

THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

CITATION

Wassmann, P., and M. Reigstad. 2011. Future Arctic Ocean seasonal ice zones and implications for pelagic-benthic coupling. *Oceanography* 24(3):220–231, <http://dx.doi.org/10.5670/oceanog.2011.74>.

COPYRIGHT

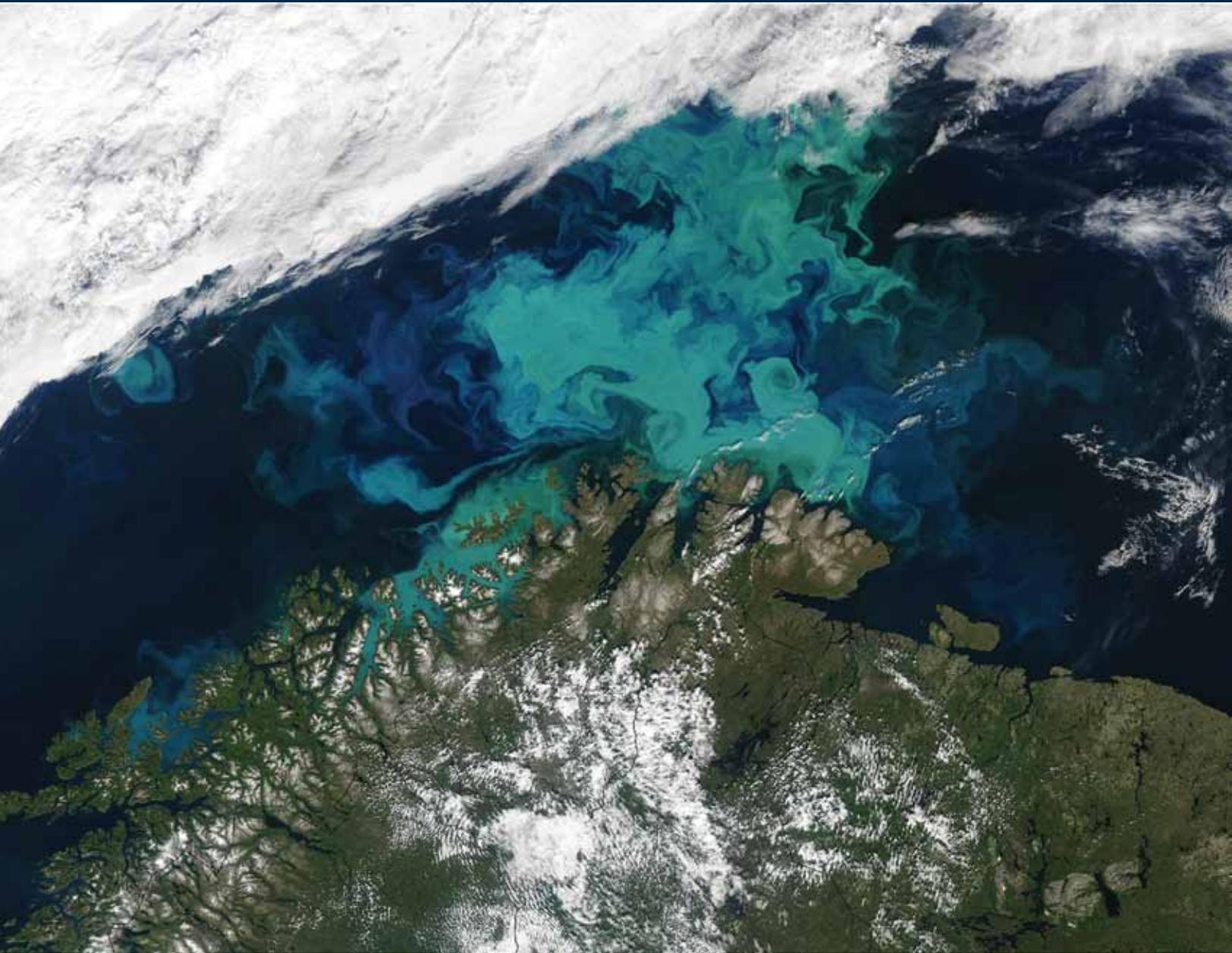
This article has been published in *Oceanography*, Volume 24, Number 3, a quarterly journal of The Oceanography Society. Copyright 2011 by The Oceanography Society. All rights reserved.

USAGE

Permission is granted to copy this article for use in teaching and research. Republication, systematic reproduction, or collective redistribution of any portion of this article by photocopy machine, reposting, or other means is permitted only with the approval of The Oceanography Society. Send all correspondence to: info@tos.org or The Oceanography Society, PO Box 1931, Rockville, MD 20849-1931, USA.

Future Arctic Ocean Seasonal Ice Zones and Implications for Pelagic-Benthic Coupling

BY PAUL WASSMANN AND MARIT REIGSTAD



The display of color in the southern Barents Sea north of Norway reveals a bloom of tiny marine plants called phytoplankton. The colors can be produced by a variety of pigments, including chlorophyll, that the plants use to harness sunlight for photosynthesis. This Moderate Resolution Imaging Spectroradiometer (MODIS) image was captured by the Aqua satellite on July 19, 2003. From http://visibleearth.nasa.gov/view_rec.php?id=16521

ABSTRACT. Despite concerns about rapid changes in Arctic Ocean physical forcing and ecosystem function, quantitative knowledge and time series are scarce. The number of reliable physical-biological coupled models and models based on remote sensing is small. To improve our comprehension of carbon flux in the most prominent Arctic Ocean feature, the seasonal ice zone, a possible first step is to evaluate how biogeochemical cycling might develop in the future by examining conceptual models that address climate warming and seasonality in ecosystem development. Here we present three conceptual models of biogeochemical cycling and climate warming in the seasonal ice zone of the Arctic Ocean. They are designed to enhance, in a conceptual and semiquantitative manner, understanding of the possible temporal sequence of future primary production development, its spatial variation, and food availability in the most productive part of the future Arctic Ocean, including pelagic-benthic coupling. We speculate that the largest changes will take place in (a) the northern portions of today's seasonal ice zone, which will expand to cover the entire Arctic Ocean, and (b) the southern portions, which will be exposed to more thermal stratification. The former change increases and the latter change decreases productivity and supply to the bottom. Lack of nutrient availability means that new production in the central Arctic Ocean will remain low. Blooms of ice and plankton algae may start earlier, depending on snow cover, providing more continuity in food supply for grazers in the upper water column. Weakening of today's highly episodic primary production in the seasonal ice zone will result in lower average food concentrations for pelagic heterotrophs. We suggest that more of the available energy will be recycled in the pelagic zone, and that vertical export of biogenic matter will be less variable and of reduced quality.

INTRODUCTION

In the Arctic Ocean, productivity, biogeochemical cycling, and pelagic-benthic coupling (i.e., the link between pelagic and benthic systems) are primarily determined by the distribution, thickness, and melt dynamics of sea ice. Global warming is reflected in decreased extent and thickness of sea ice in the Arctic Ocean (Comiso, 2003; Kwok and Rothrock, 2009). Ice cover extent has shown an overall negative trend for 1979–2006 (Stroeve et al., 2007), decreasing at an average rate of 10% per decade (Comiso et al., 2008; Polyakov et al., 2010). Melting accelerated in 2007, but a slower and still negative trend was re-established in 2008–2010. Nonetheless, the Arctic Ocean may be largely ice-free in late

summer in two to three decades, with a winter cover consisting mainly of first-year ice. In addition, the average ice thickness has decreased steadily, and the Arctic Ocean may have lost over 50% of its sea ice volume (Kwok and Rothrock, 2009). Simultaneously, freshwater inputs have increased (McPhee et al., 2009; Yamamoto-Kawai et al., 2009), and ice transport toward Fram Strait has grown in both volume and velocity (von Eye et al., 2009). Along with the reduction of sea ice cover, there has been an increase in the area of low surface salinity and stratification in the pan-Arctic meltwater

band (i.e., the seasonal ice zone). These changes have been accompanied by surface-layer warming. The amount of photosynthetic and UV radiation that reaches the water column has increased in most of the seasonal ice zone. Conversely, total incident radiation may have decreased in shelves that receive river discharges and diffuse runoff from land because of increased particle content owing to permafrost melting on land.

