

1 Identifying areas prone to coastal hypoxia - the role of topography

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10 **Abstract.** Hypoxia is an increasing problem in marine ecosystems around the world. While major advances have been made
11 in our understanding of the drivers of hypoxia, challenges remain in describing oxygen dynamics in coastal regions. The
12 complexity of many coastal areas and lack of detailed *in situ* data has hindered the development of models describing
13 oxygen dynamics at a sufficient spatial resolution for efficient management actions to take place. It is well known that the
14 enclosed nature of seafloors and reduced water mixing facilitates hypoxia formation, but the degree to which topography
15 contributes to hypoxia formation, and small-scale variability of coastal hypoxia, has not been previously quantified. We
16 developed simple proxies of seafloor heterogeneity and modelled oxygen deficiency in complex coastal areas in the northern
17 Baltic Sea. According to our models, topographical parameters alone explained ~80 % of hypoxia occurrences. The models
18 also revealed that less than 25 % of the studied seascapes were prone to hypoxia during late summer (August-September).
19 However, large variation existed in the spatial and temporal patterns of hypoxia, as certain areas were prone to occasional
20 severe hypoxia ($O_2 < 2 \text{ mg L}^{-1}$), while others were more susceptible to recurrent moderate hypoxia ($O_2 < 4.6 \text{ mg L}^{-1}$). Areas
21 identified as problematic in our study were characterized by low exposure to wave forcing, by high topographical shelter
22 from surrounding areas, and by isolation from the open sea, all contributing to longer water residence times in seabed
23 depressions. Deviations from this “topographical background” are probably caused by strong currents or by high nutrient
24 loading, thus improving or worsening oxygen status, respectively. In some areas, connectivity with adjacent deeper basins
25 may also influence coastal oxygen dynamics. Developed models could boost the performance of biogeochemical models, aid
26 developing nutrient abatement measures, and pinpoint areas where management actions are most urgently needed.

27

28

29 **1 Introduction**

30 Hypoxia is a key stressor of marine environments, occurring in over 400 physically diverse marine ecosystems worldwide
31 (Diaz and Rosenberg, 1995b, 2008;Conley et al., 2009b). Declining oxygen levels have been recorded in fjords, estuaries
32 and in coastal and open-sea areas, such as Chesapeake Bay, Gulf of Mexico, Japan Sea, Baltic Sea and the Black Sea
33 (Gilbert et al., 2010;Carstensen et al., 2014). It is clear that our oceans are losing their breath, and recent projections indicate
34 that anoxic zones devoid of higher life will be increasing in the forthcoming decades (Frölicher et al., 2009;Meier et al.,
35 2011a;Meier et al., 2012a), with severe consequences for marine ecosystems (Breitburg et al., 2018).

36 The lack of oxygen alters the structure and functioning of benthic communities (Nilsson and Rosenberg, 2000;Gray et al.,
37 2002;Karlson et al., 2002;Valanko et al., 2015), disrupts bioturbation activities (Timmermann et al., 2012;Villnas et al.,
38 2012;Villnas et al., 2013;Norkko et al., 2015), changes predator-prey relationships (Eriksson et al., 2005) and may lead to
39 mass mortalities of benthic animals (Vaquer-Sunyer and Duarte, 2008). Hypoxia does not only affect organisms of the
40 seafloor, but also influences biogeochemical cycling and benthic-pelagic coupling (Gammal et al., 2017). Hypoxia can
41 increase releases of nutrients from the sediment and thus promote planktonic primary production and sedimentation, which
42 in turn leads to enhanced microbial consumption of oxygen (Conley et al., 2002;Kemp et al., 2009;Middelburg and Levin,
43 2009). This creates a self-sustaining process, often referred to as “vicious circle of eutrophication” (Vahtera et al., 2007),
44 which may hamper the effects of nutrient abatement measures.

45 Biogeochemical processes contributing to hypoxia formation are well known. Factors affecting the development of hypoxia
46 are usually associated with the production of organic matter, level of microbial activity and physical conditions creating
47 stratification and limited exchange or mixing of water masses (Conley et al., 2009a;Rabalais et al., 2010;Conley et al.,
48 2011;Fennel and Testa, 2019). Coastal hypoxia is common in areas with moderate or high anthropogenic nutrient loading,
49 high primary productivity and complex seabed topography limiting lateral movement of the water. Shallow-water hypoxia is
50 often seasonal. It is associated with warming water temperatures and enhanced microbial processes and oxygen demand
51 (Buzzelli et al., 2002;Conley et al., 2011;Caballero-Alfonso et al., 2015;van Helmond et al., 2017).

52 Projecting patterns and spatial and temporal variability of hypoxia is necessary for developing effective management actions.
53 Thus three-dimensional coupled hydrodynamic-biogeochemical models have been created for several sea areas around the
54 world, such as Gulf of Mexico (Fennel et al., 2011;Fennel et al., 2016), Chesapeake Bay (Scully, 2013;Testa et al.,
55 2014;Scully, 2016), the North Sea (Hordoir, 2018) and the Baltic Sea (Eilola et al., 2009;Eilola et al., 2011;Meier et al.,
56 2011a;Meier et al., 2012a;Meier et al., 2012b). These models simulate various oceanographic, biogeochemical and biological
57 processes using atmospheric and climatic forcing and information on nutrient loading from rivers. While such models are
58 useful for studying processes at the scale of kilometers, and aid in defining hypoxia abatement at the basin-scale, their
59 horizontal resolution is too coarse (often 1–2 nautical miles) for accurately describing processes in coastal areas. Lack of
60 detailed data on water depth, currents, nutrient loads, stratification and local distribution of freshwater discharges (Breitburg
61 et al., 2018) (not to mention computational limitations) usually prevent the application of biogeochemical models developed

62 to large geographical areas at finer horizontal resolutions (<100 m). Understanding spatial variability of hypoxia in
63 topographically complex coastal environments has therefore been impeded by the lack of useful methods and systematic,
64 good-quality data (Diaz and Rosenberg, 2008; Rabalais et al., 2010; Stramma et al., 2012). Finding alternative ways to
65 pinpoint areas prone to coastal hypoxia could facilitate management and determining of efficient local eutrophication
66 abatement measures.

67 It is widely recognized that the semi-enclosed nature of the seafloors, and associated limited water exchange is a significant
68 factor in the formation of hypoxia in coastal waters (Diaz and Rosenberg, 1995a; Virtasalo et al., 2005; Rabalais et al.,
69 2010; Conley et al., 2011). However, to determine the degree to which seascape structure restricting water movement
70 contributes to hypoxia formation has not been quantified. Analytical and theoretical frameworks developed specifically for
71 terrestrial environments, such as landscape heterogeneity or patchiness, are analogous in marine environments, and are
72 equally useful for evaluating links between ecological functions and spatial patterns in marine context. We tested how large
73 fraction of hypoxia occurrences could be explained only by structural complexity of seascapes, without knowledge on
74 hydrographical or biogeochemical parameters. We adopted techniques and metrics from landscape ecology and transferred
75 them to marine environment, and (1) examined if spatial patterns in seascapes can explain the distribution of hypoxia, (2)
76 defined the relative contribution of seascape structure to hypoxia formation and (3) estimated the potential ranges of hypoxic
77 seafloors in coastal areas. To achieve this, we concentrated on extremely heterogeneous and complex archipelago areas in
78 the northern Baltic Sea, where coastal hypoxia is a common and an increasing problem (Conley et al., 2011; Caballero-
79 Alfonso et al., 2015).

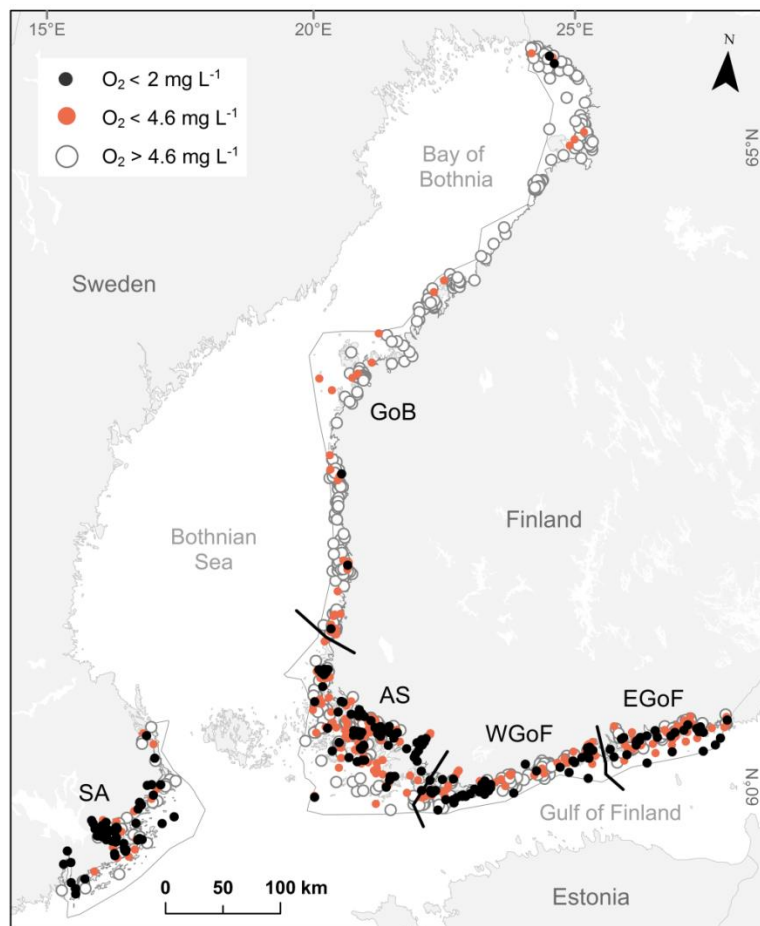
80 **2 Data and methods**

81 **2.1 Study area**

82 The studied area covers the central northern Baltic Sea coastal rim, 23 500 km² of Finnish territorial waters from the
83 Bothnian Bay to the eastern Gulf of Finland, and 5100 km² of Swedish territorial waters in the Stockholm Archipelago in the
84 Baltic Proper. Oxygen dynamics in the deeper areas of the Gulf of Finland and Stockholm Archipelago are strongly affected
85 by oceanography and biogeochemistry of the central Baltic Proper, not reflecting the dynamics of coastal hypoxia (Laine et
86 al., 1997), and were therefore excluded from this study. The outer archipelago of Finland is relatively exposed with various
87 sediment and bottom habitat types, while the inner archipelago is more complex and shallower, but maintains a higher
88 diversity of benthic habitats and sediment types (Valanko et al., 2015). The inner archipelago of Stockholm is an equally
89 complex archipelago area, with a large number of islands, straits and coves. Freshwater outflow from Lake Mälaren creates
90 an estuarine environment where freshwater meets the more saline water in the Baltic Proper.

