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Effects of bottom trawling and hypoxia on benthic invertebrate communities

P. Daniël van Denderen[1,2*], Anna Törnroos[3], Marija Sciberras[4], Hilmar Hinz[5], René Friedland[6], Rafal Lasota[7], Maria Cristina Mangano[8], Craig Robertson[9], Sebastian Valanko[10], Jan Geert Hiddink[9]

[1] Centre for Ocean Life, DTU Aqua, Technical University of Denmark, DK-2800 Kgs. Lyngby, Denmark

[2] Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA

[3] Environmental and Marine Biology, Faculty of Science and Engineering, The Sea research profile, Åbo Akademi University, 20520 Turku, Finland.

[4] The Lyell Centre, Heriot-Watt University, Edinburgh, UK, EH14 4AP

[5] Mediterranean Institute for Advanced Studies, IMEDEA (CSIC-UIB), Marine Ecosystem Dynamics, 07190 Esporles, Balearic Islands, Spain

[6] Leibniz-Institute for Baltic Sea Research Warnemünde, 18119 Rostock, Germany

[7] University of Gdansk, Faculty of Oceanography and Geography, Institute of Oceanography, Department of Marine Ecosystems Functioning, 81-378 Gdynia, Poland

[8] Department of Integrative Marine Ecology (EMI), Stazione Zoologica Anton Dohrn, Sicily, 98167 Messina, Italy

[9] Bangor University, School of Ocean Sciences, Menai Bridge, UK, LL59 5AB

[10] International Council for the Exploration of the Sea, Copenhagen, DK 1553, Denmark

Running title (max 6 words): Benthic impacts from trawling and hypoxia

25   *Corresponding author: e-mail: pdvd@aqua.dtu.dk

26 **Abstract**

27 Marine benthic habitats in continental shelf regions are increasingly impacted by hypoxia

28 caused by the combination of eutrophication and climate warming. Many regions that have the

29 potential for hypoxic conditions are being fished by mobile bottom-contacting fishing gears.

30 The combined effects of trawling and hypoxia may be synergistic and disproportionally impact

31 benthic fauna, or they may act antagonistically, leading to smaller trawl impacts in hypoxic

32 areas. Yet, few studies have quantified how bottom trawling and hypoxia interact to affect

33 benthic communities. Here we examine these combined effects on benthic community biomass

34 and abundance, the number of large organisms, the longevity distribution of the community

35 and the vertical position of fauna in the sediment in the southern Baltic Sea. We find large

36 declines in benthic biomass and abundance that co-occur with declines in near-bed oxygen

37 concentrations from 5.8 to 0.8 ml O_2 l^{-1}. Conversely, no relationships and weak positive

38 relationships are found between bottom trawl disturbance and benthic community biomass and

39 abundance. No interacting effects between hypoxia and trawling are detected. Our findings

40 therefore highlight a low likelihood of synergistic impacts of bottom trawling and hypoxia on

41 the benthic communities studied. These results suggest that management may prioritize benthic

42 protection from fishing in regions that are not in a state of oxygen stress.

43

44 **Keywords:** bottom-trawling, hypoxia, Baltic Sea, macrofauna, body size, longevity, vertical

45 position in sediment

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 two 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 disproportionally 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

4

71   al. 2016). Alternatively, when hypoxia leads to asphyxiation of sessile fauna and/or migration

72   of mobile fauna, leading to a depauperate state or even absence of benthic fauna, trawling may

73   have a negligible additional impact on the benthos. Animals that can survive hypoxia events

74   may also have life-history characteristics that make them less vulnerable to trawling (e.g. fast

75   growth and high dispersal) and trawling may not affect these species significantly. Fisheries

76   management measures in such areas will have only limited benefits to the benthic ecosystem.

77   The above highlights that depending on the cumulative effects of bottom trawling and hypoxia,

78   management of human impacts on benthic habitats may either prioritize protection from

79   fisheries of hypoxic areas or prioritize the protection of areas that are non-hypoxic. So far, few

80   studies have quantified the interactive effects of bottom trawling and hypoxia on benthic

81   communities, limiting the development of management plans that consider the cumulative

82   effects. Recent work on a continental slope off Vancouver Island found that bottom trawling

83   continues to impact benthic communities affected by an oxygen minimum zone, suggesting

84   cumulative impacts that are either additive or synergistic (De Leo et al. 2017).

85   Here we study the effects of bottom trawling and hypoxia on benthic communities in the Baltic

86   Sea. Throughout its historic past the Baltic Sea has seen hypoxic events on the seafloor (natural

87   and human induced), mainly due to limited water exchange with the Atlantic and in recent

88   decades excess nutrient input (Carstensen et al. 2014, Andersen et al. 2017). The Baltic Sea's

89   benthic communities lack large habitat forming epifauna, in particular in the deeper areas. This

90   is due to a low salinity, that in combination with its historic hypoxic past, has created the

91   characteristically low species diversity, but highly abundant benthic communities (Bonsdorff

92   2006). Most of these benthic communities consist of short-lived fauna (Törnroos et al. 2015,

93   2019, van Denderen et al. 2019), which are predicted to be largely resilient to bottom trawling

94   disturbance (Hiddink et al. 2018). Yet, approximately two thirds of the Baltic Sea bottom trawl

95   fishing footprint occurs in areas with seasonal oxygen concentrations <3.2 ml O_2 l^{-1} that may

96   impact benthic organisms (van Denderen et al. 2019). It is therefore an area where trawling

97   impacts may be severely underestimated if synergistic effects are found to occur. The objective

98   of this study is to estimate interactive effects of bottom trawling and hypoxia on macrofaunal

99   biomass and abundance, large-bodied macrofauna, benthic community longevity and the

100   vertical position of fauna in the sediment. The studied stations ranged over a gradient in near-

101   bed oxygen concentrations from 0.8 to 5.8 ml O_2 l^{-1} and in trawling intensity from little trawl

102   disturbance to up to 7 bottom trawl events per year. Our findings highlight a low likelihood of

103   synergistic effects between bottom trawling and hypoxia on the benthic communities studied.

2. MATERIAL 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 is an active fishing ground with bottom trawling by otter trawls that target cod and flounder. The area was selected as earlier work showed it has gradients in average annual oxygen concentration and trawling intensity (van Denderen et al. 2019).

