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Review

Microzooplankton Communities in a Changing Ocean: A Risk Assessment

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Abstract: Microzooplankton communities are fundamental components of marine food webs and have the potential to impact the functioning of carbon pumps. The identification of common responses of microzooplankton to global change has been challenging due to their plasticity and complex community-level interactions. However, accumulating research is providing new insights on the vulnerability of this group to different climate and other human-related hazards. Here, the current and future risk levels of microzooplankton associated with global change are assessed by identifying prevailing hazards, exposure, sensitivity, natural adaptability, and observed impacts based on available evidence. Most documented hazards for the survival and yield of microzooplankton are ocean warming, acidification, deoxygenation, and coastal eutrophication. Overall, heterotrophic protists are expected to respond and adapt rapidly to global trends. Fast growing, mixotrophy, wide internal stoichiometry, and their capacity to track optimal environmental conditions by changing species' range distribution are among the most important traits that shape their high adaptability to global change. Community-level responses to warming, however, are predicted to be amplified in polar and subpolar regions. At the individual level, the highest risk is associated with the sensitivity to deoxygenation since microzooplankton, especially ciliates, are known to reduce metabolic rates under hypoxic episodes; however, vulnerable species can be readily replaced by specialized taxa from a similar functional type. Microzooplankton seem to act as functional buffers of environmental threats, thus conferring stability, in terms of community connectedness to marine food webs and ecosystems against external disturbances.

Keywords: microzooplankton; global change; warming; acidification; deoxygenation; eutrophication; risk assessment

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1. Introduction

In the last three decades, the pace of ocean warming has revealed a two-fold intensification, thus reducing the adaptation time of ecosystems [1]. Compound effects of different climate change aspects are incrementally altering natural populations in a way that many ecosystems are reaching a threshold or tipping point, after which an irreversible shift is attained [2]. Under this scenario, global model projections anticipate a decline in marine net primary production in low latitudes as a result of reduced nutrient input to surface waters and warming anomalies exceeding the tolerance range of species (e.g., [3]). Optimal temperature for the growth of marine microbes, however, are generally above local environmental conditions, which implies that warming will theoretically accelerate the growth of small protists and the consumption and respiration of organic carbon by heterotrophic bacteria [4,5]. Furthermore, the overall population outcome to global change will depend on the overlap between evolutionary timescales and the rate of environmental change. The generation time, population size, and the underlying diversity pool of microbes provide a high likelihood to accumulate beneficial mutations and to evolve in concert with climate trends [6]. For instance, niche adaptation of phytoplankton within a 15-year timeframe with a warming trend similar to that expected to occur over the next century allowed dominant species to persist under environmental pressures [7]. Given enough nutrients, the collaborative link between bacteria and phytoplankton will strengthen and grazers will take advantage of increasing prey biomass [8]. Likewise, most observations suggest that ocean acidification will produce little effect on marine microbes [9] and can even benefit some microbial components [10]. Consequently, model projections anticipate that a higher degree of biogenic carbon will be redirected toward microbial food webs in the future [11]. In addition, ocean warming is expected to reduce the overall size of phytoplankton communities and to accelerate the respiration of organic carbon relative to autotrophic growth [12]. This implies that the relative importance of carbon export by the biological pump will decrease relative to carbon transformation within the microbial carbon pump [13]. However, many knowledge gaps remain regarding the individual responses of functional groups and mechanisms within microbial food webs to different aspects of global change and how these drivers will affect the future efficiency of carbon export toward the ocean's interior.

Microzooplankton constitute key components of microbial food webs in all aquatic environments. These organisms represent a significant proportion of the eukaryotic diversity and encompass a heterogeneous group of consumers (strict heterotrophs), many of which have the ability to photosynthesize and to thus act both as consumers and producers (mixotrophs) [14]. Their wide genetic variability and diverse ancestral origin has led to the adoption of a non-phylogenetic classification consisting of grouping organisms that respond similarly to environmental factors or "functional types" and that produces a similar effect on resource populations [15]. That is, in spite of their functional and genotypic diversity, microzooplankton collectively consume most primary production in marine ecosystems (e.g., [16]). At the global scale, microzooplankton are estimated to graze a significant amount of carbon (20–30 Pg C yr^{-1}), more than double to that grazed by mesozooplankton (5–15 Pg C yr^{-1}) [17]. Their critical role in the biological carbon pump rests on their ability to repackage phytoplankton biomass and either to respire carbon back to the atmosphere or to transfer it to fast sinking mesozooplankton [18]. They also interfere in the microbial carbon pump [19] through the ability of efficiently recycle nutrients that in turn delay the growth limitation of prey and prolong the flow of carbon within the microbial food web [20]. In addition, microzooplankton are able to photosynthesize, graze on prokaryotes, and absorb extracellular organic matter, thus gaining certain independence from resource composition and availability [21].

Microzooplankton are sensitive to most climate-related factors, and their responses to global change can produce cascading effects in marine food webs [22]. In spite of their critical role in structuring microbial communities and the fate of carbon in sunlit and in dark oceans, extracting regularities regarding microzooplankton responses to global change has remained challenging. Observable responses are usually the outcome of a complex interaction between local environmental conditions, global climatic phenomena, and interspecific interactions [22]. The insufficient number of long-term and spatially wide monitoring programs along with the difficulty to maintain stable populations of microzooplankton under culture conditions has further delayed the identification of climate and human-driven effects. In addition, unobservable factors are implicated in the configuration of emergent responses such as climate context dependencies [23] and differential evolution of physiological traits [24].

Natural communities within illuminated layers are currently faced with the joint effects of warming, acidification, enhanced stratification, deoxygenation, nutrient imbalance, and extreme weather events. Thus, the anticipation of ecosystem shifts is in most cases obscured by the multidimensional nature of ecosystems along with the occurrence of stochastic events. To reduce uncertainties in the prediction of climate effects at different organization levels, Working Group II of the Intergovernmental Panel on Climate Change (IPCC) has introduced a risk assessment methodological ensemble based on expert judgement on published research [25]. This framework has gained utility in recent years given the urgent need to extract meaningful patterns across ecosystems from the growing body of evidence reported in the literature [26]. The introduction of a structured method to enunciate judgement consensus has improved the communication of global change impacts among policymakers and helped to direct research efforts.

The aim of this work is to assess the impacts of global change on microzooplankton to identify the main risks and vulnerabilities. For this purpose, a comprehensive literature assessment was developed and the sensitivity and adaptive capacity of microzooplankton to most documented climate hazards, i.e., ocean warming, acidification, and deoxygenation, were evaluated. While not a direct climate-related stressor, the effect of eutrophication was also assessed given that it constitutes one the greatest human-driven threats in coastal ecosystems. Identifying emergent responses at the base of pelagic food webs is vital given that small changes in their function can produce strong effects on higher trophic levels and carbon export.

