The impact of hypoxia on fish communities in the Baltic sea

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Contents

1 Acknowledgements

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2 Introduction

Hypoxia has occurred intermittently over the Holocene in the Baltic Sea, but the recent expansion from less than 10000 km2 before 1950 to 60000 km2 since 2000 is mainly caused by enhanced nutrient inputs from land and atmosphere (Conley et al. [2009], Carstensen et al. [2014]). The oxygen situation in the Baltic sea has become increasingly problematic because large inflows don't occur every year and due to large nutrient inputs over time, mainly between the 1950s and the late 1980s, resulting in escalating eutrophication with increasingly severe symptoms to the Baltic Sea's ecosystem. The higher the organic matter amount in the deep water, the more oxygen is consumed, resulting in oxygen deficiency, hypoxia, and in the most severe cases to complete depletion of oxygen, anoxia. Anoxia is the condition when all oxygen has been consumed by microbial processes, and no oxygen is left in the water. If the water stays anoxic for an extended period, hydrogen sulphide (H2S) is formed, which is toxic to all higher marine life. Only bacteria and fungi can survive in a water environment with total absence of oxygen (Hansson and Viktorsson [2023]).

Many studies have shown loss of body condition in exploited marine predators as a consequence of hypoxia (Casini et al. [2016]). Yet, the connection between oxygen concentration and the occurrence of predators in the seascape is not well understood. Do individuals from different predator species avoid low oxygen concentration? If so, which species most severely are avoiding low oxygen concentration? Here we performed an analysis of the spatiotemporal trend of oxygen concentration to compare the observed and the expected frequency of individuals sampled of four predator species, cod, sprat, flounder and herring, along an oxygen gradient. Our sampling data is highly heterogeneous (see Material and Methods). Despite such a sampling heterogeneity, our results show that condition, using body weight as a proxy, and the time-series of occurrence proportions of individuals in oxygen concentrations are species-specific.

3 Material and Methods

We analyze data from the Baltic sea between 1979 and 2019 to explore time-dependent patterns for the condition of species and the occurrence proportions along oxygen concentration in the seascape. Our analysis show spatiotemporal bias in the samplings. Spatial bias of the hypoxic concentration, fish abundance and fish diets data show an heterogeneous number of sampling locations. Oxygen concentration represented a total of 572 locations, abundance data for sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) were obtained from 141 locations, and for flounder (*Platichthys flesus*) and cod (*Gadus morhua*) together contained 19 locations. Stomach data for cod and flounder were sampled from 17 locations. Temporal sampling bias was also highly heterogeneous for the predators analyzed, ranging from cod (31 years), sprat (almost 30 years), herring (almost 30 years), and flounder (3 years). In addition, oxygen value were extracted for each plot from the oxygen data for the specific-species sampled area. Because this spatiotemporal sampling bias, all figures contain axis ranges given by the specific spatiotempooral samplings analyzed. Therefore, the statistical values shown in each figure are calculated according to each specific subset of samplings. The 1+ age-class mentioned in the figures 4 and 5 for sprat and herring regroups all the classes abundance older than 1 year.

3.1 Temporal dynamics of hypoxia

Our analysis shows an uptrend in the area and volume for two values of hypoxic concentrations (Figure 1). The uptrend was more severe in late 90's and have since then continued the uptrend but with a lower slope. This pattern occurs for $[O_2] < 1$ml, and $[O_2] < 43$ml oxygen concentration for the area and the volume.

3.2 Species-specific response to hypoxia

We analyzed predator weight and prey composition data as a proxy to body condition to explore weather there is a species-specific response for each predator. While the uptrend in hypoxic concentration is a general pattern since the 80's (Figure 1), predator patterns in weight and prey composition might vary because their different trait architecture of each species. Temporal sampling bias was highly heterogeneous for the predators analyzed, ranging from cod (31 years, Figure 2), sprat (almost 30 years, Figure 4), herring (almost 30 years, Figure 5), and flounder (3 years, Figure 3). Figures 6 to 11 show the oxygen seascape for 1993, the year with the minimum area of the hypoxic zone and for 2015, the year with the maximum area of the hypoxic zone (code and flounder had no samples for the 1993 year). All the figures have the oxygen concentration trend in the background for clarity.

We test the strength of the preference for each oxygen concentration as a proxy to trait species-specific response to hypoxic concentration or the indirect response of predators given by the health status of the prey resources in the seascape. We obtained the expected occurrence for each predator in each oxygen concentration by using the theoretical expectation derived from a 2D global Brownian motion model. This expectation is given by the percentage of occurrence accounting for the area of a given oxygen concentration in the data. We notice that we only test the empirical data with the area and not the volume because we have an estimation for the expected percentage of occurrence in a 2D seascape. This expectation is the same as if we were sampling individuals moving randomly in the whole 2D sampled seascape for each predator species. We then can compare the empirical occurrence against the expected occurrence for three oxygen concentrations, low, $[O_2]<1$ml, medium, 1ml$\leq[O_2]\leq$43ml and high $[O_2]>43$ml, for the four predators, cod (Figures 6 and 7), flounder (Figures 6 and 8), sprat (Figures 9 and 10), and herring (Figures 9 and 11). We obtained the hypoxic seascape with minimum and maximum area from the samplings, the empirical and theoretical expectation for each year for the whole temporal series to find an individual in each of the three oxygen concentrations for the four main consumers in the data, cod, flounder, herring and sprat (Figures 6 to 11).

