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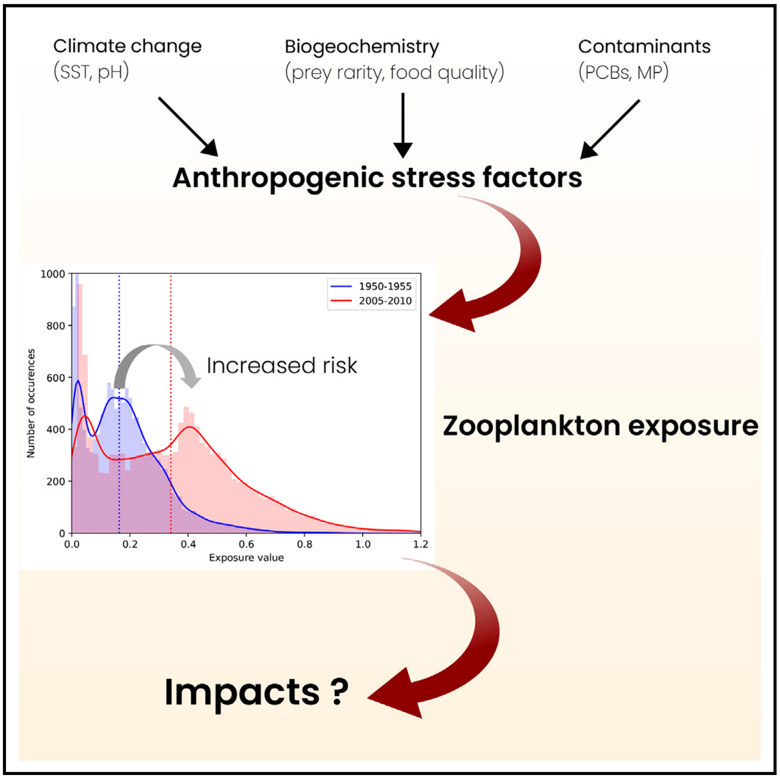
Graphical abstract



Highlights

- Multiple stress factors for zooplankton overlap in the surface ocean
- Stress brought by surface warming and acidification strongly increased in ∼50 years
- More research on anthropogenic impacts on zooplankton is urgently needed

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In brief

We established a global biogeography of anthropogenic stress factors for zooplankton at the surface ocean. Our results demonstrate that zooplankton endures stress from multiple overlapping factors. Most stress factors have increased since the 1950s and may continue to increase by the end of the century, bringing unknown consequences for zooplankton species. This study calls for new scientific and regulatory frameworks to monitor and prevent potential anthropogenic impacts on zooplankton, which are keystone species for ocean ecosystems.

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A global biogeography analysis reveals vulnerability of surface marine zooplankton to anthropogenic stressors

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SCIENCE FOR SOCIETY Oceans are instrumental for our societies through the provision of food and climate regulation. The stability of ocean ecosystems is vital for these services, and zooplankton, the smallest ocean animals, play a key role. They form the base of many marine food webs and are essential for the carbon cycle. However, human activities are impacting the oceans, exposing zooplankton to various stressors, like climate change and contaminants, thus potentially affecting their regulating role. In this work, we show a significant increase in the number and intensity of stressors in the surface ocean in recent decades, which effectively doubled the vulnerability of zooplankton to anthropogenic impacts. The unknown impacts of accumulating stressors prompt further research into anthropogenic impacts on zooplankton. This emphasizes the importance of including zooplankton in efforts to protect the ocean and planning ways to reduce the impact of human activities on these important species in the future.

SUMMARY

Anthropogenic impacts on zooplankton at the surface ocean pose an urgent challenge because these keystone species are crucial for oceanic processes. Some anthropogenic stressors for zooplankton have been identified, such as acidification due to climate change, but a multitude of other stressors exist, and the combination of these may lead to unknown impacts. We utilized global biogeochemical models to assess the temporal and spatial distribution of zooplankton stress factors, including changes in sea surface temperature, acidification, prey quantity, food quality, and contaminants. We highlighted regional hotspots where multiple stress factors overlap and revealed that most stress factors are increasing. By linking stress factors to zooplankton distribution, we introduced a zooplankton vulnerability index. We found that the zooplankton vulnerability index has doubled in 50 years, and this suggests that zooplankton populations are increasingly at risk from anthropogenic stressors. Further research is needed to develop strategies for mitigating the impacts of anthropogenic stressors on zooplankton.

INTRODUCTION

Planetary boundaries define the safe operating space for anthropogenic activities within Earth's capacity.[1] To date, several planetary boundaries have already been crossed (i.e., novel entities, biodiversity, and biogeochemical flows), pushing humanity dangerously close to several climate tipping points.[2,3] The concept of planetary boundaries has been extended to ocean ecosystems.[4] Oceans constitute 90% of the planetary habitat space and provide 61% of the world's gross domestic product.[5] However, the consequences of crossing these boundaries for planktonic organisms, which are the foundation of ocean biodiversity and biomass, have been ignored. In this context, an understanding of the different stress factors acting on marine plankton and their impacts is a key missing element necessary for an integrated assessment of planetary boundaries for ocean ecosystems.

Here, we focus on zooplankton, which are keystone organisms in ocean ecosystems but often overlooked in anthropogenic impact studies. Zooplankton are heterotroph organisms drifting along with the ocean currents. As primary consumers, their grazing activity regulates phytoplankton populations and primary productivity in many regions of the ocean.[6–8] Additionally, they constitute the largest biomass on Earth and are an indispensable food item for higher trophic levels, including fish,[9,10] birds,[11] and mammals.[12] Zooplankton also regulate ocean biogeochemistry through recycling and export of carbon and nutrients.[13–17] In spite of these essential roles, zooplankton are largely under-represented in marine ecosystem studies, and many uncertainties regarding how zooplankton respond to environmental change remain.[18,19]

In the ocean, the distribution and functioning of zooplankton is regulated by a suite of environmental conditions.[20] Biogeochemical conditions, such as prey availability and nutrient content, drive energy intake and nutrient assimilation.[21] Because they are ectotherms, temperature directly influences zooplankton physiology and metabolism.[22–24] Other environmental factors, such as pH and oxygen, also exert influence on shell formation and respiration rate of zooplankton.[25,26] Anthropogenic climate change has already caused significant changes to abiotic conditions in the ocean surface through changes in sea surface temperature (SST) and acidification.[27] Additionally, climate change modifies the biotic conditions through changes in plankton and essential nutrient distributions.[17,28,29] Climate change impact on zooplankton health is superimposed on the increasing number of anthropogenic contaminants in the ocean.[30] To date, several contaminants have been shown to harm marine ecosystems, but the toxicity of many contaminants remains unknown.[31,32] Thus, the overall fate of zooplankton is linked to several planetary boundaries (biodiversity, novel entities, climate change, ocean acidification, and biogeochemical flows). The presence of multiple stressors will likely amplify the negative effect of any stressor alone.[33] Consequently, crossing one or more of the planetary boundaries may trigger abrupt changes impacting the equilibrium of ocean biogeochemistry and food webs. This knowledge gap requires us to assess the spatial superimposition of these multifactorial stressors on zooplankton in a changing climate.

Here, we use a multistressor framework to combine different metrics, derived from modeling assessments as well as large scale datasets, into a single indicator to measure how the anthropogenic pressure on zooplankton functioning changed since the preindustrial period. This approach follows the ocean health index (OHI) of Halpern.[34] Our framework produces a global overview of zooplankton stressors linked to climate change impacts on abiotic factors (changes in SST and ocean acidification [OA]), climate change impacts on biogeochemical conditions (prey rarity and food quality), and the presence of contaminants (polychlorinated biphenyls [PCBs] and microplastics [MP] that are bioaccumulative and toxic for zooplankton.[35–39] Our stressor analysis takes into consideration the temporal evolution of each stressor since the preindustrial era, encompassing two distinct time periods characterized by exponential growth in greenhouse gas emissions and chemical release: the onset of the Anthropocene (1950–1955) and the early 21st century (2005–2010). Considering these two time periods reveals that most stress factors have increased in a few decades, revealing an intensification of anthropogenic pressure on surface zooplankton. Moreover, linking the stressors with zooplankton biomass allows drawing a biogeography of zooplankton vulnerability to anthropogenic pressure, showing that zooplankton vulnerability has been increasing (median zooplankton exposure to stressors doubled in 50 years), primarily driven by abiotic stressors (median stress from OA increased 5-fold), with likely amplification by overlapping stress from contaminants and changing biogeochemical conditions. Our understanding of the impacts of anthropogenic pressure on zooplankton is hampered by the lack of empirical knowledge about the impact of each stressor alone and in combination. With this goal in mind, we frame a scientific roadmap to understand the combined impacts of the multifactorial stressors on zooplankton at the global scale.

