Annual cycle of export fluxes of biogenic matter near Hanna Shoal in the northeast Chukchi Sea

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ABSTRACT

The Chukchi Ecosystem Observatory (CEO), a mooring array of subsurface oceanographic instruments, was established on the northeast Chukchi Sea continental shelf to obtain time-series measurements of physical, biogeochemical, and biological parameters. A sequential sediment trap was deployed on a CEO mooring 8 m above seafloor to measure export fluxes of chlorophyll *a* (chl *a*), microalgal cells, zooplankton fecal pellets, total particulate matter (TPM), particulate organic carbon (POC), and zooplankton actively entering the trap from August 2015 to July 2016. These time-series measurements allowed us to monitor sympagic and pelagic algal production, the seasonal development of the zooplankton community, pelagic-benthic coupling, and particulate matter export in relation to snow and sea-ice cover on the shallow Chukchi Sea continental shelf. Notably, chl *a* and algal fluxes were nearly as high from August to October 2015 as in June-July 2016, indicating substantial autumn production. Autumn algal fluxes were dominated by the epipelic *Cylindrotheca closterium* while summer fluxes were dominated by pennate diatoms, including *Fossula arctica* and *Neodenticula seminae*. Peaks in the export of the exclusively sympagic diatom *Nitzschia frigida* in May and June 2016 indicated the release of ice algae due to snow and ice melt events. While pelagic copepods *Calanus glacialis/marshallae*, *Pseudocalanus* spp. and *Oithona similis* were the dominant copepods collected in the sediment trap, meroplanktonic stages of benthic organisms displayed the largest abundances and reflected mixing of pelagic stages and resuspension events on the shallow Chukchi Sea shelf. Enhanced fecal pellet carbon fluxes reflected zooplankton grazing in August and September 2015 and in July 2016. Despite the grazing pressure, high chl *a*, diatom and POC fluxes during these periods allowed strong pelagic-benthic coupling in the northeast Chukchi Sea. Persistent summer and autumn production also suggest that the local benthic community benefits from a sustained food supply rather than episodic flux events. Overall, these observations demonstrate the importance of year-round monitoring for fully understanding the phenology of marine processes and set a baseline for understanding the impact of environmental changes on Arctic marine ecosystems.

Keywords: Arctic Ocean, Chukchi Sea, Export, Sediment trap, Microalgae, Zooplankton, Observatory

1. Introduction

Decades of physical and biological sampling in the Pacific Arctic region have revealed that the abundant nutrient supply of Pacific waters flowing into the Chukchi Sea through the Bering Strait supports one of the most productive marine ecosystems of the Arctic Ocean (Grebmeier and Maslowski, 2014). The constant input of nutrient-rich waters leads to sympagic algae production (~1-2 g C m^{-2}) and large pelagic blooms (up to ~200 g C m^{-2} yr^{-1}) on the southern Chukchi Shelf just north of Bering Strait (Gradinger, 2009; Hill et al., 2018; Wang et al., 2018). On the northern Chukchi Shelf, stratification following ice melt results in a seasonally nutrient-depleted surface layer over much of the shelf but production at or below the mixed layer depth may persist to the end of summer and reach up to 90 mg C m^{-2} yr^{-1} (Hill and Cota, 2005; Questel et al., 2013; Danielson et al., 2017a). The high levels of primary production at several regional hotspots in the Chukchi Sea support large populations of zooplankton, pelagic fishes, seabirds, and marine mammals (Ershova et al., 2015; Kuletz et al., 2015; Logerwell et al., 2015; De Robertis et al., 2017; Moore and Kuletz, 2018), and lead to large export fluxes of biogenic matter sustaining rich benthic communities (Grebmeier et al., 1988; Grebmeier et al., 2006b; Lalande et al., 2007; Grebmeier et al., 2015). Similar to the northern Bering Sea, the Chukchi Sea has recently experienced a rapid reduction in seasonal sea-ice cover and an increase in air and ocean temperatures that may result in a shift from Arctic to subarctic conditions (Grebmeier et al., 2006b; Shimada et al., 2006; Woodgate et al., 2012; Grebmeier et al., 2018; Baker et al., 2020).

Except for a few notable programs with shipboard operations early (May-June) in the productive season (e.g. Hill and Cota, 2005; Arrigo et al., 2012; Baker and Dickson, 2020; Danielson et al., 2020), most of the sampling effort in the Chukchi Sea takes place closer to the annual minimum sea ice cover period (July-August-September), providing snapshots of the physical conditions and marine ecosystem only relatively late in the growing season. The lack of regular ship-based observations between October and June results in a critical observational gap for the majority of the seasonal cycle. This gap motivated the establishment of the Chukchi Ecosystem Observatory (CEO), an array of subsurface oceanographic instruments deployed on the northeast Chukchi Sea continental shelf near Hanna Shoal (71º 35.976' N, 161º 31.621' W), to obtain continuous, high-resolution, and year-round measurements of physical, biogeochemical, and biological parameters (Fig. 1; Danielson et al., 2017b; Hauri et al., 2018). The CEO moorings are equipped with sensors that collectively measure temporal variations in sea-ice cover and thickness, light, currents, waves, water column structure, dissolved oxygen, nitrate, inorganic carbon, particulate matter, sympagic and pelagic algal export, and local zooplankton communities, fish populations, and marine mammal vocalizations (Danielson et al., 2017b; Hauri et al., 2018).

Here, we present results on the continuous export fluxes of biogenic matter obtained from a sequential sediment trap deployed at the CEO from August 18, 2015 to July 31, 2016. Export fluxes were used to evaluate the phenology and makeup of algal production, the seasonal development of the zooplankton community, pelagic-benthic coupling, and particulate matter export in relation to snow and sea-ice cover on the shallow Chukchi Sea continental shelf. Due to the nature of mooring deployment and recovery in seasonally ice-covered regions, the time frame of the annual cycle from late August to the following July prevented the analysis of a complete production cycle. This constraint will be eliminated by maintaining consecutive sediment trap deployments at the CEO. In the current context of a period of rapid changes, this annual cycle of export fluxes provides a benchmark against which to assess natural variability and the impact of climate change on this productive Arctic marine ecosystem.

2. Methods

2.1. Remote sensing

Daily averaged sea-ice concentrations were retrieved at a 12.5-km resolution from the Centre ERS d'Archivage et de Traitement (CERSAT) service of the French Research Institute for Exploitation of the Sea (http://cersat.ifremer.fr/). Snow depth on top of sea ice was retrieved at a 25-km resolution from the Northern Hemisphere snow depth files derived from the Scanning Multichannel Microwave Radiometer (SMMR) and the Special Sensor Microwave/Imager (SSM/I) of the National Aeronautics Space Agency (https://neptune.gsfc.nasa.gov; Comiso et al., 2003). Daily sea-ice concentration and snow depth were averaged for a delimited region above the mooring (44 x 44 km; 71.4-71.8°N; 161.4-161.9°W; Fig. 1).

2.2. Sequential sediment trap

A sequential sediment trap (Hydro-Bios, Germany) was deployed at 37 m depth, 8 m above seafloor, on the biogeochemistry mooring of the CEO (Fig. 1). CEO moorings were deployed from the R/V *Norseman II* in August 2015 and recovered from the USCGC *Healy* in August 2016. Collection cups rotated at pre-programmed intervals ranging from one week during spring and summer and to one month during winter. Because the sediment trap was recovered before the completion of the last rotation, the last open sample was excluded from the study. Collection cups were filled with filtered seawater adjusted to a salinity of 38 with NaCl and fixed with formalin (4% final solution) to preserve samples during deployment and after recovery.

