

Response to Referee #1:

Interactive comment on “Identifying areas prone to coastal hypoxia – the role of topography” by Elina A. Virtanen et al.

We wish to thank Anonymous Referee #1 for insightful ideas and comments, they improved the manuscript substantially. Our comments marked as black, Referee #1's as grey.

General comments

This study presents a GIS analysis of the ability of selected geomorphological metrics to predict the occurrence of seafloor hypoxia in the coastal sea areas of Finland and Stockholm Archipelago in the northern Baltic Sea. The selection of geomorphological metrics is well justified, and the predictive performance of the metrics is evaluated against subsets of national water quality monitoring data from 808 sites. The selected metrics have been described and published elsewhere, but used in this study in a combination that is itself novel. The key results of the analysis are that Depth-Attenuated Wave Exposure (SWM(d)) is the most important metric, and that all the metrics combined predict hypoxia correctly in >80% of the cases. The main conclusion that sluggish water exchange increases the development of hypoxia in patchy archipelago areas is not particularly new as correctly pointed out by the authors, but this study nevertheless contributes to the understanding of mechanisms driving hypoxia, and the significance of topography in particular. In general, the manuscript is well written and illustrated, and the topic is suitable for Biogeosciences. However, as usual, there is also room for improvement. Overall, I recommend this study for publication after my comments below have been adequately addressed.

This manuscript is focused on topography, while the other known drivers of hypoxia are less considered, including the other physical drivers. The coastal areas studied in the manuscript generally lie above the Baltic Sea halocline, where the seasonal development of thermocline is an important feature with respect to reduced water exchange and hypoxia. The seasonality of hypoxia is mentioned in the manuscript, but it needs to be emphasized more that the implied coastal hypoxia at large is seasonal by nature, and different from the more permanent hypoxia in areas below halocline. The authors may even consider including the word “seasonal” in the title.

Good point. We recognize that hypoxia is in many shallow areas above halocline seasonal. We have added text about this in Discussion (L286-291):

“It is notable that in areas above the permanent halocline, hypoxia is in many areas seasonal, and develops after the building of thermocline in late summer (Conley et al., 2011). It is therefore probable that many of the areas we recognized as hypoxic may well be oxygenated during winter and spring. This does not however reduce the severity of the phenomenon. Even hypoxic event of short duration, e.g. few days, will reduce ecosystem resistance to further hypoxic perturbation and affect the overall ecosystem functioning (Villnas et al., 2013).”

The authors further need to discuss the potential effects thermocline has on hypoxia in the shallow sea areas.

We also added a short notion of warming up and thermocline in Discussion, where potential effects of climate change are discussed (L294-296):

“Shallow areas also suffer from eutrophication and rising temperatures due to changing climate, and are most probably the ones that are particularly susceptible to hypoxia in the future (Breitburg et al., 2018). This suggests that seasonal hypoxia may become a recurrent phenomenon in shallow areas above the thermocline in late summer.”

The authors may even consider exploring, whether the typical depth of thermocline could be included in the analysis in order to improve the predictive ability of metrics.

The suggestion that the depth of thermocline could be included in the analysis is an interesting idea, and could be explored in further development of the model. However, our modelling approach concentrates on the role topography has, and how much of the hypoxia occurrence and variability can be explained by topographical parameters alone. It can well be that adding information about the thermocline depth could improve the model performance (although already decent: ~80 % of the hypoxia occurrences explained

against independent data). Moreover, thermocline depth can be highly variable between 1–10m, and data for defining that for prediction is not so easy to obtain. We have however included depth as an explanatory factor in our model. The analysis showed that depth was the second most important factor in explaining the variation in hypoxia (after depth-attenuated exposure; cf. Fig. 4). We therefore do not consider it possible to add thermocline *per se* in the analysis for now with the data limitations.

We have however clarified the interaction of depth with sheltered areas in Results (L233-235):

“Noteworthy is also that depth was not the most important driver of hypoxia in coastal areas. This suggests that hypoxia is not directly dependent on depth, but that depressions that are especially steep and isolated are more sheltered and become more easily hypoxic than smoother depressions.”

An important conclusion is that half of the monitoring sites in Stockholm Archipelago and one third of sites in southern Finland experienced severe hypoxia. It should be discussed whether this is an artefact resulting from the locations of monitoring sites or a true difference between these two sea areas.

A good point. We do not find any major differences in sampling strategy or methods, and do not see any reason to doubt the validity of this result. Stockholm Archipelago is characterised by a particularly steep topography, with narrow channels, where wave forcing is extremely low, making it thus very susceptible for hypoxia to develop (and confirmed by the model). This has been now further explained in text (L333-342):

“There were spatial differences in the frequency and severity of hypoxia that can be explained by topographical characteristics of the areas, external loading, and interaction with the adjacent deeper basins. For instance, in the Stockholm Archipelago severe hypoxia covered the largest percentage of seascapes of all study areas. Stockholm Archipelago is part of a joint valley landscape with deep, steep areas also in the inner parts where wave forcing is exceptionally low, making it very susceptible for hypoxia, which was also confirmed by the model. In Finland, the inner archipelago is mostly shallow, with steep but wider channels occurring only in the Archipelago Sea. Geographically, hypoxia was in Finland most prominent in the Archipelago Sea and the Gulf of Finland, where the inner archipelago is isolated from the open sea, and the complex topography results in overall poor water exchange in the existing depressions.”

We also added in the end of the same paragraph text on the possible role of external nutrient loading (L342-345):

“Both Stockholm Archipelago and the Archipelago Sea suffer from external loading from the associated watersheds, and internal loading from sediments, which probably contributes to the poor oxygen status of these areas (Walve et al., 2018; Puttonen et al., 2014). Biogeochemical factors were however not accounted for by our analysis, and cannot be used in explaining the observed spatial differences.”

The authors conclude (e.g. page 15) that hypoxia most often occurs in shallow to moderate water depths, in accordance with previous studies. However, looking at Figure 7, hypoxia seems to be developed in deep channels, which in the previous studies have been concluded to be well ventilated. This discrepancy needs to be discussed further.

Actually, the elongated, narrow channel in Fig. 7 is not very deep (mean depth 20 m), and it is not very well ventilated because it is not connected to open areas. In contrast, the channels in the Archipelago Sea are much wider and deeper, and well connected to the open sea, and thus experiencing higher water mixing. The reviewer however raises an important point, and we thank the referee for raising this issue. We emphasize that our study cannot fully take into account hydrographic factors, such as strong currents in deep, elongated channels (such as the ones crisscrossing the Archipelago Sea). We merely aim to indicate areas that are topographically susceptible to hypoxia. For instance, the deep, narrow channels of the Stockholm Archipelago are more susceptible for hypoxia formation than wider, long channels of the Archipelago Sea with connectivity to adjacent open sea areas. We have now emphasized this point even further throughout the manuscript:

In Abstract (L13-17, L23-26):

“It is well known that the enclosed nature of seafloors and reduced water mixing facilitates hypoxia formation, but the degree to which topography contributes to hypoxia formation, and small-scale variability of coastal hypoxia, has not

been previously quantified. We developed simple proxies of seafloor heterogeneity and modelled oxygen deficiency in complex coastal areas in the northern Baltic Sea. According to our models, topographical parameters alone explained ~80 % of hypoxia occurrences.”

“...Deviations from this “topographical background” are probably caused by strong currents or by high nutrient loading, thus improving or worsening oxygen status, respectively. In some areas, connectivity with adjacent deeper basins may also influence coastal oxygen dynamics.”

In Introduction (L67-70, L72-74):

“It is widely recognized that the semi-enclosed nature of the seafloors, and associated limited water exchange is a significant factor in the formation of hypoxia in coastal waters (Rabalais et al., 2010; Conley et al., 2011; Diaz and Rosenberg, 1995a; Virtasalo et al., 2005). However, to determine the degree to which seascape structure restricting water movement contributes to hypoxia formation has not been quantified.”

“... We tested how large fraction of hypoxia occurrences could be explained only by structural complexity of seascapes, without knowledge on hydrographical or biogeochemical parameters.”

In Discussion (L320-324):

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

Terminology used in the manuscript is partly confusing, and the authors may want to seek help from a colleague with background in seafloor geology/sedimentology in particular. The term “sinkhole” is widely used in the manuscript, although collapse structures are unlikely in the study area with predominantly siliciclastic sediments.

We acknowledge that “sinkhole” is a confusing term. We’ve changed that to “local depressions” were appropriate.

Specific comments

Abstract, line 12. Add “and vertical mixing” between “water circulation” and “that can”.

Added “vertical mixing”.

Abstract, line 17. Replace “sinkholes” by “local depressions”.

Sinkholes replaced with “local depressions”

Abstract, line 17. Add “seasonal” between “development of” and “hypoxia”.

Abstract reformatted thoroughly, and we speak now of hypoxia during late summer (August-September) (L10-26):

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

Page 3, line 21. Add “Sea” between “Baltic” and “coastal”. Here and elsewhere in the manuscript, note that the term Baltic when used alone refers to the Baltic States.

“Sea” added.

Page 4, line 1. Replace “archipelago” with “islands”. There is no archipelago really in GoB (except Vaasa).

Changed to “islands”

Page 4, lines 3-4. Specify the type of soft sediments in shallow areas. Organic-rich mud?

Sentence reformatted to (L96-97):

“Substrate in both areas varies from organic-rich soft sediments in sheltered locations to hard clay, till and bedrock in exposed areas.”

Page 4, line 4. Replace “rocky” with “hard clay, till and bedrock”. Rocky is an oversimplification.

Changed to “hard clay, till and bedrock”

Page 10, line 10. Replace “Contrary to” with “In contrast in”.

Replaced with “In contrast in”.

Page 11, line 7, and elsewhere in the manuscript. The use of word “sink” is very confusing in this context and should be replaced by a more correct term.

Sinkholes replaced with “local depressions” throughout the manuscript.

Page 14, line 6. The number “20 %” probably does not make much sense here, because the more sites one would sample in the Baltic Sea, the higher would be the number of hypoxic sites. It is probably sufficient to state that hypoxia is known to be widespread in the Baltic Sea.

Reformatted to (L279-280):

“Earlier studies have reported coastal hypoxia to be a global phenomenon (Diaz and Rosenberg, 2008; Conley et al., 2011), and is known to be widespread in the Baltic Sea (Conley et al., 2011).”

Page 16, line 10. Replace “canyons” with “channels”.

Canyons replaced with channels.

Page 16, line 16, and elsewhere in the manuscript. Replace “ledge” with “tongue”.

Replaced ledge with tongue.

Page 16, line 17-19. What would be the contribution of River Neva to the hydrodynamics and hypoxia in the EGoF?

Interesting point. Reformatted to (L346-357):

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

Page 16, lines 22-26. In case the authors insist that the lack coastal hypoxia in GoB is due to the lack of halocline and permanent hypoxia in central deep areas, the driving mechanisms need to be explained. Probably it is safer to just state that there is less hypoxia in GoB coastal areas because of less islands and stronger wave forcing.

We have clarified this (L358-362):

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

Page 16, lines 27-30. If valid, this conclusion needs to be better substantiated. The authors write many times in the manuscript that the deepest parts (channels) in archipelago areas are usually well oxygenated. How does that oxie deep water then transform to shallow water hypoxia?

