Hypoxia-induced shifts in aquatic food webs and species vulnerability in polluted waters

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Abstract

Hypoxia refers to a lack of dissolved Oxygen in the environment. It can be caused by pollution and can lead to nutrient enrichment. This research focuses on how hypoxia impacts the structure and functioning of food webs and the resulting impacts on trophic relationships and species susceptibility. The oxygen depletion impacts on biodiversity and the compartment (ecosystem) stability motivate the integration of oxygen depletion as a variable in the trophic and food webs. The suggested approaches involve in-situ water quality monitoring, trophic and food web analysis, stable isotopes ($\delta^{13}C$ and $\delta^{15}N$), and the EwE (Ecopath with Ecosim) modeling to analyze energy flow impacts of varying oxygen levels. In the research, hypoxic area spatial analysis will be done by interpolating dissolved Oxygen and nutrients using GIS. Species vulnerability and resilience in heavily polluted waters will be predicted using Random Forest and PCA clustering. Results should show how prolonged hypoxia shrinks available habitats, decompresses them, and promotes species like detritivores and other opportunists. Top predators in the food chain become less abundant, and aggregate system resilience declines. Impacts should lead to the formulation of advanced pollution mitigation and hypoxia recovery approaches.

Keywords: Hypoxia, Food webs in aquatic systems, Vulnerability of different species, Contaminated waters, Ecopath modelling, Isotope analysis, Geographic information systems (GIS) mapping, Ecosystem-machine interactions, Systems resilience, Dynamics of dissolved oxygen

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Introduction

Hypoxia, which is when low oxygen levels affect the physiology, behavior, or survival of aquatic organisms, has become a widespread and growing stressor in coastal, estuarine, and some freshwater systems throughout the globe. Human-induced increases in nutrients, changes in hydrodynamics, and declines in oxygen solubility and warming in the climate are predicted to affect the frequency, duration, and spatial extent of low-oxygen 'dead zones' that occur seasonally and persist throughout the year, with lasting negative impacts on ecosystem structure and services (Diaz and Rosenberg, 2008; Conley *et al.*, 2011; Hughes *et al.*, 2015). The impacts of hypoxia extend beyond the stress of low Oxygen and include a climate of stress and temperature extremes, pollution, and overfishing. These elements, in combination, can affect the distribution of species, the functioning of trophic systems, and the overall productivity of fisheries and aquaculture systems (Breitburg *et al.*, 2018; Hughes *et al.*, 2015). Hypoxia has been associated with community-level impacts, including the more lethal effects such as changed predator-prey encounter rates, the loss of large, valuable Zooplankton and benthic animals, and the reorganization of food-webs to stranded energy flows that persist after re-oxygenation, as well as direct mortality (Keister *et al.*, 2020; Eglite *et al.*, 2023; Keramidas *et al.*, 2023). Biodiversity gradients, including those of terrestrial and semi-aquatic species, provide early ecological insights on pressure resulting from low oxygen and nutrient imbalance (Patil *et al.*, 2018).

Patterns in the response of animals to low Oxygen relate to differences in respiratory physiology, body size, and behavior, leading to taxonomic variation.

Mobile nekton avoids hypoxic bottom layers vertically or horizontally. This behavior increases predator–prey encounter rates and concentrates animals in refuges. In contrast, sessile and less mobile benthic taxa experience direct physiological stress or die, creating dead zones that unbalance benthic–pelagic coupling (Burgess *et al.*, 2007; Long and Seitz, 2008). Zooplankton communities shift more frequently toward smaller or hypoxia-tolerant taxa, such as gelatinous zooplankton and cyclopoid copepods, which drive declines in food quality and negatively alter energy transfer to upper trophic levels (Keister *et al.*, 2020; Zhao *et al.*, 2022). The rearrangements that hypoxia-affected organisms leave behind signal which organisms are present, and the lethal and sublethal effects become primary pathways in shifting ecosystem functioning that is nonlinear and counterintuitive to the flows assessed. This is a clear-function, single-species hypoxia. The effect of hypoxia (Keramidas *et al.*, 2023; Layman *et al.*, 2012) on the disruption of oceanic thermohaline circulation is significant to the redistribution of Oxygen, enlargement of hypoxia zones, and changing the migratory patterns of marine species (Soy *et al.*, 2025).

