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Hypoxia zone and functional group losses in zooplankton community structure

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Abstract

The oxygen in the oceans is decreasing, and this topic is little commented on in scientific studies. The reduction in oxygen occurs mainly in places that receive a greater availability of nutrients, either naturally or anthropically, which increases the excessive proliferation of phytoplankton that develop the hypoxic zones. Hypoxic zones are increasing with the effects of land use and fertilizers, global warming, and climate change among other reasons. In this review, the following were analyzed: 1) hypoxia zone increase associated with natural anthropogenic effects such as: eutrophication, global warming and climate change, 2) the correlation found in pelagic food web with loss of functional group with emphasis on zooplankton community as a response to adaptations in the hypoxia zone. Hypoxia zones have been causing changes in the food web on a global scale, and this effect becomes even more evident if steps are not taken to reduce effluents and environmental imbalances.

Keywords: nutrients; food web; anthropogenic effects; global warming; climate change.

Zona hipóxia e perdas de grupos funcionais na estrutura da comunidade zooplanctônica

Resumo

O oxigênio nos oceanos está diminuindo, e esse tema é pouco comentado em estudos científicos. A redução do oxigênio ocorre principalmente em locais que recebem maior disponibilidade de nutrientes, seja de forma natural ou antrópica, o que aumenta a proliferação excessiva de fitoplâncton que desenvolve as zonas hipóxicas. As zonas hipóxicas estão aumentando com os efeitos do uso da terra e dos fertilizantes, do aquecimento global e das mudanças climáticas, entre outros motivos. Nesta revisão, foram analisados: 1) o aumento da zona de hipóxia associado aos efeitos antropogênicos naturais, tais como: eutrofização, aquecimento global e mudança climática; 2) a correlação encontrada na rede alimentar pelágica com a perda do grupo funcional, com ênfase na comunidade de zooplâncton como resposta às adaptações na zona de hipóxia. As zonas de hipóxia têm causado mudanças na rede alimentar em escala global, e esse efeito se tornará ainda mais evidente se não forem tomadas medidas para reduzir os efluentes e os desequilíbrios ambientais.

Palavras-chave: nutrientes; teia alimentar; efeitos antropogênicos; aquecimento global; mudança climática.

Zona hipóxica y pérdida de grupos funcionales en la estructura de la comunidad de zooplancton

Resumen

El oxígeno de los océanos está disminuyendo, y este tema es poco comentado en los estudios científicos. La reducción del oxígeno se produce principalmente en lugares que reciben una mayor disponibilidad de nutrientes, ya sea de forma natural o antrópica, lo que aumenta la proliferación excesiva de fitoplancton que desarrolla las zonas hipóxicas. Las zonas hipóxicas están aumentando con los efectos del uso de la tierra y los fertilizantes, el calentamiento global y el cambio climático, entre otras razones. En esta revisión se analizaron: 1) el aumento de las zonas de hipoxia asociado a efectos antropogénicos naturales como: eutrofización, calentamiento global y cambio climático, 2) la correlación encontrada en la red trófica pelágica con la pérdida de grupo funcional con énfasis en la comunidad de zooplancton como respuesta a las adaptaciones en la zona de hipoxia. Las zonas de hipoxia han venido provocando cambios en la red trófica a escala mundial, y este efecto se hace aún más evidente si no se toman medidas para reducir los efluentes y los desequilibrios medioambientales.

Palabras clave: nutrientes; red alimentaria; efectos antropogénicos; calentamiento global; cambio climático.

1 Introduction

The zooplankton community is composed of organisms metazoans, being represented by many invertebrates, such as Hydrozoa, Copepoda, Cladocera, Pteropoda, Chaetognatha, (Rosa; Batista; Monteiro-Ribas, 2020; Rosa *et al*., 2021; Rosa; Monteiro-Ribas; Fernandes, 2016), fish eggs and larvae (Rosa *et al*., 2016), among others. Within the zooplankton community coastal marine, copepods play an important role in energy flow, since the transfer of energy from phytoplankton to higher trophic levels occurs through zooplankton (planktonic animals), which are important for secondary production in pelagic ecosystems (Nocera; Dumont; Schloss, 2020). In vertical migration, copepods move upwards where phytoplankton are found to feed at night and downwards at dawn to protect themselves from predators, providing an export of carbon, which contributes to marine snow, mainly through the sinking of fecal pellets (zooplankton), dead organisms and detritus (La *et al*., 2018; Nocera; Dumont; Schloss, 2020; Son *et al*., 2023). Thus, part of the atmospheric carbon fixed in organic matter is transferred through the trophic chain and is retained on a biological timescale (Weber *et al*., 2016). When it reaches the seabed, some of this carbon is incorporated into the benthic trophic web and some is buried and enters the geological cycles (thousands of years) (Stasko *et al*., 2018).

