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Evaluating impacts of bottom trawling and hypoxia on benthic communities at the local, habitat and regional scale using a modelling approach

PD van Denderen¹, SG Bolam², R Friedland³, JG Hiddink⁴, K Norén⁵, AD Rijnsdorp⁶, M Sköld⁵, A Törnroos⁷, EA Virtanen⁸ & S Valanko⁹

¹ Centre for Ocean Life - Danish Technical University Aqua, Kongens Lyngby, Denmark

² Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK

³ Leibniz-Institut für Ostseeforschung Warnemünde, Rostock, Germany

⁴ School of Ocean Sciences - Bangor University, Menai Bridge, United Kingdom

⁵ Department of Aquatic Resources, Institute of Marine Research, Swedish University of Agricultural Sciences, Lysekil, Sweden

⁶ Wageningen Marine Research - Wageningen University, IJmuiden, the Netherlands

⁷ Environmental and Marine Biology - Åbo Akademi University, Turku, Finland

⁸ Marine Research Centre - Finnish Environment Institute, Helsinki, Finland

⁹ International Council for the Exploration of the Sea, Copenhagen, Denmark

Corresponding author: P. Daniël van Denderen, pdvd@aqua.dtu.dk, Centre for Ocean Life - Danish Technical University Aqua, Kongens Lyngby, Denmark

21 **Abstract**

22 Bottom trawling disturbance and hypoxia are affecting marine benthic habitats worldwide. We present
23 an approach to predict their effects on benthic communities, and use the approach to estimate the state,
24 the biomass relative to carrying capacity, of the Baltic Sea at the local, habitat and regional scale.
25 Responses to both pressures are expected to depend on the longevity of fauna, which is predicted from
26 benthic data from 1558 locations. We find that communities in low-salinity regions mostly consist of
27 short-lived species, which are, in our model, more resilient than those of the saline areas. The model
28 predicts that in 14% of the Baltic Sea region benthic biomass is reduced by at least 50%, whereas an
29 additional 8% of the region has reductions of 10-50%. The effects of hypoxia occur over larger spatial
30 scales and lead to a low state of especially deep habitats. The approach is based on a simple
31 characterization of the benthic community, which comes with high uncertainty, but allows for the
32 identification of benthic habitats that are at greatest risk and prioritization of management actions at the
33 regional scale. This information supports the development of sustainable approaches to manage impact
34 of human activities on benthic ecosystems.

35 **Keywords**

36 benthic fauna, bottom fishing, ecosystem-based management, human pressures, impact assessment,
37 oxygen deficiency, seabed disturbance

38 **Introduction**

39 Bottom trawling disturbance and hypoxia cause widespread impacts on marine ecosystems, changing the
40 physical and physico-chemical characteristics of the seabed and their associated benthic invertebrate
41 communities (Gray and Wu, 2002; Sciberras *et al.*, 2016; Hiddink *et al.*, 2017). Bottom trawl fisheries
42 account for >25% of the global fisheries capture and have a large spatial footprint, especially in
43 continental shelves (Eigaard *et al.*, 2017; Amoroso *et al.*, 2018; Watson and Tidd, 2018). Hypoxia of sea
44 bottom waters due to eutrophication is becoming increasingly widespread around the world and is
45 estimated to affect approximately 0.25 million square kilometres of shallow regional seas and coastal
46 habitats (Diaz and Rosenberg, 2008; Breitburg *et al.*, 2018).

47 Fishing vessels using bottom trawls physically disturb the seabed by towing a gear (e.g., trawls, dredges)
48 over the seafloor that damages and/or kills benthic organisms, reducing species biomass, abundance and
49 richness (de Groot, 1984; Collie *et al.*, 2000; Sciberras *et al.*, 2018). The effects of trawling are most
50 pronounced in long-lived benthic organisms as these typically take longer to recover after a trawling
51 event (Hiddink *et al.*, 2018; Kaiser *et al.*, 2018). Frequently trawled areas have been shown to exhibit
52 reductions in the biomass of long-lived organisms (Tillin *et al.*, 2006; van Denderen *et al.*, 2015).

53 Eutrophication-induced hypoxia, oxygen deficiency, and anoxia, severe hypoxia, i.e. absence of
54 dissolved oxygen, in bottom waters results from both natural processes and anthropogenic activity. The
55 impact of oxygen deficiency in benthic species depends on the severity of hypoxia. Low, but non-lethal,
56 oxygen concentrations result in various behavioural changes. Mobile organisms may move away from
57 or avoid hypoxic areas, while behavioural responses of sessile species may manifest as alterations to
58 feeding and bioturbation rates (Villnäs *et al.*, 2012). Further declines in oxygen concentrations lead to
59 mortality depending on species-specific sensitivities and the magnitude and extent of hypoxia, with

complete faunal depletion being observed in very low oxygen concentrations ($\sim 0.5 \text{ ml O}_2 \text{ l}^{-1}$) and anoxic conditions (Diaz and Rosenberg, 1995). Low oxygen concentrations, from natural processes or anthropogenic activity, can be episodic or seasonal in many estuaries, fjords or along open coasts, while more-or-less permanent in some isolated basins and shallow seas (Levin *et al.*, 2009).

In an ecosystem such as the Baltic Sea, these pressures already act on a large spatial scale, potentially affecting entire habitats and the ecosystem. Bottom trawling mainly occurs in the western and southern parts of the Baltic Sea (ICES, 2017), where otter trawls target demersal fish such as cod, brill, turbot, plaice and flounder. In such gears, the otter boards (trawl doors) penetrate the sediment, whereas the trawl sweeps and the trawl ground gear mainly impact the surface layers of the sediment (Eigaard *et al.*, 2015). Hypoxic and anoxic conditions are predominantly observed further north in the offshore waters of the Baltic Sea. The area with low oxygen conditions has greatly expanded over the last decades due to eutrophication (Conley *et al.*, 2009; Carstensen *et al.*, 2014). Even though bottom trawling and hypoxia are largely disconnected in space, an assessment of their overall impact is needed to identify benthic habitats that are at greatest risk and to facilitate the development of joint management measures at a regional scale (Korpinen *et al.*, 2012).

We developed an assessment methodology that quantitatively predicts benthic community impact from trawling disturbance and low oxygen concentrations. Impact is predicted using a population dynamic growth model (Mazor *et al.*, 2017; Pitcher *et al.*, 2017) that assumes that mortality on benthic communities is pressure-specific, whereas the responses (recovery) of benthic communities to these pressures are dependent on faunal longevity (maximum lifespan) (Rijnsdorp *et al.*, 2016, 2018; Hiddink *et al.*, 2018). Using the model, we estimate the state of the Baltic Sea benthic macrofauna community as a whole and for two specific functional groups, i.e., suspension-feeders and sediment bioturbators. We

82 validate part of the model predictions in two areas of the Baltic Sea by comparing benthic community
83 responses over gradients of trawling intensity. Finally we derive an overall state of the benthic habitat,
84 which is illustrated in a map and further summarized per habitat type.

85 **Methods**

86 Method outline

87 We examined how faunal longevity, defined as the longevity-biomass composition of the benthic
88 communities, varies in relation to different environmental variables, i.e. depth, wave exposure at the
89 seabed and bottom salinity. The analysis was undertaken for the whole community and for two subsets
90 of the benthic community responsible for filtering of the water column (suspension-feeders) and mixing
91 of sediment (bioturbators). Using the relationships between the longevity-biomass composition and the
92 environmental variables, we predicted a habitat-specific longevity composition for the whole community
93 and the two functional groups across the Baltic Sea on a 0.05·0.05 degrees grid (~15 km², hereafter: grid
94 cells). This prediction was derived in the absence of trawling and hypoxia (and anoxia) to estimate a
95 reference state. We then calculated how both pressures have impacted the benthic community in all grid
96 cells. Impact depends on the intensity of both pressures and the recovery rate, which decreases with
97 longevity (Hiddink *et al.*, 2017, 2018; Pitcher *et al.*, 2017). We estimated the uncertainty of the model
98 predictions and validated part of our model outputs using empirical data for Baltic Sea benthic
99 communities over two gradients of commercial bottom trawling effort (for overview Fig. 1).