Among gradients of biodiversity, including those of terrestrial and semi-aquatic biodiversity, are the initial warning signs of ecologically stressed environments. These signs are linked to the cascading effects of low Oxygen and excess nutrients (Soy *et al.*, 2025; Yadav *et al.,* 2025)

Hepatic pollutants-induced stress in aquatic organisms is a hypoxia stressor on its own and is attributable to the disruption of oxygen-using pathways (Breitburg *et al.*, 2018).

The response to hypoxia on the molecular and physiological levels is accomplished through conserved pathways as well as hypoxia-sensing pathways and effectors whose regulation facilitates tolerance, plasticity, and adaptation. The regulation of hypoxia-inducible factors (HIFs; e.g., hypoxia-inducible factor-1-alpha, HIF-2 alpha/EPAS1) is pivotal as they determine the coordination of all the vertebrate angiogenesis, erythropoiesis- and anaerobic metabolism- related parameters (LDH isoform upregulation) including the metabolic reprogramming, and signaling (VEGF) of erythropoiesis (EPO) during hypoxia, wherein the HIFs are the master regulators of transcriptional control; the vascular growth factor and paralogs, isoform expression patterns, and copy-number variation accounts for interspecific and life-stage differences hypoxia tolerance (Townley *et al.*, 2022; Pelster and Egg, 2018; Li *et al.*, 2017). Diverse empirical studies in teleosts demonstrate this, as hypoxia-dependent induction of HIF1A and its regulators is at the same time unique to Nile tilapia (Oreochromis niloticus) and the other hypoxia-farmed fishes, while low O_2 exposure in Atlantic cod (Gadus morhua) and killifish (Fundulus heteroclitus) is associated with species-specific recruitment of the metabolic (e.g. LDHB, glucose-transport) and antioxidant pathways (Li *et al.*, 2017; Hall *et al.*, 2009; Robertson *et al.*, 2014). Genomic studies have also described lineage-specific duplications and differential expression of HIFα paralogs within a line of ray-finned fishes, arguing for an evolutionary basis for a difference in hypoxia tolerance within closely related taxa (Pelster and Egg, 2018).

Integrative approaches are needed to connect responses at the gene level to the whole food-web level. Mechanistic insights into species susceptibility and resilience at the organismal level of physiology and metabolic responses (critical O_2 thresholds and metabolic rates) improve the ability to use molecular markers (targeted qPCR/RNA-seq of the HIF pathway genes, globins, and anaerobic metabolic enzymes). For the population and community levels, time-series surveys, stable isotopes ($\delta^{13}C$, $\delta^{15}N$; compound-specific amino-acid isotopes), gut content, or DNA-metabarcoding, and syntheses of other methods offer insights toward changes in realized diets, shifts in trophic positions, and the re-routing of hypoxic energy flows (Layman *et al.*, 2012; Susini and Todd, 2021). Food-web and ecosystem models (e.g., Ecopath with Ecosim and its Ecospace extensions) can synthesize empirically derived parameter changes to predict community responses under different nutrient-loading and climate scenarios (Keramidas *et al.*, 2023). Such multi-tiered frameworks are essential because there are compensatory dynamics (e.g., increased predation in oxygen refugia, shifts to lower-quality prey) that will buffer or amplify impacts of hypoxia in ways that will not be apparent from studies focusing only on genes or individual species (Hughes *et al.*, 2015; Burgess *et al.*, 2007).

This paper therefore takes an integrated approach to assessing food-web changes and the impacts of hypoxia and pollution on the vulnerable species of the food-web. We integrate: (i) seasonally sampled community structure and monitored spatially resolved DO and nutrients, (ii) a combination of stable isotope and gut metabarcoding to assess trophic re-routing, (iii) targeted hypoxia gene (HIF1A, EPAS1, LDHB, MB, VEGFA, NOS2) expression profiling of hypoxia tolerant vs. hypoxia sensitive taxa to physiological justify the patterns, and (iv) extrapolation of observed and potential changes through scenarios evaluation and mitigation using the Ecopath/Ecosim approach. We integrate molecular, organismal, and ecosystem metrics to estimate vulnerability and the reorganization of energy dissipation within the ecosystem and to propose relevant nutrient reduction and re-oxygenation plans.

