

RESEARCH/REVIEW ARTICLE

Responses in Arctic marine carbon cycle processes: conceptual scenarios and implications for ecosystem function

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Keywords

Sea ice; climate change; ecosystem function; carbon cycling.

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Abstract

The Arctic Ocean is one of the fastest changing oceans, plays an important role in global carbon cycling and yet is a particularly challenging ocean to study. Hence, observations tend to be relatively sparse in both space and time. How the Arctic functions, geophysically, but also ecologically, can have significant consequences for the internal cycling of carbon, and subsequently influence carbon export, atmospheric CO₂ uptake and food chain productivity. Here we assess the major carbon pools and associated processes, specifically summarizing the current knowledge of each of these processes in terms of data availability and ranges of rates and values for four geophysical Arctic Ocean domains originally described by Carmack & Wassmann (2006): inflow shelves, which are Pacific-influenced and Atlantic-influenced; interior, river-influenced shelves; and central basins. We attempt to bring together knowledge of the carbon cycle with the ecosystem within each of these different geophysical settings, in order to provide specialist information in a holistic context. We assess the current state of models and how they can be improved and/or used to provide assessments of the current and future functioning when observational data are limited or sparse. In doing so, we highlight potential links in the physical oceanographic regime, primary production and the flow of carbon within the ecosystem that will change in the future. Finally, we are able to highlight priority areas for research, taking a holistic pan-Arctic approach.

The Arctic Ocean's (AO's) physically and biologically unique environment appears sensitive to recently documented changes to the global climate system. Arctic sea ice has been diminishing dramatically in recent decades as the northern polar region has been warming (Rhein et al. 2013). Larger ice-free areas increase the absorption

of solar radiation by surface waters in summer, further increasing temperatures and reducing winter sea-ice formation, resulting in further reductions in sea-ice extent (Polyakov et al. 2010; Serreze & Barry 2011). Other mechanisms contributing to the decline of Arctic sea ice are increased oceanic heat transport from the Atlantic (Miles

et al. 2014), increase in cloudiness and increased atmospheric heat flux from the sub-Arctic (Serreze & Barry 2011). These positive feedbacks may be significant for the global climate system (Symon et al. 2005; Rhein et al. 2013) but may also have large implications for the functioning of Arctic marine ecosystems and subsequent consequences for the marine carbon cycle in these polar waters. Indeed, ecosystem structure changes have already been observed in the Arctic (e.g., Wassmann & Reigstad 2011; Grebmeier 2012; Weydmann et al. 2014).

Arctic food webs, typically, are relatively simple, with short connectivity between trophic levels. This makes them potentially sensitive to changes in the magnitude and direction of energy flow (e.g., Wassmann & Reigstad 2011). Considering carbon as the unit of energy cycled through the food chain, and biology as an important component of the carbon cycle, it is clear that changes in the Arctic's physical regimes causing shifts in the ecosystem dynamics will have consequences for the sequestration of carbon. Extensive sea-ice cover restricting ocean-atmosphere exchange and low-light conditions resulting in relatively low biological production (Symon et al. 2005; Arrigo et al. 2008) are the reason the AO has not historically been considered a significant carbon sink. However, the amount of carbon sequestered by the AO is likely to increase significantly as sea-ice cover becomes less extensive (Symon et al. 2005; Manizza et al. 2013) and primary production increases (Bates et al. 2006; Brown & Arrigo 2012). The response of the Arctic marine carbon cycle to changes in climate is therefore a major issue of global concern (Symon et al. 2005) that calls for investigating holistically how shifting Arctic regimes impact the ecosystem and its functions, and the resulting consequences for carbon cycling. This study uses an interdisciplinary approach to combine an assessment of Arctic ecosystems under differing geophysical regimes, such as those outlined by Carmack & Wassmann (2006), with respect to carbon cycling.

Previous reviews of the Arctic carbon cycle commonly have assessed either the whole carbon cycle, i.e., ocean, terrestrial and atmospheric components (e.g., McGuire et al. 2009), or singular aspects of the oceanic component, such as inorganic carbon cycle (Bates & Mathis 2009; Bates et al. 2013), the microbial carbon cycle (e.g., Nguyen & Maranger 2011; Ortega-Retuerta et al. 2012) or the organic carbon cycle (e.g., Stein & Macdonald 2004), while few directly assessed links between the carbon cycle and ecosystem function. Here we synthesize data on the Arctic marine carbon cycle by explicitly considering both inorganic and organic carbon within the surface ocean (Fig. 1), linking the carbon flow to the ecosystem and its functioning within four differing geophysical

domains: Pacific- and Atlantic-influenced inflow shelves; river-influenced shelves (RIS); and the central basins (CBs), equivalent to the multi-year ice regions that Carmack & Wassmann (2006) showed to be physically, and therefore ecologically, different. Specifically we aim to present a conceptual understanding of the important contemporary processes in the Arctic marine carbon cycle, linking carbon to ecosystem function. By doing so, we provide a mechanism for assessing how the carbon cycle may respond to future climate change, as well as identify research priorities that can fill critical knowledge gaps and aid in refining the models needed to capture, simulate and predict (project) the complex non-linear dynamics of the Arctic marine carbon cycle.

The Arctic marine carbon cycle

AO water masses are a composition of water from both the Atlantic and the Pacific oceans (Fig. 1). Broadly, there are three main water masses recognized within the AO water column (Coachman & Aagaard 1974): Surface or Arctic Water (SW), which occupies the top 200 m of the water column and is influenced by rivers, precipitation, sea-ice melt and formation and relatively fresh Pacific Water (PW); Atlantic Water (AW), from approximately 200 to 900 m; and Deep or Bottom Water (BW) from about 900 m to the seafloor. A strong halocline exists between the relatively fresh, cold SW and the more saline but warmer AW. Waters originating on the shelves form during winter freezing and are advected towards the centre of the basins. Because ice cover reduces wind-induced vertical mixing relative to other oceans, the water masses preserve source water properties over relatively long distances (Aagaard et al. 2008). In the multi-year ice-covered central ocean basins the halocline persists throughout the year, restricting vertical exchange between cold SW and underlying warmer AW.

The Arctic surface ocean interacts with other systems, including the atmosphere (through heat and gas exchange), land (through river discharge and coastal erosion), deep water and connecting oceans (through advection of water from both the Pacific and the Atlantic). Here, we will not discuss the cycling of carbon within each of these adjoining systems, but rather consider their relative interactions with the surface ocean system.

Carbon pools

Our conceptual overview of the five dominant pools of carbon and associated processes is summarized in Fig. 2 and Table 1. Here we define each of the carbon pools considered.

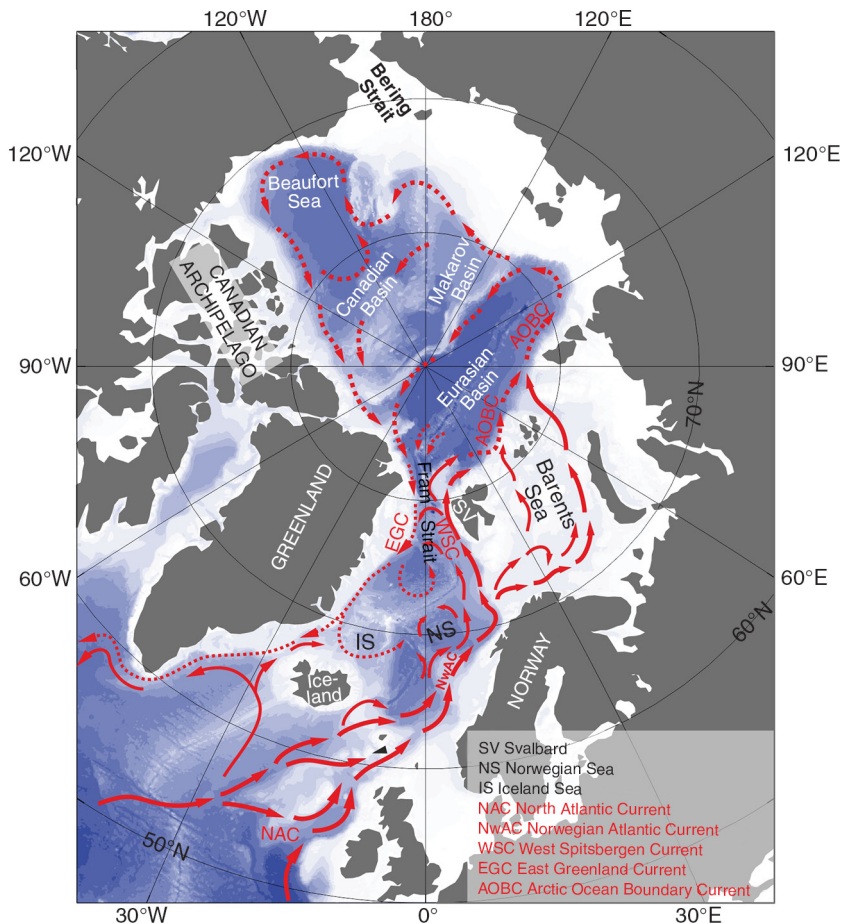


Fig. 1 Upper layer circulation in the Nordic seas and Arctic Ocean. Warm Atlantic inflow is shown with red solid lines, Arctic outflow with dashed red lines (A. Beszczynska-Möller, pers. comm.).

The abiotic particulate pools (particulate organic carbon [POC], PIC; box labelled 1 in Fig. 2) and the abiotic dissolved pools (dissolved inorganic carbon [DIC], dissolved organic carbon [DOC]; 2 in Fig. 2) essentially constitute carbon, which is bioavailable but is not bound in, or to, a biologically active organism. The carbon inventory in the oceans is dominated by inorganic carbon within the water column. Abiotic-POC is commonly referred to, or is inclusive of, the detrital pool (or detritus).

The autotrophic pool (3 in Fig. 2) constitutes phytoplankton, sea-ice algae and photosynthetic bacteria, which take up inorganic carbon from the abiotic pool to form particulate inorganic and organic carbon structures. Within a seasonal cycle the size of the autotrophic-POC pool varies substantially. Ice-associated micro-organisms are considered in this paper as external sources to the surface water, and although some discussion is given to their relative importance, they are not considered part of the surface water autotrophic pool.

The bacterial (heterotrophic) pool (4 in Fig. 2) is formed when heterotrophic bacteria create or modify organic carbon structures and contribute to the recycling of organic carbon back to the abiotic pools. Focusing on Arctic surface waters and assuming that the majority of this water mass is not oxygen limited, we consider only aerobic bacteria.

The heterotrophic (non-bacterial) pool (5 in Fig. 2) includes the pelagic zooplankton (micro- and mesozooplankton) in Arctic surface waters. These consumers are unable to gather carbon directly from the abiotic dissolved pool, but can utilize carbon from any of the other organic pools. Because of their relatively small impact on the cycling of marine carbon we do not consider higher trophic levels in this assessment.

Internal processes

The processes that transfer carbon from one pool to another are described below, where possible in the

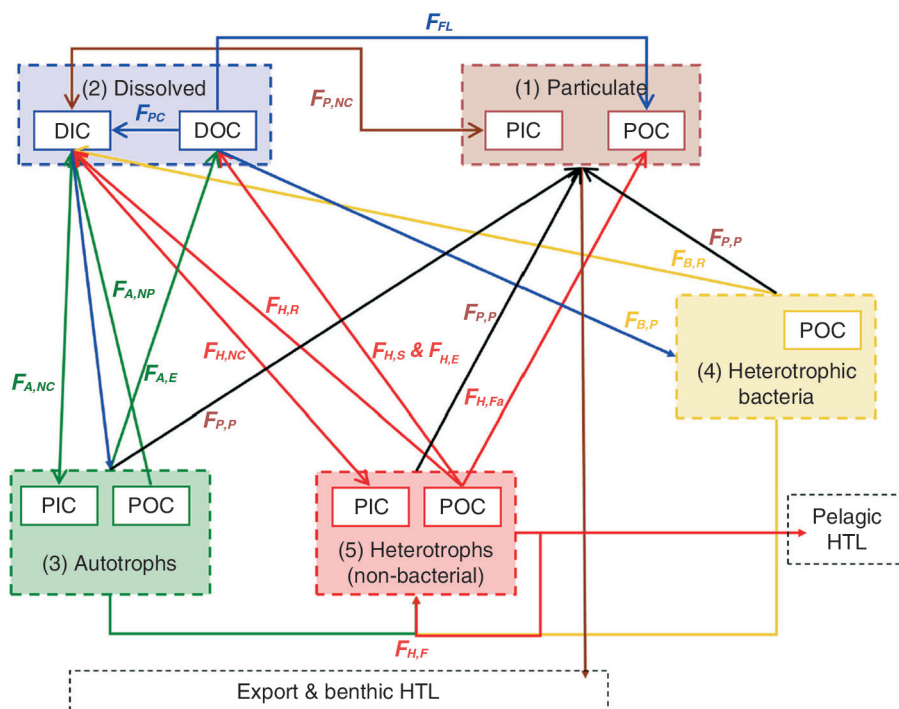
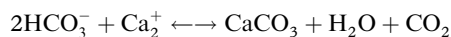


Fig. 2 The major internal pools and fluxes within the surface ocean, through which carbon can circulate: dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), particulate organic carbon (POC) and particulate inorganic carbon (PIC); see Table 2 for details of the fluxes. The numbers in brackets in each box relate to the list of the five main carbon pools described in the text. Higher trophic level is abbreviated to HTL.

context of the AO. Where there is limited information about how these processes are regulated in the Arctic, details come from lower latitude studies.

Particulate net mineralization ($F_{P,NC}$). Mineralization (transferring carbon from the abiotic-DIC to the abiotic-PIC) is the processes of forming calcium carbonate minerals (CaCO_3) from bicarbonate (HCO_3^-) and calcium ions (Ca^{2+}). Dissolution is the reverse of this process. Hence, $F_{P,NC}$ is a product of gross mineralization and gross dissolution of calcium carbonate minerals.



Mineralization releases CO_2 to the surrounding water. Although this process, which locks away carbon molecules into calcium carbonate, is a sink for carbon, it also results in an increase in dissolved CO_2 (Frankignoulle et al. 1994). The saturation state, a ratio of the ion concentrations ($[\text{Ca}^{2+}] \times [\text{CO}_3^{2-}]$) to the solubility constant (K_{sp}), which is a function of salinity, temperature and pressure (Morse & Berner 1972), is a common measure of when mineralization or dissolution should theoretically dominate. Importantly for the Arctic, recent evidence (Nomura et al. 2013) suggests that ikaite, a specific calcium carbonate mineral, can form in sea ice as

a result of CO_3^{2-} and Ca^{2+} ions being highly concentrated within brine fluids produced through brine rejection when seawater freezes and sea ice forms. Therefore, although the AO is typically characterized by a lower saturation state than other oceans due to low salinity and temperature, ice-associated ikaite production has the potential to influence the surface water carbon flux (Rysgaard et al. 2012).

Photodegradation (F_{PC}). Photodegradation is the photochemical transformation of marine dissolved organic matter (DOM, or specifically here, DOC) into low-molecular-weight compounds including formic acid, formaldehyde, acetic acid, acetaldehyde, acetone, propanol, pyruvic acid, citric acid, levulinic acid, glyoxal, methylglyoxal and glyoxylate (Miller & Moran 1997 and references therein). The marine carbon cycle is impacted through the reduction of DOC into bioavailable compounds (Moran & Zepp 1997; Mopper & Kieber 2000), and the recycling of DOC back to DIC (photomineralization) by forming CO_2 and CO (Valentine & Zepp 1993; Miller & Zepp 1995; Bélanger et al. 2006; Stubbins et al. 2006; Stubbins et al. 2011). Chromophoric, or coloured, DOM (CDOM) is the fraction of DOM that absorbs UV and visible light and is therefore subjected to photochemical reactions. The photo-processes associated with CDOM can

Table 1 Summary of pools and processes within the Arctic Ocean surface waters. Names and abbreviations are provided, as well as the source and sink pools (i.e., where carbon is transferred from and to) associated with each process.

Pools	A Autotrophs H Heterotrophs (non-bacteria) B Bacteria (heterotrophic only)		P Abiotic particulate (POC, PIC) (detritus) D Abiotic dissolved (DIC, DOC)		
	Flux	Process	Source	Sink	Net process
Biotic processes	$F_{A,R}$	Autotrophic respiration	A-POC	DIC	$F_{A,NP}$
	$F_{A,P}$	Primary production	DIC	A-POC	$F_{A,NP}$
	$F_{A,C}$	Autotrophic calcification	DIC	A-PIC	$F_{A,NC}$
	$F_{A,D}$	Autotrophic dissolution	A-PIC	DIC	$F_{A,NC}$
	$F_{A,E}$	Autotrophic excretion	A-POC	DOC	
	$F_{B,R}$	Bacterial respiration	B-POC	DIC	$F_{B,GE}$
	$F_{B,P}$	Bacterial production	DOC,POC	B-POC	$F_{B,GE}$
	$F_{H,R}$	Heterotrophic respiration	H-POC	DIC	
	$F_{H,C}$	Heterotrophic calcification	DIC	H-PIC	$F_{H,NC}$
	$F_{H,D}$	Heterotrophic dissolution	H-PIC	DIC	$F_{H,NC}$
	$F_{H,S}$	Heterotrophic sloppy feeding	H-POC	DOC	
	$F_{H,F,B}$	Heterotrophic feeding on bacteria	B-POC	H-POC	$F_{H,F}$
	$F_{H,F,A}$	Heterotrophic feeding on autotrophs	A-POC	H-POC	$F_{H,F}$
	$F_{H,F,P}$	Heterotrophic feeding on particulates	POC	H-POC	$F_{H,F}$
	$F_{H,Fa}$	Heterotrophic faecal production	H-POC	POC	
$F_{H,E}$	Heterotrophic excretion	H-POC	DOC		
Abiotic processes	$F_{P,P}$	Particulate production (death)	A-B-H-POC	POC	
	$F_{P,C}$	Particulate calcification (mineralization)	DIC	PIC	$F_{P,NC}$
	$F_{P,D}$	Particulate dissolution	PIC	DIC	$F_{P,NC}$
	$F_{P,C}$	Photodegradation	DOC	DIC	
	F_{FL}	Flocculation	DOC	POC	
External fluxes	F_{SE}	Sedimentation/export to deep waters			
	F_G	Exchange with atmosphere			
	F_R	Exchange with rivers			
	F_O	Exchange with other oceans			
	F_U	Upwelling (exchange with deep waters)			

also cause radiant heat to be trapped within the top few metres of the water column, which may influence the stratification of the water column (Granskog et al. 2007) and increase sea-ice melt (Hill 2008). Indirectly, photo-bleaching, the photochemical destruction of fluorophores within DOM, alters light penetration and absorption in the water column (Del Vecchio & Blough 2002; Helms et al. 2008). Light intensity and spectral quality, as well as temperature, are the main drivers acting on photochemical transformation processes. In the AO, seasonality in solar radiation, sea ice, stratification and river run-off can impact the temporal variations in photodegradation, while sea-ice coverage, river inputs, stratification and hydrography drive its spatial variation.