In the laboratory, zooplankton and meroplankton actively entering the collection cups (swimmers) were removed from a fraction of the samples with forceps and identified to the lowest taxonomic level possible using a dissecting microscope. Sample cups were then gently mixed before subsamples (0.1 to 3 ml) were taken with a modified micropipette to enable the collection of large particles for measurements of chl *a*, microalgal cells, zooplankton fecal pellets, total particulate matter (TPM), and particulate organic carbon (POC). Subsamples for chl *a* measurements were filtered onto GF/F filters (0.7 µm), extracted in acetone for 24 h at -20°C and measured on a Turner Design fluorometer following the methods outlined in Welschmeyer (1994). Samples were kept cool and in the dark prior to chl *a* measurements but may have experienced some degradation, even when preserved in a formalin solution. For the enumeration of algal cells, subsample volumes were adjusted to 3 ml with filtered seawater when needed before being placed in an Utermöhl chamber. A minimum of 300 algal cells were counted and identified by inverted microscopy at 100X, 200X or 400X depending on cell size according to the Utermöhl method (Utermöhl, 1931). Subsamples for the enumeration and measurement of zooplankton fecal pellets were sieved to remove small sandy particles before observation using a dissecting scope. The length and width of fecal pellets (broken or intact) were measured with an ocular micrometer and fecal pellet volumes were calculated according to their shape. Cylindrical pellets were attributed to calanoid copepods while ellipsoidal pellets were attributed to appendicularians (González et al., 1994). Fecal pellet volumes were converted to fecal pellet carbon (FPC) using a volumetric carbon conversion factor of 0.057 mg C mm^{-3} for copepod pellets and 0.042 mg C mm^{-3} for appendicularian pellets (González et al., 1994). Subsamples for TPM measurements were filtered onto pre-combusted (500°C overnight) and pre-weighed GF/F filters (0.7 µm), rinsed with distilled water to remove salt, dried at 60°C overnight, and weighed on a microbalance. The same filters were then exposed to 1N HCl overnight for removal of inorganic carbon and dried once again at 60°C overnight before encapsulation for POC measurements. POC measurements were conducted on a Perkin Elmer CHNS 2400 Series II elemental analyzer. All measurements were converted to daily flux rates depending on the open cup duration of each sample and integrated to annual fluxes.

3. Results

3.1. Sunlight, snow, sea ice, air temperature

The northeast Chukchi Sea was ice free and had >18 daylight hours at the start of the sediment trap deployment in August 2015 (Fig. 2a). Sea-ice cover began to form and snow started to accumulate at the CEO site on November 7, a few days before the CEO site entered the polar night on November 20 (sunrise and sunset times; https://aa.usno.navy.mil). Six months later in May 2016, satellite-derived snow depths revealed an early season snow melt event coinciding with the onset of the polar day on May 12, followed by gradual snow melt through June and July (Fig. 2b). The cause of the mid-May snow melt event was linked to the air temperature recorded at the nearby coastal city of Utqiaġvik (170 km east of the CEO), where air temperatures increased and remained above 0ºC for 83 consecutive hours over May 10-14, with maximum temperatures exceeding 5ºC (Fig. 2a). Although low-salinity sea-ice melt waters at the mooring position were first observed a few weeks after the end of the June snow melt (Hauri et al., 2018), sea ice remained in the region until the last sample collection in July 2016 (Fig. 2b).

3.2. *Algal fluxes*

The contribution of diatoms ranged from ~93 to 100% of the total microalgal flux at 8 m above the seafloor, with 30 to 73% of diatoms containing chloroplasts (data not shown). High chl *a* and diatom fluxes (>1.5 mg m^{-2} d^{-1} and >2000 million cells m^{-2} d^{-1}, respectively) were observed from August to October and in late June and July (Fig. 3a and b). Chlorophyll *a* fluxes drastically decreased below 0.3 mg m^{-2} d^{-1} by the end of October but a low diatom flux of ~35 million cells m^{-2} d^{-1} persisted from November to March (Fig. 3b). The lowest diatom fluxes, with ~3.5 million cells m^{-2} d^{-1} containing chloroplasts, were observed during the second half of March just before the onset of spring production. The epipelic diatom *Cylindrotheca closterium* contributed ~60-95% of the diatom fluxes from August to mid-November and 20-45% from mid-November to April (Fig. 3b and c).

The composition of the diatom fluxes gradually shifted to a greater diversity during spring (Fig. 3c). The exclusively sympagic algae *N. frigida* was first collected in the sediment trap at the end of March, and two peaks of *N. frigida* fluxes were observed during May and June (Fig. 3c and d). The onset of *N. frigida* export was quickly followed by the export of *Melosira arctica*, another exclusively sympagic algae, with most of the cells exported as resting spores (Fig. 3c and d). *Synedropsis hyperborea*, a common epiphyte on *M. arctica* (Hasle et al., 1994;

von Quillfeldt et al., 2003), was present from May to July, similar to *M. arctica*. Export fluxes of *Gyrosigma-Pleurosigma-Haslea*, a group of physiologically similar sea-ice diatoms constituting a minor proportion of the ice assemblage, were observed from February to early July (Fig. 3c). The ice-associated pennate diatoms *Achnantes taeniata*, *Fragilariopsis* spp. and *Pseudonitzschia* spp., first appeared in March and April and significantly contributed to the diatom fluxes during spring and summer (Fig. 3c). Unidentified pennate diatoms dominated algal fluxes during the bloom in June and July and fluxes included large contributions of *Fossula arctica* and *Neodenticula seminae*. The exclusively pelagic centric diatoms *Chaetoceros* spp. and *Thalassiosira* spp. increasingly contributed to the diatom fluxes at the end of July, while *Proboscia* spp. significantly contributed to the diatom fluxes from November to January (Fig. 3c).

3.3. Zooplankton and meroplankton

The suspension-feeding copepods *Calanus glacialis/Calanus marshallae* and *Pseudocalanus* spp. and the omnivorous copepod *Oithona similis* were the dominant copepods collected at the CEO site. As adults and juveniles (copepodite stages) of the Arctic *C. glacialis* and the Pacific *Calanus marshallae* are difficult to distinguish, *C. glacialis* and *C. marshallae* were aggregated and identified as *C. glacialis/marshallae* (Hopcroft et al., 2010; Questel et al., 2013; Ashjian et al., 2017). *C. glacialis/marshallae* copepodite stages C2, C3 and C4 were abundant at the beginning of the deployment in August 2015 (Fig. 4a). The *C. glacialis/marshallae* population shifted to a dominance of C5 in September and then decreased in abundance from September to March (Fig. 4a). Adult females of *C. glacialis/marshallae* were collected in the sediment trap in April (Fig. 4a). *C. glacialis/marshallae* nauplii of feeding stages N3 to N6 were observed at the end of August 2015 and from the end of June 2016 until the end of the trap deployment in July 2016 (Fig. 4b).

Pseudocalanus spp., most likely a combination of *P. minutus*, *P. acuspes* and *P. newmani* (Darnis et al., 2008), were a constant blend of adult females and males, adult females with eggs, and all copepodite stages from August to January and in July (Fig. 4c). Adult females were present from August to October and at the end of April-beginning of May (Fig. 4c). Nauplii stages of *Pseudocalanus* spp. were mostly abundant from August to December and in July (Fig. 4d). The abundance of all copepodite stages of *O. similis* increased in November and December, a few weeks later than peak in abundances of *C. glacialis/marshallae* and *Pseudocalanus* spp. (Fig. 4e). Nauplii of *O. similis* were nearly absent, apart from a few nauplii of an unidentified stage observed at the beginning of November (Fig. 4f).

