

SYNTHESIS

Future Arctic: how will increasing coastal erosion shape nearshore planktonic food webs?

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Scientific Significance Statement

Arctic permafrost coasts constitute 34% of the Earth's coasts, and they are warming nearly four times faster than the global average. This rapid warming erodes Arctic coasts which may have important implications for the functioning of coastal ecosystems, more so the productivity of planktonic organisms that form the basis of the aquatic food web. Here, we explore how Arctic coastal erosion may impact nearshore primary production and we evaluate implications for the functioning of planktonic food webs. We provide evidence that higher turbidity associated with increased erosion of permafrost coasts is likely to shift the balance between phytoplankton and bacterial production, which may lower zooplankton biomass, with negative consequences for higher trophic levels. Our findings lay out the path for future work to investigate the permafrost-carbon feedback, and how increasing Arctic coastal erosion will affect the microbial food webs.

Abstract

Arctic regimes. Currently, warming accelerates the erosion of permafrost coasts and the associated discharge of sediment, carbon, and nutrients into the Arctic Ocean. However, the impacts of coastal erosion on planktonic food webs remain understudied. We aimed to (1) understand how coastal erosion impacts nearshore carbon, nutrient, and light regimes; (2) investigate the effects on primary production and energy transfer; and (3) predict how increased erosion will impact the productivity of consumers, and the overall food web interactions. We found that sediment discharge increases turbidity (darkening). This darkening is expected to hamper phytoplankton productivity, while additional carbon input will provide bacteria with direct energy sources, and shift the balance between basal autotrophic and heterotrophic production. Since the heterotrophic pathway has a lower efficiency, its dominance might negatively affect mesozooplankton. Increased Arctic coastal erosion might therefore influence planktonic food webs by changing mechanisms of energy mobilization and transfer to higher trophic levels.

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In the last four decades, the Arctic has warmed nearly four times faster than the global average (Lim et al. 2020; Rantanen et al. 2022). This phenomenon has increased the susceptibility of Arctic permafrost coasts to thaw and erode, leading to an estimated increase in erosion rates from around 0.18 m yr^{-1} up through the mid-1970s (Nielsen et al. 2022), to 0.5 m yr^{-1} by 2012 (Lantuit et al. 2012). Accelerating coastal retreat is caused by a combination of many different factors, which vary locally and regionally. The main environmental drivers leading to faster erosion are longer open water periods, more severe, frequent, and longer-lasting storms, rising sea levels, and higher water and air temperatures (Irrgang et al. 2022). These environmental drivers all result in greater wave impacts and less resilient shorelines (Casas-Prat and Wang 2020; Irrgang et al. 2022). Since Arctic permafrost coasts constitute 34% of Earth's coastlines, and since one-third of settlements built on permafrost are close to the coast (Lantuit et al. 2012; Fritz et al. 2017; Ramage et al. 2021), increased erosion in the Arctic has broad consequences for the functioning of coastal ecosystems, as well as for the sustainability of livelihoods and infrastructure (Fritz et al. 2017).

Permafrost coastal erosion mobilizes sediments, nutrients, and carbon, which are subsequently transported from the land to the ocean, and are predicted to greatly alter Arctic planktonic food webs by changing light and nutrient regimes. Currently, coastal erosion is estimated to release an average of 15.4 Tg (10^{12} g) of total carbon, and 1.6 Tg yr^{-1} of nitrogen into the Arctic Ocean (Terhaar et al. 2021). However, the specific effects of carbon and nutrient input on coastal planktonic food webs are murky, due to high variabilities, interdependencies, and interactions among watersheds and in the coastal zone. Tank et al. (2012) posed that nitrogen from land only supports a small proportion of photosynthesis in the Arctic Ocean, while Terhaar et al. (2021) estimated that coastal erosion sustains about one-fifth of net primary production. Further, there is paucity of information on the impacts of terrigenous material on turbidity, and the balance between phytoplankton and bacterioplankton energy pathways in the nearshore zones (zones shallower than 20 m water depth). These zones account for 7.5% of the Arctic Ocean (Fritz et al. 2017), a much greater proportion compared to other oceans. They also play a major role in Arctic biogeochemical cycling and primary production by determining the fate of the material released from terrestrial ecosystems (Fritz et al. 2017). The increased introduction of terrestrial material into the nearshore zone might lead to the darkening of coastal waters (increased turbidity due to high concentrations of suspended material) (Wegner et al. 2015), which will negatively affect primary production in those zones (Lindemann et al. 2016; Szeligowska et al. 2021). Additionally, intensifying Arctic coastal erosion may affect planktonic community structure and the overall food web functioning in the nearshore zone (Calbet 2008; Vrede et al. 2011; Schmoker et al. 2013).

