

Seafloor primary production in a changing Arctic Ocean

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Phytoplankton and sea ice algae are traditionally considered to be the main primary producers in the Arctic Ocean. In this Perspective, we explore the importance of benthic primary producers (BPPs) encompassing microalgae, macroalgae, and seagrasses, which represent a poorly quantified source of Arctic marine primary production. Despite scarce observations, models predict that BPPs are widespread, colonizing ~3 million km² of the extensive Arctic coastal and shelf seas. Using a synthesis of published data and a novel model, we estimate that BPPs currently contribute ~77 Tg C y⁻¹ of primary production to the Arctic, equivalent to ~20 to 35% of annual phytoplankton production. Macroalgae contribute ~43 Tg C y⁻¹, seagrasses contribute ~23 Tg C y⁻¹, and microalgae-dominated shelf habitats contribute ~11 to 16 Tg C y⁻¹. Since 2003, the Arctic seafloor area exposed to sunlight has increased by ~47,000 km² y⁻¹, expanding the realm of BPPs in a warming Arctic. Increased macrophyte abundance and productivity is expected along Arctic coastlines with continued ocean warming and sea ice loss. However, microalgal benthic primary production has increased in only a few shelf regions despite substantial sea ice loss over the past 20 y, as higher solar irradiance in the ice-free ocean is counterbalanced by reduced water transparency. This suggests complex impacts of climate change on Arctic light availability and marine primary production. Despite significant knowledge gaps on Arctic BPPs, their widespread presence and obvious contribution to coastal and shelf ecosystem production call for further investigation and for their inclusion in Arctic ecosystem models and carbon budgets.

marine primary production | Arctic ecosystems | macroalgae | seagrasses | microalgae

1. Marine Pelagic Primary Production in the Arctic

Marine primary producers in the water column and sea ice zones of the Arctic Ocean currently convert ~400 teragrams of C per year (Tg C y⁻¹) into biomass via photosynthesis (equivalent to ~1.5 Gt CO₂ y⁻¹) through phytoplankton [~391 Tg C y⁻¹, (1)] and sea ice algae production [~18 Tg C y⁻¹, (2, 3)]. This sustains a unique marine ecosystem (4), globally important industrial fisheries (5), and a way of life for Arctic peoples within the world's northernmost edge (6). Vast expanses of the Arctic Ocean sea ice cover are now melting sooner in the year, freezing up later, and experiencing a more extended melt season (7), altogether yielding a thinner, younger ice pack as well as larger and longer open water periods that are expected to increase further in the coming decades (8). The diminishing Arctic ice pack has important implications for marine primary production: Sea ice algal

communities and the biodiversity they support will likely decline in summer (9–11), favoring phytoplankton that benefit from a longer growing season and increased open water habitat (1, 12, 13). Sustained by increased nutrients from lateral eddy transport, upwelling, river inputs, coastal erosion, and enhanced oceanic connectivity with lower latitudes (14–16), annual Arctic Ocean phytoplankton production has increased steadily over the past ~20 y, with significant positive trends in production being observed on regional- and pan-Arctic scales (1, 12, 17). With increasing phytoplankton production, the biomass of consumers such as krill and fish has also increased in some parts of the Arctic, reflecting a more productive and a more connected ocean (15, 18, 19). Our capacity to understand Arctic marine ecosystems hinges on a robust knowledge of how different groups of primary producers respond to climate change.

2. Seafloor Primary Producers in the Arctic

As the Arctic Ocean continues a path toward sea ice-free conditions in summer and increasing solar irradiance in

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marine waters (20), it becomes increasingly important to understand the distribution and dynamics of marine primary production. Will photosynthetic primary production continue to increase with increasing light availability, or will it stabilize or even decrease because of other changes such as decreased water transparency (increased turbidity) or increased nutrient limitation? In addition to sea ice algae and phytoplankton, a third source of marine primary production in the Arctic are microalgae, macroalgae, and seagrasses living on the seafloor (benthos). The presence of benthic primary producers (BPPs) has important implications for biogeochemical functioning, food-web connections, and energy transfer through to the highest trophic levels (21). However, the quantitative importance of BPPs in the Arctic coastal and shelf seas is poorly resolved and remains largely unknown (22). In this Perspective, we explore the roles of photosynthetic BPPs in the Arctic. We provide a better quantification of their extent and primary production rates, and we compare their contributions to other known sources while highlighting key knowledge gaps to focus future research.

The Arctic harbors an extensive coastline exceeding 250,000 km, and ~6 million km² of its seafloor is shallower than 200 m (23). Its rocky coasts are suitable for canopy-forming macroalgae such as kelps and fucoid brown algae, which, despite a short growing season and the prevailing low temperatures, can maintain high biomass and primary production rates in the intertidal and subtidal zones (24). The same is true for seagrasses. The eelgrass *Zostera marina* is the only seagrass species extending to the Arctic, where it can grow on sandy, soft sediment seafloor in shallow protected areas that occasionally experience water temperatures around 0 °C at its northern limit (25, 26). The broader Arctic continental shelf is sedimentary consisting predominantly of muds and clays (27–29), and millions of km² of this region are expected to receive sufficient sunlight to drive BPP, likely in the form of microalgal-dominated habitats, during some months of the year (30–32). The broadest regions of the Arctic shelf comprising the Chukchi, East Siberian, Laptev, Kara, and Barents seas (altogether ~4.5 million km²) are already almost ice-free in late summer (8) (Fig. 1A). As the

