

A no-take zone and partially protected areas are not enough to save the Kattegat cod, but enhance biomass and abundance of the local fish assemblage

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To supplement catch and effort regulations with the purpose to rebuild the cod (*Gadus morhua*) stock in Kattegat, Sweden and Denmark established a large (426 km²) year-round no-take zone (NTZ) surrounded by partially protected areas (PPAs) in 2009. The purpose of these spatial regulations was to prohibit cod fishing on the spawning grounds and to displace fisheries bycatch of cod from areas where mature cod aggregate in the Kattegat. The aim of this study is to evaluate the effects of the established NTZ and PPAs on the local fish assemblage, including cod. Based on a spatially high-resolution bottom trawl survey in the Kattegat (covering 2008–2021), multivariate analyses revealed significant shifts in the fish assemblage. A closer analysis indicated that six to seven fish species, including cod increased in the NTZ relative to control areas depending on if abundance or biomass was used as dependent variable. Univariate analysis showed that two flatfish species dab (*Limanda limanda*) and lemon sole (*Microstomus kitt*), and Norway lobster (*Nephrops norvegicus*) significantly increased in biomass in the NTZ, and turbot (*Scophthalmus maximus*) in the PPA relative to the control areas. These results suggest that the NTZ protected even relatively mobile species in an open sea system, such as the Kattegat. However, neither cod abundance nor biomass showed a significant increase as an effect of the NTZ and PPA despite two relatively strong year classes in 2012 and 2013, which possibly would have helped the recovery of the cod stock. As assessed by the International Council for the Exploration of the Sea in 2022, Kattegat cod continuously suffer from being severely overfished with low recruitment, and high discard rates in the mixed *N. norvegicus* fishery, is considered the major driver behind the reinforced depletion of the stock.

Keywords: bottom trawling, cod, flatfish, MPA, *Nephrops norvegicus*.

Introduction

Spatial restrictions for fisheries are used both for conservation and fisheries management purposes, and marine protected areas (MPAs) are increasingly used in policy and management as tools to protect species, habitats, and ecosystem functioning, and minimize destructive impact from e.g. bottom trawl fisheries. The most restrictive spatial protection is often termed no-take zones (NTZs) or fully protected areas where all extractive uses are prohibited (Fenberg *et al.*, 2012; Grorud-Colvert *et al.*, 2021). NTZs often show strong responses enhancing biomass of whole fish assemblage relative to fished reference areas and may also increase species richness and body size of organisms (Halpern, 2003; Lester *et al.*, 2009). Partially protected areas (PPAs) may also show positive ecological effects relative to open access areas, but often less in terms of biomass than in NTZs, primarily due to the exclusion of target species in NTZs (Sciberras *et al.*, 2013a, b; Zupan *et al.*, 2018). Theoretical and empirical studies show that the effectiveness and potential of MPAs to increase species density depend on their mobility and is related to the size of the MPA (Hastings and Bootsford, 2003; Claudet *et al.*, 2008). Most NTZs, but also PPAs, that have been studied are, however, small (NTZs 0.1–30.5 km²; PPAs 1.9–140.1 km²) and often dominated by reef areas with hard substrate inhabiting fish assemblages with low dispersal and low mobility (Sciberras

et al., 2013a). In contrast, temperate areas with commercial fish species often have high dispersal and are highly mobile, but theoretical studies indicate that combining catch quota with large, closed areas may be effective in protecting and managing such stocks (Stefansson and Rosenberg, 2005). Accordingly, a few studies of temperate NTZs indicate increasing abundance, size, and biomass in NTZs (Stewart *et al.*, 2008; Lester *et al.*, 2009).

The scientific literature of effects of MPAs has grown over the last 20 years, although there are still few studies of NTZs and PPAs from temperate areas with soft seafloor habitats. This shortage of studies is surprising given the global extent and intensity of bottom trawl fisheries on soft seafloor habitats in temperate areas (Eigaard *et al.*, 2016; Amoroso *et al.*, 2018). However, it also indicates that NTZs are predominantly used as a conservation measure to protect iconic species and habitats, including reefs and associated organisms. NTZ are, thus in many cases, measures to satisfy policy directives and stakeholders and do not necessarily have the intention to minimize impact of ongoing fisheries on fish stocks. In addition, there are few studies of NTZs that have strong experimental designs such as Before-After-Control-Impact (BACI), which can account for both spatial and temporal processes (Sciberras *et al.*, 2013a), making it difficult to detect effects of NTZs.

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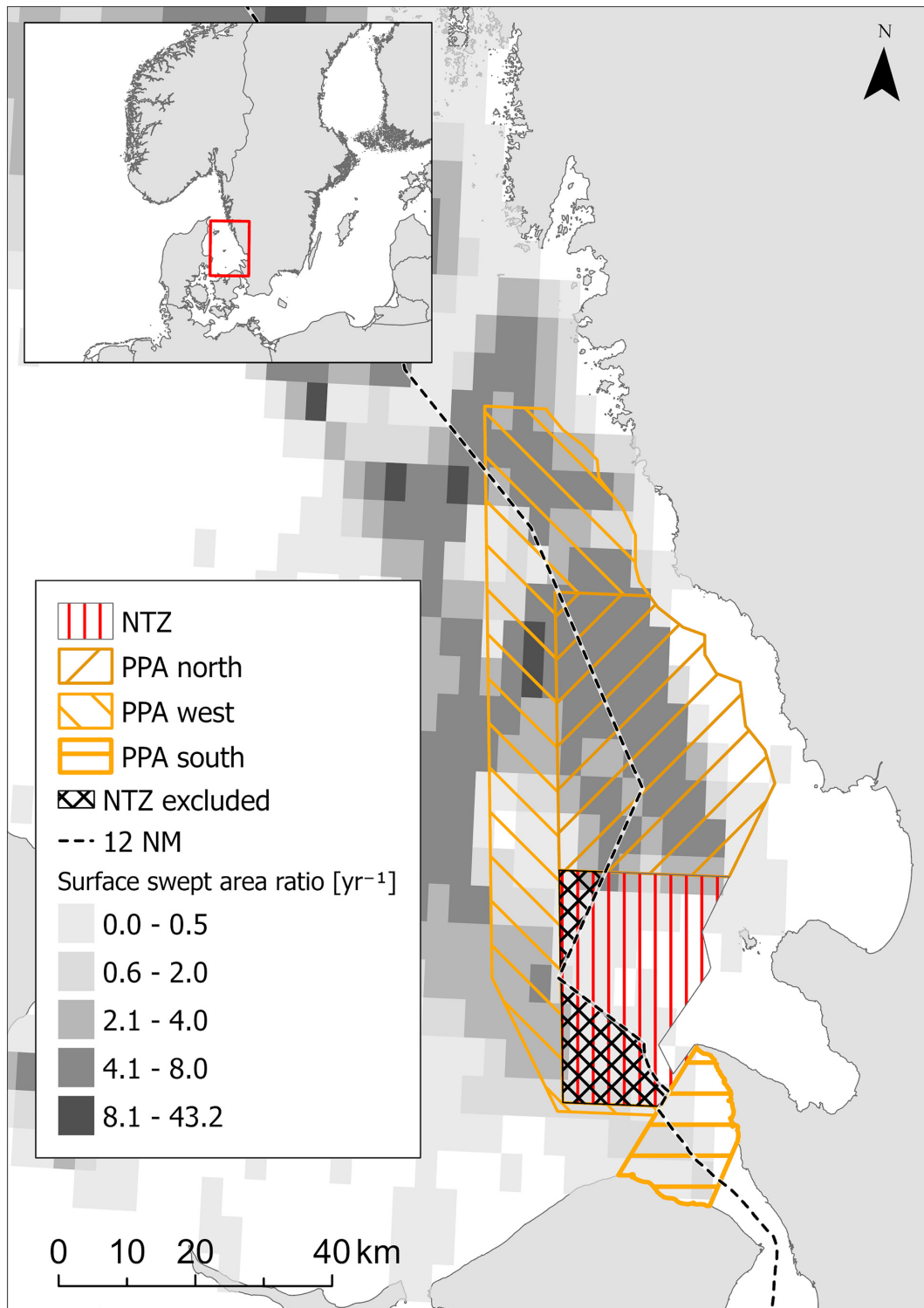


Figure 1. Map view of the enforced NTZ and PPA areas in the southern Kattegat. German vessels have access to exclusive economic zone (EEZ) waters outside 12 NM of the member states (indicated as NTZ excluded). In the northern area (PPA north), fishing is prohibited during the first quarter (January–March), i.e. the spawning period for cod, and during the rest of the year, fishing is allowed with the above mentioned selective gear. In the western area (PPA west), fishing is permitted all year round with the restriction that selective gear must be used in the first quarter. In the southern area (PPA south), the same premises prevail as in PPA west, but the period is from February to March. Surface swept area ratio (SAR) estimates define the swept area as the cumulative area contacted by bottom trawlers within a grid cell over 1 year. The SAR here is from 2017 to 2020 and averaged per year (ICES, 2021b).