The foundation of the Arctic pelagic food web is primary production by single-celled phytoplankton and sea ice algae. These autotrophs use light and nutrients to store energy in the form of compounds like polysaccharides, which can later be passed to higher trophic levels via consumption (Bluhm and Rolf 2008; Murphy et al. 2020). In Arctic coastal regions, both underwater light regimes and nutrient supplies are affected by sea ice dynamics, the circulation of water masses, and seasonal permafrost thawing (Popova et al. 2010; Ardyna et al. 2017). Arctic coastal zones are typically characterized by strong vertical and horizontal stratification in the water column and low nutrient levels in the surface layers. However, episodic nutrient inputs can trigger phytoplankton blooms that may account for up to half of the regional production within a season (Mundy et al. 2009). This autotrophic primary production can also be supported by bacterioplankton through heterotrophic production. Indeed, bacterioplankton consume dissolved and particulate organic matter and hence play a key role in remineralizing processes (Piontek et al. 2021). Consumption of autotrophic and heterotrophic production by microzooplankton ($< 200 \mu\text{m}$ in equivalent spherical diameter) and mesozooplankton (between 0.2 and 20 mm) (Negrete-García et al. 2022), subsequently passes energy and nutrients to higher-order consumers, such as planktivorous fish. The top of Arctic pelagic food webs is characterized by fish species like cod and Arctic char, as well as mammals such as seals and whales, upon which local subsistence fishers and hunters rely (Zeller et al. 2011; Galappaththi et al. 2019). Given that the structure and functioning of Arctic pelagic food webs depend on the interplay between nutrients and light availability (Polimene et al. 2022), changing environmental conditions have the potential to alter the ecosystem services provided to local communities.

While the link between Arctic coastal erosion and primary productivity has been studied to some extent (Sipler et al. 2017; Terhaar et al. 2019, 2021; Polimene et al. 2022), the implications for the balance between autotrophic and heterotrophic energy pathways, and the overall food web efficiency in the nearshore zone, remain largely untested. With ongoing warming, coastal erosion fluxes in the Arctic have the potential to increase by an order of magnitude by 2100 (Rantanen et al. 2022). Taken together, the increase in organic carbon (OC) and the decrease in light availability will have consequences for planktonic energy pathways, but the exact ways these factors interact remain unclear. Understanding the cascading effects of increasing Arctic coastal erosion on the nearshore food web is crucial for conservation efforts and the implementation of climate change mitigation measures, as human communities in the Arctic depend on local marine biological resources to a large extent (Fritz et al. 2017; Galappaththi et al. 2019).

In this review, we assess the potential effects of Arctic coastal erosion on planktonic community structure and food web interactions in nearshore environments. We focus on (1)

understanding how coastal erosion impacts carbon, nutrient, and light availability in the nearshore zones; (2) investigating how these changes could affect autotrophic and heterotrophic production, and energy transfer to higher trophic levels; and (3) understanding how the increase in Arctic coastal erosion will impact the productivity of consumers, and the overall food web interactions and efficiency.

Arctic coastal erosion and its impacts on carbon, nutrients, and light distribution

Arctic coastal systems have a high geomorphic variability (Lantuit et al. 2012), and include lithified and unlithified coasts. Lithified coasts consist of solid rocks and show little erosion. They are characterized by a mix of fjords, pocket beaches, bluffs, and low-lying rocky shorelines (Overduin et al. 2014). Unlithified coasts are composed of unconsolidated sediments and are cemented and solidified by ground ice. They are characterized by ice-rich permafrost bluffs (Lantuit et al. 2012) and are mostly found in Canadian, U.S., and Russian coastal margins, making up two-thirds of the coasts facing the Arctic Ocean (Lantuit et al. 2012; Farquharson et al. 2018; Kupilik et al. 2020; Lim et al. 2020). Permafrost areas comprise a seasonally active layer that thaws during the warm season. Underneath the active layer lies perennially frozen ground that contains substantial amounts of ice. Erosion of the active layer makes Arctic coasts exceptionally vulnerable to degradation upon thaw and mechanical abrasion when in contact with seawater.

Unlithified permafrost coasts store large amounts of OC that are increasingly eroded into the Arctic Ocean. OC stored in permafrost and the active layer above it across the Northern Hemisphere is about 1,300,000 Tg, with an uncertainty range of $\sim 1,100,000$ Tg to $\sim 1,500,000$ Tg, which exceeds the amount of carbon stored in all other soil regions of the world (Hugelius et al. 2014). Warming accelerates permafrost thawing and erosion (Cohen et al. 2014; Fritz et al. 2017; Underwood et al. 2019). Compared to stabilized permafrost coasts (Fig. 1a), coastal areas with retrogressive thawing slumps (Fig. 1b), actively eroding cliffs (Fig. 1c), active layer detachment, and low bluffs, are substantially degraded (Grotheer et al. 2020; Tanski et al. 2021). Under the RCP 8.5 scenario, these phenomena are projected to decrease near-surface permafrost areas by $69 \pm 20\%$ by 2100 (Slater and Lawrence 2013). The erosion of the Arctic coast is further enhanced by sea level rise and the intensification of storms (Atkinson 2005). Even though seasonal coastal erosion is a natural process, current global warming and the associated increase in extreme weather events intensify sediment and carbon transport from the land (Wegner et al. 2015). While geomorphological studies on coastal erosion processes are manifold, little is known about how these processes influence carbon bioavailability in nearshore areas, and the subsequent uptake of OC by planktonic communities in the Arctic Ocean.

