

THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

CITATION

Grebmeier, J.M., B.A. Bluhm, L.W. Cooper, S.G. Denisenko, K. Iken, M. Kędra, and C. Serratos. 2015. Time-series benthic community composition and biomass and associated environmental characteristics in the Chukchi Sea during the RUSALCA 2004–2012 Program. *Oceanography* 28(3):116–133, <http://dx.doi.org/10.5670/oceanog.2015.61>.

DOI

<http://dx.doi.org/10.5670/oceanog.2015.61>

COPYRIGHT

This article has been published in *Oceanography*, Volume 28, Number 3, a quarterly journal of The Oceanography Society. Copyright 2015 by The Oceanography Society. All rights reserved.

USAGE

Permission is granted to copy this article for use in teaching and research. Republication, systematic reproduction, or collective redistribution of any portion of this article by photocopy machine, reposting, or other means is permitted only with the approval of The Oceanography Society. Send all correspondence to: info@tos.org or The Oceanography Society, PO Box 1931, Rockville, MD 20849-1931, USA.

Time-Series Benthic Community Composition and Biomass and Associated Environmental Characteristics in the Chukchi Sea During the RUSALCA 2004–2012 Program

By Jacqueline M. Grebmeier, Bodil A. Bluhm, Lee W. Cooper, Stanislav G. Denisenko,
Katrin Iken, Monika Kędra, and Carlos Serratos



ABSTRACT. Benthic macrofaunal and epifaunal composition and biomass and associated environmental drivers were evaluated for time-series stations occupied during three cruises of the RUSALCA (Russian-American Long-term Census of the Arctic) program undertaken in August 2004, September 2009, and September 2012. We focus on the benthic communities collected at repeat stations in the southern Chukchi Sea and the key environmental characteristics that could influence benthic population structure and biomass. These characteristics included bottom water temperature, salinity, and chlorophyll *a* (chl *a*); integrated chl *a*; export production via sediment oxygen uptake rates as an indicator of food supply to the benthos; and surface sediment parameters that are known to influence benthic population community composition and biomass, such as grain size, carbon content, and chl *a*. Overall, both the macrofaunal and epibenthic community composition at the time-series sites in the southern Chukchi Sea have remained relatively constant over the time period of this study (2004–2012). However, some of the more sedentary macrofauna are showing significant declines in biomass since 2004, particularly in the center of a macrobenthic hotspot that has been persistent for decades in the southern Chukchi Sea. While biomass estimates were more variable for the more motile epibenthic fauna, there was also an indication of declining epifaunal biomass since 2009. We highlight here as a case study the benthic time-series efforts during RUSALCA that are also part of the Distributed Biological Observatory (DBO) international network, which is tracking the status and trends of Arctic ecosystem response to the changing physical drivers in the southern Chukchi Sea.

INTRODUCTION

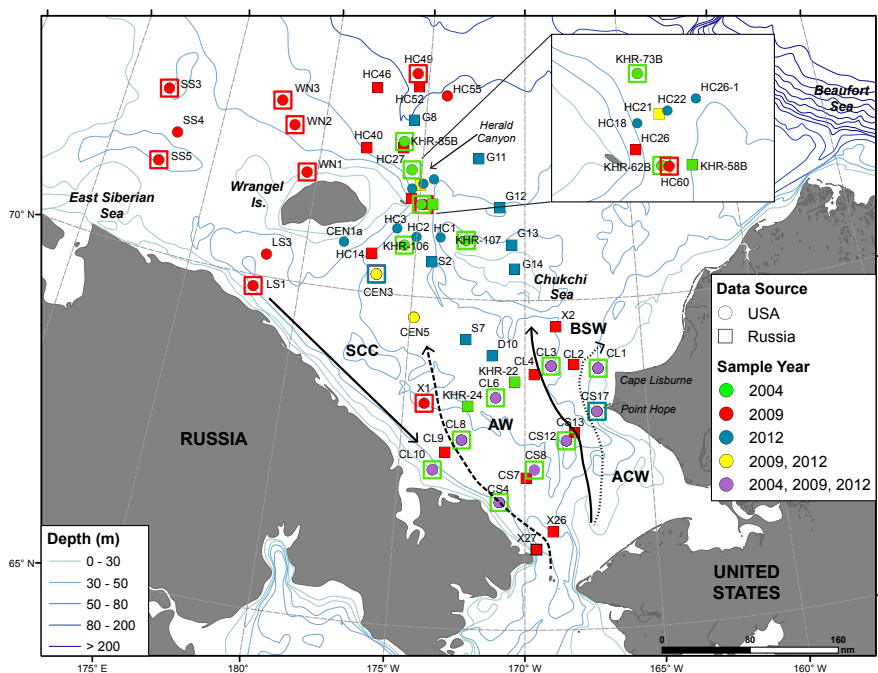
Changing seasonal sea ice conditions and seawater temperatures strongly influence biological processes and marine ecosystems at high latitudes (Grebmeier et al., 2006a; Kędra et al., 2015). Understanding the impacts of reduced seasonal sea ice and warming seawater on water column

and benthic processes is essential for tracking and forecasting ecosystem responses in the Pacific Arctic region, where the greatest changes in Arctic seasonal sea ice duration and extent have been observed (Grebmeier et al., 2010; Frey et al., 2015). Two important questions concern how the developing new

system in the Pacific Arctic will influence system-level ecological processes and what the potential tipping points are in biological community structure and biodiversity (Moore and Stabeno, 2015). A primary goal of our study was to investigate the benthic ecological response to these changing physical driving factors by evaluating time-series benthic collections in the southern Chukchi Sea between the United States and Russia.

Using samples collected during three cruises of the Russian-American Long-term Census of the Arctic (RUSALCA) in 2004, 2009, and 2012 by both Russian and American scientists (Figure 1), we investigated key processes that influence the Pacific Arctic benthic ecosystem (both macrofauna and epifauna). Over the observation period, the southern Chukchi Sea benthic habitat has increasingly been exposed to significantly longer open-water periods as seasonal sea ice has declined (Frey et al., 2014, 2015). We have collected and developed, with colleagues, a large data set of benthic macrofaunal, and to a limited degree epifaunal, abundance and biomass in the eastern Chukchi Sea over the last three decades (Feder et al., 2005, 2007; Grebmeier et al., 2006a, 2015 and references therein;

FIGURE 1. Distribution of RUSALCA benthic sampling stations with sampling years color-coded: 2004 in green, 2009 in red, and 2012 in blue, and repeat time-series sites for two of the years in yellow and all three years in purple. The circles represent collections by US scientists and the squares by Russian scientists. The general current flow (dotted and solid lines with arrows) is modified from Grebmeier et al. (2015). This paper focuses on the southern Chukchi Sea time-series sites indicated by purple dots along the CS (Chukchi South) and CL (Cape Lisburne) lines. ACW = Alaska Coastal Water. BSW = Bering Sea Water. AW = Anadyr Water. SCC = Siberian Coastal Current.



Bluhm et al., 2009; Iken et al., 2010; Blanchard et al., 2013a; S. Denisenko et al., 2015, in this issue). Other related studies have assessed carbon cycling in general (reviewed in Grebmeier, 2012; Mathis et al., 2014; Grebmeier et al., 2015). However, there have been very limited oceanographic and biological studies on the continental shelf regions of the western Chukchi Sea and East Siberian Sea, which were focus areas for the RUSALCA program. RUSALCA (and the previous

US-Russian/Soviet programs such as BERPAC [Bering-Pacific studies]), as well as time-series studies in other regions of the Chukchi Sea continental shelf, have identified “footprints” of persistent benthic biomass, dominant fauna, and export of carbon to the sediments in the Pacific Arctic region (Grebmeier et al., 2015).

The RUSALCA macrofaunal and epibenthic studies have been undertaken since 2004, specifically along the Chukchi South (CS) and Cape Lisburne

(CL) transect lines (Figure 1), in conjunction with the Distributed Biological Observatory (DBO) program initiated in 2010 (Grebmeier et al., 2010) that also includes a subset of stations on the CS line (see Box 1). These time-series stations are also part of the Circumpolar Biodiversity Monitoring Program (CBMP), which is part of the Conservation of Arctic Flora and Fauna (CAFF) activity of the Arctic Council (CAFF, 2013). The international aspects of the RUSALCA program add

BOX 1. TIME-SERIES BENTHIC BIOMASS ON THE RUSALCA DBO/CS LINE

The RUSALCA time-series stations on the Chukchi South (CS) transect (Figure B1, left panel) have been incorporated into the international Distributed Biological Observatory (DBO), which is tracking the status and trends of benthic communities and environmental conditions in the region. The RUSALCA data have been instrumental in delineating the benthic biomass hotspot that extends across the US-Russian border, thereby providing coordinates for an enhanced suite of ecosystem observations in this region. Data have been collected in this area not only by RUSALCA during the first decade of this century but also during prior Russian and US cruises, including the joint Bering-Pacific cruises (BERPAC) in 1988

(*Akademik Koralev*), in 1993 (*Okean*), in 1995 (*Alpha Helix*), and annually since 1998 during DBO cruises with international collaborators aboard *CCGS Sir Wilfrid Laurier* (only in US waters).

