Temporal and spatial trends in marine carbon isotopes in the Arctic Ocean and implications for food web studies

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Temporal and spatial trends in marine carbon isotopes in the Arctic Ocean and implications for food web studies

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Abstract

The Arctic is undergoing unprecedented environmental change. Rapid warming, decline in sea ice extent, increase in riverine input, ocean acidification and changes in primary productivity are creating a crucible for multiple concurrent environmental stressors, with unknown consequences for the entire arctic ecosystem. Here, we synthesized 30 years of data on the stable carbon isotope ($\delta^{13}C$) signatures in dissolved inorganic carbon ($\delta^{13}C$-DIC; 1977–2014), marine and riverine particulate organic carbon ($\delta^{13}C$-POC; 1986–2013) and tissues of marine mammals in the Arctic. $\delta^{13}C$ values in consumers can change as a result of environmentally driven variation in the $\delta^{13}C$ values at the base of the food web or alteration in the trophic structure, thus providing a method to assess the sensitivity of food webs to environmental change. Our synthesis reveals a spatially heterogeneous and temporally evolving $\delta^{13}C$ baseline, with spatial gradients in the $\delta^{13}C$-POC values between arctic shelves and arctic basins likely driven by differences in productivity and riverine and coastal influence. We report a decline in $\delta^{13}C$-DIC values (−0.011‰ per year) in the Arctic, reflecting increasing anthropogenic carbon dioxide (CO_2) in the Arctic Ocean (i.e. Suess effect), which is larger than predicted. The larger decline in $\delta^{13}C$-POC values and $\delta^{13}C$ in arctic marine mammals reflects the anthropogenic CO_2 signal as well as the influence of a changing arctic environment. Combining the influence of changing sea ice conditions and isotopic fractionation by phytoplankton, we explain the decadal decline in $\delta^{13}C$-POC values in the Arctic Ocean and partially explain the $\delta^{13}C$ values in marine mammals with consideration of time-varying integration of $\delta^{13}C$ values. The response of the arctic ecosystem to ongoing environmental change is stronger than we would predict theoretically, which has tremendous implications for the study of food webs in the rapidly changing Arctic Ocean.

KEYWORDS

base of the food web, dissolved inorganic carbon, isoscape, marine mammals, particulate organic matter, sea ice decline, Suess effect, $\delta^{13}C$

1 | INTRODUCTION

The Arctic is changing rapidly (IPCC, 2013), warming twice as fast as the global average (Carmack et al., 2015; Hoegh-Guldberg & Bruno, 2010) and causing sea ice to decline in both extent and thickness (Kwok, 2018; Lind, Ingvaldsen, & Furevik, 2018). Sea ice underpins the entire arctic ecosystem and the decline in this seasonal habitat is affecting the entire food web. Primary production has increased by 30% from 1998 to 2012 owing to an increase in light under reduced ice conditions (Arrigo & van Dijken, 2015). Arctic predators, such as seals and polar bears, that rely on sea ice for foraging, moulting and breeding are also adversely affected by the loss of sea ice (Laidre et al., 2008). Other climate-induced changes are occurring in tandem and include acidification (Yamamoto, Kawamiya, Ishida, Yamanaka, & Watanabe, 2012), shifts in wind patterns and enhanced wind field in the Western Arctic (Overland & Wang, 2010), increased coastal erosion, river flow and melting of permafrost and glaciers (Haine et al., 2015; Jones et al., 2009; Mars & Houseknecht, 2007). These multiple concurrent stressors have far-reaching implications for the arctic marine ecosystem at multiple trophic levels, and there is an urgent need to understand the ecosystem response in this unique polar habitat.

The ratio of stable carbon isotopes, ^{13}C and ^{12}C, expressed as $\delta^{13}C$ (‰), provides a powerful tool for studying food webs. The $\delta^{13}C$ values of particulate organic carbon (POC), consisting of fresh phytoplankton, microzooplankton, bacteria and marine and terrestrial detritus, (Fry & Sherr, 1989; Lobbes, Fitznar, & Kattner, 2000; Michener & Kaufman, 2007; Wassmann et al., 2004), represent the base of the food web or 'baseline'. The $\delta^{13}C$ values of POC ($\delta^{13}C$-POC) are generally transferred with a ^{13}C enrichment of 1‰–2‰ between each trophic level, creating an inextricable link between the base of the food web and consumers (Fry, Anderson, Entzeroth, Bird, & Parker, 1984). Spatial trends in $\delta^{13}C$-POC values controlled by environmental factors have been used to decipher the foraging and migratory patterns of consumers on a regional scale (Hoffman, 2016; Iken, Bluhm, & Dunton, 2010; Polito et al., 2017; Wassenaar, 2019) and more recently on a global scale in the construction of global 'isoscapes' (Bird et al., 2018; Bowen & West, 2008; Firmin, 2016; Graham, Koch, Newsome, McMahon, & Aurioles, 2010; McMahon, Hamady, & Thorrold, 2013b). However, spatial and temporal trends in the $\delta^{13}C$ values of high trophic levels may also reflect changes in food web structure such as loss or addition of species, consumer's diet or a combination of factors. To disentangle the drivers of spatial and temporal trends in the $\delta^{13}C$ values of consumers in the Arctic, it is crucial to establish spatial and temporal variations in $\delta^{13}C$ values at the base of the food web, allowing the sensitivity of marine arctic consumers to environmental change to be quantified.

It is challenging to isolate phytoplankton-POC for analysis and so the nominal definition of $\delta^{13}C$-POC values typically assumes that the bulk of POC is derived from phytoplankton only, although $\delta^{13}C$-POC values can be influenced by other factors such as bacterial activity and detritus (Michener & Kaufman, 2007). While the detrital fraction of POC may be degraded by bacteria, potentially altering the $\delta^{13}C$ values of that fraction, we assume that photosynthetic phytoplankton are responsible for transforming the bulk of $\delta^{13}C$-POC values in time and space. $\delta^{13}C$ value of phytoplankton, which underpins the $\delta^{13}C$-POC values, is controlled by fractionation during photosynthesis. This equates to the difference between the $\delta^{13}C$ values of the carbon source, either dissolved inorganic carbon (DIC) or carbon dioxide (CO_2), and the $\delta^{13}C$-POC values (Cassar, Laws, Bidigare, & Popp, 2004; Young, Bruggeman, Rickaby, Erez, & Conte, 2013). Factors such as phytoplankton growth rate, availability or concentration of carbon, light and nutrient availability affect isotopic fractionation and the $\delta^{13}C$-POC values (Burkhardt, Riebesell, & Zondervan, 1999; Keeley & Sandquist, 1992). As such, environmental conditions can create distinct patterns in these values. $\delta^{13}C$-POC values become enriched in ^{13}C in an environment where replenishment of the CO_2 pool is slow or restricted, for example, during periods of rapid phytoplankton growth (Rau, Takahashi, Des Marais, Repeta, & Martin, 1992) or in sea ice associated with sympagic primary production (Budge et al., 2008; Hobson et al., 2002; Søreide et al., 2013; Wang, Budge, Gradinger, Iken, & Wooller, 2014). Conversely, an increase in CO_2 concentration will lead to a carbon pool depleted in ^{13}C (Rau et al., 1992) creating a ^{13}C-deplete POC pool. Terrestrially derived POC delivered via rivers and coastal erosion also tends to be depleted in ^{13}C relative to marine-derived POC (Boutton, 1991; Keeley & Sandquist, 1992). While global isoscapes capture the large-scale spatial trends in $\delta^{13}C$ values related to oceanographic provinces (shelf vs. open ocean) and latitude (Bird et al., 2018; Bowen & West, 2008; Graham et al., 2010; McMahon et al., 2013b), they do not include the Arctic Ocean. We expect the $\delta^{13}C$ values of POC in the Arctic to be influenced by the strong regional trends in sea ice, productivity and terrestrial influence including riverine input and coastal erosion, all of which vary along the water mass circulation pathways from the inflow shelves, which receive water from the Atlantic and Pacific oceans, to the arctic basins and interior shelves (Sakshaug, 2004; Tremblay & Gagnon, 2009; Varela, Crawford, Wrohan, Wyatt, & Carmack, 2013).

Imprinted on the regional trends is a temporal trend in $\delta^{13}C$ values worldwide. Enhanced atmospheric CO_2 since the industrial period (Tagliabue & Bopp, 2008) is causing an increase in oceanic CO_2 (Sabine et al., 2004) and a decline in the $\delta^{13}C$ values of DIC ($\delta^{13}C$-DIC), known as the Suess effect, as a result of ^{13}C-depleted anthropogenic CO_2 (Quay, Sonnerup, Westby, Stutsman, & McNichol, 2003). $\delta^{13}C$-DIC values in the Arctic Ocean are predicted to change at a rate of −0.006‰ to −0.008‰ per year, compared to the global average of −0.017‰ per year (Tagliabue & Bopp, 2008). However, several studies have already shown that decadal trends in the $\delta^{13}C$ values of marine mammals in the Arctic (Misarti, Finney, Maschner, & Wooller, 2009; Nelson, Quakenbush, Mahoney, Taras, & Wooller, 2018; Newsome et al., 2007; Schell, 2001) are larger than the Suess effect alone, implying that other factors are altering their $\delta^{13}C$ signatures on decadal timescales.

The main objective of this study was to quantify how regional differences and temporal trends in the arctic environment have altered the $\delta^{13}C$ values in DIC and POC, representing the base of the food web

or 'baseline'. We compared these trends at the base of the food web to trends in $\delta^{13}C$ values in arctic marine mammals to investigate how environmental change (e.g. Suess effect, loss of sea ice) may alter $\delta^{13}C$ values in the entire food web. We synthesized published data from 1977 to 2014 on $\delta^{13}C$ values of DIC and dissolved CO_2, and $\delta^{13}C$-POC values in the surface ocean (POC_{water}) and in sea ice (POC_{ice}) across the entire Arctic Ocean, alongside data from arctic rivers (POC_{riv}). We quantified regional differences in the $\delta^{13}C$ values in POC and discuss the underlying environmental drivers of the observed spatial heterogeneity. We then quantified the decadal trends in $\delta^{13}C$ values of DIC and CO_2, and $\delta^{13}C$ values of POC in the Arctic Ocean, comparing the rate of change to the Suess effect and observed trends in tissues of arctic marine mammals from the post-industrial period.

