



Effects of bottom trawling and hypoxia on benthic invertebrate communities

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ABSTRACT: Marine benthic habitats in continental shelf regions are increasingly impacted by hypoxia caused by the combination of eutrophication and climate warming. Many regions that have the potential for hypoxic conditions are being fished by mobile bottom-contacting fishing gears. The combined effects of trawling and hypoxia may be synergistic and disproportionately impact benthic fauna, or they may act antagonistically, leading to smaller trawl impacts in hypoxic areas. Yet, few studies have quantified how bottom trawling and hypoxia interact to affect benthic communities. Here we examine these combined effects on benthic community biomass and abundance, the number of large organisms, the longevity distribution of the community and the vertical position of fauna in the sediment in the southern Baltic Sea. We find large declines in benthic biomass and abundance that co-occur with declines in near-bed oxygen concentrations from 5.8 to 0.8 ml O₂ l⁻¹. Conversely, no relationships and weak positive relationships are found between bottom trawl disturbance and benthic community biomass and abundance. No interacting effects between hypoxia and trawling are detected. Our findings therefore highlight a low likelihood of synergistic impacts of bottom trawling and hypoxia on the benthic communities studied. These results suggest that management may prioritize benthic protection from fishing in regions that are not in a state of oxygen stress.

KEY WORDS: Bottom-trawling · Hypoxia · Baltic Sea · Macrofauna · Body size · Longevity · Vertical position · Sediment

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1. INTRODUCTION

Marine benthic habitats in continental shelf regions are increasingly impacted by eutrophication-induced hypoxia (Diaz & Rosenberg 2008). Hypoxic

regions are predicted to expand due to the warming of shelf waters with climate change, which increases both the oxygen demand and the strength of stratification of the water column (Breitburg et al. 2018). Many periodic hypoxic regions, such as the Baltic

and Adriatic Seas, are currently also being fished by mobile bottom-contacting fishing gears, and these bottom trawl fisheries are the most widespread source of anthropogenic physical disturbance to seabed habitats (Amoroso et al. 2018).

Since management of nutrient loads and subsequent declines of hypoxic regions might take decades to occur (Andersen et al. 2017, Van Meter et al. 2018, Ballard et al. 2019), strategic management of bottom fisheries may be used to alleviate some of the impacts on benthic fauna and the ecosystem. Such strategic management requires quantifying the cumulative impacts of the 2 pressures on benthic fauna. The cumulative impacts of trawling and hypoxia may be synergistic when hypoxic conditions make organisms more vulnerable to bottom fishing disturbance. Such effects may occur in areas where hypoxic and anoxic bottoms result in upward migration of burrowing organisms to the sediment surface (Pihl et al. 1992, Nilsson & Rosenberg 1994), thereby making these organisms more vulnerable to damage by bottom gears dragged along the seabed surface. Synergistic effects have also been proposed for brittle stars that became more vulnerable to trawl disturbance due to arm-tipping behaviour, i.e. the elevation of the central disk to escape the low oxygen concentrations closest to the seafloor (Baden et al. 1990, Diaz & Rosenberg 1995). Under this scenario, management measures that protect hypoxic or hypoxia-prone areas from bottom fishing may thus disproportionately benefit benthic fauna by reducing fishing-derived mortality of hypoxia sensitive fauna, and thus lowering the risk of benthic habitats being pushed into a permanently altered state (Riedel et al. 2016). Alternatively, when hypoxia leads to asphyxiation of sessile fauna and/or migration of mobile fauna, leading to a depauperate state or even absence of benthic fauna, trawling may have a negligible additional impact on the benthos. Animals that can survive hypoxia events may also have life-history characteristics that make them less vulnerable to trawling (e.g. fast growth and high dispersal) and trawling may not affect these species significantly. Fisheries management measures in such areas will have only limited benefits to the benthic ecosystem.

The above highlights that depending on the cumulative effects of bottom trawling and hypoxia, management of human impacts on benthic habitats may either prioritize protection from fisheries of hypoxic areas or prioritize the protection of areas that are non-hypoxic. So far, few studies have quantified the interactive effects of bottom trawling and hypoxia on benthic communities, limiting the development of

management plans that consider the cumulative effects. On a continental slope off Vancouver Island, bottom trawling continues to impact benthic communities affected by an oxygen minimum zone, suggesting cumulative impacts that are either additive or synergistic (De Leo et al. 2017).

Here we study the effects of bottom trawling and hypoxia on benthic communities in the Baltic Sea. Throughout its historic past the Baltic Sea has seen hypoxic events on the seafloor (natural and human induced), mainly due to limited water exchange with the Atlantic and in recent decades excess nutrient input (Carstensen et al. 2014, Andersen et al. 2017). The Baltic Sea's benthic communities lack large habitat forming epifauna, particularly in the deeper areas. This is due to a low salinity, which in combination with the Baltic's historic hypoxic past, has created the characteristically low species diversity, but highly abundant benthic communities (Bonsdorff 2006). Most of these benthic communities consist of short-lived fauna (Törnroos et al. 2015, 2019, van Denderen et al. 2020), which are predicted to be largely resilient to bottom trawling disturbance (Hidink et al. 2019). Yet, approximately 2 thirds of the Baltic Sea bottom trawl fishing footprint occurs in areas with seasonal oxygen concentrations $<3.2 \text{ ml O}_2 \text{ l}^{-1}$ that may impact benthic organisms (van Denderen et al. 2020). It is therefore an area where trawling impacts may be severely underestimated if synergistic effects are found to occur. The objective of this study is to estimate interactive effects of bottom trawling and hypoxia on macrofaunal biomass and abundance, large-bodied macrofauna, benthic community longevity and the vertical position of fauna in the sediment. The studied stations ranged over a gradient in near-bed oxygen concentrations from 0.8 to $5.8 \text{ ml O}_2 \text{ l}^{-1}$ and in trawling intensity from little trawl disturbance to up to 7 bottom trawl events per year. Our findings highlight a low likelihood of synergistic effects between bottom trawling and hypoxia on the benthic communities studied.

2. MATERIALS AND METHODS

2.1. Study area

The effects of bottom trawling and hypoxia were examined over a gradient of oxygen concentration and bottom trawling intensity in the Southern Baltic Sea in Polish waters (Fig. 1). The area was still an active fishing ground in 2018, the year of sampling, with bottom trawling by otter trawls that target cod and