Time-series data in the region indicate spatial and temporal variability in the benthic communities due to variable water mass dynamics and current velocities. The data overall (excluding the hotspot stations UTN5 and CS8) indicate declining benthic biomass since the 1970s, with a more rapid decline starting in the late 1990s (Figure B1, right). However, the high biomass UTN5 station on the CS line had increasing benthic biomass from 2000 to 2010, with subsequent declines after that to 2012; this decline

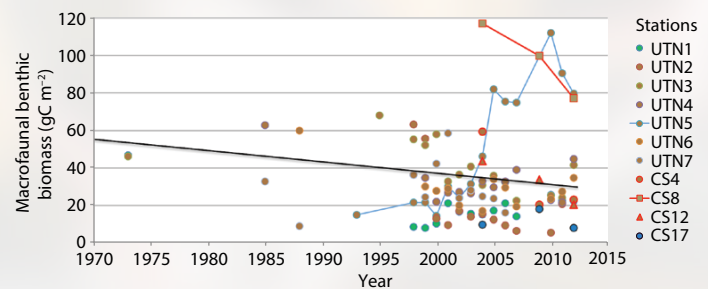
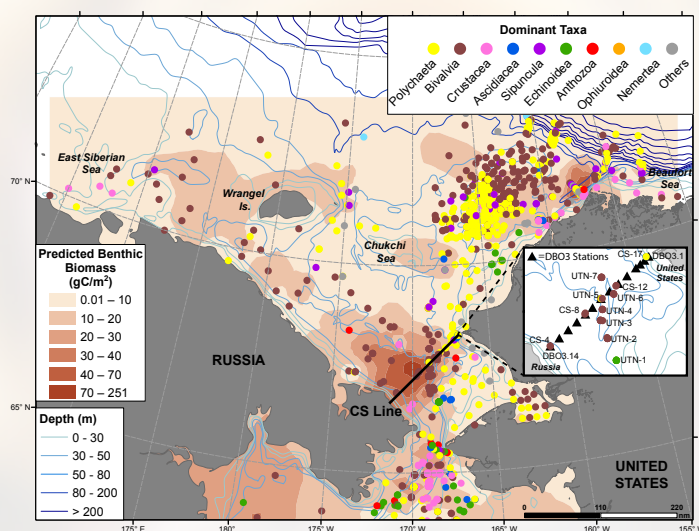


FIGURE B1. (left) Distribution of dominant benthic macrofaunal taxa type and total station biomass in the Chukchi Sea from 1973 to 2012 (updated from Grebmeier et al., 2006a). The Chukchi South (CS) line designates the RUSALCA time-series effort discussed in this paper with the time-series sites identified on the map in the blowup box. (right) Time-series macrofaunal benthic biomass measurements from 1973 to 2012 in the benthic hotspot region of the Southeast Chukchi Sea. Data indicate a decline in the dominant bivalve, *Macoma calcareo*, and other bivalves species at almost all stations (excluding the highest macrofaunal biomass UTN5 and CS8 stations), with the black line indicating this trend in macrofaunal benthic biomass ($\text{gC m}^{-2} = 1,535.83 - 0.75 \times \text{Year}$; ANOVA $F = 15.55$, $p = 0.0002$). Coincidentally, there was an increase in station biomass from about 2000 to 2010 at Station UTN5, which was dominated by bivalves (blue solid line), with a subsequent decline from 2010 to 2012. This declining trend at station UTN5 in recent years is similar, but temporally offset, from the other very high biomass station CS8 that has a declining trend since 2004 (red line), both located in the benthic hotspot.

special strength to the field effort through (1) established working relationships with other US and Russian collaborators, (2) consistency in sampling approach and access to legacy data from three RUSALCA process cruises and past sampling efforts, and (3) time-series studies of water column and benthic regions to evaluate system response to changing environmental parameters. Arctic climate change is not only predicted to impact the physical environment, such as

sea ice and seawater characteristics (Frey et al., 2015), but also may lead to multiple changes in ecosystem function, including food web structure, stability, and trophic transfer efficiency, especially by affecting the prey base, such as the benthic macro- and epifauna evaluated in this synthesis paper (Grebmeier et al., 2006a, 2015; Doney et al., 2012; Kędra et al., 2015).

As sea ice extent declines and seawater warms in this region of the Arctic, the vulnerability of its ecosystem to

environmental change is considered high (Grebmeier et al., 2006b; Wassmann et al., 2011; Duarte et al., 2012; Grebmeier, 2012). The duration and extent of seasonal sea ice, seawater temperature, and water mass structure are critical controls on water column production, organic carbon cycling, and pelagic–benthic coupling. Because the productive areas in the Chukchi Sea are associated with short food webs and shallow depths, changes in lower trophic levels can

is similar to the trend for the other high benthic time-series site (station CS8) (Figure B1–both panels; also see Figure 5 in the core paper). The overall DBO sampling approach includes collection of a series of coordinated, multitrophic-level observations that integrate physical, biogeochemical, and biological measurements along transect lines that intersect areas of high benthic biomass, including the CS line that is considered part of DBO3 (Figure B2; Grebmeier et al., 2015). The Southeast Chukchi Sea hotspot (DBO3 offshore) is maintained by export to the benthos of locally produced chlorophyll *a* (Figure B2, left panel) as well as advected organic carbon brought into the region by Pacific water transiting northward through the ecosystem (Grebmeier, 2012). This high level of organic carbon production settles to the underlying sediments to support the high biomass populations of macrofauna, with a distinct gradient at DBO3 of high

benthic biomass offshore and reduced biomass near the Alaskan coastline (Figure B2, right panel). Both walrus and gray whales are known to forage at this hotspot seasonally (Jay et al., 2012; Moore et al., 2014). Sampling in this Southeast Chukchi Sea region, including at the benthic hotspot on the CS line (Grebmeier et al., 2015), has been supported by the US National Oceanic and Atmospheric Administration and the National Science Foundation over the years, along with other US federal agencies and international partners participating in the Pacific Arctic Group. The latter is an open membership coordination entity that allows data sharing and planning of sampling opportunities among scientists and agencies from the US, Canada, China, Japan, Korea, and Russia (Grebmeier et al., 2010). Further information on the DBO and RUSALCA can be found at the following websites: <http://www.arctic.noaa.gov/dbo> and <http://www.arctic.noaa.gov/rusalca>.

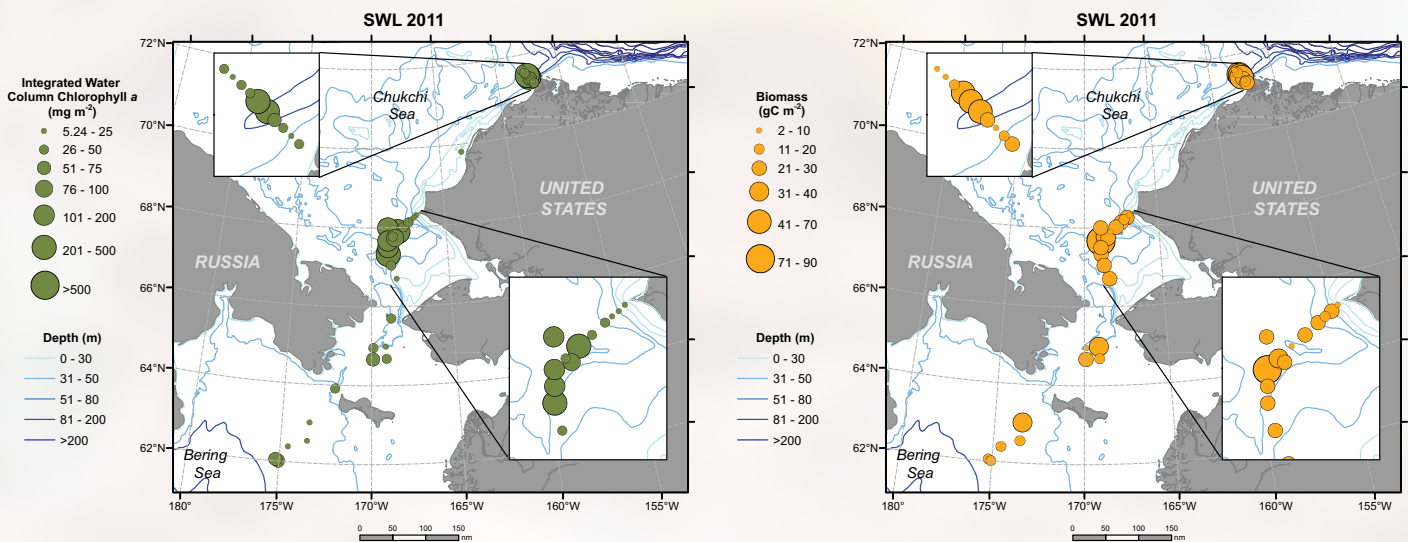


FIGURE B2. (left) Distribution of integrated chlorophyll *a* (mg m^{-2}) during July 2011 at four DBO regions over whole water column, including the DBO3 transect line in the southern Chukchi Sea. (right) Distribution of total station macrofaunal biomass (gC m^{-2}) in the same region.

rapidly impact benthic-feeding higher trophic levels, such as walruses, gray whales, and bearded seals (Grebmeier et al., 2006a, 2015; Moore et al., 2014). The recent reduction in seasonal Arctic sea ice could shift the current benthic-based food web to one more dominated by pelagic processes.

Benthic macrofaunal biomass reflects variability in interannual carbon deposition to the seafloor on the shallow Chukchi Sea continental shelf from south to north (Grebmeier et al., 2006a, 2015, and references therein). Bivalves, polychaetes, amphipods, and sipunculans are the dominant Chukchi shelf macrofauna (Grebmeier et al., 2006a, and references therein; Feder et al., 2007; S. Denisenko et al., 2015, in this issue). In addition to food supply and community composition, sediment grain size reflects local current speed and thus has an impact on carbon deposition to the benthos (Grebmeier, 2012; Grebmeier et al., 2015). Sediment grain size is a key predictor of benthic faunal community composition; by comparison, organic carbon, which is positively correlated with the smaller silt and clay grain particles, is a key predictor of biomass (Grebmeier and Cooper, 1995; Grebmeier et al., 2006a, and references therein).

Echinoderms (brittle stars, sea stars, and sea cucumbers), arthropods (crabs and shrimps), and mollusks (gastropods) dominate the epibenthic communities of the Chukchi Sea. Echinoderms are widespread, and although brittle stars are numerically dominant in the northern part of the sea, they are more variable in biomass, depending on species type, and instead sea stars dominate by biomass (Feder et al., 2005; Bluhm et al., 2009; Ravelo et al., 2014). Multiple environmental factors, including seawater temperature, food supply, and sediment grain size, can drive epibenthic biomass and community structure, similar to their influences on macrofaunal communities (Feder et al., 2005; Grebmeier et al., 2006a; Bluhm et al., 2009; Blanchard et al., 2013a,b; Petryashov et al., 2013;

Schonberg et al., 2014). A higher percent of arthropod biomass in the southern Chukchi Sea gives way to proportionally more echinoderms poleward (Feder et al., 2005; Ravelo et al., 2014). The dominant snow crab, *Chionoecetes opilio*, is the major contributor to the arthropod biomass on parts of the Chukchi Sea shelf (Bluhm et al., 2009; Ravelo et al., 2014). Its core distribution range has shifted northward over the past decades (Orensanz et al., 2004; Mueter and Litzow, 2008), and population size in the Chukchi Sea has possibly increased since the 1970s (Feder et al., 2005; Bluhm et al., 2009). However, very cold bottom water temperatures can limit populations on the northern Chukchi Sea shelf (Foyle et al., 1989). By comparison, echinoderms are released from competitive and predation pressures in the absence of large crabs (and fishes) in the northern Chukchi waters, allowing them to become more dominant (Feder et al., 2005).