Flocculation (F_{FL}). Flocculation, the formation of particulate matter from colloids or dissolved material, transfers carbon from the abiotic-DOC pool to the abiotic-POC pool. This process is widespread in aquatic environments especially in regions with strong salinity gradients, such as estuaries (Sholkovitz 1976). Sholkovitz

(1976, 1978) demonstrated that only 3–10% of riverine DOM could be removed as a result of mixing in estuaries, of which a major fraction is high-molecular-weight dissolved humic acids. In the AO, the flocculation process is not believed to be very important because recent evidence from Siberian rivers, for example, the Ob, Yenisei, and Lena, suggests that DOM mixes conservatively with seawater, with only minor losses (< 5%) due to flocculation (Amon & Meon 2004 and sources therein).

Bacterial production ($F_{B,P}$). Through secondary production, heterotrophic bacteria utilize organic carbon to build new bacterial biomass, converting abiotic-DOC, including total dissolved amino acids (TDAA) and CDOM, and autotrophic-POC to bacterial-POC. While total $F_{B,P}$ could be determined by the amount of available organic substrates (Kirchman et al. 2009; Ortega-Retuerta et al. 2012), in particular TDAA, it is also highly regulated by temperature (Ortega-Retuerta et al. 2012). In the AO, temperature has been shown to have a linear (log–log) relationship with $F_{B,P}$, with the rate apparently being

very similar between the euphotic zone, below the mixed layer and in rivers, e.g., the Mackenzie River (Ortega-Retuerta et al. 2012). In contrast, the TDAA or DOC (log–log) relationships with $F_{B,P}$ appear to be more representative of a saturation curve, such that there is a higher rate of production below the mixed layer, with the rate decreasing through the upper SW and into rivers (e.g., the Mackenzie River), where these components are found in higher concentrations (Ortega-Retuerta et al. 2012).

Primary production ($F_{A,P}$). Photosynthesis occurs in the cells of autotrophic organisms, such as phytoplankton, photosynthesizing bacteria and sea-ice algae and is a process that converts inorganic carbon (abiotic-DIC) to organic matter (autotrophic-POC). Necessary drivers for this process are light, which provides the energy for photosynthesis, and nutrients (Harrison & Cota 1991), while temperature affects the rate of this process (Eppley 1972; Smith & Sakshaug 1990; Harrison & Cota 1991). The amount of carbon fixed through photosynthesis is referred to as primary production ($F_{A,P}$).

In the AO, light and temperature are the strongest regulating factors for photosynthesis. In cold Arctic waters photosynthetic rates tend to be slower than at lower latitudes (Hegseth 1998). Above the Arctic Circle, autotrophs have a narrow time window of three to four months in summer (the growing season) with enough light to form organic matter (Søreide et al. 2006). Light is further limited in the AO by ice cover, especially if this is overlain by snow, which substantially reduces the amount of light transmitted through the ice (Mundy et al. 2005; Grenfell et al. 2006; Light et al. 2008). During the growing season, $F_{A,P}$ in the upper euphotic zone becomes limited by nutrient availability once the waters above the pycnocline become depleted of nutrients (Carmack et al. 2006; Wassmann & Reigstad 2011). Some $F_{A,P}$ can continue in the lower euphotic zone within subsurface chlorophyll maxima. In the AO, the primary limiting nutrient is nitrate, which is primarily advected from the Atlantic and Pacific oceans, but can be upwelled to the euphotic zone in some areas, commonly along the shelf break (Cottier et al. 2007; Popova et al. 2012). Other regional processes, such as Ekman pumping (McLaughlin & Carmack 2010) and storm-driven or tidal mixing (Lenn et al. 2011; Pnyushkov & Polyakov 2012), can also inject nutrients into the upper sunlit layer and affect $F_{A,P}$ in the AO.

Respiration (bacterial: $F_{B,R}$, autotrophic: $F_{A,R}$, heterotrophic: $F_{H,R}$). Here respiration refers to the oxidation of organic matter (POC) to yield energy, and the release of CO_2 (abiotic-DIC) as a waste product. The

rate of respiration is affected by temperature but also the elemental composition of the organic matter being metabolized. Where estimates are available for polar and sub-polar regions, bacterial respiration ($F_{B,R}$) accounts for the bulk of community respiration; ranging from 50 to >90% (Ngyuyen & Maranger 2011). A frequently used index of efficiency for bacteria is bacterial growth efficiency (BGE), which quantifies the prevalence of bacterial production ($F_{B,P}$) over $F_{B,R}$. BGE can be considered as a determinate of the fate of organic carbon, where a higher BGE implies more carbon remains in organic form, and hence is retained within the microbial food web, rather than being respired back into inorganic forms.

The relationship between $F_{H,R}$ and temperature has been well characterized, and described by the Q10 approximation: $Q10 = (k1/k2)^{10/(t1-t2)}$, where $k1$ and $k2$ are the respiration rates corresponding to the temperatures $t1$ and $t2$. Pelagic crustaceans throughout much of the world's ocean usually have a Q10 in the range of 2.1–2.7 (Ivleva 1980). Arctic copepods' respiration rates have been found to increase with temperature (Hirche 1987), but the relationship does not always appear to follow the Q10 formula. For example, respiration estimates for the Arctic copepod *Calanus glacialis* show a general rate increase with temperature but the associated Q10 varies according to life stage, season and the ambient temperature range (Tande 1988; Vaquer-Sunyer et al. 2010).

It was previously thought that the low temperature of Arctic waters caused low $F_{H,R}$, but this low $F_{H,R}$ was responsible for high vertical export of carbon relative to lower latitudes (Rivkin & Legendre 2001). However, it was recently suggested that the availability of food is more important than temperature for microbial, zooplankton and benthic respiration rates (Takahashi et al. 2002; Renaud et al. 2007; Morata et al. 2015). For example, a threefold increase in *C. hyperboreus* $F_{H,R}$ was observed when fed with excess food (Takahashi et al. 2002) and the absence of food can reduce copepod $F_{H,R}$ (Ikeda & Skjoldal 1989; Ikeda et al. 2001). As Arctic communities are food restricted throughout much of the year, food limitation may currently be a limiting driver of $F_{H,R}$. Recently, light availability has also been shown to affect respiration rates in a key Arctic copepod (Morata & Søreide 2015).

Autotrophic excretion ($F_{A,E}$). During photosynthesis, autotrophs can excrete by-products that form dissolved organic matter products (DOC). These products include labile CDOM and TDAAAs, discussed above, that are particularly important for fuelling bacterial production.

Heterotrophic feeding ($F_{H,F}$), heterotrophic faecal production ($F_{H,Fa}$), heterotrophic sloppy feeding ($F_{H,S}$), heterotrophic excretion ($F_{H,E}$). Transferring carbon through the food chain occurs by secondary consumers (here “heterotrophs”) feeding on available organic carbon ($F_{H,F}$), and then either being eaten by larger predators, or producing waste products in particulate form (faecal pellets [$F_{H,Fa}$]) and dissolved form (excretion [$F_{H,E}$] and sloppy feeding [$F_{H,S}$]). Feeding rates are linked to lifestyle, food quality and abundance, season and reproductive state, as well as other factors, such as temperature and respiration rate. The specificities of these are beyond the scope of this study.

The role of zooplankton has been recognized as very important for influencing the distribution of oceanic carbon (Ducklow et al. 2001). An important pathway for transferring autotrophic-POC to bacterial-POC (via abiotic-DOC) is through the by-products of heterotrophic ingestion and digestion rather than via direct excretion of DOC from intact phytoplankton ($F_{A,E}$). Copepods, which dominate Arctic zooplankton communities in terms of biomass, generate significant amounts of DOM via sloppy feeding (49% of consumed suspended carbon [Kosobokova & Hirche 2009]), as well as via excretion and leaching from egested faecal pellets (Møller 2007; Saba et al. 2011). Release of DOM via sloppy feeding, the physical breakage of the food source and the food loss to the surrounding water (Roy et al. 1989), is greatest when cells are too large to be ingested whole (Møller 2005, 2007). DOM release from faecal pellets is also higher during spring blooms (Møller & Nielsen 2001) because the pellets contain a higher percentage of undigested carbon. Blooms of large-sized phytoplankton, typical in the Arctic with persistent sea ice, may result in the high rates of DOC production by copepods (Møller 2005).

The initial concentration of DOC within faecal pellets quickly leaches out of the pellets due to diffusion gradients between the pellet and the surrounding water (Jumars et al. 1989). The amount of DOC that leaches from copepod faecal pellets is dependent on their food source; amounts being higher when feeding on dinoflagellates compared to diatoms (Thor et al. 2003), and when feeding on other heterotrophs compared to phytoplankton (Urban-Rich 1999). Diffusion of DOC from faecal pellets occurs on very short timescales of minutes to hours, in contrast to excretion of DOC from heterotrophs, which occurs over a relatively long timescale of hours to days (Jumars et al. 1989; Urban-Rich 1999). Leakage of DOC from faecal pellets was found to represent only 6% of carbon removed from suspension (Urban-Rich 1999). However, more recently, Saba et al. (2011)

have suggested that excretion may be a more important source of DOC than sloppy feeding.

Biological net calcification ($F_{A,NC}$, $F_{H,NC}$). Biological calcification (or biomineralization) is the process of forming calcium carbonate (CaCO_3) materials as part of an organism’s structure. Like abiotic particulate net mineralization ($F_{P,NC}$), this process utilizes calcium (Ca^{2+}) and carbonate ions (CO_3^{2-}), although the carbon substrate extracted from seawater for calcification is actually, in most cases, bicarbonate ions (HCO_3^-), which are converted to CO_3^{2-} internally via proton regulation and/or catalytic reaction using the enzyme carbonic anhydrase (see Findlay et al. 2011). The difference between mineralization and biological calcification really comes from the biological control that has been found to regulate the type, as well as the rate of formation, of CaCO_3 minerals, in addition to the conditions of the surrounding seawater. While dissolution is the reverse of this reaction, in some shelled organisms the CaCO_3 structure is not directly exposed to seawater and can be covered by a periostracum or mixed with an organic matrix, both of which act to stabilize and/or protect the mineral structure (Taylor & Kennedy 1969). Like $F_{P,NC}$, the saturation state of the seawater does influence the dissolution rate of any exposed material.

The main CaCO_3 mineral forms secreted in organisms are, in order from least soluble to most soluble: calcite, aragonite, or high-magnesium calcite. In the AO there are representative calcifying organisms in the water column, the sea ice and on the seafloor that produce a range of these mineral forms. Cold-water corals tend to have aragonite skeletons, coralline algae tend to produce high-magnesium calcite; and benthic molluscs, bryozoans, echinoderms, crustaceans and foraminifera and pelagic coccolithophores, foraminifera and pteropods produce a mix of two or three of these CaCO_3 forms. While the benthic communities are potentially important for influencing the carbon budget in the AO, the extent of pelagic calcification in the SW under consideration is limited primarily to pteropods, and further south, to coccolithophores.

Particulate production: mortality ($F_{P,P}$). Mortality of organisms results in a cessation of biological processes that can mediate many of the physicochemical dynamics. Hence a flux of carbon material passes from living organisms back to an abiotic particulate pool (POC). Although there are many different causes and drivers for mortality, we do not explore them here.

Contemporary carbon cycling in four Arctic regions

Four case studies—Pacific-influenced shelves (PiS), Atlantic-influenced shelves (AiS), RiS and CBs—were used to conceptualize the carbon cycle in the surface waters of the AO in different physical settings, with distinct geophysical drivers. These regions are based on the original AO domain concepts proposed by Carmack & Wassmann (2006). The relative importance of temperature, ice cover, wind stress and light are different within each region (Fig. 3). These environmental conditions, together with the advection of water masses from outside the AO, influence the carbon cycle dynamics and ecosystem functions, as described in the following sections.

Pacific-influenced shelves

Here we consider the shelf regions of the Arctic predominantly influenced by PW; the western AO comprising the Chukchi and Bering seas. The approximate volume flux of the PW inflow is on average 0.8 Sv, although it is higher in summer and lower in winter (Woodgate & Aagaard 2006). Recent research has shown that this volume transport can reach up to 1.1 Sv (Woodgate et al. 2012). Approximately the same amount of water exits the AO through the Canadian Archipelago (Prisenberg & Hamilton 2005). Given the concentrations of DIC, DOC, POC and PIC in the inflow waters, and considering the PW flow, the abiotic carbon transports can be estimated (Fig. 4). DIC inflow is estimated to be 600 Tg C y^{-1} , inflow of DOC is estimated to be 34 Tg C y^{-1} and POC is believed to be orders of magnitude smaller, at around 0.2 Tg C y^{-1} . PIC inflow is difficult to quantify and rarely measured (McGuire et al. 2009).

In the summer, inflowing PW is a source of less saline, less dense seawater, relatively rich in carbon and nutrients (McLaughlin et al. 1996). In the winter, PW cools to freezing temperatures and salinity increases (Woodgate et al. 2012). Stratification, which helps autotrophs to remain within the euphotic zone, tends to be well developed, and dominated by salinity changes through freshwater supply from the formation and melt of ice through the year (Carmack & Wassmann 2006). Although the signature of the PW varies between years (Bourgain et al. 2013), continuous inflow of nutrient-rich PW into the western AO is considered to be the dominant factor controlling regional $F_{A,P}$. As the nutrient-rich inflow spreads north through the Bering Strait it supports a short but intense photosynthetic season in the Bering Sea (160 mg C $m^{-2} d^{-1}$ [Lee et al. 2013]) and Chukchi Sea (up to 1600 mg C $m^{-2} d^{-1}$ [Lee et al. 2013]); hence, the autotrophic carbon pool tends to be large throughout the growing

season. The phytoplankton community appears to be dominated by large phytoplankton (60–96% cells $> 20 \mu m$ [Lee et al. 2013]).

Despite high $F_{A,P}$, cool water temperatures and limited shallow shelf connection with the Pacific through the Bering Strait results in low zooplankton abundance, dominated by smaller copepods ($> 5000 \text{ mg m}^{-2}$ [Springer et al. 1989]) and microzooplankton (ciliates and heterotrophic dinoflagellates [Sherr et al. 2009]). Cold temperatures also result in lower grazing rates (about 16–22% of consumed primary production [Grebmeier et al. 1988; Sherr et al. 2009]; 40 mg d^{-1} microzooplankton grazing rate [Sherr et al. 2009]) and detrital degradation rates by bacteria (Grebmeier et al. 1988). As such, a sizable portion of the SW POC sinks to the sea bed (Lovvorn 2005; Moran et al. 2005) creating a tight benthic-pelagic coupling. Recent estimates suggest about 56–60% of total $F_{A,P}$ is exported from SW to the benthos (Campbell et al. 2009; Whitehouse 2011; Hunt et al. 2013). Moran et al. (2005) estimated that up to 30% of the autotrophic-POC is converted to abiotic-POC within the SW, and approximately 6% is converted to DOC through exudation. A large fraction of POC and DOC is also likely advected by horizontal transport off the shelf and into the deep CBs (Dunton et al. 2005).

$F_{B,P}$ has been shown to be relatively low in the PiS (ca. 6 mg C $m^{-2} d^{-1}$); however, $F_{B,R}$ has been suggested to account for $> 40\%$ of total community respiration in the Chukchi Sea, increasing towards land (Kirchman et al. 2009). Assuming a BGE of 12% (Kirchman et al. 2009), $F_{B,R}$ can be estimated to be about 44 mg C $m^{-2} d^{-1}$. Bacteria therefore appear to play an important role in producing DIC on the PiS.

As the zooplankton community in this region is dominated by microzooplankton and small copepods, grazing on the dominant large diatoms would be expected to result in high rates of DOC loss through excretion ($F_{H,E}$) and sloppy feeding ($F_{H,S}$). Observations also suggest that up to 38% of sampled POC is in the form of faecal pellets (Lalande 2006). This rather significant amount of POC production from heterotrophs, yet relatively low consumption on phytoplankton, suggests that zooplankton may be consuming other organic material (Fig. 5), as suggested by experiments on microzooplankton grazing (Sherr et al. 2009), although further studies are required.

