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Review Article

Ecological roles, climate-driven responses, and critical knowledge gaps of krill in the global ocean

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Abstract

Human-induced global climate change and other anthropogenic stressors are fundamentally altering our oceans. Understanding the ecological and societal implications of these changes is critical for developing mitigation strategies and conservation measures. However, major components of the marine pelagic ecosystem remain poorly understood. This is true for euphausiids ("krill"), which are a crucial part of marine food webs and play an important role in elemental cycling, including in the biological carbon pump, but for which we know surprisingly little. In this review, we first provide an overview of the ecological and socio-economic value of krill, highlighting their function in marine food webs and biogeochemical cycling. Next, we describe what is currently known regarding the response of krill to climate change and other anthropogenic stressors, focusing on changes in their biogeography, physiology, life history, as well as the impacts of krill fishing and their association with pathogens and parasites. We identify five key gaps in our current knowledge of krill: (1) the effects of krill on food web dynamics and stability, (2) the effects of changing predator and/or prey communities on krill populations, (3) the identification of important krill habitats, (4) the understanding of vertical and horizontal range shifts, and (5) the combined effects of multiple climate change and other anthropogenic stressors on krill. We also highlight the krill species, regions, and habitats that are understudied. Finally, we propose strategies to improve our understanding of this ecologically important taxonomic group, including the sustained funding for time series; implementation of novel research technologies; expanding research on understudied species and regions; and creating a global community of krill researchers.

Keywords euphausiids, krill, climate change, anthropogenic stressors, fisheries, carbon pump, ecosystem health

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Introduction

Krill (Euphausiacea; Dana 1850), hereafter referred to collectively as "krill," are a fundamental component of global marine ecosystems supporting extensive fish stocks and populations of marine megafauna (Everson 2000). Krill can be found in every ocean, from the poles to the equator and from the surface ocean to the deep sea (Baker et al. 1990, Brinton et al. 2015). A recent functional size spectrum model of zooplankton in marine ecosystems suggests that if krill were removed, fish biomass may decrease by up to 80% (Heneghan et al. 2020). Healthy krill populations are thus critical to both global food security and economies. The ecological importance of krill in global marine ecosystems is not limited to their fundamental role in food webs. Due to their relatively large body size and tendency to form dense aggregations, many krill species are significant mediators of carbon sequestration and are important components in global biogeochemical cycles, including the biological carbon pump and the cycling of other elements necessary for primary production, such as nitrogen and iron (Fortier et al. 1994, Robinson et al. 2010, Schmidt et al. 2011, 2016, Cavan et al. 2019, Franco-Cisterna et al. 2022, 2024).

The combined effects of human-induced global climate change (including ocean warming, ocean acidification, and deoxygenation) and other anthropogenic activities, such as overfishing and pollution, exert a suite of stressors on marine pelagic ecosystems. These stressors are causing cascading effects and reducing energy transfer efficiency through marine food webs with the potential to disrupt fisheries and destabilize global food security through trophic amplification (Heneghan et al. 2023, Atkinson et al. 2024). Warming oceans favor smaller organisms (Campbell et al. 2021) and there is evidence of shifts in the composition of pelagic zooplankton communities from those dominated by larger crustaceans, like large calanoid copepods and krill, to those dominated by smaller taxa, primarily small calanoid and cyclopoid copepods (Heneghan et al. 2023). In this shifting seascape, krill emerge as potential early-warning indicators of broader ecological changes due to their pivotal role in global marine ecosystems and their sensitivity to changes in ocean temperature and chemistry (Díaz-Astudillo et al. 2022a, Werner 2013, Fiechter et al. 2020, Dorman et al. 2023).

Even if CO_2 emissions are reduced in the near future, the global oceans are predicted to warm by ˜1.42°C by the end of the century (Kwiatkowski et al. 2020). Marine heatwaves (MHWs) will likely become more frequent, more intense, and of longer duration. For example, recent Coupled Model Intercomparison Project Phase 6 (CMIP6) models predict the Indian Ocean to experience a marine heatwave-state for over 6 months of the year by 2050 (Dalpadado et al. 2024b, Roxy et al. 2024). The current worst-case scenario predicts a 41-fold increase in the number of MHWs from present-day values by the end of the century (Frolicher and Laufkotter 2018, Frolicher et al. 2018). In addition, a general deoxygenation of marine systems is predicted (Bakun 2017, Shepherd et al. 2017, Kwiatkowski et al. 2020), and oxygen minimum zones (OMZs) are expected to expand, shoaling into surface waters (Stramma et al. 2008, 2012). Furthermore, with continued anthropogenic emissions of CO_2, we can expect to see increased ocean acidification (OA; Doney et al. 2020). Compounding the impacts of human-induced climate change, other anthropogenic stressors like pollution and overfishing affect marine life in a myriad of ways that are overall detrimental to the health of marine organisms. There is thus a pressing need to understand the implications of human-induced climate change and other anthropogenic stressors on marine ecosystems.

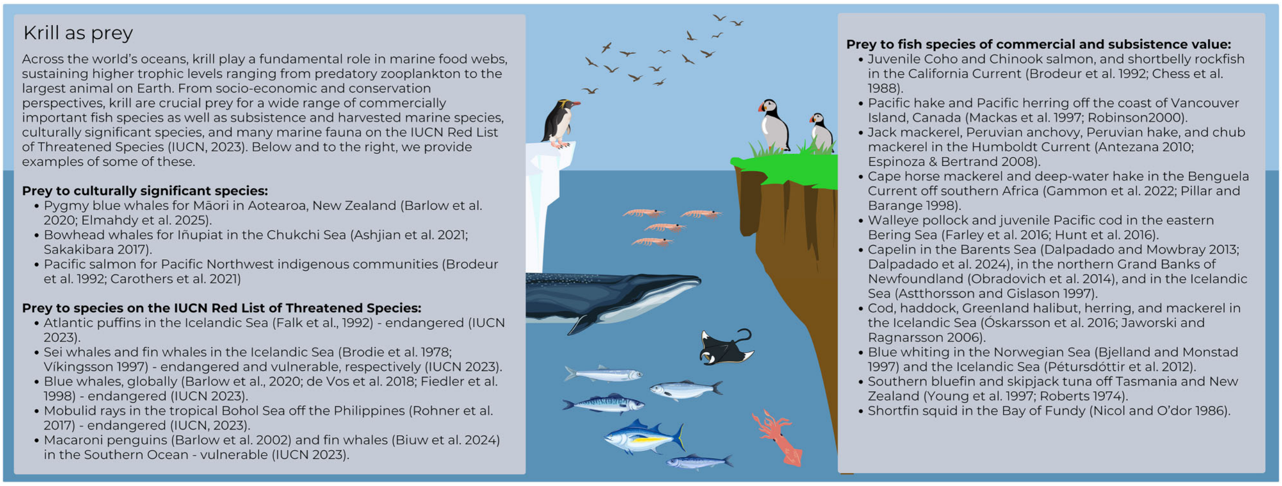
Despite the critical role that krill play in global marine food webs and biogeochemical cycles, and the clear direct impacts climate-induced declines in their populations have on marine ecosystems, very few of the 87 known krill species [86 in Baker et al. (1990), plus the addition of *Hansarsia einarssoni* by Kulagin et al. (2024)] have been studied in depth, and krill are rarely considered adequately in Earth system models. In the present review, we first highlight the ecological and socio-economic significance of krill in their role as vital trophic intermediaries supporting commercially and culturally significant higher trophic level predators and their contribution to global biogeochemical cycles. Next, we synthesize current understanding of the responses of global krill to human-induced climate change and other anthropogenic stressors, focusing on changes in species biogeography, physiology, life history, the impacts of krill fisheries, and interactions with pathogens and parasites. Using a Delphi-style approach (Linstone and Turoff 1975) to reach academic consensus, we identified the top five gaps in our current knowledge on global krill and provide an overview of the future research directions necessary to address them.

The importance of krill in global marine ecosystems

Trophic intermediaries

Krill provide a crucial link between primary producers at the base of the food web and top predators in many ocean habitats from the Antarctic to the Arctic and in between (Dalpadado et al. 2024a, Laws 1977, Everson 2000, Antezana 2010, Savenkoff et al. 2013, Hunt et al. 2016, Trathan and Hill 2016). As consumers, krill exhibit versatile feeding behaviors reflected in the morphological characteristics of their different feeding apparatus, with most species being considered omnivorous (reviewed in Mauchline 1989). The diets and trophic levels of krill are dynamic, varying with life stage, time of day, season, and region (Schmidt 2010, Park et al. 2011, Schmidt and Atkinson 2016, Färber-Lorda and Murcia-Riaño 2021). This versatility in feeding strategies enables krill to optimally use their seasonally or regionally variable food resources. For instance, the diet of dominant krill species differs between the California Current and eastern tropical North Pacific, with individuals of *Thysanoessa spinifera* and *Euphausia pacifica* in California occupying lower trophic positions than *Euphausia diomiedeae* and *Euphausia distinguenda* in the eastern tropical Pacific (Färber-Lorda and Murcia-Riaño 2021).