The specific objectives of our study were (1) to determine abundance, biomass, and community structure of macrofauna and epifauna at time series (repeat) stations in 2004, 2009, and 2012 in the southern Chukchi Sea in the context of average macrofaunal biomass patterns across the southern and western Chukchi Sea, and (2) to interpret the resulting patterns in the light of hydrography, food availability, and sediment properties.

METHODS

The data for this RUSALCA synthesis effort are based upon sample collections from three multidisciplinary cruises in the Chukchi Sea, including biological, chemical, and physical sampling of the water column and benthos using R/V *Professor Khromov*: RUSALCA 2004 from August 8–25, 2004; RUSALCA 2009 from September 4–27, 2009; and RUSALCA 2012 from September 2–24, 2012. The time-series data collected in the southern Chukchi Sea included: (1) determinations of macrofaunal and epifaunal abundance, biomass, and

community structure, (2) measurements of sediment parameters and food availability, including sediment chl *a* content, total organic carbon (TOC) and nitrogen (TON) content, sediment grain size, and sediment community oxygen consumption (SCOC; an indicator of carbon supply to the benthos), and (3) hydrographic measurements from other RUSALCA team members of bottom water temperature and salinity (directed by Principal Investigator [PI] Robert Pickart, Woods Hole Oceanographic Institution; Pisareva et al., 2015, in this issue) as well as water column chl *a* content (PI Terry Whitledge, University of Alaska Fairbanks). See the RUSALCA webpage for cruise reports and/or <http://www.whoi.edu/science/PO/people/pickart/newFieldPrograms.htm> for hydrographic data.

Summary of Physical Observations

A combination of cold and high-salinity Anadyr Water (AW; >32.5) and Bering Sea Water (BSW; 31.8–32.5), or mixtures thereof, characterize the bottom waters throughout the southern Chukchi Sea and as far north as 72°N in Herald Canyon in 2004, 2009, and 2012 (Figure 1, Table 1; Coachman, 1987; Grebmeier et al., 1988; Bluhm et al., 2009; Ershova et al., 2015). In addition, relatively warm and fresh Alaska Coastal Water (ACW) normally occurs on the eastern side of the Chukchi Sea in all years (Weingartner et al., 2005; Grebmeier et al., 2006a, 2015; Bluhm et al., 2009; Pisareva et al., 2015, in this issue). The western side of the southern Chukchi Sea can include a more freshwater component of East Siberian Sea water and coastal runoff (Münchow et al., 1999; Khim et al., 2003), which we call Russian Coast (RC) water to follow the nomenclature of Bluhm et al. (2009).

Macrofaunal Communities

Macroinfauna were sampled at 114 stations during RUSALCA cruises in 2004, 2009, and 2012 in both Russian and US waters (Figure 1). Three to four replicate macrofaunal samples were collected

using 0.1 m² van Veen or Okean grabs, with sediment sieved over 1 mm screens and the remaining macrofauna preserved in 10% buffered seawater formalin. Nine time-series stations were sampled in the southern Chukchi Sea over the three RUSALCA cruise years. Macroinfauna were later identified to family and/or species (or to the lowest taxon possible), with all taxa subsequently counted and weighed. Data were analyzed for abundance and biomass, although here we focus on biomass. Data for all collections (Russian and American) were converted to dry weight carbon values based on previously verified correction factors (Stoker, 1978; Grebmeier et al., 1989) in order to reduce the bias of calcium carbonate on weight values.

Epifaunal Communities

Epibenthic data were collected at most of the benthic stations occupied during the three RUSALCA cruises (Figure 1, Table 1). Of these multiyear collections, eight time-series stations were sampled in the southern Chukchi Sea each year. Quantitative sampling for epibenthic fauna in each of the three years followed methods outlined in Bluhm et al. (2009). Briefly, a plumb-staff beam trawl (2.26 m opening and a 7 mm mesh net with a 4 mm cod end liner) was used. Tow duration ranged from 1.5 to 5 min at speeds of ~1 to 1.5 knots for a trawled area ranging from 135 m² to 823 m². Large catches were quantitatively subsampled from a well-mixed haul. Epifauna samples from trawl hauls were rinsed, sorted

to lowest practical taxonomic level, and counted and weighed (wet weight) onboard using spring or digital hanging scales; field identifications were later confirmed or corrected in the home lab (for details see Bluhm et al., 2009). For colonial organisms (e.g., bryozoans, hydrozoans), only wet weights were recorded. Area trawled was used to estimate abundance and biomass as catch per unit effort (CPUE), which were then normalized to 1,000 m⁻². Given the semi-quantitative nature of trawl surveys, these data should be considered gross estimates (Bluhm et al., 2009; Eleftheriou and Moore, 2013). Taxonomic names used for macro- and epifauna follow the currently accepted names in the World Register of Marine Species (<http://www.marinespecies.org>).

TABLE 1. Summary of station parameters for each of the time-series stations during RUSALCA cruises in 2004, 2009, and 2012.

Cruise Data							Bottom Water (BW)			Chlorophyll		
Cruise	Station Number	Station Name	Time Series ID	Date (yr-mo-d)	Latitude (°N)	Longitude (°W)	Depth (m)	Temp (°C)	Salinity	Oxygen (ml L ⁻¹)	BW (mg m ⁻³)	Integrated chl <i>a</i> (mg m ⁻²)
RUSALCA04	7	KHR-11	CS4	2004-08-11	66.937	170.997	40	1.69	33.17	6.20	0.47	1.04
RUSALCA04	9	KHR-13	CS8	2004-08-12	67.432	169.620	49	2.47	32.93	5.15	0.30	3.86
RUSALCA04	11	KHR-15	CS12	2004-08-12	67.868	168.328	55	2.77	32.58	6.11	0.52	6.89
RUSALCA04	13	KHR-17	CS17	2004-08-13	68.297	167.051	39	7.00	31.00	5.13	0.58	1.28
RUSALCA04	14	KHR-18	CL1	2004-08-13	68.950	166.912	48	7.95	31.30	5.00	0.34	1.13
RUSALCA04	16	KHR-20	CL3	2004-08-13	69.006	168.895	54	3.69	32.27	7.21	0.11	2.54
RUSALCA04	19	KHR-23	CL6	2004-08-15	68.524	171.214	56	2.21	32.91	5.25	0.59	3.91
RUSALCA04	21	KHR-25	CL8	2004-08-15	67.870	172.551	49	1.70	33.05	5.17	0.79	2.29
RUSALCA04	23	KHR-27	CL10	2004-08-16	67.397	173.653	31	-1.52	32.87	5.48	0.30	0.99
RUSALCA09	7	CS4	CS4	2009-09-26	66.934	170.986	42	3.95	31.37	6.87	1.18	1.04
RUSALCA09	11	CS8	CS8	2009-09-27	67.431	169.610	50	1.83	32.68	3.72	1.39	5.25
RUSALCA09	15	CS12	CS12	2009-09-27	67.874	168.314	56	1.91	32.79	3.34	1.84	6.89
RUSALCA09	20	CS17	CS17	2009-09-28	68.298	167.044	39	3.75	31.88	5.50	1.06	1.28
RUSALCA09	23	CL1	CL1	2009-09-24	68.949	166.916	46	3.23	32.03	6.26	0.42	1.13
RUSALCA09	25	CL3	CL3	2009-09-25	69.005	168.896	53	2.31	32.19	5.03	0.35	2.54
RUSALCA09	28	CL6	CL6	2009-09-25	68.518	171.462	54	1.77	32.84	3.14	1.95	3.91
RUSALCA09	30	CL8	CL8	2009-09-26	67.867	172.553	48	-0.09	33.00	3.15	1.14	2.87
RUSALCA09	32	CL10	CL10	2009-09-27	67.630	169.020	40	2.19	28.67	7.37	1.92	3.80
RUSALCA12	1	CS4	CS4	2012-09-29	66.933	170.985	44	1.40	32.40	6.30	0.10	0.52
RUSALCA12	6	CS17	CS17	2012-09-01	68.298	167.042	40	6.73	30.51	6.89	0.03	1.12
RUSALCA12	8	CL1	CL1	2012-09-02	68.948	166.918	47	3.19	32.19	7.21	0.02	1.10
RUSALCA12	10	CL3	CL3	2012-09-02	69.003	168.894	54	2.01	32.57	7.32	0.02	1.17
RUSALCA12	14	CL6	CL6	2012-09-02	68.519	171.462	55	1.28	32.92	5.44	0.02	5.00
RUSALCA12	45	CL8-1	CL8	2012-09-13	67.869	172.548	49	1.11	32.93	4.25	0.42	9.23
RUSALCA12	51	CS8R	CS8	2012-09-14	67.431	169.603	52	-0.81	33.28	3.81	0.08	2.27
RUSALCA12	54	CS12R	CS12	2012-09-01	67.874	168.314	58	0.99	32.58	3.88	0.01	2.20
RUSALCA12	48	CL10	CL10	2012-09-14	67.409	173.576	34	1.21	32.36	6.03	0.01	1.02

Sediment Characteristics

The upper layer of sediment (top 0–1 cm) was collected from one van Veen grab (via a door opened prior to the grab being emptied), bagged, frozen, and analyzed for grain size and organic carbon content at the Chesapeake Biological Laboratory using standard procedures (Cooper et al., 2002, and 2015, in this issue). Surface sediment organic carbon and nitrogen ratios were determined on acidified aliquots of dried sediment using an elemental analyzer. Sediment chlorophyll *a* (sed chl *a*) samples were collected by syringe subcores from the same grab, extruded into pre-weighed plastic tubes, and processed shipboard. Briefly, the sediment samples were stored for 12 hr in 90% acetone at 4°C in the dark. Chl *a* concentrations were subsequently determined fluorometrically on a Turner Designs 10-AU fluorometer. The mean of two chl *a* concentration measurements for each station were converted to chl *a* per m² of surface sediment. SCOC experiments were run on duplicate 133 cm² subcores to measure sediment oxygen uptake over a 12–24 hr period. Further details on the analyses are provided in Cooper et al. (2002, 2012, 2015, in this issue).