4 Results

4.1 Temporal dynamics of hypoxia

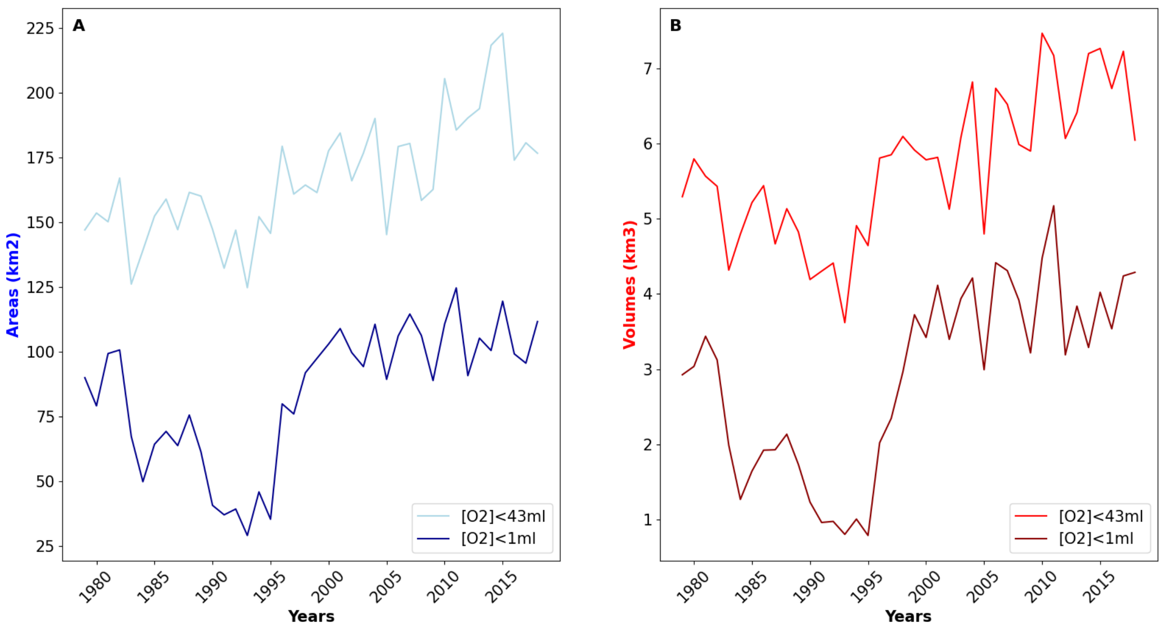

Figure 1: Area (A) and Volume (B) of hypoxic seafloor as a function of time for two oxygen concentrations, $[O_2]$<1ml (dark blue (A), dark red (B)) and $[O_2]$<43ml (light blue (A) and red (B)).

4.2 Species-specific response to hypoxia

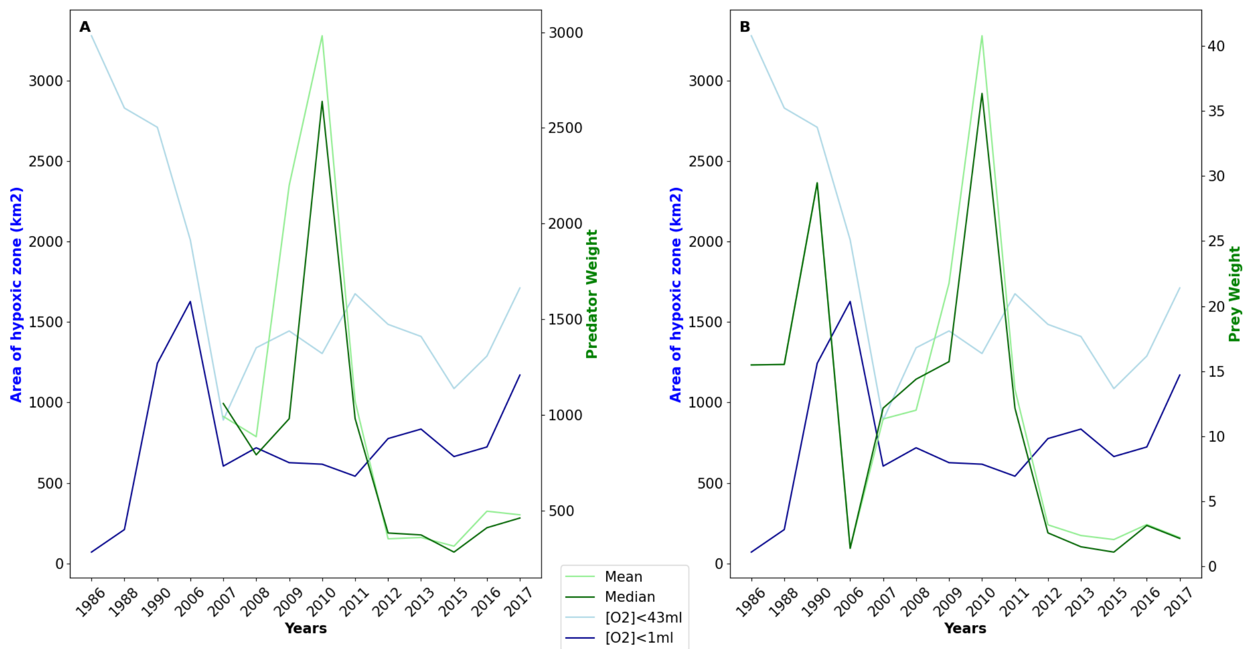

Figure 2: Average weight of predators for cod (A, mean, light green, and median, dark green) and average weight of preys (B, mean, light green and median, dark green) as a function of time together with area of hypoxic seafloor for $[0_2]<1$ml (dark blue, A and B) and $[0_2]<43$ml (light blue, A and B).

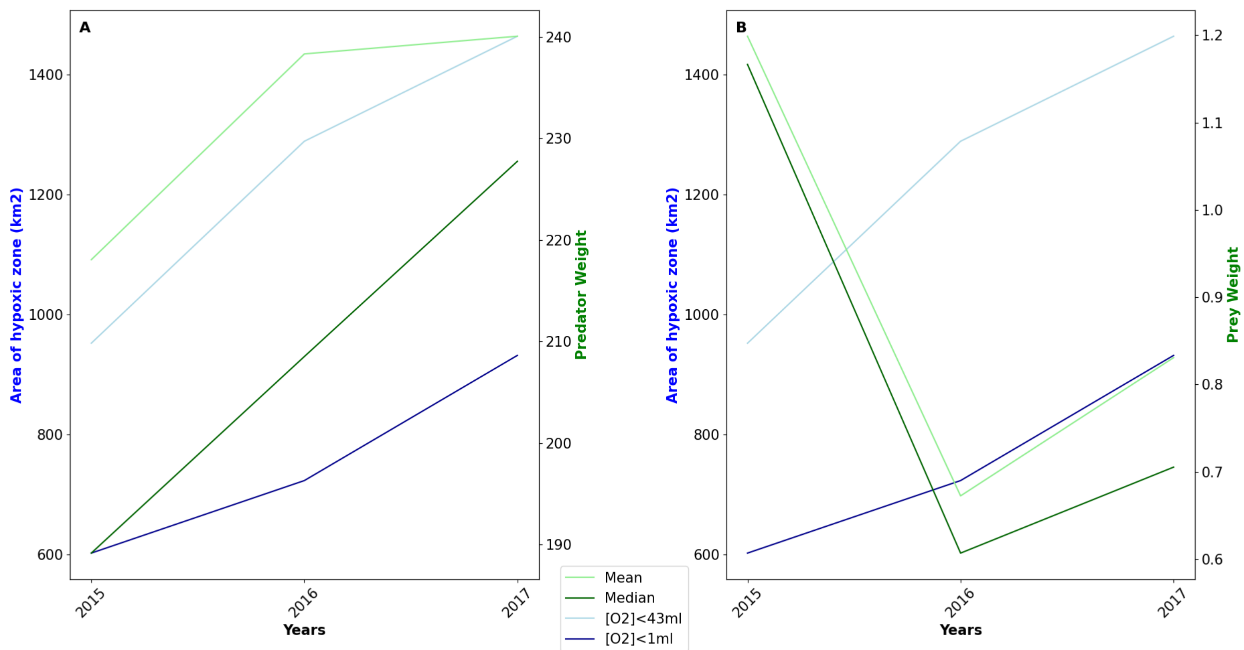

Figure 3: Average weight of predators for flounder (A, mean, light green, and median, dark green) and average weight of preys (B, mean, light green and median, dark green) as a function of time together with area of hypoxic seafloor for $[0_2]$<1ml (dark blue, A and B) and $[0_2]$<43ml (light blue, A and B).

