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Models of Plankton Community Changes during a Warm Water Anomaly in Arctic Waters Show Altered Trophic Pathways with Minimal Changes in Carbon Export

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Carbon flow through pelagic food webs is an expression of the composition, biomass and activity of phytoplankton as primary producers. In the near future, severe environmental changes in the Arctic Ocean are expected to lead to modifications of phytoplankton communities. Here, we used a combination of linear inverse modeling and ecological network analysis to study changes in food webs *before*, *during*, and *after* an anomalous warm water event in the eastern Fram Strait of the West Spitsbergen Current (WSC) that resulted in a shift from diatoms to flagellates during the summer (June–July). The model predicts substantial differences in the pathways of carbon flow in diatom- vs. *Phaeocystis*/nanoflagellate-dominated phytoplankton communities, but relatively small differences in carbon export. The model suggests a change in the zooplankton community and activity through increasing microzooplankton abundance and the switching of meso- and macrozooplankton feeding from strict herbivory to omnivory, detritivory and coprophagy. When small cells and flagellates dominated, the phytoplankton carbon pathway through the food web was longer and the microbial loop more active. Furthermore, one step was added in the flow from phytoplankton to mesozooplankton, and phytoplankton carbon to higher trophic levels is available via detritus or microzooplankton. Model results highlight how specific changes in phytoplankton community composition, as expected in a climate change scenario, do not necessarily lead to a reduction in carbon export.

Keywords: phytoplankton, flagellates, food web, carbon cycling, inverse model

INTRODUCTION

The Arctic Ocean is one region where climate change is most pronounced, impacting the pelagic environment with observed effects on stratification, pH and currents. The consequences of these effects on phytoplankton are complex. Spatial shifts in latitude as well as timing of biological events affect phytoplankton bloom phenology, microalgal species distribution and trophic interactions

(Aberle et al., 2012). A third major effect is the decrease in cell size distribution (Peter and Sommer, 2012), the focus of this study. A decrease in cell size can come about by direct effects of the environment on phytoplankton, e.g., higher temperature increasing metabolism, or indirectly, where environmental conditions alter grazing pressure on phytoplankton abundance, composition and cell size (Winder and Sommer, 2012). In the Arctic, warmer climate increases stratification, with warmer and less saline mixed layers, lower nitrate concentrations and higher picoplankton abundance (Li et al., 2009). Similarly, reduced sea ice cover in Lake Erie has been associated with smaller-sized cells that attain lower total biomass than during periods of ice cover that instead promotes chain-forming diatoms (Beall et al., 2016). Temperature could affect cell size of a given species or may facilitate larger vs. small species abundance, or both. However, this is not a given (Rüger and Sommer, 2012). Alternatively, it has been proposed that at higher temperatures grazing could intensify in a size-selective mode, affecting phytoplankton cell size distribution by top-down controls. Results are variable, with no cell size changes observed at higher temperatures (Rüger and Sommer, 2012 but see Daufresne et al., 2009) or grazing causing a reduction in cell size (Peter and Sommer, 2012). Although the importance of the grazers in the food chain is considered key to sedimentation (e.g., Reigstad et al., 2011) there is no large-scale consensus that small cells contribute substantially to sedimentation (but see Richardson and Jackson, 2007). Large zooplankton (e.g., *Calanus* spp.) feeding on the phytoplankton spring bloom, usually dominated by large cells, is known to produce a pulse of sedimentation through fecal pellet formation (Forest et al., 2010). Within this paradigm, it is expected that an absence of large cells, i.e., diatoms, will decrease the flux of material to the sediments (Wohlers et al., 2009).

In the Arctic, Atlantic water coming from the south becomes the West Spitsbergen Current (WSC); west of Svalbard, this current has a subsurface core at about 250 m depth and a surface expression. The current brings 6.6–8.5 Sv (or 10^6 m^3 s^{-1}) with a northward flow (Beszczynska-Möller et al., 2011). A cooling occurs as the water moves north, losing heat at the surface in contact with the atmosphere as well as sub-surface cross-front exchange with fresher and colder water from sea ice and/or glacial melting (Rudels et al., 2005). The Atlantic water cooling and freshening as it is transported north has a 5-to-6-year cycle in its salinity and temperature properties. Temperatures >2°C, with a mean temperature in the WSC of 3.1 ± 0.1°C characterize the Atlantic water at these latitudes (Beszczynska-Moller et al., 2012). Only one third of the heat carried by the WSC is transported into the Arctic Ocean, the rest is lost in westward transport and sea surface cooling (Kawasaki and Hasumi, 2016). In the 1997–2010 period, the trend is one of increased temperature but no significant change in volume transport (Beszczynska-Moller et al., 2012). The Warm Water Anomaly in 2005–2007 was defined as a northward advance of Atlantic water, a warm tongue more than 350 km north, reaching the Fram Strait northwest of Svalbard with waters 1°C higher than average (Walczowski et al., 2012).

The observed biological changes in eastern Fram Strait, and their implication for the Central Arctic Ocean, were tightly coupled with changes in the hydrography. Although the WSC shows pronounced inter-annual variability in primary productivity, phytoplankton and zooplankton abundance and composition (Wassmann et al., 2010; Carstensen et al., 2012; Kwasniewski et al., 2012), large changes in phytoplankton and zooplankton were associated with the warm water anomaly from 2005 to 2007 (Beszczynska-Moller et al., 2012; Nöthig et al., 2015; Soltwedel et al., 2016). This is best reflected in the long-term data set of the HAUSGARTEN observatory at 79°N, 4°E (Long-Term Ecological Research in the deep Arctic Ocean) that demonstrated a shift in phytoplankton community structure and in the composition of the sedimenting particulate carbon (Alcaraz et al., 2010; Lalande et al., 2013). The main diatoms found in the Atlantic waters of the WSC before the warm water event were large centric or chain-forming species, including *Thalassiosira* spp., *Chaetoceros* spp. (very often *Chaetoceros socialis*), chains of pennate diatoms of the genus *Fragilariopsis* spp., *Navicula* spp., *Achnanthes taeniata* and *Fossula arctica* in different proportions. Sometimes a few *Rhizosolenia* spp, *Nitzschia*/*Pseudonitzscha* sp., or *Cylindrotheca* sp., were observed (Degerlund and Eilertsen, 2010). At the time of the warm water pulse, higher phytoplankton biomass was observed in the water column, protistan plankton >3 μm changed in composition, and diatoms that dominated the period before the warm event switched to a dominance by coccolithophores in 2004, followed by *Phaeocystis pouchetii* dominance in 2006 (Nöthig et al., 2015). Several of these changes remained after the warm-water event, with *Phaeocystis* sp., still being prominent in the community (Metfies et al., 2016), although there has been a decrease in water temperature and in *Phaeocystis* sp. abundance from 97 to 48% from 2007 to 2011 (Soltwedel et al., 2016) whereas diatom concentration remained low and nanoflagellates increased to 43% (Nöthig et al., 2015). The ecosystem responded to the observed pelagic changes: there was an increase in food availability to the benthos in 2006–2007 when *Phaeocystis* sp., and flagellates dominated the overlying plankton community, which altered the abundance and community structure of the benthic bacteria and meiofauna, while macrofauna response lagged by a year (Jacob, 2014; Soltwedel et al., 2016).

Biological changes in the Fram Strait might foreshadow expected future changes in the Central Arctic, as this is the largest sub-Arctic water feeding the Arctic Ocean. In fact, what was observed in the Fram Strait during the warm period is seen throughout the Arctic Ocean and Arctic Seas: an increase of 20% in phytoplankton productivity due to more ice-free days during the growth season (e.g., Arrigo and van Dijken, 2011), a decrease in phytoplankton cell size associated with freshening and nitrate depletion in the mixed layer (Li et al., 2009), and changes in bloom phenology, both by an early sea ice retreat and late summer blooms (Kahru et al., 2011; Harrison et al., 2013; Ji et al., 2013; Ardyna et al., 2014).

In this study, we used a combination of linear inverse modeling and ecological network analysis to characterize and quantify the pathways of carbon flow through pelagic food webs of the eastern Fram Strait. We were particularly interested in how variations in phytoplankton community composition and in cell size *before*, *during*, and *after* the anomalously warm period of

2005–2007 affected the ecosystem trophic dynamics, including the transfer of carbon to higher trophic levels (planktivorous fish and cod) and export of carbon out of surface waters.

METHODS

Model Construction

We constructed food webs for the WSC region of the eastern Fram Strait (**Figure 1**) using published data for the late spring/summer of 2003 (*before* the warming event), 2006 (*during*), and 2010 (*after*), or as close as possible to the time period (but always within 1 year). The same model structure was used for each time period (**Figure 2**). Each web comprised 42 flows that represented carbon flows between two compartments, or from one compartment to a sink (**Table 1**). The structure of the food webs was based on the assumption that sizes of the producers and consumers were major determinants of the trophic dynamics of these systems, i.e., small grazers are restricted to small algae. Choices of compartments and trophic relationships were a compromise between achieving biological reality and keeping the total number of flows in the system reasonable. The living components included two phytoplankton compartments, three zooplankton compartments, one compartment for small planktivorous fish, one for cod, and one compartment for heterotrophic bacteria. The phytoplankton were divided into "small" (0.2 to ∼10 μm; assumed to be mainly picophytoplankton, coccolithophores, *Phaeocystis* sp., and small autotrophic flagellates) and "large" (> 10 μm; mainly diatoms and larger dinoflagellates; Kilias et al., 2014; Nöthig et al., 2015). Zooplankton size classes were the microzooplankton (20–200 μm; ciliates and flagellates), the mesozooplankton (200 to ∼1,000 μm; mainly small copepods) and macrozooplankton (chaetognaths, euphausiids, and *Calanus* copepods >1,000 μm; Bamstedt et al., 1991; Hop et al., 2006; Blachowiak-Samolyk et al., 2007; Calbet, 2008; Pasternak et al., 2008; De Laender et al., 2010; Svensen et al., 2011; Monti and Minocci, 2013). Small planktivorous fish were assumed to be mainly capelin and herring but this compartment also includes carnivorous zooplankton, such as amphipods (Wassmann et al., 2006; Dalpadado et al., 2016). The top predator in the system was cod (Wassmann et al., 2015)

All living compartments contributed to a labile dissolved organic carbon (DOC) pool through excretion and to the detrital pool through mortality or defecation. Sloppy feeding was implicitly included as excretion to DOC. Detritus was transformed to DOC by chemically- or bacterially-mediated dissolution (Jumars et al., 1989). All living compartments lost carbon by respiration. Other forms of mortality (e.g., viral lysis or natural cell mortality) were implicitly included in flows to detritus and DOC. All non-respiratory losses from the system were represented by flows to an "external" compartment that served as a mathematical closure term. These losses included particulate organic carbon (POC) export by detrital settling, DOC loss by advection, and removal of cod through the fishery or via consumption by higher trophic levels.