Biological calcification ($F_{A,NC}$) occurs in the Bering Sea during coccolithophore blooms in the summer months (Merico et al. 2004). Currently these blooms do not extend into the Chukchi Sea. However, it is possible that the calcified liths are advected through the Bering Strait, as PIC, into this region of the AO, although we are aware of little information on this in the literature. At present,

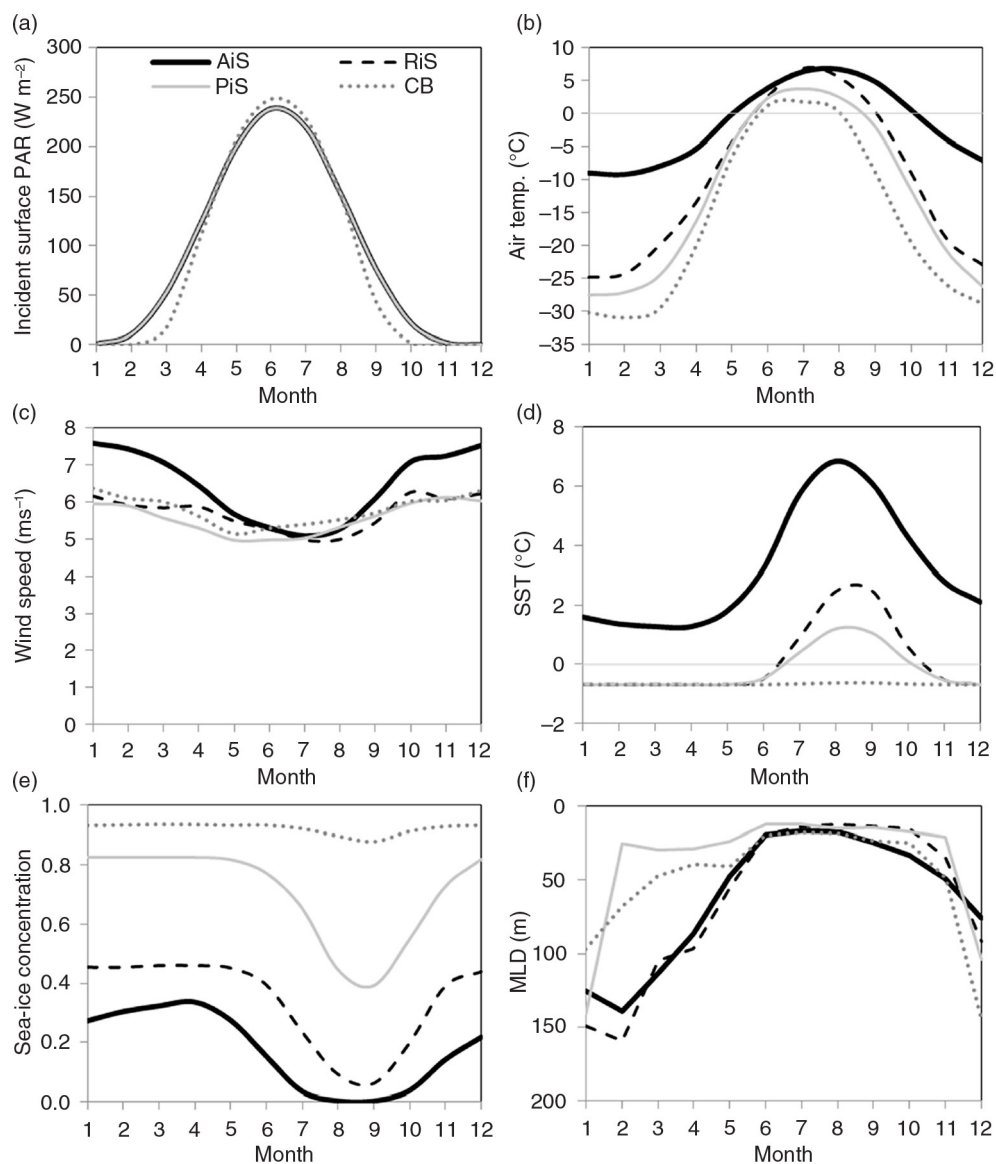


Fig. 3 Mean monthly conditions for (a) incident photosynthetically active radiation (PAR), (b) air temperature (at 2 m), (c) wind speed, (d) sea surface temperature (SST), (e) sea-ice concentration, and (f) mixed layer depth (MLD) for each of the four case study regions. Data are averaged for the regions—Atlantic-influenced shelves (AiS), Pacific-influenced shelves (PiS), river-influenced shelves (RiS), and central basins (CB)—for the period 1979–2013 (for ice, air temperature and PAR, SST and wind speed) using National Centers for Environmental Prediction reanalysis data provided by the Physical Sciences Division of the Earth System Research Laboratory (National Oceanic and Atmospheric Administration) in Boulder, CO, from their website (<http://www.esrl.noaa.gov/psdl/>) and for the period 1961–2008 for MLD, using MLD density-calculated climatology from de Boyer Montegut et al. (2004).

the seasonal ice cover, and hence seasonal brine formation, could provide the opportunity for mineralization of particulate CaCO_3 ($F_{P,NC}$); however, to-date observations of ikaite are rare. The saturation state in the surface waters of the PiS region have been shown to be relatively low compared to the global average, but higher than other AO regions, such as the RiS (aragonite $\Omega < 2$ [Jutterström & Anderson 2005]).

The tight benthic–pelagic coupling in this region results in an efficient transfer of carbon out of AO surface waters (Fig. 5). A strong biological pump and lack of large zooplankton present to graze efficiently on the large phytoplankton also means that a large amount of POC is transported off the shelves into the deep ocean (Dunton et al. 2005). However, the relatively rapid removal of DIC and nutrients from PW as it passes through the Bering

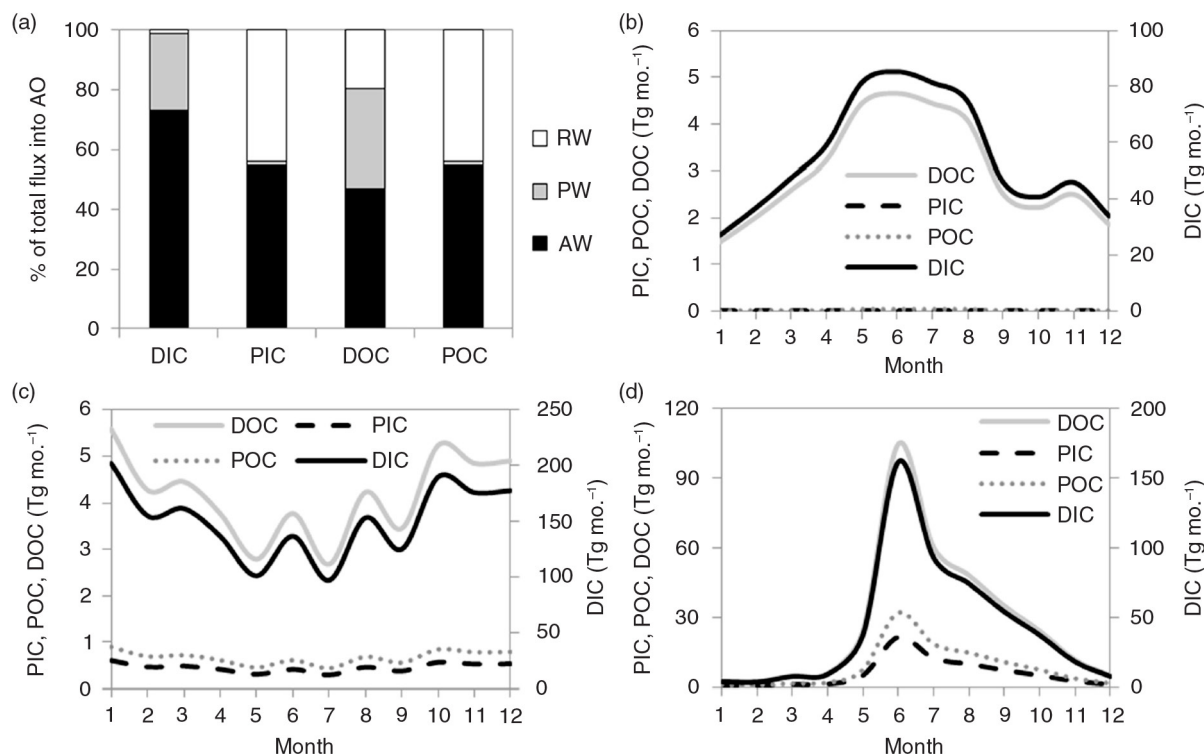


Fig. 4 (a) Relative fluxes of abiotic carbon into the Arctic Ocean (AO) over an average year from the main water inflows: Pacific Water (PW); Atlantic Water (AW) river water (RW). (b–d) relative flux of dissolved inorganic carbon (DIC), particulate inorganic carbon (PIC), dissolved organic (DOC) and particulate organic carbon (POC) into each of the focus regions within the AO: (b) Pacific-influenced shelves, (c) Atlantic-influenced shelves and (d) river-influenced shelves. Note the scales are different on the y-axis and PIC is estimated from a constant PIC:POC ratio of 0.67 (Striegli et al. 2007; McGuire et al. 2009).

Strait and Chukchi Sea leaves the water replete with respect to these inorganic components as it advects further along the shelves or into central Arctic. The removal of carbon from the surface water on the shelf helps to maintain low $p\text{CO}_2$ levels and therefore the region acts a sink for CO_2 from the atmosphere especially during summer months (11–53 Tg C y^{-1} [Bates & Mathis 2009]; 9 Tg C y^{-1} [Arrigo et al. 2010]; 2.3 Tg C y^{-1} [Manizza et al. 2013]).

Atlantic-influenced shelves

The Atlantic-influenced part of the surface AO includes the Nordic seas (Greenland, Iceland and Norwegian seas) and the Barents Sea. Estimates of mean AW transport within the West Spitsbergen Current vary depending on calculation methods but average volume transport ranges from 5.6 to 10 Sv (Aagaard et al. 1973; Hanzlick 1983; Fahrbach et al. 2001; Schauer et al. 2004). High seasonal variability in the AW transport via the West Spitsbergen Current has also been observed, with lowest fluxes in spring (1.4 Sv [Hanzlick 1983]) and highest in autumn and winter (11.6 Sv [Walczowski et al. 2005]). The total

AW inflow to the AO is up to 10 times larger than the PW inflow. Focusing specifically on the Barents Sea, for example AiS, the mean AW inflow across the Barents Sea opening into the AO is around 2.0–2.2 Sv (Jeansson et al. 2011; Smedsrud et al. 2013). Average DIC transport from the Atlantic into the Barents Sea is estimated to be about 1.8 Pg C y^{-1} , DOC inflow is estimated to be 50 Tg C y^{-1} and POC around 8 Tg C y^{-1} (Jeansson et al. 2011) (Fig. 4).

Warm, saline AW, and cooler, fresher Arctic waters interact in AiS. Stratification in these regions is primarily driven by temperature and is therefore very seasonal (Loeng 1991). However, stratification also tends to be weaker than other Arctic regions because of limited sea-ice and river influences, and strong vertical mixing due to the frequent passage of low pressure systems (Ådlandsvik & Loeng 1991).

$F_{A,B}$ mainly by diatoms, lasts from early March to May and varies between 200 and 500 $\text{mg C m}^{-2} \text{d}^{-1}$ (Rey 2004; Loeng & Drinkwater 2007). Assuming that a minimum of 6% $F_{A,P}$ is excreted as DOC (Moran et al. 2005) would give an $F_{A,E}$ of up to 30 $\text{mg C m}^{-2} \text{d}^{-1}$. $F_{A,NC}$ during coccolithophore blooms is high in the Nordic and Barents seas: for the period from 1998 to

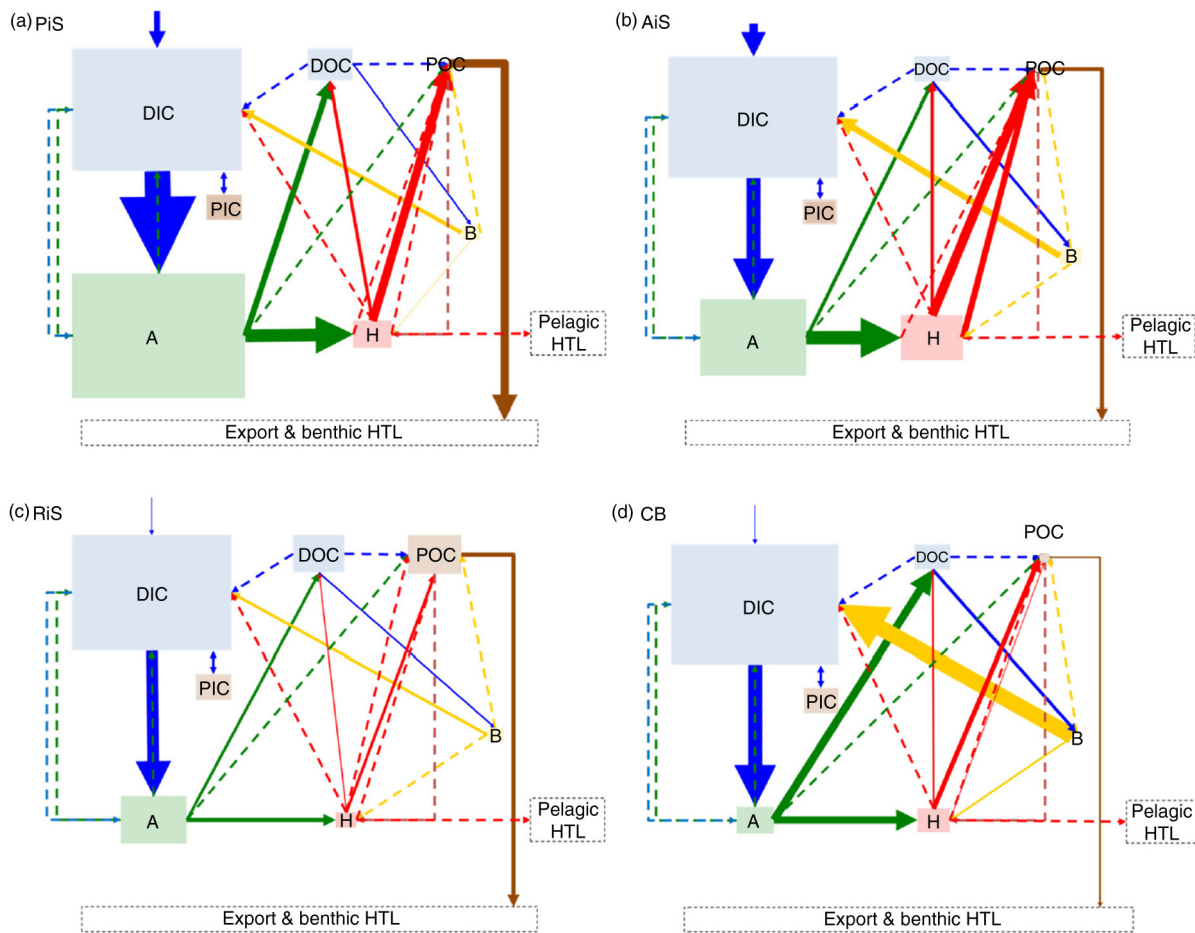


Fig. 5 Relative size of extant (using data available in the literature between the years 1990 and 2013) pools and fluxes at each of the Arctic Ocean regions: (a) Pacific-influenced shelves, (b) Atlantic-influenced shelves, (c) river-influenced shelves and (d) the central basins. The pools include dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), particulate organic carbon (POC) and particulate inorganic carbon (PIC), with the area of these boxes representing by the relative concentrations in $\mu\text{mol kg}^{-1}$ (except for PIC, where no data are available) and autotrophs (A), heterotrophs (H) and bacteria (B), with the size of these boxes representing the relative biomass in g C m^{-2} . Solid lines indicate fluxes for which there are data available, and are relative sizes in $\text{mg C m}^{-2} \text{d}^{-1}$, except for the atmospheric CO₂ flux which is provided in Tg C y^{-1} . Dashed lines indicate fluxes where data are unavailable. Higher trophic level is abbreviated to HTL.

2001, gross annual calcite production, estimated from ocean colour remote sensing data of blooms in the Barents Sea, varied from 0.48 to 1.59 Tg C y^{-1} (Hovland et al. 2013). Much of this PIC is exported from the surface waters and sediment trap data showing that PIC production is highly seasonal, with high vertical flux in May to October (57% calcareous material in sediments) and low rates of flux between December and April (approximately 36% of calcareous material in the sediments [Samtleben & Bickert 1990]). In general, the saturation state of the warmer AiS tends to be higher than other Arctic regions (SW aragonite $\Omega > 2$ [Skogen et al. 2014]), which provides suitable conditions for CaCO₃ formation, although the lower seasonal ice cover here will prevent high rates of F_{BNC} forming minerals such as ikaite in large quantities.

Relatively high stocks of zooplankton are sustained in the AiS compared to the PiS because of the higher $F_{\text{A,P}}$, greater depth and larger advection of deeper waters (Carmack & Wassmann 2006). The zooplankton community tends to be dominated by larger mesozooplankton and supports a longer pelagic food web (Hunt et al. 2013). Despite this longer food web between 34–47% of total $F_{\text{A,P}}$ is exported to the benthos in the Barents Sea (Hunt et al. 2013). Estimates of total $F_{\text{A,P}}$ consumed within the pelagic range from 36 to 86 $\text{g C m}^{-2} \text{y}^{-1}$ (Reigstad et al. 2008). However, larger *Calanus* copepod species are believed to feed on heterotrophic microzooplankton such as ciliates and heterotrophic dinoflagellates as opposed to directly on the autotrophs (Levinsen et al. 2000). Despite this, grazing rates have been found

to be quite high on the AiS, with microzooplankton grazing rates of about 240 mg d^{-1} , and consumption of over 75% of daily $F_{A,P}$ (Verity et al. 2002). Less information is available for bacterial production and respiration rates. However, studies have shown that in the AiS region, active bacteria are abundant with $F_{B,P}$ up to $18 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Howard-Jones et al. 2002). Assuming a BGE of 15% (Kirchman et al. 2009), $F_{B,R}$ for the AiS region can be estimated to be up to $105 \text{ mg C m}^{-2} \text{ d}^{-1}$. These levels of bacterial abundance and activity are similar to those found at lower latitude open ocean sites, and imply that the microbial food web is a significant component of carbon cycling in the AiS (Howard-Jones et al. 2002). This level of bacterial activity would suggest some heterotrophs are feeding on bacteria ($F_{H,F,B}$); however, few rate data are available for this region. The greater standing stocks of heterotrophs also influenced POC and DOC through faecal pellet production ($F_{H,Fa}$), sloppy feeding ($F_{H,S}$) and excretion ($F_{H,E}$). $F_{H,Fa}$ rates have been observed between 20 and $104 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the AiS (Riser et al. 2002), while the rate of $F_{H,E}$ —based on carbon consumption—would be between 9 and $28.8 \text{ mg C m}^{-2} \text{ d}^{-1}$ and $F_{H,S}$ would be between 74 and $235 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Fig. 5).

The longer food web associated with the high $F_{A,P}$ implies that the biological pump is less efficient because more carbon is cycled internally in the SW or passed onto higher trophic levels (Fig. 5). At present the AiS are generally a large sink for atmospheric CO_2 ($44\text{--}77 \text{ Tg C y}^{-1}$ [Bates & Mathis 2009]; 24 Tg C y^{-1} [Arrigo et al. 2010]; $23\text{--}24 \text{ Tg C y}^{-1}$ [Manizza et al. 2013]). The horizontal transport of carbon through the Nordic seas into the AO is approximately two orders of magnitude larger than the CO_2 uptake from the atmosphere (Jeansson et al. 2011); indeed about 40% of the total anthropogenic carbon inflow reaches the AO, although most carbon likely gets sequestered at deeper depths (Kivimae et al. 2010).