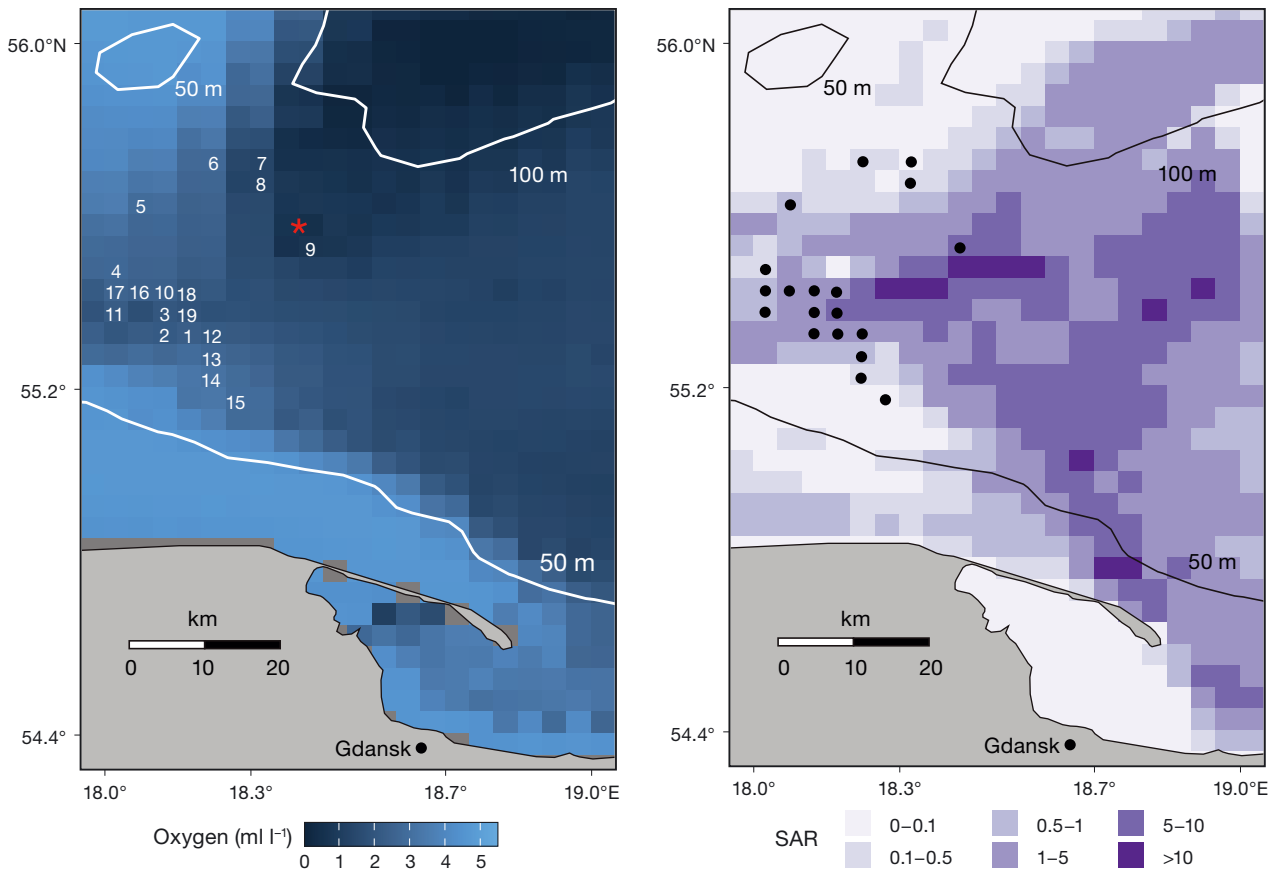


Fig. 1. Sampling station locations in the southern Baltic Sea (numbers correspond to Table S1). The oxygen concentrations (left) show the lowest seasonal concentration in the year based on modelled bottom oxygen concentrations from an ecosystem model (see van Denderen et al. 2020). The red asterisk shows a location close to Stn 9 with time-series of near-bed oxygen measurements (see Fig. 3). The trawling intensity data (right) show average SAR (swept area ratio per year) values for the period 2013–2017. Depth contours were extracted from the Baltic Sea Hydrographic Commission (2013). The oxygen and depth data were solely used to select sampling stations as depth and oxygen data used in the analysis were measured in-situ at each station

flounder (but note that cod fishing was prohibited in 2019). The area was selected as earlier work showed it has gradients in average annual oxygen concentration and trawling intensity (van Denderen et al. 2020).

We selected sampling stations that covered a wide range of expected oxygen concentrations and trawling intensities in a limited depth range (62–102 m; Table S1 in the Supplement at www.int-res.com/articles/suppl/m694p013_supp.pdf), and aimed to cover all crossed combinations of trawling and oxygen to end up with a design where the effects of trawling and oxygen could be disentangled. Unsurprisingly, we could not identify any stations that had a high fishing effort at very low oxygen, as no fish can survive in those conditions, but we did sample several stations with fishing and relatively low oxygen concentrations (Fig. 2, Table S1). All sampling stations were found in an area of 30 × 62 km, and the distance from any station to its nearest neighbour varied between 3 and 18 km.

2.2. Sampling of benthic fauna

Sampling was carried from on board the research vessel RV Oceanograf between 3 and 8 September 2018. Five replicate box core and 2 replicate dredge samples were collected from each station. The box core was used to collect information on infauna and small epifauna, and a dredge for larger epifauna and more mobile species. Box core samples (sampling area 0.06 m² per core, average seafloor penetration depth 24 cm) were taken in a star pattern, one at the selected position and 4 more, 100 m away in each direction, using the vessel's Dynamic Positioning System. At times, the box core came up empty or lost most of the sample before retrieval because the jaws did not close fully when pebbles or stones jammed the mechanism. When sampling was unsuccessful, the ship was moved 10s of meters and the box core redeployed. Three 4.5 cm diameter sub-cores up to a

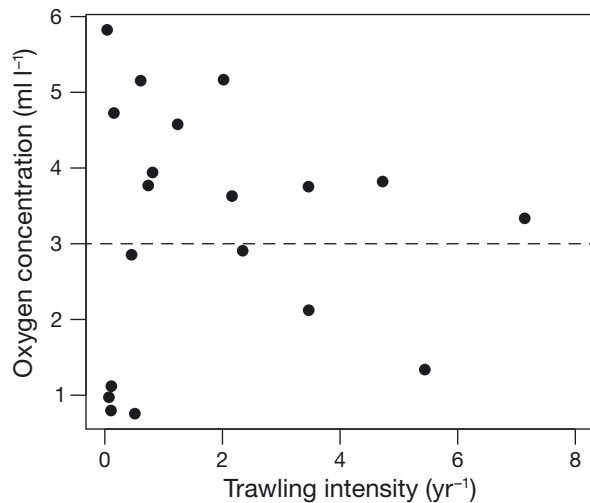


Fig. 2. Trawling intensity (average SAR) and oxygen concentration of the sampling stations. We analysed all sampling stations together to examine the combined effect of trawling intensity and oxygen concentration, as well as a subset of stations with oxygen concentrations $>3 \text{ ml O}_2 \text{ l}^{-1}$ (stations above dashed line) to explore trawling effects in isolation. This threshold was chosen as no effect of oxygen on benthic biomass or abundance is observed above this concentration (Fig. S2)

maximum depth of 17 cm were collected from the first 2 intact box core samples collected at each station to assess the vertical distribution of fauna in the sediment in areas of different oxygen and fishing levels. Each sub-core was sliced into 4 sections (0–2 cm, 2–4 cm, 4–8 cm, >8 cm) and sieved to obtain the fauna at different sediment depths. The rest of the box core sample was sieved through a 0.5 mm sieve. Most samples had a solid clay layer below a surficial mud, sand and/or gravel layer (surficial layer was ca. 8–18 cm deep); the solid clay layer was not sieved as macrofauna cannot (and did not) occur in this solid layer. To separate the smaller fauna from the remaining gravel and stones, samples were back-washed at least 7 times to obtain the fauna, by adding water, stirring the sample and draining the water over a sieve to capture suspended animals. The remaining sediment was checked for any further large fauna.

Semi-quantitative dredge samples were obtained using an Agassiz trawl type dredge (56 wide \times 31 cm high, outer net mesh size 1×1 cm, inner net mesh size 0.5×0.5 cm), except for Stn 1 (see below). The dredge was towed for 2 min at 1 knot and was generally full on retrieval. Samples were searched visually for fauna. In most dredge samples where fauna was present, a subsample was taken that was searched visually and abundance and biomass of the total

sample was afterwards calculated based on the relative size of the subsample. Stn 1 was sampled with a Naturalist dredge (60 cm wide \times 30 cm high) that was towed for 10 and 5 min at 1 knot. We expect that the alternative methodology did not affect the resulting data in Stn 1 as, in all cases, the dredge was full on retrieval (it likely filled up quickly and stopped sampling afterwards). Inspection of the data does not suggest the dredge data in Stn 1 is an obvious outlier. Since the dredge samples provided semi-quantitative information, the dredge was only used as a complementary method to the box core (note that both sampling devices show similar results).

All biota in box core and dredge were identified to the lowest taxonomic level possible and their individual wet weight was measured. For some species in some dredge samples, abundance was greater than approximately 100 individuals. For each of these species and samples, length was measured for all individuals whereas weight was measured for 50 individuals of a range of lengths. For the remaining individuals, we converted length to weight using the established length–weight relationship of the 50 individuals.

