

Synoptic evaluation of carbon cycling in Beaufort Sea during summer: contrasting river inputs, ecosystem metabolism and air–sea CO₂ fluxes

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Abstract

The accelerated decline in Arctic sea ice combined with an ongoing trend toward a more dynamic atmosphere is modifying carbon cycling in the Arctic Ocean. A critical issue is to understand how net community production (NCP; the balance between gross primary production and community respiration) responds to changes and modulates air–sea CO₂ fluxes. Using data collected as part of the ArcticNet-Malina 2009 expedition in southeastern Beaufort Sea (Arctic Ocean), we synthesize information on sea ice, wind, river, water column properties, metabolism of the planktonic food web, organic carbon fluxes and pools, as well as air–sea CO₂ exchange, with the aim of identifying indices of ecosystem response to environmental changes. Data were analyzed to develop a non-steady-state carbon budget and an assessment of NCP against air–sea CO₂ fluxes. The mean atmospheric forcing was a mild upwelling-favorable wind (~5 km h⁻¹) blowing from the N-E and a decaying ice cover (< 80 % concentration) was observed beyond the shelf, the latter being fully exposed to the atmosphere. We detected some areas where the surface mixed layer was net autotrophic owing to high rates of primary production (PP), but the ecosystem was overall net heterotrophic. The region acted nonetheless as a sink for atmospheric CO₂ with a mean uptake rate of $-2.0 \pm 3.3 \text{ mmolCm}^{-2} \text{ d}^{-1}$. We attribute this discrepancy to: (1) elevated PP rates (> 600 mgCm⁻² d⁻¹) over the shelf prior to our survey, (2) freshwater dilution by river runoff and ice melt, and (3) the presence of cold surface waters offshore. Only the Mackenzie River delta and localized shelf areas directly affected by upwelling were identified as substantial sources of CO₂ to the atmosphere (> 10 mmolCm⁻² d⁻¹). Although generally < 100 mgCm⁻² d⁻¹, daily PP rates cumulated to a total PP of $\sim 437.6 \times 10^3 \text{ tC}$, which was roughly twice higher than the organic carbon delivery by river inputs ($\sim 241.2 \times 10^3 \text{ tC}$). Subsurface PP represented 37.4 % of total PP for the whole area and as much as $\sim 72.0 \%$ seaward of the shelf break. In the upper 100 m, bacteria dominated (54 %) total community respiration ($\sim 250 \text{ mgCm}^{-2} \text{ d}^{-1}$), whereas protozoans, metazoans, and benthos, contributed to 24 %, 10 %, and 12 %, respec-

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tively. The range of production-to-biomass ratios of bacteria was wide (1–27 % d⁻¹), while we estimated a narrower range for protozoans (6–11 % d⁻¹) and metazoans (1–3 % d⁻¹). Over the shelf, benthic biomass was twice higher (~5.9 g C m⁻²) than the biomass of pelagic heterotrophs (~2.4 g C m⁻²), in accord with high vertical carbon fluxes on the shelf (956 ± 129 mg C m⁻² d⁻¹). Threshold PP (PP at which NCP becomes positive) in the surface layer oscillated from 20–152 mg C m⁻² d⁻¹, with a pattern from low-to-high values as the distance from the Mackenzie River decreased. We conclude that: (1) climate change is exacerbating the already extreme biological gradient across the Arctic shelf-basin system; (2) the Mackenzie Shelf acts as a weak sink for atmospheric CO₂, implying that PP exceeds the respiration of terrigenous and marine organic matter in the surface layer; and (3) shelf break upwelling can transfer CO₂ to the atmosphere, but massive outgassing can be attenuated if nutrients brought also by upwelling support diatom production. Our study underscores that cross-shelf exchange of waters, nutrients and particles is a key mechanism that needs to be properly monitored as the Arctic transits to a new state.

1 Introduction

As the seasonal ice zone (SIZ) expands with the ongoing retreat in summer ice (Parkinson and Comiso, 2013), increased transport of water, solutes and particles is expected across the Arctic shelf break (Carmack and Chapman, 2003; Forest et al., 2007; Anderson et al., 2010). This is because sea ice and newly opened waters are both exposed to a more dynamic atmospheric forcing, which is a collateral effect of the amplified warming taking place at high northern latitudes (Francis and Vavrus, 2012). The synergy between a fractured, more mobile, sea ice cover and the development of large areas devoid of sea ice creates the ideal pre-conditioning for increased cross-shelf exchange (e.g. O'Brien et al., 2011; Janout et al., 2013). The trend in atmospheric circulation over the Arctic since the late 1990's is an acceleration of the anticyclonic (clockwise) regime (Ogi and Rigor, 2013), recently exacerbated (since ~2007) by a marked in-

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5 tensification of the Beaufort Sea High (a prominent feature of high sea-level pressure) in early summer, which now frequently extends from northern North America to over Greenland (Overland et al., 2012; Moore, 2012). Although the cyclonic (anticlockwise) regime is apparently in a declining trend in the Arctic during summer (Moore, 2012),
10 coastal storminess is increasing (Vermaire et al., 2013) and the late summer season is affected by a significant rise in the strength and size of cyclones (Simmonds and Keay, 2009). This trend in late summer storm activity apparently culminated in 2012 with the development of the so-called great Arctic cyclone (Simmonds and Rudeva, 2012; Zhang et al., 2013). As a result, stronger winds induced by both intensified high-
15 pressure systems and large-scale storms increase the potential for momentum transfer and facilitate cross-shelf exchange during and around the period of minimum sea ice.

A prime consequence of increased lateral cross-shelf exchange for ecosystem function and biogeochemical cycling in the Arctic is the upwelling of nutrient-rich and CO₂-rich (acidic) halocline waters (> 100 m) along the continental slope and over shallow
20 shelves. On the one hand, upwelled nutrients sustain high primary production and associated vertical carbon export, thus resulting in the uptake of CO₂ by the surface biota and its subsequent storage at depth through the biological pump (e.g. Anderson et al., 2010; Tremblay et al., 2011). This process is however tightly linked to the structure of the pelagic food web, which dictates the pathways of biogenic carbon flow in the
25 water column (Forest et al., 2011). For example, a large biomass of microbial and/or metazoan heterotrophs in the surface layer could possibly negate the potential for CO₂ uptake if respiration exceeds primary production (e.g. Ortega-Retuerta et al., 2012). But if the respiration occurs below the mixed layer instead, such as when animals migrate to depth during the day or at the end of summer, heterotrophic respiration might actually contribute to CO₂ storage in deeper waters (e.g. Darnis and Fortier, 2012; Kobari et al., 2013). On the other hand, upwelling brings upward acidic waters super-saturated in CO₂ with respect to the atmosphere (up to > 600 ppm), promoting CO₂ outgassing and possibly impairing pelagic and benthic organisms sensitive to low pH (Yamamoto-Kawai et al., 2009; Mathis et al., 2012). These phenomena can be particu-

larly strong in the Pacific sector of the Arctic Ocean where a water layer of Pacific origin containing ca. twice as much CO₂ as the deep Atlantic water mass lies at intermediate depths (see Lansard et al., 2012 for details).

Analyzing the interplay between hydrodynamics and ecosystem metabolism is a critical task if the implications of increased cross-shelf exchange for ocean acidification and CO₂ sink-source balance are to be understood. Despite being utterly needed, such analysis is challenging to realize, as a synoptic view of physical forcings, geochemical setting, and planktonic food web structure, is logistically difficult to obtain – especially for the Arctic marine environment. Such evaluation is also complexified by the multiple time-scales affecting the environmental and biological factors that govern carbon flux dynamics. Ecosystem metabolic balance can be simplified as the net result of carbon fixation by autotrophic organisms minus that used by the whole biological community for respiration, which encompasses numerous processes in between (e.g. trophic transfer, reproduction, somatic maintenance, motility). However, studies on ecosystem metabolism rarely go beyond the quantification of organic carbon production vs. remineralization, so the phenology of production vs. respiration, the food web components at play, and the implications for air–sea CO₂ exchange remain often unexplored.

Here, we synthesize information on atmospheric and hydrographic forcings, biogeochemical context, plankton metabolism, and air–sea CO₂ fluxes, as measured during the ArcticNet-Malina campaign that took place in July–August 2009 across the Mackenzie Shelf region (southeastern Beaufort Sea, Arctic Ocean). This spatial-temporal window was particularly relevant to investigate the potential effects of changing atmospheric and sea ice patterns on the Arctic marine ecosystem. Over that period, the Beaufort Sea has been influenced by a shift from a high-pressure system fostering clear sky and strong northerly winds to a more cyclonic regime that promoted clouds and ice melt across the area (NSIDC, 2009). Our objective is to evaluate quantitatively the different fluxes and reservoirs of carbon across the shelf-basin interface to identify key indices of ecosystem response to climate change. Hence, we pose three questions that will form the crucible for concluding on the potential interactions and feedbacks be-

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tween ecological and biogeochemical processes with respect to carbon fluxes in the future Arctic Ocean: (1) to which extent net ecosystem metabolism was coupled with sea-to-air CO₂ fluxes? (2) What were the roles of cross-shelf exchange, river inputs and sea ice in driving carbon fluxes? (3) How did the planktonic food web respond and feed back to organic and inorganic carbon cycling?

2 Material and methods

2.1 Study area and sampling strategy

The Mackenzie Shelf in southeastern Beaufort Sea is a narrow rectangular shelf (120 km width × 530 km length) bordered by the Alaskan Beaufort Shelf on the west, the Amundsen Gulf on the east, and by the Canada Basin to the north (Fig. 1). Galley et al. (2013) reviewed the atmospheric and sea ice conditions of the southern Beaufort Sea from 1996 to 2010. Over that period, ocean currents and sea ice circulation patterns were closely coupled, showing an anomalous anti-cyclonic pattern associated with an accentuated Beaufort Sea High when compared with the mean over 1981–2010 (Overland, 2009). The Beaufort Sea High was particularly strong in 2007 when Arctic sea ice extent dramatically declined to 4.1×10^6 km². Although less developed, a similar atmospheric pattern prevailed in summer 2008 and for most of summer 2009 (i.e. until August; NSIDC, 2009). Sea ice in southern Beaufort Sea typically reaches a maximum thickness of ~2–3 m in March–April and is usually melted by mid-September (Barber and Hanesiak, 2004). In April 2009, Haas et al. (2010) surveyed sea ice thicknesses in the region and found a wide range of conditions, from a multi-year sea ice cover of 2.3–3.3 m advected south by the anti-cyclonic motion of the Beaufort Gyre, to a thin first-year ice of 1.1 m northwest of the Mackenzie Canyon.

Despite being the fourth largest river input in terms of freshwater discharge (330 km³ yr⁻¹), the Mackenzie River ranks first for sediment load among Arctic rivers, with an annual mean of 124×10^6 yr⁻¹ (Gordeev, 2006). In 2009, the water dis-

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charge from the Mackenzie was above the mean of 1998–2008 from May to July (~ 20.5 vs. $\sim 17.4 \times 10^3 \text{ m}^3 \text{ s}^{-1}$) as well as during September–October (~ 12.8 vs. $\sim 10.5 \times 10^3 \text{ m}^3 \text{ s}^{-1}$), but remained overall in the envelope covered by standard deviation (from ± 0.5 to $\pm 7.4 \times 10^3 \text{ m}^3 \text{ s}^{-1}$) during summer (Forest et al., 2013). Typically in summer, ice melt and river runoff generate a stratified surface layer in the top 5–10 m of the water column (Carmack and Macdonald, 2002). Water masses in the region come from various sources and comprise: sea ice melt water, the Mackenzie River, the polar mixed-layer (above ~ 50 m), summer and winter water of Pacific origin (~ 50 – 200 m), Atlantic Water (~ 200 – 800 m), and Canada Basin deep water (> 800 m depth) (Lansard et al., 2012). Ocean circulation is complex and driven by wind and sea ice dynamics. Northwesterly winds retain surface waters and the Mackenzie River plume inshore (downwelling conditions), whereas easterlies push them seaward (upwelling conditions) (Macdonald and Yu, 2006). The recent wind-driven acceleration of the Beaufort Gyre (strengthening of the Beaufort Sea High) has promoted the upwelling regime. Accordingly, a progressive switch from eastward to northwestward routing of surface waters has been observed since 2002 (Fichot et al., 2013).

Primary production (PP) in the Beaufort Sea is usually known as being low when compared with other Arctic shelves, with an annual range from 30 to $70 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Sakshaug, 2004; Carmack et al., 2004). With the ongoing transformation of the atmosphere-ice regime in the Beaufort Sea, the vertical transport of nutrient-rich intermediate waters to the surface through wind-driven upwelling appears to be able to increase PP on the shelf (Tremblay et al., 2011) and at its periphery (Forest et al., 2011). The strength of the spring bloom is closely related to the renewal of nitrate in the upper water column during winter (Tremblay et al., 2008). Then, a subsurface chlorophyll maximum (SCM) rapidly develops and progressively lowers the nitracline over summer (Martin et al., 2010). While large-sized diatom cells dominate the spring bloom, the SCM harbors a more diverse phytoplankton community, numerically dominated by small flagellates. Planktonic and benthic food webs in the Mackenzie Shelf region are fuelled by both allochthonous and autochthonous carbon sources (Parsons

et al., 1989; Morata et al., 2008; Connelly et al., 2012). But the exact contribution of riverine material to overall ecosystem metabolism remains difficult to quantify, especially as stable isotopes and elemental ratios might provide a distorted view on food web linkages in the Beaufort Sea – i.e. biased toward terrigenous inputs while PP is the primary organic carbon source (Sallon et al., 2011; Pineault et al., 2013). Nevertheless, it is impossible to dismiss the large organic matter flux from the Mackenzie River, so studies comparing heterotrophic carbon demand against autochthonous marine productivity typically used river input as the major factor for explaining any imbalance between these two (e.g. Garneau et al., 2008; Ortega-Retuerta et al., 2012). While this might be appropriate for microbial communities, metazooplankton activity (dominated by copepods) is rather linked to pulses in fresh food supply during spring-summer (e.g. Forest et al., 2011, 2012). Similarly, carbon turnover by benthic organisms is largely related to the distribution of phyto-detritus in surface sediments (Renaud et al., 2007).

Here we used data from the ArcticNet and Malina oceanographic expeditions that successively investigated the southeastern Beaufort Sea in July–August 2009 from the Canadian research icebreaker CCGS Amundsen. The ArcticNet sampling stations were located within a small, enclosed area at the shelf break; whereas the Malina sampling grid was primarily composed of 7-shelf-basin transects (Fig. 1). Two of the Malina transects extended to very shallow waters (~3 m depth) where sampling was conducted using a zodiac or a barge (see Doxaran et al., 2012). The ensemble of sampling stations conducted in July–August 2009 constitutes one of the most comprehensive spatial coverage of the Mackenzie Shelf region, within which a wide range of hydrographic, cryospheric and biogeochemical conditions were thoroughly sampled over a ~1 month period.