100 101 Benthic data across the Baltic Sea

102 To estimate faunal longevity across the Baltic Sea, we used sampling data collated by Gogina et al.
103 (2016). The dataset comprises 2268 5x5 km cells (hereafter: locations) with information on species
104 biomass in wet weight, including calcareous structures, without tubes (Fig. 2). Each location contains
105 one or multiple sampling events, taken in different years or at different periods in the year, which are
106 aggregated to the 5x5 km cell and expressed as the average biomass in mg per m². As such, local variation
107 in space and time in each location is ignored in this dataset, which means that our estimation of faunal

108 longevity only captures large-scale spatial patterns. At all locations, benthic samples were collected with
109 either box-cores or grab-samplers that both provide a quantitative estimate of the smaller epi- and
110 infaunal part of the benthic community, for details on sampling etc. see Gogina *et al.* (2016). Following
111 Gogina *et al.* (2016), we assumed that the locations are quantitatively comparable across the Baltic Sea.

112 For each of the locations, benthic species were linked to a species-by-trait matrix with trait information
113 on longevity (maximum lifespan). Benthic trait information was derived from available literature
114 (Törnroos and Bonsdorff, 2012; Bolam *et al.*, 2014, 2017). Longevity was subdivided into four trait
115 classes (<1 year, 1-3, 3-10 and >10 years). For each species-longevity combination, a score of one was
116 assigned to a single class when a species longevity matched a longevity class. Otherwise, fractional
117 scores that summed to one were assigned to multiple longevity classes, following Bolam *et al.*, (2014).

118 From this species-by-longevity matrix, including in some cases higher taxonomic levels, a table of
119 locations by biomass-weighted trait longevity classes was calculated by multiplying the total biomass
120 per species by the longevity score. These were then summed by longevity class and divided by the total
121 biomass of the location to produce a proportional biomass-weighted longevity table for all locations.

122 A biomass-weighted longevity table was also calculated for two functional groups of the benthic
123 community that are responsible for key ecosystem processes. The first subset contains all suspension-
124 feeders (e.g. *Mya arenaria*, *Cerastoderma glaucum*, *Phoronis* sp.), which account for 60% of the total
125 biomass in the dataset and filter the near-bed water, facilitating benthic-pelagic coupling processes. The
126 second subset contains all bioturbators, which account for 35% of the total biomass in the dataset and
127 mix the sediment, e.g. diffusive mixers and upward/downward conveyors (for terminology see Bolam *et*
128 *al.* 2017). When a taxon was only partly affiliated with the functional group, we proportionally allocated
129 its biomass to the subset.

130 Environmental variables

131 To examine how the longevity-biomass composition varies across the Baltic Sea, we obtained different
132 environmental variables. The Baltic Sea is a semi-enclosed sea with a large salinity gradient that strongly
133 affects the composition of benthic communities (Bonsdorff, 2006). Bottom salinity data were obtained
134 from the ICES data portal and interpolated to cover a Baltic-wide grid based on all data from 2005 to
135 2015. Depth was extracted from the Baltic Sea Hydrographic Commission (2013). Wave exposure at the
136 seabed was derived following the principles of Bekkby *et al.* (2008) and was calculated for the whole
137 Baltic Sea. No continuous sediment data were available for the entire Baltic Sea, and fractions mud,
138 gravel and sand were obtained for part of the region from the global dbSeabed database (Jenkins, 1997);
139 no data were available in the northern Baltic Sea. Sediment fractions had little effect on the statistical
140 model (not shown) and were left out of the analysis as the estimates are uncertain and limited in spatial
141 extent. Wave exposure at the seabed and depth were both transformed to improve model fit as $\ln(x+1)$.
142 The different habitat conditions were weakly correlated between each other. The correlation coefficient
143 between wave exposure and depth is -0.46, depth and salinity is -0.03 and wave exposure and salinity is
144 -0.06.

145 Oxygen deficiency and bottom trawling

146 We obtained data on bottom oxygen concentrations and bottom trawling intensities for the Baltic Sea.
147 Bottom oxygen concentrations ($\text{ml O}_2 \text{ l}^{-1}$) were extracted as seasonal means over five years (2006-2010)
148 from an ecosystem model simulation (Fig. 3a). This model setup, using the coupled hydrographical and
149 biogeochemical system ERGOM-MOM (Schernewski *et al.*, 2015), covers the whole Baltic Sea with a
150 horizontal grid of 1 to 3 nautical miles. Trawling intensity was calculated based on average annual
151 estimates of the amount of seabed disturbed by mobile bottom-contacting fishing gears (surface abrasion)

152 on a 0.05·0.05 degrees grid between 2012 and 2016 (ICES, 2017). Bottom trawling intensity was
153 expressed as the ratio between the area of a grid cell that is trawled each year (on average) and the total
154 area of the grid cell (Fig. 3b). There is a temporal mismatch between trawling intensity (2012-2016) and
155 bottom oxygen concentrations (2006-2010) due to lack of bottom oxygen data covering the whole Baltic
156 Sea in recent years.

157 Longevity-biomass composition of the benthic community

158 We estimated the longevity-biomass composition of the sampling locations across the Baltic Sea in
159 relation to different environmental variables. The estimation was done using only sampling locations that
160 are largely undisturbed by both pressures (but see discussion), in order to derive a reference state. For
161 trawling disturbance, Bolam *et al.* (2017) showed that it is possible to use both untrawled (i.e., a zero
162 fishing pressure estimate) locations and locations with low trawling intensity (up to ≈ 0.1 per year for the
163 more sensitive habitats) to derive the reference state. For that reason, we used all sampling locations with
164 average trawling intensities < 0.1 per year. We used all sampling locations with minimum oxygen
165 concentrations $> 3.2 \text{ ml O}_2 \text{ l}^{-1}$, see below for rationale of the oxygen value. The relatively undisturbed
166 locations ($n=1558$) represent the range of habitat characteristics of the Baltic Sea, but with an
167 overrepresentation of nearshore regions (Appendix 1).

168 To statistically estimate the longevity composition in relation to environmental drivers, we converted the
169 biomass by longevity to a cumulative biomass by calculating the biomass proportion with longevity that
170 is smaller than or equal to 1, 3 and 10 years in each location. We assumed, following Rijnsdorp *et al.*
171 (2018), that the shape of this cumulative biomass proportions - longevity relationship is a sigmoidal
172 (logistic) function, which starts at 0 and approaches 1 when longevity becomes large (Fig. 4). The
173 cumulative proportions in each sample are not independent of each other. The dependence may have an

174 effect on the standard error estimation but will not affect the estimated relationships between the
175 longevity composition and the environmental drivers (which can therefore be used to predict the
176 longevity-biomass composition for the Baltic Sea). We estimated the biomass-longevity composition
177 using a statistical model, with the cumulative biomass proportions (Cb) as the response variable and
178 longevity (l) and environmental conditions (Hab) as the predictor variables. We used a logistic mixed
179 effect model with a random intercept per location (Rijnsdorp *et al.* 2018):

$$180 \quad Cb \sim \beta_0 + \beta_1 \ln(l) + \beta_2 Hab + \beta_3 \ln(l) \cdot Hab + \varepsilon_1 + \varepsilon_2 \quad (\text{eq. 1})$$

181 where longevity (l) is ln transformed, the first error term (ε_1) has a binomial distribution and the second
182 normally distributed error term (ε_2) represents the random effect on the intercept per sampling location.
183 The random effect had a variance component that was (very close to) zero in all analyses, but was retained
184 in the model to incorporate the dependency of the cumulative biomass proportions per location.