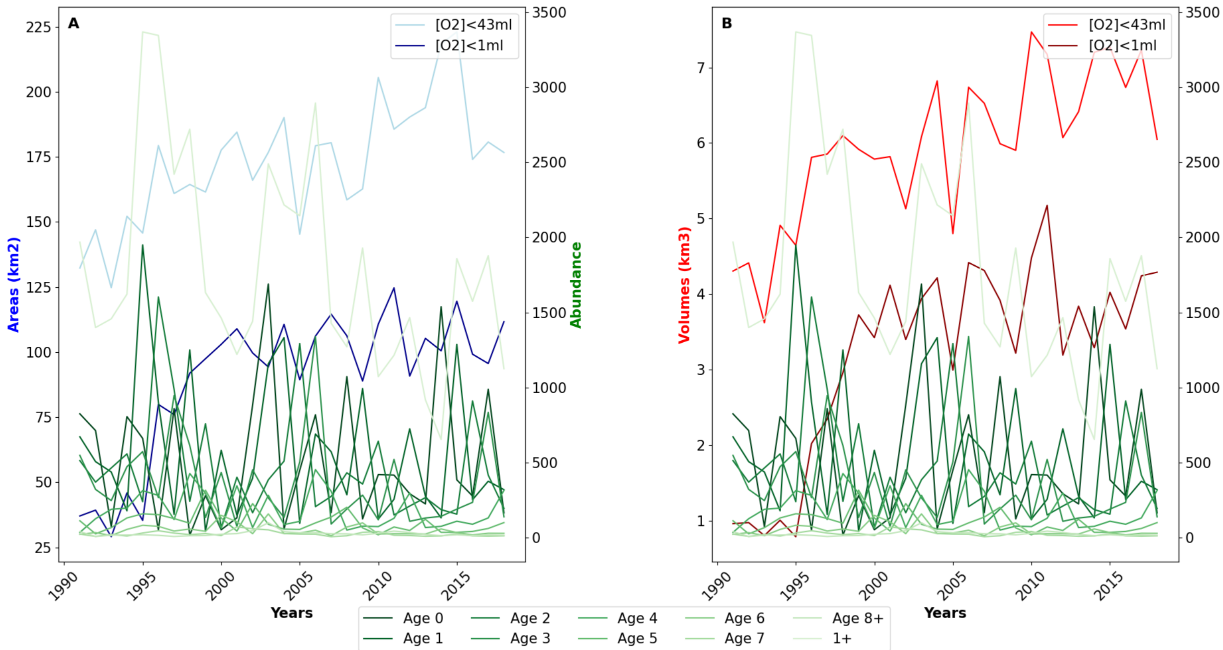

Figure 4: Area of hypoxic seafloor (A, for [0_2]<1ml, dark blue, and [0_2]<43ml, light blue) and volume of hypoxic seafloor (B, for [0_2]<1ml, dark red, and [0_2]<43ml, red) as a function of time together with abundance of sprat by age group (green gradient, A and B).

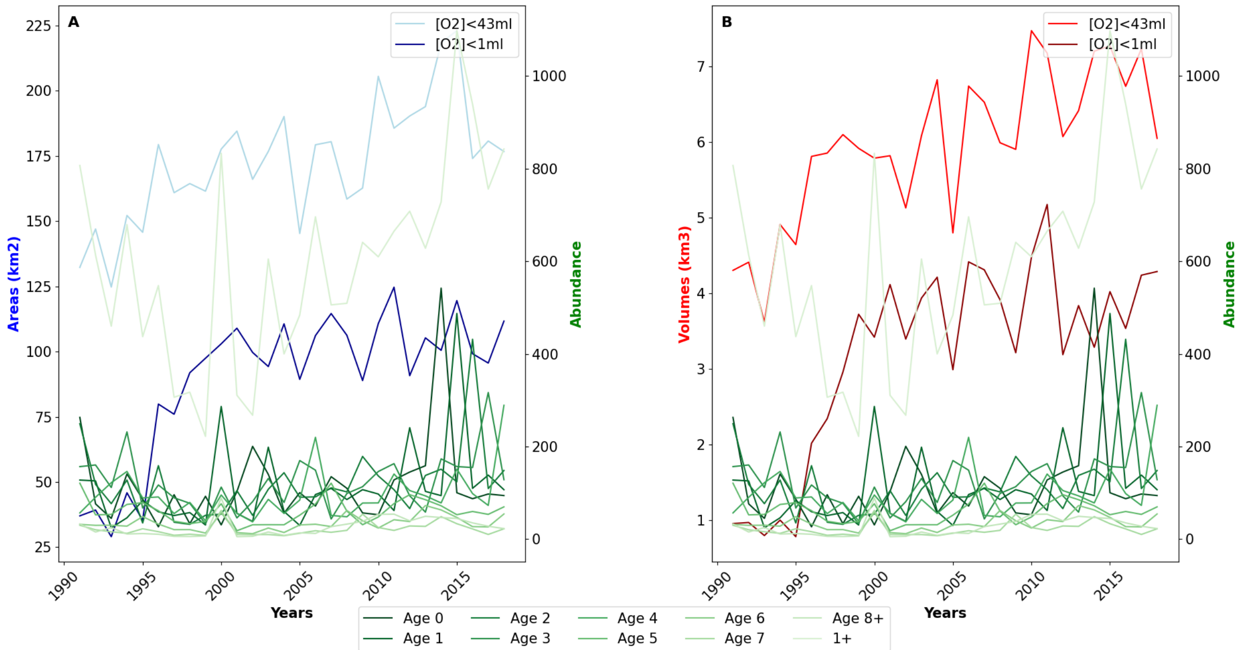

Figure 5: Area of hypoxic seafloor (A, for $[0_2]$<1ml, dark blue, and $[0_2]$<43ml, light blue) and volume of hypoxic seafloor (B, for $[0_2]$<1ml, dark red, and $[0_2]$<43ml, red) as a function of time together with abundance of herring by age group (green gradient, A and B).