The deep elongated, but wide channels are well-ventilated in the Archipelago Sea due to the connectivity to adjacent open areas, and potentially due to strong currents, as opposite to the narrow channels of Stockholm Archipelago, which occur in the inner parts of the archipelago. When we refer to “the deeper basins” we refer to the Baltic Proper and deep parts of the Gulf of Finland. This is now clarified in the text (L333-342):

“There were spatial differences in the frequency and severity of hypoxia that can be explained by topographical characteristics of the areas, external loading, and interaction with the adjacent deeper basins. For instance, in the Stockholm Archipelago severe hypoxia covered the largest percentage of seascapes of all study areas. Stockholm Archipelago is part of a joint valley landscape with deep, steep areas also in the inner parts where wave forcing is exceptionally low, and disconnected from the open sea, making it very susceptible for hypoxia, which was also confirmed by the model. In Finland, the inner archipelago is mostly shallow, with steep but wider channels occurring only in the Archipelago Sea. These elongated channels are connected to adjacent open sea areas, and thus well-ventilated, as opposite to the narrow channels of Stockholm Archipelago. Geographically, hypoxia was in Finland most prominent in the Archipelago Sea and the Gulf of Finland, where the inner archipelago is isolated from the open sea, and the complex topography results in overall poor water exchange in the existing depressions.”

And (L364-366):

“... While we suggest that coastal hypoxia can be formed entirely based on local morphology and local biogeochemical processes, the relatively low occurrence of hypoxia in the Gulf of Bothnia, and differences in frequency of hypoxia in different parts of the Gulf of Finland, both highlight the interaction of these coastal areas with the Baltic Proper.”

The Conclusions section as it is currently written is more about the implications of findings than the actual conclusions of the study.

Noted. More findings added to the conclusions (L391-407):

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

The electronic supplement to this manuscript only has one figure. This figure is quite informative, and the authors may wish to consider including it as a figure in the actual paper.

We only refer to this figure when speaking of BPI differences in GoB and other areas, and as such we would prefer to keep it in the Supplementary material.

That ends my referee comments.

Response to Referee#2: Interactive comment on “Identifying areas prone to coastal hypoxia – the role of topography” by Elina A. Virtanen et al.

Anonymous Referee #2

We thank Referee #2 for insightful comments on our manuscript that improved it substantially. We have now taken into account all the comments received and edited text accordingly. Referee #2 comments marked as grey and our responses as black.

Thank you for inviting me to review “Identifying areas prone to coastal hypoxia -the role of topography” by Virtanen et al, submitted to Biogeosciences. In general, this is a very well written, well-structured and interesting study where the authors use new approaches to quantify the impact of topography on bottom-water [O₂]. I strongly recommend it to be published in Biogeosciences and I hope the approaches presented will be widely used for also other geographical areas. My major objection is the following statements in the beginning of the manuscripts: “We hypothesized that the enclosed nature of seafloors facilitates hypoxia formation.” “We discovered that topographically sheltered seafloors and sinkholes with stagnant water are prone to the development of hypoxia” It is text book knowledge that topography (i.e. sills, deep basins, restricted morphology, skerries etc.) has a large impact on residence time and water circulation, hence also on dissolved [O₂] in the bottom water. I honestly don’t think this was new knowledge for the authors and hence the main driver of the study. However, and here is where the study becomes more interesting, to determine the degree to which a restricted setting affects the [O₂] (i.e. the quantification) and then model that effect. That is interesting and new. I would like to see the author rephrasing their aim and their hypothesis.

We have now edited the aims and hypothesis of our manuscript, and changed texts in Abstract and in Introduction.

In Abstract (L13-14):

“It is well known that the enclosed nature of seafloors and reduced water mixing facilitates hypoxia formation, but the degree to which topography contributes to hypoxia formation, and small-scale variability of coastal hypoxia, has not been previously quantified.”

And (L16-17):

“We developed simple proxies of seafloor heterogeneity and modelled oxygen deficiency in complex coastal areas in the northern Baltic Sea. According to our models, topographical parameters alone explained ~80 % of hypoxia occurrences. The models also revealed that less than 25 % of the studied seascapes were prone to hypoxia during late summer (August-September).”

In Introduction (L67-70):

“...It is widely recognized that the semi-enclosed nature of the seafloors, and associated limited water exchange is a significant factor in the formation of hypoxia in coastal waters (Rabalais et al., 2010;Conley et al., 2011;Diaz and Rosenberg, 1995a;Virtasalo et al., 2005). However, to determine the degree to which seascape structure restricting water movement, contributes to hypoxia formation has not been quantified. ...”

And (L72-74):

“We tested how large fraction of hypoxia occurrences could be explained only by structural complexity of seascapes, without knowledge on hydrographical or biogeochemical parameters.”

Minor details: It would help the reader to use abbreviations as sparingly as possible and to remind us what the geographical abbreviations stand for in the beginning of the result/discussion section, and preferable use the names of the regions more in the text.

Abbreviations replaced with place names accordingly in the text to help the reader, both in the results section and in the discussion.

I find it slightly difficult to accept the term normoxic and that is defined as > 4.6 mg/l. What is the “normal”/norm for a deep-water in a coastal setting, should we expect fully oxygenated conditions, should that our reference value? It is important to think about in these type of studies.

We agree that “normal oxygen conditions” are difficult to define in an environment like the Baltic Sea.

We have deleted the term “normoxic” and edited text accordingly:

“...to discriminate a hypoxic site from a **normoxic** one” changed to:

“...to discriminate a hypoxic site from **an oxic one**”

“...AS, EGoF and SA were **normoxic**...” changed to:

“...AS, EGoF and SA were **not hypoxic**...”

“...channels are mostly **normoxic**...” changed to:

“...channels are not **usually hypoxic**...”

“...many local depressions are more often hypoxic than **normoxic**...” changed to:

“...many local depressions are **often hypoxic**...”

The threshold for hypoxia admittedly varies in literature, but here we define it as $O_2 > 4.6$ mg/l. This limit is mentioned Section 2.2. Hypoxia data (L113-116):

“Here we define hypoxia based on two ecologically meaningful limits: moderately hypoxic < 4.6 mg L⁻¹ O_2 – as this has been estimated to be a minimum safe limit for species survival, behavior and functioning in benthic communities (Norkko et al., 2015)”

Dead zones is a popular science word which isn't really accurate, dead zones are devoid of higher life but not of all organisms. It should be used within “”, if used at all in this type of publications.

Dead zones deleted from the text, and now we talk about anoxic areas and anoxic zoned devoid of higher life throughout the text.

The conclusions are very short, general and undersell the study. I would suggest the authors to be more detailed and really highlight the specific conclusions from the study. One of them is: topographically prone areas to deoxygenation represent less than 25 % of the investigated seascapes.

Conclusions (and Abstract) are now thoroughly edited to highlight the key findings of the study (L394-402):

“We found that a surprisingly large fraction (~80 %) of hypoxia occurrences could be explained by topographical parameters alone. Modelling results also suggested that less than 25 % of the studied seascapes were prone to hypoxia during late summer. Large variation existed in the spatial and temporal patterns of hypoxia, however, with certain areas being prone to occasional severe hypoxia ($O_2 < 2$ mg/L), while others were more susceptible to recurrent moderate hypoxia ($O_2 < 4.6$ mg/L). Sheltered, topographically heterogeneous areas with limited water exchange were susceptible for developing hypoxia, in contrast to less sheltered areas with high wave forcing. In some areas oxygen conditions were either better or worse than predicted by the model. We assume that these deviations from the “topographical background” were caused by processes not accounted for by the model, such as hydrographical processes, e.g. strong currents causing improved mixing, or by high external or internal

nutrient loading, inducing high local oxygen consumption. We conclude that formation of coastal hypoxia is probably primarily dictated by local processes, and can be quite accurately projected using simple topographical parameters, but that interaction with the associated watershed and the adjacent deeper basins of the Baltic Sea can also influence local oxygen dynamics in many areas..”

The link to SMHI doesn't work (paragraph 2.2).

Hyperlink changed to a link that works: <https://www.smhi.se/data/oceanografi/havsmiljodata>

The references are not consistently formatted.

References checked and reformatted (EndNote problems solved with alphabetical ordering of authors).

I can't evaluate the modelling approaches, as that is far from my field, and I hope a second reviewer can do that.

I'm looking forward to see the study published.

Identifying areas prone to coastal hypoxia - the role of topography

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Abstract. Hypoxia is an increasing problem in marine ecosystems around the world, ~~and recent projections indicate that anoxic “dead zones” will be spreading in the forthcoming decades.~~ While major advances have been made in our understanding of the drivers of hypoxia, ~~it fundamentally hinges on patterns of water circulation that can be difficult to resolve~~ challenges remain in describing oxygen dynamics in coastal regions. The complexity of many coastal areas and lack of detailed *in situ* data has hindered the development of models describing oxygen dynamics at a sufficient spatial resolution for efficient management actions to take place. ~~We hypothesized~~ It is well known that the enclosed nature of seafloors and reduced water mixing facilitates hypoxia formation, but the degree to which topography contributes to hypoxia formation, and small-scale variability of coastal hypoxia, has not been previously quantified. We developed simple proxies of seafloor heterogeneity and modelled oxygen deficiency in complex coastal areas in the northern Baltic Sea. ~~We discovered that topographically sheltered seafloors and sinkholes with stagnant water are prone to the development~~ According to our models, topographical parameters alone explained ~80 % of hypoxia. Approximately half occurrences. The models also revealed that less than 25 % of the monitoring sites studied seascapes were prone to hypoxia during late summer (August-September). However, large variation existed in Stockholm Archipelago the spatial and one third temporal patterns of sites in southern Finland experienced hypoxia, as certain areas were prone to occasional severe hypoxia ($O_2 \leq 2 \text{ mg L}^{-1}$). Based only on topography, area potentially affected), while others were more susceptible to recurrent moderate hypoxia ($O_2 < 4.6 \text{ mg L}^{-1}$). Areas identified as problematic in our study were characterized by hypoxia is smaller than anticipated. low exposure to wave forcing, by high topographical shelter from surrounding areas, and by isolation from the open sea, all contributing to longer water residence times in seabed depressions. Deviations from this “topographical background” are probably caused by strong currents or by high nutrient loading, thus improving or worsening oxygen status, respectively. In some areas, connectivity with adjacent deeper basins may also influence coastal oxygen dynamics. Developed models could boost the performance of numerical biogeochemical models, aid developing nutrient abatement measures, and pinpoint areas where management actions are most urgently needed.

1 Introduction

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

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

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

Projecting patterns and spatial and temporal variability of hypoxia is necessary for developing effective management actions. Thus three-dimensional coupled hydrodynamic-biogeochemical models have been created for several sea areas around the world, such as Gulf of Mexico (~~Fennel et al., 2011~~; ~~Fennel et al., 2016~~); (~~Fennel et al., 2011~~; ~~Fennel et al., 2016~~), Chesapeake Bay (~~Scully, 2013~~; ~~Testa et al., 2014~~; ~~Scully, 2016~~); (~~Scully, 2013~~; ~~Testa et al., 2014~~; ~~Scully, 2016~~), the North Sea (~~Hordoir, 2018~~); (~~Hordoir, 2018~~) and the Baltic Sea (Eilola et al., 2009; ~~Eilola et al., 2011~~; ~~Meier et al., 2011b~~; ~~Meier et al., 2011a~~; ~~Meier et al., 2012a~~; ~~Meier et al., 2012b~~); (~~Meier et al., 2012a~~; ~~Meier et al., 2012b~~). These models simulate various oceanographic, biogeochemical and biological processes using atmospheric and climatic forcing and information on nutrient loading from rivers. While such models are useful for studying processes at the scale of kilometers, and aid in defining hypoxia abatement at the basin-scale, their horizontal resolution is too coarse (often 1–2 nautical miles) for accurately describing processes in coastal areas. Lack of detailed data on water depth, currents, nutrient loads, stratification and local distribution of freshwater discharges (~~Breitburg et al., 2018~~); (~~Breitburg et al., 2018~~) (not to mention computational limitations) usually prevent the application of biogeochemical models developed to large geographical areas at finer horizontal resolutions (<100 m).