The recovery of overfished individual fish species in areas with mixed fisheries is a widespread problem and a particular challenge to fisheries management. Approaches to mitigate these problems often involve time/area and gear restrictions

to allow fisheries on exploitable resources (Murawski, 2010). In 2009, Sweden and Denmark established a large (426 km²) NTZ surrounded by PPAs in the temperate sea Kattegat. The background for the spatial regulations in Kattegat was that

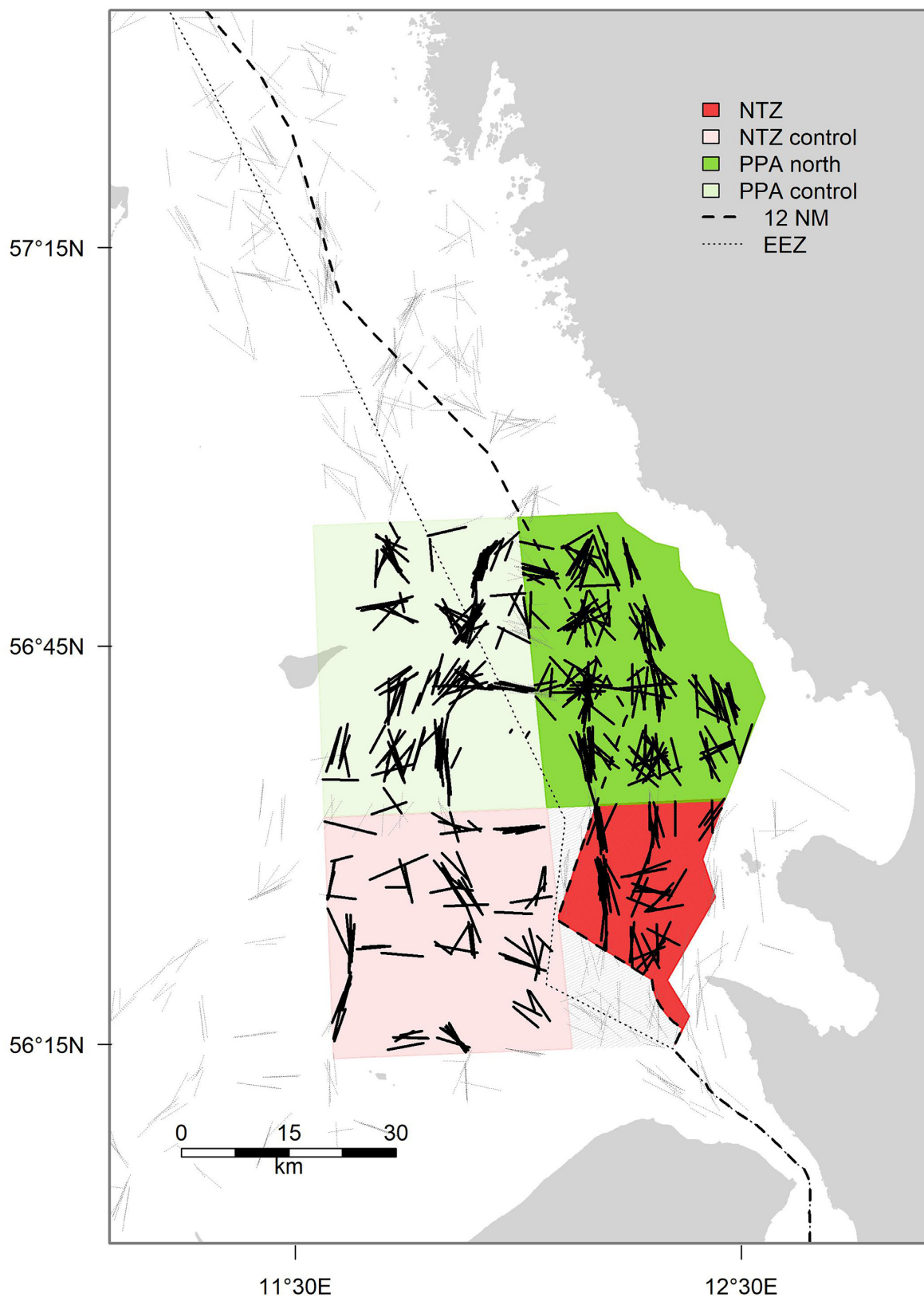


Figure 2. Map showing hauls during the period 2008–2021 in the regulated areas (NTZ in red and PPA north in green), and the areas used as control in the analyses. Only trawls hauls with 75% or more of their length in one of the four areas were used in the analyses.

the cod, *Gadbus morhua*, stock in Kattegat had been severely overfished, and the spawning stock biomass (SSB) has been very low since the turn of the millennium. The stock decline coincided with the disappearance of large spawning aggrega-

tions (Cardinale and Svedäng, 2004). Historically, cod fishing has been carried out on the spawning grounds in the south-eastern Kattegat during the first quarter both by Denmark and Sweden, and for several years >70% of the annual Swedish

Table 1. Number of hauls by year and area used in the analyses.

Year	NTZ	NTZ control	PPA control	PPA north
2008	4	7	12	17
2009	4	6	16	17
2010	6	5	11	18
2011	6	2	13	16
2012	No survey	-	-	-
2013	4	6	9	15
2014	5	4	9	14
2015	5	7	10	10
2016	4	4	11	13
2017	5	9	11	11
2018	7	8	9	13
2019	7	8	14	10
2020	6	8	14	11
2021	0	5	12	12

cod quota in the Kattegat, were caught in the targeted fishing for spawning cod in this area (Vitale *et al.*, 2008). In 2002, the International Council for the Exploration of the Sea (ICES) advised a total stop of cod catches. As a result, the cod quotas were reduced, but cod mortality was still too high, and the stock biomass continued to decline. The reason for the continued high fishing mortality was that cod were caught both as a targeted species during the spawning period and in a demersal mixed fishery for demersal fish and Norway lobster, *Nephrops norvegicus*, where cod are by-caught and discarded when the quota is fully used (ICES, 2021a). To supplement the unsuccessful catch regulations, Swedish and Danish researchers outlined a proposal to close the remaining functional cod spawning grounds to fishing (Hjelm *et al.*, 2008). The purpose of establishing a large year-round NTZ, surrounded by a PPA, was to prohibit targeted cod fishing on the spawning grounds and displace fisheries bycatching cod from areas where mature cod aggregate both during and after spawning (Vitale *et al.*, 2008; Börjesson *et al.*, 2013). In addition, the intention of

the proposal was to allow fisheries on other species, mainly *N. norvegicus* and flatfish to continue in other areas, and also after the cod spawning season. The Swedish and Danish fisheries ministers agreed on measures based on the researchers' proposal, however, with major modifications, including significantly reduced area coverage of the NTZ and the PPA.

Aim of the study

The area provides unique possibilities to study effects of a large soft sediment habitat dominated NTZ on the mobile fish assemblage of the Kattegat. The established NTZ was implemented to displace fisheries that could catch cod from the spawning and main habitat for cod, but also has the potential to protect other species of fish and *N. norvegicus* within its boundaries. The aim of this study was to analyse trends of the fish assemblage within and between the NTZ, the most restrictive PPA and control areas where fisheries persist, using a combination of multi- and univariate approaches.

Materials and methods

Study area

The Kattegat is a shallow sea area (mean depth 27 m) and connects to the North Sea in the north and to the Baltic Sea via narrow straits in the south (Figure 1). The low saline surface waters from the Baltic Sea create a typical estuarine circulation pattern and 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 >32 PSU (Andersson and Rydberg, 1988). Seafloor substrates vary with shallow areas, including offshore banks with rocks, gravel, and sandy sediments and deeper, often mixed soft sand, silt, and mud sediments in the east (Hallberg *et al.*, 2010). Fishing by bottom trawling has a long history and developed by steam trawlers already in the early 1900s in the Kattegat (Bartolino *et al.*, 2012). Today fisheries are dominated by demersal otter trawling targeting a mix-

Table 2. PERMANOVA and correlation of species with CAP of the two most explanatory CAP axes.

Abundance of species years 2008–2020			NTZ vs. PPA north			PPA north vs. PPA control		
NTZ vs. NTZ control			Pseudo $F_{11,203} = 1.7079$, $p = 0.0001$			Pseudo $F_{11,278} = 1.9537$, $p = 0.0001$		
Species	CAP1	CAP2	Species	CAP1	CAP2	Species	CAP1	CAP2
<i>A. radiata</i>	0.42	-0.05	<i>G. morhua</i>	0.72	0.39	<i>G. morhua</i>	0.71	-0.25
<i>G. morhua</i>	0.46	-0.19	<i>H. platessoides</i>	0.42	-0.04	<i>H. platessoides</i>	0.63	-0.07
<i>H. platessoides</i>	0.72	0.13	<i>L. limanda</i>	0.08	-0.49	<i>M. merluccius</i>	0.32	-0.40
<i>M. merluccius</i>	0.49	-0.25	<i>M. merluccius</i>	0.49	-0.29	<i>M. kitt</i>	0.03	-0.46
<i>M. kitt</i>	0.40	-0.30	<i>Platichthys flesus</i>	-0.22	-0.53	<i>T. draco</i>	-0.44	-0.35
<i>S. rhombus</i>	0.18	-0.41						
<i>S. maximus</i>	0.42	-0.09						
<i>T. draco</i>	-0.30	-0.50						
Biomass of species years 2008–2020			NTZ vs. PPA north			PPA north vs. PPA control		
NTZ vs. NTZ control			Pseudo $F_{11,203} = 2.2335$, $p = 0.0001$			Pseudo $F_{11,113} = 1.9537$, $p = 0.0001$		
Species	CAP1	CAP2	Species	CAP1	CAP2	Species	CAP1	CAP2
<i>A. radiata</i>	0.50	-0.14	<i>A. radiata</i>	0.005	0.62	<i>G. morhua</i>	0.83	-0.25
<i>G. morhua</i>	0.65	0.32	<i>G. morhua</i>	0.87	-0.14	<i>Glyptocephalus cynoglossus</i>	-0.06	-0.42
<i>H. platessoides</i>	0.62	-0.32	<i>M. merluccius</i>	0.26	0.56	<i>H. platessoides</i>	0.61	-0.07
<i>M. merluccius</i>	0.37	-0.60	<i>M. kitt</i>	0.24	0.46	<i>M. kitt</i>	0.09	-0.46
<i>P. flesus</i>	-0.44	0.01	<i>Platichthys flesus</i>	-0.39	0.45	<i>P. platessa</i>	0.52	-0.27
<i>S. maximus</i>	0.51	-0.23	<i>P. platessa</i>	0.44	0.26	<i>T. draco</i>	-0.44	-0.29

Species that correlate with $r > 0.4$ to one or both CAP axes are included. Significant correlations are indicated in bold (α level 0.05, $df = 24$).