2. Methods

The methodological approach used here follows the comprehensive assessment of the impacts of climate change on organisms and ecosystems introduced by Working Group II of the Intergovernmental Panel on Climate Change (IPCC) [25] and recently used for marine systems in the Special Report on the Ocean and Cryosphere in a Changing Climate (SROCC) [1]. Hence, the vulnerability of microzooplankton to global change was assessed according to Bindoff et al. [1], considering the risk of community changes at present day based on historical and currently observed impacts. This assessment took into account recent peer-reviewed research (2000–present) to summarize relevant hazards and related impacts on microzooplankton communities that serve as a tool for future research.

The levels of risk, i.e., low, moderate, and high, depend on the vulnerability of microzooplankton to hazards (e.g., ocean warming, acidification, and deoxygenation). Here, risk is defined as the potential for negative consequences on communities in response to the impacts of global change. The vulnerability is assessed based on sensitivity to harm, exposure, and adaptive capacity to specific hazards. Exposure is defined by the biogeographic distribution of the assessed community. For instance, warming has emerged at the global scale (at different regional rates) and affects microzooplankton communities worldwide, with different degrees of impacts depending on local biotic and abiotic settings. In contrast, deoxygenation occurs at coastal waters and spatially confined deep open zones, which sets a lower level of exposure to planktonic communities. The adaptive capacity is defined as the ability of organisms to respond, adjust, and take advantage of potential damage.

Based on data availability, only the impacts of four hazards were assessed: ocean warming, acidification, deoxygenation, and coastal eutrophication. The risk associated with other climate-related hazards, such as shoaling of the remineralization depth and nutrient imbalance, was not assessed due to the lack of observations and judgement consensus. Instead, a brief review on the potential impacts of both climate-related drivers is provided. Multiple lines of evidence were assessed: observed impacts from long-term observations, fingerprints (e.g., tolerance curves along spatial environmental gradients and biotic records during extreme events), experimental surveys, and modelling data. The vulnerability in present day and future scenarios was assigned a confidence level based on the reference amount and agreement (i.e., the amount of available observations reporting effects of similar size and sign). The confidence levels were low, medium, high, and very high, according to IPCC calibrated language. To improve data interpretation, the overall effect of global hazards at the community level was expressed as negative (−), neutral (0), or positive (+).

The term *microzooplankton* was defined by Sieburth et al. [27] as a group of heterotrophic and mixotrophic plankton within a determined size fraction (20–200 µm). This classification does not consider phylogenetic origin; in fact, the size compartment includes not only protists but also small metazoans. In spite of this, the term gained acceptance due to its ecological relevance and operative convenience. The term *microzooplankton*, as used here, encompasses protistan organisms with the ability to consume prey by different mechanisms, although this may not be the unique energy acquisition method. That is, many protists are able to combine phago-heterotrophy with a phototrophic mode of nutrition in variable degrees. Hence, the present assessment includes several functional types as described in Mitra et al. [15]: phago-heterotrophs, constitutive mixotrophs, generalist non-constitutive mixotrophs, plastidic specialist-non-constitutive mixotrophs, and endosymbiotic specialist-non-constitutive mixotrophs. Some protist species considered here may fall outside the size fraction defined by Sieburth et al. [27] and thus the term *microzooplankton* should be taken with caution. Parasitic forms are not included in the present assessment.

3. Global Hazards to Planktonic Communities

Over the last six decades, ocean conditions revealed a significant trend beyond natural variability. Better-quantified trends in the ocean are rising water temperature, acidification, expansion of hypoxic zones, enhanced water column stratification, and sea level rise. The upper 75 m warmed at a decadal rate of >0.1 °C, which along with regional-scale freshening, led to an increase in the stability of the water column in the last four decades [28]. Consequently, an accumulation of heat, a mass reduction in the cryosphere, a higher density stratification, and a higher frequency of extreme events have been documented since 1970 [1]. In addition, ocean warming decreases the solubility of oxygen while intensifying the organism's respiration, which in the last 50 years, translated into an overall 2% decrease in the global oxygen inventory [29]. It also decreases water viscosity, which may accelerate particle sinking by 25% in 2100 [30].

Increased atmospheric $p\mathrm{CO}_2$, on the other hand, leads to a higher solubility of carbon dioxide in the surface ocean that involves the release of hydrogen ions (H^+) and a decrease in ocean pH. Since preindustrial times, the ocean pH has decreased by more than 0.1 units to an average of 8.17, although important variability exists at the regional scale [1]. The recent development of low-uncertainty models revealed that the rate of ocean warming accelerated by 23% since 1991 [31]. By 2090, surface temperature is expected to be 2.7 °C higher than in 1990 under a RCP8.5 scenario [3]. Under the same scenario, the global oxygen inventory in the ocean will drop by 1–7% in 2100 [32], while surface pH is expected to drop by 0.33 pH units [3].

Human activities and population growth has also exacerbated nutrient enrichment in coastal areas. Although not a direct consequence of climate change, this issue has become the most widespread human-driven negative effect on water quality in marine coastal areas [33]. Nitrogen is the primary element associated with coastal eutrophication, and the resulting nutrient excess is linked with the development of harmful algal blooms [34]. The cumulative effect of nutrient enrichment has led to the expansion of hypoxic areas [35]. In addition, eutrophication can interact with warming, thus promoting bacterial respiration and the acidification of coastal waters [36], as well as the establishment of invasive species [37]. A projected increase on river runoff as a consequence of the intensification of total precipitations is expected to exacerbate eutrophication in many coastal areas of the world [38].

4. Observed Impacts and Projected Risk to Microzooplankton as a Consequence of Global Hazards

The observed impacts of global change on microzooplankton are the outcomes, either negative, neutral, or beneficial, to specific hazards at the individual and community levels. In the following sections, the realized outcomes of human and climate-related drivers are assessed, while the related uncertainties associated with reference extent and agreement are evaluated. The main impacts and corresponding references are compiled in Table 1.

Table 1. Observed and projected impacts of global hazards on microzooplankton: the reference agreement refers to both the extent and agreement among published research. Most impacts of ocean acidification (OA) are projected for the worst-case climate scenario.