Water Column Data

Water column temperature and salinity were obtained from the RUSALCA hydrographic sampling system; data are available at the WHOI RUSALCA website mentioned previously. Water samples were collected at standard depths via bottles on the conductivity-temperature-depth (CTD) rosette for chl *a*. Chl *a* was extracted and either processed on board or frozen for post-cruise processing using Turner Designs 10-AU fluorometers (Terry Whitledge, University of Alaska Fairbanks, *pers. comm.*, 2015; Lee et al., 2013). Time-series stations were assigned to water masses based on average bottom water salinity using the definitions of Grebmeier et al. (1988), which are based on Coachman (1987). Stations with bottom water salinity <31.8 were assigned to ACW, stations with bottom

water salinity between 31.8 and 32.5 were assigned to BSW, and stations with bottom water salinity values >32.5 were assigned to AW. The RC designation was given to the westernmost station, which included local freshwater runoff as well as Siberian Coastal Water (SCW; Münchow et al., 1999).

Data Analysis of Biotic and Abiotic Parameters

Benthic macrofaunal and epifaunal communities and various environmental variables were analyzed for the three RUSALCA cruises using the PRIMER statistical package (v.6, Clarke and Gorley, 2006) as well as the JMP statistical software (SAS, Cary, North Carolina). GIS kriging was utilized to predict macrobenthic biomass distribution using ArcGIS 10.1. Temporal patterns in macrofauna and epifaunal biomass were mapped using bin size breaks according to Jenks's natural breaks.

Time-series macrofaunal and epibenthic community structures were analyzed for 2004, 2009, and 2012. A Bray-Curtis similarity matrix was created using fourth-root transformed biomass data to reduce the influence of dominant taxa on the analyses. A hierarchical cluster analysis was used to group stations by similarity (group average) based on the similarity matrix, and a SIMPROF test was run to test the significance of clusters ($\alpha = 0.05$). Nonmetric multidimensional scaling (nMDS) plots were then used at the designated similarity level (45%) for macrofauna and epifauna to visualize community similarity. A similarity of percentages (SIMPER) routine was run to identify the taxa contributing the most (~50–70%) to similarities within station clusters. Analysis of similarity (ANOSIM) was used to test similarity of community structure among years. Environmental variables were normalized to a common measurement scale and then correlated with the biological matrix based on biomass (fourth-root transformed) for each year using the BIO-ENV suite within PRIMER.

Temporal comparisons of benthic communities were conducted using data from the three years of repeat stations in 2004, 2009, and 2012 occupied in the southern Chukchi Sea on the CS and CL lines (macrofauna: $n = 9$, and epibenthos: $n = 8$). Because certain macrofauna and epibenthic taxa were identified to different taxonomic levels in different years, all species lists were collapsed to the lowest common taxonomic level found across all study years, separately for macro- and epifauna. The environmental variables available for all three study years included latitude, longitude, depth, bottom water salinity, temperature, dissolved oxygen, chl *a* content, integrated chl *a* content over the whole water column, variable sediment substrate size (ϕ), modal size (ϕ), TOC and TON content, C/N ratio, and surface sediment chl *a* concentrations. Sediment substrate was determined as a percent composition of the composite total of very coarse sand and gravel ($\leq 0 \phi$), coarse sand (1 ϕ), medium sand (2 ϕ), fine sand (3 ϕ), very fine sand (4 ϕ), 1–4 ϕ combined as the sand component, and silt/clay ($\geq 5 \phi$), along with modal size (largest percent of grain size). SCOC data were only available for a limited number of stations, so these values were only used in a correlation analysis with gC biomass.

RESULTS AND DISCUSSION

Benthic Macroinfauna and Carbon Export Studies

Highest macrofaunal benthic biomass for all the RUSALCA cruises combined was observed at the head of Herald Valley and the southeast Chukchi Sea in the known hotspot of tellinid bivalves (*Macoma calcarea* and *M. moesta*), which extends across the US-Russian boundary (Table 2, Figure 2; Grebmeier, 1992, 1993, 2006a, 2015; Sirenko and Koltun, 1992; Feder et al., 2007; S. Denisenko et al., 2015, in this issue). At this location, biomass ranges from 30 to ~120 gC m⁻² (Figure 3a–c). This high biomass results from seasonally high productivity and subsequent carbon load in the Anadyr

TABLE 2. Summary of time-series macrofauna and epifauna station parameters for each of the RUSALCA cruises in 2004, 2009, and 2012. Average values are provided for parameters for each cruise.

Cruise Data				Macrofaunal			Epifaunal	
Cruise	Station Number	Station Name	Time Series ID	Abundance (# m ⁻²)	Biomass (gww m ⁻²)	Biomass (gC m ⁻²)	Abundance (1,000 kg m ⁻²)	Biomass (g ww 1,000 m ⁻²)
RUSALCA04	7	KHR-11	CS4	7,568	1,339.69	59.36	15,437	16,644
RUSALCA04	9	KHR-13	CS8	14,058	3,005.09	116.96	9,712	30,478
RUSALCA04	11	KHR-15	CS12	6,505	1,008.01	43.59	nd	nd
RUSALCA04	13	KHR-17	CS17	3,303	254.26	9.79	1,828	17,027
RUSALCA04	14	KHR-18	CL1	903	22.67	1.44	6,133	60,249
RUSALCA04	16	KHR-20	CL3	2,765	94.18	5.90	16,594	64,475
RUSALCA04	19	KHR-23	CL6	3,283	543.29	24.46	11,605	7,821
RUSALCA04	21	KHR-25	CL8	3,095	826.03	35.69	10,848	9,693
RUSALCA04	23	KHR-27	CL10	4,845	101.73	5.79	2,858	1,628
RUSALCA04 Average				5,147	799.44	33.66	8,511	26,002
RUSALCA09	7	CS4	CS4	2,015	434.74	20.47	8,709	47,544
RUSALCA09	11	CS8	CS8	3,200	2,765.35	99.71	8,663	95,043
RUSALCA09	15	CS12	CS12	3,200	756.91	33.73	nd	nd
RUSALCA09	20	CS17	CS17	4,728	671.03	19.09	2,110	46,565
RUSALCA09	23	CL1	CL1	1,048	14.41	0.77	4,824	28,794
RUSALCA09	25	CL3	CL3	770	15.32	0.93	782	24,966
RUSALCA09	28	CL6	CL6	880	406.04	16.15	9,870	117,004
RUSALCA09	30	CL8	CL8	2,228	1,151.24	42.53	33,295	96,470
RUSALCA09	32	CL10	CL10	1,463	53.83	2.30	5,765	13,349
RUSALCA09 Average				2,170	696.54	26.19	9,252	58,717
RUSALCA12	1	CS4	CS4	8,298	490.96	23.07	6,180	24,636
RUSALCA12	6	CS17	CS17	4,840	247.90	8.23	2,715	10,915
RUSALCA12	8	CL1	CL1	2,733	20.34	0.92	1,475	5,593
RUSALCA12	10	CL3	CL3	2,420	84.41	4.00	1,664	13,729
RUSALCA12	14	CL6	CL6	5,265	610.51	22.32	13,314	11,419
RUSALCA12	45	CL8-1	CL8	3,638	1,116.93	44.56	20,104	27,256
RUSALCA12	51	CS8R	CS8	12,225	2,082.12	77.12	29,230	48,312
RUSALCA12	54	CS12R	CS12	8,818	452.09	19.39	3,6715	103,876
RUSALCA12	48	CL10	CL10	555	58.88	2.44	14,796	11,875
RUSALCA12 Average				5,421	573.79	22.45	14,021	28,623

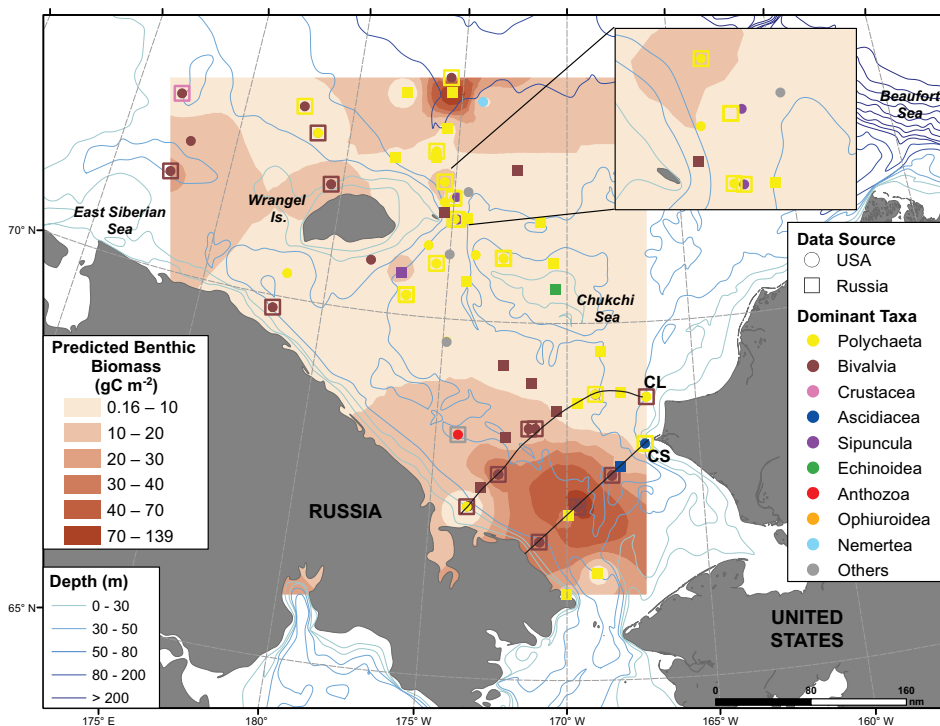


FIGURE 2. Distribution of macrofaunal station biomass (gC m⁻²) for all RUSALCA cruises—2004, 2009, and 2012—by US and Russian scientists, with dominant faunal taxa type color-coded on the map.

Water as it flows north through Bering Strait (Walsh et al., 1989), with tight pelagic-benthic coupling between the upper water column primary production zone and underlying benthos as currents begin to slow down and deposition occurs (Grebmeier et al., 1988, 2006a, 2015, and references therein; Cooper et al., 2015, in this issue). Lowest macrofaunal biomass ($0.1\text{--}10\text{ g C m}^{-2}$) occurred in the central and northwest areas of the Chukchi Sea, excluding stations at the mouth of Herald Canyon (Figure 2). Patches of higher benthic biomass within Herald Canyon, northwest of Wrangel Island, and in the East Siberian Sea, are evaluated in S. Denisenko et al. (2015, in this issue) and will not be discussed in this paper. Bivalves and polychaetes dominate macrofaunal biomass at most of the southern and western Chukchi Sea sites sampled during all the three RUSALCA cruise periods combined (Figure 2).