91 In order to evaluate differences in oxygen deficiency between coastal areas, the study area was divided into five regions as
92 defined by the EU Water Framework Directive (2000/60/EC) (WFD, 2000): the Archipelago Sea (AS), the Eastern Gulf of
93 Finland (EGoF), the Gulf of Bothnia (GoB), Stockholm Archipelago (SA) and the western Gulf of Finland (WGoF) (Figure

94 1). Small skerries and sheltered bays characterize AS, EGoF and WGoF, whereas narrower band of islands forms relatively
95 exposed shores in GoB. Deep, elongated channels of bedrock fractures can reach depths of over 100 m in AS, similarly to
96 SA where narrow, deep valleys separate mosaics of islands and reefs. Substrate in both areas varies from organic-rich soft
97 sediments in sheltered locations to hard clay, till and bedrock in exposed areas. At greater depths, soft sediments are
98 common due to limited water movement. As a whole, the study area with rich topographic heterogeneity forms one of the
99 most diverse seabed areas in the world (Kaskela et al., 2012). In many areas hypoxia is a result of strong water stratification,
100 slow water exchange and complex seabed topography, creating pockets of stagnant water (Conley et al., 2011; Valanko et al.,
101 2015; Jokinen et al., 2018). Thus, the area is ideal for testing hypotheses of topographical controls for hypoxia formation.
102



103
104 **Figure 1.** Study areas in Finland: AS – Archipelago Sea, WGoF – Western Gulf of Finland, EGoF – Eastern Gulf of Finland,
105 GoB – Gulf of Bothnia, and Sweden: SA – Stockholm Archipelago. Orange dots represent sites of moderately hypoxic ($O_2 <$
106 4.6 mg L^{-1}) black dots severely hypoxic ($O_2 < 2 \text{ mg L}^{-1}$) and white circles denote sites with $O_2 > 4.6 \text{ mg L}^{-1}$. Grey and
107 black lines illustrate boundaries of Water Framework Directive areas.

108 2.2 Hypoxia data

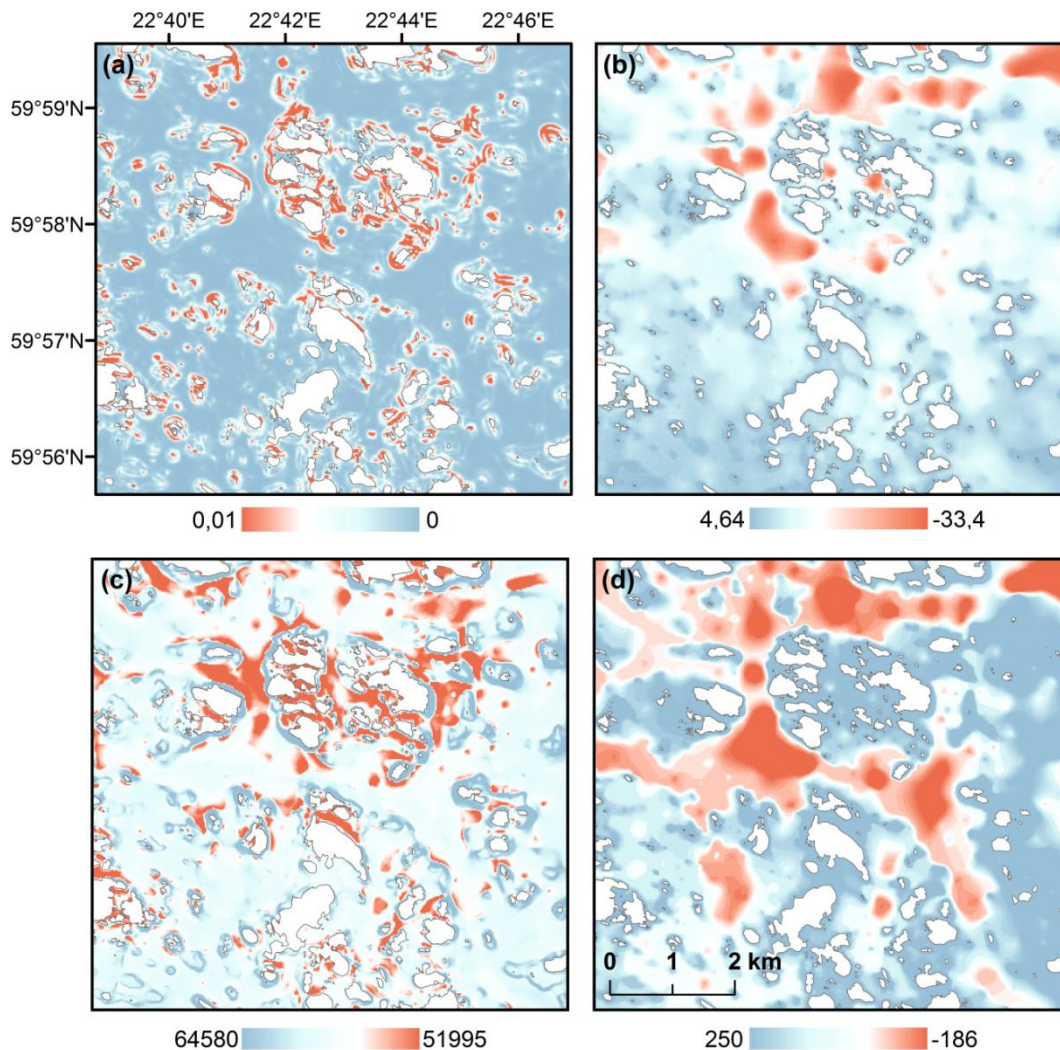
109 Bottom-water hypoxia is the main factor structuring benthic communities in the Baltic Sea (Villnas et al., 2012;Norkko et
110 al., 2015). Two mg L⁻¹ of O₂ is usually considered a threshold where coastal organisms start to show symptoms of the lack
111 of oxygen, and this limit has been commonly used in various global reviews (Diaz and Rosenberg, 1995b, 2008). Some
112 studies have however concluded that 2 mg L⁻¹ is below the empirical sublethal and lethal oxygen limit for many species
113 (Vaquer-Sunyer and Duarte, 2008;Conley et al., 2009b). Here we define hypoxia based on two ecologically meaningful
114 limits: moderately hypoxic <4.6 mg L⁻¹ O₂ – as this has been estimated to be a minimum safe limit for species survival,
115 behavior and functioning in benthic communities (Norkko et al., 2015) – and severely hypoxic <2 mg L⁻¹ O₂, which
116 describes zones where larger marine organisms suffer from severe mortality (Vaquer-Sunyer and Duarte, 2008). As no
117 reference values exist for severity of hypoxia to marine organisms based on the frequency of hypoxic events (Norkko et al.,
118 2012;Villnas et al., 2012;Norkko et al., 2015), we here define a site to be prone to hypoxic events, i.e. occasionally hypoxic,
119 if it experienced hypoxia (O₂<2 mg L⁻¹ and <4.6 mg L⁻¹) at least once during the study period. If hypoxia was recorded ≥20
120 % of the visits, it was categorized as frequently hypoxic. We consider this to be ecologically relevant, as species develop
121 symptoms already from short exposures to hypoxia (Villnas et al., 2012;Norkko et al., 2015). This is also justified, as our
122 oxygen data is from ~1 m above the seafloor, suggesting that the actual oxygen concentrations at sediment where benthic
123 species live are probably lower.

124 Data from oxygen profiles were collated from the national monitoring environmental data portals Hertha
125 (http://www.syke.fi/en-US/Open_information) and SHARK (<https://www.smhi.se/data/oceanografi/havsmiljodata>). Data was
126 available from 808 monitoring sites. Only months of August and September 2000–2016 were considered, as hypoxia is
127 usually a seasonal phenomenon occurring in late summer when water temperatures are warmest (Conley et al., 2011).

128 2.3 Predictors

129 For modelling hypoxia occurrences, we developed five geomorphological metrics: (1) Bathymetric Position Indices (BPI)
130 with varying search radii, (2) Depth-Attenuated Wave Exposure (SWM(d)), (3) Topographical Shelter Index (TSI), (4) Arc-
131 Chord Rugosity (ACR) and (5) Vector Ruggedness Measure (VRM). BPI is a marine modification of the terrestrial version
132 Topographic Position Index (TPI), originally developed for terrestrial watersheds (Weiss, 2001). BPI is a measure of a
133 bathymetric surface to be higher (positive values) or lower (negative values) than the overall seascape. BPI values close to
134 zero are either flat areas or areas with constant slope. Here, BPIs represent topographical depressions and crests at scales of
135 0.1, 0.3, 0.5, 0.8, and 2 km calculated with Benthic Terrain Modeler (v3.0) (Walbridge et al., 2018). SWM(d) estimates
136 dominant wave frequency at a given location with the decay of wave exposure with depth, and takes into account diffraction
137 and refraction of waves around islands (Bekkby et al., 2008). SWM(d) characterizes areas where water movement is slower,
138 i.e. where water resides longer. In terrestrial realms, landform influence on windthrow patterns, i.e. exposure to winds, have
139 been noted in several studies, e.g. Kramer (2001) and Ashcroft et al. (2008). Here, we introduce an analogous version of

140 “windthrown-prone” areas to the marine realm, i.e. a “wave-prone” metric: Topographical Shelter Index (TSI), which
141 differentiates wave directions and takes into account the sheltering effects of islands (i.e. exposure above sea-level).
142 Identification of “wave-prone” areas was calculated for the azimuths multiple of 15 (0° – 345°), and for altitudes
143 (corresponding to the angle of light source) ranging from 0.125° to 81° . For each altitude the produced “wave-prone areas”
144 were combined to an index value for each grid cell. Surface roughness is a commonly used measure of topographical
145 complexity in terrestrial studies, and has been used in marine realms as well (see e.g. Dunn and Halpin (2009) for modelling
146 habitats of hard substrates and Walker et al. (2009) for complexity of coral reef habitats). Here, we consider two approaches
147 for estimating seascape rugosity; Arc-Chord Rugosity (ACR) and Vector Ruggedness Measure (VRM). ACR is a landscape
148 metrics, which evaluates surface ruggedness using a ratio of contoured area (surface area) to the area of a plane of best fit,
149 which is a function of the boundary data (Du Preez, 2015). VRM on the other hand, is a more conservative measure of
150 surface roughness developed for wildlife habitat models, and is calculated using a moving 3×3 window where a unit vector
151 orthogonal to the cell is decomposed using the three dimensional location of the cell center, the local slope and aspect. A
152 resultant vector is divided by the number of cells in the moving window (Sappington et al., 2007). Both rugosity indices
153 were used here to identify areas with complex marine geomorphology. Differences of predictor variables are illustrated in
154 Fig. 2. We also included geographical study areas as predictors, in order to highlight the differences between WFD areas.



