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**Review Article**

# Impact of Global Climate Shifts on the Biodiversity and Functionality of Marine Zooplankton Communities

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## ABSTRACT

Climate change represents one of the biggest crises confronting humanity today. Its effects are not limited to human populations but extend to the marine environment, including zooplankton communities, which are critical components of the marine food chain. This study provides a review of the impacts of global climate shifts on the biodiversity and functioning of marine zooplankton communities. Specifically, it examines how changes in temperature, ocean acidification, and other environmental stressors affect zooplankton populations. The study also includes an analysis of case studies and regional variations in the impacts of climate change on these communities, alongside a discussion of methodologies used in studying these effects. Furthermore, the research evaluates existing knowledge gaps and identifies future research directions that are necessary to enhance our understanding of these impacts. Through this latest evaluation, the study underscores the importance of continuous monitoring and the adoption of a multi-stressor research approach. It also highlights the need for designing effective adaptation strategies for marine zooplankton communities, which are crucial for the development of sustainable marine conservation policies in the future. The findings of this study emphasise the urgency of further research to preserve the integrity of marine ecosystems in the face of global climate change challenges.

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# INTRODUCTION

## Background Related to Climate Change

### Definition and Causes of Climate Change

The climate is generally understood as a synthesis of atmospheric parameters such as temperature, precipitation, humidity, and wind patterns over significant periods (Ching-Ruey 2020; Kalkuhl & Wenz 2020). This broader concept encompasses both short-term weather fluctuations and long-term climate variations that span geological timescales (Safia et al. 2023). The Earth's climate system is a complex, interconnected network involving the atmosphere, oceans, ice masses, land surfaces, and vegetation, each influencing the others in intricate ways (Li et al. 2016; Fyke et al. 2018). Oceans, covering approximately 70 % of the Earth's surface, play a critical role in climate regulation through heat absorption and release, as well as the distribution of atmospheric moisture (Zardi 2024). Ocean circulation patterns, such as major ocean currents, impact regional and global climates by transporting warm water to polar regions and influencing humidity levels. Additionally, oceans serve as a significant carbon sink, affecting atmospheric $CO_2$ levels and, consequently, global climate (Doney et al. 2009). Vegetation interacts with climate by reflecting radiant energy, transferring water and latent heat, and influencing air movement, thereby forming a complex cycle of interactions within the Earth system that governs the dynamics and balance of the global environment (López-Pacheco et al. 2021; Wunderling et al. 2024).

Climate change represents one of the most pressing crises facing humanity today (Cornell & Gupta 2019). It encompasses variations in weather conditions, such as changes in precipitation levels, deviations from normal temperature ranges, and shifts in global temperatures (López-Pacheco et al. 2021). Riebeek (2011) defines climate change as a global phenomenon primarily driven by fossil fuel combustion, leading to increased greenhouse gas concentrations in the atmosphere. This results in global warming, rising sea levels, melting ice masses, altered plant and flower blooming patterns, and more frequent extreme weather events. The causes of climate change are twofold: natural and anthropogenic. Natural factors include variations in solar output, changes in Earth's orbit, volcanic activity, shifts in ocean currents, and continental drift (Sigl et al. 2015). In contrast, human activities such as greenhouse gas emissions from burning fossil fuels, land conversion, deforestation, and industrial activities significantly contribute to climate change by enhancing the greenhouse effect and increasing atmospheric $CO_2$ concentrations. Additionally, urbanisation and infrastructure development further exacerbate $CO_2$ emissions. Public awareness of climate variations spans short-term seasonal and annual changes to long-term decadal shifts (Smith et al. 2014). Therefore, understanding these intricate climate dynamics is essential for developing effective strategies to mitigate climate change impacts and adapt to future environmental conditions, ensuring the sustainability of ecosystems and human societies alike.

### An Overview of Global Warming and Ocean Acidification

Global warming, driven by increased greenhouse gas emissions from human activities, is leading to increased atmospheric and ocean temperatures. This warming trend manifests in observable phenomena such as rising global temperatures, melting polar ice, and an increase in extreme weather events (Smith et al. 2014). Ocean acidification is another critical issue associated with global warming. It results from the absorption of $CO_2$ by seawater through diffusion, where it reacts to form carbonic acid. This acid then dissociates into bicarbonate and hydrogen ions, lowering the pH of seawater and increasing its acidity. Additionally, phytoplankton also absorbs $CO_2$ through photosynthesis, but their contribution to ocean acidification is much smaller than diffusion (Houghton 2012). Future projections indicate that under worst-case scenarios, ocean pH could drop by an additional 0.3 to 0.5 units by 2100, which would severely impact marine biodiversity, leading to the collapse of coral reef ecosystems and disrupting marine food webs (Caldeira & Wickett 2005). Ocean acidification negatively impacts marine organisms that rely on calcium carbonate to form their shells and skeletons, including corals and mollusks. The interaction between global warming and ocean acidification exacerbates both issues: higher sea temperatures reduce the ocean's capacity to absorb $CO_2$ due to decreased gas solubility. Meanwhile, phytoplankton is important for $CO_2$ absorption through photosynthesis, however, warming and ocean acidification disrupt their productivity and the global carbon cycle in complex ways. A decline in nutrient availability and changes in the ecosystem also reduce phytoplankton's ability to absorb $CO_2$, even though they still require $CO_2$ for photosynthesis (Tai et al. 2021). Together, these phenomena pose significant threats to marine ecosystems and overall planetary health (Figure 1). Addressing these interconnected challenges requires comprehensive mitigation strategies that involve both local and global efforts. These strategies include reducing $CO_2$ emissions through the transition to renewable energy sources, enhancing carbon sequestration in marine ecosystems such as seagrasses and mangroves, and implementing marine protected areas to support biodiversity resilience (Gattuso et al. 2018). What equally important is the role of international cooperation in tackling the root causes of climate change and ocean acidification, highlighting the necessity of collective action to safeguard marine ecosystems for future generations (IPCC 2019).