2.3. Environmental conditions

A sub-core measuring 4 cm in diameter was collected from the first box core sample at each station to determine the sediment grain size composition of the upper 4 cm of the seabed. This sub-core sample did include most gravel but not the larger gravel/pebbles. Particle size distributions were determined using a Malvern laser diffraction particle sizer (Blott & Pye 2001). Sediment particle analysis showed that most of the stations had a high percentage of sand (Table S1). Visual inspection of the box core samples showed that the sandy sediment was sometimes mixed with pebbles, gravel or mud and typically accompanied by a deeper layer of glacial clay. Some stations had ferromanganese nodules on the seafloor surface. Despite the fact that most stations had largely similar depth and sediment conditions, there were larger differences in some of these variables in a few stations (Table S1, Fig. S1). After verifying that results were robust against the exclusion of these stations, we decided to maintain all stations within our analysis.

Bottom water was collected at 20 cm above the seabed with a Niskin bottle and oxygen saturation (YSI model 58) and temperature and salinity (WTW Multiset 340i with TetraCon 325) were immediately measured after bringing the sample to the surface.

Three replicate water samples were collected at each station (with the exception of the first few stations, where only a single measurement was taken) (Table S1). Temperature and salinity information was used to convert near-bed oxygen saturation into oxygen concentration in ml per litre following Benson & Krause (1984) (Table S1). About a quarter of the stations were azoic and sediment had a strong smell of H_2S and a clear black surface layer. Of these azoic stations, only 3 had measured near-bed oxygen concentrations below $1 \text{ ml O}_2 \text{ l}^{-1}$.

In addition to the oxygen measurements taken at the sampling stations, we analysed a time series of near-bed oxygen concentration measurements collected from a nearby site at 90 m depth (red asterisk in Fig. 1) between 2012 and 2018. Monthly oxygen concentration was calculated by averaging oxygen measurements at depths less than 5 m from the seafloor per month (where available). Data used were obtained from HELCOM secretariat and based on ICES dataset on Ocean Hydrography. Lastly, we compared the field measurements of oxygen with model simulations of daily bottom oxygen concentrations from an ecosystem model simulation. This model simulation is based on the coupled system ERGOM-MOM with a horizontal grid of 1 nautical mile covering the whole Baltic Sea (Neumann et al. 2017, 2020, 2021). The biogeochemical module ERGOM simulates the marine carbon, nitrogen and phosphorus cycles, while production and consumption of oxygen is included in the biogeochemical processes via stoichiometric ratios. The modelled oxygen concentrations have been validated against recent observations, e.g. Meier et al. (2018). We extracted 3 different oxygen metrics from the model to obtain an indication how the simulated temporal history of each sampling station correlates with the oxygen field measurement: (1) the mean simulated oxygen concentration of the preceding 6 mo, (2) the closest hypoxia event with high likelihood of mass-mortality pre-sampling, defined as the first day in a period of 20 consecutive days with simulated oxygen concentrations below $0.5 \text{ ml O}_2 \text{ l}^{-1}$, and (3) the number of days in the last 2 yr preceding sampling where simulated oxygen concentrations are above $0.5 \text{ ml O}_2 \text{ l}^{-1}$. The oxygen threshold of $0.5 \text{ ml O}_2 \text{ l}^{-1}$ was chosen as mass-mortality of benthic fauna typically occurs below this value (Diaz & Rosenberg 1995).

Bottom trawling intensity data were obtained at a $0.05^\circ \times 0.05^\circ$ grid resolution (ICES 2019) and expressed as the ratio of the area that is swept each year by trawl gears relative to the total SAR surface area (hereafter termed swept-area-ratio, SAR). The grid

resolution used implies that we represent trawling intensity on a relatively large spatial scale that may overlook local effects along the trawl passage. We used average SAR values per grid cell for the period 2013–2017, since we were interested in chronic effects of fishing, and recovery following trawling disturbance may last >1 yr (Hiddink et al. 2017). An average intensity (based on multiple years) is therefore expected to better represent the state of a community than a single-year estimate.

2.4. Data analysis

We analysed the effect of trawling intensity and oxygen concentration on community biomass and abundance, the number of large organisms, the biomass–longevity distribution of the benthic community and the vertical position of fauna in the sediment. In all analyses, we estimated biomass and abundance as the sum of all box core or dredge samples per station. All results show biomass of bivalves with shell. Since the biomass patterns are strongly driven by bivalve weights, we verified that similar results are obtained when shell-free wet weight is used (based on a wet weight to shell-free wet weight conversions as shown in Table S2). The data have been deposited in the Marine Data Archive repository (van Denderen et al. 2022). Scripts and output are available on Github (<https://doi.org/10.5281/zenodo.5579600>). All statistical analyses were done in program R (version 4.1.0; R Core Team 2021) using the R packages VGAM (1.1-5; Yee 2021) and vegan (2.5-7; Oksanen et al. 2020).

2.4.1. Community biomass and abundance

We tested the effect of trawling intensity and oxygen concentration and their interaction on community biomass and abundance with a Tobit regression model and selected the best model using the Akaike Information Criterion (AIC); when models differed by <2 AIC-units, the model with fewest parameters was selected. Tobit regression is designed to estimate relationships assuming a normal distribution for the response variable with left/right censoring, i.e. where the response variable data above/below a threshold value are censored (Tobin 1958). We used Tobit regression as it was expected that a range of sampling stations at low oxygen concentrations had zero biomass and abundance and we therefore set the threshold for censoring our data at zero biomass

and abundance. The full dataset was used to examine the combined effect of trawling intensity and oxygen concentration, whereas a subset of stations with oxygen concentrations $>3 \text{ ml O}_2 \text{ l}^{-1}$ was used to examine the effect of bottom trawling in oxygenated conditions (Fig. 2). The oxygen threshold value ($3 \text{ ml O}_2 \text{ l}^{-1}$) was chosen because benthic biomass and abundance did not correlate with oxygen at values above this threshold (Fig. S2). The value has also some empirical basis as results of a meta-analysis indicate that concentrations above $3.2 \text{ ml O}_2 \text{ l}^{-1}$ (equivalent to $4.6 \text{ mg O}_2 \text{ l}^{-1}$) cause notably less mortality in benthic fauna (Vaquer-Sunyer & Duarte 2008). We analysed the effect of trawling intensity on benthic biomass and abundance in this data subset using linear regression.

2.4.2. Large organisms

Since the impact of bottom trawling is larger on larger benthic organisms ($>4 \text{ mm}$) (McLavery et al. 2020), we included a separate analysis to study the effect of oxygen concentration and trawling intensity on the abundance of large individuals in the benthic community. The analysis used the box core data and the same Tobit regression model as described above. We used 2 length thresholds, $>4 \text{ mm}$ and $>15 \text{ mm}$. Since we did not measure the length of the sampled animals in the box core data, we approximated individual length using length–weight relationships from the literature (Table S3).

2.4.3. Community longevity

Long-lived fauna are more impacted by bottom trawling as they recover more slowly (Rijnsdorp et al. 2018, Hiddink et al. 2019). We therefore examined the effect of trawling intensity and oxygen concentration on the longevity biomass distribution of the benthic community. We used the box core data to study changes in the biomass–longevity composition as these data provide a more controlled estimate of biomass (the dredge was full upon retrieval, as noted above). Using information on species longevity of benthic fauna in the Baltic Sea (Törnroos & Bonsdorff 2012, van Denderen et al. 2020), we classified biota in 3 longevity groupings: maximum lifespan of 0–1, 1–3 and 3–10 yr (no fauna were classified with a longevity $>10 \text{ yr}$). The resulting taxon-by-trait matrix was combined with the taxon biomass-by-station ($\text{g wet weight m}^{-2}$) matrix to create the final station-by-

trait matrix. We used a PERMANOVA analysis to examine if changes in trawling intensity and/or oxygen concentrations had a significant effect on the distribution of benthic biomass in these 3 longevity groupings. This analysis was done on absolute and fractional biomass values per longevity grouping and sampled station.