185 We examined main effects and two-way interaction terms in all statistical procedures with model fits
186 being evaluated using the Akaike Information Criterion (AIC). The best candidate model, i.e. lowest
187 AIC, yet with a difference of less than 2 AIC units, the model with the fewest parameters was chosen,
188 was used to extrapolate the longevity distribution and to calculate seabed sensitivity on a Baltic-wide
189 scale (0.05·0.05 degrees grid) using the environmental conditions.

190 The longevity composition of the two different functional groups was estimated using a similar method
191 as described above, except only these two functional groups were selected from the benthic community
192 for each sampling location.

193 Seabed state and impact

194 For bottom trawling, Pitcher et al. (2017) derived a method to assess the relative state of the benthic
195 community, the biomass relative to its carrying capacity, per grid cell by solving the logistic growth
196 model:

197
$$\text{Community state} = B/K = 1 - F \frac{d}{r} \quad (\text{eq. 2})$$

198 where B is the community biomass, K the carrying capacity, r the intrinsic growth rate per year of the
199 benthic community, F bottom trawling intensity per year and d the proportional decline of benthic
200 biomass caused by a single trawl pass.

201 The effects of oxygen deficiency on benthic communities substantially differ from those of trawling as
202 oxygen concentrations have an effect that is dependent on both the severity and duration of oxygen
203 deficiency (Vaquer-Sunyer and Duarte, 2008). For that reason, we formulated a temporal dynamic
204 benthic model following van Denderen et al. (2015) to study the effects of both pressures:

205
$$B(t + 1) = B(t) + r_d B(t) \left(\frac{K - B(t)}{K} \right) - (df(t) + O_{def}(t))B(t) \quad (\text{eq. 3})$$

206 where t is time in days, f defines whether there is a trawling event ($f=1$) or no event ($f=0$) at a particular
207 day, d shows the decline of benthic biomass (as a fraction) caused by a single trawl pass (similar to eq.
208 2), r_d the intrinsic growth rate per day and O_{def} describes mortality from oxygen deficiency at each day
209 (detailed below). In the temporal model, trawling events were randomly distributed over the year based
210 on the annual trawling frequency F at each grid cell. The temporal model was run for 100 years through
211 the 1-year period to derive an average state (see further below).

212 The trawling mortality parameter d is derived from a global meta-analysis (Hiddink *et al.*, 2017), where
213 d is shown to be dependent on the penetration depth of the gear. Since essentially all bottom fishing

214 vessels in the Baltic Sea use otter trawls (ICES, 2017), we use d estimates derived in the meta-analysis
215 for otter trawling ($d = 0.06$). An analysis of model uncertainty for parameter d is described below (see
216 model uncertainty).

217 Similar syntheses of benthic community mortality from oxygen deficiency do not exist due to the
218 difficulties of controlling for both the severity of oxygen deficiency and its duration. Studies of oxygen
219 deficiency typically suggest that mass mortality occurs with seasonal concentrations around 0.5 ml O₂ l⁻¹
220 ¹ (Diaz and Rosenberg, 1995). Oxygen concentrations above which species do not suffer any mortality
221 are highly species dependent. Concentrations of less than 1.4 ml O₂ l⁻¹ are defined as hypoxic waters, but
222 sensitive species experience lethal effects from oxygen deficiency at these concentrations (Vaquer-
223 Sunyer and Duarte, 2008). Concentrations above 3.2 ml O₂ l⁻¹ cause notably less mortality (Vaquer-
224 Sunyer and Duarte, 2008) so a concentration of 3.2 ml O₂ l⁻¹ was adopted as the seasonal oxygen
225 concentration where the biomass of a healthy community is not declining.

226 We chose a function that defined mortality from oxygen deficiency (O_{def}) in such a way that a healthy
227 community will experience *i*) mass mortality in a season where oxygen concentrations are around 0.5 ml
228 O₂ l⁻¹ (O_{crit}), *ii*) little mortality in a season with oxygen concentrations ≥ 1.4 ml O₂ l⁻¹, and *iii*) no mortality
229 in a season with oxygen concentrations ≥ 3.2 ml O₂ l⁻¹. The above assumptions resulted in the following
230 oxygen deficiency mortality function:

$$231 \quad O_{def} = d_o(1 + O_{conc} - O_{crit})^{-6} \quad (\text{eq. 4})$$

232 where O_{conc} is the daily concentration (where the daily concentration is the same for all days in a season;
233 92 days in winter and 91 days in the other seasons) and d_o a factor that scales the degree of daily mortality,
234 parameterized as 0.01 (see Appendix 2 for examples of seasonal mortality from oxygen deficiency).
235 Similar to bottom trawling, mortality induced by oxygen deficiency affects all longevities equally. The

236 exact parameterization of O_{crit} and d_O , in combination with the intrinsic growth rate r of the community,
237 will determine the benthic community state. An analysis of model uncertainty is described below (see
238 model uncertainty).

239 We used an intrinsic growth rate of the community r that is independent of the type of disturbance, either
240 from bottom trawling, oxygen deficiency or both, because the mechanism of recovery, i.e. recruitment
241 and growth following mortality, is assumed to be the same. Recovery rates are derived from field
242 estimates of a global meta-analysis of recovery after trawling disturbance, where recovery is shown to
243 be dependent on longevity (recovery rate per year = $r = H/\text{longevity}$, with $H = 5.31$, Hiddink *et al.* 2018).
244 We used this formula to calculate the recovery rate and we divided r in the temporal dynamic model by
245 365 to get an intrinsic growth rate per day r_d . Uncertainty in H and the predicted longevity distribution
246 for the grid cells is evaluated (see model uncertainty). The approach is based on a simple characterization
247 of recovery; other important factors such as larval strategy and mobility are considered in the discussion
248 section.

249 We discretized the longevity distribution into 15 longevity-classes (1-14 and ≥ 15), and hence 15
250 recovery rates ($r = H/\text{longevity}$, with longevity from 1 to 15), to run the temporal dynamic model in eq.
251 3. The model was run with 15 r_d values and the final B/K values, bounded between 0.001 and 1, were
252 multiplied with the 15 longevity-class biomass fractions and summed to estimate the community state.
253 We ran the model for each grid cell that is affected by oxygen deficiency and/or bottom trawling for 100
254 years through the 1-year period, where trawling events each year are randomly distributed and oxygen
255 deficiency follows a seasonal pattern. After the simulation, we calculated the average B/K from the final
256 50 years to derive the average state of the benthic community.

257 Model uncertainty

258 We estimated model uncertainty for the depletion d and recovery H parameters and for the predicted
259 biomass-longevity composition at each grid cell. The estimation of uncertainty was done by calculating
260 benthic state 1500 times at each grid cell based on a resampling of the density distributions of the
261 parameters. The value of d had a logit-normal distribution with $\mu = \text{logit}(0.06)$ and $\sigma = 0.68$ (Hiddink *et*
262 *al.*, 2017), the value of H a log-normal distribution with mean = $\log(5.31)$ and standard deviation = 0.39
263 (Hiddink *et al.*, 2018) and the biomass-longevity model estimates were assumed to be normally
264 distributed. Uncertainty in benthic state was afterwards expressed as the difference between the 75th and
265 25th percentile. We also examined uncertainty in the oxygen deficiency parameters. Since these
266 parameters are unquantified, we did not include them in the main uncertainty analysis, but tested oxygen
267 deficiency separately in two scenarios where no fauna will occur on a location when oxygen
268 concentrations in one season are either below 0.3 or 0.5 ml O₂ l⁻¹, whereas all other grid cells are
269 unaffected, *i.e.* on-off response.