This study represents an effort to synthesize a wide range of observations made during the ArcticNet-Malina campaign in the context of previous work in the region and comprises diverse datasets acquired through distinct approaches. Hence, to facilitate the reading of the following methodological sections, we provide a diagram (Fig. 2) showing which variables have been directly measured on the field, vs. which ones

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have been calculated using a combination of in situ data and empirical models, or rather estimated using knowledge from the literature or deduced from previous regional studies. For a detailed description of equations linking metabolic pathways of planktonic and benthic compartments, please see Appendix B in Forest et al. (2011).

2.2 Sea ice conditions, wind reanalysis and ocean color remote sensing

Daily-averaged sea ice concentrations (% of cover) were obtained from the Ifremer-CERSAT Team (<http://cersat.ifremer.fr/>) as initially acquired from the Special Sensor Microwave Imager (SSM/I) located onboard the orbiting sensor of the Defense Meteorological Satellite Program (DMSP). The CERSAT team processes ice maps at 12.5 km resolution using the daily brightness temperature maps from the National Snow and Ice Data Center (NSIDC; Maslanik and Stroeve, 1999) combined with the Artist Sea Ice algorithm of Kaleschke et al. (2001). Sea ice concentrations for the study area were averaged over two 35 day periods (14 June–19 July and 20 July–24 August) to produce gridded composites of sea ice conditions in summer 2009.

Daily mean wind velocity and direction (meridional and zonal wind at 10 m) were obtained from the National Centers for Environmental Prediction (NCEP) North American Regional Reanalysis (NARR) (<http://www.esrl.noaa.gov/psd/data/gridded/data.narr.html>). The NARR data are obtained from the high resolution NCEP Eta Model (32 km, 45 layers) together with the Regional Data Assimilation System (RDAS) and converted to a Northern Lambert Conformal Conic grid. Wind composites for the same periods as sea ice averages were computed.

Ocean color images from the Moderate Resolution Imaging Spectroradiometer (MODIS-Aqua; Level-3 daily Rrs at 412, 443, 488, 531, 555 and 667 nm) were downloaded from the NASA Goddard Earth Sciences Data and Information Services Center (<http://oceancolor.gsfc.nasa.gov>). For each image, PP rates were calculated using the processing chain and the photosynthesis-irradiance model of Bélanger et al. (2013). This procedure makes use of the state-of-the-art development in ocean color remote sensing and combines sea ice and cloud properties in order to model the incident spec-

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tral solar irradiance below the sea surface. It also accounts for absorption by colored dissolved organic matter (CDOM) and non-algal particles, which are known to increase artificially the ratio of chlorophyll (*chl*) *a* concentration to the diffuse attenuation coefficient of photosynthetically usable radiation. As this problem still remains a major issue in the coastal Arctic Ocean where river inputs are important (Mustapha et al., 2012), we set a maximum *chl a* threshold of 30 mgm⁻³ (Ardyna et al., 2013). The final products were daily maps of PP (4.64 km resolution) that we averaged for the same periods as sea ice and wind conditions.

2.3 Ocean properties, mixed layer depth and sea-to-air CO₂ fluxes

A conductivity-temperature-depth system (CTD, Seabird SBE-911+) was deployed at every sampling station across the study area (Fig. 1). CTD data were calibrated and verified following the Unesco Technical Papers (Crease, 1988). Water samples, collected with a rosette system equipped with 22 × 12 L Niskin bottles, were taken for salinity calibration using a Guildline Autosol salinometer. All verified CTD data were averaged over 1 m bins.

The mixed layer depth (MLD) was calculated using the method proposed by Holte and Talley (2009), but modified for the Arctic waters by using only the density profiles. In brief, this algorithm first calculates 4 possible MLD values with different methods (i.e. threshold value method at 0.05 kgm⁻³, maximum density gradient, intersection between straight line on the mixed-layer of density and fitted line on pycnocline, and gradient method) and then analyses the groupings and patterns within the possible MLDs to select a final MLD estimate (see Holte and Talley, 2009 for a detailed description of each step of the MLD calculation).

Water samples for the determination of total alkalinity (TA) and pH were collected at sea following the protocol of Mucci et al. (2010). TA and pH were measured onboard within 4 h of sample collection. TA was measured using an automated Radiometer potentiometric titrator and a Red Rod combination pH electrode. The pH of samples with salinity > 20 was determined colorimetrically using a UV visible diode array spec-

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trophotometer and a 5 cm quartz cell. Phenol red and *m*-cresol purple were used as indicators. The pH of brackish water samples (salinity < 20) was measured with a potentiometric electrode setup. In situ seawater CO₂ fugacity ($f\text{CO}_2\text{-sw}$) and total inorganic carbon (TIC) concentration were calculated from TA and pH measurements with the freeware CO2SYS (Lewis and Wallace, 1998) and the carbonate dissociation constants of Mehrbach et al. (1973) as refit by Dickson and Millero (1987). In addition to bottle sampling, a continuous sampling of $p\text{CO}_2\text{-sw}$ was conducted using an underway system (General Oceanics model 8050; Pierrot et al., 2009) delivering water from a nominal depth of ~ 5 m and equipped with a flow-through CTD (Idronaut Ocean Seven 315) as described in Else et al. (2013a). CO₂ data from the underway system were corrected for thermodynamic effects and were discarded when the flow to the equilibrator was below 2 L per min. Validated $p\text{CO}_2\text{-sw}$ data from the underway system were merged with the bottle dataset to provide a comprehensive overview of sea surface CO₂ concentrations across the study area. Conversion of $f\text{CO}_2$ to $p\text{CO}_2$ and vice-versa was made using the virial equation of Weiss (1974).

Sea-to-air CO₂ fluxes were calculated using the bulk formulation, linearly scaled to sea ice concentration (e.g., Bates et al., 2006; Mucci et al., 2010; Else et al., 2012):

$$\text{FCO}_2 = k\alpha(p\text{CO}_2\text{-sw} - p\text{CO}_2\text{-atm})(100 - \text{SIC}/100) \quad (1)$$

where FCO₂ is the flux of CO₂ (mmolm⁻²d⁻¹, negative values indicate a sink into the ocean while positive values indicate a source for the atmosphere), k is the gas transfer velocity, α is the solubility of CO₂ in seawater, $p\text{CO}_2$ is the partial pressure of CO₂ in the atmosphere (atm) and surface seawater (sw), and SIC is the sea ice concentration from 0 to 100%. $p\text{CO}_2\text{-atm}$ over the study area was calculated using atmospheric CO₂ mixing ratio from the Scripps Facility located in Point Barrow (Keeling et al., 2001; <http://scrippsco2.ucsd.edu>), according to the equations of Weiss (1974) and Weiss and Price (1980) that make use of in situ sea surface temperature (SST), sea surface salinity, and barometric pressure (from the ship meteorological tower). We

Matsuoka et al. (2012) ($\text{DOC} = 486 - 16 \times \text{salinity}$; $r^2 = 0.89$; $p < 0.0001$) and a salinity of zero.

Concentrations of POC in the water column were determined using two methodologies. The first one involved the filtration of known volumes of seawater in triplicates through pre-weighed and pre-combusted 25 mm GF/F Whatman filters (0.7 μm pore size). These samples were stored at -80°C on the ship before further acidification (to remove the inorganic carbon fraction) followed by a classical CHN analysis (Perkin Elmer 2400, combustion at 925°C) on land (as described in Doxaran et al., 2012). The second method used a similar filtration procedure, but the determination of POC was carried using the wet-oxidation technique of Raimbault et al. (1999a). In total, 130 samples were processed with the CHN and 248 samples were analyzed with the wet-oxidation method. The two datasets were subsequently compared for coherency and combined into one single database.

Samples for the determination of total organic carbon were collected into 50 mL Glass Schott bottles, immediately acidified with H_2SO_4 and stored for further analysis. Prior to oxidation, samples were bubbled with a high purity oxygen/nitrogen gas stream for 15 min. Persulfate wet-oxidation was used to digest the organic matter in these unfiltered samples (Raimbault et al., 1999b). The concentration of DOC was calculated from the total organic fraction by subtracting POC values obtained from the corresponding GF/F fraction. Reference water from the Sargasso Sea was used to verify the calibration of DOC (Hansell Laboratory, Bermuda Biological Station for Research). All reagents and blanks were prepared using fresh Millipore Milli-Q plus water.

Vertical POC fluxes during ArcticNet-Malina 2009 were determined using a combination of sediment trap measurements and camera recordings (Forest et al., 2013). Briefly, particles in the range 0.08–4.2 mm (in equivalent spherical diameter, ESD) recorded with an Underwater Vision Profiler 5 (UVP5, Picheral et al., 2010) were transformed into vertical POC fluxes with a regional empirical algorithm linking sediment trap fluxes and the UVP5 dataset. The algorithm was developed using an optimization procedure following Guidi et al. (2008) and provided a good agreement between sedi-

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ment trap POC fluxes and UVP5 fluxes ($r^2 = 0.68$, $n = 21$). This methodology allowed us to obtain vertical POC fluxes at high vertical resolution at 154 stations.

2.5 Nutrients, gross primary production and phytoplankton dynamics

Nutrient samples were collected at standard depths in the water column (Tremblay et al., 2008; Martin et al., 2010). Samples for the determination of nitrate [NO_3^-] and nitrite [NO_2^-] were dispensed into polyethylene flasks and poisoned with mercuric chloride (Kirkwood, 1992) for later analysis. Nitrate and nitrite were measured using a Technicon AutoAnalyzer II (Tréguer and LeCorre (1975) following Raimbault et al., 1990). Ammonium concentration [NH_4^+] was measured directly on board using the sensitive fluorescent method of Holmes et al. (1999). The reproducibility of nutrient measurements was also assessed using in-house standards compared with commercial products (<http://www.osil.co.uk/Products/SeawaterStandards>).

Rates of carbon fixation, nitrate and ammonium uptake were measured using a dual $^{13}\text{C}/^{15}\text{N}$ isotopic technique as described by Raimbault and Garcia (2008) (see also Ortega-Retuerta et al., 2012). Briefly, water samples were collected at 6 depths between the surface and the 1–0.3% light irradiance and poured into acid-cleaned polycarbonate flasks. Labeled ^{13}C sodium bicarbonate ($\text{NaH}^{13}\text{CO}_3$) and ^{15}N -tracers (K^{15}NO_3 or $^{15}\text{NH}_4\text{Cl}$) were added to each bottle to obtain $\approx 10\%$ final enrichment. Incubations were carried out immediately following tracer addition. On-deck incubators consisted of 6–8 opaque boxes allowing 50%, 25%, 15%, 8%, 4%, 1% and 0.3% light penetration. Incubators were maintained at sea-surface temperature ($\sim 0^\circ\text{C}$) with ice packs for 24 h. Incubations were terminated by filtration through precombusted (450°C) Whatman GF/F filters (25 mm diameter, $0.7\ \mu\text{m}$ pore) using a low vacuum pressure to measure the final $^{15}\text{N}/^{13}\text{C}$ enrichment ratio in the particulate organic matter and the concentrations of particulate carbon and particulate nitrogen. The f -ratios were calculated as the ratio of nitrate uptake to the sum of nitrate and ammonium uptake as measured on particles retained on filters (Tremblay et al., 2006). The dual isotopic

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enrichment analysis was performed on an Integra-CN mass spectrometer. Net, daily fixation rates of ¹³C into particulate organic matter were calculated from the mean of 2 replicates according to Collos and Slawyk (1984), with a time 0 enrichment of 1.085 % ±0.009 % (*n* = 15). We estimated gross PP by summing the net particulate rates and estimates of respiration and DOC production, assuming that these components represent 10 and 15 % of gross PP, respectively (cf. Forest et al., 2011).

Phytoplankton biomass estimates were based on 88 samples acquired at 20 stations across the study area. Samples for microscopic analysis were preserved in acidic Lugol's solution and stored in the dark at 4 °C until analysis. Counting was performed following the Utermöhl method (Lund et al., 1958) using an inverted microscope (Wild & Zeiss Axiovert 10). Phytoplankton abundance obtained by taxonomy (cells > 3 µm) and cytometry (picoeukaryotes 1–3 µm) were converted into carbon biomass by multiplying the mean cellular carbon content by abundance (Menden-Deuer and Lessard, 2000) by abundance.

2.6 Biomass, respiration and production of bacteria, zooplankton and benthos

Bacterial biomass and bacterial production (BP) during Malina 2009 were obtained from Ortega-Retuerta et al. (2012) (see also Forest et al., 2013). Bacterial abundance was estimated at sea using a FACS ARIA cytometer (Becton Dickinson, San Jose, USA) after DNA staining with SYBR Green. Abundance was converted to biomass using a cell-to-carbon conversion factor of 15.2 fg C cell⁻¹ as based on a mean estimated cellular biovolume of 0.040 ± 0.009 µm³ and the factor of 380 fg C µm⁻³ from Lee and Fuhrman (1987). BP was measured using the ³H-leucine incorporation method (Kirchman, 1993) as modified by Smith and Azam (1992). Leucine incorporation rates were converted into carbon production using the conversion factor of 1.2 kg C produced per mole of leucine (Forest et al., 2011, 2013). Bacterial respiration (BR) was calculated using the equation:

$$BR = (BP/BGE) - BP \quad (3)$$

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where BGE is the bacterial growth efficiency. Here, we implemented BGEs as variable parameters (from 0.5 to 25) depending on the stratum (surface or subsurface) within which BR was estimated. Varying BGEs in the surface layer were calculated using a linear relationship found between the surface BGEs estimated from field measurements by Ortega-Retuerta et al. (2012) and the water column standing stocks of chl *a* (mg chl am^{-2}) assessed by Forest et al. (2013) during Malina. The relationship provided the following equation: $0.952(\text{chl } a) + 2.21$ ($r^2 = 0.99, n = 5$). Since there was only one subsurface BGE value available in Ortega-Retuerta et al. (2012), the subsurface BGEs were rather calculated using the linear relationship of Nguyen et al. (2012) linking BP and BGE in southern Beaufort Sea.

The abundance of protozooplankton was measured using taxonomic work (Utermöhl method) on Lugol-preserved samples and the carbon biomass was estimated following Menden-Deuer and Lessard (2000), as for phytoplankton. We further estimated protozooplankton respiration according to the log-log equation of Caron et al. (1990) linking the biovolume of protozoans to weight-specific respiration rates. Since this equation provides respiration rates normalized to 20 °C, protozoan respiration estimates were corrected for in situ temperature using a Q_{10} of 2 (Fenchel, 2005). Biovolume conversion factors for the different protist species were compiled from Olenina et al. (2006) or estimated based on cell shape and dimensions (Bérard-Therriault et al., 1999) using appropriate geometric formulas (Olenina et al., 2006).

