

Effects of bottom trawling and hypoxia on benthic invertebrate communities

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1 **Effects of bottom trawling and hypoxia on benthic invertebrate**
2 **communities.**

3

4 P. Daniël van Denderen^{1,2*}, Anna Törnroos³, Marija Sciberras⁴, Hilmar Hinz⁵, Rafal Lasota⁶,
5 Maria Cristina Mangano^{7,8}, Craig Robertson⁹, Sebastian Valanko¹⁰, Jan Geert Hiddink⁹

6

7 ¹ Centre for Ocean Life, DTU Aqua, Technical University of Denmark, Lyngby, Denmark

8 ² Graduate School of Oceanography, University of Rhode Island, Narragansett, USA

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

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

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

14 ⁶ University of Gdansk, Faculty of Oceanography and Geography, Institute of Oceanography,
15 Department of Marine Ecosystems Functioning, 81-378 Gdynia, Poland

16 ⁷ Department of Integrative Marine Ecology (EMI), Stazione Zoologica Anton Dohrn, Sicily

17 ⁸ Marine Centre, Lungomare Cristoforo Colombo (complesso Roosevelt) 90149, Palermo, Italy

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

19 ¹⁰ International Council for the Exploration of the Sea, Copenhagen, Denmark

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

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

23 **Abstract**

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

40

41 **Keywords:** bottom-trawling, hypoxia, Baltic Sea, macrofauna, body size, longevity, vertical
42 position in sediment

43 **1. INTRODUCTION**

44 Marine benthic habitats in continental shelf regions are increasingly impacted by
45 eutrophication-induced hypoxia (Diaz & Rosenberg 2008). Hypoxic regions are predicted to
46 expand due to the warming of shelf waters with climate change, which increases both the
47 oxygen demand and the strength of stratification of the water column (Breitburg et al. 2018).
48 Many periodic hypoxic regions, such as the Baltic and Adriatic Seas, are currently also being
49 fished by mobile bottom-contacting fishing gears, and these bottom trawl fisheries are the most
50 widespread source of anthropogenic physical disturbance to seabed habitats (Amoroso et al.
51 2018).

52 Since management of nutrient loads and subsequent declines of hypoxic regions will take
53 decades to centuries to occur, strategic management of bottom fisheries may be used to
54 alleviate some of the impacts on benthic fauna and the ecosystem. Such strategic management
55 requires quantifying the cumulative impacts of the two pressures on benthic fauna. The
56 cumulative impacts of trawling and hypoxia may be synergistic when hypoxic conditions make
57 organisms more sensitive to bottom fishing disturbance. Such effects may occur in areas where
58 hypoxic and anoxic bottoms result in upward migration of burrowing organisms to the sediment
59 surface (Pihl et al. 1992, Nilsson & Rosenberg 1994), thereby making these organisms more
60 vulnerable to damage by bottom gears dragged along the seabed surface. Synergistic effects
61 have also been proposed for brittle stars that became more sensitive to trawl disturbance due to
62 arm-tipping behaviour, i.e. the elevation of the central disk to escape the low oxygen
63 concentrations closest to the seafloor (Baden et al. 1990, Diaz & Rosenberg 1995). Under this
64 scenario, management measures that protect hypoxic or hypoxia-prone areas from fishing may
65 thus disproportionately benefit benthic fauna by reducing fishing-derived mortality of hypoxia
66 sensitive fauna, and thus lowering the risk of benthic habitats being pushed into a permanently
67 altered state (Riedel et al. 2016). Alternatively, when hypoxia leads to asphyxiation of sessile

68 fauna and/or migration of mobile fauna, leading to a depauperate state or even absence of
69 benthic fauna, trawling may have a negligible additional impact on the benthos. Animals that
70 can survive hypoxia events may also have physical characteristics that make them less
71 vulnerable to trawling and trawling may not affect these species significantly. Fisheries
72 management measures in such areas will have only limited benefits to the benthic ecosystem.

73 The above highlights that depending on the cumulative effects of bottom trawling and hypoxia,
74 management of human impacts on benthic habitats may either prioritize protection from
75 fisheries of hypoxic areas or prioritize the protection of areas that are non-hypoxic. So far, few
76 studies have quantified the interactive effects of bottom trawling and hypoxia on benthic
77 communities, limiting the development of management plans that consider the cumulative
78 effects. Recent work on a continental slope off Vancouver Island found that bottom trawling
79 continues to impact benthic communities in hypoxic areas, suggesting cumulative impacts that
80 are either additive or synergistic (De Leo et al. 2017).

81 Here we study the effects of bottom trawling and hypoxia on benthic communities in the Baltic
82 Sea. Throughout its historic past the Baltic Sea has seen hypoxic events on the seafloor (natural
83 and human induced), mainly due to limited water exchange with the Atlantic and in recent
84 decades excess nutrient input (Carstensen et al. 2014, Andersen et al. 2017). The Baltic Sea's
85 benthic communities lack large habitat forming epifauna, in particular in the deeper areas. This
86 is due to a low salinity, that in combination with its historic hypoxic past, has created the
87 characteristically low species diverse, but highly abundant benthic communities (Bonsdorff
88 2006). Most of these benthic communities consist of short-lived fauna (Törnroos et al. 2015,
89 2019, van Denderen et al. 2019), which are predicted to be largely resilient to bottom trawling
90 disturbance (Hiddink et al. 2018). Yet, approximately two thirds of the Baltic Sea bottom trawl
91 fishing footprint occurs in areas with seasonal oxygen concentrations $<3.2 \text{ ml O}_2 \text{ l}^{-1}$ that may
92 impact benthic organisms (van Denderen et al. 2019). It is therefore an area where trawling

93 impacts may be severely underestimated if synergistic effects are found to occur. The objective
94 of this study is to estimate interactive effects of bottom trawling and hypoxia on macrofaunal
95 biomass and abundance, large-bodied macrofauna, benthic community longevity and the
96 vertical position of fauna in the sediment. The studied stations ranged over a gradient in near-
97 bed oxygen concentrations from 0.8 to 5.8 ml O₂ l⁻¹ and in fishing intensity from little trawl
98 disturbance to up to 7 bottom trawl events per year. Our findings highlight a low likelihood of
99 synergistic effects between bottom trawling and hypoxia on the Baltic Sea benthic communities
100 studied.

101 **2. MATERIAL AND METHODS**

102 **2.1 Study area**

103 The effects of bottom trawling and hypoxia were examined over a gradient of oxygen and
104 bottom trawling intensity in the Southern Baltic Sea in Polish waters (Fig. 1). The area is an
105 active fishing ground with bottom trawling by otter trawls that target cod and flounder. The
106 area was selected as earlier work showed it has gradients in oxygen concentration and bottom
107 trawling intensity (van Denderen et al. 2019).