River-influenced shelves

Here we consider the Arctic shelves that are predominantly influenced by rivers, including the White Sea, Kara Sea, Laptev Sea, East Siberian Sea and the Beaufort Sea. These shelves vary in depth (from ca. 50 to 200 m) and width (ca. 100 to >1000 km). Complex interaction with the coasts occurs on these shelves, including river run-off, erosion and seasonal ice cover. Ice, particulate matter and CDOM input from the rivers can severely limit the light availability in these regions.

About 90% of the annual riverine delivery to the AO takes place during the ice-free period from May to July (Dittmar & Kattner 2003). In winter, rivers are fed

by groundwater rich in nutrients and poor in organic matter, while in spring and summer, taiga and tundra soils are percolated by the melting of snow which brings abundant organic substances to the rivers. Therefore, nutrient and DIC concentrations in the rivers generally are at a minimum in summer and a maximum in early spring, while organic carbon concentrations parallel water discharge with maximum concentrations in summer (McGuire et al. 2009). The export flux of the DIC from all rivers to the coastal areas of the AO is estimated as 43 Tg C y^{-1} (Fig. 4; McGuire et al. 2009). According to Dittmar & Kattner (2003), about 80% of the total organic carbon is delivered by rivers in the form of DOC, with concentrations ranging from 200 and $1600 \mu\text{M}$ (Stedmon et al. 2011). The total annual DOC discharge by the Arctic rivers is estimated to be $18\text{--}37 \text{ Tg C y}^{-1}$ (Dittmar & Kattner 2003; McGuire et al. 2009; Holmes et al. 2011), which is comparable to the DOC flux of the Amazon (Dittmar & Kattner 2003). The total riverine POC discharge to the AO is about 6 Tg C y^{-1} (Fig. 4; McGuire et al. 2009), which includes a discharge of highly refractory black carbon POC of ca. $0.2\text{--}0.6 \text{ Tg C y}^{-1}$ (Guo et al. 2004; Elmquist et al. 2008). POC is also added to the AO from coastal erosion (ca. $6\text{--}7 \text{ Tg C y}^{-1}$ [Rachold et al. 2004]) and from wind erosion (ca. 2 Tg C y^{-1} [Stein & MacDonald 2004]). Observations of PIC in rivers entering the AO are scarce. However, indirect estimates of PIC fluxes based on PIC to POC relationships (Yukon River) give a pan-Arctic value of $3\text{--}4 \text{ Tg C y}^{-1}$ (Striegl et al. 2007; McGuire et al. 2009).

RiS tend to be relatively stratified, primarily salinity-driven, due to the input of warm, fresh river waters (RWs). However, these regions will periodically experience mixing due to storm events. Unlike the PiS, which also have salinity-dominated stratification, the RiS tend to additionally have a large spatial temperature gradient, with warmer waters running out of the rivers on to the shelves. The warmer temperatures and high nutrient inputs in summer tend to result in moderate levels of $F_{A,P}$ on these shelves ($20\text{--}359 \text{ mg C m}^{-2} \text{ d}^{-1}$ [Hirche et al. 2006]). Le Fouest et al. (2013) showed that only between 1 and 8.3% of new $F_{A,P}$ was due to local river nitrate inputs (Fig. 5). RiS can therefore become nutrient limited in the summer months. However, probably as a result of temperature gradients, $F_{A,P}$ has also been shown to decrease with distance from the river (Deubel et al. 2003), with community composition of the autotrophic pool also changing from blue-green algae- to diatom-dominated from river mouths to the open ocean (Deubel et al. 2003; Morata et al. 2008). There is no evidence of calcifying phytoplankton in the RiS, and the low salinity inputs make the regions relatively low in CaCO_3

saturation state (Beaufort Sea aragonite $\Omega < 1.5$ [Steinacher et al. 2009]; Kara Sea aragonite $\Omega < 1.8$ [Juggerstrom & Anderson 200]). This is also likely to prevent high rates of $F_{P,NC}$. Furthermore, in some areas, upwelling events, through changes in the atmospheric forcing and storm events, have been found to bring high pCO_2 , from biological remineralization in deep water, to the surface, causing localized outgassing of CO_2 and lowered saturation state conditions in the SW (Mathis et al. 2012).

Although there are large fluxes of DOC and POC from rivers, much of the POC is fairly degraded (Fahl et al. 2001; Morata et al. 2008) and likely represents low-quality food. A substantial fraction of the POC (28–66% $F_{A,P}$) on RiS is believed to be deposited to the seafloor (Stein & MacDonald 2004) and recent studies suggest that on shallow shelves riverine POC may still fuel benthic food webs (Kędra et al. 2012). Low grazing rates in the SW may contribute to this high flux (see below). Furthermore, this might imply flocculation (F_{FL}) to be important. However, only about 5% of DOC has been found to be lost through this process (Amon & Meon 2004). Indeed, the fate of DOC in the AO is still not well understood (Granskog et al. 2012). Despite this, experimental work, adding riverine waters to samples in order to follow the effect on $F_{B,P}$ showed only minor DOC consumption by bacteria (Stein & MacDonald 2004), suggesting that the DOC input from rivers may be refractory and acts conservatively (e.g., Dittmar & Kattner 2003) and is more likely to be transported across the shelf than cycled locally (Fig. 5).

Bacteria abundance and production have often been found to be correlated with temperature and DOM and inversely correlated with salinity (Saliot et al. 1996; Ortega-Retuerta et al. 2012; Boeuf et al. 2013). In the Laptev Sea, influenced by the Lena River, $F_{B,P}$ was found to be highest near the river (ca. 2–3 $pmol\ l^{-1}\ h^{-1}$ or approx. 5.7–8.6 $mg\ C\ m^{-2}\ d^{-1}$) and lowest at salinities > 19 (Saliot et al. 1996). A similar pattern was observed on the Mackenzie Shelf, influenced by the Mackenzie River, where $F_{B,P}$ in August was $7.8 \pm 9.16\ mg\ C\ m^{-2}\ d^{-1}$. Rates generally decreased with distance from the river, and were controlled by temperature and availability of labile organic matter (Ortega-Retuerta et al. 2012). Rates of $F_{B,B}$ together with a BGE of 27% would suggest a low $F_{B,R}$ of about 21 $mg\ C\ m^{-2}\ d^{-1}$. A strong correlation between $F_{A,P}$ and $F_{B,P}$ has also been observed (Meon & Amon 2004). Given that about 22 $mg\ C\ m^{-2}\ d^{-1}$ DOC could be excreted from autotrophs ($F_{A,E}$), it seems likely that $F_{B,P}$ is enhanced by DOC and POC production from autochthonous $F_{A,P}$ (Fig. 5), which in turn is stimulated by nutrient inputs, and thus $F_{B,P}$ is not directly reliant on refractory river-DOC (Meon & Amon 2004).

Photodegradation of DOC from rivers (F_{PC}) could also be critical for fuelling additional $F_{B,P}$ on RiS (Garneau et al. 2009), and experiments which expose RW to sunlight have found an increase in bio-lability of DOC (Vallières et al. 2008). Bélanger et al. (2006) reported that on average (for the period 1979–2003) F_{PC} of terrestrial DOC was estimated to be $36.6 \pm 7.1\ Gg\ C\ y^{-1}$ for the Mackenzie Shelf, Amundsen Gulf and Canada Basin, which represent 2.25–3.35% of the annual input of terrestrial DOC to the region (Telang et al. 1991). At the same time, these estimates correspond to a photoproduction of DIC of $66.5 \pm 18.5\ Gg\ C\ y^{-1}$. Although, F_{PC} processes are severely constrained by the strong attenuation of UV radiation by CDOM and suspended particulate material in RWs, as well as by the ice cover, anticipated further sea-ice retreat and potential depletion of stratospheric ozone can increase the importance of the F_{PC} in the AO (Bélanger et al. 2006). To our knowledge, there are no available estimates of F_{PC} of autochthonously produced DOC/DOM in any regions of the AO. F_{PC} of this usually labile organic matter could become more relevant in the future in light of Arctic sea-ice retreat and potential increase in marine $F_{A,P}$.

The RiS have been found to have relatively low heterotrophic abundance (Hopcroft et al. 2005; Hirche et al. 2006), with herbivorous copepods comprising almost half the mesozooplankton in the central Kara Sea, for example (Hirche et al. 2006). Early studies suggested that river POC was important for sustaining heterotrophs during periods of low productivity (Vinogradov et al. 1995). However, further studies of the carbon demand of zooplankton suggest that grazing on autotrophs ranges from about 0.1 to 12.5% of $F_{A,P}$ (Hirche et al. 2006). The relative abundance of autotrophs to heterotrophs is about 0.1, which suggests that there is sufficient $F_{A,P}$ to support these communities (Hirche et al. 2006). The lower levels of heterotrophs mean that relatively small amounts of POC and DOC are recycled through grazing activity by sloppy feeding ($< 22\ mg\ C\ m^{-2}\ d^{-1}$) and excretion ($< 2.64\ mg\ C\ m^{-2}\ d^{-1}$) (Fig. 5).

Overall the RiS have a large input of carbon in all forms from rivers, but the majority of this allochthonous carbon acts conservatively, is removed by sedimentation or is biologically unavailable. The areas nearest to the river mouths tend to be net autotrophic for short periods in the growing season, resulting in DIC removal. However, the system quickly becomes net heterotrophic with increasing distance from the rivers. The strength of the biological pump, as well as capacity for RiS regions to be sinks or sources of carbon to/from the atmosphere will vary spatially; despite this, the net CO_2 flux currently ranges from about 0.6 to 9.6 $Tg\ C\ y^{-1}$ with the ocean

acting primarily as a sink for CO₂ (Bates & Mathis 2009; Arrigo et al. 2010; Manizza et al. 2013).

Central basins (multi-year ice domains)

The perennially ice-covered Eurasian and Canadian basins are considered here together as the CB region. The CB SW are predominately low light and highly stratified, with an upper cold, fresh layer above a steep pycnocline. Little vertical mixing occurs in the CB because wind-forcing is limited by the ice cover. Therefore, horizontal advection of water masses provides the dominant flux of material to the CB. Although there are differences between the Eurasian and Canadian basins, both regions tend to be perennially oligotrophic, with low inorganic nutrient concentrations. The surface water concentrations of DIC and DOC are relatively similar, or slightly lower than, the PiS and AiS regions, reflecting the transport of dissolved carbon from these regions into the CB, with some transformation taking place from river influence and freshening by sea-ice processes (Fig. 5, Table 2).

The CB are dominated by bottom-up control of $F_{A,P}$ by physical factors, including ice cover, light and horizontal

advection (Wassmann 2011). Even in mid-summer, during 24 h daylight, continual ice cover limits the depth of the euphotic zone. The high level of stratification maintains autotrophs within the shallow euphotic zone, which is beneficial until nutrients are depleted. In the Canadian basin, lower salinity originating from the Pacific results in a stronger year-round pycnocline. The stronger pycnocline, together with the low supply of nutrients to this region (because of high production rates in the PiS consuming nutrients), causes the lowest $F_{A,P}$ of the AO ($1-5 \text{ g C m}^{-2} \text{ y}^{-1}$ [Codispoti et al. 2013]; $50-140 \text{ mg C m}^{-2} \text{ d}^{-1}$ [Olli et al. 2007]). Although the Eurasian basin is also limited primarily by bottom-up factors, the slightly enhanced vertical mixing resulting from saltier AW influence, means $F_{A,P}$ is slightly higher in this region ($10-15 \text{ g C m}^{-2} \text{ y}^{-1}$ [Codispoti et al. 2013]). Low-light conditions and cold temperature prevent calcifying autotrophs from existing in the CB. While observations of CaCO₃ saturation state have been relatively limited in this region, the data that are available suggest that the saturation states are also relatively low in the CB SW (aragonite $\Omega < 1.8$ [Jutterström & Anderson 2005]). Despite this, the continual formation of sea ice in this region, together with cold temperatures, may be conducive to

Table 2 Ranges of values for each of the processes (flux as listed in Table 1), as available from the literature, for Pacific-influenced shelves (PiS), Atlantic-influenced shelves (AiS), river-influenced shelves (RiS) and central basins (CB).

Flux	Units	PiS	AiS	RiS	CB
$F_{A,NP}$	$\text{mg C m}^{-2} \text{ d}^{-1}$	180–1630 ^a	200–500 ^b	20–359 ^c	50–140 ^d
$F_{A,NC}$	Tg C y^{-1}	nd	0.48–1.59 ^e	nd	nd
$F_{A,E}$	$\text{mg C m}^{-2} \text{ d}^{-1}$	11.0–98 ^f	12.0–30 ^f	1.2–22 ^f	4.5–156 ^f
$F_{B,R}$	$\text{mg C m}^{-2} \text{ d}^{-1}$	44 ^g	105 ^g	21 ^g	69–664 ^g
$F_{B,P}$	$\text{mg C m}^{-2} \text{ d}^{-1}$	6 ^h	18 ⁱ	7.8 ^j	6.0–57.7 ^k
$F_{H,R}$			Dependent on zooplankton type		
$F_{H,NC}$		nd	nd	nd	nd
$F_{H,S}$	$\text{mg C m}^{-2} \text{ d}^{-1}$	15–191 ^l	74–235 ^l	0.01–22 ^l	0.6–64 ^l
$F_{H,F,B}$	$\text{mg C m}^{-2} \text{ d}^{-1}$	0.8 ^m	nd	nd	0.1–8.9 ^m
$F_{H,F,A}$	$\text{mg C m}^{-2} \text{ d}^{-1}$	30–390 ⁿ	150–480 ⁿ	0.02–44.9 ⁿ	1–130 ⁿ
$F_{H,F,P}$		nd	nd	nd	nd
$F_{H,Fa}$	$\text{mg C m}^{-2} \text{ d}^{-1}$	nd	20–104 ^o	nd	0.4–1.7 ^p
$F_{H,E}$	$\text{mg C m}^{-2} \text{ d}^{-1}$	1.8–23.5 ^q	9–28.8 ^q	0.001–2.64 ^q	0.08–8.3 ^q
$F_{P,P}$	Gg C y^{-1}	nd	nd	nd	nd
$F_{P,NC}$		nd	nd	nd	nd
F_{PC}		nd	nd	66.5 ± 18.5 ^r	nd
F_{FL}		nd	nd	nd	nd
F_{SE}	$\text{mg C m}^{-2} \text{ d}^{-1}$	90–970 ^s	70–240 ^s	5.6–239.9 ^s	0.9–31.2 ^s
F_G	Tg C y^{-1}	Sink 11–53 ^t	Sink 44–77 ^t	Sink 1.0–5.7 ^t	Sink 6–9 ^t
F_R	Sv				0.1
F_O	Sv	0.8	2.2		
F_U					

^aLee et al. 2013. ^bRey 2004. Loeng & Drinkwater 2007. ^cHirche et al. 2006. ^dOlli et al. 2007. ^eHovland et al. 2013. ^fCalculated from estimate of 6% primary production ($F_{A,NP}$) for PiS, AiS and RiS, 30% for CB. ^gCalculated from estimate of 12% bacterial growth efficiency (BGE) for PiS (avg. shelf/slope values [Kirchman et al. 2009]), 15% BGE for AiS, 8% BGE for CB (avg. CB values [Kirchman et al. 2009]) and 27% BGE for RiS (Meon & Amon 2004). ^hKirchman et al. 2009. ⁱHoward-Jones et al. 2002. ^jOrtega-Retuerta et al. 2012. ^kSherr et al. 2003. Wheeler et al. 1996. ^lCalculated from estimate of 49% C-intake. ^mCalculated from% bacterial production ($F_{B,P}$) (PiS 13–22%; CB 1.1–32%). ⁿCalculated from% PP (PiS 16–22%; AiS 75–95%; CB 6.7–25%). ^oRiser et al. 2002. ^pOlli et al. 2007. ^qCalculated from estimate of 6% C-intake. ^rTelang et al. 1991. ^sCalculated from% $F_{A,NP}$ (PiS 50–60%; AiS 34–47%; RiS 28–66%; CB 6%). ^tBates & Mathis 2009.

CaCO₃ mineral formation ($F_{P,NC}$) within the ice, as has been found for thick, multi-year ice in the Antarctic (Dieckmann et al. 2008).

Advection plays an important role in bringing heterotrophs to the CB (Fig. 5). However, standing stocks of autotrophs, bacteria and heterotrophs are all comparatively low in CB as a result of cold temperatures, low-light and low-nutrient conditions (Fig. 5). Wheeler et al. (1996) demonstrated that the ratio between $F_{B,P}$ and $F_{A,P}$ ranged from about 0.95 to 1.50 in the higher latitude CB areas between 81 and 90°N, showing that $F_{B,P}$ equalled or even outweighed $F_{A,P}$. Wheeler et al. (1996) also suggested that up to about 30% of the POC produced by autotrophs is returned to DOC through exudation ($F_{A,E}$). While $F_{A,P}$ is light-limited over the seasonal cycle, with greatest abundance and production occurring in the summer time, $F_{B,P}$ has the potential to occur throughout the winter, although both $F_{B,P}$ and bacterial biomass increase by about twofold from winter to summer in the CB (e.g., Sherr et al. 2003), with bacteria responding strongly to $F_{A,P}$. Thus, similar to RiS, the additional DOC exudation from phytoplankton likely fuels further $F_{B,P}$ during the summer months. The high levels of bacteria suggest that $F_{B,R}$ is also significant. A maximum estimate, assuming 8% BGE (Kirchman et al. 2009), would give a $F_{B,R}$ of over 660 mg C m⁻² d⁻¹ (Fig. 5).

Grazing rates ($F_{H,F}$) have been suggested to be relatively high in the CB because of advection of mesozooplankton with multi-year life stages from the Atlantic. The ratio of autotrophs to heterotrophs in the CB is high (0.74) and therefore bacterivory is important in sustaining the heterotrophic community. Microzooplankton, such as heterotrophic dinoflagellates, ciliates and protists have been found to be important grazers on bacteria, with bacterivory grazing rates of 0.1–8.9 mg m⁻² d⁻¹, or 1.1–31.7% of $F_{B,P}$ (Sherr et al. 1997). Indeed, grazing rate resulted in a relatively dynamic turnover of the POC produced in the upper layers, although faecal pellet production rates was low, between 0.4 and 1.7 mg C m⁻² d⁻¹ (Olli et al. 2007). The high turnover prevents a large build-up of organic material in the SW and provides a continual, albeit relatively small (6% $F_{A,P}$; Fig. 5), export of organic matter to depth (Carmack & Wassmann 2006). While export of POC occurs, the greater depths of these basins and high levels of stratification prevent a significant coupling to the benthos. Finally, relatively small amount of DOC and POC are therefore likely to be recycled through heterotrophic feeding activities via $F_{H,E}$ (< 8.3 mg C m⁻² d⁻¹) and $F_{H,S}$ (< 64 mg C m⁻² d⁻¹), respectively (Fig. 5).