Filling this knowledge gap on OC transformation and uptake is fundamental in understanding the biogeochemical pathways of OC in the warming Arctic.

Coastal erosion is a natural process resulting from wind and wave action and has always caused substantial OC and nutrient fluxes into the coastal Arctic Ocean. For example, the pan-Arctic average loss from coastal erosion has been estimated at 6.9 Tg C yr^{-1} during the period 1850–1950 (McGuire et al. 2009; Nielsen et al. 2022). However, these rates have increased up to $15.4 \text{ Tg C yr}^{-1}$ in 2021 (Wegner et al. 2015; Terhaar et al. 2021). The increase in terrestrial input could drastically impact fluxes of key elements like carbon, nitrogen, and phosphorus into and within the coastal ecosystems and their feedback on nearshore local communities and food webs. This raises the question of the exact consequences in the nearshore zones.

Coastal erosion will increase organic matter supply. The Arctic nearshore system receives considerable amounts of particulate organic carbon (POC) and, to a smaller degree, dissolved organic carbon (DOC). For example, on the Yukon coast, POC : DOC is supplied in the ratio of 900 : 1 (Tanski et al. 2016). These organic compounds are derived from remnants of animals and plants that have accumulated in the permafrost over millennia (Barker et al. 2006). Increased contact between organic soil horizons and water through thawing processes enhances organic matter mobilization into the water column or leaching from the sediment and soils, leading to higher OC concentrations in nearshore systems (Vonk et al. 2013; Jong et al. 2020). Additionally, the small amount of OC stored in ice wedges and other ground ice also gets released during the thawing of ice-rich permafrost (Fritz et al. 2015; Tanski et al. 2016).

Permafrost erosion also has the potential to increase nutrient transport to coastal waters (Thompson et al. 2012). For instance, an estimate of 1.6 Tg N yr^{-1} of total nitrogen almost entirely in particulate organic form is delivered through coastal erosion (Terhaar et al. 2021). This input is particularly relevant since Arctic systems are nitrogen-limited. The deficiency of dissolved inorganic nitrogen (DIN) in the Arctic waters occurs due to the connectivity of the Arctic Ocean to other oceans, and its circulation (Tremblay et al. 2015). DIN is lost within the Arctic Ocean through denitrification on Arctic shelves while additional surface DIN inventories are depleted after ice retreat, leading to nutrient limitation of primary production during the rest of the season when light is sufficient. In addition to nitrogen, phosphorus (P) is also supplied by permafrost thaw, river runoff, and ice melting in the Arctic environment (Hawkings et al. 2016). Climate-related changes to permafrost erosion, therefore, have particular significance in increasing nutrient supply into the Arctic Ocean.

Unlike carbon and nutrients, light availability might be reduced in the Arctic nearshore systems (Fig. 1d). Allochthonous material originating from permafrost erosion brings an array of humic compounds that significantly



Fig. 1. Examples of different coastal landforms along the Yukon coast in the western Canadian Arctic. Stabilized permafrost coasts show little or no erosion (**a**). However, slump-affected sites (**b**) and coasts with actively eroding cliffs (**c**) exhibit higher erosion and substantial transfer of sediment and OC into the water column. The discharge of the eroded material increases turbidity in the nearshore zones (**d**). Photos were taken by C. Weber in July 2022.

attenuate light and reduce the depth of the euphotic zone (Lefebvre et al. 2013; Brett et al. 2017; Mann et al. 2021; Szeligowska et al. 2021). For example, between 2003 and 2020, the attenuation of light in the coastal Arctic Ocean with depth < 100 m, increased by 22% (Singh et al. 2022). Similarly, high sediment loads from Arctic rivers lead to a reduction in light penetration throughout the water column (Wegner et al. 2015), a major consequence given that the Arctic Ocean receives more than 10% of the global river discharge (McClelland et al. 2012). Changes in long-term river discharge into the Arctic Ocean have also been observed, with a 7% increase recorded between 1936 and 1999 (Peterson et al. 2002). The river-driven brownification occurs mainly in spring and early summer. This is linked to maximal riverine runoff, and the highest absolute sediment flux into the ocean (Golubeva et al. 2019). In late summer, large loads from

coastal erosion drive turbidity (Terhaar et al. 2021), whereas in winter, little or no runoff occurs due to the freezing of the land and the rivers. Discharge of freshwater either directly from land or through rivers also lowers surface salinity (Park et al. 2023), thereby increasing surface layer stratification. Because climate change is elongating and intensifying, permafrost thaw, coastal erosion, and seasonal river runoff are expected to further reduce light intensity (Brett et al. 2017; Mann et al. 2021; Szeligowska et al. 2021).