270 Model validation of bottom trawling

271 We validated the impact assessment with empirical data of Baltic Sea benthic communities over two
272 gradients of commercial bottom trawling effort in the Kattegat and Gotland Basin. In both areas, benthic
273 sampling has been conducted in locations with relative constant environmental conditions and along a
274 trawling gradient (see Appendix 3 for further information). We first compared biomass proportions per
275 longevity class for all undisturbed sampling stations (fishing intensity <0.1 y⁻¹) with predicted
276 proportions based on the model for the same locations. To allow a direct comparison, we used depth from
277 the gradient studies as input parameter in the model, whereas salinity and wave exposure at the seabed
278 were taken from the Baltic-wide dataset. Afterwards, we examined the effects of fishing on total

279 community biomass in the gradient studies and compared the empirical outcomes with the predicted
280 impact from the model. We did not validate the effects of hypoxia (see further discussion).

281 Data accessibility

282 Output and code of the assessment model and benthic trait information are available on Github with DOI:
283 <http://doi.org/10.5281/zenodo.3346899>.

284 **Results**

285 Longevity composition of the benthic community

286 Table 1 shows an overview of the statistical models that fitted the data best for both the total benthic
287 community and the specific functional groups. The cumulative biomass proportions across longevity of
288 the overall benthic community are best described by salinity, longevity and depth and their interactions
289 (with a greater longevity in deep and high-salinity areas), while wave stress at the seabed has a negative
290 effect. Using the statistical model outcome, the longevity composition of the benthic community is
291 predicted across the Baltic Sea (Fig. 5a) based on the underlying environmental conditions (Fig. 3d-f).
292 The prediction shows a large spatial variation in the longevity composition that is largely driven by
293 salinity and the interactive effects between salinity and depth. Low salinity and depth correlate with
294 communities whose biomass is dominated by short-lived taxa, e.g. *Monoporeia affinis* (amphipod),
295 *Marenzelleria* spp. (polychaete) and *Saduria entomon* (isopod), whereas those of the relatively high-
296 salinity Kattegat are dominated by long-lived species such as *Amphiura* spp. (brittle stars) and *Arctica*
297 *islandica* (bivalve).

298 The best candidate model for the longevity composition of suspension-feeders is similar to the statistical
299 model for the whole benthic community (Table 1) and results in a similar spatial pattern with somewhat
300 longer lived fauna (Fig. 5b). The best candidate model for bioturbators does not include an interaction
301 between longevity and salinity (Table 1). The median longevity of bioturbators is lower than that for
302 suspension-feeders in areas with high salinity, while in the remaining parts of the Baltic Sea median
303 longevities are generally comparable (Fig. 5c).

304 Predicting the state of the benthic community

305 For all three faunal groups, the low salinity in most regions of the Baltic Sea correlates with a longevity
306 distribution of mostly short-lived species. These communities are, in our model, predicted to be more
307 resilient to the effects of both pressures than the high-salinity communities in the Kattegat. The predicted
308 state of the benthic community in response to both pressures is shown in Fig. 6a. In 22% of the Baltic
309 Sea, the state of benthic habitats is below 0.90 (a state of 1 is un-impacted) and the state is below 0.50 in
310 14% of the Baltic Sea (Fig. 7). Impact is summarized in Table 2 per main habitat type (see Fig. 3c for a
311 map of the main habitats). This shows that deep mud is most affected, with on average a community
312 state of 0.42. Deep mud is spatially extensive and covers 16% of the seabed, predominantly in the middle
313 part of the Baltic Sea where oxygen deficiency is greater. Another relatively deep benthic habitat, deep
314 mixed sediment that covers 6% of the Baltic Sea, also displays a low community state (state = 0.48).
315 Mixed sediment, the most spatially dominant habitat, has a relatively unimpacted state of 0.94, whereas
316 shallow mud has a state of 0.84. Suspension-feeders and bioturbators have a similar state as the whole
317 community in all habitat types (Table 2).

318 Results of the uncertainty analysis show that the predicted impacts are most uncertain in areas with a
319 high predicted faunal longevity and high bottom fishing intensity, *i.e.* Kattegat (Fig. 6b). The uncertainty
320 in oxygen deficiency is low in the middle part of the Baltic Sea and hence limitedly affected by
321 uncertainty in faunal longevity or parameter H . The impact of oxygen deficiency mainly depends on the
322 oxygen concentrations that cause mass mortality (Appendix 4). The community state of the main habitats
323 varies maximally ± 0.1 from the main result based on the 25th and 75th percentile (Appendix 4).

324 In 6% of the Baltic Sea region benthic biomass is reduced by at least 10% due to the combined impact
325 of bottom trawling and oxygen deficiency. The average state of these areas is 0.59 (Table 3). In our
326 model specification, we have assumed that the effects of bottom trawling and oxygen deficiency on
327 benthic ecosystems are additive, resulting in a combined impact as illustrated in Fig. 8. The combined
328 impact always results in a lower benthic state than the effect of a single pressure. Changes in impact are
329 non-linear because low oxygen concentrations, or high bottom trawling intensities, shift the community
330 to a younger mean age by disproportionally removing long-living biota.

331 Model validation

332 The longevity composition of the benthic community differs markedly between the Kattegat and Gotland
333 Basin (Fig. 9a, b). Most organisms in the Gotland Basin have longevitys of 3-10 years, whereas longer-
334 lived (>10 years) organisms are predominant in the Kattegat. These distributions of longevity are also
335 predicted with the model, despite an underestimation of the proportion of long-lived organisms in the
336 Kattegat (Fig. 9a, b). Both the model and the data show a decline in community biomass in the Gotland
337 Basin with increased trawling, although the decline is stronger in the data (Fig. 9c). There is no clear
338 biomass change, and large variability, in the Kattegat in response to trawling, whereas the model predicts
339 a reduction (Fig. 9d). The large variability in biomass is not captured in the model as we assumed a
340 carrying capacity K that is calculated as the average community biomass of all undisturbed stations (see
341 further Appendix 3).

342 **Discussion**

343 Our results show that the low salinity in most regions of the Baltic Sea correlates with a community
344 biomass-longevity distribution that is heavily biased towards short-lived species. In our model, these
345 communities are more resilient to the effects of hypoxia and bottom trawling than those of the highly
346 saline areas where biomass is comprised of relatively long-lived species. We find that in 14% of the
347 Baltic Sea region benthic biomass is reduced by at least 50% (state <0.5), whereas 8% of the region has
348 reductions of 10-50%. About one quarter of these impacted areas is affected by both pressures,
349 corresponding to 6% of the Baltic Sea region with cumulative impacts. The effects of hypoxia cover
350 larger areas and lead to a low habitat state of deep mud and deep mixed sediment.

351 Longevity distribution of the Baltic Sea benthic community

352 For the estimated reference conditions, the longevity-biomass distribution of the benthic community
353 differed substantially between habitats. Changes in longevity are primarily driven by the salinity gradient
354 from the Kattegat towards the Gotland Basin and the Bothnian Sea, which has been shown to strongly
355 influence the benthic community (Bonsdorff, 2006; Törnroos *et al.*, 2015). In the high-salinity waters of
356 the Kattegat, the longevity distribution is comparable to that predicted for the neighbouring North Sea
357 (Rijnsdorp *et al.*, 2018), and in both regions suspension-feeders consist of a higher fraction of longer-
358 lived species than the bioturbators. The longevity of all groups declines notably in the low-salinity waters
359 of the Baltic Sea.