Copepods are often the dominant organisms (90%) of the coastal marine zooplankton assembly and recent studies have confirmed the dominance of copepods in estuaries (Valentin *et al*., 2021), as well as hypersaline estuaries (Rosa; Batista, 2020) and in oceanic regions (Bonecker *et al*., 2014). In addition, they are excellent indicators of water characteristics (i.e. temperature, salinity and nutrient availability) (Björnberg, 1981; Dias; Araujo, 2006; Rosa; Batista; Monteiro-Ribas, 2020; Leonor; Muxagata, 2024). Due to the diversity of shapes and sizes of organisms, copepods occupy a variety of ecological niches and show physiological plasticity (Rosa *et al*., 2023).

Seasonality has an influence on the composition and abundance of the copepod assemblage, since during the rainy season (spring and summer) estuaries receive a much higher amount of organic matter than during the dry season (winter and fall) (Silva-Junior; Paranhos; Vianna, 2016; Valentin *et al*., 1999), which consequently provides a greater availability of food (phytoplankton) for copepod assemblage (Hunt *et al*., 2017). However, phytoplankton biomass can also increase due to anthropogenic effects such as the discharge of effluents that favor the disorderly proliferation of phytoplankton. Impacts by effluents can also harm the diversity of the copepod assemblage, since it is the eutrophication sites that have a high phytoplankton biomass, but despite their abundance they are of low quality and not palatable or toxic (Jessim, 2020). In these areas, the copepod assemblage suffers in terms of predation, growth, egg production and food quality, among other factors (Elliott; Pierson; Roman, 2013).

Changes in food habits, composition and diversity in the copepod assemblage may also be related to other factors such as changes in temperature, salinity and climate change (Mcginty *et al*., 2021; Leonor; Muxagata; 2025), which cause alterations in the functioning of the marine ecosystem, with a direct impact on fisheries production on a global scale (Karl, 1999; Pompeu; Godinho, 2003). Identifying patterns of species composition and associations in the plankton makes it possible to assess or monitor the effect of climate change and other environmental variations, from regional to global scales (Brandão *et al*., 2021; Kaartvedt, 2008).

Zooplankton is very sensitive to changes in temperature, salinity, and dissolved oxygen (DO). However, when DO is present in low concentration in many marine environments, it is called a hypoxia zone (Steube; Altenritter; Walther, 2021). Hypoxia is considered to be a low oxygen concentration (2 mg.L^{-1}) and thereby causes a stress on the organisms present in the aquatic environment (Breitburg *et al.*, 2018; Roman *et al.*, 2019). Hypoxia occurs mainly in eutrophic places, can be natural as in estuarine plume regions (Castello; Krug, 2015), upwelling (Chen *et al.*, 2022) and by anthropogenic action (Horta *et al.*, 2021) (Table 1).

Eutrophicated sites have a high phytoplankton biomass, but little energy transfer occurs to the upper trophic levels, because despite the abundance of phytoplankton they are of low quality, not palatable or toxic (Jessim, 2020). In these areas, the zooplankton community is impaired in terms of grazing activity, predation, growth, egg production, among other factors (Elliott; Pierson; Roman, 2013) (Table 1).

Water temperature controls both oxygen solubility and metabolic demand of aquatic organisms. Thus, to assess the impacts of hypoxia, it is necessary to consider the effects of temperature, both on oxygen availability and on the metabolism of organisms. One of the consequences of global warming is climate change, which has been increasingly documented, but its relationship to worsening hypoxia, is still underreported on a global scale (Roman *et al.*, 2019).