RESULTS

Global distribution of zooplankton stress factors

In 1950–1955, the stress factors for zooplankton functioning had limited spatial extent and intensity (Figure 1). Most of the stress for zooplankton functioning was linked to the already perceivable effects of climate change on the surface ocean via changes in SST and OA (Figures 1A and 1B). In particular, relatively low stress from OA (around 0.3) was detectable in almost every region. The highest intensity of stress from OA (over 0.8) was found in the Indian sector of the Southern Ocean (around 100°E). The early impacts of climate change on SST were mostly found in the North Atlantic and North Pacific regions, with stress between 0.5 and 0.6 around 40°N (Figure 1A; see Note S1 for a regional analysis of the stress factors).

Overall, the impacts of climate change on surface biogeochemistry (prey rarity and food quality; Figures 1C and 1D) were limited in 1950–1955 (hence, the stress factors below 0.5 in most regions; Figures 1C and 1D). However, there is a strong spatial variability in the stress from prey rarity (Figure 1C). This factor is highest in the Arctic region and dominates over the stress from OA (Note S1). There was almost no stress associated with food quality changes between the preindustrial era and 1950–1955, except for a small region surrounding the South Pacific gyre, which may be linked to an expansion of the South Pacific gyre (Figure 1D). This high stress value is linked to the decreased food quality between the preindustrial period and 1950–1955 because of the changes in ocean dynamics that lead to changes in micronutrient concentrations and prey stoichiometry.

In 1950–1955, ocean contamination from PCBs was confined to the northern hemisphere. Accordingly, the highest stress occurs in the western Atlantic, closest to the largest PCB sources[40] (Figures 1E; Note S1). Finally, MP contamination was null in 1950–1955 because the global plastic production was low.

The distributions and intensities of all stress factors significantly changed between 1950–1955 and 2005–2010 (Figure 2). Stress factors linked to abiotic climate change (changes in SST and OA) expanded and intensified in almost all regions (stress factor from OA over 0.5 in almost every region in Figure 2B and

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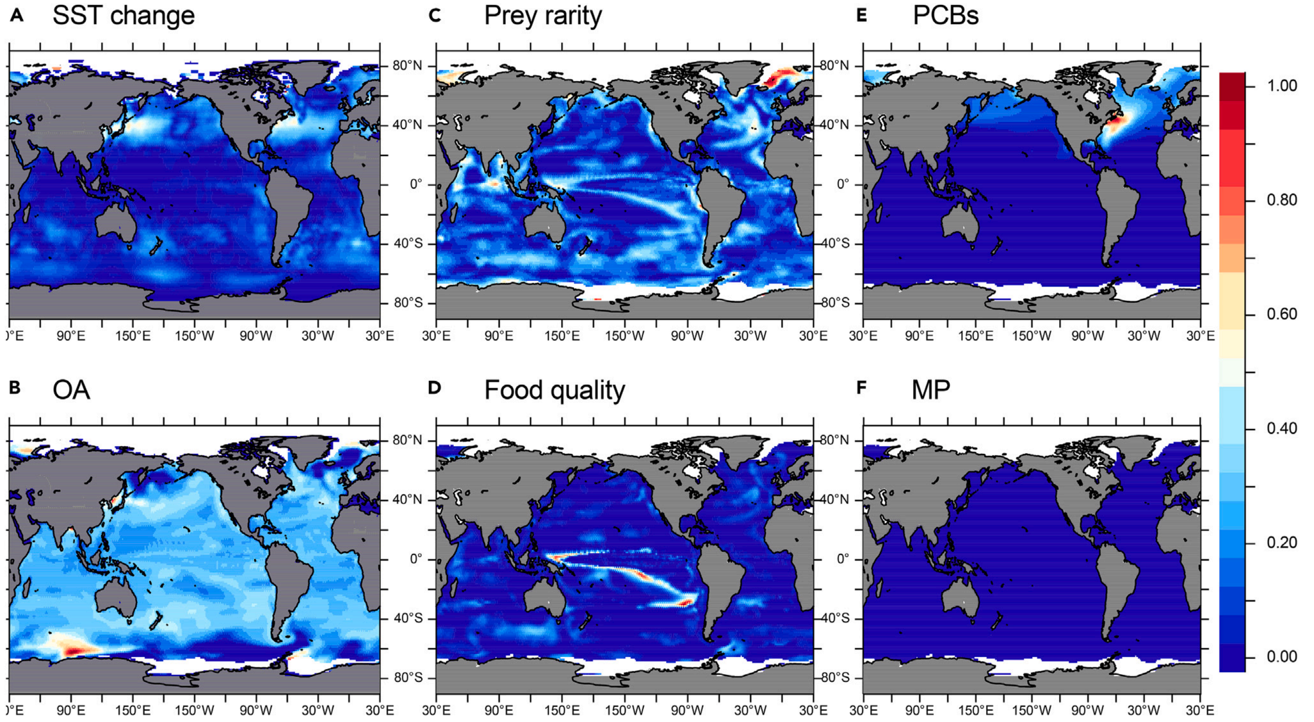

Figure 1. Maps of the stress factors for the 1950–1955 period

(A and B) The climatic stress factors: changes in SST since the preindustrial (PI) period $(SST_{(1950-1955)} - SST_{(PI)})/\sigma(SST_{PI})$ (A) and ocean acidification (OA) on the surface (B).

(C and D) The changes in biogeochemical indexes (changes in biogeochemical conditions since the PI period): prey rarity $((1 - \overline{\sum_i^j (P_i \times p_i^j)})_{1950-1955} - (1 - \overline{\sum_i^j (P_i \times p_i^j)})_{PI})$ (C) and food quality $(\sum_m |\overline{1 - FQ_m}|_{1950-1955} - \sum_m |\overline{1 - FQ_m}|_{PI})$ (D).

(E and F) The stress factors from contaminants: polychlorinated biphenyl (PCB) concentration (E) and microplastics (MP) concentration (0 in the 1950–1955 period) (F).

All stress factor values are log transformed and normalized between 0 and 1 (see experimental procedures for details). White areas are ice covered and masked out.

Note S2). The stress factor from changes in SST spread from the mid to the lower latitudes, with stress increases between 0.1 and 0.2 in the equatorial regions, coastal areas, and Indian and South Pacific oceans (see Figure S1 for difference maps). In the North Atlantic, stress from changes in SST has not significantly changed (average stress values changed from 0.23 to 0.28 between 1950–1955 and 2005–2010; Note S1). Furthermore, stress from changes in SST in the southern hemisphere below 40°S decreased locally, even when the average stress value in the Southern Ocean increased from 0.06 in 1950–1955 to 0.11 in 2005–2010 (Figures 2A and S3; Note S2). The local cooling may be linked with modeled changes in ice melt.[41,42] The intensification of OA stress is particularly pronounced at high latitudes (stress values reaching locally over 0.60 over 40° in both hemispheres; Figure 2B). The increase and spread of the stress factors linked to climate change impacts on abiotic conditions between 1950–1955 and 2005–2010 indicate that the impacts of climate change on the surface ocean intensified over the second half of the 20th century.

The biogeochemical stress factors evolved differently between 1950–1955 and 2005–2010 (Figures 2C and 2D). Changes in stress from prey rarity display a patchy pattern (Figure S1C), with a decrease of 0.01 in the Southern Ocean but a strong intensification in the North Atlantic and the equatorial Atlantic (stress value increased over 0.5; Figures 2C and S1C; Note S1). Additionally, stress from prey rarity decreased along the Eastern Pacific coasts (between −0.1 and −0.4) and along the Western Indian coasts, while a limited increase (between 0.1 and 0.2) is observed along 40°S and between 30°N and 50°N in the Pacific. These changes are the result of the spatially contrasted impacts of climate change on plankton production, which affects the biomass of zooplankton prey. In contrast, overall food quality decreased between the two time periods, resulting in higher stress (Figures 2D and S1). Climate change impacts modified the nutrient stoichiometry of zooplankton prey, leading to a reduced food quality index (i.e., further from the optimum value of 1;[43] Figures S4–S6).[43] The largest changes in food quality occurred in the Southern Ocean, with stressor values rising from 0 to 0.4 (Figures 1D and 2D), indicating important changes in trace nutrient biogeochemistry in the region.[17]