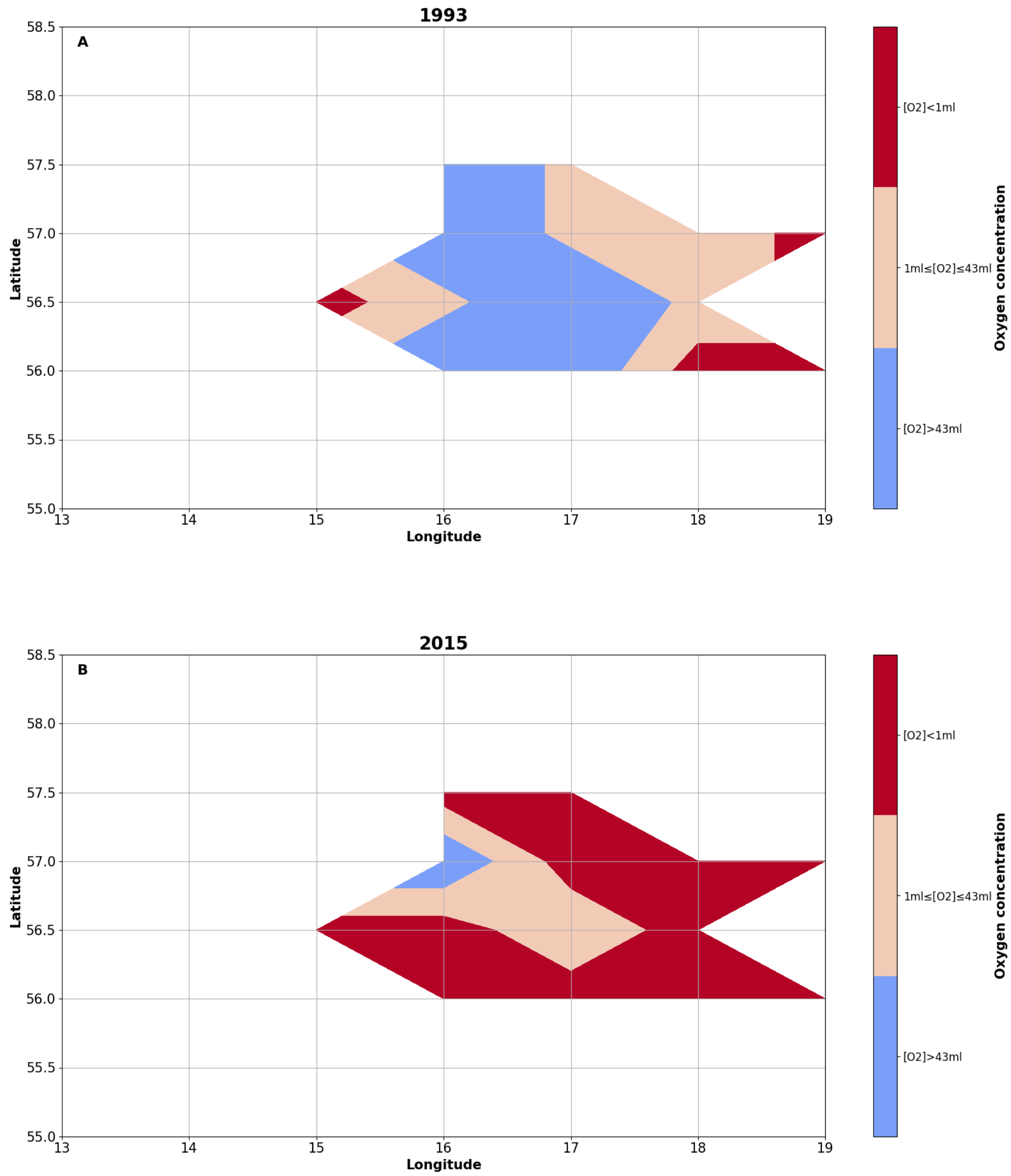

Figure 6: Hypoxic seascape of the seafloor with minimum (year 1993, A) and maximum (year 2015, B) area for cod and flounder. Empirical (red, peach and blue) concentrations $[0_2]$<1ml, 1ml$\leq[0_2]\leq$43ml, and $[0_2]$>43ml.