Thus, the entire physical forcing that determines productivity, biogeochemical cycling, and the relationship between algae and grazers has already changed and continues to do so steadily (see Box 1). Clearly, these environmental alterations have also had an impact on pelagic-benthic coupling (e.g., export of fresh algae, zooplankton fecal pellets, and other detritus from the water column to the bottom). The largest share of pelagic-benthic coupling is composed of vertical export or gravitational flux. Vertical flux depends, first of all, on primary production, but also upon the feeding intensity of zooplankton in the upper layers that simultaneously impoverishes their feeding grounds (Wassmann, 1998). Vertical flux of organic matter also influences atmospheric carbon dioxide drawdown, which is of global significance in the Arctic Ocean (Bellerby et al., 2005). When the Arctic Ocean is subjected to new physical regimes and rapid changes, ecological responses and adjustments of both pelagic and bottom-dwelling organisms as well as changes in biogeochemical cycling are likely to ensue.

Paul Wassmann (*paul.wassmann@uit.no*) is Professor, and **Marit Reigstad** is Professor, Institute of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economy, University of Tromsø, Tromsø, Norway.

BOX 1 | PHYSICAL FORCING INFLUENCING CARBON FLUX IN THE ARCTIC OCEAN: AN OVERVIEW

Annual primary production by ice algae and phytoplankton in the seasonal ice zone is determined by nutrient availability (generally low winter accumulated concentrations, except in regions of advection or shelf breaks), light (determined primarily by ice, snow cover, and atmospheric conditions), upper-layer stratification (depending mainly on ice melt, but in some regions also on river discharge), and type of algae present (ice or phytoplankton algae). Based upon predicted changes in climate, we can identify factors that would be expected to *increase* primary production in the future Arctic Ocean:

- Episodic nutrient availability (upwelling at shelf breaks and low-pressure passages)
- Increased light availability due to ice melt and reduced snow cover (due to rain and warm-weather spells)
- Increased nutrient discharge from rivers

By the same token, we can identify factors that would *decrease* primary production:

- Increased stratification (ice melt and river discharge)
- Increased denitrification on the shallow shelves in the Pacific sector
- Decrease in incident light (more cloudy weather in the low-pressure belt)
- Increased turbidity in river discharge regions (permafrost melt, beach erosion, river discharge, wind-driven resuspension)

How can pan-Arctic changes in primary production (see Box 2 for terminology details) and ecosystem function be described and understood? This timely question is presently difficult, if not impossible, to answer adequately. Historical impediments—practical and political—have prevented intensive research in the Arctic so that ongoing and future change in the Arctic must be measured against comparatively weak baseline knowledge (Wassmann et al., 2011). The future ecology of the seasonal ice zone and pelagic-benthic coupling are thus difficult to depict, let alone predict. In addition, the Arctic Ocean

is complex, composed of five ecosystems that contribute to productivity and biogeochemical cycling. There are three different shelf ecosystem types (Carmack and Wassmann, 2006): inflow (Barents and Bering Seas), outflow (Fram Strait and Canadian Archipelago), and interior (Siberian and Beaufort shelves). And, there are two deep basins (the Nansen/Amundsen and Canadian Basins), separated by the Lomonosov Ridge, that function differently.

In a region as remote, vast, and inaccessible as the Arctic Ocean, the only practical method for addressing climate change and primary production over the

entire region is to apply mathematical models developed from and validated by existing measurements of the physical, chemical, and biological oceanography from areas that have been investigated. The number of well-documented changes in planktonic and benthic systems in the Arctic Ocean is surprisingly low (Wassmann et al., 2011). Likewise, the number of available physical-biological coupled models for the region is low, but this field is rapidly developing (e.g., Popova et al., 2010; Zhang et al., 2010; Slagstad et al., 2011). Despite the alarming nature of warming and its potentially strong effects on the Arctic Ocean, little research is being done to evaluate the impacts of climate change in a balanced manner over the entire region.

GOAL AND INTENTIONS

To determine how productivity and pelagic-benthic coupling in the Arctic Ocean will evolve in the near future, and to develop more realistic mathematical models, we apply future ecosystem scenarios as the basis for designing suitable dedicated investigations. Conceptual models for the Arctic Ocean have been presented previously (e.g., Hunt and Stabeno, 2002; Carmack and Wassmann, 2006; Leu et al., 2011; Wassmann, 2011). Some of them are re-edited and compiled here, with the goal of shedding light on the fate of carbon in the Arctic Ocean by focusing upon rapid transitions and future ecosystem states, in particular. To this end, we display semiquantitative scenarios that focus on the physical forcing of primary production and pelagic-benthic coupling. For a “bird’s-eye” perspective of future primary production in the Arctic Ocean, see Box 3.

We focus mostly upon the European Arctic Corridor (Fram Strait to Kara Sea) and adjacent basins, the climate “motor” of the Arctic Ocean. More than 80% of the total water exchange between the Arctic Ocean and the adjacent Atlantic and Pacific Oceans takes place within this corridor. The Barents Sea alone, comprising about 30% of the total shelf area in the Arctic Ocean, provides over half of the ocean’s total primary production (Sakshaug, 2004; Wassmann et al., 2010). Thus, we focus largely on the Arctic Ocean’s most important carbon cycling region, and less on other regions such as the Bering Strait/Chukchi Sea and the Siberian shelves. Also, little attention is paid here to the interior shelves whose significant terrigenous supply of biogeochemical matter, turbidity, and shallowness has particular primary production and pelagic-benthic coupling constraints.

Alternative scenarios of climate forcing and ecosystem function for today’s and the future Arctic Ocean exist. One of them, the Oscillating Control Hypothesis (e.g., Hunt and Stabeno, 2002), characterizes the shallow parts of the Bering Sea shelf (50–100 m depth), but may have application for adjacent regions. The region is characterized by low Arctic latitude, ~ 55° N, an unusual range of Arctic temperatures (–1.8 to 14°C), strong wind forcing (when ice-free), and zooplankton species that can cope with extensive environmental variability. Thus, the ice-covered Bering Strait is, by definition, a part of the Arctic Ocean, but has noticeable subarctic and boreal features. These conditions deviate strongly from the core of the Arctic Ocean and the Oscillating Control Hypothesis and are, therefore,

not included in the scenarios presented here. An all-encompassing ecosystem development theory for the Arctic Ocean has still to be developed.

How Will Global Warming Change the Timing of Primary Production in the Ice-Covered Arctic Ocean?

The growth of ice algae depends primarily on light availability, as determined by solar angle, ice thickness, and snow cover. Ice algae production is patchy and highly variable, averaging 5–10 g C m⁻² yr⁻¹; the concomitant production of Arctic phytoplankton is higher, averaging 12–50 g C m⁻² yr⁻¹,

depending on latitude and the duration of ice-free periods (Legendre et al., 1992; Gosselin et al., 1997). In areas with more extensive ice cover, ice algae are of comparatively greater importance. In the central Arctic Ocean’s multiyear ice pack, for instance, ice algae contribute, on average, 57% of the total primary production (Gosselin et al., 1997). The relative contribution of ice algae to primary production and vertical export in the various sectors of the seasonal ice zone is uncertain, as it has not been quantified. For an overview of ice algae and phytoplankton in the Arctic, see Poulin et al. (2011). Some ice algae diatoms form

BOX 2 | NOT SO EASY: THE VARIOUS TERMS AND ASPECTS OF PRIMARY PRODUCTION

Primary production is the production of organic compounds from atmospheric or aquatic carbon dioxide, principally through the process of photosynthesis. Almost all life on Earth is directly or indirectly reliant on primary production. The organisms responsible for primary production are known as *primary producers* or autotrophs, and they form the base of the food chain. In aquatic ecoregions, algae are primarily responsible for primary production. We distinguish net and gross primary production. Net primary production is the dynamic balance between gross primary production and cell respiration.