Understanding spatial variability of hypoxia in topographically complex coastal environments has therefore been impeded by the lack of useful methods and systematic, good-quality data (Diaz & Rosenberg, 2008; ~~Rabalais et al., 2010~~; ~~Stramma et al., 2012~~); (~~Rabalais et al., 2010~~; ~~Stramma et al., 2012~~). Finding alternative ways to pinpoint areas prone to coastal hypoxia could facilitate management and determining of efficient local eutrophication abatement measures. ~~Several studies have suggested~~

~~It is widely recognized~~ that the semi-enclosed nature of the seafloors, and associated limited water exchange, is a significant factor in the formation of hypoxia in coastal waters (Diaz & Rosenberg, 1995a; ~~Virtasalo et al., 2005~~; ~~Rabalais et al., 2010~~; ~~Conley et al., 2011~~); (~~Virtasalo et al., 2005~~; ~~Rabalais et al., 2010~~; ~~Conley et al., 2011~~); ~~but. However, to our knowledge this hypothesis has not been tested or quantified.~~

~~Here, we estimate how topography, i.e. determine the degree to which~~ seascape structure, ~~restricting water movement~~ contributes to ~~the hypoxia~~ formation of hypoxia. ~~has not been quantified.~~ Analytical and theoretical frameworks developed specifically for terrestrial environments, such as landscape heterogeneity or patchiness, are analogous in marine environments, and are equally useful for evaluating links between ecological functions and spatial patterns in marine context. We ~~hypothesized that tested how large fraction of hypoxia occurrences could be explained only by~~ structural complexity of seascapes ~~facilitates the formation of hypoxia, without knowledge on hydrographical or biogeochemical parameters.~~ We adopted techniques and metrics from landscape ecology and

transferred them to marine environment, and (1) examined if spatial patterns in seascapes can explain the distribution of hypoxia, (2) defined the relative contribution of seascape structure to hypoxia formation and (3) estimated the potential ranges of hypoxic seafloors in coastal areas. To achieve this, we concentrated on extremely heterogeneous and complex archipelago areas in the northern Baltic Sea, where coastal hypoxia is a common and an increasing problem ([Conley et al., 2011](#); [Conley et al., 2011](#); Caballero-Alfonso et al., 2015).

2 Data and methods

2.1 Study area

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

In order to evaluate differences in oxygen deficiency between coastal areas, the study area was divided into five regions as defined by the EU Water Framework Directive (2000/60/EC) ([WFD, 2000](#)) ([WFD, 2000](#)): the Archipelago Sea (AS), the Eastern Gulf of Finland (EGoF), the Gulf of Bothnia (GoB), Stockholm Archipelago (SA) and the western Gulf of Finland (WGoF) (Figure 1). Small skerries and sheltered bays characterize AS, EGoF and WGoF, whereas narrower band of [archipelagoislands](#) forms relatively exposed shores in GoB. Deep, elongated channels of bedrock fractures can reach depths of over 100 m in AS, similarly to SA where narrow, deep valleys separate mosaics of islands and reefs. Substrate in both areas varies from [organic-rich](#) soft [unconsolidated](#) sediments in sheltered locations to [rocky substrates](#) [hard clay, till and bedrock](#) in exposed areas. At greater depths, soft sediments are common due to limited water movement. As a whole, the study area with rich topographic heterogeneity forms one of the most diverse seabed areas in the world ([Kaskela et al., 2012](#)) ([Kaskela et al., 2012](#)). In many areas hypoxia is a result of strong water stratification, slow water exchange and complex seabed topography, creating pockets of stagnant water ([Conley et al., 2011](#); [Valanko et al., 2015](#); [Jokinen et al., 2018](#)) ([Conley et al., 2011](#); [Valanko et al., 2015](#); [Jokinen et al., 2018](#)). Thus, the area is ideal for testing hypotheses of topographical controls for hypoxia formation.

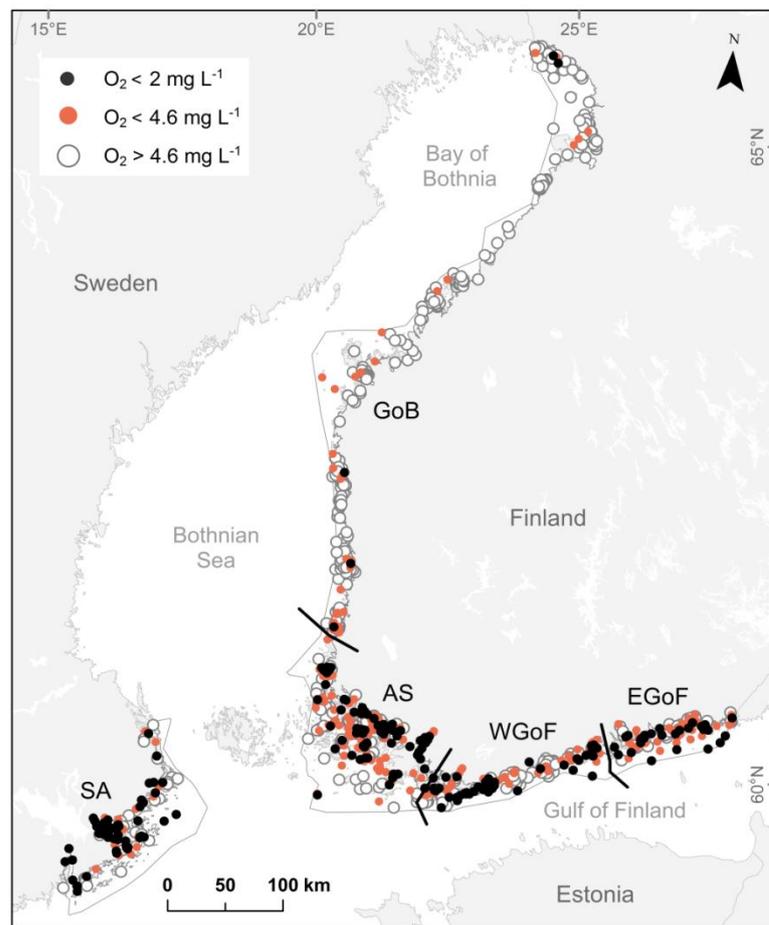


Figure 1. Study areas in Finland: AS – Archipelago Sea, WGoF – Western Gulf of Finland, EGoF – Eastern Gulf of Finland, GoB – Gulf of Bothnia, and Sweden: SA – Stockholm Archipelago. Orange dots represent sites of moderately hypoxic ($O_2 \leq 4.6 \text{ mg L}^{-1}$) black dots severely hypoxic ($O_2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

2.2 Hypoxia data

Bottom-water hypoxia is the main factor structuring benthic communities in the Baltic Sea (Villnas *et al.*, 2012; Norkko *et al.*, 2015)(Villnas *et al.*, 2012;Norkko *et al.*, 2015). Two mg L^{-1} of O_2 is usually considered a threshold where coastal organisms start to show symptoms of the lack of oxygen, and this limit has been commonly used in various global reviews (Diaz & Rosenberg, 1995b, 2008). Some studies have however concluded that 2 mg L^{-1} is below the empirical sublethal and lethal oxygen limit for many species (Vaquer-Sunyer & Duarte, 2008; Conley *et al.*, 2009a)(Vaquer-Sunyer and Duarte, 2008;Conley *et al.*, 2009b). Here we define hypoxia based on two ecologically meaningful limits: moderately hypoxic $< 4.6 \text{ mg L}^{-1} O_2$ – as this has been estimated to be a minimum safe limit for species survival, behavior and functioning in benthic communities (Norkko *et al.*, 2015)(Norkko *et al.*, 2015) – and severely hypoxic $< 2 \text{ mg L}^{-1} O_2$, which describes dead-zones for where larger marine organisms suffer from severe mortality (Vaquer-Sunyer & Duarte, 2008)(Vaquer-Sunyer and Duarte, 2008). As no reference values exist for severity of hypoxia to marine organisms based on the frequency of hypoxic events (Norkko *et al.*, 2012; Villnas *et al.*, 2012; Norkko *et al.*, 2015); Villnas *et al.*, 2012;Norkko *et al.*, 2015), we here define a site to be prone to hypoxic events, i.e. occasionally hypoxic, if it experienced hypoxia ($O_2 < 2 \text{ mg L}^{-1}$ and $< 4.6 \text{ mg L}^{-1}$) at least once during the study period. If hypoxia was recorded $\geq 20\%$ of the visits, it was categorized as frequently hypoxic. We consider this to be ecologically relevant, as species develop symptoms already from short exposures to hypoxia (Villnas *et al.*, 2012; Norkko *et al.*, 2015)(Villnas *et al.*, 2012;Norkko *et al.*, 2015). This is also justified, as our oxygen data is from $\sim 1 \text{ m}$ above the seafloor, suggesting that the actual oxygen concentrations at sediment where benthic species live are probably lower.

Data from hypoxia oxygen profiles were collated from the national monitoring environmental data portals Hertta (http://www.syke.fi/en-US/Open_information) and SHARK (<https://www.smhi.se/klimatdata/oceanografi/havsmiljodata/marinamiljoovervakningsdata>); (<https://www.smhi.se/d ata/oceanografi/havsmiljodata>). Data was available from 808 monitoring sites. Only months of August and September 2000–2016 were considered, as hypoxia is usually a seasonal phenomenon occurring in late summer when water temperatures are warmest (Conley *et al.*, 2014)(Conley *et al.*, 2011).

