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Climate Change increases the risk of metal toxicity in Arctic zooplankton

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This mini-review outlines major climate-change exacerbated sources of metal to the Arctic marine environment, leading to measured concentrations sometimes exceeding levels considered environmentally safe, and thus potentially impacting arctic marine zooplankton. We review the bioavailability of metals in Arctic marine environments and the current state of knowledge on metal toxicity in marine copepods. Toxicity response mechanisms to metals included oxidative stress as well as genetic processes of DNA damage and repair. We highlight species-specific differences in metal impacts within the diverse group of planktonic copepods. We summarize observed responses at multiple levels of biological organization, and note that studies on arctic species are scarce and need expansion, as results from temperate and tropical species may not be readily transferable to arctic counterparts. We further provide an updated view on impacts of metals in combination with other stressors in the Arctic marine system in light of increasing attention to multiple stressors of climate change and pollution. For arctic marine zooplankton, a number of research gaps are identified, including a need for integrating effects responses across levels of biological organization, for studies into mechanisms of heritable changes and long-term transgenerational impacts, and considering interspecific capacity for response and adaptation.

KEYWORDS

Calanus, Acartia longiremis, genotoxicity, temperature increase, LC_{50} , multistress, metals

Introduction

The Arctic is strongly affected by global warming, resulting in altered environmental processes both on land and at sea that affect marine ecosystems and communities. Rising temperatures can impact the dynamics of metals in the arctic region, with subsequent consequences of their elevated availability for marine species. Metal transport rates to arctic coastal waters via riverine runoff are intensified by thawing permafrost, coastal erosion, and melting glaciers, while local human activities and long-range transport from distant

anthropogenic sources add to these inputs. Metals can surpass environmental quality standards and toxicity levels under changing physical environments (e.g. warming), and some are toxic even at low concentrations (e.g. mercury, lead), posing risks for environmental and human health (Elnabi et al., 2023). Estimates of toxicity are largely based on studies of species with boreal, temperate, or tropical distributions, while examples from polar regions are scarce. Additionally, there is the need to integrate the knowledge on effects across different stressors and contaminants, providing a multi-stressor assessment of risk in exposed communities (Dinh et al., 2023; Orr et al., 2024).

Zooplankton are a diverse functional group of marine invertebrates exposed to multiple terrestrial contamination sources as well as large scale changing water conditions in the Arctic. Here, we summarize current knowledge on availability of metals for arctic marine zooplankton, examine species-specific metal toxicity in selected planktonic species, and summarize known ecological, physiological, and genetic responses of zooplankton to metal contamination. In addition, we examine the state of knowledge on their capacity to cope with additional stressors, such as climate change-related elevated temperature and ocean acidification, and chemical pollution, to highlight important knowledge gaps for combined and interactive effects of metal toxicity in a multiple stress context.

Metal sources to Arctic coastal marine systems

Metals occur naturally in the arctic environment as constituents of weathering bedrock, rock eroded by glaciers, tundra soil, and riverine runoff to coastal waters and marine sediments (Lu et al., 2013; Zaborska et al., 2017). Background levels of metals can be supplemented with metals transported by e.g. volcanic eruptions (Edmonds et al., 2022), and human activities can also add to the metal inventory, resulting in local variations in sediment and water concentrations. Metals from anthropogenic sources enter the Arctic Ocean from all around the Arctic, including Baffin Island (Zdanowicz et al., 2013), Greenland (Søndergaard et al., 2015), Svalbard (Zaborska, 2017; Zaborska et al., 2017, 2020), Alaska (Schuster et al., 2018; Perryman et al., 2020), and Siberia (Lim et al., 2020). Metals reach the Arctic marine environment through either autochthonous sources (locally derived) or allochthonous sources (long range transport pathways) (Figure 1). Climateimpacted changes in transport pathways include increased rates of permafrost thawing and coastal erosion (Kim et al., 2020; Nicu et al., 2021), glacial melt (Zaborska et al., 2017), and increased industrial and human activity (mining, aquaculture, shipping, tourism) enabled by retreating seasonal sea ice (Lasserre and Faury, 2019; Brockington, 2020; Emenike et al., 2022) (Figure 1).