108 We selected sampling stations that covered a wide range of expected oxygen concentrations
109 and trawling intensities on muddy sediment in a limited depth range (61 - 102 metres, Table
110 S1-1), and aimed to cover all crossed combinations of trawling and oxygen to end up with a
111 design where the effects of trawling and oxygen could be disentangled. Unsurprisingly, we
112 could not identify any stations that had a high fishing effort at very low oxygen, as no fish can
113 survive in those conditions, but we did sample several stations with fishing and relatively low
114 oxygen concentrations (Fig. 2 and Table S1-1). All sampling stations were found in an area of
115 30 by 62 km, and the distance to the nearest station varied between 3 and 18 km.

116 **2.2 Sampling of benthic fauna**

117 Sampling was carried from on board the research vessel RV Oceanograf between 3 and 8
118 September 2018. Five replicate box corers and two replicate dredge samples were collected
119 from each station. Box corer samples (catching area 0.06 m² per core) were taken in a star
120 pattern, one at the selected position and four 100 m in each direction, using the vessel's
121 Dynamic Positioning System. At times, the box corer came up empty or lost most of the sample
122 before retrieval because the jaws did not close fully when pebbles or stones jammed the
123 mechanism. When sampling was unsuccessful, the ship was moved 10s of meters and the box
124 core redeployed. Three 4.5 cm diameter sub-cores up to a maximum depth of 17 cm were

125 collected from the first two intact box core samples collected at each station to assess the
126 vertical distribution of fauna in the sediment in areas of different oxygen and fishing levels.
127 Each sub-core was sliced into four sections (0-2 cm, 2-4 cm, 4-8 cm, >8 cm) and sieved to
128 obtain the fauna at different sediment depths. The rest of the box core sample was sieved over
129 0.5 mm sieve. Most samples had a solid clay layer below a surficial mud, sand and/or gravel
130 layer (surficial layer was ca. 8-18 cm deep); the clay layer was not sieved as no macrofauna
131 can and did occur in this solid layer. To separate the smaller fauna from the remaining gravel
132 and stones, samples were back-washed at least 7 times to obtain the fauna, by adding water,
133 stirring the sample and draining the water over a sieve to capture suspended animals. The
134 remaining sediment was checked for any further large fauna.

135 Semi-quantitative dredge samples were obtained using an Agassiz trawl type dredge (56 wide
136 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
137 1 (see below). The dredge was towed for 2 minutes at 1 knot and was generally full on retrieval.
138 Samples were searched visually for fauna. Station 1 was sampled with a Naturalist dredge (60
139 cm wide x 30 cm high) that was towed for 10 and 5 minutes at 1 knot. We expect that the
140 alternative methodology did not affect the resulting data in Station 1 as, in all cases, the dredge
141 filled up quickly and stopped sampling afterwards. Inspection of the data does not suggest the
142 dredge data in Station 1 is an obvious outlier.

143 All biota were identified to the lowest taxonomic level possible and their individual wet weight
144 was measured. For dredge samples, where species abundance was greater than approximately
145 100 individuals, a subsample was taken per species. In the subsample, length was measured for
146 all individuals whereas weight was measured for 50 individuals of a range of lengths. For the
147 remaining individuals, we converted length to weight using the established length-weight
148 relationship. We afterwards calculated abundance and biomass of the total sample based on the
149 relative size of the subsample.

150 **2.3 Environmental conditions**

151 A sub-core measuring 4 cm in diameter core by 4 cm in depth was collected from the first box
152 core sample collected at each station to determine sediment grain size composition. Particle
153 size distributions were determined using a Malvern laser diffraction particle sizer (Blott & Pye
154 2001). Sediment particle analysis showed that most of the stations had a high percentage mud
155 (Table S1-1). Visual inspection of the box cores showed that the muddy sediment was
156 sometimes mixed with pebbles, gravel or sand and typically with a deeper layer of glacial clay.
157 Some stations had ferromanganese nodules on the seafloor surface. A principal component
158 analysis on depth and sediment conditions shows that stations 5 and 16 could be outliers due
159 to a relatively high sand / gravel fraction, respectively (Fig. S1-1). Results showed similar
160 patterns and trends when these stations were excluded from the analysis. It was therefore
161 decided to maintain these stations within the analysis, despite small differences in sediment
162 composition.

163 Bottom water was collected at 20 cm above the seabed with a Niskin bottle and oxygen
164 saturation (YSI model 58) and temperature and salinity (WTW Multiset 340i with TetraCon
165 325) were measured from three replicate water samples collected at each station (with the
166 exception of the first few stations where only a single measurement was taken) (Table S1-1).
167 Temperature and salinity information was used to convert oxygen saturation into oxygen
168 concentration in ml per litre following Benson and Krause (1984). A large fraction of stations
169 was azoic, with concentrations below 1 ml O₂ l⁻¹ and with a strong smell of H₂S and a clear
170 black surface layer. In addition to the oxygen measurements taken at the sampling stations, we
171 analysed a time series of bottom oxygen concentration measurements collected from a nearby
172 site at 90 m depth (red asterisk in Fig. 1) between 2012 and 2018. Monthly bottom oxygen
173 concentration was calculated by averaging oxygen measurements at depths less than five

174 meters from the seafloor per month (where available). Data used were obtained from HELCOM
175 secretariat and based on ICES dataset on [Ocean Hydrography](#).

176 Bottom trawling intensity data were obtained at a $0.05^\circ \times 0.05^\circ$ grid resolution (ICES 2019),
177 and expressed as the ratio of the area that is swept each year by trawl gears relative to the total
178 surface area (hereafter termed swept-area-ratio, SAR). We used average SAR values per grid
179 cell for the period 2013-2017, as we were interested in chronic effects of fishing and since
180 recovery following trawling disturbance may last more than one year.

181 **2.4 Data analysis**

182 We analysed the effect of trawling and oxygen concentrations on community biomass and
183 abundance, the number of large organisms, the biomass-longevity distribution of the benthic
184 community and the vertical position of fauna in the sediment. In all analyses, we estimated
185 biomass and abundance as the sum of all box core or dredge samples per station. All results
186 show biomass of bivalves with shell. Since the biomass patterns are strongly driven by bivalve
187 weights, we verified that similar results are obtained when shell-free wet weight is used (based
188 on a wet weight to shell-free wet weight conversions as shown in Table S1-2). The dataset, R
189 scripts and output are available on Github with DOI: [10.5281/zenodo.5579600](https://doi.org/10.5281/zenodo.5579600).

190 Community biomass and abundance

191 We tested the effect of trawling and oxygen and their interaction on community biomass and
192 abundance with a Tobit regression model and selected the best model using the Akaike
193 Information Criterion (AIC); when models differ less than 2 AIC-units, the model with fewest
194 parameters is selected. Tobit regression is designed to estimate relationships assuming a normal
195 distribution for the response variable with left/right censoring, i.e. where a threshold value is
196 set to the response variable above/below the response variable data are censored (Tobin
197 1958). We used Tobit regression as it was expected that a range of sampling stations at low

198 oxygen concentrations had zero biomass and abundance and we therefore set the threshold for
199 censoring our data at zero biomass and abundance. The community biomass and abundance
200 analyses were done considering all stations, to examine the combined effect of trawling and
201 oxygen concentration, as well as for a subset of stations with oxygen concentrations $> 3 \text{ ml O}_2$
202 l^{-1} to examine the effect of bottom trawling in isolation (Figure 2). The oxygen threshold value
203 was chosen since benthic biomass and abundance no longer correlate with oxygen above this
204 value.