High abundances of appendicularians were collected at 37 m in July 2016 (Fig. 4g). While the majority of appendicularians were identified as *Fritillaria borealis* (~95%), a few *Oikopleura vanhoeffeni* (~5%) were observed from September to February (data not shown). Meroplanktonic stages of benthic organisms were also abundant in the sediment trap, with bivalve veliger, polychaete larvae, barnacle larvae, and even polychaetes observed from August to November 2015 (Fig. 4h). Polychaete larvae and a few barnacle larvae were also observed at the end of June and in July 2016 (Fig. 4h).

3.4. Particulate matter and carbon fluxes

FPC fluxes declined from 21.6 to 4.9 mg C m^{-2} d^{-1} from August to October, with copepod FPC contributing to >58% of the FPC fluxes during this period (Fig. 5a). A peak in copepod FPC flux (12.9 mg C m^{-2} d^{-1}) contributing to 98% of the total FPC flux was recorded at the end of May (Fig. 5a). Highest FPC fluxes were recorded in early July (28 mg C m^{-2} d^{-1}), with appendicularian FPC contributing to >70% of the FPC flux at that time (Fig. 5a). TPM and POC fluxes (~60 g m^{-2} d^{-1} and ~1.0 g C m^{-2} d^{-1}, respectively) were 15 to 20 times higher during August than at their lowest values at the end of March (Fig. 5b). TPM and POC fluxes steadily decreased until the end of March and remained low until the end of May except for a short period of increased fluxes in the first half of April (Fig. 5b). TPM and POC fluxes increased from the beginning of June until the end of the deployment in July (Fig. 5b).

4. Discussion

4.1. Algal fluxes

Continuous export fluxes obtained at the CEO site from August 2015 to July 2016 reflected pelagic processes occurring over a year, encompassing the full range of annual sunlight and sea-ice conditions on the shallow Chukchi Sea shelf. These year-long measurements provide an invaluable dataset to track the seasonal development of the Chukchi marine ecosystem, particularly for the rarely-sampled winter and early spring periods. Enhanced chl *a* (3-5 mg m^{-2} d^{-1}) and diatom fluxes (>4000 million cells m^{-2} d^{-1}) during June and July 2016 were higher than daily chl *a* fluxes (<2.5 mg m^{-2} d^{-1}) obtained from May to August 2004 in the Chukchi Sea

(Lalande et al., 2007) and under-ice algal fluxes (~120 million cells m^{-2} d^{-1}) recorded in April and May 2008 and 2009 in the Bering Sea (Szymanski and Gradinger, 2016). Elevated chl *a* (>1 mg m^{-2} d^{-1}) and diatom fluxes (>2000 million cells m^{-2} d^{-1}) were also observed in the absence of ice cover from mid-August to October 2015 at the CEO site. These results reflect exceptionally high algal biomass and export during summer and autumn that led to annual fluxes of chl *a* and diatoms reaching 225 mg m^{-2} yr^{-1} and ~320 billion cells m^{-2} yr^{-1}, respectively, on the shallow northeast Chukchi Sea shelf.

Diatoms have been reported as the dominant or the second most abundant taxa (after flagellates) in the Chukchi Sea (Sukhanova et al., 2009; Giesbrecht et al., 2018). Whereas small flagellates have low sinking rates, diatom aggregates may sink at rates >100 m d^{-1} and rapidly reach the seafloor on the shallow Chukchi Sea continental shelf, therefore contributing to the majority of algal flux, pelagic-benthic coupling, and potential carbon sequestration (Legendre et al., 1992; McDonnell and Buesseler, 2010). Since most diatom cells exported in autumn and summer contained chloroplasts, these fluxes clearly reflected the export of recent and local algal production.

Commonly found on shallow shelves, *C. closterium* has a rapid growth rate when transported into the euphotic zone during mixing events (Kingston, 2009). Strong winds (>10 m s^{-1}) and frequent wind direction reversals recorded in Utqiaġvik were associated with periodic depressions of the pycnocline from August to November 2015 at the nearby CEO freeze-up detection mooring (Hauri et al., 2018). The strong wind-induced mixing of surface waters was accompanied by elevated chl *a* fluorescence under decreasing levels of photosynthetically active radiation until November at the same site, supporting an autumn bloom (Hauri et al., 2018). The elevated fluxes of *C. closterium* containing chloroplasts observed from August to October reflected the enhanced algal production when ice was absent and sunlight was sufficient for growth on the shallow Chukchi Sea shelf. The large proportion of *C. closterium* and other diatom cells without chloroplasts composing the algal flux during winter suggested a sustained resuspension of sedimented material beneath the ice cover. However, the constant contribution of diatoms with chloroplasts to these wintertime diatom fluxes (at least 10 million cells m^{-2} d^{-1}) indicated that a considerable fraction of resuspended diatoms remained alive throughout the polar night, providing a continual carbon source for benthic suspension feeders and surface deposit feeders. In contrast, ~5 million diatom cells with chloroplasts m^{-2} d^{-1} reached the seafloor at 2430 m during a spring peak diatom export event in the deep Fram Strait (Lalande et al., 2016). The close proximity of the seafloor and the extended periods of pelagic export clearly factor into the tight pelagic-benthic coupling and elevated benthic biomasses reported for the Chukchi continental shelf (Grebmeier et al., 2006a).

Sea-ice algal production in nutrient-rich waters such as in the Chukchi Sea is often limited by light, either related to photoperiod or snow cover (Legendre et al., 1992; Rysgaard et al., 2001). Sea-ice algae grow and accumulate at the bottom of the ice, in melt ponds, or in the ice brine channel matrix from the time sunlight is sufficient until their release into the water column at the onset of melting processes. In the Chukchi Sea, high sea-ice algal abundance has previously been observed in early March (Szymanski and Gradinger, 2016). Peaks in the ice algal bloom have been reported from mid to late May (Selz et al., 2018). While many diatom species composing the ice algal community in the Arctic Ocean are both sympagic and pelagic, key species such as *N. frigida* and *M. arctica* are exclusively sympagic (Poulin et al., 2011; Poulin et al., 2014). *N. frigida*, a pennate diatom forming arborescent colonies, usually dominates the biomass on the ice underside and sinks out of the water relatively quickly when melt is initiated, without maintaining a planktonic population (Michel et al., 1993; von Quillfeldt et al., 2003; Olsen et al., 2017; Lalande et al., 2019). The two distinct peaks in *N. frigida* fluxes observed in May and June therefore reflected ice algae release. These two peaks coincided with the snow melt event recorded on May 15 and with the combined snow and ice melt observed at the end of June. While *M. arctica*, a chain-forming centric diatom, has been reported as sporadically abundant in the Chukchi Sea (Ambrose et al., 2005; Wang et al., 2018), only low fluxes of *M. arctica* were measured during the 2015-2016 deployment, most of them at the onset of ice melt at the end of June. The constant, albeit relatively low fluxes of *N. frigida*, *M. arctica* and *Gyrosigma-Pleurosigma-Haslea* observed from February to July reflected a continuous release of ice algae from the drifting sea ice above the mooring site, contrasting with model-derived results that suggest a brief sea-ice algal seeding period in the Chukchi Sea (Selz et al., 2018).

The ice-associated pennate diatoms *Achnantes taeniata*, *Fragilariopsis* spp. and *Pseudonitzschia* spp., common phytoplankton spring bloom taxa thriving in both ice and the water column in the Chukchi Sea (Sukhanova et al., 2009; Selz et al., 2018; Wang et al., 2018), first appeared in March and April and significantly contributed to the diatom fluxes during spring and summer. The boreal pennate diatom *Neodenticula seminae*, a common species in the northern North Pacific and Bering Sea (Reid et al., 2007), increasingly contributed to the export fluxes from May to July, reflecting the influence of inflowing Pacific waters from the Bering Sea into the study area. The substantial increase of chl *a* and diatom fluxes at the end of June clearly reflected a large bloom during snow and ice melt. The dominant diatom exported at the onset of the bloom was the pennate diatom *Fossula arctica*, another species known to thrive well in both ice and water and common in early phytoplankton blooms (Szymanski and Gradinger, 2016).