The variability in krill diets, and consequently their dynamic trophic position within the food web, alters their quality as prey to higher trophic levels (Färber-Lorda et al. 2009, Färber-Lorda and Mayzaud 2010, Bernard et al. 2022) and modifies the efficiency of energy transfer through marine food webs. Those krill species for which diatoms represent a large component of their diet, like *Euphausia superba* in the Southern Ocean (Stowasser et al. 2012, Cleary et al. 2018) or *Thysanoessa inermis* in the Barents Sea (Dalpadado and Mowbray 2013), provide an efficient energy transfer from primary producers to higher trophic levels. Krill species that occupy comparatively higher trophic positions (i.e. are predomi-



Krill as prey

Across the world's oceans, krill play a fundamental role in marine food webs, sustaining higher trophic levels ranging from predatory zooplankton to the largest animal on Earth. From socio-economic and conservation perspectives, krill are crucial prey for a wide range of commercially important fish species as well as subsistence and harvested marine species, culturally significant species, and many marine fauna on the IUCN Red List of Threatened Species (IUCN, 2023). Below and to the right, we provide examples of some of these.

Prey to culturally significant species:

- Pygmy blue whales for Māori in Aotearoa, New Zealand (Barlow et al. 2020; Elmahdy et al. 2025).
- Bowhead whales for Iñupiat in the Chukchi Sea (Ashjian et al. 2021; Sakakibara 2017).
- Pacific salmon for Pacific Northwest indigenous communities (Brodeur et al. 1992; Carothers et al. 2021)

Prey to species on the IUCN Red List of Threatened Species:

- Atlantic puffins in the Icelandic Sea (Falk et al., 1992) - endangered (IUCN 2023).
- Sei whales and fin whales in the Icelandic Sea (Brodie et al. 1978; Víkingsson 1997) - endangered and vulnerable, respectively (IUCN 2023).
- Blue whales, globally (Barlow et al., 2020; de Vos et al. 2018; Fiedler et al. 1998) - endangered (IUCN 2023).
- Mobulid rays in the tropical Bohol Sea off the Philippines (Rohner et al. 2017) - endangered (IUCN, 2023).
- Macaroni penguins (Barlow et al. 2002) and fin whales (Biuw et al. 2024) in the Southern Ocean - vulnerable (IUCN 2023).

Prey to fish species of commercial and subsistence value:

- Juvenile Coho and Chinook salmon, and shortbelly rockfish in the California Current (Brodeur et al. 1992; Chess et al. 1988).
- Pacific hake and Pacific herring off the coast of Vancouver Island, Canada (Mackas et al. 1997; Robinson2000).
- Jack mackerel, Peruvian anchovy, Peruvian hake, and chub mackerel in the Humboldt Current (Antezana 2010; Espinoza & Bertrand 2008).
- Cape horse mackerel and deep-water hake in the Benguela Current off southern Africa (Gammon et al. 2022; Pillar and Barange 1998).
- Walleye pollock and juvenile Pacific cod in the eastern Bering Sea (Farley et al. 2016; Hunt et al. 2016).
- Capelin in the Barents Sea (Dalpadado and Mowbray 2013; Dalpadado et al. 2024), in the northern Grand Banks of Newfoundland (Obradovich et al. 2014), and in the Icelandic Sea (Astthorsson and Gislason 1997).
- Cod, haddock, Greenland halibut, herring, and mackerel in the Icelandic Sea (Óskarsson et al. 2016; Jaworski and Ragnarsson 2006).
- Blue whiting in the Norwegian Sea (Bjelland and Monstad 1997) and the Icelandic Sea (Pétursdóttir et al. 2012).
- Southern bluefin and skipjack tuna off Tasmania and New Zealand (Young et al. 1997; Roberts 1974).
- Shortfin squid in the Bay of Fundy (Nicol and O'dor 1986).

Figure 1. The ecological importance of krill as prey in global marine food webs. Depiction of predator guilds (fish, squid, whales, penguins, and seabirds) and the central role of krill in sustaining global marine biodiversity and fisheries productivity.

nantly carnivorous), such as *Meganyctiphanes norvegica*, also play an important role in marine food webs and can be the food of a wide range of fish species, squid, shrimp, whales, and even brittle stars (Simard and Harvey 2010).

The nutritional quality of krill is linked to their diet and physiology and varies by species, season, and life stage (Riquelme-Bugueño et al. 2020a, Hagen et al. 2007, Ju et al. 2009, Färber-Lorda and Mayzaud 2010, Harvey et al. 2012, Hellessey et al. 2018, Fisher et al. 2020, Bernard et al. 2022). Those species and/or life stages that have higher lipid contents tend to be the preferred prey of top predators. For instance, in the California Current, *T. spinifera* has a higher average lipid content than *E. pacifica* (Fisher et al. 2020, Färber-Lorda and Murcia-Riaño 2021) and is preferentially preyed upon by blue whales (Nickels et al. 2018) and humpback whales (Rockwood et al. 2020, Kaplan et al. 2025) despite being less abundant than *E. pacifica*. In Southwest Alaska and Antarctica, humpback whales target adult krill rather than immature individuals that have reduced lipid contents (Szabo 2015, Cade et al. 2022).

Globally, krill are key prey for some of the largest and most lucrative commercially fished species as well as many subsistence fisheries (Fig. 1). In addition, numerous seabirds and marine megafauna, many of which are currently listed on the IUCN Red List of Threatened Species (a comprehensive, science-based information source on the global extinction risk of plants, animals, and fungi) or have cultural significance (either as a subsistence food source or as a spiritual symbol) feed directly on krill (Fig. 1). Although total annual consumption of krill by higher trophic levels has not been assessed globally, it has been estimated at the regional scale. For example, in the Lower St. Lawrence Estuary, Canada, a community of higher trophic level predators ranging from carnivorous macrozooplankton to blue whales consumed an estimated 14.2 tonnes km^{-2} $year^{-1}$ of *M. norvegica* and 19.3 tonnes km^{-2} $year^{-1}$ of *Thysanoessa raschii*, which equated to an average of 35% of the krill biomass estimated between 2008 and 2010 for that region (Savenkoff et al. 2013). In Icelandic waters, dominated by *M. norvegica*, *Thysanoessa longicaudata*, and *T. inermis* (Astthorsson and Gislason 1997), annual consumption of krill by cetaceans was estimated to be 3.4 million tonnes (Sigurjónsson and Víkingsson 1997), while seabirds consumed ∼34 000 tonnes each year (Lilliendahl and Solmundsson 1997). In the eastern Bering Sea, where *T. raschii* and *T. inermis* are the main krill species, walleye pollock alone consumed between 17% and 29% of the summer krill production each year between 1999 and 2009 (Hunt et al. 2016). Off the coast of Vancouver Island, Canada, the fish community (including Coho and Chinook salmon, dogfish, sablefish, herring, hake and Pacific cod) consumed an annual average of 268 400 metric tonnes of krill—which primarily consist of *E. pacifica* and *T. spinifera* (Evans et al. 2021)—between 1985 and 1989 (Robinson 2000). Marine mammals and seabirds in the Scotia Sea, Southern Ocean, consume at least 55 million tonnes of *E. superba* annually (Trathan and Hill 2016). Recent estimates of annual summer *E. superba* consumption by fin whales alone amount to ∼8 million tonnes (Biuw et al. 2024). Consequently, the health of global krill populations is vital to sustaining thriving top predator populations with the potential for serious ramifications for commercial fisheries and conservation efforts when krill abundances decrease.

Role in biogeochemical cycles

Krill play an important role in the biological carbon pump, the suite of biologically driven processes that are responsible for transferring photosynthetic carbon from surface waters to the ocean interior (Sarmiento and Gruber 2013, Boyd et al. 2019). Although traditionally described in terms of the gravitational pump—the sinking of particulate organic carbon in the form of faecal pellets and detritus—the biological carbon pump is now recognized as a composite of several interconnected processes, including the mesopelagic migrant pump, which involves active transport by migrating organisms and the release of dissolved and suspended carbon at depth (Boyd et al. 2019). Krill play a key role in both the gravitational and migrant pumps.

The role of krill in the gravitational pump is particularly evident in the Southern Ocean, where the large individual body size and extraordinary abundances of *E. superba* result in the dominance of krill-derived particles (faecal pellets) at depth, especially during spring and summer (Gleiber et al. 2012, Cavan et al. 2015, Belcher et al. 2019, Manno et al. 2020, 2024). Furthermore, regular moulting throughout the krill life cycle produces a continuous flux of carbon-rich exuviae, recently shown to contribute as much to carbon export in the Scotia Sea as faecal pellets (Manno et al. 2020). Another potentially important but poorly constrained pathway is the passive export of carbon associated with the descent and mortality of krill embryos (Thorpe et al. 2019), which sink to depth during development but for which direct estimates of mortality-driven carbon flux are lacking. Sinking carcasses add a further important pathway for carbon flux. In waters off southwest Greenland, the euphausiids *T. raschii* and *M. norvegica* were found to sink at rates of 1500–3000 m d^{-1}, with minimal carbon loss ($<10\%$) during descent (Franco-Cisterna et al. 2022). Such rapid export enhances the efficiency of sequestration and supports benthic productivity by supplying organic carbon and nutrients (Franco-Cisterna et al. 2022). As an important counterpoint, swimming behavior of *E. pacifica* off Southern California was shown to fragment marine snow aggregates into smaller particles, potentially altering sinking rates and attenuating levels of carbon export (Dilling and Alldredge 2000).