2 | MATERIALS AND METHODS

2.1 | Data collation

Data on bulk $\delta^{13}C$-POC_{water}, $\delta^{13}C$-POC_{ice} and $\delta^{13}C$-POC_{riv} values, focusing on suspended particulate organic matter above the thermocline, were collated from tables and figures in 37 original manuscripts and two open access databases for both marine (PANGAEA; http://www.pangaea.de) and riverine (articGRO; https://arcticgreatrivers.org/) environments, in Arctic and sub-Arctic regions, as defined by the Köppen–Geiger climate classification (Kottek, Grieser, Beck, Rudolf, & Rubel, 2006). The database included 354 data points for marine $\delta^{13}C$-POC_{water} values (Brown et al., 2014; Connelly, McClelland, Crump, Kellogg, & Dunton, 2015; Forest et al., 2010; Griffith et al., 2012; Guo, Tanaka, Wang, Tanaka, & Murata, 2004; Hallanger et al., 2011; Hobson, Ambrose, & Renaud, 1995; Hobson et al., 2002; Iken et al., 2010; Iken, Bluhm, & Gradinger, 2005; Ivanov, Lein, Zakharova, & Savvichev, 2012; Kohlbach et al., 2016; Kuliński, Kędra, Legeżyńska, Gluchowska, & Zaborska, 2014; Kuzyk, Macdonald, Tremblay, & Stern, 2010; Lin et al., 2014; Lovvorn et al., 2005; O'Brien, Macdonald, Melling, & Iseki, 2006; Parsons et al., 1989; Roy et al., 2015; Sarà et al., 2007; Schubert & Calvert, 2001; Smith, Henrichs, & Rho, 2002; Søreide et al., 2008; Søreide, Hop, Carroll, Falk-Petersen, & Hegseth, 2006; Tamelander, Reigstad, Hop, & Ratkova, 2009; Tamelander et al., 2006; Tremblay, Michel, Hobson, Gosselin, & Price, 2006; Zhang et al., 2012), 69 data points for $\delta^{13}C$-POC_{ice} values (Forest et al., 2010; Hobson et al., 1995; 2002; Iken et al., 2005; Kohlbach et al., 2016; Lovvorn et al., 2005; Roy et al., 2015; Schubert & Calvert, 2001; Søreide et al., 2006, 2008; Tamelander et al., 2006; Tremblay et al., 2006) and 383 data points for riverine $\delta^{13}C$-POC_{riv} values (Goni, Yunker, Macdonald, & Eglinton, 2000; Holmes, McClelland, Tank, Spencer, & Shiklomanov, 2018; Kuzyk et al., 2010; Lobbes et al., 2000). Data were available over different temporal scales: marine $\delta^{13}C$-POC_{water} values from 1986 to 2013, $\delta^{13}C$-POC_{ice} from 1993 to 2012 and riverine $\delta^{13}C$-POC_{riv} values from 1987 to 2016.

To relate the temporal trend in $\delta^{13}C$-POC_{water} values to the predicted decline of $\delta^{13}C$-DIC and $\delta^{13}C$-CO_2 values, a compilation of data on $\delta^{13}C$-DIC values was extracted from three publications (Bauch, Polyak, & Ortiz, 2015; Schmittner et al., 2013; Young et al., 2013) and two databases (Becker et al., 2016; Key et al., 2015). $\delta^{13}C$-CO_2 values were determined from the $\delta^{13}C$-DIC values and absolute temperature following the Equation (1) (Rau, Riebesell, & Wolf-Gladrow, 1996). $\delta^{13}C$-DIC and $\delta^{13}C$-CO_2 values included 1,333 data points covering 1977–2014.

$$\delta^{13}C\text{-}CO_2 = \delta^{13}C\text{-}DIC + 23.644 - 9{,}701.5/T, \quad (1)$$

where T is the temperature in Kelvin.

To determine if the temporal trend in $\delta^{13}C$-POC values was reflected in higher trophic levels within the Arctic Ocean, $\delta^{13}C$ data were collated from arctic marine mammals covering years following the industrial period (post 1950). We collated $\delta^{13}C$ data from teeth of ringed seals (*Pusa hispida*) from 1986 to 2006 from East Greenland (Aubail, Dietz, Rigét, Simon-Bouhet, & Caurant, 2010) and northern fur seals (*Callorhinus ursinus*) from 1950 to 2000 from the Bering Sea and Gulf of Alaska (Newsome et al., 2007). Additionally, $\delta^{13}C$ data were collated from teeth of Beluga whales (*Delphinapterus leucas*) from 1963 to 2008 from the Hudson Bay and from 1976 to 2001 from the Baffin Bay (Matthews &

FIGURE 1 Map indicating the locations of the arctic regions considered in this study. Circulation pathways are highlighted and modified from Carmack and Wassmann (2006). The yellow arrows represent the intermediate Pacific water and the red arrows represent the Atlantic water. White arrows indicate the mouths of the arctic rivers. The black circles point to the approximate location of the North Water Polynia in the Northern Baffin bay, North-East Water Polynia in Northeast Greenland and Svalbard marine coastal area. Chu., Churchill River; Gr.Wh., Great Whale River; Hay., Hayes River; Inn., Innuksuac River; Li.Wh., Little Whale River; Nas., Nastapoca River; Nel., Nelson River; Win., Winisk River; Bathymetry and coast lines were from the software Ocean Data View (Schlitzer, 2016)

TABLE 1 Location and description of marine regions and rivers, and regional means ± *SD* of $\delta^{13}C$ values in dissolved inorganic carbon (DIC), ocean dissolved CO_2, POC_{water}, POC_{ice} and POC_{riv}

Marine regions	Description	Regional mean ± *SD* (*n* = number of observations)				References
		$\delta^{13}C$-DIC (‰)	$\delta^{13}C$-CO_2 (‰)	$\delta^{13}C$-POC_{water} (‰)	$\delta^{13}C$-POC_{ice} (‰)	
Outer shelves						
South Iceland	Atlantic influenced	1.3 ± 0.2 (*n* = 560)	−9.3 ± 0.2 (*n* = 560)	−19.9 ± 3.3 (*n* = 4)	NA	Becker et al. (2016); Key et al. (2015); Sarà et al. (2007); Schmittner et al. (2013); Young et al. (2013)
Norwegian sea	Atlantic influenced	1.4 ± 0.4 (*n* = 183)	−10.0 ± 0.4 (*n* = 183)	NA	NA	Bauch et al. (2015); Becker et al. (2016); Key et al. (2015)
Southeast Greenland	Atlantic influenced	1.3 ± 0.1 (*n* = 267)	−9.9 ± 0.2 (*n* = 267)	NA	NA	Becker et al. (2016); Key et al. (2015)
Hudson bay	Atlantic influenced; fresh water influenced	NA	NA	−24.7 ± 1.3 (*n* = 19)	NA	Kuzyk et al. (2010)
Bering sea	Pacific influenced	1.3 ± 0.6 (*n* = 11)	−9.8 ± 0.8 (*n* = 11)	−23.9 ± 0.7 (*n* = 62)	−21.5 ± 0.9 (*n* = 2)	Guo et al. (2004); Lin et al. (2014); Lovvorn et al. (2005); Schmittner et al. (2013); Smith et al. (2002); Young et al. (2013); Zhang et al. (2012)
Gulf of Alaska	Pacific influenced	0.8 ± 0.2 (*n* = 50)	−10.3 ± 0.3 (*n* = 50)	NA	NA	Schmittner et al. (2013); Young et al. (2013)
Inflow shelves						
Barents sea	Atlantic influenced	1.0 ± 0.4 (*n* = 10)	−10.3 ± 0.5 (*n* = 10)	−23.7 ± 1.6 (*n* = 12)	−19.3 ± 2.6 (*n* = 12)	Becker et al. (2016); Søreide et al. (2006); Tamelander et al. (2006, 2009)
Svalbard	Northwest of the Barents sea inflow shelf	1.3 ± 0.4 (*n* = 17)	−10.0 ± 0.4 (*n* = 17)	−24.5 ± 0.9 (*n* = 12)	−23.0 ± 0.7 (*n* = 6)	Becker et al. (2016); Søreide et al. (2006, 2008); Tamelander et al. (2009)
Svalbard fjords	Fresh water influenced; Northwest of the Barents sea inflow shelf	NA	NA	−26.5 ± 1.2 (*n* = 11)	NA	Hallanger et al. (2011); Kuliński et al. (2014)
Chukchi sea	Pacific influenced	0.8 ± 0.5 (*n* = 21)	−10.8 ± 0.7 (*n* = 21)	−22.7 ± 0.1 (*n* = 36)	NA	Bauch et al. (2015); Iken et al. (2010); Ivanov et al. (2012); Zhang et al. (2012)
Interior shelves						
Siberian coast	Fresh water influenced; consists of the East Siberian sea	NA	NA	−24.5 ± 0.5 (*n* = 7)	NA	Iken et al. (2010); Ivanov et al. (2012)
Beaufort sea	Fresh water influenced; North American coast	NA	NA	−26.7 ± 2.2 (*n* = 43)	−26.4 ± 0.5 (*n* = 8)	Connelly et al. (2015); Forest et al. (2010); Iken et al. (2005); O'Brien et al. (2006); Parsons et al. (1989); Zhang et al. (2012)
Outflow shelves						
Fram strait	Northeast of Greenland	1.3 ± 0.4 (*n* = 102)	−10.5 ± 0.4 (*n* = 102)	NA	NA	Bauch et al. (2015); Becker et al. (2016)

(Continues)

TABLE 1 (Continued)

Marine regions	Description	Regional mean ± *SD* (*n* = number of observations) δ^{13}C-DIC (‰)	δ^{13}C-CO_2 (‰)	δ^{13}C-POC_{water} (‰)	δ^{13}C-POC_{ice} (‰)	References
North-East Water Polynia	Recurring mesoscale areas of open water within areas of pack ice (Sakshaug, 2004); Northeast of Greenland	NA	NA	−27.7 ± 0.6 (*n* = 3)	−18.6 ± 0.2 (*n* = 3)	Hobson et al. (1995)
North Water Polynia	Recurring mesoscale areas of open water within areas of pack ice (Sakshaug, 2004); North Baffin bay	NA	NA	−21.9 ± 0.6 (*n* = 30)	−17.7 ± 3.5 (*n* = 20)	Hobson et al. (2002); Tremblay et al. (2006)
Canadian archipelago	Complex straits and channels, terrestrial influence	NA	NA	−25.9 ± 1.4 (*n* = 21)	−18.9 ± 2.3 (*n* = 9)	Roy et al. (2015)
Arctic basins						
Arctic oceanic basins	Includes Amundsen, Nansen and Canadian basins	1.0 ± 0.2 (*n* = 134)	−11.1 ± 0.2 (*n* = 134)	−26.3 ± 1.6 (*n* = 88)	−22.1 ± 2.4 (*n* = 9)	Bauch et al. (2015); Brown et al. (2014); Griffith et al. (2012); Ivanov et al. (2012); Kohlbach et al. (2016); Schubert and Calvert (2001); Søreide et al. (2006); Tamelander et al. (2009); Zhang et al. (2012)
Riverine regions	**Description**			**δ13C-POC_{riv} (‰)**		**References**
Siberian rivers	Includes the large rivers of Lena, Ob and Yenisei and smaller rivers of Kolyma, Indigirka, Yana, Olenek, Vakina and Mezen	NA	NA	−29.5 ± 2.1 (*n* = 237)	NA	Holmes et al. (2018); Lobbes et al. (2000)
North American rivers	Consists of the large rivers of Mackenzie and Yukon, as well as the smaller rivers surrounded the Hudson Bay (Figure 1)	NA	NA	−29.5 ± 1.7 (*n* = 146)	NA	Goni et al. (2000); Holmes et al. (2018); Kuzyk et al. (2010)

Ferguson, 2014), and baleen plates of bowhead whales (*Balaena mysticetus*) from 1950 to 1998 from the Bering and Chukchi Seas (Schell, 2001).