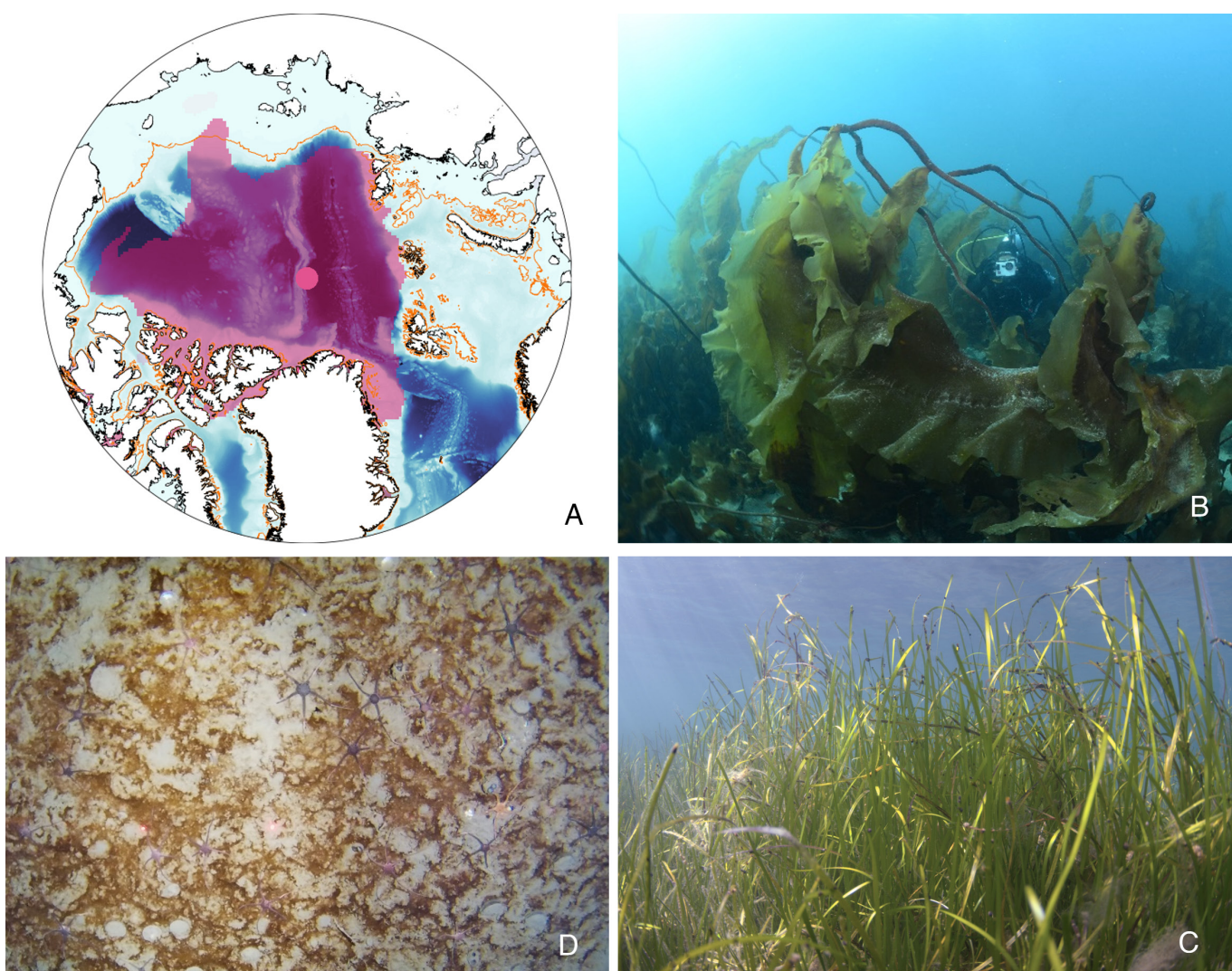


Fig. 1. (A) Arctic bathymetry, showing the shallow shelves in light blue color, with 100-m isobath indicated with an orange line. The minimum sea ice extent for 2022 is indicated as the shaded area in purple (data from NSIDC). (B) Macroalgal forest near Nunavut, northern Canada (photo credit: Ignacio Garrido, ArcticKelp), (C) eelgrass (*Zostera marina*) meadow near Nuuk, southwest Greenland (photo credit: Peter Bondo Christensen), and (D) microphytobenthos on the seafloor (yellow/brown sediment discoloration) in Young Sound, northeast Greenland (photo credit: Amalia Al-Hababbeh).

duration of the ice-free season increases, higher sunlight availability, warmer waters, and less ice scour could permit a larger proportion of the coastline and the seafloor to become habitable for BPPs from the temperate zone, which form the majority of Arctic macrophytes (33). Extensive marginal areas where these ecosystems occur but are constrained by sea ice could also become more productive, expanding their realm in a warming Arctic (25, 34, 35).

Benthic primary producers have long been observed in the Arctic, but given the vastness and remoteness of this region, indications of an active benthic phototrophic community across the whole Arctic are mainly inferred through models. Broad-scale distribution estimates of BPPs are based on a) estimates of the photosynthetically active radiation (PAR; 400 to 700 nm) reaching the seabed, as estimated from satellite-based remote sensing of ocean color (30, 31) in combination with the minimum light requirement of key phototrophic communities determined experimentally [compiled by Gattuso et al. (36)], and b) through niche models for specific taxa such as macroalgae that consider determinants of coverage such as substrate type, wave exposure, and sea ice (25, 34, 37). Model predictions indicate that seafloor PAR can exceed the minimum light requirement of Arctic BPPs over ~3 million km² of the shelf region (30, 36), and the niche models roughly predict the widespread occurrence of intertidal and subtidal macrophytes over >1 million km² along the Arctic coastline (34). BPPs could therefore be present in ~3 million km² of the Arctic Ocean (~half of its shelf) and likely are a generally important component of the ecosystem, as reported for individual locations in the Arctic (38). Their further expansion into the Arctic could be sustained by enhanced nutrient loads already linked to a larger phytoplankton production (14–16). Additionally, macrophytes maintain internal nutrient pools that sustain their production when external nutrient sources are limiting (39), thereby reallocating growth to BPP biomass with higher C:N and likely altering food webs, C cycling, and C sequestration pathways (40). Understanding the dynamics of BPPs in relation to other known primary producers and against a backdrop of a changing Arctic is a key research frontier.