2.3 Predictors

For modelling hypoxia occurrences, we developed five geomorphological metrics: (1) Bathymetric Position Indices (BPI) with varying search radii, (2) Depth-Attenuated Wave Exposure (SWM(d)), (3) Topographical Shelter Index (TSI), (4) Arc-Chord Rugosity (ACR) and (5) Vector Ruggedness Measure (VRM). BPI is a marine modification of the terrestrial version Topographic Position Index (TPI), originally developed for terrestrial watersheds (Weiss, 2001)(Weiss, 2001). BPI is a measure of a bathymetric surface to be higher (positive values) or lower (negative values) than the overall seascape. BPI values close to zero are either flat areas or areas with constant slope. Here, BPIs represent topographical depressions, sinkholes and crests at scales of 0.1, 0.3, 0.5, 0.8, and 2 km calculated with Benthic Terrain Modeler (v3.0)(Walbridge *et al.*, 2018)(Walbridge *et al.*, 2018). SWM(d) estimates dominant wave frequency at a given location with the decay of wave exposure with depth, and takes into account diffraction and refraction of waves around islands (Bekkby *et al.*, 2008)(Bekkby *et al.*, 2008). SWM(d) characterizes areas where water movement is slower, i.e. where water resides longer. In terrestrial realms, landform influence on windthrow patterns, i.e. exposure to winds, have been noted in several studies, e.g. (Kramer, 2001) and (Ashcroft *et al.*, 2008)Kramer (2001) and Ashcroft *et al.* (2008). Here, we introduce an analogous version of “windthrown-prone” areas to the marine realm, i.e. a “wave-prone” metric: Topographical Shelter Index (TSI), which differentiates wave directions and takes into account the sheltering effects of islands (i.e. exposure above sea-level). Identification of “wave-prone” areas was calculated for the azimuths multiple of 15 (0°–345°), and for altitudes (corresponding to the angle of light source) ranging from 0.125° to 81°. For each altitude the produced “wave-prone areas” were combined to an index value for each grid cell. Surface roughness is a commonly used measure of topographical complexity in terrestrial studies, and has been used in marine realms as well (see e.g. (Dunn & Halpin, 2009) for modelling habitats of hard substrates and (Walker *et al.*, 2009)Dunn and Halpin (2009) for modelling habitats of hard substrates and Walker *et al.* (2009) for complexity of coral reef habitats). Here, we consider two approaches for estimating seascape rugosity; Arc-Chord Rugosity (ACR) and Vector Ruggedness Measure (VRM). ACR is a landscape metrics, which evaluates surface ruggedness using a ratio of contoured area (surface area) to the area of a plane of best fit, which is a function of the boundary data (Du Preez, 2015). VRM on the other hand, is a more conservative measure of surface roughness developed for wildlife habitat models, and is calculated using a moving 3×3 window where a unit vector orthogonal to the cell is decomposed using the three dimensional location of the cell center, the local slope and aspect. A resultant vector is divided by the number of cells in the moving window (SAPPINGTON *et al.*, 2007)(Sappington *et al.*, 2007). Both rugosity indices were used here to identify areas with complex marine geomorphology. Differences of predictor variables are illustrated in Fig. 2. We also included geographical study areas as predictors, in order to highlight the differences between WFD areas.

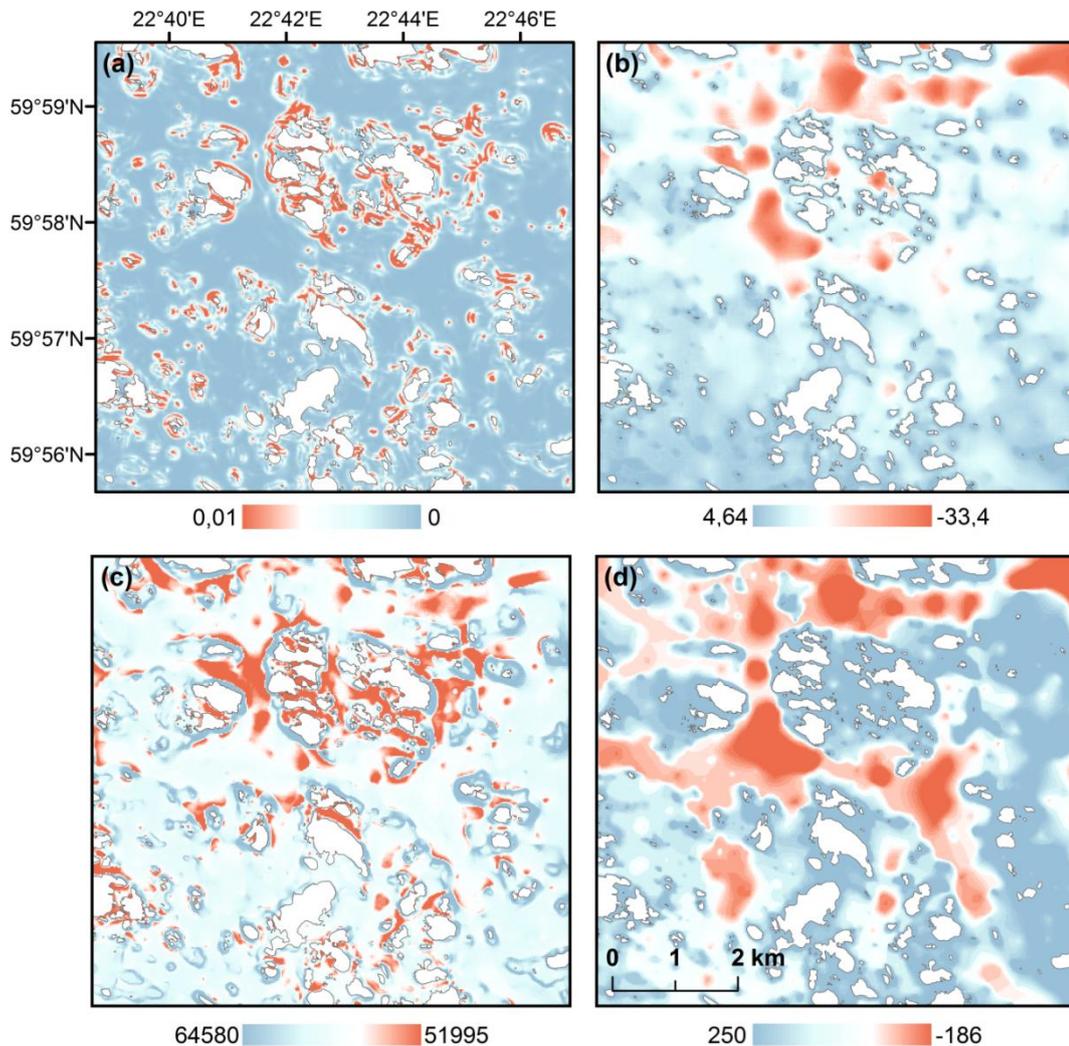


Figure 2. Predictor variables developed for hypoxia ensemble models: a) Vector Ruggedness Measure (VRM), b) Depth-Attenuated Wave Exposure (SWM(d)), c) Topographical Shelter Index (TSI) and (d) Bathymetric Position Index (BPI) with a search radius of 2 km. Red color represents rugged seafloors (VRM),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

2.4 Hypoxia models

Based on the ecologically meaningful limits of hypoxia (see section “Hypoxia data”), we built four separate oxygen models 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 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 Boosted Regression Models (GBM) and its extension Boosted Regression Trees (BRT), a method from statistical and machine learning traditions (De’ath & Fabricius, 2000; Hastie et al., 2001; Schapire, 2003; Schapire, 2003). BRT optimizes predictive performance through integrated stochastic gradient boosting (Natekin & Knoll, 2013), and forms the best model for prediction based on several models. Ideal model tuning parameters (learning rate, bag fraction, tree complexity) for our hypoxia models were based on optimizing the model performance, i.e. minimizing the prediction error. The learning rate was set to 0.001 to determine the contribution of each successive tree to the final model. We varied the number of decision rules controlling model interaction levels, i.e. tree complexities, between 3 and 56. We shuffled the hypoxia data randomly into ten subsets for training (70 %) and testing (30 %), while preserving the prevalence ratio of hypoxia occurrence. Hypoxia models were developed based on 10-fold cross-validation, and resulting final, best models leading to smallest predictive errors were chosen to predict the probability of detecting hypoxia across the study region at a resolution of 20 m. We believe such a high resolution is necessary due to the complexity of archipelagoes of Finland and Sweden. Model predictions for the whole seascape were repeated ten times with different models, model fits from data subsets (40 separate model predictions), to identify areas where models agree on the area to be potentially hypoxic. Model performances were estimated against the independent data (test data 30 %), not used in model fitting in order to evaluate the potential overfitting of the models. Analyses were performed in R 3.5.0. (R, 2018)(R, 2018) with R libraries ‘gbm’ (Greenwell et al., 2018)(Greenwell et al., 2018), ‘PresenceAbsence’ (Freeman & Moisen, 2008) and relevant functions from (Elith et al., 2008)(Freeman and Moisen, 2008) and relevant functions from Elith et al. (2008).

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

Estimation of model fits and predictive performances was based on the ability to discriminate a hypoxic site from a normoxic one, evaluated with Area Under the Curve (AUC) ([Jiménez-Valverde & Lobo, 2007](#))([Jiménez-Valverde and Lobo, 2007](#)) and simply with Percent Correctly Classified (PCC) ([Freeman & Moisen, 2008](#))([Freeman and Moisen, 2008](#)). AUC is a measure of detection accuracy of true positives (sensitivity) and true negatives (specificity), and AUC values above 0.9 indicate excellent, 0.7–0.9 good, and below 0.7 poor predictions. We transformed hypoxia probability predictions into binary classes of presence/absence, and estimated the relative area of potentially hypoxic due to topographical reasons. Although dichotomization of probability predictions flattens the information content, it facilitates the interpretation of results, and is needed for management purposes. Predicted range of hypoxia and the potential geographical extent enables the identification of problematic areas and facilitates management actions in a cost-effective way. There are various approaches for determining thresholds, which are based on the confusion matrix, i.e. how well the model captures true/false presences or true/false absences. Usually the threshold is defined to maximize the agreement between observed and predicted distributions. Widely used thresholds, such as 0.5, can be arbitrary unless the threshold equals prevalence of presences in the data, i.e. the frequency of occurrences (how many presences of the total dataset) ([Liu *et al.*, 2005](#))([Liu *et al.*, 2005](#)). Here, we define thresholds objectively based on an agreement between predicted and observed hypoxia prevalence. This approach underestimates areas potentially hypoxic (see section “Hypoxia areas”) and is expressed here as a conservative estimate.

3 RESULTS

3.1 Hypoxia in complex coastal archipelagos

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

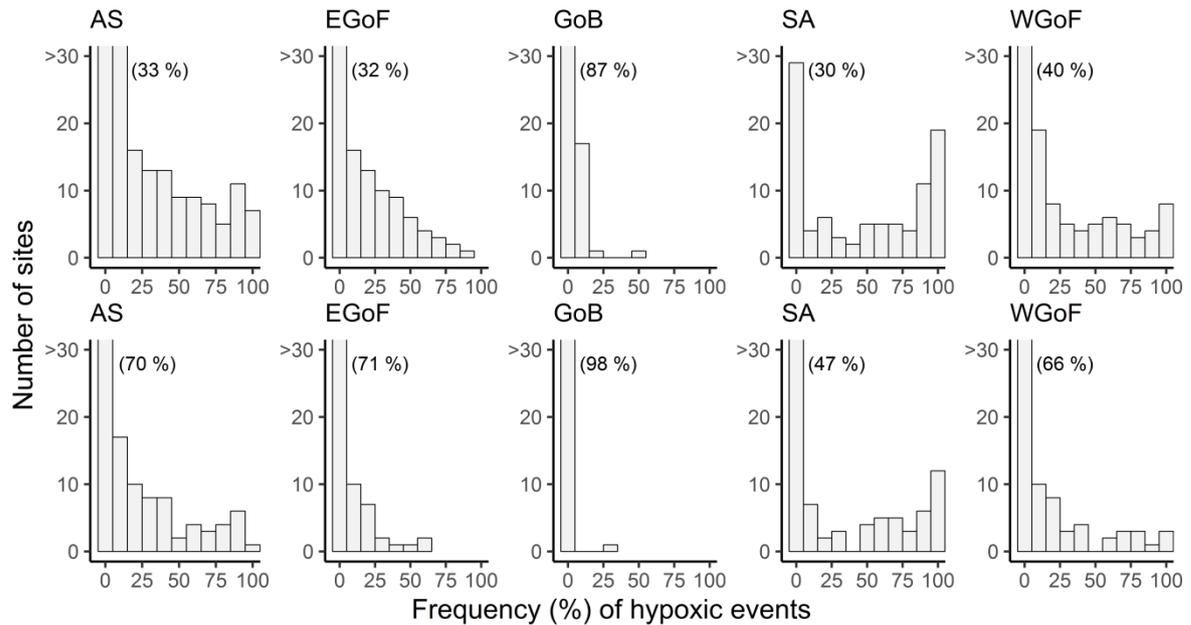


Figure 3. Frequencies of hypoxic events at coastal monitoring sites across Water Framework Directive areas (upper: Archipelago Sea (AS), Eastern Gulf of Finland (EGoF), Gulf of Bothnia (GoB), Stockholm Archipelago (SA) and Western Gulf of Finland (WGoF). Upper panels indicate $\text{O}_2 < 4.6 \text{ mg L}^{-1}$, lower panels $\text{O}_2 < 2 \text{ mg L}^{-1}$. Numbers in brackets indicate the 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.