360 The longevity distribution of the benthic community is used in the present study as a proxy of benthic
361 sensitivity to trawling and oxygen deficiency. The use of this proxy is based on the findings by Hiddink
362 *et al.* (2018) who showed that the intrinsic rate of population growth r , which drives the recovery rate, is

363 proportional to the reciprocal of longevity. It is also supported by other studies that show shifts towards
364 shorter-lived species in response to trawling (Tillin *et al.*, 2006; van Denderen *et al.*, 2015; Rijnsdorp *et*
365 *al.*, 2018) and hypoxia (Diaz and Rosenberg, 1995). Although longevity is a key trait that correlates with
366 habitat sensitivity and recovery, estimating the longevity of benthic taxa is uncertain because benthic
367 taxa cannot be aged and other factors, besides longevity, affect benthic sensitivity. Large variations in
368 recovery rates within longevity classes were observed in the meta-analysis of Hiddink *et al.* (2018),
369 highlighting uncertainty in using longevity to estimate benthic recovery. Uncertainty is also shown in
370 our model validation analysis, where the model underestimates the effect of fishing in the Gotland Basin,
371 where short-lived fauna dominate, and overestimates the fishing effect on long-lived organisms in the
372 Kattegat (Fig. 9). For the Kattegat, long-lived organisms seem to be largely insensitive to trawling, which
373 is contradictory to the meta-analysis by Hiddink *et al.* (2018). The limited effect of fishing on long-lived
374 organisms in the Kattegat is most likely due to an increase in the long-living and abundant brittle stars
375 (*Amphiura* spp.) under intermediate trawling disturbance (Sköld *et al.*, 2018). Hence, further work is
376 needed to elucidate when responses of the benthic community are not (solely) dependent on the longevity
377 of fauna. Studying the response of biological-trait groupings to various pressures (Villnäs *et al.*, 2017)
378 or incorporating the food-web dynamics and the possibility of having non-linear and non-negative
379 responses to pressures, see for example for trawling van Denderen *et al.*, (2013) and Sköld *et al.*, (2018),
380 offer two potential approaches in this respect. Nevertheless, from our model validation we are unable to
381 determine whether the response of Baltic Sea benthic communities systematically differs from the results
382 of the global meta-analysis (Hiddink *et al.*, 2018), *i.e.* the recovery rate is proportional to the reciprocal
383 of longevity.

384 The longevity composition of the benthic community was derived using only sampling locations that
385 were assumed to be largely undisturbed by the pressures. It is likely that most undisturbed sampling
386 locations are not in ‘pristine’ condition, e.g. sampling locations might have been at a state of recovery
387 from historic fishing, hypoxia or are impacted by other pressures. The sampling locations used to predict
388 the longevity are also predominantly shallow, limiting the accuracy of our longevity prediction in deeper
389 areas. In our estimation of the reference condition, we also did not include that a minor part of the Baltic
390 Sea seafloor is naturally, and historically, disturbed by hypoxia (Carstensen *et al.*, 2014). Furthermore,
391 our predictions are uncertain by a lack of continuous sediment data, as sediment conditions will likely
392 affect faunal longevity. The reference state is hence based on the best condition currently available and
393 may be updated when new information becomes available.

394 The effects of bottom trawling and hypoxia

395 Our results show that 6% of the Baltic Sea region (approx. 30000 km²) is currently impacted by both
396 bottom trawling and oxygen deficiency. We have assumed that the effects of bottom trawling and oxygen
397 deficiency on benthic ecosystems are additive and both shift the community to a younger mean age.
398 Evidence also suggests potential synergistic effects through other mechanisms, as oxygen deficiency can
399 induce burrowing organisms to migrate to the sediment surface (Baden *et al.*, 1990; Hansson *et al.*, 2000)
400 making them potentially more vulnerable to trawling impacts. To date, however, no targeted study has
401 been conducted to determine the nature of any cumulative impacts of these two pressures. Synergistic
402 effects, if shown to occur, could be included in the assessment model and are likely to result in a reduced
403 benthic habitat state in areas with both pressures, compared to our model predictions. Understanding the
404 interactive effects is important as hypoxic conditions are predicted to expand in the Baltic Sea (Bendtsen

405 and Hansen, 2013) and in coastal areas in general (Breitburg *et al.*, 2018) with climate warming,
406 potentially increasing the area that is affected by both pressures.

407 Model parametrization

408 The effects of oxygen deficiency in the model are largely based on the assumption of mass mortality at
409 0.5 ml O₂ l⁻¹ and changes in this parameter affect the average state of especially deep offshore habitats
410 (Appendix 4). Part of these deep offshore habitats have oxygen concentrations close to or even zero and
411 these areas are, even in a best-possible scenario, highly impacted. The response of benthic communities
412 at higher oxygen concentrations (>1 ml O₂ l⁻¹) is assumed to cause little mortality to the benthic
413 community (Appendix 2). A proper validation of these model results across regions and benthic
414 communities is needed, both in relation to the concentration and duration of oxygen deficiency. The
415 oxygen concentrations used to predict impact are now also based on seasonal averages, whereas a few
416 hours/days of anoxic conditions may already result in mass mortality (Villnäs *et al.*, 2012). A finer
417 temporal resolution of the simulated bottom oxygen conditions, in combination with an improved
418 parametrization of oxygen deficiency, will refine our modelling results.

419 The intrinsic growth rate of the community r , which drives the recovery rate, is independent of the type
420 of disturbance in our model. Recovery rates are likely to differ between trawling and hypoxia as the
421 physical and physico-chemical conditions and the spatial scale of these disturbances differ. Trawling is
422 patchy in space and time (Rijnsdorp *et al.*, 1998; Van Denderen *et al.*, 2015) which enhances the potential
423 for local, less disturbed communities to facilitate recolonization through larval dispersal and post-
424 settlement movement. In contrast, the relatively continuous and spatially-extensive nature of severely
425 hypoxic areas hinders such recolonization processes (Whitlatch *et al.*, 1998). The severe hypoxic areas
426 are also characterized by mud and mud may harbour a specific benthic community, further limiting

427 successful recolonization from neighbouring (non-muddy) habitats. Our models may, therefore, be
428 improved by allowing recovery rates to be dependent on the community (dis)continuity, or degree of
429 patchiness. Additionally, larval dispersal mechanisms by the benthos are limited due to the lack of tidal
430 currents in the Baltic Sea (Valanko *et al.*, 2010) and recovery rates may potentially differ from those of
431 other regions.

432 Conclusion

433 We have applied a method for assessing the combined effects of trawling disturbance and hypoxia on
434 benthic communities. The approach is based on a simple characterization of the benthic community.
435 With the exception of the estimation of faunal longevity, the parameterization of depletion and recovery
436 rates are derived from meta-analyses outside the Baltic Sea. The approach comes as such with high
437 uncertainty. The approach has been used to identify regions that are most at risk, so as to prioritize
438 management actions. The approach can be used to monitor changes over time by evaluating benthic state
439 with temporal pressure data. The assessment methodology can be transferred to other regions where the
440 benthic longevity-biomass composition can be estimated and where high-resolution pressure data are
441 available. The method allows to aggregate results from a local scale ($\sim 15 \text{ km}^2$) to the main habitats (and
442 potentially any other assessment unit), as well as to the regional scale (Baltic Sea; $\sim 450000 \text{ km}^2$). We
443 expect our findings and the assessment method to be of relevance to managers as it objectively highlights
444 how bottom trawling and oxygen deficiency act on benthic habitats. Within a regional policy context,
445 such an assessment method is required to evaluate benthic seafloor integrity and how changes may be
446 occurring over time. Information on benthic seafloor integrity will facilitate the development of
447 sustainable management strategies and assist in the assessment of trade-offs between human activities
448 and their environmental impact on the seabed.