205 Large organisms

206 Since previous work showed that the impact of bottom trawling is larger on larger benthic
207 organisms ($> 4 \text{ mm}$) (McLaverly et al. 2020), we included a separate analysis to study the effect
208 of oxygen and trawling on the number of large organisms in the benthic community. The
209 analysis used the same Tobit regression model as described above. We used two length
210 thresholds: $>4 \text{ mm}$ and $>15 \text{ mm}$. We estimated individual length using length-weight
211 relationships from the literature (Table S1-3).

212 Community longevity

213 Previous work has further shown that long-lived fauna are more impacted by bottom trawling
214 (Rijnsdorp et al. 2018, Hiddink et al. 2018). We therefore examined the effect of trawling and
215 oxygen on the longevity biomass distribution of the benthic community. We used the box core
216 data to study changes in the biomass-longevity composition as these data provide a more
217 controlled estimate of biomass (the dredge filled up quickly, as noted above). Using
218 information on species longevity of benthic fauna in the Baltic Sea (Törnroos & Bonsdorff
219 2012, van Denderen et al. 2019), we classified biota in four longevity groupings: maximum
220 lifespan of 0-1 years, 1-3 years, 3-10 years and > 10 years. The resulting taxon-by-trait matrix
221 was combined with the taxon biomass-by-station (gram wet weight per 0.3 m^2) matrix to create
222 the final station-by-trait matrix. We used a PerMANOVA analysis to examine if changes in

223 trawling intensity and/or oxygen concentrations had a significant effect on the distribution of
224 benthic biomass in these four longevity groupings. This analysis was done on absolute and
225 fractional biomass values per longevity grouping and sampled station.

226 Vertical position

227 We also used a PerMANOVA analysis to examine if changes in oxygen concentrations and
228 trawling intensity affected the vertical distribution of fauna in the sediment. Since the number
229 of observations was low in the vertical sub-cores, we limited our analysis to examining
230 community changes in the vertical position using the abundance and biomass data, whereas we
231 did not examine species-specific vertical changes. The analyses were done on absolute and
232 fractional abundance/biomass data per vertical section and sampled station.

233 3. RESULTS

234 3.1 Temporal and spatial stability in fishing and near-bed oxygen

235 We used average fishing intensities per grid cell for the period 2013-2017 to examine the
236 chronic effects of fishing. A cross-comparison of fishing intensities between all years shows
237 clear correlations, with an average Pearson product-moment correlation of 0.89. These strong
238 correlations show there is temporal stability in the spatial fishing patterns studied. The studied
239 gradient in fishing intensities is conserved in 2018, the year of sampling (Pearson correlation
240 of 0.85 when compared with the annual average for the period 2013-2017), although the
241 average level of fishing in the area in 2018 is marginally lower (average SAR in 2018 for all
242 stations is 1.0, whereas it varies between 1.3 and 2.9 in the other years).

243 The time series of near-bed oxygen concentrations (Fig. 3a) shows large fluctuations between
244 months, with maximum concentrations close to 5 and minimum less than 0.5 ml O₂ l⁻¹. The
245 median near-bed oxygen concentrations are lower in summer and autumn (Q3 and Q4, Fig.
246 3b), although very low oxygen concentrations have been found in all seasonal quarters. The
247 time series highlights that there are significant uncertainties in the temporal history of near-bed
248 oxygen in our sampled stations (see further *Discussion* section).

249 3.2 Community biomass and abundance

250 The biomass of the community is dominated by the bivalves *Astarte elliptica*, *Mytilus trossulus*
251 and *Limecola balthica* (formerly known as *Macoma balthica*). Together these species
252 comprised 90% of total biomass in the box core data and 99% in the dredge. Abundance is
253 dominated by the bristleworm *Scoloplos armiger* (27% of total abundance) in the box core data
254 and by *A. elliptica* (81% of total abundance) in the dredge. No biota is found at stations with
255 oxygen concentrations below 2 ml l⁻¹. All stations with oxygen concentrations above 3 ml l⁻¹
256 had some fauna.

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

265 To explore further the community response to trawling, we examined changes in biomass for
266 the six most dominant species (in terms of biomass) in the box core samples and the five most
267 dominant in the dredge samples collected at stations with relatively high oxygen concentrations
268 ($> 3 \text{ ml l}^{-1}$). It is worth noting that all species have a non-significant relationship with oxygen
269 in this subset (not shown). We find no significant relationship between biomass and trawling
270 intensity for most dominant species, except for the priapulid worm *Halicryptus spinulosus*
271 where a significant positive relationship is observed between its biomass and trawling in both
272 dredge and box core data (Fig. 6).

273 **3.3 Large organisms**

274 Individuals larger than 4 mm comprised $>99\%$ of total biomass and 85% of total abundance.
275 For these individuals ($n = 1587$), we find a significant positive relationship between oxygen
276 and abundance and between trawling intensity and abundance (Table 1). Individuals larger than
277 15 mm comprised 30% of total biomass and 6% of total abundance. For these individuals ($n =$
278 110), there is again a significant positive relationship between oxygen and abundance, whereas
279 tobit regression indicates no support for a model that includes trawling (Table 1). The dominant
280 species contributing to the 'larger than 15 mm' group are the bivalve *A. elliptica* ($n = 34$), the
281 isopod *Saduria entomon* ($n=19$) and the bristleworm *Terebellides stroemii* ($n=16$). The number

282 of individuals larger than 15 mm varies among stations between 0 and 21 per 0.3 m² (the sum
283 of the five box cores); high numbers are only found in areas with relatively high oxygen
284 concentrations (> 3.5 ml l⁻¹) (Fig. 7).

285 **3.4 Community longevity**

286 Almost 90% of the total biomass is grouped as fauna with longevities between 3 and 10 years
287 and no species are found with lifespans more than 10 years. PerMANOVA analysis shows no
288 support for a change in the biomass longevity composition of the community with changes in
289 oxygen and/or trawling intensity (Table S1-4).

290 **3.5 Vertical position**

291 In total, 143 individuals are found in the vertical sub-cores across the stations. Most fauna (102
292 individuals, representing 90% of total biomass) are in the upper 0-2 cm of the sediment.
293 Different polychaete species (*Pygospio elegans*, *Aricidea catherinae*, *Nereis diversicolor* and
294 *Streblospio benedicti*), nematodes and ostracods are found in low abundance at depths deeper
295 than 4 cm (in total 11 individuals, representing 1% of total biomass). PerMANOVA analysis
296 shows no support for a change in the vertical distribution of fauna with changes in oxygen
297 and/or trawling intensity (Table S1-5). The vertical biomass and abundance distribution is for
298 each species shown in Figure S1-2 and S1-3.

