

Section 4

Subchapter 4A

Plankton

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Key points

- Plankton are overwhelmingly the biomass-dominant organism in the open oceans; thus, their activity sets the rates of biogeochemical cycles and propagates to higher trophic levels.
- With short generation times, large population sizes and high diversity, plankton are responsive to changing ocean conditions. However, this responsiveness presents challenges when it comes to capturing changes at the appropriate spatial and temporal scales.
- As addressed in the second *World Ocean Assessment*, it is predicted that the productivity, composition and distribution of plankton will be altered due to global change-driven alterations in temperature, nutrient fluxes and ocean acidification, among other factors (see sect. 3). However, in the absence of observable ecosystem tipping points, the period 2018-2023 largely continued previously observed trends. We identify gaps in data on plankton responses to long-term environmental change, as there is little long-term data aside from that on phytoplankton and zooplankton that can be used to establish trends. However, we identify stronger support for event-driven compositional and functional shifts in response to, inter alia, storms, fires and marine heat waves.
- Current global observing networks and models still under-sample plankton or treat them as a “black box”, failing to capture their dynamics in the pelagic oceans and particularly in dynamic coastal ecosystems (see subsect. 5A, chap. 9).

1. Introduction

Marine plankton comprise the majority of biomass in the open oceans and drive key biogeochemical cycles and support higher trophic levels by providing essential resources such as food and oxygen. Marine plankton (here excluding larvae of larger organisms) encompass a diversity of forms and functions, including viruses; bacterioplankton; archaea; phototrophic, heterotrophic and mixotrophic microeukaryotes; and zooplankton. Prior *World Ocean Assessments* and the scientific literature have contained predictions on plankton responses to long-term global change, including temperature-driven poleward shifts and changes in community composition; decreasing phytoplankton cell size due to stratification; reduced transfer of carbon and energy to metazoan food webs and to the deep ocean; reductions in primary production at mid-latitudes and increases at the poles; loss of calcifying taxa due to ocean acidification; shifts towards carnivorous and gelatinous filter-feeding zooplankton; and high temperatures potentially driving localized extinctions or evolution in the tropics (Bopp and others, 2013; Beaugrand and others, 2019; Affairs, 2021; Heneghan and others, 2023; Knecht and others, 2023).

Many of these predictions and models, which generally concern roughly the next 100 years, have been focused on primary producers, which tend to have more clearly defined thermal niches and nutrient requirements compared with other plankton groups (Bopp and others, 2013). Particularly neglected are predictions for heterotrophic eukaryotes (e.g. fungi, labyrinthulomycetes) (Jones and others, 2022), which are generally not measured in time series or molecular surveys. In addition to data gaps and biased methods (e.g. exclusion of fragile rhizarians in net samples (Soviadan and others, 2024) or exclusion of specific taxa by molecular techniques), it can be difficult to determine whether shifts in plankton composition are driven directly by global change or indirectly through interactions with other trophic levels. For example, as phytoplankton serve as the base of the marine food web alterations in their composition and physiology propagate to bacteria and zooplankton consumers (Hunt and Ward, 2015). While there is growing confidence in measurements of environmental change and models of plankton responses (Beaugrand and others, 2019), we lack unambiguous, empirical evidence that long-term climate pressures are reshaping plankton communities. Shifts in plankton abundance and community composition are assumed to be driven primarily by temperature, followed by nutrients and salinity (Frémont and others, 2022). However, many environmental parameters co-vary, and the same characteristics that make plankton good sentinels or bioindicators for ecosystem change, such as short generation times and responsiveness to environmental conditions, make it difficult to identify the proximal drivers of community and biomass changes. Further complicating identification of long-term trends, plankton are also shaped by mesoscale physical and temporal forces, including seasonal changes, large-scale multi-year oscillations (e.g. El Niño/Southern Oscillation (ENSO)), stochasticity and drift (Vellend, 2010).