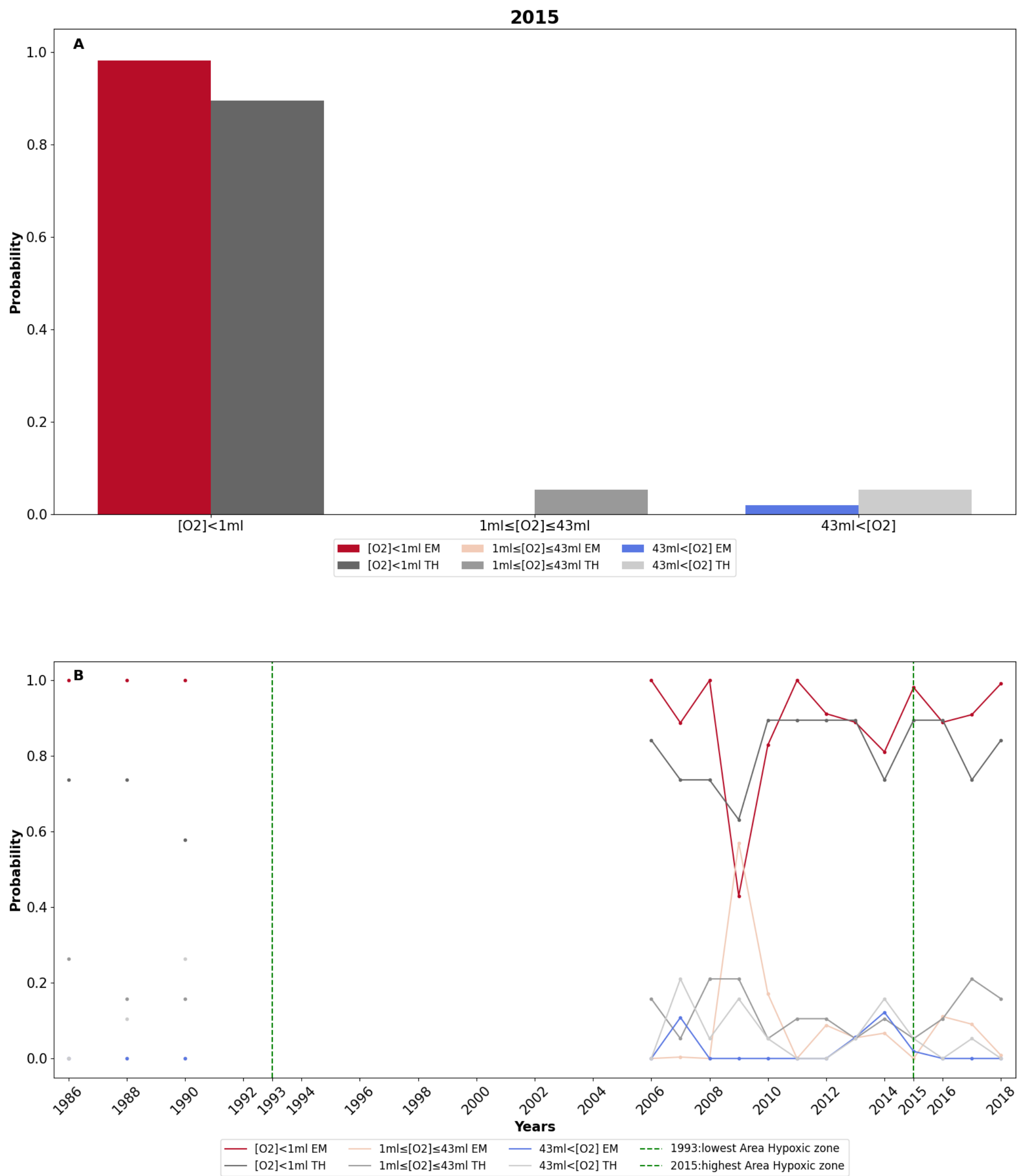

Figure 7: (A) Empirical (red, peach and blue) and theoretical (grey) expectation to find a cod individual in the maximum hypoxic area in the seafloor for year 2015 with concentrations $[0_2]<1ml$, $1ml \leq [0_2] \leq 43ml$, and $[0_2]>43ml$. (B) Time series of the empirical (EM) and theoretical probability (TH) for the three hypoxic areas, $[0_2]<1ml$ (red, EM and grey TH), $1ml \leq [0_2] \leq 43ml$ (peach, EM and grey TH), and $[0_2]>43ml$ (light blue, EM and grey TH).

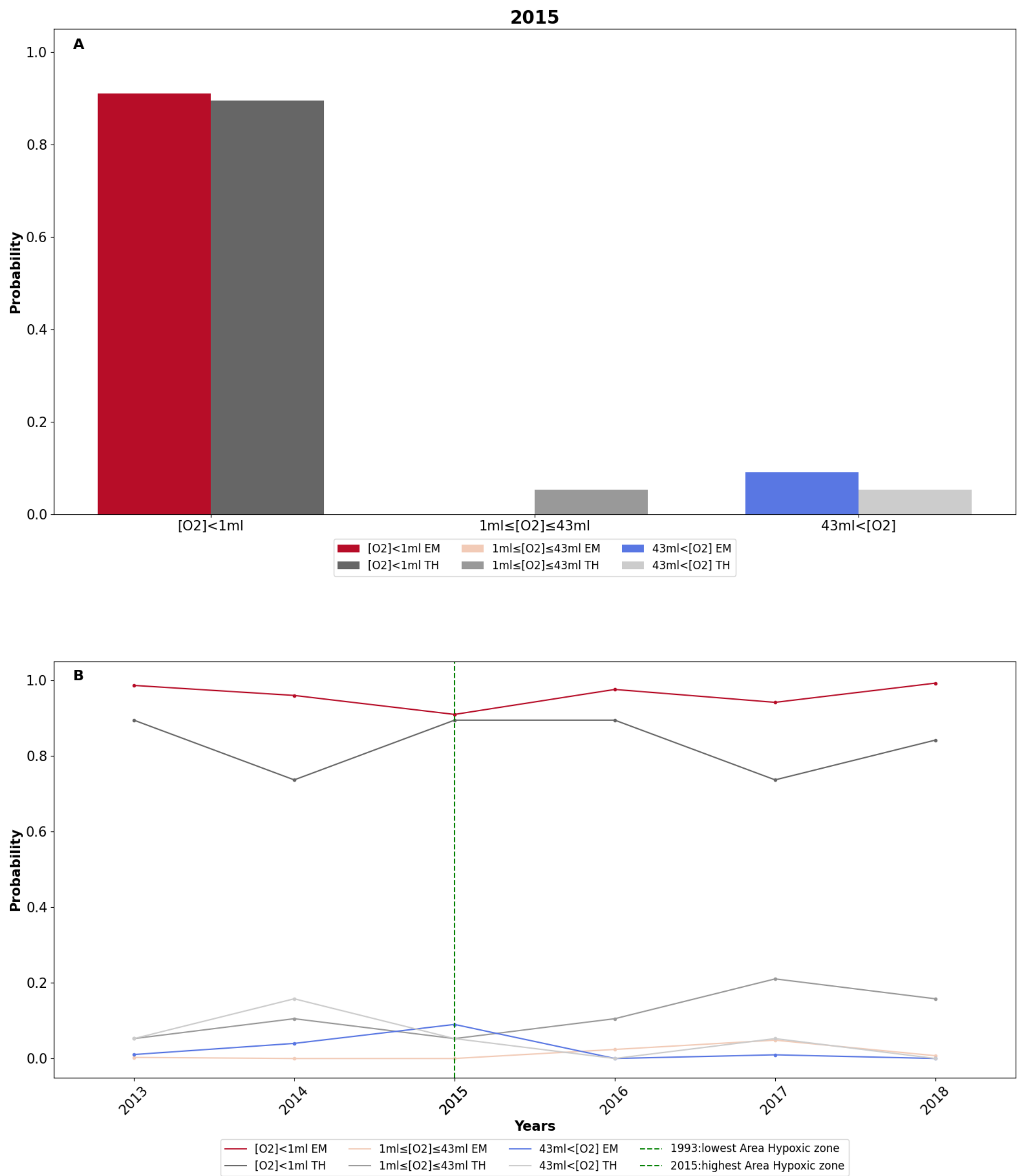

Figure 8: (A) Empirical (red, peach and blue) and theoretical (grey) expectation to find a flounder individual in the maximum hypoxic areas in the seafloor for year 2015 with concentrations $[0_2]<1$ml, 1ml$\leq[0_2]\leq$43ml, and $[0_2]>43$ml. (B) Time series of the empirical and theoretical probability for the three hypoxic areas, $[0_2]<1$ml (red, EM and grey TH), 1ml$\leq[0_2]\leq$43ml (peach, EM and grey TH), and $[0_2]>43$ml (light blue, EM and grey TH).