3. Toward Pan-Arctic Estimates of Seafloor Primary Production

Models for pan-Arctic phytoplankton production have existed since the 1980s (e.g., ref. 41) and are being improved and updated continuously (1, 12). These models are based on either a) satellite remote sensing of clouds, ice, and phytoplankton (Chl *a*) used in combination with experimentally determined functional relationships between light availability, phytoplankton biomass, and photosynthesis to investigate the dynamics of Arctic phytoplankton production over the satellite record spanning >20 y (1, 42, 43), or b) coupled physical-biological models (44–46). These models have yielded remarkable insights into primary and secondary production dynamics over broad spatiotemporal scales by identifying Arctic hotspots of biomass, production, and change over time. This now permits good representation of Arctic phytoplankton production in global ecological and biogeochemical models while formulating novel hypotheses. Similarly, large-scale production models for sea ice-associated

(sympagic) algae are also available, although ice algae are less studied than phytoplankton (2). There is, therefore, scope to develop a similar broad-scale understanding of Arctic BPP.

Along coasts with rocky substrate, the growth of several species of macrophytes is initiated in winter and early spring when nutrients are abundant. Later in the year, when sunlight is abundant, macrophytes benefit from a deep photic zone of tens of meters in depth (47), and often extend well into the mesophotic zone (>30 m depth) (e.g., refs. 48 and 49). On the Arctic shelves, where models predict widespread occurrence of light-exposed soft sediments such as muds and clays (27–29), we expect BPP to be dominated by microalgae living on or within the sediments with occasional macroalgae colonizing glacial drop stones. Detailed knowledge of coastal bathymetry and substrate type is therefore important, but the seafloor is poorly mapped in many areas (50). The sedimentary photic zone in the Arctic remains poorly described (51), but studies from other locations document that sunlight reaching the sediment surface is rapidly attenuated with sediment depth, yielding a photic zone of just a few millimeters deep (52–54), thousands of times smaller than the photic zone in the water column. In marine sediments, macronutrients are typically not limiting, as sediments host high densities of heterotrophic bacteria and fauna that degrade sedimentary organic matter and release bioavailable nutrients such as ammonium (NH₄⁺) and nitrate (NO₃[−]), which benthic phototrophs take up (thereby affecting nutrient budgets and competing with other nutrient-consuming processes, such as denitrification) (55–57). Light- and nutrient-replete surface sediments constitute an important niche for benthic diatoms, the predominant primary producer in Arctic sedimentary environments (32, 58–60), which have evolved both structurally [e.g., the shape of the silica cell wall frustule; (61–63)] and behaviorally [e.g., motility, adhesion, chemokinesis, and chemotaxis; (52, 64–68)] to exploit the dynamic conditions in surface sediments (69). Field observations of high benthic microalgal density and Arctic surface sediment chlorophyll-*a* (Chl-*a*) concentration often exceeding 50 mg Chl *a* m^{−2} is evidence of their success (32, 60).

Challenges that are unique to the benthos include the vastly different and heterogeneous habitats, species, and life strategies of Arctic BPPs, which range from microscopic algae and encrusting coralline algae to canopies of seagrasses and towering macroalgae, and which colonize substrates ranging from soft sediments to bedrock (Fig. 1) (47, 70). Accordingly, the methods that are used to estimate BPP vary widely. Studies investigating net primary production by Arctic macroalgae (BPP_{macro}) and eelgrass (BPP_{eel}) largely employ biomass accumulation methods, which are practical and integrate over the growth season, but underestimate net production due to grazing and other processes that erode biomass growth throughout the year (24). Side-by-side comparisons of BPP_{macro} using biomass accumulation and biogeochemical flux measurements (the latter known to much better approximate net primary production) are scarce but indicate substantial increases in annual net primary production using the latter method. For instance, a seasonal study on the perennial brown macroalga *Fucus vesiculosus*, a species common to Arctic waters, estimated an annual net primary production of 0.2 kg C m^{−2} y^{−1} using biomass accumulation and 0.4 kg C m^{−2} y^{−1} using flux measurements

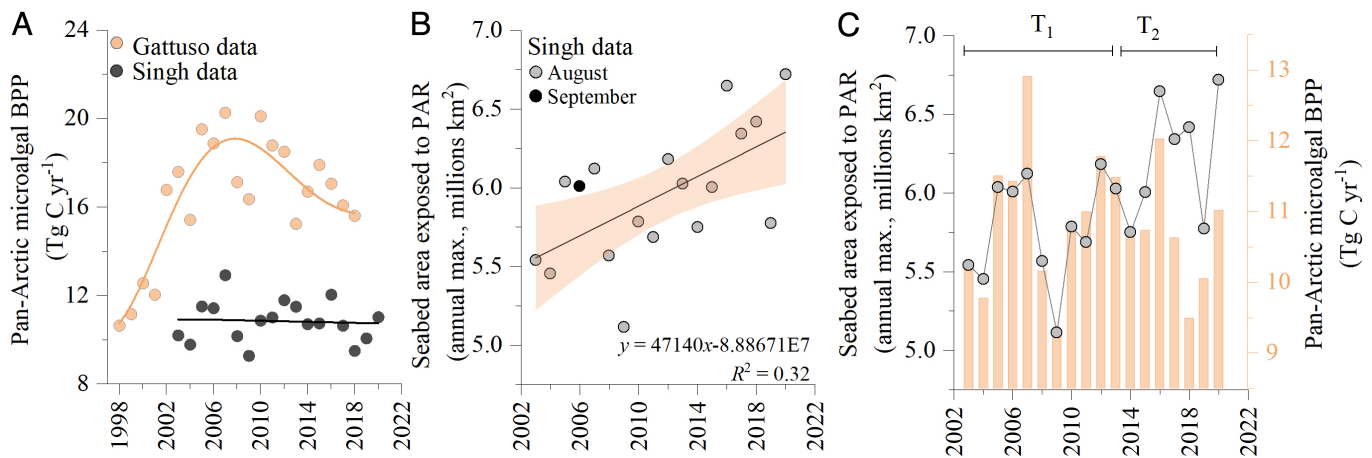


Fig. 2. (A) Pan-Arctic microalgal BPP (BPP_{micro}) based on the seabed PAR models by Gattuso et al. (30) and Singh et al. (31). Trendlines are illustrated as a damped sine wave function for the Gattuso data ($R^2 = 0.71$) and as a linear regression to the Singh data ($R^2 = -0.06$). The slope of the linear regression is not significantly different from zero. (B) Trend in the annual maximum Arctic seafloor area exposed to photosynthetically active radiation (PAR) and (C) seabed area and pan-Arctic BPP_{micro} . T₁ illustrates a period when area and BPP_{micro} generally correlate well (2003 to 2014), while during T₂ (2015 to 2020) area and BPP_{micro} seemingly become less correlated. Analyses for (B) and (C) based on ref. 31.