PCB contamination expanded toward new regions, mostly in the northern hemisphere, between 1950–1955 and 2005–2010 (Figure 2E). This expansion was due to increasing releases over this time period and the wider redistribution of these highly persistent contaminants through atmospheric transport and ocean currents. The distribution of the stress factor from MP in

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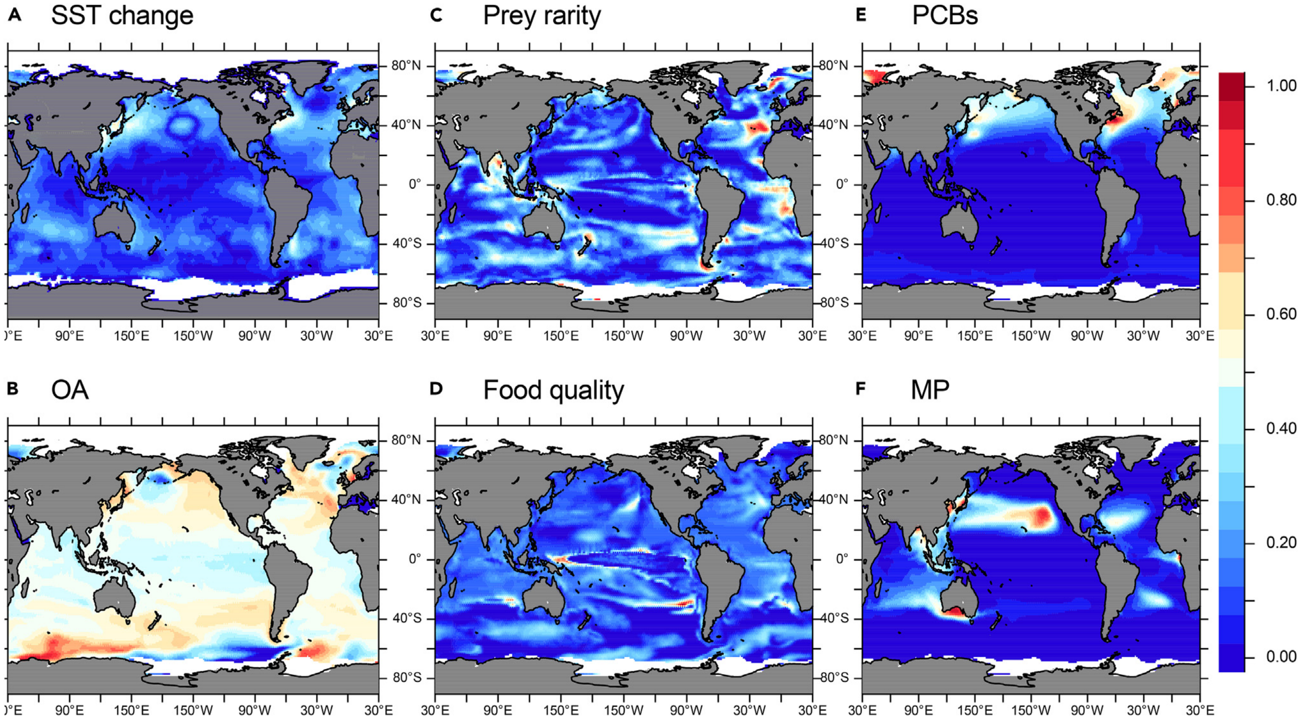

Figure 2. Maps of the stress factors for the 2005–2010 period

(A and B) The climatic stress factors: changes in SST since the PI period $(SST_{(2005-2010)} - SST_{(PI)})/\sigma(SST_{PI})$ (A) and OA on the surface (B).

(C and D) The changes in biogeochemical indexes (changes in biogeochemical conditions since the PI period): prey rarity ($(1 - \overline{\sum_i^j (P_i \times p_i^j)})_{2005-2010} - (1 - \overline{\sum_i^j (P_i \times p_i^j)})_{PI}$) (C) and food quality ($\sum_m |1 - FQ_m|_{2005-2010} - \sum_m |1 - FQ_m|_{PI}$) (D).

(E and F) The stress factors from contaminants: PCB concentration (E) and MP concentration (F).

2005–2010 represents the current distribution of MP in the surface ocean (Figure 2F; see also Richon et al.[44]). The surface convergence zones (subtropical gyres and coastal areas close to MP sources) accumulate high concentrations of MP, thus leading to maximum stress factor values. Overall, multiple stress factors for zooplankton functioning occur simultaneously at the surface of the ocean. Moreover, anthropogenic activities led to an expansion and intensification of almost all stress factors within a few decades since the 1950s.

Identifying stress factor dominance and overlap

In Figure 3, we identified the dominant stress factor in each point of the surface ocean as the factor that exhibits the largest change since the preindustrial period. In most areas of the surface ocean, climate change (in particular OA) constitutes the dominant anthropogenic stress category for zooplankton (Figure 3). In 1950–1955, climate change impacts on abiotic factors (changes in SST or OA) were the dominant stressors in about 82% of the ocean surface (276 Mkm^2; Figure 3C). Thus, among the range of stress factors that we calculated, changes in SST and pH exhibited the largest variability since the preindustrial period. In 2005–2010, the intensification of climate change impacts led to warming and acidification dominating over 300 Mkm^2 (88% of ocean's surface), while areas dominated by stress from changes in biogeochemical conditions (prey rarity or food quality) were reduced 3-fold between the two periods. Prey rarity and food quality were the dominant stressors in 17 Mkm^2 in 2005–2010 (5% of the total surface area versus 16% in 1950–1955 because of the large regions in the Southern Ocean dominated by prey rarity stress). The emergence and rapid contamination of surface ocean by MP led to MP concentration becoming the dominant stress factor for zooplankton functioning in large areas of the subtropical North Pacific and the South Australian coast (Figure 3B). Overall, 2.1% of the ocean surface area was dominated by contamination-related stressors from PCBs and MP in 2005–2010, which remained stable in proportion since 1950–1955. In 1950–1955, the contamination stressor, which consisted only of PCBs, was the dominant stress factor in a substantial part of the North Atlantic.

The intensification, spatial expansion, and emergence of new stress factors between 1950–1955 and 2005–2010 exposed large areas of the ocean to overlapping stress factors (Figure S2). In 2005–2010, over 16 Mkm2 (5% of the global ocean surface) were exposed to 2 or more stress factors compared with 0.9 Mkm2 (<1%) in 1950–1955 (Figures 3C and S2). The changes in stress factor dominance were driven by the changes in each stress factor distribution and intensity between 1950–1955 and 2005–2010 (Figure S1). As also seen in Figure 2, the climatic stress factors mostly intensified and expanded, whereas the biogeochemical stress factors intensified in some regions but decreased in others. Stress factors linked to the contaminants considered in this study mostly intensified and spread

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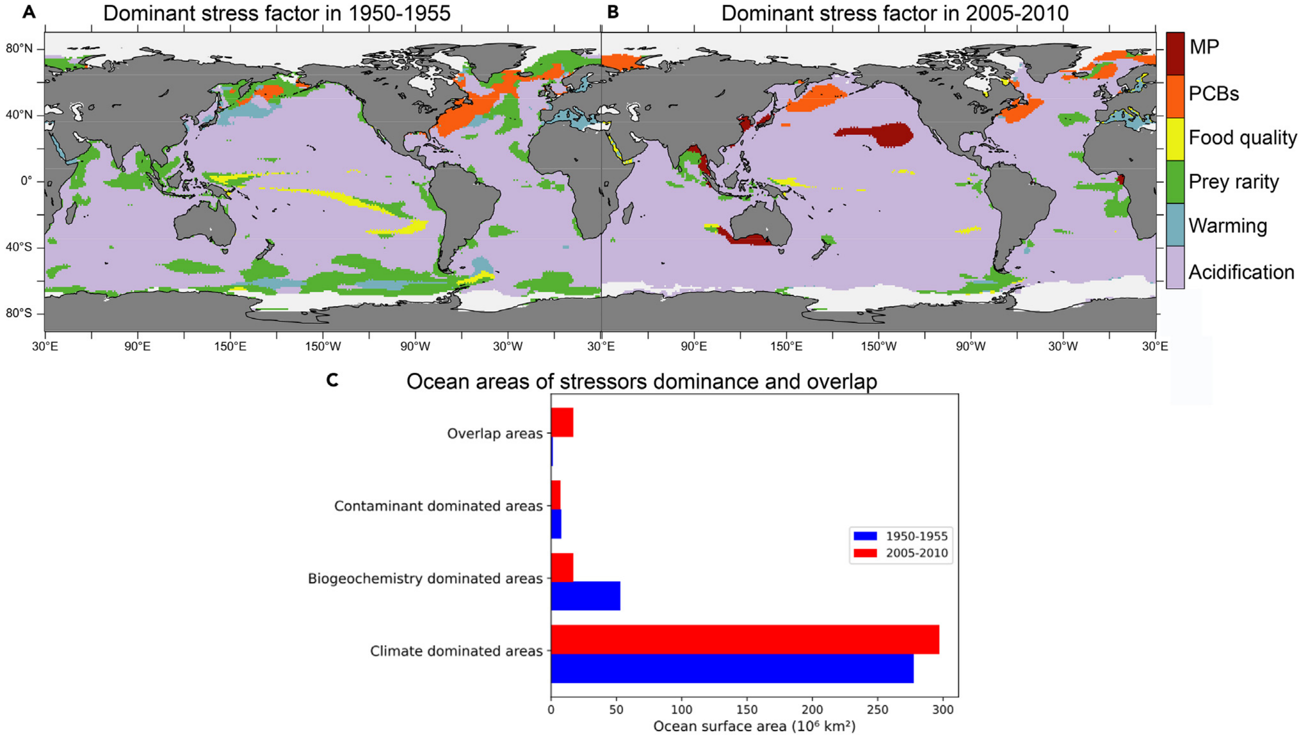