Data

We used published data from Fram Strait to calculate input ("known") values for 7 of the 42 carbon flows: small and large phytoplankton primary productivity, bacterial productivity,

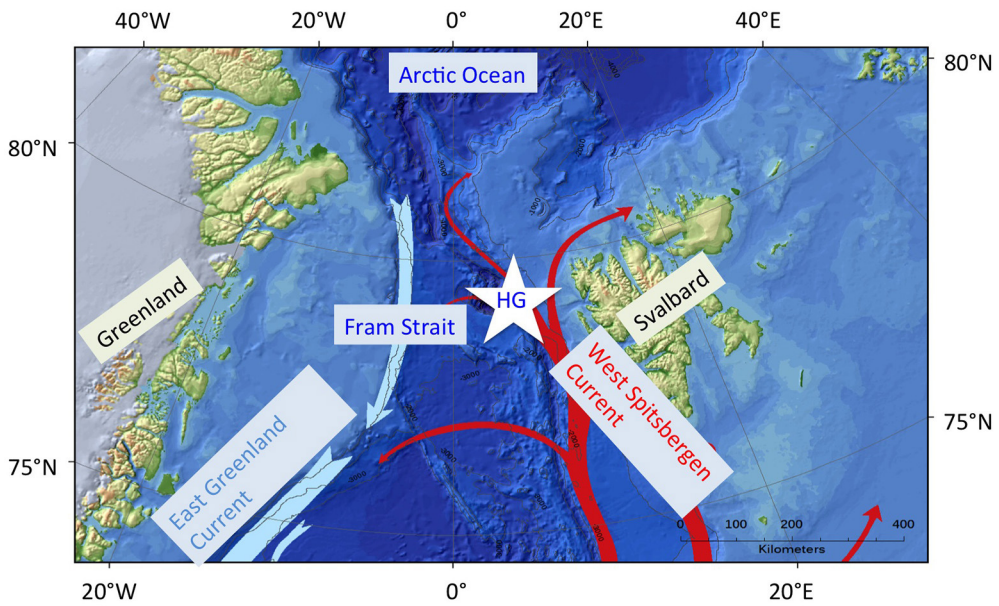

FIGURE 1 | Map of the Fram Strait region with the northward moving, warm Atlantic water carrying West Spitsbergen Current (WSC) in the eastern Fram Strait (red arrows); blue arrows indicate the outflow of polar water in the East Greenland Current in the western Fram Strait. The center of the star is at 79°N and 4°E indicating the source of the data used in this study, HG is HAUSGARTEN observatory. (Map was produced with ArcGIS 10.3 using GEBCO 08, modified by Laura Hehemann from the Alfred Wegener Institute, Germany).

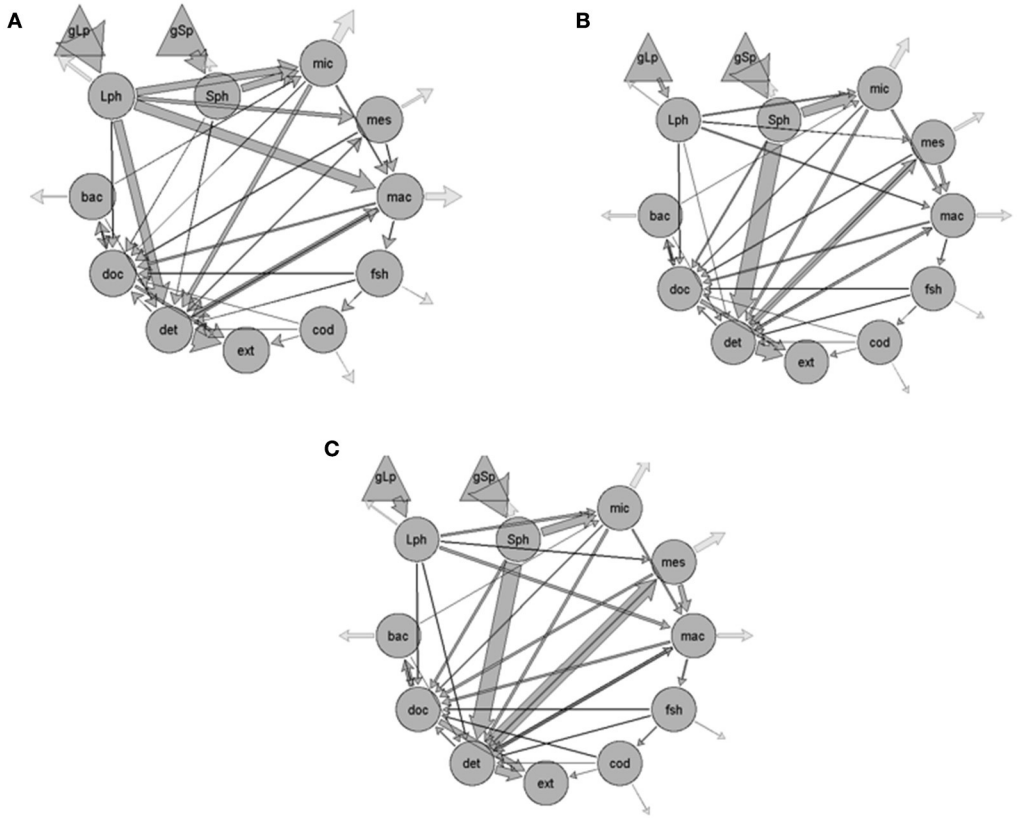

FIGURE 2 | Flows of carbon (mgC m^{-2} d^{-1}) through the food web of the West Spitzbergen Current in the eastern Fram Strait **(A)** before, **(B)** during, and **(C)** after the warm water anomaly of 2005–2007. Primary productivity was dominated by the large phytoplankton (Lph), primarily diatoms, before the warm event and by small phytoplankton (Sph; primarily *Phaeocystis*) during and afterwards. Phytoplankton were grazed by microzooplankton (mic), mesozooplankton (mes), and macrozooplankton (mac). Planktivorous fish (fsh) and cod (cod) generally consumed the larger grazers. Carbon could flow to detritus (det) as particulate material, or be remineralized as dissolved organic carbon (doc) to fuel bacterial productivity (bac). Gray arrows to nowhere represent respiration losses. gLp, gross primary productivity of the Lph; gSp, gross primary productivity of the Sph.

microzooplankton grazing on small phytoplankton and flagellates, microzooplankton grazing on large phytoplankton, ingestion rates for the small fish and ingestion rates for cod (**Table 2**). Total primary productivity rates were taken from remote sensing estimates by Arrigo et al. (2008), Arrigo and van Dijken (2011, 2015) and daily production was estimated assuming annual primary production was evenly distributed over the period of open water. Contributions of flagellates vs. large phytoplankton to total primary productivity were assumed to be proportional to their size-specific contributions to biomass and were calculated from chlorophyll *a* measurements and phytoplankton community composition data of Nöthig et al. (2015, their Table 2). Accordingly, small phytoplankton and flagellates constituted 20% of the total phytoplankton biomass for the *before* models and 80% were considered large phytoplankton; *Phaeocystis* sp. and other flagellates accounted for 97 and ∼50% of the small phytoplankton biomass for the *during* and *after* models, respectively.

Conversions from chlorophyll *a* to carbon units were done using an average C:chl ratio of 53 (g:g) to avoid seasonal biases (Svensen et al., 2011). The C:chl ratio of 53 for phytoplankton was chosen as a compromise between spring and summer values and those for small and large phytoplankton cells as shown by mesocosm experiments in which C:chl ratio of diatoms, dinoflagellate and mixed composition were 95, 45, and 60, respectively (Svensen et al., 2011; Spilling et al., 2014). Similarly, phytoplankton in the Fram Strait in May and August 2014 had a C:chl ratio of 41 (Marit Reigstad, personal communication). The ratio of 53 was used when converting from chl *a* estimates in the field (in mg chl*a* m^{-2}) to phytoplankton carbon (mg C m^{-2}). A different C:chl ratio would either increase or decrease phytoplankton biomass in the model constraints but has no effect where phytoplankton biomass is an unknown.

There is difficulty in obtaining reliable and consistent data in high latitude environments due to the effort and cost of such studies. The data from Nöthig et al. (2015) as well as other field campaigns are based on cruises of a few weeks length, in the June and July time period, with the exception of estimates of fish abundance, provided by year. In this way, it is possible to compare year-to-year summer variability. Data from cruises from other times of the year (either April–May or August–September) were not included in this study.

TABLE 1 | Carbon flows in food webs constructed for *before*, *during* and *after* anomalously warm waters in the eastern Fram Strait.