(71, 72). On the other hand, studies investigating net primary production by Arctic benthic microalgae (BPP_{micro}) commonly use gas exchange methods (typically O_2 flux) and assume an $O_2:CO_2$, termed a photosynthetic quotient (PQ), of ~ 1.2 to convert to C equivalents (32). Here, fluxes represent net primary production rates of benthic microalgae, but can include additional heterotrophic components of the habitat, such as benthic fauna, depending on the spatial scale of investigation. Isotope incorporation techniques commonly used to approximate phytoplankton net primary production (^{14}C - or ^{13}C -labeling) are challenging to use in benthic systems. Uncertainties in inorganic C speciation and the presence of steep gradients in solutes and light make it challenging to determine the specific labeling of dissolved inorganic C by photosynthesizing benthic microalgae (32). Net primary production comparisons between benthic habitats and across sea ice, pelagic, and benthic ecosystems are therefore inexact due to methodological differences. While these remain the best available estimates, methodological differences would propagate into the pan-Arctic estimates of BPP_{macro} , BPP_{eel} , and BPP_{micro} presented in this study.

3.1. Seafloor Microalgal Primary Production on Arctic Shelves.

Pan-Arctic models of PAR availability on the seafloor based on ocean color remote sensing (30, 31) in combination with the growing database of Arctic microalgal benthic primary production (BPP_{micro}) measurements make it possible to estimate BPP_{micro} of the Arctic shelves. Two models for estimating PAR availability on the Arctic seafloor are available: a) the global model by Gattuso et al. (30), which provides daily integrated seafloor PAR (mol photons $m^{-2} d^{-1}$) for 5 mo of the year (June to October) over 21 y (1998 to 2018), and b) the model by Singh et al. (31), which similarly provides daily integrated seafloor PAR but for 18 y (2003 to 2020). Given the relatively coarse spatial resolution of these models, i.e., 4.6 km for Gattuso et al. (30) and 1 km for Singh et al. (31), these data effectively capture the broader Arctic shelves but exclude near-shore areas including the many Arctic fjords and embayments. Some overlap in areas with macrophyte-dominated habitats can be expected, but microalgae and

macrophytes are likely to co-occur in these regions. The two models consider different approaches for computing seafloor PAR. Therefore, their estimates of absolute PAR values are independent and can differ (discussed in ref. 31).

Regarding net primary production of microalgae-dominated benthic habitats, we focused on BPP_{micro} data collected using the aquatic eddy covariance method (73, 74). This method is particularly suited to upscaling to daily PAR models because it is noninvasive, allowing functional relationships between PAR and BPP_{micro} to be developed with confidence. It also integrates over a relatively large seafloor area in its measurement (typically 10 to 100 m^2), which is important given that benthic habitats are notoriously patchy (75, 76). The aquatic eddy covariance database currently includes 35 multiple-day deployments from around Greenland targeting microalgal-dominated benthic habitats in different locations, depths, and seasons (58, 77, 78) (SI Appendix, Fig. S1). These measurements reveal a significant positive relationship between daily BPP_{micro} (expressed in $mmol O_2 m^{-2} d^{-1}$) and the daily integrated PAR measured just above the seabed (in mol photons $m^{-2} d^{-1}$) (SI Appendix, Fig. S2). The focus on daily primary production as a measure of photosynthesis has similarly been employed in phytoplankton studies (79). The functional relationship in SI Appendix, Fig. S2 provides a means to upscale point measurements to the pan-Arctic models by Gattuso et al. (30) and Singh et al. (31) and doing so reveals that pan-Arctic BPP_{micro} over the satellite record has ranged from 10.6 to 20.3 $Tg C y^{-1}$ (average = $16.4 \pm 2.8 Tg C y^{-1}$; $n = 21$) for the PAR model by Gattuso et al. (30), and from 9.3 to 12.9 $Tg C y^{-1}$ (average = $10.8 \pm 0.9 Tg C y^{-1}$, $n = 18$) for the PAR model by Singh et al. (31) (Fig. 2A). These values are comparable to primary production by sea ice algae [$\sim 18 Tg C y^{-1}$; (2, 3)] and compare well to previous pan-Arctic estimates of BPP_{micro} by Glud et al. (32) ($16 Tg C y^{-1}$).

The trend in annual BPP_{micro} based on the Gattuso et al. (30) PAR model shows a doubling of BPP_{micro} from 1998 to 2005 followed by a rapid decline from 2005 to 2018 (Fig. 2A). BPP_{micro} based on the Singh et al. (31) PAR model shows some temporal variations although overall annual BPP_{micro} has neither increased nor decreased significantly since 2003 (Fig. 2A). The

higher annual BPP_{micro} obtained when using the Gattuso et al. (30) PAR model is expected, as this model generally overestimates benthic PAR by not considering PAR reflection at the water surface and PAR absorption by dissolved organic matter in the water column, both of which are considered in the model by Singh et al. (31). Overall, the trends in BPP_{micro} starkly contrasts pan-Arctic phytoplankton production, which has increased quasi-linearly at $\sim 6.8 \text{ Tg C y}^{-1}$ since 1998, equivalent to a 57% increase between 1998 and 2018 (1, 12).