2.4.4. Vertical position

A PERMANOVA analysis was carried out to examine the effect of oxygen concentration and trawling intensity on the vertical distribution (0–2, 2–4, 4–8 and $>8 \text{ cm}$) of fauna in these 4 sediment layers within the sediment. Since the number of observations was low in the vertical sub-cores, we estimated biomass and abundance for each sediment layer as the sum of all observations in all sub-cores per sampled station. The analyses were done on absolute and fractional abundance/biomass data per vertical section and sampled station. We did not examine species-specific vertical changes in relation to oxygen concentrations and trawling intensity (but see Figs. S3 & S4 for the vertical biomass and abundance distribution per species summed across all stations).

3. RESULTS

3.1. Temporal and spatial stability in fishing and near-bed oxygen

We used average trawling intensities per grid cell for the period 2013–2017 to examine the chronic effects of fishing. A cross-comparison of trawling intensities between all years showed clear correlations, with an average Pearson product-moment correlation of 0.89, which implies there is temporal stability in the spatial fishing patterns studied. The studied gradient in trawling intensities was conserved in 2018, the year of sampling (Pearson correlation of 0.85 when compared with the annual average for the period 2013–2017), although the average level of fishing in the area in 2018 was marginally lower (average SAR in 2018 for all stations was 1.0, whereas it varied between 1.3 and 2.9 in the other years).

We observed large fluctuations between months in the time series of near-bed oxygen concentrations (Fig. 3a), with maximum concentrations close to 5 and minimum less than $0.5 \text{ ml O}_2 \text{ l}^{-1}$. The median near-bed oxygen concentrations were lower

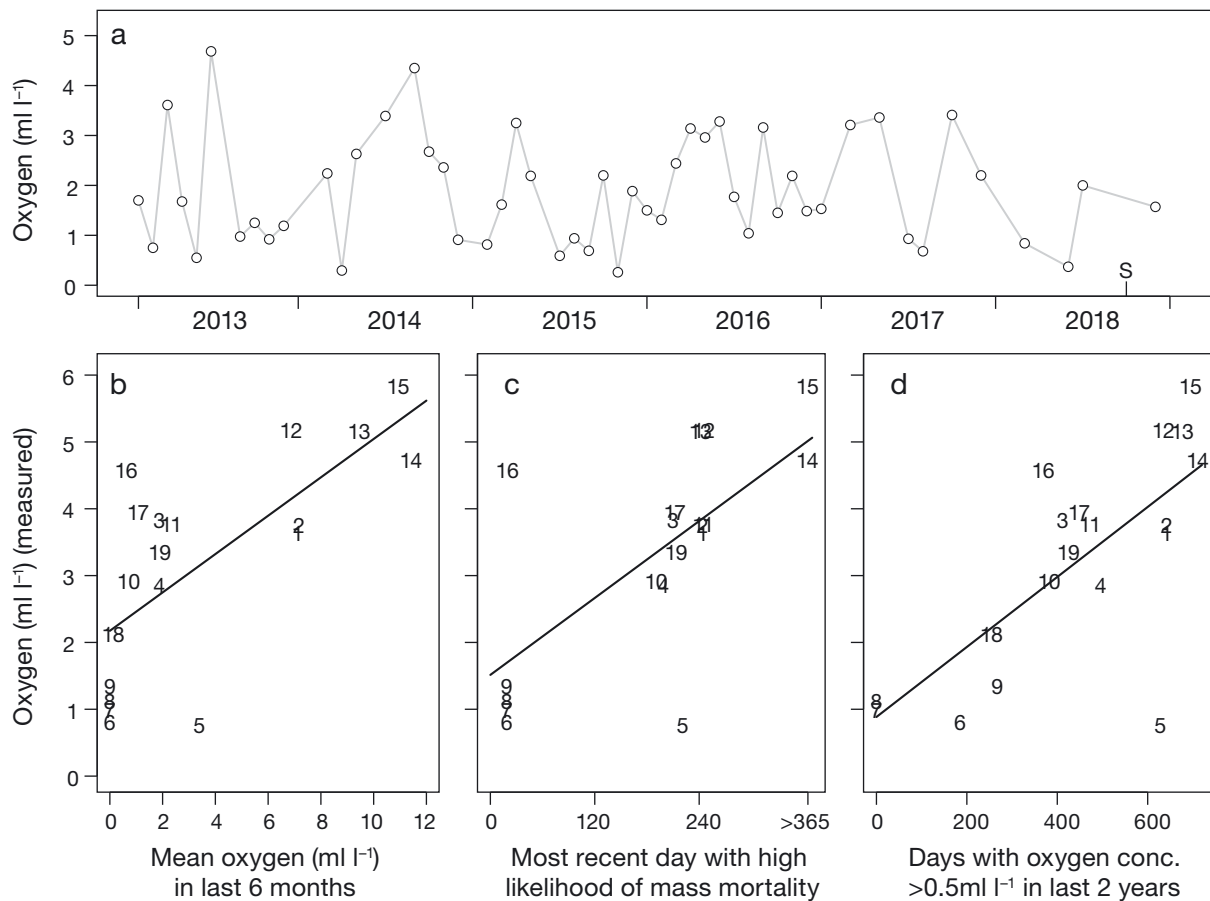


Fig. 3. (a) Time series of near-bed oxygen concentrations at a location close to Stn 9 (red asterisk in Fig. 1) from 2013 to 2018. The letter 'S' indicates when we sampled the study area. (b–d) Comparison of measured near-bed oxygen concentrations with 3 metrics of oxygen from ecosystem model simulations for the same locations (numbers correspond to Fig. 1 and Table S1): (b) mean oxygen concentration of the preceding 6 mo, (c) the most recent hypoxia event with high likelihood of mass-mortality prior to sampling (Fig. S7), and (d) number of days preceding sampling where simulated oxygen concentrations were above 0.5 ml l^{-1} within previous last 2 yr. Lines were constructed using linear regression

in summer and autumn (Q3 and Q4; Fig. S5), although very low oxygen concentrations have been measured in all seasonal quarters. These fluctuations highlight that there are significant uncertainties in the temporal history of near-bed oxygen in sampled stations. Despite these large fluctuations, the measured near-bed oxygen gradient in the field is correlated (Pearson correlation between 0.70–0.72) with 3 different oxygen metrics based on ecosystem model simulations (Fig. 3b–d; see Fig. S6 for simulated time series per station). The correlations imply that the benthic communities at sampling stations with high measured oxygen conditions have likely experienced healthier oxygen conditions prior to sampling than benthic communities at low oxygen conditions. It is therefore expected that the oxygen gradient measured in the field is coherent in time and representative for

describing the state of the benthic community, albeit with noise due to temporal fluctuations in the concentrations (see Section 4.1).

3.2. Community biomass and abundance

The biomass of the community was dominated by the bivalves *Astarte elliptica*, *Mytilus trossulus* and *Macoma balthica*. Together these species comprised 90% of total biomass in the box core data and 99% in the dredge. Abundance was dominated by the bristleworm *Scoloplos armiger* (27% of total abundance) in the box core data and by *A. elliptica* (81% of total abundance) in the dredge. No biota was found at stations with oxygen concentrations below 2 ml l^{-1} . All stations with oxygen concentrations above 3 ml l^{-1} had some fauna.