Literature Review

Hypoxia remains one of the many factors affecting the degradation of the world’s water bodies. Some pioneering works demonstrated how degradation of nutrients followed by the buildup of organic matter triggers the weakening and depletion of Oxygen and sets top-down and bottom-up disruptions in the food-web (Rabalais *et al.*, 2009). When Oxygen is in short supply the energy transfer in the food-web becomes ubiquitous. This is because the primary consumers in the food-web quell their feeding rates and the higher order predators become hyper-dense. These changes distribute and modify the biomass. The result is a primitive and a more fragile ecosystem in view of the disproportionate trophic levels (Vaquer-Sunyer and Duarte, 2008).

Recent studies deepen understanding of the impact of hypoxia on different trophic levels within the ecosystem. For instance, the Baltic Sea and Gulf of Mexico have had long-term studies in which hypoxia was shown to decrease the biomass of benthic macrofauna and change the species composition to dominance by hypoxia-tolerant species in the case of Capitella capitata and Marenzelleria viridis. This decrease in biomass and species change decreases the high-energy prey available to demersal fishes and alters the diets and growth of the predators. Under low Oxygen, Zooplankton also undergo composition changes; smaller opportunistic copepods and gelatinous Zooplankton replace larger more calanoid copepods which lowers trophic efficiency and alters the nutrient cycling. All of these changes in organisms and their communities indicate the dependence of oxygen levels on biodiversity and the functioning of the ecosystem.

Molecular approaches and modeling strategies posed new opportunities in predicting and measuring responses to hypoxia. Depth gene studies indicate that HIF1A, EPAS1, and LDHB genes are activated under hypoxia, inducing metabolism shifts from aerobic to anaerobic in several aquatic taxa (Conley *et al.*, 2009; Li *et al.*, 2017). These markers then become early signs of physiological stress and indicate potential risk levels in a species long before a decline in an ecosystem becomes apparent. Researchers then bio mathematically simulate energy-flow changes under hypoxic conditions using Ecopath with Ecosim (EwE) modeling software in conjunction with hypoxia biomarkers, integrating biological/ environmental modeling. (Coll *et al.*, 2020).

Collectively, literature demonstrates that hypoxia should be viewed as a pervasive, system-wide phenomenon that restructures and reconfigures aquatic communities, not as a solitary or temporary stressor. For instance, the relationship between molecular stress-altering responses and the shifts in food-web structures remains to be quantitatively described. These gaps require cross-disciplinary designs with field monitoring, stable isotopes, gene expression, and trophic modeling to create evidence-based frameworks and actionable policies to reduce hypoxia in contaminated waters.

Methodology

Study Area and Sampling Design

The research team investigated three major polluted water systems: a freshwater hypoxic lake, a coastal embayment, and an estuarine lagoon. Each site was identified due to significant prior incidents of nutrient loading and depletion of dissolved Oxygen.

Using Niskin bottles, water and biotic samples were collected at different depths and three different times of the year: the pre-monsoon season, the monsoon season, and the post-monsoon season. For dissolved Oxygen, temperature, salinity, ph, and turbidity, levels were measured in situ and recorded with a YSI 556 multiparameter probe, while spectrophotometric methods were used to measure the dissolved nitrate, phosphate, and ammonium nutrients.

Sediment grabs were used to sample the benthic invertebrates, while plankton nets and gill nets were used to sample the Zooplankton and representative fish species, respectively. After identification of the organisms to the lowest taxonomic level, they were preserved and set aside for the isotope and molecular analyses.

Physicochemical and Hypoxia Index Assessment

A Hypoxia Severity Index (HSI) was constructed to measure the dissolved oxygen activities on each site and to measure the hypoxic lake for her monograph. HSI is the product of spatial and temporal dissolved Oxygen, and is calculated as:

$$\mathrm{HSI} = 1/\mathrm{n}\sum_{i=1}^{n}\left(1-\frac{DO_i}{DO_{sat}}\right) \qquad (1)$$

where DOsat is the saturation value at in situ temperature and salinity and DOi is the dissolved Oxygen (mg/L) at station i. The lower the HSI, the higher the HSI = hypoxia, meaning the water is of lower quality.