FIGURE 1

Major sources of metals to the Arctic marine ecosystem. White arrows depict movement through the environmental compartments. Created with BioRender.com.

Bioavailability of metals in arctic marine environments

Combined understanding of metal concentrations, availability, and toxicity is required to assess overall environmental risk. The degree to which metals present in the environment are available for interactions with organisms, i.e. their bioavailability, depends on their accessibility, lability, chemical activity, and metal absorption, uptake, and regulation mechanisms of organisms (Grotti et al., 2013). In water, free metal ions exist in equilibrium with metal ions complexed with inorganic or organic ligands, such as carbonate, chloride, humic and fulvic acids, and chelators, or adsorbed on particulates (Sigg and Xue, 1994). Metal concentrations are classified according to environmental quality standards and thresholds set by national and international organisations (e.g. the European Union through their Environmental Quality Standards EQS and the United States Environmental Protection Agency USEPA). These are selected according to the level of risk to the environment and biota, with risk defined according to standardised metrics such as the median concentration eliciting a 50% mortality response (LC50), or the concentration eliciting no detected effects (NEC).

The form in which metals are present determines their bioavailability to biota and thus their toxicity. Dissolved metals are subject to currents and vertical oceanographic processes within the water column and are more readily bioavailable for uptake in pelagic species than metals bound in sediments (Hansson et al., 2020). A high ratio of water-dissolved to sediment-bound particulates indicates overall increased risk of negative impact on marine biota (Zaborska et al., 2017, 2020). Elevated dissolved metal concentrations above background levels have been reported from Arctic fjords, with multiple sediment measurements exceeding safe environmental thresholds in fjords in Svalbard (Grotti et al., 2013; Lu et al., 2013; Zaborska et al., 2017), the Beaufort Sea (Sweeney and Naidu, 1989; Trefry et al., 2013), the Chukchi Sea (Lu and Kang, 2018), the Bering Strait (Lu and Kang, 2018), and the Barents Sea (Zaborska et al., 2017). In Hornsund, Svalbard, reported dissolved cadmium and copper concentrations of up to 4.99 and 6.28 µg/L, respectively, surpass the US EPA maximum concentration for acute exposure; resident Svalbard marine biota are thus at risk of metal toxicity (Zaborska et al., 2020).

Metal toxicity in arctic marine zooplankton

Not all metals are toxic and some are essential, such as iron (essential in blood) and magnesium (chlorophyll) (Soetan et al., 2010). They can be toxic in high concentrations or when in a certain chemical form, e.g. as free ions, soluble compounds or organometallic molecules (George, 2018)), whilst others such as lead, cadmium, and mercury are harmful at all concentrations (Ansari et al., 2004). In seawater, most metals are complexed with organic ligands; organic matter interacts with metal molecules and the resulting complexes determine both bioavailability, uptake, and toxic effects on marine animals (Ansari et al., 2004). Toxicity of metals varies 3-4 orders of magnitude governed by seawater

residence times (Dong et al., 2015). The degree of toxicity varies both among metals and between species (Ansari et al., 2004), described through quantification of standardized LC_{50} 's to provide a basis for risk assessments across contaminant groups and impacted environments.

Zooplankton are a useful bioindicator group for understanding impacts of metals in marine systems (Battuello et al., 2016; Bat et al., 2016). A review of toxicity effects of metals on marine invertebrates (Chiarelli and Roccheri, 2014) suggests meroplanktonic sea urchin larvae are sensitive bioindicators, and zooplankton species diversity can change along gradients of types and concentrations of metals (Cardoso et al., 2013). Copepods are the most abundant and widely distributed zooplankton group, and published LC50 values for copepods exposed to metals are compiled in Table 1. LC₅₀ values for copepods can vary immensely depending on metal, species, and biogeography. The temperate copepod A. tonsa showed no significant change in mortality when exposed to copper but considerable reduction in reproductive rates (Bielmeyer et al., 2006). Data for arctic species are virtually absent, except for one study that included C. glacialis exposed to mercury, highlighting an urgent knowledge gap for Arctic taxa.