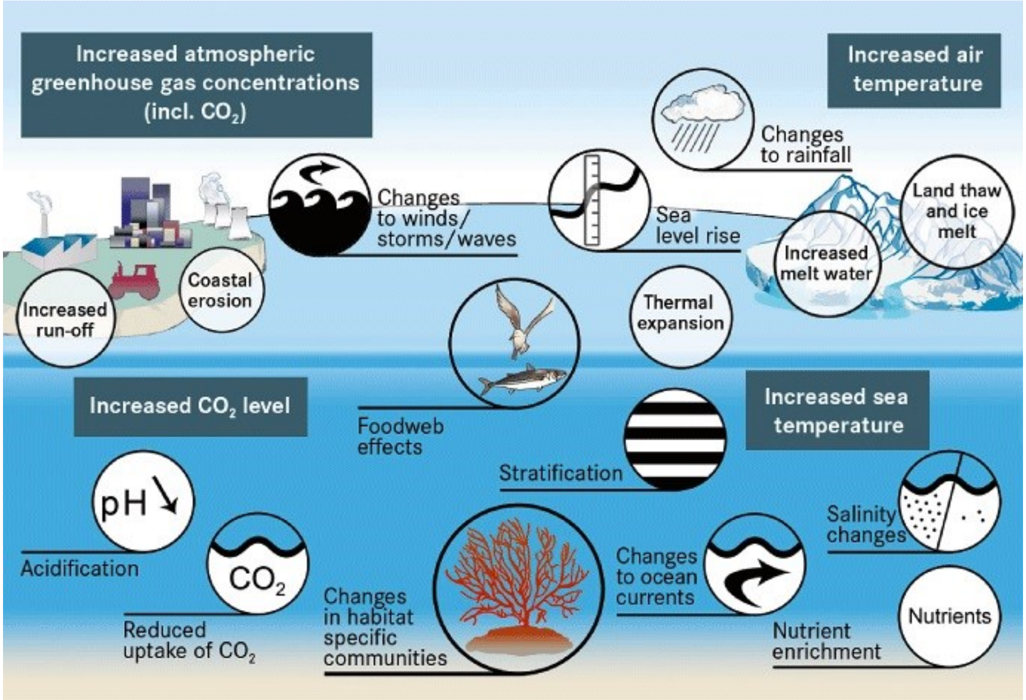


**Figure 1.** Overview of the effects caused by climate change and ocean acidification. (Source: Ospar Commission 2010).

## The Importance of Zooplankton in Marine Ecosystems

Zooplankton are essential for food web stability, serving as a primary food source for many marine organisms, as well as a crucial link between phytoplankton and higher-level consumers such as fish and marine mammals. They are also essential for energy transfer and ecosystem sustainability. By regulating phytoplankton populations, zooplankton help to prevent harmful algal blooms that can degrade water quality and negatively impact marine life (Ratnarajah et al. 2023). Additionally, zooplankton contribute significantly to biogeochemical cycles, including the carbon and nitrogen cycles, through processes such as biological pumping and nutrient regeneration (Steinberg &

Landry 2017). With an estimated 28,000 marine zooplankton species, they are diverse and vital for maintaining nutrient balances that support primary productivity (Bucklin et al. 2021). However, they face significant challenges from rapid environmental changes, including shifts in temperature and acidity, which may disrupt their life cycles and availability as prey, ultimately destabilising marine ecosystems (Richardson 2008).

### Study Objectives

This research review aims to achieve four core objectives. *First*, it seeks to analyse the impacts of temperature changes, ocean acidification, and other stressors on marine zooplankton communities, identifying shifts in biodiversity and ecosystem function that are crucial for ocean sustainability. *Second*, it incorporates case studies and explores regional variations to understand how climate change affects zooplankton across different marine ecosystems. This approach is vital for developing effective, region-specific adaptation strategies. *Third*, the review details the methodologies used to assess climate impacts on zooplankton, aiming to enhance the accuracy and reliability of data. Improved research methods are expected to yield more valid data, supporting better conservation policies and strategies. *Fourth*, it identifies existing knowledge gaps and outlines future research directions necessary to address these gaps. Addressing these gaps is essential for developing a comprehensive understanding of zooplankton-climate interactions and for crafting effective mitigation and adaptation strategies. Overall, this study provides insights into the effects of climate change on zooplankton, offers guidance on improving research methodologies, and supplies region-specific information for local policy development. It is anticipated to contribute significantly to global efforts to protect marine biodiversity and sustain ecosystem functions that are essential for life on Earth.

## IMPACT OF TEMPERATURE INCREASE ON ZOOPLANKTON

Climate variability impacts zooplankton distribution and abundance in complex ways, with patterns differing across ocean basins (Ratnarajah et al. 2023). Deep waters have experienced warming ranging from 0.3 °C to 0.6 °C under different emissions scenarios, with the Southern Ocean projected to see the most significant warming (Ciais et al. 2013) (Figure 2). Rising global temperatures have led to shifts in zooplankton distribution, such as the northward migration of North Atlantic species like *Calanus finmarchicus* due to warming waters, while *Calanus glacialis* has declined in the western Barents Sea (Beaugrand et al. 2002). These shifts, driven by changes in sea ice conditions, impact predator-prey dynamics and disrupt marine food webs, potentially leading to imbalances in ecosystem dynamics (Møller & Nielsen 2020). The arrival of new zooplankton species can also alter predator-prey relationships and impact marine biodiversity. In addition, increased sea temperatures accelerate zooplankton metabolism and reproduction rates but may reduce larval survival and overall population density, affecting fisheries productivity and global climate dynamics through changes in carbon sequestration (Hays et al. 2005; Richardson 2008).

Rising ocean temperatures disrupt zooplankton reproduction and life cycles by altering spawning times and reducing larval survival, as reproductive cycles are closely tied to water temperature and phytoplankton availability (Edwards & Richardson 2004). Misalignment with food availability can lead to declines in predator populations, causing cascading effects throughout marine ecosystems (Durant et al. 2007). Elevated temperatures also induce thermal stress, reducing egg production and increasing embryo mortality, as observed in copepods (Byrne et al. 2009). Accelerated development from egg to adult may decrease longevity and body size, leading to shorter life cycles and increased generational turnover, which can affect population stability and predator-prey interactions (Møller & Nielsen 2020). Changes in diet, such as copepods shifting to protozoa when phytoplankton are scarce and furtherly influence primary production and predator-prey relationships (Atkinson 1996).