In addition to these gravitational pathways, diel vertical migration (DVM; Hays 2003) may provide an active transport route for carbon to depth in krill species that exhibit this behavior. By feeding near the surface and respiring, excreting, and egesting at depth, vertically migrating krill actively inject organic carbon into the mesopelagic zone (Steinberg et al. 2000, Darnis et al. 2017, Boyd et al. 2019). However, not all DVM is equal. In krill, DVM includes (i) the vertical migration of epipelagic species between the epipelagic and mesopelagic (e.g. Taki 2008, Haraldsson and Siegel 2014, Sogawa et al. 2016), (ii) the vertical migration of epipelagic species within the epipelagic (e.g. Taki 2008, Conroy et al. 2020), and (iii) the vertical migration of mesopelagic species between the mesopelagic and epipelagic (e.g. Steinberg et al. 2000). These migrations are typically upward at night, but the reverse has also been observed (Meyer et al. 2017). There is often a seasonal component to DVM, particularly in regions with strongly seasonal food supply (Werner and Buchholz 2013, Haraldsson and Siegel 2014, Sogawa et al. 2016, Darnis et al. 2017, Smith et al. 2025).

Through feeding, egestion, and excretion in surface waters, krill release essential elements—such as iron (Tovar-Sanchez et al. 2007, Schmidt et al. 2016), ammonium (Atkinson and Whitehouse 2000, Steinberg et al. 2002, Ikeda 2012, Lehette et al. 2012, Kiko et al. 2016, Darnis et al. 2017), and dissolved organic carbon (Steinberg et al. 2000, Ruiz-Halpern et al. 2011)—that are required for primary and microbial production. Furthermore, by migrating to the seafloor, ingesting lithogenic particles with high iron content, and returning to surface waters, krill redistribute this essential trace metal throughout the water column, locally enhancing primary productivity, particularly in regions with low iron concentrations such as the Southern Ocean where *E. superba* has been shown to transport iron to the surface waters (Schmidt et al. 2016, Cavan et al. 2019).

Response of krill to a changing ocean world

The global oceans are changing rapidly with significant ramifications for marine ecosystem functioning and productivity (Richardson 2008, Brierley and Kingsford 2009, Poloczanska et al. 2013, 2016). Warming associated with long-term human-induced climate change is causing a general poleward shift in isotherms, resulting in the contraction of biogeographic habitat for some species and expansion for others. Changes in large-scale ocean circulation patterns, frontal positions, and upwelling are modifying transport, advection, and nutrient delivery (Bakun et al. 2015, Hunt et al. 2016, Wilson et al. 2016, Ashjian et al. 2021, Lévy et al. 2024). In addition to long-term ocean warming, many parts of the world ocean are also experiencing acute MHWs, the ecological effects of which are not yet fully understood. Ocean warming has also reduced ventilation (through increased stratification) and solubility of the global oceans (de Boer et al. 2007, Shepherd et al. 2017). These processes, in combination with altered ocean circulation, increased biological oxygen demand, and greater eutrophication near the coast, have resulted in the deoxygenation of several oceanic regions (Bakun 2017, Kwiatkowski et al. 2020) with profound negative consequences for marine life (Kwiatkowski et al. 2020, Morée et al. 2023). While this is problematic at a global scale, deoxygenation has a particularly strong negative impact on marine organisms living above OMZs, which are a predominant feature in the Eastern North and South Pacific, the Arabian Sea, and the Bay of Bengal (Dalpadado et al. 2024b, Fernández-Álamo and Färber-Lorda 2006, Paulmier and Ruiz-Pino 2009). In addition to warming and deoxygenation, rapidly increasing atmospheric CO_2 concentrations have led to an increase in dissolved CO_2 and inorganic carbon concentrations in seawater, resulting in a reduction in pH and changes to the acid-base chemistry of marine environments (Orr et al. 2005, Fabry et al. 2008, Doney et al. 2009).

Human-induced climate change is, justifiably, a dominant theme in marine research, but we would be remiss to neglect the review of other anthropogenic stressors, including pollution (nano- and microplastics, heavy metal contamination, anthropogenic noise, and eutrophication) and fishing. These additional stressors can act to compound those caused by climate change, further exacerbating the negative effects on marine ecosystems and organisms. Considering the ecological and socio-economic importance of krill, it is vital to establish an overview of how our changing oceans will affect their populations. In this section, we discuss the various implications of changing oceanic conditions for global krill populations, including changes in their biogeography, physiology, life history, the impacts of krill fishing, and interactions with pathogens and parasites.

Changes in biomass and species distribution

The biogeography of krill has been comprehensively described by Brinton et al. (2015) in the online resource "Euphausiids of the World Ocean." This work, that includes all known species at the time of publication (86 species), provides a valuable baseline from which to quantify climate driven shifts in biogeography. Understanding the changing biogeography of krill species globally is complex and requires time-series spanning multiple decades to disentangle (Ducklow et al. 2022). Such programs are rare for krill but, where they have been maintained, they shed light on the varied responses of different krill species to climate-driven stressors (e.g. those outlined in Ducklow et al. 2022). These stressors can be categorized as (i) press (long-term, directional change, e.g. long-term warming), (ii) pulse (intense, short-term deviations from the norm, e.g. MHWs), or (iii) oscillating (annual, decadal to multidecadal climate modes, e.g. ENSO).

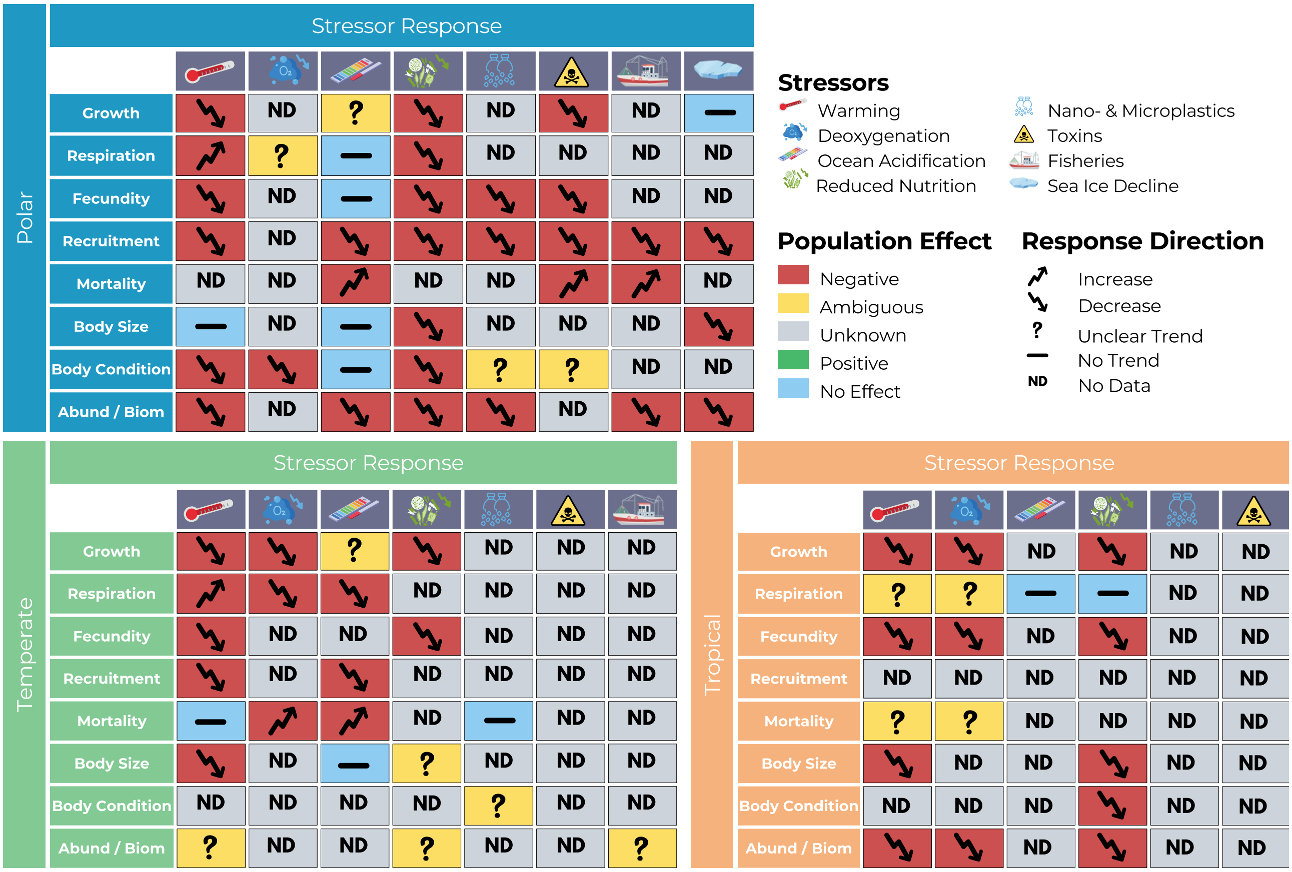
Poleward range shifts, by which species alter their distribution to keep pace with moving isotherms, is one of the "universal" responses to long-term warming (Chen et al. 2011). In the Atlantic sector of the Southern Ocean, long-term warming (Meredith and King 2005) coincided with a poleward range contraction of *E. superba* (Atkinson et al. 2019), associated with climatic controls on spawning and recruitment within a series of localized hotspots (Atkinson et al. 2022). In the Barents Sea and Scotian Shelf of the Arctic, increased ocean heat transport and a decline in sea ice (Smedsrud et al. 2022) have coincided with an increase in subarctic and boreal krill species, such as *M. norvegica* and *T. inermis* (Orlova et al. 2015, Eriksen et al. 2016, ICES 2021) and a decrease in the Arctic species *T. raschii* (Silva et al. 2014, Edwards et al. 2021). Even larger range shifts have been observed with the subtropical species *Hansarsia megalops* (previously *Nematoscelis megalops*) recently being recorded in the Barents Sea (Zhukova et al. 2009, Ingvaldsen et al. 2023) and *Stylocheiron affine* observed in sub-Antarctic waters of the Indian Ocean (Sutton and Beckley 2022). Not all species are able to shift their range polewards, however. For example, a 60-year dataset of krill abundances obtained from Continuous Plankton Recorder (CPR) surveys in the North Atlantic provides evidence that the decline in krill biomass in that region may have been caused by the fact that those species were spatially constrained due to ocean currents and strong thermal boundaries, such as the polar front, limiting their northward expansions (Edwards et al. 2021). With continued warming under those conditions, neritic krill with narrower thermal tolerances, such as *T. raschii* (Hünerlage and Buchholz 2015), will experience habitat compression and may not adapt fast enough, resulting in regional population collapse.