2. Environmental change since the second *World Ocean Assessment*

Given the vast diversity in plankton phylogeny, trophic levels, form and function, a comprehensive review of the predicted impacts of global change on marine plankton is beyond the scope of the present *World Ocean Assessment* update, which covers the period 2018—2023. Instead, we focus on the evidence of observed responses to: (a) sustained changes in the environment (e.g. ocean warming) as assessed by time series and (b) shorter-term climate-related extreme events (e.g. storms, fires). research has highlighted not only long-term trends, but also the importance of extreme events, including floods, storms and heat waves, which may themselves be driven by global change or may add to underlying climate trends (e.g. a marine heat wave occurring alongside long-term warming).

3. Long-term trends

Measuring changes in plankton requires long-term time series to separate annual and interannual variability from global change-driven trends. Environmental observations, experiments and models are largely focused on phytoplankton due to their relatively simple nutrient requirements, the abundant long-term data on them and the ease of measurement. However, even trends in phytoplankton are somewhat mixed within general shifts towards smaller phytoplankton, including cyanobacteria (see table 1). Globally, phytoplankton blooms have increased in area by 13.2% and in frequency by 59% between 2003 and 2020, although with regional differences and compositional changes (Dai and others, 2023). Moreover, despite predicted decreases in tropical ocean primary production, the Hawaii Ocean Time-series shows increasing primary production, driven mainly by higher concentrations of cyanobacteria and picoeukaryotes (Kwon and others, 2022). Similarly, long-term trends in zooplankton reveal mixed responses: in some regions biomass has decreased, while in others there have been increases in biomass

and shifts in community composition (Pitois and Fox, 2006; Couret and others, 2023; Fernandez de Puellas and others, 2023).

Table 1

Predicted impacts of global change and extreme events on plankton

	Long-term global change		Heat waves		Fires		Storms	
	Abundance	Community	Abundance	Community	Abundance	Community	Abundance	Community
Large zooplankton	Mixed	Shifts in composition	Decreasing	Favouring smaller species	Neutral/minor impact	Minor shifts	Decreasing	Favouring tolerant species
Small zooplankton	Mixed	Shifts in composition	Increasing	Smaller species dominance	Minor increase	Minor shifts	Mixed	Shifts in composition
Eukaryotic phytoplankton	Decreasing	Favouring smaller species	Mixed	Favouring smaller species	Increase	-	Potential increases	-
Harmful algal blooms	Mixed	Mixed	Increasing	-	-	-	Mixed	-
Cyanobacteria	Increasing	Shifts in composition	Increasing	Shifts in ecotypes	-	-	-	Shifts in composition
Eukaryotic heterotrophs	-	Shifts in composition	-	-	-	-	-	-
Bacterioplankton	Increasing	Shifts in composition	-	Shifts in composition	-	Shifts to tolerant groups	Potential increases	Minor changes

Source: Prepared by the writing team.

Note: A dash indicates inconclusive or non-existent data.

While it is generally assumed that temperature drives most changes in plankton (Richardson, 2008), other environmental factors play a role in plankton dynamics. For example, a strengthening of the East Australian Current tropicalized temperate cyanobacteria and heterotrophic bacteria and altered phytoplankton community composition (Ajani and others, 2016; Messer and others, 2020). Nutrients represent another key anthropogenic influence on plankton. Harmful algal blooms have increased in geographic range and frequency in coastal areas since the 1980s in response to increased riverine nutrient inputs (Glibert, 2020). Similarly, zooplankton community changes have been attributed to the combined increases in temperature and nutrients (Holland and others, 2023; Marques and others, 2024) or gradients in salinity and oxygen (Peña and others, 2019a). However, we did not find reports of long-term trends for eukaryotic heterotrophs, as they are not measured in many time series (Xie and others, 2021). To add a further complication, viral abundances are rarely measured and are linked to their hosts, rendering it difficult to differentiate global change’s direct impacts on viruses from shifts in host communities.