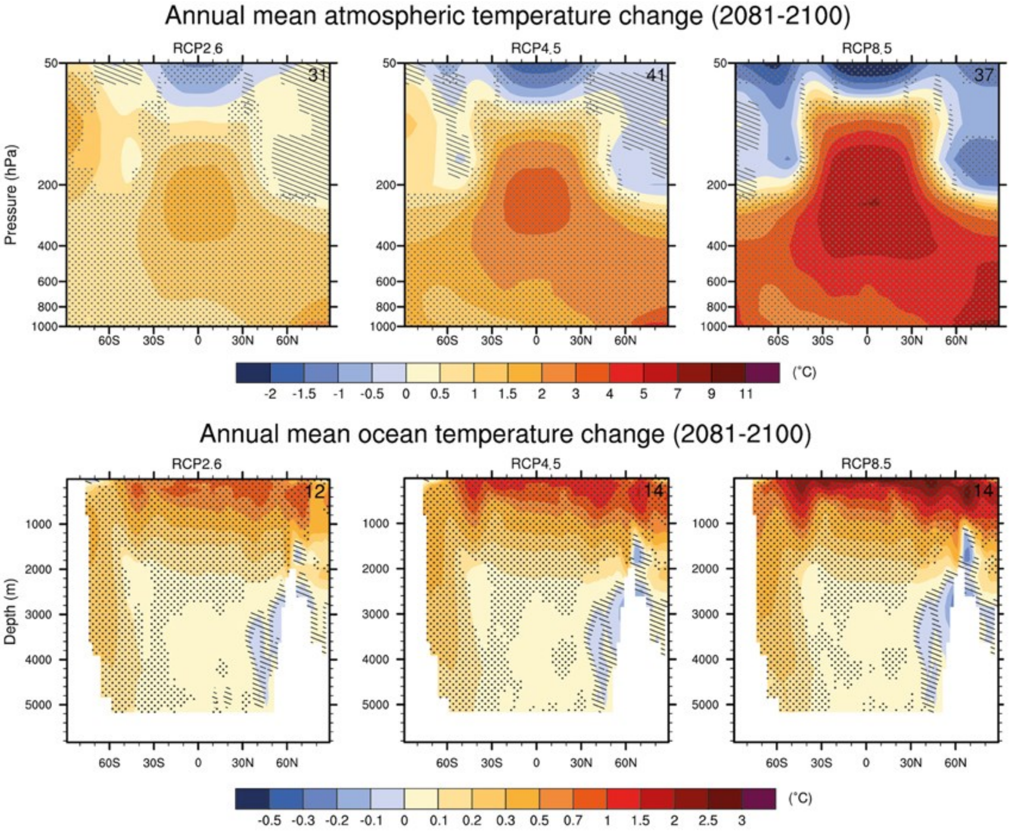


**Figure 2.** Changes in zonal annual mean temperature in the atmosphere and oceans, as projected by the Multi-Model Coupled Model Intercomparison Project Phase 5 (CMIP5), compared to the period 1986-2005 for the years 2081-2100. Projections are presented for the Representative Concentration Pathways (RCP) scenarios RCP2.6 (left), RCP4.5 (middle), and RCP8.5 (right). RCPs represent different greenhouse gas concentration trajectories. Shaded areas indicate regions where the multi-model averages fall below one standard deviation of internal variability. The dotted area highlights regions where the multi-model average exceeds two standard deviations of internal variability and where 90 % of the models exhibit consistent directional changes. (Source: Collins et al. 2013).

Zooplankton exhibit genetic adaptation to rising temperatures through changes in gene expression related to metabolism, reproduction, and stress tolerance. While rapid adaptation can occur in some species, the ability to adapt varies and may be limited by the rate of temperature change and other selective pressures (Geerts et al. 2014). Rapid or extreme temperature changes can exceed the genetic adaptability of zooplankton, potentially leading to population declines or local extinctions. Furthermore, adaptation to one stressor may impair the ability to cope with others, such as salinity changes or food scarcity (Bell & Collins 2008). In addition to genetic adaptation, zooplankton exhibit behavioural and physiological responses that depend on food availability, such as phytoplankton, which serve as a primary food source. They alter their vertical migration patterns to avoid warmer surface waters and forage in cooler depths. Furthermore, they produce heat shock proteins to enhance their thermal tolerance and resilience which is crucial in the face of temperature changes (Record et al. 2014).

## IMPACT OF OCEAN ACIDIFICATION ON ZOOPLANKTON

Ocean acidification imposes significant physiological stress on zooplankton, particularly those with calcium carbonate structures such as pteropods and foraminifera. As seawater's pH declines, the availability of carbonate ions necessary for shell formation decreases, resulting in more brittle and vulnerable shells. For instance, the pteropod *Clio pyramidata* has shown a 35 % reduction in shell thickness under lower pH conditions, increasing its susceptibility to predation and environmental damage (Comeau et al. 2009). This weakening of shells compromises the ecological function of these zooplankton in contributing calcium carbonate to marine sediments and disrupts metabolic processes critical for survival, such as respiration and excretion (Fabry et al. 2008). Consequently, increased mortality and decreased reproductive success, such as the 20 % reduction observed in the copepod *Acartia tonsa*, can impact population dynamics and lead to significant ecological consequences, including potential long-term genetic adaptations or changes in community composition (Cripps et al. 2014).

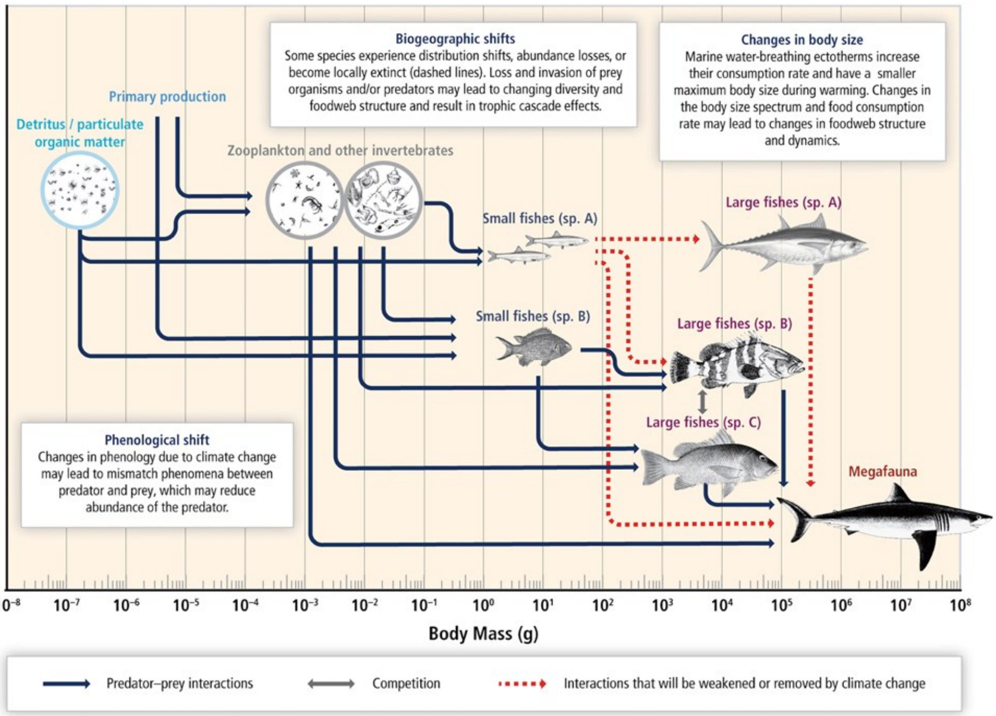
Apart from inducing physiological stress, ocean acidification also impacts the feeding behaviour and growth of zooplankton. The decreased pH disrupts sensory mechanisms crucial for detecting and capturing food, leading to reduced feeding efficiency and slower growth rates. For example, copepods like *C. finmarchicus* experience up to a 15 % reduction in feeding efficiency under acidic conditions (Cripps et al. 2014). This reduction in feeding efficiency results in lower zooplankton biomass, which is critical for sustaining marine food webs. Furthermore, acidification diminishes the nutritional quality of zooplankton, including essential fatty acids such as omega-3 in species like *A. tonsa*, impacting their predators and disrupting marine ecosystems (Bairagi et al. 2019). At the ecosystem level, the consequences of ocean acidification are profound. Declines in zooplankton populations and their nutritional quality lead to reduced food availability for predators, including fish, crustaceans, seabirds, and mammals such as whales. This disruption can affect commercially important fish species such as herring and salmon, which rely on zooplankton during their early life stages (Orr et al. 2005). As a specific example, reducing copepod populations can decrease the biomass of small pelagic fish, impacting larger predatory fish and seabirds. Alterations in zooplankton community structure can disturb marine food webs, affecting ecosystem stability and energy transfer, ultimately diminishing marine biodiversity and ecosystem resilience (Fabry et al. 2008; Doney et al. 2009). Moreover, the economic impacts of ocean acidification are substantial, as declining zooplankton populations can lead to reduced fish stocks, adversely affecting fisheries and coastal communities that depend on them for livelihoods (Mangi et al. 2018). Mitigation strategies should focus on reducing $CO_2$ emissions through policy changes and transitioning to sustainable energy sources, while further research is crucial to understand the long-term effects of acidification on marine ecosystems and to develop adaptive management strategies (Doney et al. 2009)

## INTERACTIVE EFFECTS OF VARIOUS STRESSORS

### The Combined Impact of Warming and Acidification

Global warming and ocean acidification present significant synergistic stressors for zooplankton, with their combined effects often intensifying physiological stress beyond the impact of each stressor individually. Key stressors include elevated sea temperatures which accelerate zooplankton metabolism and increase energy demands, also ocean acidification which disrupts calcification and metabolic functions. Together, these factors lead to heightened oxidative stress, reduced feeding efficiency, and impaired reproductive health (Byrne & Przeslawski 2013). The interactions between these stressors can vary significantly among zooplankton species. Typically, the copepod *C. finmarchicus* demonstrates significant declines in survival and reproduction under simultaneous high temperatures and low pH conditions, while other species may show differing levels of tolerance (Lewis et al. 2013). The compounded effects of these stressors can manifest as altered behaviour, such as reduced swimming ability in pteropods and disrupted migration patterns, impacting predator-prey interactions and marine food webs (Bednaršek et al. 2012).