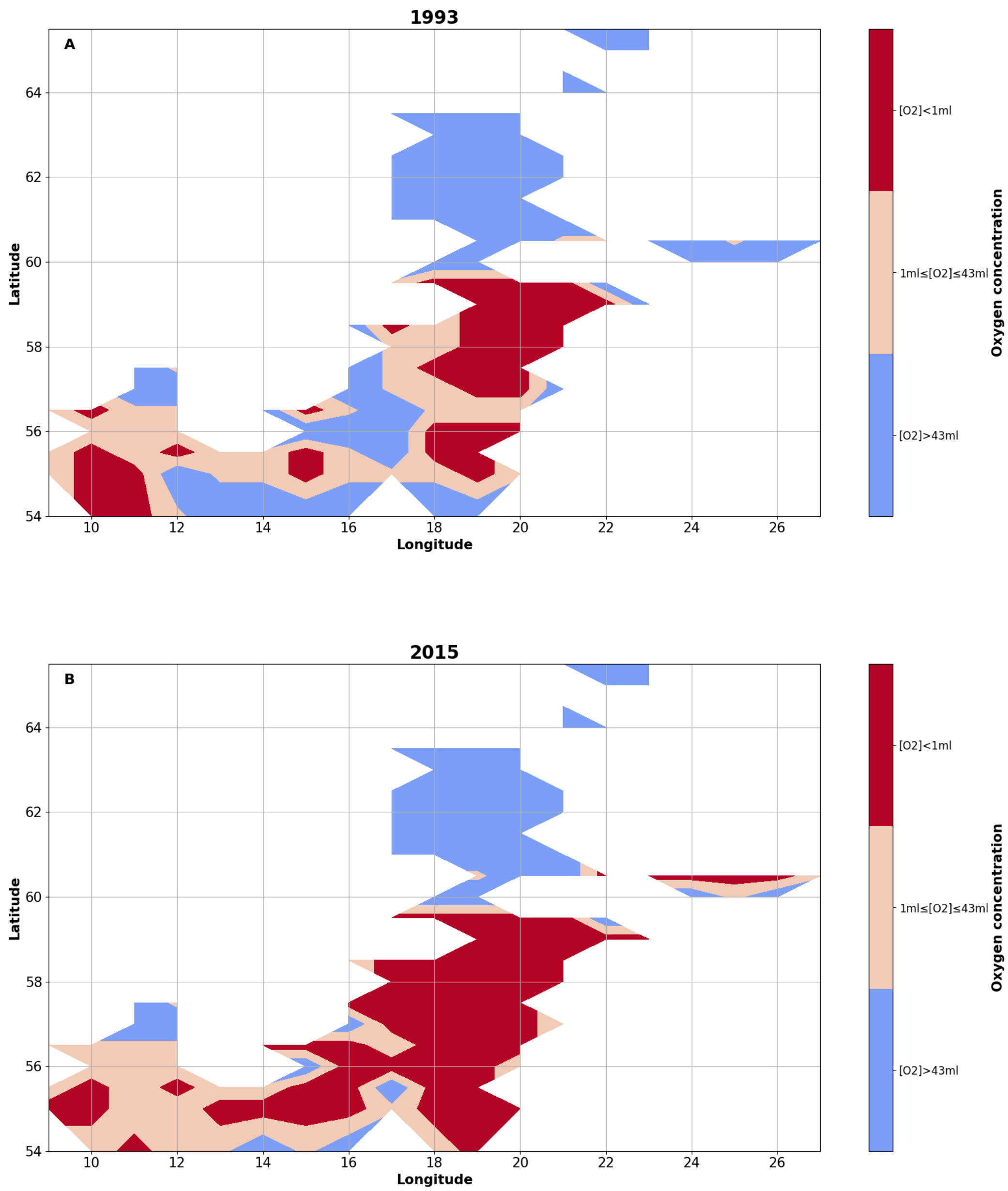

Figure 9: Hypoxic seascape of the seafloor with minimum (year 1993, A) and maximum (year 2015, B) area for sprat and herring. Empirical (red, peach and blue) concentrations $[0_2]<1$ml, 1ml$\leq[0_2]\leq$43ml, and $[0_2]>$43ml.

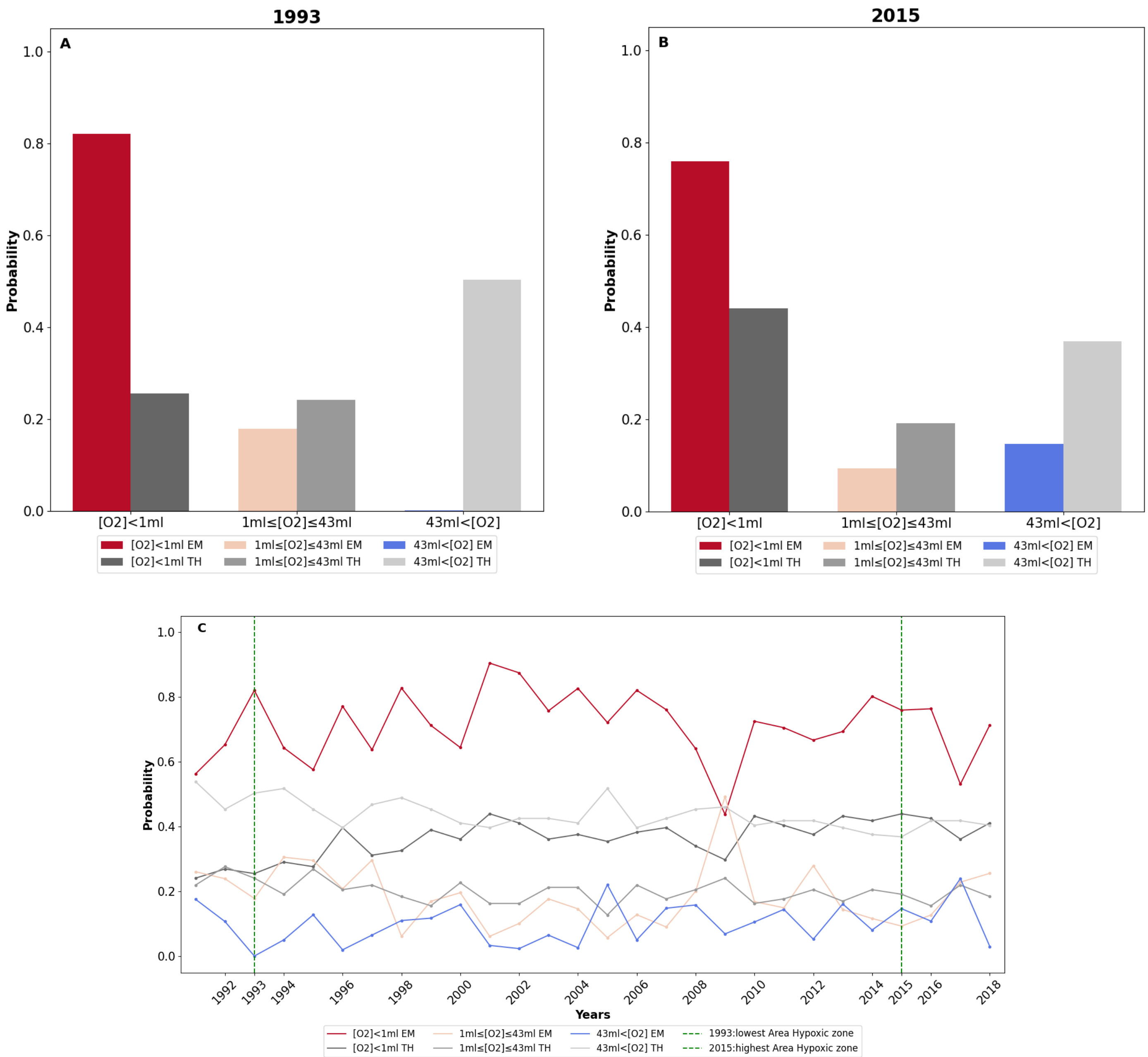

Figure 10: Empirical (red, peach and blue) and theoretical (grey) expectation to find a sprat individual in the minimum and maximum areas in the seafloor for years 1993 (A) and 2015 (B), respectively, for concentrations $[0_2]<1$ml, 1ml$\leq[0_2]\leq$43ml, and $[0_2]>43$ml. (C) Time series of the empirical and theoretical probability for the three hypoxic areas, $[0_2]<1$ml (red, EM and grey TH), 1ml$\leq[0_2]\leq$43ml (peach, EM and grey TH), and $[0_2]>43$ml (light blue, EM and grey TH).