We selected sampling stations that covered a wide range of expected oxygen concentrations and trawling intensities in a limited depth range (62 - 102 metres, Table S1), 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 and Table S1). All sampling stations were found in an area of 30 by 62 km, and the distance to the nearest station 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 two 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 m^2 per core, average seafloor penetration depth 24 cm) were taken in a star pattern, one at the selected position and four 100 m 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

128   sampling was unsuccessful, the ship was moved 10s of meters and the box core redeployed.

129   Three 4.5 cm diameter sub-cores up to a maximum depth of 17 cm were collected from the

130   first two intact box core samples collected at each station to assess the vertical distribution of

131   fauna in the sediment in areas of different oxygen and fishing levels. Each sub-core was sliced

132   into four sections (0-2 cm, 2-4 cm, 4-8 cm, >8 cm) and sieved to obtain the fauna at different

133   sediment depths. The rest of the box core sample was sieved over 0.5 mm sieve. Most samples

134   had a solid clay layer below a surficial mud, sand and/or gravel layer (surficial layer was ca. 8-

135   18 cm deep); the solid clay layer was not sieved as no macrofauna can and did occur in this

136   solid layer. To separate the smaller fauna from the remaining gravel and stones, samples were

137   back-washed at least 7 times to obtain the fauna, by adding water, stirring the sample and

138   draining the water over a sieve to capture suspended animals. The remaining sediment was

139   checked for any further large fauna.

140   Semi-quantitative dredge samples were obtained using an Agassiz trawl type dredge (56 wide

141   x 31 cm high, outer net mesh size 1 x 1 cm, inner net mesh size 0.5 x 0.5 cm), except for Station

142   1 (see below). The dredge was towed for 2 minutes at 1 knot and was generally full on retrieval.

143   Samples were searched visually for fauna. In most dredge samples where fauna was present, a

144   subsample was taken that was searched visually and abundance and biomass of the total sample

145   was afterwards calculated based on the relative size of the subsample. Station 1 was sampled

146   with a Naturalist dredge (60 cm wide x 30 cm high) that was towed for 10 and 5 minutes at 1

147   knot. We expect that the alternative methodology did not affect the resulting data in Station 1

148   as, in all cases, the dredge was full on retrieval (it likely filled up quickly and stopped sampling

149   afterwards). Inspection of the data does not suggest the dredge data in Station 1 is an obvious

150   outlier. Since the dredge samples provided semi-quantitative information, the dredge was only

151   used as a complementary method to the box core (note that both sampling devices show similar

152   results).

153   All biota in box core and dredge were identified to the lowest taxonomic level possible and

154   their individual wet weight was measured. For some species in some dredge samples,

155   abundance was greater than approximately 100 individuals. For each of these species and

156   samples, length was measured for all individuals whereas weight was measured for 50

157   individuals of a range of lengths. For the remaining individuals, we converted length to weight

158   using the established length-weight relationship of the 50 individuals.

159   **2.3 Environmental conditions**

160   A sub-core measuring 4 cm in diameter was collected from the first box core sample at each

161   station to determine the sediment grain size composition of the upper 4 cm of the seabed. This

162   sub-core sample did include most gravel but not the larger gravel/pebbles. Particle size

163   distributions were determined using a Malvern laser diffraction particle sizer (Blott & Pye

164   2001). Sediment particle analysis showed that most of the stations had a high percentage sand

165   (Table S1). Visual inspection of the box core samples showed that the sandy sediment was

166   sometimes mixed with pebbles, gravel or mud and typically with a deeper layer of glacial clay.

167   Some stations had ferromanganese nodules on the seafloor surface. Despite that most stations

168   had largely similar depth and sediment conditions, there were larger differences in some of

169   these variables in a few stations (Table 1, Fig. S1). After verifying that results were robust

170   against the exclusion of these stations, we decided to maintain all stations within our analysis.

171   Bottom water was collected at 20 cm above the seabed with a Niskin bottle and oxygen

172   saturation (YSI model 58) and temperature and salinity (WTW Multiset 340i with TetraCon

173   325) were immediately measured after bringing to the surface. Three replicate water samples

174   were collected at each station (with the exception of the first few stations where only a single

175   measurement was taken) (Table S1). Temperature and salinity information was used to convert

176   near-bed oxygen saturation into oxygen concentration in ml per litre following Benson and

177   Krause (1984) (Table S1). About a quarter of stations was azoic and sediment had a strong

9

178   smell of H₂S and a clear black surface layer. Of these azoic stations, only three had measured

179   near-bed oxygen concentrations below 1 ml O_2 l^{-1}.

180   In addition to the oxygen measurements taken at the sampling stations, we analysed a time

181   series of near-bed oxygen concentration measurements collected from a nearby site at 90 m

182   depth (red asterisk in Fig. 1) between 2012 and 2018. Monthly oxygen concentration was

183   calculated by averaging oxygen measurements at depths less than five meters from the seafloor

184   per month (where available). Data used were obtained from HELCOM secretariat and based

185   on ICES dataset on Ocean Hydrography. Lastly, we compared the field measurements of

186   oxygen with model simulations of daily bottom oxygen concentrations from an ecosystem

187   model simulation. This model simulation is based on the coupled system ERGOM-MOM with

188   a horizontal grid of 1 nautical mile covering the whole Baltic Sea (Neumann et al. 2017, 2020,

189   2021). The biogeochemical module ERGOM simulates the marine carbon, nitrogen and

190   phosphorus cycles, while production and consumption of oxygen is included in the

191   biogeochemical processes via stoichiometric ratios. The modelled oxygen concentrations have

192   been validated against recent observations, e.g. Meier et al. (2018). We extracted three different

193   oxygen metrics from the model to obtain an indication how the simulated temporal history of

194   each sampling station correlates with the oxygen field measurement:1) the mean simulated

195   oxygen concentration of the preceding six months, 2) the closest hypoxia event with high

196   likelihood of mass-mortality pre-sampling, defined as the first day in a period of 20 consecutive

197   days with simulated oxygen concentrations below 0.5 ml O_2 l^{-1}, and 3) the number of days in

198   the last two years preceding sampling where simulated oxygen concentrations are above 0.5

199   ml O_2 l^{-1}. The oxygen threshold of 0.5 ml O_2 l^{-1} was chosen as mass-mortality of benthic fauna

200   typically occurs below this value (Diaz & Rosenberg 1995).