Consequences of increasing coastal erosion for the nearshore planktonic food web

Elevated inputs of permafrost material along the Arctic coast are expected to (1) intensify by 70% to 150% by 2100 in zones already receiving high terrestrial input (e.g., estuaries

and nearshore areas) (Nielsen et al. 2022), (2) increase in zones that until now received little terrestrial input, and (3) increase the overall coastal area influenced by terrestrial inputs. These processes may have wide-ranging consequences for Arctic marine ecological dynamics, including influencing species interactions, productivity, and energy transfer. Here, we explore the potential impacts of increasing coastal erosion on plankton productivity and food web interactions, focusing on the poorly studied yet highly relevant lower trophic levels.

Phytoplankton

Two main processes are associated with the influence of erosion on nearshore primary production: a decrease in light availability, and an increase in carbon and nutrient concentrations. Although nitrogen is limited in the Arctic Ocean, coastal erosion mobilizes nutrients and supports 28–51% of net primary production in the coastal zone (Terhaar et al. 2021). However, terrestrial input influences nearshore marine habitats by decreasing the extent of the euphotic zone (McGovern et al. 2020; Szeligowska et al. 2021). Given the increase of up to $0.01 K_d^{\text{PAR}[m^{-1} \text{ yr}^{-1}]}$ in light attenuation between 2003 and 2020 (Singh et al. 2022), turbidity can be expected to increase by $\sim 80\%$ by 2100. Lower light availability might reduce phytoplankton photosynthetic rates and phytoplankton productivity. Szeligowska et al. (2021) found lower phytoplankton abundances in turbid and glacier-influenced waters than in clear waters due to higher particle abundance. A model study by Polimene et al. (2022) on the Arctic shelf also found that primary productivity decreased by 4% to 16% with a 25% to 100% increase in terrestrial dissolved organic matter (DOM). The decrease in primary production was due to the interplay of light limitation and grazing pressure on primary producers. By attenuating underwater light, permafrost erosion may also shift the competitive balance between autotrophs and mixotrophs to favor the latter, with groups such as Dinophyceae and Cryptophyceae growing substantially better than pure autotrophs such as Bacillariophyceae (Szeligowska et al. 2020, 2021). Changes in phytoplankton community composition have already been observed in the Arctic Ocean around eastern Fram Strait, with chain-forming and large, centric diatoms such as *Achnanthes taeniata*, *Navicula* spp, *Chaetoceros* spp, and *Thalassiosira* spp being replaced by mixotrophic nanoflagellates and coccolithophorids due to warming and increased sediment inputs (Bauerfeind et al. 2009; Nöthig et al. 2015).

Apart from reducing the extent of the euphotic zone, low salinity from freshwater discharge might also negatively affect biodiversity. Brackish water tends to favor euryhaline plankton, leading to lower biodiversity when compared to marine water (Carmack et al. 2016; Hopwood et al. 2020). By increasing upper water column stratification, freshwater discharge also reduces vertical nutrient flux, consequently decreasing new production, and shifting the algal communities towards smaller cell sizes (Carmack et al. 2016). Smaller cells are more

effective in acquiring nutrients and less susceptible to gravitational settling than larger cells. In the Arctic Ocean, Li et al. (2009) found that phytoplankton with smaller cells thrived while larger cells languished due to increasing discharge of freshwater.

The elemental composition of autotrophs varies substantially as a function of carbon, solar energy, and mineral nutrient availabilities (Sterner and Elser 2003). Relative to nitrogen (N) and phosphorus (P), the higher input of terrigenous carbon might increase the elemental ratios of C : P and C : N in the Arctic coasts. This means that phytoplankton might be forced to utilize low cellular N and P quotas for growth sustenance, resulting in biomass with a disproportionate accumulation of C relative to N and P (Fig. 2). It remains unclear whether the negative effects of increased OC and light attenuation on primary production will be compensated by the positive influence of increased nutrient supply in the nearshore zones.

Bacterioplankton

Bacterioplankton have high carbon requirements and often rely on C-rich algal exudates for growth (Baines and Pace 1991). However, high inputs of allochthonous carbon can uncouple bacterial reliance on phytoplankton carbon exudates, a phenomenon that has been observed in high-latitude lakes (Tranvik 1988; Jansson et al. 2007). Hence, increased coastal erosion might stimulate bacterial production via greater labile C-rich terrestrial organic matter availability. Bacterioplankton and phytoplankton compete for nutrients such as nitrogen and phosphorus, and the expected negative influence of higher terrestrial C inputs on phytoplankton biomass may benefit bacterioplankton. By decreasing light availability and subsidizing with allochthonous C, elevated terrestrial inputs should favor heterotrophic bacterial production over autotrophic phytoplankton production (Sandberg et al. 2004; Figueroa et al. 2016). In support of this hypothesis, a 76% increase in freshwater discharge resulted in doubled the bacteria to phytoplankton production in the northern Baltic Sea due to inputs of colored humic substances and deeper mixed layers (Wikner and Andersson 2012). In another study, Meunier et al. (2017) observed that carbon enrichment decreases phytoplankton biomass and increases bacteria biomass, and suggested that bacteria outcompete phytoplankton where an alternate, readily bioavailable carbon source is accessible.