The biomass of mesozooplankton was obtained from Forest et al. (2012, 2013) who documented the mesozooplankton community structure in summer 2009 across the Mackenzie Shelf with a combination of zooplankton net tows (1 m^2 , 200 μm mesh size) and underwater images obtained with the UVP5 (validated manually). The mean ratio between the biomass of mesozooplankton and the one of small zooplankton and copepod nauplii collected with a 50 μm mesh size (Robert et al., 2011) at the Arctic-Net stations (Fig. 1) was used to correct the whole metazooplankton biomass with the aim of providing biomass estimates for the broadest size spectrum as possible. We then divided the whole metazooplankton biomass into two size categories (< 1 mm and

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> 1 mm) as based on their apparent ESD. The biomass in the > 1 mm size-class was dominated by large calanoid copepods, while cyclopoids and small calanoids dominated in the < 1 mm size-class (see Forest et al., 2012 for further details). Biomass of metazooplankton was converted into respiration outflows using the conversion factors of Darnis and Fortier (2012) who measured specific respiratory carbon rates per unit of dry weight (DW) biomass on bulk size-fractions (< 1 mm and > 1 mm) of zooplankton over a quasi-annual cycle in the Beaufort Sea in 2007–2008. For our study spanning late-July to mid-August, we used a conversion factor of $10 \mu\text{gCmgDW}^{-1} \text{d}^{-1}$ for the large zooplankton fraction and a factor of $15 \mu\text{gCmgDW}^{-1} \text{d}^{-1}$ for the small fraction.

The inverse modeling estimates of zooplankton gross growth efficiency and assimilation efficiency of Forest et al. (2011) (see their Table 7) were used to calculate the secondary production of protozoans and metazooplankton on the basis of carbon respiration outflows.

Respiration fluxes from the benthos were based on the benthic oxygen fluxes measured in triplicates at 8 stations across the study area (see Table 2 in Link et al., 2013) and a molar ratio of oxygen to carbon of 1.25 (Langdon, 1988). It is known that oxygen fluxes are not perfect proxies for carbon turnover rates (Link et al., 2013), but they provide at least minimal estimates that can be used to obtain a rough picture of benthic activity. Benthic carbon demand was calculated assuming a net growth efficiency of 0.3 and an assimilation efficiency of 0.8 (Brey, 2001). The relationship of Renaud et al. (2007) linking benthic carbon demand to epifaunal biomass in Beaufort Sea ($r^2 = 0.86$, $p < 0.001$, $n = 11$) was used to provide a coarse estimation of benthic biomass.

2.7 Data analyses, mapping and net community production estimates

The various datasets collected during ArcticNet-Malina were analyzed to explore spatial variability and large-scale differences in physical, biogeochemical and ecological functioning. Sub-regions and sub-layers were defined as follows. The mixed-layer depth was used to delimit the boundary between the surface and subsurface layer, while the

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subsurface layer extended down to 100 m depth maximum. The threshold between the on-shelf and off-shelf region was set at the 100 m isobath. The northward bound of the off-shelf zones was set to the 2000 m isobath. The western, central and eastern regions used for averaging diverse values corresponded to the areas delimited by 136–141° W, 131–136° W and 126–131° W, respectively. The whole study region was defined as the area confined within 126–141° W and within the 2–2000 m isobaths. It corresponds to a parallelogram of ca. 254.5 km width × 550.5 km length ($\sim 140.1 \times 10^3 \text{ km}^2$).

All observational data maps presented in this study were computed using the *Gridfit* function developed for Matlab (MathWorks, USA) by D'Errico (2006). *Gridfit* is a powerful modeling tool that produces a surface representing the behavior of supplied data as closely as possible. It handily allows for replicates, regular and scattered data, noise and extreme values – as it builds a mesh-grid directly from the data instead of interpolating a linear estimate to a 2-D surface. As such, it is more convenient than Kriging and standard interpolation methods (e.g. nearest neighbor, linear) when working with irregular oceanographic data. *Gridfit* is also able to smoothly extrapolate beyond the convex envelope of the supplied dataset in a more clever way than polynomial models. It is fully flexible and uses a differential equation solver to compute a set of nodes forming a rectangular lattice that contains the data points. For further details on the methodological and philosophical underpinnings of *Gridfit*, see D'Errico (2006).

Net community production (NCP) estimates were calculated using the following equation:

$$\text{NCP} = \text{GPP} - \text{CR} \quad (4)$$

where CR is the total community respiration calculated as the sum of all respiration fluxes from phytoplankton, bacteria, protozooplankton, as well as small and large metazooplankton. Respiration fluxes from the benthos over the shelf (< 100 m isobath) were included in the NCP estimates of the subsurface layer that extended from the MLD down to 100 m maximum.

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Linear regressions of NCP against GPP were conducted with the aim of estimating threshold GPP, i.e. the GPP value at which NCP becomes positive (Duarte and Regaudie-de-Gioux, 2009). Here, threshold GPPs were used as further indicators of the spatial variability of heterotrophy vs. autotrophy across the Mackenzie Shelf. Given that GPP and NCP are both dependent variables, regressions were computed using a model II least squares bisector equation (Geometric Mean Functional Relationship; Sprent and Dolby, 1980). These linear models determine the slope of the line (through the centroid) that bisects the minor angle between the regressions of Y-on-X and X-on-Y. The Matlab function *lsqbisec* (Peltzer, 2008) was used to compute the model II least squares bisector regressions.

3 Results

3.1 Overview of sea ice, wind and satellite-derived primary productivity

Sea ice and wind conditions in summer 2009 in the Beaufort Sea were influenced by a shift in the atmospheric pattern that occurred between July and August. Over the early summer, the region was affected by a high-pressure system (anticyclone) located around 70° N 156° W that brought clear sky conditions, southward advection of old sea ice from the Arctic pack (Fig. 3a), and persistent northerly winds (Fig. 3c). In early August, the atmospheric conditions that were observed in the months of June and July collapsed and the mid-to-late summer season was characterized by a low-pressure system that caused cloudy conditions. This cyclone had a catalytic effect on the melt of sea ice through the dispersal of ice floes, which resulted in what can be seen in Fig. 3b – i.e. large areas of open water over the Mackenzie Shelf and a maximum ice concentration of ~80% over the deep basin. The mean wind pattern observed over the field campaign (Fig. 3d) was computed as a weak easterly wind (< 5 km h⁻¹) consequential of the disruption of the anticyclone.

Remote sensing estimates of PP (Fig. 3d and e) showed that surface productivity was restricted to the shelf environment (< 100 m isobath), although this was expected as pixels with more than 10 % of sea ice were discarded during the MODIS processing chain. Satellite images showed that PP appeared to be primarily intertwined with the Mackenzie River plume that propagated westward along the Alaskan coast under the influence of northerly winds in June–July. Hence, given the easterly wind pattern that was calculated for late July–August, turbid waters from the Mackenzie River had, presumably, no impact at all on PP estimates east of Kugmallit Valley or Canyon in summer 2009.

3.2 Sea surface physics, inorganic carbon and sea-to-air CO₂ fluxes

The trajectory of the Mackenzie River plume during July–August was clearly visible on the map of sea surface salinity (Fig. 4a). This confirmed that the eastern portion of the study area was not influenced by any substantial freshwater input. Even surface waters on the eastern shelf remained around a salinity of 30, which is not a particularly low value for the Beaufort Sea. Surface waters with a salinity < 20 were restricted to the inner shelf close to the Mackenzie delta. Brackish surface waters were also generally characterized by increased temperature (up to ~ 10 °C in very shallow waters, Fig. 4b). Near-0 °C surface waters were associated with the presence of sea ice and a transition from 0 °C to 10 °C was measured as the distance to the ice edge increased.

The vertical extent of the MLD generally increased as sea surface salinity increased and as temperature decreased (Fig. 4c). There was no clear difference between stations affected by the absence or presence of sea ice. Mapping of MLDs showed that the mouth of the Amundsen Gulf was the zone where the MLD extended the deepest (down to ~ 17 m), but MLD values were small overall, with a mean ± standard deviation (SD) of 8.1 ± 3.1 m for the whole study area. Here, MLDs were used to delimit the surface and subsurface layers.

Gridded concentrations of TIC at the ocean surface showed a clear gradient from west to east (Fig. 4d). TIC concentrations were significantly ($p < 0.01$) related to salinity

(S) in the mixed-layer ($TIC = 48.4 \times S + 562.6$; $r^2 = 0.88$; $n = 77$) if we omit data strongly influenced by the Mackenzie River plume (i.e. the inner shelf).

The spatial variability of CO_2 fugacity at the sea surface was high (ranging from 198 to 660 μatm , mean \pm SD of $322 \pm 60 \mu\text{atm}$), with marked maxima on the outer eastern shelf, near the Mackenzie River delta and toward the Alaskan coast, and to some extent in the Amundsen Gulf (Fig. 4e).

The computation of sea-to-air CO_2 fluxes revealed that the zones affected by elevated CO_2 fugacity were the only regions acting as sources of carbon to the atmosphere (Fig. 4f), especially the river delta (up to $\sim 20 \text{ mmolCm}^{-2} \text{d}^{-1}$) and the localized hotspot northwest of Cape Bathurst (up to $\sim 10 \text{ mmolCm}^{-2} \text{d}^{-1}$). Other areas were acting as a carbon sink, with maximum drawdown of CO_2 on the mid-to-outer shelf north of the Mackenzie River delta and near the Banks Island shelf (down to $\sim -10 \text{ mmolCm}^{-2} \text{d}^{-1}$). Overall, the southeastern Beaufort Sea acted as a weak sink of atmospheric CO_2 in July–August 2009 with a mean uptake of $-2.0 \pm 3.3 \text{ mmolCm}^{-2} \text{d}^{-1}$.

3.3 Bulk budget of organic carbon pools, river inputs and vertical fluxes

We developed a non-steady-state budget of bulk carbon fluxes and pools for the Mackenzie Shelf in July–August 2009 (Fig. 5) using estimates of organic carbon inputs from the Mackenzie River and Anderson River, POC and DOC measurements in the water column, and vertical POC fluxes. The budget summary is presented as spatial averages across the western, central and eastern zones of the study area as delimited by $136\text{--}141^\circ \text{W}$, $131\text{--}136^\circ \text{W}$ and $126\text{--}131^\circ \text{W}$, respectively.

The main result of this bulk budget is the fact that POC inventories were overall higher on the eastern shelf than on the central and western shelf, despite the tremendous POC input from the Mackenzie River, which delivered a daily average load of $3253 \pm 2183 \text{ t POCd}^{-1}$ in these two zones combined. The mean total inventory of POC (integrated vertically, sum of the surface and subsurface layers) in the eastern region

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(Fig. 5c) was $18.3 \pm 1.5 \text{ gCm}^{-2}$, whereas it was $9.6 \pm 1.0 \text{ gCm}^{-2}$ in the western zone (Fig. 5a) and $11.7 \pm 1.6 \text{ gCm}^{-2}$ in the central region (Fig. 5b). Similarly, the quantity of POC relative to ambient DOC roughly doubled from west to east (from $\sim 6.0\%$ to $\sim 13.7\%$; Fig. 5), which suggests that DOC was relatively homogenous across the study area when integrated vertically in the upper 100 m.

A second key result of this summary concerns vertical POC fluxes that did not follow the same pattern as POC inventories. When averaged across the three zones, mean vertical POC fluxes were higher in the central zone ($1790 \pm 122 \text{ mgCm}^{-2} \text{ d}^{-1}$), compared against the eastern ($897 \pm 98 \text{ mgCm}^{-2} \text{ d}^{-1}$) and western ($669 \pm 141 \text{ mgCm}^{-2} \text{ d}^{-1}$) regions. In addition, vertical POC fluxes injected into the benthic boundary layer (as derived from UVP5 recordings) were particularly high on the inner-mid shelf ($< 60 \text{ m}$ isobath, $\sim 1200\text{--}4100 \text{ mgCm}^{-2} \text{ d}^{-1}$) when compared to the relatively low POC inventories found in shallow waters ($\sim 1600\text{--}2900 \text{ mgCm}^{-2}$), implying that the turnover of POC near the coast was high and/or that the inner-mid shelf was affected by resuspension. Overall, estimates of vertical POC fluxes over the shelf were one to two orders of magnitude than offshore.

3.4 Nutrient dynamics, phytoplankton biomass and primary production

During ArcticNet-Malina 2009, nitrate represented 96.6% of the total nitrogenous nutrient concentrations in the upper 100 m, while nitrite and ammonium accounted for 1.4% and 2.0%, respectively. In surface waters, nitrate concentrations were typically lower than $0.01 \mu\text{M}$, except close to the Mackenzie River delta, where undiluted fresh-water with a nitrate of $3.6 \mu\text{M}$ was found. Below the surface mixed layer (Fig. 4c), nitrate remained depleted typically down to 40–50 m depth, followed by a clear nitracline associated with the increasing presence of Pacific-derived waters that occupied the 50–200 m layer. A three-dimensional view of nitrate concentrations (as measured at the Malina cross-shelf transects) provided synoptic insights on the geographical and vertical variability of the nitracline during our study (Fig. 6). In this figure, we can observe

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a clear cross-shelf flow of nitrate-rich waters that propagated inshore within the bottom 10–15 m of the water column. This oblique expansion of the nitracline from the basin to the shelf was particularly visible at transects conducted north of Cape Bathurst and in the Mackenzie Canyon. In the head of the Canyon, we estimated using Delaunay triangulation that waters just below the surface contained nitrate concentration up to 6–7 μM (Fig. 6).

Relatively high GPP rates ($\sim 200\text{--}500\text{ mgCm}^{-2}\text{d}^{-1}$) during our field survey were confined to the surface (above MLD) inshore environment (within the 20 m isobath) and to some extent to the mid-shelf region close to Cape Bathurst (Fig. 7a). Elsewhere, GPP in surface waters remained at very low levels ($\sim 10\text{--}50\text{ mgCm}^{-2}\text{d}^{-1}$). Beyond the inner shelf, GPP was actually higher below the surface (below MLD) than within the surface mixed layer, with rates up to $75\text{--}90\text{ mgCm}^{-2}\text{d}^{-1}$. When spatially averaged over the whole study area ($\sim 140.1 \times 10^3\text{ km}^2$), GPP in the surface layer was $55.9 \pm 82.7\text{ mgCm}^{-2}\text{d}^{-1}$, which represented on the average 62.6% of the total GPP in the upper 100 m ($89.2 \pm 102.1\text{ mgCm}^{-2}\text{d}^{-1}$). Using a study period of 35-days for ArcticNet-Malina, this yielded a cumulated GPP of $3.1 \pm 3.6\text{ gCm}^{-2}$. And also provided a total GPP for the whole study region of $\sim 437.6 \times 10^3\text{ t C}$, which was roughly twice higher than the total organic carbon delivery (POC + DOC) by the Mackenzie and Anderson River ($\sim 241.2 \times 10^3\text{ t C}$) from 20 July to 24 August 2009.