Evidence on a global scale has shown that the concentration of DO in the oceans is decreasing over the years (Breitburg *et al.*, 2018; Vaquer-Sunyer; Duarte, 2008) and this is related to the increase of organic matter by the excess nutrients released into the marine environment (Breitburg *et al.*, 2018). As well as climate change, which is also causing a change in the biogeochemical cycle of the oceans, which in turn increases oxygen consumption (Breitburg *et al.*, 2018). Hypoxic zones are also growing in spatial scale (Roman *et al.*, 2012) and temporal (Lashaway; Carrick, 2010). The thermal change begins most often in late spring and/or early summer, when the surface temperature inhibits vertical water mixing, and with it an aggravating reduction in DO, especially in tropical environments (Vigouroux *et al.*, 2021) (Table 1).

Thus the objectives of this review are: 1) examine the main published information on hypoxic zones that cause zooplankton stress at eutrophication sites (estuarine plume, upwelling and anthropogenic activity); 2) analyze the factors that influence the migration of zooplankton between the hypoxia zone and the zone of higher DO availability (surface); 3) the correlation found in pelagic trophic chains with the loss of functional groups with emphasis on the zooplankton community and its adaptations in the hypoxia zone; 4) evaluate the results found in the last decade on the relationship between trophic interactions and stress. This review will focus on the patterns and zone of hypoxia of the zooplankton community in coastal regions.

Table 1. Definitions of terminology and their interaction with the hypoxic zone used in the review (continued)

Term	Concept	Reference
Eutrophication	Hypoxia, triggered largely by eutrophication, exerts a great deal of stress on coastal ecosystems. The increase in nutrients due to natural, but mainly anthropogenic, causes a very high proliferation of microalgae and, as a consequence, a reduction in oxygen, conditioning many species to live in stressful environments.	Breitburg *et al.*, (2018)
Estuarine Plume and Upwelling	In estuarine plumes and upwelling areas, eutrophication occurs naturally, but there is also a hypoxic zone that can cause stress as well as anthropogenic eutrophication.	Chen *et al.*, (2022)
Climate Change	Water temperature controls both the solubility of oxygen and the metabolic demand of an aquatic ecosystem. Hypoxia is increasing with climate change. Therefore, in order to assess the impacts of hypoxia, it is necessary to consider the effects of temperature on both oxygen availability and animal metabolism.	Roman *et al.*, (2019)

Table 1. Definitions of terminology and their interaction with the hypoxic zone used in the review (conclusion)

Term	Concept	Reference
Trophic interactions under stress	In an environment with a hypoxic zone, zooplankton need to adapt to stress (hypoxic zone) or to a local surface with high oxygen availability and many predators.	Steube *et al.*, (2021)
Zooplankton dispersal	Most zooplankton groups prefer to locate themselves near the surface where there is a higher concentration of oxygen, but other groups resort to the hypoxic zone to avoid predators. However, not all groups and/or life stages are able to maintain stress for a long period of time.	Steube *et al.*, (2021)
Loss of Functional Groups	Zooplankton is the link between primary production and subsequent trophic levels and the loss of one species can have an irreparable impact on the trophic chain.	Tang; Yang; Sun, (2022)

Source: Prepared by the author (2024)
Note: Citations do not necessarily indicate the author who introduced the term, but rather the reference where a widely used definition can be found.