Studies indicate that about 30% of terrestrial DOC entering the Arctic coastal zones is readily bioavailable (Vonk et al. 2013, 2015; Mann et al. 2015). Beyond this carbon's lability and quality, the selective forces of these carbon compounds in structuring the bacterioplankton community should be considered (Gómez-Consarnau et al. 2012; Sosa et al. 2015). For instance, Niemi et al. (2014) found that DOM released from melting Arctic sea ice led to a 2.1–3.2-fold increase in bacterial cell size. Adding terrestrial DOM extracted

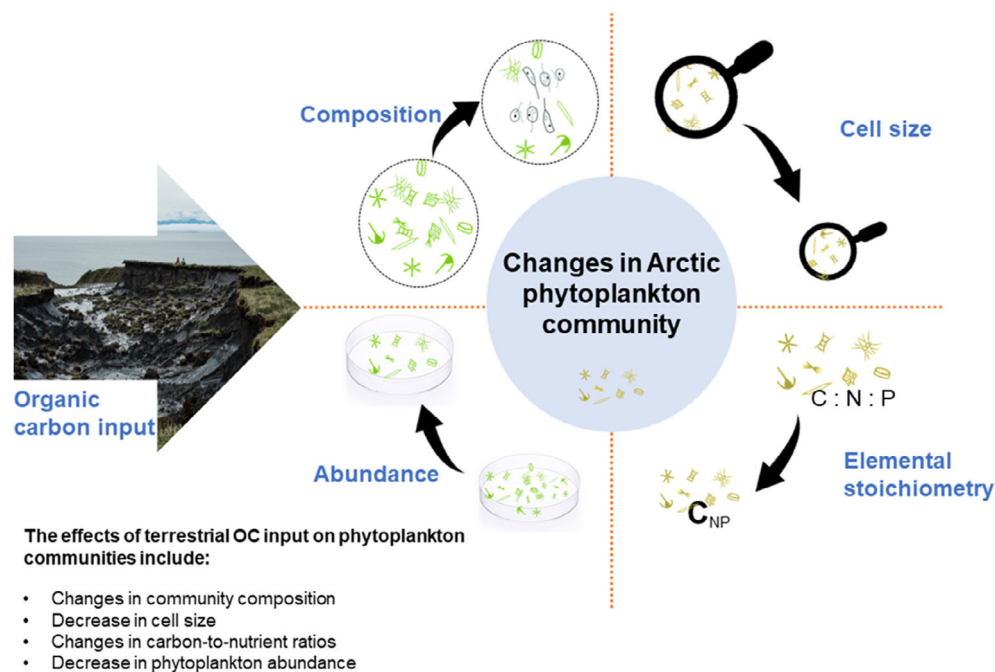


Fig. 2. Schematic illustration of the effects of terrestrial OC input from permafrost thaw and erosion on phytoplankton communities in the Arctic near-shore zone. The arrows indicate anticipated shifts in phytoplankton community structure and include changes in species composition, a decrease in cell size, changes in the elemental stoichiometry, and a reduction in phytoplankton abundance.

from the active permafrost layer to aquatic bacterial communities also shifts community composition by increasing the number of high nucleic acid-containing bacteria (Müller et al. 2018). This outcome may be due to the ability of larger bacteria to metabolize a broader spectrum of DOM than smaller bacteria (Grunert et al. 2021). While these shifts in bacterial communities may have large implications for overall carbon and nutrient cycling, these aspects remain largely unexplored in the coastal Arctic.

In short, increased coastal erosion and associated terrestrial DOC input benefit bacterioplankton and impair phytoplankton, which may affect higher trophic levels. The planktonic food web can be subdivided into two energy pathways, the photoautotrophic (phytoplankton-based) energy pathway, and the heterotrophic (bacterial-based) energy pathway (Azam et al. 1983; Meunier et al. 2016), which have different efficiencies (Fig. 3). In the following section, we explore the potential consequences of shifts in production at the base of the food chain for higher trophic levels.

Zooplankton

Phytoplankton-based food chains typically transfer carbon more efficiently to higher trophic levels than bacteria-based food chains (Berglund et al. 2007; Brett et al. 2009). However, it remains a fundamental question whether bacterial-derived carbon represents an addition to autotrophic energy sources or if it replaces it to some degree. As a potential supplement, a study by Degerman et al. (2018) in the Baltic Sea found an increase in

zooplankton production due to the channeling of energy via both the phytoplankton and bacterial pathways. Similar changes may be expected in the Arctic when higher bacterial biomass dominates the heterotrophic food chain in the early spring months, before the phytoplankton bloom (Polimene et al. 2022). In another study by Karlsson et al. (2005) in high-latitude, unproductive lakes, they found a close association between the input of allochthonous OC sources and the input of limiting inorganic nitrogen and phosphorus. Bacteria have a higher affinity for inorganic nutrients than phytoplankton. In the northern Baltic Sea, Berglund et al. (2007) discovered that a noteworthy portion of the biomass in higher trophic levels may originate from terrestrial carbon sources, potentially mobilized by bacterioplankton. For instance, increased biomass of bacterioplankton could be advantageous for microzooplankton, such as certain ciliates known for their efficient consumption of bacteria (Berglund et al. 2007; Lefebure et al. 2013). Although microzooplankton is later consumed by mesozooplankton (Fig. 3), this additional trophic link reduces food web efficiency (Berglund et al. 2007; Jansson et al. 2007), as respiratory energy losses occur at each trophic transfer step, especially in cases where energy is limiting (Gan et al. 2023). Degerman et al. (2018) found minimal bacterial carbon transfer to consumers like mesozooplankton and fish.