3.2 Importance of predictors

Models developed on 566 sites, based on 10-fold cross-validation and ten repeated predictions, the most influential predictor (averaged across models) was SWM(d), with a mean contribution of 33 % (± 5 %) (Fig. 4). The contribution of SWM(d) was highest for frequent, severe hypoxia (FH₂) (41 \pm 3 %), whereas for occasional, moderate hypoxia (OH_{4.6}) the influence was markedly lower (25 \pm 5 %). This supports the hypothesis that in sheltered areas, where water movement is limited, severe oxygen deficiency is likely to develop. Noteworthy is also that depth was not the most important driver of hypoxia in coastal areas. This suggests that coastal hypoxia is not directly dependent on depth, but that depressions that are especially steep and isolated are more sheltered and become more easily hypoxic than smoother depressions.

Across models, BPIs identifying wider sinks (BPI2 and BPI0.8) were more influential than BPIs identifying smaller sinks (BPIs 0.1, 0.3 and 0.5), and terrain ruggedness measures, VRM and ACR, were more important for frequent severe hypoxia (FH₂) than for moderate hypoxia (FH_{4.6}). The relatively high contribution of topographical shelter (TSI 7 \pm 2 %) indicates that, in areas where there are higher islands, the basins between are prone to hypoxia formation.

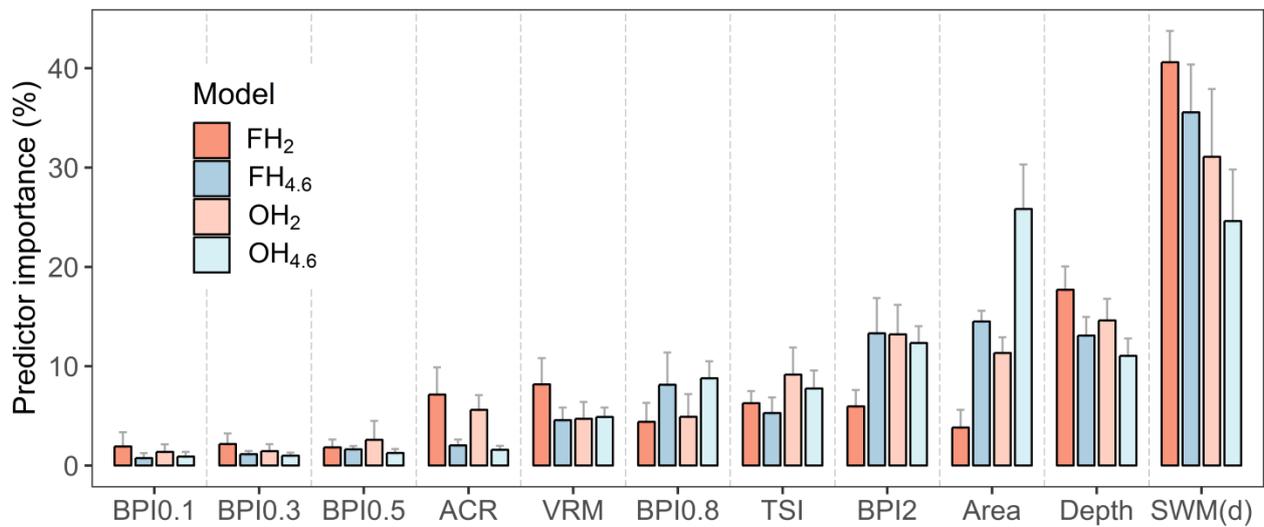


Figure 4. Importance of predictors based on ten prediction rounds. Predictors are colour-coded based on models. FH₂= frequent, severe hypoxia ($O_2 < 2 \text{ mg L}^{-1}$), FH_{4.6}= frequent, moderate hypoxia ($O_2 < 4.6 \text{ mg L}^{-1}$), OH₂= occasional, severe hypoxia ($O_2 < 2 \text{ mg L}^{-1}$),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

3.3 Model performance

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

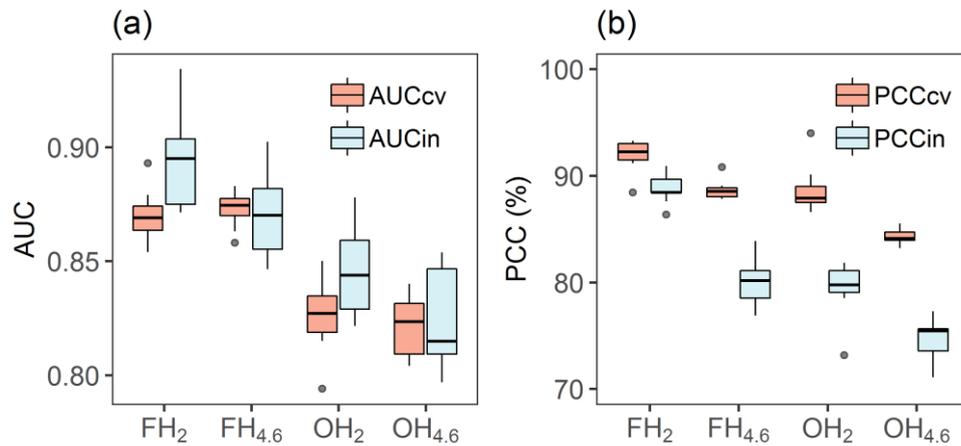


Figure 5. Model performances based on (a) Area Under the Curve values with 10-fold cross-validation (AUCcv), and against independent test data (30 % of sites) (AUCin), (b) Percent of Correctly Classified with 10-fold cross-validation (PCCcv) and against independent data (PCCin).

3.4 Hypoxic areas

Although hypoxia was commonly recorded in all WFD areas, except in ~~GoB~~the Gulf of Bothnia, the potential geographical extent of hypoxic seafloors shows rather different pattern. Based on models, topographically prone areas represent only a small part 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 ~~AS and SA~~the Archipelago Sea and Stockholm Archipelago, although representing only a small fraction of the total areas (on average 1.5 and 3.7 %, respectively). Problematic areas based on the models are ~~AS, SA and WGoF~~Archipelago Sea, Stockholm Archipelago and Western Gulf of Finland. Those areas seem to be topographically prone to oxygen deficiency. Moreover, around 10 % of areas in ~~EGoF~~Eastern Gulf of Finland are vulnerable to occasional moderate hypoxia, but less to severe hypoxia. Areas predicted as hypoxic in ~~GoB~~Gulf of Bothnia were less than $< 2 \%$, which supports our hypothesis of the facilitating role that topography potential has. ~~The prevalence of~~There are fewer depressions, i.e. potential sinks in ~~GoB~~ is non-existent (Supporting Fig. 1), and the seafloor is less topographically less complex than that in the other study areas.

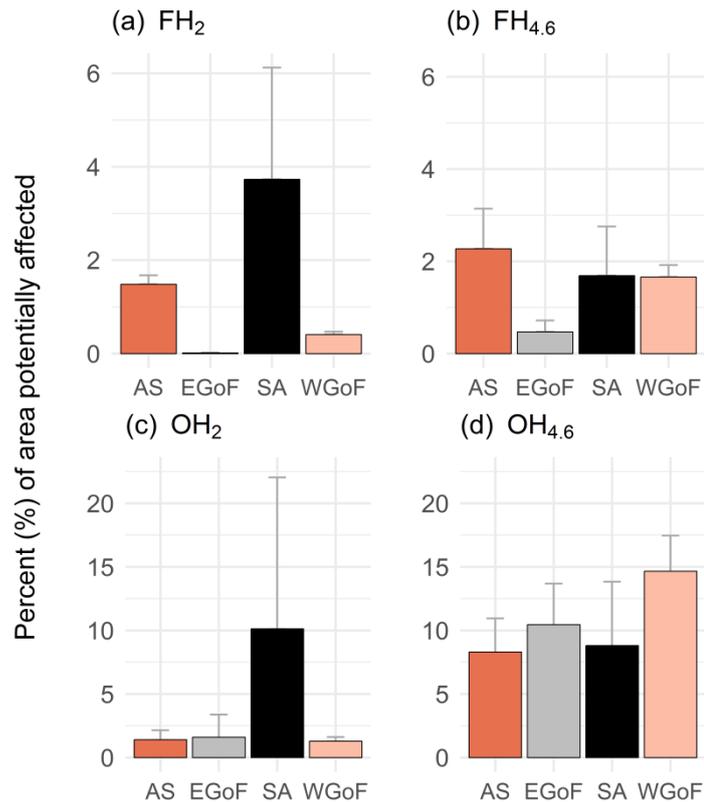


Figure 6. Percent (%) of areas potentially affected by hypoxia with varying frequencies (occasional and frequent) and hypoxia severities ($O_2 < 4.6 \text{ mg L}^{-1}$ and $O_2 < 2 \text{ mg L}^{-1}$). AS=Archipelago Sea, EGoF=Eastern Gulf of Finland, SA=Stockholm Archipelago and WGoF=Western Gulf of Finland. GoB not reported as areas potentially affected were below 2 % across all models.

4 DISCUSSION (1200)

Hypoxia has been increasing steadily since the 1960s, and ~~dead zones~~anoxic areas are seizing the seafloor, suffocating marine organisms on the way (~~Diaz & Rosenberg, 2008~~)(Diaz and Rosenberg, 2008; Breitburg et al., 2018). Understanding the factors affecting the severity and spatial extent of hypoxia is essential in order to estimate rates of deoxygenation and its consequences to the marine ecosystems (~~Breitburg et al., 2018~~)(Breitburg et al., 2018). Earlier studies have reported coastal hypoxia to ~~occur globally at more than 500 sites~~be a global phenomenon (Diaz ~~&~~and Rosenberg, 2008; ~~Conley et al., 2011~~)(Conley et al., 2011), ~~of which 20 % were reported from and is known to be widespread in~~ the Baltic Sea (~~Conley et al., 2011~~)(Conley et al., 2011). ~~Our results confirmed this, and showed that coastal hypoxia is perhaps a more common phenomenon than previously anticipated.~~ According to our results, over 50 % of sites in the complex archipelagoes of Finland and Sweden experienced hypoxia that is ecologically significant ($O_2 < 4.6 \text{ mg L}^{-1}$). Especially alarming was the intensity of it. For instance, Stockholm Archipelago suffered frequently from severe hypoxia ($O_2 < 2 \text{ mg L}^{-1}$), as approximately half of the coastal monitoring sites were hypoxic across our study period (Fig. 3). This demonstrates that deoxygenated seafloors are probably even more common in coastal environments than previously reported (~~Karlsson et al., 2010; Conley et al., 2011~~)(Karlsson et al., 2010; Conley et al., 2011).