Net primary production creates the base of new production that is determined by the availability of the limiting nutrient (e.g., nitrate; Eppley and Peterson, 1979). Organisms ultimately metabolize nitrogenous organic molecules, which are returned to the water column as ammonium, in a process known as regeneration. Total primary production is thus comprised of new production (nitrate) and regenerated production (ammonium).

New production can also be designated harvestable production (i.e., the maximum biomass that can be extracted from the system without destroying its carrying capacity). The balance between gross and net primary production has direct implications for ecosystems, biogeochemical cycling, pelagic-benthic coupling, and fisheries. The maximum marine harvest and the annual vertical carbon export from the upper layers (also termed export production) are limited upward by net or new production.

meter-long threads that hang from multi-year ice. Their existence in an environment where heterotrophs' need for food far exceeds the amount of food available (Olli et al., 2007) implies that these algae must be difficult for planktivores to graze or digest. However, for organisms at the seafloor, these ice algae are reported to constitute a food source (e.g., Carroll and Carroll, 2003). Further information on annual and seasonal phytoplankton production in several Arctic Ocean ecosystems can be found in, for example, Sakshaug (2004), Tremblay et al. (2006), and Appolonio and Matrai (2010).

Figure 1 depicts the present-day temporal development of ice and plankton algae along a transect through

the seasonal ice zone from the southernmost, stratified domain (D), where sea ice melts early in the season, to the central Arctic Ocean close to the North Pole (A). As the sea ice cover shrinks due to global warming, we may find that the seasonal development of ice and plankton algae at a specific latitude of the seasonal ice zone changes from one scenario (C or D) to one more closely resembling that seen in areas without any sea ice cover, where there is often little or no stratification, such as in the northeastern North Atlantic (E). A new scenario is introduced at the southern rim of today's open ocean and seasonal ice zone (F). The open, weakly stratified water of the southern Barents Sea will

become increasingly prone to thermal stratification, resulting in decreased primary production. This scenario will have negative implications for harvestable production and most probably for one of the world's most significant fisheries.

Temporal Development in the Seasonal Ice Zone and Pelagic-Benthic Coupling in Times of Global Warming: A Simple View

The polar night, sun's height, and changing thickness of snow all play roles in the annual development of the pelagic ecosystem in the Arctic Ocean's seasonal ice zone (Figure 2). Some nutrients from nutrient-rich deeper water diffuse into the surface layer during the polar night. Presently, in the seasonal ice zone, thinning of relatively thick ice in spring (increased stratification) and disappearance of the snow cover (increased light) are followed by a brief, intense phytoplankton bloom (Figure 2A). The water depth to which nutrients are depleted (roughly the euphotic zone) decreases continuously during the productive period. In spring, algae growth exceeds degradation (autotrophic biomass prevails). Heterotrophic processes (red in Figure 2) gradually take over the spring dominance of autotrophy (green). The ice algae bloom decline is accompanied by a distinct vertical export of algae. The production, consumption, and regeneration cycles in the pelagic zone are reflected in the quantity and quality of vertically exported biogenic matter leaving the euphotic layers (vertical arrows). Vertical export and its regulation are greatly dependent upon the role and presence of key zooplankton species and the microbial food web. Two distinct pulses of biogenic matter

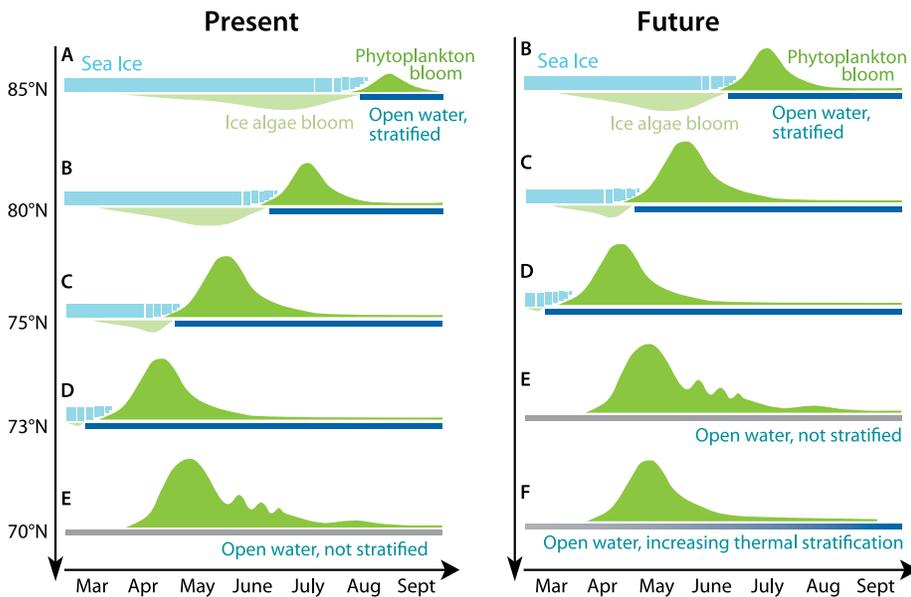


Figure 1. Timing of ice algae and phytoplankton bloom development along a latitudinal axis of the open water-seasonal ice zone region (ranging from 75–85°N) with long to short productive periods in open water (70–75°N) and heavy ice-covered regions (> 73–75°N) in the European Arctic Corridor, respectively. Present-day scenario (left) and predicted future scenario with a warmer climate (right) along the same latitudes. Notice how today's bloom development in scenario A disappears while scenario F enters the latitudinal gradient in the future. Panels E and F exemplify the course of primary production in the scenario of continuously open water in the Barents Sea, characterized by no major freshwater source and weak and slow development of surface water stratification. The variable production in June (Panel E) arises through variations in nutrient supply caused by vertical mixing events triggered by low-pressure passage after the end of the spring bloom. Panel F projects future primary production at 70°N after global warming leads to increasing thermal stratification and decreased primary production. Modified from Figure 1 in Leu et al. (2011)

dominated by autotrophic cells (green) are followed by less-distinct pulses of degrading matter (reddish).

Climate warming extends the ice-free period, with melt starting earlier in spring and freeze up occurring later in fall (Figure 2B). Consequently, both the Arctic ice and plankton algae blooms start earlier (Kahru et al., 2011; Perrette et al., 2011), nutrients are consumed faster, and the period when heterotrophic processes dominate lasts longer. Stratification caused by melting sea ice persists, and nutrient availability does not increase with the increase of photosynthetically active radiation. The vertical export of ice and plankton algae takes place earlier in the season and the time interval dominated by regenerated production becomes longer.

However, winter accumulation (diffusion and vertical mixing) determines nutrient availability in the surface waters. Increasing stratification prevents increased supplies in the future. New, harvestable, and exported production under conditions of increased radiation depicted in scenario B will be similar to scenario A. Vertical export will spread over longer time periods, with consequences for benthos and zooplankton (earlier availability of food after winter depletion, longer period of food availability but at lower concentrations).