201   Bottom trawling intensity data were obtained at a 0.05° x 0.05° grid resolution (ICES 2019)

202   and expressed as the ratio of the area that is swept each year by trawl gears relative to the total

203   surface area (hereafter termed swept-area-ratio, SAR). The used grid resolution implies that we

204   represent trawling intensity on a relatively large spatial scale that may overlook local effects

205   along the trawl passage. We used average SAR values per grid cell for the period 2013-2017,

206   as we were interested in chronic effects of fishing and since recovery following trawling

207   disturbance may last more than one year (Hiddink et al. 2017). An average intensity (based on

208   multiple years) is therefore expected to better represent the state of a community than a single

209   year estimate.

210   **2.4 Data analysis**

211   We analysed the effect of trawling intensity and oxygen concentration on community biomass

212   and abundance, the number of large organisms, the biomass-longevity distribution of the

213   benthic community and the vertical position of fauna in the sediment. In all analyses, we

214   estimated biomass and abundance as the sum of all box core or dredge samples per station. All

215   results show biomass of bivalves with shell. Since the biomass patterns are strongly driven by

216   bivalve weights, we verified that similar results are obtained when shell-free wet weight is used

217   (based on a wet weight to shell-free wet weight conversions as shown in Table S2). The data

218   have been deposited in the Marine Data Archive repository (van Denderen et al. 2022). Scripts

219   and output are available on Github with DOI: 10.5281/zenodo.5579600. All statistical analyses

220   were done in program R (version 4.1.0) using the R package VGAM (1.1-5) and vegan (2.5-

221   7).

222   2.4.1 Community biomass and abundance

223   We tested the effect of trawling intensity and oxygen concentration and their interaction on

224   community biomass and abundance with a Tobit regression model and selected the best model

225   using the Akaike Information Criterion (AIC); when models differ less than 2 AIC-units, the

226   model with fewest parameters is selected. Tobit regression is designed to estimate relationships

227   assuming a normal distribution for the response variable with left/right censoring, i.e. where

228   the response variable data above/below a threshold value are censored (Tobin 1958). We used

229   Tobit regression as it was expected that a range of sampling stations at low oxygen

230   concentrations had zero biomass and abundance and we therefore set the threshold for

231   censoring our data at zero biomass and abundance. The full dataset was used to examine the

232   combined effect of trawling intensity and oxygen concentration, whereas a subset of stations

233   with oxygen concentrations > 3 ml O_2 l^{-1} was used to examine the effect of bottom trawling in

234   oxygenated conditions (Fig. 2). The oxygen threshold value (3 ml O_2 l^{-1}) was chosen because

235   benthic biomass and abundance did not correlate with oxygen at values above this threshold

236   (Fig. S2). The value has also some empirical basis as results of a meta-analysis indicate that

237   concentrations above 3.2 ml O_2 l^{-1} (equivalent to 4.6 mg O_2 l^{-1}) cause notably less mortality in

238   benthic fauna (Vaquer-Sunyer & Duarte 2008). We analysed the effect of trawling intensity on

239   benthic biomass and abundance in this data subset using linear regression.

240   2.4.2 Large organisms

241   Since previous work showed that the impact of bottom trawling is larger on larger benthic

242   organisms (> 4 mm) (McLaverty et al. 2020), we included a separate analysis to study the effect

243   of oxygen concentration and trawling intensity on the abundance of large individuals in the

244   benthic community. The analysis used the box core data and the same Tobit regression model

245   as described above. We used two length thresholds: >4 mm and >15 mm. Since we did not

246   measure the length of the sampled animals in the box core data, we approximated individual

247   length using length-weight relationships from the literature (Table S3).

248   2.4.3 Community longevity

249   Previous work has further shown that long-lived fauna are more impacted by bottom trawling

250   as they recover more slowly (Rijnsdorp et al. 2018, Hiddink et al. 2018). We therefore

251   examined the effect of trawling intensity and oxygen concentration on the longevity biomass

252   distribution of the benthic community. We used the box core data to study changes in the

12

253 biomass-longevity composition as these data provide a more controlled estimate of biomass

254 (the dredge was full upon retrieval, as noted above). Using information on species longevity of

255 benthic fauna in the Baltic Sea (Törnroos & Bonsdorff 2012, van Denderen et al. 2019), we

256 classified biota in three longevity groupings: maximum lifespan of 0-1 years, 1-3 years and 3-

257 10 years (no fauna were classified with a longevity > 10 years). The resulting taxon-by-trait

258 matrix was combined with the taxon biomass-by-station (gram wet weight per m^2) matrix to

259 create the final station-by-trait matrix. We used a PerMANOVA analysis to examine if changes

260 in trawling intensity and/or oxygen concentrations had a significant effect on the distribution

261 of benthic biomass in these three longevity groupings. This analysis was done on absolute and

262 fractional biomass values per longevity grouping and sampled station.

263 2.4.4 Vertical position

264 A PerMANOVA analysis was carried out to examine the effect of oxygen concentration and

265 trawling intensity on the vertical distribution (0-2 cm, 2-4 cm, 4-8 cm, >8 cm) of fauna in these

266 four sediment layers within the sediment. Since the number of observations was low in the

267 vertical sub-cores, we estimated biomass and abundance for each sediment layer as the sum of

268 all observations in all sub-cores per sampled station. The analyses were done on absolute and

269 fractional abundance/biomass data per vertical section and sampled station. We did not

270 examine species-specific vertical changes in relation to oxygen concentrations and trawling

271 intensity (but see Fig. S3 and S4 for the vertical biomass and abundance distribution per species

272 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 ml O_2 l^{-1}. The median near-bed oxygen concentrations were lower 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 three 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 further *Discussion* section).

3.2 Community biomass and abundance

The biomass of the community was dominated by the bivalves *Astarte elliptica*, *Mytilus trossulus* and *Limecola balthica* (formerly known as *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.

We found a significant positive relationship between oxygen concentration and community biomass and abundance for both box core and dredge data (Fig. 4). In three of the four 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 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 six most dominant species (in terms of biomass) in the box core samples and the five most dominant in the dredge samples collected at stations with relatively high oxygen concentrations (> 3 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* where a significant positive relationship was observed between its biomass 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 indicates no support for a model that includes trawling (Table 1). The dominant species contributing to the 'larger than 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 larger than 15 mm varied among stations between 0 and 70 per m^2; 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 years. 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 (supplementary text S1).