The advection of phytodetritus from upstream production passing through Bering Strait and in situ production in

the southern Chukchi Sea annually provide the high food supply that supports the persistence of this benthic hotspot in the southern Chukchi Sea time-series area (Grebmeier et al., 2015). SCOC and surface sediment chl *a*, both indicators of carbon export to the sediments (Grebmeier, 2012), were highest within AW in the Southeast Chukchi Sea and in portions of the East Siberian Sea and Long Strait (Table 3), indicating efficient organic carbon export to the benthos. The areas of highest carbon export to the benthos (SCOC, integrated and sediment chl *a*) match the areas of greatest macrofaunal biomass that are important foraging areas for walrus, gray whales, and bearded seals (Grebmeier et al., 2015). Nonparametric statistical evaluation indicates significant relationships between macrofaunal biomass and water mass type (defined by BW salinity, $\rho = 0.725$, $p < 0.0001$), sediment grain size (2 phi, $\rho = -0.471$, $p < 0.01$), food supply (SCOC, $\rho = 0.733$, and integrated chl *a*, $\rho = 0.456$, both $p < 0.02$), and food

quality (sediment C/N, $\rho = -0.544$, $p = 0.003$), supporting previous findings by Grebmeier et al. (2006a).

The similarity cluster analysis and nMDS analyses of station macrofaunal composition and biomass, as well as individual cruise results for each period of time (2004, 2009, and 2012; not shown) and the time series analysis (Figure 4a,b), indicate four major macrofaunal communities: the core AW group, the transitional ACW/BSW group, the ACW group off Alaska, and the western Russian Coast station (Table 4). The ANOSIM results indicate that there are distinct groupings with repeat macrofaunal time series stations (Global R = 0.8, $p = 0.001$), with little influence relating to the year sampled (Global R = 0.1, $p = 0.08$). This finding suggests strong community composition overlap for the AW stations and within each of the other groups (Figure 4a,b) and relatively consistent macrofaunal community composition geographically across the sampling years, despite variability in absolute biomass. The hotspot

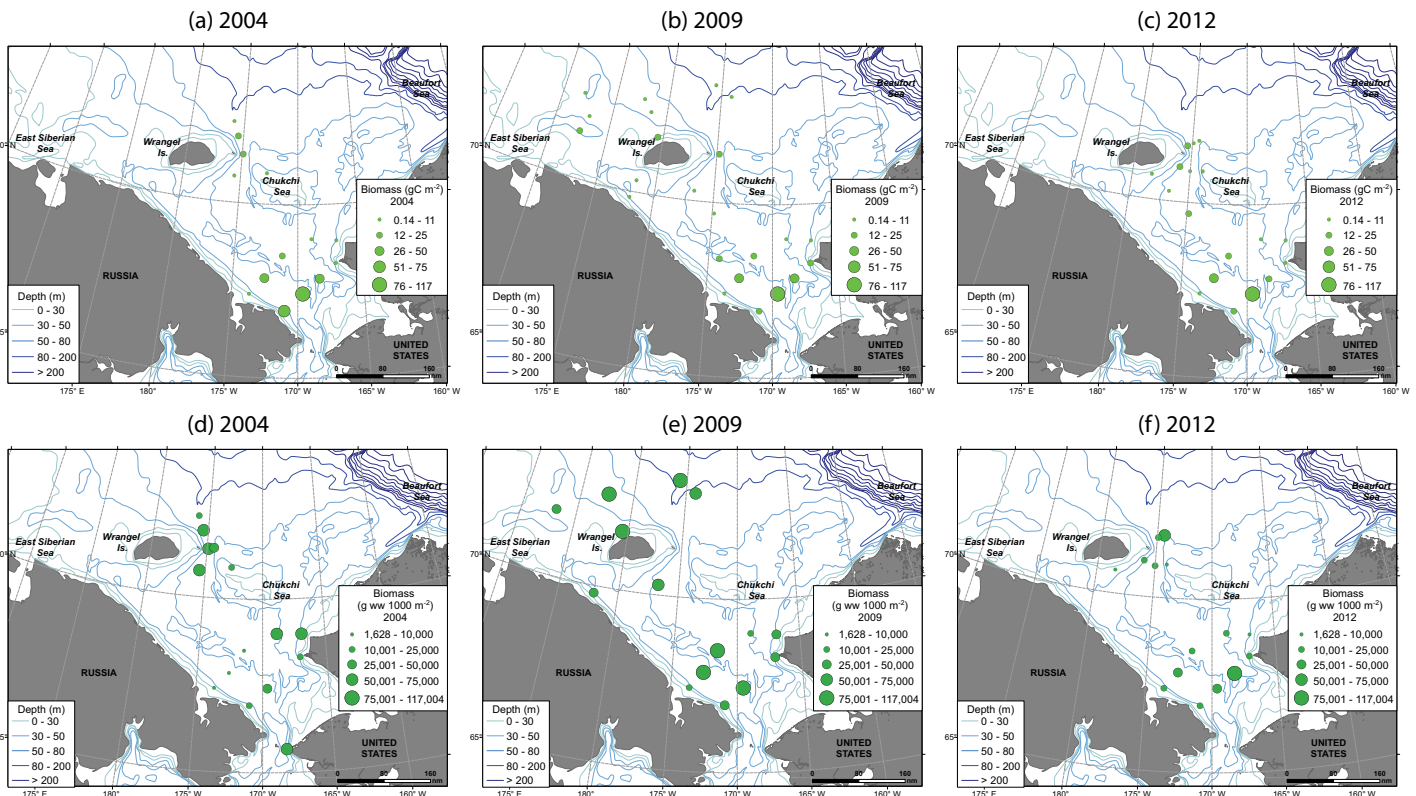


FIGURE 3. Benthic biomass for RUSALCA 2004, 2009, and 2012 (US collections only) for (a–c) macrofauna (g C m^{-2}) and (d–f) epifauna ($\text{g wet weight} \times 1,000\text{ m}^{-2}$).

TABLE 3. Summary of surface sediment parameters for each of the time series stations during RUSALCA cruises in 2004, 2009, and 2012. TOC = Total organic carbon. TON = Total organic nitrogen. Sed chl α = Sediment chlorophyll α .

Cruise	Time Series Stations	Sediment Grain Size (%)							Surface Sediment					Sediment
		≤0 phi	1 phi	2 phi	3 phi	4 phi	1–4 phi	≥5 phi	Modal Size (phi)	TOC (%)	TON (%)	C/N (wt/wt)	Sed chl α (mg m ⁻²)	Community Oxygen Uptake (mM m ⁻² d ⁻¹)
RUSALCA04	CS4	0.00	0.10	0.10	9.07	41.04	50.31	49.69	5	0.67	0.14	4.91	21.82	
RUSALCA04	CS8	1.77	0.68	0.16	0.47	17.61	20.68	79.32	5	1.22	0.25	4.82	0.15	
RUSALCA04	CS12	0.00	0.08	0.08	0.23	0.91	1.28	98.72	5	1.77	0.36	4.98	0.37	
RUSALCA04	CS17	58.44	9.32	4.63	6.44	6.98	85.80	14.20	0	0.44	0.07	6.25	0.11	
RUSALCA04	CL1	1.31	0.15	0.20	2.01	17.70	21.37	78.63	5	0.89	0.12	7.66	0.13	
RUSALCA04	CL3	0.00	0.05	0.05	0.21	2.02	2.33	97.67	5	1.01	0.19	5.23	0.14	
RUSALCA04	CL6	0.06	0.17	0.11	0.28	1.14	1.77	98.23	5	1.61	0.35	4.65	0.19	
RUSALCA04	CL8	0.56	0.05	0.05	0.51	1.38	2.55	97.45	5	1.59	0.32	5.03	0.17	
RUSALCA04	CL10	94.87	0.38	0.10	0.10	0.05	95.49	4.51	0	0.22	0.05	4.52	0.13	
RUSALCA09	CS4	0.05	0.05	0.19	11.47	52.33	64.04	35.91	4	0.46	0.07	6.57	14.90	
RUSALCA09	CS8	0.00	0.05	0.05	0.69	27.69	28.47	71.53	5	1.13	0.18	6.28	11.56	19.93
RUSALCA09	CS12	0.00	0.00	0.05	0.05	1.64	1.73	98.27	5	1.92	0.29	6.62	21.98	11.16
RUSALCA09	CS17	47.84	8.85	5.96	6.11	10.72	31.63	20.53	0	0.63	0.08	7.88	18.12	
RUSALCA09	CL1	1.68	0.10	0.21	1.41	18.48	20.21	78.12	5	1.26	0.13	9.69	9.16	5.26
RUSALCA09	CL3	0.10	0.10	0.15	1.58	10.14	11.97	87.93	5	1.39	0.19	7.32	15.13	6.46
RUSALCA09	CL6	0.00	0.00	0.05	0.10	0.83	0.99	99.01	5	2.01	0.30	6.70	17.01	11.07
RUSALCA09	CL8	0.00	0.05	0.05	0.10	1.64	1.84	98.16	5	2.45	0.38	6.45	16.88	11.18
RUSALCA09	CL10	91.76	5.13	1.26	0.85	0.30	7.54	0.70	0	0.15	0.03	5.00	4.24	
RUSALCA12	CS4	0.00	0.05	0.14	11.37	54.94	66.51	33.49	4	0.52	0.09	5.78	18.31	
RUSALCA12	CS17	20.72	4.46	4.46	10.78	19.09	38.80	40.48	5	0.64	0.08	8.00	1.12	
RUSALCA12	CL1	0.00	0.04	0.08	1.15	18.01	19.28	80.72	5	1.09	0.13	8.38	12.89	
RUSALCA12	CL3	0	0.05	0.05	0.62	5.69	6.41	93.59	5	1.22	0.17	7.18	13.28	
RUSALCA12	CL6	0.00	0.00	0.00	0.05	1.10	1.16	98.84	5	1.76	0.27	6.52	18.70	15.20
RUSALCA12	CL8	0.00	0.00	0.05	0.05	0.15	0.25	99.75	5	2.20	0.36	6.11	12.40	20.23
RUSALCA12	CS8	0.00	0.00	0.05	0.47	24.57	25.08	74.92	5	1.13	0.18	6.28	18.44	39.54
RUSALCA12	CS12	0.00	0.00	0.00	0.14	2.16	2.31	97.69	5	1.45	0.23	6.30	21.62	26.83
RUSALCA12	CL10	50.98	14.85	4.50	4.22	0.75	24.32	24.70	0	0.92	0.14	6.57	6.45	