Analysis of the seafloor area exposed to sunlight reveals that the light-exposed area of the Arctic seafloor peaks in August or September and has been increasing at a rate of $\sim 47,000 \text{ km}^2 \text{ y}^{-1}$ between 2003 and 2020 (Fig. 2B). For comparison, the Arctic Ocean open-water area has expanded by $95,000 \text{ km}^2 \text{ y}^{-1}$ between 1998 and 2008, and by $32,000 \text{ km}^2 \text{ y}^{-1}$ between 2009 and 2018 (1). The extent of the benthic area seems to correlate well with annual pan-Arctic BPP_{micro} up until around 2014 (illustrated by period T₁ in Fig. 2C). Since 2014, however, area and BPP_{micro} are less correlated (period T₂ in Fig. 2C), suggesting that despite a larger light-exposed seafloor area, the annually integrated light availability on the seafloor could have decreased in some regions resulting in lower BPP_{micro}. Regional trends in BPP_{micro} and PAR can be illustrated for the different Arctic regions by investigating the trend for each pixel of data over the satellite record (Fig. 3). In doing so, it becomes evident that despite substantial sea ice loss, BPP_{micro} only increased in a few regions of the Arctic shelf (Fig. 3D). In regions that remained the same or that experienced a reduction in BPP_{micro}, we expect that the increase in PAR transmittance due to sea ice loss was counterbalanced by reduced water transparency due to, e.g., increased concentration of phytoplankton, suspended sediment, and/or chromophoric dissolved organic matter (CDOM) (31). This is illustrated by an increase in the attenuation coefficient of PAR, K_d(PAR), in many Arctic regions over the past 20 y (Fig. 3C). The factors influencing PAR absorbance and their dynamics across the various Arctic regions remain to be explored further.

The BPP_{micro} model predicts that 50 to 60% of the annual BPP_{micro} activity takes place in July and August. In these months, Arctic waters are relatively transparent, as phytoplankton growth is limited by nutrient availability (predominantly nitrate) (12, 81) and terrestrial runoff has decreased from the spring peak (82). With the ice cover at a minimum and a low phytoplankton biomass, benthic microalgae might become a main source of autochthonous produced organic matter, fueling food webs during the short but productive Arctic summer (83, 84). The PAR model by Gattuso et al. (30) considers only the period from June to October, whereas the Singh et al. (31) PAR model is year-round. Our BPP_{micro} model based on ref. 31 suggests that 15 to 21% (average = $17 \pm 2\%$, $n = 18$) of the annual BPP_{micro} occurs outside of the June to October period. Understanding the phenology and distribution of BPP_{micro} is important. Furthermore, an increasing number of field observations document dense coverage of BPPs under extreme low PAR irradiance and/or under highly turbid waters, challenging existing paradigms (60, 85, 86) (Fig. 4). These observations add to the growing literature documenting the low light requirements of Arctic primary producers (87, 88). Conditions leading to development of high standing benthic microalgal biomass in turbid and dimly lit waters is still unclear, but it is known that sedimentation

strongly influences the structure of benthic communities in polar environments, favoring rapid colonizers and pioneer species such as diatoms and highly mobile fauna, while excluding other common grazers (89, 90) (Fig. 4). Microalgae such as diatoms are capable of rapid colonization, and their motility and ability to optimize light exposure could be advantageous in these dynamic settings (65, 69, 91).

3.2. Primary Production by Macrophytes in the Arctic Coastal Zone.

For macroalgae colonizing the coastal zone, it is possible to coarsely estimate pan-Arctic primary production by combining recently published niche distribution models (37) predicting their likelihood of occurrence for each of the 19 Arctic coastal ecoregions (92), with annual per-area BPP_{macro} data for key orders of Arctic brown macroalgae (Laminariales, Tilopteriales, Fucales, and Desmarestiales) (reviewed in refs. 24 and 37). The per-area BPP_{macro} is highly variable, ranging from 8 to $966 \text{ g C m}^{-2} \text{ y}^{-1}$ (mean $\pm \text{SE} = 194 \text{ g C m}^{-2} \text{ y}^{-1} \pm 55$, $n = 17$), and regional BPP_{macro} ranges from 0.06 Tg C y^{-1} in the White Sea, Russia, to $12.29 \text{ Tg C y}^{-1}$ in the Hudson Complex, Canada, and a total pan-Arctic BPP_{macro} = $\sim 43 \text{ Tg C y}^{-1}$. Notably, abundant encrusting coralline algae, understudied Arctic red, green, and some brown algae are excluded from this estimate (26, 34, 93, 94). Other considerable uncertainties underpinning this estimate include area and depth distribution of macrophytes and the fraction of suitable substrates along the coasts, which remain unverified for many Arctic regions. Field observations document macroalgae growing at 50 to 60 m depth in coastal areas with sea ice (95, 96), which is deeper than the 30 m depth limit used in current distribution models. For example, estimates of kelp BPP in the Eastern Canadian Arctic range from 4 to 11 Tg C y^{-1} when calculated using a 15 m depth limit compared to 7 to 21 Tg C y^{-1} using a 30 m depth limit, both limits that frequently occur along different regions of coastline (97). State-of-the-art assessments (25, 37) currently assume suitable substrate based on land features [e.g., coastal cliffs (98)], as maps of seafloor type and high-resolution bathymetry data are rare. The growing database of regional analyses of macroalgal distribution and observational data, such as those for the Nordic (99–102) and Canadian regions (97, 103), serve as an important ground truthing of large-scale models and permit moving beyond regional averages by considering additional key variables such as sea ice, latitude, and wave fetch.

The eelgrass *Zostera marina*, the only known Arctic seagrass, is distributed along the coasts of Russia, Norway, Iceland, southern Greenland, and Canada (34, 104). Estimates of eelgrass benthic primary production (BPP_{eel}) in the Arctic and subarctic are scarce, but the study by Olesen et al. (26) enables a first-order estimate. Aboveground production, in $\text{g C m}^{-2} \text{ y}^{-1}$, was estimated from aboveground biomass, C content, and leaf production-to-biomass ratios. Belowground production, also in $\text{g C m}^{-2} \text{ y}^{-1}$, was estimated from belowground biomass, C content, and maximum rhizome age. Eelgrass production was computed as the sum of above- and belowground annual production ($\text{g C m}^{-2} \text{ y}^{-1}$). Pan-Arctic estimates of annual BPP_{eel}, in Tg C y^{-1} , were approximated using the distribution model by Jayatilake and Costello (104), adjusted for the proportion of sedimentary areas (98), and computed as the product of annual production and extent. Using this approach, annual per-area BPP_{eel} ranges from 75 to $348 \text{ g C m}^{-2} \text{ y}^{-1}$, which when upscaled to its potential Arctic