299 **4. DISCUSSION**

300 We examined the effects of bottom trawl disturbance and oxygen on benthic community
301 biomass and abundance, the number of large-bodied individuals, community longevity and the
302 vertical position of fauna in the sediment. Our results show that changes in near-bed oxygen
303 concentrations have a large impact on benthic fauna, whereas trawling had a weak positive
304 effect on some species and community metrics and no effect on others. The lack of negative
305 effects of trawling on most parameters, and a positive effect on some community metrics and
306 the priapulid worm *Halicryptus spinulosus*, are somewhat unexpected given the high annual
307 trawling frequencies at some sampling stations. We discuss below whether these non-negative
308 effects may be a true effect or the result of different confounding factors. Whatever the reason,
309 our findings highlight that bottom trawling appears to have limited impacts on the benthic
310 communities studied here.

311 **4.1 Non-negative trawl effects on benthic fauna**

312 Bottom trawl impacts depend on the frequency of trawl disturbance, the amount of mortality
313 (depletion) that bottom gears cause and the recoverability of the benthic community (Pitcher
314 et al. 2017). The fisheries data shows that all trawling in the area occurs with a demersal otter
315 trawl. This is a relatively light gear that is associated with a low depletion rate of 0.03, i.e.
316 causing a biomass decline of 3% each time a benthic community is swept by this trawl (Hiddink
317 et al. 2017, Rijnsdorp et al. 2020). All fauna in the studied region are further relatively short
318 lived (<10 years), potentially the result of selection by environmental filtering due to low
319 salinity and variable oxygen levels (Bonsdorff 2006). Short-lived species have relatively high
320 recovery rates (Hiddink et al. 2018). Therefore, low trawl impacts may be expected in this area.
321 Nonetheless, model predictions based on the observed longevity and the above depletion rate
322 suggest a 20% decline of community biomass relative to carrying capacity in a location with a
323 chronic fishing frequency of SAR = 7 a year (see SI 2 for the calculation). Although this is a

324 substantial effect, the variation in the recorded benthic communities is large due to natural
325 variation and sampling error, and the power to detect such an effect may have been limited.

326 Biomass comparisons with the Kattegat and the more northern Gotland Basin reveal that box
327 core biomass in our study area is on average 6 to 10 times lower than in those areas (Sköld et
328 al. 2018, van Denderen et al. 2019). Since low oxygen conditions tend to affect relatively large
329 areas homogenously, the low biomass in our study area may be the result of low and variable
330 oxygen levels that have hindered recruitment and recolonization from neighbouring regions
331 (Whitlatch et al. 1998). Recruitment in the Baltic Sea is also more stochastic and dependent on
332 wind-induced waves since it is a non-tidal system (Valanko et al. 2010). It may therefore be
333 hypothesized that any survivors and/or new arrivals in the area will have little competition for
334 space and food and high growth rates, thus resulting in lower trawl impacts than expected.

335 The large fluctuations in oxygen concentration may also have limited our ability to detect
336 negative bottom trawl effects given that we sampled at only one point in time. Some sampled
337 stations with high oxygen measurements during our survey may have experienced lower levels
338 in earlier months that would have killed a large fraction of the biota, causing a large amount of
339 noise on the trawl impact signal. Nonetheless, all areas with relatively high oxygen
340 concentrations were found to have some large-bodied (> 15 mm) individuals in the box core
341 (Fig. 7). This suggests that the historic oxygen conditions were sufficient to allow the benthos
342 to survive and grow to a large size. Moreover, most species sampled have minimal mobility so
343 are unlikely to have moved from neighbouring regions.

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

348 effect on priapulid abundances (Bonsdorff et al. 1995). *S. entomon* shows a negative trend with
349 trawling intensity that albeit non-significant may have lowered predation pressure on infaunal
350 prey in fished areas. Although speculative, the declining trend of *S. entomon* with trawling can
351 itself also be driven by predation, since cod, an important predator on *S. entomon* (Neuenfeldt
352 et al. 2020), may be found at higher abundances in areas of high fishing.

353 **4.2 Low oxygen conditions and the absence of fauna**

354 We found no benthic fauna in locations with oxygen concentrations less than 2 ml l⁻¹. Mass-
355 mortality of benthic fauna typically occurs around 0.5 ml O₂ l⁻¹ (Diaz & Rosenberg 1995) and
356 it is therefore likely that these sampling locations had lower oxygen levels earlier in the year.
357 We also found no benthic fauna in Station 9, where an oxygen concentration of 1.3 ml l⁻¹ was
358 measured. Station 9 is only 3.7 km away from the location with a time series of near-bed
359 oxygen (Fig. 1, Fig. 3), making it likely that the time series reflect the temporal oxygen history
360 of Station 9. The time series shows that oxygen concentrations dropped below 0.5 ml O₂ l⁻¹ in
361 May 2018, which is four months before sampling. This drop is likely the moment where the
362 mass-mortality occurred that led to the defaunation of Station 9. Importantly, in June 2018
363 oxygen concentrations were again 2 ml O₂ l⁻¹, showing the fine-scale temporal fluctuations in
364 oxygen conditions. These results highlight that models predicting mortality on benthic fauna
365 from hypoxia need near-bed oxygen data that captures these fine-scale temporal fluctuations
366 in oxygen, as predictions will otherwise be at risk of significantly underestimating the effect.
367 For example, all seasonal averages of the time series are well above 1 ml O₂ l⁻¹ and these values
368 would not suggest a benthic defaunation of the area. A conclusion that warrants a reassessment
369 of oxygen condition monitoring for assessing and disentangling seabed disturbance activities
370 in the future.

371 The fishing intensity at Station 9 declined most severely in comparison to all stations, over the
372 period 2013-2018. The station exhibited values close to SAR = 10 in 2013 and 1 in 2018. Fig.

373 S1-4 shows there is a strong and positive relation between the annual fishing intensities at
374 Station 9 and the maximum yearly oxygen concentrations from the time series (linear model
375 shows a p-value of 0.01 and an adjusted R^2 of 0.78), whereas no relation is found for minimum
376 or average yearly oxygen conditions. This finding may imply that peaks in oxygen, which are
377 still below $5 \text{ ml O}_2 \text{ l}^{-1}$, attract fish and subsequently fisheries in this area. Catch rates of cod, an
378 important target species, have been shown to peak at these intermediate oxygen conditions in
379 the neighbouring Bornholm Basin (Neuenfeldt & Beyer 2003). Since cod feeds on pelagic sprat
380 as well as benthic animals (especially motile ones), cod abundance may be high in areas where
381 the state of the seafloor is low. This could explain why there is no relationship between trawling
382 intensity and the average or minimum yearly oxygen conditions. If correct, there is an
383 important temporal aspect to the interactive impacts of trawling and hypoxia on benthic fauna,
384 where trawl disturbance will be highest in periods with relatively healthy oxygen conditions.