Further climate warming not only reduces the thickness of the ice cover but also, to a lesser degree, the late winter ice extent. This warming may result in earlier ice algae blooms, as more light may be available. Zooplankton,

overwintering at depth and food-deprived since the previous summer, will ascend earlier to utilize this attractive nutrient source (Leu et al., 2011). The slow-growing ice algae may provide food for pelagic heterotrophs more continuously, and food supply may be less pulsed, implying that less biogenic matter is exported vertically. Ice thickness and snow cover determine whether ice algae and plankton algae can thrive in concert. Nutrient availability will not increase, and primary production will be spread over a longer time period. This scenario will favor smaller plankton (Li et al., 2009; Rokkan Iversen and Seuthe, 2010) and reduce the intense pulsing of the present-day ice-edge bloom climate scenario that supports large mesozooplankton (e.g., Søreide et al., 2006) and

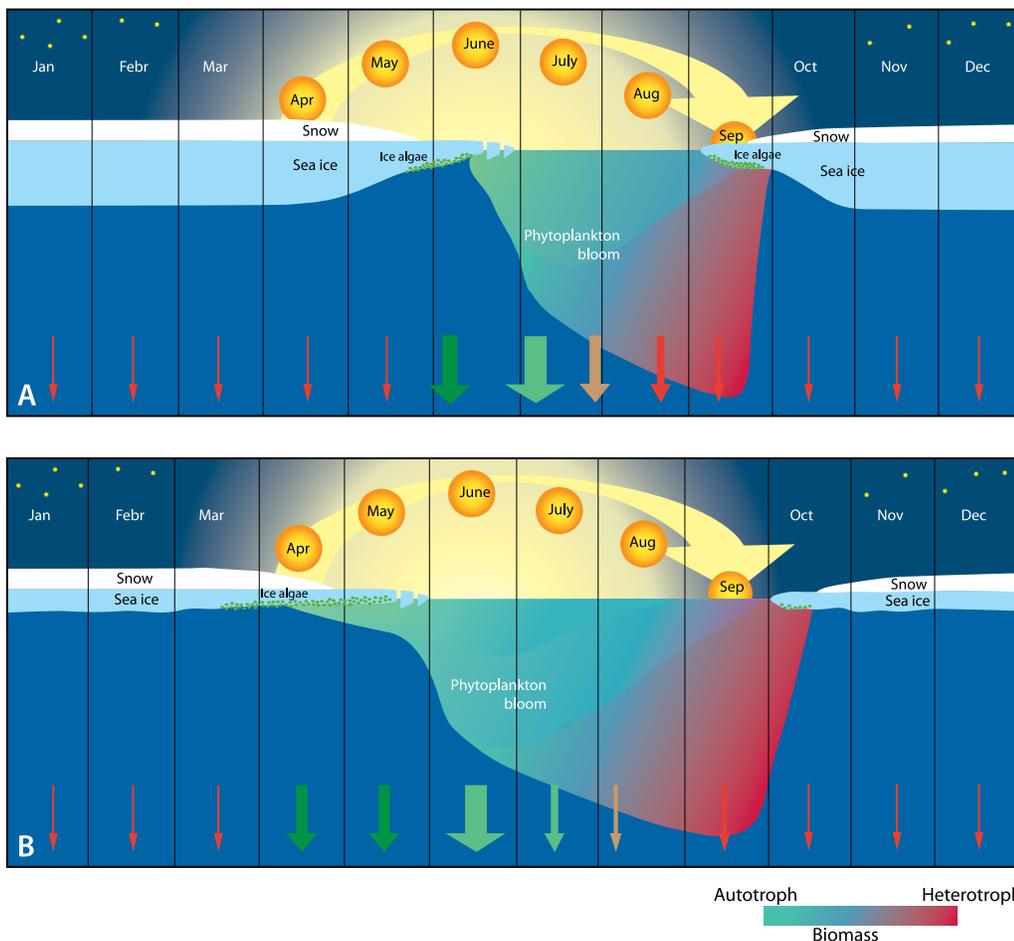


Figure 2. Seasonality in bloom development and in downward carbon export in present-day climate and ice conditions (A), and a future warmer climate with thinner ice in winter and more melting of summer ice, causing a widening of the seasonal ice zone (B). The green-to-red gradient indicates the balance of suspended biomass from autotrophic to heterotrophic sources. The new and export production in both scenarios is similar because stratification limits nutrient availability. The width and color of the vertical arrows illustrate the semi-quantitative magnitude and key composition of vertically exported organic matter. Dark green = ice algae-derived carbon. Light green = phytoplankton-derived carbon. Orange and red arrows = increasing degree of detritus (nonliving particulate organic material). Modified from Wassmann (2011)

rich benthos (e.g., Piepenburg et al., 2011) on the shelves. Consequently, the heavily phased nature of today's seasonal ice zone will be replaced by more evenly distributed (nutrient-limited) primary production and food availability.

During winter, by far the longest period of the year, when the ice is thick and snow-covered, and the sun is below the horizon, productivity is negligible, suspended biomass accumulation is minimal, and vertical carbon export from the upper layers is usually very low (Olli et al., 2002; Forest et al., 2008). The fate of the ice algae blooms in early spring is still not well understood, but they are clearly an important food source for zooplankton (Leu et al., 2011) and benthos (Carroll and Carroll, 2003). It is generally assumed that a considerable amount of the biomass sinks ungrazed as high-quality input to the benthos (Figure 2A). As the season proceeds, with more light, ice melting, and the development of a pelagic bloom in the marginal ice zone (Reigstad et al., 2002; Søreide et al., 2010; Leu et al., 2011), grazing intensity will determine this bloom's fate. High grazing impact can reduce vertical export in terms of carbon and the quality of the settling organic matter, but usually a peak in vertical carbon export is observed following the pelagic bloom and its large component of phytoplankton cells (Figure 2A; Olli et al., 2002; Reigstad et al., 2008). The post-bloom and summer periods are characterized by regenerated production, and they are controlled by stratification and recycling of nutrients in the euphotic zone. This ecosystem structure facilitates recycling, allowing less material to be exported below the euphotic zone, where nutrients will then be lost

to further incorporation (Wassmann, 1998). Investigations in the Barents Sea seasonal ice zone revealed that the vertically exported material is more degraded during this period (Figure 2A; Reigstad et al., 2008).

A future seasonal ice zone characterized by thinner ice, earlier snowmelt, and earlier onset of the productive season will widen the productive time window by 40% or more. This amplification allows heterotrophic pelagic organisms more time to respond with growth and reproduction to optimize use of available food. Thus, pelagic organisms graze a larger proportion of both ice and phytoplankton algae, and less biogenic matter is exported to the benthic communities. Therefore, we can predict seasonal pattern shifts that will result in vertical export increases earlier in the season following low winter export, but instead of today's intense pulses derived from the accumulation of algae during marginal ice edge blooms, export of organic material will be lower but steadier (Figure 2B). As most of the large copepods in the Arctic Ocean are in diapause in deeper waters from mid-summer to the following spring, the share of the bloom not grazed by microzooplankton and smaller winter-active copepods can be exported (Figure 2B). The seasonal dynamics in vertical export in a future scenario with a longer productive season will most likely be characterized by lower daily average rates, but the annual downward carbon export may be equal to or most likely higher than today's. The quality may also be lower as the material will be recycled or degraded rather than being fresh input directly exported from the peak bloom.

Temporal Development in the Seasonal Ice Zone and Pelagic-Benthic Coupling in Times of Global Warming: A More Complex View

Physical forcing—through vertical mixing, stratification, and ice cover—determines primary production and vertical export through the upper 200 m of the water column along a gradient from the North Pole to the subarctic seas (Figure 3). The open subarctic sectors of the Pacific and Atlantic Oceans lie at the southernmost end of the gradient through the Arctic seasonal ice zone; ice cover never influences these areas (known as alpha oceans, *sensu* Carmack, 2007). They are characterized by extensive vertical mixing, high productivity but relatively low phytoplankton biomass, and a deep euphotic zone (Figure 3A). The European Arctic Ocean sector's alpha ocean is uniquely characterized by very low vertical stability caused by a lack of freshwater sources. North of the alpha ocean, on the outskirts of the Arctic Ocean, lies the beta ocean—a region where melting of seasonal sea ice produces robust, long-lasting vertical stratification (*sensu* Carmack, 2007). Vertical mixing ceases, the euphotic zone is closer to the surface, and zooplankton grazing increases. Consequently, primary production decreases (per m²), but phytoplankton biomass may be high (per m³). Characteristics of the multiyear ice zone situated north of the seasonal ice zone include strong stratification, a relatively shallow euphotic zone, and an intense, transient phytoplankton bloom. Under the ice, the euphotic zone is extremely shallow, and productivity and phytoplankton biomass are low.