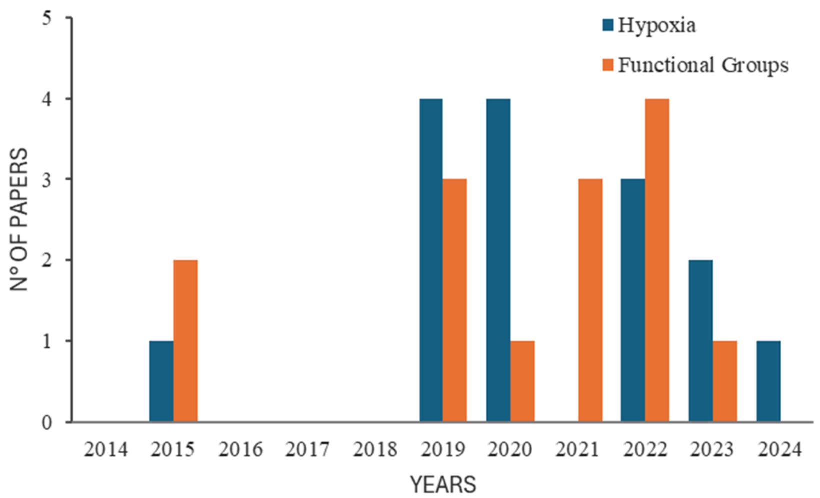
2 Material and Methods

The production of general knowledge on hypoxic zones and loss of zooplankton functional groups was analyzed in this systematic review based on scientific articles with less than ten years of publication, where the following protocol was created to systematize the searches and data analysis: 1) eutrophication and its potential for hypoxic zone formation; 2) hypoxic zone and its consequences for the copepod assemblage; 3) loss of functional group and its direct relationship with the hypoxic zone; 4) extracting the data from the studies found; 5) synthesizing the data extracted; and 6) describing the main results or trends. Thus, a primary definition of the exclusion criteria and insertion of the articles into the systematic review database was carried out. The articles were first selected by their abstracts and then by their results, after which they were assessed and considered for their relevance to this study when compared to the objectives presented here.

3 Results

The results of the database search returned to a total of 29 articles, 15 of which were in the hypoxic zone and 14 on functional groups. 2019 and 2020 were the years in which the most articles were published on marine zooplankton in the hypoxic zone and 2022 was the year with the most publications on marine zooplankton with functional groups. In 2014, no articles were found on either topic, nor in the period from 2016 to 2018 (Figure 1). The following keywords were used to search for articles on marine zooplankton: functional group losses, functional group zooplankton, functional group copepods, functional group losses cladocera, hypoxia zooplankton, hypoxia copepods, hypoxia cladocera, hypoxia marine, hypoxia upwelling zone, hypoxia estuary.

Figure 1. Number of articles published per year during the period 2012-2022, which contain a study of functional groups and hypoxia in zooplankton in the title or abstract



Source: Prepared by the author (2024)
Note: The search was carried out on the Web of Science database.

3 Loss of functional group and hypoxia zone in zooplankton dispersal in the food web

In the coastal region as areas currently exhibiting signs of eutrophication that are at risk of developing hypoxia, in the last 65 years, there has been a tenfold increase in the number of hypoxic areas resulting from eutrophication. However, in the last decades, a reduction of hypoxia is occurring mainly in North America and Europe, well-studied locations when compared to other places in the world (Diaz; Rosenberg; Sturdivant, 2019).

The largest natural form of eutrophication occurs in upwelling regions such as Arraial do Cabo, off the coast of Brazil (Rosa *et al.*, 2023), in the coastal region of California (United States) (Quilfen *et al.*, 2021), in Chile (Rivera *et al.*, 2023) and in southern Benguela (Angola) (Ortega-Cisneros *et al.*, 2018). Although upwelling is a form of natural eutrophication, hypoxia zone can also be found. The association between the impact of upwelling and hypoxia is still poorly reported on a global scale (Chen *et al.*, 2022).

The continental inputs, which generate estuarine plumes due to the high freshwater inflow, are the main sources of nutrients for the coastal region (Guinder *et al.*, 2015). The region between the limit of the estuarine plume and the sea, has high primary productivity and concentrates organisms of different trophic levels (Castello; Krug, 2015).

Environments that have combinations of estuarine plume and coastal upwelling, as in the Changjiang estuary and the East China Sea, are among the best known hypoxic aquatic environments. Upwelling pushes oxygen-poor water to the surface and together with the estuarine plume provides a hypoxia zone. Furthermore, combined with the offshore effect that shifts the coastal water mass into the ocean that amplifies the spatial distribution of the hypoxia zone. Despite this great relevance for hypoxia zone studies the Changjiang estuarine and East China Sea is still poorly studied (Wei *et al.*, 2021).

The interference of the hypoxia zone in the ecosystem can lead to a lack of functional group in the zooplankton community. Due to its ecological importance, its loss in relation to environmental changes will impact the relationships in the functioning of the ecosystem (Tang; Yang; Sun, 2022).

In order to understand the trophic interactions of different groups in the Sontecomapan, a tropical estuarine in the southern Gulf of Mexico, Sanvicente-Añorve *et al.* (2022) explained the relation of zooplankton in this environment where collections were made in the upper and lower zones of the estuarine, since it was expected to find different species in the two zones with different feeding habits. On the surface, herbivorous filter-feeding organisms were found, with high or medium transparency, and that it is easier to float. In this group were classified the Hydromedusa, Thaliacea, Ostracoda, Cladocera Heteropoda, Pteropoda and Chaetognatha. In the lower part predators predominate, with average or low transparency, and which use their appendages for vertical buoyancy or have faster swimming for protection against predators. In this group were the Luciferidae, Mysidacea, Copepod, Decapoda, and the fish larvae.