Global Hazard	Impact	Reference Agreement	References
Warming	Higher growth rate	high	[39–53]
	Higher grazing rate	high	[44,45,47,49–51,54–63]
	Higher trophic coupling with phytoplankton in polar and subpolar ecosystems	high	[42,45,46,49,51,57,64–69]
	Poleward range expansion of warm-water species	medium	[70–80]
	Shifts in timing	medium	[45,49,52,69,71,74]
	Increased predation risk on ciliates, especially in oligotrophic areas	low	[49,81–85]
	Higher relative contribution of heterotrophy to the growth of primarily heterotrophic mixotrophs	low	[47,86]
	Cell volume reduction	low	[43,51,53,87]
	Trophic mismatch	low	[79]
OA and $p\text{CO}_2$ Increase	Weak or no direct impact to non-calcifying organisms	high	[69,88–100]
	Weak or nondetectable effect on composition and diversity	high	[69,90–92,94,96,97,101]
	Weak to moderate effect on grazing rate	medium	[88,96,101]
	Positive effect on biomass due to increasing prey edibility	low	[56,96,98]
	Negative effect on biomass due to decreasing prey edibility and/or nutritional quality	low	[68,99,101,102]
	Growth inhibition of calcifying organisms	low	[103]
	Growth stimulation of primarily phototrophic mixotrophs	low	[98,104]
Deoxygenation	Ciliates species replacement	medium	[105–107]
	Diversity loss	medium/high	[106–110]
Coastal Eutrophication	Species replacement	high	[111–120]
	Lower trophic coupling	high	[55,68,118,119,121–126]
	Increased biomass	medium	[55,120,126,127]
	Stimulation of mixotrophic taxa	medium	[128–138]

4.1. Warming

4.1.1. Temperature Effect on Growth Rate

Temperature is a key factor in modulating the growth rate of protists in marine environments [41]. Microzooplankton usually have a wide range of thermal tolerance, and although a simple relationship between temperature and growth has not yet been described [22], its long-term effect on microzooplankton metabolism and ecology cannot be ignored. The Metabolic Theory of Ecology (MTE) predicts the response of metabolic rate to body size and temperature and how this rate determines resource allocation from the individual to the ecosystem levels [139]. The conceptual ensemble provided by the MTE generated the notion that thermal dependence or activation energy (Ea) differs among phototrophs (0.32 eV) and heterotrophs (0.65 eV) and that the latter are able to respond more rapidly to an increase in temperature [140]. However, the functional complexity of plankton implies some deviations from theory. In the first place, the temperature dependence of phytoplankton predicted by the MTE is based on terrestrial C3 plants; however, the significantly lower CO_2 concentration in water than on air and its active accumulation within cells in some phytoplankton groups contribute increasing the Ea with respect to terrestrial plans [52]. On the other hand, the response of microzooplankton growth to temperature is shaped, and even masked, by their abundance or closeness to carrying capacity [48], community composition [52,60], the resource availability and specific nutritional requirements [40,43,46,50,57,141,142], the concentration of predators [143] and the life history of consumers, e.g., starved vs. food-replete conditions [46,144]. The shifting hierarchy of these factors among short periods of time (hours to days) further complicates the interpretation of field measurements. For instance, short-lived interactions among resources and temperature occur when starved ciliates are offered food. Under such conditions, ciliates compensate the temperature-driven growth limitation by a rapid ingestion of prey and a parallel increase in the maximum growth rate [46]. The growing recognition of such complexity has encouraged the incorporation of taxon-specific responses into models [52] as well as the implementation of multifactorial experimental approaches (e.g., [68]).

Several models have been proposed to predict the response of microzooplankton growth to temperature under controlled conditions [42,145,146]. According to these models, the growth rate is an exponential function of temperature, although linear responses have also been reported (Montagnes et al., 2003, Yang et al., 2016, Franzè and Menden-Deuer 2020). Recently, improvements in the estimation of Ea of phototrophs and heterotrophs were made by Wang et al. [52]. The authors predicted a higher Ea of both groups to that predicted by the MTE, and although Ea varied widely among taxa, the highest departure from theory occurred in phototrophic taxa. A growing body of evidence indicates that these discrepancies may be related to the ability of protists to implement dual nutritional modes. Between 40 and 60% of protists traditionally viewed as heterotrophs are actually mixotrophs [147]. The so-called non-constitutive mixotrophs have higher gross growth efficiencies than strict heterotrophs and can double their biomass in natural conditions, especially under low food supply [148]. This high efficiency is attained because the degree of phototrophic and heterotrophic activities is not predetermined but is rather a direct response to environmental conditions, such as light, nutrients, and prey availability. Hence, the nutritional plasticity of mixotrophs compensates growth inhibition occurring among strict phototrophs and heterotrophs when species-specific resources are scarce and is thought to contribute to the underestimation of theoretical Ea.

Experimental and modelling data support the idea that the discrepancy between the thermal sensitivity of phototrophs and heterotrophs maximizes and tends toward theoretical values when predator–prey systems are represented by strict phototrophs and strict heterotrophs or by primarily heterotrophic mixotrophs [50]. In fact, higher than predicted temperature-dependence of mixotrophs, including ciliates and dinoflagellates, was reported in field experiments in the Barents Sea [48]. Moreover, under light-saturated conditions, both phototrophic and heterotrophic growth of the mixotrophic *Ochromonas* sp. showed higher temperature-dependence to that predicted by the MTE [47]. These authors reported that heterotrophy increased more strongly with temperature than phototrophy, suggesting that, under a future scenario of ocean warming, mixotrophic organisms may rely more on heterotrophy to sustain growth [47,149,150]. Likewise, the modelled mixotrophic maximum growth rate of *Karlodinium veneficum* exceeded that of its heterotrophic form while warming was predicted to enhance mixotrophic over heterotrophic growth only under nutrient-limiting conditions [86]. In such cases, future warming may increase the grazing pressure on phototrophic communities and even constrain the magnitude of algal blooms. However, the relative stimulation of heterotrophy under increased temperature showed no temperature dependence on *Dinobryon* species, which are primarily phototrophic mixotrophs [151,152], suggesting that warming-induced heterotrophy may only occur in primarily heterotrophic mixotrophs.

Overall, warming is predicted to stimulate the growth of microzooplankton, setting closer coupling with prey pulses. A higher contribution of heterotrophy to the growth of primary heterotrophic mixotrophs is also anticipated. High uncertainties are posed by the strong influence of the temperature dependence of prey, by the changing hierarchy of interacting drivers (i.e., prey offer, predation pressure, and nutrient ratios), and by the nutritional plasticity of non-strict heterotrophic protists.