The ratios of new production to total GPP (f -ratio, as based on nitrate and ammonium uptake) were relatively low in the surface layer (~ 0.2), except close to Cape Bathurst (~ 0.4) and near the Mackenzie River delta (~ 0.6), which reflected localized sources of nitrate from upwelling and riverine input, respectively (Fig. 7c). Below the surface mixed layer, f -ratios were also very variable, but relatively high f -ratios (> 0.6) were found along the Alaskan coast, close to Cape Bathurst and at few locations offshore (Fig. 7d). At some stations west of the Mackenzie Canyon and on the outer eastern shelf, diatoms overwhelmingly dominated ($> 80\%$) phytoplankton biomass. At stations where the abundance of diatoms was low, autotrophic flagellates dominated the phytoplankton assemblage (not shown).

Further details on the geographic and vertical variability of phytoplankton biomass (B) and production (P) are presented in Table 1. This enables us to calculate an ensemble of $P : B$ ratios. Highest $P : B$ ratios (up to $\sim 41 \% d^{-1}$) were found within the surface mixed layer, whereas $P : B$ ratios found in association with subsurface productivity were 5–10 times lower (Table 1).

3.5 Biomass, production and respiration of bacteria, zooplankton and benthos

Estimates (and 95 % confidence intervals) of biomass and secondary production of pelagic heterotrophs are listed in Table 1. Secondary production within the surface layer was equally dominated by protozoans (48 %) and bacteria (47 %), while metazooplankton (sum of the two size-fractions) accounted for 5 %. Below the surface layer, metazooplankton represented 28 % of the secondary production, whereas bacteria and protozoans contributed on the average to 33 % and 39 %, respectively. Relative biomass of heterotrophs in the surface layer was more homogenous than their production (i.e. protozoans 48 %, bacteria 29 %, metazooplankton, 24 %). Below the surface, protozoans and bacteria accounted for 16 % and 24 %, while metazooplankton dominated at 60 % the total heterotroph biomass. It is worth mentioning that the biomass of metazooplankton was roughly 300 % greater in the central and eastern zones than in the western region of the study area, which was affected by the Mackenzie River plume. A spatial match between the biomass of metazooplankton and phytoplankton was detected in the eastern on-shelf subsurface layer where these two groups accounted for 87 % of the whole plankton biomass.

Unsurprisingly, bacteria and protozooplankton had higher $P : B$ ratios (range ~ 1.2 – $26.8 \% d^{-1}$) than metazooplankton (range ~ 0.8 – $2.8 \% d^{-1}$), likely because of their low structural carbon content (i.e. high carbon turnover capacity). Highest bacterial $P : B$ ratio ($\sim 26.8 \% d^{-1}$) was found in the surface layer of the eastern on-shelf region, while the production of protozoans relative to their biomass was strongest ($\sim 11.4 \% d^{-1}$) in the central on-shelf zone. Interestingly, the $P : B$ ratios of protozoans was ca. 3 times

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higher than that of bacteria in the subsurface layer off the shelf, an opposite situation to what was seen in other areas (Table 1).

The gridded maps of respiration fluxes (Fig. 8) complemented the biomass and production data of Table 1 by providing an overview of the spatial variability of heterotrophic activity. When averaged over the whole study area (see definition in Sect. 2.7), respiration outflows from bacteria in the surface and subsurface layers (48 ± 44 and $87 \pm 88 \text{ mgC m}^{-2} \text{ d}^{-1}$, respectively) were both statistically greater (Mann-Whitney U test, $p < 0.001$) than those of protozoans (23 ± 30 and $38 \pm 14 \text{ mgC m}^{-2} \text{ d}^{-1}$, respectively), which were themselves both statistically higher (same test and p -value) than those of total metazooplankton (2 ± 3 and $23 \pm 21 \text{ mgC m}^{-2} \text{ d}^{-1}$). Therefore, an interesting feature that we can discern from the respiration maps is the emergence of an anti-correlation pattern between respiration by bacteria and respiration by protozoans (Fig. 8a and b vs. Fig. 8c and d); and between respiration by protozoans and respiration by metazooplankton (Fig. 8c and d vs. Fig. 8e and f). For example, protozoan activity was high in the Mackenzie River delta, a zone where bacterial respiration was surprisingly low. Similarly, protozoan respiration was low on the central and eastern shelf, exactly where metazooplankton activity was greatest.

Estimates of benthic respiration on the shelf (derived from field measurements) are presented in Fig. 9. A straightforward conversion of these rates to production was achieved using a net growth efficiency of 30% (net growth efficiency = production/[production + respiration]) and yielded values ranging from 15–40 $\text{mgC m}^{-2} \text{ d}^{-1}$. Further estimates of epifaunal benthic biomass on the shelf (based on a relationship between carbon demand and biomass from the literature) lead thus to a range of ~ 3.4 – 8.9 gC m^{-2} . This implies that, on the average, benthic biomass was at minimum more than twice higher ($\sim 5.9 \text{ gC m}^{-2}$) than the cumulated biomass of pelagic heterotrophs in the surface and subsurface layers on the shelf ($\sim 2.4 \text{ gC m}^{-2}$) – even if respiration fluxes were overwhelmingly dominated ($\sim 88\%$) by pelagic organisms (Fig. 9).

3.6 Ecosystem metabolic balance and net community production estimates

The ecosystem metabolic balance, as being defined as the interplay between GPP and CR, is depicted schematically in Fig. 9 and via the surface and subsurface gridded maps of Fig. 10. The cross-shelf averages of GPP and respiration outflows (Fig. 9) aim at simplifying the large spatial variability presented in Figs. 7 and 8. As seen above, bacteria dominated the overall organic carbon remineralization across the study region, but protozoans were important players near the Mackenzie River delta and beyond the shelf break. The importance of metazooplankton was only really noticed in the subsurface layer of the central and eastern regions (Fig. 9b and c).

Generally, respiration in the surface mixed layer exceeded GPP, which resulted in the NCP map shown in Fig. 10a. Surface NCP was clearly positive only near to shore and around Cape Bathurst, where increased GPP has been estimated through both remote sensing (Fig. 3f) and in situ field measurements (Fig. 7a). However, surface NCP was close to zero and/or slightly positive in some regions affected by the persistent presence of sea ice (Fig. 3b). Below the surface layer down to 100 m depth, NCP was negative everywhere (Fig. 10b) with a signal dominated by BR (Fig. 8b). When averaged for the whole region, NCP in the surface and subsurface layer was $-22.6 \pm 70.6 \text{ mg C m}^{-2} \text{ d}^{-1}$ and $-142.4 \pm 109.4 \text{ mg C m}^{-2} \text{ d}^{-1}$, respectively.

Model II regressions of NCP against GPP for all the cells contained in the distinct regions provided estimates of threshold GPPs in the surface layer (Fig. 11). We did not attempt any regression of NCP against GPP for subsurface values, as NCP was always negative in the subsurface layer. Threshold GPPs were much higher on the shelf than offshore, with a maximum value of $152 \pm 7 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the region influenced by the Mackenzie River plume. Lowest threshold GPP ($20 \pm 1 \text{ mg C m}^{-2} \text{ d}^{-1}$) was found in the central off-shelf region where both NCP and GPP were also very low. The only region where a threshold GPP could not be estimated was the western off-shelf region barely characterized by any positive NCP values (Fig. 11b).

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4 Discussion

4.1 To which extent sea-to-air CO₂ fluxes were coupled with surface mixed layer NCP?

Computations of air–sea CO₂ exchange in regions affected by strong environmental variability, such as continental margins, require a high-resolution dataset of $\Delta p\text{CO}_2$ (Anderson et al., 2010). A location-by-location approach (Else et al., 2012) is particularly needed in Arctic shelf seas where multiple physical, geochemical and biological processes influence air–sea CO₂ exchange (e.g., photosynthesis, respiration, vertical mixing, upwelling, surface warming and cooling, lateral advection, ice melt and formation, as well as river runoff). Air–sea CO₂ fluxes in the southeast Beaufort Sea were previously documented by Mucci et al. (2010), Shadwick et al. (2011), and Else et al. (2013a, b), but none of these studies had the fine-scale geographical coverage that the ArcticNet-Malina 2009 sampling strategy provided across the Mackenzie Shelf and slope.

That being said, our results generally corroborate the pattern in air–sea CO₂ fluxes deciphered for the region in summer. First, we estimated a weak net sink of $-2.0 \text{ mmol C m}^{-2} \text{ d}^{-1}$, a mean value close to the ones obtained by Mucci et al. (2010) and Else et al. (2013a) (i.e. -2.3 and $-2.4 \text{ mmol C m}^{-2} \text{ d}^{-1}$, respectively). These mean rates were, however, much lower (in terms of sink) than the air–sea flux of Shadwick et al. (2011) who estimated an average sink of $-7.2 \text{ mmol C m}^{-2} \text{ d}^{-1}$ for July–August 2008. While the study area of Shadwick et al. (2011) was a small box in Amundsen Gulf unaffected by CO₂ outgassing from both river input and upwelling of CO₂-rich waters at Cape Bathurst, this value may also have been biased towards CO₂ uptake due to undersampling. Using a higher resolution dataset of $\Delta p\text{CO}_2$, Else et al. (2013b) observed that the Amundsen Gulf shifted from a weak source to a weak sink of CO₂ over the July–August time period, with a mean value around $-2.5 \text{ mmol C m}^{-2} \text{ d}^{-1}$. In our study, we observed – similarly to Else et al. (2013b) – that the Amundsen Gulf was near equilibrium or was slightly outgassing CO₂ to the atmosphere, potentially due

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to warming, net heterotrophy or upwelling. The exact factor or combination of factors that stimulated such a weak outgassing in Amundsen Gulf during our survey remains elusive, however.

Second, we identified a sharp transition from a CO₂ source to a CO₂ sink when transiting away from the Mackenzie River delta. This shift was previously detected through snapshot measurements of pCO₂ (cf. Vallières et al., 2008; Mucci et al., 2010; Else et al., 2012), but our mapping of air–sea CO₂ fluxes clearly defined the transition zone. Interestingly, the mid-shelf area bordering the zone of CO₂ outgassing in the delta was the sub-region characterized by the strongest CO₂ sink (Fig. 4f), suggesting that PP combined with riverine freshwater diluted into cold oceanic waters acted synergistically to facilitate CO₂ uptake. Third, the coastal area west of Herschel Island (Fig. 1) was identified as a small zone super-saturated in CO₂ and acting as a source of CO₂. This area exactly matches the one where Mathis et al. (2012) detected CO₂ super-saturation during a cruise in October 2011, when strong easterly winds prevailed in coastal Beaufort Sea as a result of an intensified atmospheric pressure gradient between the Beaufort Sea High and an Aleutian low. Actually, Williams and Carmack (2008) previously identified this area as often affected by shelf-break upwelling developing in the Mackenzie Canyon owed to isobath divergence on the northeastern side of Herschel Island.

Fourth, we have detected a localized zone of strong CO₂ outgassing on the northeastern shelf break which corresponds to the region nearby Cape Bathurst now well known to be sensitive to wind-driven coastal upwelling (Williams and Carmack, 2008; Mucci et al., 2010; Tremblay et al., 2011; Else et al., 2012). What was indeed different here was the configuration of the patch of increased fCO₂–sw (Fig. 4e), which was more spatially limited when compared to what Else et al. (2012) observed in the fall of 2007 during a massive upwelling event; and which was slightly larger and displaced to the north relative to what Mucci et al. (2010) observed during the relatively quiescent summer of 2004 (when compared to 2008 for example; see Tremblay et al., 2011). This underscores that, although the eastern Mackenzie Shelf along Cape Bathurst is fre-

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quently affected by upwelling events, the exact pattern of CO₂ outgassing is obviously dictated by the persistence and direction of winds (i.e. pattern of Ekman transport), but also by the balance between PP and total community respiration. However, quantifying the precise contribution of each physical and biological factor that modulates air–sea CO₂ exchange remains a challenging task, especially since various time-scales are involved with respect to ocean circulation and ecosystem response.

A way to explore to what extent sea-to-air CO₂ fluxes were coupled with ecosystem metabolism during Malina is to actually sum up surface NCP and CO₂ fluxes. Following such addition, positive values would mean that the potential for CO₂ sink due to a positive NCP (net autotrophy) were dampened by external forcings that increased $p\text{CO}_2\text{-sw}$ at the surface (e.g. upwelling of CO₂-rich waters, warming/evaporation, photomineralization). While negative values would mean that the potential for a given zone to be a CO₂ source due to negative NCP (net heterotrophy) was compensated by other factors that lowered $p\text{CO}_2\text{-sw}$ (e.g. cooling, downwelling, dilution). This new metric, as mapped on Fig. 12, illustrates that most of the study region was affected by factors lowering $p\text{CO}_2\text{-sw}$, which were somehow counteracting the net heterotrophy that generally prevailed across the southeastern Beaufort Sea during July–August 2009. The main factor that could explain this discrepancy is the strong PP that developed over the shelf prior to the field campaign, as measured with ocean color remote sensing (Fig. 3e). Since it takes several months for gas exchange to replace CO₂ uptake driven by PP (e.g. Else et al., 2013a), it is not surprising that $p\text{CO}_2\text{-sw}$ was still undersaturated at the time of our study. These findings also imply that mechanisms favoring carbon export below the surface mixed layer before and during Malina were greater than the potential for organic carbon remineralization near the surface. Indeed, amazingly high vertical POC fluxes (up to > 5000 mgC m⁻² d⁻¹; Forest et al., 2013, see also Fig. 5) were detected in the neritic zones affected by the most negative values in Fig. 12. On the shelf, vertical export during July–August was roughly one order of magnitude greater than the total community respiration estimate (~ 250 mgC m⁻² d⁻¹). Of course, the system can be expected to equilibrate over time as the decrease in

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nutrients and light availability progressively limits PP, while heterotrophs continue to remineralize organic carbon previously brought by PP and river inputs. This temporal lag between CO₂ exchange and heterotrophic respiration probably explains why Else et al. (2013a) did not measure particularly low pCO₂-sw values across the Mackenzie Shelf (300–370 μatm) just after our field survey.