4. Short-term events

The present part of the subchapter contains an examination of a number of short-term extreme events which are themselves the products of global change (table 1). Marine heat waves, which are persistent anomalously warm ocean temperatures, highlight the thermal sensitivity of plankton communities. However, observed changes in phytoplankton communities during heat waves, such as a shift towards smaller phytoplankton (Peña and others, 2019b; Brown and others, 2024) or a shift away from frustule-forming diatoms due to low silicate (Arteaga and Rousseaux, 2023), may reflect co-varying environmental changes, including warming and reduced nutrient inputs through stratification. Zooplankton communities may also transition towards smaller, thermally tolerant species, which can reduce grazing pressure on phytoplankton as well as total zooplankton biomass (Huỳnh and others, 2024). With respect to bacterioplankton, heat waves have shifted the microbiome towards more thermally tolerant taxa and favour rare taxa (Brown and others, 2024.) Moreover, in one system studied, heat wave-induced bacterial community composition changes did not recover once temperatures returned to seasonal averages (Larkin and others, 2020).

Wildfires. Although they are terrestrial in origin, fires can release growth-limiting resources (e.g. nitrogen, iron) through both wind- and water-based dispersal that fuel phytoplankton blooms (Ardyna and others, 2022). While less is known about heterotrophs' responses to wildfires, wildfires can increase marine organic matter (Coward and others, 2022), which could stimulate heterotrophic growth and the remineralization of carbon dioxide.

Storms. Similarly, strong storms (e.g. tropical cyclones), can be multifaceted disturbances that alter a number of environmental factors, making it difficult to identify the proximal drivers of shifts in plankton. Somewhat surprisingly, such storms do not necessarily fuel dramatic or long-term changes in bacterioplankton, despite altered environmental factors, but appear to transiently drive shifts in the relative abundance of existing taxa and increase photosynthetic biomass, potentially favouring eukaryotic algae over cyanobacteria (Ares and others, 2020; Gronniger and others, 2022; Johnson and others, 2025). Similarly, zooplankton are often resistant to tropical cyclone impacts, except when higher primary production fuels a zooplankton bloom (Topor and others, 2022). Although little is known about eukaryotic heterotrophs, salinity changes and terrestrial or phytoplankton detritus in coastal waters can cause transient blooms of specific microeukaryotes (Duan and others, 2018; Xie and others, 2021).

Other events. While we have focused on a number of discrete events as described above, additional factors, such as ocean oscillations, deoxygenation, nutrient influxes and changes in terrestrial influences (e.g. salinity and terrestrial organic matter) may also influence plankton dynamics. For example, harmful algal blooms resulting in fish kills have been linked to drought conditions influenced by the Southern Annular Mode (Mardones and others, 2021). Ocean deoxygenation (e.g. increases in oxygen minimum zones) are predicted to affect organisms, especially those sensitive to low oxygen levels, but without discernible affect on heterotrophic eukaryotes (Herrera and others, 2019; Li and others, 2024). Due to the severe under-sampling of coastal oceans and the lack of baseline data needed to identify anomalies from a high-variability baseline, it is likely that a number of critical events and responses among plankton are unknown.

5. Region-specific changes

A full review of changes observed in plankton communities at the regional scale is beyond the scope of the present subchapter due to the high diversity of plankton organisms and to the paucity of long-term monitoring programmes. Ratnarajah and others (2023) have recently reviewed long-term zooplankton monitoring programmes, which shows earlier phenology and poleward range expansion of some groups in the North Atlantic and North Pacific oceans. In the Southern Ocean, Antarctic krill (*Euphausia superba*) and salps showed poleward shifts. However, the seasonality of the pteropod *Limacina helicina* and the distribution of copepod species remained resilient to warming patterns and did not show apparent changes. The absence of patterns observed in other areas can be partially explained by the limited number of long-term monitoring programmes in areas beyond North America and western Europe and particularly in the global South. However, the overall absence of more examples of seasonal or geographical shifts in distribution across all regions can also be related to reduced accessibility to data from long-term plankton time series (see figure 3 in Ratnarajah and others, 2023). Although there have been significant improvements in automated or semi-automated analyses of plankton, research is hampered by the lack of experts in morphological and molecular identification of a diverse and complex group of organisms.

Other apparent patterns of change have been observed in other taxonomic groups at the regional scale since the second *World Ocean Assessment* (2018–2023) that show the complexity of plankton dynamics and the difficulties of observing conspicuous long-term trends at the global scale.