Habitat compression is also occurring in response to the warming-induced expansion (both horizontally and vertically) and intensification of OMZs (Bograd et al. 2008, Stramma et al. 2008, Deutsch et al. 2011, 2012). Seawater dissolved oxygen is a controlling variable of krill species distribution and vertical migration in many ecosystems (see for example the Habitat Contraction Hypothesis of Fernández-Álamo and Färber-Lorda 2006). It is to be noted that, although the amount of fully oxygenated water column may have become reduced, a viable oxygenated part of the water column remains available both horizontally and vertically. Nevertheless, compression of the oxygenated habitat has implications for krill behavioral and life-history strategies and for predator–prey interactions (Wishner et al. 2013, Seibel et al. 2016, Tremblay et al. 2020, Díaz-Astudillo et al. 2024). In such environments, there may be some advantage for euphausiid species that can physiologically tolerate low dissolved oxygen environments. For instance, recent analyses of multiyear data collected off northern Chile show that projected increases in upwelling intensity and expansion of the OMZ could favor the low-oxygen-adapted *Euphausia mucronata* over oxygen-sensitive species like *Euphausia eximia* and *S. affine* (Díaz-Astudillo et al. 2024).

MHWs are increasingly reshaping krill biogeography by driving abrupt distributional shifts, local absences, and altered regional dominance patterns. In the northeast Pacific, the prolonged 2014–2016 MHW (one of the most intense on record) was linked to the near-disappearance of *E. pacifica* and *T. spinifera* from extensive areas of the California Current System (Cavole et al. 2016, Peterson et al. 2017, Brodeur et al. 2019, Santora et al. 2020), likely reflecting poleward displacement or vertical redistribution to cooler habitats. In contrast, during the same MHW, no detectable decline in krill biomass was observed off the west coast of Vancouver Island, suggesting the presence of local refugia or behavioral plasticity that may buffer some populations against short-term warming (Evans et al. 2023). In the southwest Pacific, the 2015–2016 and 2017–2018 Tasman Sea MHWs coincided with sharp declines in Nyctiphanes australis abundances off New Zealand (Barlow et al. 2020) and shifts in larval krill distributions off southeast Australia (Evans et al. 2020). Although empirical data are still lacking for the Southern Ocean, the rising frequency and persistence of MHWs there (Fernández-Barba et al. 2024) suggest similar risks of transient habitat loss and poleward or vertical displacement for Southern Ocean krill species.

The impacts of warming associated with climate oscillations, such as El Niño Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), the Southern Annular Mode (SAM), and others, are also evident in krill populations, though the direction of change varies between species and region. The California Current System, in the northeast Pacific Ocean, is a highly productive, temperate eastern boundary upwelling system (EBUS) strongly influenced by ENSO and PDO events (Chelton et al. 1982, Huyer 1983, Checkley and Barth 2009). These climate modes can reorganize krill communities in the California Current, with some species declining and others increasing, depending on their thermal affinities, habitat associations, and latitudinal position (Brinton and Townsend 2003). For instance, during years of increased sea-surface temperature associated with positive ENSO (i.e. El Niño) and positive PDO, abundances of cold-water temperate species (e.g. *E. pacifica*) decreased while abundances of warm-water subtropical species (e.g. *Nyctiphanes simplex*) increased (Marinovic et al. 2002, Brinton and Townsend 2003, Lilly and Ohman 2021, Phillips et al. 2022, Dorman et al. 2023) (Fig. 2). Further south, in northern Baja California, *E. pacifica* abundances decreased to near-absence at the southern edge of their distribution range while the warm-water species, *E. eximia*, increased in abundance and expanded its distribution range northwards during a strong El Niño event in 1997–1998 (Parés-Escobar et al. 2018). In the Humboldt Current System—another highly productive temperate EBUS—the warmer, saltier, and more oxygenated conditions brought on by El Niño events corresponded to a decline in overall krill biomass and abundance (Díaz-Astudillo et al. 2022a, González et al. 2000) but no apparent shift in community composition, though there was evidence of high resilience in the Humboldt Current endemic *E. mucronata* to episodic warming associated with El Niño (Díaz-Astudillo et al. 2024) (Fig. 2).

Adding further complexity, the response of krill species to different expressions of El Niño—Eastern Pacific (EP) or Central Pacific (CP)—varies in species-specific ways (Parés-Escobar et al. 2018, Lilly and Ohman 2021). Off southern California, EP El Niño events result in a shoreward compression, poleward retraction, and decline in abundances of *E. pacifica,* while CP El Niño events typically result in a weaker response (Lilly and Ohman 2021). Another cool temperate species, *T. spinifera*, can become particularly sparse during EP El Niño events when the upwelling habitat collapses. *Thysanoessa spinifera* abundances are more variable during CP El Niño and can even rebound if upwelling persists (Lilly and Ohman 2021). The subtropical *N. simplex* exhibits a stronger response during EP compared to CP El Niño events, extending poleward in the nearshore during the former (Lilly and Ohman 2021). Off Baja Cal-



Polar

Stressor Response

	🌡	O₂	▤	🌿	⁘	⚠	🚢	🧊
Growth	🟥↘	ND	🟨?	🟥↘	ND	🟥↘	ND	🟦—
Respiration	🟥↗	🟨?	🟦—	🟥↘	ND	ND	ND	ND
Fecundity	🟥↘	ND	🟦—	🟥↘	🟥↘	🟥↘	ND	ND
Recruitment	🟥↘	ND	🟥↘	🟥↘	🟥↘	🟥↘	🟥↘	🟥↘
Mortality	ND	ND	🟥↗	ND	ND	🟥↗	🟥↗	ND
Body Size	🟦—	ND	🟦—	🟥↘	ND	ND	ND	🟥↘
Body Condition	🟥↘	🟥↘	🟦—	🟥↘	🟨?	🟨?	ND	ND
Abund / Biom	🟥↘	ND	🟥↘	🟥↘	🟥↘	ND	🟥↘	🟥↘

Stressors

🌡 Warming
O₂ Deoxygenation
▤ Ocean Acidification
🌿 Reduced Nutrition
⁘ Nano- & Microplastics
⚠ Toxins
🚢 Fisheries
🧊 Sea Ice Decline

Population Effect

🟥 Negative
🟨 Ambiguous
⬜ Unknown
🟩 Positive
🟦 No Effect

Response Direction

↗ Increase
↘ Decrease
? Unclear Trend
— No Trend
ND No Data

Temperate

Stressor Response

	🌡	O₂	▤	🌿	⁘	⚠	🚢
Growth	🟥↘	🟥↘	🟨?	🟥↘	ND	ND	ND
Respiration	🟥↗	🟥↘	🟥↘	ND	ND	ND	ND
Fecundity	🟥↘	ND	ND	🟥↘	ND	ND	ND
Recruitment	🟥↘	ND	🟥↘	ND	ND	ND	ND
Mortality	🟦—	🟥↗	🟥↗	ND	🟦—	ND	ND
Body Size	🟥↘	ND	🟦—	🟨?	ND	ND	ND
Body Condition	ND	ND	ND	ND	🟨?	ND	ND
Abund / Biom	🟨?	ND	ND	🟨?	ND	ND	🟨?

Tropical

Stressor Response

	🌡	O₂	▤	🌿	⁘	⚠
Growth	🟥↘	🟥↘	ND	🟥↘	ND	ND
Respiration	🟨?	🟨?	🟦—	🟦—	ND	ND
Fecundity	🟥↘	🟥↘	ND	🟥↘	ND	ND
Recruitment	ND	ND	ND	ND	ND	ND
Mortality	🟨?	🟨?	ND	ND	ND	ND
Body Size	🟥↘	ND	ND	🟥↘	ND	ND
Body Condition	ND	ND	ND	🟥↘	ND	ND
Abund / Biom	🟥↘	🟥↘	ND	🟥↘	ND	ND

Figure 2. Region-specific stressor–response matrices for euphausiids in tropical, temperate, and polar ecosystems. Each matrix summarizes observed or inferred responses of euphausiids to key environmental and anthropogenic stressors—warming, deoxygenation, ocean acidification, declining food quality and quantity, pollution, fisheries, and (for polar regions only) sea-ice loss. Responses are shown for eight biological or population-level metrics: growth, respiration, fecundity, recruitment, mortality, body size, body condition, and abundance/biomass. Icons indicate the direction of response, while box colors represent the overall consequence for population health. Fisheries targeting euphausiids are absent in tropical systems; thus, only the temperate and polar matrices include a fisheries column. References used to inform the matrices are provided in the Supplementary materials.

ifornia, *N. simplex* abundances increase during EP El Niños, but show the opposite during CP events (Parés-Escobar et al. 2018).