449 **Supplementary information**

450 The following supplementary material is available at *ICESJMS*: a comparison of environmental variables
451 between sampling locations and the Baltic Sea region (appendix 1), the effects of oxygen deficiency in
452 the model (appendix 2), information on empirical data in the Kattegat and Gotland Basin used for
453 validation (appendix 3) and model uncertainty predictions (appendix 4).

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472 **Author contributions**

473 PDvD, JGH, ADR, MS, AT and SV conceived the ideas. AT and SGB collated benthic trait data. RF and
474 EAV derived environmental modeled data. KN and MS collated benthic validation data. PDvD
475 performed the analyses with support of JGH, ADR, KN and MS. PDvD and SV led the writing and all
476 authors contributed critically to the drafts.

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608 **Tables**

609 Table 1. Model selection for the cumulative biomass proportions in relation to longevity and habitat
 610 conditions for the total community and different functional groups. L = ln(longevity), S = salinity, D =
 611 ln(depth +1), W= ln(wave exposure at the bottom+1).

Total community (n = 1558)

Model	df	AIC	Formula
L+S+D+W+L·S+S·D+L·D	9	2525	Y = -4.2 + 3.7 L + 0.1 S + 0.2 D - 0.1 W - 0.1 L·S - 0.04 S·D + 0.3 L·D
L+S+D+W+L·S+L·D	8	2530	-
L+S+D+L·S+S·D+L·D	8	2560	-
L+S+D+W	6	2600	-

Suspension-feeders (n = 1487)

Model	df	AIC	Formula
L+S+D+W+L·S+S·D+L·D	9	2457	Y = -4.5 + 3.3 L + 0.2 S -0.1 D - 0.1 W - 0.1 L·S - 0.05 S·D + 0.5 L·D
L+S+D+W+L·S+L·D	8	2503	-
L+S+D+L·S+S·D+L·D	8	2474	-
L+S+D+W	6	2598	-

Bioturbators (n = 1536)

Model	df	AIC	Formula
L+S+D+W+S·D+L·D	8	2577	Y = -1.9 + 2.1 L + 0.001 S -0.3 D - 0.18 W - 0.03 S·D + 0.5 L·D
L+S+D+W+L·D	7	2589	-
L+S+D+W+L·S+L·D	8	2590	-
L+S+D+W	6	2617	-

612

613 Table 2. Overview of impact (presented as the average grid cell state) by both pressures for the total
614 community and for different functional groups in the most common habitat types (cl is circalittoral, il is
615 infralittoral, ocl is offshore circalittoral). Fraction of area is the surface area of a habitat type divided by
616 the total assessed area.

Habitats	State (community)	State (susp feeders)	State (bioturbators)	Fraction of area
Baltic Sea region	0.85	0.84	0.85	1
Mixed sediment (cl)	0.94	0.94	0.94	0.27
Mud (cl)	0.84	0.84	0.84	0.19
Deep mud (ocl)	0.42	0.41	0.43	0.16
Sand (cl)	0.97	0.97	0.97	0.09
Shallow mixed sediment (il)	1	1	1	0.06
Deep mixed sediment (ocl)	0.48	0.47	0.48	0.06
Others	0.98	0.98	0.98	0.17

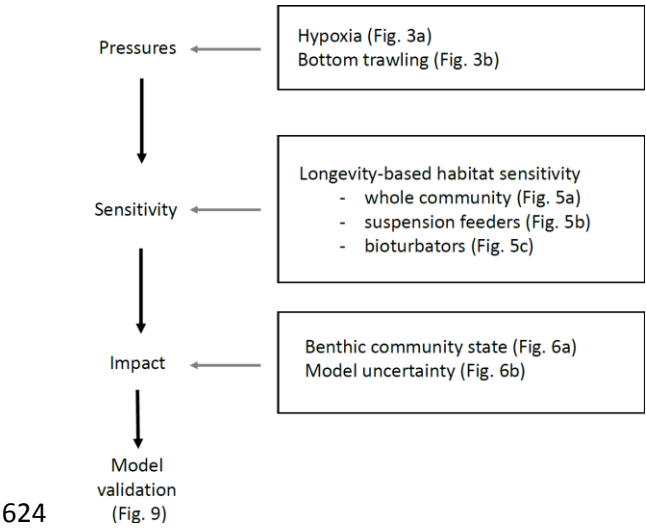
617

618 Table 3. Overview of the average state and areal extent of grid cells where benthic biomass is reduced
619 by at least 10% (state <0.90) due to bottom trawling, oxygen deficiency or both. The total area of the
620 Baltic Sea with a state <0.9 is 22% (see Fig. 7). F is bottom trawling intensity, O is the minimum
621 seasonal oxygen concentration in ml O₂ l⁻¹.

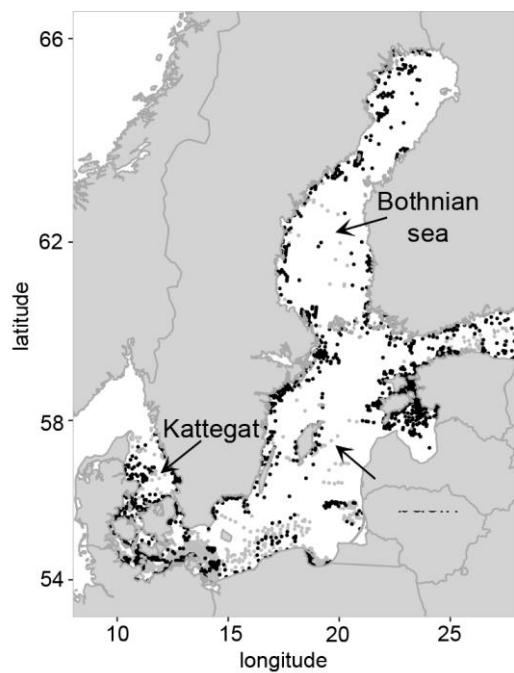
Pressure	Average state	Fraction of the total Baltic Sea region
Bottom trawling (F >0.1, O ≥3.2)	0.71	0.03
Oxygen deficiency (F ≤0.1, O < 3.2)	0.11	0.13
Both (F > 0.1, O < 3.2)	0.59	0.06