The exclusively pelagic centric diatoms *Chaetoceros* spp. and *Thalassiosira* spp. increasingly contributed to the diatom fluxes at the end of July. However, while *Chaetoceros* spp. and *Thalassiosira* spp. have been reported as dominant components of pelagic algal blooms in the Chukchi Sea (Sukhanova et al., 2009; Arrigo et al., 2012; Wang et al., 2018), they never dominated diatom fluxes during summer, rather reflecting a steady contribution from August 2015 to July 2016. *Proboscia* spp., a genus observed in late summer blooms following wind forcing or the influence of small eddies (Sukhanova et al., 2009), significantly contributed to the diatom fluxes from November to January. A similar increase in the relative abundance of *Proboscia* was observed at ~200 m over the Northwind Abyssal Plain, north of the CEO site, in October and November 2011 (Onodera et al., 2015).

4.2. Zooplankton and meroplankton

Year-round studies on zooplankton abundance and stage succession are rare in the Arctic Ocean due to the remoteness and difficult accessibility of polar regions (e.g. Kosobokova, 1982; Darnis and Fortier, 2014). Although sediment traps are not designed to quantitatively collect zooplankton, zooplankton entering the traps have effectively been identified to partly reflect the seasonal development of the zooplankton community (e.g. Dezutter et al., 2019). On a very shallow shelf, swimmers are more likely to be trapped and thereby accurately reflect the relative abundance and composition of the zooplankton community. In the Chukchi Sea, the copepods *C. glacialis/marshallae*, *Pseudocalanus* spp., and *O. similis* dominate the zooplankton communities in terms of abundance and biomass (Hopcroft et al., 2010; Questel et al., 2013; Ashjian et al., 2017). Accordingly, they were the dominant copepods collected in the CEO sediment trap. A few individuals of *C. hyperboreus,* the most abundant copepod in the adjacent deep Arctic basin (Campbell et al., 2009), were collected in January (~5-10 individuals) and March (~30-35 individuals; data not shown), possibly reflecting the aperiodic upwelling of deep continental slope waters onto the shallow shelf (Ashjian et al., 2017; Danielson et al., 2017a). Pacific copepods *Eucalanus bungii* and *Metridia pacifica* were also sporadically collected from August to October (data not shown). Although zooplankton typical of Pacific origin water can be absent near Hanna Shoal (Lane et al., 2008), other studies do find them on occasion (Hopcroft et al., 2010).

The large proportion of young copepodid stages of *C. glacialis/marshallae* collected at the beginning of the deployment in August corroborated with the dominance of *C. glacialis/marshallae* copepodid stages C1-C3 collected using vertical net tows on Hanna Shoal in August 2012 and 2013 (Ashjian et al., 2017). The gradual transition from a high abundance of *C. glacialis/marshallae* C2, C3 and C4 to a low abundance of C5 during autumn may have reflected high predation and/or early life stage mortality. It also reflects the accrual of energy and growth of *C. glacialis/marshallae* into a lipid-rich stage for the winter (Falk-Petersen et al., 2009). While *C. glacialis/marshallae* typically attempts to enter diapause within cold bottom-water pools in the region (Ashjian et al., 2017; Elliott et al., 2017), it is unclear to what extent the decline of C5s after November reflected decreased swimming activity, permanent descent below the depth of the trap, or advection into deeper waters off the shelf. The limited but lasting presence from September to January of *C. glacialis/marshallae* C5 on the shallow Chukchi Sea shelf suggests the advection of the overwintering stage from nearby deeper areas into the region (Darnis et al., 2008; Ashjian et al., 2017). After months of quiescence, *C. glacialis/marshallae* rapidly develops its gonads using internal lipid reserves (Falk-Petersen et al., 2009), reflected by the collection of *C. glacialis/marshallae* adult females in the sediment trap in April (Fig. 4a). The near complete absence of *C. glacialis/marshallae* at 37 m following their maturation presumably reflected their distribution nearer the ice-water interface to feed on ice algae and spawn prior to the pelagic bloom, and in the subsurface chlorophyll maximum during the bloom (Niehoff et al., 2002; Campbell et al., 2009; Søreide et al., 2010; Leu et al., 2011; Daase et al., 2013; Darnis and Fortier, 2014; Durbin and Casas, 2014). The subsequent collection of *C. glacialis/marshallae* nauplii of feeding stages N3 to N6 at the onset on the pelagic bloom 8 to 10 weeks later reflected nauplii development in the region in time to feed on the pelagic bloom to fuel their growth (Søreide et al., 2008; Søreide et al., 2010; Leu et al., 2011; Wold et al., 2011; Dezutter et al., 2019). The presence of *C. glacialis/marshallae* nauplii during August 2015 may have reflected the production of nauplii by populations advected in the region from the Bering Sea, or an extended nauplii production period on the Chukchi Sea shelf.

In contrast to *C. glacialis/marshallae,* the period of high abundance of *Pseudocalanus* spp. copepodites coincided with high abundance of their nauplii from August to December. The presence of young nauplii stages N2, N3 and N4 during November and December suggested sustained spawning until ice formation on the Chukchi Sea shelf. The *Pseudocalanus* spp. complex exploited the prolonged productive period to sustain growth, maturation, lipid accumulation, and reproduction during autumn before a rapid decline of the population occurred at the beginning of the polar night. Similar to *C. glacialis/marshallae*, the lower abundance of *Pseudocalanus* spp. in spring and summer likely indicated their distribution at the ice-water interface to feed on ice algae from the bottom of the ice (Conover et al., 1986; Campbell et al., 2009).

An increased abundance of the small omnivorous copepod *O. similis* was observed in November and December, a few weeks later than peak in abundances of *C. glacialis/marshallae* and *Pseudocalanus* spp. The increased abundance matched with a seasonal peak in the abundance of *O. similis* in November in Kongsfjorden (Lischka and Hagen, 2005) and suggests that *O. similis* thrives when larger copepods are not present (Zamora-Terol et al., 2014). Relatively high abundances of adult females and males during winter support previous reports that *O. similis* uses a year-round reproduction strategy and remains active during winter (Zamora-Terol et al., 2013), although only a few unidentified nauplii were collected in November. The presence of all copepodite stages from November to January and scattered throughout the sampling period reflected the continuous reproduction of *O. similis*, with all stages typically present throughout the year (Ashjian et al., 2003; Lischka and Hagen, 2005; Zamora-Terol et al., 2013).

Appendicularians and meroplankton may contribute to a large proportion of the zooplankton community in terms of abundance and biomass during summer on the Chukchi Sea shelf, but are also extremely variable in their abundances from year to year (Hopcroft et al., 2010; Questel et al., 2013; Ashjian et al., 2017). While nearly all appendicularians were collected in July during the bloom, extremely large abundances of larvae of polychaetes and barnacles from mid-August to November suggest that meroplanktonic stages exploited the autumn production during resuspension events. Ashjian et al. (2017) also reported high abundances of barnacle larvae and polychaete larvae in the water column in August on Hanna Shoal. The presence of adult polychaetes 8 m above seafloor from August to November and in June and July further reflects resuspension and the rich benthic ecosystem of the Chukchi Sea.