In the Southern Ocean, ENSO and the SAM are among the dominant large-scale climate modes affecting krill biogeography. In the SW Atlantic sector, positive SAM (warmer, windier conditions) resulted in a decrease in *E. superba* biomass and a southward contraction of their population centre (Atkinson et al. 2019). At the northern Antarctic Peninsula, La Niña (colder, more productive conditions) was associated with increased abundances of *E. superba* (Loeb and Santora 2015). By contrast, along the western Antarctic Peninsula, *E. superba* showed no directional long-term trend (Steinberg et al. 2015). Responses of *E. superba* to ENSO and SAM likely arise through their effects on sea ice, upper-ocean stratification or mixed-layer structure, and primary productivity, which together influence reproductive development and recruitment (Saba et al. 2014, Steinke et al. 2021, 2024, Atkinson et al. 2022) (Fig. 2). Responses of other Southern Ocean krill species are also variable, and appear to reflect differences in thermal tolerances, habitat affinity, and position along latitudinal gradients. At the northern Antarctic Peninsula, *Euphausia crystallorophias*, *Euphausia frigida*, and larval *Thysanoessa macrura* increased in abundance following a shift to more La Niña and Niño-neutral conditions, whereas the sub-Antarctic *Euphausia triacantha* tended to increase during warmer El Niño conditions (Loeb and Santora 2015). Along the western Antarctic Peninsula, *E. crystallorophias* was more abundant under higher-ice conditions and was best explained by SAM and MEI variability rather than by a simple long-term warming response (Steinberg et al. 2015).

The responses of krill to climate modes may also reflect cumulative integration of environmental variability over organismal life history. Di Lorenzo and Ohman (2013) showed that variability in the abundance of *N. simplex* was better explained by an integrated PDO signal than by the PDO itself, and referred to this as the Double Integration Hypothesis—a concept under which atmospheric variability is first integrated by the ocean and then by population dynamics over the species' lifespan. While double-integration explained variability in abundances of *N. simplex*, it could not explain patterns in abundance of *E. pacifica*, which exhibited a more direct, single-integration response. The double-integration framework has important implications for interpreting lags, apparent regime shifts, and climate-change signals in krill time series.

Effects on physiology

The additive effects of increased seawater temperatures with low pO_2 and elevated pCO_2 concentrations, in addition to pollution (including microplastics) and shifting food quality and quantity leads to a particularly stressful physiological challenge. The response of different krill species to the stressors brought on by human-induced climate change and other anthropogenic activities may be varied, but some general themes emerge and are outlined below (Fig. 2).

Impacts of warming, deoxygenation, and OA

As ectotherms, krill are susceptible to the effects of warming, and their metabolic rates increase as temperatures rise. For stenothermic species with a narrow thermal tolerance range, warming can have a significant impact on their physiology and vital rates. Higher metabolic rates correspond with greater dissolved oxygen consumption and energy expenditure and consequently energy demand (Portner 2010). Because warming is frequently associated with shifts toward smaller plankton (Campbell et al. 2021, Benedetti et al. 2021, Zhan et al. 2024), the quality and quantity of food available to krill is altered with implications for their growth and reproductive maturation (Bernard et al. 2022, Steinke et al. 2022) (Fig. 2). Sensitivity to temperature changes has been observed in krill moulting and growth (Lagos et al. 2022b, Iguchi and Ikeda 1995, 2005, Atkinson et al. 2006, Robertson and Bjorkstedt 2020, Saba et al. 2021 a), maturation (Brown et al. 2010), mortality (Saba et al. 2021), lipid content (Lagos et al. 2022a, Hellessey et al. 2020), and body size (Wiedenmann et al. 2008, Robertson and Bjorkstedt 2020, Killeen et al. 2022, Shaw and Fisher 2026) (Fig. 2).

Elevated metabolic rates require higher oxygen consumption and, in regions where deoxygenation is occurring or where an already-present OMZ is expanding, this may push species to alter their physiology and/or behavior. For example, during oxygen depletion, adult *E. superba* may form smaller or less dense swarms or adopt deeper positions below warmer surface layers to reduce short-term hypoxic exposure, adjustments that could negatively impact their feeding capability (Tremblay et al. 2024). Many species inhabiting naturally hypoxic systems have morphological, physiological, and metabolic adaptations to cope with their low-oxygen environment (Antezana 2002, Tremblay et al. 2010, 2020, Seibel 2011, Seibel et al. 2016, Tremblay and Abele 2016, Riquelme-Bugueño et al. 2020b). However, because tolerance to hypoxia is dependent on environmental conditions, increased temperature and reduced pH may lower hypoxia tolerance (Tremblay et al. 2010, Seibel et al. 2016, Parouffe et al. 2023). For instance, some krill that are adapted to moving in and out of OMZs, often on a diel basis, do so by suppressing their aerobic metabolism by >50% and maintaining low critical oxygen partial pressures (P_{crit}—the minimum partial pressure of oxygen at which a particular organism can maintain its standard metabolic rate) (Seibel et al. 2016). But the metabolic stress associated with ocean warming and acidification is predicted to raise P_{crit} levels, potentially reducing hypoxia tolerance (Seibel et al. 2016).

Studies examining the effects of OA on krill are still rare compared to other taxonomic groups and focus only on a few krill species, often with contradictory results making interpretation of the findings ambiguous (Fig. 2). For instance, short-term exposure to elevated $p\text{CO}_2$ (670 μatm) increased feeding and nutrient excretion rates of adult *E. superba*, likely due to increased metabolism associated with internal acid-base regulation (Saba et al. 2012), but sub-adults of *Nyctiphanes couchii* in the North Atlantic and adults of *T. inermis* in the Arctic showed no significant effects of increasing $p\text{CO}_2$ on various biological response variables (including survival, moulting, growth, and respiration), though mortality increased significantly at 1700 μatm (Sperfeld et al. 2014, Venello et al. 2018, Opstad et al. 2018). In *E. superba*, embryonic development was sensitive to increased $p\text{CO}_2$ levels (1000–2000 μatm) due to the inability of embryos to regulate intracellular acid-base balance (Kawaguchi et al. 2013). For *E. pacifica*, embryonic development was not affected at reduced pH, but larval survival was impaired (20% reduction in survival rates) at pH levels (7.69) currently observed in Puget Sound suggesting the species is already living near the limits of its pH tolerance (McLaskey et al. 2016). No effects on the behavior of adult *E. superba* were observed under high $p\text{CO}_2$ conditions (Yang et al. 2018).

The compound effects of OA with warming and/or deoxygenation can further disrupt physiological processes in krill, complicating their response to these environmental stressors. A long-term experimental study found that feeding rates in *E. superba* were reduced at higher temperatures (3°C) and lower pH (7.7) compared to ambient conditions, and that survival rates decreased significantly under these combined stressors (Saba et al. 2021). *Euphausia pacifica* regularly experiences a wide range in $p\text{CO}_2$ levels during DVM in the North Pacific (McElhany and Shallin Busch 2013) but showed decreasing respiratory potential and metabolic suppression in low oxygen and high $p\text{CO}_2$ waters (Cooper et al. 2016, McLaskey and Keister 2021). In contrast, *E. eximia*, which undergoes DVM in another low-oxygen environment, the Humboldt Current, showed resilience to low oxygen and high $p\text{CO}_2$ conditions (Riquelme-Bugueño et al. 2020b).

Impacts of other anthropogenic stressors

Krill have been observed ingesting microplastic in laboratory settings (Desforges et al. 2014, Dawson et al. 2018, Valdez-Cibrián et al. 2024) and microplastics have been seen in the digestive tract of krill collected in their natural environment (Wilkie Johnston et al. 2023, Primpke et al. 2024), with impacts on their physiology and behavior (Fig. 2), as well as on their role in biogeochemical cycles (Bergami et al. 2020, Rowlands et al. 2023, Manno et al. 2024). Further, oxidative stress caused by nanoplastics may negatively impact immune responses and could trigger cellular defence mechanisms in krill (Rowlands et al. 2021b). Interestingly, laboratory evidence suggests that krill may actively discard larger microplastic particles in food boluses (Butterley et al. 2025), potentially reducing ingestion but also altering particle processing and organic matter export. Other anthropogenic stressors include seismic air-gun surveys for petroleum resources, which have been shown to kill larval krill with intense, low-frequency acoustic impulse signals (McCauley et al. 2017). Toxic heavy metals have also been observed in krill (Yamamoto et al. 1987, Rainbow 1989, Bocher et al. 2003, Korejwo et al. 2023), likely with physiological impacts, the extent of which is not yet clear.

Effects on life history

Human-induced climate change and other anthropogenic stressors can disrupt life history patterns and population dynamics of krill. For instance, krill may respond to the elevated metabolic costs associated with warming by evolving shorter life spans and smaller body sizes (Gómez-Gutiérrez et al. 2012, Atkinson et al. 2019, Robertson and Bjorkstedt 2020, Lagos et al. 2021, Killeen et al. 2022, Shaw and Fisher 2026) (Fig. 2). Ocean warming, deoxygenation, acidification, and exposure to nanoplastics may also disproportionately affect early life stages of krill, reducing recruitment to the population (Kawaguchi et al. 2013, Meyer et al. 2017, Rowlands et al. 2021a, b) (Fig. 2). For example, in the Humboldt Current System, larval krill abundances were lower during El Niño compared to La Niña conditions (Aronés et al. 2019, Díaz-Astudillo et al. 2022b). The decrease in abundance of krill in the California Current System during anomalously warm years was likely the result of lower spring recruitment and adult survival throughout the year due, in part, to increased metabolic requirements and decreased food availability (Marinovic et al. 2002). Reduced food availability in response to warming has an adverse effect on early life stages in high latitude regions too, where changes in the timing of the spring phytoplankton bloom may result in a temporal mismatch between krill larvae and their phytoplankton food (Silva et al. 2014).