The biological pump can be considered to be relatively efficient in the CB. However, it is weak because of the

limited production in the region. Carbon exchange with the atmosphere is generally relatively low because of the prolonged ice cover, but is currently a net sink for CO₂ with a range between 0.5 and 9 Tg C y⁻¹ (Bates & Mathis 2009; Manizza et al. 2013).

Modelling, future carbon cycling and research priorities

Progress and challenges in modelling the Arctic marine carbon cycle

Models of the AO carbon cycle can help interpret observed changes in the carbon budget, as well as predict likely future changes. In the face of a rapidly changing Arctic, such model predictions may act as early warning systems for changes to the relative contribution to the global carbon budget as well as for the impact on the Arctic marine ecosystem.

As discussed above, the relative importance of carbon pools and fluxes in the Arctic varies by region, while the physical processes drive the overall biogeochemical cycles. Despite these obvious regional differences, regional modelling in the Arctic is challenging because the prevalence of sea ice in the physical system compounds (or exacerbates) the difficulty (or complicates the problem) of finding adequate boundary conditions. Although regional one-dimensional models have been developed for various Arctic shelves (e.g., Lavoie et al. 2009), a pan-Arctic approach is usually taken when modelling the system in three dimensions. The computational limitations required for the spatial coverage necessitate a compromise on the horizontal resolution. Today, horizontal spatial scales range from ca. 1 degree (ca. 111 km) in global models down to ca. 9 km (Maslowski & Lipscomb 2003). In an attempt to better capture smaller scale circulation features (likely important to the Arctic carbon system) new, finer resolution models currently under development cover the whole Arctic (e.g., Curchitser et al. 2013).

The ideal Arctic marine carbon cycle model would explicitly and adequately resolve all of the important organic and inorganic carbon pools and associated processes we have highlighted. In today's models there is a wide range of variability with respect to what state variables are included and the level of detail to which various fluxes are resolved. Importantly, a large part of this diversity comes from the range of questions that the models were initially intended to answer. Many carbon cycle models largely ignore or oversimplify some of the processes that we have highlighted as important for the AO regions, either because of insufficient knowledge of the processes or computational limitations. This raises the

question as to whether such models will be sufficiently parameterized to capture AO carbon cycle dynamics as the ocean rapidly moves into a new state. Past evaluations of a number of models found that only a quarter of them performed adequately relative to a data-based skill metric (Matsumoto et al. 2004).

Biogeochemical-focused models (e.g., Yool et al. 2010) well represent DOC, DIC and alkalinity while ecosystem-focused models tend to simplify these processes but more adequately represent the various autotrophic and heterotrophic components of the Arctic marine food web (Zhang et al. 2010; Dupont 2012). Most models applied in a global or regional setting can reasonably simulate the production of carbon by phytoplankton ($F_{A,P}$). However, even within the growing collection of ecosystem models, only a handful presently include calcifying organisms, e.g., coccolithophores, as part of the food web structure (Gregg & Casey 2007). Most models continue to simplify the formation and dissolution of CaCO_3 (e.g., Najjar et al. 2007). If considered at all, calcifying phytoplankton are often oversimplified in models, e.g., calcification and dissolution of calcium carbonate is modelled as proportional to a temperature-dependent fraction of the phytoplankton (Moore et al. 2004). While this approach may be appropriate for a present-day applications, such a parameterization may not hold for future conditions with different ocean circulation and surface water fluxes, and this shortcoming may hinder our ability to understand the relative contribution of these processes to the Arctic carbon budget.

Most models transfer the material following mortality of autotrophs and heterotrophs into one or more particulate “detritus” pools (abiotic-POC), which are prescribed with specific sinking rates (often “slow” or “fast” depending on the carbon source) and remineralization rates. DOM may be explicitly differentiated into labile and non-labile (Moore et al. 2004) but to date there has not been any attempts to include representations of the coloured fraction (CDOM). Schwarz et al. (2002) have shown that to adequately represent this component in a model, it would require incorporation as a state variable. CDOM and the associated photochemical processes are highlighted here as important for carbon cycling into the microbial and autotrophic components of the food web, particularly in the RiS, but it is not clear that sufficient data exist to support development of such a component at this time.

To realistically represent the processes associated with the microbial food web, biogeochemical models need explicitly to represent the bacterial loop processes, including $F_{B,P}$ and $F_{B,P}$, as well as the exudation of DOC from autotrophs and heterotrophs. These internal processes

have been highlighted here as potentially important for the contemporary CB and the RiS. While these important bacterial processes have been explicitly represented in some marine ecosystem models (Lancelot et al. 2000), to date these processes have been included in Arctic ecosystem models only through implicit representation of bacteria. Explicit representations of flocculation (F_{Fl}) and photodegradation (F_{PC}) dynamics are also not common. Again, realistic representations of these processes are hindered by lack of a clear understanding of the mechanistic processes and a shortage of data for model formulations and parameterization. Furthermore, the fluvial input of carbon into RiS can play an important role in carbon cycling. However, it remains common for simulated river inputs to carry no dissolved tracers, only freshwater, to the model (Long et al. 2013). Even in models designed specifically for continental shelves, the incorporation of a time invariant DOC and POC input with river flow cannot be seen as much of an improvement (Hofmann et al. 2011). A significant advance forward was made with the explicit time varying representation of riverine DOC in the regional AO model MITgcm (Marshall et al. 1997; Manizza et al. 2009; Manizza et al. 2011); this model, however, has its own shortcomings in representing the marine carbon cycle as it does not formally include any ecosystem components.

Due to substantial variability in the simulated depth of winter mixing, ecosystem models applied to the Arctic still have a fundamental disagreement as to whether light or nutrients is the limiting factor (Popova et al. 2012). Likely, as we have seen for the differing regions, there is no single control over a pan-Arctic perspective. Indeed, the physical environment, specific to each region is important in this respect, and this lingering uncertainty highlights that the model of physical environment has to be well tuned. In particular, the importance of salinity and ice in contributing to stratification makes the Arctic environment a particularly challenging region to model. While much progress has been made on this front many of the Intergovernmental Panel on Climate Change models were found to underestimate sea-ice thinning by a factor of four (Balcerak 2011) and models cannot yet simulate salinity anomalies in a robust manner (Jahn et al. 2012). Any uncertainties in the representation of the physical Arctic environment will potentially hamper understanding of the biogeochemical processes.

One of the key difficulties in modelling is verifying model behaviour through comparisons with often sparse and disjointed data (Doney et al. 2003). This problem remains a particularly big challenge when looking to model the Arctic marine carbon cycle because of the lack of pan-Arctic observational data (Gerdes et al. 2009).

Ice and cloud problems make satellite chlorophyll *a* observations very limited and sampling of other ecosystem components and processes generally requires in situ experiments, which are expensive and logistically challenging in this region. These limitations make for poorly spatially- and temporally-resolved data for model tuning and validation. Lower cost, user-friendly analytical systems are needed to enable temporal and spatial coverage of data relevant to understanding carbon cycling. Thoughtful model development, in concert with measurements and experimental efforts on the underrepresented components of the Arctic marine carbon cycle will result in more robust models with data assimilative capabilities and more reliant predictive capabilities.

Future carbon cycling and ecosystem dynamics

A number of studies have attempted to draw together interpretations of Arctic ecosystem functioning to assess how changes in physical regimes might impact carbon cycling in the Arctic in the future, particularly via changes to primary production (e.g., Wassmann & Reigstad 2011). Our assessment provides limited new insight into these projections for primary production, hence only a summary of these impacts and potential changes are provided in Table 3 for each region. However, by discussing the current state of processes within a more detailed conceptual food web and carbon cycle for each region, we are able to suggest potential impacts on other processes (Table 3), highlight knowledge gaps and areas for future research.

Considering one of the most significant changes that is occurring in the Arctic is warming (with atmospheric warming occurring at a much faster rate than in the surface ocean; Fig. 6), most of the processes discussed here (especially the biological processes) are, to some degree, temperature dependent (e.g., growth, feeding and respiration rates). The time and effort required to conduct ecosystem-level experiments to investigate the sensitivity of all these processes to warming makes it incredibly challenging. Modelling studies will therefore be important to help to simulate and investigate how, for example, increased feeding rates might be related to increased primary production in the future.

Many of these biological processes are also substrate, or food, dependent. For example, bacterial production is related to organic substrate (and its lability), phytoplankton to nutrients, and heterotrophic feeding rate is depending on food quantity and also quality. Changes to any of these closely linked trophic levels can have wide consequences. Shifts in community structure, including increases in new “invasive” organisms expanding their

ranges northwards (Cheung et al. 2009) and shifts in ecological interactions can have significant impacts on the function of the ecosystem resulting in changes in the flow of carbon. Indeed, recent evidence suggests shifts in the microbial community are already occurring: Li et al. (2009) highlight a size-shift in Arctic phytoplankton in the PiS region with larger nanoplankton being replaced by picoplankton. These shifts co-occur with long-term trends of freshening and warming that is leading to increased stability of the upper water column, and a concomitant decrease in nitrate concentration (Li et al. 2009; Comeau et al. 2011). Comeau et al. (2011) also found more subtle shifts in diversity and species composition within the bacterial communities in this region. A decrease in diversity of bacteria, and an increase in the small size-fraction within the phytoplankton, will likely lead to a change in carbon cycling through the ecosystem, best illustrated by comparing the extant system of the Arctic CB (cf. Fig. 5a, d).

In addition to ocean warming, and the associated melting of ice and increased land run-off, ocean acidification is also an important topic to consider in the Arctic, as the AO may be the one of the most rapidly acidifying oceans (Steinacher et al. 2009). The seasonality of the AO plays an important role in governing the seasonal ability for the oceans to take up CO₂, and the consequential seasonal changes in pH and calcium carbonate saturation states (Shadwick et al. 2013). This seasonality is driven by a combination of physicochemical and biological processes (e.g., Findlay et al. 2008; Bates & Mathis 2009; Mathis et al. 2010). Ocean acidification, the decrease in seawater pH and the associated decline in carbonate ions, has the potential to cause the AO SW to become corrosive, with respect to aragonite, within the next few decades (Popova et al. 2014). Acidification is most likely to, more immediately, impact calcifying marine organisms (Kroeker et al. 2013) and some instances of pteropods dissolution have been observed in both the laboratory and the field (Bednaršek et al. 2012; Comeau et al. 2012). Less direct impacts of acidification could come from a change in the energetics of organisms (e.g., Findlay et al. 2011), and thus alter the quality of food (e.g., Rossoll et al. 2012). Changes in energetics or food quality have significant implications for rates of many processes, and the resultant carbon cycling within the surface waters. That said, an increase in food quality has also been shown to counter potential impacts of acidification (e.g., Seibel et al. 2012). However, acidification may be of more concern for benthic organisms, in particular in shelf regions that are already experiencing undersaturated conditions, for example, the PiS (Mathis et al. 2012). The well coupled pelagic–benthic exchange in the PiS means higher trophic

Table 3 The potential impacts of change on physical, biogeochemical and ecological systems and the consequences for the carbon cycle, highlighting the regions—Pacific-influenced shelves (PIS), Atlantic-influenced shelves (AIS), river-influenced shelves (RIS) and central basins (CB)—most affected by each aspect.

Potential change	Consequences to physical, biogeochemical, and ecological systems	Potential impact on C cycle	Region	Ref. ^a
River (land) influence				
↑Freshwater discharge	<ul style="list-style-type: none"> · ↑ Stratification, ↓ nutrients supply, ↓ $F_{A,NP}$ · ↑ Nutrients supply, ↑ $F_{A,NP}$, · Favour species tolerating low salinity, 	<ul style="list-style-type: none"> ↓ C drawdown in SW. ↓ C cycling ↑ C drawdown in SW. ↑ C cycling ? 	Mostly RIS, possibly some influence into the CB	1, 2
↑Riverine supply of organic matter (old, refractory)	<ul style="list-style-type: none"> · ↓ Light, ↓ $F_{A,NP}$ · ↑ Radiative heating or ↑ scattering · ↑ OM remineralization, ↓ pH 	<ul style="list-style-type: none"> ↓ C drawdown in SW. ↓ C cycling ? ↓ ocean CO₂ sink 	RIS	3 4 5
↑Supply of fresh (labile) organic matter	<ul style="list-style-type: none"> · ↑ Labile material, ↑ heterotrophic processes 	<ul style="list-style-type: none"> ↓ ocean CO₂ sink 	RIS	6
Oceanic influence				
Major changes in sea-ice regime (switch from multi-year cover to seasonal ice cover)	<ul style="list-style-type: none"> · ↑ Coastal erosion, ↑ organic matter fluxes · ↑ Vertical mixing, ↑ nutrient supply, ↑ $F_{A,NP}$ · ↑ Vertical mixing, ↓ euphotic zone, ↓ $F_{A,NP}$ · ↓ Ice cover, ↑ light availability, ↑ $F_{A,NP}$ · ↑ Gas-exchange opportunities · Changes in freshwater delivery · Disturbed formation of cold water masses · Food web reorganization 	<ul style="list-style-type: none"> (see river influences) ↑ C drawdown in SW. ↑ C cycling ↓ C drawdown in SW. ↓ C cycling ↑ C drawdown in SW. ↑ C cycling Changes to C gas exchange Changes to C gas exchange Changes to C pump and export Changes to C pump and export 	All, especially CB	2, 7
↑Pacific inflow	<ul style="list-style-type: none"> · ↑ Nutrients supply, ↑ $F_{A,NP}$, · ↑ Temperature, ↑ biological rates · ↑ Advection of heterotrophs, ↑ grazing · Water inflow further north, expands $F_{A,NP}$ 	<ul style="list-style-type: none"> ↑ C drawdown in SW. ↑ C cycling Multiple level impacts ↓ C drawdown in SW. ↓ C cycling Larger area for C drawdown 	PIS (& CB)	8
↑Atlantic inflow	<ul style="list-style-type: none"> · ↑ Higher salinity water, ↑ stratification, ↓ nutrients supply, ↓ $F_{A,NP}$ · ↑ Temperature, ↑ biological rates 	<ul style="list-style-type: none"> ↓ C drawdown in SW. ↓ C cycling Multiple level impacts 	AiS (& CB)	9
Atmospheric influence				
Atmospheric warming (air temperature ↑)	<ul style="list-style-type: none"> · ↓ Ice cover & volume (see ice changes above) 		All	10
Oceanic warming (sea-surface temperature ↑)	<ul style="list-style-type: none"> · ↓ Ice cover & volume (see ice changes above) · ↑ Stratification, ↓ nutrients supply, ↓ $F_{A,NP}$ · ↑ Temperature, ↑ biological rates 	<ul style="list-style-type: none"> ↓ C drawdown in SW. ↓ C cycling Multiple level impacts 	All	2
↑Atmospheric CO ₂ concentration	<ul style="list-style-type: none"> · ↑ CO₂ uptake, ↓ pH 	<ul style="list-style-type: none"> Potentially alter ocean C sink, CaCO₃ processes, biological C processes 	All (depends on season and region)	11, 12, 13
Changes in large scale patterns of atmospheric circulation	<ul style="list-style-type: none"> · Changes in sea ice, ↑ precipitation, and change in cloud cover. Impact on light and mixing regimes 	<ul style="list-style-type: none"> Multiple level impacts 	CB (All)	14
Stratospheric ozone depletion	<ul style="list-style-type: none"> · ↑ UV radiation, ↓ $F_{A,NP}$ 	<ul style="list-style-type: none"> ↓ C drawdown in SW. ↓ C cycling 	All	15
Increase in cloudiness	<ul style="list-style-type: none"> · ↓ PAR, ↓ $F_{A,NP}$ 	<ul style="list-style-type: none"> ↓ C drawdown in SW. ↓ C cycling 	All	16

^a1. Tremblay & Gagnon 2009; 2. Wassmann & Reigstad 2011; 3. Bélanger et al. 2013; 4. Hill 2008; 5. Granskog et al. 2007; 6. Peterson et al. 2002; 7. Vancoppenolle et al. 2013; 8. Woodgate et al. 2012; 9. Schauer et al. 2004; 10. Miller et al. 2010; 11. Steiner et al. 2014; 12. Popova et al. 2014; 13. Shadwick et al. 2013; 14. Dickson et al. 2000; 15. Manney et al. 2011; 16. Bélanger et al. 2013.

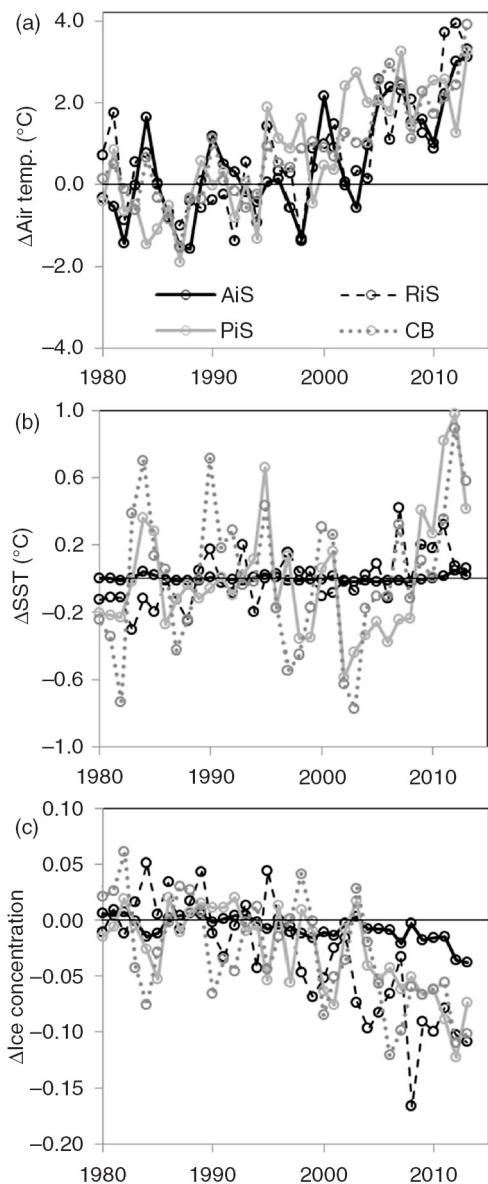


Fig. 6 Anomalies in (a) air temperature (AT), (b) sea-surface temperature (SST), and (c) ice cover (%) since 1979, relative to the 1979–2013 mean, for each of the Arctic ocean regions: Pacific-influenced shelves (PiS), Atlantic-influenced shelves (AiS), river-influenced shelves (RiS) and central basins (CB). Data are National Centers for Environmental Prediction reanalysis data provided by the Physical Sciences Division of the Earth System Research Laboratory (National Oceanic and Atmospheric Administration) in Boulder, CO, via the website <http://www.esrl.noaa.gov/psd/>.

levels and local fisheries are reliant on this benthic link (Hunt et al. 2013). Additional stress on benthic organisms from acidification, primarily occurring in the early-life stages, such as on crustacean (Whiteley 2011) or molluscs and echinoderms (Kroeker et al. 2013), will have knock-on socio-economic implications. Combined with evidence

that pelagic communities are shifting (Li et al. 2009; Comeau et al. 2010), resulting in a possible reduction in carbon export to the benthos and, hence, lower food availability, acidification could be a significant challenge to address in this region. These more complicated aspects of the carbon cycle warrant modelling exercises to help elucidate potential interactive and synergetic effects of multiple stressors on marine ecosystems and the feedback to the carbon cycle.