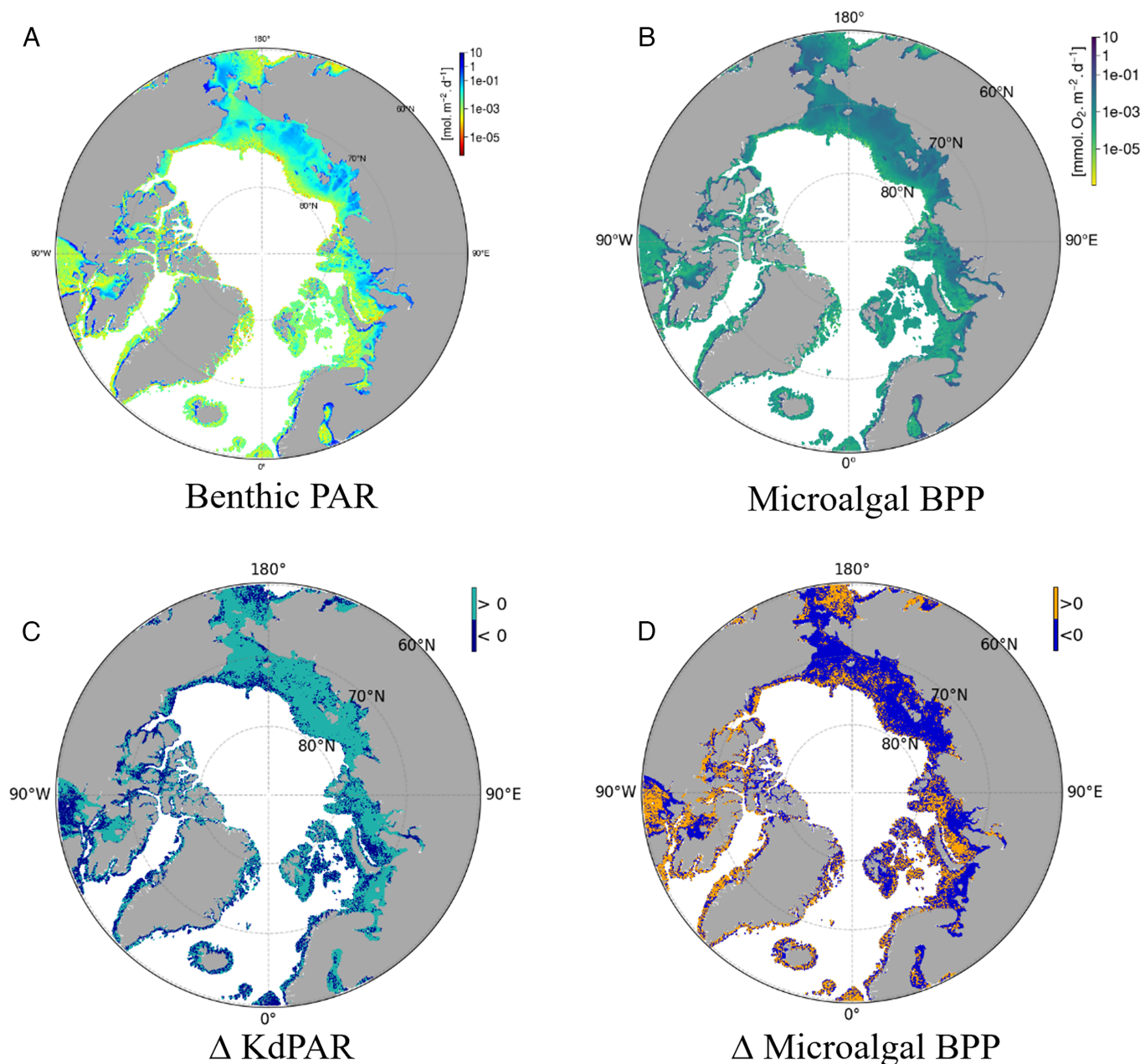


Fig. 3. August estimates for (A) benthic photosynthetic active radiation (PAR) from ref. 31, (B) rates of microalgal BPP (BPP_{micro}), (C) trend in the light attenuation coefficient (KdPAR) over the satellite record (2003 to 2020), where >0 suggests more turbid waters and vice-versa, and (D) trend in BPP_{micro} as in (C). The KdPAR was computed from MODIS-Aqua data acquired from NASA Ocean Biology Distributed Active Archive Center using the method described by Saulquin et al. (80).

distribution ($\sim 77,000 \text{ km}^2$) yields a BPP_{eel} range ~ 6 to 27 Tg C y^{-1} (median $BPP_{eel} \sim 23 \text{ Tg C y}^{-1}$) and thus about twice as high as BPP_{micro} ($\sim 11 \text{ Tg C y}^{-1}$) and $\sim$ half of BPP_{macro} ($\sim 43 \text{ Tg C y}^{-1}$). Overall, it appears that BPP_{eel} could be considerable, but this value should be interpreted with caution, as further measurements of distribution and areal BPP_{eel} are needed to better constrain annual production within different Arctic coastal ecoregions.

4. What Models Predict for the Sunlit Arctic Shelf

From the models by Gattuso et al. (30) and Singh et al. (31), we can make several inferences about the benthic light

climate we expect Arctic phototrophs to experience. Both models predict August and September as the months where benthic PAR and the light-exposed seafloor area are at its greatest (Fig. 2B). In terms of PAR irradiance, $\sim 60\%$ of the photic seafloor in August receives a low daily integrated PAR irradiance of 0.1 to $1.0 \text{ mol m}^{-2} \text{ d}^{-1}$ (phototrophs exposed to $1.0 \text{ mol photons m}^{-2} \text{ d}^{-1}$ under a 12 h light-dark cycle at 64°N would experience a maximum instantaneous PAR irradiance of about $40 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$). The aquatic eddy covariance database for Arctic BPP_{micro} suggests that habitats receiving $<1 \text{ mol photons m}^{-2} \text{ d}^{-1}$ photosynthesize more efficiently per photon reaching the seafloor than habitats receiving higher light intensities (~ 3.8 -fold higher; *SI Appendix, Fig. S2*), supporting the still scarce evidence for acclimation