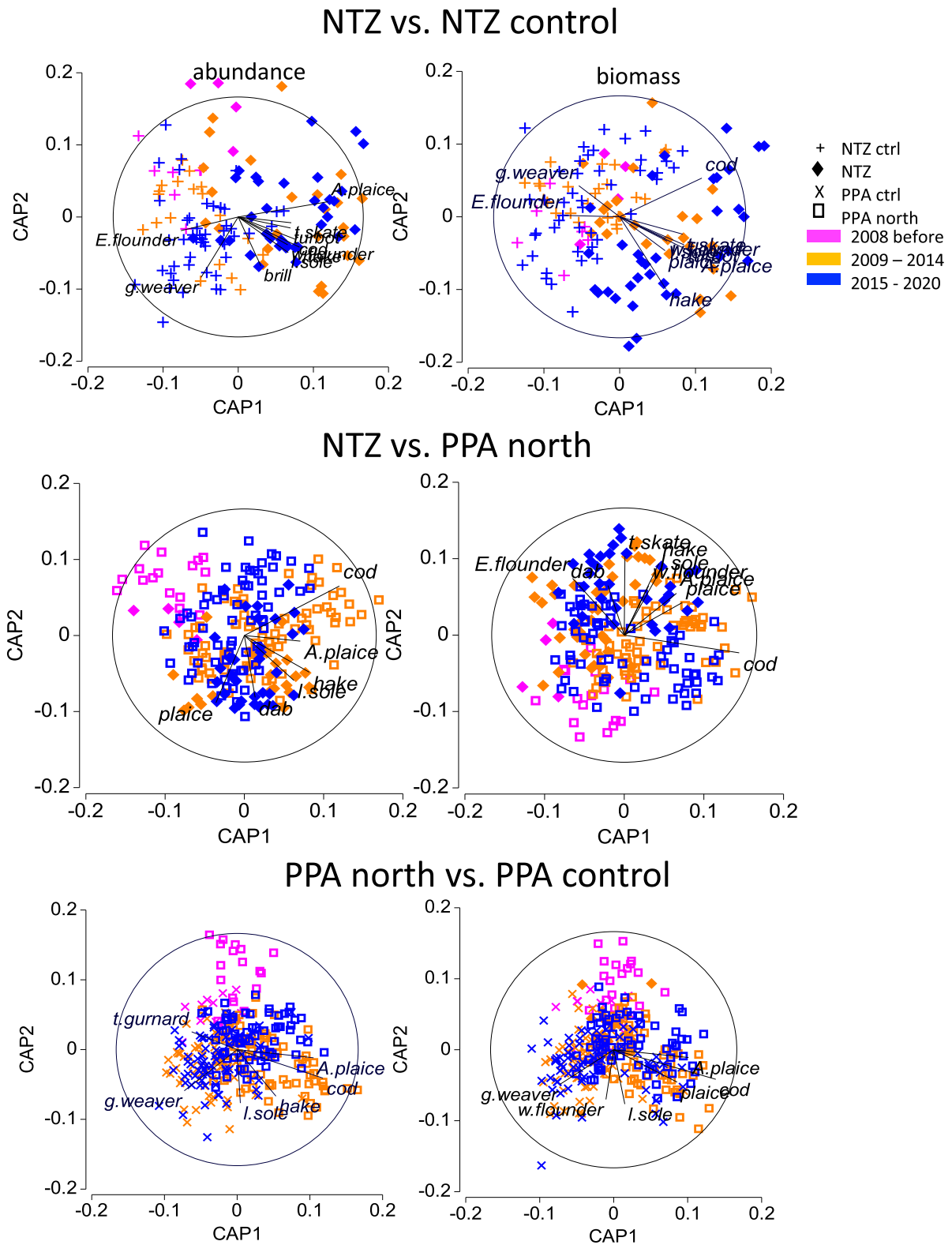


Figure 3. CAP plot for the visual presentation of composition by abundance or biomass of species as shaped by the interaction term treatment \times year. Species that correlate with $r > 0.4$ to one or both CAP axes are shown on the plot. See Table 2 for further details. Abbreviations for species: A. = American, E. = European, g. = greater, l. = lemon, t. = thorny, and w. = witch.

ture of *N. norvegicus* and fish, mainly plaice (*Pleuronectes platessa*), sole (*Solea solea*), and cod (ICES, 2021b). The MPA covered parts of the spawning areas of cod that before the enforcement of the NTZ were fished by other trawlers tar-

getting aggregated cod during the spawning season (Vitale *et al.*, 2008), and a mixture of *N. norvegicus* and demersal fish (Hornborg *et al.*, 2016) (Figure 1). Gears defined as selective and allowed in PPA north are bottom trawls equipped

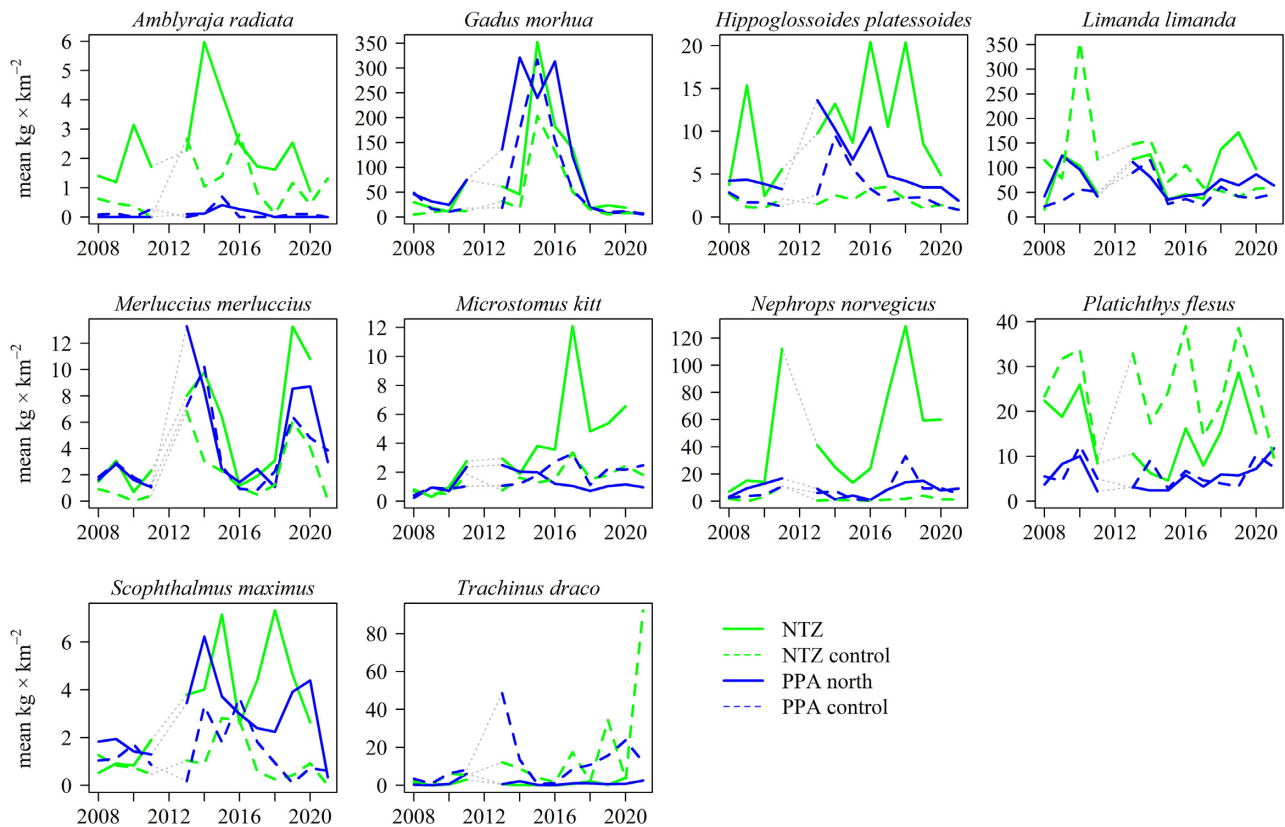


Figure 4. Average catch per unit effort in $\text{kg} \times \text{km}^{-2}$ of selected species in the regulated areas and in the control areas during the period 2008–2021. Solid green and blue lines represent the NTZ and the PPA north, respectively. The dashed lines of the same colours represent the control areas. No survey was conducted in 2012, and in 2021, no stations were sampled in the NTZ.

with a Swedish sorting grid or SELTRA 300 and described in detail in Madsen and Valentinsson (2010), and creels for *N. norvegicus*. The activity by demersal otter trawlers is presented as surface swept area ratio estimates for the years 2017–2020 for bottom otter trawlers ≥ 12 m and averaged per year within a 0.05×0.05 -degree grid, as provided by ICES (2021b).

Biological data collection and analysis

All analysis of fish is based on the joint Swedish and Danish survey for cod in the Kattegat (Jørgensen *et al.*, 2019). The survey has been conducted in November–December every year since 2008 except for 2012. 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 34-m-long commercial bottom trawl with a 70 mm diamond mesh in the cod-end.