Krill fisheries

Commercial exploitation of krill began in the 1970s, spurred by projections that global catches could reach 50–100 million tonnes annually for human consumption (Gulland 1972, Sprague and Arnold 1972). In practice, present-day catches remain far lower, marginally over 0.5 million tonnes per year and dominated by the Southern Ocean fishery for *E. superba* (~0.5 Mt), alongside smaller fisheries targeting *E. pacifica* in Japanese (~20 000 t) and Canadian (<250 t) waters (Fisheries and Oceans Canada 2022, Wakamatsu et al. 2022, CCAMLR 2024) (Fig. 2). These harvests represent only a small fraction of total stock biomass—less than 1% in the case of *E. superba* (Hill et al. 2020)—yet the growing demand for fishmeal and omega-3 supplements has driven substantial corporate investment, with companies collectively spending hundreds of millions of dollars on modern krill-fishing fleets (Cappell et al. 2022). Exploratory harvesting has also been considered in other regions, including the Icelandic Sea (Gíslason et al. 2021, Sigurðardóttir and Gíslason 2021). Krill populations are naturally variable in abundance and distribution, influencing both fishery yields and prey availability for predators (Wakamatsu et al. 2022). In the North Pacific, *E. pacifica* fisheries compete with major krill-feeding fish such as Pacific cod and Alaska pollock, whose annual krill consumption equals 15%–64% of the commercial catch (Yamamura et al. 1998).

In the Southern Ocean, *E. superba* supports the world's largest krill fishery, managed under the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Current catch limits theoretically allow a 22-fold increase in legal harvest (Nicol and Foster 2016), although quotas have remained unchanged for more than a decade. Recent studies highlight the tension between industrial expansion and ecosystem needs: catch concentrations around the Antarctic Peninsula are intensifying local depletion and predator competition (Freer et al. 2025, Trathan et al. 2025). Meyer et al. (2025) propose a "krill-stock hypothesis" framework that integrates climate variability, spatial connectivity, and recruitment dynamics into adaptive management. Together, these findings indicate that, as commercial demand for krill products continues to grow, governance reforms and more spatially responsive regulation will be essential to sustain both the fishery and the broader Southern Ocean ecosystem.

Interactions with pathogens and parasites

Impacts of pathogens and parasites on krill individuals can range from mild to severe including sluggish, erratic swimming, loss of body transparency, black spots on exoskeleton, slow or desynchronized heartbeat, opaque and/or nonfunctional chromatophores, abnormal digestive gland and intestinal function prolonged fasting, malnutrition, weight loss, irregular growth and moulting, impairment in reproduction, castration, or death (Gómez-Gutiérrez 2003, Gómez-Gutiérrez and Morales-Ávila 2016, Gómez-Gutiérrez et al. 2017, Cleary et al. 2024, 2025). Krill may also serve as intermediate hosts, transmitting parasites on to vertebrate predators (Hays et al. 1998, Cleary et al. 2019, Flores-Cascante et al. 2019). Little is currently known on how infections impact the susceptibility of krill to external stressors, nor on the impact of external stressors on susceptibility of krill to pathogens and parasites. Some linkages would appear mechanistically likely. For example, the common krill protistan parasites Gregarines (Apicomplexa) infest gut tissue and reduce digestion efficiency; related gregarine parasites in insects increase susceptibility to negative impacts of food limitation, which may also occur in krill, though this phenomenon is not yet documented (Takahashi et al. 2011, Randall et al. 2013). Some have speculated that the euphausiid trait of continuous moulting throughout the life-cycle, which is unusual in crustaceans, may be an adaptation to reduce parasitic infections (Tarling and Cuzin-Roudy 2008). It has been suggested that pathogenic and parasitic organisms globally may have larger impacts on host individuals and populations in a warmer world because smaller organisms typically respond metabolically more rapidly to increases in temperature (Byers 2021). But shifting distributions of both krill and parasites, as well as their intertwined coevolutionary histories and thermal niches makes this difficult to predict (Studer et al. 2010, Danovaro et al. 2011).

Knowledge gaps

Due to the challenges with studying krill, there are numerous gaps in our knowledge about this group, globally. We conducted a Delphi-style assessment among the coauthors to gain consensus on the top five gaps in our knowledge on krill (Fig. 3; see the Supplementary material for details on this assessment approach). In addition, we have identified understudied species, regions, and habitats.

Top five knowledge gaps

The role of krill in controlling trophic dynamics and affecting the stability of marine food webs

The term *wasp-waist* has been used to define ecosystems where a single mid-trophic level species exerts top-down control on lower trophic levels and bottom-up control on higher trophic levels (Curry et al. 2000, Atkinson et al. 2014). This attribute has been ascribed to *E. superba* in the Southern Ocean, and it implies that the removal of the species would have severe consequences for all levels of the food web, potentially disrupting its stability. Given the

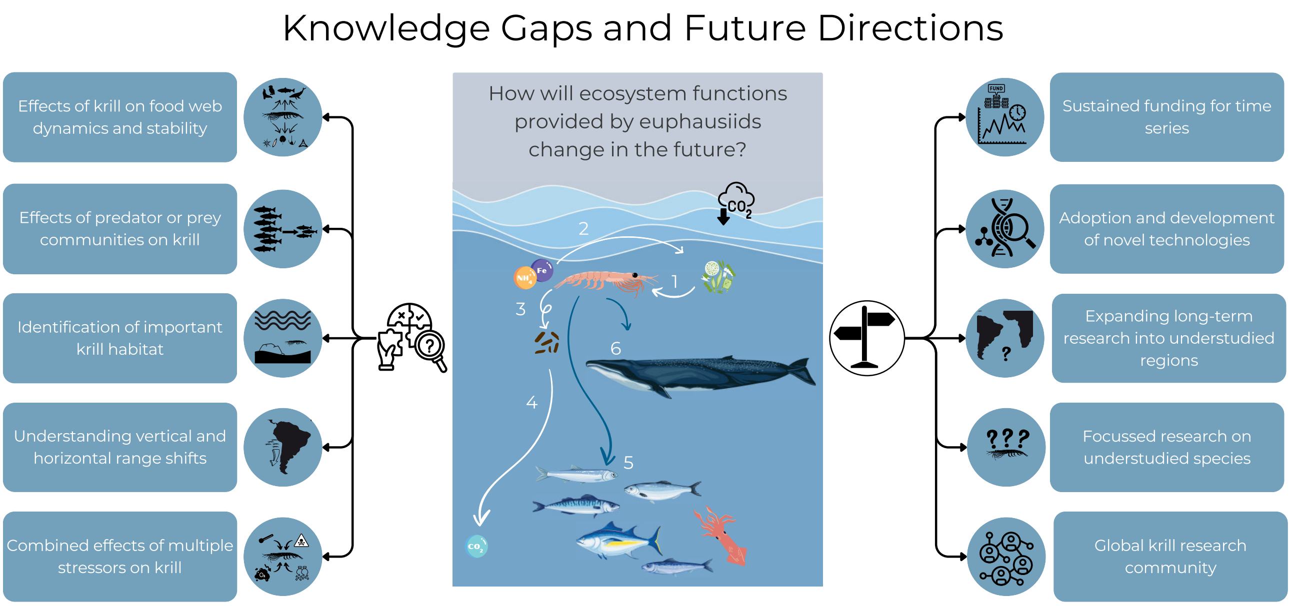


Figure 3. Knowledge gaps and future directions for understanding euphausiid ecology and ecosystem roles. Central panel illustrates key ecosystem functions mediated by krill, including nutrient recycling (1), grazing and carbon export (2–4), and their role as prey for fish and megafauna (5–6). Surrounding panels summarize priority research needs. On the left, major knowledge gaps, on the right, strategic actions needed to address these gaps.

role of other krill species as critical consumers and prey in other regions of the global ocean, there is potential for krill in other regions to play similarly crucial roles in their respective ecosystems, influencing both primary productivity and predator populations. Consequently, shifts in krill populations due to environmental changes or exploitation could destabilize these ecosystems, underscoring the need for region-specific studies on their ecological functions and vulnerabilities.

Impacts of changing food webs on global krill

Surface ocean stratification has increased globally due to rising temperature, preventing vertical mixing and the resupply of nutrients from deeper water (Li et al. 2020). Such conditions favor smaller phytoplankton taxa that lack essential polyunsaturated fatty acids (Marañón 2009, Schmidt et al. 2020, 2024) and thereby reduce the efficiency of trophic transfer from primary producers to zooplankton consumers, including krill (Atkinson et al. 2024). Simultaneously, the recovery of marine megafauna, including fur seals, humpback and fin whales (Baines et al. 2021, Forcada et al. 2023), from human exploitation has led to an increase in predation on krill. Additionally, anthropogenic activities such as overfishing and eutrophication have resulted in localized increases in gelatinous zooplankton (Richardson et al. 2009, Brodeur et al. 2018), with increased predation on krill larvae (Suchman et al. 2008) and the potential to outcompete krill for food resources (Bernard et al. 2012, O'Loughlin et al. 2020). Understanding the ramifications of food web shifts on krill is essential for predicting future krill population changes.