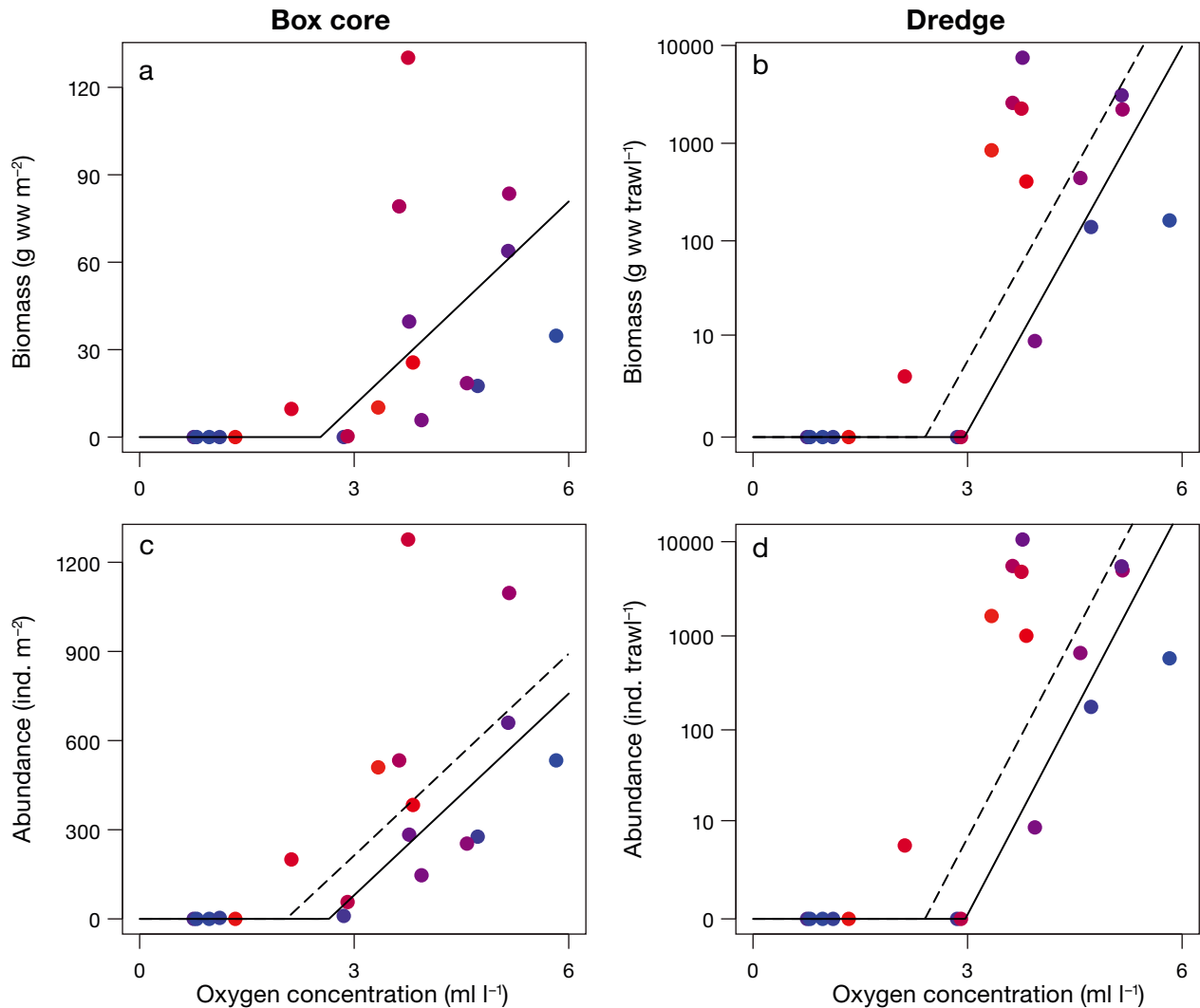


Fig. 4. Relationships between oxygen concentration and (a,b) total faunal biomass and (c,d) abundance collected using the box core (a,c) and dredge (b,d). Lines are fitted with a Tobit-regression. In (b–d) where trawling intensity is part of the best model (Table 1), the solid lines show the prediction without fishing (SAR = 0) and the dashed lines with SAR = 2. Points are coloured using a linear colour gradient from the station with the lowest (blue, SAR = 0.04) to highest (red, SAR = 7.14) trawling intensity. The dredge data is $\log_{10}(x + 1)$ transformed because there are 4 orders of magnitude variation between stations

We found a significant positive relationship between oxygen concentration and community biomass and abundance for both box core and dredge data (Fig. 4). In 3 of the 4 datasets, trawling intensity had a positive effect (Table 1). An interaction term between oxygen concentration and trawling intensity did not provide a better fit to any model (note that for box core abundance the interaction term has a p-value of 0.05, but the AIC value differed less than 2 units from a model without the interaction; Table 1). When analysing a subset of sampled stations with relatively high oxygen concentrations ($>3 \text{ ml l}^{-1}$), trawling intensity had no relationship with community biomass or abundance (Fig. 5).

To explore further the community response to trawling, we examined changes in biomass along the gradient in trawling intensity for the 6 most dominant species (in terms of biomass) in the box core samples and the 5 most dominant in the dredge samples collected at stations with relatively high oxygen concentrations ($>3 \text{ ml l}^{-1}$). It is worth noting that all species have a non-significant relationship with oxygen concentration in this subset (not shown). We found no significant relationship between biomass and trawling intensity for most dominant species, except for the priapulid worm *Halicryptus spinulosus*, for which a significant positive relationship was observed between its biomass

Table 1. Model selection and coefficients. B: benthic biomass; A: benthic abundance; T: trawling intensity (yr^{-1}); O: measured oxygen concentration (ml l^{-1}). Tobit regression lower limit was set at zero biomass/abundance. The Tobit model includes an ancillary statistic, termed σ , which describes the log-standard deviation of the latent variable. Asterisks show best model based on AIC (when models differ less than 2 AIC-units, the model with fewest parameters is selected). Since Hauck-Donner effects were observed in some p-value estimates using Wald statistics, p-values were obtained by conducting a likelihood ratio test

Model	σ	p-values	AIC
Box core biomass (g ww per m²)			
$B = -59.04 + 23.31 \cdot O$	3.56	$p_O < 0.001$	148.4*
$B = -77.91 + 25.28 \cdot O + 5.73 \cdot T$	3.52	$p_O < 0.001$; $p_T = 0.20$	148.8
$B = -53.68 + 18.47 \cdot O - 13.32 \cdot T + 5.78 \cdot T \cdot O$	2.27	$p_O = 0.01$; $p_T = 0.41$; $p_{T \cdot O} = 0.21$	149.2
Box core abundance (per m²)			
$A = -442.18 + 218.13 \cdot O$	5.73	$p_O < 0.001$	223.8
$A = -598.88 + 226.18 \cdot O + 67.05 \cdot T$	5.64	$p_O < 0.001$; $p_T = 0.06$	222.4* ^a
$A = -368.60 + 155.34 \cdot O - 152.55 \cdot T + 69.04 \cdot T \cdot O$	5.53	$p_O = 0.005$; $p_T = 0.20$; $p_{T \cdot O} = 0.05$	220.5
Dredge biomass (g ww per trawl)			
$\text{Log}_{10}(B+1) = -2.57 + 1.16 \cdot O$	0.24	$p_O < 0.001$	52.4
$\text{Log}_{10}(B+1) = -3.87 + 1.31 \cdot O + 0.36 \cdot T$	0.10	$p_O < 0.001$; $p_T = 0.03$	49.5*
$\text{Log}_{10}(B+1) = -2.70 + 1.01 \cdot O - 0.27 \cdot T + 0.19 \cdot T \cdot O$	0.03	$p_O < 0.001$; $p_T = 0.60$; $p_{T \cdot O} = 0.21$	49.9
Dredge abundance (per trawl)			
$\text{Log}_{10}(A+1) = -2.78 + 1.26 \cdot O$	0.30	$p_O < 0.001$	53.8
$\text{Log}_{10}(A+1) = -4.28 + 1.44 \cdot O + 0.41 \cdot T$	0.14	$p_O < 0.001$; $p_T = 0.02$	50.2*
$\text{Log}_{10}(A+1) = -3.02 + 1.12 \cdot O - 0.24 \cdot T + 0.19 \cdot T \cdot O$	0.07	$p_O < 0.001$; $p_T = 0.66$; $p_{T \cdot O} = 0.22$	50.7
Box core abundance (individuals >4 mm per m²)			
$A = -536.92 + 221.99 \cdot O$	5.76	$p_O < 0.001$	210.3
$A = -843.04 + 254.76 \cdot O + 90.91 \cdot T$	5.62	$p_O < 0.001$; $p_T = 0.02$	207.0*
$A = -541.84 + 174.36 \cdot O - 99.54 \cdot T + 56.96 \cdot T \cdot O$	5.55	$p_O = 0.005$; $p_T = 0.45$; $p_{T \cdot O} = 0.12$	206.7
Box core abundance (individuals >15 mm per m²)			
$A = -47.20 + 17.80 \cdot O$	2.92	$p_O < 0.001$	114.7*
$A = -62.41 + 19.92 \cdot O + 3.30 \cdot T$	2.89	$p_O < 0.001$; $p_T = 0.21$	115.2
$A = -47.80 + 16.21 \cdot O - 5.80 \cdot T + 2.61 \cdot T \cdot O$	2.86	$p_O < 0.001$; $p_T = 0.58$; $p_{T \cdot O} = 0.37$	116.4
^a Note that a model without trawling intensity (Model 1) differs less than 2 AIC values from the selected model (Model 2). Yet, a model with interaction (Model 3) is more than 3 AIC units lower than Model 1. Model 2 is therefore selected as best intermediate model.			