Experimental set-up and statistics

Abundance and biomass of fish for the years 2008–2021 were used to evaluate the effect of the NTZ and PPA north on the temporal development of the species assemblage. Control areas were identified as trawled areas west of the treatment areas within the same depth interval and dominating soft seafloor substrate as the treatment areas, i.e. the NTZ or PPA north (Figure 2). The PPA west is considered fished and is included in the control areas having only minimal difference in impact by the bottom trawl fisheries, and only during the first quar-

ter of the year. In total, 470 hauls from 2008 to 2021 were available for analyses (Table 1).

Multivariate abundance and biomass of fish for the years 2008–2020 were used to evaluate the effect of the NTZ and PPA north on the temporal development of the species assemblage by PERMANOVA using the software PERMANOVA+ for PRIMER (Anderson *et al.*, 2008). Control areas were identified as continuously trawled areas west of the treatment areas within the same depth interval and dominating seafloor substrate as the treatment area (Figure 2). The effect of the NTZ will be the interaction between year of sampling and treatment. Dependent variables examined were species composition weighted by abundance or biomass divided by the area (km^2) swept by the trawl during the haul. Since this survey uses 70 mm diamond mesh-size nets, only species with a maximum size >20 cm were included since smaller species are only likely to be caught occasionally. Results were visualized with canonical analysis of principal coordinates (CAP) for the interaction between treatment and year of sampling. Data were transformed (square root) and evaluated with a distance-based test for homogeneity of multivariate dispersions using the function PERMDISP.

Univariate trend analyses were carried out on the differences in average abundance and biomass between areas, by generalized least-squares regression, including AR-1 autocorrelation between years using the nlme package in R (Pinheiro *et al.*, 2020). An increasing difference, i.e. an upward trend between the NTZ and the control, or between the NTZ and the PPA over time, indicates that the implementation of the NTZ had a positive impact on the species.

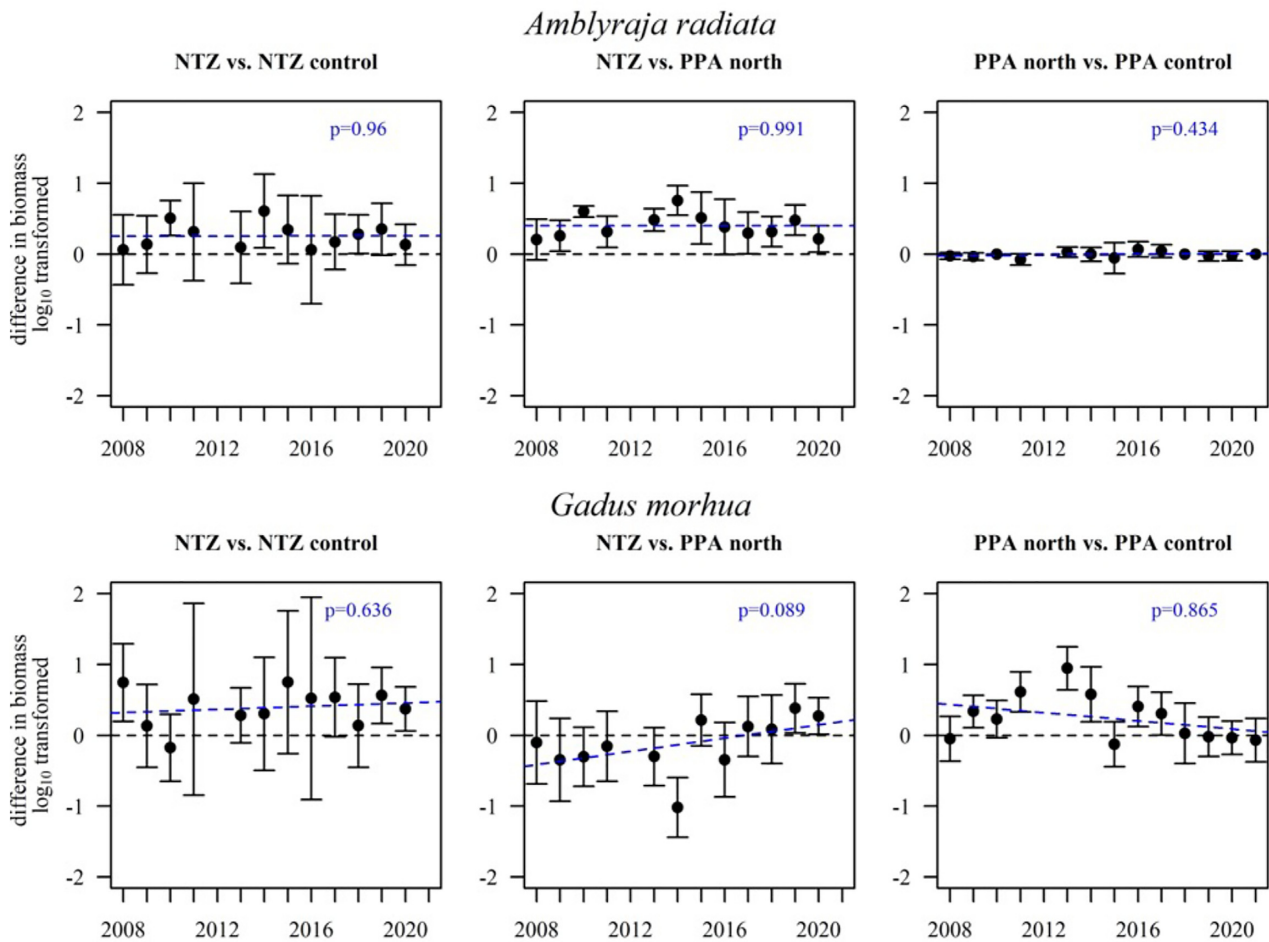


Figure 5. Trend analysis for selected species in 2008–2021. The left panels show differences in biomass (mean \pm 95% CI) between the NTZ and the control area. CIs that do not overlap with the dashed line indicate a significant difference. The middle panels show the difference between the NTZ and PPA north, and the right panels show differences in biomass between PPA north and the control area. The dotted line with the associated p_{GLS} value shows the trend over time and is the significance of the generalized least-squares fitted linear model.

Results

The multivariate analysis of the fish assemblage showed a significant effect for the sought-after interaction between the treatment (NTZ and PPA north areas, and the respective control areas and years), i.e. shifts in assemblage composition over the years (Table 2). Also, the temporal development in the NTZ vs. the PPA north differed. Resolving the multivariate results using CAP for the interaction (treatment \times year) and overlaying the two most explanatory axes with correlating species from the matrix indicated that a limited number of species contributed to the differences. American plaice (*Hippoglossoides platessoides*), turbot (*Scophthalmus maximus*), cod, hake (*Merluccius merluccius*), lemon sole (*Microstomus kitt*), dab (*Limanda limanda*), plaice (*Pleuronectes platessa*), and starry ray (*Amblyraja radiata*) all increased in abundance and biomass in the NTZ relative to the NTZ control or the PPA north. Greater weaver (*Trachinus draco*) decreased along CAP axis 2 but showed no consistent patterns for abundance and biomass (Figure 7; Table 2). Fishing restrictions in PPA north also influenced the fish assemblage, with some species of fish becoming more abundant over time and having a higher biomass in PPA north compared to PPA control, where fishing was allowed (Figure 3; Table 2).

The univariate analyses detected significant positive trends in biomass over time for the following species identified in the multivariate analysis: *L. limanda*, *M. kitt*, and *N. norvegicus* when the NTZ was contrasted with the control area; and *M. kitt*, *S. maximus*, and *N. norvegicus* when the NTZ was contrasted with PPA north. A positive trend for *G. morhua* was indicated for the NTZ in comparison to the PPA north area albeit only at a significance level of $\alpha = 0.10$ (Figures 4 and 5; Table 3). A similar pattern was found for abundance, although the trends were less distinct than for biomass (Figures 6 and 7; Table 4). No trends were detected for *M. merluccius*, *P. platessa*, *H. platessoides*, *P. flesus*, *T. draco*, and *A. radiata* that correlated with the CAP axes for treatment \times years in the multispecies analyses (Tables 3 and 4).

Discussion

The NTZ with buffer zones was introduced in the Kattegat in 2009 and with the present fishing regulations been effective for over 13 years at the time of this study. The fish assemblage showed a positive response to the establishment of the NTZ during the observed period. This effect was observed in the interaction between the spatial treatment, i.e. with the