4.1.2. Temperature Effect on Grazing Rate

Warming is expected to increase the overall grazing exerted by microzooplankton since the ingestion rate is an exponential function of temperature [153]. However, the differential effect of temperature on the metabolism of grazers and their prey determines the degree of primary productivity that is either remineralized or exported toward bottom layers. A review by Rose and Caron [42] that included 1308 growth rate estimates of heterotrophic protists revealed that the slope of log-transformed rates was significantly higher to that computed by Eppley [154] for marine phytoplankton but with a lower y-intercept. Their findings imply that a temporal trophic decoupling between microzooplankton and phytoplankton may occur at the low extreme of the temperature range due to the higher temporal lag of heterotrophs in activating growth. The mechanisms behind the differential temperature dependence of heterotrophic and phototrophic protists are primarily driven by metabolic constraints associated with energy-producing reactions that imply a higher Ea in heterotrophs compared to phototrophs [140,155]. This differential response was later supported by Chen et al. [57], who extracted the general temperature dependence of the proportion of daily primary productivity grazed by microzooplankton, defined as the quotient between grazing (m) and phytoplankton growth (μ) rates, from published research. The authors found that, in eutrophic environments with high chlorophyll content, m:μ are minimal at the extremes of the temperature range while maximum values occur at intermediate temperatures. Moreover, global recompilations of grazing rates obtained by the dilution technique reported minimum values of m:μ in polar seas [16,156]. This does not necessarily imply that the temperature limitation on microzooplankton clearance rate sets a lower absolute grazing rate in polar and subpolar regions. In fact, microzooplankton can attain significant grazing rates at low temperatures, leading to a net removal of phytoplankton biomass [48,157,158]. Instead, warmer conditions are expected to stimulate a higher trophic coupling of microzooplankton and phytoplankton in polar and subpolar regions (e.g., [64]). Moreover, the gross growth efficiency of ciliates is known to decrease with temperature [17], implying that a higher trophic efficiency will occur in cold regions under future warming. On the other hand, the decrease in m:μ under maximum temperatures predicted by Chen et al. [57], both in oligotrophic and eutrophic environments, usually does not hold true in nature, since the mean grazing pressure in the tropics is among the highest across the latitudinal gradient [16,156]. However, this situation may be associated with the higher biomass and the closeness to the carrying capacity of microzooplankton in the tropics [17].

It is important to note that transient warming events may produce contrasting results. For instance, the warming effect on natural, un-acclimated polar assemblages was tested by Manden-Deuer et al. [158]. The authors found that a 6 °C increase in in situ temperature produced a stimulation of phytoplankton growth and a significant reduction in microzooplankton grazing, resulting in a lower m:μ and a trophic decoupling. Moreover, the exposure of three herbivorous dinoflagellates to experimental temperature gradients of 5–7 °C resulted in a high mortality rate [53]. These authors also reported asymmetric acclimation times to temperature on the three species, which required twice as long to acclimate to colder than to warmer conditions.

A stronger top-down control on microzooplankton in high latitudes may also reduce the net grazing rate of natural communities. In fact, field studies in the Arctic Sea revealed that copepods prey preferentially on microzooplankton even under high phytoplankton concentrations [159–161]. In addition, the effect of temperature on grazing was also shown to interact with prey composition [50,62]. The differential effect of prey on temperature dependence of growth and grazing rates determines no universal outcome of warming on microzooplankton yield. In spite of difficulties on the individualization of temperature effects, observations indicate that microzooplankton will show a higher trophic coupling and transfer efficiency in polar and subpolar regions in response to warming. In contrast, trophic transfer efficiency may be reduced in temperate and eutrophic environments as a result of a lower gross growth efficiency of ciliates with ongoing warming.

4.1.3. Latitudinal Range Shift and Temporal Redistribution

The delimitation of microzooplankton species distribution is often challenging as significant dispersion limits do not exist in the ocean. A review analysis revealed that only 8.5% of ciliates' morphospecies exhibit restricted distribution or endemism [162]. The Tara Oceans expedition, which uncovered unprecedented taxonomic discrimination of the majority of ciliate's clades, reported that only 17% of taxa were distributed among all oceanic regions. The analysis of DNA sequences showed a close correlation between ciliate's diversity and environmental factors of local relevance (temperature, chlorophyll, salinity, and inorganic nutrients) but no clear large-scale latitudinal gradients [163]. On the other hand, the wide genotypic diversity of microzooplankton creates numerous ecotypes shaped by local environmental conditions [164].

In spite of these limitations, field observations reported the range expansion of microzooplankton species among long-surveyed marine areas. For instance, the arrival in the early 2000s of the radiolarian *Ceratocyrtis histricosus* to the Western Arctic Ocean has been suggested as the consequence of warming of the deep Atlantic waters coming from the North Atlantic Ocean and as the persistent positive anomalies of the North Atlantic Oscillation that are responsible for the inflow of North Atlantic waters into the Arctic Ocean [70,78]. Likewise, several species of the foraminifera *Amphistegina* have shown a northwestward range expansion in the Mediterranean Sea in response to warming ([75] and the references therein). In the southern hemisphere, a southward range expansion of 8 km year^{-1} since 1987 in *Amphistegina* from the south African coastline was attributed mainly to temperature trends [77]. Similarly, an increasing dominance of warm-water species parallel to a decreasing trend of temperate and subpolar species was attributed to warming in the California current [72]. Planktonic foraminifera species also revealed a mean 600 km latitudinal displacement relative to the pre-industrial state consistent with warming magnitude and sign in a global compilation of sediment samples [80]. The dinoflagellate *Noctiluca scintillans* showed a similar poleward spreading driven by temperature in the NE Atlantic [71]. Similarly, a range expansion of *N. scintillans* since 1960 from Australian coasts toward the Southern Ocean was documented in parallel to the southward movement of the Eastern Australian Current [73]. Like all western boundary currents, the Eastern Australian Current experiences faster warming compared to the global mean and poleward migration since 1900 [165]. This implies that the range expansion of thermally tolerant species may accelerate in subtropical areas facilitated by the encroachment of western boundary currents [166].

The Continuous Plankton Recorder (CPR) has gathered data over the last 60 years in the North Atlantic Ocean. This unique monitoring program has allowed us to identify large-scale trends of plankton populations in open waters. The relatively large pore size of the plankton net contained in the CPR (270 μm) determines that phytoplankton and microzooplankton size classes are not conservatively sampled. Also, delicate, unarmored organisms are frequently damaged by the sample filtration and retention mechanisms. Consequently, the information provided by this tool is limited and research has relied on group-specific trends of large, armored species such as dinoflagellates and diatoms over periods long enough to allow the emergence of trend [167]. Based on these data and accounting for the abovementioned limitations, Hinder et al. [74] analyzed the long-term, semiquantitative pattern of five tintinnid species in the NE Atlantic and the North Shelf Sea. The authors found contrasting trends among open and shelf waters. In the NE Atlantic, tintinnid species showed a positive trend and a northward range shift during the period 1996–2009, while in the North Shelf Sea, tintinnids evidenced a negative abundance trend and no clear relocation pattern. Accordingly, neither environmental nor biotic factors explained the observed changes, suggesting that the emergent response of tintinnids was shaped by region-specific drivers that, in turn, depends on their ecological niches. In spite of these contrasting responses, all tintinnid taxa showed a progressive widening of their seasonal occurrence period during 1960–2009, in concurrence with warming and shifts in phytoplankton communities [71]. Dinoflagellates showed a completely different response in the area during 1960–2009. During this period, a shift in local wind patterns promoted the intensification of water mixing and turbulence. The authors suggested that increased turbulence may have promoted the retention of diatoms within illuminated layers and that, under these conditions, outcompeted dinoflagellates, leading to their progressive exclusion [168]. The relevance of local environmental factors over global climate signals is also well illustrated by the geographic range shift toward lower latitudes of the mixotrophic dinoflagellate *Ceratium arcticum*. This cold-adapted species showed an equatorial expansion into the temperate Atlantic Ocean during the period 1960–2000, and although no significant warming trend was detected in this area during the examined period, the authors attributed the shift to the establishment of favourable large-scale stratification patterns [169]. These contrasting responses suggest that the effect of global climate signals are expected to emerge over considerably long periods of time. Although long-term observations of microzooplankton are scarce, fossil records may offer some insights into the responses to climate trends. For instance, paleontological records of Polycystina (radiolaria) revealed that only one third of species were able to track optimal environmental conditions over the last 10 million years in the Southern Ocean [170].