Future decrease in sea ice cover will

influence primary production and suspended phytoplankton biomass. Ice will disappear, and stratification in the outer reaches of today's seasonal ice zone will be eroded by wind, particularly during the passage of low-pressure systems that is expected to happen more frequently. Consequently, the alpha ocean will expand northward (Figure 3B), possibly resulting in increased annual primary production in the southernmost realms of today's seasonal ice zone. Another result will be decreased vertical mixing in the northernmost region of the alpha ocean (caused by increased thermal stratification). Preliminary modeling results suggest that primary production may decrease by up to 30% in the

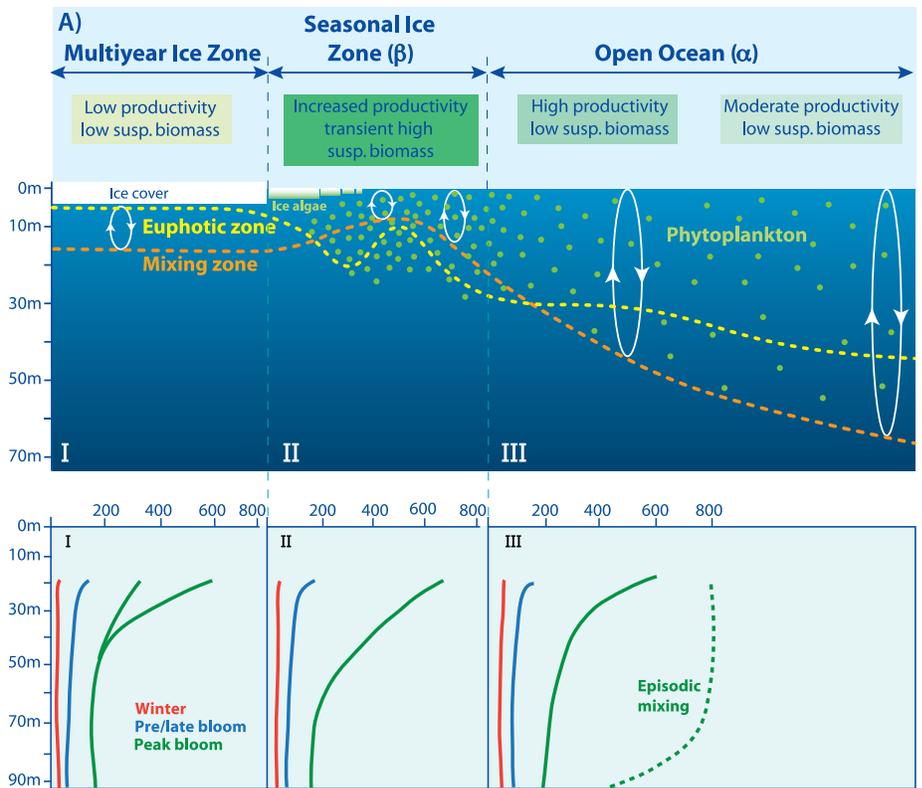
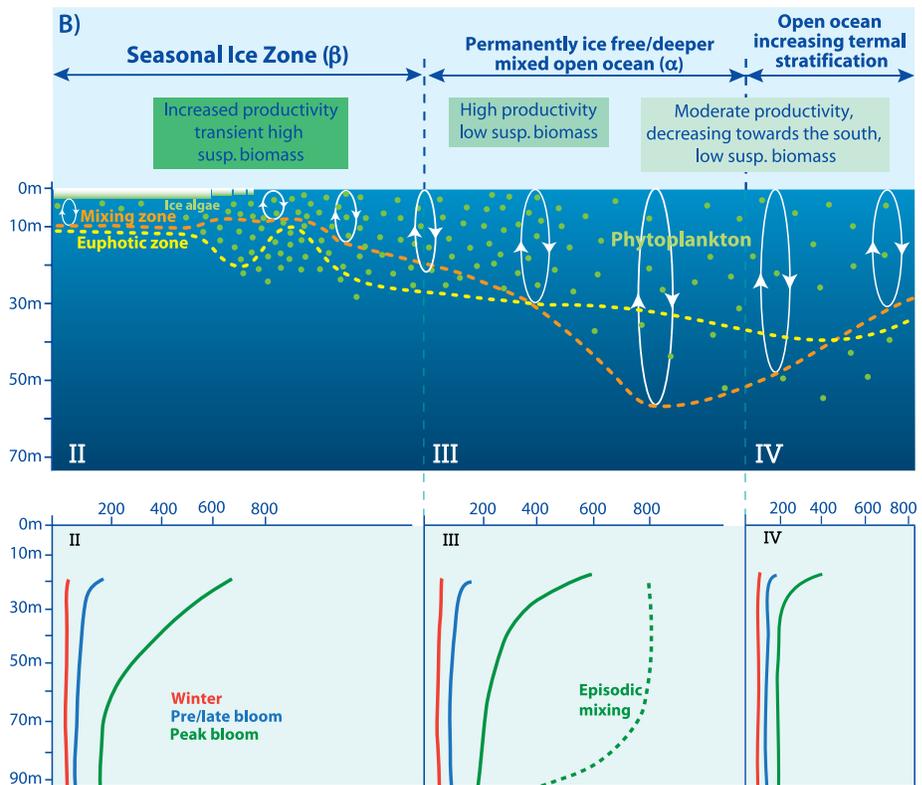


Figure 3. (A) Generic scheme illustrating the basic features and function of the multiyear ice zone (I), seasonal ice zone (II), and permanently open water outside the seasonal ice zone continuum (III), with the marginal ice zone toward open water being the most conspicuous feature of zone II. Zonation, functional ocean types (alpha/beta), and ice cover are indicated at the top. Primary production, the depth of the euphotic zone, and the mixed layer are also shown, as are phytoplankton concentrations and ice algae. Below each scenario, the principal profiles of vertical export of particulate organic carbon for winter (red), spring bloom/episodic mixing (green), and summer (blue) are illustrated in a semi-quantitative manner. The stippled lines indicate variability in phytoplankton bloom strength (II) and the result of episodic mixing (III). (B) The generic scheme after shrinkage and disappearance of the multiyear ice zone (I) in a future Arctic Ocean. The entire Arctic Ocean turns into a seasonal ice zone (II). Erosion of stratification in the outer section of the seasonal ice zone results in expansion of the vertically mixed alpha ocean northwards (III), but there is a simultaneous increase of thermal stratification in the south, which is a new and presently non-existent scenario (IV). Below each scenario the principal profiles of vertical export of particulate organic carbon for winter (red), spring bloom/episodic mixing (green), and summer (blue) are illustrated in a semi-quantitative manner. *Partly redrawn and modified from Carmack and Wassmann (2006) and Wassmann (2011)*



most productive region of the southern Barents Sea toward the end of the century (Slagstad et al., 2011).

Vertical carbon export and retention of sinking material in the upper layers create the characteristic vertical flux curve, which is described as an attenuation curve, similar to light attenuation (Wassmann et al., 2003; Buesseler et al., 2007). Grazing by heterotrophic organisms, biological degradation by bacteria, or physical breakup of sinking particles

determine vertical flux attenuation. The attenuation curvature therefore depends on (a) the vertical distribution of biomass that can potentially settle through the upper layers, (b) the distribution of grazers of sinking material, and (c) the upper-layer mixing regime (Carmack and Wassmann, 2006). As biomass accumulation is restricted to the euphotic zone, and grazers tend to accumulate at layers with high food concentrations, the physical characteristics of

the upper water column are important. Ice, wind exposure, heat loss, and stratification strength determine nutrient supply in the euphotic zone (Reigstad et al., 2008). A subsurface chlorophyll *a* maximum often develops at the nutricline, determined by the light, and the highest export rates are often observed at this depth. Physical environments from multiyear ice, to the seasonal ice zone, to open water form a gradient that is also reflected in the vertical flux attenuation curve and, consequently, affects pelagic-benthic coupling.