Identification of key habitats for global krill

Krill exist in a highly advective environment and their capacity to control their spatial distribution continuously develops over their life cycle. Consequently, krill occupy a range of marine habitats that may vary by life stage or behavior. This means that hotspots for spawning or aggregations of early developmental stages can often be considerably displaced from those of the adults (Perry et al. 2019). For most krill species, we do not know which habitats are vital at which stages. For instance, while we know that sea ice is important for the winter survival of larval and juvenile *E. superba* in Antarctica (Meyer 2012, Meyer et al. 2017, Bernard et al. 2018), we do not know if this is true for other polar krill. Spawning and recruitment locations are unknown for almost all krill species, yet this information is critical to understand population dynamics and predict population fluctuations, which will in turn inform marine food web and biogeochemical models, fisheries management, and conservation efforts. Different life-stages may be exposed to contrasting environments and rates of change. Identifying which krill life cycle stages are most vulnerable is a fundamental requirement in krill ecology.

Habitat compression and distribution shifts in response to climate change

Ocean warming and expanding OMZs impose major stresses on krill, and their response in terms of distributional shifts was identified as a major knowledge gap. Studies of krill and other plankton species have shown that ranges cannot simply be predicted from water temperature alone, with highly nonlinear and sometimes counter-intuitive distribution shifts observed (Chivers et al. 2017, Edwards et al. 2021, Atkinson et al. 2022). Likewise, expansion of the horizontal and vertical extent of OMZs may compress the vertical habitat (Fernández-Álamo and Färber-Lorda 2006, Färber-Lorda and Färber-Data 2023) with species showing variable responses in terms of acclimation and adaptation. Understanding the mechanisms behind these redistributions is crucial for distinguishing long-term distribution shifts from short-term population responses to climatic drivers like ENSO or SAM or extreme events like MHWs.

Response of krill to multiple human-induced stressors

Exposure of krill to multiple human-induced stressors may adversely impact their robustness to environmental change, as combined stressors can lower biological thresholds (Hunter et al. 2024). For example, simultaneous exposure to OA and nanoplastics reduces krill larval development more than the exposure to each stressor individually (Rowlands et al. 2021a). Studying single drivers can therefore produce misleading conclusions about individual or population responses to multiple stressors (Bopp et al. 2013), which can vary by region, habitat, species, and life stage (Hobday and Lough 2011). Recent studies increasingly use multifactorial designs to address this complexity (Saba et al. 2021, Rowlands et al. 2021b). However, interactions between stressors—whether additive, synergistic, or antagonistic—make it difficult to extrapolate from single-stressor responses, often producing conflicting results (Riebesell and Gattuso 2015). Addressing this complexity demands interdisciplinary work involving modeling, empirical, and experimental efforts.

Understudied species, regions, and habitats

A review of Web of Science searches (conducted on 10 November 2025) for each of the Euphausiacea species revealed that the number of publications per year on krill has increased over time since 1965, dominated almost entirely by research on polar krill species (Fig. 4A). Since 1965, there have been nearly 4000 publications on polar krill species, ~1000 on temperate species, and <500 on tropical species. The number of publications on polar krill have increased at a rate of ~2.4 per year, compared to 0.5 per year for temperate krill and 0.05 per year for tropical species. Research on polar krill thus far exceeds both the total number of publications and the rate of increase in publication numbers for either temperate or tropical species (Fig. 4A).

Of the 87 known species, research and the scientific literature focus predominantly on the Antarctic krill, *E. superba* (2708 publication counts since 1965, Fig. 4A and B). Species for which at least 100 articles have been published include *M. norvegica* (592 counts), *E. pacifica* (379 counts), *T. inermis* (240 counts), *T. raschii* (137 counts), *E. crystallorophias* (134 counts), and *T. macrura* (127 counts). *Euphausia superba* and *E. pacifica* are both the focus of fisheries, and *E. pacifica, M. norvegica*, *T. inermis*, and *T. raschii* are major prey items of commercially fished species in their respective regions. *Euphausia crystallorophias* and *T. macrura* are relatively abundant in the Southern Ocean, where substantial research effort on krill has focused. These seven species occur primarily in northern hemisphere temperate-polar waters, or in the Southern Ocean (Fig. 4C). Notably, none of these species occur in the tropical ocean or in the temperate southern hemisphere.

Fish consumption in the global south is an important source of nutrition (Allegretti and Hicks 2023, Maulu et al. 2024). Commercially important and subsistence fish in those regions depend on krill species that we currently lack even the basic biological information on. For instance, *E. eximia* (23 publication counts) and *E. mucronata* (37 counts) in the Humboldt Current off the coasts of Chile and Peru, *Nyctiphanes capensis* (25 counts) and *Euphausia lucens* (71 counts) in the Benguela Current off the west coast of South Africa and Namibia, and *N. australis* (78 counts) in the Tasman Sea and waters off New Zealand all are vital prey for commercially fished species.

Of the 11 genera of Euphausiacea, the *Euphausia* genus has received by far the most attention, roughly five times the publication counts than the next most mentioned genus, *Thysanoessa*, and two orders of magnitude more than the least mentioned genera: *Nematobrachion*, *Bentheuphausia*, and *Tessarabrachion* (Fig. 4D). Species in these latter genera occur predominantly in the meso- and bathypelagic realms, which are severely understudied krill habitat (Fig. 4E). The role of meso- and bathypelagic krill in carbon sequestration and open-ocean fisheries is likely immense (Irigoien et al. 2014, Siegel et al. 2023, Burd 2024), but inadequately quantified. Another krill habitat that remains poorly studied is the sea floor (Fig. 4E). Anthropogenic activities on the sea floor (dredging, mining, benthic trawling, and drilling) may negatively impact krill populations that rely on this habitat, but at present we do not know how important sea floor interactions are for krill. In the polar regions, sea ice is also an important habitat for some krill species (Fig. 4E), but global warming is reducing this habitat and the consequences of this to polar krill species have not yet been fully resolved.

Future directions

To better anticipate future changes in ecosystem functions provided by krill that influence the health and resilience of our oceans (e.g. food to higher trophic levels, carbon sequestration, and biogeochemical cycling), research aimed at addressing the top five knowledge gaps and increasing the representation of understudied species, regions, and habitats is critical (Fig. 3). This includes improved long-term monitoring, implementing the use of new technologies, enhanced global networking, and expanding research on understudied regions and species.

Improved long-term monitoring of global krill abundances, species composition, and distribution patterns

Long-term monitoring is critical to understand the response of marine ecosystems to a changing climate but faces a wide range of challenges (Benway et al. 2019). These include the need to maintain sufficiently long time series for statistical power to reveal climate change responses, the fact that most research funding is shorter term (1–5 years), that traditional ship-based sampling is suffering funding cuts worldwide (Mackas and Beaugrand 2010, Mackas et al. 2012, Vucetich et al. 2020, Ratnarajah et al. 2023), and that taxonomic expertise requires training and is a skill that develops over years. Notwithstanding these challenges, a few ocean-basin scale surveys are on-going, a notable example being the CPR survey. However, most long-term surveys are at regional scales, run by national monitoring programs that recognize the importance of krill in commercially exploited food webs. Good examples include work in the California Current (Lilly and Ohman 2021, Phillips et al. 2022, Dorman et al. 2023), off Iceland (Silva et al. 2014), and the Peru–Chile upwelling (Díaz-Astudillo et al. 2022a). Long-term monitoring of krill could be expanded (both temporally and regionally) by employing nontraditional survey platforms such as ships of opportunity (as is often used by the CPR program) and krill fishing vessels (Meyer et al. 2020).