2.2 | Data treatment

We analysed the $\delta^{13}C\text{-}POC_{water}$, $\delta^{13}C\text{-}POC_{ice}$, $\delta^{13}C\text{-}DIC$ and $\delta^{13}C\text{-}CO_2$ values in 17 marine arctic regions (Figure 1; Table 1). In addition, the $\delta^{13}C\text{-}POC_{water}$ values from arctic rivers were grouped into two large riverine regions: the Siberian rivers and the North American rivers (Figure 1; Table 1). The regions were defined based on their location, and physical and biological characteristics. Most of the data were collected in summer and $\delta^{13}C\text{-}POC_{water}$ did not vary seasonally (Appendix S1). In order to achieve the best spatial coverage, data from all seasons and years were combined for the spatial comparison. Regional means were calculated for $\delta^{13}C\text{-}POC_{water}$, $\delta^{13}C\text{-}POC_{ice}$, $\delta^{13}C\text{-}POC_{riv}$, $\delta^{13}C\text{-}DIC$ and $\delta^{13}C\text{-}CO_2$ values (Table 1).

The decadal variation of regional marine $\delta^{13}C\text{-}POC_{water}$ values in arctic regions was assessed where data were available for at least three different years covering a period of at least 5 years. This included the following regions: arctic basins, Beaufort Sea, Chukchi Sea and Bering Sea. Svalbard and the Barents Sea, which had similar $\delta^{13}C\text{-}POC_{water}$ values and $\delta^{13}C\text{-}POC_{ice}$ values (Table S2: ANOVA3 and 4), were combined into the 'European Arctic' to achieve the best temporal coverage. The mean decadal trend (all regions combined) was calculated for $\delta^{13}C\text{-}POC_{water}$, $\delta^{13}C\text{-}POC_{ice}$, $\delta^{13}C\text{-}DIC$ and $\delta^{13}C\text{-}CO_2$ values.

2.3 | Statistical analyses

Quantile–quantile plots of the residuals were plotted to check how closely the data follow a normal distribution (Becker, Chambers, & Wilks, 1988). The data were normally distributed, and therefore, we used a one-way ANOVA (α = 0.005; Zuur, Ieno, & Smith, 2007) followed by post hoc Tukey pairwise comparison tests in R (R Core Team, 2018) to spatially compare: (a) the $\delta^{13}C\text{-}POC_{water}$ data between arctic shelves and arctic basins (ANOVA1), between arctic shelves and arctic rivers (ANOVA2) and between all arctic shelves (ANOVA3); and (b) the $\delta^{13}C\text{-}POC_{ice}$ values between all marine arctic regions where data were available (ANOVA4). We used a two-way ANOVA followed by post hoc Tukey pairwise comparison test to compare the $\delta^{13}C\text{-}POC_{ice}$ values with $\delta^{13}C\text{-}POC_{water}$ values (factor 'origin') for regions (factor 'region') where both data sets were available (ANOVA5). Arctic regions with less than five data points were excluded from statistical analyses. Relevant *p*-values of the post hoc Tukey pairwise comparison tests following ANOVA1 to 5 are shown in Table S2.

We applied linear models in R (R Core Team, 2018) to quantitatively assess the latitudinal gradient in $\delta^{13}C\text{-}DIC$, $\delta^{13}C\text{-}CO_2$ and $\delta^{13}C\text{-}POC_{water}$ values, and the temporal trends in $\delta^{13}C$ values of marine POC_{water}, POC_{ice}, DIC, dissolved CO_2 and arctic marine mammals. The significance and robustness of the linear models were assessed based on the *p*-values of the slopes and intercepts, the R^2, the *F*-values and *df* (Table S3; Zuur et al., 2007).

3 | RESULTS

3.1 | Spatial trends in the $\delta^{13}C$ of the baseline

The Atlantic and Pacific waters entering the Arctic via the South Iceland and Norwegian Sea, and Gulf of Alaska and Bering Sea, respectively (Figure 1; Table 1), had similar $\delta^{13}C\text{-}CO_2$ values and were depleted by up to 2‰ relative to the $\delta^{13}C\text{-}CO_2$ values in the arctic basins (Table 1). We observed a significant depletion in $\delta^{13}C\text{-}CO_2$ and $\delta^{13}C\text{-}POC_{water}$ values with increasing latitude (Figure 2). $\delta^{13}C\text{-}DIC$ did not vary with latitude (Figure 2a).

We analysed the $\delta^{13}C\text{-}POC_{water}$, $\delta^{13}C\text{-}POC_{ice}$ and $\delta^{13}C\text{-}CO_2$ values in 17 marine arctic regions (Figure 1; Table 1). $\delta^{13}C$ values of POC_{water} varied significantly between arctic regions (Figure 3a). POC_{water} from arctic shelves was significantly enriched in ^{13}C compared to POC_{water} from arctic basins and POC_{riv} (Figure 3a; Table S2: ANOVA1 and ANOVA2). The $\delta^{13}C\text{-}POC_{water}$ values were ^{13}C depleted in arctic shelves (Beaufort Sea, Svalbard fjords, Canadian archipelago and the Hudson Bay) influenced by fresh water (Table 1; Figure 1) relative to the inflow (Chukchi Sea and Barents Sea) shelves and the North Water Polynya (Figure 3a; Table S2: ANOVA3).

$\delta^{13}C\text{-}POC_{ice}$ values followed the same regional trend as $\delta^{13}C\text{-}POC_{water}$ values, with $\delta^{13}C\text{-}POC_{ice}$ values enriched in ^{13}C in the inflow and outflow shelves (Barents Sea, North Water Polynya) compared to the interior shelf Beaufort Sea and the arctic basins (Figure 3b; Table S2: ANOVA4).

3.2 | Comparison between $\delta^{13}C$ of POC_{ice} and POC_{water}

Generally, $\delta^{13}C$ values of POC_{ice} were significantly ^{13}C-enriched compared to those of POC_{water} ($p < .005$; Table S2: ANOVA5), with $\delta^{13}C\text{-}POC_{water}$ being enriched by 4.4‰ in the Barents Sea, by 4.2‰ in the North Water Polynya and by 7.0‰ in the Canadian archipelago (Table 1). There were no significant differences between POC_{ice} and POC_{water} in the Svalbard region, the arctic basins and the Beaufort Sea (Table S2: ANOVA5). $\delta^{13}C\text{-}POC_{ice}$ values were highly variable in most of the arctic regions (Figure 3b).

3.3 | Temporal trends in the $\delta^{13}C$ of the baseline and Arctic marine mammals

In all arctic regions combined, $\delta^{13}C\text{-}DIC$ (1977–2014), $\delta^{13}C\text{-}CO_2$ (1977–2014) and $\delta^{13}C\text{-}POC_{water}$ (1986–2013) values became significantly ^{13}C depleted by 0.011 ± 0.001, 0.011 ± 0.002 and 0.149 ± 0.020‰ per year respectively (Figure 4a; Table 2). The temporal trends in $\delta^{13}C\text{-}POC_{water}$ values were statistically significant in the Beaufort Sea (−0.117 ± 0.033‰ per year; 1987–2013) and in the arctic basins (−0.256 ± 0.057‰ per year; 1997–2012) and not statistically significant in the European Arctic, Bering Sea and Chukchi Sea (Figure 4b; Table 2; Table S3). The temporal trend in $\delta^{13}C\text{-}POC_{ice}$ values was not significant (Figure 4d; Table 2; Table S3). The $\delta^{13}C$ values in the teeth of northern fur seals, ringed seals and beluga whales, and in baleen

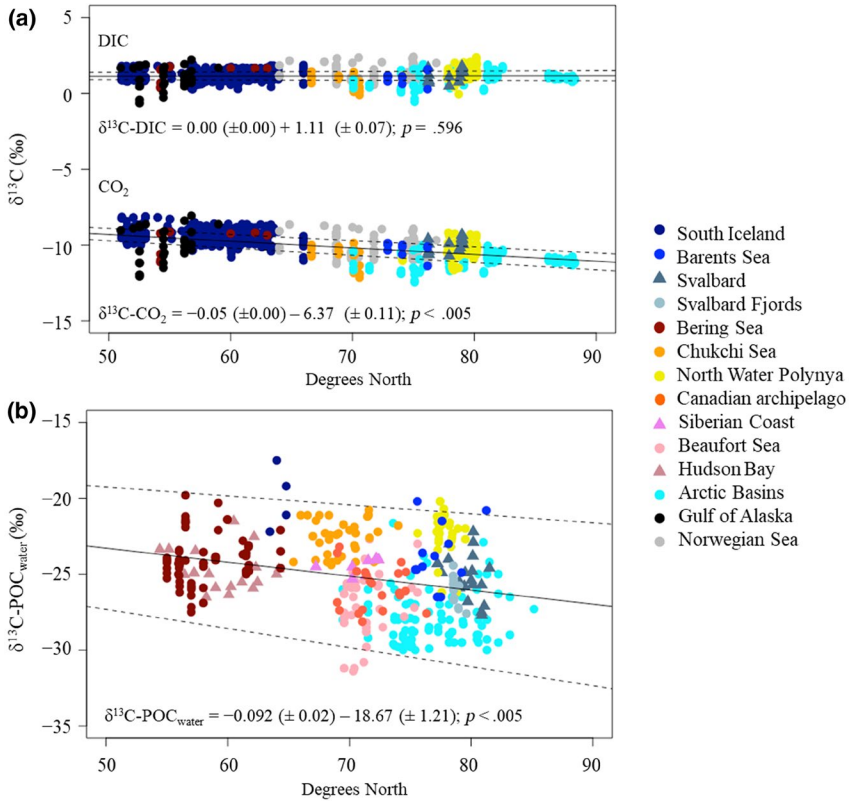

FIGURE 2 Stable carbon isotope values ($\delta^{13}C$, in ‰) of (a) marine dissolved inorganic carbon (DIC; n = 1,333) and marine dissolved CO_2 (n = 1,333) and (b) marine POC_{water} (n = 354) in the surface waters with latitude; each dot is a single data point; the solid line represents the slope of the linear regression; dashed lines indicate the 95% confidence interval of the linear regression. The equations and p-values of the linear regressions are shown on the figure. Trends are considered significant when p < .005

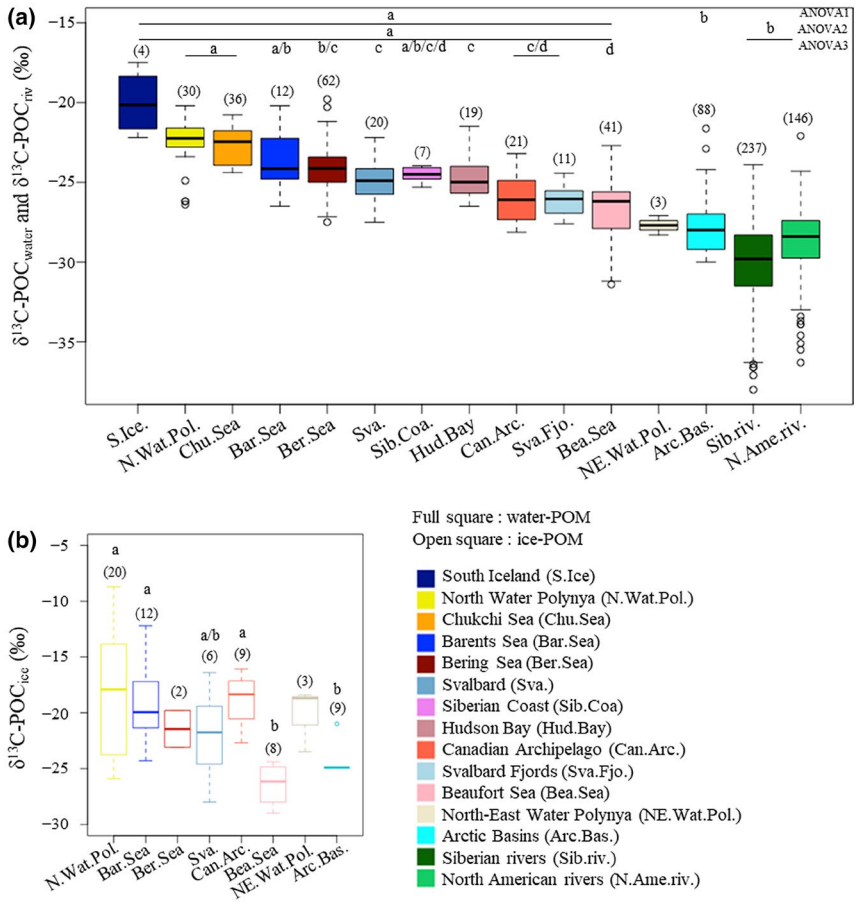

FIGURE 3 Regional stable carbon isotope values ($\delta^{13}C$, in ‰) of (a) POC_{water} and POC_{riv} and (b) POC_{ice}; Numbers of observations are shown as number on top of the boxplots. Results of post hoc Tukey tests following (a) ANOVA1 to ANOVA3 and (b) ANOVA4 are expressed as letters on top of the boxplots. Different letters indicate significant differences (p < .005) between regions. The p-values of each test are shown in Table S2

