MS led the writing of the manuscript, and all authors contributed to writing and editing the manuscript and approved the final draft.

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DATA AVAILABILITY STATEMENT

The data underlying this article will be provided as Appendix S1 to the published article.

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SUPPORTING INFORMATION

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

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