622

623 **Figures**

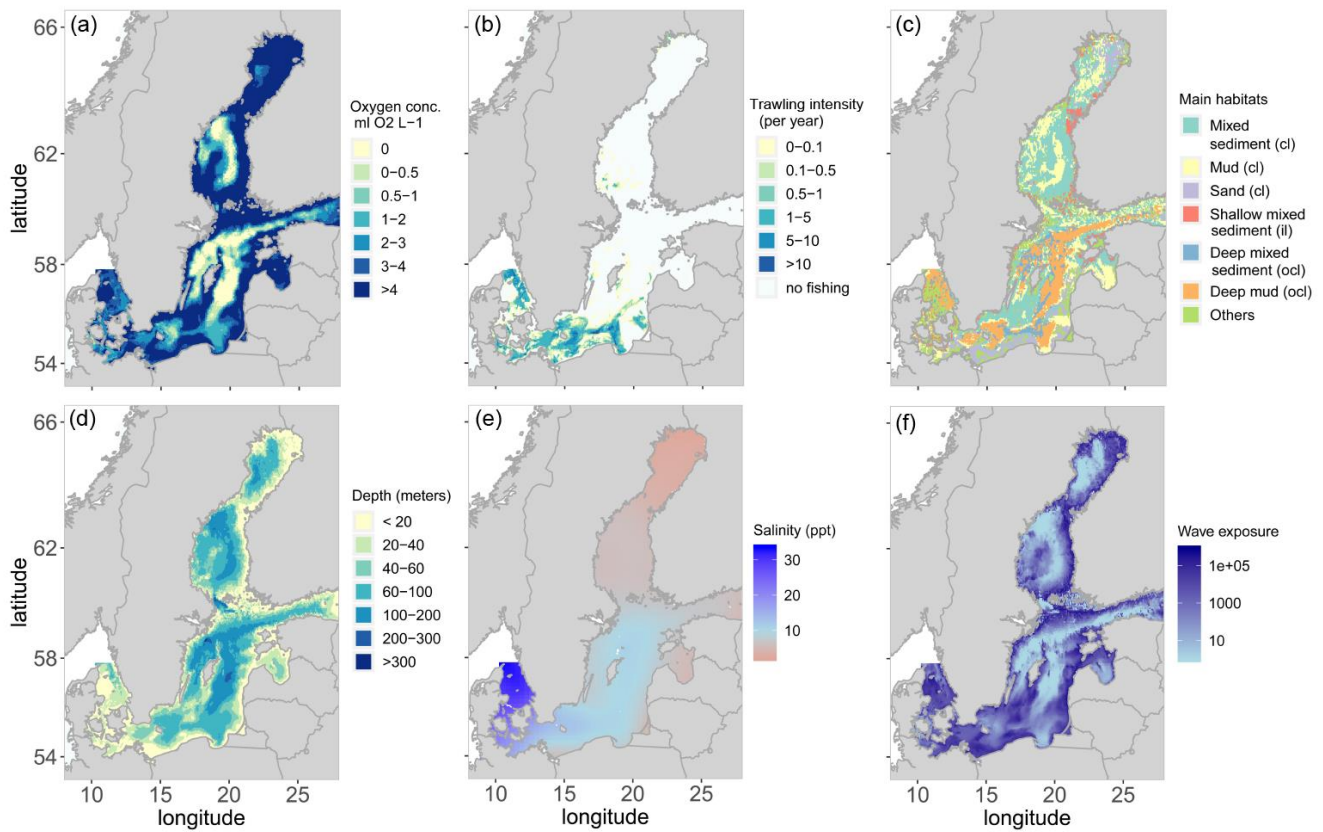


625 Figure 1. Outline of the method and results.



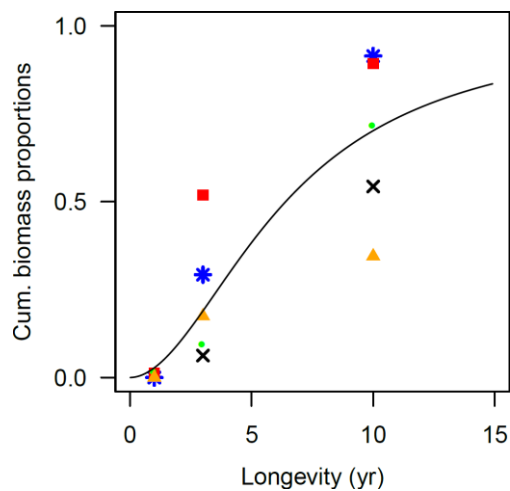
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627 Figure 2. Sampling locations (based on aggregated benthic data) collated by Gogina et al. (2016). All
 628 black dots (n=1558) were used in the analysis to predict fauna longevity. All grey dots (n=710) were
 629 not used as pressure levels were too high.



630

631 Figure 3. Map of (a) oxygen concentrations, here presented as the lowest seasonal concentration in the
 632 year, (b) trawling intensities, (c) the Marine Strategy Framework Directive Benthic Broad Habitat Types
 633 for the Baltic Sea region as downloaded from <http://www.emodnet-seabedhabitats.eu/>, (d) depth, (e)
 634 salinity and (f) wave exposure at the seabed (unitless). See data sources and explanation in main text.



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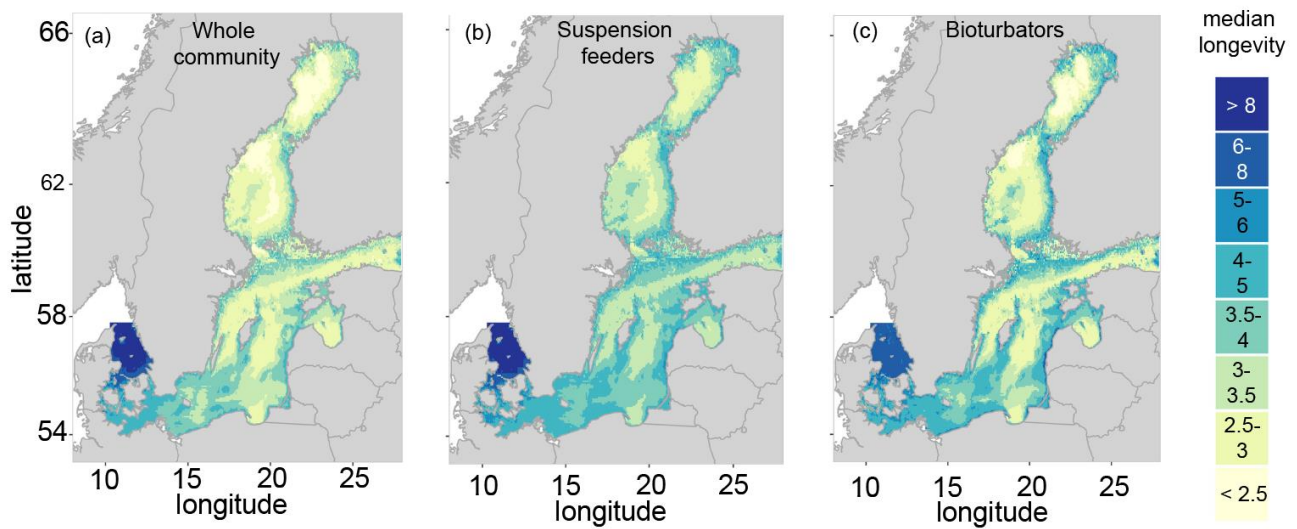
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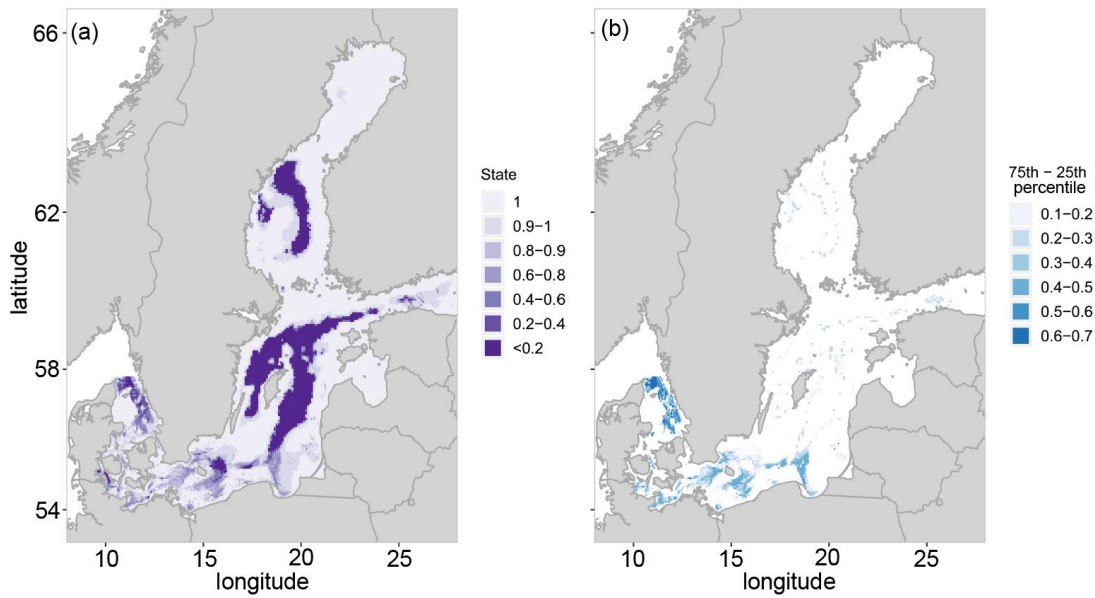
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Figure 4. Illustration of five sampling stations with similar environmental conditions and their biomass-longevity compositions. Dots show cumulative biomass at longevitys of 1, 3 and 10 based on benthic data (each station is a different colour and symbol). Line is fitted (for illustration) with a binomial model where longevity is ln transformed. Salinity 25-27 ppt, depth 10-13 m, wave exposure $3 \cdot 10^5$ - $5 \cdot 10^5$, fishing intensity <0.1 per year and minimum seasonal oxygen concentration >4 ml O_2 per litre.