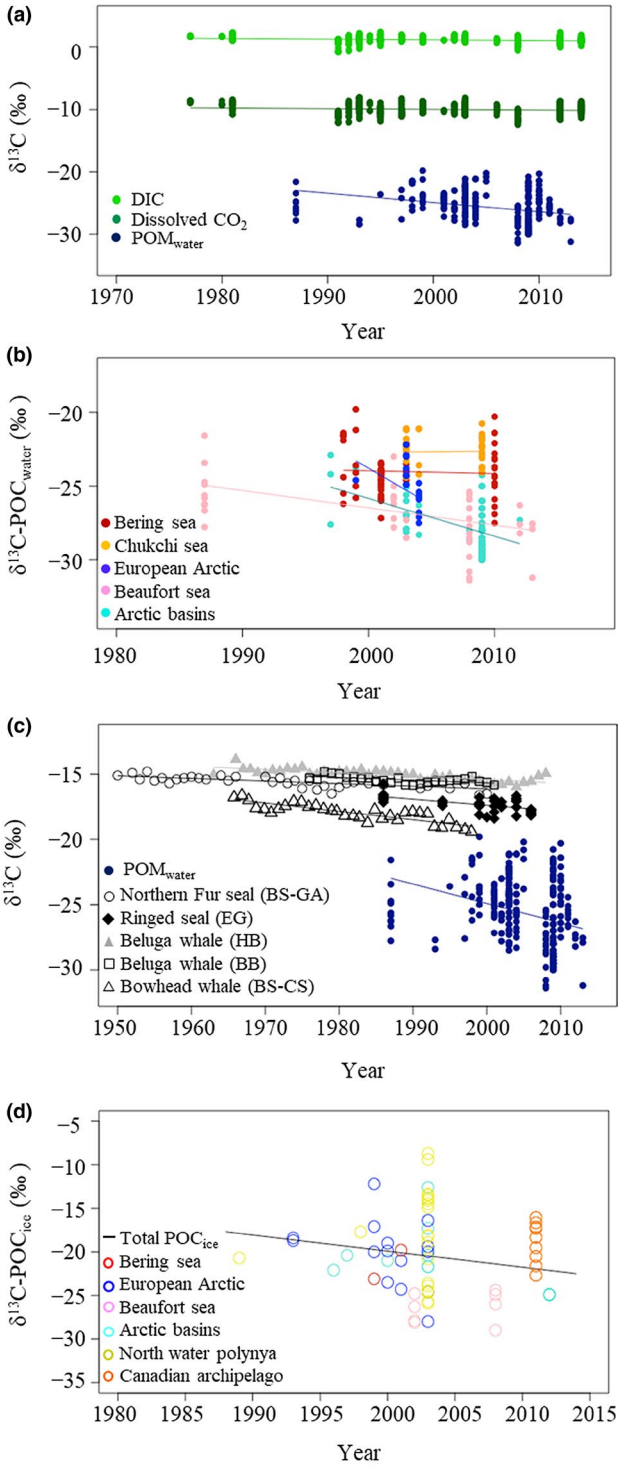

FIGURE 4 Decadal trend in $\delta^{13}C$ values of: (a) dissolved inorganic carbon (DIC), dissolved CO_2 and POC_{water}, (b) POC_{water} for each arctic region, (c) POC_{water} and arctic marine mammal tissues and (d) POC_{ice} for each arctic region. BS, Bering sea; CS, Chukchi sea; EG, East Greenland; GA, Gulf of Alaska; HB, Hudson bay. Results of the linear models can be found in Table 2 and Table S3. Number of observations can be found in Table 2

plates of bowhead whales were significantly depleted in ^{13}C with time (Figure 4c; Table 2). The decline in $\delta^{13}C$ values in teeth ranged from 0.020 ± 0.003‰ per year in northern fur seals from the Gulf of Alaska (1950–2000) to −0.046 ± 0.012‰ per year in ringed seals from East Greenland (1986–2006; Table 2). The $\delta^{13}C$ in the baleen plates of bowhead whales from the Bering and Chukchi Seas significantly decreased by 0.064 ± 0.010‰ per year (1965–1998; Table 2). The decline in $\delta^{13}C$ values of POC_{water} and marine mammals was larger than decline in $\delta^{13}C$-DIC and $\delta^{13}C$-CO_2 values (0.011‰ per year, this study). Details of the linear models are shown in Table S3.

4 | DISCUSSION

4.1 | Ice versus water

The ^{13}C-enrichment in POC_{ice} compared to POC_{water} in arctic regions has been observed previously and attributed to carbon limitation around ice algae within sea ice (Budge et al., 2008; Hobson et al., 2002; Søreide et al., 2006; Wang et al., 2014). The termination of the spring ice edge bloom can cause ^{13}C at the base of the food web to be altered when ^{13}C-enriched ice algae were added to ^{13}C-depleted pelagic phytoplankton (Søreide et al., 2006). The similarity in the $\delta^{13}C$-POC_{ice} and $\delta^{13}C$-POC_{water} values in some regions (see Section 2.2) and the high intra-regional variability of the $\delta^{13}C$-POC_{ice} values may be explained by differences in ice porosity, allowing replenishment of DIC from water to ice (Thomas & Papadimitriou, 2011). $\delta^{13}C$-POC_{ice} values were likely to have been influenced by light availability and the high bacterial activity in sea ice compared to open water (Wang et al., 2014). Thus, variation in the sampling month for sea ice might also contribute to the high variability in $\delta^{13}C$-POC_{ice}. This highlights that caution is required when using bulk $\delta^{13}C$ values of POC_{ice} and POC_{water} to distinguish between open water versus ice-dependent food webs in the Arctic (Søreide et al., 2006). The challenge of disentangling the contribution of carbon derived from sympagic production to the food web has been successfully resolved by using compound-specific stable isotope analyses (e.g. $\delta^{13}C$ values of fatty acids; Graham, Oxtoby, Wang, Budge, & Wooller, 2014; Oxtoby, Budge, Iken, Brien, & Wooller, 2016; Oxtoby et al., 2017; Wang et al., 2015).

4.2 | Spatial trends

Spatial trends in the $\delta^{13}C$ values of POC_{water} and POC_{ice} were similar, implying that they were influenced by the same environmental drivers within specific regions of the Arctic Ocean.

Low temperature, high wind speed and high productivity enhance the atmospheric CO_2 uptake by the Arctic Ocean (Takahashi et al., 2002), driving strong latitudinal gradients in concentration and $\delta^{13}C$ values of oceanic CO_2 with ^{13}C-CO_2 being more depleted in the Arctic Ocean (≈−10‰, Young et al., 2013; −10.2 ± 0.5‰, this study) relative to the tropics (≈−7 ‰, Young et al., 2013). In the marine environment, more than 90% of DIC is composed of bicarbonate ions (HCO_3^-; Boutton, 1991). Fractionation between HCO_3^- and atmospheric CO_2 increases in cold water (Zhang, Quay, & Wilbur, 1995) leading

TABLE 2 Slopes ± *SD* and *p*-values of the decadal linear models of $\delta^{13}C$ values in dissolved inorganic carbon (DIC), ocean dissolved CO_2, POC_{water}, POC_{ice} and arctic marine mammal tissues

	Slope ± *SD*	*p*-value	Time period	Number of observations
POC_{water}				
Beaufort sea	**−0.117 ± 0.033**	**<.005**	**1987–2013**	**71**
European Arctic	−0.499 ± 0.265	.076	1999–2004	20
Arctic basins	**−0.256 ± 0.057**	**<.005**	**1997–2012**	**87**
Bering sea	−0.019 ± 0.046	.679	1998–2010	62
Chukchi sea	+0.008 ± 0.071	.906	2003–2009	36
All data	**−0.149 ± 0.020**	**<.005**	**1987–2013**	**311**
POC_{ice}				
All data	−0.185 ± 0.106	.084	1993–2012	69
DIC				
All data	**−0.011 ± 0.001**	**<.005**	**1977–2014**	**1,333**
CO_2				
All data	**−0.011 ± 0.002**	**<.005**	**1977– 2014**	**1,333**
Marine mammals				
Northern fur seal—Bering sea/Gulf of Alaska	**−0.020 ± 0.003**	**<.005**	**1950–2000**	**40**
Ringed seal—East Greenland	**−0.046 ± 0.012**	**<.005**	**1986–2006**	**36**
Beluga whale—Hudson Bay	**−0.026 ± 0.003**	**<.005**	**1963–2008**	**42**
Beluga whale—Baffin Bay	**−0.021 ± 0.006**	**<.005**	**1976–2001**	**26**
Bowhead whale—Bering sea/Chukchi sea	**−0.064 ± 0.007**	**<.005**	**1965–1998**	**34**

Note: Lines in bold are considered significant ($p < .005$).
Detailed statistics of the linear models are shown in Table S3.

to ^{13}C enrichment of $\delta^{13}C$-DIC values with increasing latitude (Tagliabue & Bopp, 2008), as observed in this study (Figure 2a). $\delta^{13}C$-POC_{water} values became ^{13}C-depleted with increasing latitude (Figure 2b, this study; Goericke & Fry, 1994; McMahon et al., 2013b), reflecting the latitudinal trend in $\delta^{13}C$-CO_2 values as well as multiple additional factors, including temperature, phytoplankton growth rates, bacterial activity and isotopic fractionation, that also vary with latitude (Fouilland et al., 2018; Thomas, Kremer, Klausmeier, & Litchman, 2012; Young et al., 2013). A latitudinal trend in $\delta^{13}C$ values of zooplankton was observed in the western Arctic (i.e. Bering and Chukchi Sea; Dunton, Saupe, Golikov, Schell, & Schonberg, 1989), demonstrating the transfer of this $\delta^{13}C$ signature to the next trophic level.