and trawling in both dredge and box core data (Fig. 6).

3.3. Large organisms

Individuals larger than 4 mm comprised >99% of total biomass and 85% of total abundance. For these individuals ($n = 1587$), we found a significant positive relationship between oxygen concentration and abundance and between trawling intensity and abundance (Table 1). Individuals larger than 15 mm comprised 30% of total biomass and 6% of total abundance. For these individuals ($n = 110$), there was again a significant positive relationship between oxygen concentration and abundance, whereas tobit regression indicated no support for a model that includes trawling (Table 1). The dominant species contributing to the '>15 mm' group were the bivalve *A. elliptica* ($n = 34$), the isopod

Saduria entomon ($n = 19$) and the bristleworm *Terebellides stroemii* ($n = 16$). The number of individuals >15 mm varied among stations between 0 and 70 per m²; high numbers were only found in areas with relatively high oxygen concentrations (>3.5 ml l⁻¹) (Fig. 7).

3.4. Community longevity

Almost 90% of the total biomass was grouped as fauna with longevities between 3 and 10 yr. PERMANOVA analysis showed no support for a change in the biomass longevity composition of the community with changes in oxygen concentration and/or trawling intensity (Table S4). Since the longevity of the dominant bivalve *Astarte elliptica* was uncertain in our sampling region, we verified that the same results were obtained when *Astarte elliptica* was classified with a different maximum age (Text S1).

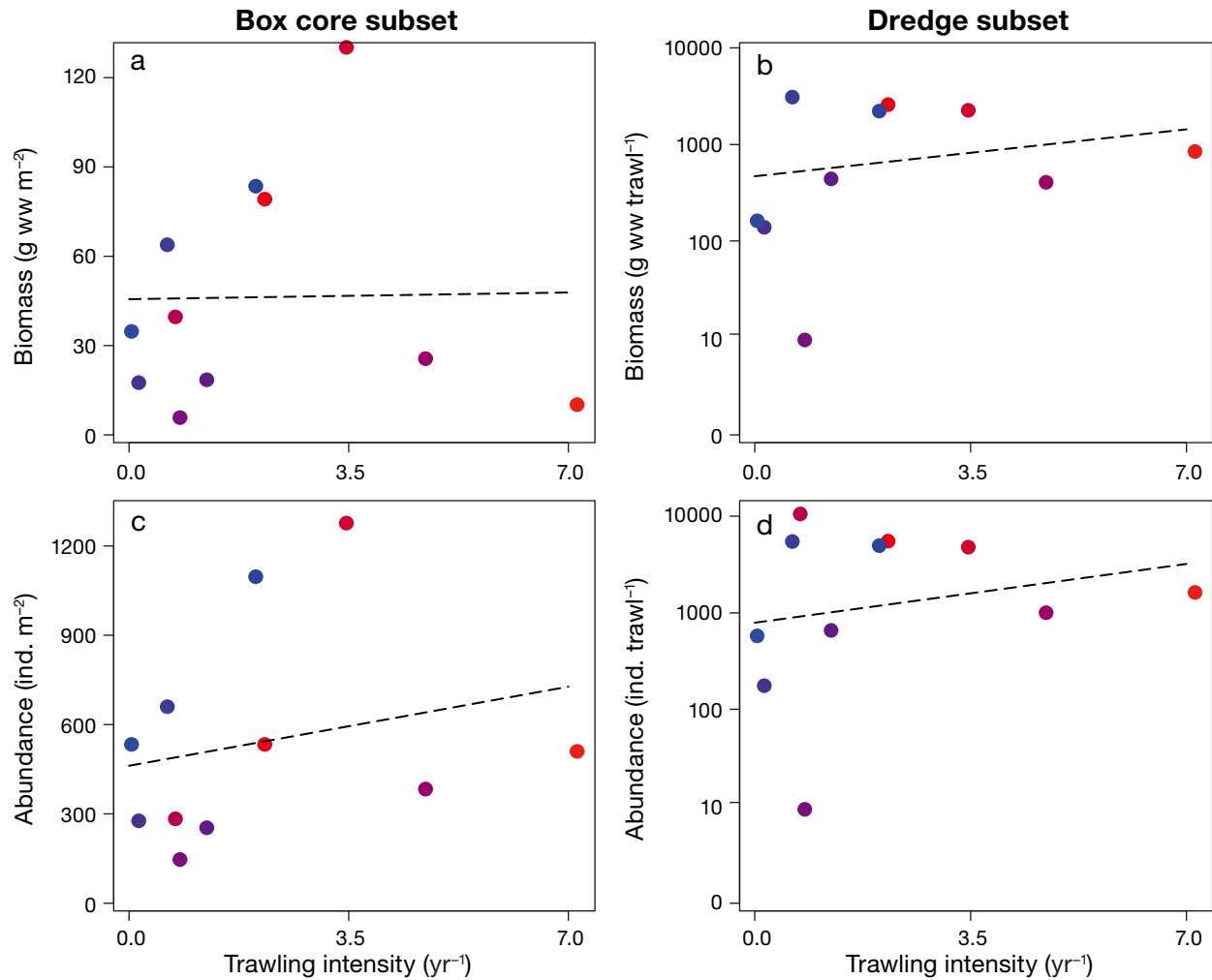


Fig. 5. Relationship between trawling intensity (average SAR) and (a,b) faunal biomass and (c,d) abundance of box core and dredge for stations with oxygen concentrations above 3 ml l⁻¹. The relationships are all non-significant based on linear regression. Points are coloured using a linear colour gradient from the station with the lowest oxygen concentration (red, 3.3 ml l⁻¹) to the highest (blue, 5.8 ml l⁻¹) in this data subset

3.5. Vertical position

In total, 143 individuals were found in the vertical sub-cores across the stations. Most fauna (102 individuals, representing 90% of total biomass) were in the upper 0–2 cm of the sediment. Different polychaete species (*Pygospio elegans*, *Aricidea* spp., *Hediste diversicolor* and *Terebellides stroemii*), nematodes and ostracods were found in low abundance at depths deeper than 4 cm (in total 11 individuals, representing 1% of total biomass). PERMANOVA analysis showed no support for a change in the vertical distribution of fauna with changes in oxygen concentration and/or trawling intensity (Table S5). The vertical distribution of species abundance and biomass are shown in Figs. S3 & S4, respectively.

4. DISCUSSION

We examined the effects of bottom trawl disturbance and oxygen concentration on benthic community biomass and abundance, the number of large-bodied individuals, community longevity and the vertical position of fauna in the sediment. We found that changes in near-bed oxygen concentrations had a large impact on benthic fauna, whereas trawling intensity had a weak positive effect on some species and community metrics and no effect on others. The lack of negative effects of trawling intensity on most parameters, and a positive effect on some community metrics and on the priapulid worm *Halicryptus spinulosus*, are somewhat unexpected given the high annual trawling frequencies at some sampling stations.