Research priorities

There is clearly much less information available specifically for the AO about how carbon is cycled through the microbial food web, the contribution of heterotrophs to secondary production and the fate of carbon from these biological cycles. This is highlighted by the large number of dashed lines in Fig. 5 that are associated with these processes, and as indicated by the gaps in data in Table 2. Figure 5 and Table 2 also demonstrate that significantly more data are available for some regions than others. Of particular importance is the fact that the majority of studies have been conducted in spring, summer or autumn, with very few data coming from winter-time. Technological advancements are now making year-round measurements possible and need to be utilized more within the AO: monitoring stations, buoys and remotely operated vehicles, such as gliders and Argo floats, will undoubtedly require deployment in the Arctic over the coming years.

Organic matter measurements, both particulate and dissolved, are often restricted to export studies, which have limited use for understanding the residence time in the SW and the contribution to the microbial carbon cycle, which, as highlighted, is important in at least two of Arctic domains—RiS and CB—considered here. The transformation of refractory material into labile material (e.g., through photodegradation and heterotrophic feeding) is understudied. Mounting evidence suggests that food supply, as well as food quality, are important for marine organisms to survive in general, and also to overcome shifts and changes in the environment (e.g., Seibel et al. 2012). Enhanced organic matter input may well alleviate some of the potentially detrimental impacts of climate change and ocean acidification. To fully assess this demands an improved knowledge of the physiochemical processes, as well as microbial communities, transforming carbon at cold temperatures. Field observations together with controlled process-experiment studies are required to understand the fate of carbon as it is transferred internally within the surface waters. A deeper understanding of how the microbial loop functions at

cold temperatures is required, in combination with the application of knowledge from warmer conditions to the rapidly changing AO regions.

There are still many uncertainties surrounding the heterotrophic consumers (small zooplankton) in the AO. In particular, questions remain about the temperature-dependent responses and respiratory quotient (RQ) for high-latitude species, the interactive response of organisms to warming, ocean acidification and increased organic matter input, and the contributions to carbon cycling through processes such as sloppy feeding, excretion and exudation, which may well play a crucial role in providing labile DOC for bacterial production, as shown here.

The RQ (the ratio of CO₂ eliminated to O₂ consumed) is often used to characterize the efficiency of respiration, which is directly related to the type of organic matter being metabolized. An RQ of 1, for example, represents oxidation of a pure carbohydrate. Phytoplankton generally have RQs ranging from 0.71 to 1.23 (Rodrigues & Williams 2001), depending on their composition, e.g., proteins, lipids, carbohydrates and nucleic acids. Estimates of $F_{H,R}$ using CO₂ consumption methods require knowledge of the RQ value for the organism under investigation. However, most Arctic studies have referred to RQs determined in Antarctica or sub-polar latitudes, e.g., RQs of 0.77, 0.97 and 0.85 were used for Arctic micro-zooplankton communities (Sherr & Sherr 2003), for larger zooplankton (Alcaraz et al. 2010) and for benthos (Renaud et al. 2007), respectively. Hence $F_{H,R}$ estimates in the majority of Arctic studies are based on the assumption that the composition of these organic compounds does not vary across geophysical gradients, such as temperature regimes or through seasons.

Changes in sea-ice distribution, thickness and cover pose important questions about the timing of spring ice algae blooms and their coupling to zooplankton communities. Concomitant increases in light availability in the upper ocean layer in summer due to sea-ice retreat and thinning will certainly have consequences for the carbon cycling in the AO that need to be thoroughly investigated in the future, including the impact on the rate and amount of photochemical processes, and the influence of UV on marine organisms.

Model development is required not only to project how the AO will transition into a new state in the future, but additionally to help facilitate the understanding of the carbon cycle and ecosystem function of these difficult to measure locations. The major limitation to both model development and the primary understanding of several of the key processes highlighted in this review comes from a lack of observational and experimental data that is

specific to the cold water and unique AO environment. There is already information from the modelling community on which regions, such as sea-ice zones, and which processes, such as nitrate limitation, produce the most uncertainty within Earth system model simulations (Vancoppenolle et al. 2013), and hence require immediate attention. As interest in the AO increases, both politically and economically, there should be increased opportunity to study this region. International, multidisciplinary and coordinated efforts, including joint efforts between the modelling and observational communities, are needed to rapidly gain new knowledge and make a concerted effort to understand the AO environment.

Acknowledgements

This paper resulted from a joint Arctic in Rapid Transition—Association for Polar Early Career Scientists workshop supported by the International Arctic Science Committee, the Prince Albert II of Monaco Foundation, the Polish Academy of Sciences and the Institute of Oceanology, the Polish Scientific Committee on Oceanic Research, the International Arctic Research Center, the National Center for Scientific Research—Laval Takuvik Joint Laboratory, the Alfred Wegener Institute for Polar and Marine Research and the Department of Fisheries and Oceans Canada.

References

- Aagaard K., Anderson R., Swift J. & Johnson J. 2008. A large eddy in the central Arctic Ocean. *Geophysical Research Letters* 35, L09601, doi: 10.1029/2008GL033461.
- Aagaard K., Darnall C. & Greisman P. 1973. Year-long current measurements in the Greenland–Spitsbergen passage. *Deep-Sea Research and Oceanographic Abstracts* 20, 743–746.
- Ådlandsvik B. & Loeng H. 1991. A study of the climatic system in the Barents Sea. *Polar Research* 10, 45–50.
- Alcaraz M., Almeda R., Calbet A., Saiz E., Duarte C.M., Lasternas S., Agusti S., Santiago R., Movilla J. & Alonso A. 2010. The role of Arctic zooplankton in biogeochemical cycles: respiration and excretion of ammonia and phosphate during summer. *Polar Biology* 33, 1719–1731.
- Amon R.M.W. & Meon B. 2004. The biogeochemistry of dissolved organic matter and nutrients in two large Arctic estuaries and potential implications for our understanding of the Arctic Ocean system. *Marine Chemistry* 92, 311–330.
- Arrigo K.R., Pabi S., van Dijken G.L. & Maslowski W. 2010. Air–sea flux of CO₂ in the Arctic Ocean, 1998–2003. *Journal of Geophysical Research—Biogeosciences* 115, G04024, doi: 10.1029/2009JG001224.
- Arrigo K.R., van Dijken G. & Pabi S. 2008. Impact of a shrinking Arctic ice cover on marine primary production.

- Geophysical Research Letters* 35, L19603, doi: 10.1029/2008GL035028.
- Balcerak E. 2011. Models fail to capture Arctic ice thinning, drift trends. *Eos, Transactions of the American Geophysical Union* 92, 384.
- Bates N.R. & Mathis J.T. 2009. The Arctic Ocean marine carbon cycle: evaluation of air–sea CO₂ exchanges, ocean acidification impacts and potential feedbacks. *Biogeosciences* 6, 2433–2459.
- Bates N.R., Moran S.B., Hansell D.A. & Mathis J.T. 2006. An increasing CO₂ sink in the Arctic Ocean due to sea-ice loss. *Geophysical Research Letters* 33, L23609, doi: 10.1029/2006GL027028.
- Bates N.R., Orchowka M.I., Garley R. & Mathis J.T. 2013. Summertime calcium carbonate undersaturation in shelf waters of the western Arctic Ocean—how biological processes exacerbate the impact of ocean acidification. *Biogeosciences* 10, 5281–5309.
- Bednaršek N., Tarling G.A., Bakker D.C.E., Fielding S., Jones E.M., Venables H.J., Ward P., Kuzirian A., Lézé B., Feely R.A. & Murphy E.J. 2012. Extensive dissolution of live pteropods in the Southern Ocean. *Nature Geoscience* 5, 881–885.
- Bélanger S., Cizmeli S.A., Ehn J., Matsuoka A., Doxaran D., Hooker S. & Babin M. 2013. Light absorption and partitioning in the Arctic Ocean surface waters: impact of multiyear ice melting. *Biogeosciences* 10, 6433–6452.
- Bélanger S., Xie H., Krotkov N., Larouche P., Vincent W.F. & Babin M. 2006. Photomineralization of terrigenous dissolved organic matter in Arctic coastal waters from 1979 to 2003: interannual variability and implications of climate change. *Global Biogeochemical Cycles* 20, GB4005, doi: 10.1029/2006GB002708.
- Boeuf D., Cottrell M.T., Kirchman D.L., Lebaron P. & Jeanthon C. 2013. Summer community structure of aerobic anoxygenic phototrophic bacteria in the western Arctic Ocean. *FEMS Microbiology Ecology* 85, 417–132.
- Bourgain P., Gascard J.C., Shi J. & Zhao J. 2013. Large-scale temperature and salinity changes in the upper Canadian Basin of the Arctic at a time of a drastic Arctic Oscillation inversion. *Ocean Science* 9, 447–460.
- Brown Z.W. & Arrigo K.R. 2012. Contrasting trends in sea ice and primary production in the Bering Sea and Arctic Ocean. *ICES Journal of Marine Science* 69, 1180–1193.
- Campbell R.G., Sherr E.B., Ashjian C.J., Plourde S., Sherr B.F., Hill V. & Stockwell D.A. 2009. Mesozooplankton prey preference and grazing impact in the western Arctic Ocean. *Deep-Sea Research Part II* 56, 1274–1289.
- Carmack E., Barber D., Christensen J., Macdonald R., Rudels B. & Sakshaug E. 2006. Climate variability and physical forcing of the food webs and the carbon budget on panarctic shelves. *Progress in Oceanography* 71, 145–181.
- Carmack E. & Wassmann P. 2006. Food webs and physical–biological coupling on pan-Arctic shelves: unifying concepts and comprehensive perspectives. *Progress in Oceanography* 71, 446–477.
- Cheung W.W.L., Lam V.W.Y., Sarmiento J.L., Kearney K., Watson R. & Pauly D. 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* 10, 235–251.
- Coachman L.K. & Aagaard K. 1974. Physical oceanography of Arctic and Subarctic seas. In Y. Herman (ed.): *Marine geology and oceanography of Arctic seas*. Pp. 1–72. New York: Springer.
- Codispoti L.A., Kelly V., Thessen A., Matrai P., Suttles S., Hill V., Steele M. & Light B. 2013. Synthesis of primary production in the Arctic Ocean: III. Nitrate and phosphate based estimates of net community production. *Progress in Oceanography* 110, 126–150.
- Comeau A.M., Li W.K.W., Tremblay J.-E., Carmack E.C. & Lovejoy C. 2011. Arctic Ocean microbial community structure before and after the 2007 record sea ice minimum. *PLoS One* 6, e27492, doi: 10.1371/journal.pone.0027492.
- Comeau S., Alliouane S. & Gattuso J.-P. 2012. Effects of ocean acidification on overwintering juvenile Arctic pteropods *Limacina helicina*. *Marine Ecology Progress Series* 456, 279–284.
- Cottier F.R., Niksen F., Inall M.E., Gerland S., Tverberg V. & Svendsen H. 2007. Wintertime warming of an Arctic shelf in response to large-scale atmospheric circulation. *Geophysical Research Letters* 34, L10607, doi: 10.1029/2007GL029948.
- Curchitser E.N., Hedstrom K., Danielson S. & Weingartner T. 2013. *Adaptation of an Arctic circulation model*. OCS Study BOEM 2013–202. Herndon, VA: Bureau of Ocean Energy Management, US Department of the Interior.
- de Boyer Montegut C., Madec G., Fischer A.S., Lazarus A. & Ludicone D. 2004. Mixed layer depth over the global ocean: an examination of profile data and a profile-based climatology. *Journal of Geophysical Research—Oceans* 109, C12003, doi: 10.1029/2004JC002378.
- Del Vecchio R. & Blough N.V. 2002. Photobleaching of chromophoric dissolved organic matter in natural waters: kinetics and modeling. *Marine Chemistry* 78, 231–253.
- Deubel H., Engel M., Fetzer I., Gagaev S., Hirche H.-J., Klages M., Larionov V., Lubin P., Lubina O., Nöthig E.-M., Okolodkov Y. & Rachor E. 2003. The southern Kara Sea ecosystem: phytoplankton, zooplankton and benthos communities influenced by river run-off. In R. Stein et al. (eds.): *Siberian river run-off in the Kara Sea*. Amsterdam: Elsevier.
- Dickson R.R., Osborn T.J., Hurrell J.W., Meincke J., Blindheim J., Adlandsvik B., Vinje T., Alekseev G. & Maslowski W. 2000. The Arctic Ocean response to the North Atlantic oscillation. *Journal of Climate* 13, 2671–2696.
- Dieckmann G.S., Nehrke G., Papadimitriou S., Göttlicher J., Steininger R., Kennedy H., Wolf-Gladrow D. & Thomas D.N. 2008. Calcium carbonate as ikaite crystals in Antarctic sea ice. *Geophysical Research Letters* 35, L08501, doi: 10.1029/2008GL035540.
- Dittmar T. & Kattner G. 2003. The biogeochemistry of the river and shelf ecosystem of the Arctic Ocean: a review. *Marine Chemistry* 83, 103–120.
- Doney S.C., Lindsay K. & Moore J.K. 2003. Global ocean carbon cycle modelling. In M.J.R. Fasham (ed.): *Ocean biogeochemistry*. Pp. 217–238. Berlin: Springer.

- Ducklow H.W., Steinberg D.K. & Buesseler K.O. 2001. Upper ocean carbon export and the biological pump. *Oceanography* 14, 50–58.
- Dunton K.H., Goodall J.L., Schonberg S.V., Grebmeier J.M. & Maidment D.R. 2005. Multi-decadal synthesis of benthic–pelagic coupling in the western arctic: role of cross-shelf advective process. *Deep-Sea Research Part II* 52, 3462–3477.
- Dupont F. 2012. Impact of sea-ice biology on overall primary production in a biophysical model of the pan-Arctic Ocean. *Journal of Geophysical Research—Oceans* 117, C00D17, doi: 10.1029/2011JC006983.
- Elmquist M., Semiletov I., Guo L. & Gustafsson O. 2008. Pan-Arctic patterns in black carbon sources and fluvial discharges deduced from radiocarbon and PAH source apportionment markers in estuarine surface sediments. *Global Biogeochemical Cycles* 22, GB2018, doi: 10.1029/2007GB002994.
- Eppley R.W. 1972. Temperature and phytoplankton growth in the sea. *Fishery Bulletin* 70, 1063–1085.
- Fahl K., Cremer H., Erlenkeuser H., Hanssen H., Hölemann J.A., Kassens H., Knickmeier K., Kosobokova K.N., Kunz-Pirrung M., Lindemann F., Markhaseva E., Lischka S., Petryashov V., Piepenburg D., Schmid M.K., Spindler M., Stein R. & Tuschling K. 2001. Sources and pathways of organic carbon in the modern Laptev Sea (Arctic Ocean): implications from biological, geochemical and geological data. *Polarforschung* 69, 193–205.
- Fahrbach E., Meincke J., Østerhus S., Rohardt G., Schauer U., Tverberg V. & Verduin J. 2001. Direct measurements of volume transports through Fram Strait. *Polar Research* 20, 217–224.
- Findlay H.S., Tyrrell T., Bellerby R.G.J., Merico A. & Skjelvan I. 2008. Carbon and nutrient mixed layer dynamics in the Norwegian Sea. *Biogeosciences* 5, 1395–1410.
- Findlay H.S., Wood H.L., Kendall M.A., Spicer J.I., Twitchett R.J. & Widdicombe S. 2011. Comparing the impact of high CO₂ on calcium carbonate structures in different marine organisms. *Marine Biology Research* 7, 565–575.
- Frankignoulle M., Canon C. & Gattuso J.-P. 1994. Marine calcification as a source of carbon dioxide: positive feedback of increasing atmospheric CO₂. *Limnology and Oceanography* 39, 458–462.
- Garneau M.-E., Vincent W.F., Terrado R. & Lovejoy C. 2009. Importance of particle-associated bacterial heterotrophy in a coastal Arctic ecosystem. *Journal of Marine Systems* 75, 185–197.
- Gerdes R., Kauker F. & Köberle C. 2009. Long term perspective on Arctic sea ice from AOMIP hindcasts and coupled climate models. Presentation at Arctic Ocean Model Intercomparison Project Workshop 12. 14–16 January, Woods Hole, MA, USA.
- Granskog M.A., Macdonald R.W., Mundy C.J. & Barber D.G. 2007. Distribution, characteristics and potential impacts of chromophoric dissolved organic matter. *Continental Shelf Research* 27, 2032–2050.
- Granskog M.A., Stedmon C.A., Dodd P.A., Amon R.M.W., Pavlov A.K., de Steur L. & Hansen E. 2012. Characteristics of colored dissolved organic matter (CDOM) in the Arctic outflow in the Fram Strait: assessing the changes and fate of terrigenous CDOM in the Arctic Ocean. *Journal of Geophysical Research—Oceans* 117, C12021, doi: 10.1029/2012JC008075.
- Grebmeier J. 2012. Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. *Annual Review of Marine Science* 4, 63–78.
- Grebmeier J.M., McRoy C.P. & Feder H.M. 1988. Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi seas. I. Food supply source and benthic biomass. *Marine Ecology Progress Series* 48, 57–67.
- Gregg W.W. & Casey N.W. 2007. Modeling coccolithophores in the global oceans. *Deep-Sea Research Part II* 54, 447–477.
- Grenfell T.C., Light B. & Perovich D.K. 2006. Spectral transmission and implications for the partitioning of short-wave radiation in Arctic sea ice. *Annals of Glaciology* 44, 1–6.
- Guo L., Semiletov I., Gustafsson O., Ingri J., Andersson P., Dudarev O. & White D. 2004. Characterization of Siberian Arctic coastal sediments: implications for terrestrial organic carbon export. *Global Biogeochemical Cycles* 18, GB1036.
- Hanzlick D.J. 1983. *The West Spitsbergen Current: transport, forcing and variability*. PhD thesis, University of Washington.
- Harrison W.G. & Cota G.F. 1991. Primary production in polar waters: relation to nutrient availability. *Polar Research* 10, 87–104.
- Hegseth E.N. 1998. Primary production of the northern Barents Sea. *Polar Research* 17, 113–123.
- Helms J.R., Stubbins A., Ritchie J.D., Minor E.C., Kieber D.J. & Mopper K. 2008. Absorption spectral slopes and slope ratios as indicators of molecular weight, source, and photobleaching of chromophoric dissolved organic matter. *Limnology and Oceanography* 53, 955–969.
- Hill V.J. 2008. Impacts of chromophoric dissolved organic material on surface ocean heating in the Chukchi Sea. *Journal of Geophysical Research—Oceans* 113, C07024, doi: 10.1029/2007JC004119.
- Hirche H.-J. 1987. Temperature and plankton. II. Effect on respiration and swimming activity in copepods from the Greenland Sea. *Marine Biology* 94, 347–356.
- Hirche H.J., Kosobokova K.N., Gaye-Haake B., Harms I., Meon B. & Nöthig E.-M. 2006. Structure and function of contemporary food webs on Arctic shelves: a panarctic comparison. The pelagic system of the Kara Sea—communities and components of carbon flow. *Progress in Oceanography* 71, 288–313.
- Hofmann E.E., Cahill B., Fennel K., Friedrichs M.A., Hyde K., Lee C., Mannino A., Najjar R.G., O'Reilly J.E., Wilkin J. & Xue J. 2011. Modeling the dynamics of continental shelf carbon. *Annual Review of Marine Science* 3, 93–122.
- Holmes R.M., McClelland J.W., Peterson B.J., Tank S.E., Bulygina E., Eglinton T.I., Gordeev V.V., Gurtovaya T.Y., Raymond P.A., Repeta D.J., Staples R., Striegl R.G., Zhulidov A.V. & Zimov S.A. 2011. Seasonal and annual fluxes of nutrients and organic matter from large rivers to the Arctic Ocean and surrounding seas. *Estuaries and Coasts* 35, 369–382.
- Hopcroft R.R., Clarke C., Nelson R.J. & Raskoff K.A. 2005. Zooplankton communities of the Arctic's Canada Basin: the contribution by smaller taxa. *Polar Biology* 28, 198–206.