4.3. Pelagic-benthic coupling

Elevated chl *a*, diatom and POC fluxes reflected a tight coupling between water column primary production and benthic secondary production on the shallow Chukchi Sea shelf. These fluxes (annual POC flux: ~145 g C m^{-2} yr^{-1}) are more than sufficient to support the rich benthic biomass (<20 g C m^{-2}) of amphipods and bivalves that constitute the food base for benthic-feeding marine mammals in the Hanna Shoal region (Grebmeier and Barry, 1991; Grebmeier et al., 2015). Campbell et al. (2009) reported a low grazing impact of the zooplankton community on algal production due to low zooplankton biomass during spring in the Chukchi Sea, concluding that grazers are not able to exert much control over algal blooms in this region. Therefore, the majority of the water column primary production is directly available for local export to the benthos or for offshore transport into the adjacent basin. Acoustics-derived data recently obtained north of the Bering Strait also reflected low zooplankton biomass during the spring phytoplankton bloom on the Chukchi Sea shelf, further implying that low grazing impact resulted in tight pelagic-benthic coupling in the region (Kitamura et al., 2017). Export fluxes of rapidly-sinking fecal pellets at the CEO showed a peak in copepod FPC fluxes reaching ~13 mg C m^{-2} d^{-1} at the end of May. This peak followed the appearance of *C. glacialis/marshallae* and *Pseudocalanus* spp. adult females in April and reflected enhanced grazing by copepods after the onset of ice algae release in May. Similar FPC fluxes (up to ~25 mg C m^{-2} d^{-1}) were previously obtained from under-ice drifting sediment trap deployments at nearby East Hanna Shoal and Barrow Canyon during May and June (Lalande et al., 2007). A peak in appendicularian FPC fluxes in July 2016 coincided with the large abundance of *Fritillaria borealis* in the sediment trap, reflecting the high grazing and growth rates of these filter feeders (Deibel, 1998). The summertime peak in FPC fluxes on the shallow Chukchi Sea shelf was 30 times higher than at 200 m in the eastern Fram Strait in June and 5 times higher than at 25 m in the Central Arctic Ocean in July and August (Lalande et al., 2014; Lalande et al., 2016). Elevated FPC fluxes at the CEO from August to November also indicated enhanced grazing pressure during autumn, consistent with high abundance of copepods, mostly of older stages. Overall, FPC fluxes indicated that a fair proportion of algal production was channeled into the pelagic ecosystem during autumn and summer. Despite this grazing pressure, the prolific chl *a*, diatom and POC fluxes clearly indicate that tight pelagic-benthic coupling prevails on the shallow Chukchi Sea shelf, in agreement with acoustics-derived and experimental results (Campbell et al., 2009; Kitamura et al., 2017).

4.4. Particulate matter and carbon fluxes

Elevated TPM and POC fluxes throughout the mooring deployment show that multiple processes combine to regulate the export of particulate matter on the Chukchi Sea shelf. In qualitative agreement with elevated *C. closterium* fluxes, high TPM and POC fluxes during autumn can be attributed to resuspension of sediments and diatoms blooming as a result of fall storms in the absence of ice cover. Despite substantial fecal pellet export (~2 g C m^{-2} yr^{-1}), the annual FPC flux only contributed to a small fraction (<2%) of the annual POC flux, and the annual POC flux (~145 g C m^{-2} yr^{-1}) represented <3% of the annual TPM flux (~5600 g C m^{-2} yr^{-1}). Enhanced TPM and POC fluxes in April and from the beginning of June until the end of the deployment in July 2016 likely corresponded to the release of particulate matter during snow and ice melt events. A large quantity of particulate matter is incorporated into ice during freeze-up on shallow shelves and is later released during melt (Wegner et al., 2005; Lalande et al., 2014). Because the potential for incorporation of particulate matter into sea ice likely increases with decreasing depth, ice-released material likely contributed considerably to TPM and POC fluxes during spring and summer on the very shallow Chukchi Sea shelf. High diatom fluxes during the spring bloom from the end of June to the end of the deployment in July likely contributed to enhanced POC fluxes for that period. Overall, export fluxes on the shallow Chukchi Shelf were extremely high relative to fluxes recorded in deeper Arctic regions, displaying winter fluxes as high as spring and summer fluxes in the Beaufort Sea, northern Baffin Bay, Laptev Sea, and Fram Strait (Lalande et al., 2009; Lalande et al., 2016). These substantial export fluxes of biogenic matter reflected the combined effect of extensive primary production driven by high nutrient loads, ice-released material, and resuspension on a shallow Arctic shelf.

5. Conclusions

Continuous export flux measurements of biogenic matter obtained at intervals ranging from one week to one month from August 2015 to July 2016 captured the local products of elevated primary production during summer and autumn. While autumn fluxes obtained at the end of the productive cycle of 2015 were possibly affected by different wind-forcing, water masses and circulation patterns than in autumn 2016, these fluxes nonetheless set a baseline for production dynamics in the northeast Chukchi Sea. These collections documented the release of ice algae due to snow melt during spring, the onset of the under-ice phytoplankton bloom triggered by ice melt enabling stratification during summer, high appendicularian grazing in the presence of ice during summer, and high copepod grazing in the absence of ice cover during autumn. These high-resolution biological time-series measurements provided critical information to track biodiversity, phytoplankton phenology, seasonal development of zooplankton communities, and food supply to the benthos. Most importantly, these results showed a 4-month period of sustained elevated primary and secondary production on the Chukchi Sea shelf validated by elevated fluorescence and intense acoustic backscatter of zooplankton at the CEO during the same period (Hauri et al., 2018), suggesting that the local benthic community benefits from a sustained food supply rather than episodic flux events. In spite of the apparent continuous food supply during the polar day, the benthic macrofauna near the CEO site only reach half the biomass of benthic communities found in the southeast Chukchi Sea (Grebmeier et al., 2006a; Grebmeier et al., 2015), possibly due to lower nutrient content (Giesbrecht et al., 2018). Long-term biological and biogeochemical measurements such as these are uncommon but imperative for fully understanding the impact of environmental changes such as warmer water temperature and reduced sea-ice cover. With the need to better monitor and understand the rapidly changing Arctic coupled with technological advances that enable reliable year-round observations, we anticipate better biological monitoring at high latitudes through the future addition of sequential sediment traps on year-round moorings.