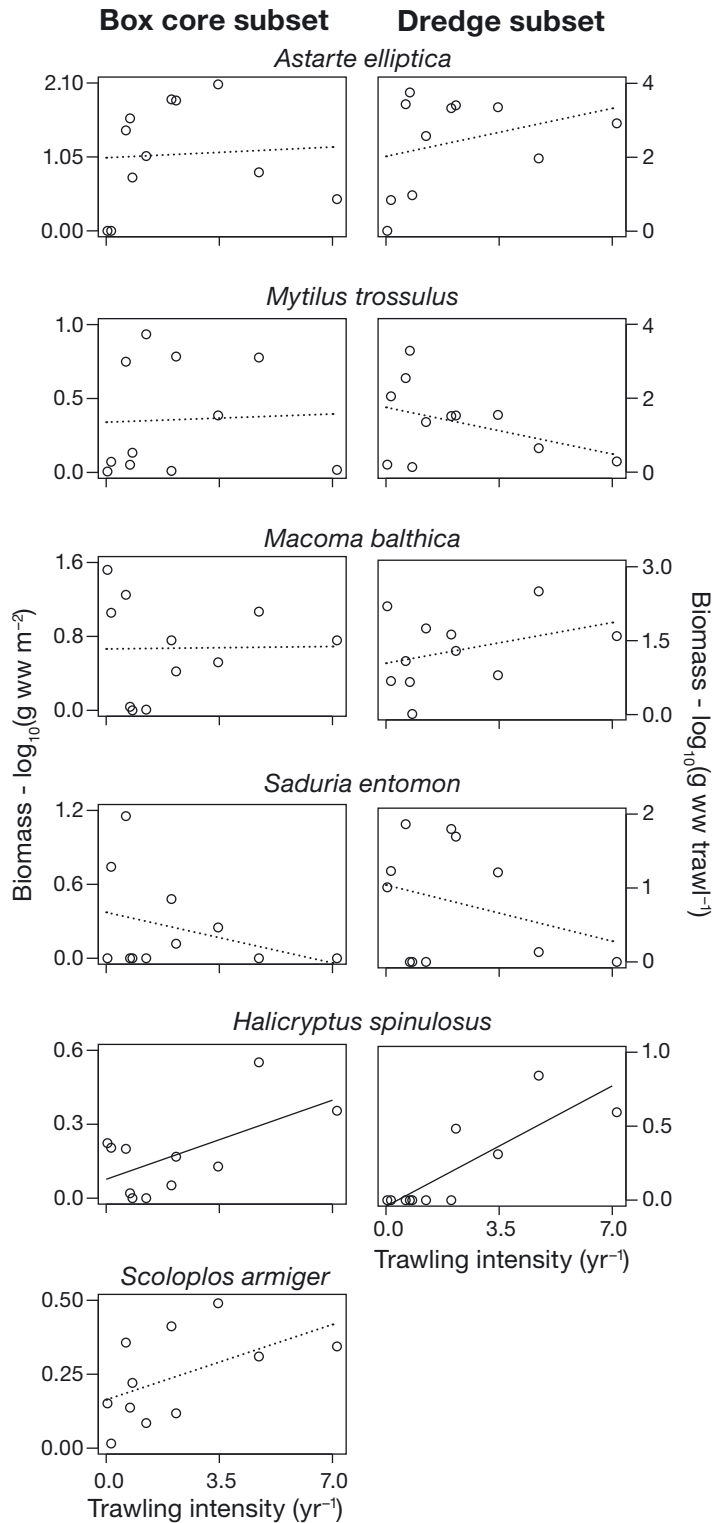


Fig. 6. Relationship between trawling intensity (average SAR) and biomass of different dominant species in box core and dredge for all stations with oxygen concentrations above 3 ml l^{-1} . Solid lines: significant relationships ($p < 0.05$); dotted lines: non-significant. Note that all species in this subset have a non-significant relationship with oxygen concentration

We discuss below whether these non-negative effects may be a true effect or the result of different confounding factors. Whatever the reason, our findings highlight that bottom trawling appears to have limited impacts on the benthic communities studied here.

4.1. Fluctuations in near-bed oxygen concentrations

Both the time series (Fig. 3a) and oxygen model simulations (Fig. S6) showed fluctuations of the bottom oxygen conditions. The study region is a highly dynamic region where bottom waters from Bornholm Basin, Eastern Gotland Basin and Gdansk Deep are transported in and out (Meier et al. 2006, Neumann et al. 2017, Zhurbas et al. 2012). All these waters have different oxygen concentrations, and this results in frequent fluctuations of the bottom oxygen conditions, forced by the hydrodynamics. The fluctuations in oxygen concentration may have limited our ability to detect negative bottom trawl effects given that we sampled at only one point in time (but see Fig. 3b–d).

The oxygen model simulations further suggest that most sampled stations with high oxygen measurements during our survey may have experienced lower levels in earlier months that would have killed a large fraction of the biota (Fig. 3c). This could cause a large amount of noise on the trawl impact signal. However, a comparison of the oxygen model simulation with the time series data shows that the simulation is on average lower and has multiple periods with zero oxygen, which is not observed in the data (Fig. S7). The comparison therefore suggests that the model overestimates hypoxic and anoxic conditions in this area. All sampling stations with relatively high measured oxygen concentrations were also found to have some large-bodied ($>15 \text{ mm}$) individuals in the box core (Fig. 7). Most of these large-bodied individuals have minimal mobility and are unlikely to have moved from neighbouring regions. This suggests that the historic oxygen conditions were sufficient to allow the benthos to survive and grow to a large size, which takes multiple years for the bivalve *A. elliptica* (Trutschler & Samtleben 1988), the dominant species con-

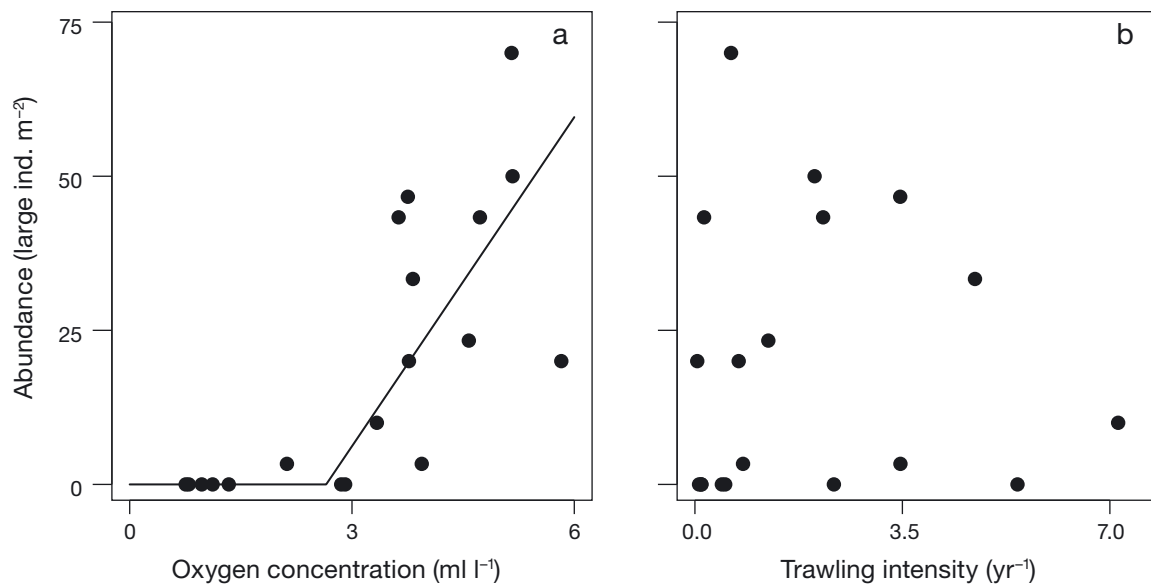


Fig. 7. Relationships between the number of large individuals (>15 mm) and (a) oxygen concentration and (b) trawling intensity (average SAR) for all box core sampling stations. The solid line is based on Tobit regression. There is no support for a model with trawling (Table 1)

tributing to the large-bodied group. This finding corroborates that the simulated oxygen concentrations are likely lower than the natural conditions.