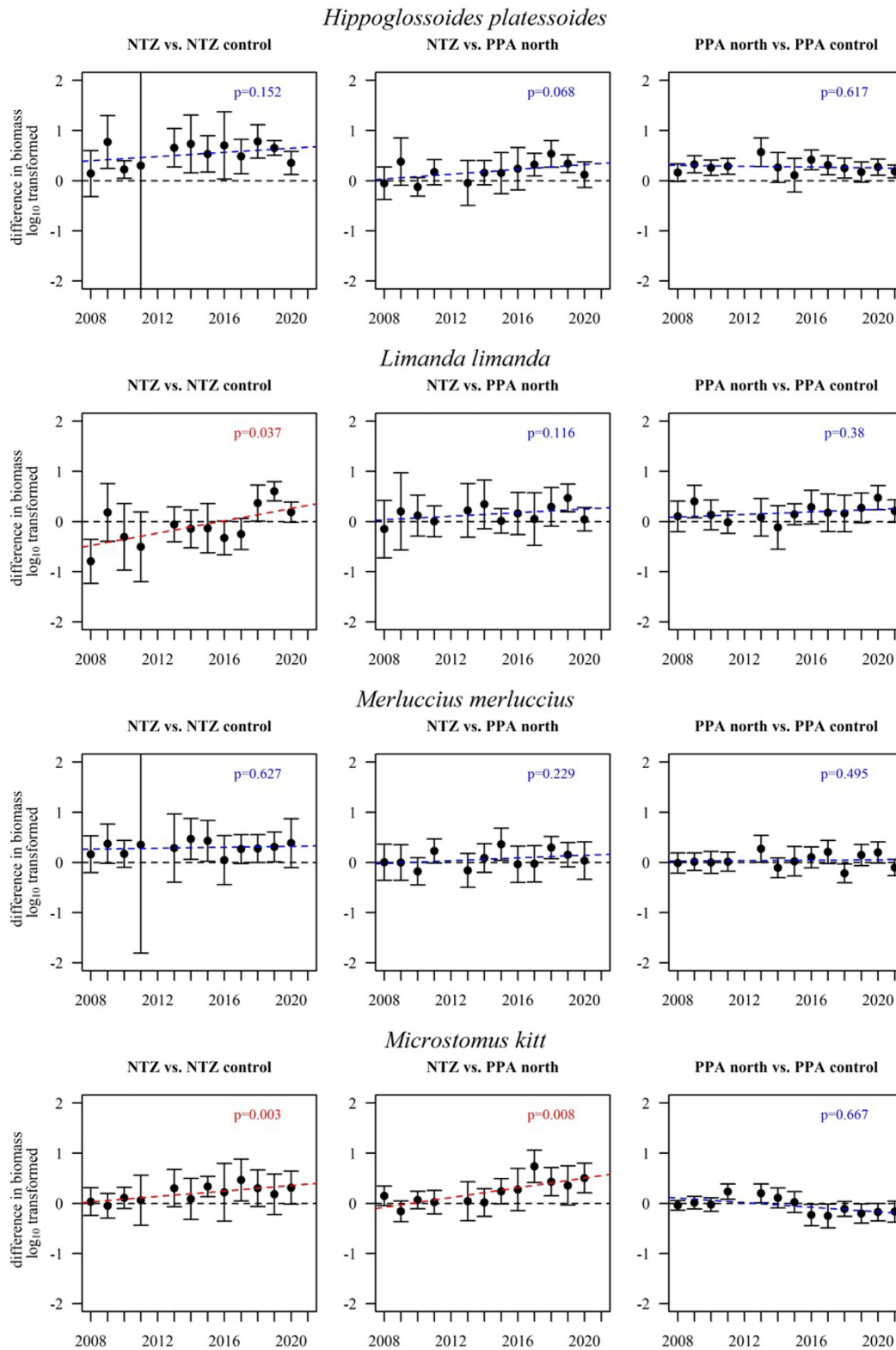


Figure 5. Continued.

NTZ with PPA north the control areas, and years. Several of the investigated fish species showed increasing biomass and abundance over time in the NTZ relative to the NTZ control and the PPA north, while no increase was found in the weakly protected PPA north relative to the control area. These find-

ings show that an NTZ dominated by soft seafloor habitat like Kattegat, despite being present in a temperate open ecosystem, can lead to the increase in abundance and biomass in mobile species such as fish. Our findings that most of the analysed fish species showed a positive response to the reduced fishing

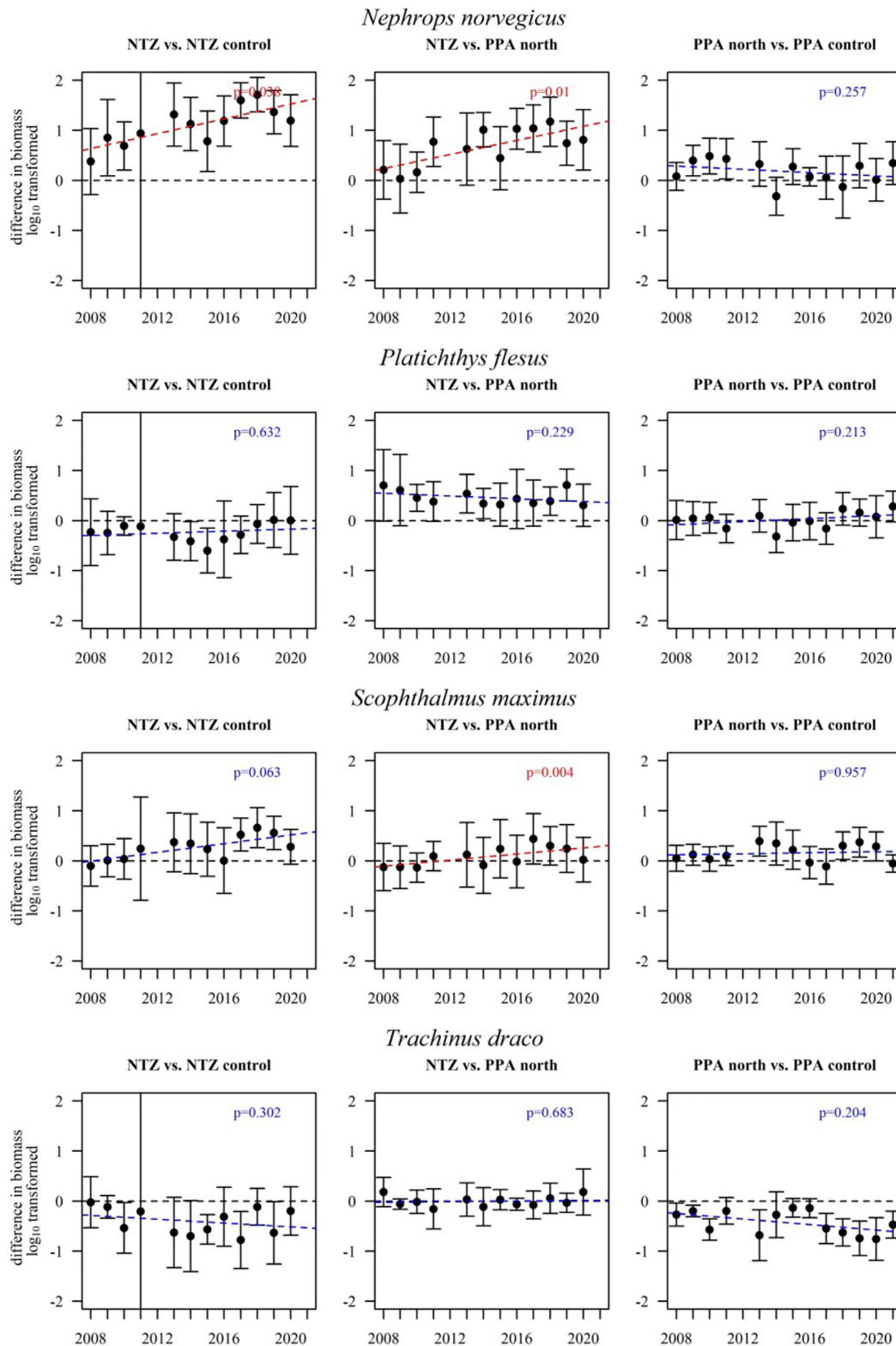


Figure 5. Continued

pressure should be considered as a minimum effect on the fish assemblage since the survey trawl mesh size precluded comparisons for all small-bodied species ($L_{inf} < 20$ cm). Hence, this suggests that the effects of an NTZ may have effects on more fish species and other fauna.

A strong biomass response to the introduction of the NTZ was found in three of the flatfish species investigated. Dab showed a significant biomass increase in the NTZ relative to the control area. For lemon sole, there was a biomass increase in the NTZ relative to both the control area and PPA

Table 3. Univariate trend analyses of difference in biomass of species indicating contributing trends to explanatory axes in the CAP analysis of treatment (area) \times years.

Species	Parameter	NTZ vs. NTZ control					NTZ vs. PPA north					PPA north vs. PPA control				
		ρ_{bi}	ρ_{AR1}	Value	SE	ρ_{gls}	ρ_{bi}	ρ_{AR1}	Value	SE	ρ_{gls}	ρ_{bi}	ρ_{AR1}	Value	SE	ρ_{gls}
<i>A. radiata</i>	Intercept			0.25	0.12	0.07			0.38	0.15	0.03			-0.03	0.03	0.30
	Year	0.09	0.80	0.00	0.02	0.96	0.39	0.31	0.00	0.02	0.99	0.11	0.73	0.00	0.00	0.43
<i>G. morhua</i>	Intercept			0.31	0.18	0.10			-0.47	0.20	0.05			0.23	0.56	0.69
	Year	0.03	0.95	0.01	0.02	0.64	-0.04	0.91	0.05	0.03	0.09	0.80	0.12	-0.01	0.06	0.86
<i>H. platessoides</i>	Intercept			0.39	0.11	0.01			0.01	0.10	0.89			0.31	0.07	0.00
	Year	-0.22	0.57	0.02	0.01	0.15	-0.14	0.70	0.02	0.01	0.07	-0.04	0.93	0.00	0.01	0.62
<i>L. limanda</i>	Intercept			-0.56	0.21	0.03			0.02	0.08	0.79			0.08	0.12	0.54
	Year	0.13	0.70	0.06	0.03	0.04	-0.18	0.64	0.02	0.01	0.12	0.31	0.36	0.01	0.01	0.38
<i>M. merluccius</i>	Intercept			0.26	0.07	0.01			-0.04	0.09	0.69			0.00	0.06	0.95
	Year	-0.03	0.93	0.00	0.01	0.63	-0.13	0.68	0.01	0.01	0.23	-0.41	0.22	0.00	0.01	0.49
<i>M. kitt</i>	Intercept			0.00	0.06	0.95			-0.12	0.12	0.34			0.02	0.28	0.96
	Year	-0.13	0.69	0.03	0.01	0.00	0.15	0.71	0.05	0.01	0.01	0.89	0.02	-0.01	0.03	0.67
<i>N. norvegicus</i>	Intercept			0.56	0.25	0.05			0.17	0.18	0.35			0.31	0.13	0.03
	Year	0.45	0.33	-0.07	0.03	0.04	0.09	0.82	0.07	0.02	0.01	-0.10	0.79	-0.02	0.01	0.26
<i>P. flesus</i>	Intercept			-0.25	22.28	0.99			0.57	0.10	0.00			-0.10	0.10	0.36
	Year	1.00	0.00	0.02	0.04	0.63	0.18	0.62	-0.02	0.01	0.23	0.09	0.78	0.02	0.01	0.21
<i>S. maximus</i>	Intercept			-0.03	0.16	0.84			-0.16	0.07	0.05			0.14	0.20	0.49
	Year	0.39	0.38	0.04	0.02	0.06	-0.29	0.47	0.03	0.01	0.00	0.60	0.11	0.00	0.02	0.96
<i>T. draco</i>	Intercept			-0.27	0.15	0.10			-0.03	0.06	0.62			-0.24	0.16	0.17
	Year	-0.12	0.75	-0.02	0.02	0.30	-0.20	0.72	0.00	0.01	0.68	0.30	0.35	-0.03	0.02	0.20

ρ_{bi} represents the autocorrelation between years, ρ_{AR1} is the significance of the autoregressive component, and ρ_{gls} is the significance of the generalized least-squares fitted linear model.