In different phases of the productive season the vertical flux curve differs along the north-south gradient (lower panel of Figure 3A). During winter, vertical export is low throughout the water column, reflecting low biomass and low export at all depths. This is similar along the entire gradient from open water to multiyear ice, but with lowest vertical export in the multiyear ice zone. The pre- and post-bloom scenarios are often reflected in slightly higher export rates in surface waters (close to the nutricline and the bottom of the euphotic zone) and a noticeable but relatively small reduction with depth (Figure 3A). Vertical export is higher than during winter, but still moderate. The bloom scenarios with high biomass accumulation result in different vertical attenuation patterns determined by the depth and intensity of upper-water-column stratification. In the multiyear ice zone (I in Figure 3A), attenuation takes place at shallower depths compared to the marginal ice zone (II), where the euphotic zone is deeper. Export from the upper layers in the multiyear ice may vary considerably depending on nutrient availability, biomass accumulation, and

BOX 3 | PRIMARY PRODUCTION CARBON FLUX IN THE UPPER COLUMN OF THE ARCTIC OCEAN OF THE FUTURE: A BIRD'S-EYE PERSPECTIVE OF BASIC FACTS

- As the upper layers of the Arctic Ocean receive more radiation, heat, and freshwater, vertical mixing processes no longer provide enough nutrients for additional phytoplankton growth (e.g., Tremblay and Gagnon, 2009)
- Increased radiation will increase new (or harvestable) production only to a limited degree in the Arctic Ocean (e.g., Slagstad et al., 2011)
- More consumption than production in parts of the Arctic Ocean may be caused by:
 1. Increased import of mesozooplankton from warming subarctic regions (e.g., Olli et al., 2007)
 2. Increased respiration of heterotrophs (in particular, microbes; Vaquer-Sunyer et al., 2010)
 3. Relatively small increases in primary production (low supply of nutrient from nutrient-rich waters)
- With increasing temperature, respiration increases much faster than primary production, creating a scenario where the Arctic Ocean turns from a sink into a producer of atmospheric carbon dioxide (e.g., Vaquer-Sunyer et al., 2010; Kritzbeg et al., 2010)
- With increasing temperature and decreasing salinity, the cell size of autotrophs decreases, providing more strength to the microbial loop (e.g., Li et al., 2009; Rokkan Iversen and Seuthe, 2010)
- When ice cover permits vessels to enter the Arctic Ocean basins, an Arctic fishery cannot be expected there because of persistently low harvestable production

grazing pressure. In the less-stratified open water, episodic mixing facilitates high-export scenarios when accumulated algal biomass is mixed below the euphotic zone before restratification enables production of new biomass fueled by new nutrients imported during mixing. The suspended biomass that has been mixed down sinks further downward, and can double the daily vertical carbon export to the benthos on Arctic shelves like the Barents Sea (Figure 3A, III; Reigstad et al., 2008).

First-year ice has already replaced multiyear ice over large areas, considerably widening the seasonal ice zone in summer (Figure 3B). It is expected that this process will continue in a warmer climate, potentially eliminating multi-year ice from the Arctic Ocean. It is difficult to predict how warmer air and sea temperatures will influence thermal stratification, but model simulations (Slagstad et al., 2011) suggest increased thermal stratification in regions that are presently weakly stratified and where the passage of low atmospheric pressure induces episodic mixing (Figure 3B). The high productivity and vertical export that currently characterize these regions may thus be reduced through increased thermal stratification, preventing nutrients from being mixed upward in the future (Wassmann, 2011). Consequently, the pulsed, downward mixing of accumulated biomass will decrease (Figure 3B, IV). Along the gradient from multiyear ice to open water, benthic communities are exposed to higher vertical food supply. In the multiyear ice in the north, the reduced ice cover may facilitate increased productivity and vertical export in the future, provided that new nutrients become available.

TRENDS AND EXPECTATIONS FOR CARBON FLUX IN A WARMING ARCTIC OCEAN

Before closing, we pause to speculate about how and when marine ecosystems may be affected by climate change and what trends can be expected.

- The largest changes will occur in the northern sections of today's seasonal ice zone, which will expand to cover the entire Arctic Ocean. Primary production will increase slightly in the currently low-productive Arctic Ocean basins.
- The stratified and nutrient-poor surface waters prevent further increases in new production that would otherwise be expected as light availability increases. The exceptions are regions subjected to large-scale advection (e.g., the Chukchi Sea, the southern Barents Sea, western Spitsbergen, and possibly parts of the Canadian Archipelago). New production in the central Arctic Ocean will remain low. Thus, the fisheries of the subarctic regions—currently the world's richest—may not expand from the shelves into the Arctic Ocean basins when the ice cover shrinks.
- The southernmost sector of today's seasonal ice zone may turn into an alpha ocean because passage of atmospheric low pressure may erode stratification. Today's highly productive southern subarctic regions could experience more thermal stratification and receive fewer nutrients. Primary production thus appears likely to increase in the former and decrease in the latter zones. Fisheries may need to move northward onto shelves.
- The significance of ice algae for total Arctic Ocean primary production

may increase in the central part of this ocean but decrease in the outer seasonal ice zone as a result of ice thinning. Blooms of ice and plankton algae will extend to encompass longer time periods.

- Weakening of today's highly episodic primary production and algae blooms in the seasonal ice zone may result in more continuous, but lower, food concentrations. Consequently, there may be more recycling of biogenic matter, changes in plankton life-cycle strategies, and less-variable vertical export.
- Increased freshwater discharge by rivers is predicted to introduce more nutrients into interior shelves of the Arctic Ocean, but turbidity is also very likely to increase because of melting permafrost. Thus, primary production may decrease rather than increase on the shelves exposed to Arctic rivers.
- Freshening of the Arctic Ocean, nutrient limitation, and a prolonged growing season will shift community composition toward smaller phyto- and zooplankton forms, more retention of suspended biomass, and decreased seasonality in pelagic-benthic coupling. While the quantity of vertical carbon export may increase, the quality of the biogeochemical material injected into the benthic boundary layer may decrease.

To improve estimates of primary production and carbon flux in the Arctic Ocean, attempts must be made to increase our basic knowledge about, in particular, the poorly investigated central Arctic Ocean basins and the Siberian shelf in its entirety (Wassmann et al., 2011). Before initiating efforts to

better understand the ecology of the Arctic Ocean in light of climate change, conceptual schemes presented here and elsewhere may be applied to guide and systemize this work. Although the three schemes presented here primarily depict ecosystem function and development within the European sector, they may guide research in the entire central Arctic Ocean. There is a particularly urgent need for information regarding the horizontal and vertical distributions of nutrients, which are currently not well known, except in a few Arctic Ocean shelf subregions (e.g., Tremblay and Gagnon, 2009). The processes that make nutrients available to the euphotic zone—mixing, diffusion, tidal movements, and wind stress—also need considerable attention (e.g., Sundfjord et al., 2007).

Remotely sensed information on phytoplankton distribution in the Arctic Ocean (e.g., Pabi et al., 2008) needs quality control and validation, and the algorithms that convert chlorophyll into primary production need to be carefully considered for the specific Arctic Ocean conditions. The few existing physical-biological coupled models that cover the Arctic Ocean (e.g., Popova et al., 2010; Zhang et al., 2010; Slagstad et al., 2011) must be improved with regard to physical forcing (e.g., how available light for photosynthesis is affected by low sun angle, an atmosphere with high probability for fog and haze, the thickness of ice, and variable snow cover). There is also a need for more information on temperature-dependent respiration and metabolism at low, but increasing, temperatures (e.g., Kritzberg et al., 2010; Vaquer-Sunyer et al., 2010), and on how key zooplankton conquer new or lose former habitats (e.g., Kosobokova et al., 2011). The processes depicted in

Figures 1–3 cannot be studied using permanent moorings or remote sensing. They require process studies that focus primarily on rates, not biomass. Last, but not least, more basic data from the entire Arctic Ocean, in particular its central sections, must be obtained in order to validate numerical and remote-sensing models.