4.2. Non-negative trawl effects on benthic fauna

Bottom trawl impacts depend on the frequency of trawl disturbance, the amount of mortality (depletion) that bottom gears cause and the recoverability of the benthic community (Pitcher et al. 2017). The fisheries data shows that all trawling in the area occurs with a demersal otter trawl. This is a relatively light gear that is associated with a low depletion rate of 0.03, i.e. causing a biomass decline of 3% each time a benthic community is swept by this trawl (Hiddink et al. 2017, Rijnsdorp et al. 2020). All fauna in our study area are further relatively short lived (<10 yr), potentially the result of selection by environmental filtering due to low salinity and variable oxygen levels (Bonsdorff 2006). Short-lived species have relatively high recovery rates (Hiddink et al. 2019). Therefore, low trawl impacts may be expected in this area (but note that the area may have harboured more organisms vulnerable to trawling before the emergence of eutrophication-induced hypoxia and industrial trawling). Nonetheless, model predictions based on the observed longevities and the above depletion rate suggest a 20% decline of community biomass relative to carrying capacity in a location with a chronic trawling in-

tensity of SAR = 7 per year (see Text S2 for the calculation). Although this is a substantial effect, the variation in the recorded benthic communities is large due to natural variation and sampling error, and the power to detect such an effect may have been limited (as noted in Section 4.1).

Biomass comparisons with the Kattegat and the more northern Gotland Basin reveal that box core biomass in our study area is on average 6 to 10 times lower than in those areas (Sköld et al. 2018, van Denderen et al. 2020). Since low oxygen conditions tend to affect relatively large areas homogeneously, the low biomass in our study area may be the result of low and variable oxygen levels that have hindered recruitment and recolonization from neighbouring regions (Whitlatch et al. 1998). Recruitment in the Baltic Sea is also more stochastic and dependent on wind-induced waves since it is a non-tidal system (Valanko et al. 2010). It may therefore be hypothesized that any survivors and/or new arrivals in the area will have little competition for space and food and high growth rates, thus resulting in lower trawl impacts than expected.

We observed a positive relation between trawling intensity and some community metrics and the biomass of the priapulid worm *H. spinulosus*. These increases may be linked to changes in the biomass and abundance of *Saduria entomon*, an important benthic predator in the Baltic Sea, with trawling. In field enclosure experiments, *S. entomon* has been found

to have a negative effect on priapulid abundances (Bonsdorff et al. 1995). *S. entomon* shows a negative trend with trawling intensity that albeit non-significant may have lowered predation pressure on infaunal prey in fished areas. The declining trend of *S. entomon* with trawling may itself also be driven by predation, since cod, an important predator on *S. entomon* (Neuenfeldt et al. 2020), may be found at higher abundances in areas of high fishing. Although the importance of these feeding interactions is speculative and largely hypothetical, it highlights how indirect food web effects can complicate relationships between bottom trawling and benthic communities (Sköld et al. 2018, van de Wolfshaar et al. 2020).

4.3. Low oxygen conditions and the absence of fauna

We found no benthic fauna in locations with oxygen concentrations less than $2 \text{ ml O}_2 \text{ l}^{-1}$. Mass-mortality of benthic fauna typically occurs around $0.5 \text{ ml O}_2 \text{ l}^{-1}$ (Diaz & Rosenberg 1995) and model simulations indicate that these sampling locations had lower oxygen levels earlier in the year (Fig. 3c,d). We also found no benthic fauna in Stn 9, where an oxygen concentration of $1.3 \text{ ml O}_2 \text{ l}^{-1}$ was measured. Time series data of near-bed oxygen at an area that is 90 m deep and located only 3.7 km away from Stn 9 (marked by red asterisk in Fig. 1; Fig. 3) shows that oxygen concentrations dropped to below $0.5 \text{ ml O}_2 \text{ l}^{-1}$ in May 2018, just 4 mo before our sampling campaign took place. Although the 2 stations are not in exactly the same location, their vicinity suggests that the temporal changes in oxygen concentrations at the 90 m depth location are representative of those occurring at Stn 9. This drop may have led to the mass-mortality of macrofauna at Stn 9, hence the absence of fauna in our observations at this station. Importantly, in June 2018, oxygen concentrations were again $2 \text{ ml O}_2 \text{ l}^{-1}$, showing the fine-scale temporal fluctuations in oxygen conditions that occur there.

The trawling intensity at Stn 9 declined most severely in comparison to all stations over the period 2013–2018. The station exhibited values close to $\text{SAR} = 10$ in 2013 and 1 in 2018. Fig. S8 shows there is a strong and positive relation between the annual trawling intensities at Stn 9 and the maximum yearly oxygen concentrations from the time series (linear model shows a p-value of 0.01 and an adjusted R^2 of 0.78), whereas no relation is found for minimum or average yearly oxygen conditions. This finding may imply that peaks in oxygen, which are still below

$5 \text{ ml O}_2 \text{ l}^{-1}$, attract fish and subsequently fisheries in this area. Catch rates of cod, an important target species, have been shown to peak at these intermediate oxygen conditions in the neighbouring Bornholm Basin (Neuenfeldt & Beyer 2003). Since cod feeds on pelagic sprat as well as benthic animals (especially motile ones), cod abundance may be high in areas with a depauperate benthic community. If correct, there is an important temporal aspect to the interactive impacts of trawling and hypoxia on benthic fauna, where trawling intensity will be highest in years with relatively healthy oxygen conditions.

4.4. No synergistic effects

We found no evidence of synergistic effects between trawling and hypoxia in our study. Compared to other regions, 2 characteristics of the benthic community and the environment may have reduced the potential for synergistic effects in this area. We hypothesized that trawling impacts on the benthic community in the study area would be exacerbated by hypoxia, as the latter may increase the vulnerability of burrowing organisms to trawling as these move closer to the surface to avoid asphyxiation (Pihl et al. 1992, Nilsson & Rosenberg 1994). However, most samples were characterized by a layer of sand sitting on top of a deeper layer of glacial clay. Very few deep-bioturbating species were observed and 99% of the total macrofaunal biomass was found in the upper 4 cm. This therefore limits the potential of increasing trawl impacts with hypoxia, because all fauna are already found in the upper surface layers. These fauna and sediment conditions are widespread in the Baltic Sea basin (Pikies & Jurowska 1992, Gogina et al. 2016), suggesting our findings may be more general for this region. Furthermore, ophiuroids and asteroids do not occur in the Baltic Sea basin, thus so-called arm-tipping behaviour (individuals standing on their arm-tips, elevating their bodies above the oxygen depleted substrate) does not increase the vulnerability of benthos to trawling impacts. Other regions, with a different benthic fauna and sediment composition, may show a different response.

4.5. Management implications

The benthic communities in the study area appear to be predominantly impacted by low oxygen concentrations, despite the high annual trawling intensities at some sampling stations. The studied benthic

communities are therefore expected to benefit most from management actions targeting reductions of nutrient loads and reversing eutrophication and hypoxia. Long-term improvements of the benthic communities after removal of bottom trawl fishing are less likely, given the current oxygen conditions, but cannot be ruled out due to uncertainty in the oxygen gradient studied that may have limited our ability to detect negative bottom trawl effects. However, impacts of bottom trawls on the benthic community do not seem to be amplified in the low oxygen areas in our studied region, as has been suggested for other regions (e.g. Baden et al. 1990, Diaz & Rosenberg 1995). This finding may allow management to prioritize benthic protection from bottom fishing in other areas, more prone to fishing impact, to ensure effective allocation of resources and maximize conservation returns.

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