Furthermore, measuring the impact of these stressors on zooplankton diversity involves assessing various physiological and ecological responses, such as changes in biomass, reproductive success, and community composition across different environmental conditions (Pörtner et al. 2014). Techniques like controlled laboratory experiments and long-term field studies can provide valuable insights into how these stressors affect zooplankton populations (Richardson et al. 2009). Over time, the interactions between warming and acidification can alter marine ecosystem structure and function by reducing zooplankton biomass and disrupting marine food chains, which affects higher trophic levels such as fish and marine mammals (Bednaršek et al. 2012). Therefore, understanding the synergistic impacts of these stressors is crucial for accurately predicting the effects of climate change on marine ecosystems (Byrne & Przeslawski 2013). Comprehensive research is essential to fully understand the long-term effects of these synergistic stressors on zooplankton health and ecological dynamics (Figure 3).



**Biogeographic shifts**
Some species experience distribution shifts, abundance losses, or become locally extinct (dashed lines). Loss and invasion of prey organisms and/or predators may lead to changing diversity and foodweb structure and result in trophic cascade effects.

**Changes in body size**
Marine water-breathing ectotherms increase their consumption rate and have a smaller maximum body size during warming. Changes in the body size spectrum and food consumption rate may lead to changes in foodweb structure and dynamics.

**Phenological shift**
Changes in phenology due to climate change may lead to mismatch phenomena between predator and prey, which may reduce abundance of the predator.

**Figure 3.** Schematic estimated response to climate change in seafood webs. This framework illustrates how interconnected pelagic and benthic food webs, organised by body size spectrum, respond to climate change. Warming, hypoxia, and ocean acidification cause reductions in body size, shifts in biogeography, changes in species composition and abundance, and alterations in trophic relationships. Fishing further reduces large-sized species, narrowing the body size spectrum and complicating the detection of climate change impacts on food webs. Arrows denote species interactions, such as predation and competition, while the dotted line represents potential losses in population and trophic relationships due to climate change. (Source: Pörtner et al. 2014).

### Effects of Additional Stressors (e.g., pollution and hypoxia)

Anthropogenic pollution, including heavy metals, pesticides, and microplastics, compounds the effects of ocean warming and acidification on zooplankton, exacerbating physiological stress and reducing their adaptability to environmental changes (Gobler & Talmage 2013). Pollutants can accumulate in zooplankton, leading to cellular damage, reproductive issues, and increased mortality, while also impairing detoxification processes and increasing susceptibility to toxicity (Wang et al. 2022). Furthermore, pollutants like microplastics can disrupt nutrient digestion and absorption, impacting growth and development (Richon et al. 2022). In addition to pollution, declining oxygen levels or hypoxia, which are often linked to eutrophication and nutrient runoff, further stress zooplankton by reducing oxygen availability, increasing metabolic strain, and altering vertical distribution. This can enhance predation risks and disrupt feeding behaviors (Gobler & Baumann 2016). These cumulative stressors can lead to significant declines in zooplankton populations, affecting marine food webs and ecosystem dynamics. The combined effects of these stressors suggest that managing and protecting marine ecosystems requires a comprehensive understanding of their interactive impacts (Pörtner et al. 2014) (Figure 3).

## CASE STUDIES AND REGIONAL VARIATIONS

Various studies underscore the significant impact of climate change on zooplankton communities. In the North Sea, rising ocean temperatures have led to shifts in zooplankton distribution and abundance, affecting local marine ecosystems and commercial fisheries (Beaugrand et al. 2002). In the Barents Sea, melting sea ice and temperature changes have altered zooplankton community composition, impacting predators such as Arctic cod and seabirds (Dalpadado et al. 2012). The Continuous Plankton Recorder (CPR) data from the Atlantic Ocean reveal long-term changes in zooplankton communities over recent decades, indicating that climate change disrupts zooplankton timing and spatial distribution, which can affect predator-prey interactions and energy transfer efficiency in marine ecosystems (Richardson et al. 2006). Research in the Southern Ocean showed that ocean acidification negatively affects pteropods, crucial zooplankton in the region, by impairing their shell formation and thus reducing their survival and reproduction (Bednaršek et al. 2012).

### Polar Region

Zooplankton in polar regions are confronting distinct challenges due to rapid climate change. In the Arctic, rising temperatures accelerate sea ice melt, disrupting the habitat and life cycles of ice-dependent species such as *C. glacialis*. This disruption extends to algal phenology and food quality, negatively impacting zooplankton reproduction and growth. Additionally, ocean acidification impairs calcium carbonate exoskeleton formation, further increasing mortality rates among these organisms (Søreide et al. 2010; Bednaršek et al. 2012; Hatlebakk et al. 2022). In Antarctica, warming temperatures and reduced sea ice are affecting Antarctic krill (*Euphausia superba*), a vital food source for many predators, potentially altering the entire ecosystem's dynamics. These changes also impact krill larvae's reproduction and survival (Atkinson et al. 2004; Flores et al. 2012). Despite some species showing resilience, the combined effects of warming and acidification present significant challenges, necessitating further research to understand the broader impacts on polar ecosystems (Kebir et al. 2023). Case studies highlight these issues: in the Arctic Chukchi Sea, the research indicated that warming and acidification have led to declines in sea ice-dependent zooplankton and an increase in species tolerant to warmer conditions, affecting marine food webs and ecosystem sustainability (Questel et al. 2013; Brower et al. 2018). In Antarctica, warming has shifted Antarctic krill distribution southward and negatively affected larval survival due to acidification, while studies in the Weddell Sea show how hydrographic variability influences zooplankton migration patterns and alters the behaviour of large predators such as elephant seals (Biuw et al. 2010; Flores et al. 2012).