Figure 3. Stress factor dominance and overlap

(A and B) Dominant stress factor (i.e., the stress factor showing the highest variation since the PI period) for each grid point in 1950–1955 (A) and 2005–2010 (B).
(C) Histograms of the ocean areas dominated by each stressor category.

(Figures 2E, 2F, and S1), but this intensification overlapped in space with the climatic stress factors, notably in the North Atlantic and North Pacific regions. The stronger changes in SST and acidification that occurred in these regions between 1950–1955 and 2005–2010 caused the dominance of climatic stress factors and explained the small decrease in contaminant-dominated areas in 2005–2010.

Our analysis of stress factor dominance and overlap sheds light on the temporal fluctuations in environmental conditions since the 19th century. However, it is important to note that this assessment does not quantify the severity of potential impacts on zooplankton from the stressors. In other words, the identification of a dominant stress factor using our methodology does not imply that it should yield negative impacts on zooplankton, nor does it suggest that it will have more pronounced effects compared with a stressor that would be less variable.

Calculating zooplankton exposure

The zooplankton stress factor framework provides evidence for which regions are hotspots for stressors (i.e., regions where stress factor overlap and/or stress factor values increased over time) and identifies the most important stress factors in a given region. The risk of anthropogenic impacts on zooplankton functioning is quantified via an exposure term (Figure 4). Exposure is calculated as the product of normalized zooplankton simulated biomass (called the zooplankton index in Figure 4; see also Note S2 for zooplankton index evaluation) with the sum of all stress factors (total stress factors). Exposure of zooplankton to risks from stress factors has already been used by Richon et al.[44]

The zooplankton index (i.e., normalized zooplankton biomass) enables estimations of zooplankton biomass distribution and spatial variability, providing a unitless exposure factor. The zooplankton index mirrors the distribution of surface productivity in the ocean, with highest values observed in upwelling and coastal regions (Figures 4A and 4D). In the high latitudes of the Arctic and Southern Ocean, the zooplankton index is intermediate (between 0.4 and 0.6) but likely downplays strong seasonal variability. Overall, there is very little modification of the zooplankton index between 1950–1955 and 2005–2010 (Figures 4A and 4D), which indicates no significant change in zooplankton biomass distribution during our simulation. In 1950–1955, the total stress factor value was below 2 in all oceanic regions (Figure 4B). Highest exposure occurred off Eastern Canada, where the maximum stress from PCBs occurred. In contrast, the spread and intensification of almost all stress factors in 2005–2010 (Figure 2) yielded to high values of total stress factors over the entire surface ocean (over 1.5 in most regions and up to 2.5 in the North Atlantic and North Pacific; Figure 4E).

Due to the relatively low total stress factors in 1950–1955, zooplankton exposure remained limited (Figure 4C). Only the western North Atlantic and Pacific regions showed potential significant exposure (approximately 0.8). This exposure was influenced by the combined effect of high stress factors related to changes in SST, prey rarity, and PCBs (Figure 2) as well as an elevated zooplankton index (around 0.6–0.7). Consequently,

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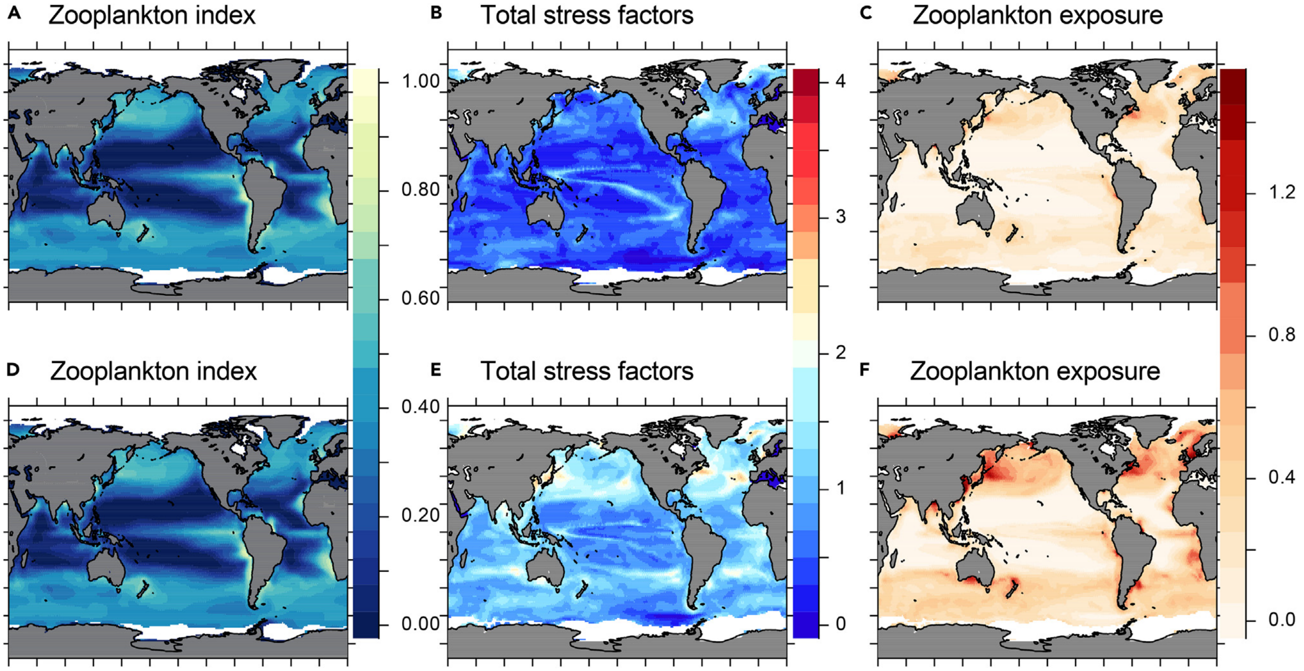

Figure 4. Biogeography of zooplankton exposure to human impacts

Shown are maps of the zooplankton index (normalized zooplankton biomass, simulated with NEMO/PISCES, see Richon and Tagliabue[17]) (A and D), total stress factors (sum, B and E), and zooplankton exposure to total stress factors (C and F). (A)–(C) are averaged over 1950–1955, and (D)–(F) are averaged over 2005–2010.

the North Atlantic and Pacific regions were most likely to experience anthropogenic impacts on zooplankton functioning during the 1950–1955 period.

Zooplankton exposure was increased by 2005–2010, raising the importance of anthropogenic impacts on zooplankton. Because there were only minor changes in the zooplankton index by 2005–2010, the increased zooplankton exposure in this period was driven by the increase in the total stress factor. This was particularly visible in the North Pacific and North Atlantic between 30°N and 50°N, where the total stress factor almost doubled, and, to a lower extent, in the southern hemisphere (Figure 4). Despite the increase in total stress factor value in the North Pacific gyre (from around 0.5 to 1.5), the change in zooplankton exposure was small because this region is oligotrophic with a low zooplankton index and low temporal variability (Figures 4A and 4D). The biogeography of zooplankton exposure to stress factors permitted by our global assessment highlighted the areas where the most important anthropogenic impacts on zooplankton may occur and suggested that the regions that combine a high zooplankton index with increasing stress factors (e.g., the North Atlantic, the North Pacific, and some coastal regions, such as the South of Australia, the Indian and South-East Asian coasts, or the western African coasts) require attention regarding potential impacts of anthropogenic activities on zooplankton. Between 1950–1955 and 2005–2010, the median exposure of zooplankton doubled (from 0.17 to 0.35; Figure 5). Although exposure values in 1950–1955 were generally close to 0, many areas exhibited values above 0.15, as indicated by the peak between 0.15 and 0.22. In 2005–2010, the peaks of exposure occurrences shifted to 0.08 and 0.45. This demonstrates a significant increase in zooplankton exposure to multiple stressors since 1950–1955. The rise in exposure values can be attributed to the higher stress factor values (see Figure 6 for stress factor distributions).