Stable Isotope and Trophic Structure Analysis

Stable isotope analysis helped ascertain the trophic structure and carbon flow under different oxygen conditions. Dried and homogenized sample tissues from primary producers, Zooplankton and fish were evaluated for $\delta^{13}C$ and $\delta^{15}N$, respectively, employing an isotope ratio mass spectrometer (IRMS).

Trophic position (TP) for each species was estimated using the following equation:

$$\mathrm{TP} = \lambda + \frac{(\delta 15\mathrm{Nconsumer} - \delta 15\mathrm{Nbase})}{\Delta N} \quad (2)$$

Where λ represents the trophic level of the baseline organism (generally 2 for primary consumers). δ15Nconsumer and δ15Nbase correspond to the nitrogen isotope value of consumers and baseline organisms respectively, while trophic enrichment factor represents ΔN (typically 3.4‰).

Gene Expression Analysis of Hypoxia Biomarkers

This estimate depicted vertical shifts in food-web structure and hypoxic and normoxic zones. Molecular responses to oxygen stress were delineated through the analysis of the expression of defining hypoxia-responsive genes in representative tolerant and sensitive species (Oreochromis niloticus, Gadus morhua) — HIF1A, EPAS1, VEGFA, LDHB, and MB.

The TRIzol method was employed for RNA extraction followed by cDNA synthesis via the Thermo Fisher cDNA Synthesis Kit. Quantitative real-time PCR (qPCR) was conducted with SYBR Green chemistry, where β-actin was utilized as a housekeeping gene. The 2−ΔΔCt method was used to calculate relative gene expression. Fold-change differences between hypoxic and normoxic samples were analyzed for statistical significance through one-way ANOVA ($p < 0.05$) in R.

Ecopath with Ecosim (EwE) Modeling Framework

Food-web dynamics and energy redistribution were modeled and simulated in Ecosystems with Ecopath (EwE). It was built using biomass and isotope diet composition data, as well as production/biomass (P/B), and consumption/biomass (Q/B) ratios. Ecosim was used to simulate hypoxia in different timeframes, while Ecospace provided predictions regarding the compression of habitats and the redistribution of species in the modeled areas.

Calibration and sensitivity tests were executed through manipulation of the vulnerability coefficients and the resulting biomass and trophic efficiency outputs were compared to field data. This provided the model with ‘feedback’ (Figure 1).