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.*, *Nereis diversicolor* and *Streblospio benedicti*), nematodes and ostracods were found in low abundance at depths deeper

345   than 4 cm (in total 11 individuals, representing 1% of total biomass). PerMANOVA analysis

346   showed no support for a change in the vertical distribution of fauna with changes in oxygen

347   concentration and/or trawling intensity (Table S5). The vertical biomass and abundance

348   distribution is for each species shown in Fig. S3 and S4.

4. DISCUSSSION

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 find 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 the priapulid worm *Halicryptus spinulosus*, are somewhat unexpected given the high annual trawling frequencies at some sampling stations. 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. Previous work has shown that 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

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373   noise on the trawl impact signal. However, a comparison of the oxygen model simulation with

374   the time series data shows that the simulation is on average lower and has multiple periods with

375   zero oxygen, which is not observed in the data (Fig. S7). The comparison therefore suggests

376   that the model overestimates hypoxic and anoxic conditions in this area. All sampling stations

377   with relatively high measured oxygen concentrations were also found to have some large-

378   bodied (> 15 mm) individuals in the box core (Fig. 7). Most of these large-bodied individuals

379   have minimal mobility and are unlikely to have moved from neighbouring regions. This

380   suggests that the historic oxygen conditions were sufficient to allow the benthos to survive and

381   grow to a large size, which takes multiple years for the bivalve *A. elliptica* (Trutschler &

382   Samtleben 1988), the dominant species contributing to the large-bodied group. This finding

383   corroborates that the simulated oxygen concentrations are likely lower than the natural

384   conditions.

385   **4.2 Non-negative trawl effects on benthic fauna**

386   Bottom trawl impacts depend on the frequency of trawl disturbance, the amount of mortality

387   (depletion) that bottom gears cause and the recoverability of the benthic community (Pitcher

388   et al. 2017). The fisheries data shows that all trawling in the area occurs with a demersal otter

389   trawl. This is a relatively light gear that is associated with a low depletion rate of 0.03, i.e.

390   causing a biomass decline of 3% each time a benthic community is swept by this trawl (Hiddink

391   et al. 2017, Rijnsdorp et al. 2020). All fauna in our study area are further relatively short lived

392   (<10 years), potentially the result of selection by environmental filtering due to low salinity

393   and variable oxygen levels (Bonsdorff 2006). Short-lived species have relatively high recovery

394   rates (Hiddink et al. 2018). Therefore, low trawl impacts may be expected in this area (but note

395   that the area may have harboured more organisms vulnerable to trawling before the emergence

396   of eutrophication-induced hypoxia and industrial trawling). Nonetheless, model predictions

397   based on the observed longevities and the above depletion rate suggest a 20% decline of

398 community biomass relative to carrying capacity in a location with a chronic trawling intensity

399 of SAR = 7 a year (see supplementary text S2 for the calculation). Although this is a substantial

400 effect, the variation in the recorded benthic communities is large due to natural variation and

401 sampling error, and the power to detect such an effect may have been limited (as noted in

402 section 4.1).

403 Biomass comparisons with the Kattegat and the more northern Gotland Basin reveal that box

404 core biomass in our study area is on average 6 to 10 times lower than in those areas (Sköld et

405 al. 2018, van Denderen et al. 2019). Since low oxygen conditions tend to affect relatively large

406 areas homogenously, the low biomass in our study area may be the result of low and variable

407 oxygen levels that have hindered recruitment and recolonization from neighbouring regions

408 (Whitlatch et al. 1998). Recruitment in the Baltic Sea is also more stochastic and dependent on

409 wind-induced waves since it is a non-tidal system (Valanko et al. 2010). It may therefore be

410 hypothesized that any survivors and/or new arrivals in the area will have little competition for

411 space and food and high growth rates, thus resulting in lower trawl impacts than expected.

412 We observed a positive relation between trawling intensity and some community metrics and

413 the biomass of the priapulid worm *H. spinulosus*. These increases may be linked to changes in

414 the biomass and abundance of *Saduria entomon*, an important benthic predator in the Baltic

415 Sea, with trawling. In field enclosure experiments, *S. entomon* has been found to have a

416 negative effect on priapulid abundances (Bonsdorff et al. 1995). *S. entomon* shows a negative

417 trend with trawling intensity that albeit non-significant may have lowered predation pressure

418 on infaunal prey in fished areas. The declining trend of *S. entomon* with trawling may itself

419 also be driven by predation, since cod, an important predator on *S. entomon* (Neuenfeldt et al.

420 2020), may be found at higher abundances in areas of high fishing. Although the importance

421 of these feeding interactions is speculative and largely hypothetical, it highlights how indirect

422 food web effects can complicate relationships between bottom trawling and benthic

423 communities (Sköld et al. 2018, van de Wolfshaar et al. 2020).

424 **4.3 Low oxygen conditions and the absence of fauna**

425 We found no benthic fauna in locations with oxygen concentrations less than 2 ml l^{-1}. Mass-

426 mortality of benthic fauna typically occurs around 0.5 ml O$_2$ l^{-1} (Diaz & Rosenberg 1995) and

427 model simulations indicate that these sampling locations had lower oxygen levels earlier in the

428 year (Fig. 3c and d). We also found no benthic fauna in Station 9, where an oxygen

429 concentration of 1.3 ml l^{-1} was measured. Time series data of near-bed oxygen at an area 90 m

430 depth and located only 3.7 km away from Station 9 (marked by red asterisk in Fig. 1, Fig. 3)

431 shows that oxygen concentrations dropped to below 0.5 ml O$_2$ l^{-1} in May 2018, just four months

432 before our sampling campaign took place. Although the two stations are not exactly in the same

433 location, their vicinity suggests that the temporal changes in oxygen concentrations at the 90

434 m depth location are representative of those occurring at Station 9. This drop may have led to

435 the mass-mortality of macrofauna at Station 9, hence the absence of fauna in our observations

436 at this station. Importantly, in June 2018 oxygen concentrations were again 2 ml O$_2$ l^{-1}, showing

437 the fine-scale temporal fluctuations in oxygen conditions.

438 The trawling intensity at Station 9 declined most severely in comparison to all stations, over

439 the period 2013-2018. The station exhibited values close to SAR = 10 in 2013 and 1 in 2018.