Arctic Ocean

The most dramatic changes in the Arctic Ocean have been driven by warming and reduced sea ice cover (Ardyna and Arrigo, 2020; see also sect. 4, chap. 3). Increased open water has led to a 30% increase in net primary production, accompanied by the loss of sea ice-associated plankton (Hop and others, 2020; Ardyna and others, 2022). Furthermore, global change is increasing the “Atlantification” of the Arctic Ocean; for example, *Emiliana huxleyi*, a calcifying coccolithophore, has expanded its range poleward (Oziel and others, 2020), among others. These changes in arctic phytoplankton communities and sea ice affect zooplankton phenology, production and community composition (Wang and others, 2015); however, less is known about other plankton, such as ciliates (Wang and others, 2023)

North Atlantic Ocean, Baltic Sea, Black Sea, Mediterranean Sea and North Sea

In the Baltic Sea, phytoplankton blooms have occurred one to two weeks earlier over the past two decades, which is associated with increased sunshine and a decrease in strong wind conditions. Higher temperatures are linked with earlier and decreasing diatom blooms and a higher proportion of dinoflagellates (Hjerne et al 2019). In the Black Sea, shifts in the composition of the dominant species have been observed together with an increase in the proportion of dinoflagellates, particularly in the fall (Stelmakh and others, 2023). In the Mediterranean Sea, the concentration of diatoms is decreasing and the concentration of cyanobacteria is increasing, and the whole Mediterranean Sea is shifting to an eastern Mediterranean state (Hourany and others, 2021).

Pacific Ocean

The warm anomaly in the Gulf of Alaska in 2014 reduced silica supply and led to a switch in community composition from diatoms to dinoflagellates, resulting in an increase in surface ocean chlorophyll during

the summer and fall. A more dramatic change was observed in the equatorial Pacific, where the extreme warm conditions of the 2016 El Niño resulted in a major decline of about 40% in surface chlorophyll, which was associated with a near-total collapse in diatoms (Arteaga and Rousseaux, 2023). The 2023 El Niño may have provoked similar dramatic effects, although its consequences for plankton have yet to be documented.

Southern Ocean

This region has experienced greater warming than other regions, resulting in declines in sea ice and nutrient influxes that have led to phytoplankton blooms (Ferreira and others, 2024). However, despite warming, mesozooplankton communities in the South Atlantic and West Antarctic Peninsula did not significantly change, suggesting possible thermal resilience (Tarling and others, 2018). This region is also subject to the influence of short-term events; for instance, a marine heat wave in the western Antarctic Peninsula showed a 60% decrease in microbial community biomass and a shift from a cryptophyceae-dominated community towards nanoflagellates and heterotrophic plankton (Latorre and others, 2023). In addition, the 2019/20 Australian wildfires were linked to months-long phytoplankton blooms in the Southern Ocean, potentially due to fertilization of iron-limited waters (Tang and others, 2021).

6. Key remaining knowledge and capacity gaps

We advocate for long-term time series to both capture long-term trends and situate extreme events in context, in order to clarify whether these events result in statistically discernible impacts on plankton and persistent altered plankton states. However, we make the case that specific groups (notably, heterotrophic bacteria and eukaryotes) and regions (e.g. the global South and depths below the photic zone) are underrepresented relative to their biogeochemical importance. We also lack long-term data (and event-driven sampling) on bacterioplankton and heterotrophic eukaryotes. Considering these groups' critical functions in decomposing organic matter and secondary production, global change and extreme events can significantly affect marine biogeochemical cycles. However, we should not discount the fact that non-determinative factors (e.g. drift) shapes plankton communities; therefore, care should be taken when interpreting long-term trends as being driven by global change or when predicting the reproducibility of short-term disturbance responses. To understand the dynamics of plankton in the context of climate variability and extreme events, long-term high-resolution plankton observatories are needed, ideally across taxonomic groups, so that transmission of impacts can be tracked across food webs (Hunt and Ward, 2015). Therefore, we advocate for sustained and even expanded support for plankton observatories in the face of a changing climate.

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