ACKNOWLEDGEMENTS

We thank Janet Holmén for language support, Frøydis Strand for assistance with the figures, and two anonymous referees. The Norwegian Research Council's *Norklima* and *IPY* programmes (e.g., iAOS-Norway; <http://www.iaaos.no>), the *Arctic Tipping Points* project (<http://www.eu-atp.org>) funded by FP7 of the European Union (contract #226248), and the project *Fate of organic material in the ocean: Controlling mechanisms in vertical flux regulation* financed through Tromsø Forskningstiftelse (<http://conflux.arctosresearch.net>) supported this study. The ARCTic marine ecOSystem research network, ARCTOS (<http://www.arctosresearch.net>), a northern-Norwegian network that addresses large-scale, pan-Arctic questions in marine Arctic oceanography, provided a scientifically inspiring background for this publication. 

REFERENCES

- Apollonio, S., and P. Matrai. 2011. Marine primary production in the Canadian Arctic. 1956. *Polar Biology* 34:767–774, <http://dx.doi.org/10.1007/s00300-010-0928-3>.
- Bellerby, R.G.J., A. Olsen, T. Furevik, and L.A. Anderson. 2005. Response of the surface ocean CO₂ system in the Nordic Seas and North Atlantic to climate change. Pp. 189–198 in *Climate Variability in the Nordic Seas*. H. Drange, T.M. Dokken, T. Furevik, R. Gerdes, and W. Berger, eds, Geophysical Monograph Series, American Geophysical Union, Washington, DC.
- Buesseler, K.O., C.H. Lamborg, P.W. Boyd, P.J. Lam, T.W. Trull, R.R. Bidigare, J.K.B. Bishop, K.L. Casciotti, F. Dehairs, M. Elskens, and others.

2007. Revisiting carbon flux through the ocean's twilight zone. *Science* 316:567–570, <http://dx.doi.org/10.1126/science.1137959>.
- Carmack, E. 2007. The alpha/beta ocean distinction: A perspective on freshwater fluxes, convection, nutrients and productivity in high-latitude seas. *Deep-Sea Research Part II* 54:2,578–2,598, <http://dx.doi.org/10.1016/j.dsr.2.2007.08.018>.
- Carmack, E., and P. Wassmann. 2006. Food webs and physical-biological coupling on pan-Arctic shelves: Comprehensive perspectives, unifying concepts and future research. *Progress in Oceanography* 71:446–477, <http://dx.doi.org/10.1016/j.pocean.2006.10.004>.
- Carroll, M.L., and J. Carroll. 2003. The Arctic Seas. Pp. 127–156 in *Biogeochemistry of Marine Systems*. K. Black and G. Shimmield, eds, Blackwell Publishing, Oxford.
- Comiso, J.C. 2003. Warming trends in the Arctic from clear sky satellite observations. *Journal of Climate* 16:3,498–3,510, [http://dx.doi.org/10.1175/1520-0442\(2003\)016<3498:WTITAF>2.0.CO;2](http://dx.doi.org/10.1175/1520-0442(2003)016<3498:WTITAF>2.0.CO;2).
- Comiso, J.C., C.L. Parkinson, R. Gersten, and L. Stock. 2008. Accelerated decline in the Arctic sea ice cover. *Geophysical Research Letters* 35, L01703, <http://dx.doi.org/10.1029/2007GL031972>.
- Eppley, R.W., and B.J. Peterson. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* 282:677–680, <http://dx.doi.org/10.1038/282677a0>.
- Forest, A., M. Sampei, R. Makabe, H. Sasaki, H. Hattori, M. Fukuchi, D. Barber, Y. Gratton, P. Wassmann, and L. Fortier. 2008. Annual cycle of particulate organic carbon export in the Franklin Bay (Canadian Arctic): Environmental control and food web implications. *Journal of Geophysical Research* 113, C03S05, <http://dx.doi.org/10.1029/2007JC004262>.
- Gosselin, M., M. Levasseur, P.A. Wheeler, R.A. Horner, and B.C. Booth. 1997. New measurements of phytoplankton and ice algal production in the Arctic Ocean. *Deep-Sea Research Part II* 44:1,623–1,644, [http://dx.doi.org/10.1016/S0967-0645\(97\)00054-4](http://dx.doi.org/10.1016/S0967-0645(97)00054-4).
- Hunt, G.L., and P.J. Stabenro. 2002. Climate change and the control of energy flow in the southeastern Bering Sea. *Progress in Oceanography* 55:5–22, [http://dx.doi.org/10.1016/S0079-6611\(02\)00067-8](http://dx.doi.org/10.1016/S0079-6611(02)00067-8).
- Kahru, M., W. Brotas, M. Manzano-Sarabia, and B.G. Mitchel. 2011. Are phytoplankton blooms occurring earlier in the Arctic? *Global Change Biology* 17:1,733–1,739, <http://dx.doi.org/10.1111/j.1365-2486.2010.02312.x>.
- Kosobokova, K.N., R.R. Hopcroft, and H.-J. Hirche. 2011. Patterns of zooplankton diversity through the depth of the Arctic's central basins. *Marine Biodiversity* 41:29–50, <http://dx.doi.org/10.1007/s12526-010-0057-9>.
- Kritzberg, E.S., C.M. Duarte, and P. Wassmann. 2010. Changes in Arctic marine bacterial carbon metabolism in response to increasing temperature. *Polar Biology* (Special Issue: Impacts of Climate Warming on Polar Marine and Freshwater Ecosystems) 33:1,673–1,682, <http://dx.doi.org/10.1007/s00300-010-0799-7>.