- Hovland E.K., Dierssen H.M., Ferreira A.S. & Johnsen G. 2013. Dynamics regulating major trends in Barents Sea temperatures and subsequent effect on remotely sensed particulate inorganic carbon. *Marine Ecology Progress Series* 484, 17–32.
- Howard-Jones M.H., Ballard V.D., Allen A.E., Frischer M.E. & Verity P.G. 2002. Distribution of bacterial biomass and activity in the marginal ice zone of the central Barents Sea during summer. *Journal of Marine Systems* 38, 77–91.
- Hunt G.L. Jr., Blanchard A.L., Boveng P., Dalpadado P., Drinkwater K.F., Eisner L., Hopcroft R.R., Kovacs K.M., Norcross B.L., Renaud P., Reigstad M., Renner R., Skjoldal H.R., Whitehouse A. & Woodgate R.A. 2013. The Barents and Chukchi seas: comparison of two Arctic shelf ecosystems. *Journal of Marine Systems* 109–110, 43–68.
- Ikeda T., Kano Y., Ozaki K. & Shinada A. 2001. Metabolic rates of epipelagic marine copepods as a function of body mass and temperature. *Marine Biology* 139, 587–596.
- Ikeda T. & Skjoldal H.R. 1989. Metabolism and elemental composition of zooplankton from the Barents Sea during early Arctic summer. *Marine Biology* 100, 173–183.
- Ivleva I.V. 1980. The dependence of crustacean respiration rate on body mass and habitat temperature. *International Review of Hydrobiology* 65, 1–47.
- Jahn A., Aksenov Y., de Cuevas B., de Steur L., Hakkinen S., Hansen E., Herbaut C., Houssais M.-N., Karcher M.J., Kauker F., Lique C., Nguyen A.T., Pemberton P., Worthen D.L. & Zhang J. 2012. Arctic Ocean freshwater: how robust are model simulations? *Journal of Geophysical Research—Oceans* 117, C00D16, doi: 10.1029/2012JC007907.
- Jansson E., Olsen A., Eldevik T., Skjelvan I., Omar A.M., Lauvset S.K., Nilsen J.E.Ø., Bellerby R.G.J., Johannessen T. & Falck E. 2011. The Nordic Sea carbon budget: sources, sinks, and uncertainties. *Global Biogeochemical Cycles* 25, GB4010, doi: 10.1029/2010GB003961.
- Jumars P.A., Penry D.L., Baross J.A., Perry M.J. & Frost B.W. 1989. Closing the microbial loop—dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. *Deep-Sea Research Part I* 36, 483–495.
- Jutterström S. & Anderson L.G. 2005. The saturation of calcite and aragonite in the Arctic Ocean. *Marine Chemistry* 94, 101–110.
- Kędra M., Kuliński K., Walkusz W. & Legeżyńska J. 2012. The shallow benthic food web structure in the High Arctic does not follow seasonal changes in the surrounding environment. *Estuarine, Coastal and Shelf Science* 114, 183–191.
- Kirchman D.L., Hill V., Cottrell M.T., Gradinger R., Malmstrom R.R. & Parker A. 2009. Standing stocks, production, and respiration of phytoplankton and heterotrophic bacteria in the western Arctic Ocean. *Deep-Sea Research Part II* 56, 1237–1248.
- Kivimäe C., Bellerby R.G.J., Fransson A., Reigstad M. & Johannessen T. 2010. A carbon budget for the Barents Sea. *Deep-Sea Research Part I* 57, 1532–1542.
- Kosobokova K. & Hirche H.-J. 2009. Biomass of zooplankton in the eastern Arctic Ocean—a base line study. *Progress in Oceanography* 82, 265–280.
- Kroeker J.K., Kordas R.L., Crom R., Hendriks I.E., Ramajo L., Singh G.S., Duarte C.M. & Garruso J.-P. 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Global Change Biology* 19, 1884–1896.
- Lalande C. 2006. *Vertical export of biogenic matter in the Chukchi and Barents seas*. PhD thesis, University of Tennessee.
- Lancelot C., Hannon E., Becquevort S., Veth C. & De Baar H.J.W. 2000. Modeling phytoplankton blooms and carbon export production in the Southern Ocean: dominant controls by light and iron in the Atlantic sector in Austral spring 1992. *Deep-Sea Research Part I* 47, 1621–1662.
- Lavoie D., Macdonald R.W. & Denman K.L. 2009. Primary productivity and export fluxes on the Canadian shelf of the Beaufort Sea: a modelling study. *Journal of Marine Systems* 75, 17–32.
- Lee S.H., Yun M.S., Kim B.K., Saitoh S., Kang C.-K., Kang S.-H. & Whitedge T. 2013. Latitudinal carbon production in the Bering and Chukchi seas during summer in 2007. *Continental Shelf Research* 59, 28–36.
- Le Fouest W., Babin M. & Tremblay J.-E. 2013. The fate of riverine nutrients on Arctic shelves. *Biogeosciences* 10, 3661–3677.
- Lenn Y.D., Rippeth T.P., Old C.P., Bacon S., Polyakov I., Ivanov V. & Hölemann J. 2011. Intermittent intense turbulent mixing under ice in the Laptev Sea continental shelf. *Journal of Physical Oceanography* 41, 531–547.
- Levinsen H., Turner J.T., Nielsen T.G. & Hansen B.W. 2000. On the trophic coupling between protists and copepods in arctic marine ecosystems. *Marine Ecology Progress Series* 204, 65–77.
- Li W.K.W., McLaughlin F.A., Lovejoy C. & Carmack E.C. 2009. Smallest algae thrive as the Arctic Ocean freshens. *Science* 326, 539.
- Light B., Grenfell T.C. & Perovich D.K. 2008. Transmission and absorption of solar radiation by Arctic sea ice during the melt season. *Journal of Geophysical Research—Oceans* 113, C03023, doi: 10.1029/2006JC003977.
- Loeng H. 1991. Features of the physical oceanographic conditions of the Barents Sea. *Polar Research* 10, 5–18.
- Loeng H. & Drinkwater K. 2007. An overview of the ecosystems of the Barents and Norwegian seas and their response to climate variability. *Deep-Sea Research Part II* 54, 23–26.
- Long M.C., Lindsay K., Peacock S., Moore J.K. & Doney S.C. 2013. Twentieth-century oceanic carbon uptake and storage in CESM1 (BGC). *Journal of Climate* 26, 6775–6800.
- Lovvorn J.R., Cooper L.W., Brooks M.L., De Ruyck C.C., Bump J.K. & Grebmeier J.M. 2005. Organic matter pathways to zooplankton and benthos under pack ice in late winter and open water in late summer in the north-central Bering Sea. *Marine Ecology Progress Series* 291, 135–150.
- Manizza M., Follows M.J., Dutkiewicz S., McClelland J.W., Menemenlis D., Hill C.N., Townsend-Small A. & Peterson B.J. 2009. Modeling transport and fate of riverine dissolved organic carbon in the Arctic Ocean. *Global Biogeochemical Cycles* 23, GB4006, doi: 10.1029/2008GB003396.

- Manizza M., Follows M.J., Dutkiewicz S., Menemenlis D., Hill C.N. & Key R.M. 2013. Changes in the Arctic Ocean CO₂ sink (1996–2007): a regional model analysis. *Global Biogeochemical Cycles* 27, 1108–1118.
- Manizza M., Follows M.J., Dutkiewicz S., Menemenlis D., McClelland J.W., Hill C.N., Peterson B.J. & Key R.M. 2011. A model of the Arctic Ocean carbon cycle. *Journal of Geophysical Research—Oceans* 116, C12020, doi: 10.1029/2011JC006998.
- Manney G.L., Santee M.L., Rex M., Livesey N.J., Pitts M.C., Veefkind P., Nash E.R., Wohltmann I., Lehmann R., Froidevaux L., Poole L.R., Schoeberl M.R., Haffner D.O., Davies J., Dorokhov V., Gernandt H., Johnson B., Kivi R., Kyrö E., Larsen N., Levelt P.F., Makshtas A., McElroy C.T., Nakajima H., Conception Parrondo M., Tarasick D.W., von der Gathen P., Walker K.A. & Zinoviev N.S. 2011. Unprecedented Arctic ozone loss in 2011. *Nature* 478, 469–475.
- Marshall J., Hill C., Perelman L. & Adcroft A. 1997. Hydrostatic, quasi-hydrostatic, and nonhydrostatic ocean modelling. *Journal of Geophysical Research—Oceans* 102, 5733–5752.
- Maslowski W. & Lipscomb W.H. 2003. High resolution simulations of Arctic sea ice, 1979–1993. *Polar Research* 22, 67–74.
- Mathis J.T., Cross J.N., Bates N.R., Bradley Moran S., Lomas M.W., Mordy C.W. & Stabeno P.J. 2010. Seasonal distribution of dissolved inorganic carbon and net community production on the Bering Sea shelf. *Biogeosciences* 7, 1769–1787.
- Mathis J.T., Pickart R.S., Byrne R.H., McNeil C.L., Moore G.W.K., Juranek L.W., Liu X., Ma J., Easley R.A., Elliot M.M., Cross J.N., Reisdorph S.C., Bahr F., Morison J., Lichendorf T. & Feely R.A. 2012. Storm-induced upwelling of high pCO₂ waters onto the continental shelf of the western Arctic Ocean and implications for carbonate mineral saturation states. *Geophysical Research Letters* 39, L07606, doi: 10.1029/2012GL051574.
- Matsumoto K., Sarmiento J.L., Key R.M., Bullister J.L., Caldeira K., Campin J.-M., Doney S.C., Drange H., Dutay J.-C., Follows M., Gao Y., Gnanadesikan A., Gruber N., Ishida A., Joos F., Lindsay K., Maier-Reimer E., Marshall J.C., Matear R.J., Monfray P., Najjar R., Platter G.-K., Schlitzer R., Slater R., Swathi P.S., Totterdell I.J., Weirig M.-F., Yamanaka Y., Yool A. & Orr J.C. 2004. Evaluation of ocean carbon cycle models with data-based metrics. *Geophysical Research Letters* 31, L07303, doi: 10.1029/2003GL018970.
- McGuire A.D., Anderson L.G., Christensen T.R., Dallimore S., Guo L., Hayes D.J., Heimann M., Lorenson T.D., Macdonald R.W. & Roulet N. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs* 79, 523–555.
- McLaughlin F.A. & Carmack E.C. 2010. Deepening of the nutricline and chlorophyll maximum in the Canada Basin interior, 2003–2009. *Geophysical Research Letters* 37, L24602, doi: 10.1029/2010GL045459.
- McLaughlin F.A., Carmack E.C., Macdonald R.W. & Bishop J.K. 1996. Physical and geochemical properties across the Atlantic/Pacific water mass front in the southern Canadian Basin. *Journal of Geophysical Research—Oceans* 101, 1183–1197.
- Meon B. & Amon R.M.W. 2004. Heterotrophic bacterial activity and fluxes of dissolved free amino acids and glucose in the Arctic rivers Ob, Yenisei and the adjacent Kara Sea. *Aquatic Microbial Ecology* 37, 121–135.
- Merico A., Tyrrell T., Lessard E.J., Oguz T., Stabeno P.J., Zeeman S.I. & Whitledge T.W. 2004. Modelling phytoplankton succession on the Bering Sea shelf: role of climate influences and trophic interactions in generating *Emiliania huxleyi* blooms 1997–2000. *Deep-Sea Research Part I* 51, 1803–1826.
- Miles M.W., Divine D.V., Furevik T., Jansen E., Moros M. & Ogilvie A.E.J. 2014. A signal of persistent Atlantic multi-decadal variability in Arctic sea ice. *Geophysical Research Letters* 41, 463–469.
- Miller G.H., Brigham-Grette J., Alley R.B., Anderson L., Bauch H.A., Douglas M.S.V., Edwards M.E., Elias S.A., Finney B.P., Fitzpatrick J.J., Funder S.V., Herbert T.D., Hinzman L.D., Kaufman D.S., MacDonald G.M., Polyak L., Robock A., Serreze M.C., Smol J.P., Spielhagen R., White J.W.C., Wolfe A.P. & Wolff E.W. 2010. Temperature and precipitation history of the Arctic. *Quaternary Science Reviews* 29, 1679–1715.
- Miller W.L. & Moran M.A. 1997. Interaction of photochemical and microbial processes in the degradation of refractory dissolved organic matter from a coastal marine environment. *Limnology and Oceanography* 42(6), 1317–1324.
- Miller W.L. & Zepp R.G. 1995. Photochemical production of dissolved inorganic carbon from terrestrial organic matter: significance to the oceanic organic carbon cycle. *Geophysical Research Letters* 22, 417–420.
- Møller E.F. 2005. Sloppy feeding in marine copepods: prey-size-dependent production of dissolved organic carbon. *Journal of Plankton Research* 27, 27–35.
- Møller E.F. 2007. Production of dissolved organic carbon by sloppy feeding in the copepods *Acartia tonsa*, *Centropages typicus*, and *Temora longicornis*. *Limnology and Oceanography* 52, 79–84.
- Møller E.F. & Nielsen T.G. 2001. Production of bacterial substrate by marine copepods: effects of phytoplankton biomass and cell size. *Journal of Plankton Research* 23, 527–536.
- Moore J.K., Doney S.C. & Lindsay K. 2004. Upper ocean ecosystem dynamics and iron cycling in a global three-dimensional model. *Global Biogeochemical Cycles* 18, GB4028, doi: 10.1029/2004GB002220.
- Mopper K. & Kieber D.J. 2009. Marine photochemistry and its impact on carbon cycling. In S. de Mora et al. (eds.): *The effects of UV radiation on the marine environment*. Pp. 101–129. Cambridge: Cambridge University Press.
- Moran M.A. & Zepp R.G. 1997. Role of photoreactions in the formation of biologically labile compounds from dissolved organic matter. *Limnology and Oceanography* 42, 1307–1316.
- Moran S.B., Kelly R.P., Hagstrom K., Smith J.N., Grebmeier J.M., Cooper L.W., Cota G.F., Walsh J.J., Bates N.R., Hansell D.A., Maslowski W., Nelson R.P. & Mulsow S. 2005. Seasonal changes in POC export flux in the Chukchi Sea and implications for water column–benthic coupling in Arctic shelves. *Deep-Sea Research Part II* 52, 3427–3451.