The stress factors linked to climate change showed the largest distribution shift (Figure 6). The median value of stress from changes in SST was close to 0 in 1950–1955 and around 0.05 in 2005–2010. The median value of stress from OA increased 5-fold between 1950–1955 and 2005–2010. On the contrary, climate change impacts on biogeochemical stress factors (prey rarity and food quality) were overall limited, with only slight shifts in their distributions. Finally, the distribution of stress factors from the contaminants showed median values close to 0 in both time periods. This strongly skewed distribution was linked to the limited spatial extent of contaminant-related stressors (Figures 1 and 2). As also shown by Figure 3C, the most intense changes of stress factors for zooplankton at the surface ocean were directly linked to climate change. By the end of the 21st century, as climate change impacts continue to affect the surface ocean, the distribution of stressors from changes in SST and OA may shift further toward much higher values (see 4-fold increase in median SST stress factor and the OA stress peak around 0.8 in Figure S3).

DISCUSSION

Toward a global health index for zooplankton?

In this study, we quantify anthropogenic pressure on zooplankton in the global surface ocean, which is a first step toward addressing the knowledge gap regarding anthropogenic

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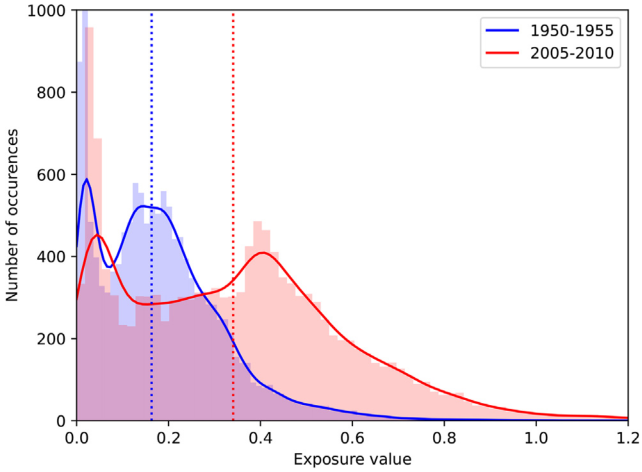

Figure 5. Bar plot of the zooplankton exposure distributions for the two time periods

Blue bars represent 1950–1955, and red bars represent 2005–2010. The number of occurrences represents the number of observed exposure values in every grid point of the modeled surface ocean. Dotted lines indicate the median exposure values for the 1950–1955 period (blue) and for the 2005–2010 period (red). Solid lines represent the kernel density estimates (kdes) of the exposure distribution for both periods (calculated with the Seaborn Python package[45]).

impacts on marine zooplankton. Addressing this knowledge gap is important because of the key role played by zooplankton in ocean ecosystems. Thus, identifying and quantifying anthropogenic stress factors for these keystone species is a necessary first step toward understanding the links between zooplankton functioning and the planetary boundaries and to find ways to mitigate their impacts. The stress factors and exposure based on global observations and biogeochemical model output[17,44,46] provide useful insights into the direct and indirect potential impacts of anthropogenic activities on zooplankton.

Our results highlight the multifactorial and overlapping nature of anthropogenic climate change, biogeochemical changes, and contamination. Between 1950 and 2010, the presence of stress factors has expanded dramatically and intensified as a result of the ongoing climate change impacts and chemical releases to the ocean. The variety of the stress factors occurring at the ocean surface may expose zooplankton to increasing impacts (Figures 4 and 5) and may lead to a decrease in zooplankton health. However, many uncertainties and knowledge gaps regarding zooplankton and stress factors hamper our ability to reach firm conclusions regarding the ultimate impacts on zooplankton biomass and dynamics.

First, the representation of the stress factors in current biogeochemical models carries uncertainties. Changes in SST and OA are probably the best constrained stress factors thanks to the breadth of observations and models representing these abiotic factors.[47,48] In this study, we focused on climate change impacts on the surface abiotic conditions (SST and pH), but observations have shown that climate change impacts on some abiotic factors, such as pH or oxygen concentration, also occur (and sometimes may be greater) below the surface.[49,50] As a consequence, different zooplankton species that inhabit different depth strata may experience stress factors that differ from those examined here. Thus, complementary investigations using the stress factor framework we developed should be applied to various species and specific depth ranges of the ocean. Moreover, the distribution of the biogeochemical stress factors (prey rarity and food quality) is linked to the distribution and composition of plankton.[43] Even when the representation of global planktonic biomass distribution is satisfyingly captured by our model (Note S2), its evolution with climate is still largely uncertain.[19,27,51,52] Currently, the number of global biogeochemical models representing anthropogenic contaminants is limited due to the large uncertainties regarding their sources, sinks, distribution, and transformations in the ocean. The toxicity of PCBs and MPs to zooplankton has been demonstrated in previous work.[53] Thus, we used two state-of-the-art biogeochemical models that include PCB[46] and MP[44] distribution, respectively. These models are based on the current understanding of these contaminants' distributions, but large uncertainties regarding their distributions, transformations, and impacts persist. However, while PCBs have been regulated under the Stockholm Convention, and their concentrations in the ocean have been declining in the last decade, release of the majority of other chemicals (including MP) to the ocean continue to increase, following increases in global chemical production,[54] suggesting that the contaminant-related stress factor is, in fact, larger than shown in this analysis.

To link the exposure of zooplankton to stressors with impacts on marine ecosystems, several knowledge gaps must be addressed. Here, we calculated exposure based on the co-occurrence of zooplankton and the stressors, but the duration of zooplankton exposure was not considered because our model does not explicitly represent zooplankton lifespan. However, this exposure time may influence stressors impacts. Moreover, experimental studies show that stressor impacts on zooplankton differ depending on the stress and the species considered.[55] Moreover, the stress factors impact various aspects of zooplankton physiology and, hence, fitness (respiration, grazing, growth, reproduction, survival) and sometimes impact several aspects at once.[56] For instance, contrasting effects of warming and OA may be observed depending on the intensity of both stress factors.[57] The impacts of changes in temperature on zooplankton have also been extensively studied. The general understanding regarding temperature impacts on zooplankton is based on the Arrhenius equation linking zooplankton metabolic rates (e.g., respiration, mortality) exponentially to temperature increase.[58,59] However, some functional traits (i.e., morphological, physiological and/or phenological characteristics that impacts organisms' fitness and functioning)[60] may be maximized at an optimal temperature that varies between species (e.g., reproduction, growth).[18,61,62] These complex effects complicate the simple formulation of an empirical relationship between stress factor and zooplankton dynamics.

To address the knowledge gap regarding the impacts of stressors on zooplankton, a deeper understanding of zooplankton physiology and biology is required to (1) identify the metrics that best describe zooplankton functioning and (2) quantify each stress factor's impact on zooplankton. Such a framework necessarily relies on simplified assumptions. Building empirical relationships between stress factors and zooplankton functioning (e.g., growth, mortality) is difficult because this group