385 **4.3 No synergistic effects**

386 Despite significant uncertainties in the impact of trawling on benthic fauna and the temporal
387 history of oxygen conditions, it is clear from our study that trawling impacts are not
388 underestimated for this area because of clear synergistic effects between low oxygen conditions
389 and trawling. Compared to other regions, two characteristics of the benthic community and the
390 environment may have reduced the potential for synergistic effects in this area. Firstly, most
391 samples had a deeper layer of glacial clay and few deep-bioturbating species; 99% of total
392 biomass was found in the upper 4 cm. This limits the potential of increasing trawl impacts with
393 hypoxia due to upward migration of burying organisms to the sediment surface as observed in
394 other regions (Pihl et al. 1992, Nilsson & Rosenberg 1994), because all fauna is already found
395 in the upper surface layers. Secondly, there were no ophiuroids and asteroids present in the
396 area, limiting the potential of high trawl impacts with hypoxia due to arm-tipping behaviour.

397 This highlights that other regions with a different benthic fauna and sediment composition may
398 show a different response, as is also observed by De Leo et al., (2017).

399 **4.4 Management implications**

400 Our results suggest that significant long-term improvements of benthic communities in this
401 area are not to be expected when the area is solely protected from bottom trawl disturbance
402 (even though significant negative effects of trawling in certain months of the year cannot be
403 ruled out). Management of bottom trawl fisheries could therefore prioritize the protection of
404 neighbouring non-hypoxic regions, under the assumption that trawl impacts do take place in
405 these regions. Bottom fisheries management targeting non-hypoxic regions can thus be used to
406 improve the overall status of benthic fauna in these specific areas within a relatively short
407 period of time, which could have positive spill-over effects for neighbouring seasonal or more
408 permanent hypoxic areas. Continued reductions of nutrient loads and subsequent declines of
409 hypoxic regions would also benefit the state of the benthic ecosystem, but such management
410 actions targeting eutrophication and hypoxia take decades before they yield positive results on
411 the benthic ecosystem (Carstensen et al. 2014).

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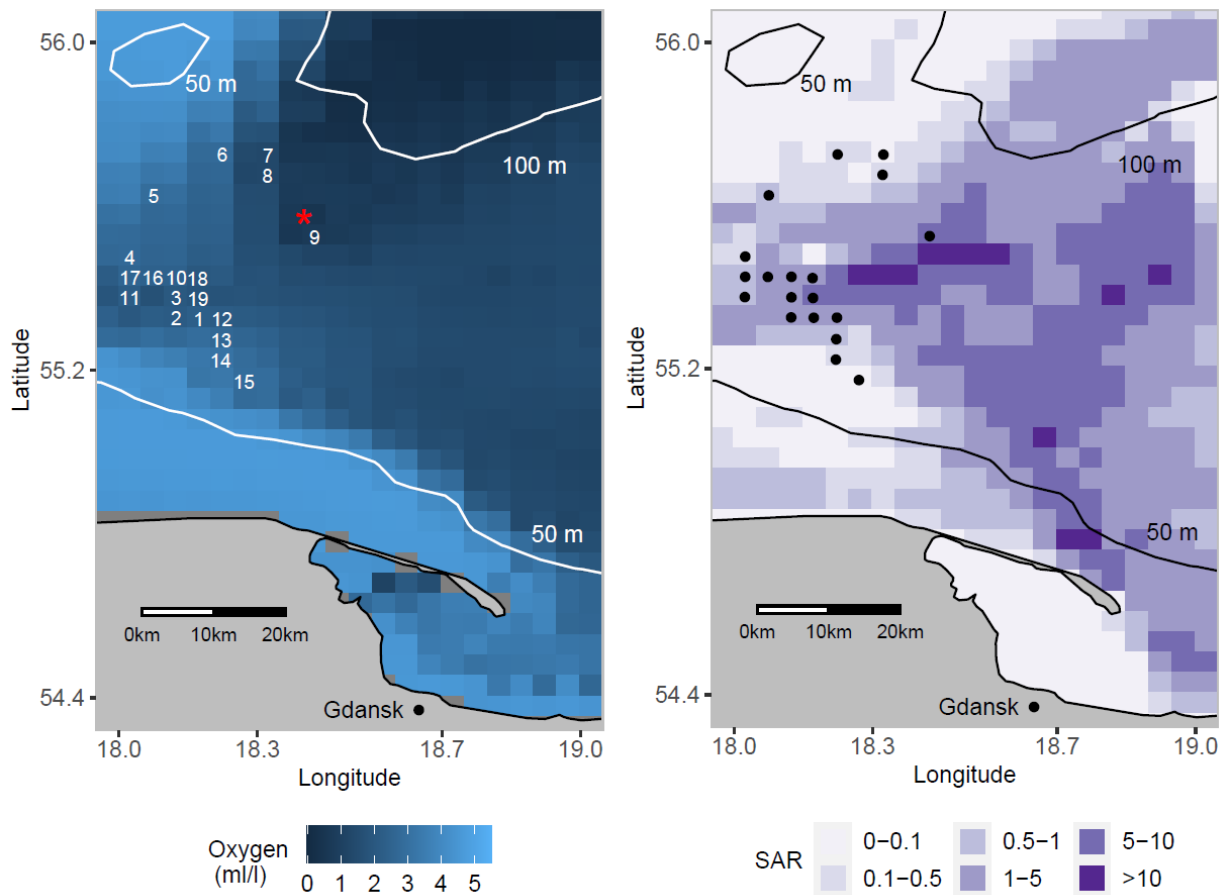
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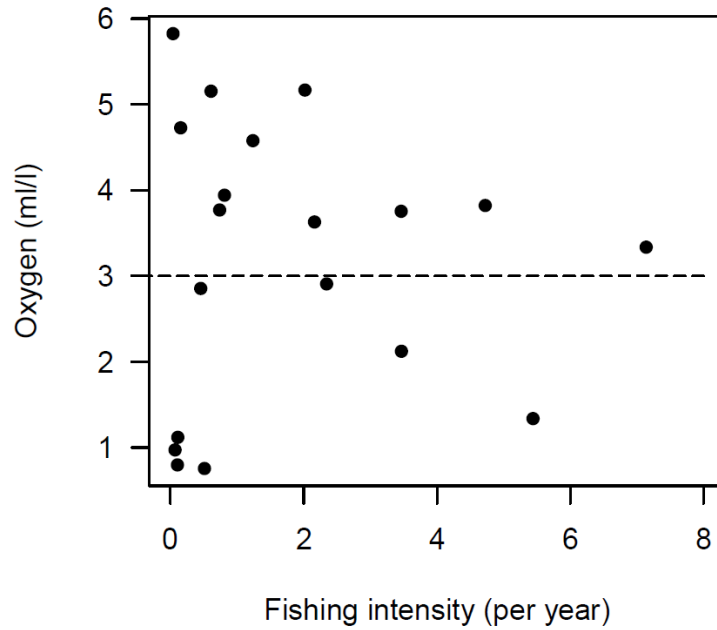
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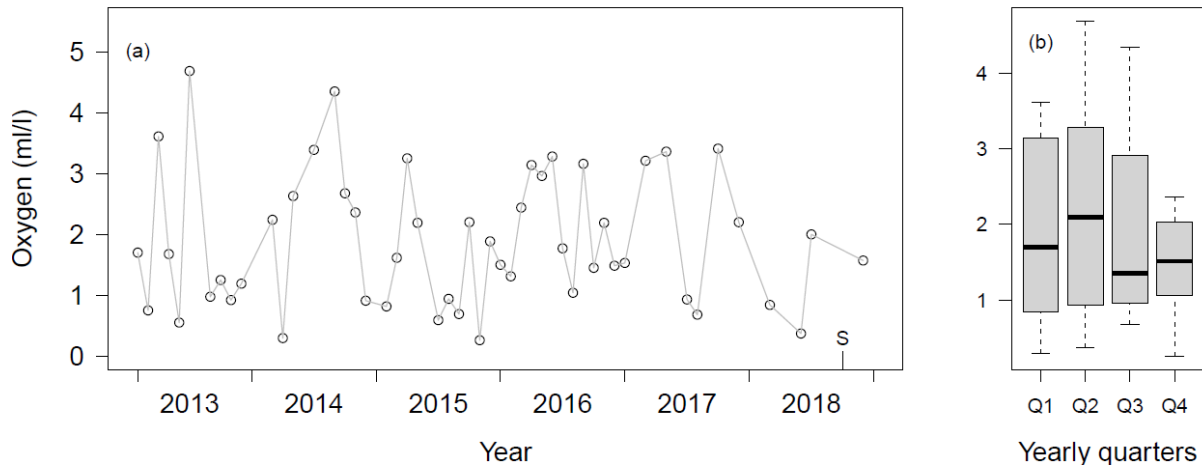
525

