

Contribution of marine zooplankton time series to the United Nations Decade of Ocean Science for Sustainable Development

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Zooplankton play a central role in marine trophic webs, influencing both biogeochemistry and productivity of the oceans. Changes in their communities are important indicators of overall ecosystem health and global change impacts. With increasing exploitation and pressures on the marine environment, there is a growing need for high-resolution monitoring of marine zooplankton to provide detailed information about seasonal to decadal changes at local, regional, and global scales. This crucial knowledge is gathered mainly through long-term time series, which are key to characterizing and forecasting changes in marine zooplankton assemblages. In this Introduction, and through the articles included in this Themed Article Set, we bring together new insights, issuing from data time series, into zooplankton population dynamics. We also take up the application of such time series to the understanding of global change impacts on marine ecosystems and in providing advice on sustainable management of marine ecosystem resources and services. We highlight the importance of maintaining and supporting long-term marine zooplankton time series as key contributors to the development and advancement of the United Nations' Decade of Ocean Science for Sustainable Development Goal 13–Climate action and Goal 14–Life below water.

Keywords: global change, ICES, marine food webs, pelagic ecosystems, population dynamics, time series, WGZE, zooplankton monitoring.

Background and motivation for this article themed set

This themed article set (TS) is intended as an homage to Steve Hay who sadly passed away on 25th June 2020 at the age of 70 (see In memoriam—Steve Hay (https://www.ices.dk/news-and-events/news-archive/news/Pages/Steve_Hay.aspx)).

Steve was one of Scotland's leading marine zooplankton ecologists. He spent many years investigating the life history and the overwintering ecology of *Calanus finmarchicus*. Steve played an integral role in establishing the long-term monitoring sites at Stonehaven and Loch Ewe, which have become key components of the Scottish Coastal Observatory.

Steve joined the ICES Working Group on Zooplankton Ecology (WGZE) at its beginning in the early 1990's and was a strong contributor until his retirement, including serving as Chair in the early 2000s. In 2009, Steve proposed a new ICES Study Group on Integrated Morphological and Molecular Taxonomy (now WGIMT), providing visionary leadership in promoting new molecular approaches to revolutionize monitoring and the study of marine species and ecosystems. Since 2010, he was an active promoter of the calibration of biochemical indices of growth against somatic growth rates (ICES, 2010), and incorporated enzymatic production measurements into the data routinely collected by the Stonehaven time series. He was also one of the first supporters of reviving the ICES Leaflets for Plankton identification (https://www.ices.dk/Science/publications/Pages/ID_leaflets_plankton.aspx).

Steve was a true seagoing marine scientist, and a source of information and experience on all aspects of zooplankton. Many members of the WGZE remember him as being friendly, generous and very supportive when they first joined the group,

and we all feel privileged to have had the opportunity to work with him. Steve will certainly be missed, and his contributions remembered by the zooplankton community and beyond. After 42 years working on diverse studies of marine plankton Steve retired in 2011. One of his last contributions was the review The ICES Working Group on Zooplankton Ecology: Accomplishments of the first 25 years (Wiebe *et al.*, 2016).

Relevance of zooplankton time series

In its now over 30 years of existence, the WGZE has been essential to the advancement of the understanding of zooplankton community structure and population dynamics in the world's oceans, in particular the compilation and integration of allometric relationships for zooplankton species, and evaluation of new methodologies for the study of zooplankton distribution, abundance, physiology, and genetics. A particular accomplishment of the Group was the development of zooplankton time series, which now includes over a hundred sites covering the entire North Atlantic Ocean and its adjacent seas (Figure 1).

The objective of this TS was to bring together process-oriented contributions based on marine zooplankton time series data sets and their application to the understanding of global change and sustainable management of marine ecosystem resources and services and/or to test marine ecological or fisheries oceanographic hypotheses, to support the development of the United Nations' (UN) Decade of Ocean Science for Sustainable Development (<https://www.oceandecade.org/>) by addressing UN SDG 13 (Climate action) and 14 (Life below water).