Based on satellite imagery, our cartography of PP prior to the field campaign bears some uncertainty in the off-shelf region affected by the presence of sea ice. It is possible that under-ice PP developed there, but given the oligotrophic nature of the central Arctic basin (e.g. Ardyna et al., 2013), it is most probable that the main factor explaining any decoupling between NCP and air–sea CO₂ fluxes beyond the shelf was related to surface dilution by sea ice melt water, which causes a reduction in surface pCO₂ (e.g., Denman et al., 2011). By contrast, the most positive values in Fig. 12 were restrained to the very nearshore environment and to the region around Cape Bathurst, which were thus affected by some factors diminishing the net autotrophy of these zones (Fig. 10a). Along Cape Bathurst, it appears now evident that the upwelling of deep acidic waters has brought enough CO₂ to reduce the potential for CO₂ uptake through PP and export. Of course, this would be true only if the time scale is long enough (e.g. several days to weeks) so that the net result of such successive biophysical events can be discerned. Interestingly, the balance in air–sea CO₂ exchange near Cape Bathurst shifted from a sink to a source only in the localized patch apparently characterized by no substantial PP prior to Malina (Fig. 3e). This suggests that as a general rule, upwelling-induced CO₂ outgassing across the Mackenzie Shelf (or at least the “kind” of upwelling observed in summer 2009) can be compensated by PP through CO₂-fixation, if a concomitant upward flux of nitrate favors the new production of large and rapidly-sinking diatoms (Fig. 7e and f). An analogue situation appeared to prevail near the coast where the impact of very high PP rates on NCP was attenuated by excess CO₂ outgassed from riverine waters leaving the inner estuary (as also described in the review of Chen et al., 2012).

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4.2 What was the interplay between upwelling, river plume and sea ice in driving C fluxes?

The common view on upwelling in Beaufort Sea is one that would induce the replacement of the warm upper-layer water over the shelf by cold nitrate-rich water from the intermediate Pacific-derived water layer (e.g., Williams and Carmack, 2008; Tremblay et al., 2011; Pickart et al., 2013). Here, we did not observe any features in sea surface temperature that could have informed us on the presence of an upwelling reaching the surface (Fig. 4b). Cross-shelf nitrate sections rather showed that the on-shelf flux was a terrain-following pattern with variable penetration and intensity. Given that the dominant wind pattern in summer 2009 was a strong northerly flow followed by weak easterlies (Fig. 3), the resulting Ekman transport of surface waters to the west-northwest would have favored the entrainment of subsurface waters to the east-southeast. Although the true south-eastward (up-the-shelf) component of the subsurface flow was likely not very strong in this situation, it was thus sufficient enough to bend isopycnals and bring nitrate into the lower euphotic zone over the shelf (see also Tremblay et al., 2013). The slanting of deep waters across the shelf was evident everywhere, except at the transect 400 visited at the end of the campaign, which reflected the development of a cyclonic regime over August (NSIDC, 2009) and the subsequent relaxation of isopycnals. This is in accord with Williams and Carmack (2008) who demonstrated that upwelling is a broad circulation pattern over the entire Canadian Beaufort Shelf that leads to topographically-intensified upwelling at Cape Bathurst and in the Mackenzie Canyon. Intrusion of nitrate-rich waters over a sloping bottom also supports our pattern in gross PP, which was predominantly occurring at depth on the mid-to-outer shelf and enhanced at surface on the inner-to-mid shelf. Based on our f ratios, we can roughly estimate that the increased PP rates observed near the coast were fuelled at $\sim 30\%$ by nitrate advected laterally from offshore. In the Mackenzie River delta, an additional 30% of the PP was apparently supported by nitrate coming from the Mackenzie River itself (f ratio ≈ 0.6).

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Under the effect of the west-northwest surface water circulation, the relatively intense surface PP rates measured nearshore would lead to the transport, aggregation and sinking of phytoplankton in the mid-to-outer shelf regions. In fact, this is exactly what we estimated based on our field measurements. Phytoplankton biomass (dominated by diatoms up to > 80 %) was greatest in the subsurface layer over the outer shelf (~ 767–1480 mgC m⁻²), also in agreement with the POC inventories that were highest in this water layer (Fig. 5). Further propagation of this seaward, descending, flux would lead to the sinking of large phyto-detritus over the slope. An oblique flux of large particles is precisely what we observed at the eastern shelf break and in the vicinity of the Mackenzie canyon within a previous study on vertical POC fluxes during Malina (Forest et al., 2013). Furthermore, the longitudinal gradient in POC concentration (increasing inventories from west-to-east, following phytoplankton biomass) is another confirmation that autochthonous processes govern the overall particulate carbon cycling over the Mackenzie Shelf despite some very large riverine inputs (cf. Macdonald et al., 1998; O'Brien et al., 2006; Tolosa et al., 2013).

With the influence of northerly/easterly winds resulting from a predominant high-pressure system (anticyclonic Beaufort Sea High) in early summer 2009, the river plume expanded to the west-northwest, leaving potentially the eastern Mackenzie Shelf and Amundsen Gulf unaffected by substantial freshwater and terrigenous inputs. In fact, in regions where surface salinity was above 25.5 in our study (Fig. 4a), the percentage of Mackenzie River water in surface waters averaged only 4.7 % ± 2.1 % (Lansard et al., unpublished data; see also Tremblay et al., 2013). This view contrasts with the results of Fichot et al. (2013) presenting the southern Beaufort Sea as a region plagued with terrigenous DOC (see their Fig. 3) as based on the spectral slope of CDOM which is correlated to lignin phenols. This illustrates that even less than 5 % of river water containing high CDOM concentration can make the terrigenous fraction still dominating the spectral signature. This nonetheless provides insights on the transport and quality of the terrigenous organic matter delivered on Arctic shelves. In the Beaufort Sea, particulate matter from the Mackenzie River sink quasi-exclusively (~ 97 %) near to coast

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(O'Brien et al., 2006; Magen et al., 2010), thus rapidly excluded from remineralization processes within the shallow surface mixed layer; while riverine dissolved organic matter in the region (presumably dominated by highly-degraded “refractory” lignin carbon; Goñi et al., 2000) appears to be of limited bioavailability as based on its amino acid content (Shen et al., 2012). This likely explains why the Mackenzie Shelf is systematically described as a sink for atmospheric CO₂ (e.g., Mucci et al., 2010; this study). By contrast, on large Siberian Shelves, the decomposition of a more labile terrestrial organic matter near the surface induces an excess of DIC that is expected to be outgassed to the atmosphere (Anderson et al., 2009). Indeed, Vonk et al. (2013) determined that DOC derived from ancient carbon permafrost in coastal Siberia is highly biolabile as based on DOC losses during incubation experiments. Hence, understanding the routing and quality of terrestrial matter delivered to the Arctic Ocean is as important as monitoring the quantity of the load at discrete source points.

Assuming that the eastern Mackenzie Shelf during our study was not affected by substantial riverine inputs implies conversely a difficult interpretation of our remotely-sensed estimates of PP (Fig. 3e and f). On the one hand, it appears obvious that CDOM contaminated the phytoplankton signal everywhere on the inner shelf and west of the Mackenzie Canyon (Matsuoka et al., 2013), potentially leading to over-estimations of PP as based on satellite imagery. On the other hand, the patterns in PP measured in situ at the ocean surface and the MODIS-derived PP estimates during the period from 20 July to 24 August were surprisingly similar, suggesting that remote sensing is indeed suitable for estimating PP over this shelf. However, linear regression of net PP measured in situ against PP estimated with ocean color during that period revealed that MODIS roughly overestimated PP by a factor of 2.3–2.7 ($r^2 = 0.3$) due to an over-estimation of chl owed to CDOM (Mustapha et al., 2012). In any case, an important fact to underscore is that the area with high measured PP levels and the Mackenzie River plume were fully intertwined (see also Tremblay et al. (2013) for a detailed discussion on the geographical variability of PP during Malina). With the aim of evaluating to which extent the Mackenzie River supported PP during Malina, we can use the re-

cent budget of Le Fouest et al. (2013). Using a concentration of $3.8 \text{ mmol nitrate m}^{-3}$ and the cumulated runoff of the Mackenzie River for our 35 day sampling period, this yields a cumulative flux of $\sim 2.4 \times 10^3 \text{ t N}$. When converted into carbon production using a C:N ratio of 8 (Tremblay et al., 2008) and a mean f ratio of 0.6 (as recorded near the Mackenzie Delta), this provides a total GPP of $32 \times 10^3 \text{ t C}$, which is about 7.4 % of the total GPP measured in situ during ArcticNet-Malina ($\sim 437.6 \times 10^3 \text{ t C}$). But if we compare this river-based estimate to GPP measured only in the region truly affected by the Mackenzie River plume (i.e., western shelf and slope; where $\text{GPP} \approx 114.1 \times 10^3 \text{ t C}$), the river plume appears to have supported approximately 28 % of GPP in this area.

With a deep nitracline (Fig. 6), the presence of an ice cover up to 80 % concentration, and a limited influence of the Mackenzie River nutrient flux, the offshore Canada Basin environment strongly inhibits PP, which limits its capacity as a CO_2 sink, and prevents the development of an active herbivorous food web. Indeed, numerous studies demonstrated that PP in the Canada Basin is not expected to increase substantially despite the ongoing sea ice retreat (e.g., Cai et al., 2010; Carmack and McLaughlin, 2011; Bélanger et al., 2013; Else et al., 2013a), and might rather be affected by a progressive shift toward the dominance of small cells, microbial looping, and regenerated production (Li et al., 2009; Comeau et al., 2011; Codispoti et al., 2013). This trend appears to be induced by an increased surface stratification (which impedes vertical mixing and deepens the nutricline) due to freshwater storage facilitated by an intensified Beaufort Sea High paralleled by an increase in the cyclonic circulation over the Eurasian basins (Timmermans et al., 2011; Morison et al., 2012; Bourgain et al., 2013). In line with these studies, our results confirm that the biogeochemical gradient in carbon and nitrogen cycling between the shelf, slope and basin environments in the Beaufort Sea is exacerbated with the ongoing environmental change. Hence, a key related issue is now to understand how the structure and metabolism of pelagic and benthic food webs respond and feed back to such an extreme biogeochemical setting.

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4.3 How did the food web respond and feed back to organic and inorganic C cycling?

There is no other variable that more effectively connects biogeochemical carbon cycling with food web activities than NCP. It accounts for the balance between PP and respiration, and thus of other metabolic processes in between such as biomass build-up and reproduction. Since NCP is tightly linked with both CO₂ and O₂ cycling, NCP is typically based on an assertion of O₂ dynamics using bottle incubations or geochemical tracers. At the heart of such NCP estimates currently lies a very active debate on the inconsistency between the results of in vitro O₂ bottle incubations and in situ O₂/Ar-based mixed-layer NCP, as exhaustively reviewed by Ducklow and Doney (2013). Here, we adopted another approach by summing up respiration rates of food web components, which were subsequently subtracted from gross PP estimates that were also assessed empirically. While our approach has its own uncertainties (e.g., conversion factors, plankton biomass estimates), we are confident that the overall picture of ecosystem metabolism across the complex Arctic shelf system that we sampled was better estimated this way. In fact, assuming a steady-state between mixed-layer NCP and sea-to-air fluxes (as the O₂/Ar methodology requires) would have yielded a wrong portrait of ecosystem metabolism since the temporal decoupling between autotrophic and heterotrophic processes was obvious. In addition, O₂ bottle incubations would have provided only snapshot bulk measurements without having the possibility to verify which food web components were influencing ecosystem metabolism.

Overall, our results support the conclusion of Ortega-Retuerta et al. (2012) that the southeastern Beaufort Sea during Malina was net heterotrophic, but our calculations based on a different strategy enabled us to identify more zones where autotrophy could be observed in the surface mixed layer (Fig. 10a). Ortega-Retuerta et al. (2012) compared bacterial carbon demand against net PP using a fixed and relatively low BGE of 0.077, and by integrating values over the whole euphotic layer, which was extending tens of meters below the mixed-layer depth. They found net heterotrophy everywhere,

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except on the eastern side of the Mackenzie River delta ahead of Tuktoyaktuk. Accordingly, they found a strong imbalance between bacterial carbon demand and PP, most likely because the subsurface layer during Malina contained substantial inventories of organic carbon (Fig. 5) resulting from past PP (as discussed in 4.1). Moreover, BGE is a highly variable parameter (~ 0.01 – 0.4) in the Arctic Ocean (e.g., Kirchman et al., 2009; Nguyen et al., 2012) and we surmise that our approach based on a flexible BGE embraces this variability. Also, it should be noted that a carbon demand lower than net PP is not necessarily the sign of an unbalanced situation. As summarized by Legendre and Niquil (2013), respiration is the only appropriate metric to assess ecosystem metabolism given that heterotrophic production is not an additive property of food web flows (i.e. the same carbon may be part of both production and respiration). Of course, this does not mean that bacteria were not partly fuelled by allochthonous DOC or by local PP supported by riverine nutrients, but it indicates at least that caution should be exerted when comparing snapshot measurements of bacterial carbon demand against PP.

By contributing to ca. 54 % of respiration outflows in the upper 100 m, bacteria were in any case the dominant actor of organic carbon remineralization. The most negative values in subsurface NCP were obviously driven by bacteria, and a spatial match between bacterial respiration and high concentration of surface DIC could be discerned (Fig. 4d). Such observations could indicate that the shallow mixed-layer depth in Beaufort Sea is not an impermeable barrier to turbulent exchange, as suggested by Mucci et al. (2010). This is because a significant fraction of the surface stress can be, in fact, transmitted below the MLD – so that shear production and interaction with existing shear that develops across the mixed-layer can occur (Belcher and Grant, 2011). This phenomenon could develop preferentially in areas where baroclinic tidal mixing is enhanced by a steep topography, such as in the northeastern corner of the Mackenzie Shelf (Kulikov et al., 2004). When excluding benthic respiration, the contribution of bacteria to pelagic respiration raised to ca. 61 %. This percentage is slightly higher than the contribution of bacteria to community respiration measured in the Amundsen Gulf

in spring-early summer 2008 (~ 45 %; Forest et al., 2011). But given that the Mackenzie River was expected to influence shelf metabolism and that our study occurred during a late-summer period when the ecosystem was more mature, the contribution of bacteria to respiration outflows was not “that” overwhelmingly dominant. Of key importance in our study was the role of protozoans (e.g., ciliates, heterotrophic dinoflagellates) that apparently showed an anti-correlation pattern with bacterial activity (e.g. Fig. 8a–d; Table 1). The contrast between protozoans and bacteria was particularly evident in the Mackenzie River delta and beyond the shelf break. Top-down regulation of bacteria by protozoan grazing in these zones cannot be excluded, but remains difficult to firmly establish. It has been demonstrated that bacteria in Arctic pelagic environments are generally regulated by bottom-up factors, such as carbon and nutrient availability (Garneau et al., 2008; Kirchman et al., 2009; Ortega-Retuerta et al., 2012), and are usually less affected by the weak grazing pressure from heterotrophic protists from spring to autumn (Vaqué et al., 2008; Forest et al., 2011; Sanders and Gast, 2012). Hence, the strength of trophic linkages between bacteria and protozoans remains an open question in our study, especially as strong spatial and seasonal variability appear to affect bacterivory rates in Arctic waters (Bussey, 2003).