Complicating their potential importance, bacterioplankton is generally considered poor-quality food for most mesozooplankton consumers because bacterioplankton lacks certain sterols and essential fatty acids (FAs; Brett and Müller-

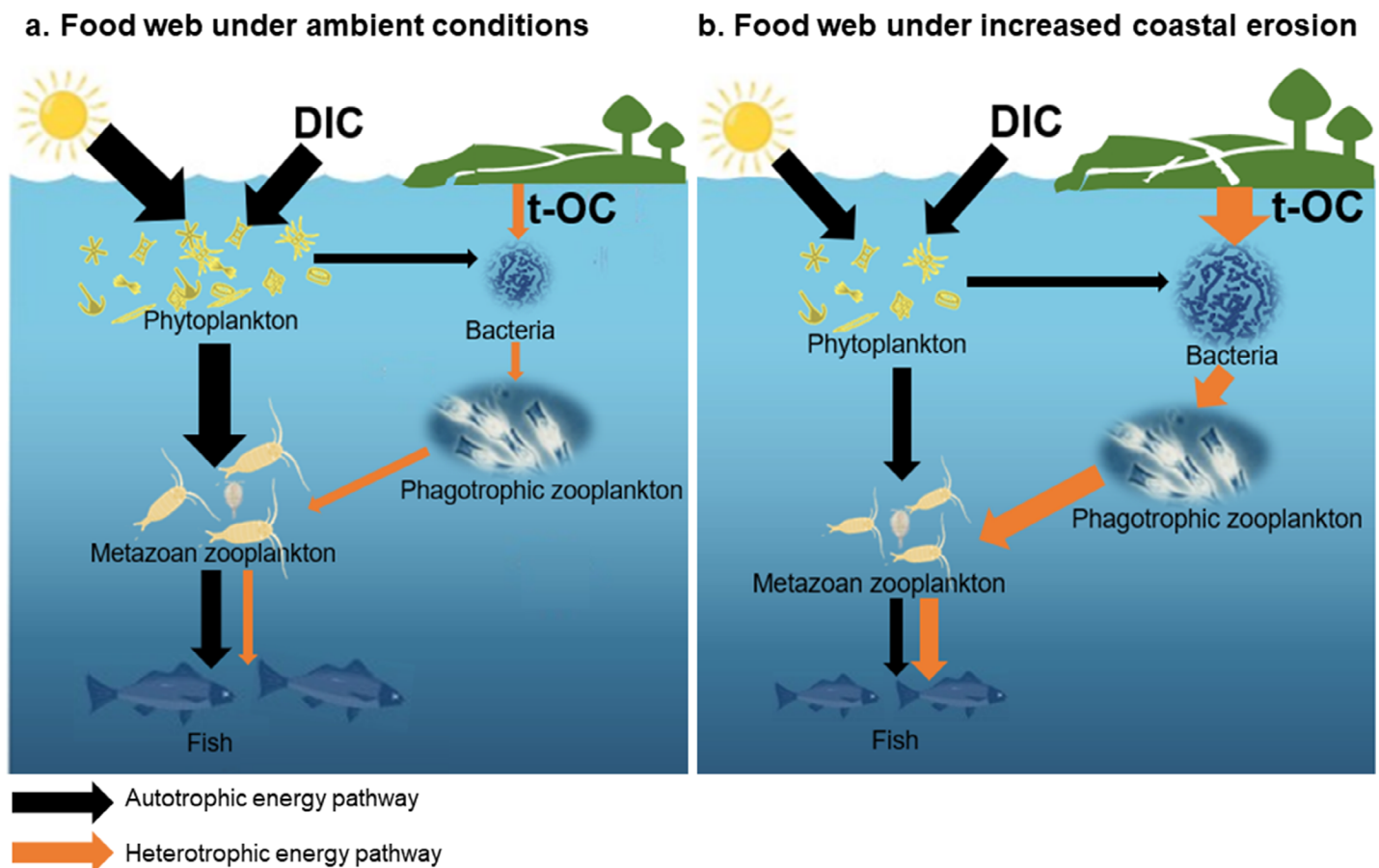


Fig. 3. Conceptual model on Arctic planktonic food webs under present conditions and increased coastal erosion. In both figures, relative arrow width represents the amount of energy passed between links; relative organism size represents shifts in abundance. **(a)** When there is less terrestrial organic carbon (t-OC) input, the autotrophic energy pathway (black arrows) dominates. Energy mobilization for primary and secondary production comes from phytoplankton photosynthesis using solar radiation and dissolved inorganic carbon (DIC). Phytoplankton carbon and energy are then transferred to higher trophic levels. **(b)** Under increased coastal erosion, the heterotrophic energy pathway (orange arrow) dominates. Increased discharge of t-OC enhances bacterial production, which becomes a major source of energy mobilization in addition to phytoplankton-derived carbon. This energy is then transferred to the mesozooplankton (0.2–20 mm) and fish through phagotrophic zooplankton (< 200 μm). However, much of the energy is dissipated due to additional links in the heterotrophic chain.