Flow No	Flow symbol	Description	*Before*	During	*After*
1	gSpTOSph	Gross PP of small phytoplankton (Sph)	157 ± 14	679 ± 44	583 ± 40
2	gLpTOLph	Gross PP of large phytoplankton (Lph)	555 ± 22	77 ± 12	173 ± 24
3	SphTOres	Respiration of Sph	30 ± 13	105 ± 44	75 ± 38
4	SphTOmic	Grazing of Sph by microzooplankton (mic)	**117 ± 0.0**	**206 ± 0.0**	**170 ± 0.0**
5	SphTOdet	Detritus (det) production by Sph	5.4 ± 0	348 ± 0	313 ± 0
6	SphTOdoc	Dissolved Organic Carbon (doc) production by Sph	4.8 ± 2.0	20 ± 7.0	24 ± 12
7	LphTOres	Respiration of Lph	55 ± 22	15 ± 7.0	27 ± 14
8	LphTOmic	Grazing of Lph by mic	**117 ± 0.0**	**25 ± 0.0**	**42 ± 0.0**
9	LphTOmes	Grazing of Lph by mesozooplankton (mes)	60 ± 31	2.0 ± 1.0	16 ± 7.0
10	LphTOmac	Grazing of Lph by macrozooplankton (mac)	164 ± 15	21 ± 1.0	55 ± 5.0
11	LphTOdet	Production of det by Lph	148 ± 36	1.0 ± 1.0	8 ± 6.3
12	LphTOdoc	Production of doc by Lph	12 ± 2.0	11 ± 9.0	25 ± 19
13	micTOres	Respiration of mic	144 ± 17	134 ± 18	117 ± 19
14	micTOmac	Consumption of mic by mac	19 ± 16	36 ± 22	32 ± 22
15	micTOdet	Production of det by mic	69 ± 22	57 ± 25	58 ± 24
16	micTOdoc	Production of doc by mic	2.5 ± 2.0	10 ± 8.4	17 ± 13
17	mesTOres	Respiration of mes	41 ± 17	109 ± 34	71 ± 26
18	mesTOdet	Production of det by mes	20 ± 11	0.8 ± 0.4	5.0 ± 2.7
19	mesTOdoc	Production of doc by mes	11 ± 4.0	38 ± 16	25 ± 10
20	mesTOmac	Consumption of mes by mac	12 ± 8.0	97 ± 35	51 ± 18
21	macTOres	Respiration of mac	109 ± 21	79 ± 14	75 ± 13
22	macTOdet	Production of det by mac	72 ± 18	60 ± 17	45 ± 14
23	macTOdoc	Production of doc by mac	24 ± 3.0	31 ± 11	36 ± 13
24	macTOfsh	Consumption of mac by small fish (fsh)	**8.6 ± 0.0**	**10 ± 0.0**	**30 ± 0.0**
25	fshTOcod	Consumption of fsh by cod	**2.0 ± 0.0**	**1.0 ± 0.0**	**5.0 ± 0.0**
26	fshTOdet	Production of det by fsh	2.3 ± 1.5	2.9 ± 2.0	9.0 ± 6.0
27	fshTOres	Respiration of fsh	2.3 ± 1.5	2.9 ± 2.0	7.0 ± 5.4
28	fshTOdoc	Production of doc by fsh	1.9 ± 1.2	3.2 ± 1.9	9.0 ± 4.7
29	codTOres	Respiration of cod	0.6 ± 0.3	0.3 ± 0.2	1.0 ± 0.8
30	codTOdet	Production of det by cod	0.4 ± 0.3	0.2 ± 0.2	1.0 ± 0.8
31	codTOdoc	Production of doc by cod	0.6 ± 0.3	0.3 ± 0.2	1.0 ± 0.7
32	codTOext	Removal (export) of cod from the ecosystem	0.4 ± 0.3	0.2 ± 0.2	1.0 ± 0.8
33	docTObac	Bacterial (bac) production	**22 ± 0.0**	**59 ± 0.0**	**90 ± 0.0**
34	bacTOres	Respiration of bac	18 ± 0.8	46 ± 4.5	59 ± 10
35	bacTOmic	Grazing of bac by mic	1.6 ± 1.0	5.6 ± 4.0	12 ± 9.2
36	bacTOdoc	Production of doc by bac	0.5 ± 0.5	2.6 ± 2.4	6.0 ± 5.3
37	bacTOdet	Production of det by bac	1.5 ± 1.0	4.9 ± 3.5	13 ± 9.8
38	detTOdoc	Remineralization of det to doc	2.3 ± 2.1	26 ± 24	22 ± 21
39	detTOmac	Consumption of det by mac	18 ± 14	25 ± 17	48 ± 28
40	detTOmes	Consumption of det by mes	**24 ± 16**	**242 ± 67**	**137 ± 43**
41	docTOext	Export of doc from the ecosystem	37 ± 3.2	84 ± 18	77 ± 30
42	detTOext	Export of det (as particles) from the ecosystem	274 ± 30	182 ± 38	246 ± 35

*Flow symbols are used in **Figure 1**. Flows for which data were used directly (as knowns) are shown in bold; the inverse approach was used to calculate all other flows. Units are mg C m^{-2} d^{-1}. Values presented are means ± standard deviations of 10,000 runs of each model.*

Bacterial productivity values were calculated by multiplying bacterial abundance data by a C-specific production of 0.109 ± 0.89 d^{-1} (L. Seuthe, personal communication) an integrated over 0–45 m during cruises to NW Spitsbergen in 2014 ($n = 7$), and a biomass of 10 fg C $cell^{-1}$ (Fukuda et al., 1998). Microzooplankton grazing rates were estimated from Verity et al. (1999, 2002) in the Barents Sea and Calbet et al. (2011) in the Fram Strait. For the *before* model, we assumed that microzooplankton grazing would be higher on small phytoplankton and flagellates (0.2 d^{-1}) than on the larger phytoplankton (0.05 – 0.1 d^{-1}) based on Strom et al. (2001). In contrast, for the models of *during* and *after* the warm period, when *Phaeocystis* sp. dominated the

phytoplankton community, we assumed that microzooplankton grazing rates on small phytoplankton and *Phaeocystis* sp. were also low (0.05 d^{-1} for *during* and 0.1 d^{-1} for *after*) and no more than 8% of the phytoplankton standing stock based on previous studies (see also Caron et al., 2000; Calbet et al., 2011). *After* the warm period, grazing of microzooplankton on non-*Phaeocystis* sp. was 0.2 d^{-1}. Ingestion rates for the small fish and cod were calculated from annual fish biomass in ICES ASWG 2014 and a conservative C-specific ingestion rate of 0.017 d^{-1} for cod (range of 0.017–0.057 d^{-1}, De Laender et al., 2010) and an average C-specific ingestion rate of 0.04 d^{-1} for capelin and herring (range of 0.01–0.1 d^{-1}, Ajiad and Pushchaeva, 1992; Megrey et al., 2007).

Sources of biomass for compartments are detailed in **Table 3**; these data are used to formulate the constraints used to set bounds on the flows predicted by the model (see Section Inverse Analysis below) (**Table 4**). The conversion factor of 0.132 was used to estimate carbon from wet weight in fishes (Sakshaug et al., 1994). Microzooplankton biomass was estimated from cell counts by the conversion factors of Verity and Lagdon (1984) and Menden-Deuer and Lessard (2000).

Inverse Analysis

The linear inverse modeling approach of Vézina and Platt (1988) was used in conjunction with the Monte Carlo solutions approach of Donali et al. (1999) for estimating the range of values for all flows in our constructed food webs. Model code was run in Matlab R2011b and was kindly provided by Dr. Nathalie Niquil (Centre National de la Recherche Scientifique, Caen, France). The approach taken assumes that biomass in any compartment is in steady state, i.e., the total flows entering any compartment are equal to the flows leaving it without any accumulation or decrease (with the exception of the "external" compartment), although modifications to the approach can be made to accommodate

TABLE 2 | Rates used as "known" flows for the inverse analysis, in units of mg C m^{-2} d^{-1}.

Rate (mg C m^{-2} d^{-1})	*Before*	Sources	*During*	Sources	*After*	Sources
Small Phytoplankton Primary Productivity	122	Arrigo et al., 2008; Arrigo and van Dijken, 2011; Nöthig et al., 2015	554	Arrigo and van Dijken, 2015; Nöthig et al., 2015	483	Arrigo and van Dijken, 2015; Nöthig et al., 2015
Large Phytoplankton Primary Productivity	488	Arrigo et al., 2008; Arrigo and van Dijken, 2011	50	Arrigo and van Dijken, 2015	121	Arrigo and van Dijken, 2015; Nöthig et al., 2015
Bacterial Productivity	22	Tan and Rüger, 1990; Meiners et al., 2003; Seuthe et al., pers. commun.	59	Boras et al., 2010; Seuthe et al., pers. commun.	90	Holding et al., 2013; Le Moigne et al., 2015; Piontek et al., 2015; Seuthe et al., pers. commun.
Microzooplankton grazing on small phytoplankton	117	Verity et al., 1999, 2002; Strom et al., 2001	206	Calbet et al., 2011	170	Verity et al., 1999, 2002; Strom et al., 2001
Microzooplankton grazing on large phytoplankton	117	Strom et al., 2001; Calbet et al., 2011	25	Calbet et al., 2011	42	Strom et al., 2001; Calbet et al., 2011
Cod ingestion	2	De Laender et al., 2010	1	De Laender et al., 2010	5	De Laender et al., 2010
Small Fish ingestion	9	Ajiad and Pushchaeva, 1992; Megrey et al., 2007	10	Ajiad and Pushchaeva, 1992; Megrey et al., 2007	30	Ajiad and Pushchaeva, 1992; Megrey et al., 2007

Values were derived using information in the source materials according to the methods described in the text.

TABLE 3 | Biomass values (mg C m^{-2}) used for the formulation of constraint equations for the inverse analysis.

Compartment	Before	Sources	During	Sources	After	Sources
Small Phytoplankton	583	Nöthig et al., 2015	4113	Nöthig et al., 2015	1696	Nöthig et al., 2015
Large Phytoplankton	2332	Nöthig et al., 2015	127	Nöthig et al., 2015	424	Nöthig et al., 2015
Microzooplankton	100	Svensen et al., 2011	84	Svensen et al., 2011; Monti and Minocci, 2013	209	
Mesozooplankton	550	Blachowiak-Samolyk et al., 2007; Svensen et al., 2011,	1000	Svensen et al., 2011	550	Svensen et al., 2011
Macrozooplankton	4779	Carstensen et al., 2012; Weydmann et al., 2014	2496	Carstensen et al., 2012; Weydmann et al., 2014	2628	Carstensen et al., 2012; Weydmann et al., 2014
Small Fish	216	ICES, 2014; Dalpadado et al., 2016	250	ICES, 2014; Dalpadado et al., 2016	216	ICES, 2014; Dalpadado et al., 2016
Cod	120	ICES, 2014	19	ICES, 2014	120	ICES, 2014
Bacteria	200	Tan and Rüger, 1990; Meiners et al., 2003	519	Boras et al., 2010	454	Holding et al., 2013; Le Moigne et al., 2015; Piontek et al., 2015

Values were derived using information in the source materials according to the methods described in the text. For the phytoplankton, chlorophyll values were taken from Nöthig et al. (2015) and were converted to carbon biomass using a C:chl ratio of 53 (g:g; Svensen et al., 2011). Size fractions were apportioned according to Nöthig et al. (2015) (see text for details).