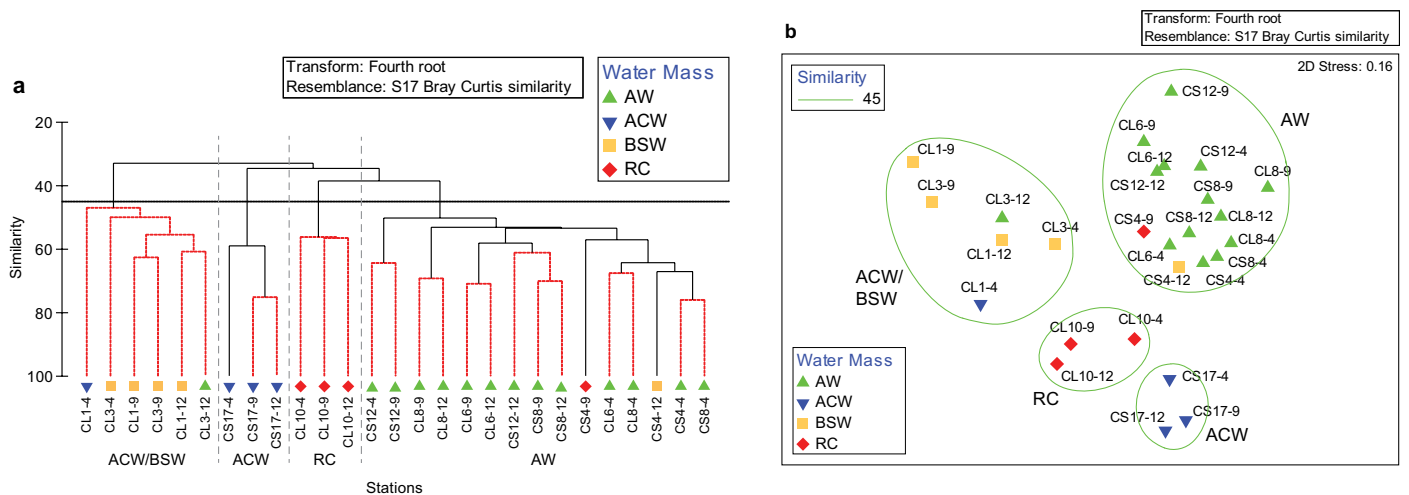


FIGURE 4. Time-series grouping of macrofaunal stations by (a) clustering of stations by macrofaunal composition, by carbon biomass (transformed fourth root), using Bray-Curtis similarity, and (b) nonmetric multidimensional scaling (nMDS), with both analyses using a 45% similarity cutoff. In (a) the transition from red dotted lines to solid black lines indicates the level of similarity grouping where there was a significant similarity between stations ($\alpha = 0.05$). The clustered stations were subsequently identified within specific water masses, based on bottom salinity values as defined by Grebmeier et al. (1988), which are based upon Coachman (1987) and also used by Bluhm et al. (2009): RC = Russian coast as influenced by East Siberian Sea Water. AW = Anadyr Water (>32.5). BSW = Bering Sea Water (31.8–32.5). ACW = Alaska Coastal Water (<31.8).

site (station CS8) had the highest macrofaunal bivalve biomass over the full study period (2004–2012, Figure 3a–c, Table 4). In fact, bivalves dominated all time-series stations located within AW (CS4, CS8, CS12, CL6 and CL8), followed by polychaetes and amphipods (Table 4). By comparison, the lowest total station biomass values on the time-series lines occurred in the ACW/BSW water masses as well as along the Russian coast (Figures 2, 3a–c), with variable taxon dominance (Table 4). Note that although the AW group had the highest similarity of faunal composition

between groups, there was high variability for the interface stations between water masses (Figure 4a,b): station CL3 was assigned to BSW in 2004 and 2009, but to AW in 2012. Similarly, CL1 off Alaska was assigned to ACW in 2004, but to BSW in 2009 and 2012, and CS4 near the Russian coast was assigned to AW (2004), RC (2009), and BSW (2012). This variability was likely due to seasonal changes in transport conditions through Bering Strait and to wind events (see Pisareva et al., 2015, in this issue).

Macrofaunal biomass at the nine

time-series RUSALCA sites indicated spatial variability within different water masses (Figure 5). When evaluating the key environmental factors related to the macrofaunal cluster group compositions, we found that water mass type, sediment grain size composition, and food quality (C/N values) together were the most statistically relevant factors (Spearman's rho = 0.681, p = 0.05). The offshore regions of the southern Chukchi Sea had the largest combined cluster group at the 45% similarity level within AW and included stations CS4, CS8, CS12, and CL6 and

TABLE 4. Composition of dominant macrofauna as determined by the Similarity of Percentages (SIMPER) analysis within clustered groups defined at the ~50–70% similarity level of the Bray-Curtis similarity results (shown in Figure 4) for the RUSALCA time-series stations occupied in 2004, 2009, and 2012. A = Ascidiacea. Amp = Amphipoda. B = Bivalvia. C = Crustacea. P = Polychaeta. S = Sipuncula. Other taxa identified to single taxon level.

Stations	Cluster Similarity Index	Dominant Macrofauna Taxa (50–70% combined) with Each Cluster Group
WATER MASS ID: Anadyr Water		
CS4-4, CS8-4, CL6-4, CL8-4	69	Nuculidae (B), Yoldiidae (B), Tellinidae (B), Nemertea, Anthozoa, Lumbrineridae (P), Scalibregmidae (P)
CS12-4, CS12-9	64	Tellinidae (B), Nuculidae (B), Nephtyidae (P), Capitellidae (P)
CS4-9	Single station	Tellinidae (B)
CL6-9, CL6-12	71	Tellinidae (B), Yoldiidae (B), Nuculidae (B), Nephtyidae (P), Terebellidae (P)
CL8-9, CL8-12	69	Tellinidae (B), Nuculidae (B), Veneridae (B), Anthozoa, Lumbrineridae (P)
CS4-12, CS8-12	69	Tellinidae (B), Yoldiidae (B), Isaeidae (Amp), Nephtyidae (P), Haustoriidae (Amp), Nuculidae (B), Flabelligeridae (P), Anthozoa, Veneridae (B), Polynoidae (P), Pectinariidae (P)
CS12-12	Single station	Nuculidae (B)
WATER MASS ID: Alaska Coastal Water		
CS17-4 (KHR-17)	Single station	Mogulidae (A), Lumbrineridae (P), Sabellaridae (P)
CS17-9, CS17-12	75	Pyuridae (A), Rhodosomatidae (A), Nephtyidae (P), Molgulidae (A), Cardiidae (B), Maldanidae (P), Lumbrineridae (P), Phascolionidae (P), Sabellidae (P), Oweniidae (P), Ascidiacea (A), Nemertea, Brachipoda, Syllidae (P), Golfingiidae (S)
WATER MASS ID: Alaska Coastal Water/Bering Sea Water		
CL1-4, CL3-4, CL1-9, CL3-9, CL1-12, CL3-12	52	Nephtyidae (P), Sternaspidae (P), Nuculidae (B), Nuculanidae (B), Cirratulidae (P), Capitellidae (P)
WATER MASS ID: Russian Coast		
CL10-4, CL10-9, CL10-12	56	Veneridae (B), Tellinidae (B), Nemertea, Lysianassidae (C), Ophelidae (P), Styelidae (A), Nephtyidae (P), Ampharetidae (P)

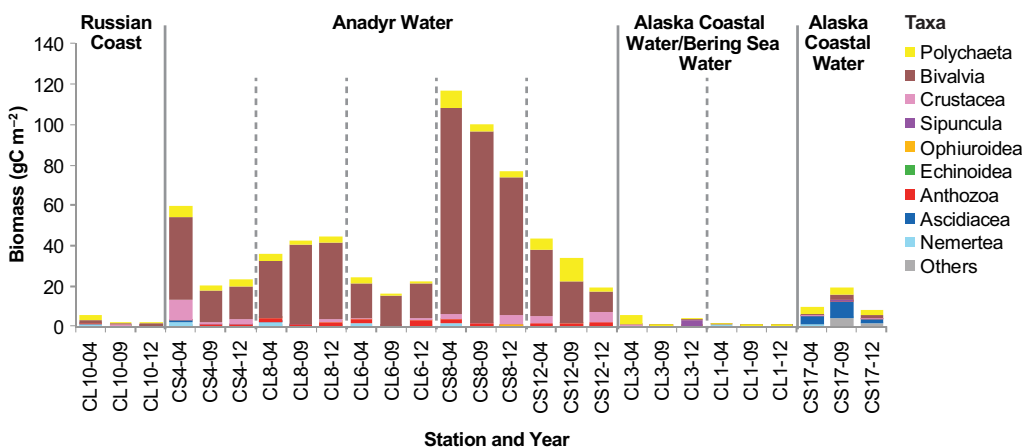


FIGURE 5. Macrofaunal biomass at nine time-series stations on the CS and CL lines for RUSALCA 2004, 2009, and 2012 (gC m⁻²) in the southern Chukchi Sea plotted from west to east (left to right). The individual stations were grouped by similarity clustering (separated by solid lines, see Figure 4), with the dotted lines separating multiple stations within each cluster group.

CL8 (Figure 4a,b, Table 4). The macrofaunal taxa composition was dominated by tellinid, nuculid, nuculanid, veneriid, and yoldiid bivalves, and secondarily by nephtyid polychaetes (Figure 5, Table 4). The ACW/BSW stations (CL1 and CL3) were dominated by nephtyid and sternaspid polychaetes, nuculid and nuculanid bivalves, and multiple other families of polychaetes. The station within the ACW (CS17) was dominated by molgulid and pyrid ascidians and nephtyid, sabellarid, and maldanid polychaetes. Finally, the Russian coast station (CL10) was characterized by venerid and tellinid bivalves, nemerteans, lysianassid amphipods, and various polychaetes.