- Morata N., Michaud E. & Włodarska-Kowalczyk M. 2015. Impact of early food input on the Arctic benthos activities during the polar night. *Polar Biology* 38, 99–114.
- Morata N., Renaud P.E., Brugel S., Hobson K.A. & Johnson B.J. 2008. Spatial and seasonal variations in the pelagic–benthic coupling of the southeastern Beaufort Sea revealed by sedimentary biomarkers. *Marine Ecology Progress Series* 371, 47–63.
- Morata N. & Søreide J.E. 2015. Effect of light and food on the metabolism of the Arctic copepod *Calanus glacialis*. *Polar Biology* 38, 67–73.
- Morse J.W. & Berner R.A. 1972. Dissolution kinetics of calcium carbonate in seawater: II. A kinetic origin for the lysocline. *American Journal of Science* 272, 840–851.
- Mundy C.J., Barber D.G. & Michel C. 2005. Variability of snow and ice thermal, physical and optical properties pertinent to sea ice algae biomass during spring. *Journal of Marine Systems* 58, 107–120.
- Najjar R.G., Jin X., Louanchi F., Aumont O., Caldeira K., Doney S.C., Dutay J., Follows M., Gruber N., Joos F. & Lindsay K. 2007. Impact of circulation on export production, dissolved organic matter, and dissolved oxygen in the ocean: results from Phase II of the Ocean Carbon-cycle Model Intercomparison Project (OCMIP-2). *Global Biogeochemical Cycles* 21, GB3007, doi: 10.1029/2006GB002857.
- Ngyuyen D. & Maranger R. 2011. Respiration and bacterial carbon demand in Arctic sea ice. *Polar Biology* 34, 1843–1855.
- Nomura D., Assmy P., Nehrke G., Granskog M.A., Fischer M., Dieckmann G.S., Fransson A., Hu Y.B. & Schnetger B. 2013. Characterization of ikaite ($\text{CaCO}_3 \cdot 6\text{H}_2\text{O}$) crystals in first-year Arctic sea ice north of Svalbard. *Annals of Glaciology* 54, 125–131.
- Olli K., Wassmann P., Reigstad M., Ratkova T.N., Arashkevich E., Pasternak A., Matrai P.A., Knulst J., Tranvik L., Klais R. & Jacobsen A. 2007. The fate of production in the central Arctic Ocean—top-down regulation by zooplankton expatriates? *Progress in Oceanography* 72, 84–113.
- Ortega-Retuerta E., Joux F., Jeffrey W.H. & Ghiglione J.F. 2012. Spatial variability of particle-attached and free-living bacterial diversity in surface waters from the Mackenzie River to the Beaufort Sea (Canadian Arctic). *Biogeosciences Discussion* 9, 17401–17435.
- Peterson B.J., Holmes R.M., McClelland J.W., Vörösmarty C.J., Lammers R.B., Shiklomanov A.I., Shiklomanov I.A. & Rahmstorf S. 2002. Increasing river discharge to the Arctic Ocean. *Science* 298, 2171–2173.
- Pnyushkov A.V. & Polyakov I.V. 2012. Observations of tidally induced currents over the continental slope of the Laptev Sea, Arctic Ocean. *Journal of Physical Oceanography* 42, 78–94.
- Polyakov I.V., Timokhov L.A., Alexeev V.A., Bacon S., Dmitrenko I.A., Fortier L., Frolov I.E., Gascard J.-C., Hansen E., Ivanov V.V., Laxon S., Mauritzen C., Perovich D., Shimada K., Simmons H.L., Sokolov V.T., Steele M. & Toole J. 2010. Arctic Ocean warming contributes to reduced polar ice cap. *Journal of Physical Oceanography* 40, 2743–2756.
- Popova E.E., Yool A., Aksenov Y., Coward A.C. & Anderson T.R. 2014. Regional variability of acidification in the Arctic: a sea of contrasts. *Biogeosciences* 11, 293–308.
- Popova E.E., Yool A., Coward A.C., Dupont F., Deal C., Elliott S., Hunke E., Jin M., Steele M. & Zhang J. 2012. What controls primary production in the Arctic Ocean? Results from an intercomparison of five general circulation models with biogeochemistry. *Journal of Geophysical Research—Oceans* 117, C00D12, doi: 10.1029/2011JC007112.
- Prisenberg S.J. & Hamilton J. 2005. Monitoring the volume, freshwater and heat fluxes passing through Lancaster Sound in the Canadian Arctic Archipelago. *Atmosphere–Ocean* 43, 1–22.
- Rachold V., Eiken H., Gordeev V.V., Grigoriev M.N., Hubberten H.-W., Lisitzin A.P., Shevchenko V.P. & Schirrmeister L. 2004. Modern and terrigenous organic carbon input to the Arctic Ocean. In R. Stein & R.W. Macdonald (eds.): *The organic carbon cycle in the Arctic Ocean*. Pp. 33–55. Berlin: Springer.
- Reigstad M., Wexels Riser C., Wassmann P. & Ratkova T. 2008. Vertical export of particulate organic carbon: attenuation, composition and loss rates in the northern Barents Sea. *Deep-Sea Research Part II* 55, 2308–2319.
- Renaud P.E., Riedel A., Michel C., Morata N., Gosselin M., Juul-Pedersen T. & Chiuchiolo A. 2007. Seasonal variation in benthic community oxygen demand: a response to an ice algal bloom in the Beaufort Sea, Canadian Arctic? *Journal of Marine Systems* 67, 1–12.
- Rey F. 2004. Phytoplankton: the grass of the sea. In H.R. Skjoldal (ed.): *The Norwegian Sea ecosystem*. Pp. 97–136. Trondheim: Tapir Academic Press.
- Rhein M., Rintoul S.R., Aoki S., Campos E., Chambers D., Feely R.A., Gulev S., Johnson G.C., Josey S.A., Kostianoy A., Mauritzen C., Roemmich D., Talley L.D. & Wang F. 2013. Observations: ocean. In T.F. Stocker et al. (eds.): *Climate change 2013. The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Pp. 255–315. Cambridge: Cambridge University Press.
- Riser C.W., Wassmann P., Olli K., Pasternak A. & Arashkevich E. 2002. Seasonal variation in production, retention and export of zooplankton faecal pellets in the marginal ice zone and central Barents Sea. *Journal of Marine Systems* 38, 175–188.
- Rivkin R.B. & Legendre L. 2001. Biogenic carbon cycling in the upper ocean: effects of microbial respiration. *Science* 291, 2398–2400.
- Rodrigues R.M.N.V. & Williams P.J.I.B. 2001. Heterotrophic bacterial utilization of nitrogenous and nonnitrogenous substrates, determined from ammonia and oxygen fluxes. *Limnology and Oceanography* 46, 1675–1683.
- Rossoll D., Bermudez R., Hauss H., Schulz K.G., Riebesell U., Sommer U. & Winder M. 2012. Ocean acidification-induced food quality deterioration constrains trophic transfer. *PLoS One* 7, e34737, doi: 10.1371/journal.pone.0034737.
- Roy S., Harris R.P. & Poulet S.A. 1989. Inefficient feeding by *Calanus helgolandicus* and *Temora longicornis* on *Coscinodiscus*

- walleisii*—quantitative estimation using chlorophyll-type pigments and effects on dissolved free amino acids. *Marine Ecology Progress Series* 52, 145–153.
- Rysgaard S., Glud R.N., Lennert K., Cooper M., Halden N., Leakey R.J.G., Hawthorne F.C. & Barber D. 2012. Ikaite crystals in melting sea ice—implications for pCO₂ and pH levels in Arctic surface waters. *Cryosphere* 6, 901–908.
- Saba G.K., Steinberg D.K. & Bronk D.A. 2011. The relative importance of sloppy feeding, excretion, and fecal pellet leaching in the release of dissolved carbon and nitrogen by *Acartia tonsa* copepods. *Journal of Experimental Marine Biology and Ecology* 404, 47–56.
- Saliot A., Cauwet G., Cahet G., Mazaudier D. & Dauma R. 1996. Microbial activities in the Lena River delta and Laptev Sea. *Marine Chemistry* 53, 247–254.
- Samtleben C. & Bickert T. 1990. Coccoliths in sediment traps from the Norwegian Sea. *Marine Micropaleontology* 16, 39–64.
- Schauer U., Fahrbach E., Osterhus S. & Rohardt G. 2004. Arctic warming through the Fram Strait: oceanic heat transport from 3 years of measurements. *Journal of Geophysical Research—Oceans* 109, C06026, doi: 10.1029/2003JC001823.
- Schwarz J.N., Kowalczyk P., Kaczmarek S., Cota G.F., Mitchell B.G., Kahru M., Chavez F.P., Cunningham A., McKee D., Gege P., Kishino T., Phinney D.A. & Raine R. 2002. Two models for absorption by coloured dissolved organic matter (CDOM). *Oceanologia* 44, 209–241.
- Seibel B.A., Maas A.E. & Dierssen H.M. 2012. Energetic plasticity underlies a variable response to ocean acidification in the pteropod, *Limacina helicina Antarctica*. *PLoS One* 7, e30464, doi: 10.1371/journal.pone.0030464.
- Serreze M.C. & Barry R.G. 2011. Process and impacts of Arctic amplification: a research synthesis. *Global and Planetary Change* 77, 85–96.
- Shadwick E.H., Trull T.W., Thomas H. & Gibson J.A.E. 2013. Vulnerability of polar oceans to anthropogenic acidification: comparison of Arctic and Antarctic seasonal cycles. *Scientific Reports* 3, article no. 2339, doi: 10.1038/srep02339.
- Sherr B.F. & Sherr E.B. 2003. Community respiration/production and bacterial activity in the upper water column of the central Arctic Ocean. *Deep-Sea Research Part I* 50, 529–542.
- Sherr E.B., Sherr B.F. & Fessenden L. 1997. Heterotrophic protists in the central Arctic Ocean. *Deep-Sea Research Part II* 44, 1665–1682.
- Sherr E.B., Sherr B.F. & Hartz A.J. 2009. Microzooplankton grazing in the western Arctic Ocean. *Deep-Sea Research Part II* 56, 1264–1273.
- Sherr E.B., Sherr B.F., Wheeler P.A. & Thompson K. 2003. Temporal and spatial variation in stocks of autotrophic and heterotrophic microbes in the upper water column of the central Arctic Ocean. *Deep-Sea Research Part I* 50, 557–571.
- Sholkovitz E.R. 1976. Flocculation of dissolved organic and inorganic matter during the mixing of river water and seawater. *Geochimica et Cosmochimica Acta* 40, 831–845.
- Sholkovitz E.R. 1978. The flocculation of dissolved Fe, Mn, Al, Cu, Ni, Co and Cd during estuarine mixing. *Earth and Planetary Science Letters* 41, 77–86.
- Skogen M.D., Olsen A., Borsheim K.Y., Sando A.B. & Skjelvan I. 2014. Modelling ocean acidification in the Nordic and Barents seas in present and future climate. *Journal of Marine Systems* 131, 10–20.
- Smedsrud L.H., Esau I., Ingvaldsen R.B., Eldevik T., Haugan P.M., Camille L., Lien V.S., Olsen A., Omar A.M., Otterå O.H., Risebrobakken B., Sandø A.B., Semenov V.A. & Sorokina S.A. 2013. The role of the Barents Sea in the Arctic climate system. *Reviews of Geophysics* 51, 415–449.
- Smith W.O. Jr. & Sakshaug E. 1990. Polar phytoplankton. In W.O. Smith Jr (ed.): *Polar oceanography. Part B. Chemistry, biology and geology*. Pp. 477–525. New York: Academic Press.
- Søreide J.E., Hop H., Carroll M.L., Falk-Petersen S. & Hegseth E.N. 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.
- Springer A.M., McRoy C.P. & Turco K.R. 1989. The paradox of pelagic food webs in the northern Bering Sea. II. Zooplankton communities. *Continental Shelf Research* 9, 359–386.
- Stedmon C.A., Amon R.M.W., Rinehart A.J. & Walker S.A. 2011. The supply and characteristics of colored dissolved organic matter (CDOM) in the Arctic Ocean: pan Arctic trends and differences. *Marine Chemistry* 124, 108–118.
- Stein R. & Macdonald R.W. 2004. Organic carbon budget: Arctic Ocean vs. global ocean. In R. Stein & R.W. Macdonald (eds.): *The organic carbon cycle in the Arctic Ocean*. Pp. 315–322. Berlin: Springer.
- Steinacher M., Joos F., Froelicher T.L., Plattner G.K. & Doney S.C. 2009. Imminent ocean acidification in the Arctic projected with the NCAR global coupled carbon cycle–climate model. *Biogeosciences* 6, 515–533.
- Steiner N.S., Christian J.R., Six K.D., Yamamoto A. & Yamamoto-Kawai M. 2014. Future ocean acidification in the Canada Basin and surrounding Arctic Ocean from CMIP5 earth system models. *Journal of Geophysical Research—Oceans* 119, 332–347.
- Striegl R.G., Dornblaser M.M., Aiken G.R., Wickland K.P. & Raymond P.A. 2007. Carbon export and cycling by the Yukon, Tanana, and Porcupine rivers, Alaska, 2001–2005. *Water Resources Research* 43, W02411, doi: 10.1029/2006WR005201.
- Stubbins A., Law C.S., Uher G. & Upstill-Goddard R.C. 2011. Carbon monoxide apparent quantum yields and photoproduction in the Tyne estuary. *Biogeosciences* 8, 703–713.
- Stubbins A., Uher G., Law C.S., Mopper K., Robinson C. & Upstill-Goddard R.C. 2006. Open-ocean carbon monoxide photoproduction. *Deep-Sea Research Part II* 53, 1695–1705.
- Symon C., Arris L. & Heal B. 2005. *Arctic climate impact assessment*. Cambridge: Cambridge University Press.
- Takahashi K., Nagao N. & Taguchi S. 2002. Respiration of adult female *Calanus hyperboreus* (Copepoda) during spring in the North Water Polynya. *Polar Biosciences* 15, 45–51.
- Tande K.S. 1988. The effects of temperature on metabolic rates of different life stages of *Calanus glacialis* in the Barents Sea. *Polar Biology* 8, 457–461.

- Taylor J.D. & Kennedy W.J. 1969. The influence of the periostracum on the shell structure of bivalve molluscs. *Calcified Tissue Research* 3, 274–283.
- Telang S.A., Pocklington R., Naidu A.S., Romankevich E.A., Gitelson I.I. & Gladyshev M.I. 1991. Carbon and mineral transport in major North American, Russian Arctic, and Siberian rivers: the St Lawrence, the Mackenzie, the Yukon, the Arctic Alaskan rivers, the Arctic basin rivers in the Soviet Union, and the Yenisei. *Biogeochemistry of Major World Rivers* 42, 75–104.
- Thor P., Dam H.G. & Rogers D.R. 2003. Fate of organic carbon released from decomposing copepod fecal pellets in relation to bacterial production and ectoenzymatic activity. *Aquatic Microbial Ecology* 33, 279–288.
- Tremblay J.E. & Gagnon J. 2009. The effects of irradiance and nutrient supply on the productivity of Arctic waters: a perspective on climate change. In C.J. Nihoul & A.G. Kostianoy (eds.): *Influence of climate change on the changing Arctic and Subarctic conditions*. Pp. 73–92. Berlin: Springer.
- Urban-Rich J. 1999. Release of dissolved organic carbon from copepod fecal pellets in the Greenland Sea. *Journal of Experimental Marine Biology and Ecology* 232, 107–124.
- Valentine R.L. & Zepp R.G. 1993. Formation of carbon monoxide from the photodegradation of terrestrial dissolved organic carbon in natural waters. *Environmental Science & Technology* 27, 409–412.
- Vallières C., Retamal L., Ramlal P., Osburn C.L. & Vincent W.F. 2008. Bacterial production and microbial food web structure in a large Arctic river and the coastal Arctic Ocean. *Journal of Marine Systems* 74, 756–773.
- Vancoppenolle M., Bopp L., Madec G., Dunne J., Ilyina T., Halloran P.R. & Steiner N. 2013. Future Arctic Ocean primary productivity from CMIP5 simulations: uncertain outcome, but consistent mechanisms. *Global Biogeochemical Cycles* 27, 605–619.
- Vaquier-Sunyer R., Duarte C.M., Santiago R., Wassmann P. & Reigstad M. 2010. Experimental evaluation of planktonic respiration response to warming in the European Arctic Sector. *Polar Biology* 33, 1661–1671.
- Verity P.G., Wassmann P., Frischer M.E., Howard-Jones M.H. & Allen A.E. 2002. Grazing of phytoplankton by microzooplankton in the Barents Sea during early summer. *Journal of Marine Systems* 38, 109–123.
- Vinogradov M.E., Shushkina E.A., Lebedeva L.P. & Gagarin V.I. 1995. Mesoplankton in the eastern part of the Kara Sea and Ob and Yenisei rivers estuaries. *Oceanology* 34, 716–723.
- Walczowski W., Piechura J., Osinski R. & Wieczorek P. 2005. The West Spitsbergen Current volume and heat transport from synoptic observations in summer. *Deep-Sea Research Part I* 52, 1374–1391.
- Wassmann P. 2011. Arctic marine ecosystems in an era of rapid climate change. *Progress in Oceanography* 90, 1–17.
- Wassmann P. & Reigstad M. 2011. Future Arctic Ocean seasonal ice zones and implications for pelagic–benthic coupling. *Oceanography* 24, 220–231.
- Weydmann A., Carstensen J., Goszczko I., Dmoch K., Olszewska A. & Kwasniewski S. 2014. Shift towards the dominance of boreal species in the Arctic: inter-annual and spatial zooplankton variability in the West Spitsbergen Current. *Marine Ecology Progress Series* 501, 41–52.
- Wheeler P.A., Gosselin M., Sherr E., Thibault D., Kirchman D.L., Benner R. & Whitley T.E. 1996. Active cycling of organic carbon in the central Arctic Ocean. *Nature* 380, 697–699.
- Whitehouse A. 2011. *Modeling the eastern Chukchi Sea food web with a mass-balance approach*. Master's thesis, School of Aquatic and Fishery Sciences, University of Washington, Seattle.
- Whiteley N.M. 2011. Physiological and ecological responses of crustaceans to ocean acidification. *Marine Ecology Progress Series* 430, 257–271.
- Woodgate R., Weingartner T. & Lindsay R. 2012. Observed increases in Bering Strait oceanic fluxes from the Pacific to the Arctic from 2001 to 2011 and their impacts on the Arctic ocean water column. *Geophysical Research Letters* 39, L24603, doi: 10.1029/2012GL054092.
- Woodgate R.A. & Aagaard K. 2006. Monthly temperature, salinity, and transport variability of the Bering Strait through flow. *Geophysical Research Letters* 32, L04601, doi: 10.1029/2004GL021880.
- Yool A., Oschlies A. & Nurser A.J.G. 2010. A model-based assessment of the TrOCA approach for estimating anthropogenic carbon in the ocean. *Biogeosciences* 7, 723–751.
- Zhang J., Spitz Y.H., Steele M., Ashjian C., Campbell R., Berlin L. & Matrai P. 2010. Modeling the impact of declining sea ice on the Arctic marine planktonic ecosystem. *Journal of Geophysical Research—Oceans* 115, C10015, doi: 10.1029/2009JC005387.