Toxicity response mechanisms to metals

How organisms respond to toxic exposure to metals can differ across species and metals, with differences according to the level of biological effects measured. Biological effects can be scaled by factors of time and concentration, and can be ordered according to the continuum from lethal to sublethal effects (Van Leeuwen, 1995), with high concentrations leading to mortality and lesser exposure conditions affecting lower levels of biological organisation such as reproduction, development, behaviour, physiology, molecular processes, and genetic integrity and regulation (Schuijt et al., 2021). In zooplankton, exposure to copper can lead to increased mortality (Dinh et al., 2021), reduced developmental rates (Kwok et al., 2008), maturation delays (Lode et al., 2018), and reduced clutch size and hatching success (Dinh et al., 2021). Egg (embryo) quality is lowered when exposed to high copper concentrations, caused by downregulation in the vitellogenin gene (Ki et al., 2009; Dinh et al., 2021), a primary yolk protein that is a vital nutrient for embryonic copepods (Lauritano et al., 2021). Some copepod females have been reported to abort their egg sacs when exposed to high concentrations of copper (Biandolino et al., 2018), which may exacerbate reproductive failure. Mercury has been shown to inactivate cellular enzymes in C. finmarchicus, with overexcitation of neurotoxicity receptors and uncoupling of oxidative phosphorylation (Tollefsen et al., 2017). Upregulation of genes from the GST family typically involved in general stress responses, detoxification, and defence against oxidative stress (Hayes et al., 2005) has been observed in many copepod species following acute sublethal metal exposure (Lee et al., 2008; Ki et al., 2009; Wang and Wang, 2009; Øverjordet et al., 2014; Farkas et al., 2020); however, the regulatory mechanism behind the induction of

Metal	Species	Distribution	T (°C)	LC ₅₀		Reference
				96 h	168 h	
Ag	Tigriopus brevicornis	Temperate	20	76.0		Barka et al., 2001
	Calanus finmarchicus	Boreal	10	147.0		Farkas et al., 2020
Cd	Eurytemora affinis M	Temperate	18	127.8		Zidour et al., 2019
	Eurytemora affinis F	Temperate	18	90.0		Zidour et al., 2019
	Tigriopus brevicornis	Temperate	20	47.9		Barka et al., 2001
	Oncaea curvata	Antarctic	0		901.0	Zamora et al., 2015
	Paralabidocera antarctica	Antarctic	0		237.0	Zamora et al., 2015
	Stephos longipes	Antarctic	0		1250.0	Zamora et al., 2015
Cu	Tigriopus japonicus	Tropical	25	1 024.0		Kwok and Leung, 2005
	Tigriopus japonicus	Tropical	4	20 000.0		Li et al., 2014
	Tigriopus japonicus	Tropical	15	9 300.0		Li et al., 2014
	Tigriopus japonicus	Tropical	25	2 500.0		Li et al., 2014
	Tigriopus japonicus	Tropical	32	243.0		Li et al., 2014
	Tigriopus japonicus	Tropical	38	1.1		Li et al., 2014
	Eurytemora affinis M	Temperate	18	25.0		Zidour et al., 2019
	Eurytemora affinis F	Temperate	18	38.0		Zidour et al., 2019
	Tigriopus brevicornis	Temperate	20	150.0		Barka et al., 2001
	Oncaea curvata	Antarctic	0		64.0	Zamora et al., 2015
	Paralabidocera antarctica	Antarctic	0		20.0	Zamora et al., 2015
	Stephos longipes	Antarctic	0		56.0	Zamora et al., 2015
Hg	Tigriopus brevicornis	Temperate	20	52.7		Barka et al., 2001
	Calanus finmarchicus	Boreal	10	34.0		Tollefsen et al., 2017
	Calanus finmarchicus	Boreal	10	41.6		Øverjordet et al., 2014
	Calanus glacialis	Arctic	2	35.3		Øverjordet et al., 2014
Ni	Tigriopus brevicornis	Temperate	20	206.9		Barka et al., 2001
	Eurytemora affinis M	Temperate	18	90.0		Zidour et al., 2019
	Eurytemora affinis F	Temperate	18	161.0		Zidour et al., 2019
Zn	Tigriopus brevicornis	Temperate	20	715.2		Barka et al., 2001

TABLE 1 Lethal concentrations (LC_{50} s) for marine copepods from various climates exposed to metals (μ g/L) for 4 (96 hours) or 7 days (168 hours) at a given temperature (T).