155

156 **Figure 2.** Predictor variables developed for hypoxia ensemble models: a) Vector Ruggedness Measure (VRM), b) Depth-
 157 Attenuated Wave Exposure (SWM(d)), c) Topographical Shelter Index (TSI) and (d) Bathymetric Position Index (BPI) with
 158 a search radius of 2 km. Red color represents rugged seafloors (VRM), sheltered areas (SWM(d), TSI) and depressions
 159 (BPI2). Islands shown as white.

160 2.4 Hypoxia models

161 Based on the ecologically meaningful limits of hypoxia (see section “Hypoxia data”), we built four separate oxygen models
 162 based on frequency and severity of hypoxia: occasional with O_2 limits <4.6 and <2 $mg\ L^{-1}$ (hereafter referred as $OH_{4.6}$ and
 163 OH_2) and frequent hypoxia with O_2 limits <4.6 and <2 $mg\ L^{-1}$ (hereafter referred as $FH_{4.6}$ and FH_2). We used Generalize
 164 Boosted Regression Models (GBM) and its extension Boosted Regression Trees (BRT), a method from statistical and

165 machine learning traditions (De'ath and Fabricius, 2000;Hastie et al., 2001;Schapire, 2003). BRT optimizes predictive
166 performance through integrated stochastic gradient boosting (Natekin and Knoll, 2013), and forms the best model for
167 prediction based on several models.

168 Ideal model tuning parameters (learning rate, bag fraction, tree complexity) for our hypoxia models were based on
169 optimizing the model performance, i.e. minimizing the prediction error. The learning rate was set to 0.001 to determine the
170 contribution of each successive tree to the final model. We varied the number of decision rules controlling model interaction
171 levels, i.e. tree complexities, between 3 and 6. We shuffled the hypoxia data randomly into ten subsets for training (70 %)
172 and testing (30 %), while preserving the prevalence ratio of hypoxia occurrence. Hypoxia models were developed based on
173 10-fold cross-validation, and resulting final, best models leading to smallest predictive errors were chosen to predict the
174 probability of detecting hypoxia across the study region at a resolution of 20 m. We believe such a high resolution is
175 necessary due to the complexity of archipelagoes of Finland and Sweden. Model predictions for the whole seascape were
176 repeated ten times with different model fits from data subsets (40 separate model predictions), to identify areas where
177 models agree on the area to be potentially hypoxic. Model performances were estimated against the independent data (test
178 data 30 %), not used in model fitting in order to evaluate the potential overfitting of the models. Analyses were performed in
179 R 3.5.0. (R, 2018) with R libraries 'gbm' (Greenwell et al., 2018), 'PresenceAbsence' (Freeman and Moisen, 2008) and
180 relevant functions from Elith et al. (2008).

181 Variable selection in BRT is internal by including only relevant predictors when building models. The importance of
182 predictors is based on the time each predictor is chosen in each split, averaged over all trees. Higher scores (summed up to
183 100 %) indicate that a predictor has a strong influence on the response (Elith et al., 2008). Although BRT is not sensitive to
184 collinearity of predictors, the ability to identify strongest predictors by decreasing the estimated importance score of highly
185 correlated ones detracts the interpretability of models (Gregorutti et al., 2017). Selecting only optimal and a minimal set
186 of variables for modelling, i.e. finding all relevant predictors and keeping the number of predictors as small as possible,
187 reduces the risk of overfitting and improves the model accuracy. Here, most of the predictors describe seascape structure and
188 are somehow related to the topography of the seabed. We estimated the potential to drop redundant predictors, i.e. those that
189 would lead to marked improvement in model performance if left out from the model building. For this, we used internal
190 backward feature selection in BRT. However, we did not find marked differences in predictive performances, and used all
191 predictors.

192 Estimation of model fits and predictive performances was based on the ability to discriminate a hypoxic site from an oxic
193 one, evaluated with Area Under the Curve (AUC) (Jiménez-Valverde and Lobo, 2007) and simply with Percent Correctly
194 Classified (PCC) (Freeman and Moisen, 2008). AUC is a measure of detection accuracy of true positives (sensitivity) and
195 true negatives (specificity), and AUC values above 0.9 indicate excellent, 0.7–0.9 good, and below 0.7 poor predictions.

196 We transformed hypoxia probability predictions into binary classes of presence/absence, and estimated the relative area of
197 potentially hypoxic due to topographical reasons. Although dichotomization of probability predictions flattens the
198 information content, it facilitates the interpretation of results, and is needed for management purposes. Predicted range of

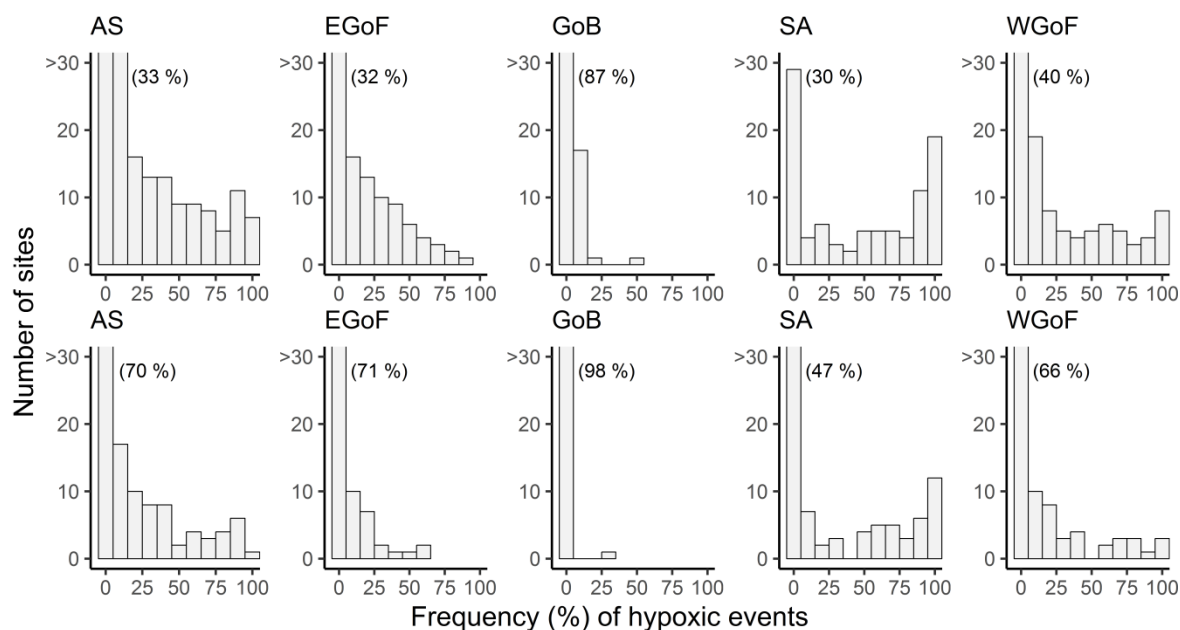
199 hypoxia and the potential geographical extent enables the identification of problematic areas and facilitates management
200 actions in a cost-effective way. There are various approaches for determining thresholds, which are based on the confusion
201 matrix, i.e. how well the model captures true/false presences or true/false absences. Usually the threshold is defined to
202 maximize the agreement between observed and predicted distributions. Widely used thresholds, such as 0.5, can be arbitrary
203 unless the threshold equals prevalence of presences in the data, i.e. the frequency of occurrences (how many presences of the
204 total dataset) (Liu et al., 2005). Here, we define thresholds objectively based on an agreement between predicted and
205 observed hypoxia prevalence. This approach underestimates areas potentially hypoxic (see section “Hypoxia areas”) and is
206 expressed here as a conservative estimate.

207

208

210 3.1 Hypoxia in complex coastal archipelagos

211 During 2000–2016 hypoxia was rather common throughout the whole study region. In Finland, hypoxia mostly occurred on
 212 the southern coast, as in Archipelago Sea (AS), Eastern Gulf of Finland (EGoF) and Western Gulf of Finland (WGoF)
 213 hypoxic events were recorded frequently. Only ~30 % of coastal monitoring sites in AS, EGoF and SA were not hypoxic,
 214 i.e., oxygen concentrations were always above 4.6 mg L^{-1} (cf. percentages in brackets in Fig. 3). Coastal areas in Stockholm
 215 Archipelago (SA) were also regularly hypoxic, with 70 % of the sites moderately ($\text{O}_2 < 4.6 \text{ mg L}^{-1}$) and 53 % severely ($\text{O}_2 <$
 216 2 mg L^{-1}) hypoxic. Severe hypoxia was quite a localized phenomenon in Finland, as it was recorded at ca. 30 % of sites in
 217 AS and EGoF. However, in WGoF there are sites where severe hypoxia is rather persistent, as every sampling event was
 218 recorded as hypoxic. Same applies to SA, as there are quite a few sites repeatedly severely hypoxic. In contrast in the
 219 northern study area, Gulf of Bothnia (GoB), hypoxic events occurred rather infrequently, as in 98 % of sites O_2 was above 2
 220 mg L^{-1} and in 87 % O_2 was above 4.6 mg L^{-1} (Fig. 3).