The two orders of magnitude difference in phytoplankton production between the nutrient-rich arctic shelves and the ice covered nutrient depleted arctic basin (Sakshaug, 2004) may partially explain the relatively large difference in $\delta^{13}C$-POC_{water} values of 2.3‰ between the arctic shelf (−24.0 ± 1.2‰) and arctic basins (−26.3 ± 1.6‰). High rates of primary production cause ^{13}C enrichment of the $\delta^{13}C$-POC values (Boutton, 1991; McMahon, Hamady, & Thorrold, 2013a). The highly productive Bering Sea and Barents Sea account for up to two-thirds of the total arctic phytoplankton production (Sakshaug, 2004). Advection of nutrients from the arctic outflow and early exposure to sunlight enhance phytoplankton productivity in the North Water Polynya (Sakshaug, 2004). In contrast, high turbidity and strong stratification caused by fresh water inflow from rivers onto the interior shelves reduce light and restrict phytoplankton production (Dittmar & Kattner, 2003). Lower phytoplankton productivity in the river influenced Beaufort Sea and Siberian Coast, as well as the North-East Water Polynia (Sakshaug, 2004) could explain the depleted $\delta^{13}C$-POC values observed in these regions relative to the more productive regions.

The ^{13}C depletion in $\delta^{13}C$-POC_{water} values observed in the interior shelves, Svalbard fjords, Hudson Bay and Canadian archipelago compared to other arctic shelf regions likely reflects the contribution of ^{13}C-depleted terrestrially derived POC (Boutton, 1991) from rivers, coastal erosion and glacial streams. Seventy-two arctic rivers supplying 40% of the total freshwater input from the surrounding continents of Eurasia and North America enter the Arctic Ocean via the interior shelves of the Siberian coast and the Beaufort Sea (Table 1; Figure 1) at a rate of 2,500–4,200 km^3/year (Haine et al., 2015). In addition, terrestrially derived POC input resulting from coastal erosion may be equal to or larger than input from river discharge in some regions, for instance along the Siberian coast (Rachold et al., 2000). Finally, glacial fjords on Svalbard are fed with freshwater by large glaciers and streams with the highest freshwater inflow in summer during ice and snow

melt (Cottier et al., 2005). Any temporal alteration of the riverine inputs or the drainage basins would likely alter the δ^{13}C-POC$_{water}$ values in the interior shelves and subsequently alter the base of the food web.

4.3 | Temporal trends at the baseline

The increasing concentration of anthropogenic CO_2, known as the Suess effect, is predicted to decrease the oceanic δ^{13}C-DIC values by an average of 0.017‰ per year, with high spatial variability from 0‰ per year in the Southern Ocean to 0.024‰ per year in the subtropical gyres (Tagliabue & Bopp, 2008). In the Arctic Ocean, the δ^{13}C-DIC values are predicted to decrease by 0.006‰ to 0.008‰ per year (Tagliabue & Bopp, 2008). We observed a decreasing trend in δ^{13}C-DIC values of 0.011 ± 0.001‰ per year from 1977 to 2014 across all arctic regions, which is larger than the predicted trend. Although CO_2 represents less than 0.5% of the total DIC pool, it is the only component that is exchangeable with the atmosphere. In polar regions, especially the Arctic Ocean, the decline in sea ice has led to an expansion of open water (Arrigo & van Dijken, 2015). This facilitates atmospheric exchange and enhances the dissolved CO_2 concentration (Yamamoto et al., 2012) resulting in an additional ^{13}C depletion of δ^{13}C-CO_2 values (Rau et al., 1992) which may explain the larger decrease in δ^{13}C-CO_2 values (0.011 ± 0.002‰ per year) and in turn the larger decrease in δ^{13}C-DIC values (0.011 ± 0.001‰ per year) in the Arctic Ocean compared to the predicted decrease of 0.006–0.008‰ per year (Tagliabue & Bopp, 2008).

The decadal decline in δ^{13}C-POC$_{water}$ values (1987–2013) was more than 10 times larger than the trend in δ^{13}C values of CO_2 (or DIC) implying that other factors are influencing the δ^{13}C values in POC in the Arctic Ocean. Since the mid-1990s, sea ice extent has declined by 8.3 ± 0.6% per decade across the entire Arctic (Comiso, 2012). Sea ice algae are up to 7 ‰ enriched in ^{13}C relative to pelagic phytoplankton (this study) and a decline in sea ice could decrease the contribution of ice algal biomass to total productivity and reduce the total mean δ^{13}C values of POC$_{water}$. For example, the open water area of the Barents sea has increased by 15,789 km^2 or 1.3% per year between 1998 and 2012, alongside a 28% increase in net primary production over the same time period (Arrigo & van Dijken, 2015). Assuming distinct end members for δ^{13}C-POC$_{water}$ (−25.0 ± 1.7‰) and δ^{13}C-POC$_{ice}$ (−20.0 ± 1.3‰) values, sea ice decline would cause the entire pool of δ^{13}C-POC values to decrease by 0.06 ± 0.15‰ per year. Additionally, the photosynthetic isotopic fractionation factor for phytoplankton in the Arctic Ocean has increased by 0.045‰ per year since the 1960s, compared to a global average of 0.022‰ per year (Young et al., 2013). The combined effect of a decline in ice algae (0.06 ± 0.15‰ per year, this study), increase in fractionation factor (0.045‰ per year, Young et al., 2013) and Suess effect (i.e. dissolved CO_2, 0.011 ± 0.001‰ per year, this study) could potentially cause the δ^{13}C-POC values to decrease by 0.116 ± 0.15‰ per year, which is of the same order of magnitude as the observed annual decrease in δ^{13}C-POC$_{water}$ values in the whole Arctic (0.149 ± 0.028‰ per year) and in the Beaufort Sea (0.126 ± 0.020‰ per year; Table 2). In support of this argument, the difference between the temporal trend or slope in δ^{13}C-CO_2 and δ^{13}C-POC values (Figure 4a) increased by 0.138 ± 0.028‰ per year in agreement with the sum of the contributions from a change in ice (0.06 ± 0.15‰ per year), fractionation (0.045‰ per year) and Suess effect (0.011 ± 0.001‰ per year) influencing δ^{13}C-POC$_{water}$ values.

Other factors contributing to the decline in δ^{13}C-POC values in the Arctic Ocean include river run-off, coastal erosion, primary production and bacterial activity. Increased riverine run-off (Haine et al., 2015) and coastal erosion (Jones et al., 2009; Mars & Houseknecht, 2007) resulting from ongoing climate change in the Arctic could contribute to the decline in δ^{13}C-POC values by adding ^{13}C-deplete terrestrially derived material to the marine POC pool. Changes in primary productivity will also influence the δ^{13}C-POC values. For example, the decline of δ^{13}C values in Bowhead whales from the Bering/Chukchi Sea was interpreted by Schell (2000) as reflecting a 30%–40% decrease in seasonal primary productivity in the Bering Sea over the last 30 years. Increasing bacterial activity with increasing temperature (Vaqué et al., 2019; Vernet, Richardson, Metfies, Nöthig, & Peeken, 2017) and dissolved CO_2 concentration (Grossart, Allgaier, Passow, & Riebesell, 2006) in the Arctic may also influence the δ^{13}C values of POC.

4.4 | Implications for food web

The reliability of stable carbon isotopes in deciphering the provenance of feeding or migratory patterns of consumers is heavily dependent on knowledge of δ^{13}C values at the base of the food web. Maps that convey the geographical and temporal trends of δ^{13}C values in the baseline, termed isoscapes (Bowen et al., 2009; Graham et al., 2010), have become a necessity for interpreting trophic structure using δ^{13}C (or δ^{15}N) values (Hansen, Hedeholm, Sünksen, Christensen, & Grønkjær, 2012; Newsome, Clementz, & Koch, 2010). Although isoscapes have been constructed for the atmosphere (Bowen et al., 2009), terrestrial environment (Bowen & West, 2008; Firmin, 2016) and the Atlantic and Pacific Oceans (Graham et al., 2010; McMahon et al., 2013b), this study provides a first view of δ^{13}C-POC values or carbon isoscape of the Arctic Ocean. We found spatially heterogeneous and temporally evolving δ^{13}C values in the POC pool, which has ramifications for the study of food webs in space and time.

Previous studies have noted that the decline in δ^{13}C in Arctic marine mammals is larger than the Suess effect alone (e.g. Matthews & Ferguson, 2014; Newsome et al., 2007), but the lack of δ^{13}C baseline information prevented these authors from disentangling the driving factors (Cullen, Rosenthal, & Falkowski, 2001; Schell, 2000, 2001). Generally, the temporal decline in the δ^{13}C values in marine mammals was larger than in δ^{13}C-DIC and δ^{13}C-CO_2 values (both of −0.011 ± 0.001‰ per year) but smaller than the decline observed in δ^{13}C-POC$_{water}$ values (−0.149 ± 0.028‰ per year). The δ^{13}C signature in phytoplankton or a consumer represents an average ratio related to the lifetime of the organism and tissue turnover time (Vander Zanden, Clayton, Moody, Solomon, & Weidel, 2015). Previous studies have shown that the seasonal variation in δ^{13}C values of POC was higher than in higher trophic levels

reflecting the strong seasonal growth cycle of phytoplankton and shorter time period over which they integrate carbon (O'reilly, Hecky, Cohen, & Plisnier, 2002). In contrast, consumers from zooplankton to predators are long-lived and thus integrate $\delta^{13}C$ values over their seasonal foraging and migratory routes (Aubail et al., 2010; Schell, Saupe, & Haubenstock, 1989) with the time of integration depending on the tissue type (Vander Zanden et al., 2015) or the animals' lifetime (O'reilly et al., 2002). The effect of yearly averaging of the $\delta^{13}C$ values in marine mammal teeth and baleen plates used to reconstruct decadal trends may have reduced the larger, short-lived variation observed in $\delta^{13}C$-POC values mainly representing summer in this study. The gradual linear decline in $\delta^{13}C$ values in arctic seals and whales likely reflects alterations to the $\delta^{13}C$-POC values. A change in diet, for example, a shift towards foraging closer to freshwater (Nelson et al., 2018), or more pelagic feeding habits (Aubail et al., 2010), may also contribute to the temporal decline in $\delta^{13}C$ values observed in predators.

This study demonstrates that to disentangle factors driving variation in the $\delta^{13}C$ values in a consumer, it is vital to know the spatial heterogeneity and temporal evolution of $\delta^{13}C$ values of the baseline in the Arctic Ocean in order to avoid inaccurate interpretation of changes in food web structures. Some studies have attempted to correct the $\delta^{13}C$ values in arctic marine mammals for the Suess effect using modelled and predicted values for large geographical regions, prior to interpreting decadal trends in $\delta^{13}C$ values (Carroll, Horstmann-Dehn, & Norcross, 2013; Misarti et al., 2009; Nelson et al., 2018). However, the Suess effect varies spatially (Tagliabue & Bopp, 2008), and therefore, local values should be used for this correction. For example, the Suess effect in the Arctic Ocean (0.011 ± 0.001‰ per year, this study) differs from the predicted modelled values (0.006–0.008‰ per year; Tagliabue & Bopp, 2008), implying that other factors, such as the loss of sea ice, are accelerating the influence of anthropogenic CO_2 in the Arctic. In addition, the decline in $\delta^{13}C$-POC values, representing the base of the food web, is larger than the decline in $\delta^{13}C$-DIC values (this study). This suggests that interpretation about diet shift should be done after consideration of temporal trends in $\delta^{13}C$-POC values and not only in $\delta^{13}C$-DIC (Suess effect). These results also highlight the importance of considering time-averaging effects when studying different trophic levels and/or tissues having, respectively, variable lifetime and turnover time. Insight from this study has direct implications for how we interpret changes in $\delta^{13}C$ values in consumers, especially in environments experiencing rapid change.