Interestingly, we also observed an anti-correlation pattern between metazooplankton and protozoans, suggesting the presence of a trophic cascade in the planktonic food web (i.e. metazoans controlled protozoans who controlled bacteria). Over the eastern shelf where the biomass of metazooplankton was high (mainly dominated by copepods; see Forest et al., 2012), the biomass of protozoans was surprisingly low (Table 1). As a result, the coupling between copepods and diatoms was tight nearby Cape Bathurst (Table 1), supporting previous evidences that the ecological setting of this zone favors trophic transfer to vertebrates (Sampei et al., 2011; Tremblay et al., 2011; Walkusz et al., 2012). Actually, the trophic coupling appears to be catalyzed by the episodic, but frequent, upwelling events that foster the development of diatom production (see Sect. 4.2) and the transport of lipid-rich calanoid copepods from the deep Amundsen Gulf to the eastern Mackenzie Shelf (Walkusz et al., 2012). In particular, such mecha-

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nism appears to sustain conditions attractive to bowhead whales that congregate annually on the eastern Mackenzie Shelf. Here, we confirmed this view of a biological hotspot, but we also present signs of a further expansion of the zooplankton biomass toward the central shelf, presumably as a result of the dominant westward flow that developed under the influence of northerly winds. Between the inner and outer shelf (20–100 m isobath), vertical POC fluxes (Fig. 5) and benthic carbon turnover (Fig. 9) in the central region were also greater than in the western and eastern areas, suggesting that the strong northerlies that prevailed prior to Malina induced a general displacement of food web activities westward of Cape Bathurst.

Threshold GPPs as estimated from model II regressions between NCP and GPP (Fig. 11) offered further indications that the ecosystem we sampled could not be considered in steady state. In fact, if we would have used NCP integrated over the whole euphotic layer, threshold GPPs would have been disproportionately high, with values roughly 2–3 times higher than what we estimated in the surface mixed layer only. Given the high temporal variability of PP in Beaufort Sea during summer (Ardyna et al., 2013), it is reasonable to assume that a substantial fraction of net heterotrophy was linked to the ingestion of organic matter produced earlier in the season and not detected by our measurements of PP during the campaign. This could also include marine organic matter freshly deposited on the sea bottom and resuspended by winds or upwelling currents (O'Brien et al., 2006). Over the shelf, the east-to-west increase in threshold GPP can thus be interpreted as the extra-heterotrophic activity supported by DOC and POC from the Mackenzie River. Since threshold GPPs were overall in the same order of magnitude on the eastern shelf (apparently unaffected by the Mackenzie River) than on the western and central zones, we can consider that riverine carbon input did not dramatically increase net heterotrophy, most probably because the river brought also nutrients that fuelled GPP. Offshore, threshold GPPs were substantially lower than on the shelf, reflecting the low primary and secondary production occurring in the slope-basin environment (see Fig. 9). As well, the negative slope computed for the western off-shelf zone likely represented the most profound example on how the Canada basin

is evolving with climate change, i.e. an oligotrophic ecosystem within which the planktonic food web does not develop beyond a microbial loop dominated by picophytoplankton, bacteria and protozoans.

5 Summary and implications

Our study illustrates that the consequences of Arctic changes on marine carbon cycling are not geographically uniform, even at the regional scale. In the attempt to synthesize our observations, we created a schematic that represents the food web structure and environmental forcings that drive synergistically ecosystem metabolism and air-sea CO₂ fluxes along the shelf-basin gradient in the Beaufort Sea during summer (Fig. 13). As the atmospheric and sea ice conditions shift in the Arctic in response to Global Change, the biogeochemical gradient between the shallow shelves and the deep basins is exacerbated. The strengthening of the anticyclonic Beaufort Sea High accompanied by an enlargement of the cyclonic regime over the Eurasian Arctic (i.e. Arctic dipole; Overland et al., 2012) leads to an intensification of easterly-northeasterly winds favorable to on-shelf upwelling and clear sky conditions in the western Arctic. As a result of increased solar heating and momentum transfer at the ocean surface, sea ice is getting thinner and younger, and melts more rapidly. This implies that the shelf would be fully exposed to the atmosphere in summer while a decaying sea ice cover would still cover the basin. However, during the current transitional stage, large sea ice floes from the central Arctic pack might easily get transported southward, as we observed during July–August 2009 under the effect of strong northerly winds. Hence, when the “true” upwelling-favorable winds are of short-duration and/or not very strong (such as in the present study), the so-called upwelling events may take the form of a sloping flux of deep waters across the shelf break and over the shelf bottom, which never truly reaches the surface except, possibly, in the nearshore environment. In any case, both upwelling and sloping currents bring upward substantial amount of dissolved CO₂ and nutrients. Surface outgassing of CO₂ over the shelf can be attenuated if the

concomitant flux of nitrate boosts PP (CO₂-fixation) and enhances vertical export – such as for example when large rapidly-sinking diatoms would dominate the phytoplankton assemblage. In the case where PP remains low, CO₂ outgassing has the potential to be massive even if it is fed through turbulent eddy diffusion resulting from wind-driven or tidal mixing from below and across the mixed-layer (Fig. 13). Therefore, monitoring the upwelling flow along the Arctic margin (e.g. through moorings, remote-sensing) is a key issue if insightful time-series of deep-water invasion over shallow shelf areas of biological importance are to be produced (cf. Pickart et al., 2013).

The balance between PP and heterotrophic respiration is a further process that will dictate if a given region might shift from a sink or a source of CO₂ (Fig. 13). Over the Mackenzie Shelf, pelagic and benthic heterotrophic activity is typically linked to pulses in fresh food supply (Renaud et al., 2007; Forest et al., 2011) and appears to be relatively rebarbative to terrigenous carbon, which appears to be bioavailable low – at least in its dissolved phase (Shen et al., 2012). We cannot dismiss that bacteria and protozoans might utilize allochthonous carbon to partly support their growth and metabolism, especially around the delta. But to which extent terrigenous carbon is incorporated and transferred into the Beaufort Sea food web is still an issue not fully resolved. Based on our analyses, the transfer of riverine carbon from microorganisms to higher trophic levels through calanoid copepods would be difficult given the spatial decoupling between mesozooplankton biomass and the routing of the river plume. Mesozooplankton were rather concentrated in the sub-surface layer, in association with large biomass of diatoms nearby Cape Bathurst (as observed by Walkusz et al., 2012). The Mackenzie River indeed provided substantial amount of nutrients that enhanced PP locally in the plume where the strongest CO₂ sink was detected (Fig. 4f). This implies that riverine DOC is not fully respired and contrasts with the Mackenzie estuary just a few km's nearby, where high respiration, warm surface temperature, and potential nearshore upwelling, contribute to make this area the strongest CO₂ source (cf. Chen et al., 2012). With the collapse of permafrost and the projected increase in freshwater runoff, the Mackenzie River discharge and its organic components might be potentially very dif-

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ferent, both qualitatively and quantitatively, in a few decades. This critical issue cannot be properly addressed without the implementation of a series of monitoring stations across the estuary and over the shelf that would help resolving the balance between PP and respiration and improve remote sensing estimates.

5 Concurrently to the development of a more dynamic carbon cycling over the Mackenzie Shelf (see also Tremblay et al., 2011; Tolosa et al., 2013), the Canada Basin is accumulating freshwater from ice melt and riverine input, thus getting more stratified (Fichot et al., 2013; McLaughlin et al., 2013). As a result, the limited vertical exchange of nutrients and organic carbon between the surface and sub-surface layer in the Canada Basin is inducing a food web above the MLD exclusively based on recycling and small unicellulars (Fig. 13). This region still acts as a weak sink for atmospheric CO₂, essentially because of sea ice melt (cf. Else et al., 2013a). Below the surface, a diluted food web is present (see also Forest et al., 2012), which benefits from the weak local PP as well as from lateral inputs from the shelf (e.g. advection of eroded sediment, oblique flux of phyto-detritus). But with the progressive deepening of the nutricline and chl *a* maximum in the Canada Basin (Carmack and McLaughlin, 2011), lateral inputs from the shelf could become the dominant energy pathway for sustaining the pelagic food web in the deep Canada Basin (cf. Forest et al., 2012; Shah et al., 2013). This underscores that the cross-shelf flux of organic matter over the slope and in the basin is also among the most important variables to monitor if the future Arctic marine carbon cycling and the implications for food web capacity and efficiency are to be accurately understood and modeled.

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Table 1. Spatial averages (mean \pm 0.95 confidence interval) of biomass (B), production (P), and $P : B$ ratios (expressed in % day⁻¹), of pelagic autotrophs (phytoplankton) and heterotrophs (bacteria, protozoans and metazooplankton) as estimated from the ArcticNet-Malina dataset collected over July–August 2009 in southeast Beaufort Sea (Fig. 1). The mean mixed-layer depth delimits the boundary between the surface and subsurface layer. The subsurface layer extends down to 100 m maximum. The threshold between the on-shelf and off-shelf region is the 100 m isobath. The western, central and eastern regions correspond to the areas delimited by 136–141° W, 131–136° W and 126–131° W, respectively.

		Surface (above mixed layer depth)						Subsurface (below mixed layer depth until 100 m)					
		On-shelf region			Off-shelf region			On-shelf region			Off-shelf region		
		Western	Central	Eastern	Western	Central	Eastern	Western	Central	Eastern	Western	Central	Eastern
Phytoplankton	Production (mg C m ⁻² d ⁻¹)	63.4 ± 13.5	68.2 ± 9.6	153 ± 13	15.8 ± 1.2	12.0 ± 1.1	43.3 ± 3.8	32.1 ± 3.1	37.4 ± 1.9	37.2 ± 3.4	40.5 ± 1.8	26.8 ± 1.8	25.5 ± 1.3
	Biomass (mg C m ⁻²)	264 ± 36	328 ± 20	374 ± 13	69.6 ± 3.8	64.1 ± 4.1	128 ± 7	795 ± 55	767 ± 40	1480 ± 54	341 ± 11	535 ± 23	886 ± 27
	P:B ratio (% per day)	24.0 ± 3.6	20.8 ± 1.6	40.8 ± 2.0	22.7 ± 1.3	18.8 ± 1.3	33.8 ± 2.1	4.0 ± 0.3	4.9 ± 0.3	2.5 ± 0.1	11.9 ± 0.4	5.0 ± 0.2	3.7 ± 0.1
Bacteria	Production (mg C m ⁻² d ⁻¹)	18.0 ± 2.8	18.6 ± 1.9	22.2 ± 1.0	3.1 ± 0.5	1.5 ± 0.2	7.4 ± 0.6	25.8 ± 4.1	19.5 ± 1.4	24.9 ± 2.0	9.3 ± 0.6	5.7 ± 0.5	12.2 ± 1.2
	Biomass (mg C m ⁻²)	126 ± 4	120 ± 5	92.9 ± 3.7	74.7 ± 4.4	37.1 ± 2.2	67.3 ± 4.3	437 ± 36	328 ± 12	241 ± 27	557 ± 14	486 ± 22	732 ± 49
	P:B ratio (% per day)	14.3 ± 0.7	15.5 ± 0.8	26.8 ± 1.2	4.1 ± 0.3	3.9 ± 0.2	11.0 ± 0.7	5.9 ± 0.5	5.9 ± 0.2	10.3 ± 1.1	1.7 ± 0.0	1.2 ± 0.1	1.7 ± 0.1
Protozooplankton	Production (mg C m ⁻² d ⁻¹)	28.5 ± 3.9	19.1 ± 1.7	5.7 ± 0.4	6.6 ± 0.5	5.1 ± 0.3	6.1 ± 0.4	19.6 ± 0.6	15.2 ± 0.4	15.2 ± 0.6	17.2 ± 0.8	22.9 ± 0.9	22.6 ± 1.0
	Biomass (mg C m ⁻²)	333 ± 34	167 ± 12	93.1 ± 5.1	95.4 ± 6.9	84.7 ± 4.1	110 ± 3	335 ± 10	257 ± 5	273 ± 4	284 ± 15	378 ± 13	351 ± 12
	P:B ratio (% per day)	8.6 ± 0.9	11.4 ± 0.9	6.2 ± 0.3	6.9 ± 0.5	6.1 ± 0.3	5.6 ± 0.2	5.9 ± 0.2	5.9 ± 0.1	5.6 ± 0.1	6.1 ± 0.3	6.1 ± 0.2	6.4 ± 0.2
Nauplii and small metazooplankton	Production (mg C m ⁻² d ⁻¹)	0.2 ± 0.0	1.6 ± 0.1	1.5 ± 0.1	0.1 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.6 ± 0.1	6.4 ± 0.5	6.1 ± 0.6	0.8 ± 0.1	1.6 ± 0.2	1.6 ± 0.2
	Biomass (mg C m ⁻²)	13.9 ± 2.2	66.3 ± 5.2	69.1 ± 5.5	3.2 ± 0.4	5.3 ± 1.4	8.5 ± 1.0	21.9 ± 4.0	274 ± 23	215 ± 18	36.9 ± 3.2	78.6 ± 10.7	73.4 ± 7.3
	P:B ratio (% per day)	1.3 ± 0.2	2.3 ± 0.2	2.1 ± 0.2	2.1 ± 0.3	2.1 ± 0.6	2.2 ± 0.3	2.8 ± 0.5	2.3 ± 0.2	2.8 ± 0.2	2.2 ± 0.2	2.0 ± 0.3	2.2 ± 0.2
Large metazooplankton	Production (mg C m ⁻² d ⁻¹)	0.2 ± 0.0	0.5 ± 0.0	1.5 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	0.5 ± 0.1	1.9 ± 0.2	19.7 ± 1.6	16.7 ± 1.2	4.4 ± 0.3	7.9 ± 0.6	9.9 ± 0.6
	Biomass (mg C m ⁻²)	17.8 ± 2.4	38.9 ± 3.7	139 ± 13	4.1 ± 0.4	13.0 ± 2.0	47.5 ± 4.9	86.2 ± 32.3	1820 ± 149	1603 ± 143	519 ± 30	1004 ± 55	1052 ± 100
	P:B ratio (% per day)	1.3 ± 0.2	1.2 ± 0.1	1.1 ± 0.1	1.3 ± 0.1	1.2 ± 0.2	1.1 ± 0.1	2.2 ± 0.8	1.1 ± 0.1	1.0 ± 0.1	0.9 ± 0.0	0.8 ± 0.0	0.9 ± 0.1
Total heterotrophs	Production (mg C m ⁻² d ⁻¹)	46.8 ± 6.8	39.8 ± 3.7	31.0 ± 1.8	9.7 ± 1.1	6.9 ± 0.5	14.2 ± 1.1	47.9 ± 5.0	60.7 ± 3.9	62.9 ± 4.3	31.7 ± 1.7	38.2 ± 2.2	46.3 ± 2.8
	Biomass (mg C m ⁻²)	491 ± 43	395 ± 26	384 ± 28	177 ± 12	140 ± 10	233 ± 13	880 ± 63	2680 ± 190	2332 ± 193	1397 ± 63	1956 ± 101	2209 ± 168
	P:B ratio (% per day)	9.5 ± 0.9	10.1 ± 0.7	8.1 ± 0.6	5.5 ± 0.4	4.9 ± 0.3	6.1 ± 0.4	5.4 ± 0.5	2.3 ± 0.2	2.7 ± 0.2	2.3 ± 0.1	2.0 ± 0.1	2.1 ± 0.2
Total heterotroph-to-autotroph production ratio (unitless)		0.74 ± 0.14	0.58 ± 0.07	0.20 ± 0.02	0.62 ± 0.06	0.57 ± 0.05	0.33 ± 0.03	1.49 ± 0.15	1.63 ± 0.10	1.69 ± 0.13	0.78 ± 0.04	1.42 ± 0.09	1.81 ± 0.10
Total heterotroph-to-autotroph biomass ratio (unitless)		1.86 ± 0.19	1.20 ± 0.08	1.03 ± 0.05	2.55 ± 0.16	2.18 ± 0.15	1.82 ± 0.10	1.11 ± 0.09	3.49 ± 0.23	1.58 ± 0.10	4.09 ± 0.17	3.66 ± 0.18	3.22 ± 0.22