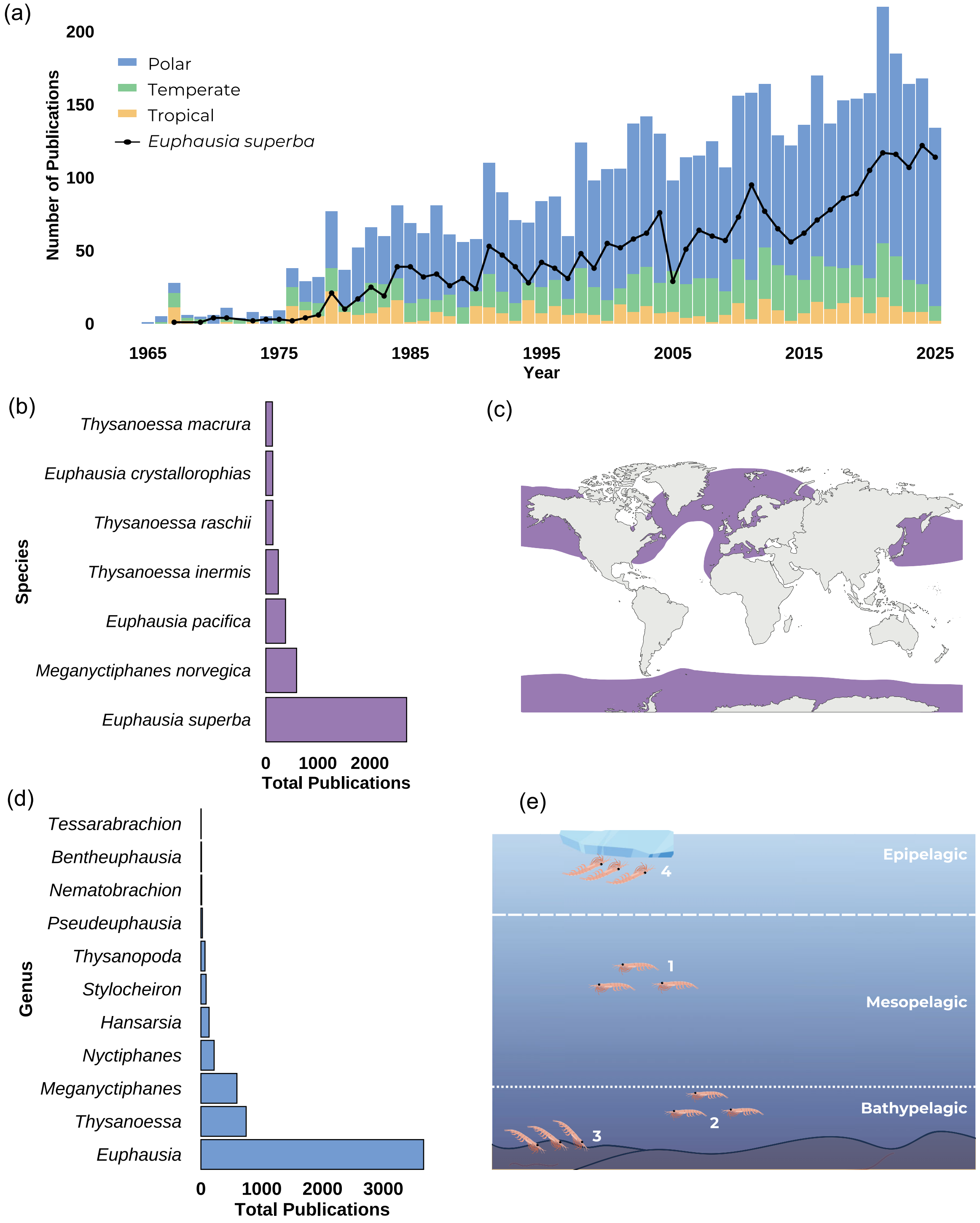


Figure 4. Global research effort and distribution patterns for euphausiids (krill) based on a Web of Science survey conducted on 10 November 2025. (A) Annual number of krill-related publications from 1965 to 2025, categorized by habitat domain (Polar, Temperate, and Tropical), with the black line showing annual number of publications for *Euphausia superba*. (B) Total publications for the seven most frequently studied (at least 100 publications) euphausiid species. (C) Geographic ranges of those seven species (*E. superba*, *E. crystallorophias*, *T. macrura* in Antarctica, *M. norvegica* in the North Atlantic, and *E. pacifica*, *T. inermis*, and *T. raschii* in the North Pacific) illustrating the uneven global coverage of euphausiid research, with most effort concentrated in high-latitude and North Atlantic–North Pacific systems. (D) Total publications by genus, highlighting the taxonomic bias toward *Euphausia* and *Thysanoessa*. (E) Conceptual schematic showing major euphausiid habitats where research remains limited: (1) mesopelagic, (2) bathypelagic, (3) seafloor, and (4) under-ice environments.

Most long-term surveys are not explicitly designed for the collection of postlarval krill, although exceptions do exist (e.g. surveys for *E. superba* in the Southern Ocean), and frequently use nets that are designed to more effectively capture smaller zooplankton, like copepods. Postlarval krill are notorious for their net avoidance capabilities (Wiebe et al. 1982, 2004) and it is likely that larger individuals are significantly underrepresented in catches made with smaller nets, such as the Bongo or WP2 nets used in many zooplankton surveys. Many, though not all, long-term surveys include active acoustics, which allows for the detection of krill swarms within the water column (e.g. Reiss et al. 2008, Fielding et al. 2014, Santora et al. 2018). However, estimates of krill biomass from acoustic backscatter data rely on accurate krill length–frequency data, which can often be skewed by the net collection method chosen (large individuals avoid the nets typically used in these surveys). Efforts should be made to improve long-term monitoring capabilities by (i) adding larger nets that are more effective at collecting post-larval krill (e.g. Multiple Opening–Closing Net and Environmental Sensing System—MOCNESS; Isaacs-Kidd Midwater Trawls—IKMT; Rectangular Midwater Trawls (RMT); Tucker Trawls), (ii) consistently including simultaneous multi-frequency acoustic surveys for krill, (iii) expanding geographic coverage into poorly studied regions, (iv) sustaining long-term monitoring programs into the future, and (v) incorporating research specifically on eggs and larval stages of krill.

Implementation of new technologies

The relatively large size and aggregation behavior of krill make them a useful model organism for developing new observation and analytical techniques (Hill et al. 2024). Developments in tethered and autonomous underwater vehicles provide unique opportunities to observe krill behavior *in situ*. These vehicles can incorporate low power, miniature acoustic- and optical-based instruments that can collect data showing how krill interact within aggregations and respond to predators and prey (Ainley et al. 2015, 2020, Benoit-Bird et al. 2018, Ohman et al. 2019, Reiss et al. 2021). From above, low-flying aircraft, aerial drones, and satellites have the potential to visualize krill surface swarms through high-resolution photography and onboard hyperspectral image detectors. The red pigment astaxanthin, present in many krill species, is perceptible by these detectors (Basedow et al. 2019, Belcher et al. 2021). Satellites may often be cloud-obscured but lower altitude long-range aircraft and aerial drones can overcome this. Through this collection of novel autonomous approaches, researchers have already observed and quantified swimming, feeding, and reproductive behaviors in krill (Gutt and Siegel 1994, Kawaguchi et al. 2011, Kubilius et al. 2015, Kane et al. 2018, 2021, Zabroda et al. 2020, Bernard et al., unpublished work).

Molecular techniques can provide insights into present day distributions, historical connectivity levels and population size variance (Dong et al. 2019, Choquet et al. 2023, Bucklin et al. 2023). They can also indicate trophic interactions and symbiotic relationships (Cleary et al. 2018, 2019, Clarke et al. 2021, Carreiro et al. 2023). Information on physiological function and seasonal adaptation has further been resolved by studying genetic expression patterns (Meyer et al. 2015, Höring et al. 2021). The recent publication of the *E. superba* genome (Shao et al. 2023) is a powerful tool with which to develop this work further. While these new technologies offer exciting potential, physical sampling with nets will likely always be required to improve the existing time series' statistical power, understand recruitment and the early life cycle, verify acoustic targets, and provide material for experimentation or biochemical analyses.

Expanding research on understudied regions and species

Krill research has been particularly unbalanced, both in terms of the regions in which most investigations have been carried out and in the limited number of species studied. This has meant that only a handful of species have been relatively well-studied in limited geographic areas (Fig. 4C). In fact, this issue extends beyond just krill to zooplankton in general (Ratnarajah et al. 2023). The response of individual krill species to climate change and other anthropogenic stressors can only be fully understood by also considering that of the wider krill species community. Consequently, even in regions where certain krill species have been relatively well-studied, we lack a nuanced understanding of community-level changes. Larger scale studies, both in the horizontal and vertical realm, are needed to set baselines for the present state of krill community structure. This will not only provide a means of detecting future change but also greater insight into the functional role of krill within pelagic and benthic ecosystems and how that might change in the future.

Progress can be accelerated through applying advances made on well-studied krill species to lesser studied ones. For instance, regular moulting is a key krill trait utilized to study growth, swimming capacity, and behavior of *E. superba* (Buchholz 1985, Quetin et al. 2003, Johnson and Tarling 2008), which can be equally applied in other species. Approaches to understand the impacts of heatwaves on *E. pacifica* can be used more widely to other krill species (Killeen et al. 2022). Research on krill that form aggregations can adapt multifrequency acoustics protocols originally developed for *E. superba* (Brierley et al. 1998, Chu and Wiebe 2005). The broadening of research approaches across a wider spectrum of krill species can be facilitated by improved global networking within the krill research community.

Improved global networking within the krill research community

With great pressure on the funding of new fieldwork, cost-effective progress can be made through maximizing the use of existing resources. This has several facets at the levels of the field sampling, the data produced, and among the scientists themselves. Dedicated scientific fora, for example the Global Ocean Observing System Biology and Ecosystem Panel (Miloslavich et al. 2018, Bax et al. 2019, Satterthwaite et al. 2021), the ICES working Group on Zooplankton Ecology across the north Atlantic (ICES, 2023), and the SCAR Krill Expert Group in the Southern Ocean (Meyer et al. 2020, Hill et al. 2024, Kawaguchi et al. 2024), provide a link between science and policy and enable networking, information sharing, capacity building, and exchange opportunities that are especially valuable for early career scientists. Such initiatives can be expanded to include better integration and communication with the modeling community, improved harmonization of sampling and experimental methods, and the development of affordable technologies and experimental protocols that can be implemented in resource-limited settings. This would improve the geographic coverage of research and promote more equitable participation in global scientific efforts.

Another major benefit of such fora is that they facilitate the process of joining various time series together to form networks (O'Brien 2017, Benson et al. 2021, Van de Putte et al. 2021). Large amounts of data are not yet publicly available or in a user-friendly format for researchers to analyse, and large scale initiatives such as the Ocean Biodiversity Information System and the Global Biodiversity Information Facility (Van de Putte et al. 2021), as well as the zooplankton-specific KRILLBASE (Atkinson et al. 2017) and COPEPOD (COPEPOD—the global plankton database project) compile databases and make them more easily available following FAIR (Findable, Accessible, Interoperable, and Reusable) data sharing principles (Wilkinson et al. 2016). This improved networking is essential to provide both spatial and temporal coverage that is necessary to answer some of the key questions that we identified in our gap analysis.

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Supplementary data

Supplementary material is available at *ICES Journal of Marine Science* online.

Conflict of interest

The authors have no conflict of interest to declare.

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Data availability

No new data were generated or analysed.

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