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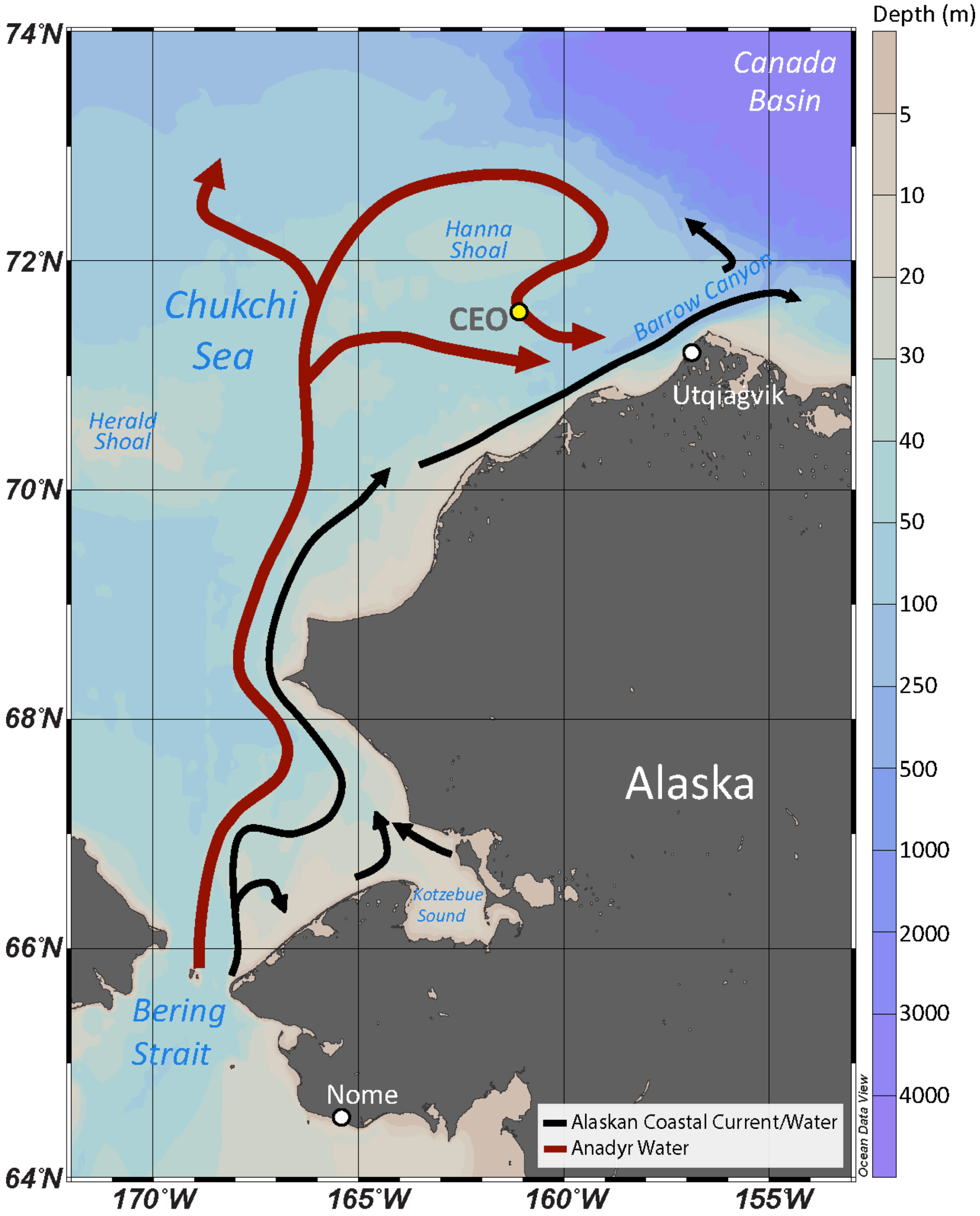
Fig. 1. Location of the Chukchi Ecosystem Observatory in the Chukchi Sea (71º 35.976' N, 161º 31.621' W).

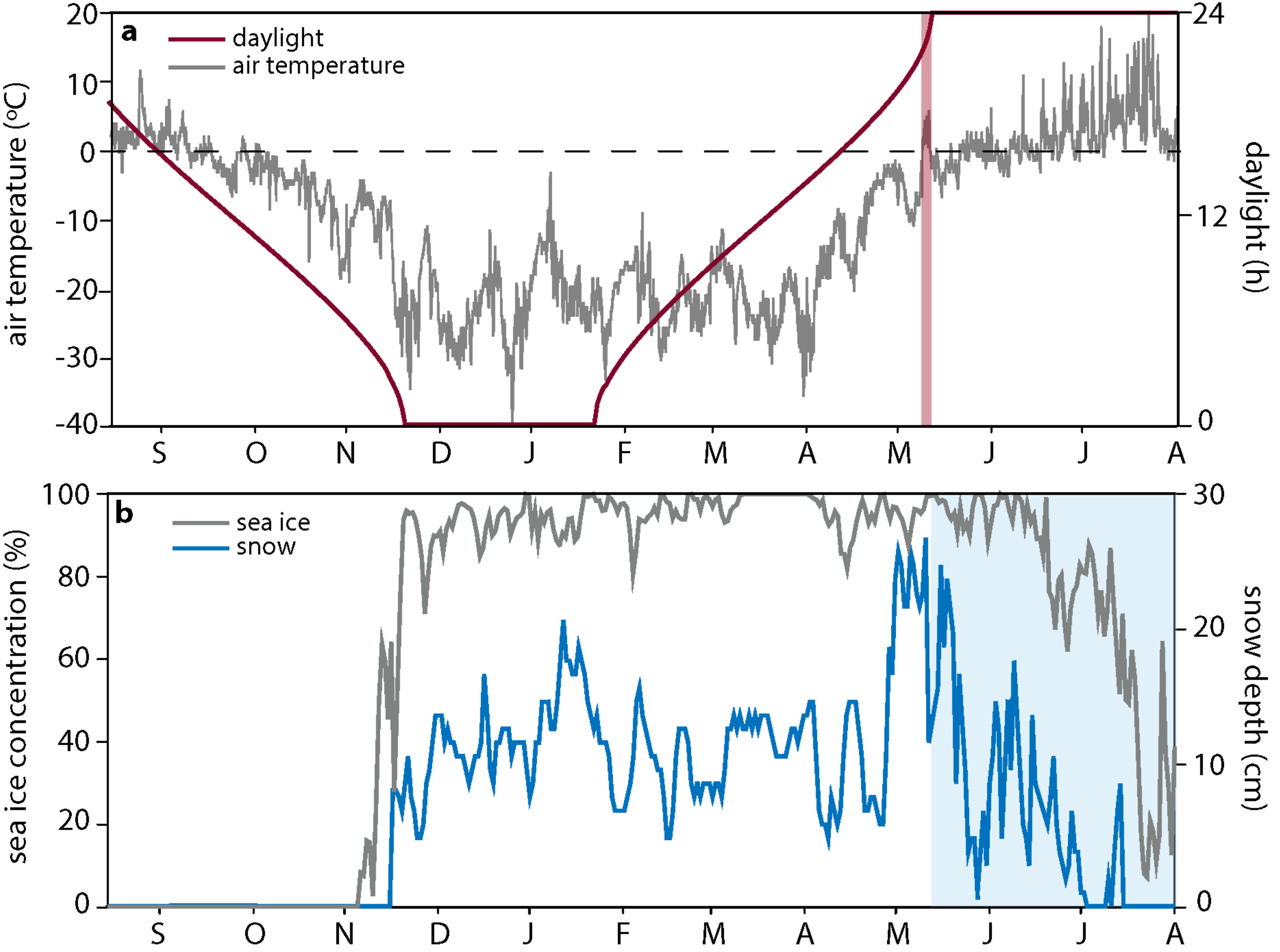
Fig. 2. a) Daylight duration and air temperature recorded at the coastal city of Utqiaġvik (170 km east of the CEO), and b) satellite-derived daily sea-ice concentration and snow depth above the mooring position (71.4-71.8ºN, 161.4-161.9ºW) during the CEO sediment trap sampling period. Shaded areas represent the early warm air temperature episode (red) and the snow and sea ice melt period (blue).