526 Figure 1. Maps of the sampling station locations in the southern Baltic Sea (numbers
 527 correspond to Table S1-1). The oxygen concentrations (left) show the lowest seasonal
 528 concentration in the year based on modelled bottom oxygen concentrations from an ecosystem
 529 model representative of 2006-2010 (Schernewski et al. 2015). The red asterisk shows a nearby
 530 location with time-series of near-bed oxygen measurements (see further Fig. 3). The fishing
 531 intensity data (right) show average SAR (Swept Area Ratio per year) values for the period
 532 2013-2017. Depth contours were extracted from the Baltic Sea Hydrographic Commission
 533 (2013). The oxygen and depth data were solely used to select sampling stations as depth and
 534 oxygen data used in the analysis were measured in-situ at each station.



535

536 Figure 2. Fishing intensity (average SAR, per year) and oxygen concentration of the sampling
 537 stations. We analysed all sampling stations together to examine the combined effect of trawling
 538 and oxygen concentration, as well as a subset of stations with oxygen concentrations > 3 ml O₂
 539 l⁻¹ (stations above dashed line) to explore trawling effects in isolation. This threshold was
 540 chosen as no effect of oxygen on benthic biomass or abundance is observed above this
 541 concentration.



542

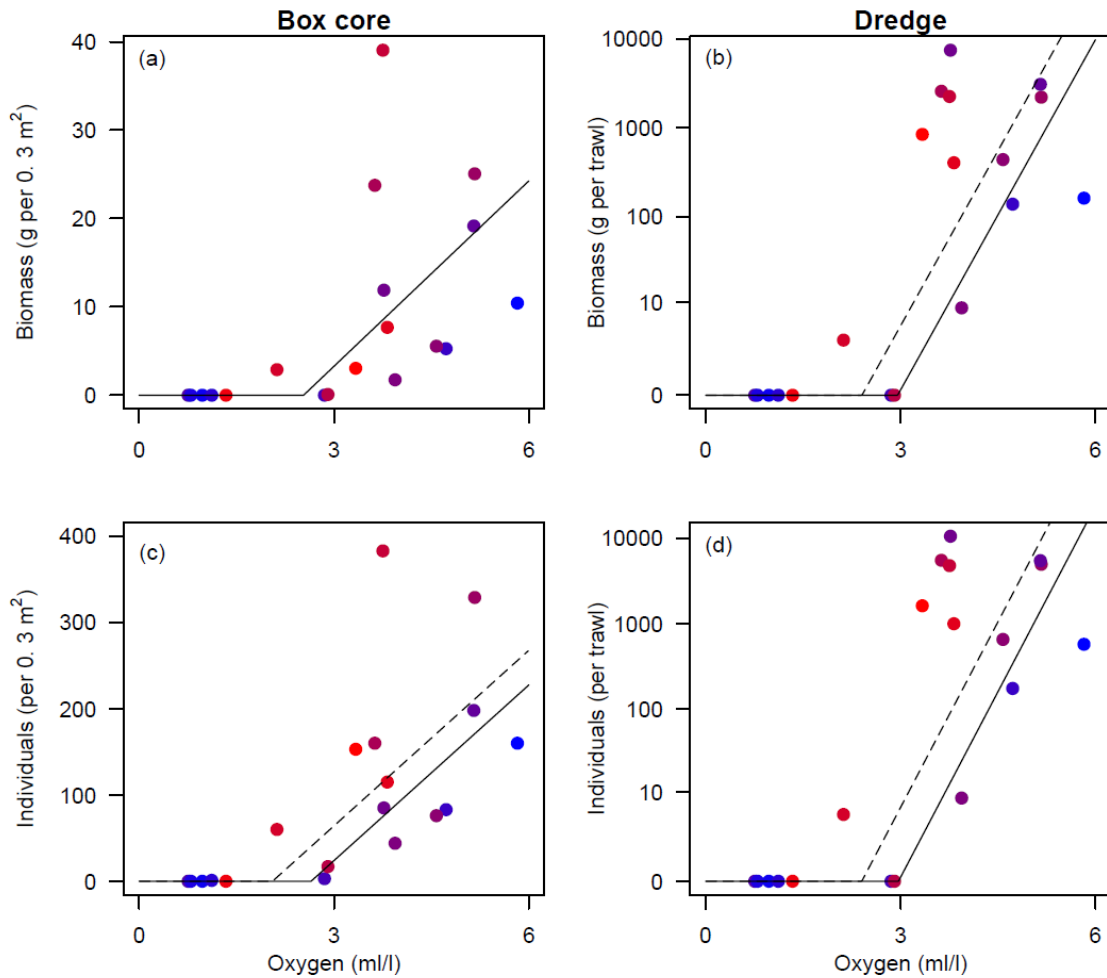
543 Figure 3. (a) Time series of near-bed oxygen concentrations at a nearby location of our study

544 area (red asterisk in Fig. 1) from 2013 to 2018. The letter “S” indicates when we sampled the

545 study area. (b) Boxplot of oxygen concentrations for each seasonal quarter based on all data