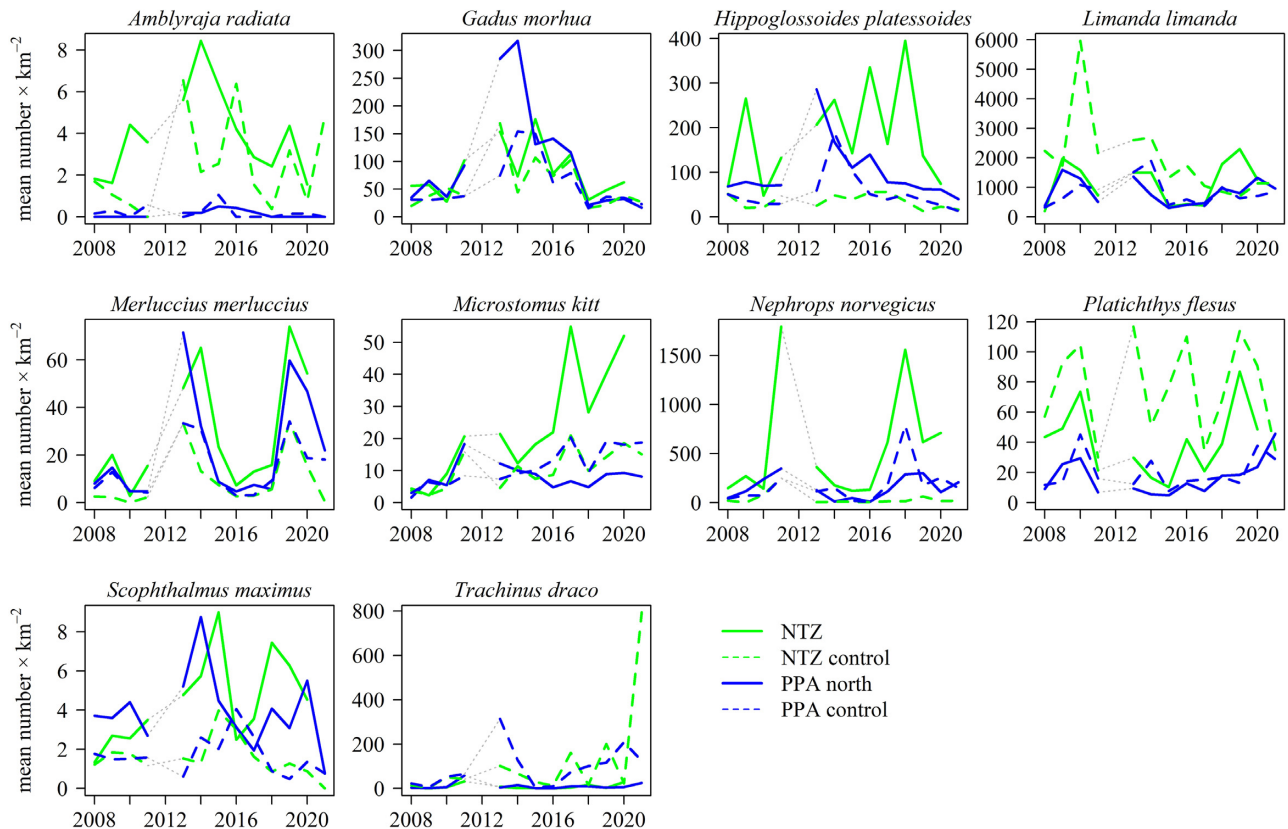


Figure 6. Average catch per unit effort in numbers \times km⁻² of selected species in the regulated areas and in the control areas during the period 2008–2021. Solid green and blue lines represent the NTZ and the PPA north, respectively. The dashed lines of the same colours represent the control areas. No survey was conducted in 2012, and in 2021 no stations were sampled in the NTZ.

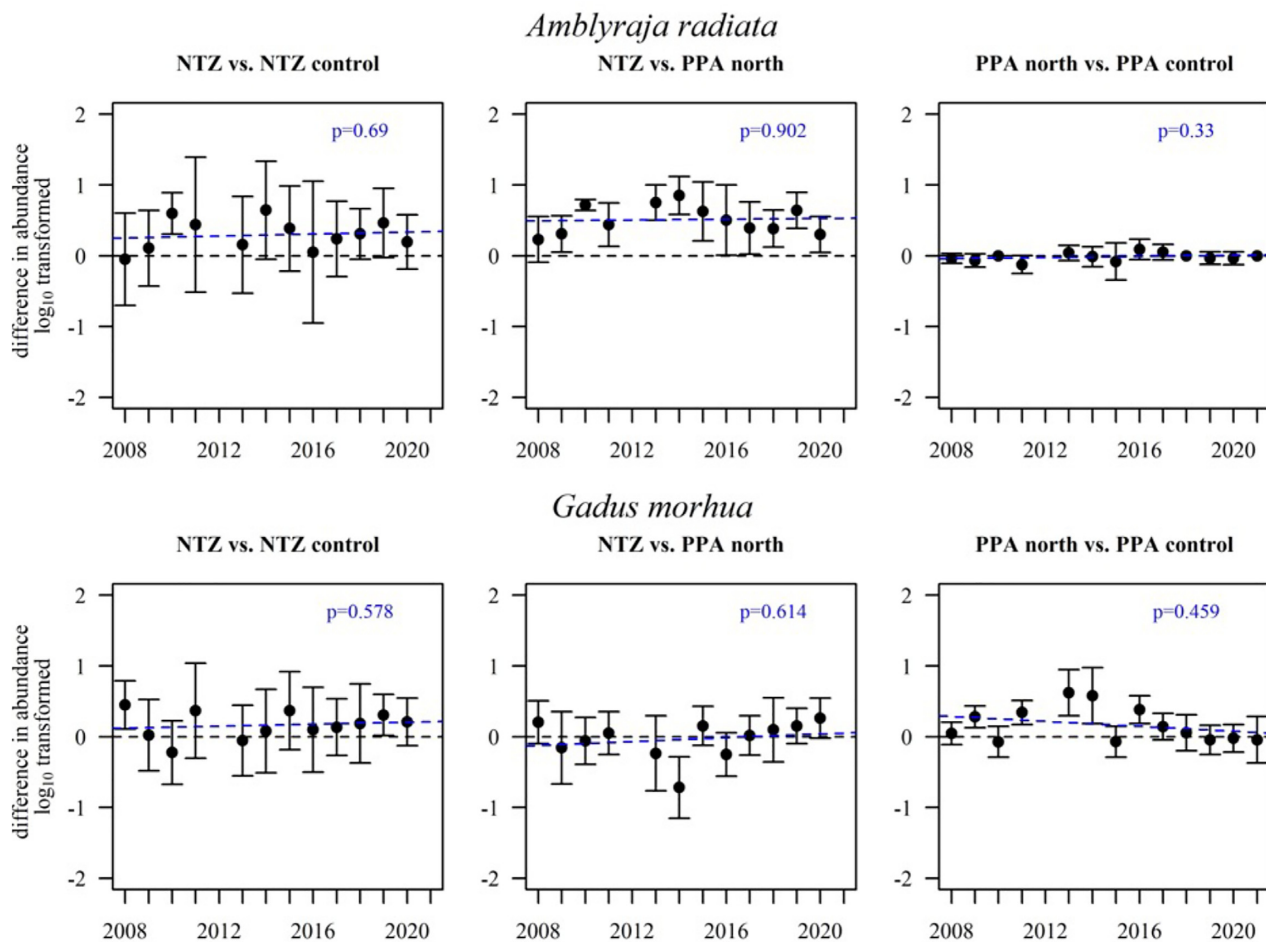


Figure 7. Trend analysis for selected species in 2008–2021. The left panels show differences in abundance (mean \pm 95% CI) between the NTZ and the control area. CIs that do not overlap with the dashed line indicate a significant difference. The middle panels show the difference between the NTZ and PPA north, and the right panels show differences in biomass between PPA north and the control area. The dotted line with the associated p_{GLS} value shows the trend over time and is the significance of the generalized least-squares fitted linear model.

north. This trend was also significant for abundance of this species. The biomass and abundance trends for turbot were positive in the NTZ relative to PPA north since the establishment of the area closed for fishing. These flatfish species are caught to varying degrees together with other species, such as plaice, flounder, and sole, in the trawl and gillnet fisheries in the Kattegat (Bergenius *et al.*, 2018). Turbot and brill (*Scophthalmus rhombus*) have been shown in tagging experiments to only have short seasonal migrations in the Kattegat moving to deeper waters in the autumn and winter and returning to shallow waters in the spring (Bagge, 1987). Turbot have also showed positive response with increased abundance and older individuals in an NTZ in the Baltic Sea (Florin *et al.*, 2013). *Microstomus kitt* and *P. platessa* tagging in the English Channel indicated limited migration as opposed to *P. platessa*, which were recaptured in a larger part of the North Sea (Jennings *et al.*, 1993). Tagging of *L. limanda* in the southern North Sea suggests relatively high mobility of adults as reported in Rijnsdorp *et al.*, (1992). Tagging of flatfish species in the NTZ and surrounding Kattegat would be required to further distinguish migration patterns of these species, which could be used to develop the closed areas and an increased protection of these species. The results, nevertheless, show that an NTZ generating an effort reallocation of the local

fishery in Kattegat can increase the local biomass and abundance of demersal fish species despite their mobility. The large fishing closures on Georges Bank (USA and Canada) have led to variable results but included increased biomass of flatfish and bivalve molluscs, while migratory fish like cod and haddock (*Melanogrammus aeglefinus*) gained little protection from these closed fishing areas (Murawski *et al.*, 2000; Link *et al.*, 2005). However, in a later assessment, a combination of strict fishing measures (closures, effort reductions, and gear selectivity) has been considered to have contributed to the recovery of haddock in this area (Brodziak *et al.*, 2008).