Navarra 1997; Martin-Creuzburg et al. 2011; Degerman et al. 2018). Mesozooplankton primarily obtain the essential highly unsaturated FAs, such as eicosapentaenoic acid and docosahexaenoic acid from phytoplankton they consume (Kattner and Hagen 2009). Feeding trials in a freshwater lake showed that *Daphnia* cannot survive on a diet containing only bacteria due to lack of these FAs (Martin-Creuzburg et al. 2011). Degerman et al. (2018) also found that fish production decreased due to the channeling of energy via the less efficient and longer bacterial pathway.

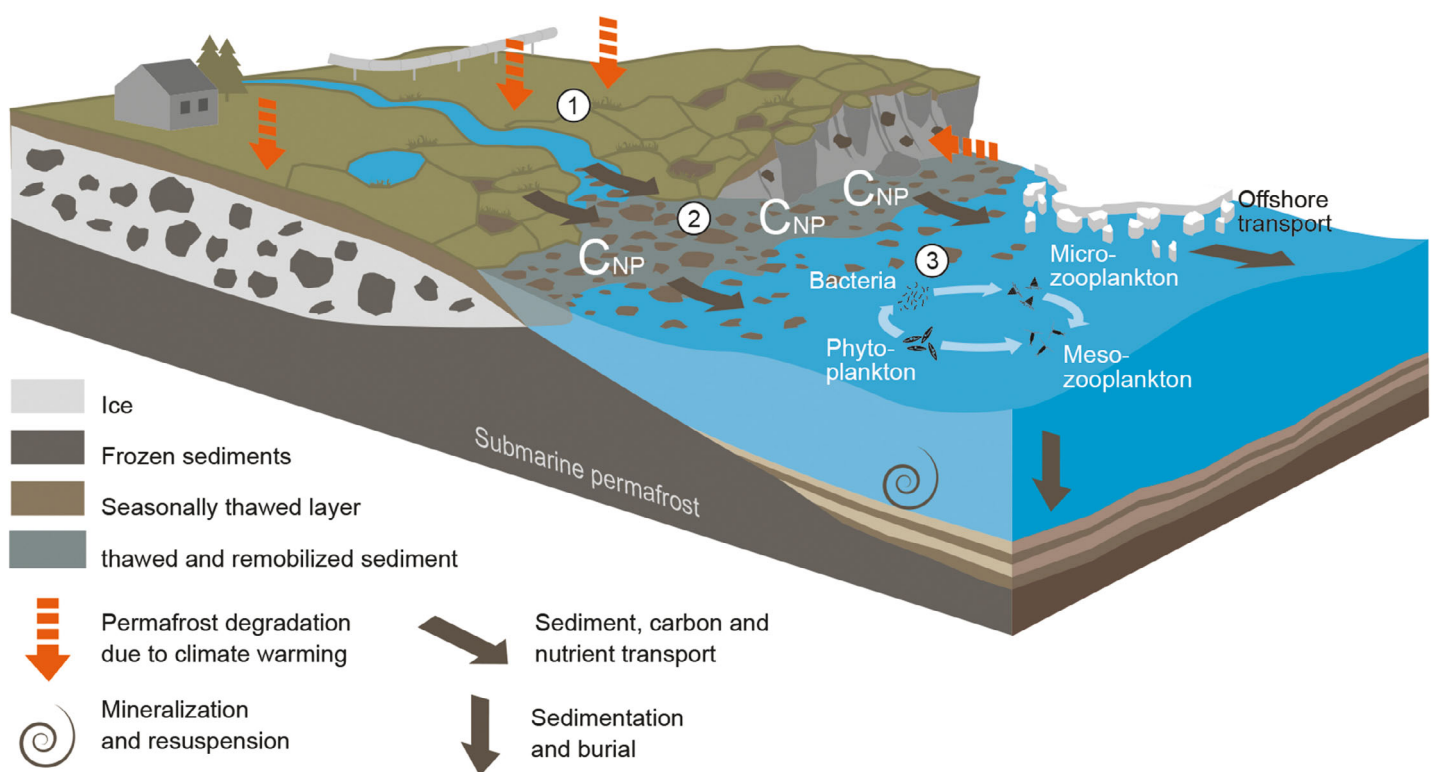
Suspended matter may also affect mesozooplankton filter and interception feeding (Margalef 1978), as well as grazing efficiency. Fine sediment loads in the water column can reduce the visibility of zooplankton. They are, therefore, forced to either invest additional energy in finding suitable food particles within the turbid water column or fill their gut with inorganic

particles (Sommaruga 2015). Additional energy is also required to locate phytoplankton that sinks from the euphotic zone (Arendt et al. 2011), decreasing energy allocation to reproduction and somatic growth. Although suspended matter might shelter zooplankton from visual predators, it might also increase their specific weight through agglutination of cells, reducing their hunting activity (Margalef 1978; Szeligowska et al. 2021). To the best of our knowledge, no study to date has dealt with changes in the stoichiometric qualities and physiology of phytoplankton, bacteria, and zooplankton in the Arctic. Future studies should aim to fill this gap by manipulating primary producers' light and nutrient conditions to predict better how changes in food quality will influence zooplankton growth, development, and physiology in the Arctic.