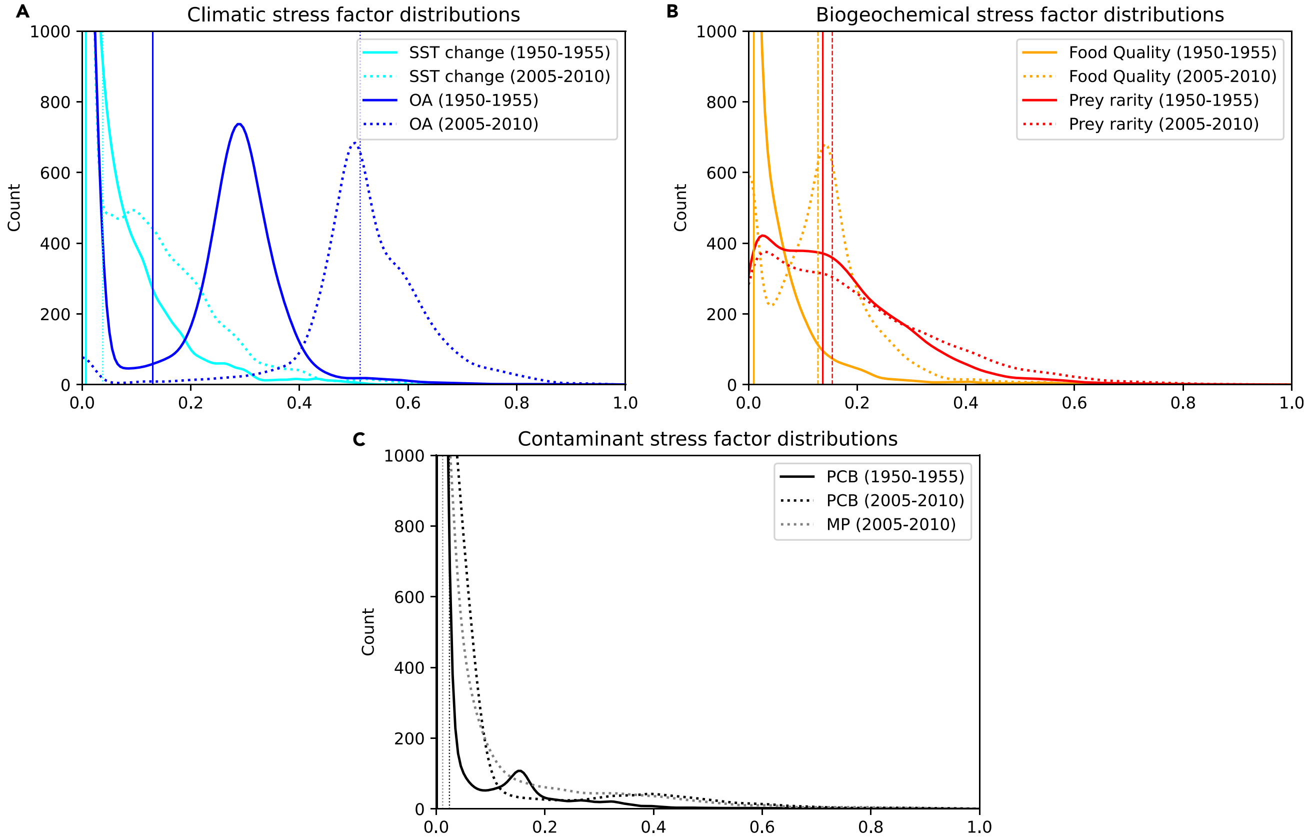

Figure 6. Stress factor global distributions

Lines represent the kernel density estimates of stress factor distributions in 1950–1955 (solid lines) and 2005–2010 (dotted lines): distributions of the climatic stress factors (sea surface temperature [SST] and OA) (A), the biogeochemical stress factors (food quality and prey rarity) (B), and the contaminant stress factor (PCBs and MP) (C). The vertical lines represent the median stress factor values. MP contamination is set to 0 at the onset of the Anthropocene (1950–1955).

is composed of many different species that are adapted to different conditions. Finally, the tolerance for each individual to combined stressors remains unknown, which precludes quantifying a planetary boundary for zooplankton health.

Ultimately, our assessment of zooplankton exposure to anthropogenic stressors represents two examples per stressor category. Given the rapid rise in anthropogenic footprint on the oceans, this assessment, which describes the best known stress factors, is incomplete. Other stressors, such as deoxygenation or other contaminants have already been identified and should be included in future studies as global distributions on decadal timescales become available.[63]

Challenges in predicting stress factor impacts

Zooplankton is a taxon comprising tens of thousands of different species with different life history traits and tolerance for each stress factor. Solan and Whiteley[64] listed some combined impacts of stress factors on marine invertebrates and noted that the responses depend on the species, the stress factors, the life stage, and the conditions of the experiment. Therefore, an integrative framework is needed to represent the impacts of multiple simultaneous stress factors on communities beyond single-species assessments. Because they integrate results from different experimental conditions across different species, global biogeochemical models are a good tool to build such a framework.

The overlap of stress factors (highlighted in Figures 3 and S4) may underlie interactions between stress factors, influencing their net impacts on zooplankton. Experimental evidence showed that the combined impacts of two or more stress factors on zooplankton are difficult to observe and predict.[25,56] Modeling and experimental studies have shown that two simultaneous stress factors may lead to synergistic (more than the sum), antagonistic (less than the sum), or simple additive impacts on zooplankton.[65] Crain et al.[33] have shown that interactive effects of stressors are often synergistic (i.e., worse than the sum) but that different responses may be observed depending on the species and experimental conditions. However, conducting experiments on the impact of multiple stressors on diverse zooplankton remains challenging.

Given the difficulty in studying more than two stress factors at a time, predicting the combined effects of all of the stress factors at once is, at present, almost impossible because cocktail experiments are long and expensive, and the list of potential contaminants and stress factors to zooplankton is ever increasing.

Potential adaptation of zooplankton

In the context of changing environmental conditions, the potential for zooplankton adaptation must be addressed. By the end of

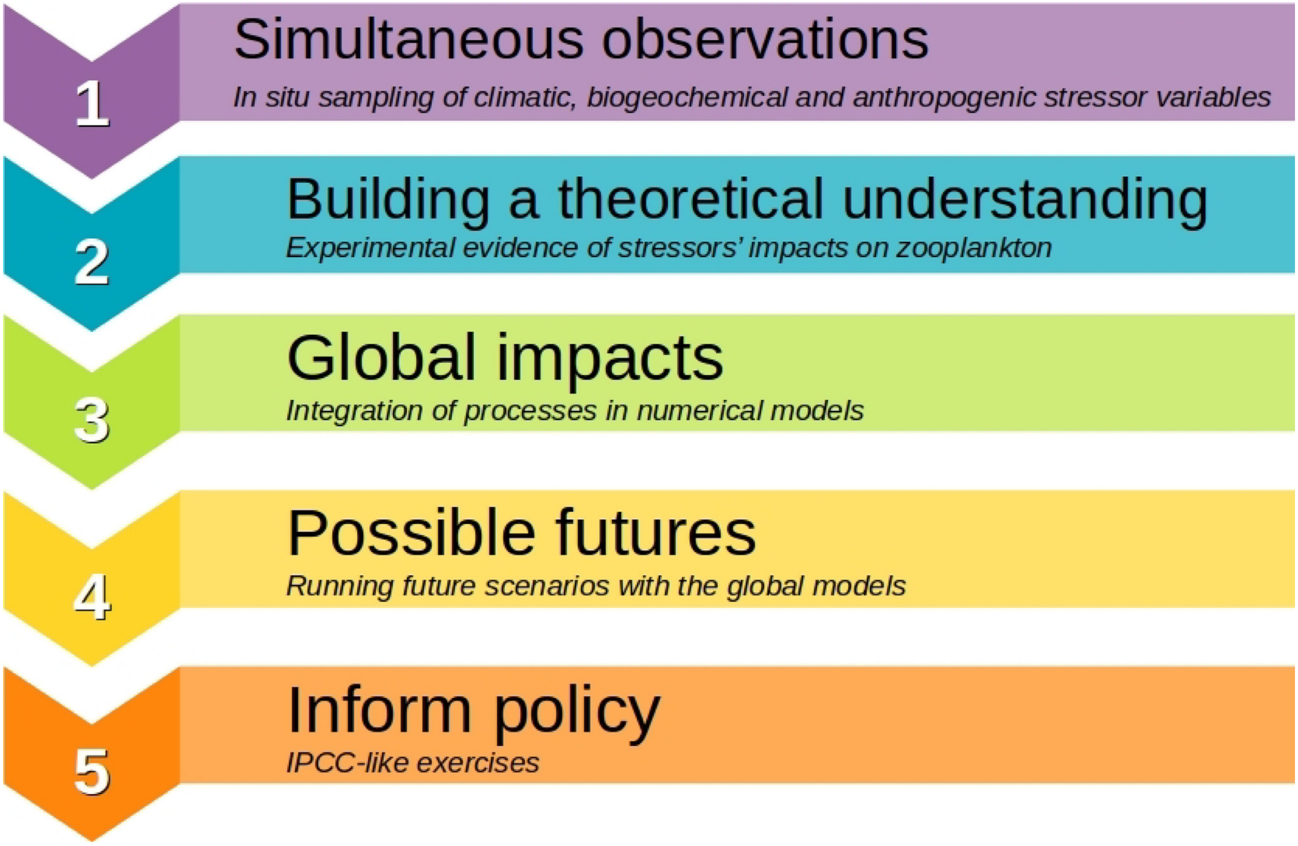

Figure 7. Scientific and regulatory framework toward a global understanding of the multifactorial stress factors to zooplankton functioning

the century, continued variations in climatic conditions may lead to new environmental conditions for zooplankton.[66] For instance, if the average seawater temperature may reach outside of some species' thermal window, most zooplankton species are adapted to variations in seawater temperature and other environmental factors (i.e., prey concentration, salinity) on short timescales to cope with seasonal succession and diel vertical migration. In this context, the ability of zooplankton to adapt to long-term environmental changes is unclear. On the other hand, species found in naturally stable environments, such as tropical regions, may be more sensitive to changes in environmental conditions. Evolutionary biologists hypothesized that the changing environmental conditions may promote evolutionary responses of zooplankton.[67] Finally, the combination of warming with other stress factors (such as acidification and oxygen loss) may lead to growing "compound" events.[68,69] The ability of zooplankton to survive such extreme events is unclear.