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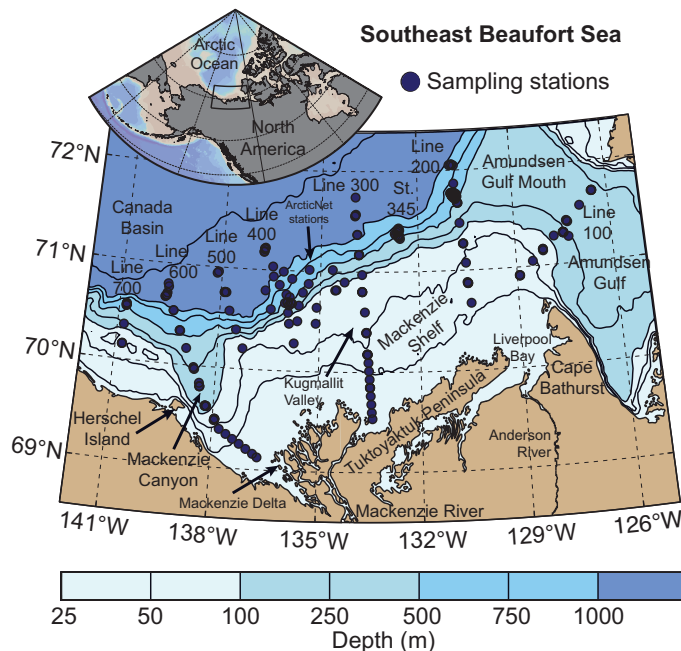


Fig. 1. Map of the Mackenzie Shelf region (Beaufort Sea, Arctic Ocean) with position of sampling stations visited in July–August 2009 as part of the ArcticNet-Malina campaign. The ArcticNet sampling stations were located within the exploration license area EL446, whereas transects 100–700 and station 345 correspond to the Malina sampling grid. On each Malina transect, station numbers are listed in descending order from south to north (e.g. stations 170 to 110 from south to north on line 100). In this study, we used the following geographical limits when discussing the spatial variability: (i) the boundary between the shelf and the slope/basin is delineated by the 100 m isobath; and (ii) the western, central and eastern regions correspond to the areas delimited by 136–141° W, 131–136° W and 126–131° W, respectively.

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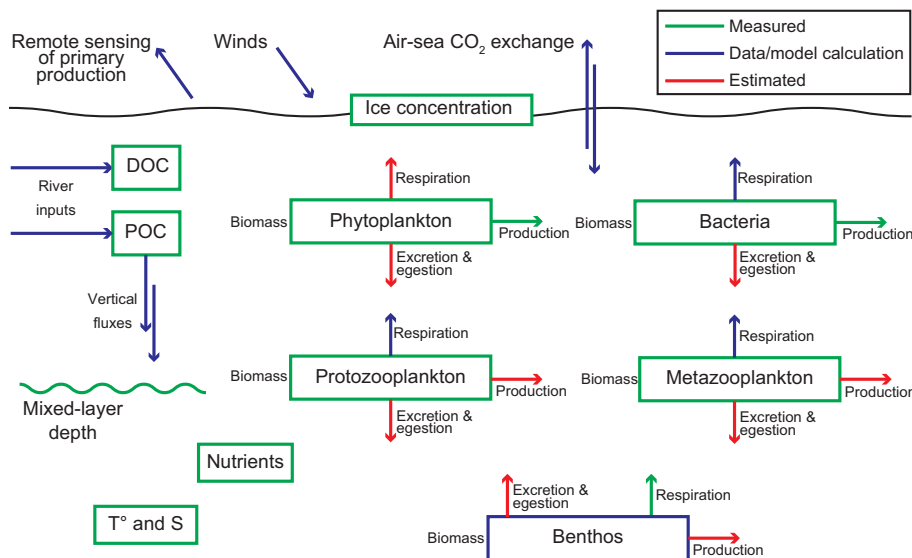


Fig. 2. Diagram showing which variables have been directly measured on the field during ArcticNet-Malina, vs. which ones have been calculated using a combination of in situ data and empirical models, or rather estimated using knowledge from the literature or deduced from previous regional studies. This schematic aims at facilitating the reading of the methodological Sects. 2.2–2.6. The biophysical context at a regional scale prior and during the field campaign was documented using sea ice, wind and ocean color PP estimates gathered from different sources. For a detailed description of equations linking metabolic pathways of the planktonic and benthic compartments, please see the Appendix B in Forest et al. (2011).

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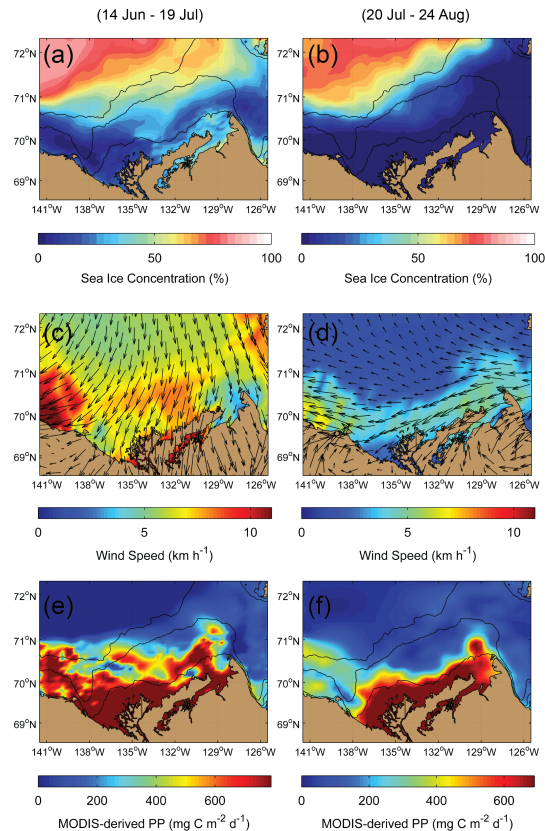


Fig. 3. Composites of (a, b) sea ice concentration (% ice coverage) from the SSM/I-DMSP orbiting sensor, (c, d) wind velocity and vectors from the NCEP-NARR reanalysis, and (e, f) rates of primary production (PP) derived from the MODIS satellite, as averaged for the 35 day period just before (14 June–19 July, left panels) and just during (20 July–24 August, right panels) the ArcticNet-Malina field campaign. Bathymetric contours are 20, 100 and 1000 m.

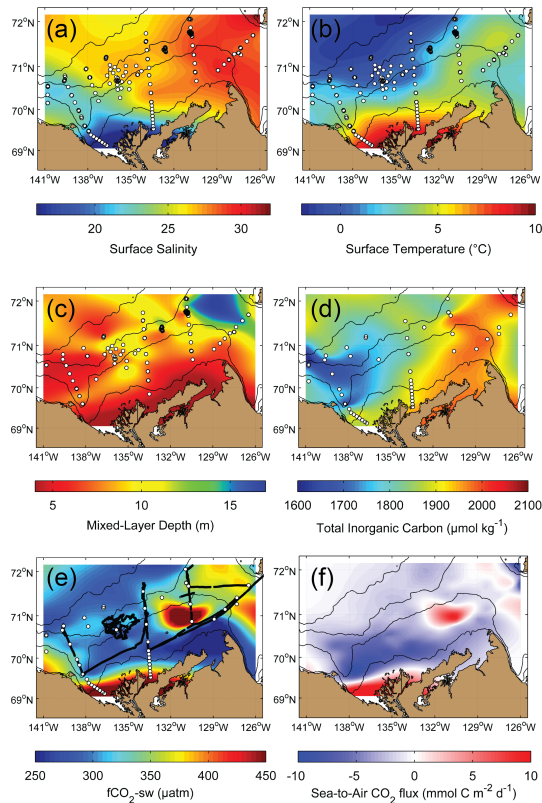


Fig. 4. Gridded composites of in situ physico-chemical data obtained at the sampling stations (white dots) conducted in Beaufort Sea in mid-summer 2009 (Fig. 1): **(a)** surface salinity, **(b)** surface temperature, **(c)** depth of the mixed-layer delimiting the surface and subsurface layers as used in this study, **(d)** concentration of dissolved inorganic carbon, **(e)** sea surface CO_2 fugacity (combined dataset from the underway system and bottle data), and **(f)** the sea-to-air CO_2 fluxes (blue: flux to the ocean; red: to the atmosphere) as computed following the methodology described in Sect. 2.3. Bathymetric contours are 20, 100, 1000, and 2000 m.

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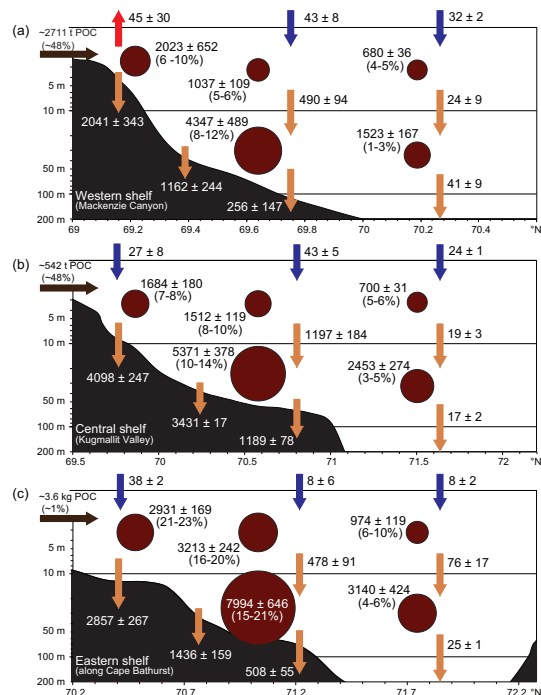


Fig. 5. Cross-shelf averages (mean ± 0.95 confidence interval) of particulate organic carbon (POC) inventories (dark brown circles), vertical POC fluxes (light brown arrows), riverine POC inputs (black arrows), and sea-to-air CO₂ fluxes (red and dark blue arrows). All pool units (circles) are in mg C m⁻² and all flux units (arrows) are in mg C m⁻² d⁻¹, except the riverine inputs (which are in t POC day⁻¹ or kg POC day⁻¹). The percentage in brackets associated with every POC inventory and river input is the percentage of POC in total (particulate + dissolved) organic carbon that each value represents. The western, central and eastern regions correspond to the areas delimited by 136–141° W, 131–136° W and 126–131° W, respectively (Fig. 1). For a detailed description on how each variable has been estimated, please see Sect. 2.4.

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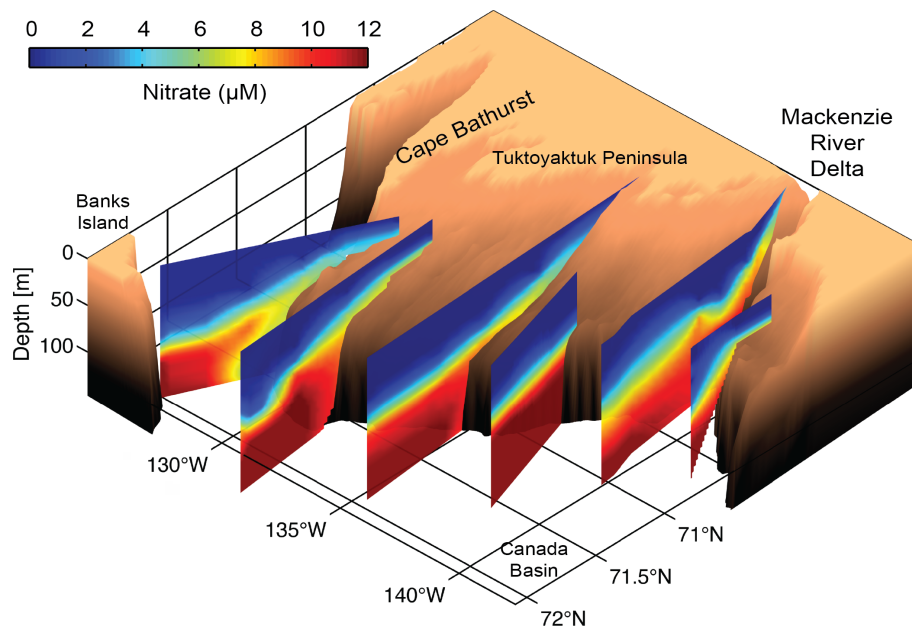


Fig. 6. Three-dimensional view of the Mackenzie Shelf region showing the nitrate concentration as measured at transects 100, 200, 300, 400, 600 and 700 (from left to right) during the Malina expedition (Fig. 1). Each vertical slice corresponds to a gridded composite of nitrate concentration measured at standard depths along the cross-shelf sampling line.