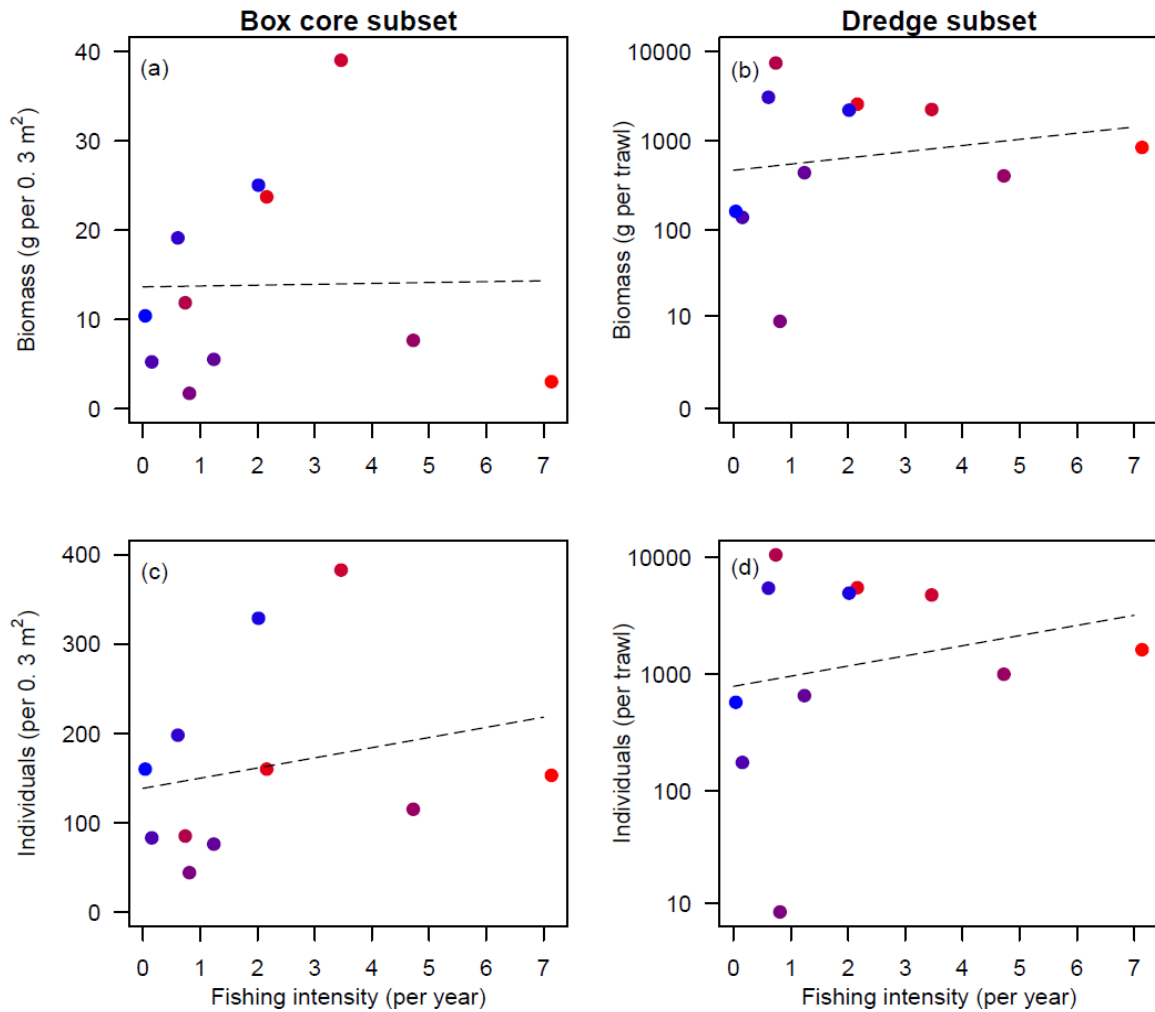
546 points in (a), indicating lower median oxygen concentrations in quarter 3 and 4. Data used were

547 obtained from HELCOM secretariat and based on ICES dataset on [Ocean Hydrography](#).