M and F indicate male or female.

GST in different copepod species is not well understood. Detoxification and stress response systems differ between species and organism groups; therefore, effects are the net result from a combination of toxic impact as well as response. Inclusion of mechanistic toxicity and response effects in experimental zooplankton studies could shed light on why extent and impacts of exposure can differ between species, metals, and exposure situations, as previously shown for sea urchin larvae (Reinardy and Bodnar, 2015).

Dissolved metals have been linked to structural damage of DNA, lipids, enzymes, and proteins through enhanced

intracellular production of reactive oxygen species (ROS), and resulting oxidative stress (e.g. Reinardy et al., 2013). Genome integrity is fundamental for maintaining cellular, physiological, and organismal functions, and genetic damage from exposure to environmental metal contaminants can disrupt all levels of biological functions (Reinardy and Bodnar, 2015). The mechanism by which individual effects link to longer-term population and even species-level impacts is through heritable changes in either the genome or epigenome: changes can be beneficial for adaptation or negative through inherited genome instability. DNA repair is the main mechanism to mitigate damaged DNA, and DNA repair pathways are largely conserved across a wide range of phyla, reflecting the fundamental importance of maintaining genome integrity (El-Bibany et al., 2014). Zooplankton are susceptible to DNA damage from genotoxic exposure (Halsband et al., 2021); however, studies on DNA repair in zooplankton are limited (Reinardy and Bodnar, 2015; Bailey et al., 2017; Park et al., 2023). This approach of comparative susceptibility and toxicity response is of importance when considering realistic, complex, and fluctuating changing environmental conditions and presence of contaminants, and should be further developed for ecologically essential zooplankton.

There is evidence for metal toxicity through oxidative stress response and genotoxicity in zooplankton. Copper can induce oxidative stress, antioxidant defence systems, and genotoxicity in copepods. Copper caused oxidative stress in harpacticoid T. japonicus indicated by significant upregulation of the catalase gene (Rhee et al., 2013) and reduced the body load of the antioxidant astaxanthin (Weaver et al., 2016). DNA damage, hypothesized through DNA cross-links, measured in C. finmarchicus and Acartia longiremis exposed to 20 µg/L copper was correlated with induction of oxidative stress genes and suggested that the mechanism of toxicity leading to mortality was a ROS-induced oxidative stress DNA damage response (Thomsen et al., in review¹). However, lethal responses in Temora longicornis, T. brevicornis, and Acartia tonsa exposed to 6 and 60 µg/L copper were not linked to detected DNA damage as measured by the DNA strand break comet assay (Sahlmann et al., 2019). The mechanisms of sublethal toxicity from copper, and the link to different forms and levels of DNA damage, are therefore still unclear. The arctic congener C. glacialis more rapidly induced transcription of GST when exposed to mercury compared with boreal C. finmarchicus, and the species differences likely do not lie in metabolic differences as both species were kept at their metabolic optimum (Øverjordet et al., 2014). This result would be in line with the hypothesis that toxicity should decrease from the tropics to the poles (Chapman and Riddle, 2005). Arctic copepods could be more resilient to metal contamination than their boreal and tropical counterparts, possibly due to rapid and effective initiation of antioxidant and stress response systems (Øverjordet et al., 2014). Energy reserves in the form of storage lipids are an important component of Arctic copepod survival (Falk-Petersen et al., 2009) and may play an alleviating role in metal toxicity. Phenotypic plasticity (Sasaki and Dam, 2021) and cellular and genetic stress response variability (Collins et al., 2023) may also underpin inter- and intra-specific variability in zooplankton stress responses, but are little studied in relation to metal contamination.