In the study by Zheng *et al.* (2022) of seasonal changes in the Changjiang River estuary in China, it is showed that in spring and winter it favored the smaller herbivores like Copepod. With the rise in temperature and the summer runoff, there has been a change in zooplankton community for larger herbivores and carnivores. The functional group and diversity can also vary according to the seasons.

In the world's largest hypersaline estuarine, salinity is an environmental factor little addressed in functional group loss but is also one of the main factors providing changes in zooplankton composition and abundance. These changes have recently been noted by Rosa and Batista (2020), which found a salinity variation over decades and this reflected in the zooplankton community. In the years 2012 to 2013, Rosa e Batista (2020) found dominance of *Acartia tonsa* and Cirripedia larvae at a mean salinity of 46, but Rodrigues (1998) in the years 1993 to 1995 found dominance of *Oithona hebes* and Mitilidae larvae with an average salinity of 52 and in the 1970s Monteiro-Ribas (1978) found Copepod dominance *Acartia lilljeborgi* with an average salinity of 64.

The loss of functional group, as well as hypoxic zones, are also related to global warming, because temperature has a direct relationship with the composition of the plankton, due to the different tolerance ranges of the species. The change in phytoplankton composition requires an adaptation in the feeding habits of zooplankton and other trophic levels, which often cannot be restructured, thus causing a change in the ecosystem (Brandão *et al.*, 2021; Kaartvedt, 2008). Brandão *et al.* (2021) evaluated the Copepod assemblage in Polar, Temperate and Tropical zones, with different Copepod families that changed according to the localities studied. However, constant temperature changes due to anthropogenic effects can permanently impact on the food web (Richardson, 2008).

The trophic interactions of the zooplankton community are also directly related to the problems of hypoxia and anoxia, which must be taken into account, because when hypoxia stresses fish, crabs, shrimp, and other organisms, they swim to areas of higher oxygen concentration, gathering in dense assemblages along the edge of low oxygen zones. This phenomenon is the origin of the term dead zone, a place where fishermen find nothing to catch due to the migration of mobile animals out of the affected area. With this, it becomes a habitat that encourages the "escape" of pelagic organisms and the death of sessile ones. Organisms experience lost growth potential due to a shift to less suitable habitat and increased competition for resources through crowding (Diaz; Rosenberg; Sturdivant, 2019).

Hypoxia can restructure the food web in relation to different predators and prey, where some species with higher stress tolerance are able to take refuge in a zone with low oxygen. This can occur at certain opportune moments or continuously when the organism is resistant because it has the appropriate physiological conditions (Elliott; Pierson; Roman, 2013).

For example, copepodites (non-mature adult stage of copepoda) can be abundant in the hypoxia zone to take refuge from predators and thereby offset the consequences of stress in this zone. The copepodites of *Acartia tonsa* have low buoyancy and are located closer to the bottom. The hypoxia zone can cause nauplii mortality, but not that of copepodites (Elliott; Pierson; Roman, 2013). The Ctenophora Mnemiopsis leidyi, are also tolerant of low oxygen levels when compared to fish in the Chesapeake Bay and can use hypoxic areas that fish cannot tolerate (Breitburg *et al*., 2018).

In general, the most abundant zooplankton groups like Appendicularians, Cladocerans and Copepods have higher biomass in the upper layer compared to the lower layer of the water column (Batziakas *et al*., 2020). Adult copepods may be avoiding hypoxic conditions, but this can lead to predation mortality in the upper layer. Zooplankton organisms eventually reduce in abundance under these conditions. This pattern was observed in the Chesapeake Bay, where zooplankton abundance is highest at the surface and where increased predation mortality occurs. To avoid predation, zooplankton needs to resort to the hypoxia zone on the bottom (Elliott; Pierson; Roman, 2013).

There are still few studies of the effect of hypoxia on trophic interaction between predators and prey along the marine food web (Batziakas *et al*., 2020). The hypoxia zone can be a paradox for fishery production, because in the short term, can result in an increase of fish in the local fishery, when the fish assembly is compressed in the minimum high oxygen zone. However, in the long term, these conditions are unsustainable and can result in ecosystem collapse (Breitburg *et al*., 2018).