TABLE 4 | Constraints on carbon flows for the inverse analysis.

Process-Compartment	Bound	Description	Equation	References
Respiraton-Bacteria	Lower	At least 30% of total DOC production	0.3×(Total DOC production)	Niquil et al., 2011
	Upper	No more than the maximum specific respiration (d^{-1}); a function of cell size (W; pgC $cell^{-1}$) and temperature (T)×bacterial biomass (mgC m^{-3})	$1.7W^{-0.25} \times e^{(0.0693 \times (T-20))} \times$ Biomass	Moloney and Field, 1989
Respiration-Small and Large Phytoplankton	Lower	At least 5% of Small or Large Phyto GPP	0.05×(GPP)	Vézina and Platt, 1988
	Upper	No more than 30% of Small or Large Phyto GPP	0.3×(GPP)	Vézina and Platt, 1988
Respiration-Microzooplankton	Lower	At least 20% of total ingestion	0.2×(Total ingestion by microzooplankton)	Vézina and Pace, 1994; Vézina et al., 2000
	Upper	No more than the maximum specific respiration (d^{-1}); a function of body size (W; pgC $cell^{-1}$) and temperature (T)×microzooplankton biomass (mgC m^{-3})	$14W^{-0.25} \times e^{(0.0693 \times (T-20))} \times$ Biomass	Moloney and Field, 1989
Respiration-Mesozooplankton	Lower	At least 20% of total ingestion	0.2×(Total ingestion of mesozooplankton)	Vézina and Pace, 1994; Vézina et al., 2000
	Upper	No more than the maximum specific respiration (d^{-1}); a function of body size (W; pgC $cell^{-1}$) and temperature (T) ×mesozooplankton biomass (mgC m^{-3})	$14W^{-0.25} \times e^{(0.0693 \times (T-20))} \times$Biomass	Moloney and Field, 1989
Respiration-Macrozooplankton	Lower	At least 20% of total ingestion	0.2×(Total ingestion of macrozooplankton)	Vézina and Pace, 1994; Vézina et al., 2000
	Upper	No more than the maximum specific respiration (d^{-1}); a function of body size (W; pgC $cell^{-1}$) and temperature (T) ×macrozooplankton biomass (mgC m^{-3})	$14W^{-0.25} \times e^{(0.0693 \times (T-20))} \times$Biomass	Moloney and Field, 1989
Excretion-Small and Large Phytoplankton	Lower	No <2% of NPP	0.02×(NPP)	Baines and Pace, 1991
	Upper	No more than 55% of NPP	0.55×(NPP)	Baines and Pace, 1991
Excretion-Microzooplankton	Lower	10% of total ingestion	0.1×(Total ingestion by microzooplankton)	Vézina and Pace, 1994
	Upper	100% of Respiration	1×(microzooplankton respiration)	Vézina and Platt, 1988
Excretion-Mesozooplankton	Lower	10% of total ingestion	0.1×(Total ingestion by mesozooplankton)	Vézina and Pace, 1994
	Upper	100% of Respiration	1×(mesozooplankton respiration)	Vézina and Platt, 1988
Excretion–Macrozooplankton	Lower	10% of total ingestion	0.1×(Total ingestion by macrozooplankton)	Vézina and Pace, 1994
	Upper	100% of Respiration	1×(mesozooplankton respiration)	Vézina and Platt, 1988
Excretion–Small Fish	Lower	6.6% of total ingestion	0.066×(small fish ingestion)	Klumpp and von Westernhagen, 1986
Excretion–Cod	Lower	10% of total ingestion	0.1×(cod ingestion)	Holdway and Beamish, 1984
Macrozooplankton Grazing	Lower	30% of Large Phytoplankton NPP	0.3×(NPP of Large Phytoplankton)	Based on Wassmann et al., 2006
Assimilation Efficiency–Microzooplankton	Lower	50% of total ingestion	0.5×(microzooplankton ingestion)	Straile, 1997
	Upper	90% of total ingestion	0.9×(microzooplankton ingestion)	Straile, 1997
Assimilation Efficiency–Mesozooplankton and Macrozooplankton	Lower	50% of total ingestion	0.5×(mesozooplankton or macrozooplankton ingestion)	Straile, 1997
	Upper	80% of total ingestion	0.8×(mesozooplankton or macrozooplankton ingestion)	Straile, 1997
Bacterial Growth Efficiency	Lower	30% of ingestion	0.3×(bacterial ingestion of DOC)	Straile, 1997
	Upper	90% of ingestion	0.9×(bacterial ingestion of DOC)	Straile, 1997
Gross Growth Efficiency–all zooplankton groups	Lower	25% of total group-specific ingestion	Excretion × Respiration losses = 75% of group-specific ingestion	Straile, 1997
	Upper	50% of total group-specific ingestion	Excretion × Respiration losses = 50% of group-specific ingestion	Straile, 1997

GPP, gross primary productivity; NPP, net primary productivity; DOC, dissolved organic carbon. Values used for carbon content (W) were 6.3 fg C $cell^{-1}$ for bacteria (Kawasaki et al., 2011), 1.7 pg C $individual^{-1}$ for microzooplankton, 2214 pg C $individual^{-1}$ for mesozooplankton and 2.31 × 10^8 pg C $individual^{-1}$ for the macrozooplankton (Bamstedt et al., 1991). Temperatures were assumed to be 3.5, 5, and 4°C for before, during, and after the warm anomaly, respectively (Beszczynska-Moller et al., 2012).

non-steady state scenarios by allowing residual flows to balance the system (e.g., Richardson et al., 2003).

As described above, data from the scientific literature were used to formulate 7 input equations. Combined with the 10 mass balance equations (one for each compartment; see **Table 5**), there were 17 equations available to describe the system with 42 flows. We reduced the number of possible solutions for this underdetermined system by applying a set of biological constraints (provided in **Table 4**). Allometric constraints based on published relationships incorporated available biomass data and provided upper and lower bounds on the rates and efficiencies of biological processes. For example, the respiration of all phytoplankton was constrained to be at least 5% but no more than 30% of the gross primary productivity (GPP) (Vézina and Platt, 1988). Growth efficiencies were assumed to be 25–50% of ingestion for the zooplankton groups (Straile, 1997). Bounds on assimilation efficiencies for all grazers were 50–90% of ingestion for the microzooplankton (Vézina and Platt, 1988; Straile, 1997) and 50–80% for the macrozooplankton (Straile, 1997). We also set a lower bound on the macrozooplankton grazing such that they consumed at least 30% of the large phytoplankton productivity (based on Wassmann et al., 2006). Other constraints are detailed in **Table 4**. We used temperatures of 3.5, 5, and 4°C for the *before*, *during* and *after* models, respectively (Beszczynska-Moller et al., 2012).

Application of constraints reduces the range of possible solutions, but does not provide a unique solution. The Monte Carlo approach of Donali et al. (1999) (see also the review by Niquil et al., 2012) calculates 10,000 possible solutions for each set of flows, thus we were able to calculate both an average and a standard deviation for each flow in the food web.

Econetwork Analysis of Inverse Solutions

After food webs were constructed for the *before*, *during* and *after* warm water event, the structure and function of each web was assessed using EcoNetwork analysis software (available at https://www.cbl.umces.edu/~ulan/ntwk/network.html; see also Ulanowicz and Kay, 1991; Ulanowicz, 2004). Michaels and Silver (1988), Ducklow et al. (1989), and McManus (1991) used earlier versions of this program to examine flows of nitrogen and energy, respectively, through microbial food webs to higher trophic levels in planktonic systems. We chose a key index from the output, *input/export vectors*, to calculate how much of each input flow (i.e., primary production of the two phytoplankton groups) eventually was exported through the three possible routes of export (via cod, detritus, or DOC). This calculation allowed us to break down the export flows into the relative contributions by the flagellate (small) vs. diatom (large) phytoplankton.

RESULTS

Food webs constructed for *before*, *during*, and *after* the warm anomaly (**Figure 2**) differ substantially with respect to the input flows (contributions by the small phytoplankton and flagellates vs. large phytoplankton), trophic transformations, and predicted export pathways (**Figure 2**, **Table 1**). While diatoms (or large phytoplankton) dominated primary productivity before the warm anomaly in the WSC, *Phaeocystis* sp. accounted for 97% of the primary productivity during the warm years, and small phytoplankton (*Phaeocystis* sp. and flagellates) continued to dominate for almost 4 years after the peak in water temperature. The dominance of *Phaeocystis* sp. and low grazing of this material by the microzooplankton *during* the warm water event (see also Calbet et al., 2011) resulted in the model prediction of more carbon from flagellates (or small phytoplankton) going to detritus, which then became an important source of food for mesozooplankton or macrozooplankton (**Figure 3**).

In general, the zooplankton diet in the model reflected the dominant phytoplankton community composition (**Figure 3**). When large phytoplankton dominated *before* the warm water event, the microzooplankton fed equally on small and large phytoplankton, but consumed mostly carbon originating from small cells and flagellates in the *during* and *after* periods. The mesozooplankton diet changed *during* and *after* the warm anomaly to rely more heavily on detritus than on the large phytoplankton, while the carbon flow increased

TABLE 5 | Mass balance equations (inputs–outputs = 0) for the inverse analysis.