POC from permafrost could also directly supplement food webs. For example, in freshwater lakes, POC has been shown

to contribute between 33% and 73% of the carbon incorporated into nearshore zooplankton, and between 20% and 50% of the carbon incorporated into fish (Cole et al. 2006). Even though some zooplankton species readily consume particulates, some studies found that high proportions of terrestrial POC in the diet of zooplankton from freshwater lakes reduce their growth and survival performance due to poor digestibility, and lack of essential biochemicals (FAs) and minerals (P) (Wenzel et al. 2012, 2021). Our current understanding of how zooplankton in marine coastal habitats will respond to OC from permafrost is severely hindered by the lack of studies on these ecosystems, and we recognize that some biogeochemical

processes in marine systems might differ from freshwater habitats. However, similar biological processes such as increased heterotrophy under higher OC, have been observed in both systems. We can therefore hypothesize that elevated permafrost OC will favor heterotrophic energy pathways, which will have negative consequences for mesozooplankton biomass, and may further impact fish if it replaces the autotrophic energy pathway. Studies that disentangle and combine assessments of Arctic primary productivity under varying carbon concentrations and light intensities can better elucidate the primary drivers of biological shifts in the microbial food web and the potential impacts on higher trophic communities.



Potential impacts of increased permafrost thaw and erosion on coastal biogeochemical processes

① Coastal habitat

- Increase in permafrost degradation
- Increase in active layer depth
- Thawing of coastal sediment
- Increase of coastal erosion

② Nearshore habitat

- Increase in sediment and turbidity
- Reduction in light conditions
- Increase in C input, relative to N and P
- Loss of fishing grounds

③ Marine food web

- Decrease in primary productivity
- Increase in bacterial production
- Shifts to heterotrophic bacterial-based energy pathway
- Additional trophic steps in the food web

Fig. 4. Potential impacts of increased permafrost thaw and erosion on coastal biogeochemical processes. (1) Increased warming might lead to an increase in active layer depth and thawing of permafrost sediment at the coast. (2) In the nearshore zone, increased discharge of sediment nutrients and carbon might enhance turbidity in the nearshore zones, as well as higher C input, relative to N and P. Additionally, coastal erosion might lead to loss of fishing ground, as well as migration to offshore areas with lower turbidity. (3) Higher turbidity and C input might support bacterial production shifting the energy pathway to a heterotrophic bacterial-based pathway. Such shifts might lead to longer trophic links for zooplankton and fish. Figure adapted from Fritz et al. (2017), and modified by Yves Nowak (AWI).

Conclusions and future perspectives

Climate warming is particularly rapid in the Arctic, accelerating the thawing and erosion of permafrost. Elevated erosion of permafrost material along the Arctic coast is expected to increase the overall coastal area influenced by terrestrial inputs. The seawater in these areas will become more turbid and have higher dissolved and particulate carbon content. We expect that this darkening will reduce phytoplankton productivity due to light limitation, and alter plankton species composition, and biomass (Fig. 4).

The input of t-DOM might also supply bacteria with a direct energy source, enhancing bacterial production and the heterotrophic energy pathway. In this case, the phytoplankton energy pathway might be replaced to some degree in the coastal marine habitats. Although bacterial energy might be a supplement for some organisms, we suggest that the effects of low nutrient-use efficiency and low energy transfer efficiency induced by heterotrophic energy mobilization will negatively affect size-structured dynamics among zooplankton and subsequently reduce food availability for fish.

To date, literature on coastal erosion dynamics and the associated effects on nearshore food webs is characterized by small datasets. It remains an open question of how different permafrost coasts (stable and degraded coasts) influence carbon and nutrient input, as well as the phytoplankton and zooplankton community structures in the nearshore zones. Additionally, it has been demonstrated that organisms at higher trophic levels can be supported by either phytoplankton or bacterial energy pathways, depending on the intensity of carbon input. Isotopic analysis can elucidate the sources of OC and its transfer through the trophic chain. Moreover, no studies in the Arctic have directly compared zooplankton growth, reproduction, and survival, when fed with bacterial, algal, or t-DOM-dominated diets. Experimental studies with manipulated quantities of light and carbon at different trophic levels will help predict the potential effects of increasing erosion on both top-down and bottom-up processes. Clarifications on these aspects should substantially enhance our understanding of the manifold ways the Arctic ecosystem is changing in response to Arctic warming, and thus guide Arctic coastal management towards a greater focus on sustainable nearshore ecosystem conservation.

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Conflict of Interest

None declared.

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