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REFERENCES

Arrigo, K. R., & van Dijken, G. L. (2015). Continued increases in Arctic Ocean primary production. *Progress in Oceanography*, *136*, 60–70. https://doi.org/10.1016/j.pocean.2015.05.002

Aubail, A., Dietz, R., Rigét, F., Simon-Bouhet, B., & Caurant, F. (2010). An evaluation of teeth of ringed seals (*Phoca hispida*) from Greenland as a matrix to monitor spatial and temporal trends of mercury and stable isotopes. *Science of the Total Environment*, *408*(21), 5137–5146. https://doi.org/10.1016/j.scitotenv.2010.07.038

Bauch, D., Polyak, L., & Ortiz, J. (2015). A baseline for the vertical distribution of the stable carbon isotopes of dissolved inorganic carbon ($\delta^{13}C$-DIC) in the Arctic Ocean. *Arktos*, *1*(1), 15. https://doi.org/10.1007/s41063-015-0001-0

Becker, M., Andersen, N., Erlenkeuser, H., Humphreys, M. P., Tanhua, T., & Körtzinger, A. (2016). An internally consistent dataset of $\delta^{13}C$-DIC in the North Atlantic Ocean–NAC13v1. *Earth System Science Data*, *8*(2), 559–570. https://doi.org/10.5194/essd-8-559-2016

Becker, R. A., Chambers, J. M., & Wilks, A. R. (1988). *The new S language: A programming environment for data analysis and graphics*. Pacific Grove, CA: Wadsworth & Brooks/Cole Advanced Books & Software.

Bird, C. S., Veríssimo, A., Magozzi, S., Abrantes, K. G., Aguilar, A., Al-Reasi, H., … Trueman, C. N. (2018). A global perspective on the trophic geography of sharks. *Nature Ecology & Evolution*, *2*(2), 299–305. https://doi.org/10.1038/s41559-017-0432-z

Boutton, T. W. (1991). Stable carbon isotope ratios of natural materials: II. Atmospheric, terrestrial, marine and freshwater environments. In D. C. Coleman & B. Fry (Eds.), *Carbon isotope techniques* (pp. 173–186). San Diego, CA: Academic Press.

Bowen, G. J., & West, J. B. (2008). Isotope landscapes for terrestrial migration research. *Terrestrial Ecology*, *2*, 79–105. https://doi.org/10.1016/s1936-7961(07)00004-8

Bowen, G. J., West, J. B., Vaughn, B. H., Dawson, T. E., Ehleringer, J. R., Fogel, M. L., … Still, C. J. (2009). Isoscapes to address large-scale earth science challenges. *EOS, Transactions American Geophysical Union*, *90*(13), 109–110. https://doi.org/10.1029/2009EO130001

Brown, K. A., McLaughlin, F., Tortell, P. D., Varela, D. E., Yamamoto-Kawai, M., Hunt, B., & Francois, R. (2014). Determination of particulate organic carbon sources to the surface mixed layer of the Canada Basin, Arctic Ocean. *Journal of Geophysical Research: Oceans*, *119*(2), 1084–1102. https://doi.org/10.1002/2013JC009197

Budge, S., Wooller, M., Springer, A., Iverson, S. J., McRoy, C., & Divoky, G. (2008). Tracing carbon flow in an arctic marine food web using fatty acid-stable isotope analysis. *Oecologia*, *157*(1), 117–129. https://doi.org/10.1007/s00442-008-1053-7

Burkhardt, S., Riebesell, U., & Zondervan, I. (1999). Stable carbon isotope fractionation by marine phytoplankton in response to daylength, growth rate, and CO_2 availability. *Marine Ecology Progress Series*, *184*, 31–41. https://doi.org/10.3354/meps184031

Carmack, E., Polyakov, I., Padman, L., Fer, I., Hunke, E., Hutchings, J., … Winsor, P. (2015). Toward quantifying the increasing role of oceanic heat in sea ice loss in the New Arctic. *Bulletin of the American Meteorological Society*, *96*(12), 2079–2105. https://doi.org/10.1175/bams-d-13-00177.1

Carmack, E., & Wassmann, P. (2006). Food webs and physical–biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. *Progress in Oceanography*, *71*(2), 446–477. https://doi.org/10.1016/j.pocean.2006.10.004

Carroll, S. S., Horstmann-Dehn, L., & Norcross, B. L. (2013). Diet history of ice seals using stable isotope ratios in claw growth bands. *Canadian Journal of Zoology*, *91*(4), 191–202. https://doi.org/10.1139/cjz-2012-0137

Cassar, N., Laws, E. A., Bidigare, R. R., & Popp, B. N. (2004). Bicarbonate uptake by Southern Ocean phytoplankton. *Global Biogeochemical Cycles*, *18*(2). https://doi.org/10.1029/2003GB002116

Comiso, J. C. (2012). Large decadal decline of the arctic multiyear ice cover. *Journal of Climate*, *25*(4), 1176–1193. https://doi.org/10.1175/jcli-d-11-00113.1

Connelly, T. L., McClelland, J. W., Crump, B. C., Kellogg, C. T., & Dunton, K. H. (2015). Seasonal changes in quantity and composition of suspended particulate organic matter in lagoons of the Alaskan Beaufort Sea. *Marine Ecology Progress Series*, *527*, 31–45. https://doi.org/10.3354/meps11207

Cottier, F., Tverberg, V., Inall, M., Svendsen, H., Nilsen, F., & Griffiths, C. (2005). Water mass modification in an Arctic fjord through cross-shelf exchange: The seasonal hydrography of Kongsfjorden, Svalbard. *Journal of Geophysical Research*, *110*. https://doi.org/10.1029/2004jc002757

Cullen, J. T., Rosenthal, Y., & Falkowski, P. G. (2001). The effect of anthropogenic CO_2 on the carbon isotope composition of marine phytoplankton. *Limnology and Oceanography*, *46*(4), 996–998. https://doi.org/10.4319/lo.2001.46.4.0996

Dittmar, T., & Kattner, G. (2003). The biogeochemistry of the river and shelf ecosystem of the Arctic Ocean: A review. *Marine Chemistry*, *83*(3–4), 103–120. https://doi.org/10.1016/S0304-4203(03)00105-1

Dunton, K. H., Saupe, S. M., Golikov, A. N., Schell, D. M., & Schonberg, S. V. (1989). Trophic relationships and isotopic gradients among arctic and subarctic marine fauna. *Marine Ecology Progress Series*, *56*, 89–97. https://doi.org/10.3354/meps056089

Firmin, S. M. (2016). *The spatial distribution of terrestrial stable carbon isotopes in North America, and the impacts of spatial and temporal resolution on static ecological models*. University of Denver.

Forest, A., Galindo, V., Darnis, G., Pineault, S., Lalande, C., Tremblay, J.-É., & Fortier, L. (2010). Carbon biomass, elemental ratios (C:N) and stable isotopic composition ($\delta^{13}C$, $\delta^{15}N$) of dominant calanoid copepods during the winter-to-summer transition in the Amundsen Gulf (Arctic Ocean). *Journal of Plankton Research*, *33*(1), 161–178. https://doi.org/10.1093/plankt/fbq103

Fouilland, E., Floc'h, E. L., Brennan, D., Bell, E. M., Lordsmith, S. L., McNeill, S., … Leakey, R. J. G. (2018). Assessment of bacterial dependence on marine primary production along a northern latitudinal gradient. *FEMS Microbiology Ecology*, *94*(10), fiy150. https://doi.org/10.1093/femsec/fiy150

Fry, B., Anderson, R. K., Entzeroth, L., Bird, J. L., & Parker, P. L. (1984). ^{13}C enrichment and oceanic food web structure in the northwestern Gulf of Mexico. *Contributions in Marine Science*, *27*, 49–63.

Fry, B., & Sherr, E. B. (1989). $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. In P. W. Rundel, J. R. Ehleringer, & K. A. Nagy (Eds.), *Stable isotopes in ecological research* (pp. 196–229). New York, NY: Springer.

Goericke, R., & Fry, B. (1994). Variations of marine plankton $\delta^{13}C$ with latitude, temperature, and dissolved CO_2 in the world ocean. *Global Biogeochemical Cycles*, *8*(1), 85–90. https://doi.org/10.1029/93gb03272

Goni, M. A., Yunker, M. B., Macdonald, R. W., & Eglinton, T. I. (2000). Distribution and sources of organic biomarkers in arctic sediments from the Mackenzie River and Beaufort Shelf. *Marine Chemistry*, *71*(1–2), 23–51. https://doi.org/10.1016/S0304-4203(00)00037-2

Graham, B. S., Koch, P. L., Newsome, S. D., McMahon, K. W., & Aurioles, D. (2010). Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In J. B. West, G. J. Bowen, T. E. Dawson, & K. P. Tu (Eds.), *Isoscapes* (pp. 299–318). Dordrecht, the Netherlands: Springer.

Graham, C., Oxtoby, L., Wang, S. W., Budge, S. M., & Wooller, M. J. (2014). Sourcing fatty acids to juvenile polar cod (*Boreogadus saida*) in the Beaufort Sea using compound-specific stable carbon isotope analyses. *Polar Biology*, *37*(5), 697–705. https://doi.org/10.1007/s00300-014-1470-5

Griffith, D. R., McNichol, A. P., Xu, L., McLaughlin, F. A., Macdonald, R. W., Brown, K. A., & Eglinton, T. I. (2012). Carbon dynamics in the western Arctic Ocean: Insights from full-depth carbon isotope profiles of DIC, DOC, and POC. *Biogeosciences*, *9*(3), 1217–1224. https://doi.org/10.5194/bg-9-1217-2012

Grossart, H.-P., Allgaier, M., Passow, U., & Riebesell, U. (2006). Testing the effect of CO_2 concentration on the dynamics of marine heterotrophic bacterioplankton. *Limnology and Oceanography*, *51*(1), 1–11. https://doi.org/10.4319/lo.2006.51.1.0001

Guo, L., Tanaka, T., Wang, D., Tanaka, N., & Murata, A. (2004). Distributions, speciation and stable isotope composition of organic matter in the southeastern Bering Sea. *Marine Chemistry*, *91*(1–4), 211–226. https://doi.org/10.1016/j.marchem.2004.07.002

Haine, T. W. N., Curry, B., Gerdes, R., Hansen, E., Karcher, M., Lee, C., … Woodgate, R. (2015). Arctic freshwater export: Status, mechanisms, and prospects. *Global and Planetary Change*, *125*, 13–35. https://doi.org/10.1016/j.gloplacha.2014.11.013

Hallanger, I. G., Ruus, A., Warner, N. A., Herzke, D., Evenset, A., Schøyen, M., … Borgå, K. (2011). Differences between Arctic and Atlantic fjord systems on bioaccumulation of persistent organic pollutants in zooplankton from Svalbard. *Science of the Total Environment*, *409*(14), 2783–2795. https://doi.org/10.1016/j.scitotenv.2011.03.015

Hansen, J. H., Hedeholm, R. B., Sünksen, K., Christensen, J. T., & Grønkjær, P. (2012). Spatial variability of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios in an Arctic marine food web. *Marine Ecology Progress Series*, *467*, 47–59. https://doi.org/10.3354/meps09945

Hobson, K. A., Ambrose, W. G. Jr, & Renaud, P. E. (1995). Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: Insights from $\delta^{13}C$ and $\delta^{15}N$ analysis. *Marine Ecology Progress Series*, *128*, 1–10. https://doi.org/10.3354/meps128001

Hobson, K. A., Fisk, A., Karnovsky, N., Holst, M., Gagnon, J.-M., & Fortier, M. (2002). A stable isotope ($\delta^{13}C$, $\delta^{15}N$) model for the North Water food web: Implications for evaluating trophodynamics and the flow of energy and contaminants. *Deep Sea Research Part II: Topical Studies in Oceanography*, *49*(22–23), 5131–5150. https://doi.org/10.1016/s0967-0645(02)00182-0

Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science*, *328*(5985), 1523–1528. https://doi.org/10.1126/science.1189930

Hoffman, J. C. (2016). Tracing the origins, migrations, and other movements of fishes using stable isotopes. *An Introduction to Fish Migration*, 169–196.