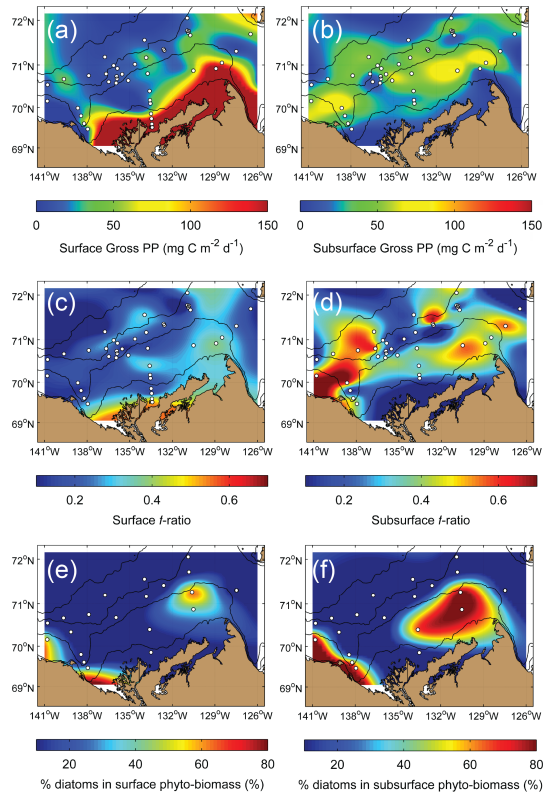


Fig. 7. Gridded composites of variables related to phytoplankton dynamics as measured in the surface and subsurface layer of the study region: **(a, b)** total gross primary production (PP) from field measurements, **(c, d)** the f ratio of new PP to total PP as estimated on the basis of nitrate and ammonium uptake incubations, and **(e, f)** the percentage of diatoms in the total phytoplankton biomass. The white dots correspond to the sampling sites. Bathymetric contours are 20, 100, 1000, and 2000 m.

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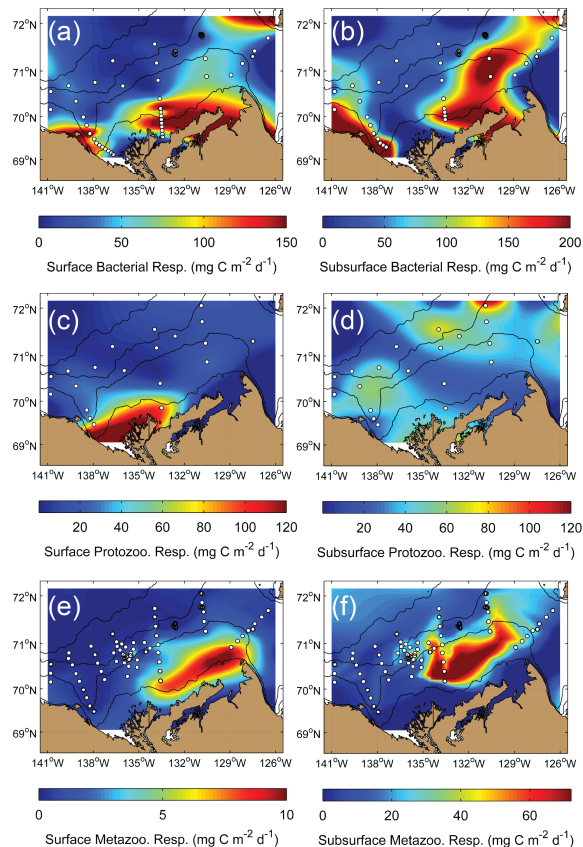


Fig. 8. Gridded composites of estimated values related to heterotroph respiration in the surface (left panels) and subsurface (right panels) layer: **(a, b)** bacterial respiration, **(c, d)** protozooplankton respiration, and **(e, f)** metazooplankton respiration. The white dots correspond to the sampling stations upon which respiration estimates were calculated. For a detailed description on how each respiration flux has been estimated, please see Sect. 2.6.

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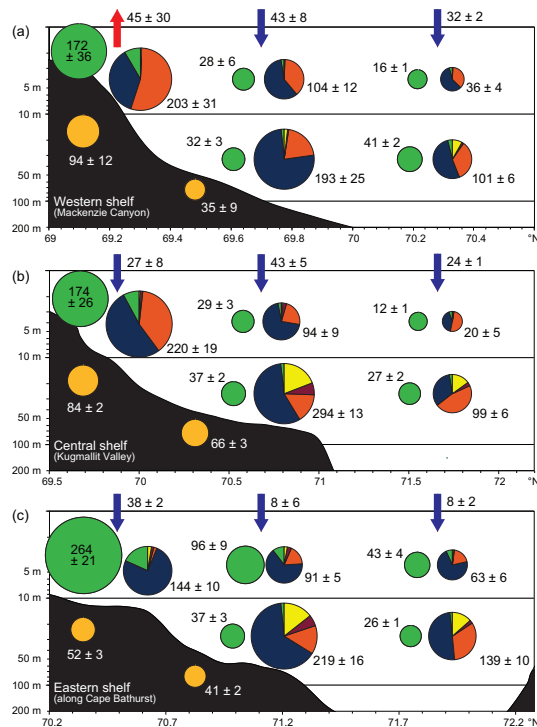


Fig. 9. Cross-shelf average estimates (mean ± 0.95 confidence interval) of gross primary production (green circles), total pelagic heterotroph respiration (pie charts), benthic respiration (orange circles in the sediment), and sea-to-air CO₂ fluxes (red and dark blue arrows; same as in Fig. 4). Every pie chart represents the combined respiration of phytoplankton (green), bacteria (dark blue), protozooplankton (dark orange), small metazooplankton and nauplii (dark red), and large metazooplankton (yellow). All units are in mg C m⁻² d⁻¹. The western, central and eastern regions correspond to the areas delimited by 136–141° W, 131–136° W and 126–131° W, respectively (Fig. 1). For a detailed description on how each variable has been estimated, please see Sects. 2.5 and 2.6.

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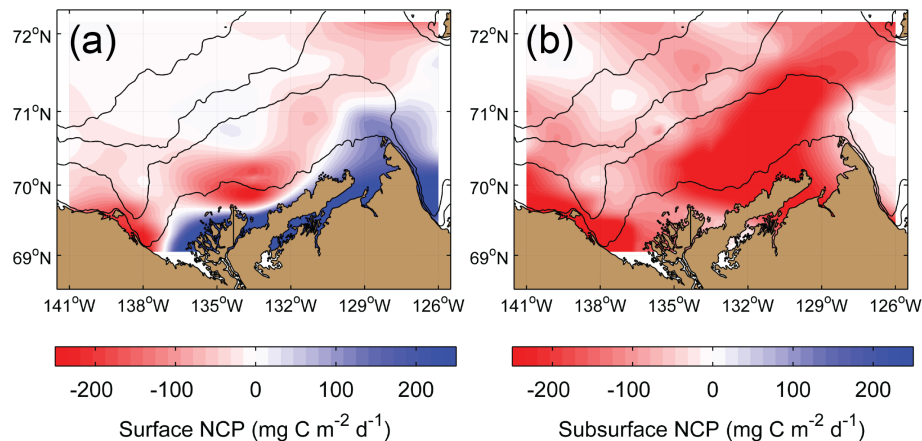


Fig. 10. Maps of net community production (NCP) in the **(a)** surface and **(b)** subsurface layer of the study area as based on total gross primary production minus total community respiration. The subsurface NCP accounts for the respiration flux from the benthos (over the shelf only, i.e. until the 100 m isobath). The mean mixed-layer depth delimits the boundary between the surface and subsurface layer; and the subsurface layer extends down to 100 m maximum. Bathymetric contours are 20, 100, 1000, and 2000 m.

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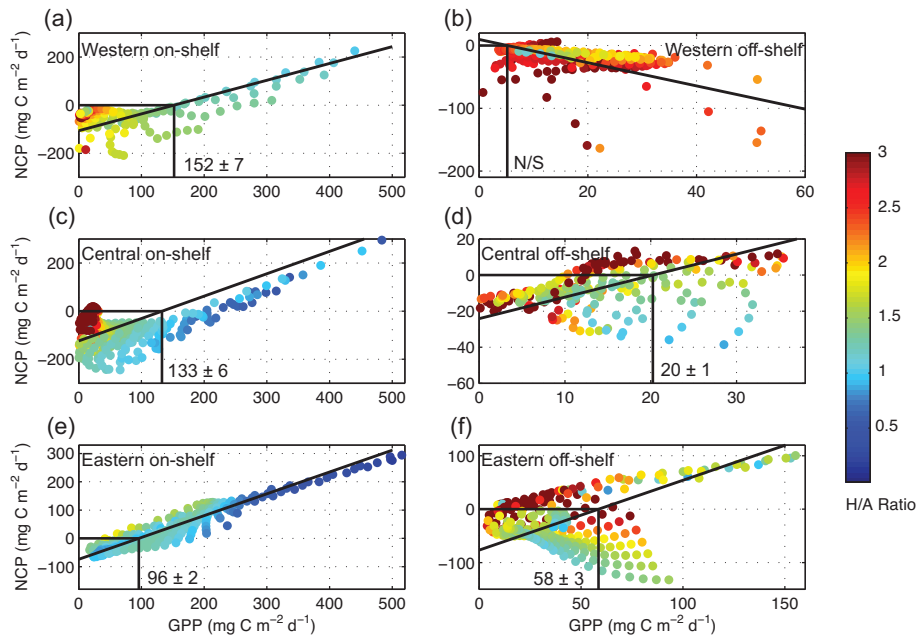


Fig. 11. Model II regressions of net community production (NCP) against gross primary production (GPP) in the surface layer of the on-shelf and off-shelf zones (delimited by the 100 m isobath). Every dot represents a pixel extracted from the gridded composites and further colored according to the total heterotroph to autotroph biomass ratio (H/A ratio). The threshold GPP (i.e. GPP at which NCP becomes positive) is shown on every image, except for the western off-shelf area where the regression was not significant (N/S). The western, central and eastern regions correspond to the areas delimited by 136–141° W, 131–136° W and 126–131° W, respectively (Fig. 1).

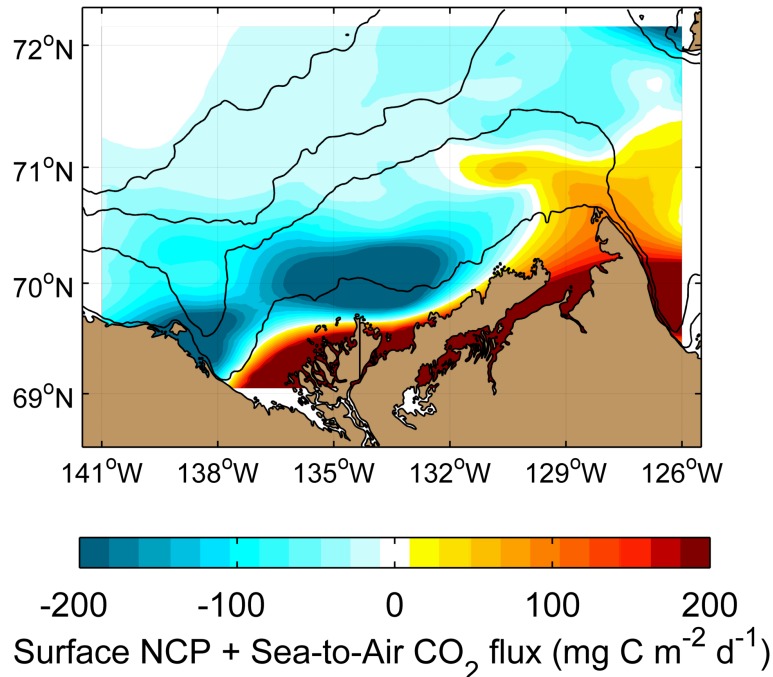


Fig. 12. Map of the sum of surface net community production (NCP) and sea-to-air CO₂ fluxes for the ArcticNet-Malina campaign of mid-summer 2009. This map aims at showing the spatial discrepancy between CO₂ fluxes and ecosystem metabolism. A positive value (reddish) means that the potential for CO₂ sink due to positive NCP is dampened by external forcings (e.g. upwelling of CO₂-rich waters, warming, photomineralization). While negative values (turquoise) mean that the potential for CO₂ source due to negative NCP is compensated by other factors (e.g. past productivity and vertical export, dilution, cooling). Bathymetric contours are 20, 100, 1000, and 2000 m.

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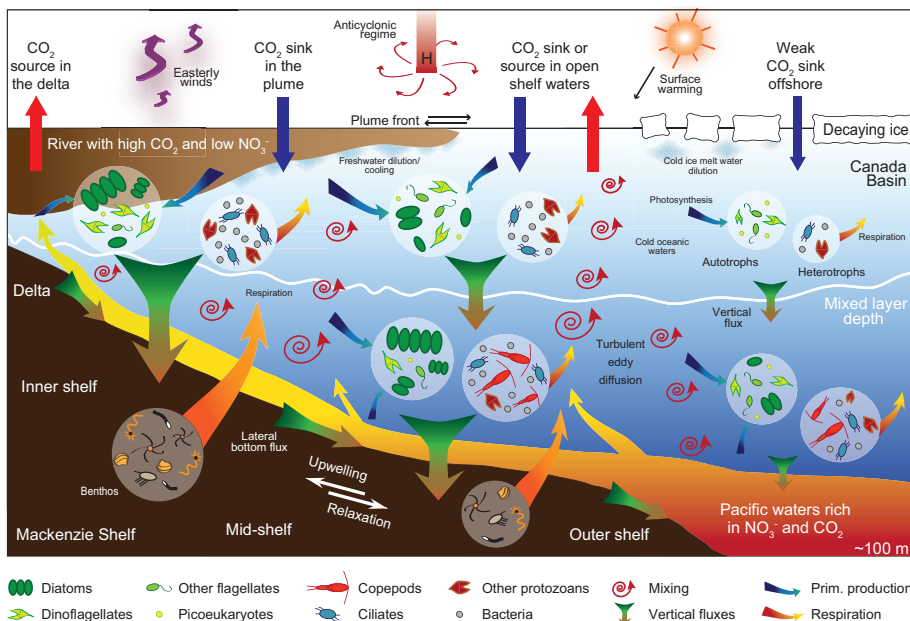


Fig. 13. Schematics of food web structure and environmental forcings that drive synergistically ecosystem metabolic balance and sea-to-air CO₂ fluxes along the shelf-basin gradient in the changing Beaufort Sea. A succinct legend is presented below the schematics, but see Sect. 5.0 for detailed explanation.

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