440 Fig. S8 shows there is a strong and positive relation between the annual trawling intensities at

441 Station 9 and the maximum yearly oxygen concentrations from the time series (linear model

442 shows a p-value of 0.01 and an adjusted R^2 of 0.78), whereas no relation is found for minimum

443 or average yearly oxygen conditions. This finding may imply that peaks in oxygen, which are

444 still below 5 ml O$_2$ l^{-1}, attract fish and subsequently fisheries in this area. Catch rates of cod, an

445 important target species, have been shown to peak at these intermediate oxygen conditions in

446 the neighbouring Bornholm Basin (Neuenfeldt & Beyer 2003). Since cod feeds on pelagic sprat

447   as well as benthic animals (especially motile ones), cod abundance may be high in areas where

448   the state of the seafloor is low. If correct, there is an important temporal aspect to the interactive

449   impacts of trawling and hypoxia on benthic fauna, where trawling intensity will be highest in

450   years with relatively healthy oxygen conditions.

451   **4.4 No synergistic effects**

452   We found no evidence of synergistic effects between trawling and hypoxia in our study.

453   Compared to other regions, two characteristics of the benthic community and the environment

454   may have reduced the potential for synergistic effects in this area. We hypothesized that

455   trawling impacts on the benthic community in the study area would be exacerbated by hypoxia,

456   as the latter may increase the vulnerability of burrowing organisms to trawling as these move

457   closer to the surface to avoid asphyxiation (Pihl et al. 1992, Nilsson & Rosenberg 1994).

458   However, most samples were characterized by a layer of sand sitting on top of a deeper layer

459   of glacial clay. Very few deep-bioturbating species were observed and 99% of the total

460   macrofaunal biomass was found in the upper 4 cm. This therefore limits the potential of

461   increasing trawl impacts with hypoxia, because all fauna are already found in the upper surface

462   layers. These fauna and sediment conditions are widespread in the Baltic Sea basin (Pikies &

463   Jurowska 1992, Gogina et al. 2016), suggesting our findings may be more general for this

464   region. Furthermore, ophiuroids and asteroids do not occur in the Baltic Sea basin, thus so-

465   called arm-tipping behaviour (individuals standing on their arm-tips, elevating their bodies

466   above the oxygen depleted substrate) does not increase the vulnerability of benthos to trawling

467   impacts. Other regions, with a different benthic fauna and sediment composition, may show a

468   different response.

469   **4.5 Management implications**

470   The benthic communities in the study area appear to be predominantly impacted by low oxygen

471   concentrations, despite the high annual trawling intensities at some sampling stations. The

472   studied benthic communities are therefore expected to benefit most from management actions

473   targeting reductions of nutrient loads and reversing eutrophication and hypoxia. Long-term

474   improvements of the benthic communities after removal of bottom trawl fishing are less likely,

475   given the current oxygen conditions, but cannot be ruled out due to uncertainty in the oxygen

476   gradient studied that may have limited our ability to detect negative bottom trawl effects.

477   However, impacts of bottom trawls on the benthic community do not seem to be amplified in

478   the low oxygen areas in our studied region, as has been suggested for other regions e.g. Baden

479   et al. (1990), Diaz & Rosenberg (1995). This finding may allow management to prioritize

480   benthic protection from bottom fishing in other areas, more prone to fishing impact, to ensure

481   effective allocation of resources and maximize conservation returns.

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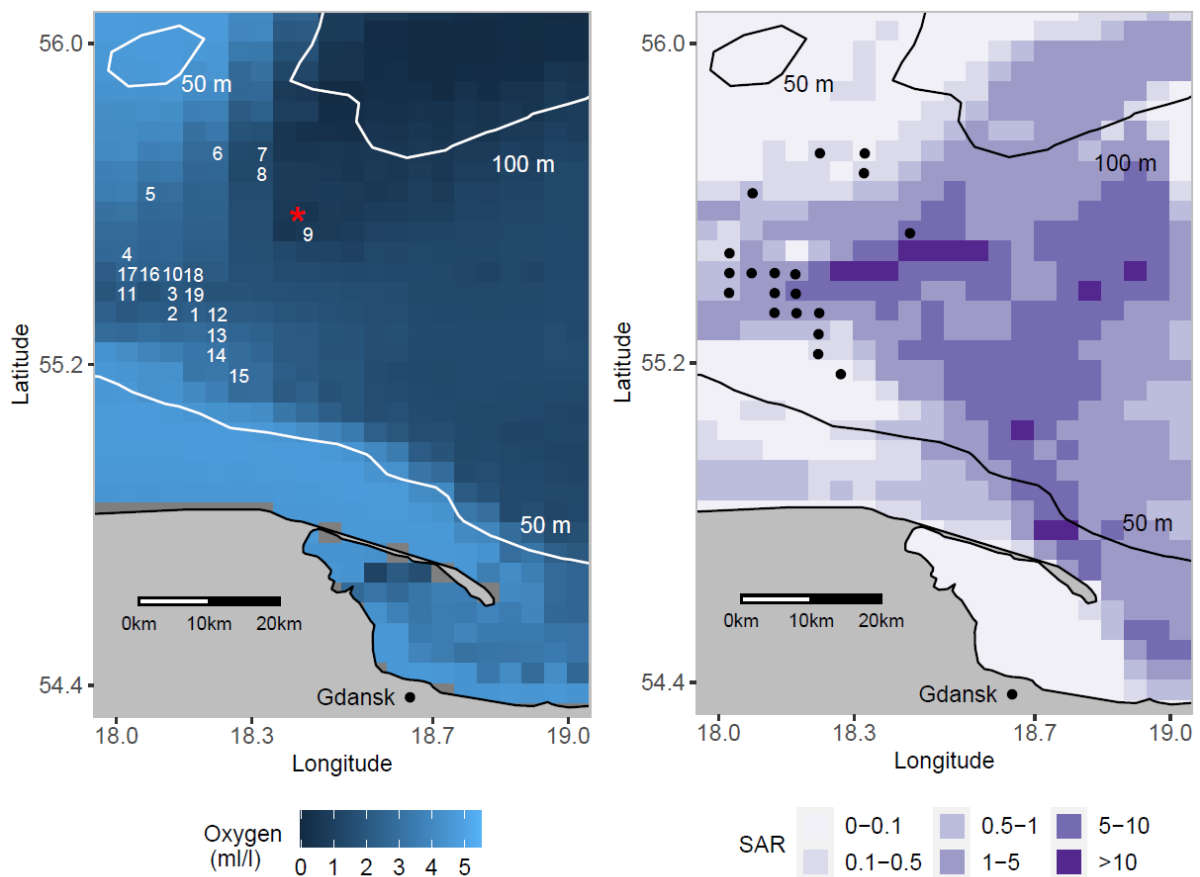
Figures