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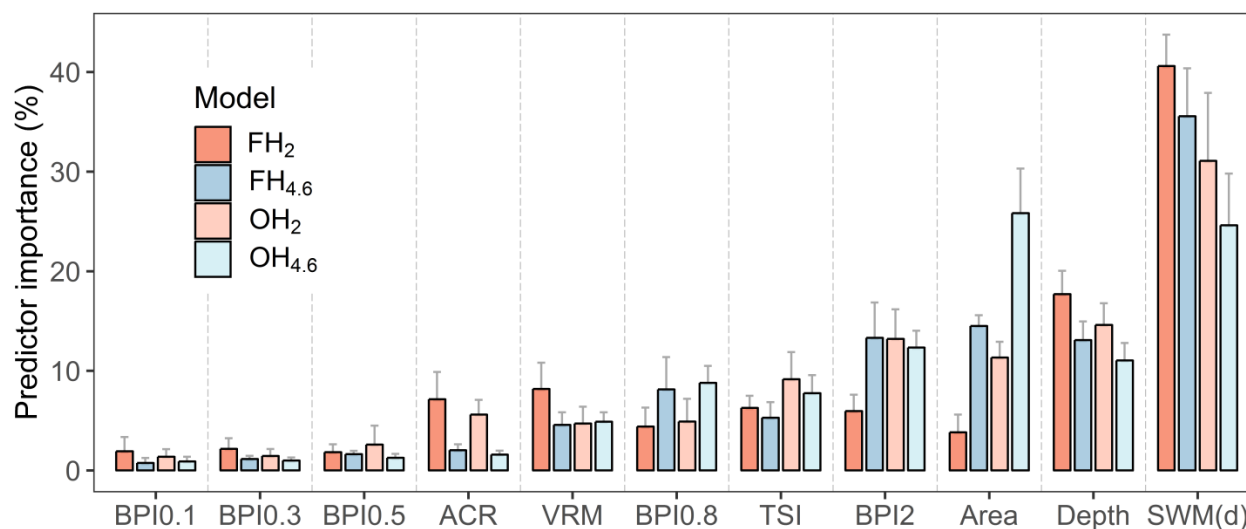
222 **Figure 3.** Frequencies of hypoxic events at coastal monitoring sites across Water Framework Directive areas: Archipelago
 223 Sea (AS), Eastern Gulf of Finland (EGoF), Gulf of Bothnia (GoB), Stockholm Archipelago (SA) and Western Gulf of
 224 Finland (WGoF). Upper panels indicate $\text{O}_2 < 4.6 \text{ mg L}^{-1}$, lower panels $\text{O}_2 < 2 \text{ mg L}^{-1}$. Numbers in brackets indicate the
 225 percentage of sites with $\text{O}_2 > 4.6$ (upper panel) and $\text{O}_2 > 2 \text{ mg L}^{-1}$ (lower panel). Sites >30 are not shown.

226

227

228 3.2 Importance of predictors

229 Models developed on 566 sites, based on 10-fold cross-validation and ten repeated predictions, the most influential predictor
230 (averaged across models) was SWM(d), with a mean contribution of 33 % (± 5 %) (Fig. 4). The contribution of SWM(d) was
231 highest for frequent, severe hypoxia (FH₂) (41 ± 3 %), whereas for occasional, moderate hypoxia (OH_{4,6}) the influence was
232 markedly lower (25 ± 5 %). This supports the hypothesis that in sheltered areas, where water movement is limited, severe
233 oxygen deficiency is likely to develop. Noteworthy is also that depth was not the most important driver of hypoxia in coastal
234 areas. This suggests that coastal hypoxia is not directly dependent on depth, but that depressions that are especially steep and
235 isolated are more sheltered and become more easily hypoxic than smoother depressions.
236 Across models, BPIs identifying wider sinks (BPI2 and BPI0.8) were more influential than BPIs identifying smaller sinks
237 (BPIs 0.1, 0.3 and 0.5), and terrain ruggedness measures, VRM and ACR, were more important for frequent severe hypoxia
238 (FH₂) than for moderate hypoxia (FH_{4,6}). The relatively high contribution of topographical shelter (TSI 7 ± 2 %) indicates
239 that, in areas where there are higher islands, the basins between are prone to hypoxia formation.

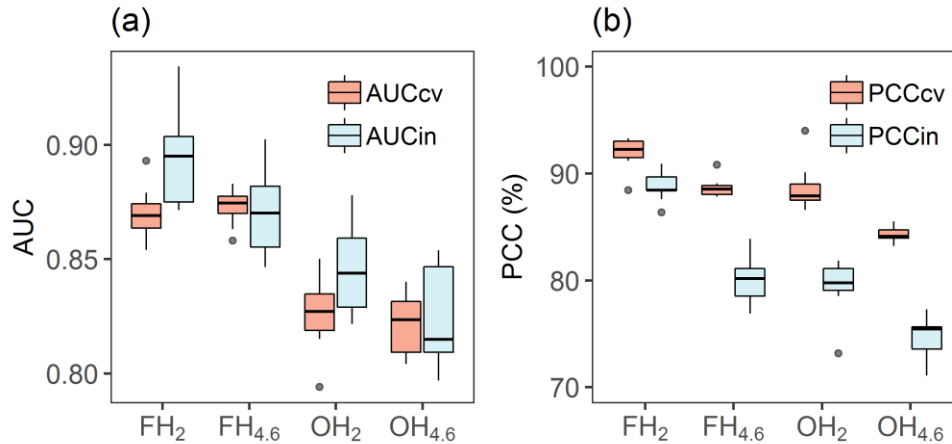


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241 **Figure 4.** Importance of predictors based on ten prediction rounds. Predictors are colour-coded based on models. FH₂=
242 frequent, severe hypoxia ($O_2 < 2 \text{ mg L}^{-1}$), FH_{4,6}= frequent, moderate hypoxia ($O_2 < 4.6 \text{ mg L}^{-1}$), OH₂= occasional, severe
243 hypoxia ($O_2 < 2 \text{ mg L}^{-1}$), and OH_{4,6}= occasional, moderate hypoxia ($O_2 < 4.6 \text{ mg L}^{-1}$). Whiskers represent standard
244 deviations.

245 **3.3 Model performance**

246 Predictive ability of models to detect sites as hypoxic across models was good, with a mean 10-fold cross-validated AUC of
247 0.85 (± 0.02) and mean AUC of 0.86 (± 0.03) when evaluated against independent test data for 242 sites (30 % of sites) (Fig.
248 5a). Models classified on average 88 % sites correctly (PCCcv in Fig. 5b), and performed only slightly worse when
249 evaluated against independent data, with 81 % (± 3 %) correctly classified (PCCin in Fig. 5b). Models developed for
250 frequent hypoxia (FH₂ and FH_{4,6}) were better (mean AUCin 0.88 \pm 0.03) compared to occasional hypoxia models (mean
251 AUCin 0.84 \pm 0.04). This suggests that other factors beyond topographical proxies contribute relatively more to the
252 occurrence of occasional hypoxia than for frequent hypoxia.



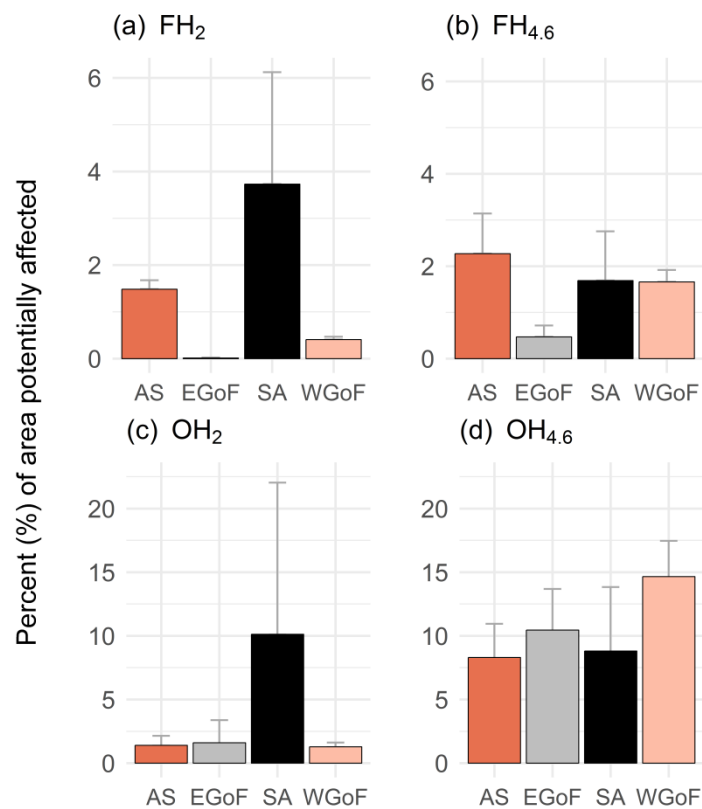
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254 **Figure 5.** Model performances based on (a) Area Under the Curve values with 10-fold cross-validation (AUCcv), and
255 against independent test data (30 % of sites) (AUCin), (b) Percent of Correctly Classified with 10-fold cross-validation
256 (PCCcv) and against independent data (PCCin).

257

258 3.4 Hypoxic areas

259 Although hypoxia was commonly recorded in all WFD areas, except in the Gulf of Bothnia, the potential geographical extent
260 of hypoxic seafloors shows rather different pattern. Based on models, topographically prone areas represent only a small part
261 of the coastal areas, with less than 25 % affected (Fig. 6). Frequent, severe hypoxia ($O_2 < 2 \text{ mg L}^{-1}$) was most prominent in
262 the Archipelago Sea and Stockholm Archipelago, although representing only a small fraction of the total areas (on average
263 1.5 and 3.7 %, respectively). Problematic areas based on the models are Archipelago Sea, Stockholm Archipelago and
264 Western Gulf of Finland. Those areas seem to be topographically prone to oxygen deficiency. Moreover, around 10 % of
265 areas in Eastern Gulf of Finland are vulnerable to occasional moderate hypoxia, but less to severe hypoxia. Areas predicted
266 as hypoxic in Gulf of Bothnia were less than $< 2 \%$, which supports our hypothesis of the facilitating role that topography
267 potential has. There are fewer depressions (Supporting Fig. 1), and the seafloor is topographically less complex than in the
268 other study areas.
269



270
271 **Figure 6.** Percent (%) of areas potentially affected by hypoxia with varying frequencies (occasional and frequent) and
272 hypoxia severities ($O_2 < 4.6 \text{ mg L}^{-1}$ and $O_2 < 2 \text{ mg L}^{-1}$). AS=Archipelago Sea, EGoF=Eastern Gulf of Finland, SA=Stockholm

273 Archipelago and WGoF=Western Gulf of Finland. GoB not reported as areas potentially affected were below 2 % across all
274 models.