Nephrops norvegicus is economically the most important species in the Kattegat with a large fishery (ICES, 2021b) and showed a positive response to the introduction of the NTZ. This result is not surprising, as tagging experiments have shown that movement by *N. norvegicus* is limited and recaptures are close (<9 km) to the site of release (Chapman, 1980,). Given the size of the NTZ investigated here, a large proportion of the *N. norvegicus* could be regarded as residents in the area. The biomass of *N. norvegicus* in the NTZ has more than doubled over time relative to both NTZ control and PPA north, and the biomass is presently higher in the NTZ compared to the other areas. The pattern is more variable in the abundance data, indicating that the main effect is increase in

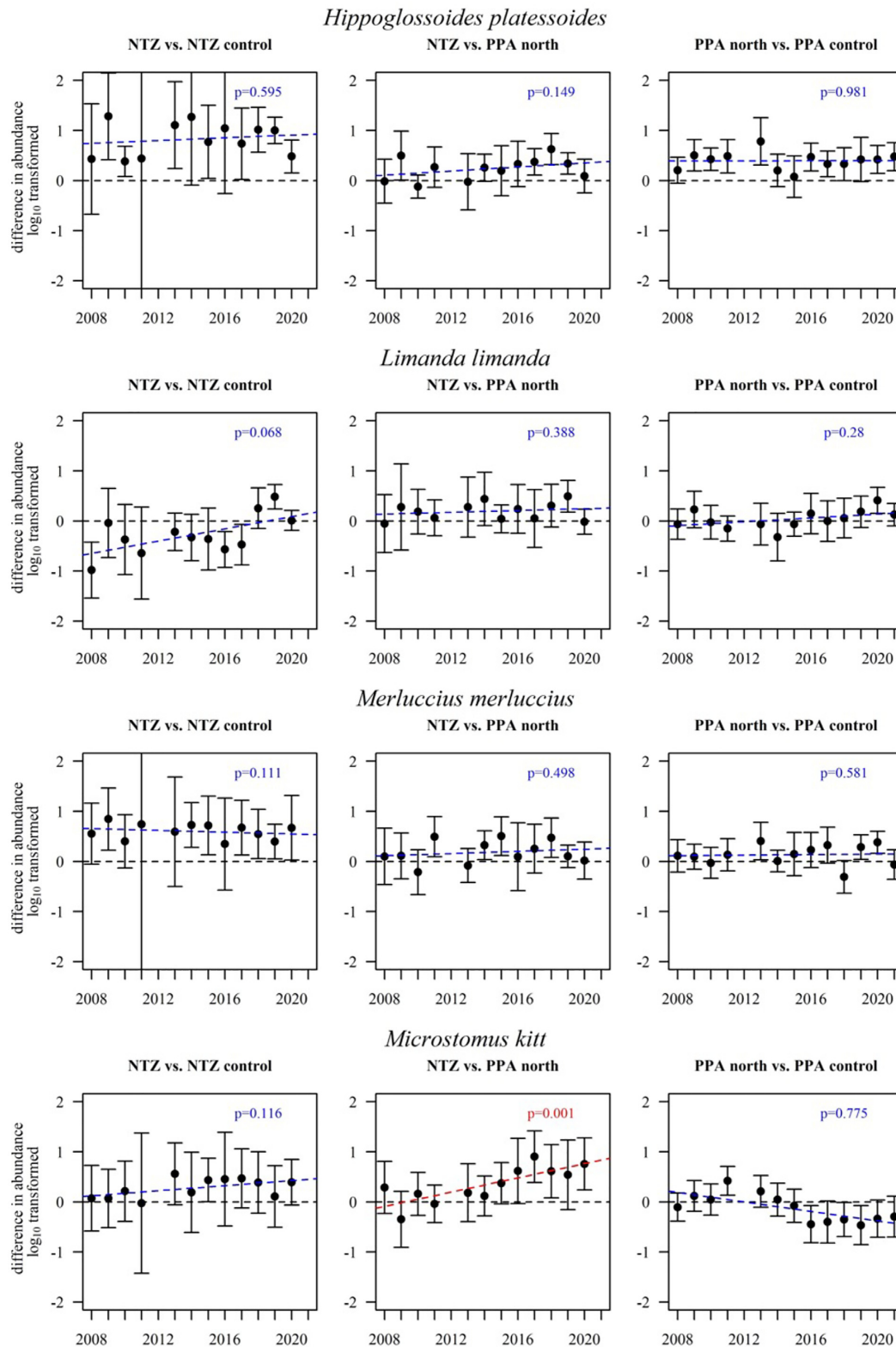


Figure 7. Continued.

the mean size of *N. norvegicus*, but also a trend towards more individuals in the NTZ compared to the fished areas. The *N. norvegicus* stock in Kattegat-Skagerrak is presently fished at levels below F_{msy} (ICES, 2021c), and the results show that significant effects of an NTZ can be detected despite being ex-

ploited at sustainable levels within a management area like the Kattegat.

The NTZ was primarily introduced to protect large individuals of the Kattegat cod stock forming spawning aggregations during the first quarter of the year by closing and displacing

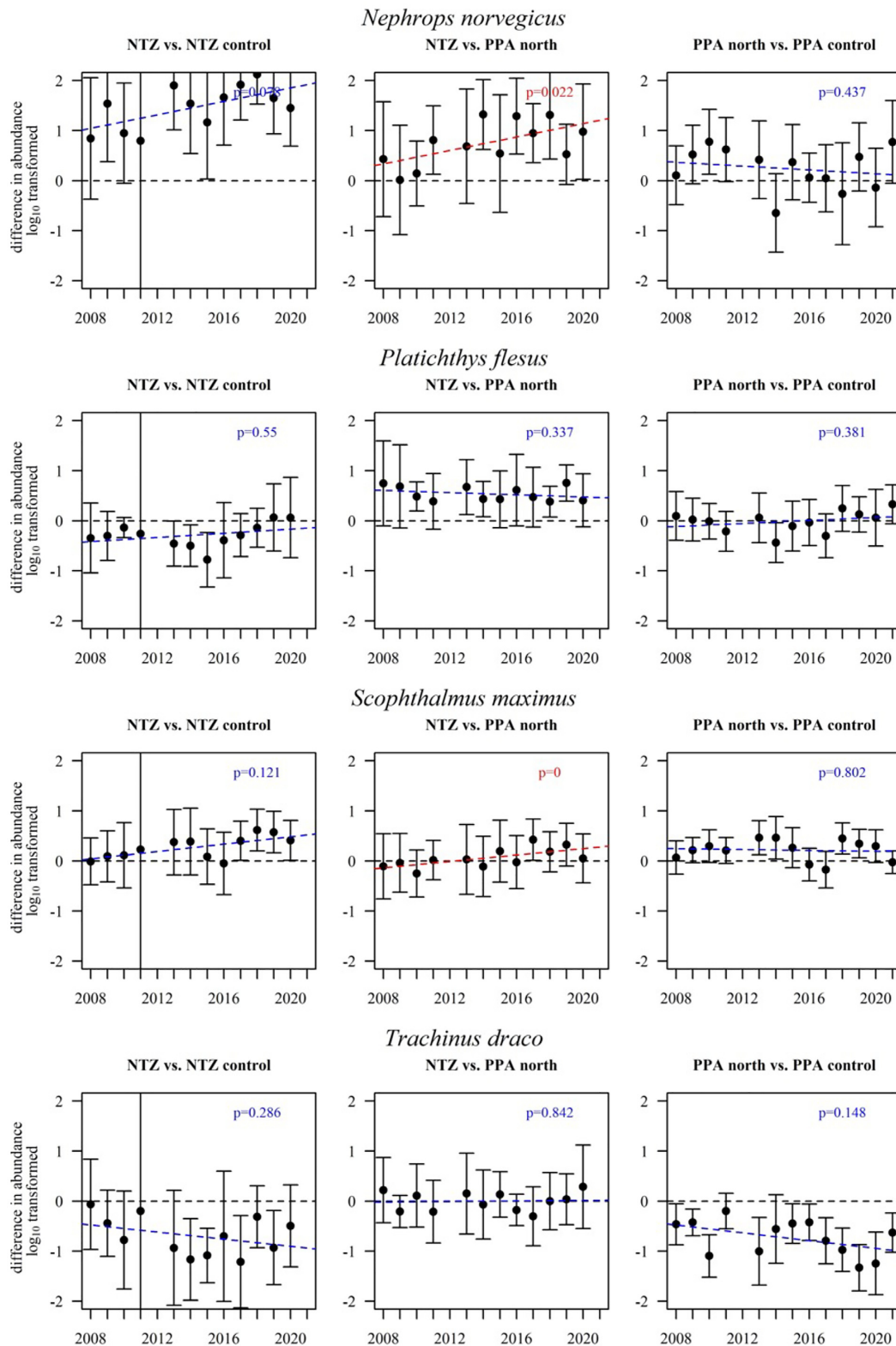


Figure 7. Continued.

fisheries in space and time. Within the NTZ and the PPA north, we found contributions to the shift in the fish assemblage by cod, but no trend in biomass or abundance compared to the control areas during the whole period. The yearly ICES stock assessments for Kattegat cod are in line with our results and

show that cod increased following two relatively successful recruitment events in 2011 and 2012. However, these recruits were partly inflow of North Sea cod, which use the Kattegat area as nursery grounds and migrate back to the North Sea for spawning (ICES, 2021d). The cod stock status deteri-

Table 4. Univariate trend analyses of difference in abundance of species indicating contributing trends to explanatory axes in the CAP analysis of treatment (area) × years.