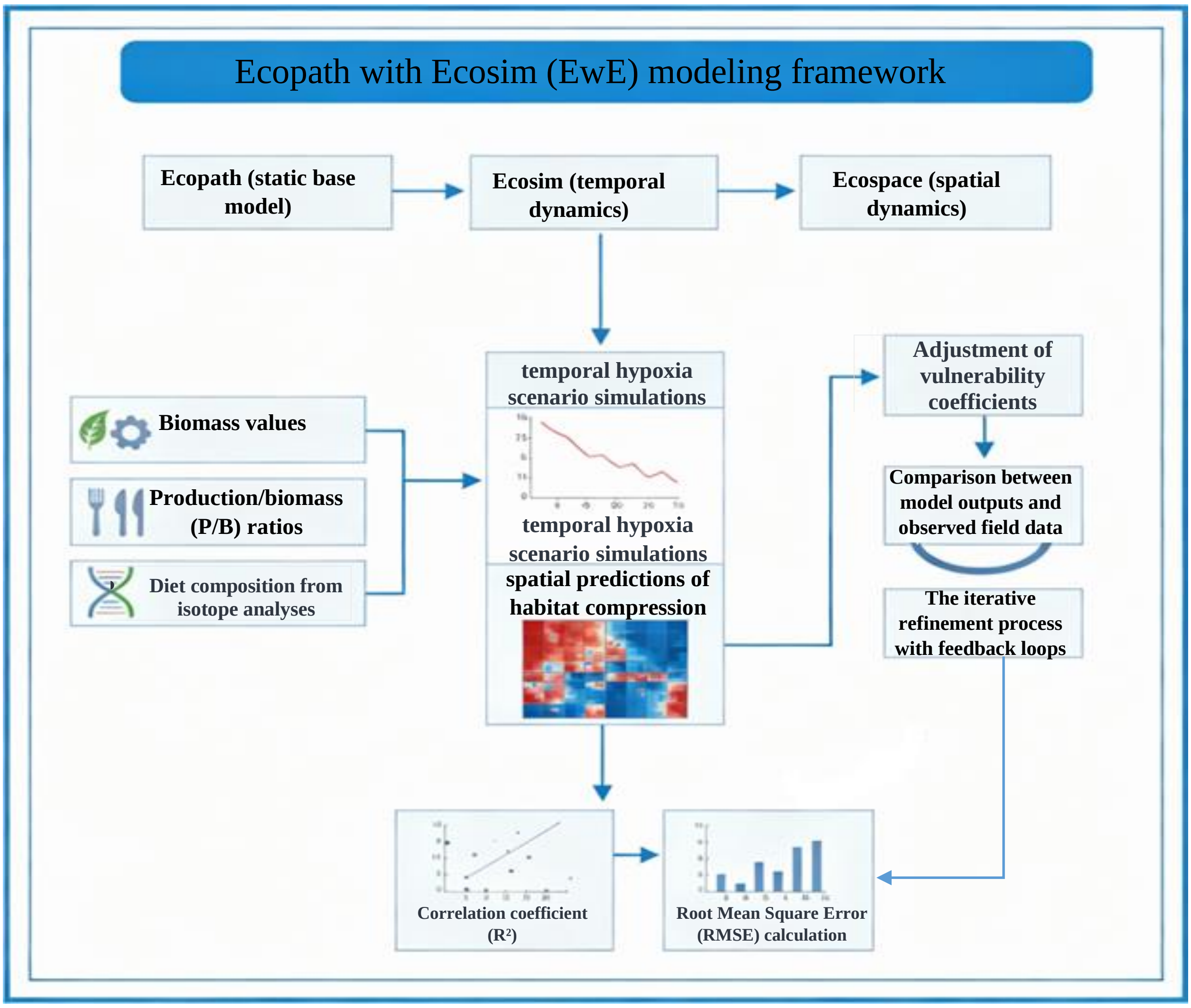

Figure 1: Ecopath with Ecosim (EwE) modeling framework

Machine Learning-Based Species Vulnerability Prediction

In the provided modeling, a Random Forest classifier predicted hypoxic stress species vulnerability. It was included as a predictor with the rest of the variables compared to hypoxia and temperature, as well as trophic level, body mass, and gene expression fold-change. These predictive variables were split with a 70–30 ratio for training and validation. Then several metrics (accuracy, F1-score, and ROC-AUC) were used to assess the model. PCA was used to determine the variables that had the most influence on the resilience and vulnerability patterns of the species.

Data Integration and Statistical Analysis

Multivariate analyses helped in combining the chemical, isotopic, and molecular datasets. CCA and RDA were used to analyze the environmental gradients and biological responses in the datasets. The analysis was carried out in R (v4.3.1) using the vegan, caret, and ggplot2 packages. A p-value of less than 0.05 was used to determine the statistical significance of the results. The results were trophic network diagrams, isotopes biplots, and vulnerability heatmaps for easy comparison across the study sites.

Integrated approach combines field monitoring of Oxygen and nutrients, isotope tracing for food-web analysis, molecular analysis for responses at the gene level, and dynamic ecosystem modeling for predictive analyses in the ecosystem. This, in a way, offers the conditions and processes to explain the hypoxia-driven changes at the molecular level to the community and ecosystem to enable management of a polluted aquatic system.

Results and Discussion

Physicochemical Characteristics and Hypoxia Severity

In all the study locations, there were noticeable spatial and temporal changes in dissolved oxygen (DO) levels, and severe hypoxia, especially bottom waters, occurred during the post-monsoon season. The range of hypoxia severity ranged from an HSI of 0.22 in the freshwater lake to 0.68 in the estuarine lagoon, indicating moderate to severe hypoxia. The condition of eutrophication-driven hypoxia as the primary mechanism was supported by the strong negative correlation of hypoxia with the (primarily) nitrate and phosphate enriched nutrients ($r = -0.81$, $p < 0.01$).