Mass balance for:	Equation
Sph	gSpTOSph–SphTOres–SphTOmic–SphTOdet-SphTOdoc=0
Lph	gLpTOLph–LphTOres–LphTOmic–LphTOmes–LphTOmac–LphTOdet–LphTOdoc=0
mic	SphTOmic+LphTOmic+bacTOmic–micTOres–micTOmac-micTOdet-micTOdoc=0
mes	LphTOmes–mesTOres–mesTOdet–mesTOdoc-mesTOmac=0
mac	LphTOmac+micTOmac+mesTOmac–macTOres–macTOdet–macTOdoc–macTOfsh=0
fsh	macTOfsh–fshTOcod–fshTOdet–fshTOres–fshTOdoc=0
cod	fshTOcod–codTOres–codTOdet–codTOdoc–codTOext=0
bac	docTObac–bacTOres–bacTOdoc–bacTOmic=0
doc	SphTOdoc+LphTOdoc+micTOdoc+mesTOdoc+macTOdoc+fshTOdoc+codTOdoc+bacTOdoc–docTObac –docTOext=0
det	SphTOdet+LphTOdet+micTOdet+mesTOdet+macTOdet+fshTOdet+codTOdet+bacTOdet–detTOdoc–detTOmes–detTOmac–detTOext=0

Sph, small phytoplankton; Lph, large phytoplankton; mic, microzooplankton; mes, mesozooplankton; mac, macrozooplankton; fsh, small fish; cod, Cod fish; bac, bacteria; doc, dissolved organic carbon; res, respiration; det, detritus. gSp and gLp are the gross primary productivity of the small and large phytoplankton, respectively. Ext refers to the export of material to an external compartment (out of the ecosystem).

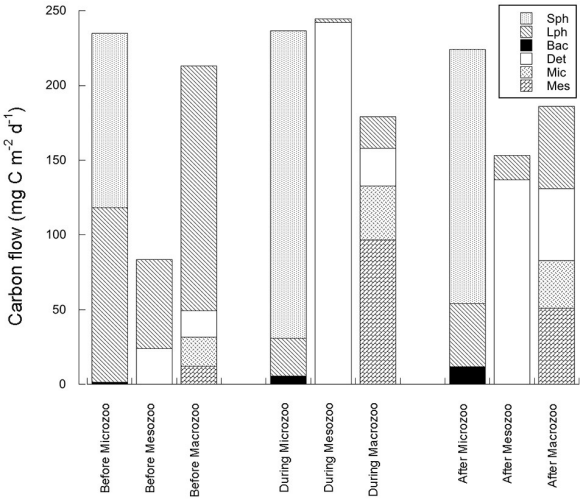

FIGURE 3 | Carbon flow, predicted by the inverse modeling, through the zooplankton compartments (microzooplankton <200 μm, mesozooplankton, 200–100 μm and macrozooplankton (>1,000 μm) during three time periods in the Fram Strait, *before, during* and *after* the warm water event of 2005–2007. Compartment identification as in **Figure 2**.

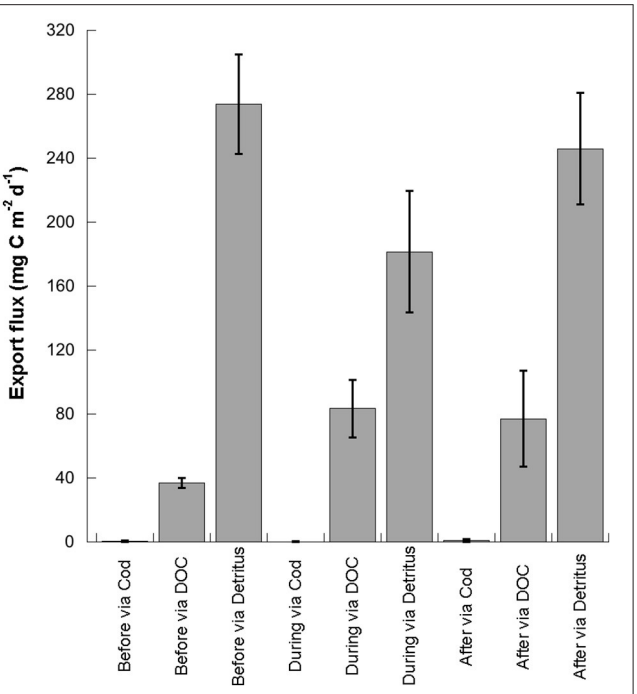

FIGURE 4 | Main pathways of carbon export, predicted by the inverse modeling, during time three periods in the Fram Strait, *before, during*, and *after* the warm water event of 2005–2007: via cod, top predator, via dissolved organic carbon (DOC) and via particulate organic carbon (POC) or detritus. Error bars indicate one standard deviation from the mean.

from $<100\,\text{mg C m}^{-2}\,\text{d}^{-1}$ to $>150\,\text{mg Cm}^{-2}\,\text{d}^{-1}$. In contrast, macrozooplankton carbon flow was predicted to remain somewhat constant through the three periods albeit important changes in the quality of diet, from mostly feeding on large phytoplankton, to a mixed diet where 50% of the carbon originated from the abundant mesozooplankton, and an even more mixed diet *after* the warm water event, with approximately equal consumption of large phytoplankton, detritus, microzooplankton and mesozooplankton (**Table 1**, **Figures 2**, **3**).

Carbon in the form of detritus dominated the export fluxes, and was generally higher in the *before* period than *during* or *after* the warm event (**Figure 4**, **Table 1**). Carbon that originated from the diatoms dominated detrital export *before* the warm anomaly (86% of the total detritus export flux vs. 14% from the flagellates), but carbon from flagellates comprised the majority of the carbon exported as detritus *during* (96% small, 4% large) and *after* (89% small, 11% large) the warm water anomaly (**Figures 4**, **5**).

Calculated rates of respiration were dominated overall by the small phytoplankton and the microzooplankton (**Figure 6**). Microzooplankton and macrozooplankton respiration were maximum *before*, and mesozooplankton respiration rates were highest in *during* the warm water event. Only planktivorous fish and bacteria showed maximum respiration in *after* period. The largest changes were from *before* to *during* in small phytoplankton and mesozooplankton.

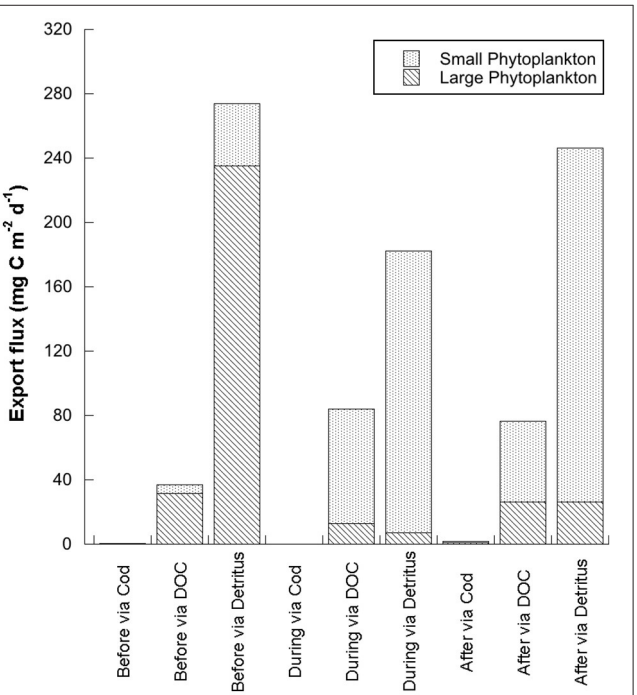

FIGURE 5 | Pathways of small (including *Phaeocystis sp.*) and large (diatom) phytoplankton carbon export: via cod, via dissolved organic carbon (DOC) and via particulate organic carbon (POC) or detritus.

DISCUSSION

Carbon flow through pelagic food webs is impacted by the composition and biomass of the primary producers, the phytoplankton. It is expected that Arctic environmental change

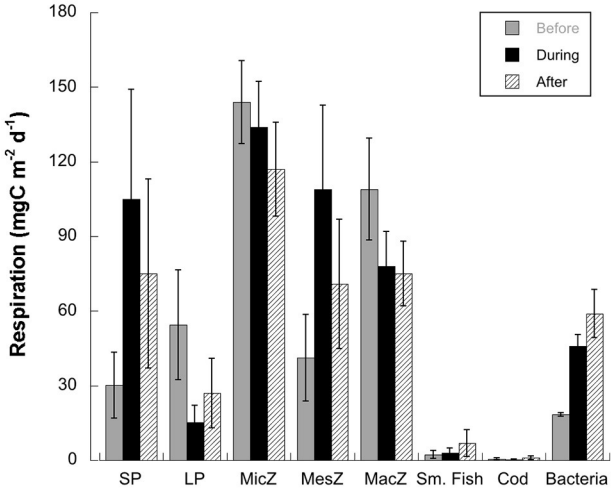

FIGURE 6 | Respiration rates of the main food web compartments, predicted by the inverse modeling, during three time periods in the Fram Strait, *before, during,* and *after* the warm water event of 2005–2007. Compartment identification as in **Figure 2**.

in response to climate warming will lead to modifications in phytoplankton species composition, cell size and biomass (Daufresne et al., 2009; Winder and Sommer, 2012). Consequences of these changes must be elucidated via field studies and modeling. We selected a modeling approach to study possible consequences in carbon cycling in the WSC, Fram Strait ecosystem from observed phytoplankton changes (Nöthig et al., 2015). Inverse modeling can synthesize and test current understanding in a system as well as provide a first approximation of carbon flows for which data are sparse. It has been applied in high latitude waters, mainly the Barents Sea (De Laender et al., 2010), the Amundsen Bay in the Canadian High Arctic (Forest et al., 2010), and in the western Antarctic Peninsula (Daniels et al., 2006; Sailley et al., 2013). The results from the model presented here are considered hypotheses about how the phytoplankton carbon could cycle in Arctic regions subject to shifts in phytoplankton composition.

The changes in carbon flow predicted by the inverse model from *before* to *after* warm water conditions parallel the changes modeled by Rivkin et al. (1996) in food webs from the Gulf of St. Lawrence. There, the structure of the food web changed from the colder spring bloom period, when large phytoplankton and herbivory by mesozooplankton dominated, to a warmer summer, microbial-dominated food web, but the amount of carbon exported in the cold vs. the warm periods was not substantially different. In summer, the mesozooplankton switched from eating large phytoplankton to consuming mainly microzooplankton. Thus, while the pathway of carbon through the system changed, the POC export flux did not. The Fram Strait system responded similarly; grazing was replaced by omnivory during warm water periods in the absence of large diatoms (**Figure 3**). The generality of the response is more striking as the post-bloom condition in the Gulf of St. Lawrence and the eastern Fram Strait were different: the first one was dominated by dinoflagellates where in the latter, diatoms were replaced by *Phaeocystis* sp. and nanoflagellates.