~~We quantified the facilitating role of seafloor complexity for the formation of hypoxia. Sheltered, topographically heterogeneous areas, where water exchange is limited are more susceptible for developing hypoxia according to our results. This statement is quite intuitive, but it has not previously been quantified. Noteworthy is that coastal hypoxia is not only related to depth; deep seafloors are not automatically hypoxic or anoxic. In our study, hypoxia was common in shallow and moderate depths of 10–45 m. For instance It is notable that in the Archipelago Sea, deep (60–100 m) canyons are mostly normoxic; areas above the permanent halocline, hypoxia is in many areas seasonal, and develops after the building of thermocline in late summer (Conley et al., 2011). It is therefore probable that many of the areas we recognized as strong currents tend to keep them hypoxic may well be oxygenated throughout during winter and spring. This does not however reduce the year (Virtasalo et al., 2005). Shallow areas can be restricted by slow water movement due to topographical reasons, thus creating opportunities for hypoxia formation. severity of the phenomenon. Even hypoxic event of short duration, e.g. few days, will reduce ecosystem resistance to further hypoxic perturbation and affect the overall ecosystem functioning. As our study suggests, topographically prone areas to deoxygenation represent less than 25 % of seascapes. However, most of the underwater nature values in the Finnish sea areas are concentrated on shallow areas where there exist enough light and suitable substrates (Virtanen et al., 2018; Lappalainen et al., 2019)(Villnas et al., 2013). Those shallow areas are also the ones that suffer from eutrophication and water heating up quickly, and are most probably the ones that are losing their breath in the future (Breitburg et al., 2018). Thus, even a fraction of hypoxic seascapes is ecologically thinking excessive.~~

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

Although extensive 3D models have been developed for the main basins of the Baltic Sea (~~Meier et al., 2011a; Meier et al., 2012a; Meier et al., 2014~~)(Meier et al., 2011b; Meier et al., 2012a; Meier et al., 2014) the previous reports on the occurrence of coastal hypoxia have mostly been based on point observations (~~Conley et al., 2009b; Conley et al., 2011~~)(Conley et al., 2009a; Conley et al., 2011). Due to the lack of data, and computational limitations, no biogeochemical model has (yet) encompassed the complex Baltic Sea archipelago with a resolution needed for adjusting local management decisions. This study provides a novel methodology to predict and identify areas prone to coastal hypoxia without data on currents, stratification or biological variables, and without complex biogeochemical models. Our approach is applicable to other low-energy and non-tidal systems, such as large shallow bays and semi-enclosed or enclosed sea areas. The benefit of this approach is that it requires far less computational power than a fine-scale 3D numerical modelling. By using relatively simple proxies describing depressions of stagnant water, we were able to create detailed hypoxia maps for the entire Finnish coastal area (23 500 km²) and Stockholm Archipelago (5100 km²), thus enabling a quick view of potentially hypoxic waters (Fig. 7).

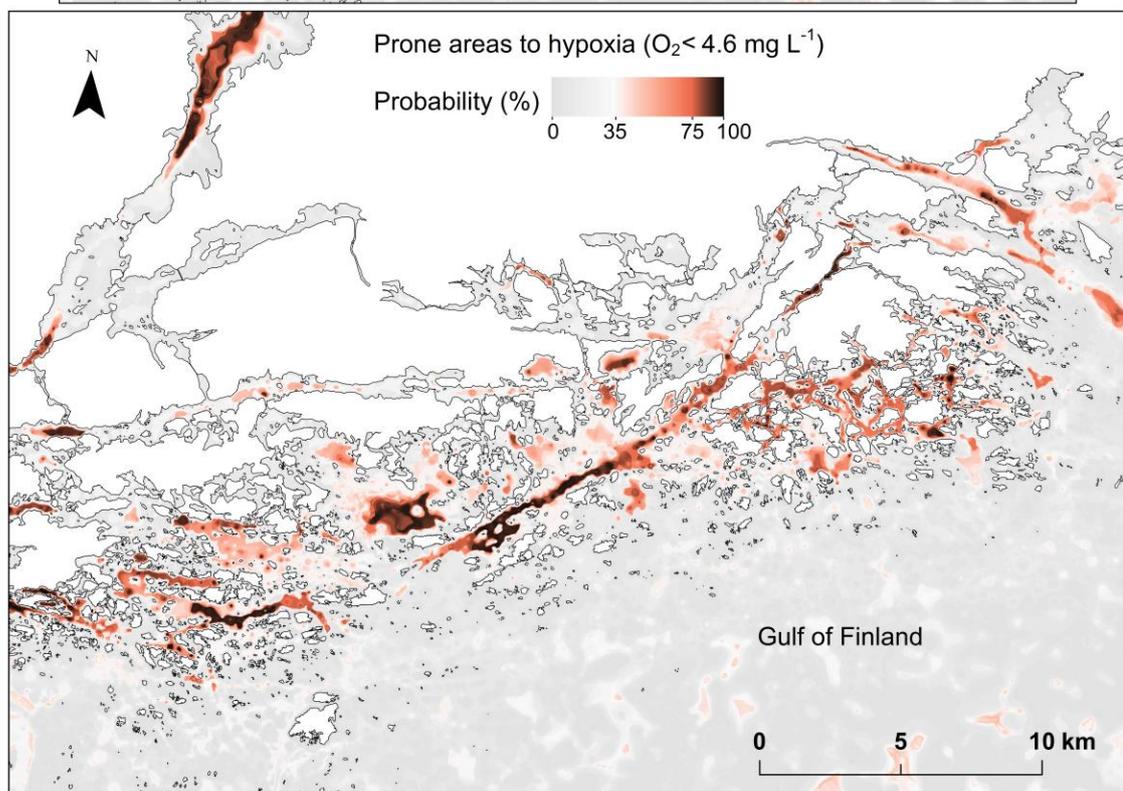
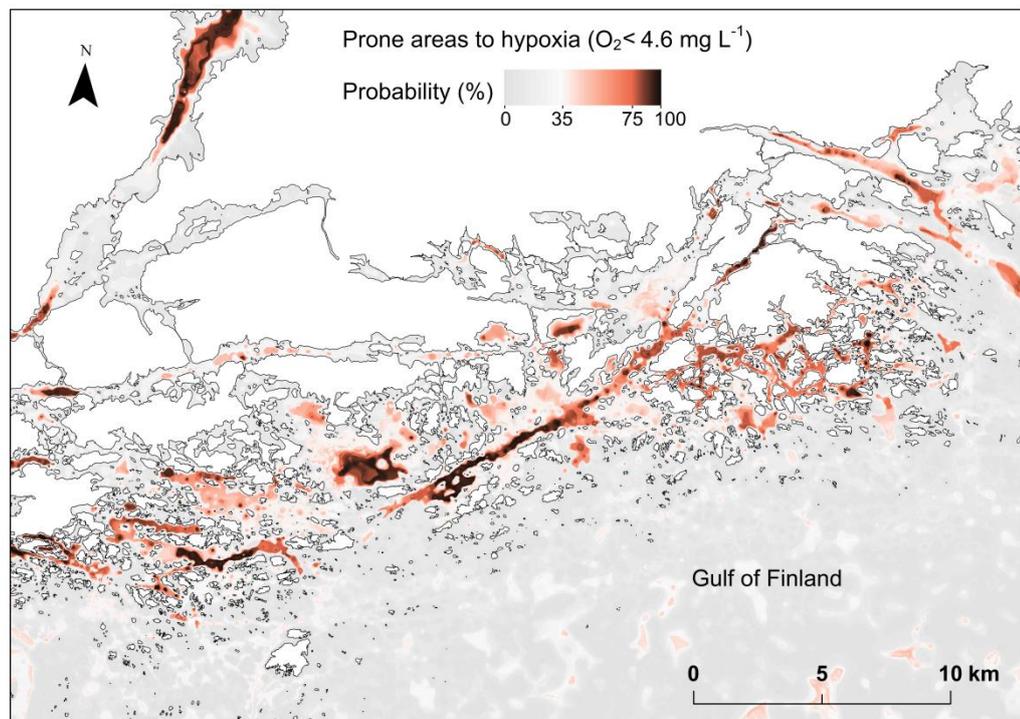


Figure 7. Modelled probability of detecting frequent hypoxia $O_2 (< 4.6 \text{ mg L}^{-1})$ in an example area in the south coast of Finland. Land shown as white color.

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

We emphasize that our models only indicate where hypoxia may occur simply due to restricted water exchange. Many otherAny deviations from this pattern are probably caused by either hydrographic factors, especiallywhich the hypoxia model based on topography did not account for (such as strong currents in elongated, wide channels), or biogeochemical factors. Especially high external loading, and local biogeochemical and biological processes; (nutrient cycling between sediment and the water), obviously modify the patterns and severity of hypoxia also in

the coastal areas. ~~Coastal systems, where oxygen~~ Oxygen deficiency has been projected to increase faster in the coastal systems than in the open sea (Gilbert et al., 2010; Altieri & Gedan, 2015). Such coastal areas are usually affected by external nutrient loading from the watershed. In larger basins and sea areas dominated by large river systems, such as the central Baltic Sea, Gulf of Mexico and Chesapeake Bay, large scale oceanographic and biogeochemical processes, or external loading, govern the depth and extent of hypoxia. This is the case also in the Baltic Sea. In areas where our models underestimate oxygen deficiency, major nutrient sources, e.g. rivers, cities or intensive agricultural areas, probably contribute to hypoxia formation. However, in extremely complex archipelago areas, such as Finnish and Swedish ~~archipelagoes~~ archipelago, physical factors limiting lateral and vertical movement of water probably facilitates, and in some areas even dictates the development of hypoxia. There were spatial differences in the frequency and severity of hypoxia that can be explained by topographical characteristics of the areas, external loading, and interaction with the adjacent deeper basins. For instance, in the Stockholm Archipelago severe hypoxia covered the largest percentage of seascapes of all study areas. Stockholm Archipelago is part of a joint valley landscape with steep topography. ~~The archipelago is extensive with~~ deep, steep areas also in the inner parts where wave forcing is low ~~exceptionally low, and disconnected from the open sea,~~ making it very susceptible for hypoxia, which was also confirmed by the model: ~~severe hypoxia covered the largest percentage of seascapes of all study areas.~~ In Finland, the inner archipelago is mostly shallow, with steep ~~canyons~~ but wider channels occurring only in the Archipelago Sea. These elongated channels are connected to adjacent open sea areas, and thus well-ventilated, as opposite to the narrow channels of Stockholm Archipelago. Geographically, hypoxia was in Finland most prominent in the Archipelago Sea and the Gulf of Finland, where the inner archipelago is isolated from the open sea, and the complex topography results in overall poor water exchange in the existing depressions. Both Stockholm Archipelago and the Archipelago Sea suffer from external loading from the associated watersheds, and internal loading from sediments, which probably contributes to the poor oxygen status of these areas (Puttonen et al., 2014; Walve et al., 2018). Biogeochemical factors were however not accounted for by our analysis, and cannot be used in explaining the observed spatial differences. In ~~addition~~ the Gulf of Finland, eutrophication increases in the open sea from west to SA, also AS and WGoF seemed to be prone to east, which has traditionally been explained by nutrient discharges from the Neva River (HELCOM, 2018). In our data there was however no clear gradient of coastal hypoxia increasing towards east. In contrast, frequent hypoxia ~~In contrast, in EGoF hypoxia was a more occasional phenomenon common in the Archipelago Sea and Western Gulf of Finland than in the Eastern Gulf of Finland, where hypoxia occurred only occasionally.~~ This may be caused by differences in ~~suggests that the coastal hypoxia is more dependent on local processes, i.e. internal loading and external nutrient loading, but loading from nearby areas, whereas open sea hypoxia is governed by basin-scale dynamics. However, the occasional nature of hypoxia in the Eastern Gulf of Finland~~ may be at least partly caused by the dependency of EGoF areas on the deep waters of the open parts of the Gulf of Finland. The Gulf of Finland is an embayment, 400 km long and 50–120 km wide, which has an open western boundary to the Baltic Proper. A ledgetongue of anoxic water usually extends from the central Baltic Sea into the Gulf of Finland along its deepest parts. Basin scale oceanographic and atmospheric processes influence how far east this ledgetongue proceeds into the Gulf of Finland each year (Alenius et al., 2016). (Alenius et al., 2016). It is possible that when this anoxic ledgetongue extends close to EGoF Eastern Gulf of Finland, it also worsens the oxygen situation of the EGoF archipelago.