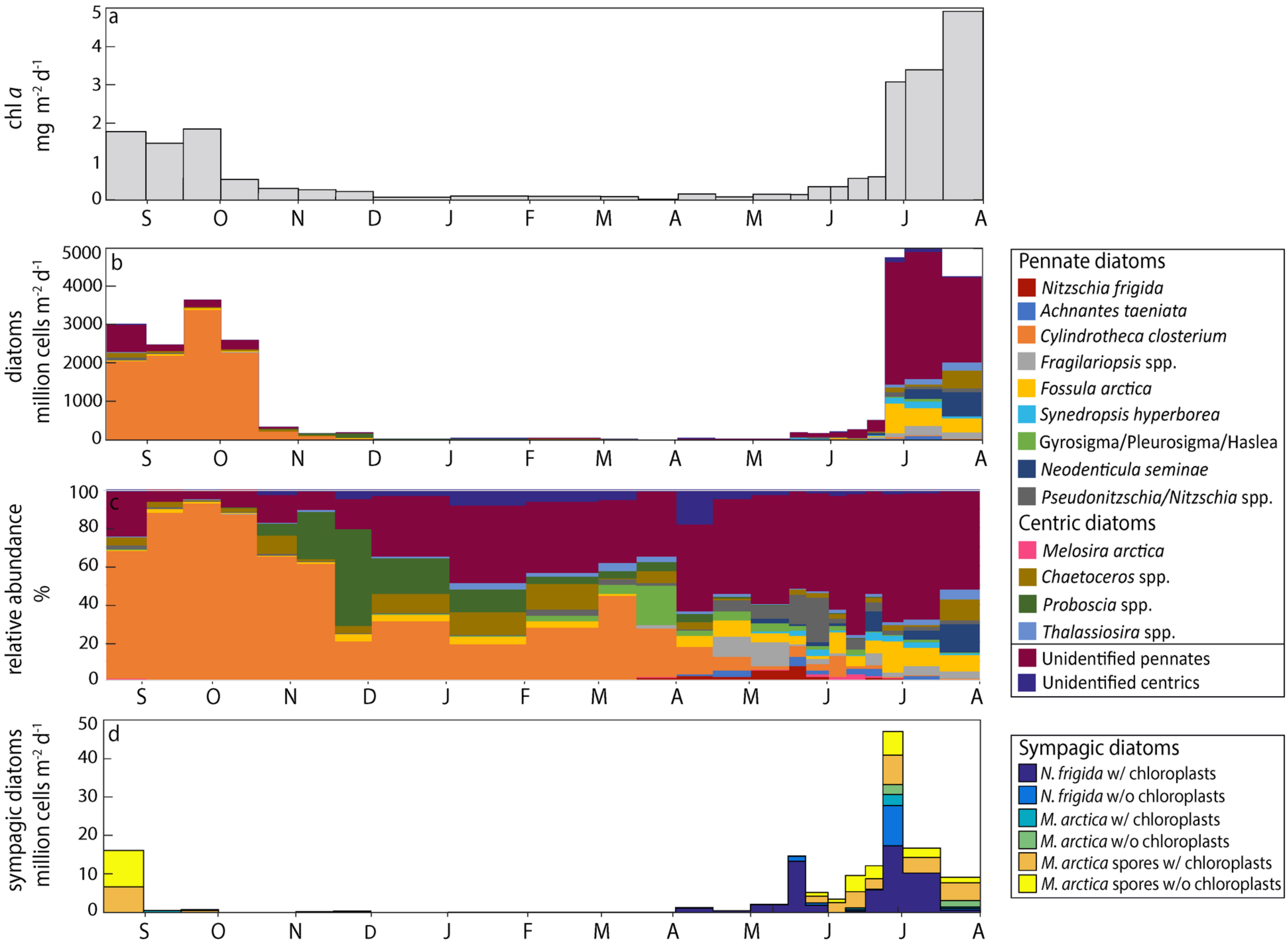
Fig. 3. Annual cycles of a) chlorophyll *a* fluxes, b) diatom fluxes, c) relative abundance of dominant diatom species and groups, and d) sympagic diatoms *N. frigida* and *M. arctica* fluxes at the CEO site from August 2015 to July 2016.

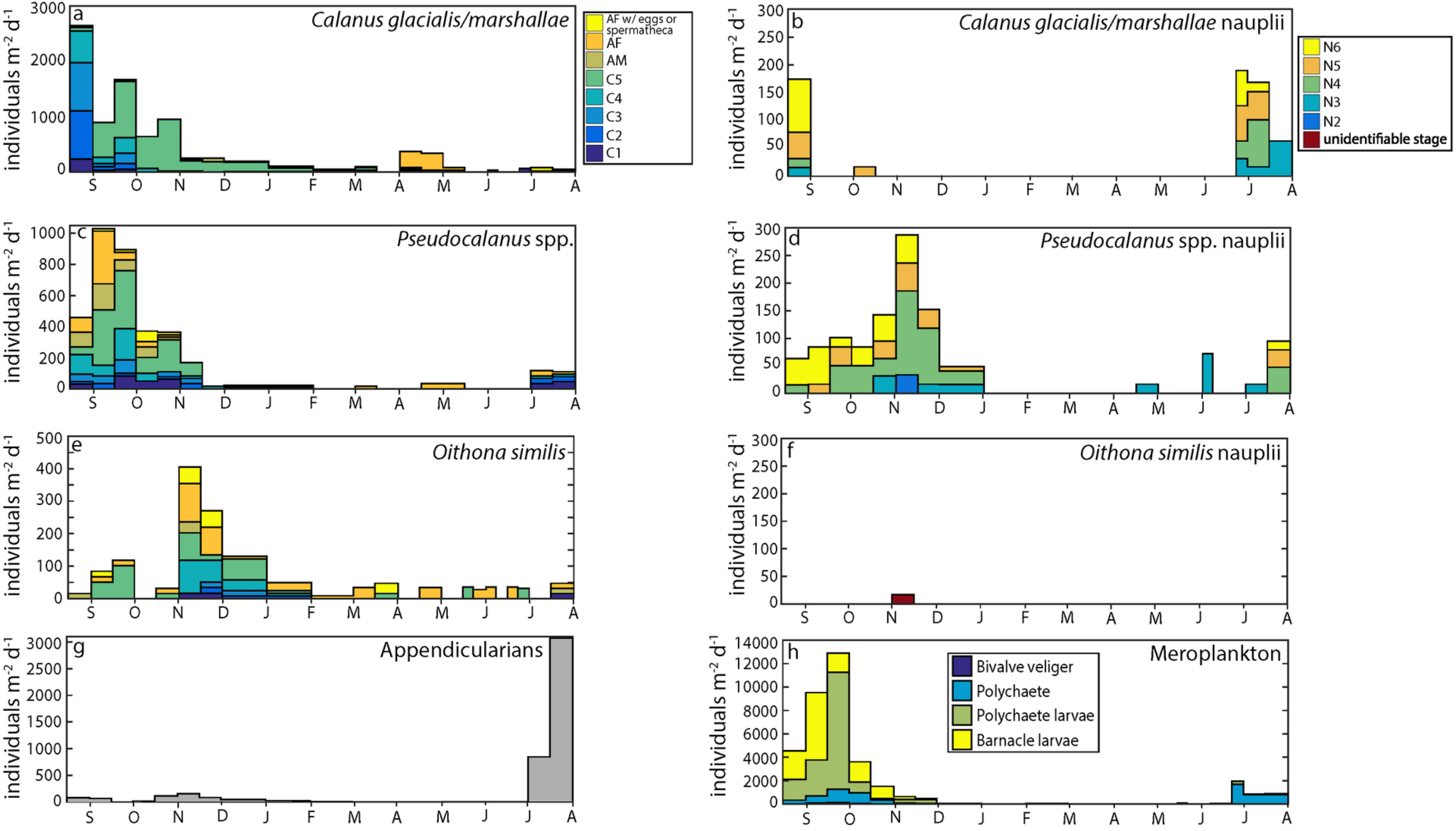
Fig. 4. Annual cycles of the abundance of a) *C. glacialis/marshallae*, b) *C. glacialis/marshallae* nauplii, c) *Pseudocalanus* spp., d) *Pseudocalanus* spp. nauplii, e) *O. similis*, f) *O. similis* nauplii, g) appendicularians, and h) meroplankton individuals at the CEO site from August 2015 to July 2016.