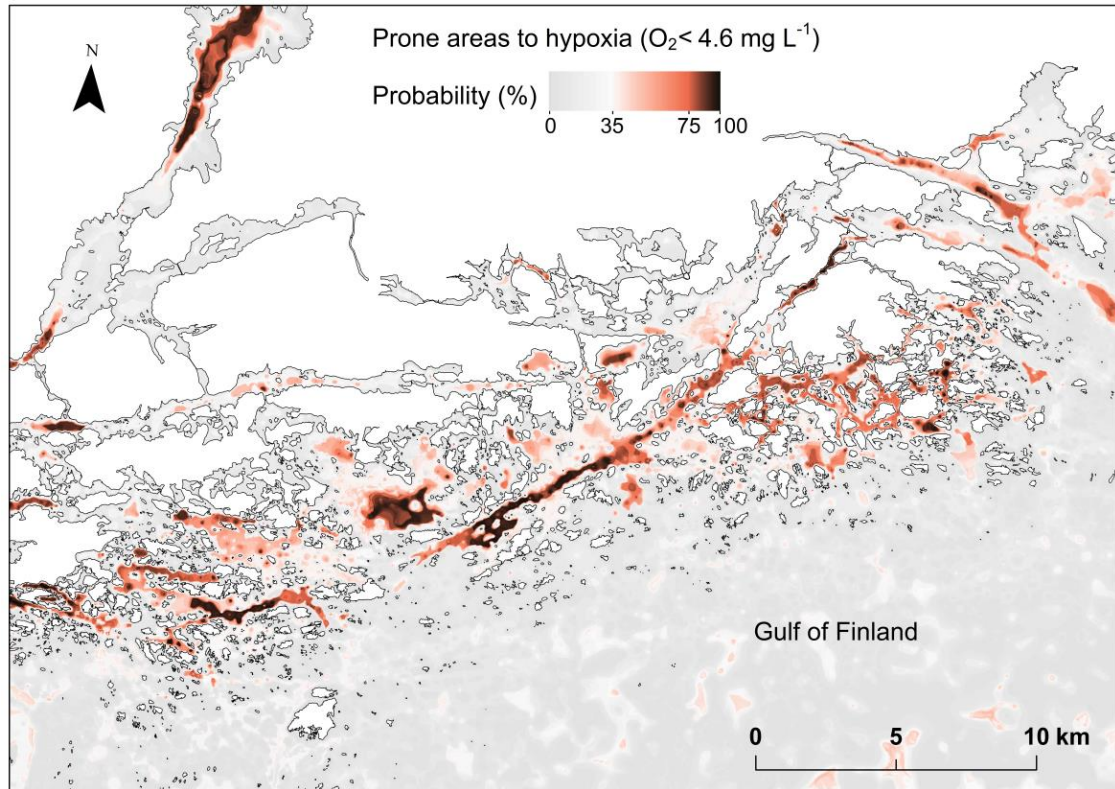
275 4 DISCUSSION

276 Hypoxia has been increasing steadily since the 1960s, and anoxic areas are seizing the seafloor, suffocating marine
277 organisms on the way (Diaz and Rosenberg, 2008;Breitburg et al., 2018). Understanding the factors affecting the severity
278 and spatial extent of hypoxia is essential in order to estimate rates of deoxygenation and its consequences to the marine
279 ecosystems (Breitburg et al., 2018). Earlier studies have reported coastal hypoxia to be a global phenomenon (Diaz and
280 Rosenberg, 2008;Conley et al., 2011), and is known to be widespread in the Baltic Sea (Conley et al., 2011). Our results
281 confirmed this, and showed that coastal hypoxia is perhaps a more common phenomenon than previously anticipated.
282 According to our results, over 50 % of sites in the complex archipelagoes of Finland and Sweden experienced hypoxia that is
283 ecologically significant ($O_2 < 4.6 \text{ mg L}^{-1}$). Especially alarming was the intensity of it. For instance, Stockholm Archipelago
284 suffered frequently from severe hypoxia ($O_2 < 2 \text{ mg L}^{-1}$), as approximately half of the coastal monitoring sites were hypoxic
285 across our study period (Fig. 3). This demonstrates that deoxygenated seafloors are probably even more common in coastal
286 environments than previously reported (Karlsson et al., 2010;Conley et al., 2011). It is notable that in areas above the
287 permanent halocline, hypoxia is in many areas seasonal, and develops after the building of thermocline in late summer
288 (Conley et al., 2011). It is therefore probable that many of the areas we recognized as hypoxic may well be oxygenated
289 during winter and spring. This does not however reduce the severity of the phenomenon. Even hypoxic event of short
290 duration, e.g. few days, will reduce ecosystem resistance to further hypoxic perturbation and affect the overall ecosystem
291 functioning (Villnas et al., 2013).

292 As our study suggests, topographically prone areas to deoxygenation represent less than 25 % of seascapes. However, most
293 of the underwater nature values in the Finnish sea areas are concentrated on relatively shallow areas where there exist
294 enough light and suitable substrates (Virtanen et al., 2018;Lappalainen et al., 2019). Shallow areas also suffer from
295 eutrophication and rising temperatures due to changing climate, and are most probably the ones that are particularly
296 susceptible to hypoxia in the future (Breitburg et al., 2018). This suggests that seasonal hypoxia may become a recurrent
297 phenomenon in shallow areas above the thermocline in late summer.

298 Although extensive 3D models have been developed for the main basins of the Baltic Sea (Meier et al., 2011b;Meier et al.,
299 2012a;Meier et al., 2014) the previous reports on the occurrence of coastal hypoxia have mostly been based on point
300 observations (Conley et al., 2009a;Conley et al., 2011). Due to the lack of data, and computational limitations, no
301 biogeochemical model has (yet) encompassed the complex Baltic Sea archipelago with a resolution needed for adjusting
302 local management decisions. This study provides a novel methodology to predict and identify areas prone to coastal hypoxia
303 without data on currents, stratification or biological variables, and without complex biogeochemical models. Our approach is
304 applicable to other low-energy and non-tidal systems, such as large shallow bays and semi-enclosed or enclosed sea areas.
305 The benefit of this approach is that it requires far less computational power than a fine-scale 3D numerical modelling. By
306 using relatively simple proxies describing depressions of stagnant water, we were able to create detailed hypoxia maps for

307 the entire Finnish coastal area (23 500 km²) and Stockholm Archipelago (5100 km²), thus enabling a quick view of
308 potentially hypoxic waters (Fig. 7).



309

310 **Figure 7.** Modelled probability of detecting frequent hypoxia O₂ (<4.6 mg L⁻¹) in an example area in the south coast of
311 Finland. Land shown as white color.

312

313 We quantified the facilitating role of seafloor complexity for the formation of hypoxia. Sheltered, topographically
314 heterogeneous areas, where water exchange is limited are more susceptible for developing hypoxia according to our results.
315 This statement is quite intuitive, but it has not previously been quantified. Noteworthy is that coastal hypoxia is not only
316 related to depth; deep seafloors are not automatically hypoxic or anoxic. In our study, hypoxia was common in shallow and
317 moderate depths of 10–45 m. For instance in the Archipelago Sea, deep (60–100 m) channels are not usually hypoxic, as
318 strong currents tend to keep them oxygenated throughout the year (Virtasalo et al., 2005). Shallow areas can be restricted by
319 slow water movement due to topographical reasons, thus creating opportunities for hypoxia formation.

320 We emphasize that our models only indicate where hypoxia may occur simply due to restricted water exchange. Any
321 deviations from this pattern are probably caused by either hydrographic factors, which the hypoxia model based on
322 topography did not account for (such as strong currents in elongated, wide channels), or biogeochemical factors. Especially
323 high external loading, and local biogeochemical and biological processes (nutrient cycling between sediment and the water),

324 obviously modify the patterns and severity of hypoxia also in the coastal areas. Oxygen deficiency has been projected to
325 increase faster in the coastal systems than in the open sea (Gilbert et al., 2010;Altieri and Gedan, 2015). Such coastal areas
326 are usually affected by external nutrient loading from the watershed. In larger basins and sea areas dominated by large river
327 systems, such as the central Baltic Sea, Gulf of Mexico and Chesapeake Bay, large scale oceanographic and biogeochemical
328 processes, or external loading, govern the depth and extent of hypoxia. This is the case also in the Baltic Sea. In areas where
329 our models underestimate oxygen deficiency, major nutrient sources, e.g. rivers, cities or intensive agricultural areas,
330 probably contribute to hypoxia formation. However, in extremely complex archipelago areas, such as Finnish and Swedish
331 archipelago, physical factors limiting lateral and vertical movement of water probably facilitates, and in some areas even
332 dictates the development of hypoxia.

333 There were spatial differences in the frequency and severity of hypoxia that can be explained by topographical characteristics
334 of the areas, external loading, and interaction with the adjacent deeper basins. For instance, in the Stockholm Archipelago
335 severe hypoxia covered the largest percentage of seascapes of all study areas. Stockholm Archipelago is part of a joint valley
336 landscape with deep, steep areas also in the inner parts where wave forcing is exceptionally low, and disconnected from the
337 open sea, making it very susceptible for hypoxia, which was also confirmed by the model. In Finland, the inner archipelago
338 is mostly shallow, with steep but wider channels occurring only in the Archipelago Sea. These elongated channels are
339 connected to adjacent open sea areas, and thus well-ventilated, as opposite to the narrow channels of Stockholm
340 Archipelago. Geographically, hypoxia was in Finland most prominent in the Archipelago Sea and the Gulf of Finland, where
341 the inner archipelago is isolated from the open sea, and the complex topography results in overall poor water exchange in the
342 existing depressions. Both Stockholm Archipelago and the Archipelago Sea suffer from external loading from the associated
343 watersheds, and internal loading from sediments, which probably contributes to the poor oxygen status of these areas
344 (Puttonen et al., 2014;Walve et al., 2018). Biogeochemical factors were however not accounted for by our analysis, and
345 cannot be used in explaining the observed spatial differences.