### Tropical Seas and Temperate Temperatures

Zooplankton in tropical and temperate regions demonstrate notable variability in their responses to environmental changes. Tropical regions, characterised by less seasonal variation and higher water temperatures, face distinct challenges. Notably, in the Indian Ocean, the El Niño phenomenon induces significant fluctuations in zooplankton abundance and distribution, necessitating rapid adaptation to shifts in temperature and food availability (Hays et al. 2005). In temperate regions such as the North Atlantic, rising temperatures have prompted shifts in zooplankton species distributions towards the poles, with cold-water species like *C. finmarchicus* being replaced by heat-tolerant species such as *Calanus helgolandicus*. This change disrupts marine food webs and ecosystems, as the latter thrives under higher temperatures while the former struggles (Falkenhaug et al. 2022). Additionally, ocean acidification impacts zooplankton differently across these regions; in tropical seas, it hinders calcium carbonate exoskeleton formation, whereas, in temperate seas, effects vary by species and local conditions, with some showing greater resilience than others (Fabry et al. 2008). Regional case studies offer further insight into these impacts. In the Caribbean Sea, ocean warming and acidification have caused declines in calcium carbonate-dependent zooplankton, highlighting the need to understand cumulative environmental stressors on tropical marine ecosystems (Howes et al. 2015). Similarly, in the Mediterranean, rising temperatures have led to shifts in zooplankton distributions, with warmer species displacing colder ones. This affects both zooplankton and their predators, such as fish and seabirds, thereby impacting temperate marine ecosystems (Raitsos et al. 2010). Furthermore, ocean acidification has been shown to reduce zooplankton abundance and diversity, particularly among calcifying species, which affects food chains and coastal ecosystem dynamics (Hall-Spencer & Harvey 2019).

## METHODOLOGY FOR STUDYING THE CLIMATE CHANGE IMPACT ON ZOOPLANKTON

### Experimental Approach

#### Laboratory Experiments and Mesocosms

Laboratory experiments and mesocosm studies are crucial for elucidating the effects of climate change on zooplankton. In controlled laboratory settings, researchers can precisely manipulate environmental variables, such as temperature, pH, and salinity, to isolate their impacts on zooplankton physiology and behaviour (Choi et al. 2021). Evidence indicates that elevated temperatures can accelerate the metabolic rates of zooplankton, subsequently influencing their developmental and reproductive processes (Richardson 2008). Furthermore, molecular techniques, including DNA and RNA analyses, facilitate the investigation of the physiological and genetic responses of zooplankton to environmental stressors, as demonstrated by Voznesensky et al. (2004). Mesocosm experiments, which are conducted in semi-controlled environments that simulate natural conditions, provide insights into the interactions between zooplankton and other components of aquatic ecosystems (Sharma et al. 2021). In mesocosm studies, zooplankton are housed in large tanks containing seawater, phytoplankton, and natural predators, enabling researchers to examine predator-prey dynamics and alterations in food webs due to environmental changes (Boyd et al. 2018). These studies are also instrumental in assessing the long-term impacts of environmental stress on zooplankton populations (Algueró-Muñiz et al. 2017). Despite their value, laboratory and mesocosm experiments have limitations. The controlled conditions of these experiments may not fully capture the complexity and variability inherent in natural marine environments (Boyd et al. 2018). Consequently, integrating findings from these experimental approaches with field data is essential for achieving a comprehensive understanding of zooplankton responses to climate change (Heneghan et al. 2023).

### Field Studies and In-Situ Observations

Field studies and in situ observations are essential for investigating the impacts of climate change on zooplankton. Researchers employ a range of tools, including plankton nets and automated sensors, to collect data on zooplankton distribution, abundance, and activity across diverse marine environments (Figures 4 and 5). Specifically, CPR has played a critical role in tracking long-term shifts in North Atlantic zooplankton communities (Richardson et al. 2006). In situ observations facilitate the direct measurement of environmental parameters such as temperature, pH, and oxygen, which are subsequently correlated with zooplankton responses to identify their preferred habitats (Mackas & Beaugrand 2010). Field studies also provide insights into how zooplankton populations react to seasonal and interannual variations, as well as extreme events such as ocean heatwaves. Research conducted in the subtropical waters of Brazil, for instance, revealed notable variations in zooplankton biomass associated with cold-water intrusions (Marcolin et al. 2015). Similarly, Xu et al. (2024) investigated the effects of marine heatwaves on zooplankton in the East China Sea using both in situ data and reanalysis techniques. Advanced technologies, including Autonomous Underwater Vehicles (AUVs) and Remotely Operated Vehicles (ROVs), have enhanced the capacity for observing zooplankton in challenging environments such as the deep ocean and polar regions. These innovations address the limitations of traditional methods and provide more detailed ecological insights (Wiebe & Benfield 2003).

## Modelling and Predictive Tools

### Using Climate Models to Project Future Impacts

Climate models are essential tools for forecasting the impacts of climate change on zooplankton populations. These models utilise historical data and future climate scenarios to simulate the effects of changes in temperature, pH, and other environmental variables on zooplankton distribution and abundance (Stock et al. 2014). Distinctly, biogeochemical models integrate data on biological and chemical processes within the ocean to project how increased atmospheric $CO_2$ and ocean acidification may influence marine food webs (Shi & Li 2024). By employing climate models, researchers can identify regions most susceptible to climate-induced changes and develop targeted mitigation strategies (Cheung et al. 2011). An illustrative case is provided by models that simulate ocean warming effects in the Bering Sea, which predict potential shifts in zooplankton distribution that could impact commercial fish populations (Whitehouse et al. 2021). Such predictions are crucial for marine resource management and ecosystem conservation (Stock et al. 2014). However, climate models have inherent limitations due to the complexity of marine ecosystems and uncertainties in future climate projections (Boyd et al. 2018). Enhancing model accuracy requires the continuous integration of empirical data and the advancement of modelling techniques (Cheung et al. 2011). Integrating climate models with field data is anticipated to yield more reliable and precise predictions.