The inverse model suggested a scenario predicted already by Weisse et al. (1994) for the North Sea *Phaeocystis* sp. blooms. This author speculated that mesozooplankton, especially small copepods like *Acartia* and *Temora*, may indirectly benefit from *Phaeocystis* sp. blooms by feeding on detrital particles or microzooplankton. Vast amounts of detritus appear in the form of marine snow during and after *Phaeocystis* sp. blooms that, when coated with bacteria and microheterotrophs, is considered nutritious (Heinle et al., 1977). This new scenario of trophic pathways is not commonly found in the literature, as very little is known about pelagic detritivory. It has been proposed that zooplankton ingestion of detritus breaks up marine snow particles, facilitating bacterial degradation that, in turn, increases the nutritional value of the organic matter (Mayor et al., 2014). Although these authors focus their hypothesis on the water column below the euphotic zone, similar processes could occur in the mixed layer.

Response of Phytoplankton to the Warming Event in Eastern Fram Strait

The prediction of the proliferation of small cells in a future warmer ocean is usually associated with flagellates, whereas larger cells are presumed to be diatoms (Li et al., 2009, but see Wright et al., 2010). In the WSC, the transition of phytoplankton communities exposed to elevated temperatures can be more complex: the prymnesiophyte *Phaeocystis* sp. is a flagellate that can form both large colonies as well as single cells (Rousseau et al., 2000). In the WSC, the warming event was associated with a proliferation of this microalga from the summer of 2005 onwards, i.e., different clades of *Phaeocystis* sp. were dominant *during* and *after* the warm water event from 2005 to 2007 (Nöthig et al., 2015). This species is not new to the Fram Strait, commonly found in the region in spring and summer (Smith, 1987; Hegseth and Tverberg, 2013; Saiz et al., 2013). *P. pouchetti* slowly decreased in concentration after 2007 with an average 45% concentration *after* the warm water event. A major consequence of this shift from diatoms to *Phaeocystis* sp. is the change in grazing pressure; *Phaeocystis* sp. experiences less grazing than other flagellates (Caron et al., 2000; Strom et al., 2001; Calbet, 2008; Calbet et al., 2011).

Blooms of single-cell *Phaeocystis* sp. are of widespread distribution, with individual cells of 3–7 μm (Vernet et al., 1996; Kozlowski et al., 2011; Metfies et al., 2016) although it is generally considered that *Phaeocystis* sp. blooms in its colonial form, with colonies in excess of 100 μm and up to 1000 μm (Schoemann et al., 2005; Lasternas and Agusti, 2010). Single-cell *Phaeocystis* sp. in the eastern Fram Strait was observed in 2012 *after* the warm event in the <3 μm phytoplankton size fraction (Metfies et al., 2016). The proportion of *P. pouchetii* in colonial or in single-cell form at the WSC in 2005–2007 is unknown; both forms were modeled in this study (Stelfox-Widdicombe et al., 2004).

The model provides realistic estimates of phytoplankton growth rates, approximated from C-specific primary production. Flagellates grew at an average 0.2, 0.13, and 0.28 d^{-1} and large

cells at an average 0.21, 0.39, and 0.28 d^{-1} within the surface layer *before*, *during* and *after* the warm water event, respectively. These rates were not measured, the biomass originated from the field (**Table 3**) and primary production from the model output (**Table 1**), which carry the inherent approximation that both phytoplankton size fractions have equal photosynthetic efficiency.

Trophic Pathways during a Shift in Phytoplankton Composition

When diatoms dominated (i.e., cells > 10 μm), the model predicted that phytoplankton were consumed by meso- and macrozooplankton herbivores, with a major carbon flow from fecal pellets to detritus and eventual export (i.e., sedimentation, **Figure 2**). Carbon also flowed to detritus and microzooplankton, accounting for the rest of the large cells, but the contribution was minor based on the small grazing pressure of microzooplankton on diatom blooms (**Figure 3**, Sherr and Sherr, 2009). The inverse model suggested that when *Phaeocystis* sp. dominated pelagic photosynthetic communities, e.g., by contributing up to 97% of the autotrophic community, phytoplankton carbon goes directly to detritus, and to a lesser extent to microzooplankton and DOC production (**Figure 3**). Mesozooplankton fed mostly on the detrital carbon, originating from phytoplankton sinking and fecal pellets, while a large proportion of the detritus was also exported. In this way, the mesozooplankton role in the food web increased when flagellates dominated but macrozooplankton role stayed rather constant, as in the case of microzooplankton. Total export out of the system decreased by 15%, due to a 35% diminution in POC export while DOC export increased (**Figure 4**). When the phytoplankton community bounced back to more diatoms, but still with ∼45% *Phaeocystis* sp., overall export of particulate carbon also recovered while DOC contribution remained high (**Figure 4**). Additionally, the increase in microzooplankton and bacterial abundance *during* and *after* the warm water period indicate an increase in substrate, as expected from Kirchman et al. (2009a,b). The modeled sedimentation flux, where the mixed phytoplankton community composed of diatoms, *Phaeocystis* sp. and nanoflagellates exported as much carbon as diatoms alone, was also expected from the sediment trap data of Lalande et al. (2013) that showed that fluxes remained the same and only the quality changed. However, these model predictions are novel and will be discussed further.

Detritus Formation

The results of the inverse model suggest that when *Phaeocystis* sp. dominated the phytoplankton community a large proportion of the biomass was not consumed by grazers and was lost to other processes, mostly routed through detritus (e.g., marine snow), DOC production and respiration. The model did not predict high DOC production (**Table 1**, see below for further discussion) and the respiration changed based mostly on the amount of carbon cycling each through each compartment (compare **Figures 2**, **3** with **Figure 6**) and to lesser extent to higher ambient temperature; the remaining possibility was for the carbon to flow to detritus as marine snow. Most of the detritus originated from phytoplankton sinking or coagulating, from 148 mg C m^{-2} d^{-1} from diatoms in the *before* conditions to 313–348 mg C m^{-2} d^{-1} in the *during* and *after* conditions, mostly from *Phaeocystis* sp. (**Table 1**). Due to lack of data, the model does not have rigid constraints for this flow that at its highest reached 50% of the *Phaeocystis sp*. primary production in the *during* and *after* time periods (compare flows 5 and 1 in **Table 1**), whereas 26% of the diatom primary production was converted to detritus in the *before* conditions. These results suggest a doubling of the phytoplankton-detritus flow *during* the warm water event compared to the *before* (diatom) conditions, similar to observations of high concentration of marine snow in the North Sea during and after *Phaeocystis* sp. blooms (Lancelot and Mathot, 1987; Riebesell et al., 1993).

Microzooplankton Grazing

High microzooplankton grazing in summer/post-bloom/*during* conditions rich in flagellates has been well documented in the field (Vernet, 1991; Verity et al., 2002; Calbet and Saiz, 2005) and grazing efficiency of the microzooplankton can be lower when feeding on large phytoplankton cells (Strom et al., 2001). In the model, microzooplankton grazed on equal amounts of diatoms and small cells *before* 2003. *During* and *after* the warm water event, this compartment grazed mainly on *Phaeocystis sp*., maintaining their overall carbon intake (flow 4, **Table 1**). Microzooplankton consumed 235, 236, and 224 mg C m^{-2} d^{-1} in the form of large and small phytoplankton and bacteria in the *before*, *during*, and *after* conditions (**Table 1**), corresponding to a grazing rate of ∼0.08, ∼0.055, and ∼0.1 d^{-1}. These grazing rates are lower than what was observed in the Barents Sea for non-*Phaeocystis* phytoplankton (0.24 ± 0.1, 0.29 ± 0.13, 0.33 ± 0.11 d^{-1}, Verity et al., 2002), and within the median value of Calbet et al. (2011) during a *Phaeocystis sp*. bloom (observed range of −0.04–0.14 d^{-1}) in the Fram Strait. The explicit grazing inhibition by *Phaeocystis sp*. in the model (see Methods) is found not only in the Fram Strait but also in Antarctica (Caron et al., 2000) and elsewhere (Strom et al., 2001). In their review, Nejstgaard et al. (2007, Table 4) report grazing rates of 0.0–0.36 d^{-1} on solitary *Phaeocystis* sp. cells (3–8 μm). For field observations, the same authors report microzooplankton grazing was positive in April 2003 (0.21 ± 0.3 d^{-1}) and negative in May 2004 (−0.23 ± 0.34 d^{-1}). Without detailed knowledge of the factors affecting *Phaeocystis sp*. grazing in the WSC after 2004, the rates in the model are in the middle of the range found in the literature, and thus considered conservative. Further estimates of microzooplankton grazing, in particular in large phytoplankton and during *Phaeocystis* sp. blooms in the Arctic, are needed in order to improve our model parameterizations and our understanding of the fate of *Phaeocystis* sp. carbon through this compartment in the food web.

Inhibition of microzooplankton grazing by *Phaeocystis sp*. is similar to observations on other Ecosystem Disruptive Algal Blooms and Harmful Algal Blooms (EDABs and HABs). Acrylic acid, released by *Phaeocystis sp*. in the conversion from dimethylsulfoniopropionate (DMSP) to dimethylsulfide (DMS),

is considered an antibiotic (Sieburth, 1960) and other growth and grazing inhibitors could be released by this species as well (Nejstgaard et al., 2007, but see Turner, 2015). The production of toxins by phytoplankton has lethal or sub-lethal effects on the microzooplankton, both for ciliates or tintinnids (Verity and Stoecker, 1982; Carlsson et al., 1990; Hansen, 1995). Rosetta and McManus (2003) concluded that ciliates may exert grazing pressure on HAB species early on, potentially contributing to the suppression and decline of *Prymnesium minimum* and *P. parvum* before they bloomed, but that ciliate grazing would be relatively ineffective once blooms (and toxicity) developed fully. In mixed diets, as long as non-toxic cells were available, ciliates survived and sometimes grew well at concentrations that otherwise would have killed them. Similar for rotifers, when exposed to a mixed diet of toxic and non-toxic phytoplankton species, these protists would tolerate and even acclimate to a toxic species (e.g., *Karenia brevis*), supporting the notion of low but positive grazing rates when *Phaeocystis* sp. was dominant (**Table 2**).