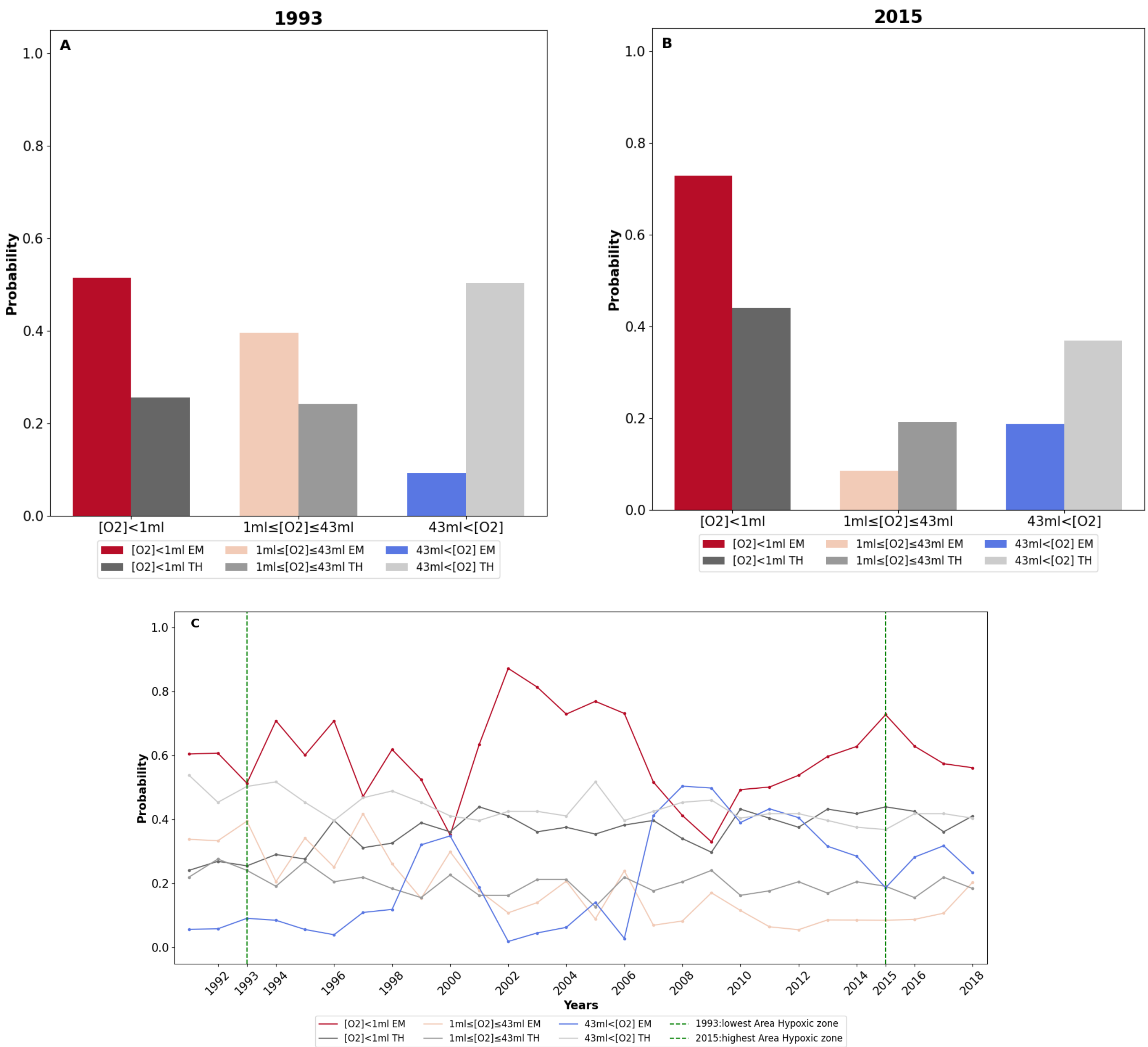

Figure 11: Empirical (red, peach and blue) and theoretical (grey) expectation to find a herring individual in the minimum and maximum in the seafloor for years 1993 (A) and 2015 (B), respectively, for concentrations $[0_2]<1$ml, 1ml$\leq[0_2]\leq43$ml, and $[0_2]>43$ml. (C) Time series of the empirical and theoretical probability for the three hypoxic areas, $[0_2]<1$ml (red, EM and grey TH), 1ml$\leq[0_2]\leq43$ml (peach, EM and grey TH), and $[0_2]>43$ml (light blue, EM and grey TH).

5 Discussion and Conclusions

Many studies in aquatic ecosystems have shown loss of body condition in exploited marine predators as a consequence of uptrend of hypoxia with time (Casini et al. [2016]) (Figure 1). It is expected that foraging strategies change as a consequence of hypoxia, for example, avoiding low oxygen concentrations. However, the connection between oxygen concentration and foraging preference for a community of predators in the seascape is not well understood. Body weight of predators and prey responded differently to hypoxia. While there was a loss in body condition in cod and its prey community, the opposite was observed for flounder with the same downtrend than cod for its prey weight (Figures 2 and 3). The response for the sprat and herring accounting for size classes also differed between the two species. Sprat age-classes showed higher amplitude along the full time series, while the herring only showed such high amplitude in the end of the series (Figures 4 and 5). To better understand the strength of the species-specific responses to hypoxia, we analyzed the temporal trend of oxygen area to contrast the empirically estimated and the expected proportion of occurrence in four fish predator species along the oxygen gradient. Our results show that while the occurrence of cod and flounder did not deviate substantially from the expected proportions for the three oxygen concentrations, the proportions of occurrence for sprat and herring substantially deviated but in opposite directions depending on the oxygen concentrations. The time series for the four predator species revealed a consistent pattern across the years (Figurs 6 to 11). Overall, these patterns suggest that the empirical occurrence of cod and flounder in low oxygen concentration is expected under a Brownian motion movement model despite a loss of body condition, suggesting that occurrence might be due to the presence of prey species in such low oxygen condition areas. Therefore understanding the response of food webs to hypoxia in the Baltic sea would require to take into account the species-specific requirements of predators and the entire community of preys to disentangle the full effect of hypoxia on ecosystems. Future research on the impact of hypoxia on food webs in the Baltic sea might take into account a modeling framework where individuals have a tolerance trait that move not only randomly, as in the case of the Brownian motion, but have an avoidance or a preference for different oxygen concentrations that is also dependent on the health status of the habitats, like the prey abundance, diversity and condition. In this way, we could gain accuracy on the impact of hypoxia on predator-prey communities and food webs on the Baltic sea.