In the Gulf of Bothnia, hypoxia was markedly less frequent and severe than in the other study areas. GoB has a relatively open coastline with only few depressions (cf. Supporting Fig. 1) and strong wave forcing, which probably ~~makes oxygen-rich water to be flushed into~~ enhances the archipelago mixing of water in the coastal areas. ~~Another reason for the relatively good oxygen conditions~~ Moreover, as the open sea areas of the Gulf of Bothnia is the are well oxygenated due to a lack of halocline and topographical isolation of GoB from the high saline deep waters of the Baltic Proper (by the relatively shallow sill between The Åland Islands and the Swedish coast. Consequently there is no halocline in the Gulf of Bothnia, which enhances mixing of water and prevents open sea hypoxia from developing these basins) (Leppäranta & Myrberg, 2009), which probably also affects the oxygen status of the coastal areas. ~~(Leppäranta and Myrberg, 2009), hypoxic water is not advected from the open sea to the coastal areas.~~

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

While our results confirm that hypoxia in most study areas is a frequently occurring phenomenon, they also show that areas affected by hypoxia are geographically quite still limited. Our modelling results indicate that overall 15, less than 25 % of the coastal studied sea areas are occasionally were afflicted by moderate some form of hypoxia, (be it recurrent or occasional), and less than 46 % of sea areas are seascapes were plagued by frequent, severe hypoxia. The relatively small spatial extent of coastal hypoxia does not mean that it is not a harmful phenomenon. In Stockholm Archipelago, severe hypoxia is a pervasive and persistent phenomenon, and also in Finland, many local depressions are more often hypoxic than normoxic. Anoxic sinkholes local depressions probably act as local nutrient sources, releasing especially phosphorus to the water column, which further enhances pelagic primary production. Such a vicious circle tends to worsen the eutrophication and maintain the environment in a poor state (Pitkänen et al., 2001; Vahtera et al., 2007)(Pitkänen et al., 2001; Vahtera et al., 2007). In this way, even small sized anoxic depressions, especially if they are many, may affect the ecological status of the whole coastal area. Moreover, as climate change has been projected to increase water temperatures and worsen hypoxia in the Baltic Sea (Meier et al., 2011b)(Meier et al., 2011a), shallow archipelago areas that typically have high productivity, warm up quickly, and are topographically prone to hypoxia, may be especially vulnerable to the negative effects of climate change.

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

CONCLUSIONS

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

ASSOCIATED CONTENT

Supporting Information

Figure S1. Boxplots showing the prevalence of depressions.

AUTHOR INFORMATION CONTRIBUTION

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Author Contributions

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

DATA AVAILABILITY

[Data and model codes will be submitted to Dryad data repository.](#)

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References:

- Alenius, P., Myrberg, K., Roiha, P., Lips, U., Tuomi, L., Pettersson, H. & Raateoja, M. (2016). Gulf of Finland Physics. In: *The Gulf of Finland assessment* eds. M. Raateoja and O. Setälä, pp. 42-57, 2016.
- Altieri, A. H. & Gedan, K. B. (2015). Climate change and dead zones. *Global Change Biology*, 21, 1395-1406. [10.1111/gcb.12754](https://doi.org/10.1111/gcb.12754), 2015.
- Ashcroft, M. B., Chisholm, L. A. & French, K. O. (2008). The effect of exposure on landscape scale soil surface temperatures and species distribution models. *Landscape Ecology*, 23, 211-225. [10.1007/s10980-007-9181-8](https://doi.org/10.1007/s10980-007-9181-8), 2008.
- Bekkby, T., Isachsen, P. E., Isaeus, M. & Bakkestuen, V. (2008). GIS modeling of wave exposure at the seabed: A depth-attenuated wave exposure model. *Marine Geodesy*, 31, 117-127. [10.1080/01490410802053674](https://doi.org/10.1080/01490410802053674), 2008.
- Breitbart, D., Levin, L. A., Oschlies, A., Grégoire, M., Chavez, F. P., Conley, D. J., Garçon, V., Gilbert, D., Gutiérrez, D., Isensee, K., 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., Telszewski, M., Yasuhara, M. & Zhang, J. (2018). Declining oxygen in the global ocean and coastal waters. *Science*, 359, [10.1126/science.aam7240](https://doi.org/10.1126/science.aam7240), 2018.
- Buzzelli, C. P., Luettich Jr, R. A., Powers, S. P., Peterson, C. H., McNinch, J. E., Pinckney, J. L. & Paerl, H. W. (2002). Estimating the spatial extent of bottom-water hypoxia and habitat degradation in a shallow estuary. *Marine ecology progress series*, 230, 103-112, 2002.
- Caballero-Alfonso, A. M., Carstensen, J. & Conley, D. J. (2015). Biogeochemical and environmental drivers of coastal hypoxia. *Journal of Marine Systems*, 141, 190-199. <https://doi.org/10.1016/j.jmarsys.2014.04.008>, 2015.
- Carstensen, J., Andersen, J. H., Gustafsson, B. G. & Conley, D. J. (2014). Deoxygenation of the Baltic Sea during the last century. *Proceedings of the National Academy of Sciences*, 111, 5628-5633. [10.1073/pnas.1323156111](https://doi.org/10.1073/pnas.1323156111), 2014.
- Conley, D. J., Carstensen, J., Vaquer-Sunyer, R. & Duarte, C. M. (2009a) *Ecosystem thresholds with hypoxia*. In: *Hydrobiologia*, pp. 21-29
- Conley, D. J., Humborg, C., Rahm, L., Savchuk, O. P. & Wulff, F. (2002). Hypoxia in the Baltic Sea and basin-scale changes in phosphorus biogeochemistry. *Environmental Science & Technology*, 36, 5315-5320. [10.1021/es025763w](https://doi.org/10.1021/es025763w), 2002.
- Conley, D., Conley, D. J., Carstensen, J., Aigars, J., Axe, P., Bonsdorff, E., Eremina, T., Hahti, B. M., Humborg, C., Jonsson, P., Kotta, J., Lannegren, C., Larsson, U., Maximov, A., Medina, M. R., Lysiak-Pastuszek, E., Remeikaite-Nikiene, N., Walve, J., Wilhelms, S. & Zillen, L. (2011) *Hypoxia Is Increasing in the Coastal Zone of the Baltic Sea*. *Environmental Science & Technology*, 45, 6777-6783.
- Conley, D. J., Björck, S., Bonsdorff, E., Carstensen, J., Destouni, G., Gustafsson, B. G., Hietanen, S., Kortekaas, M., Kuosa, H., Markus Meier, H. E., Müller-Karulis, B., Nordberg, K., Norkko, A., Nürnberg, G., Pitkänen, H., Rabalais, N. N., Rosenberg, R., Savchuk, O. P., Slomp, C. P., Voss, M., Wulff, F. & Zillen, L. (2009b). Hypoxia-Related Processes in the Baltic Sea. *Environmental Science & Technology*, 43, 3412-3420. [10.1021/es802762a](https://doi.org/10.1021/es802762a), 2009a.
- Conley, D. J., Carstensen, J., Aigars, J., Axe, P., Bonsdorff, E., Eremina, T., Hahti, B. M., Humborg, C., Jonsson, P., Kotta, J., Lannegren, C., Larsson, U., Maximov, A., Medina, M. R., Lysiak-Pastuszek, E., Remeikaite-Nikiene, N., Walve, J., Wilhelms, S., and Zillen, L.: *Hypoxia Is Increasing in the Coastal Zone of the Baltic Sea*, *Environmental Science & Technology*, 45, 6777-6783, [10.1021/es201212r](https://doi.org/10.1021/es201212r), 2011.
- De'ath, G. & Fabricius, K. E. (2000) *CLASSIFICATION AND REGRESSION TREES: Classification and regression trees: A POWERFUL YET SIMPLE TECHNIQUE FOR ECOLOGICAL DATA ANALYSIS*. *Ecology*, 81, 3178-3192. [10.1890/0012-9658\(2000\)081\[3178:CARTAP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2), 2000.
- Diaz, R. & Rosenberg, R. (1995a). Marine benthic hypoxia: A review of its ecological effects and the behavioural response of benthic macrofauna. 245-303 pp., 1995a.
- Diaz, R. J. & Rosenberg, R. (1995b). Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. in: *Oceanography and Marine Biology - an Annual Review*, Vol 33 (ed. by A. D. Ansell, R. N. A. D., Gibson, R. N., and M. Barnes), pp. 245-303. M. Oceanography and Marine Biology, U C L Press Ltd, London, 245-303, 1995b.
- Diaz, R. J. & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science*, 321, 926-929. [10.1126/science.1156401](https://doi.org/10.1126/science.1156401), 2008.
- Du Preez, C. (2015). A new arc-chord ratio (ACR) rugosity index for quantifying three-dimensional landscape structural complexity. *Landscape Ecology*, 30, 181-192. [10.1007/s10980-014-0118-8](https://doi.org/10.1007/s10980-014-0118-8), 2015.
- Dunn, D. C. & Halpin, P. N. (2009). Rugosity-based regional modeling of hard-bottom habitat. *Marine Ecology Progress Series*, 377, 1-11, 2009.
- Eilola, K., Meier, H. E. M. & Almroth, E. (2009). On the dynamics of oxygen, phosphorus and cyanobacteria in the Baltic Sea; A model study. *Journal of Marine Systems*, 75, 163-184. <https://doi.org/10.1016/j.jmarsys.2008.08.009>, 2009.
- Eilola, K., Gustafsson, B. G., Kuznetsov, I., Meier, H. E. M., Neumann, T. & Savchuk, O. P. (2011). Evaluation of biogeochemical cycles in an ensemble of three state-of-the-art numerical models of the Baltic Sea. *Journal of Marine Systems*, 88, 267-284. [10.1016/j.jmarsys.2011.05.004](https://doi.org/10.1016/j.jmarsys.2011.05.004), 2011.
- Elith, J., Leathwick, J. R. & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of Animal Ecology*, 77, 802-813. [10.1111/j.1365-2656.2008.01390.x](https://doi.org/10.1111/j.1365-2656.2008.01390.x), 2008.
- Eriksson, S. P., Wennhage, H., Norkko, J. & Norkko, A. (2005). Episodic disturbance events modify predator-prey interactions in soft sediments. *Estuarine Coastal and Shelf Science*, 64, 289-294. [10.1016/j.ecss.2005.02.022](https://doi.org/10.1016/j.ecss.2005.02.022), 2005.
- Fennel, K. & Testa, J. M. (2019) *Biogeochemical Controls on Coastal Hypoxia*. *Annual Review of Marine Science*, 11, 105-130.
- Fennel, K., Hetland, R., Feng, Y. & DiMarco, S. (2011). A coupled physical-biological model of the Northern Gulf of Mexico shelf: model description, validation and analysis of phytoplankton variability. *Biogeosciences*, 8, 1881-1899, 2011.
- Fennel, K., Laurent, A., Hetland, R., Justic, D., Ko, D. S., Lehrter, J., Murrell, M., Wang, L. X., Yu, L. Q. & Zhang, W. X. (2016). Effects of model physics on hypoxia simulations for the northern Gulf of Mexico: A model intercomparison. *Journal of Geophysical Research-Oceans*, 121, 5731-5750. [10.1002/2015jc011577](https://doi.org/10.1002/2015jc011577), 2016.
- Fennel, K., and Testa, J. M.: *Biogeochemical Controls on Coastal Hypoxia*. *Annual Review of Marine Science*, 11, 105-130. [10.1146/annurev-marine-010318-095138](https://doi.org/10.1146/annurev-marine-010318-095138), 2019.
- Freeman, E. A. & Moisen, G. (2008). PresenceAbsence: An R Package for Presence-Absence Model Analysis. *Journal of Statistical Software*, 23, 1-31, 2008.
- Frölicher, T. L., Joos, F., Plattner, G. K., Steinacher, M. & Doney, S. C. (2009). Natural variability and anthropogenic trends in oceanic oxygen in a coupled carbon cycle-climate model ensemble. *Global Biogeochemical Cycles*, 23, n/a-n/a. [10.1029/2008GB003316](https://doi.org/10.1029/2008GB003316), 2009.