Multistressor metal toxicity

There is growing attention on combined stressor impacts driven by the need for more ecologically relevant toxicity scenarios which better match the stressor profiles in environments and ecosystems (Collins et al., 2023; Dinh et al., 2023; Orr et al., 2024). Metal toxicity can be altered depending on the trajectory of climate change, especially temperature and pH, and presence of other pollutants. The solubility of metals in water increases as temperature rises, enhancing their bioavailability (Banaee et al., 2024). Elevated temperatures can increase metal toxicity in marine zooplankton (Kwok and Leung, 2005; Bai and Wang, 2020) primarily due to higher rates of uptake, increased oxidative stress, and decreased rates of intracellular detoxification processes (Sokolova and Lannig, 2008; Dinh et al., 2020). Thermal tolerance ranges of species narrow with increasing latitude (Sasaki and Dam, 2021), and species inhabiting regions at the extreme ends of their thermal tolerance are more susceptible to metal toxicity (Heuschele et al., 2022). In the tropical copepod Pseudodiaptomus incisus, survival, reproduction, grazing habits, and body size were negatively affected by individual exposures to copper and elevated temperatures, and impacts were exacerbated when stressors were combined (Dinh et al., 2021). An additive interaction was also evident in a lower 96-h LC₅₀ for copper with increasing temperatures in T. japonicus (Li et al., 2014, Table 1). Elevated temperature increases energetic demands and inactivates cellular enzymes (Rhee et al., 2009) which might especially hold true for Arctic copepods not adapted to large variations in their thermal range. Additionally, increased tolerance against copper pollution has been observed in tropical copepods after entering a dormant phase under extremely low temperature conditions (Kwok and Leung, 2005; Li et al., 2014), possibly due to improved energy supplies at the start of dormancy (Raisuddin et al., 2007). Li et al. (2014) suggested that a dormant phase lessens copper toxicity as copepods accumulate less metals due to decreased metabolism. Thomsen et al. (in review)¹ observed higher DNA damage levels from copper under elevated temperature in C. finmarchicus compared with the smaller A. longiremis, possibly due to differences in energy demands for different body sizes and thermal regimes of the two species. How trade-offs in energy demands, thermal tolerance ranges, and subsequent altered capacity for mounting detoxification and response mechanisms impact arctic zooplankton undergoing diapause is not well understood especially in extreme Arctic winters (Dinh et al., 2023).

In addition to elevated temperatures, metal contamination will often be accompanied by other climate stressors (ocean acidification, altered salinity or oxygen profiles), toxic chemicals, or biological factors (predators, parasites, health status) which can alter the metal exposure effects. Presence of additional contaminants such as persistent organic pollutants, polycyclic aromatic hydrocarbons from oil contamination (Hansen et al., 2011), or leaching chemicals (anti-fouling agents, plastic litter additives), can combine for a complex 'cocktail' of stressors (Esbaugh et al., 2018). Combined stressors may not only have negative effects, but also contribute to increased resilience through seesaw effects, cross-tolerance, and memory effects (Zhou and Wang, 2023). Integration of positive and negative effects from multiple stressors may be assisted by modelling frameworks able to quantify synergies between the effects at ecosystem level (Bailey and van der Grient, 2020).

¹ Thomsen, N., Halsband, C., Hopland-Sperre, K., and Reinardy, H. C. Multi-stress effects of copper and elevated temperature in arctic calanoid copepods.

Transgenerational effect studies consider impacts on offspring from exposed parental generations. A combined copper and elevated temperature exposure of the tropical *Pseudodiaptomus annandalei* caused reduced parent survival and nauplii production, and increased metabolism indicated by higher faecal pellet production; additionally, females showed higher mortality than males with the suggestion that the higher food demands from reproduction fuelled higher metal intake (Dinh et al., 2020). A similar combination of metal and elevated temperature exposure of *P. incises* demonstrated negative fertility and fecundity, and reduced overall fitness in offspring, which suggests that exposure effects can cascade through multiple generations with possible long-term population and food web impacts (Dinh et al., 2021).