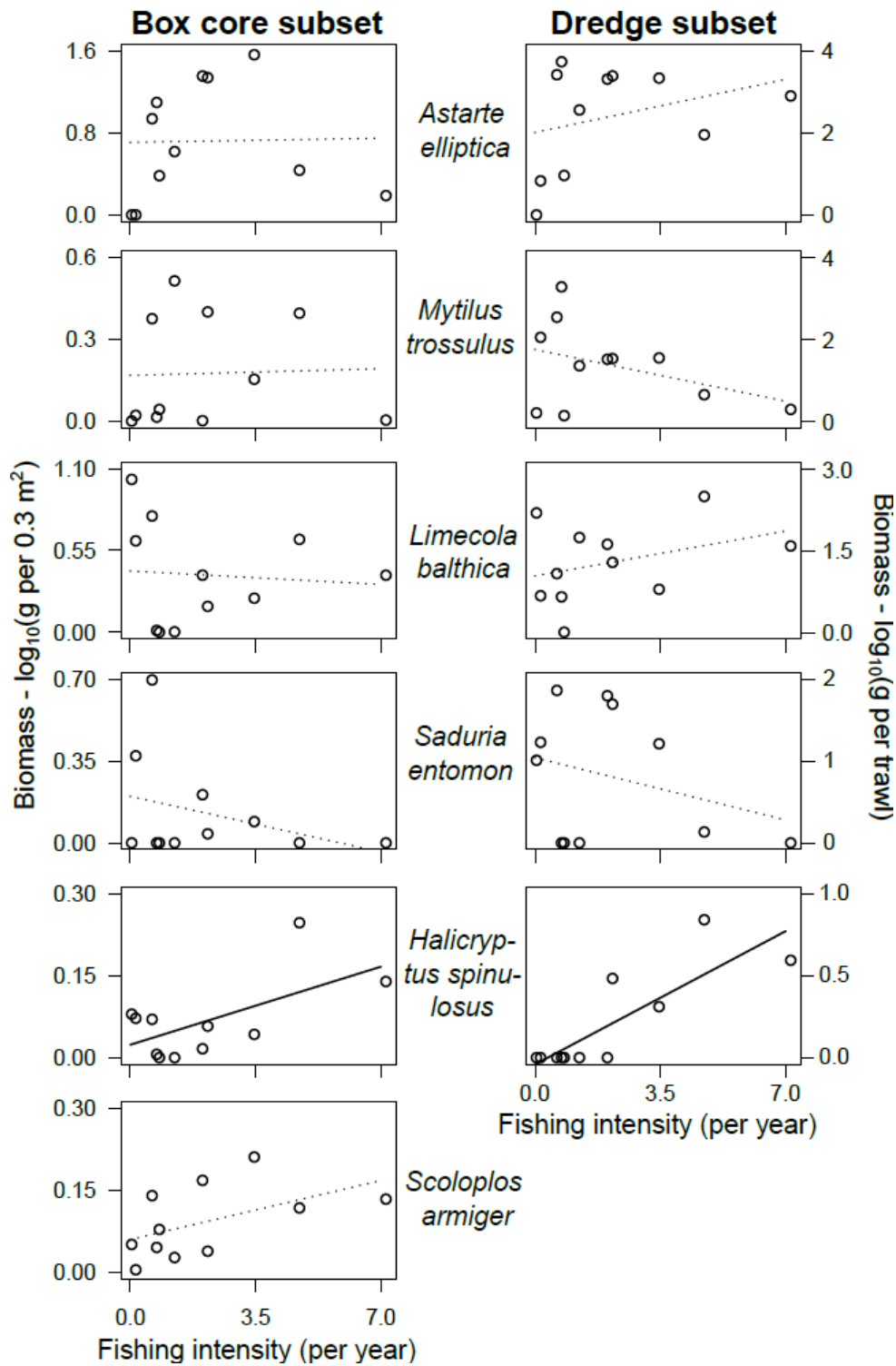
548

549 Figure 4. Relationships between oxygen and total faunal biomass and abundance collected
 550 using the box corer (a, c) and dredge (b, d). Lines are fitted with a Tobit-regression. In (b-d)
 551 where trawling intensity is part of the best model (Table 1), the solid lines show the prediction
 552 without fishing (SAR = 0) and the dashed lines with SAR = 2. Points are coloured using a
 553 linear colour gradient from the station with the lowest (blue, SAR = 0.04) to highest (red, SAR
 554 = 7.14) fishing intensity. The dredge data is $\log_{10}(x+1)$ transformed because there are four
 555 orders of magnitude variation between stations.



556

557 Figure 5. Relationship between fishing intensity (average SAR, per year) and faunal biomass
 558 and abundance of box corer and dredge for stations with oxygen concentrations above 3 ml l⁻¹
 559 ¹. The relationships are all non-significant based on linear regression. Points are coloured using
 560 a linear colour gradient from the station with the lowest oxygen concentration (red, 3.3 ml l⁻¹)
 561 to the highest (blue, 5.8 ml l⁻¹) in this data subset.



562

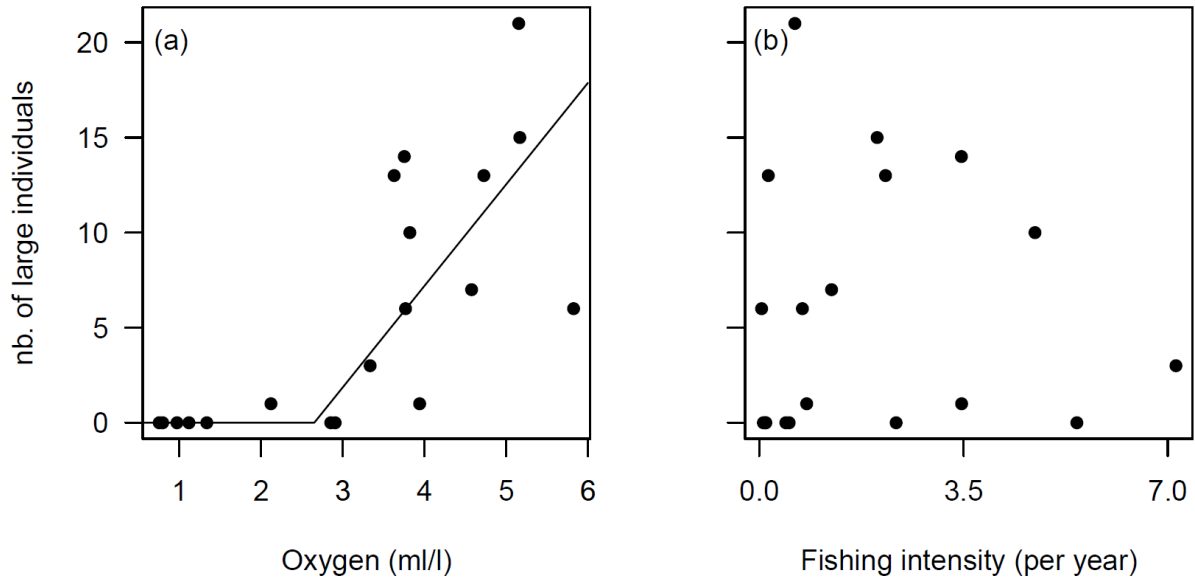
563 Figure 6. Relationship between fishing intensity (average SAR, per year) and the biomass of

564 different dominant species in box corer and dredge for all stations with oxygen concentrations

565 above 3 ml l⁻¹. Solid lines show significant relationships (p-value <0.05), dashed lines non-

566 significant. Note that all species in this subset have a non-significant relationship with oxygen

567 concentration.



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570

571

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

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

Model	σ	p-values	AIC
Box core biomass			
$B = -17.71 + 7.00 \cdot O$	2.35	$P_O < 0.001$	114.7*
$B = -23.37 + 7.58 \cdot O + 1.72 \cdot T$	2.32	$P_O < 0.001; P_T = 0.20$	115.1
$B = -16.11 + 5.54 \cdot O - 4.00 \cdot T + 1.73 \cdot T \cdot O$	2.27	$P_O = 0.01; P_T = 0.41; P_{T \cdot O} = 0.21$	115.5
Box core abundance			
$A = -132.65 + 65.44 \cdot O$	4.53	$P_O < 0.001$	187.7
$A = -179.66 + 67.86 \cdot O + 20.12 \cdot T$	4.43	$P_O < 0.001; P_T = 0.06$	186.3*±
$A = -110.58 + 46.60 \cdot O - 45.77 \cdot T + 20.71 \cdot T \cdot O$	4.32	$P_O = 0.005; P_T = 0.20; P_{T \cdot O} = 0.05$	184.4
Dredge biomass			
$\text{Log}_{10}(B+1) = -2.57 + 1.16 \cdot O$	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			
$\text{Log}_{10}(A+1) = -2.78 + 1.26 \cdot O$	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)			
$A = -161.08 + 66.60 \cdot O$	4.56	$P_O < 0.001$	176.6
$A = -252.91 + 76.43 \cdot O + 27.27 \cdot T$	4.42	$P_O < 0.001; P_T = 0.02$	173.3*
$A = -162.55 + 52.31 \cdot O - 29.86 \cdot T + 17.09 \cdot T \cdot O$	4.34	$P_O = 0.005; P_T = 0.45; P_{T \cdot O} = 0.12$	172.9
Box core abundance (individuals >15 mm)			
$A = -14.16 + 5.33 \cdot O$	1.71	$P_O < 0.001$	85.8*
$A = -18.72 + 5.98 \cdot O + 0.99 \cdot T$	1.69	$P_O < 0.001; P_T = 0.21$	86.3
$A = -14.34 + 4.86 \cdot O - 1.74 \cdot T + 0.78 \cdot T \cdot O$	1.65	$P_O < 0.001; P_T = 0.58; P_{T \cdot O} = 0.37$	87.5

± note that a model without trawling (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.

579