Stations CL1 and CL3 clustered at the 45% similarity level, although at variable levels in individual years (Figure 4a,b, Table 4). Notably in 2004, CL1 occurred within an ACW bottom water signature, with CL3 occurring within BSW, whereas in 2009 both fell within BSW. In 2012, CL1 was located within BSW and CL3 just at the interface of BSW and AW ($S = 32.57$). This variation in bottom water salinity between the years from ACW to BSW at these stations near the Alaskan coast demonstrates the seasonal and dynamic variability of the frontal zones separating the water masses in the southern Chukchi Sea, which are influenced by variable flow through Bering Strait and by wind direction (see Woodgate et al., 2015, and

Pisareva et al., 2015, both in this issue, for further discussions). The high variability in faunal types at these interface stations likely relates to the variable current velocities that cause dynamic changes in water mass boundaries, and seasonal shifts in organic carbon supplies, to the benthos (Grebmeier et al., 1989; Pisareva et al., 2015, in this issue).

By comparison to the variable transition zone between ACW and BSW, the core high biomass stations consistently grouped together within AW (CS4, CS8, CS12, CL6, and CL8), both for individual years (not shown) and across years (Figure 4a,b; Table 4). On average, the data show an overall decline in station biomass from 2004 to 2012 at the time-series sites (Table 2, Figure 5). There is a significant decline in macrofauna biomass from 2004 to 2012 at two stations in the hotspot macrobenthic biomass within AW: CS8 (ANOVA: $t = 8.49$, $p = 0.01$), and CS12 ($t = 4.59$, $p = 0.04$). There was a slight, nonsignificant increase over time in biomass at station CL8 and variable biomass at the other stations in the region. Notably, bivalves dominated all of these stations (Table 4). This hotspot region of high infaunal biomass suggests export of an annual supply of organic carbon to the benthos and reflects the seasonal persistence of high primary production in the southern Chukchi Sea (Grebmeier et al., 1988,

2015) that escapes zooplankton grazing, resulting in high pelagic-benthic coupling that supports benthic production (Grebmeier et al., 2006a). However, the decline in benthic biomass at the core of the biological hotspot during the last decade determined by this study may provide a first indication of an ecosystem response to ongoing changes in this area. Lee et al. (2013) suggested a decrease in annual primary production for this area, and changes in hydrographic parameters over the last decade have been recorded in the region with variable transport (Woodgate et al., 2015, in this issue). Thus, our findings suggest the possibility of a system-level change in this region. Note that the international community has developed the DBO program to continue to evaluate the status of and change in this region (see Box 1).

Epifauna

Epifaunal trawl collections indicate spatially variable levels of station biomass during all three RUSALCA sampling years (Figure 3d-f, Table 2). Interestingly, areas of highest macrofaunal biomass had the lowest epifaunal biomass, at least in 2004. Four epifaunal community groups were identified by similarity cluster analysis and nMDS (Figure 6a,b, respectively), and had similar spatial separation as observed for the macrofaunal communities (Figure 4a,b). As with macrofauna,

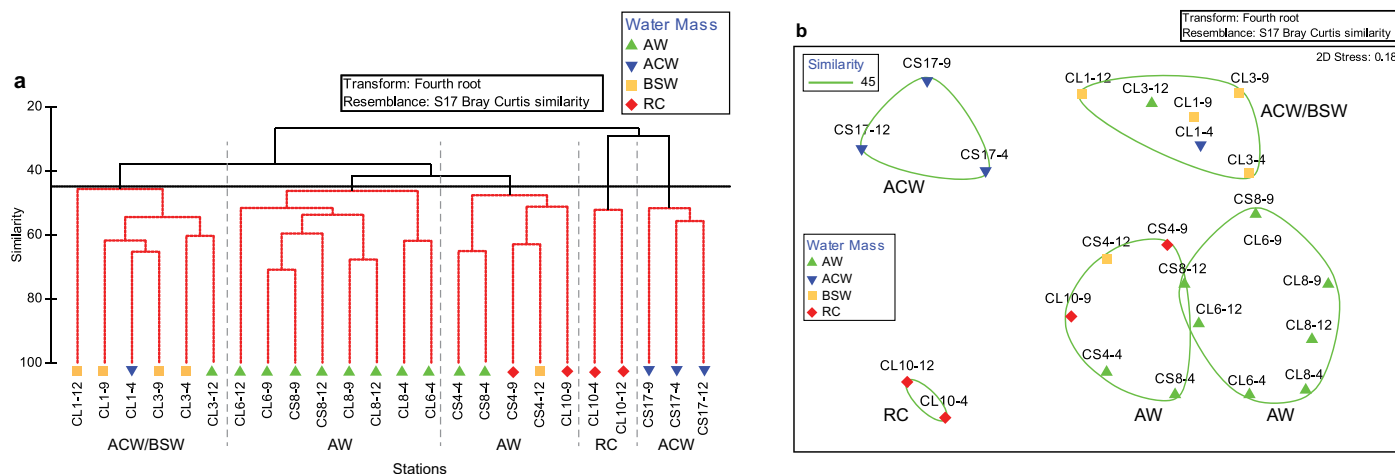


FIGURE 6. Time-series grouping of epifaunal stations by (a) clustering of stations by epifaunal composition, by biomass (transformed fourth root), using Bray-Curtis similarity, and (b) nMDS, with both analyses using a 45% similarity cutoff. See the Figure 4 caption for a description of water mass types.

epifauna generally grouped by geographical proximity rather than by sampling years (Figure 6a,b). Station CS17 near the Alaskan coast located within ACW was unique in all years and separate from the other groups. The Russian coastal station CL10 was also unique, with epifaunal communities grouping together for two of the three sampling years. Stations CL1 and CL3 clustered in all sampling years. The other repeat stations fell into two temporal clusters, and most of these stations also formed spatial clusters during individual sampling years (not shown). The ANOSIM results indicate that there are distinct groupings with repeat stations (global $R = 0.8$, $p = 0.001$) with little

influence relating to the year sampled (low global $R = 0.1$, $p = 0.06$). This finding suggests strong community overlap for the AW groupings (Figure 6a,b) and relatively consistent epibenthic community composition geographically across the sampling years, despite high temporal variability in absolute biomass.

Epifaunal biomass at the eight time series stations on the CS and CL lines indicate biomass peaks for the central regions of both the CL and CS lines (CL8 and CL6 in 2009 and consistently for CS8, respectively), occurring entirely in Anadyr Water and with arthropods as the dominant fauna (Table 5, Figure 7). Individual species can drive trends in

epifaunal biomass as indicated by fluctuations of snow crabs (the majority of Arthropoda biomass). There was also high variability (and, actually, temporally declining biomass) for the interface stations between water masses, specifically stations CL1 and CL3 off Alaska, and CS4 near the Russian coast, similar to the findings for the macrofaunal communities discussed above (Table 4). Again, this variability was likely due to variable annual transport conditions through Bering Strait and to wind events.

Over the time series, the total epifaunal biomass was significantly higher in 2009 than in 2012 (ANOVA, $p = 0.02$),

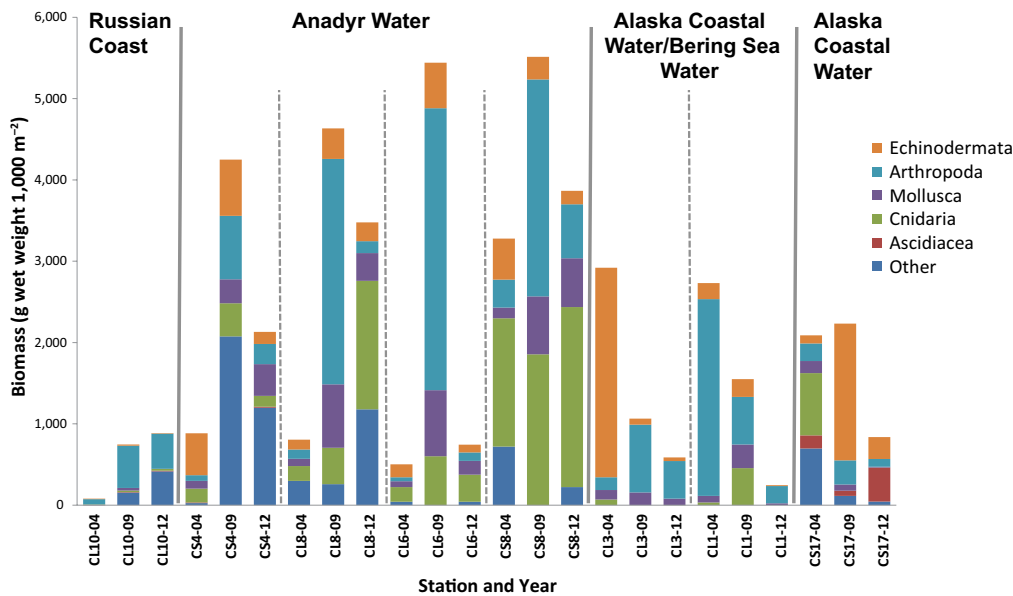


FIGURE 7. Epifaunal biomass at eight time-series stations on the CS and CL lines for RUSALCA 2004, 2009, and 2012 (g wet weight 1,000 m⁻²) in the southern Chukchi Sea plotted from west to east (left to right). The individual stations were grouped by similarity clustering (separated by solid lines, see Figure 6), with the dotted lines separating multiple stations within each cluster group. Epifauna were not collected in all years at station CS12, so its data are not included in this plot.

TABLE 5. Composition of dominant epifauna within clustered groups defined at the ~50% similarity level of the Bray-Curtis similarity analysis (shown in Figure 6) for the RUSALCA time-series stations occupied in 2004, 2009, and 2012. An = Anthozoa. B = Bivalvia. C = Crustacea. E = Echinodermata. G = Gastropoda. Other taxa identified to single taxon level.

Stations	Cluster Similarity Index	Cluster Group and Water Mass ID	Dominant Epifauna Taxa (50–70% Combined) with Each Cluster Group
CS4-4, CS8-4, CS4-9, CS4-12, CL10-9*	52	Anadyr Water, Russian Coast*	Oregoniidae** (C), Myriotrochidae (E), Naticidae (G), Buccinidae (G), Actiniaria (An)
CS17-4, CS17-9, CS17-12	53	Alaska Coastal Water	Asteriidae (E), Crangonidae (C), Cheiragonidae (C), Oregoniidae (C), Hippolytidae (C), Pectinidae (B)
CL1-4, CL3-4, CL1-9, CL3-9, CL1-12, CL3-12	54	Alaska Coastal Water/ Bering Sea Water	Oregoniidae (C), Buccinidae (G), Crangonidae (C), Asteriidae (E)
CL6-4, CL8-4, CS8-9, CL6-9, CL8-9, CS8-12, CL6-12, CL8-12	52	Anadyr Water	Naticidae (G), Oregoniidae (C), Cardiidae (B), Actiniaria (An)
CL10-4, CL10-12	52	Russian Coast	Oregoniidae (C), Uristidae (C), Crangonidae (C), Amphipoda (C)

* In 2009 the Russian Coast station CL10-9 was included in with the Anadyr Water group.