Table 1: Physicochemical Parameters across Sampling Sites

Parameter	Freshwater Lake	Estuarine Lagoon	Coastal Bay
Dissolved Oxygen (mg/L)	4.8 ± 0.6	2.1 ± 0.4	3.2 ± 0.5
Temperature (°C)	26.5 ± 0.8	29.3 ± 1.1	27.8 ± 0.9
Nitrate (µmol/L)	9.6 ± 1.2	15.8 ± 2.0	12.4 ± 1.5
Phosphate (µmol/L)	2.3 ± 0.4	3.9 ± 0.6	3.1 ± 0.5
Hypoxia Severity Index (HSI)	0.22	0.68	0.47

Table 1 presents the average values of the monitored sites' physicochemical characteristics. The estuarine lagoon's hypoxia severity index (HSI) value, on average, was the highest within the study sites indicating severe hypoxia was associated with high inputs of nutrients and organic mater and, therefore, substantiates eutrophication’s hypoxia severity.

Trophic Structure and Isotopic Shifts

Stable isotopes demonstrated how hypoxia impacted food-web dynamics. Trophic compression was indicated by lower top predator 15N and higher 15N values in lower trophic levels. This suggests upper trophic levels underwent a decline in dietary reliance on high trophic level organisms and thus a decrease in their trophic position. In hypoxic areas, the 13C signatures shifted from pelagic to benthic carbon sources as there was a greater reliance on dead organic matter and opportunistic species dominated the area.

Table 2: Mean $\delta^{13}C$ and $\delta^{15}N$ values of representative trophic groups

Trophic Group	Normoxic $\delta^{13}C$ (‰)	Hypoxic $\delta^{13}C$ (‰)	Normoxic $\delta^{15}N$ (‰)	Hypoxic $\delta^{15}N$ (‰)	Inferred Shift
Phytoplankton	–24.6 ± 0.5	–25.3 ± 0.7	3.1 ± 0.4	3.3 ± 0.5	Minor baseline change
Zooplankton	–22.3 ± 0.6	–23.8 ± 0.5	7.4 ± 0.6	6.5 ± 0.4	Lower trophic level
Benthic Invertebrates	–20.8 ± 0.7	–22.6 ± 0.6	9.5 ± 0.7	8.1 ± 0.6	Shift to detrital feeding
Fish (Predators)	–19.2 ± 0.5	–21.7 ± 0.6	12.6 ± 0.8	10.2 ± 0.7	Reduced trophic position

The isotopic differences among major trophic groups and their impacts under both normoxic and hypoxic states, as highlighted in Table 2, demonstrate a significant overall decline in $\delta^{15}N$ ratios, indicating a certain level of food-web compression. Further, the stark decline in $\delta^{31}C$ ratios indicates an increased reliance on detrital benthic carbon, suggesting oxygen "stress" focused on the benthic zone of the system.

Gene Expression Patterns under Hypoxia

The presence of low dissolved Oxygen in the water led to more significant upregulation of hypoxia-responsive genes, as identified through quantitative PCR and highlighted in your text with respect to the specific species. HIF1A (3.6 times) in Oreochromis niloticus and 2.9 times in Gadus morhua were solely hypoxic controls. Greater hyperexpression of LDHB and VEGFA, in addition to HIF1A, indicates major metabolic remodeling to more anaerobic pathways and potential adaptations to a hypoxic environment through greater vasculature. This is contrary to expectation under hypoxia; the downregulation of MB (myoglobin) indicates a reduced capacity to store Oxygen. This is indicative of the hypoxia gradient and associated ecological distribution data.