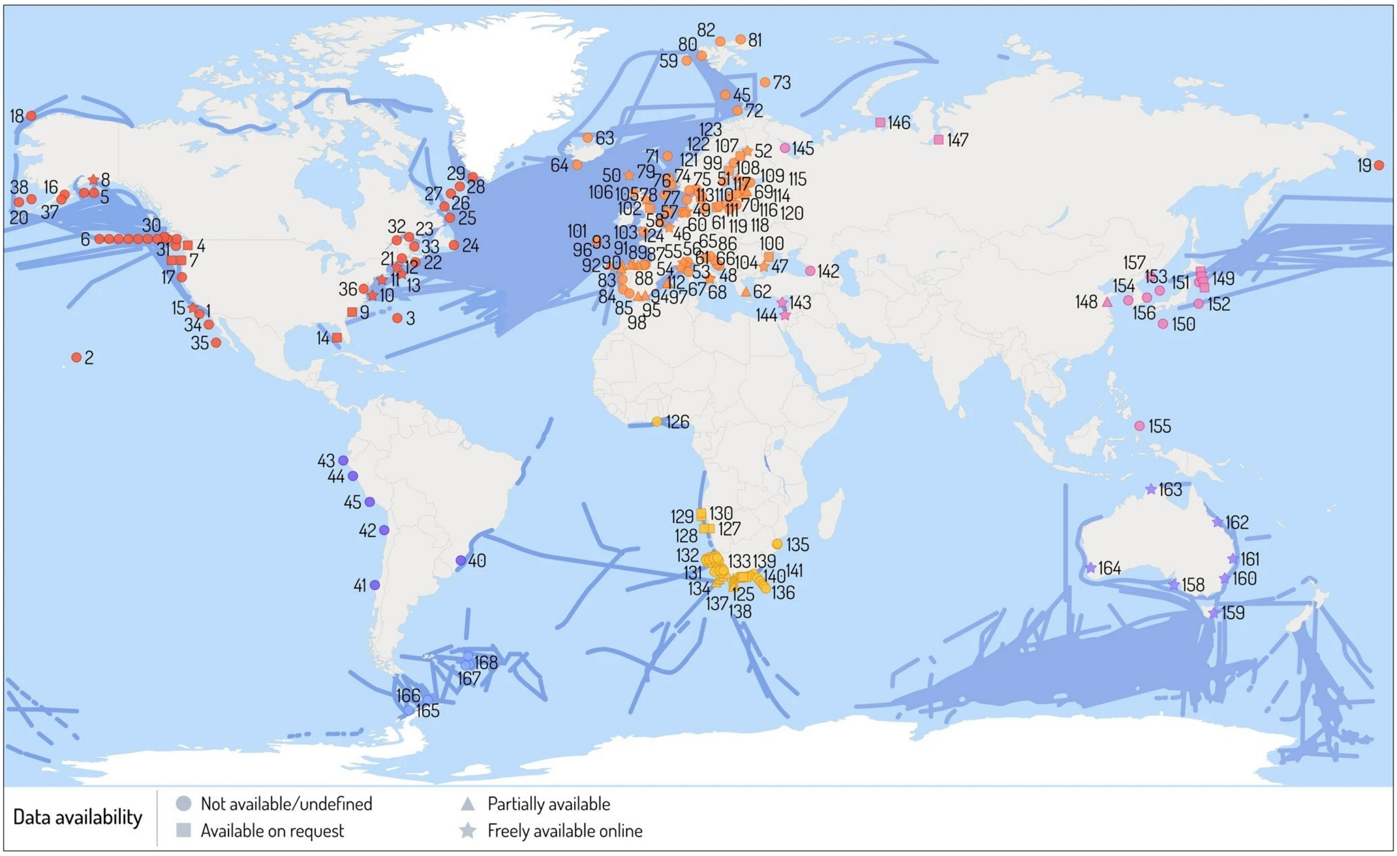


**Figure 4.** Map of long-term monitoring programs for zooplankton in the global ocean. The blue line denotes the trajectory of CPR survey, while the symbols represent the locations of specific long-term monitoring programs, with numbered locations detailed according to Ratnarajah et al. (2023). Star symbol: Indicates programs where data is available for free download. Box symbol: Represents programs with data accessible on demand. Triangle symbol: Denotes programs with partially available data. Circle symbol: Signifies programs where data is either not available or its availability is unclear. Only programs with documented coordinates are included on the map. Data sources include the Marine Ecological Time Series Database, the EuroSea survey, and additional surveys referenced in Ratnarajah et al. (2023). Detailed information and coordinates are provided in the supplementary materials of Ratnarajah et al. (2023). The map was designed by Dr. Stacey McCormack of Visual Knowledge. (Source: Ratnarajah et al. 2023).

### Integration of Empirical Data into Predictive Frameworks and Artificial Intelligence (AI)

Integrating empirical data into predictive frameworks significantly enhances the accuracy of climate models. Millette et al. (2024) underscored the importance of incorporating empirical data from both laboratory and field studies within trait-based approaches to predict zooplankton ecology. This methodology involves synthesising in situ measurements and controlled experiments to ascertain zooplankton traits, which are subsequently utilised in ecosystem models to forecast their biogeographic distribution and biogeochemical impacts. Moreover, incorporating data on zooplankton growth and reproductive rates under diverse conditions further refines model predictions (Reygondeau & Beaugrand 2011). The integration of genetic, physiological, and ecological data facilitates deeper understanding of zooplankton responses to environmental changes (Stock et al. 2014), including insights into evolutionary adaptations (Bucklin et al. 2018) and thermal tolerance limits (Alma et al. 2020). This multidisciplinary approach contributes to the development of more comprehensive models (Reusch & Boyd 2013), which are crucial for effective marine resource management (Cheung et al. 2011). Additionally, Jain et al. (2023) highlight the potential of artificial intelligence (AI) in climate change adaptation, demonstrating how AI can leverage extensive data sources to inform decision-making. However, ethical considerations must ensure that AI solutions are transparent and equitable. Advancements in AI-driven climate adaptation strategies have the potential to foster a more resilient and equitable future. Anticipated research advancements are expected to further enhance the understanding of zooplankton dynamics in the context of climate change.

## Technological Advancements

### Remote Sensing and Automated Sampling Technology

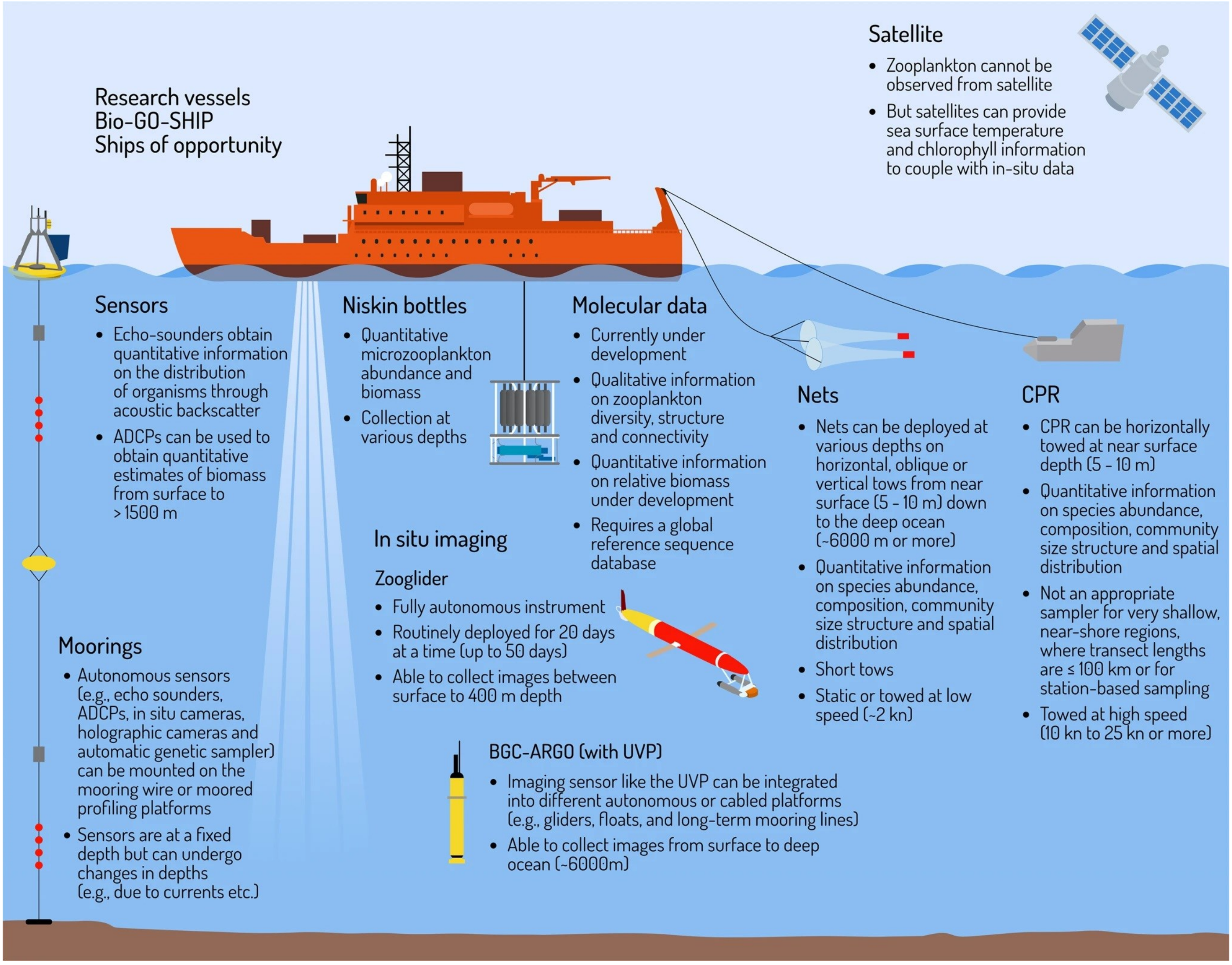
Advancements in automated sampling and remote sensing technologies, including satellites and sea surface sensors, facilitate large-scale and continuous monitoring of maritime environmental conditions (Ma et al. 2023). Environmental sensors deployed on AUVs and the SilCam imaging tool enable sustained spatial and temporal observations, thereby enhancing our comprehension of marine ecosystems and zooplankton responses to climate change (Nøland 2022). Although these techniques necessitate further refinement in taxonomic resolution and the integration of data from diverse sensors, they offer considerable promise for advancing plankton research and climate change monitoring (Wiebe & Benfield 2003). Moreover, these technologies are particularly effective in monitoring remote locations, such as the deep ocean and polar regions, which are critical for understanding global marine ecosystem dynamics (Robison 2004).