6 Supplementary material

All the figures can be reproduced from the following git repository Baltic Hypoxia. There are two ways to reproduce the figures: 1) running the python codes from the folder Python or 2) running the codes within the Jupyter notebook.

References

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7 Summary

7.1 English

Our data analysis suggests a general uptrend in the area and volume for two values of oxygen concentrations (All figures). This pattern confirms the increasing area and volume of hypoxia in the Baltic sea. The uptrend was more severe in the late 90's and have since then continued the uptrend but with lower slope. This pattern occurs for both $[O_2]$<1ml and $[O_2]$<43ml oxygen concentrations (Figure 1). Predator species responded differently to this hypoxia uptrend. While the uptrend is a general pattern since the 80's (Figure 1), predator patterns in weight and prey composition varied. There is a downtrend for the cod and prey weight (Figure 2) but an uptrend for the flounder (Figure 3, notice the Flounder time series is much shorter than the cod one.) Sprat and herring age-class time-series distribution show opposite trends for all the 141 aggregated locations. While the 1+ age-class (including all age classes over one year old) decays for the sprat (Figure 4), the opposite occurs for the herring (Figure 5). Sprat age-classes shows a higher amplitude fluctuation along the full time-series, while the herring only shows such high amplitude fluctuation in the end of the series. This pattern might be driven by the different sensitivity of species-specific age-classes to hypoxic expansion due to the direct impact of lack of oxygen or indirectly via the effect on the absence of resources. Overall, these patterns suggest that there is a trait or a set of traits like weight or body size that have species-specific response directly driven by the low oxygen concentration uptrend or indirectly by the low oxygen concentration affecting the health status of the prey community.

To explore the strength of the species-specific response to hypoxia we conducted additional analyses to contrast the empirical and the expected proportion of occurrence of individuals in the three oxygen concentrations, low, $[O_2]$<1ml, medium, 1ml≤$[O_2]$≤43ml and high $[O_2]$>43ml, for the four predators, cod and flounder (Figure 6), cod (Figure 7), flounder (Figure 8), sprat and herring (Figure 9), sprat (Figure 10), and herring (Figure 11). While the empirical occurrence proportions of cod and flounder did not deviate substantially from the expected proportion for the three concentrations (Figures 6 and 7), the proportions for sprat and herring substantially deviated but in different directions depending on the oxygen concentration. The empirical proportion of individuals found in low concentration was much higher than the theoretical expectation for both species. On the contrary, the empirical proportion of individuals found in medium and high concentrations was lower than the theoretical expectation for the two species. Overall, our results show increasing hypoxia in the Baltic sea, fish community is strongly species-dependent. Our results were obtained exploring oxygen concentration time-series, body weight as a proxy of fish condition together with the contrast of the empirical and the expected occurrence proportions along an hypoxia gradient using a Brownian motion expectations of fish movement in the seascape.

7.2 French

Cette analyse des données suggère une augmentation générale des concentrations en oxygène en surface et en volume (toutes les Figures), confirmant ainsi un accroissement de la surface et du volume de l'hypoxie. Cette tendance croissante, plus conséquente durant la fin des années 90, s'est poursuivie depuis lors avec une pente plus faible. Cette tendance se manifeste à la fois pour les concentrations en oxygène $[O_2]$<1ml et $[O_2]$<43ml (Figure 1). Les espèces prédatrices ont réagi différemment à cet accroissement global de l'hypoxie. Alors que cette tendance à la hausse est une tendance générale depuis les années 80 (Figure 1), les tendances des prédateurs en matière de masse et de composition des proies varient. Une tendance à la baisse est observée concernant la masse du cabillaud et celle de ses proies (Figure 2), contrairement à la masse du flet pour laquelle une tendance à la baisse est observée(Figure 3, remarquez que la série chronologique du flet est beaucoup plus courte que celle du cabillaud).La distribution des séries chronologiques des classes d'âge du sprat et du hareng montre des tendances opposées pour les 141 sites agrégés. Alors que la classe d'âge 1+ (regroupant toutes les classes d'âge de plus d'un an) diminue pour le sprat (Figure 4), l'inverse se produit pour le hareng (Figure 5). Les classes d'âge du sprat présentent une fluctuation de plus grande amplitude tout au long de la série temporelle, tandis que le hareng ne présente une telle fluctuation de grande amplitude qu'à la fin de la série. Ce schéma pourrait être dû à la sensibilité différente des classes d'âge, spécifiques aux espèces, à l'expansion hypoxique en raison de l'impact direct du manque d'oxygène ou indirectement par le biais des effets sur l'absence de ressources. Dans l'ensemble, ces modèles suggèrent qu'il existe un trait ou un ensemble de traits, tels que la masse ou la taille du corps, qui ont une réponse spécifique à l'espèce, directement induite par la tendance à la hausse de la faible concentration en oxygène ou indirectement par la faible concentration en oxygène qui affecte l'état de santé de la communauté des proies.

Afin d'explorer la force de la réponse spécifique des espèces à l'hypoxie, des analyses supplémentaires ont été effectuées pour contraster la proportion empirique et la proportion attendue d'occurrence des individus dans les trois concentrations d'oxygène, faible, $[O_2]$<1ml, moyenne, 1ml$\leq[O_2]\leq$43ml et élevée $[O_2]$>43ml, pour les quatre prédateurs, le cabillaud et le flet (Figure 6), le cabillaud (Figure 7), le flet (Figure 8), le sprat et le hareng (Figure 9), le sprat (Figure 10) et le hareng (Figure 11). Alors que les proportions empiriques d'occurrence du cabillaud et du flet ne s'écartent pas substantiellement de la proportion attendue pour les trois concentrations (Figures 6 et 7), les proportions pour le sprat et le hareng s'écartent substantiellement et dans des directions différentes en fonction de la concentration d'oxygène. La proportion empirique d'individus trouvés en faible concentration était beaucoup plus élevée que celle théorique pour les deux espèces. Au contraire, la proportion empirique d'individus trouvés dans des concentrations moyennes et élevées était inférieure à l'attente théorique pour les deux espèces. Dans l'ensemble, ces résultats montrent que, dans une mer Baltique de plus en plus hypoxique, la communauté de poissons dépend fortement des espèces. Ces résultats ont été obtenus en explorant les séries temporelles de concentration en oxygène, la masse corporelle comme indicateur de la condition des poissons, ainsi que le contraste entre les proportions d'occurrence empiriques et attendues le long d'un gradient d'hypoxie, en utilisant un mouvement brownien attendu du mouvement des poissons dans le paysage marin.