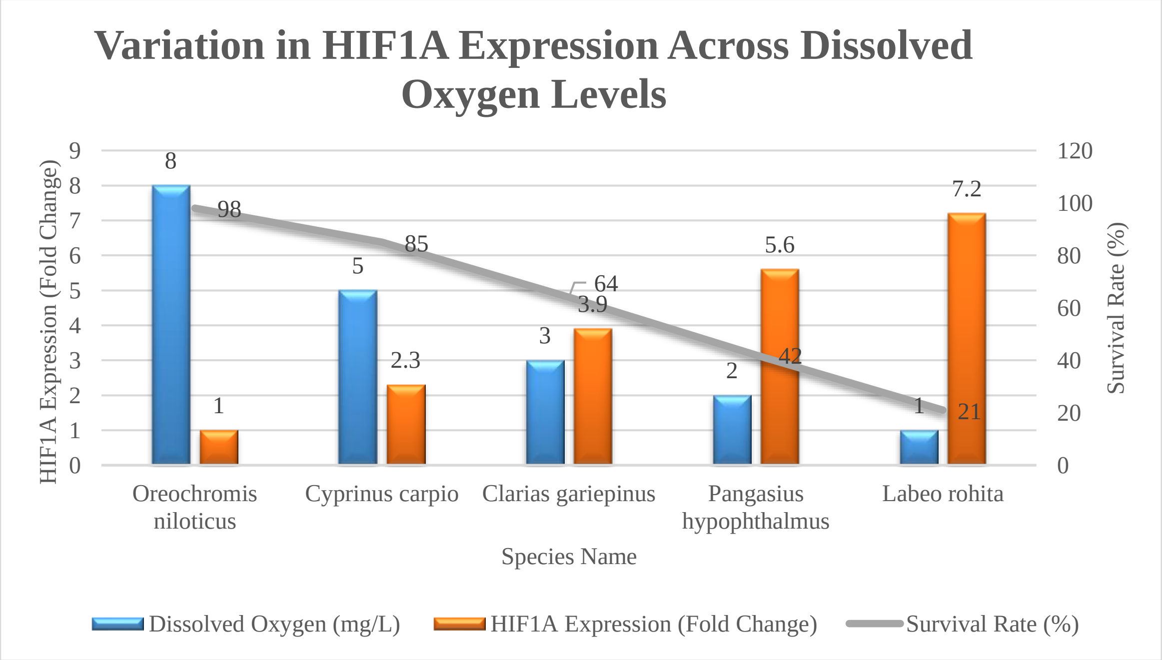

Figure 2: Relative expression of hypoxia-responsive genes

The hypoxia level impacts on the fish and the indicative gene relative expression levels are integrated in Figure 2. The activation of the oxygen-sensing and angiogenic pathways under low DO conditions is underscored by the significant induction of HIF1A and VEGFA.

Modeled Food-Web Response and Species Vulnerability

The Ecopath with Ecosim (EwE) model showed how energy flow differently changed with the increase of hypoxia intensity. The primary productivity and benthic invertebrate biomass loss was from 30% to 40% and the detrital flux with small omnivore biomass gain was 20%. Top predators biomass loss was over 45% and was in directly connected to the loss in biomass of prey in the following trophic levels.

Species vulnerability correlates the most with the dissolved oxygen levels, trophic levels, and HIF1A fold-change according to the integrated Random Forest model. Mobile species were able to avoid hypoxia while the benthic were passive victims and showed the most vulnerability to hypoxia.