The underlying cause that drives some species to survive by tracking optimal conditions while others become locally extirpated seems to be related to biotic and abiotic factors. In the first place, the threshold response to temperature is species-specific and it determines the rate of metabolic processes, thus setting the boundaries of optimal fitness. Optimal local conditions (i.e., food availability, presence/absence of symbionts and competitors, and local hydrography) may not be reproduced with isotherm migration, while physical barriers (i.e., currents, topographic anomalies, and thermohaline fonts) may restrict species relocation. According to the breadth of species niches and the region-specific rate of environmental change, evolutionary timescales may not synchronize present climate trends and will lead to the local extinction of species. This may be especially true for high-latitude biomes, which face the highest rate of climate oscillation and that encompass cold-adapted species at their warmest niche edge [171].

The latitudinal range shift of predators may additionally shape microzooplankton biomass. Warming and ice retreat in the polar seas appears to correlate with the latitudinal range shift of copepods [172]. Likewise, intense predation pressure, either by the arrival of new species or by the stimulation of resident populations due to the improvement in environmental conditions, has been linked with the decrease in tintinnids and radiolarians in the Chukchi Sea [83]. A differential latitudinal range shift of prey and predators also indirectly affects microzooplankton communities by modifying food supply and predation risk, respectively [79].

The lack of geographic boundaries along with the wide thermal tolerance of most microzooplankton species will enable the poleward range shift of many species to meet thermal niches. However, as isotherms continue to progress poleward, the vulnerability of genotypes at the warmer edge of their geographic distribution is expected to rapidly increase. The Tara Ocean expedition revealed that cosmopolitan ciliates had higher local abundances than ciliates with a restricted distribution, although in general, open-water species showed low diversity. This highlights the vulnerability of species with restricted distribution and narrow niches [163]. Shifts in microzooplankton timing are also an observed and projected response to warming as a result of temperature-driven changes in prey phenology.

4.2. Ocean Acidification

4.2.1. Direct Effects

Elevated CO_2 has shifted the ocean carbonate chemistry, causing a ca. 0.018 unit decrease in the ocean pH per decade since the pre-industrial era [1]. The emerging ocean acidification (OA) gained attention in the last two decades and is among the better documented hazards related to climate change [173]. The accumulation of CO_2 in the ocean may favor the growth of phototrophic protists, especially small algae, by increasing CO_2 availability for photosynthesis [174]. Calcifying organisms, on the other hand, may be vulnerable to ocean acidification due to restriction limits on organism’s calcification posed by a decreasing carbonate concentration [175]. The emergent phytoplankton response will therefore depend on the balance between the photosynthesis stimulation of CO_2 and the deleterious effect of pH on calcification.

Experimental data show that the tolerance of microzooplankton to pH varies widely between species [101,176]. As a general pattern, species loss and replacement are rapidly observed above pH 9 and below pH 6 [89–91,176–179]. However, a considerable amount of literature reported no detectable effect on microzooplankton growth and grazing within this range, which comprises pH values of the worst-case scenario projected for 2100 (Table 1). The lack of tangible responses to pH is especially true when considering natural communities. For instance, Suffrian et al. [88] and Aberle et al. [92] found no significant shifts in microzooplankton composition and diversity along a $p\mathrm{CO}_2$ gradient in one-month outdoor mesocosm experiments in Raunefjord (Norway) and the Arctic Sea, respectively. Calbet et al. [68] and Lischka et al. [98] found similar minor effects on ciliates among a $p\mathrm{CO}_2$ gradient expected to occur by 2100, but the response was species-specific.

Although most microzooplankton species are expected to be tolerant to present and future OA, impacts on the calcification and survival of foraminifera are anticipated. In the Southern Ocean, a 30–35% shell weight loss was recorded in modern foraminifera *Globigerina bulloides* relative to Holocene shells [103]. However, recent field evidence shows that the vulnerability of foraminifera is shaped by several factors, such as the presence of symbiotic algae, life stage, and other species-specific traits, suggesting that the vulnerability of this group may be lower than previously thought [180]. For instance, the long-term trend of pH in the North Sea was used to evaluate the response of foraminifera in the period 1958–2010. During this period, the abundance of cells showed a positive trend in spite of a 0.12 unit decrease in mean pH over the last 12 years, suggesting that either pH had no effect on foraminifera or that the effect was masked by other drivers [181].

Preliminary evidence suggests that some mixotrophs may benefit from OA. The predicted increase in $p\mathrm{CO}_2$ by 2100 stimulated the growth of *Karenia brevis*, a primarily phototrophic mixotroph [104], and the ciliate *Mesodinium rubrum* also showed significant growth stimulation under high $p\mathrm{CO}_2$ in outdoor mesocosms [98]. However, mesocosm experiments simulating post-bloom conditions revealed no clear pattern on mixotrophs in response to the addition of CO_2, probably due to strong competition with strict phototrophs [182]. The occurrence of diverse responses of natural phytoplankton communities implies that much more evidence is needed to determine whether reduced species performance due to under-calcification and the beneficial effect on mixotrophs may be a generalizable biological feedback to OA.

4.2.2. Prey-Mediated Effects

A higher CO_2 bioavailability may produce positive indirect effects on microzooplankton by stimulating the accumulation of phytoplankton biomass, either at the individual [183] or community levels [96]. Most evidence points at the relevance of prey nutritional quality and composition as an essential factor shaping the response of microzooplankton to ocean pH. A higher carbon bioavailability relative to nutrients may modify the internal stoichiometry of prey, thus reducing their nutritional value [184–186]. Excess carbon in relation to nutrients may result in nutritional deficiencies and may impact the growth efficiency of microzooplankton [99] and the growth and reproductive performance of copepods [185]. However, Rossoll et al. [94] found only transient differences in phytoplankton quality among an experimental $p\text{CO}_2$ gradient. Similarly, increasing $p\text{CO}_2$ levels in outdoor mesocosms in a Norwegian fjord produced no significant changes in essential fatty acids of plankton, reflecting no nutritional constraints to grazers [93].