346 In the Gulf of Finland, eutrophication increases in the open sea from west to east, which has traditionally been explained by
347 nutrient discharges from the Neva River (HELCOM, 2018). In our data there was however no clear gradient of coastal
348 hypoxia increasing towards east. In contrast, frequent hypoxia was more common in the Archipelago Sea and Western Gulf
349 of Finland than in the Eastern Gulf of Finland, where hypoxia occurred only occasionally. This suggests that the coastal
350 hypoxia is more dependent on local processes, i.e. internal loading and external loading from nearby areas, whereas open sea
351 hypoxia is governed by basin-scale dynamics. However, the occasional nature of hypoxia in the Eastern Gulf of Finland may
352 be at least partly caused by the dependency on the deep waters of the open parts of the Gulf of Finland. The Gulf of Finland
353 is an embayment, 400 km long and 50–120 km wide, which has an open western boundary to the Baltic Proper. A tongue of
354 anoxic water usually extends from the central Baltic Sea into the Gulf of Finland along its deepest parts. Basin scale
355 oceanographic and atmospheric processes influence how far east this tongue proceeds into the Gulf of Finland each year
356 (Alenius et al., 2016). It is possible that when this anoxic tongue extends close to Eastern Gulf of Finland, it also worsens the
357 oxygen situation of the EGoF archipelago.

358 In the Gulf of Bothnia, hypoxia was markedly less frequent and severe than in the other study areas. GoB has a relatively
359 open coastline with only few depressions (cf. Supporting Fig. 1) and strong wave forcing, which probably enhances the
360 mixing of water in the coastal areas. Moreover, as the open sea areas of the Gulf of Bothnia are well oxygenated due to a
361 lack of halocline and topographical isolation of GoB from the Baltic Proper (by the sill between these basins) (Leppäranta
362 and Myrberg, 2009), hypoxic water is not advected from the open sea to the coastal areas.

363 Such observations suggest that formation of coastal hypoxia is not totally independent from basin-scale oxygen dynamics.
364 While we suggest that coastal hypoxia can be formed entirely based on local morphology and local biogeochemical
365 processes, the relatively low occurrence of hypoxia in the Gulf of Bothnia, and differences in frequency of hypoxia in
366 different parts of the Gulf of Finland, both highlight the interaction of these coastal areas with the Baltic Proper.

367 While our results confirm that hypoxia in most study areas is a frequently occurring phenomenon, they also show that areas
368 affected by hypoxia are geographically still limited. Our modelling results indicate that overall, less than 25 % of the studied
369 sea areas were afflicted by some form of hypoxia (be it recurrent or occasional), and less than 6 % of seascapes were plagued
370 by frequent, severe hypoxia. The relatively small spatial extent of coastal hypoxia does not mean that it is not a harmful
371 phenomenon. In Stockholm Archipelago, severe hypoxia is a pervasive and persistent phenomenon, and also in Finland,
372 many local depressions are often hypoxic. Anoxic local depressions probably act as local nutrient sources, releasing
373 especially phosphorus to the water column, which further enhances pelagic primary production. Such a vicious circle tends
374 to worsen the eutrophication and maintain the environment in a poor state (Pitkänen et al., 2001; Vahtera et al., 2007). In this
375 way, even small sized anoxic depressions, especially if they are many, may affect the ecological status of the whole coastal
376 area. Moreover, as climate change has been projected to increase water temperatures and worsen hypoxia in the Baltic Sea
377 (Meier et al., 2011a), shallow archipelago areas that typically have high productivity, warm up quickly, and are
378 topographically prone to hypoxia, may be especially vulnerable to the negative effects of climate change.

379 In order to establish reference conditions and implement necessary and cost-efficient measures to reach the goals of
380 international agreements such as the EU Water Framework Directive (WFD, 2000/60/EC), the Marine Strategy Framework
381 Directive (MSFD, 2008/56/EC) and the HELCOM Baltic Sea Action Plan (BSAP), in-depth knowledge of ecological
382 functions and processes as well as natural preconditions is needed. Although eutrophication is a problem for the whole Baltic
383 Sea, nutrient abatement measures are taken locally. We therefore need to know where the environmental benefits are
384 maximized, and where natural conditions are likely to counteract any measures taken. As some places are naturally prone to
385 hypoxia, our model could aid directing measures to places where they are most likely to be efficient, as well as explain why
386 in some areas implemented measures do not have the desired effect. Our approach could be used to develop an “early-
387 warning system” for identification of areas prone to oxygen loss, and to indicate where eutrophication mitigation actions are
388 most urgently needed.

389

390 CONCLUSIONS

391 While biogeochemical 3D models have been able to accurately project basin-scale oxygen dynamics, describing spatial
392 variation of hypoxia in coastal areas has remained a challenge. Recognizing that the enclosed nature of seafloors contributes
393 to hypoxia formation, we used simple topographical parameters to model the occurrence of hypoxia in the complex Finnish
394 and Swedish archipelagoes. We found that a surprisingly large fraction (~80 %) of hypoxia occurrences could be explained
395 by topographical parameters alone. Modelling results also suggested that less than 25 % of the studied seascapes were prone
396 to hypoxia during late summer. Large variation existed in the spatial and temporal patterns of hypoxia, however, with certain
397 areas being prone to occasional severe hypoxia ($O_2 < 2$ mg/L), while others were more susceptible to recurrent moderate
398 hypoxia ($O_2 < 4.6$ mg/L). Sheltered, topographically heterogeneous areas with limited water exchange were susceptible for
399 developing hypoxia, in contrast to less sheltered areas with high wave forcing. In some areas oxygen conditions were either
400 better or worse than predicted by the model. We assume that these deviations from the “topographical background” were
401 caused by processes not accounted for by the model, such as hydrographical processes, e.g. strong currents causing improved
402 mixing, or by high external or internal nutrient loading, inducing high local oxygen consumption. We conclude that
403 formation of coastal hypoxia is probably primarily dictated by local processes, and can be quite accurately projected using
404 simple topographical parameters, but that interaction with the associated watershed and the adjacent deeper basins of the
405 Baltic Sea can also influence local oxygen dynamics in many areas. Our approach gives a practical baseline for various types
406 of hypoxia related studies and consequently, decision-making. Identifying areas prone to hypoxia helps to focus research,
407 management and conservation actions in a cost-effective way.

408 AUTHOR CONTRIBUTION

409 EAV and MV designed the study, EAV and ANS performed all analyses, EAV wrote the main text and all authors
410 contributed to the writing and editing of the manuscript.

411 DATA AVAILABILITY

412 Data and model codes will be submitted to Dryad data repository.

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References:

- 424 Alenius, P., Myrberg, K., Roiha, P., Lips, U., Tuomi, L., Pettersson, H., and Raateoja, M.: Gulf of Finland Physics, 42-57, 2016.
- 425 Altieri, A. H., and Gedan, K. B.: Climate change and dead zones, *Global Change Biology*, 21, 1395-1406, 10.1111/gcb.12754, 2015.
- 426 Ashcroft, M. B., Chisholm, L. A., and French, K. O.: The effect of exposure on landscape scale soil surface temperatures and species
427 distribution models, *Landscape Ecology*, 23, 211-225, 10.1007/s10980-007-9181-8, 2008.
- 428 Bekkby, T., Isachsen, P. E., Isaeus, M., and Bakkestuen, V.: GIS modeling of wave exposure at the seabed: A depth-attenuated wave
429 exposure model, *Marine Geodesy*, 31, 117-127, 10.1080/01490410802053674, 2008.
- 430 Breitbart, D., Levin, L. A., Oschlies, A., Grégoire, M., Chavez, F. P., Conley, D. J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K.,
431 Jacinto, G. S., Limburg, K. E., Montes, I., Naqvi, S. W. A., Pitcher, G. C., Rabalais, N. N., Roman, M. R., Rose, K. A., Seibel, B. A.,
432 Telszewski, M., Yasuhara, M., and Zhang, J.: Declining oxygen in the global ocean and coastal waters, *Science*, 359,
433 10.1126/science.aam7240, 2018.
- 434 Buzzelli, C. P., Luettich Jr, R. A., Powers, S. P., Peterson, C. H., McNinch, J. E., Pinckney, J. L., and Paerl, H. W.: Estimating the spatial
435 extent of bottom-water hypoxia and habitat degradation in a shallow estuary, *Marine ecology progress series*, 230, 103-112, 2002.
- 436 Caballero-Alfonso, A. M., Carstensen, J., and Conley, D. J.: Biogeochemical and environmental drivers of coastal hypoxia, *Journal of*
437 *Marine Systems*, 141, 190-199, <https://doi.org/10.1016/j.jmarsys.2014.04.008>, 2015.
- 438 Carstensen, J., Andersen, J. H., Gustafsson, B. G., and Conley, D. J.: Deoxygenation of the Baltic Sea during the last century, *Proceedings*
439 *of the National Academy of Sciences*, 111, 5628-5633, 10.1073/pnas.1323156111, 2014.
- 440 Conley, D. J., Humborg, C., Rahm, L., Savchuk, O. P., and Wulff, F.: Hypoxia in the Baltic Sea and basin-scale changes in phosphorus
441 biogeochemistry, *Environmental Science & Technology*, 36, 5315-5320, 10.1021/es025763w, 2002.
- 442 Conley, D. J., Björck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., Hietanen, S., Kortekaas, M., Kuosa, H., Markus
443 Meier, H. E., Müller-Karulis, B., Nordberg, K., Norkko, A., Nürnberg, G., Pitkänen, H., Rabalais, N. N., Rosenberg, R., Savchuk, O. P.,
444 Slomp, C. P., Voss, M., Wulff, F., and Zillén, L.: Hypoxia-Related Processes in the Baltic Sea, *Environmental Science & Technology*, 43,
445 3412-3420, 10.1021/es802762a, 2009a.
- 446 Conley, D. J., Carstensen, J., Aigars, J., Axe, P., Bonsdorff, E., Eremina, T., Hahti, B. M., Humborg, C., Jonsson, P., Kotta, J.,
447 Lannegren, C., Larsson, U., Maximov, A., Medina, M. R., Lysiak-Pastuszak, E., Remeikaite-Nikiene, N., Walve, J., Wilhelms, S., and
448 Zillen, L.: Hypoxia Is Increasing in the Coastal Zone of the Baltic Sea, *Environmental Science & Technology*, 45, 6777-6783,
449 10.1021/es201212r, 2011.
- 450 De'ath, G., and Fabricius, K. E.: Classification and regression trees: A powerful yet simple technique for ecological data analysis, *Ecology*,
451 81, 3178-3192, 10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2, 2000.
- 452 Diaz, R., and Rosenberg, R.: Marine benthic hypoxia: A review of its ecological effects and the behavioural response of benthic
453 macrofauna, 245-303 pp., 1995a.
- 454 Diaz, R. J., and Rosenberg, R.: Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic
455 macrofauna, in: *Oceanography and Marine Biology - an Annual Review*, Vol 33, edited by: Ansell, A. D., Gibson, R. N., and Barnes, M.,
456 *Oceanography and Marine Biology*, U C L Press Ltd, London, 245-303, 1995b.
- 457 Diaz, R. J., and Rosenberg, R.: Spreading dead zones and consequences for marine ecosystems, *Science*, 321, 926-929,
458 10.1126/science.1156401, 2008.
- 459 Du Preez, C.: A new arc-chord ratio (ACR) rugosity index for quantifying three-dimensional landscape structural complexity, *Landscape*
460 *Ecology*, 30, 181-192, 10.1007/s10980-014-0118-8, 2015.
- 461 Dunn, D. C., and Halpin, P. N.: Rugosity-based regional modeling of hard-bottom habitat, *Marine Ecology Progress Series*, 377, 1-11,
462 2009.
- 463 Eilola, K., Meier, H. E. M., and Almroth, E.: On the dynamics of oxygen, phosphorus and cyanobacteria in the Baltic Sea; A model study,
464 *Journal of Marine Systems*, 75, 163-184, <https://doi.org/10.1016/j.jmarsys.2008.08.009>, 2009.
- 465 Eilola, K., Gustafsson, B. G., Kuznetsov, I., Meier, H. E. M., Neumann, T., and Savchuk, O. P.: Evaluation of biogeochemical cycles in an
466 ensemble of three state-of-the-art numerical models of the Baltic Sea, *Journal of Marine Systems*, 88, 267-284,
467 10.1016/j.jmarsys.2011.05.004, 2011.
- 468 Elith, J., Leathwick, J. R., and Hastie, T.: A working guide to boosted regression trees, *Journal of Animal Ecology*, 77, 802-813,
469 10.1111/j.1365-2656.2008.01390.x, 2008.
- 470 Eriksson, S. P., Wennhage, H., Norkko, J., and Norkko, A.: Episodic disturbance events modify predator-prey interactions in soft
471 sediments, *Estuarine Coastal and Shelf Science*, 64, 289-294, 10.1016/j.ecss.2005.02.022, 2005.
- 472 Fennel, K., Hetland, R., Feng, Y., and DiMarco, S.: A coupled physical-biological model of the Northern Gulf of Mexico shelf: model
473 description, validation and analysis of phytoplankton variability, *Biogeosciences*, 8, 1881-1899, 2011.

474 Fennel, K., Laurent, A., Hetland, R., Justic, D., Ko, D. S., Lehrter, J., Murrell, M., Wang, L. X., Yu, L. Q., and Zhang, W. X.: Effects of
475 model physics on hypoxia simulations for the northern Gulf of Mexico: A model intercomparison, *Journal of Geophysical Research-*
476 *Oceans*, 121, 5731-5750, 10.1002/2015jc011577, 2016.

477 Fennel, K., and Testa, J. M.: Biogeochemical Controls on Coastal Hypoxia, *Annual Review of Marine Science*, 11, 105-130,
478 10.1146/annurev-marine-010318-095138, 2019.

479 Freeman, E. A., and Moisen, G.: PresenceAbsence: An R Package for Presence-Absence Model Analysis., *Journal of Statistical Software*,
480 23, 1-31, 2008.

481 Frölicher, T. L., Joos, F., Plattner, G. K., Steinacher, M., and Doney, S. C.: Natural variability and anthropogenic trends in oceanic oxygen
482 in a coupled carbon cycle–climate model ensemble, *Global Biogeochemical Cycles*, 23, n/a-n/a, 10.1029/2008GB003316, 2009.

483 Gammal, J., Norkko, J., Pilditch, C. A., and Norkko, A.: Coastal Hypoxia and the Importance of Benthic Macrofauna Communities for
484 Ecosystem Functioning, *Estuaries and Coasts*, 40, 457-468, 10.1007/s12237-016-0152-7, 2017.

485 Gilbert, D., Rabalais, N. N., Díaz, R. J., and Zhang, J.: Evidence for greater oxygen decline rates in the coastal ocean than in the open
486 ocean, *Biogeosciences*, 7, 2283-2296, 10.5194/bg-7-2283-2010, 2010.

487 Gray, J. S., Wu, R. S. S., and Or, Y. Y.: Effects of hypoxia and organic enrichment on the coastal marine environment, *Marine Ecology*
488 *Progress Series*, 238, 249-279, 10.3354/meps238249, 2002.

489 Gregorutti, B., Michel, B., and Saint-Pierre, P.: Correlation and variable importance in random forests, *Statistics and Computing*, 27, 659-
490 678, 10.1007/s11222-016-9646-1, 2017.

491 Hastie, T., Tibshirani, R., and Friedman, J. H.: *The Elements of Statistical Learning: Data Mining, Inference, and Prediction.*, Springer-
492 Verlag, New York, 2001.

493 HELCOM: Sources and pathways of nutrients to the Baltic Sea, 2018.

494 Hordoir, R., Axell, L., Höglund, A., Dieterich, C., Fransner, F., Gröger, M., Liu, Y., Pemberton, P., Schimanke, S., Andersson, H.,
495 Ljungemyr, P., Nygren, P., Falahat, S., Nord, A., Jönsson, A., Lake, I., Döös, K., Hieronymus, M., Dietze, H., Löptien, U., Kuznetsov, I.,
496 Westerlund, A., Tuomi, L., and Haapala, J.: Nemo-Nordic 1.0: A NEMO based ocean model for Baltic & North Seas, research and
497 operational applications, *Geosci. Model Dev*, in review, <https://doi.org/10.5194/gmd-2018-2>, 2018.

498 Jiménez-Valverde, A., and Lobo, J. M.: Threshold criteria for conversion of probability of species presence to either–or presence–absence,
499 *Acta Oecologica*, 31, 361-369, <https://doi.org/10.1016/j.actao.2007.02.001>, 2007.

500 Jokinen, S. A., Virtasalo, J. J., Jilbert, T., Kaiser, J., Dellwig, O., Arz, H. W., Hänninen, J., Arppe, L., Collander, M., and Saarinen, T.: A
501 1500-year multiproxy record of coastal hypoxia from the northern Baltic Sea indicates unprecedented deoxygenation over the 20th
502 century, *Biogeosciences*, 15, 3975-4001, 2018.

503 Karlson, K., Rosenberg, R., and Bonsdorff, E.: Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on
504 benthic fauna in Scandinavian and Baltic waters - A review, in: *Oceanography and Marine Biology*, Vol 40, edited by: Gibson, R. N.,
505 Barnes, M., and Atkinson, R. J. A., *Oceanography and Marine Biology*, Taylor & Francis Ltd, London, 427-489, 2002.

506 Karlsson, O. M., Jonsson, P. O., Lindgren, D., Malmaeus, J. M., and Stehn, A.: Indications of Recovery from Hypoxia in the Inner
507 Stockholm Archipelago, *Ambio*, 39, 486-495, 10.1007/s13280-010-0079-3, 2010.

508 Kaskela, A. M., Kotilainen, A. T., Al-Hamdani, Z., Leth, J. O., and Reker, J.: Seabed geomorphic features in a glaciated shelf of the Baltic
509 Sea, *Estuarine Coastal and Shelf Science*, 100, 150-161, 10.1016/j.ecss.2012.01.008, 2012.

510 Kemp, W. M., Testa, J. M., Conley, D. J., Gilbert, D., and Hagy, J. D.: Temporal responses of coastal hypoxia to nutrient loading and
511 physical controls, *Biogeosciences*, 6, 2985-3008, 2009.

512 Kramer, M. G., Hansen, A. J., Taper, M. L. and Kissinger, E. J. : Abiotic controls on long-term windthrow disturbance and temperate rain
513 forest dynamics in Southeast Alaska, *Ecology*, 2749-2768 2001.

514 Laine, A. O., Sandler, H., Andersin, A.-B., and Stigzelius, J.: Long-term changes of macrozoobenthos in the Eastern Gotland Basin and the
515 Gulf of Finland (Baltic Sea) in relation to the hydrographical regime, *Journal of Sea Research*, 38, 135-159, [https://doi.org/10.1016/S1385-](https://doi.org/10.1016/S1385-1101(97)00034-8)
516 [1101\(97\)00034-8](https://doi.org/10.1016/S1385-1101(97)00034-8), 1997.

517 Lappalainen, J., Virtanen, E. A., Kallio, K., Junttila, S., and Viitasalo, M.: Substrate limitation of a habitat-forming genus *Fucus* under
518 different water clarity scenarios in the northern Baltic Sea, *Estuarine, Coastal and Shelf Science*, 218, 31-38,
519 <https://doi.org/10.1016/j.ecss.2018.11.010>, 2019.

520 Leppäranta, M., and Myrberg, K.: *Physical Oceanography of the Baltic Sea*, Springer-Verlag, Berlin-Heidelberg-New York, 2009.

521 Liu, C., Berry, P. M., Dawson, T. P., and Pearson, R. G.: Selecting thresholds of occurrence in the prediction of species distributions,
522 *Ecography*, 28, 385-393, doi:10.1111/j.0906-7590.2005.03957.x, 2005.