### Advances in Genetic and Molecular Engineering

Advances in genetic and molecular techniques have markedly improved our capacity to investigate the effects of climate change on zooplankton. Techniques such as DNA and RNA sequencing, particularly Next-Generation Sequencing (NGS), enable researchers to identify genetic modifications and gene expression changes in response to environmental stressors (Satam et al. 2023). Research indicates that zooplankton can modulate gene expression related to metabolism, reproduction, and stress responses under fluctuating environmental conditions (DeBiasse & Kelly 2016). Genetic analyses can uncover patterns of genetic variation and potential natural adaptations across different zooplankton populations (Reusch & Boyd 2013). Additionally, molecular techniques facilitate the examination of interactions between zooplankton and microorganisms, offering insights into the health and functionality of marine ecosystems (Suttle 2005). Techniques such as RNAlater® preservation enable the collection and analysis of RNA in both experimental and field settings, providing valuable information about the physiological state of zooplankton populations (Voznesensky et al. 2004) (Figure 5).

The application of DNA metabarcoding has significantly advanced the study of marine zooplankton diversity by utilising marker gene regions such as COI and 18S nuclear rRNA (Yang et al. 2017; Bucklin et al. 2019; Blanco-Bercial 2020). Databases such as the MetaZooGene Barcode Atlas and Database (MZGdb) offer comprehensive reference sequences for marine zooplankton, thereby facilitating the identification and assessment of biodiversity (Bucklin et al. 2021). MZGdb is interconnected with NCBI GenBank and BOLD data repositories, enhancing quality control, statistical analysis, and the visualisation of genetic data. Through the MZGdb portal, over 150,000 COI sequences for approximately 5,600 documented marine metazoan plankton species—including holoplankton and meroplankton—are readily accessible.

Interestingly, Bucklin et al. (2021) employed MZGdb as a repository for COI barcode data summaries and related information for specific regions, including the North Atlantic, Arctic, North Pacific, and Southern Ocean, as well as for major taxonomic families of marine zooplankton. To assess marine ecosystems and facilitate the rapid identification of climate change impacts,


Research vessels
Bio-GO-SHIP
Ships of opportunity

Satellite
- Zooplankton cannot be observed from satellite
- But satellites can provide sea surface temperature and chlorophyll information to couple with in-situ data

Sensors
- Echo-sounders obtain quantitative information on the distribution of organisms through acoustic backscatter
- ADCPs can be used to obtain quantitative estimates of biomass from surface to > 1500 m

Niskin bottles
- Quantitative microzooplankton abundance and biomass
- Collection at various depths

Molecular data
- Currently under development
- Qualitative information on zooplankton diversity, structure and connectivity
- Quantitative information on relative biomass under development
- Requires a global reference sequence database

Nets
- Nets can be deployed at various depths on horizontal, oblique or vertical tows from near surface (5 - 10 m) down to the deep ocean (~6000 m or more)
- Quantitative information on species abundance, composition, community size structure and spatial distribution
- Short tows
- Static or towed at low speed (~2 kn)

CPR
- CPR can be horizontally towed at near surface depth (5 - 10 m)
- Quantitative information on species abundance, composition, community size structure and spatial distribution
- Not an appropriate sampler for very shallow, near-shore regions, where transect lengths are ≤ 100 km or for station-based sampling
- Towed at high speed (10 kn to 25 kn or more)

In situ imaging

Zooglider
- Fully autonomous instrument
- Routinely deployed for 20 days at a time (up to 50 days)
- Able to collect images between surface to 400 m depth

Moorings
- Autonomous sensors (e.g., echo sounders, ADCPs, in situ cameras, holographic cameras and automatic genetic sampler) can be mounted on the mooring wire or moored profiling platforms
- Sensors are at a fixed depth but can undergo changes in depths (e.g., due to currents etc.)

BGC-ARGO (with UVP)
- Imaging sensor like the UVP can be integrated into different autonomous or cabled platforms (e.g., gliders, floats, and long-term mooring lines)
- Able to collect images from surface to deep ocean (~6000m)

**Figure 5.** This illustration demonstrates the integration of traditional and modern methodologies in zooplankton studies. Conventional techniques, such as plankton nets, Niskin bottles, and the CPR, have been long-standing tools for zooplankton monitoring. However, the combination of these established methods with contemporary approaches—such as satellite observations, advanced sensors, in situ imaging techniques, and molecular analyses (including proteins, DNA, and RNA)—can significantly enhance geographic coverage, particularly in under-sampled regions, and provide more profound insights into the effects of climate change on zooplankton communities. While traditional methods like nets, CPR, and Niskin bottles are typically employed independently, their integration with modern technologies offers more comprehensive understanding of zooplankton dynamics. This integration allows for a broader spatial and temporal resolution, improving our ability to monitor and analyze zooplankton populations effectively. The image illustrating this integration was created by Dr. Stacey McCormack (Visual Knowledge) and is sourced from Ratnarajah et al. (2023).

MZGdb is designed to serve as a foundational resource for studying the diversity of marine zooplankton species through DNA barcodes and metabarcoding. The integration of metabarcoding with morphological analyses enables effective characterisation of zooplankton community structure and biomass, offering essential tools for the research, assessment, and management of marine biodiversity (Matthews et al. 2021). These genetic and molecular advancements are crucial for developing strategies to understand and mitigate the effects of climate change on marine ecosystems.