Experimental studies on multigenerational CO_2 stress impacts showed that copepods may adapt to the relatively slow pace of OA.[70] Moreover, Thor and Dupont[71] demonstrated that some impacts of OA may be the result of phenotypic plasticity, which may indicate reversibility. However, zooplankton's ability to survive changing environmental conditions sometimes implies changes in morphological and functional traits (i.e., size, biomass, metabolism),[22,72,73] with potential consequences for food web connectivity and ecosystem dynamics.[22,72,73]

Toward innovative scientific and regulatory frameworks

Zooplankton constitute a key group in ocean ecosystems but receive little attention compared with phytoplankton and bacteria. Because of their key role and the rapidly increasing scientific information regarding stress factors, greater knowledge on anthropogenic impacts on zooplankton should be urgently acquired. Concerning the increasing exposure of zooplankton to multifactorial stress factors, research should aim for a holistic understanding of zooplankton functioning in the global ocean. For instance, global ocean temperature should continue to rise until the end of the century, even in scenarios of radical decreases in greenhouse gas emissions.[47] Similarly, cleaning up the oceans from contaminants would represent tremendous effort.[74] In sum, the stress factors currently imposed on zooplankton are virtually irreversible on generational timescales. In this context, a good characterization of the impacts from all stress factors on zooplankton biomass and functioning, both in isolation and in combination, is needed to understand and anticipate the future state of these keystone species for marine ecosystems and to assess impacts that can be expected on marine biodiversity and ecosystem services.

To this aim, we propose the following plan of action (see also Figure 7).

(1) First, sampling efforts should simultaneously measure biotic and abiotic variables that constitute the stress

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factors. Simultaneous sampling of essential ocean variables (EOVs), such as temperature, plankton biomass, diversity, nutrients, and contaminant concentration, is needed as part of ocean monitoring.

(2) Experimental and observational work is instrumental to build a theoretical understanding of the impacts of the different stress factors on zooplankton communities. Classically, experimental studies focus on single or a few species that are representative of a group (e.g., *Calanus*, *Daphnia*). New ecotoxicological approaches toward more realistic experimental procedures are encouraged, including multiple species spanning several trophic levels and environmental values of multiple stress factors. Such setups are more complex to design and maintain but offer unique possibilities to observe the response of entire communities and ecosystems to simultaneous stress factors.[75].

(3) Results from such experiments must be parameterized within global models that represent the different communities and stress factors. Accounting for these new complex data in models also requires careful considerations of model and experimental design. Consistent dialogue between experimentalists and modelers is required.

(4) New socio-economic pathway scenarios must be developed to represent changes in both climate and contaminants for their combined effect to be quantified.

(5) Finally, synthesis efforts regarding the state of scientific knowledge of anthropogenic impacts on zooplankton, similar to those of the Intergovernmental Panel on Climate Change (IPCC) or Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES**)**, should be initiated. These could be initiated by international working groups focusing on marine zooplankton, such as the ICES Working Group on Zooplankton Ecology (WGZE).[76] Such synthesis would allow informing policy- and decision-makers both locally and globally on the impacts of climatic, biogeochemical, and contaminant stress factors on marine zooplankton. This effort should help to identify and quantify the planetary boundaries linked to zooplankton functioning and dynamics.

EXPERIMENTAL PROCEDURES

Resource availability

Lead contact

The lead contact for this manuscript is Camille Richon (camille.richon@univ-brest.fr).

Materials availability

No new materials were generated by this study.

Data and code availability

SST Data from the HadISST product can be found on the Met Office web page (https://www.metoffice.gov.uk/hadobs/hadisst/). Code and data from the biogeochemical models (NEMO/PISCES, PISCES-PLASTIC, and MIT General Circulation Model [MITgcm]) can be retrieved from the original articles.

Description of the global biogeochemical models

In this study, the zooplankton biomass distribution as well as the stress factors linked to OA, prey rarity, food quality, and contaminants were estimated from global coupled physical-biogeochemical models.

The distribution of zooplankton and stressors linked to OA and biogeochemistry were calculated using the NEMO/PISCES model.[77] NEMO/PISCES is a widely used modeling platform to study ocean biogeochemical cycles at various spatial and temporal scales.[78–83] The biogeochemical component of the model (PISCES) is a Monod-type model of intermediate complexity. PISCES represents the cycling of macro- and micronutrients (NO_3, NH_4, PO_4, Si, Fe, Cu, Mn, Zn, and Co) and the dynamics of two phytoplankton and two zooplankton groups (nanophytoplankton and diatoms and micro- and mesozooplankton, respectively). The performance of NEMO/PISCES at reproducing the global distribution of plankton, particles, and nutrients has been extensively evaluated in the literature.[17,77,83–86] A comparison of modeled and observed zooplankton biomass (between 0 and 200 m) is also provided in Note S2. Model outputs used to calculate the distribution of zooplankton and climatic and biogeochemical stress factors are taken from a simulation in Richon and Tagliabue.[17] This work simulated climate change impacts based on the historical reconstitution of CO_2 emissions from 1851–2005 and on the RCP8.5 scenario from 2006–2100.

PCB concentrations were taken from a global PCB ocean simulation implemented in the MITgcm. This is currently the only high-resolution model simulating the global transport of PCBs in the ocean and is driven by spatially resolved historical atmospheric inputs. The full physical-biogeochemical simulation has been described elsewhere.[46]

Finally, emerging contaminants like MP have been studied recently using the NEMO/PISCES platform.[44] This model version represents the 3D distribution of 3 MP types, differentiated by their density (floating, neutral, and sinking MP). Here, we used the MP distribution simulated by Richon et al.[44] to derive the stress factor from MP contamination. This simulation represent MP from riverine sources, simulated over a 25-year period of constant contamination. This simulated MP distribution reflects the current state of MP ocean contamination (see Richon et al.[44] for a comparison of simulated and measured MP concentrations).

Definition of the stress factors

We defined three key categories of stressors: climate change impacts on abiotic conditions, climate change impacts on biogeochemical conditions, and contamination. For each of them, we selected two of the most commonly studied biotic and abiotic factors known to impact zooplankton and assessed their change since preindustrial time in the surface ocean. They are described in the following subsections.

Anthropogenic stress emerges from the divergence of environmental conditions from that of the preindustrial period (1860–1872, for which we assumed no visible impact of anthropogenic activities). Hence, large differences in environmental conditions (climate or biogeochemical) between the preindustrial period (1860–1872 average) and 1950–1955 (2005–2010, respectively) lead to high stress factor values. We used absolute changes in SST from the preindustrial period to calculate stress. Thus, warming as well as cooling since the preindustrial period are assumed to be equally stressful for zooplankton. Conversely, we assumed that negative trends in pH (i.e., increase compared with the preindustrial average) are indicative of no stress for zooplankton functioning (stress = 0). Similarly, trends in biogeochemical conditions that lead to prey biomass increase or food quality closer to 1 lead to a stress value of 0 because these conditions are more favorable for zooplankton. Because anthropogenic contaminants mark the Anthropocene era,[87] we assume that no anthropogenic contaminants were present in the preindustrial period. A description of how the different stress factors are calculated is provided below.

Climatic stress factors

Climate change is known to impact zooplankton in different ways.[24] Most zooplankton species have a thermal preference niche,[88,89] and the ongoing warming of seawater due to climate change may bring surface temperatures outside of the zooplankton thermal niche.[24,90] Richardson[24] has shown that ocean warming may lead to shifts in zooplankton distribution and seasonality. In parallel, the rise in atmospheric CO_2 has caused decreasing ocean pH since the preindustrial period.[27] Many zooplankton species are sensitive to OA, such as calcifiers and crustaceans.[56,70,91–94]

Here, the changes in SST and surface pH since the preindustrial period constitute the climatic stress factors.