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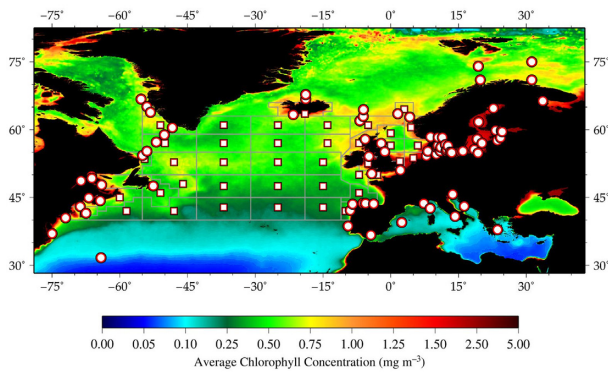


Figure 1. Locations of individual WGZE zooplankton time series monitoring sites (circles) and North Atlantic CPR Standard Areas (squares), plotted on a background of satellite-based average chlorophyll concentrations ($\text{mg}\cdot\text{m}^{-3}$). Image: Todd O'Brien (COPEPOD, NOAA).

Zooplankton play a pivotal role in the marine pelagic ecosystem, at the interface of the so-called “lower” and “upper” trophic levels, influencing both the ocean’s biogeochemical cycles and productivity. Furthermore, zooplankton are sensitive to environmental changes, and as such, changes in their abundance, biomass, community, and size structure are important indicators of overall ecosystem status (Gorokhova *et al.*, 2016). Climate-related changes in the physical and chemical oceanic environment have been considered as major drivers of significant fluctuations in zooplankton (Richardson, 2008; Poloczanska *et al.*, 2016). Micro- to macrozooplankton are key components of the marine food web. Hence, studies on their distribution, diversity, and population dynamics contribute to a more complete understanding of ecosystem dynamics.

Forecasting changes in marine zooplankton communities and their distribution and biomass is difficult. This crucial knowledge is mainly gathered through long-term time series. Such time series are key to understanding the dynamics of productivity-determining processes in marine ecosystems, such as recruitment variability and food web interactions (Beaugrand *et al.*, 2003; Brosset *et al.*, 2016; Yebra *et al.*, 2020). Understanding of such processes provides the scientific basis to support sustainable use of ecosystem goods and services (e.g. management of fisheries) and maintenance of ecosystem integrity (e.g. Good Environmental Status, *sensu* EU Marine Strategy Framework Directive, European Union (2008)). With increasing exploitation of our seas, and expanding pressure on the marine environment from a growing number of sources, there is a need to increase the information collected on zooplankton, for example, to complement existing monitoring programs with higher-resolution monitoring, in order to provide detailed information on seasonal and inter-annual changes at local, regional, and global scales (e.g. Pitois *et al.*, 2018; Scott *et al.*, 2021).

Recent advances in ICES zooplankton time series

Zooplankton production and community structure are strongly influenced by ocean circulation and environmental conditions (e.g. water column mixing and water temperature), which have been changing significantly over the last few decades. Changes in zooplankton communities have been ob-

served at sites across the North Atlantic, but the common or contrasting patterns of community change have not yet been fully assessed across time-series stations at the basin scale. Tracking and understanding changes in zooplankton community composition across time series stations and at the basin scale has applications to understanding the inter-connection of pelagic systems and their potential management and conservation.

In this Introduction, we summarize the contributions of WGZE marine zooplankton time series to the understanding of global change and to the sustainable management of marine ecosystem resources and services. The papers included in this TS describe results of research focused on key questions related to marine zooplankton time series as essential tools to understand variability in productivity-determining processes in the oceans.