Grazing by Copepods

Grazing of meso- and macrozooplankton on *Phaeocystis* sp. depends on multiple environmental factors and it is not predictable. Nejstgaard et al. (2007) conclude in their review on grazing impacts on *Phaeocystis* sp. that small copepods cannot feed on colonies whereas macrozooplankton can. It has been observed that Arctic copepods do not avoid surface waters during *Phaeocystis* sp. blooms (Norrbin et al., 2009). However, Saiz et al. (2013) reported that under these conditions the copepod ingestion rate was low in spite of positive grazing rates, making a low impact on phytoplankton standing stocks. In this way, same as with microzooplankton grazing, *Phaeocystis* sp. seems to deter herbivory of larger zooplankton.

Mesozooplankton grazing

Grazing by mesozooplankton on diatoms, flagellates and detritus was set by the model within the constraints in this compartment on assimilation efficiency, respiration, excretion and growth gross efficiency (**Table 4**). Mesozooplankton consumed diatoms and detritus in the *before* conditions; in the absence of diatoms this compartment could decrease or consume more detritus. The model predicted detritivory, with an overall increase in mesozooplankton abundance (**Figure 3**, **Table 1**). Overestimation of detritivory with respect to other mesozooplankton feeding behavior by the model is possible due to the lack of constraints on this flow. As an alternative, mesozooplankton could consume more microzooplankton (Stoecker and Capuzzo, 1990; Rivkin et al., 1996). This pathway was not explicit in the model (**Figure 1**) as flows were limited to those identified as most important in the Fram Strait literature, where small copepods are considered of minor importance (Falk-Petersen et al., 2009; Nöthig et al., 2015). However, they might play a major role during the summer (Svensen et al., 2011). Results from the inverse model suggest that mesozooplankton could be an important carbon compartment in this region's food web and their role deserves further study and experimentation.

Macrozooplankton grazing

Macrozooplankton did not change ingestion on microzooplankton or detritus when *Phaeocystis sp*. was abundant, rather they increased predation on mesozooplankton. These results contrast with those of De Laender et al. (2010) that predicted higher trophic levels in food webs in the southern Barents Sea, flooded by Atlantic waters from another branch of the Norwegian Atlantic Current, could rely on the microbial loop as a source of carbon, with a doubling of microzooplankton as food source for *Calanus* spp. copepods. These authors argue that when small zooplankton is dominant during warmer periods, their feeding strategies are more suited to ciliate predation (e.g., Svensen and Vernet, 2016). In the Fram Strait model, macrozooplankton consumed 213, 179, and 196 mg C m^{-2} d^{-1} *before*, *during* and *after* the warm water event from diatoms, microzooplankton, mesozooplankton and detritus (**Table 1**, **Figure 3**). In the absence of diatoms, large zooplankton switched their intake to 8x more mesozooplankton, 2x more microzooplankton, but remained rather constant on detritus consumption.

Results from grazing experiments do not present a clear picture on *Phaeocystis*-zooplankton interactions. In their review, Nejstgaard et al. (2007) found a large variability in grazing rates within the literature, attributed to differences in *P. globosa* and *P. pouchetii* strains, cell types, physiological state, etc. In addition to grazing, macrozooplankton has the ability to break up large marine snow aggregates into smaller ones, facilitating their decomposition and increasing their nutrition (Dilling and Alldredge, 2000). The grazing estimates in the inverse model compare well with recent experimental results in the Fram Strait: Hildebrandt (2014) reports an average concentration of 26.6 *Calanus finmarchicus* per m^3 with a grazing rate of 0.0028–0.014 μg chl*a* h^{-1} for the summer of 2012; in a 45-m upper layer and assuming 24-h feeding during boreal summer the copepods could consume up to 24 mg C m^{-2} d^{-1}. Similarly, average macrozooplankton grazing rates of 0.089, 0.205, and 0.137 d^{-1} for *Calanus glacialis*, *C. hyperboreus*, and *C. finmarchicus*, respectively, with an average rate of 0.15 d^{-1}, were reported by Weydmann et al. (2014); these copepods could consume 349, 19, and 63 mg C m^{-2} d^{-1} *before*, *during* and *after* the warm water event (based on phytoplankton biomass from **Table 3**). These calculations based on Fram Strait experiments and field data agree with results in the North Sea where of *P. globosa* was not considered a good food source for copepods (Gasparini et al., 2000). In spite of selecting for diatoms and microzooplankton, copepods suffered during a *Phaeocystis* sp. bloom; copepods consumed 27–50% of the copepod carbon weight per day during diatom dominance that decreased to 7–17% during the *Phaeocystis* sp. bloom and to 14–21% after the bloom.

Detritivorous copepods

Detritivorous copepods are usually considered to feed below the euphotic zone. Jackson (1993) suggested that this process could explain the decreased in POC sedimentation in the ocean

where only a few percentage of primary production reaches the sediments. "Flux feeding" was proposed as a major carbon flow to complement bacterial degradation of sinking organic matter that could not explain all the carbon reduction with depth. Similarly, Reigstad and Wassmann (2007) measuring recycling of *Phaeocystis* sp. phytodetritus found that between 7 and 11% of *Phaeocystis* sp. biomass reaches 40 m depth and only 3 ± 2% reaches 100 m. Assimilation efficiency of zooplankton feeding marine snow in the California Current were 64–83% (Dilling et al., 1998). Similarly, 70% retention of copepod and euphausiid fecal pellet carbon was established in the mixed layers of the Barents Sea thru flux feeding (Wexels Riser et al., 2002), but no studies exist of Arctic copepods and other planktonic organisms consuming sinking phytodetritus (Turner, 2015). For the California Current, Graham et al. (2000) explained diel variability in marine snow concentration in the upper water column to nighttime consumption by vertically migrating zooplankton. There is evidence of high mesozooplankton abundance during periods of *Phaeocystis* sp. blooms in the North Sea (Fransz and Gieskes, 1984; Weisse et al., 1986). In the Arctic, there is an increasing awareness that small copepods have been undersampled due to large mesh sizes in zooplankton nets. Svensen et al. (2011) argue the best method to sample small copepods quantitatively is with water bottles (e.g., 30-L Niskin). Small copepods have a high growth rate and reproduce year around, are not restricted in their reproduction to the spring bloom as are large copepods and thus can be very abundant year around (Svensen et al., 2011). The model results highlight the possibility that if *Phaeocystis* sp. is not consumed at a high rate, the mesozooplankton could benefit (as predicted by Weisse et al., 1994). Potential detritivory and the role of mesozooplankton during periods of *Phaeocystis* sp. dominance are ideas that deserve further study.

Bacteria

The model predicts a higher bacterial abundance and activity in warmer periods in the Arctic, when the phytoplankton community is dominated by flagellates, resulting in a more active microbial food web (**Table 1**, **Figure 6**). The bacterial activation occurs parallel to detritus formation, *during* and *after* the warm water anomaly. Bacteria decomposition of this detrital material is accounted for in the model (flow 36 in **Table 1**), so bacteria can either benefit from phytoplankton excretion or lysis as DOC, other sources of DOC production, or particulate matter degradation (**Figure 2**). Bacterial production, based on abundance and a C-specific production of $0.1 \pm 0.98\ d^{-1}$ (Seuthe, pers. commun.), is predicted at 22, 59, and 90 mg C m^{-2} d^{-1} *before, during, after* the warm water event (flow 33 in **Table 1**). These estimates are within those observed in the region. In the productive waters of Kongsfjorden, a fjord in the western coast of Spitsbergen, Iversen and Seuthe (2011) reported that for 2006, integrated over 0–50 m depth, bacterial production was 105 mg mg C m^{-2} d^{-1} and bacterial respiration 56 mg C m^{-2} d^{-1}. For open waters close to the HAUSGARTEN station, surface bacterial production is highly variable, and was estimated at 2 mg C m^{-3} d^{-1} (or 90 mg C m^{-2} d^{-1}) between 25 June and 20 July 2011 (Piontek et al., 2014, 2015).

DOC Production

In the model, DOC is produced by all living compartments via phytoplankton excretion, by bacterial activity (including detritus) and by zooplankton sloppy feeding (**Figure 1**, **Table 1**). DOC production increased during the flagellate periods, with more DOC produced in the *during* and *after* scenarios: from 57.3 to 116.1 mg C m^{-2} d^{-1} and 143 mg C m^{-2} d^{-1} as a result of bacterial activity (flow 36), of grazing by microzooplankton (flow 16), by mesozooplankton (flow 19) and by macrozooplankton (flow 23) (**Table 1**, **Figures 3**, **6**). Due to restrictions in the number of flows (see Methods) viruses and fungi, another potential source of DOC production, were not included explicitly as part of the microbial loop, but their activity was implicit in phytoplankton DOC production. The constraints for this compartment were chosen to allow for "excess" (beyond normal excretion) DOC production, up to 55% of the primary production (**Table 4**). The DOC rates from phytoplankton predicted by the model are toward the low end of this range, 2.1% to 14% for large phytoplankton, and 3–4.1% for *Phaeocystis* sp. (**Table 1**). These estimates are close to the 10% universal estimate on phytoplankton excretion even in the presence of mucilaginous colonies (Veldhuis et al., 1986), and lower than field measurements in the Arctic of up to 39% (Vernet et al., 1998; Matrai et al., 2007; Poulton et al., 2016). The extent of DOC production by viral lysis in the Arctic is not well characterized. In the North Atlantic, Mojica et al. (2016) reported elevated rates of DOC production from phytoplankton viral lysis, with a "striking reduction" toward high latitudes, where the ratio of viral lysis to grazing decreased by up to two orders of magnitude in comparison to lower latitudes. Fungi are reported to be abundant in sea ice, but have not been found in any quantity in seawater (Hassett and Gradinger, 2016). Metfies et al. (2016), analyzing data for this region, did not detect many fungi (OTUs) in the water column; they were found only occasionally in waters dominated by diatoms. Fungi seem to be mainly associated with marine snow (Bochdansky et al., 2017) and in sediment-trap material (Metfies, in prep.). Increasing the lower limit of DOC production in the model can force more carbon through the DOC compartment which might decrease other loss terms, such as detritus production *during* and *after* the warm water event, presumably channeling more carbon through the microbial loop. The complexity of the microbial food web in Arctic waters, including viruses and fungi, requires further experimentation. The model for this study (**Figure 2**) was structured to maximize all the pathways that contribute to carbon sedimentation out of surface waters in the WSC and is thus not the best vehicle to represent a complete picture of microbial processes in this region, which would probably require a model restricted to lower trophic levels only.