Gammal, J., Norkko, J., Pilditch, C. A. & Norkko, A. (2017): Coastal Hypoxia and the Importance of Benthic Macrofauna Communities for Ecosystem Functioning. *Estuaries and Coasts*, 40, 457-468. [10.1007/s12237-016-0152-7](https://doi.org/10.1007/s12237-016-0152-7), 2017.

Gilbert, D., Rabalais, N. N., Díaz, R. J. & Zhang, J. (2010): Evidence for greater oxygen decline rates in the coastal ocean than in the open ocean. *Biogeosciences*, 7, 2283-2296. [10.5194/bg-7-2283-2010](https://doi.org/10.5194/bg-7-2283-2010), 2010.

Gray, J. S., Wu, R. S. S. & Or, Y. Y. (2002): Effects of hypoxia and organic enrichment on the coastal marine environment. *Marine Ecology Progress Series*, 238, 249-279. [10.3354/meps238249](https://doi.org/10.3354/meps238249), 2002.

Greenwell, B., Boehmke, B., Cunningham, J. & Developers, G. (2018) *gbm: Generalized Boosted Regression Models. R package version 2.1.4.*

Gregorutti, B., Michel, B. & Saint-Pierre, P. (2017): Correlation and variable importance in random forests. *Statistics and Computing*, 27, 659-678. [10.1007/s11222-016-9646-1](https://doi.org/10.1007/s11222-016-9646-1), 2017.

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

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

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

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

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

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

Karlsson, O. M., Jonsson, P. O., Lindgren, D., Malmæus, J. M. & Stehn, A. (2010): Indications of Recovery from Hypoxia in the Inner Stockholm Archipelago. *Ambio*, 39, 486-495. [10.1007/s13280-010-0079-3](https://doi.org/10.1007/s13280-010-0079-3), 2010.

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

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

~~Kramer, M. G., Hansen, A. J., Taper, M. L. and Kissinger, E. J. (2001) *ABIOTIC CONTROLS ON LONG-TERM WINDTHROW DISTURBANCE AND TEMPERATE RAIN FOREST DYNAMICS IN SOUTHEAST ALASKA*. *Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in Southeast Alaska*, *Ecology*, 2749-2768, 2001.~~

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

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

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

Liu, C., Berry, P. M., Dawson, T. P. & Pearson, R. G. (2005): Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, 28, 385-393. [doi:10.1111/j.0906-7590.2005.03957.x](https://doi.org/10.1111/j.0906-7590.2005.03957.x), 2005.

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

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

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

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

Meier, H. E. M., Müller-Karulis, B., Andersson, H. C., Dieterich, C., Eilola, K., Gustafsson, B. G., Höglund, A., Hordoir, R., Kuznetsov, I., Neumann, T., Ranjbar, Z., Savchuk, O. P. & Schimanke, S. (2012b): Impact of Climate Change on Ecological Quality Indicators and Biogeochemical Fluxes in the Baltic Sea: A Multi-Model Ensemble Study. *Ambio*, 41, 558-573. [10.1007/s13280-012-0320-3](https://doi.org/10.1007/s13280-012-0320-3), 2012b.

Meier, H. E. M., Andersson, H. C., Arheimer, B., Donnelly, C., Eilola, K., Gustafsson, B. G., Kotwicki, L., Neset, T.-S., Niiranen, S., Piwowarczyk, J., Savchuk, O. P., Schenk, F., Węśławski, J. M. & Zorita, E. (2014): Ensemble Modeling of the Baltic Sea Ecosystem to Provide Scenarios for Management. *AMBIO*, 43, 37-48. [10.1007/s13280-013-0475-6](https://doi.org/10.1007/s13280-013-0475-6), 2014.

Middelburg, J. J. & Levin, L. A. (2009): Coastal hypoxia and sediment biogeochemistry. *Biogeosciences*, 6, 1273-1293, 2009.

Natekin, A. & Knoll, A. (2013): Gradient boosting machines, a tutorial. *Frontiers in Neuroinformatics*, 7, 21. [10.3389/fnbot.2013.00021](https://doi.org/10.3389/fnbot.2013.00021), 2013.

Nilsson, H. C. & Rosenberg, R. (2000): Succession in marine benthic habitats and fauna in response to oxygen deficiency: analysed by sediment profile-imaging and by grab samples. *Marine Ecology Progress Series*, 197, 139-149. [10.3354/meps197139](https://doi.org/10.3354/meps197139), 2000.

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

Norkko, J., Gammal, J., Hewitt, J. E., Josefson, A. B., Carstensen, J. & Norkko, A. (2015): Seafloor Ecosystem Function Relationships: In Situ Patterns of Change Across Gradients of Increasing Hypoxic Stress. *Ecosystems*, 18, 1424-1439. [10.1007/s10021-015-9909-2](https://doi.org/10.1007/s10021-015-9909-2), 2015.

Norkko, J., Reed, D.C., Timmermann, K., Norkko, A., Gustafsson, B.G., Bonsdorff, E., Slomp, C.P., Carstensen, J. & Conley, D.J. (2012) A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biology*, 18, 422-434.

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

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

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

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

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

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

Scully, M. E. (2013). Physical controls on hypoxia in Chesapeake Bay: A numerical modeling study. *Journal of Geophysical Research-Oceans*, 118, 1239-1256, [10.1002/jgrc.20138](https://doi.org/10.1002/jgrc.20138), 2013.

Scully, M. E. (2016). The contribution of physical processes to inter-annual variations of hypoxia in Chesapeake Bay: A 30-yr modeling study. *Limnology and Oceanography*, 61, 2243-2260, [10.1002/lno.10372](https://doi.org/10.1002/lno.10372), 2016.

Stramma, L., Oschlies, A., & Schmidtko, S. (2012). Mismatch between observed and modeled trends in dissolved upper-ocean oxygen over the last 50 yr. *Biogeosciences*, 9, 4045-4057, [10.5194/bg-9-4045-2012](https://doi.org/10.5194/bg-9-4045-2012), 2012.

Testa, J. M., Li, Y., Lee, Y. J., Li, M., Brady, D. C., Di Toro, D. M., Kemp, W. M., & Fitzpatrick, J. J. (2014). Quantifying the effects of nutrient loading on dissolved O₂ cycling and hypoxia in Chesapeake Bay using a coupled hydrodynamic-biogeochemical model. *Journal of Marine Systems*, 139, 139-158, [10.1016/j.jmarsys.2014.05.018](https://doi.org/10.1016/j.jmarsys.2014.05.018), 2014.

Timmermann, K., Norkko, J., Janas, U., Norkko, A., Gustafsson, B. G., & Bonsdorff, E. (2012). Modelling macrofaunal biomass in relation to hypoxia and nutrient loading. *Journal of Marine Systems*, 105, 60-69, [10.1016/j.jmarsys.2012.06.001](https://doi.org/10.1016/j.jmarsys.2012.06.001), 2012.

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

Valanko, S., Heino, J., Westerbom, M., Viitasalo, M., & Norkko, A. (2015). Complex metacommunity structure for benthic invertebrates in a low-diversity coastal system. *Ecology and Evolution*, 5, 5203-5215, [10.1002/ece3.1767](https://doi.org/10.1002/ece3.1767), 2015.

Walbridge, S., Slocum, N., Pobuda, M., & Wright, D. (2018). Unified Geomorphological Analysis Workflows with Benthic Terrain Modeler. *Geosciences*, 8, 94, 2018.

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

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

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

Vaquier-Sunyer, R., & Duarte, C. M. (2008). Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 15452-15457, [10.1073/pnas.0803833105](https://doi.org/10.1073/pnas.0803833105), 2008.

Weiss, A. D. (2001). Topographic position and landforms analysis. In Poster presented at the Esri User Conference, San Diego, CA, USA. http://www.jennessent.com/downloads/tpi-postertnc_18x22.pdf, 2001.

WFD (2000). Water Framework Directive. Common Implementation, 2000.

Villnas, A., Norkko, J., Lukkari, K., Hewitt, J., & Norkko, A. (2012). Consequences of Increasing Hypoxic Disturbance on Benthic Communities and Ecosystem Functioning. *Plos One*, 7, [10.1371/journal.pone.0044920](https://doi.org/10.1371/journal.pone.0044920), 2012.

Villnas, A., Norkko, J., Hietanen, S., Josefson, A. B., Lukkari, K., & Norkko, A. (2013). The role of recurrent disturbances for ecosystem multifunctionality. *Ecology*, 94, 2275-2287, [10.1890/12-1716.1](https://doi.org/10.1890/12-1716.1), 2013.

Virtanen, E. A., Viitasalo, M., Lappalainen, J., & Moilanen, A. (2018). Evaluation, Gap Analysis, and Potential Expansion of the Finnish Marine Protected Area Network. *Frontiers in Marine Science*, 5, [10.3389/fmars.2018.00402](https://doi.org/10.3389/fmars.2018.00402), 2018.

Virtasalo, J. J., Kohonen, T., Vuorinen, I., & Huttula, T. (2005). Sea bottom anoxia in the Archipelago Sea, northern Baltic Sea—Implications for phosphorus remineralization at the sediment surface. *Marine Geology*, 224, 103-122, <https://doi.org/10.1016/j.margeo.2005.07.010>, 2005.