Instead, prey composition may have a stronger impact on the prey-mediated effects of OA. Evidence shows that picophytoplankton may be benefited in a future scenario of OA due to a stimulating effect of excess carbon [10,187], thus providing more suitable food to microzooplankton. However, this phenomenon is rarely captured by short-term experiments. For instance, the experimental increase in $p\text{CO}_2$ stimulated the growth of big, inedible diatoms at the expense of smaller dinoflagellates, thus reducing the biomass of consumers and their grazing rate [102]. Cascading effects may also produce unexpected responses. In shipboard experiments conducted in the North Sea, increased temperature and $p\text{CO}_2$ caused a stimulation of both phytoplankton growth and microzooplankton grazing. After the two-week incubation, the authors reported a decrease in microzooplankton biomass in the warming treatments and suggested that selective feeding allowed the growing dominance of unpalatable prey, thus reducing available resources [56]. A similar indirect stimulation of $p\text{CO}_2$ on microzooplankton grazing was observed in >100 day outdoor mesocosms as a result of enhanced phytoplankton growth [96].

It is worth noticing that compositional shifts in phytoplankton communities do not always translates into significant modifications in microzooplankton, as seen in indoor mesocosms conducted to evaluate the combined effect of warming and high CO_2 on natural plankton communities from the Baltic Sea [69] and in outdoor mesocosms in the Arctic Sea [92]. The prey-mediated effects of OA on microzooplankton are therefore highly variable, and the three possible outcomes (neutral, positive, and negative) are documented in the literature (Table 1). To date, not enough evidence exists to attribute a higher likelihood to either undetectable, positive, or negative prey-mediated effects.

The inconsistency of responses, both at the individual and community levels, suggests a high tolerance of natural microzooplankton populations to pH. Those species unable to cope with pH variability will most likely be replaced by others from the same functional type, thus minimizing community-level responses. Although the indirect effects of OA on microzooplankton through prey edibility may yield either positive (by the dominance of small phytoplankton) or negative (by the dominance of deleterious or nutritionally poor prey) effects on maximum grazer's biomass, the overall effect is expected to be weak or even masked by interspecific interactions. Neritic species, especially estuarine, are expected to be more tolerant to future OA than those from the open ocean due to their adaptation to wide natural fluctuations on $p\text{CO}_2$. Overall, the emergent response of microzooplankton will most likely be shaped by the sensitivity of their dominant prey. The diversity of prey will therefore gain an essential role on the resilience of natural microzooplankton populations in the future.

4.3. *Deoxygenation*

Warmer waters are losing their ability to retain dissolved oxygen, thus creating oxygen minimum zones (OMZs) and threatening marine life. A recent review revealed that OMZs extend over 8% of the world's ocean area [188]. Although limited literature exists regarding the effects of climate-driven deoxygenation on microzooplankton, some observational and experimental data may help to anticipate its effects. The study of OMZs in the dark ocean has revealed high abundances of ciliates [189], and even under these seemingly hostile conditions, these organisms can attain a high degree of bacterivory [190]. However, similar to pH, the response of microzooplankton to oxygen concentration is species-specific, denoting the existence of diverse specialized oxygen niches among communities [109,191,192]. Moreover, under low oxygen conditions, the survival of some ciliates is facilitated by the association with particular endosymbiotic bacteria, while dinoflagellates may form resting stages to overcome adverse conditions [193,194].

The high specialization of ciliates to oxygen concentration is illustrated by the development of seasonal hypoxia in boreal lakes. The onset of this recurrent event revealed no significant changes in ciliate's abundance but a strong zonation on their composition, with a small number of specialized ciliates in hypoxic layers which showed a close association with bacteria [105]. Among nonspecialized ciliates, a synchronous decrease in respiration, growth and grazing rates under decreasing oxygen concentration was reported in controlled experiments, although studied species revealed specific response curves [195]. In natural conditions, some species can compensate for suboptimal oxygen concentrations by exploiting transient resource pulses during hypoxic events. For instance, a transient oxygen depletion event in a coastal embayment from Hong Kong revealed a shift from the dominance of primary producers toward ciliates and mixotrophic dinoflagellates, likely as the result of the onset of post-bloom conditions and a higher availability of bacterial prey [107]. Similarly, hypoxic conditions lead to the dominance of ciliates over the less tolerant macrozooplankton species and a lower species diversity in a coastal area of Southern California, probably linked with a higher availability of bacteria [106]. In contrast, the biomass of microzooplankton was lower within an OMZ in the eastern tropical North Pacific Ocean while no significant changes in microzooplankton composition was found. This response, however, was mostly attributed to a lower prey availability rather than to oxygen limitation [196].

At the community level, microzooplankton are tolerant to deoxygenation and may unfold adaptation tradeoff (e.g., cyst formation) to mitigate hypoxic conditions. However, the highest risk occurs at the species level since microzooplankton, especially ciliates, will reduce metabolic rates under hypoxic episodes that may become increasingly important in coastal areas exposed to eutrophication. The decrease in habitable niches driven by hypoxia will lead to a diversity loss as only highly adapted species will be able to survive under such conditions. The ability to tolerate hypoxia by endosymbiosis poses an extra level of complexity to the organism's adaptation.

4.4. Coastal Eutrophication

Microzooplankton are ubiquitous among eutrophication gradients and have long been recognized as important trophic components among self-purifying wastewater plants and natural environments receiving organic effluents ([197] and the references therein). This fact evidences that many protist species can tolerate extreme organic pollution. Observational evidence shows that microzooplankton can be indirectly benefited by eutrophication through an increase in phytoplankton availability [111]. However, noxious conditions created by phytoplankton blooms (i.e., increased pH and nocturnal hypoxia) and eutrophication itself (i.e., increased turbidity and ammonium toxicity) can eventually impair the development of microzooplankton species [198]. Consequently, sensitive species are prone to being replaced by others with higher tolerance to eutrophication, thus creating new species assemblages (Table 1).

Another common response to eutrophication is the weakening in the trophic coupling between microzooplankton and their prey. As the concentration of nutrients and the degree of eutrophication of the system increase, phototrophs respond proportionally and the prey-to-predator ratio rapidly increases [199]. In most cases, microzooplankton are able to synchronize phytoplankton productivity pulses by their rapid generation time and thus constitute one of the main factors controlling biomass accumulation in eutrophic conditions. In fact, microzooplankton have the potential to control harmful algal blooms [200–202]. However, as the frequency and magnitude of phytoplankton blooms increase, the ability of microzooplankton to control biomass accumulation decreases due to feeding saturation. Briefly, as phytoplankton reach critical concentrations (defined as the half saturation constant), the ingestion rate of microzooplankton asymptotically stabilizes at a maximum value due to predator-specific handling times. The mismatch between the clearance rate of microzooplankton with phytoplankton abundance beyond critical concentrations, has been extensively observed in dilution experiments [54,55,63,119,121,124–126,203–219]. Although the prevalence of saturated feeding has not been assessed in the context of eutrophication, almost all experiments indicating saturated feeding occurred in mesotrophic and eutrophic environments. Moreover, the occurrence of feeding saturation in oligotrophic conditions has been linked to methodological artifacts that result from trophic cascades [217]. This is related to the fact that saturated feeding is a function of phytoplankton density rather than grazer's abundance, size or temperature [219–221], and is thus expected to occur more frequently under eutrophic conditions. For instance, grazing saturation was reported in 40% and 75% of experiments conducted in two estuaries exposed to human-driven eutrophication, the Long Island Sound and the San Francisco Bay, respectively [215]. In the Bahía Blanca Estuary, saturating feeding was observed in 3 out of 14 experiments under severe eutrophication [119], and in Hong Kong coastal waters, feeding saturation was attributed to ambient nutrient enrichment [55]. It is worth noticing that microzooplankton are able to acclimate to ambient phytoplankton concentrations by adjusting their half saturation constant. This implies that these organisms can adapt to maximize resource exploitation [207,220], and that feeding saturation will not be a generalized response under more eutrophic conditions.