Holmes, R. M., McClelland, J. W., Tank, S. E., Spencer, R. G. M., & Shiklomanov, A. I. (2018). Arctic great rivers observatory. Water Quality Dataset, Version 20181010. Retrieved from https://www.arcticgreatrivers.org/data

Iken, K., Bluhm, B., & Dunton, K. (2010). Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, *57*(1–2), 71–85. https://doi.org/10.1016/j.dsr2.2009.08.007

Iken, K., Bluhm, B., & Gradinger, R. (2005). Food web structure in the high Arctic Canada Basin: Evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. *Polar Biology*, *28*(3), 238–249.

IPCC. (2013). Climate change 2013: The physical science basis. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.), *Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on*

Climate Change (pp. 255–316). Cambridge, UK: Cambridge University Press.

Ivanov, M., Lein, A. Y., Zakharova, E., & Savvichev, A. (2012). Carbon isotopic composition in suspended organic matter and bottom sediments of the East Arctic seas. *Microbiology*, *81*(5), 596–605. https://doi.org/10.1134/S0026261712050086

Jones, B. M., Arp, C. D., Jorgenson, M. T., Hinkel, K. M., Schmutz, J. A., & Flint, P. L. (2009). Increase in the rate and uniformity of coastline erosion in Arctic Alaska. *Geophysical Research Letters*, *36*(3). https://doi.org/10.1029/2008GL036205

Keeley, J. E., & Sandquist, D. (1992). Carbon: Freshwater plants. *Plant, Cell & Environment*, *15*(9), 1021–1035. https://doi.org/10.1111/j.1365-3040.1992.tb01653.x

Key, R. M., Olsen, A., van Heuven, S., Lauvset, S. K., Velo, A., Lin, X., Suzuki, T. (2015). Global ocean data analysis project, version 2 (GLODAPv2) [Miscellaneous]. https://doi.org/10.3334/CDIAC/OTG.NDP093_GLODAPv2, hdl:10013/epic.46499.

Kohlbach, D., Graeve, M., A. Lange, B., David, C., Peeken, I., & Flores, H. (2016). The importance of ice algae-produced carbon in the central Arctic Ocean ecosystem: Food web relationships revealed by lipid and stable isotope analyses. *Limnology and Oceanography*, *61*(6), 2027–2044. https://doi.org/10.1002/lno.10351

Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*,*15*(3),259–263.https://doi.org/10.1127/0941-2948/2006/0130

Kuliński, K., Kędra, M., Legeżyńska, J., Gluchowska, M., & Zaborska, A. (2014). Particulate organic matter sinks and sources in high Arctic fjord. *Journal of Marine Systems*, *139*, 27–37. https://doi.org/10.1016/j.jmarsys.2014.04.018

Kuzyk, Z. Z. A., Macdonald, R. W., Tremblay, J.-É., & Stern, G. A. (2010). Elemental and stable isotopic constraints on river influence and patterns of nitrogen cycling and biological productivity in Hudson Bay. *Continental Shelf Research*, *30*(2), 163–176. https://doi.org/10.1016/j.csr.2009.10.014

Kwok, R. (2018). Arctic sea ice thickness, volume, and multiyear ice coverage: Losses and coupled variability (1958–2018). *Environmental Research Letters*, *13*(10), 105005. https://doi.org/10.1088/1748-9326/aae3ec

Laidre, K. L., Stirling, I., Lowry, L. F., Wiig, Ø., Heide-Jørgensen, M. P., & Ferguson, S. H. (2008). Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications*, *18*(sp2). https://doi.org/10.1890/06-0546.1

Lin, F., Chen, M., Tong, J., Cao, J., Qiu, Y., & Zheng, M. (2014). Carbon and nitrogen isotopic composition of particulate organic matter and its biogeochemical implication in the Bering Sea. *Acta Oceanologica Sinica*, *33*(12), 40–47. https://doi.org/10.1007/s13131-014-0570-y

Lind, S., Ingvaldsen, R. B., & Furevik, T. (2018). Arctic warming hotspot in the northern Barents Sea linked to declining sea-ice import. *Nature Climate Change*, *8*(7), 634. https://doi.org/10.1038/s41558-018-0205-y

Lobbes, J. M., Fitznar, H. P., & Kattner, G. (2000). Biogeochemical characteristics of dissolved and particulate organic matter in Russian rivers entering the Arctic Ocean. *Geochimica et Cosmochimica Acta*, *64*(17), 2973–2983. https://doi.org/10.1016/S0016-7037(00)00409-9

Lovvorn, J. R., Cooper, L. W., Brooks, M. L., De Ruyck, C. C., Bump, J. K., & Grebmeier, J. M. (2005). Organic matter pathways to zooplankton and benthos under pack ice in late winter and open water in late summer in the north-central Bering Sea. *Marine Ecology Progress Series*, *291*, 135–150. https://doi.org/10.3354/meps291135

Mars, J., & Houseknecht, D. (2007). Quantitative remote sensing study indicates doubling of coastal erosion rate in past 50 yr along a segment of the Arctic coast of Alaska. *Geology*, *35*(7), 583–586. https://doi.org/10.1130/G23672A.1

Matthews, C. J., & Ferguson, S. H. (2014). Validation of dentine deposition rates in beluga whales by interspecies cross dating of temporal $\delta^{13}C$ trends in teeth. *NAMMCO Scientific Publications*, *10*. https://doi.org/10.7557/3.3196

McMahon, K. W., Hamady, L. L., & Thorrold, S. R. (2013a). Ocean ecogeochemistry: A review. *Oceanography and Marine Biology*, *51*, 327–373.

McMahon, K. W., Hamady, L. L., & Thorrold, S. R. (2013b). A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnology and Oceanography*, *58*(2), 697–714. https://doi.org/10.4319/lo.2013.58.2.0697

Michener, R. H., & Kaufman, L. (2007). Stable isotope ratios as tracers in marine food webs: An update. *Stable Isotopes in Ecology and Environmental Science*, *2*, 238–282. https://doi.org/10.1002/9780470691854.ch9

Misarti, N., Finney, B., Maschner, H., & Wooller, M. J. (2009). Changes in northeast Pacific marine ecosystems over the last 4500 years: Evidence from stable isotope analysis of bone collagen from archeological middens. *The Holocene*, *19*(8), 1139–1151. https://doi.org/10.1177/0959683609345075

Nelson, M. A., Quakenbush, L. T., Mahoney, B. A., Taras, B. D., & Wooller, M. J. (2018). Fifty years of Cook Inlet beluga whale feeding ecology from isotopes in bone and teeth. *Endangered Species Research*, *36*, 77–87. https://doi.org/10.3354/esr00890

Newsome, S. D., Clementz, M. T., & Koch, P. L. (2010). Using stable isotope biogeochemistry to study marine mammal ecology. *Marine Mammal Science*, *26*(3), 509–572. https://doi.org/10.1111/j.1748-7692.2009.00354.x

Newsome, S., Etnier, M., Kurle, C., Waldbauer, J., Chamberlain, C., & Koch, P. (2007). Historic decline in primary productivity in western Gulf of Alaska and eastern Bering Sea: Isotopic analysis of northern fur seal teeth. *Marine Ecology Progress Series*, *332*, 211–224. https://doi.org/10.3354/meps332211

O'Brien, M., Macdonald, R., Melling, H., & Iseki, K. (2006). Particle fluxes and geochemistry on the Canadian Beaufort Shelf: Implications for sediment transport and deposition. *Continental Shelf Research*, *26*(1), 41–81. https://doi.org/10.1016/j.csr.2005.09.007

O'Reilly, C. M., Hecky, R. E., Cohen, A. S., & Plisnier, P.-D. (2002). Interpreting stable isotopes in food webs: Recognizing the role of time averaging at different trophic levels. *Limnology and Oceanography*, *47*(1), 306–309. https://doi.org/10.4319/lo.2002.47.1.0306

Overland, J. E., & Wang, M. (2010). Large-scale atmospheric circulation changes are associated with the recent loss of Arctic sea ice. *Tellus A: Dynamic Meteorology and Oceanography*, *62*(1), 1–9. https://doi.org/10.1111/j.1600-0870.2009.00421.x

Oxtoby, L., Budge, S., Iken, K., Brien, D. O., & Wooller, M. (2016). Feeding ecologies of key bivalve and polychaete species in the Bering Sea as elucidated by fatty acid and compound-specific stable isotope analyses. *Marine Ecology Progress Series*, *557*, 161–175. https://doi.org/10.3354/meps11863

Oxtoby, L., Horstmann, L., Budge, S., O'Brien, D., Wang, S., Schollmeier, T., & Wooller, M. (2017). Resource partitioning between Pacific walruses and bearded seals in the Alaska Arctic and sub-Arctic. *Oecologia*, *184*(2), 385–398. https://doi.org/10.1007/s00442-017-3883-7

Parsons, T., Webb, D., Rokeby, B., Lawrence, M., Hopky, G., & Chiperzak, D. (1989). Autotrophic and heterotrophic production in the Mackenzie River/Beaufort Sea estuary. *Polar Biology*, *9*(4), 261–266. https://doi.org/10.1007/BF00263774

Polito, M. J., Hinke, J. T., Hart, T., Santos, M., Houghton, L. A., & Thorrold, S. R. (2017). Stable isotope analyses of feather amino acids identify penguin migration strategies at ocean basin scales. *Biology Letters*, *13*(8), 20170241. https://doi.org/10.1098/rsbl.2017.0241

Quay, P., Sonnerup, R., Westby, T., Stutsman, J., & McNichol, A. (2003). Changes in the $^{13}C/^{12}C$ of dissolved inorganic carbon in the ocean as a tracer of anthropogenic CO_2 uptake. *Global Biogeochemical Cycles*, *17*(1). https://doi.org/10.1029/2001GB001817

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rachold, V., Grigoriev, M. N., Are, F. E., Solomon, S., Reimnitz, E., Kassens, H., & Antonow, M. (2000). Coastal erosion vs riverine sediment discharge in the Arctic Shelf seas. *International Journal of Earth Sciences*, *89*(3), 450–460. https://doi.org/10.1007/s005310000113

Rau, G. H., Riebesell, U., & Wolf-Gladrow, D. (1996). A model of photosynthetic ^{13}C fractionation by marine phytoplankton based on diffusive molecular CO_2 uptake. *Marine Ecology Progress Series*, 275–285. https://doi.org/10.3354/meps133275

Rau, G., Takahashi, T., Des Marais, D., Repeta, D., & Martin, J. (1992). The relationship between $\delta^{13}C$ of organic matter and [CO_2 (aq)] in ocean surface water: Data from a JGOFS site in the northeast Atlantic Ocean and a model. *Geochimica et Cosmochimica Acta*, *56*(3), 1413–1419. https://doi.org/10.1016/0016-7037(92)90073-R

Roy, V., Iken, K., Gosselin, M., Tremblay, J.-É., Bélanger, S., & Archambault, P. (2015). Benthic faunal assimilation pathways and depth-related changes in food-web structure across the Canadian Arctic. *Deep Sea Research Part I: Oceanographic Research Papers*, *102*, 55–71. https://doi.org/10.1016/j.dsr.2015.04.009

Sabine, C. L., Feely, R. A., Gruber, N., Key, R. M., Lee, K., Bullister, J. L., … Tilbrook, B. (2004). The oceanic sink for anthropogenic CO_2. *Science*, *305*(5682), 367–371. https://doi.org/10.1126/science.1097403

Sakshaug, E. (2004). Primary and secondary production in the Arctic Seas. In R. Stein & R. W. Macdonald (Eds.), *The organic carbon cycle in the Arctic Ocean* (pp. 57–81). New York, NY: Springer.