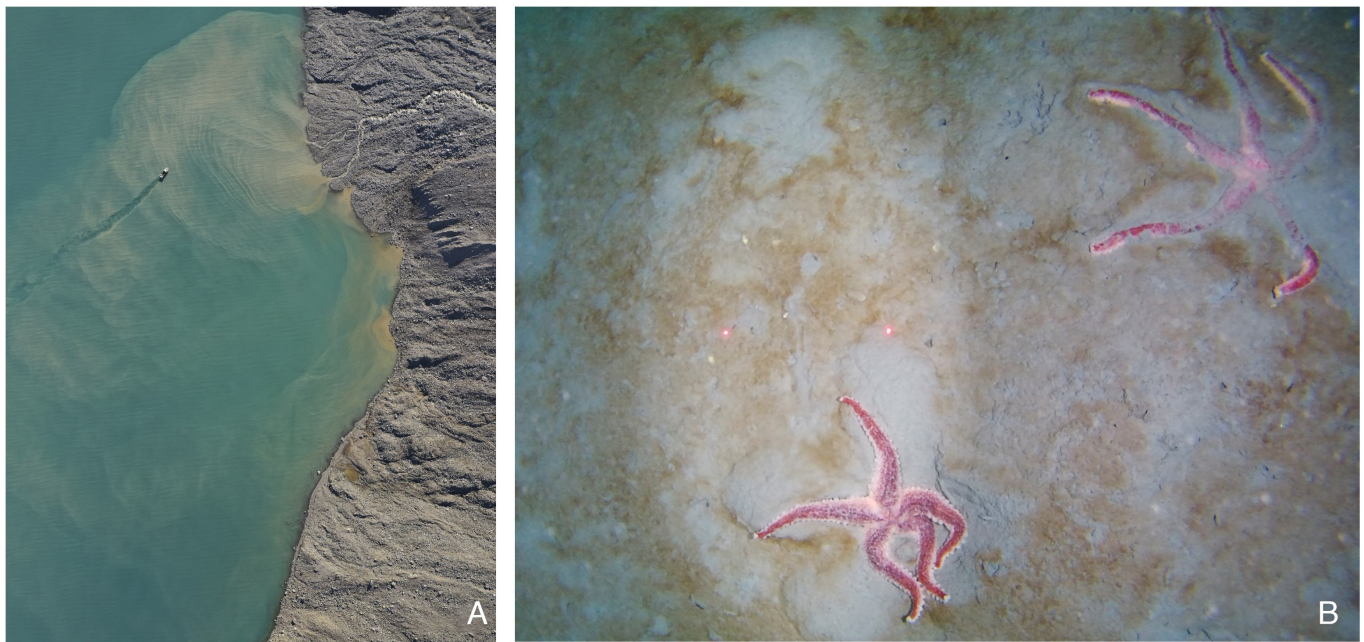


Fig. 4. (A) An aerial drone image of a meltwater runoff plume taken in NE Greenland in August 2022, showing a 10-m-long research vessel for scale, and (B) dense assemblages of benthic microalgae colonizing sediments at 20 m depth together with two Arctic sea stars (*Urasterias* sp.) beneath the turbid meltwater plume receiving a maximum PAR irradiance of $\sim 4 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Photo in (B) courtesy of Amalia Al-Hababbeh.

of benthic primary producers to life in dimly lit waters (e.g., ref. 85). Photoacclimation via upregulation of photoactive pigments and other adjustments of the photosynthetic machinery, alterations to cell shape and orientation to optimize light capture and carbon fixation efficiency, dark survival (105), and reduced metabolism are all adaptations to low or no light that remain to be studied in more detail among BPPs in the Arctic.

Marine sediments exposed to low light would yield a sediment photic zone equivalent to just a few cell layers, where light absorption is predominantly by active photopigments, yielding a higher apparent light-use efficiency (52). Thus, measurements performed under high irradiance cannot be extrapolated to low-light regions with confidence. The models by Gattuso et al. (30) and Singh et al. (31) predict that about one-third of the sunlit Arctic seafloor receives sufficient PAR irradiance for driving photosynthesis at depths >30 m, but little data are available (e.g., *SI Appendix, Fig. S1*). This implies that a substantial proportion of BPP in the Arctic occurs at mesophotic depths, where the spectrum of PAR might be modified substantially by scattering and absorption in the overlying water column before reaching the seafloor. The quality of light available for photosynthesis because of spectral attenuation by multiple components in marine coastal waters can structure both macrophyte and microalgal communities on the seafloor (61, 100, 106). The presence of dimly lit and deep photic habitats in the Arctic calls for a thorough evaluation. Given the challenges of performing research at mesophotic depth (107), it might not come as a surprise that the Arctic mesophotic zone remains poorly studied. However, understanding how these habitats function clearly is needed to grasp changes occurring within broader Arctic marine ecosystems.

5. Toward a Robust Pan-Arctic Understanding of BPP

In this Perspective, we conclude that there is ample evidence for widespread BPPs in the Arctic and that their significant contributions to primary production within Arctic coastal and shelf seas justify a need for systematic investigation and inclusion in carbon budgets and ecosystem models. Our estimate of pan-Arctic BPP of $\sim 77 \text{ Tg C y}^{-1}$, of which BPP_{macro} contribute $\sim 43 \text{ Tg C y}^{-1}$, BPP_{eel} contribute $\sim 23 \text{ Tg C y}^{-1}$, and BPP_{micro} contribute $\sim 11 \text{ Tg C y}^{-1}$, is substantial when compared to other known sources of primary production such as phytoplankton, which have varied from 221 to 391 Tg C y^{-1} over the past ~ 20 y (1), and sea ice algae, which contribute $\sim 18 \text{ Tg C y}^{-1}$ (2, 3) (Fig. 5). We also demonstrate that the light-exposed area of the Arctic seafloor has been expanding rapidly with climate change at a rate of $\sim 47,000 \text{ km}^2 \text{ y}^{-1}$ (Fig. 2B), increasing the habitable zone of BPPs in a warming Arctic. Marginal areas harboring BPPs that are presently contained by sea ice could become more productive. However, increased solar irradiance at the ice-free sea surface is being counterbalanced by reduced coastal water transparency in many regions, which reduces the total light reaching the seafloor (Fig. 3C). The spatio-temporal dynamics of water transparency, including the factors contributing to reduced transparency (i.e., increased phytoplankton, suspended sediment, and/or CDOM) require further investigation. Reduced water transparency could lead to an upward shift of the depth limit of subtidal BPPs (100).