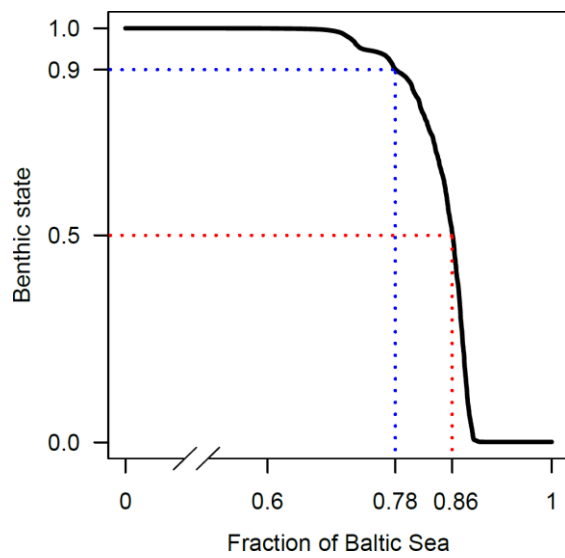
641

642 Figure 5. Predicted longevity distribution of the (a) benthic community, (b) suspension-feeders and (c)
 643 sediment bioturbators across the Baltic Sea, presented as the median longevity, the longevity in years
 644 where the cumulative biomass proportion is 0.5.



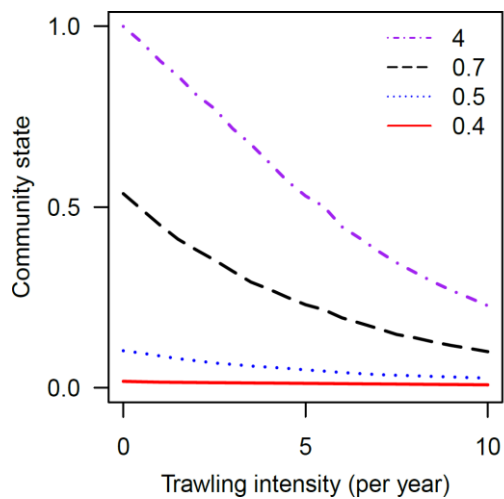
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646 Figure 6. (a) Predicted state of the benthic community impacted by fishing disturbance and oxygen
 647 deficiency (a state of 1 is un-impacted) and (b) model uncertainty measured as the difference in state
 648 between 25th and 75th percentile based on uncertainty in the depletion d and recovery H parameters and
 649 the statistical model predictions of the biomass-longevity composition at each grid cell.



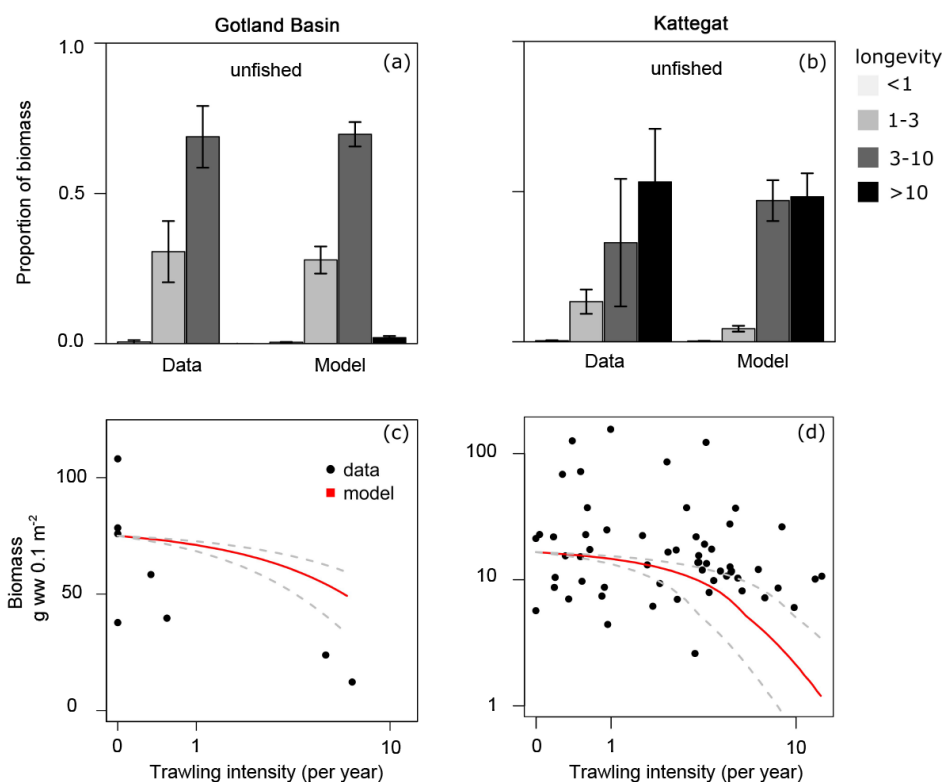
650

651 Figure 7. The benthic state per grid cell sorted from high to low and the corresponding fraction of the
 652 Baltic Sea area above or equal to that state. The figure shows that 22% ($1 - 0.78 = 0.22$) of the Baltic Sea
 653 region has a state < 0.9 and 14% ($1 - 0.86 = 0.14$) has a state < 0.5 .



654

655 Figure 8. Illustration of the combined effects of bottom trawling and oxygen deficiency on benthic
 656 community state. The lines show different summer oxygen concentrations, whereas the oxygen
 657 concentrations in the other seasons are 4 ml O₂ per litre; note that similar results are obtained when
 658 oxygen concentrations are low in another season. The longevity composition of the benthic community,
 659 used to predict impact and state, is estimated from the statistical model (Table 1) based on chosen
 660 environmental conditions (salinity 26 ppt, depth 12 m, wave exposure at the bottom $3 \cdot 10^5$, representing
 661 a location in the Kattegat). The combined effects are largely similar for other regions, but the non-linear
 662 effect becomes smaller in areas with short-lived fauna.



663

664 Figure 9. Model predictions of longevity are compared with data observations at 4 unfished stations in
 665 the Gotland Basin (a) and 3 unfished stations in the Kattegat (b). The bars show the average biomass
 666 proportion per longevity class and the error bars show the standard error. Model predictions of fishing
 667 impact are compared with data in panel c and d. The black dots show the observed community biomass
 668 at each sampling station and the red lines show the predicted biomass as a function of trawling intensity.
 669 Changes in biomass in response to trawling intensity are derived in the model by calculating impact from
 670 the predicted longevity composition in panel a and b, from fishing intensity and by assuming a carrying
 671 capacity (K) that is the average community biomass in all undisturbed stations. Model uncertainty (grey
 672 dashed lines) is estimated by resampling the depletion rate from trawling d and the longevity-specific
 673 recovery rate H 1500 times. Other sources of uncertainty are not included. The benthic data and fishing

674 intensities for each sampling station are averaged for all years of sampling. Panel d shows the y-axis on
675 a \log_{10} scale.