Research gaps

Polar species sensitivity

The duration of exposure to toxic metals might greatly affect interpretation of ecological and long-term impacts in the Arctic due to lower rates of metabolism and greater longevity in Arctic species. Contamination events with metal concentrations above legislation limits might not trigger effects in Arctic copepods as they might take longer to react due to their slower metabolism (Chapman and Riddle, 2005; Hansen et al., 2011; Zamora et al., 2015). Pulse exposure events have been investigated in temperate species (Bielmeyer et al., 2006; Hook and Fisher, 2001) but similar studies are missing for polar species. Standard 96-h acute exposure experiments generally used for toxicity testing in copepods from lower latitudes do not necessarily hold true for polar regions where stress responses to cadmium and copper have only been observed after 7 days in three Antarctic copepod species (Zamora et al., 2015; Table 1). The multitude of metal sources in the Arctic region presents an opportunity to target hotspots of multi-stressor and metal exposure as well as stable and less-exposed control sites for closely linked comparative toxicity responses, including long-term toxicity effects in Arctic populations and species.

Intra- and inter-specific toxicity differences

The interspecific differences in metal toxicity reviewed above demonstrate that more acute stress response studies on polar species are required. The overwhelming majority of studies focused on copepods, while other planktonic taxa have been rarely considered. Copper can be more toxic than cadmium in Antarctic (Zamora et al., 2015) and some temperate copepods (Verriopoulos and Moraitou-Apostolopoulou, 1982; Hutchinson et al., 1994; Zidour et al., 2019), while the opposite is true for the temperate *T. brevicornis* (Barka et al., 2001). Larval, pre-adult, and adult life stages can also differ in their sensitivity and capacity to respond. In addition, regional and local adaptive variations may cause intra-specific plasticity, resulting in wide ranges of LC_{50} 's across different populations. Different metal toxicities among closely related species highlight the need for further understanding of underlying inter-specific mechanistic differences in stressor response (Rocha-Olivares et al., 2004). Phenotypic plasticity of populations experiencing different environmental conditions and resulting cellular and molecular stress response variability require further study to disentangle inter- and intraspecific variability in zooplankton stress responses.

Genotoxic and molecular control of toxicity response

While there might be no phenotypic difference between observed LC50's and metabolic rates for any given stressor between two different copepod species, their genetic responses may vary (Øverjordet et al., 2014; Thirunavukkarasu and Hwang, 2024). If Arctic populations and food chain dynamics are more sensitive to increasing metal concentrations might be answered by comparing genotoxic responses of Arctic copepods to those of congeneric temperate or tropical counterparts. Genetic responses are, however, not as straightforward to observe as morphological changes or metabolism rates, where results can be drawn from observations of food intake and respiration rates. Differences in levels and types of sublethal genotoxicity of copper in A. longiremis and Calanus spp. indicate species-specific differences in genetic sensitivity, DNA repair responses, and downstream control of reproduction (Thomsen et al., in review¹). Individual survival and reproduction are ultimately controlled by complex genetic and molecular responses, and the fundamental mechanisms for effects beyond the individual level is through inheritable genetic and epigenetic pathways, yet studies on these pathways in Arctic zooplankton require much more expansion.

Conclusions

The review demonstrates that metal concentrations are increasing due to accelerated transport from natural and anthropogenic sources into coastal arctic systems. Hotspots with concentrations exceeding environmental quality standards pose an increasing risk in the Arctic, with implications for food web structure and function. Bioavailability of metals in Arctic marine environments is evident from some studies, however more data is required across different Arctic regions to directly assess marine concentrations in bioavailable forms to link metal sources to dissolved concentrations and uptake into zooplankton. New experimental and molecular approaches to the study of metal toxicity in a multi-stressor context can provide mechanistic understanding of a species' resilience or vulnerability, and differential capacity for adaptive evolution in a changing Arctic Ocean. The review uncovers knowledge gaps concerning speciesspecific and population-wide impacts and we call for more Arcticfocused studies on zooplankton as a key group of species in the marine trophic web. The question of sensitivity versus resilience to changing conditions, including increasing metal concentrations, and multi-stressor environment is still open for most arctic species, and mechanistic studies can illuminate different response and coping strategies in different species under future ocean

conditions to better predict and alleviate environmental risks from metal contamination in the Arctic.

Author contributions

CH: Writing – review & editing, Writing – original draft, Visualization, Supervision, Funding acquisition, Conceptualization. NT: Writing – review & editing, Writing – original draft, Visualization. HR: Writing – review & editing, Writing – original draft, Visualization, Supervision, Conceptualization.

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