Species	Parameter	NTZ vs. NTZ control			NTZ vs. PPA north			PPA north vs. PPA control			p_{gls}	
		p_{ARI}	Value	SE	p_{gls}	p_{ARI}	Value	SE	p_{ARI}	Value		SE
<i>A. radiata</i>	Intercept	0.25	0.22	0.17	0.23	0.65	0.43	0.26	0.13	-0.05	0.03	0.19
	Year	0.51	0.01	0.02	0.69	0.14	0.00	0.03	0.90	0.88	0.00	0.33
<i>G. morhua</i>	Intercept	-0.09	0.10	0.11	0.39	0.64	-0.12	0.20	0.55	0.30	0.19	0.15
	Year	0.81	0.01	0.01	0.58	0.17	0.01	0.02	0.61	0.45	-0.02	0.46
<i>H. platessoides</i>	Intercept	-0.04	0.73	0.20	0.00	-0.23	0.10	0.11	0.40	0.39	0.11	0.00
	Year	0.91	0.01	0.03	0.59	0.53	0.10	0.01	0.15	0.98	0.00	0.98
<i>L. limanda</i>	Intercept	0.26	-0.74	0.26	0.02	-0.28	0.13	0.09	0.15	-0.11	0.14	0.45
	Year	0.45	0.06	0.03	0.07	0.46	0.01	0.01	0.39	0.23	0.02	0.28
<i>M. merluccius</i>	Intercept	-0.54	0.68	0.06	0.00	-0.1	0.10	0.13	0.47	0.08	0.09	0.37
	Year	0.08	-0.01	0.01	0.11	0.77	0.01	0.02	0.50	0.335	0.01	0.58
<i>M. kitt</i>	Intercept	0.15	0.09	0.12	0.45	-0.10	-0.17	0.13	0.20	-0.07	0.92	0.94
	Year	0.65	0.03	0.01	0.12	0.81	0.07	0.02	0.00	0.02	-0.01	0.77
<i>N. norvegicus</i>	Intercept	0.23	0.98	0.27	0.00	-0.10	0.26	0.21	0.24	0.80	0.05	0.12
	Year	0.52	0.07	0.03	0.08	0.77	0.07	0.03	0.02	-0.10	0.03	0.44
<i>P. flesus</i>	Intercept	1.00	-0.38	23.92	0.99	-0.03	0.62	0.09	0.00	-0.02	0.03	0.44
	Year	0.00	0.03	0.05	0.55	0.94	-0.01	0.01	0.34	0.16	0.02	0.41
<i>S. maximus</i>	Intercept	0.53	0.01	0.17	0.95	-0.20	-0.20	0.06	0.00	0.24	0.20	0.38
	Year	0.13	0.04	0.02	0.12	-0.51	0.04	0.01	0.00	0.46	0.02	0.24
<i>T. draco</i>	Intercept	0.13	-0.43	0.26	0.13	-0.04	-0.03	0.12	0.83	-0.44	0.21	0.06
	Year	0.72	-0.04	0.03	0.29	-0.04	0.00	0.01	0.84	0.78	0.02	0.15

p_{ARI} represents the autocorrelation between years, p_{ARI} is the significance of the autoregressive component, and p_{gls} is the significance of the generalized least-squares fitted linear model.

orated again from 2016 onwards to reach a historical low in 2020 (ICES, 2022).

Why have cod not recovered?

Kattegat cod have been intensively exploited since the Viking period (Sodeland *et al.*, 2022) and have been overfished with strong indications of a collapsing stock since the beginning of the 1990s (Cardinale and Svedäng, 2004). The reduced catch quotas on Kattegat cod in the beginning of the 21st century had an insignificant effect since cod were still a major bycatch in the mixed non-selective Kattegat bottom-trawl fishery. In line with a proposal from Danish and Swedish scientists to protect the spawning grounds of cod in southeast Kattegat (Hjelm *et al.*, 2008), the Swedish and Danish ministries responsible for fisheries management in the area decided to protect cod using a combination of an NTZ with the introduction of selective gear regulations in PPAs to reduce the bycatch of cod. However, following the bilateral negotiations and pressure from the fishing industry to minimize the impact of closures on the *N. norvegicus* fishery, it was decided to implement a significantly smaller NTZ and PPAs in comparison to the scientific proposal. Closing the NTZ, PPA north and PPA south led as expected to the displacement of the fishery to other areas in Kattegat. Modelling of this displacement indicates that the negative impact of the fisheries on larger cod in the Kattegat decreased because of the NTZ, introduction of selective gears, and changes in effort (Vinther and Eero, 2013; Vinther *et al.*, 2018). Taken together, the measures of establishing the NTZ in combination with the reduction in total effort and increased selectivity decreased the mortality by up to 70% of large cod (Vinther *et al.*, 2018) and coincided in time with the temporary recovery of the cod stock. However, the fishing effort regulation, as part of the long-term cod management plan, was removed in 2016. As a result of the abolishment of the effort regulation, the main incentive to use the highly selective Swedish sorting grid was lost, a gear verified to reduce the bycatch of cod to <1.5% in the *N. norvegicus* fishery (Valentinsson and Ulmestrand, 2008). Instead, from 2017 onwards, cod in Kattegat came under the landing obligation with the rationale that bycatch of cod would be minimized and kept within the bycatch quota through an incentivized selective fishery for *N. norvegicus* and flatfish. The recorded landings of cod below minimum conservation reference size (MCRS) have, however, been negligible and discard rates of cod remain at high levels despite the new regulations (ICES, 2021d). With a diminishing stock size, these bycatches are causing a high fishing mortality for cod in the Kattegat, and ICES estimates that the discards made up ~63% of the catch weight and ~96% of the individuals caught during 2020 (ICES, 2021d).

To protect cod, the size and location of the NTZ have become even more important following the abolishment of the fishing effort regulation leading to increased fishing effort, and a reduction in the use of selective gear outside the NTZ. The present NTZ is a political compromise, i.e. significantly smaller than what was originally proposed by scientists (Hjelm *et al.*, 2008). Additionally, the changes in regulations of the *N. norvegicus* fishery, being the major source of cod bycatch, have thus increased the fishing mortality of cod in recent years. Primarily, the discontinuation of the effort regulation management system effectively removed the cap on the amount of trawling effort allowed, and recent analysis by ICES showed that the effort of the main gears catching cod

has increased to the same levels as in 2009 (ICES, 2021a). The high fishing effort observed presently is partly a consequence of a change in minimum landing size (from 40 to 32 mm carapace length) of *N. norvegicus*, which was accompanied by a significant increase in TAC to account for the fraction of small *N. norvegicus* previously discarded and now retained in the catches. Together these changes in regulations act to increase the main fishery that kill cod as bycatch in the Kattegat further from the effort limitation that was abolished in 2016 and may also have caused changes in fishing patterns. We can summarize that the management have failed to protect and rebuild cod in the Kattegat as the enforced NTZ is too small to protect cod. In addition, the overall effort has increased again, and incentives have been lost to use efficient selective gear in the *N. norvegicus* fishery due to lack of efficient control of the landing obligation.

Conclusion

The introduction of the NTZ with buffer zones in combination with effort regulations providing incentives to use selective gears initially showed promising results with signs of recovery in the age structure and biomass of the cod stock. A local increase in flatfish and *N. norvegicus* biomass in the NTZ relative to control areas also shows that the closing of an area has the potential to protect mobile species in an open system such as the Kattegat. However, when other regulations were undermined, the cod stock showed a rapid deterioration to an all-time low observed in 2020. The reported high discard rates affecting both recruits and adults of cod, despite the landing obligation, are considered a major driver behind the lack of recovery and reinforced depletion of the stock. When NTZs are used to protect main spawning areas, while allowing for the main target fisheries of *N. norvegicus* and flatfish to continue, effective management actions to reduce the bycatch of both juvenile and adult cod need to be in place. Management also needs to be patient as rebuilding an overfished stock takes time and simply depends on the survival of recruits to replace and increase the number of spawners in a stock. However, the situation for the Kattegat cod gives at present little hope for rebuilding the stock. No recovery plan exists, and cod has been classified as a “bycatch species” implying lowered management ambition for this cod stock (EU, 2018), which in the past supported the most important fishery in the Kattegat due to its high productivity.

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Authors' contributions

MS, PB, and HW contributed to the conception of the paper. MS and PB designed and conducted the data analysis. PB, KR, and JL were responsible for the coordination and collection of data. 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.

Conflict of interest statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data underlying this article will be shared on reasonable request.

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