Figure 1. Maps of the 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 further van Denderen et al. 2019). The red asterisk shows a nearby location with time-series of near-bed oxygen measurements (see further 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.
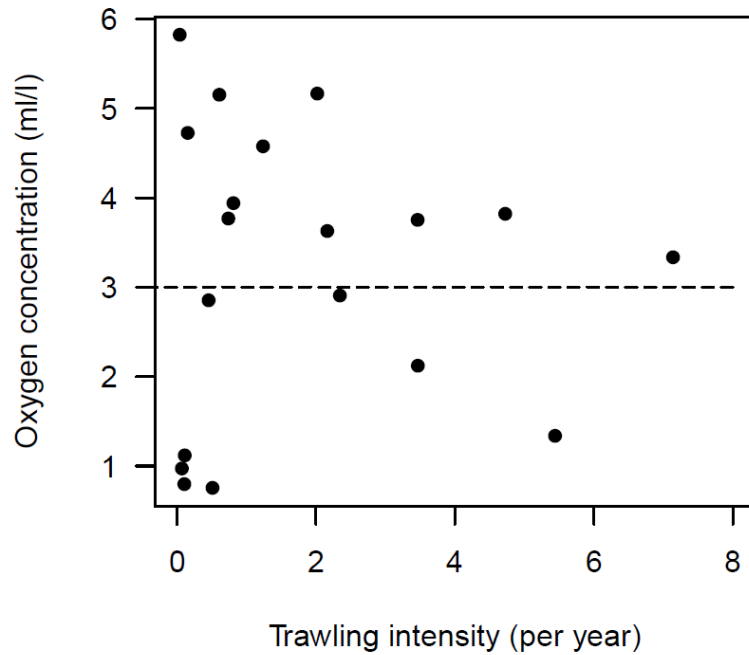
652

653   Figure 2. Trawling intensity (average SAR, per year) and oxygen concentration of the sampling

654   stations. We analysed all sampling stations together to examine the combined effect of trawling

655   intensity and oxygen concentration, as well as a subset of stations with oxygen concentrations

656   > 3 ml O_2 l^{-1} (stations above dashed line) to explore trawling effects in isolation. This threshold

657   was chosen as no effect of oxygen on benthic biomass or abundance is observed above this

658   concentration (Fig. S2).
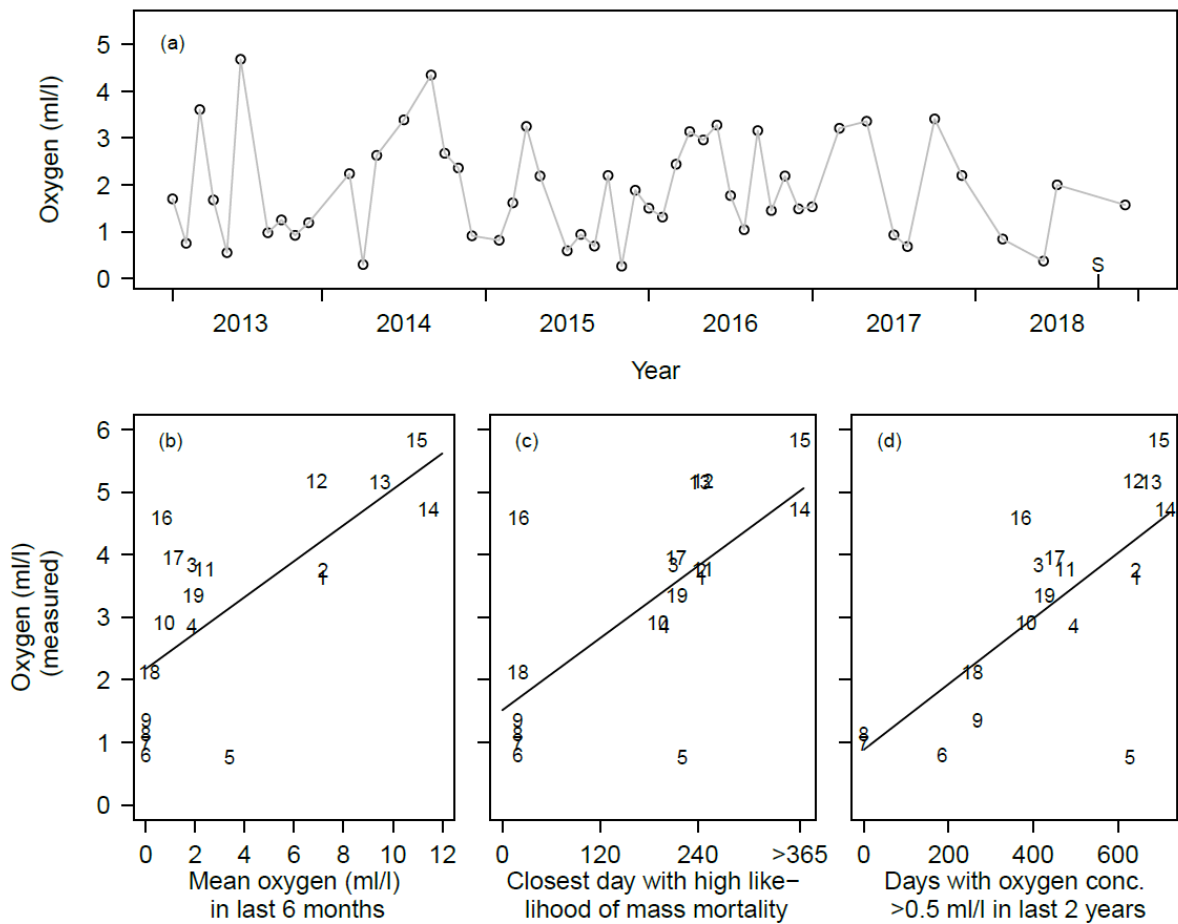
Figure 3. (a) Time series of near-bed oxygen concentrations at a nearby location of our study area (red asterisk in Fig. 1) from 2013 to 2018. The letter "S" indicates when we sampled the study area. (b - d) Comparison of measured near-bed oxygen concentrations with three metrics of oxygen from ecosystem model simulations for the same locations (numbers correspond to Fig. 1 and Table S1): (b) mean oxygen concentration of the preceding six months, (c) the closest hypoxia event with high likelihood of mass-mortality prior to sampling (Figure S7), and (d) number of days preceding sampling where simulated oxygen concentrations are above 0.5 ml/l in the last two years. The lines were constructed using linear regression.