Some demersal and pelagic fish are avoiding environments that seasonally suffer from hypoxia due to stress (Breitburg *et al*., 2018). On a global scale the temperature is usually higher in spring and summer, and this intensifies eutrophication (Vigouroux *et al*., 2021).

In summary the losses of functional groups in the zooplankton community can occur naturally as well as seasonally, temperature changes in upwelling region, but with global warming may impact the community and subsequent trophic levels. The trophic interaction between the zooplankton community and its potential predators (planktonic fish) compromises not only the zooplankton in the short term but also in the long term, as they are heavily preyed upon by the planktonic fish at the surface. However, these issues have been addressed little in scientific articles in the last 10 years.

4 State of the art on functional groups of marine zooplankton

Most functional group loss studies focusing on the analysis of community structure and related issues on marine zooplankton in Brazil have been mainly descriptive. Although the composition and spatial distribution of several taxonomic groups are currently well known, some groups, such as heterotrophic protists, ctenophores, turbellarians and ostracods, remain unstudied. Ecological studies aim to understand the mechanisms that control trophic interactions within pelagic food webs, secondary production cycles in relation to the physical environment and the distribution of zooplankton (Lopes, 2007).

Environmental variables, where conditions can favor certain functional groups, thus dictate how the ecosystem is functioning. For example, on the west coast of Vancouver Island, Canada, the similarity of functional characteristics in the southern shelf area was investigated and the relative contribution of various zooplankton functional groups to overall biomass showed no temporal trends, but some groups increased or decreased their abundance contributions. This suggests functional redundancy within groups, as smaller or larger species can dominate based on environmental conditions (Venello *et al*., 2021).

Temperature and nutrient concentration are the first-order factors that control latitudinal patterns of richness, while environmental conditions associated with upwelling systems, boundary currents and oxygen minimum zones modulate the position of richness peaks. The average annual species richness of all species diversity group patterns decreases from low to high latitudes, but the slope and shape of this decrease vary significantly according to the species diversity patterns of the plankton functional groups. Pteropods, small copepods and salps show the steepest latitudinal gradients, while amphipods and the three phytoplankton groups show the weakest gradients. The richness of all the patterns of species diversity of plankton functional groups increases with net primary production but decreases with particle size and the efficiency of the biological carbon pump. The species diversity patterns of the plankton functional groups remain poorly understood, although they are very important for the functioning of marine ecosystems (Benedetti; Gruber; Vogt, 2023).

The study by Benedetti *et al*. (2024) compares the facets of functional diversity that respond to species richness with varying strength and direction: functional richness, divergence and dispersion increase with species richness, while functional uniformity and dissimilarity of characteristics decrease. We found that primary production, mesozooplankton biomass and carbon export efficiency decrease with species richness, functional richness, divergence and dispersal. This suggests that the functioning of the ecosystem may be disproportionately influenced by the characteristics of a few dominant species.

In summary, environmental variables are directly related to the loss of functional groups, temperature, nutrient concentration and phytoplankton blooms. In addition, carbon export is related to a reduction in zooplankton community richness, functional richness, divergence and dispersion. The studies presented here are descriptive, so there is a need for more advanced sampling technology and analytical methods.

5 Final Considerations

Eutrophicated environments with a loss of functional groups, combined with the effects of climate change are rare in Brazil so far, making this study relevant on a national and global scale. These results will serve as a reference for evaluating effects such as: changes in communities, nutrient support, climate change and ecosystem effects.

Environments with high nutrient availability, whether natural or man-made, mostly have hypoxic zones that cause zooplankton stress. This stress can cause a reduction in the size class of organisms present, as well as an imbalance in the trophic chain that reflects fisheries production and can cause the loss of functional group.

Functional group loss is related to changes in temperature, salinity, and dissolved oxygen, as these are the main factors that influence the abundance and composition of the spatial and temporal distribution of zooplankton.

The hypoxic zone has a direct bearing on zooplankton migration, because some species need to locate near the surface where there is more oxygen availability and a higher number of predators, or in the hypoxic zone to protect themselves from planktonic fish.

When comparing the number of studies of zooplankton in hypoxic zone with those of functional group, more studies of zooplankton in hypoxic zone have been found so far. In general, both studies show a relationship with the trophic chain and despite this in the study of hypoxia, functional group losses also occur.

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