Estimates of SST are taken from the observational product HadISST,[95] which contains global estimates of SST averaged monthly and gridded over a regular

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1° × 1° grid since 1870. Following Halpern,[34] we calculated the stress brought by changes in SST as the mean SST anomaly for each time period normalized by the standard deviation. The average seasonal SST cycle was calculated based on the monthly data for the 3 time periods (preindustrial: 1870–1872, 1950–1955, and 2005–2010). For the time periods 1950–1955 and 2005–2010, the stress factor from changes in SST (ΔSST_{stress}) is calculated according to Equation 1:

$$\Delta SST_{stress} = \frac{(SST_{period} - SST_{preind.})}{\sigma SST_{preind.}} \qquad \text{(Equation 1)}$$

In Equation 1, $\mathrm{SST_{period}}$ and $\mathrm{SST_{preind.}}$ describe the average SST over the time periods (1950–1955 and 2005–2010) and the preindustrial period (1870–1872). $\sigma SST_{preind.}$ is the standard deviation of SST in the preindustrial period. This stress factor represents the magnitude of SST changes outside of the preindustrial range. Thus, stress from changes in SST is highest in regions where climate change brings the SST seasonal anomaly out of the preindustrial variability.

To calculate the stress factor from OA, we used the simulated seawater pH from Richon and Tagliabue.[17] The OA stress factor is calculated as the normalized changes in surface pH brought by climate change since the preindustrial period (1860–1872).

Biogeochemical stress factors

Zooplankton functioning (i.e., growth, reproduction, survival, and metabolic reactions) is prescribed by the biogeochemical conditions of their environment. In particular, zooplankton growth and biogeochemical functioning (recycling, grazing, export, etc.) is influenced both by the quantity and quality of the available prey.[8,21,43,96,97]

To calculate prey rarity stress, we calculated the prey rarity index for each time period (the preindustrial period, 1950–1955, and 2005–2010). The prey rarity index is calculated according to Equation 2:

$$Preyrarityindex = 1 - \overline{\sum\nolimits_i^j (P_i \times p_i^j)} \qquad \text{(Equation 2)}$$

where P_i is the biomass of zooplankton prey I and p_i^j the preference of zooplankton j (j = microzooplankton or mesozooplankton) for prey i, which is a constant. In PISCES, microzooplankton preys on nanophytoplankton, diatoms, and particulate organic carbon (POC), with preference set to 1, 0.5, and 0.1, respectively. Mesozooplankton preys on nanophytoplankton, diatoms, POC, and microzooplankton, with preference set to 0.3, 1, 0.3, and 1, respectively. Thus, microzooplankton preys preferably on nanophytoplankton, and mesozooplankton preys preferably on diatoms and microzooplankton. These parameters, as well as all other PISCES parameters and justifications, are detailed in Aumont et al..[77] In Equation 2, p_i^j is a constant less than 1, but the prey biomass (P_i) can reach values over 1. The normalization of this sum brings it strictly between 0 and 1. Thus, the prey rarity index varies between 0 (maximum prey availability, no stress) and 1 (no prey available, maximum stress). The stress factor from changes in prey rarity is calculated as the log-normalized difference between the prey rarity index for each time period (1950–1955 or 2005–2010) and for the preindustrial period.

The stress factor from food quality describes the difference in essential nutrient stoichiometry between zooplankton and their prey. The stoichiometric balance between predators and prey (also called food quality) was identified as a major driver of micronutrient cycling and zooplankton metabolic functions.[43,98–100]

The food quality is described in Richon et al.[43] as:

$$FQ_m = \frac{m/C_{zoo}}{m/C_{prey}} \qquad \text{(Equation 3)}$$

where FQ_m is the food quality factor calculated for nutrient m (m = Fe, Cu, Co, Mn, and Zn; see Equation 4 and Richon and Tagliabue[17]). In Equation 3, the terms m/C_{zoo} and m/C_{prey} describe the nutrient m-to-carbon ratio in zooplankton and prey, respectively. In PISCES, m/C_{zoo} is fixed for every nutrient and zooplankton group, while m/C_{prey} may vary within fixed ranges (see the supplemental information of Richon and Tagliabue[17] for the values and descriptions). When zooplankton and prey stoichiometry are similar, FQ_m is close to 1. Thus, zooplankton nutrient assimilation is optimal, and nutrient loss through recycling is minimal. Any departure from the optimal value of 1 indicates a mismatch between zooplankton and prey stoichiometry, which may result in lower nutrient assimilation and, therefore, impair zooplankton functioning (i.e., induce a stress for zooplankton).

Here, the stress factor from food quality emerges from the changes in the food quality index since the preindustrial period. The food quality index is calculated as the distance to 1 of the total food quality factor as described in Richon et al.[43] and Richon and Tagliabue:[17]

$$FoodQualityindex = \sum\nolimits_m \left|\overline{1 - FQ_m}\right| \qquad \text{(Equation 4)}$$

where FQ_m is the food quality factor calculated for nutrient m (m = Fe, Cu, Co, Mn, and Zn). Thus, the stress from changes in food quality is calculated as the log-normalized difference between the food quality index for each time period (1950–1955 or 2005–2010) and the preindustrial period.

Stress factors from anthropogenic contaminants

It is estimated that up to 100,000 chemical substances of anthropogenic origin are produced in high volumes every year.[101] For the majority, there are no regulations regarding their monitoring in the environment and no studies regarding their potential effects on ecosystems.[102] Thus, a large number of anthropogenic contaminants may be found in the ocean.[30] Although the impacts of most of these contaminants on ocean ecosystems are unknown, the global distribution and toxic effect of several contaminant groups has been widely documented. In this study, we took advantage of recent developments of global biogeochemical models to represent the stress factors from two contaminants for which spatially and temporally resolved distributions are available. Both of these contaminant classes are widely studied and have been shown to negatively impact zooplankton.

The first class of anthropogenic contaminants included in this study is PCBs. These synthetic chemicals have been widely produced since the early 20th century, and their global emissions peaked in the 1960s.[40] PCBs started to be regulated in the 1970s because of their persistence in the environment, bioaccumulation in organisms, and toxicity, and they were banned under the Stockholm Convention in 2011. Adverse impacts of PCBs on marine organisms, including zooplankton, have been documented since the 1970s,[103] and organochlorine contamination has been associated with the collapse of keystone species like orcas.[104]

The second anthropogenic contaminant considered in our study is MP. MP have been found in the ocean since the 1970s and are now ubiquitous in the global environment.[105,106] Recent experimental work has documented important concentrations of MP in accumulation zones of the ocean as well as toxic impacts on ocean zooplankton.[35,44,107] To calculate the stress to zooplankton brought by these contaminants, we used model outputs from Wagner et al.,[46] which simulate the concentrations of four PCB congeners from 1930–2015, and outputs from Richon et al.,[44] which simulate the current distribution of MP in the global ocean. Here, we assumed that potential adverse effects of PCBs and MP may result from any kind of contact (not exclusively ingestion). Hence, exposure to contaminants is calculated using the zooplankton index and not zooplankton grazing.

Calculating stress factor dominance and overlap

To ensure spatial consistency among all stress factors, we computed their values at the surface layer (0–10 m depth) to align with both the model outputs and the HadISST data, which exclusively cover the surface layer. To compare the stress factor distributions, we used the log-transformed values of each stressor and normalized them between 0 (no stress) and 1 (maximum stress). Thanks to these transformations, we are able to compare the surface distributions of stress factors and to characterize the spatial and temporal variability without taking into account the units of each stress factor metric. This transformation step is similar to the approach used by Halpern[34] and Halpern et al..[108]

In this study, we quantify each stress factor by comparing the climatic and biogeochemical conditions of the preindustrial period with those of the time periods 1950–1955 and 2005–2010. By examining the values of these stress factors, we can identify which factor has exhibited the most significant changes since the preindustrial era. In the section "Identifying stress factor dominance and overlap"2.2 and in Figure 3, we refer to the stress factor

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with the highest value at each grid point as the "dominant stress factor." This dominant stress factor highlights the specific factor that has displayed the greatest change since the preindustrial period. Furthermore, we assume that stress factors overlap in regions where the values of two or more stress factors exceed 0.5, indicating substantial changes in multiple stress factors since the preindustrial era.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2023.12.002.

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AUTHOR CONTRIBUTIONS

Conceptualization, C.R. and A.T.; methodology, C.R. and A.T.; software, C.R., C.W., E.M.S., and A.T.; investigation, C.R.; resources, C.W. and E.S.; writing—original draft, C.R., C.W., A.T., and E.M.S.; writing—review and editing, C.R., A.T., C.W., and S.-D.A.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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