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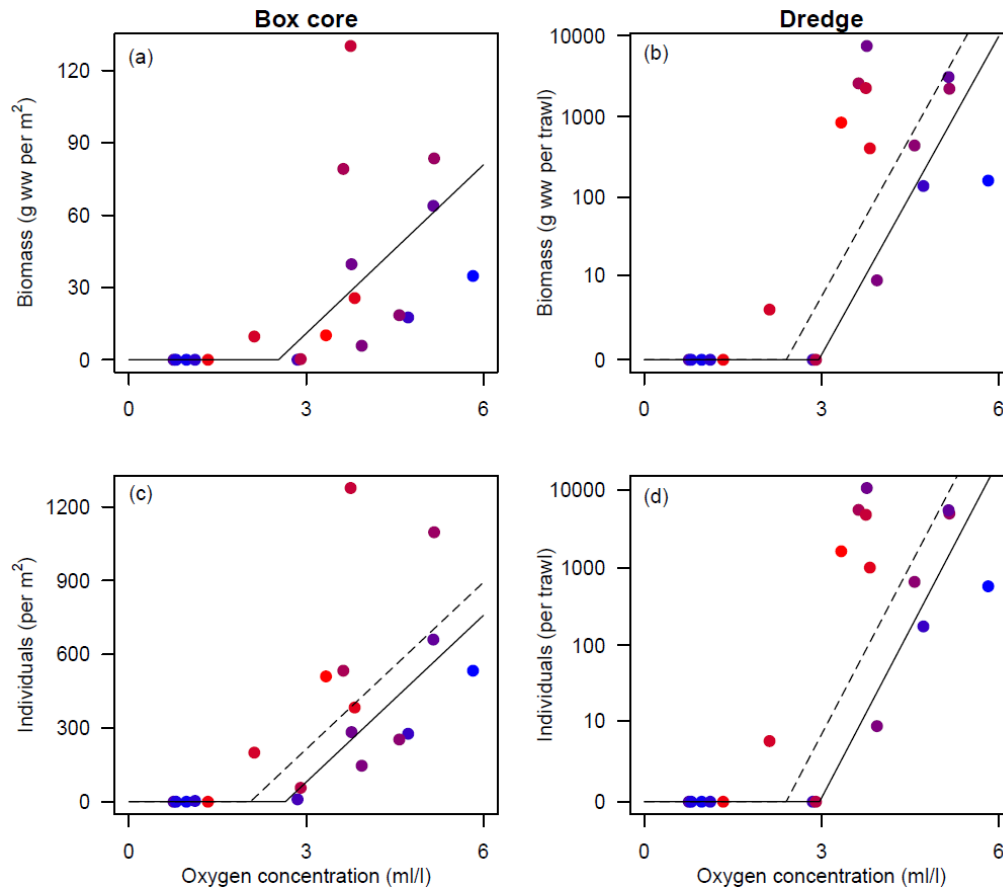
Figure 4. Relationships between oxygen concentration and total faunal biomass (gram wet weight) and abundance collected using the box core (a, c) and dredge (b, d). Lines are fitted with a Tobit-regression. In (b-d) where trawling intensity is part of the best model (Table 1), the solid lines show the 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 four orders of magnitude variation between stations.
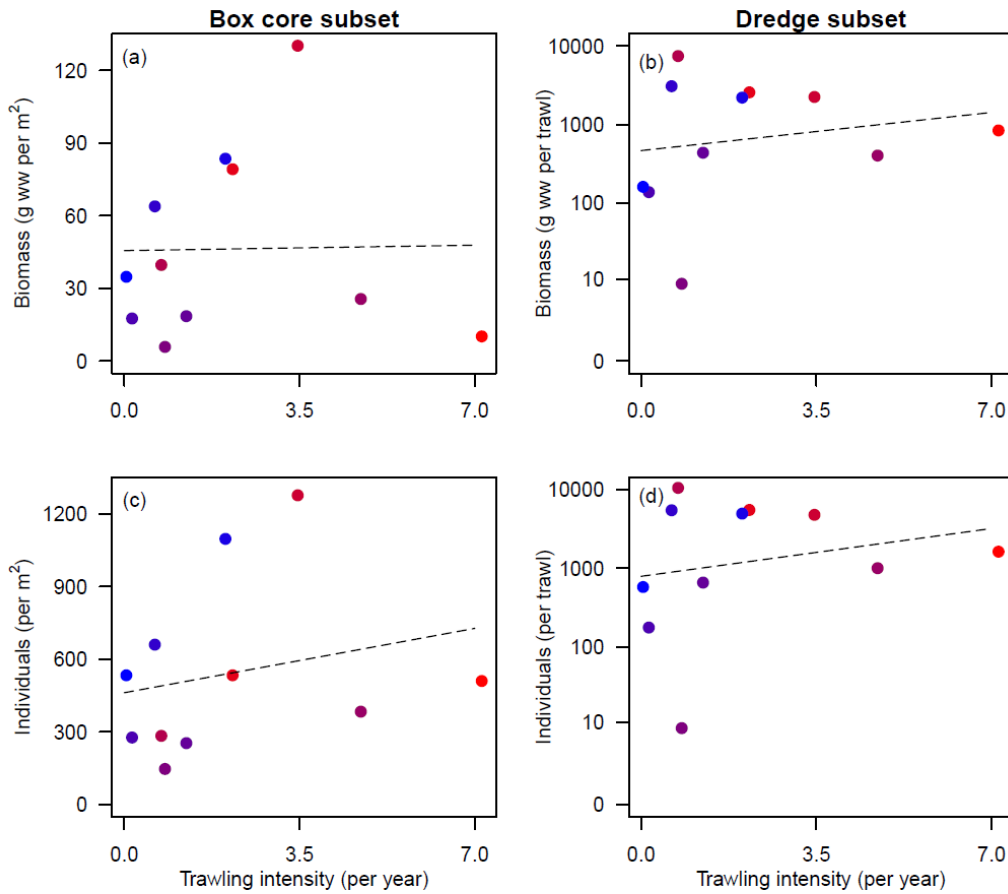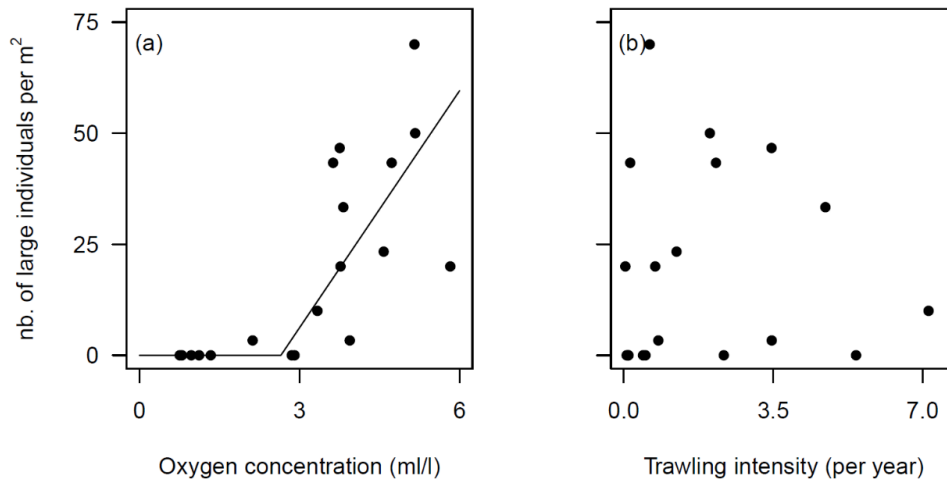
Figure 5. Relationship between trawling intensity (average SAR, per year) and faunal biomass (gram wet weight) and abundance of box core and dredge for stations with oxygen concentrations above 3 ml l^{-1}. The relationships are all non-significant based on linear regression. Points are coloured using 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.
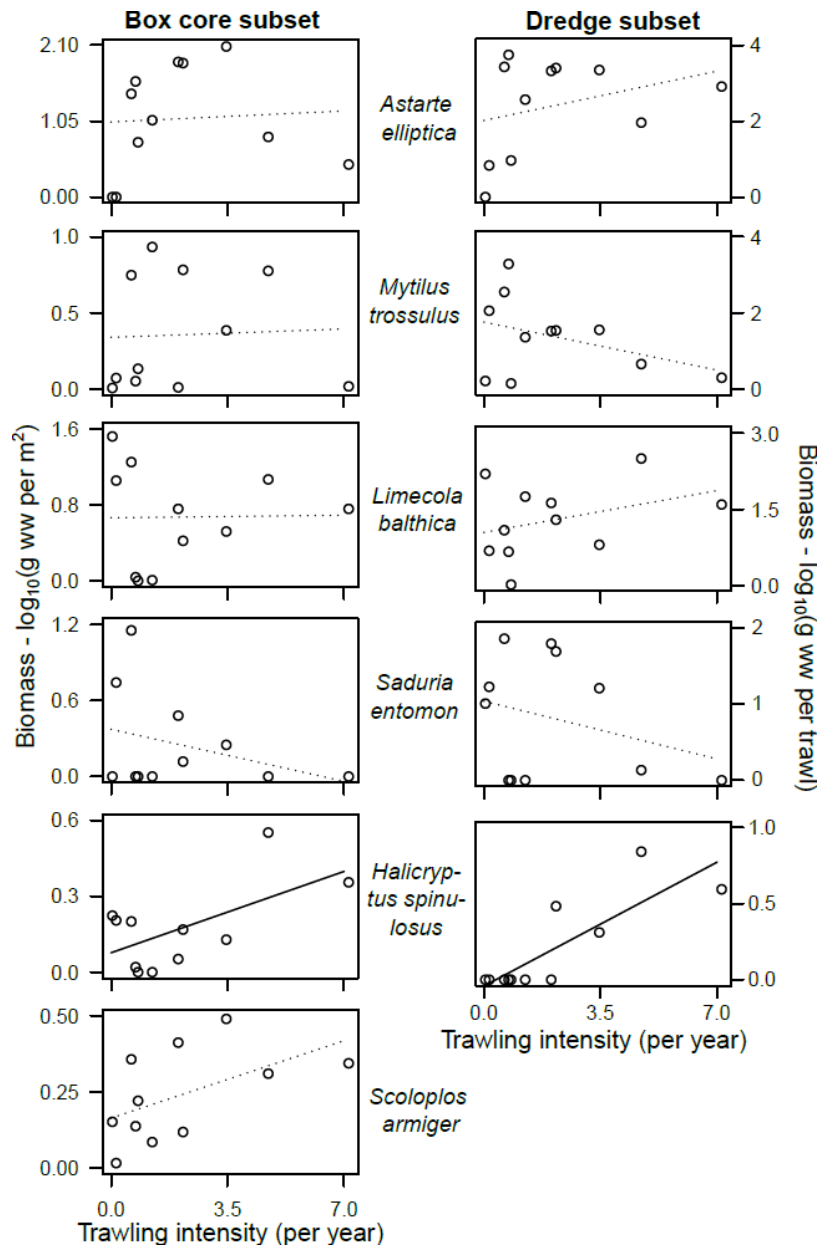
Figure 6. Relationship between trawling intensity (average SAR, per year) and the biomass (gram wet weight) of different dominant species in box core and dredge for all stations with oxygen concentrations above 3 ml l^{-1}. Solid lines show significant relationships (p-value <0.05), dashed lines non-significant. Note that all species in this subset have a non-significant relationship with oxygen concentration.

688

689 Figure 7. Relationships between the number of large individuals (>15 mm) and oxygen

690 concentration (a) and trawling intensity (average SAR, per year) (b) for all box core sampling

691 stations. The solid line is based on Tobit regression. There is no support for a model with

692 trawling (Table 1).

Tables

Table 1. Model selection and coefficients. B is benthic biomass, A is benthic abundance, T is trawling intensity (year^{-1}) and O is 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 m^2)			
$B = -59.04 + 23.31 \cdot O$	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 m^2)			
$A = -442.18 + 218.13 \cdot O$	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*±
$A = -368.60 + 155.34 \cdot O - 152.55 \cdot T + 69.04 \cdot T \cdot O$	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 m^2)			
$A = -536.92 + 221.99 \cdot O$	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 m^2)			
$A = -47.20 + 17.80 \cdot O$	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

± 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.

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