In their work, “Call to Action: A COI Reference Library for Marine Zooplankton,” Bucklin et al. (2021) issued a critical call for the development of a comprehensive COI reference sequence database for marine zooplankton. This database is essential for the widespread implementation of DNA barcoding and metabarcoding techniques, which are fundamental for effective fisheries management, environmental conservation, and assessing climate change impacts on marine ecosystems. The diversity of marine environments and the taxonomic complexity of zooplankton pose significant challenges to accurate species identification. To address these challenges, it is imperative to provide public access to accurately identified DNA barcode sequence records and tools for constructing custom databases tailored to specific taxonomic groups and geographic regions. Such resources are crucial for maintaining quality control and detecting errors, thereby enhancing species-level diversity analyses for management, monitoring, and research purposes. Prioritising the completion of a global, taxonomically comprehensive zooplankton COI reference database is vital. Key priorities include focusing on ecologically significant species, ensuring high accuracy in species-level identification, georeferencing collection sites, and analysing intra-specific variations in COI barcodes to identify errors and detect cryptic species.

# KNOWLEDGE GAPS AND FUTURE RESEARCH DIRECTIONS

## Gaps Identified in Current Research

### Areas with Limited Data and Understanding

Despite extensive research on climate change's impact on zooplankton, significant gaps remain in understanding their responses to multi-stressor variations in complex natural environments (Boyd et al. 2018). Current data often focus on individual stressors such as rising temperatures or acidification, but information on combined effects is lacking (Todgham & Stillman 2013). Additionally, there is limited knowledge about the genetic adaptation and evolution of zooplankton in response to environmental changes (Bucklin et al. 2021). Geographic variation in zooplankton responses is also under-studied, with most research concentrated in accessible regions like the North Atlantic and Eastern Pacific, while remote areas like the Indian Ocean and the Southern Ocean are poorly studied (Richardson et al. 2006). Understanding zooplankton responses in diverse habitats is crucial for predicting global climate change impacts (Morgado & Vieira 2020). Furthermore, much research is conducted in controlled laboratory settings, leading to a lack of understanding of zooplankton responses in dynamic natural ecosystems (Pörtner & Farrell 2008). Comprehensive field studies and long-term data are needed to fill this gap and provide a more accurate picture of zooplankton's response to climate change (Ducklow et al. 2007).

### The Need for Long-Term Monitoring and Studies

Long-term monitoring and studies are essential for understanding trends and changes in zooplankton populations due to climate change (Ducklow et al. 2007). These studies enable scientists to identify temporal patterns and correlate changes in zooplankton with environmental variables such as ocean temperature, pH, and food availability (Zhou et al. 2020). They are also crucial for assessing the cumulative effects of various environmental stressors on zooplankton (Mackas & Beaugrand 2010). However, such monitoring demands substantial resources and coordination among countries and research institutions (Ducklow et al. 2007). New technologies like remote sensing and automated sensors can enhance monitoring efficiency and coverage (Behrenfeld & Falkowski 1997). Expanding monitoring efforts in underrepresented regions such as the tropics, poles, and deep seas is also vital for a comprehensive understanding of climate change impacts on zooplankton (Richardson et al. 2006). A collaborative approach and advanced technologies are key to addressing these challenges.

## Future Research Advice

Future research on zooplankton should prioritise multi-stressor experiments to elucidate the complex interactions between various environmental factors, such as elevated temperatures, ocean acidification, hypoxia, and pollution, which more accurately reflect realistic conditions (Todgham & Stillman 2013). This approach will enhance our understanding of how zooplankton adapt and survive under multifactorial stress, considering variations in stress responses across different species and life stages (Pörtner & Farrell 2008). Additionally, these studies could reveal broader ecosystem impacts, including alterations in predator-prey dynamics (Boyd et al. 2018). To capture comprehensive trends, it is essential to conduct these experiments across diverse temporal and spatial scales, supported by long-term studies and extensive field observations beyond short-term experiments (Ducklow et al. 2007). Concurrently, integrating genetic, physiological, and ecological data will deepen our understanding of zooplankton responses to environmental changes. This integrative approach can link genetic variation with physiological and ecological responses, can identify stress tolerance genes, and can develop accurate models for predicting climate change impacts on zooplankton (Sunday et al. 2014). Advanced technologies, such as genomic and metagenomic analyses, will further elucidate evolutionary adaptations and physiological plasticity, aiding in the development of effective climate adaptation strategies (Weydmann et al. 2017). Moreover, the development of comprehensive models that incorporate interactions between environmental conditions and zooplankton responses is crucial for forecasting climate change impacts. These models should integrate field observations, laboratory experiments, and advanced technologies like remote sensing, accounting for temporal and spatial variability and interactions with other marine organisms (Stock et al. 2014). Continuous evaluation and validation through field data and international collaboration among research institutions will enhance the accuracy and reliability of these models, providing critical insights into marine ecosystem dynamics and climate change challenges (Boyd et al. 2018). To emphasize, the development of research models as outlined above is crucial for understanding the complexities of zooplankton responses to environmental changes, as these models can provide insights into effective conservation strategies aimed at mitigating the impacts of climate change on marine ecosystems (Orr et al. 2005; Pörtner & Farrell 2008). Incorporating these models into conservation planning will enable targeted interventions that enhance the resilience of zooplankton populations and, consequently, the broader marine food web (Hoffmann & Sgrò 2011).

## CONCLUSION

Climate change profoundly impacts zooplankton biodiversity and ecosystem functioning through key stressors such as rising ocean temperatures, acidification, and hypoxia. These stressors affect zooplankton physiology, behaviour, and distribution, leading to decreased survival and reproduction for some species, particularly those with calcium carbonate structures like pteropods, whose shell formation is impaired by acidification. Changes in zooplankton populations, in turn, influence their predators, including commercial fish, marine mammals, and seabirds that rely on zooplankton as a primary food source. Variability in responses to climate change is observed across species, locations, and ecosystem types. Polar zooplankton face challenges from melting sea ice and warming temperatures, while tropical and temperate species may shift to higher latitudes or greater depths. To address these challenges, future research should focus on multi-stressor experiments and improved integration of data across genetic, physiological, and ecological dimensions to better predict and mitigate impacts on marine ecosystems. Extensive long-term monitoring programs are essential for tracking shifts in zooplankton populations and their responses to environmental changes, particularly in underrepresented regions such as the deep ocean and polar areas.

Research should also explore zooplankton interactions with microorganisms and their roles in nutrient cycles and ecosystem health. Developing comprehensive models that incorporate various environmental conditions and biological responses, supported by international and interdisciplinary collaboration, will enhance our ability to forecast climate impacts. Mitigation efforts, including greenhouse gas reduction and habitat protection, are crucial for easing pressure on marine ecosystems and improving their resilience. Addressing these issues requires raising awareness among the public and policymakers about the importance of zooplankton for marine ecosystem health and fisheries economies to drive effective conservation and research initiatives.

## AUTHORS CONTRIBUTION

All authors contributed to the formulation and design of this study. A.P. served as the lead researcher in this study. A.P. and S.A. were also responsible for the investigation and writing of the research, including conducting information and literature searches, conceptualizing the study, drafting the initial manuscript, and performing subsequent review and editing. H.H.1, C.M., L.A.J.Q., M.R., H.H.2, M.A., R.A.S., and T.T. handled the information and literature explorations, data curation, review, editing, and financial aspects of the research. All authors read and approved the final version of the manuscript and participated in its writing and revision.

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## CONFLICT OF INTEREST

The authors declare that there are no financial conflicts of interest or personal relationships that could be perceived as influencing the content or findings of this paper.

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