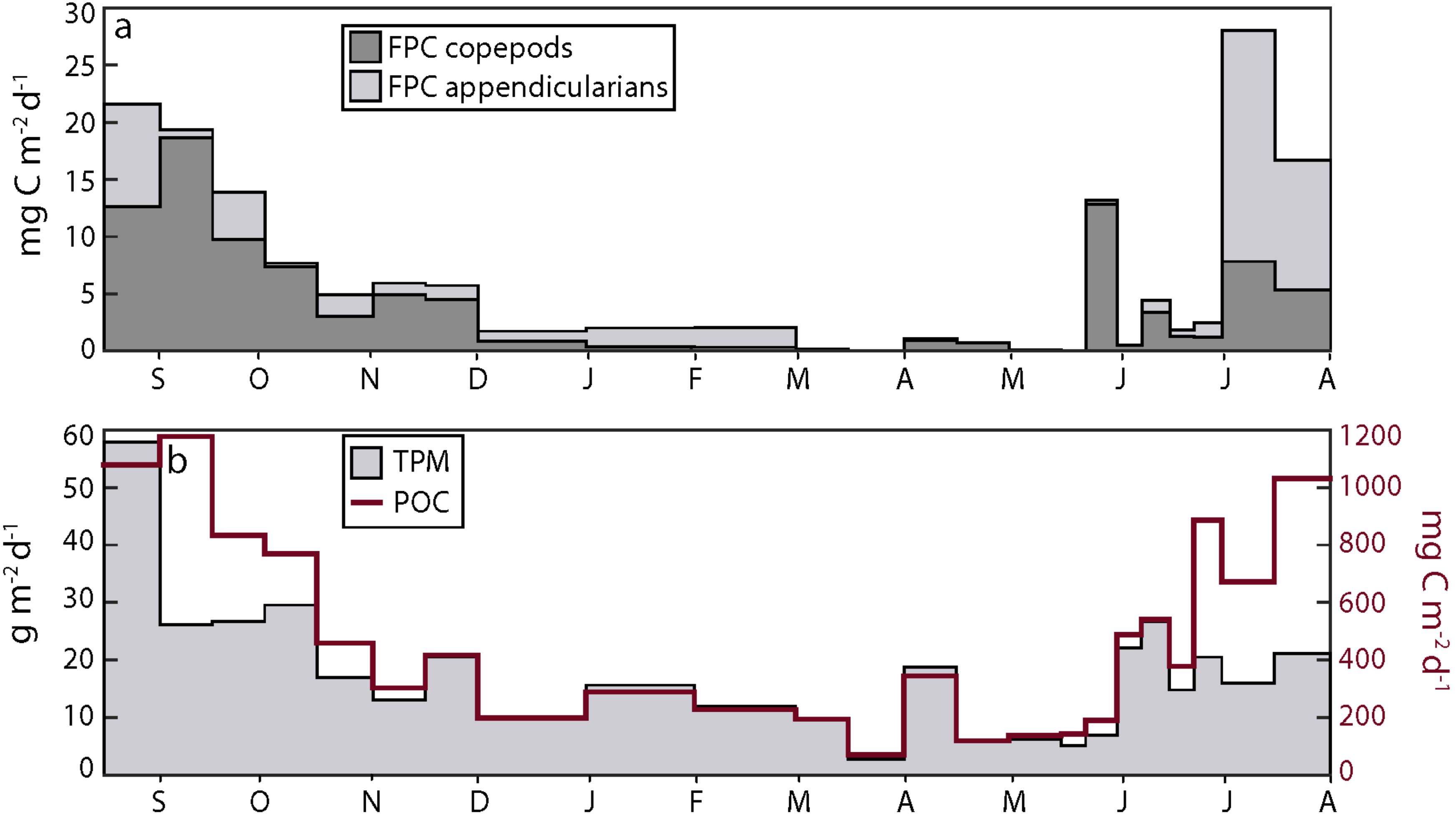
Fig. 5. Annual cycles of a) fecal pellet carbon (FPC) fluxes and b) total particulate matter (TPM) and particulate organic carbon (POC) fluxes from August 2015 to July 2016.


Depth (m)
5
10
20
30
40
50
100
250
500
1000
2000
3000
4000
74°N
72°N
70°N
68°N
66°N
64°N
170°W
165°W
160°W
155°W
Canada Basin
Hanna Shoal
Chukchi Sea
CEO
Barrow Canyon
Utqiagvik
Herald Shoal
Alaska
Kotzebue Sound
Bering Strait
Nome
Alaskan Coastal Current/Water
Anadyr Water
Ocean Data View


a
daylight
air temperature
air temperature (°C)
daylight (h)
20
10
0
-10
-20
-30
-40
24
12
0
S
O
N
D
J
F
M
A
M
J
J
A
b
sea ice
snow
sea ice concentration (%)
snow depth (cm)
100
80
60
40
20
0
30
20
10
0
S
O
N
D
J
F
M
A
M
J
J
A


a
chl *a*
mg m^{-2} d^{-1}
0
1
2
3
4
5
S
O
N
D
J
F
M
A
M
J
J
A
b
diatoms
million cells m^{-2} d^{-1}
0
1000
2000
3000
4000
5000
c
relative abundance
%
0
20
40
60
80
100
d
sympagic diatoms
million cells m^{-2} d^{-1}
0
10
20
30
40
50
Pennate diatoms
Nitzschia frigida
Achnantes taeniata
Cylindrotheca closterium
Fragilariopsis spp.
Fossula arctica
Synedropsis hyperborea
Gyrosigma/Pleurosigma/Haslea
Neodenticula seminae
Pseudonitzschia/Nitzschia spp.
Centric diatoms
Melosira arctica
Chaetoceros spp.
Proboscia spp.
Thalassiosira spp.
Unidentified pennates
Unidentified centrics
Sympagic diatoms
N. frigida w/ chloroplasts
N. frigida w/o chloroplasts
M. arctica w/ chloroplasts
M. arctica w/o chloroplasts
M. arctica spores w/ chloroplasts
M. arctica spores w/o chloroplasts


a
Calanus glacialis/marshallae
AF w/ eggs or spermatheca
AF
AM
C5
C4
C3
C2
C1
individuals m^{-2} d^{-1}
0
1000
2000
3000
S O N D J F M A M J J A
b
Calanus glacialis/marshallae nauplii
N6
N5
N4
N3
N2
unidentifiable stage
individuals m^{-2} d^{-1}
0
50
100
150
200
250
300
S O N D J F M A M J J A
c
Pseudocalanus spp.
individuals m^{-2} d^{-1}
0
200
400
600
800
1000
S O N D J F M A M J J A
d
Pseudocalanus spp. nauplii
individuals m^{-2} d^{-1}
0
50
100
150
200
250
300
S O N D J F M A M J J A
e
Oithona similis
individuals m^{-2} d^{-1}
0
100
200
300
400
500
S O N D J F M A M J J A
f
Oithona similis nauplii
individuals m^{-2} d^{-1}
0
50
100
150
200
250
300
S O N D J F M A M J J A
g
Appendicularians
individuals m^{-2} d^{-1}
0
500
1000
1500
2000
2500
3000
S O N D J F M A M J J A
h
Meroplankton
Bivalve veliger
Polychaete
Polychaete larvae
Barnacle larvae
individuals m^{-2} d^{-1}
0
2000
4000
6000
8000
10000
12000
14000
S O N D J F M A M J J A


a
FPC copepods
FPC appendicularians
mg C m-2 d-1
30
25
20
15
10
5
0
S
O
N
D
J
F
M
A
M
J
J
A
b
TPM
POC
g m-2 d-1
60
50
40
30
20
10
0
1200
1000
800
600
400
200
0
mg C m-2 d-1
S
O
N
D
J
F
M
A
M
J
J
A