Contributions mainly cover the North Atlantic Ocean, from polar to subtropical waters, the Mediterranean, and the Black Seas. Long-term data on the distribution (spatial and temporal), abundance, composition, and species diversity of zooplankton are explored. These include the traditionally studied mesozooplankton, but also changes in the macrozooplankton, microzooplankton, and gelatinous zooplankton communities. Several topics are addressed to fill some current gaps in knowledge, including new information on long-term changes and trends, their impact on fish stock recruitment, regional comparisons among sites, and the challenges of optimizing zooplankton field monitoring.

Dynamics of zooplankton populations

Changes in zooplankton communities have been observed at sites across the North Atlantic, but the common or contrasting patterns of community change have not yet been fully assessed across WGZE time-series stations at the basin scale. For example, datasets spanning the Western English Channel, Celtic Sea, and the Bay of Biscay to the Cantabrian Sea, revealed a latitudinal effect, both with more diversity in the southernmost locations and with the seasonal cycles of *Calanus helgolandicus* and *Acartia clausi*. No clear interannual trends in abundance were detected, but some coherent events among the several data sets revealed a regional response to environmental forcing factors (Valdés *et al.*, 2022).

In the subarctic NE Pacific, moulting zooplankton biomass and temperature were identified as key drivers of biomass production rates (BPR) for the entire crustacean community. The authors showed that BPR is affected by changes in the zooplankton community structure and that high crustacean zooplankton biomass does not necessarily equate to high BPR, as BPR was generally lower in years with reduced juvenile copepod biomass or increased biomass of non-copepod crustaceans and gelatinous zooplankton (Venello *et al.*, 2022). In the California Current Ecosystem (CCE), Killeen *et al.* (2022) tested the hypothesis that body length of three dominant species of krill declined during a recent marine heatwave off California, and that this was related to elevated seawater temperatures and reduced upwelling in the region. They found that these trends were not strongly driven by increased seawater temperatures but were linked to reduced upwelling and indicators of food availability, thus providing new insight into the environmental drivers of krill length and how pelagic ecosystems respond to the expected increase in frequency of marine heatwaves.

Several studies support a better understanding of the dynamics of *Calanus finmarchicus* in the North Atlantic, including spatiotemporal patterns, time from ascent, and vital rates, such as egg production and grazing rates compared to environmental parameters in the Gulf of Maine (Ji *et al.*, 2022) and subpolar basins (Espinasse *et al.*, 2022; Jónasdóttir *et al.*, 2022). Case studies focus on changes in vertical distribution of *Calanus finmarchicus* in the water column over a >30 year period in the Barents Sea (Kvile *et al.*, 2022), and the formulation of the hypothesis that warming north of Iceland may lead to an increase of *C. finmarchicus* through increased recruitment and a decrease of *C. hyperboreus*, which may in turn influence upper trophic levels, in particular plankton feeders in the region such as capelin (Gislason *et al.*, 2022; Jónasdóttir *et al.*, 2022).

Zooplankton as indicators of global change and ecosystem resilience

Zooplankton time series are an important tool in the development of indicators to track the impacts of global change and anthropogenic pressure on marine ecosystems.

Major changes in zooplankton communities in recent decades in several locations have been linked to climate change but the precise environmental variables driving this change are rarely clear. These changes can be abrupt or gradual. For example, Iriarte *et al.* (2022) report an abrupt community shift in the patterns of copepod densities in 2013–2014, in the southeastern Bay of Biscay, towards an increase of species normally associated with summer months. Similarly, a study in the west of Scotland suggests that changes in freshwater input, expected as a result of climate change, may adversely impact coastal zooplankton communities and the predators that depend on them (Wells *et al.*, 2022). In the Chesapeake Bay, seasonal deoxygenation in coastal and estuarine systems leads to decreased available habitat for a variety of planktonic organisms, but Pierson *et al.* (2022) argue that constraints other than oxygen may also be important for copepod habitat quality.