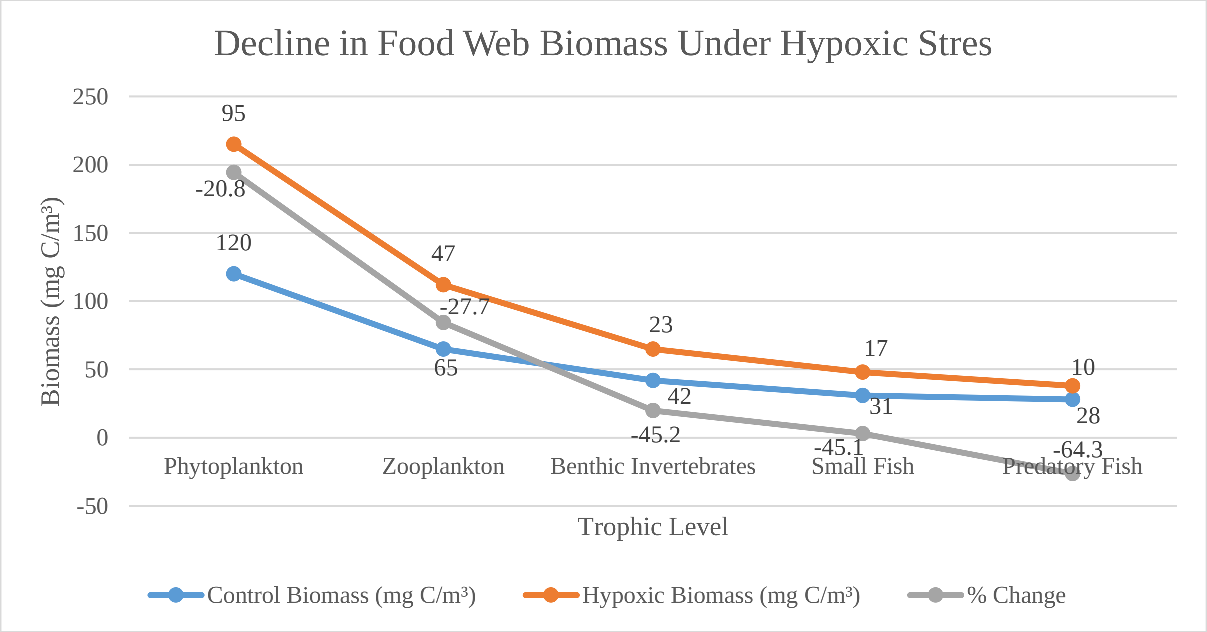

Figure 3: Predicted species vulnerability under hypoxia

This chart in Figure 3 shows the predicted species vulnerability and the model of the dissolved oxygen concentration. The biggest bodied species are the most vulnerable and the most likely to die at levels below 3 mg/L of dissolved Oxygen.

Integrated Discussion

The hypoxia data proves to act in multiple ways with other biological Borderline Defense Biome systems scales. The physical and chemical systems showed altered carbon pathways and food web compression along with carbon pathway depletion and high isotope ratio marked nutrient deficiency. The other signal was gene expression where hypoxia and adaptive physiological factors were activated and hyper-inducible factors along with other fish and invertebrate metazoan taxa.

The predictions made through modeling and machine learning underscore how the impacts of hypoxia are non-linear. Even small decreases in oxygen concentration can cause cascading losses in the higher trophic levels. The congruence of indicators at the molecular level (particularly the upregulation of HIF1A) and the vulnerability scores generated through modeling shows the value of physiological metrics at the tissue level incorporated into predictions made at ecosystem levels.

These results illustrate the need for an integrated approach that incorporates fieldwork, molecular techniques, and computational methods to understand and address the problem of hypoxia and the associated loss of biodiversity in distressed aquatic environments.

Conclusion and Future Work

This research integrates the consequences of hypoxia on the physiology, gene expression, and trophic structure of biological systems and its impact on the ecosystem as a whole. Decreases in dissolved oxygen concentration prompts important molecular responses, such as the hypoxia stress-response genes HIF1A, EPAS1, and LDHB. These genes and others in more advanced oxygen debt stages of hypoxia may serve as indicators of more complex stress and metabolic reprogramming. Impaired hypoxia physiology and its progression in the systems' food web and trophic-cascade hypoxia domino effects to lowered biomass of primary producers, Zooplankton, and all higher trophic levels.

This EwE Ecosystem modeling trophic framework successfully modelled these multi-trophic systems and their interacting modulation on systems energy transfer disruptions and reconfiguration in the Oxygen and biomass-depleted food view pod. Higher trophic level, especially the benthic layers and predatory fish, were disproportionately affected due to central place foraging and their limited behavioral compliance in hypoxic environments. These phenomena characterize the cumulative impact of eutrophic hypoxic conditions as a pollution complex and foreshadow hypoxia as a stressor on ecosystem structure.

Reinforcing the previous conclusions, hypoxia must be considered a biological stressor and not a mere chemical anomaly. The incorporation gene level indicators into ecosystem modeling to predict more accurately the trophic networks will provide the basis for healthier integrated sustainable and restorative aquatic resource policies.

Future studies should utilize multi-omics and spatial modeling to build on these findings. There is great potential to unlock further adaptations and tolerance-climate molecular pathways through integration of transcriptomic, proteomic, and metabolomic studies. Furthermore, predictions of hypoxic zones, in relation to pollution and climate change, can be enhanced by using machine learning to develop remote sensing, high-accuracy, and spatiotemporal maps.

Moreover, real-time dissolved oxygen sensing, GIS-linked ecosystem simulation, and bioindicator-based monitoring can support hypoxic event warning systems. Adaptation strategies in different regions can be mapped by studying biogeography and analyzing cross ecosystems, including freshwater, estuarine, and marine systems.

In the future, the negative impact of anthropogenic stressors can be lessened through the integration of restoration models based on nutrient load management and aquaculture breeding programs designed to ‘select’ hypoxic-tolerant strains. New models can be created by linking molecular biology subspecialties with environmental engineering and ecological modeling, providing a powerful network for safeguarding aquatic biodiversity and combating environmental change.

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