523 Meier, H. E. M., Andersson, H. C., Eilola, K., Gustafsson, B. G., Kuznetsov, I., Müller-Karulis, B., Neumann, T., and Savchuk, O. P.:
524 Hypoxia in future climates: A model ensemble study for the Baltic Sea, *Geophysical Research Letters*, 38, n/a-n/a,
525 10.1029/2011GL049929, 2011a.

526 Meier, H. E. M., Eilola, K., and Almroth, E.: Climate-related changes in marine ecosystems simulated with a 3-dimensional coupled
527 physical-biogeochemical model of the Baltic Sea, *Climate Research*, 48, 31-55, 2011b.

528 Meier, H. E. M., Hordoir, R., Andersson, H. C., Dieterich, C., Eilola, K., Gustafsson, B. G., Hoglund, A., and Schimanke, S.: Modeling the
529 combined impact of changing climate and changing nutrient loads on the Baltic Sea environment in an ensemble of transient simulations
530 for 1961–2099, *Climate Dynamics*, 39, 2421–2441, 10.1007/s00382-012-1339-7, 2012a.

531 Meier, H. E. M., Muller-Karulis, B., Andersson, H. C., Dieterich, C., Eilola, K., Gustafsson, B. G., Hoglund, A., Hordoir, R., Kuznetsov,
532 I., Neumann, T., Ranjbar, Z., Savchuk, O. P., and Schimanke, S.: Impact of Climate Change on Ecological Quality Indicators and
533 Biogeochemical Fluxes in the Baltic Sea: A Multi-Model Ensemble Study, *Ambio*, 41, 558–573, 10.1007/s13280-012-0320-3, 2012b.

534 Meier, H. E. M., Andersson, H. C., Arheimer, B., Donnelly, C., Eilola, K., Gustafsson, B. G., Kotwicki, L., Neset, T.-S., Niiranen, S.,
535 Piwowarczyk, J., Savchuk, O. P., Schenk, F., Weślowski, J. M., and Zorita, E.: Ensemble Modeling of the Baltic Sea Ecosystem to Provide
536 Scenarios for Management, *AMBIO*, 43, 37–48, 10.1007/s13280-013-0475-6, 2014.

537 Middelburg, J. J., and Levin, L. A.: Coastal hypoxia and sediment biogeochemistry, *Biogeosciences*, 6, 1273–1293, 2009.

538 Natekin, A., and Knoll, A.: Gradient boosting machines, a tutorial, *Frontiers in Neuroinformatics*, 7, 21, 10.3389/fnbot.2013.00021, 2013.

539 Nilsson, H. C., and Rosenberg, R.: Succession in marine benthic habitats and fauna in response to oxygen deficiency: analysed by
540 sediment profile-imaging and by grab samples, *Marine Ecology Progress Series*, 197, 139–149, 10.3354/meps197139, 2000.

541 Norkko, J., Reed, D. C., Timmermann, K., Norkko, A., Gustafsson, B. G., Bonsdorff, E., Slomp, C. P., Carstensen, J., and Conley, D. J.: A
542 welcome can of worms? Hypoxia mitigation by an invasive species, *Global Change Biology*, 18, 422–434, 10.1111/j.1365-
543 2486.2011.02513.x, 2012.

544 Norkko, J., Gammal, J., Hewitt, J. E., Josefson, A. B., Carstensen, J., and Norkko, A.: Seafloor Ecosystem Function Relationships: In Situ
545 Patterns of Change Across Gradients of Increasing Hypoxic Stress, *Ecosystems*, 18, 1424–1439, 10.1007/s10021-015-9909-2, 2015.

546 Pitkänen, H., Lehtoranta, J., and Räsänen, A.: Internal Nutrient Fluxes Counteract Decreases in External Load: The Case of the Estuarial
547 Eastern Gulf of Finland, *Baltic Sea*, 195–201 pp., 2001.

548 Puttonen, I., Mattila, J., Jonsson, P., Karlsson, O. M., Kohonen, T., Kotilainen, A., Lukkari, K., Malmaeus, J. M., and Rydin, E.:
549 Distribution and estimated release of sediment phosphorus in the northern Baltic Sea archipelagos, *Estuarine, Coastal and Shelf Science*,
550 145, 9–21, <https://doi.org/10.1016/j.ecss.2014.04.010>, 2014.

551 R. C. T.: R: A language and environment for statistical computing. , R foundation for Statistical Computing, Vienna, Austria, 2018.

552 Rabalais, N. N., Diaz, R. J., Levin, L. A., Turner, R. E., Gilbert, D., and Zhang, J.: Dynamics and distribution of natural and human-caused
553 hypoxia, *Biogeosciences*, 7, 585–619, 2010.

554 Sappington, J. M., Longshore, K. M., and Thompson, D. B.: Quantifying Landscape Ruggedness for Animal Habitat Analysis: A Case
555 Study Using Bighorn Sheep in the Mojave Desert, *SPIE*, 8 pp., 2007.

556 Schapire, R.: The boosting approach to machine learning – an overview, in: *MSRI Workshop on Nonlinear Estimation and Classification*,
557 2002, edited by: Denison, D., Hansen, M. H., Holmes, C., B., M., and B., Y., Springer, New York, 2003.

558 Scully, M. E.: Physical controls on hypoxia in Chesapeake Bay: A numerical modeling study, *Journal of Geophysical Research-Oceans*,
559 118, 1239–1256, 10.1002/jgrc.20138, 2013.

560 Scully, M. E.: The contribution of physical processes to inter-annual variations of hypoxia in Chesapeake Bay: A 30-yr modeling study,
561 *Limnology and Oceanography*, 61, 2243–2260, 10.1002/lno.10372, 2016.

562 Stramma, L., Oeschlies, A., and Schmidtko, S.: Mismatch between observed and modeled trends in dissolved upper-ocean oxygen over the
563 last 50 yr, *Biogeosciences*, 9, 4045–4057, 10.5194/bg-9-4045-2012, 2012.

564 Testa, J. M., Li, Y., Lee, Y. J., Li, M., Brady, D. C., Di Toro, D. M., Kemp, W. M., and Fitzpatrick, J. J.: Quantifying the effects of
565 nutrient loading on dissolved O-2 cycling and hypoxia in Chesapeake Bay using a coupled hydrodynamic-biogeochemical model, *Journal*
566 *of Marine Systems*, 139, 139–158, 10.1016/j.jmarsys.2014.05.018, 2014.

567 Timmermann, K., Norkko, J., Janas, U., Norkko, A., Gustafsson, B. G., and Bonsdorff, E.: Modelling macrofaunal biomass in relation to
568 hypoxia and nutrient loading, *Journal of Marine Systems*, 105, 60–69, 10.1016/j.jmarsys.2012.06.001, 2012.

569 Vahtera, E., Conley, D. J., Gustafsson, B. G., Kuosa, H., Pitkanen, H., Savchuk, O. P., Tamminen, T., Viitasalo, M., Voss, M., Wasmund,
570 N., and Wulff, F.: Internal ecosystem feedbacks enhance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic
571 Sea, *Ambio*, 36, 186–194, 10.1579/0044-7447(2007)36[186:iefenc]2.0.co;2, 2007.

572 Valanko, S., Heino, J., Westerborg, M., Viitasalo, M., and Norkko, A.: Complex metacommunity structure for benthic invertebrates in a
573 low-diversity coastal system, *Ecology and Evolution*, 5, 5203–5215, 10.1002/ece3.1767, 2015.

574 Walbridge, S., Slocum, N., Pobuda, M., and Wright, D.: Unified Geomorphological Analysis Workflows with Benthic Terrain Modeler,
575 *Geosciences*, 8, 94, 2018.

576 Walker, B. K., Jordan, L. K. B., and Spieler, R. E.: Relationship of Reef Fish Assemblages and Topographic Complexity on Southeastern
577 Florida Coral Reef Habitats, *SPIE*, 10 pp., 2009.

578 Walve, J., Sandberg, M., Larsson, U., and Lannergren, C.: A Baltic Sea estuary as a phosphorus source and sink after drastic load
579 reduction: seasonal and long-term mass balances for the Stockholm inner archipelago for 1968–2015, *Biogeosciences*, 15, 3003–3025,
580 10.5194/bg-15-3003-2018, 2018.

581 van Helmond, N. A., Krupinski, N. B. Q., Loughheed, B. C., Obrochta, S. P., Andrén, T., and Slomp, C. P.: Seasonal hypoxia was a natural
582 feature of the coastal zone in the Little Belt, Denmark, during the past 8 ka, *Marine Geology*, 387, 45–57, 2017.

583 Vaquer-Sunyer, R., and Duarte, C. M.: Thresholds of hypoxia for marine biodiversity, Proceedings of the National Academy of Sciences
584 of the United States of America, 105, 15452-15457, 10.1073/pnas.0803833105, 2008.
585 Weiss, A. D.: Topographic position and landforms analysis., In Poster presented at the Esri User Conference, San Diego, CA, USA. ,
586 http://www.jennessent.com/downloads/tpi-postertnc_18x22.pdf, 2001.
587 WFD: Water Framework Directive, Common Implementation, 2000.
588 Villnas, A., Norkko, J., Lukkari, K., Hewitt, J., and Norkko, A.: Consequences of Increasing Hypoxic Disturbance on Benthic
589 Communities and Ecosystem Functioning, Plos One, 7, 10.1371/journal.pone.0044920, 2012.
590 Villnas, A., Norkko, J., Hietanen, S., Josefson, A. B., Lukkari, K., and Norkko, A.: The role of recurrent disturbances for ecosystem
591 multifunctionality, Ecology, 94, 2275-2287, 10.1890/12-1716.1, 2013.
592 Virtanen, E. A., Viitasalo, M., Lappalainen, J., and Moilanen, A.: Evaluation, Gap Analysis, and Potential Expansion of the Finnish
593 Marine Protected Area Network, Frontiers in Marine Science, 5, 10.3389/fmars.2018.00402, 2018.
594 Virtasalo, J. J., Kohonen, T., Vuorinen, I., and Huttula, T.: Sea bottom anoxia in the Archipelago Sea, northern Baltic Sea—Implications
595 for phosphorus remineralization at the sediment surface, Marine Geology, 224, 103-122, <https://doi.org/10.1016/j.margeo.2005.07.010>,
596 2005.
597