A higher concentration of nutrients also promotes the development of large phytoplankton with lower nutrient affinities and enhanced defensive skills [222–224]. In addition, noxious or unpalatable phytoplankton may be stimulated under eutrophic conditions [225,226]. Hence, eutrophication may also reduce trophic efficiency by increasing the proportion of inedible phytoplankton [55,118,119,123]. In this scenario, dinoflagellates may be stimulated since they are able to graze on a wide range of prey size and, in particular, athecate forms can take advantage from the occurrence of large diatom blooms [227].

Under natural conditions, the outcomes of eutrophication are difficult to generalize since this phenomenon acts in concert with other climate-driven stressors. In this sense, a multi-factorial experiment combining the effect of eutrophication, warming, and acidification was conducted in a Norwegian fjord [68]. Although heterotrophic protists showed a high adaptability to shifting prey exposed to combined hazards and group-specific cascading effects, the overall community-level response denoted a lower trophic efficiency under a global change scenario in coastal ecosystems [68]. This denotes that the joint effect of human-related and climate drivers, in spite of generating higher resource availability, can disrupt trophic links by the predominance of low-quality food.

Under eutrophic conditions, mixotrophic protists can take advantage of both the direct uptake of nutrients and the consumption of prey that is stimulated by nutrient pulses [132]. In addition, the nutritional plasticity of mixotrophs allows them to growth efficiently and to even cause harmful algal blooms under nutrient-deficient conditions, a situation that frequently arises under human-driven nutrient pollution [132,137,228]. These traits are likely to confer an adaptive advantage to mixotrophic taxa in a more eutrophic ocean.

Overall, microzooplankton are expected to be indirectly favored by the consumption of abundant and diverse prey stimulated by nutrient pulses. However, eutrophication provides heterogeneous spatiotemporal pulses of nutrients, thus creating less predictable phytoplankton blooms and a weaker trophic coupling with grazers. Although microzooplankton have the potential to control phytoplankton blooms under eutrophic conditions, most evidence suggests that, under these conditions, microzooplankton grazing have a lower reactivity to resource pulses, either by feeding saturation, a lower food palatability, or a combination of both.

4.5. Other Hazards

4.5.1. Shoaling of the Remineralization Depth

Enhanced density stratification in the upper ocean, especially in the tropics, occurs as a result of the heat imbalance between the ocean and the atmosphere. This inhibits the free exchange of nutrients with deeper waters, resulting in more severe nutrient limitation to phototrophic growth [229]. In the ocean, reduced prey (nutrient) availability in low and mid-latitudes, where density stratification is expected to intensify in the future, will likely favor smaller heterotrophs (phototrophs), which are able to prosper under low resource concentration [230]. Under these conditions, i.e., low nutrient concentration and the dominance of small prey, mixotrophic taxa are expected to dominate microbial food webs [231]. Despite the fact that the response of microzooplankton to this hazard is largely undocumented, it is important to note that the reduction in plankton biomass resulting from shoaling of the surface layer where carbon is remineralized will reduce the vertical boundary of carbon release and thus, restrict the ocean's capacity to remove atmospheric CO_2 [232]. Research is therefore urgently needed to assess the risk of pelagic food webs, which play a central role on marine biogeochemical processes.

4.5.2. Shifts in N:P Ratios

The projected increases in water column stratification in the tropics, the Arctic, the North Atlantic, and the North Pacific Oceans are expected to reduce the upwelling of nutrient-rich deep waters into the euphotic zone [233]. Besides the general negative trend of nutrient concentration in the euphotic zone, a changing N:P ratio is expected to occur at low latitudes with ongoing climate change. In particular, phosphorus is expected to decline at a higher rate than that of nitrogen due to biological N-fixation in the tropics [234].

Prey quality in terms of internal stoichiometry may shape grazer communities [235]. In turn, the internal conversion of carbon by heterotrophic protists, either by its direct respiration or by its investment on cell maintenance and organelle build-up, implies widespread consequences on the C:N ratio of suspended materials and the magnitude of exported carbon [236]. Ciliates and dinoflagellates may allow their internal N:P ratio to vary among wide-ranging intervals and are therefore able to thrive on nutrient-deficient prey [237]. However, modelling approaches revealed that microzooplankton grazing efficiency decreases when prey stoichiometry is unbalanced [18]. Moreover, some ciliates may control their internal homeostasis among narrower limits than dinoflagellates while not as narrow as metazoans [238]. This poses a higher risk to ciliates' growth inhibition when offered nutrient-deficient prey [239], a situation that may arise in a future, more oligotrophic ocean. On the other hand, the growth of dinoflagellates is significantly stimulated when offered P-rich prey [240], implying that, under P-limitation, the yield of primarily heterotrophic dinoflagellates may be reduced. A mesocosm study revealed that the addition of nitrogen and glucose produced little effects on microzooplankton abundance and compositions and that nutrient effects were overridden by a high diversity of both protistan and metazoan grazers [241]. Likewise, experimental [242] and modelling [86] approaches revealed that, under nutrient starvation, heterotrophy in primarily phototrophic dinoflagellates is stimulated.

To date, limited research regarding the impacts of nutrient imbalance on microzooplankton exists, thus preventing a confident risk assessment. In spite of high uncertainties, species interactions and trophic cascades seem to have strong mediating effects on shifting nutrient ratios, thus providing some resilience to natural populations.

5. Projected Impacts on Carbon Export

In the coming decades, microzooplankton are expected to play a predominant role within microbial-mediated carbon sequestration mechanisms in both eutrophic and oligotrophic habitats. This is mainly related to their trophic plasticity and community-level multifunctionality, which allow them to prey on various prey types from bacteria to diatom chains and other heterotrophic protists, as well as to gain some independence from prey by harvesting light [137]. These traits confer microzooplankton with a higher ability to adapt to changing food availability compared to metazoans, and are thus assumed to play a fundamental role in rapidly changing habitats [243].