- Kwok, R., and D.A. Rothrock. 2009. Decline in Arctic sea ice thickness from submarine and ICESat records: 1958–2008. *Geophysical Research Letters* 36, L15501, <http://dx.doi.org/10.1029/2009GL039035>.
- Legendre, L., S.F. Ackley, G.S. Dieckmann, B. Gulliksen, R. Horner, T. Hoshiai, A. Melnikov, W.S. Reeburg, W.S. Spindler, and C.W. Sullivan. 1992. Ecology of sea ice biota. 2. Global significance. *Polar Biology* 12:429–444, <http://dx.doi.org/10.1007/BF00243114>.
- Leu, E., J.E. Søreide, D.O. Hessen, S. Falk-Petersen, and J. Berge. 2011. Consequences of changing sea ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. *Progress in Oceanography* 90:18–32, <http://dx.doi.org/10.1016/j.pocean.2011.02.004>.
- Li, W.K.W., F.A. McLaughlin, C. Lovejoy, and E.C. Carmack. 2009. Smallest algae thrive as the Arctic Ocean freshens. *Science* 326:539, <http://dx.doi.org/10.1126/science.1179798>.
- McPhee, M.G., A. Proshutinsky, L.H. Morison, M. Steele, and M.B. Alkire. 2009. Rapid change in freshwater content of the Arctic Ocean. *Geophysical Research Letters* 36, L10602, <http://dx.doi.org/10.1029/2009GL037525>.
- Olli, K., P. Wassmann, M. Reigstad, T.N. Ratkova, E. Arashkevich, A. Pasternak, P. Matrai, and J. Knulst. 2007. Suspended concentration and vertical flux of organic particles in the upper 200 m during a 3 week ice drift at 88°N. *Progress in Oceanography* 72:84–113, <http://dx.doi.org/10.1016/j.pocean.2006.08.002>.
- Olli, K., C. Wexels Riser, P. Wassmann, T. Ratkova, E. Arashkevich, and A. Pasternak. 2002. Seasonal variation in vertical export of biogenic matter in the marginal ice zone and the central Barents Sea. *Journal of Marine Research* 38:189–204, [http://dx.doi.org/10.1016/S0924-7963\(02\)00177-X](http://dx.doi.org/10.1016/S0924-7963(02)00177-X).
- Pabi, S., G.L. Van Dijken, and K. Arrigo. 2008. Primary production in the Arctic Ocean, 1998–2006. *Journal of Geophysical Research* 113, C08005, <http://dx.doi.org/10.1029/2007JC004578>.
- Perrette, M., A. Yool, G.D. Quartly, and E.E. Popova. 2011. Near-ubiquity of ice-edge blooms in the Arctic. *Biogeosciences* 8:515–524, <http://dx.doi.org/10.5194/bg-8-515-2011>.
- Piepenburg, D., P. Archambault, W.G. Ambrose, A.L. Blanchard, B.A. Bluhm, M.L. Carroll, K.E. Conlan, M. Cusson, H.M. Feder, J.M. Grebmeier, and others. 2011. Towards a pan-Arctic inventory of the species diversity of the macro- and megabenthic fauna of the Arctic shelf seas. *Marine Biodiversity* 41:51–70, <http://dx.doi.org/10.1007/s12526-010-0059-7>.
- Polyakov, I.V., L.A. Timokov, V.A. Alexeev, S. Bacon, I.A. Dimitrenko, L. Fortier, I.E. Frolov, J.-C. Gascard, E. Hansen, V.V. Ivanov, and others. 2010. Arctic Ocean warming contributes to reduced Polar ice cap. *Journal of Physical Oceanography* 40:2,743–2,756, <http://dx.doi.org/10.1175/2010JPO4339.1>.
- Popova, E.E., A. Yool, A.C. Coward, Y.K. Aksenov, S.G. Alderson, B.A. de Cuevas, and T.R. Anderson. 2010. Control of primary production in the Arctic by nutrients and light: Insights from a high resolution ocean general circulation model. *Biogeosciences* 7:3,569–3,591, <http://dx.doi.org/10.5194/bg-7-3569-2010>.
- Poulin, M., N. Daugbjerg, R. Gradinger, L. Ilyash, T. Ratkova, and C. von Quillfeldt. 2011. The pan-Arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: A first-attempt assessment. *Marine Biodiversity* 41:13–28, <http://dx.doi.org/10.1007/s12526-010-0058-8>.
- Reigstad, M., C. Wexels Riser, S. Øygarden, P. Wassmann, and F. Rey. 2002. Variation in hydrography, nutrients and suspended biomass in the marginal ice zone and the central Barents Sea. *Journal of Marine Systems* 38:9–29, [http://dx.doi.org/10.1016/S0924-7963\(02\)00167-7](http://dx.doi.org/10.1016/S0924-7963(02)00167-7).
- Reigstad, M., C. Wexels Riser, P. Wassmann, and T. Ratkova. 2008. Vertical export of particulate organic carbon: Attenuation, composition and loss rates in the northern Barents Sea. *Deep-Sea Research Part II* 55:2,308–2,319, <http://dx.doi.org/10.1016/j.dsr2.2008.05.007>.
- Rokkan Iversen, K., and L. Seuthe. 2010. Seasonal microbial processes in a high-latitude fjord (Kongsfjorden, Svalbard). I. Heterotrophic bacteria, picoplankton and nanoflagellates. *Polar Biology* 34:731–749, <http://dx.doi.org/10.1007/s00300-010-0929-2>.
- Sakshaug, E. 2004. Primary and secondary production in the Arctic Seas. Pp. 57–81 in *The Organic Carbon Cycle in the Arctic Ocean*. R. Stein and R.W. Macdonald, eds, Springer-Verlag, Berlin, http://dx.doi.org/10.1007/978-3-642-18912-8_3.
- Slagstad, D., I.H. Ellingsen, and P. Wassmann. 2011. Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: An experimental simulation approach. *Progress in Oceanography* 90:117–131, <http://dx.doi.org/10.1016/j.pocean.2011.02.009>.
- Søreide, J.E., H. Hop, M.L. Carroll, S. Falk-Petersen, and E.N. Hegseth. 2006. Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. *Progress in Oceanography* 71:59–87, <http://dx.doi.org/10.1016/j.pocean.2006.06.001>.
- Søreide, J.E., E. Leu, J. Berge, M. Graeve, and S. Falk-Petersen. 2010. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Global Change Biology* 16:2,913–3,169, <http://dx.doi.org/10.1111/j.1365-2486.2010.02175.x>.
- Stroeve, J., M.M. Holland, W. Meier, T. Scambos, and M. Serreze. 2007. Arctic sea ice decline: Faster than forecast. *Geophysical Research Letters* 34, L09501, <http://dx.doi.org/10.1029/2007GL029703>.
- Sundfjord, A., I. Fer, Y. Kasajima, and H. Svendsen. 2007. Observations of turbulent mixing and hydrography in the marginal ice zone of the Barents Sea. *Journal of Geophysical Research* 112, C05008, <http://dx.doi.org/10.1029/2006JC003524>.
- Tremblay, J.E., and J. Gagnon. 2009. The effects of irradiance and nutrient supply on the productivity of Arctic waters: A perspective on climate change. Pp. 73–92 in *Influence of Climate Change on the Changing Arctic and Subarctic Conditions*. C.J. Nihoul and A.G. Kostianoy, eds, Springer Science, Berlin, http://dx.doi.org/10.1007/978-1-4020-9460-6_7.
- Tremblay, J.-E., H. Hattori, C. Michel, M. Ringuette, Z.P. Mei, C. Lovejoy, L. Fortier, K.A. Hobson, D. Amiel, and K. Cochran. 2006. Trophic structure and pathways of biogenic carbon flow in the eastern North Water Polynya. *Progress in Oceanography* 71:402–425, <http://dx.doi.org/10.1016/j.pocean.2006.10.006>.
- Vaquer-Sunyer, R., C.M. Duarte, P. Wassmann, R. Santiago, and M. Reigstad. 2010. Experimental evaluation of planktonic respiration response to warming in the European Arctic Sector. *Polar Biology* 33:1,661–1,671, <http://dx.doi.org/10.1007/s00300-010-0788-x>.
- von Eye, M., A. von Eye, and J. Rodrigues. 2009. *Global Warming and Changes in Sea Ice in the Greenland Sea: 1979–2007*. R. Graf, ed., InterStat, 27 pp. Available online at <http://interstat.statjournals.net/YEAR/2009/abstracts/0905003.php> (accessed June 13, 2011).
- Wassmann, P. 1998. Retention versus export food chains: Processes controlling sinking loss from marine pelagic systems. *Hydrobiologia* 363:29–57, <http://dx.doi.org/10.1023/A:1003113403096>.
- Wassmann, P. 2011. Arctic marine ecosystems in an era of rapid climate change. *Progress in Oceanography* 90:1–17, <http://dx.doi.org/10.1016/j.pocean.2011.02.002>.
- Wassmann, P., C.M. Duarte, S. Agusti, and M. Sejr. 2011. Footprints of climate change in the Arctic marine ecosystem. *Biological Global Change* 17:1,235–1,429, <http://dx.doi.org/10.1111/j.1365-2486.2010.02311.x>.
- Wassmann, P., K. Olli, C. Wexels Riser, and C. Svensen. 2003. Ecosystem function, biodiversity and vertical flux regulation in the twilight zone. Pp. 279–287 in *Marine Science Frontiers for Europe*. G. Wefer, F. Lamy, and F. Mantoura, eds, Springer Verlag.
- Wassmann, P., D. Slagstad, and I. Ellingsen. 2010. Primary production and climatic variability in the European sector of the Arctic Ocean prior to 2007: Preliminary results. *Polar Biology* 33:1,641–1,650, <http://dx.doi.org/10.1007/s00300-010-0839-3>.
- Yamamoto-Kawai, M., F.A. McLaughlin, E.C. Carmack, S. Nishino, K. Shimada, and N. Kurita. 2009. Surface freshening of the Canada Basin, 2003–2007: River runoff versus sea ice meltwater. *Journal of Geophysical Research* 114, C00A05, <http://dx.doi.org/10.1029/2008JC005000>.
- Zhang, I., Y.H. Spitz, M. Steele, C. Ashjian, R. Campbell, L. Berline, and P. Matrai. 2010. Modeling the impact of declining sea ice on the Arctic marine planktonic ecosystem. *Journal of Geophysical Research* 115, C10015, <http://dx.doi.org/10.1029/2009JC005387>.