Understanding the distribution, quantity, and phenology of BPPs is important given that currently, Arctic Ocean carbon budgets are bound by large uncertainty. For instance, vertical carbon export rates measured in the pelagic zone are not sufficient to sustain carbon demands of the underlying pelagic

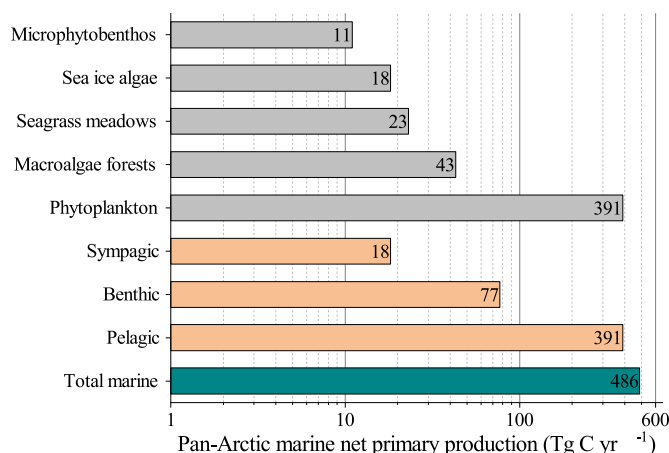


Fig. 5. Contemporary estimates of Arctic marine photosynthetic net primary production by known sources. The value for sea ice algae production is the median value estimated from the studies by Tedesco et al. (2) and Vancoppenolle and Tedesco (3). Phytoplankton production is the 2018 value in ref. 1.

and benthic habitats (108), suggesting that other sources such as lateral flows of organic matter produced by BPPs are likely important (109–111). Other primary producers, such as chemoautotrophs, also contribute to marine primary production. Globally, sediment chemoautotrophy represents around 5% of marine primary production (112). In the Arctic, maximum areal rates of sediment chemoautotrophy appear low ($\sim 0.6 \text{ mmol C m}^{-2} \text{ d}^{-1}$) when compared to BPP_{micro} in adjacent sediments ($\sim 140 \text{ mmol C m}^{-2} \text{ d}^{-1}$) (77, 113). However, chemosynthesis can proceed in the absence of sunlight, extending to a much larger area of the seafloor, and takes place throughout the year, making it potentially significant.

To stimulate Arctic BPP research and to move this research field forward, we have identified priority areas for research, which will improve our understanding of BPPs in the Arctic (SI Appendix, Table S1). Arctic bathymetry and seafloor type emerge as knowledge gaps of key importance, with errors propagating into BPP distribution and production estimates. Despite the latest available models providing a grid cell-size resolution on a Polar Stereographic projection of $200 \text{ m} \times 200 \text{ m}$ [IBCAO Version 4.0, (23)], the digital bathymetric grid lacks measurements in major parts of the shelf such as parts of the Chukchi, East Siberian, Laptev, Kara and Barents seas (50); areas where we expect to find significant BPP activity (Fig. 3B). Collection and provisioning of seafloor bathymetry for the Arctic coastal zone is important, and here, we note major ongoing initiatives, such as the Nippon Foundation—GEBCO Seabed 2030 project, which aims to map all shallow waters at $100 \text{ m} \times 100 \text{ m}$ grid resolution by 2030 [reviewed by Jakobsson et al. (50)].

Sunlight availability is another key variable for benthic phototrophs, and the models by Gattuso et al. (30) and Singh et al. (31) represent the best available estimates for the Arctic. New initiatives such as the European Space Agency's Sentinel program and NASA's Plankton, Aerosol, Cloud, ocean Ecosystem (PACE) program are much anticipated and will improve estimates significantly. Describing the sedimentary photic zone in the Arctic, including the spectral quality of light, will help to understand the importance of light in structuring biotic communities and biogeochemical cycles. Models projecting light availability into the future coastal ocean are

needed to better constrain the expansion of BPPs into the Arctic, which is expected to be substantial (34).

With regard to BPP estimates, it is evident that macroalgae and seagrasses could be important to Arctic marine primary production. Here, direct measurements are sparse, so new measurements are required to better approximate their area coverage and net primary production rates. In addition to rocky substrates, macroalgal forests often are encountered colonizing glacial drop stones in sedimentary and permafrost areas, and may even colonize scattered cobbles (96). Further observational data (e.g., in situ imaging) in combination with environmental data and seafloor mapping would improve our understanding of suitable substratum and distribution models. These efforts would allow moving beyond regional averages and toward dynamic models that can better be compared to phytoplankton and benthic microalgal production. Although we assume light to be a predominant driver of BPP (SI Appendix, Fig. S2), top-down controls on biomass, such as grazing by sea urchins, appear to be important in some Arctic coastal regions (e.g., Nuuk fjord, Greenland), but not in others (e.g., in the northern part of Hudson Bay, Canada) (96, 114). Understanding what factors determine grazing pressure on local scales and developing a broad-scale understanding of its impacts on biomass and production of Arctic BPPs is important.

Overall, BPPs are key to contemporary and future Arctic ecosystem functioning. To achieve a comprehensive understanding of Arctic BPPs, it is important to engage in collaborative multidisciplinary endeavors that integrate field and laboratory experiments. This synergy would improve our knowledge base and, when combined with modeling and data science tools, would permit extrapolation of point measurements with more confidence, enabling further exploration of the expansive and understudied Arctic Ocean.

Data, Materials, and Software Availability. Arctic bathymetry and sea ice extent are openly available from the International Bathymetric Chart of the Arctic Ocean and from the National Snow and Ice Data Center. Benthic PAR climatology by Gattuso et al. (30) is openly available on PANGAEA (115). All data presented in this paper are openly available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.n2z34tn49>.

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