Sarà, G., Pirro, M., Romano, C., Rumolo, P., Sprovieri, M., & Mazzola, A. (2007). Sources of organic matter for intertidal consumers on Ascophyllum-shores (SW Iceland): A multi-stable isotope approach. *Helgoland Marine Research*, *61*(4), 297–302. https://doi.org/10.1007/s10152-007-0078-3

Schell, D. M. (2000). Declining carrying capacity in the Bering Sea: Isotopic evidence from whale baleen. *Limnology and Oceanography*, *45*(2), 459–462. https://doi.org/10.4319/lo.2000.45.2.0459

Schell, D. M. (2001). Carbon isotope ratio variations in Bering Sea biota: The role of anthropogenic carbon dioxide. *Limnology and Oceanography*, *46*(4), 999–1000. https://doi.org/10.4319/lo.2001.46.4.0999

Schell, D., Saupe, S., & Haubenstock, N. (1989). Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by $\delta^{13}C$ techniques. *Marine Biology*, *103*(4), 433–443.

Schlitzer, R. (2016). *Ocean data view*. Retrieved from http://odv.awi.de

Schmittner, A., Gruber, N., Mix, A., Key, R., Tagliabue, A., & Westberry, T. (2013). Biology and air–sea gas exchange controls on the distribution of carbon isotope ratios ($\delta^{13}C$) in the ocean. *Biogeosciences*, *10*(9), 5793–5816. https://doi.org/10.5194/bg-10-5793-2013

Schubert, C. J., & Calvert, S. E. (2001). Nitrogen and carbon isotopic composition of marine and terrestrial organic matter in Arctic Ocean sediments: Implications for nutrient utilization and organic matter composition. *Deep Sea Research Part I: Oceanographic Research Papers*, *48*(3), 789–810. https://doi.org/10.1016/S0967-0637(00)00069-8

Smith, S. L., Henrichs, S. M., & Rho, T. (2002). Stable C and N isotopic composition of sinking particles and zooplankton over the southeastern Bering Sea shelf. *Deep Sea Research Part II: Topical Studies in Oceanography*, *49*(26), 6031–6050. https://doi.org/10.1016/S0967-0645(02)00332-6

Søreide, J. E., Carroll, M. L., Hop, H., Ambrose, W. G. Jr, Hegseth, E. N., & Falk-Petersen, S. (2013). Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers. *Marine Biology Research*, *9*(9), 831–850. https://doi.org/10.1080/17451000.2013.775457

Søreide, J. E., Falk-Petersen, S., Hegseth, E. N., Hop, H., Carroll, M. L., Hobson, K. A., & Blachowiak-Samolyk, K. (2008). Stable carbon and nitrogen isotope ratios of suspended particulate organic matter in waters around Svalbard archipelago. *PANGAEA*. https://doi.org/10.1594/PANGAEA.786711. In supplement to: Søreide, JE et al. (2008): Seasonal feeding strategies of Calanus in the high-Arctic Svalbard region. Deep Sea Research Part II: Topical Studies in Oceanography, 55(20-21), 2225-2244, https://doi.org/10.1016/j.dsr2.2008.05.024

Søreide, J. E., Hop, H., Carroll, M. L., Falk-Petersen, S., & Hegseth, E. N. (2006). Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. *Progress in Oceanography*, *71*(1), 59–87. https://doi.org/10.1016/j.pocean.2006.06.001

Tagliabue, A., & Bopp, L. (2008). Towards understanding global variability in ocean carbon-13. *Global Biogeochemical Cycles*, *22*. https://doi.org/10.1029/2007GB003037

Takahashi, T., Sutherland, S. C., Sweeney, C., Poisson, A., Metzl, N., Tilbrook, B., … Nojiri, Y. (2002). Global sea–air CO_2 flux based on climatological surface ocean pCO_2, and seasonal biological and temperature effects. *Deep Sea Research Part II: Topical Studies in Oceanography*, *49*(9–10), 1601–1622. https://doi.org/10.1016/S0967-0645(02)00003-6

Tamelander, T., Reigstad, M., Hop, H., & Ratkova, T. (2009). Ice algal assemblages and vertical export of organic matter from sea ice in the Barents Sea and Nansen Basin (Arctic Ocean). *Polar Biology*, *32*(9), 1261–1273. https://doi.org/10.1007/s00300-009-0622-5

Tamelander, T., Renaud, P. E., Hop, H., Carroll, M. L., Ambrose, W. G. Jr, & Hobson, K. A. (2006). Trophic relationships and pelagic–benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements. *Marine Ecology Progress Series*, *310*, 33–46. https://doi.org/10.3354/meps310033

Thomas, D. N., & Papadimitriou, S. (2011). Biogeochemistry of sea ice. In V. P. Singh, P. Singh, & U. K. Haritashya (Eds.), *Encyclopedia of snow, ice and glaciers* (pp. 98–102). Dordrecht, the Netherlands: Springer.

Thomas, M. K., Kremer, C. T., Klausmeier, C. A., & Litchman, E. (2012). A global pattern of thermal adaptation in marine phytoplankton. *Science*, *338*(6110), 1085–1088. https://doi.org/10.1126/science.1224836

Tremblay, J.-É., & Gagnon, J. (2009). The effects of irradiance and nutrient supply on the productivity of Arctic waters: A perspective on climate change. In J. Nihoul (Ed.), *Influence of climate change on the changing arctic and sub-arctic conditions* (pp. 73–93). Dordrecht, the Netherlands: Springer.

Tremblay, J.-E., Michel, C., Hobson, K. A., Gosselin, M., & Price, N. M. (2006). Bloom dynamics in early opening waters of the Arctic Ocean. *Limnology and Oceanography*, *51*(2), 900–912. https://doi.org/10.4319/lo.2006.51.2.0900

Vander Zanden, M. J., Clayton, M. K., Moody, E. K., Solomon, C. T., & Weidel, B. C. (2015). Stable isotope turnover and half-life in animal tissues: A literature synthesis. *PLoS ONE*, *10*(1), e0116182. https://doi.org/10.1371/journal.pone.0116182

Vaqué, D., Lara, E., Arrieta, J. M., Holding, J., Sà, E. L., Hendriks, I. E., … Duarte, C. M. (2019). Warming and CO_2 enhance Arctic heterotrophic microbial activity. *Frontiers in Microbiology*, *10*, 494. https://doi.org/10.3389/fmicb.2019.00494

Varela, D. E., Crawford, D. W., Wrohan, I. A., Wyatt, S. N., & Carmack, E. C. (2013). Pelagic primary productivity and upper ocean nutrient dynamics across Subarctic and Arctic Seas. *Journal of Geophysical Research: Oceans*, *118*(12), 7132–7152. https://doi.org/10.1002/2013JC009211

Vernet, M., Richardson, T. L., Metfies, K., Nöthig, E.-M., & Peeken, I. (2017). Models of plankton community changes during a warm water anomaly in arctic waters show altered trophic pathways with minimal changes in carbon export. *Frontiers in Marine Science*, *4*, 160. https://doi.org/10.3389/fmars.2017.00160

Wang, S. W., Budge, S. M., Gradinger, R. R., Iken, K., & Wooller, M. J. (2014). Fatty acid and stable isotope characteristics of sea ice and pelagic particulate organic matter in the Bering Sea: Tools for estimating sea ice algal contribution to Arctic food web

production. *Oecologia*, *174*(3), 699–712. https://doi.org/10.1007/s00442-013-2832-3

Wang, S. W., Budge, S. M., Iken, K., Gradinger, R. R., Springer, A. M., & Wooller, M. J. (2015). Importance of sympagic production to Bering Sea zooplankton as revealed from fatty acid-carbon stable isotope analyses. *Marine Ecology Progress Series*, *518*, 31–50. https://doi.org/10.3354/meps11076

Wassenaar, L. I. (2019). Introduction to conducting stable isotope measurements for animal migration studies. In G. J. Viljoen, A. G. Luckins, & I. Naletoski (Eds.), *Tracking animal migration with stable isotopes* (pp. 25–51). Amsterdam, the Netherlands: Elsevier.

Wassmann, P., Bauerfeind, E., Fortier, M., Fukuchi, M., Hargrave, B., Moran, B., … Peinert, R. (2004). Particulate organic carbon flux to the Arctic Ocean sea floor. In R. Stein & R. W. Macdonald (Eds.), *The organic carbon cycle in the Arctic Ocean* (pp. 101–138). Berlin/Heidelberg, Germany: Springer.

Yamamoto, A., Kawamiya, M., Ishida, A., Yamanaka, Y., & Watanabe, S. (2012). Impact of rapid sea-ice reduction in the Arctic Ocean on the rate of ocean acidification. *Biogeosciences*, *9*(6), 2365–2375. https://doi.org/10.5194/bg-9-2365-2012

Young, J., Bruggeman, J., Rickaby, R., Erez, J., & Conte, M. (2013). Evidence for changes in carbon isotopic fractionation by phytoplankton between 1960 and 2010. *Global Biogeochemical Cycles*, *27*(2), 505–515. https://doi.org/10.1002/gbc.20045

Zhang, J., Quay, P. D., & Wilbur, D. O. (1995). Carbon isotope fractionation during gas-water exchange and dissolution of CO_2. *Geochimica et Cosmochimica Acta*, *59*(1), 107–114. https://doi.org/10.1016/0016-7037(95)91550-D

Zhang, R., Chen, M., Guo, L., Gao, Z., Ma, Q., Cao, J., … Li, Y. (2012). Variations in the isotopic composition of particulate organic carbon and their relation with carbon dynamics in the western Arctic Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, *81*, 72–78. https://doi.org/10.1016/j.dsr2.2011.05.005

Zuur, A., Ieno, E. N., & Smith, G. M. (2007). *Analyzing ecological data*. New York, NY: Springer Science & Business Media.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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