Carbon Export

What the inverse model in this study provides is a picture of possible carbon pathways within Arctic food webs that could explain how to maintain an important contribution of phytoplankton carbon to deep water in the absence of a diatom bloom. Export of carbon originating from non-diatoms is not surprising (**Figure 4**). Picoplankton and flagellates have

been observed in sedimenting matter for the last 30 years: *Synechococcus* was a major contributor to fluxes to the deep sea (Lochte and Turley, 1988) and has been detected in the South Pacific (Waite et al., 2000), tropical Pacific (Stukel et al., 2013) and in equatorial Pacific, Atlantic and Indian Oceans (e.g., Lampitt et al., 1993). High abundance of *Synechococcus* has been recently reported for the eastern Fram Strait, included here as cells <10 μm (Paulsen et al., 2016). Similarly, the ubiquitous *Micromonas* sp. in Arctic waters has been detected in this region by sediment traps, and associated with increased ^{234}Thorium adsorption in the Central Arctic (Charles Bachy, pers. commun., Roca-Marti et al., 2016). Great quantities of *Phaeocystis* sp. were observed at the ocean bottom in the Ross Sea, at >500 m depth (DiTullio et al., 2000). In the Fram Strait, highest export was observed during a *Phaeocystis* sp. bloom, equivalent to the export efficiency, or % of primary production that sediments, by diatoms (Le Moigne et al., 2015). In the Gulf of St. Lawrence, the export efficiency increased from 10% during the diatom bloom to 10–5% in post-bloom conditions (Rivkin et al., 1996). In the Canadian Arctic, flagellates were associated with high export ratios of 0.38–0.69 (Lapoussiere et al., 2013). Similarly, the inverse model in the Fram Strait predicts an export efficiency of 51, 44, and 53.5% *before*, *during* and *after* the warm water event (**Table 1**). In this way, *Phaeocystis* sp. and flagellates can fuel the biological pump, transferring an important proportion of surface primary production to depth.

Carbon export in the model originated from either diatoms or detritus that *during* the warm period is overwhelmingly dominated by *Phaeocystis* sp. carbon (**Figure 5**). By which processes can flagellates contribute to export out of the surface layer? High biomass, stickiness, and presence of ballast all correlate with increased phytoplankton sedimentation by coagulation (e.g., Passow and Alldredge, 1999; Jouandet et al., 2014). In general, diatoms and coccolithophores are considered to sink faster than other phytoplankton and their silicon frustule (opal) or carbonate coccoliths are assumed to act as ballast for phytoplankton sinking and zooplankton fecal pellets, activating the biological pump (Armstrong et al., 2001; Klaas and Archer, 2002; Ploug et al., 2008). Ballast for phytoplankton could originate also from intracellular carbohydrates, minerals or carbonate precipitated within sea ice (Richardson and Cullen, 1995; Iversen and Ploug, 2010). *Phaeocystis* sp. blooms are reported to have very high sinking rates (Wassmann et al., 1990; DiTullio et al., 2000 but see Schoemann et al., 2005). DMSP, known to be elevated in *Phaeocystis* sp., has recently been suggested as ballast for this species (Lavoie et al., 2015, but see Boyd and Gradmann, 2002). Coagulation of cells in turbulent environments, in particular species with a sticky surface as observed in senescent *Phaeocystis* sp. blooms, generates marine snow; this process is considered a widespread venue of removing cells from the upper ocean (Passow and Wassmann, 1994; Logan et al., 1995). Mucus webs of pteropods are also known to be an efficient transport vehicle for pico-plankton particles (Noji et al., 1997). High stickiness in Arctic phytoplankton is expected; diatoms excrete large amounts of polysaccharides (Myklestad, 1995) and Arctic phytoplankton, both diatoms and flagellates, can excrete as much as 70% of their daily primary production as DOC (Vernet et al., 1998; Matrai et al., 2007; Poulton et al., 2016), which can be considered a source of stickiness (Schoemann et al., 2005). Marine snow is part of the detrital carbon, and is difficult to detect and quantify. TEP (transparent exo-polymers) is believed to comprise most of the marine snow and its sinking speed is also related to size, porosity and ballast usually provided by its constituents (Passow, 2002; Bach et al., 2016). For example, porosity of marine snow is lower when flagellates dominate in comparison with diatom-rich aggregates, thus providing another mechanism by which non-diatom aggregates can export carbon (Bach et al., 2016).

The changes in carbon export predicted by the model when *Phaeocystis* sp. dominated agree in large extent to the observations from sediment traps in the eastern Fram Strait. Flux of (POC) at 179–280 m depth from 2002 to 2008, with 20 sampling cups per year collecting material from 59 days in winter and 7 days in summer, showed POC sedimentation associated with biogenic silica (bSi) pulses (Lalande et al., 2013). Before the fall of 2004, these pulses occurred in spring (April to June), sometimes associated with the ice edge and in the late summer (August to October) due to atmospheric heating of the upper water column. Before 2004 the pulses ranged from 30 to 50 mg C m^{-2} d^{-1} and 10–30 mg bSi m^{-2} d^{-1}. From late 2004 to the summer of 2008, during the warm water event, the consistency of the spring and late summer bSi pulses disappeared, with a few peaks in sedimentation in either May or August (∼10 mg bSi m^{-2} d^{-1}) remaining and the rest of the time sedimentation was <5 mg bSi m^{-2} d^{-1} (Figure 2f, Lalande et al., 2013). The pulses of POC remained unchanged throughout this period, both in magnitude and time of the year (Figure 2e, Lalande et al., 2013).

Any differences between model predictions and sediment trap data on sedimentation rates are expected, as export in the model represents carbon loss out of the surface layer (<100 m) while the sediment traps were deployed at ∼250 m depth. In the field, the changes in flux of bSi correlated with other important changes in the nature and quality of the sedimenting matter: lower fecal pellet carbon and an increase in the amount of small fecal pellets, attributed to dominance of smaller zooplankton (Lalande et al., 2013). The inverse model predicts the change in quality of sedimenting matter can be attributed to the dominant phytoplankton community, diatoms vs. *Phaeocystis* sp. and to the changes in trophic pathways in the food web (**Figure 5**, see Section Discussion. for a detailed discussion on carbon flow through the modeled food web). The predicted changes in the biomass of the different compartments are reflected in higher respiration *during* and *after* the warm water event for small phytoplankton, mesozooplankton (small copepods) and bacteria and lower respiration from large phytoplankton (**Figure 6**).

Our model results present an alternative hypothesis that warming and flagellates could bring increased heterotrophy to the Arctic, expressed as the ratio of respiration to primary production (**Table 1**, **Figure 6**). The paradigm that flagellates will decrease sedimentation corresponds to a scenario of higher retention of organic carbon in surface waters and higher respiratory losses (Forest et al., 2010; Vaquer-Sunyer et al., 2010). Similarly, predictions of lower sedimentation are associated with an activation of the microbial loop (Kirchman et al., 2009b).

High export in absence of diatoms in the Arctic is also possible as shown in this study, or when dinoflagellates replace diatoms (Rivkin et al., 1996); high sedimentation by flagellates has been observed in the field even when diatoms are abundant in surface waters (Amacher et al., 2013). A high export is possible if a link between the classical and microbial food webs develops through the consumption of microzooplankton and detritus by copepods.

CONCLUSIONS

1. In conclusion, more proliferation of flagellates, such as *Phaeocystis sp*. in Arctic waters as a response to warming, presumably increasing stratification and reducing nitrate availability through the halocline, is predicted by the inverse model to alter the amount of carbon sedimentation by <20%, and thus the biological pump remains effective. The consumers in the Arctic food web can adjust to the change from diatoms to flagellates by increasing microzooplankton abundance, by switching meso- and macrozooplankton feeding from herbivory to omnivory, detritivory and coprophagy. When *Phaeocystis sp*. dominates, the pathway of carbon through the food web is longer, at least one step is added in the flow from phytoplankton to mesozooplankton. Phytoplankton carbon to higher trophic levels is available either as detritus or as microzooplankton biomass.
2. Results from the inverse model provide several important hypotheses in relation to the carbon cycling in Arctic food webs subject to warming and presumable to a decrease in diatoms and an increase in flagellates, including *Phaeocystis sp*. The hypotheses in relation to the role of grazing by microzooplankton and small copepods, the role of detritivore copepods in consuming marine snow and other detrital carbon and the relative importance of the microbial vs. the classical food web need to be tested experimentally, both in the laboratory and in the field.
3. Inverse modeling provides a snapshot of conditions over short timescales, here during summer cruises to the eastern Fram Strait. The emphasis is on studies of trophic interactions. The quality of the results is based on previous knowledge of the food web and trophic interactions as well as the availability of rate processes at critical times through the growth season (April to September). Technological advances will help provide a better understanding of inter-annual and intra-annual variability in Arctic systems. As more data becomes available the quality of model predictions, as well as their accuracy, will increase.

AUTHOR CONTRIBUTIONS

MV organized the study, was responsible for searching the majority of data used in the model, participated in model interpretation and was in charge of the writing. TR was in charge of the model development, participated in interpretation of results and writing the manuscript. IP, EN, and KM provided data for the model and participated in food web construction, data interpretation and writing.

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