Most model projections agree on the enhancement of water column stratification in the tropics, the Arctic, the North Atlantic, and the North Pacific Oceans, which is assumed to reduce the upwelling of nutrient-rich waters to the euphotic zone with a concomitant decrease in the net primary productivity and photosynthetic CO_2 assimilation [233,244]. A parallel reduction in the mean phytoplankton size is anticipated in tropical and subtropical areas as a consequence of the overall reduction in available resources. The opposite occurs in polar and subpolar areas due to more efficient mixing processes that bring nutrients toward the surface, along with the migration of isotherms and the consequent expansion of environmental niches [230,245]. In addition, heterotrophic bacteria may take advantage of the direct effects of warming on metabolism [246], and has been shown to be resilient to ocean acidification [9]. Moreover, marine cyanobacteria is also expected to be favored by warming and acidification [247].

Under the predominance of small prey, microzooplankton will efficiently repackage phototrophic prey beyond the size range accessible to metazoans. Microzooplankton will therefore constitute a buffering link to the formation of mesozooplankton-derived particulate organic matter thus compensating the reduction in carbon export by small, slow sinking phytoplankton [243]. This will be especially the case in oligotrophic areas, where omnivorous copepods are expected to exert a higher top-down control over microzooplankton due to a lower availability of primary producers [81]. On the other hand, enhanced respiration and labile dissolved organic matter excretion due to warming, intraguild predation, and nutrient regeneration are expected to deviate carbon from the biological carbon pump [21]. The relatively lower reduction in heterotrophic biomass compared to that of phototrophs in low and mid-latitudes will likely produce a negative trophic amplification of climate change, thus reducing the export of carbon toward bottom layers, while a positive trophic amplification is anticipated at higher latitudes [248]. As the main source of phytoplankton mortality, consuming an average of 66% of annual primary production and a 10% of bacterial production globally, microzooplankton will likely set the paths and boundaries of carbon transfer within microbial food webs in future oceans [21].

6. Conclusions

This assessment revealed that the risk level of negative consequences on microzooplankton to the evaluated global hazards is low with a medium confidence level (Table 2). Compared to phytoplankton and mesozooplankton, the amount of data regarding the responses of microzooplankton to global change is still limited. The lack of sustained observations in the field and under controlled laboratory conditions prevents the identification of consistent regularities on several aspects of species- and community-level responses. Hence, to allow the emergence of trends beyond short-term variability, further investigations will be required to increase the confidence of the present assessment. In spite of these limitations, existing data evidence a general consensus on the robustness of microzooplankton communities under present and future global change. This robustness resides in (1) their short generation time and relatively simple life history, (2) their nutritional plasticity, (3) their diverse interspecific interactions such as predator–prey and symbiotic relationships, and (4) the enormous functional diversity contained in their genetic reservoir. These traits and interactions confer microzooplankton with a buffering capacity that helps maintain community connectivity and stabilize marine food webs exposed to climatic and other human-driven hazards.

Table 2. Associated vulnerability of microzooplankton to the main global hazards: exposure, sensitivity, and adaptive capacity define the level of vulnerability, which in turn determines the global risk of assessed communities.

Hazard	Exposure	Sensitivity	Adaptive Capacity	Overall Effect	Vulnerability
Warming	high	high	Moderate/high: most species will be stimulated by higher temperatures due to a lower thermal restriction on metabolism. Species can shift their range distribution toward the poles and can widen their productive windows to meet thermal niches and to match prey pulses.	+	low
OA and $p\mathrm{CO}_2$ Increase	high	low	High: most non-calcifying species can tolerate the projected pH for 2100. Most community-level effects will be mediated by prey composition and quality. Mixotrophy and wide internal stoichiometry are adaptations to cope with shifts in prey driven by increasing pCO_2.	+/0/−	low
Deoxygenation	low	high	Moderate/low: at the community level, oxygen depletion can be compensated with species replacement. Some species may form cysts to overcome periodic hypoxic events. However, ciliates have specific oxygen niches and sustained hypoxic conditions cannot be coped with individual plasticity but with species replacement. Neritic species will show the highest vulnerability given the increasing frequency and magnitude of hypoxic events in coastal areas.	0/−	medium/high
Coastal Eutrophication	medium	medium	High: many species are able to tolerate severe organic pollution and can compensate for a drop in water quality by species replacement. Species will take advantage of the abundant prey stimulated by nutrient pulses. Mixotrophic species will be benefited under nutrient imbalance conditions due to their trophic plasticity. However, a lower trophic efficiency is expected due to feeding saturation and a relative increase in unpalatable prey.	+/−	low

Microzooplankton species are generally tolerant to temperature and pH values projected by the worst-case climate scenario, while emergent community-level responses to both warming and acidification are strongly influenced by prey and specific nutritional requirements. Warming will reduce metabolic constraints of microzooplankton in polar and subpolar regions, thus stimulating trophic coupling with phytoplankton. The thermally driven stimulation of heterotrophic growth will contribute to controlling deleterious bloom formation and to prolonging the residence time of carbon in the sunlit ocean. At the individual level, the highest risk is associated with the vulnerability to deoxygenation since non-specialist ciliates are known to reduce metabolic rates under hypoxic episodes. The oxygen niches of ciliates seem to be strongly species-specific, suggesting that small shifts in oxygen content cannot be coped with individual plasticity but with species replacement. The specificity of species niches regarding temperature, oxygen, pH, and eutrophication highlights the crucial role of the "rare biosphere" in providing genotypic diversity to cope with present and future global trends.

In addition to the lack of long-term data on microzooplankton, the medium level of confidence of this assessment is associated with uncertainties in the prediction of common responses by the changing hierarchy of factors that interact with prey and the nutritional plasticity of non-strict heterotrophic protists. The robustness of risk assessments will therefore increase with new research and the implementation of a standard numerical framework for the management of big datasets. Moreover, the identification of microzooplankton risks among specific ecosystems is especially relevant in order to map vulnerabilities. Considering the current pace of environmental change, the improvement and standardization of technical summaries gains critical application in communicating climate impacts and in guiding policy discussions.

Specific methodological approaches are encouraged for future research to minimize the identified uncertainties. In the first place, microzooplankton are expected to shift with resource trends; hence, the quantification of size effects produced by well-known phytoplankton responses to global trends (e.g., cell-size reduction, shifts in phenology, and biogeographic distribution) is highly relevant in optimizing prediction models. Response curves and niche delimitations will be accomplished with taxon-specific experiments exposed to multifactorial settings. This approach has been proven useful to identify dominant predictors and nonlinear effects. To assess the impacts at the ecosystem level, a community-based approach, either based on sustained ocean observations or on the experimental simulation of near-natural conditions, is better suited in order to integrate ecological interactions with taxon-specific climate responses. Multifactorial approaches gain critical relevance considering the intensification of interactive effects between climate and other human-driven stressors and the emergence of irregular, local, and regional-scale responses of plankton. Moreover, the effects of global hazards such as enhanced density stratification and upwelling, nutrient imbalance, and increased frequency of extreme events remain largely under-documented. The extent to which species evolution can compensate projected impacts will be also required to reduce uncertainties. These urge for coordinated research efforts to observe and model protistan responses under a multidimensional environment.

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