Further north, in the arctoboreal environment of the southwestern Barents Sea and northeastern Norwegian Sea, a 35 year time series on the spatial and temporal dynamics of gelatinous zooplankton showed that the occurrence of medusae, but not ctenophores and chaetognaths, was consistently higher in warm than in cold years, suggesting that the role of medusae is most profound during warm periods (Yaragina *et al.*, 2022). Finally, in the NW Mediterranean, changes in the mesozooplankton coastal communities were not directly related to increases in temperature but may have been related to the biotic interactions among plankton (Feuilloley *et al.*, 2022). The authors concluded that understanding marine ecosystem dynamics requires integrated long-term monitoring from phytoplankton to fish, rather than single compartment approaches.

Optimizing monitoring strategies

Zooplankton cover a wide range of diversity of organisms in terms of size, shape, and behaviour. This renders monitoring of zooplankton challenging as no single plankton sampler, or combination of plankton samplers, can provide an accurate estimate of abundance for all components of the plankton at any given time (Batten *et al.*, 2013). This is well evidenced by Head *et al.* (2022) who compared time series data collected with different gear and found that characterization of zoo-

plankton communities is also influenced by sampling methodology, including gear type, net mesh size, and sampling depth. Therefore, any sampling system will be biased toward a specific component of the plankton and it is important to select the adequate sampling gear for each target group.

For example, zooplankton sampling traditionally uses nets that target the mesozooplankton component (range 0.2–2 cm); thus, missing the smaller organisms such as planktonic foraminifera (generally smaller than 0.5 mm). Jonkers *et al.* (2022) highlight the unique potential of these calcifying marine zooplankton to bridge the gap between biology and geology, as planktonic foraminifera may substantially extend our view on plankton dynamics because their skeletal remains are preserved for millions of years in deep-sea sediments. Sampling frequency is also an important feature of monitoring programs, to make sure the peak of biomass is not missed and most taxa are recorded. Recommendations on sampling frequency are provided that optimize the value of heterotrophic microplankton monitoring programs by Lehtiniemi *et al.* (2022).

The role of zooplankton in the sustainable management of marine ecosystem services

Zooplankton, as prey, has an important role in the recruitment variability of fish stocks. For example, as ice-free years become the norm in the Bering Sea, negatively impacting the abundance of *Calanus* copepods, a decline of walleye pollock recruitment can be anticipated in the Berings Sea (Hunt *et al.*, 2022). In the Black Sea, an ecosystem influenced by eutrophication, overfishing, and invasive ctenophore species, Vereshchaka *et al.* (2022) provide deeper insight into adaptive strategies of both invading ctenophores and their interaction with mesozooplankton over the period 1991–2017. In the North Sea, Cook *et al.* (2022) provide evidence of the potential for copepods (an important food source for fish larvae and commercial pelagic fish such as mackerel and herring) to act as a vector for algal toxins to higher trophic levels, through their ability to accumulate toxins, but without being affected themselves by the presence of such toxins in the water column.

Conclusions

Analysis of long-term datasets allow for the detection of changes in zooplankton communities, potential regime shifts, and the drivers behind them. The results presented in this collection of papers illustrate the importance of time series for the study of climate change driven variations in the physical and biological environment on zooplankton community structure and distribution, and the resulting impact of warming seas on marine ecosystems and the services that they provide. To address current and future challenges highlighted by the UN Sustainable Development Goals 13 (Climate action) and 14 (Life below water), an increased and continued support of current zooplankton monitoring efforts is needed. Moving forwards, as technologies continue evolving towards automation of data collection and/or analysis (e.g. acoustics, molecular, image analysis, and machine learning tools), allowing for higher resolution and more comprehensive data, it will be important to integrate these newer methods with traditional ones so as to ensure continuity of existing time series from a more diverse suite of plankton sampling equipment. Concomitant monitoring of zooplankton and nekton would facilitate

the inclusion of zooplankton data into fisheries models, thus enhancing the scientific based evidence for an ecosystem approach to management; ultimately, supporting international policies promoting sustainable exploitation of our seas.

Data availability statement

The work does not include collection or use of any data.

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Conflict of interest

The authors declare that they have no conflicts of interest.

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