**Although Opilio crabs are currently listed in the F. Oregoniidae (C), many prior research results identify these crabs to the F. Majidae.

but the same for 2009 and 2004 (ANOVA, $p = 0.06$; Table 2). The low biomass in 2012 was reflected in reduced biomass in all major phyla (Figure 7). Echinoderm biomass decreased from 2004 to 2012, mostly because of declines in the brittle star *Ophiura sarsii* and the sea cucumber *Myriotrochus rinkii*. Arthropod and mollusk biomass both peaked in 2009 due to high biomasses of the snow crab *C. opilio* and the moon snail *Cryptonatica affinis*, respectively (Serratos, 2015). It is notable that the biomasses of both the mobile epifauna and the immobile macrofauna have declined in the southern Chukchi Sea. These declines took place after 2009 for the mobile epifauna and even earlier for the immobile macrofauna, coincident with the changing hydrographic conditions in the region and seasonal declines in primary productivity. Alternatively, the epifaunal decline could just be variability in *C. opilio* stock size. Regardless, such declines in multiple biological components (macro- and epifauna) may be a bellweather of system change associated with reduced sea ice duration, variability of current flow, and changing phenology of seasonal production events, suggesting the continued need to track status and trends in this southern Chukchi Sea system.

Across all years, substrate category was the most consistent driver of benthic community structure in the multivariate analysis for epifaunal community structure, similar to findings for the macrofauna. Consistent spatial patterns in epibenthic and macrofaunal community structure were observed in 2004, 2009, and 2012, reflecting the influence of biogeography and environmental forcing. We found that spatial patterns in benthic community composition, by biomass, in the southern Chukchi Sea differed among water masses. Although variable levels of epifaunal biomass and composition were observed among the three sampling years for the epibenthos, we observed a significant decline in benthic macrofaunal biomass at central stations within the core flow of Anadyr Water.

It should be noted that both the macrofaunal and epibenthic communities in the southern Chukchi Sea represent a transition zone between Pacific and Arctic Ocean waters. This area is characterized by Pacific-boreal communities, with a gradual poleward increase in the occurrence of Arctic fauna (Petryashov et al., 2013; N. Denisenko and Grebmeier, 2015, in this issue). The southern CS line exhibits a larger portion of Pacific-boreal species compared to the northern CL line (e.g., Golikov, 1989). Central Chukchi Sea epibenthic communities located on the time-series lines (stations CL3, CL6, CL8, CS12, CS8; Figure 6) differed in all years from communities found along the Alaskan (CL1, CS17) and the Russian (CL10, CS4) coasts, and they were characterized by a large biomass of predators-scavengers, especially the snow crab *C. opilio* (F. Oregoniidae; often also listed as F. Majidae) and the predatory gastropod *C. affinis* (F. Naticidae; Table 5). *C. opilio* is in general a major contributor to epibenthic biomass from the northern Bering and southern Chukchi Seas (Grebmeier et al., 2006a; Bluhm et al., 2009; present study), the central to the northeastern Chukchi shelf (Bluhm et al., 2009; Blanchard et al., 2013b; Ravelo et al., 2014), and into the western Beaufort Sea (Rand and Logerwell, 2011; Ravelo et al. 2015).

High prey densities are needed to support high densities of predatory snow crab (Kolts et al., 2013), and the pronounced aggregation of snow crab in the southern Chukchi Sea may thus be related to a macrobenthic hotspot (sensu Grebmeier et al., 2015) of macrofaunal prey on the central shelf. Kolts et al. (2013) found the infaunal bivalves common at the hotspot location to be among the dominant prey items for snow crab. This is borne out by the results of the present study in which measures of food availability (i.e., macrofaunal biomass, sediment, and water column chlorophyll) were determined to be important drivers of epibenthic community composition, with sediment and water column

chlorophyll also important drivers for macrofauna community composition.

As found earlier in the same region (Feder et al., 2005; Bluhm et al., 2009), our data also showed high mollusk biomass in the benthic communities of the south central Chukchi Sea. The predatory moon snail *C. affinis* was often dominant in the south central part of the study area that overlaps with the macrobenthic hotspot region (Grebmeier et al., 2006a, 2015). The macrobenthic community contains dense populations of infaunal bivalves dominated by *Macoma calcerea* (Sirenko and Gagaev, 2007; Grebmeier, 2012), which is an important food source for the predatory moon snail *C. affinis* (Feder et al., 1994). Inshore epibenthic communities along both eastern and western margins of the southern Chukchi Sea sampled during all three years are influenced by the river runoff and the coastal currents that shape the Alaskan and Russian coastal domains (Carmack et al., 2015). Nearshore communities living on coarse substrate are normally dominated by a diverse mix of suspension feeders (Feder et al., 2005). In the eastern sector along the Alaskan coast there is variable influx of freshwater and terrestrial matter within the ACW, derived mostly from Yukon River discharge into the Bering Sea (Walsh et al., 1989), with hard substrate also prevalent along the Russian coast in the western Chukchi Sea.

We found no consistent relationship between food supply and epibenthic community composition or biomass on the southern Chukchi shelf. This finding is in contrast to the strong link between food supply and macrofaunal community structure and biomass determined by the current study and previous findings (Grebmeier, 1992; Sirenko and Koltun, 1992; Feder et al., 2005; Grebmeier et al., 2006a). The lack of a strong pelagic-benthic coupling within the epibenthic communities on the southern Chukchi shelf is probably due to the mobility of the dominant predatory/scavenging feeding guild (Bluhm et al., 2009; Serratos, 2015).

The high mobility of these larger organisms allows them to exploit multiple food sources by moving among patches of high organic matter deposition and different water masses. This motility can thus be expected to decouple the relationship between epifaunal communities and primary production in the overlying water column, compared with the more stationary macrofauna that feed on phytodetritus that either settles seasonally from production in the water column and/or is advected into the southern Chukchi Sea from upstream sources in the northern Bering Sea brought northward in Pacific water transiting Bering Strait (Grebmeier et al., 2015).

Water Mass Characteristics, Circulation, and Sediment Dynamics

Interconnected processes sustain the persistent high benthic biomass in the Southeast Chukchi Sea (Grebmeier et al., 2015). This region north of Bering Strait receives Pacific water inflow with entrained organic carbon (e.g., phytodetritus) components. The major currents flow northward through Bering Strait and separate into three parts: a continuation of the Anadyr Water to the northwest, the more diffuse and less saline Bering Sea Water transiting northward, and the northeast flowing Alaska Coastal Water (Figure 1; also see Woodgate et al., 2015, in this issue). Generally, currents slow down north of Bering Strait as the water masses spread out (Pisareva et al., 2015, in this issue). Suspended material that settles out from these waters to the benthos includes phytodetritus from both in situ production and material advected into the system as the ice retreats in spring and early summer. In both the Atlantic and Pacific gateways to the Arctic, advection is a critical driver of key water mass characteristics (temperature and salinity) and food supply (Wassmann, 2015), and it also impacts current speed and sediment composition.

Benthic Community Shifts

Sirenko and Gageav (2007) indicate some northward species shifts as do N. Denisenko and Grebmeier (2015, in this issue), who identify many new species records of bryozoans in the Chukchi Sea. Similar to our findings, the latter study determined that advective regimes in the Chukchi Sea drive bryozoan biogeography along with increased seasonal seawater temperatures that have a direct impact on the habitat and reproductive potential of bryozoan fauna.

In addition, increasingly large copepod biomass was found in the southern Chukchi Sea biological hotspot from 2004 to 2012 (Ershova et al., 2015). These increased biomasses have the potential to consume more phytoplankton than in the past, which could limit export production and thus account at least in part for the declines in benthic biomass we found at sites underlying the CS and CL lines of the current study. In addition, Lee et al. (2007, 2013) detected a decline in seasonal primary production in late summer/fall in the southern Chukchi Sea over the RUSALCA study time period that also may indicate a potential biological response to the ongoing physical changes occurring in this region. In spite of our observation of local biomass declines for macrofauna, and to a lesser degree for epifauna, in some areas of the southern Chukchi Sea, the overall benthic biomass in this region is still very high for an Arctic continental shelf (Grebmeier et al., 2015). It is worth noting that this finding of a decline in benthic macrofaunal biomass in the Southeast Chukchi Sea hotspot is similar to observations at two other hotspots under the productive Anadyr Water, specifically the declining biomass at the benthic hotspot south of St. Lawrence Island (Grebmeier, 2012) and a spatial contraction of the amphipod footprint in the Chirikov Basin just south of Bering Strait (author Grebmeier, unpublished data, see <http://www.arctic.noaa.gov/dbo/dbo2-related-time-series>; Coyle et al., 2007). Although it has been assumed that zooplankton cannot crop

the seasonally high annual phytoplankton biomass produced in this region to the extent required to impose food limitations, the observations of a decline in benthic standing stock in this Southeast Chukchi hotspot in combination with the declines in the two northern Bering Sea regions may be a “first response” observation of a changing ecosystem in this region.

We conclude that there is a need to evaluate mechanisms of climate change and their influence on the production/biomass of benthic fauna. The Figure 8 schematic suggests a scenario that could provide a basis for such evaluation through field and modeling efforts. Specifically, increased transport of Pacific water through Bering Strait could enhance the input of Anadyr Water and its associated nutrients, thus increasing seasonal primary production, food supply, macrofaunal growth increments, and overall production and biomass of benthic fauna. Increased seawater temperatures could also increase growth rates and result in increased benthic production and biomass. However, reduced transport through Bering Strait would have a negative impact on food supply and temperatures that could result in decreased benthic growth rates, production, and biomass. Lower temperatures would decrease benthic growth increments and reduce benthic production and biomass. The development of testable hypotheses through multidisciplinary studies on seasonal and interannual time scales at the southern Chukchi time series sites, including process studies, are needed to address this hydrographic influence question.

SUMMARY

Overall, both macrofaunal and epibenthic community compositions at the RUSALCA time-series sites in the southern Chukchi Sea have remained relatively constant over the time period considered in this study (2004–2012). Although estimates of biomass were at times highly variable for the more motile epibenthic

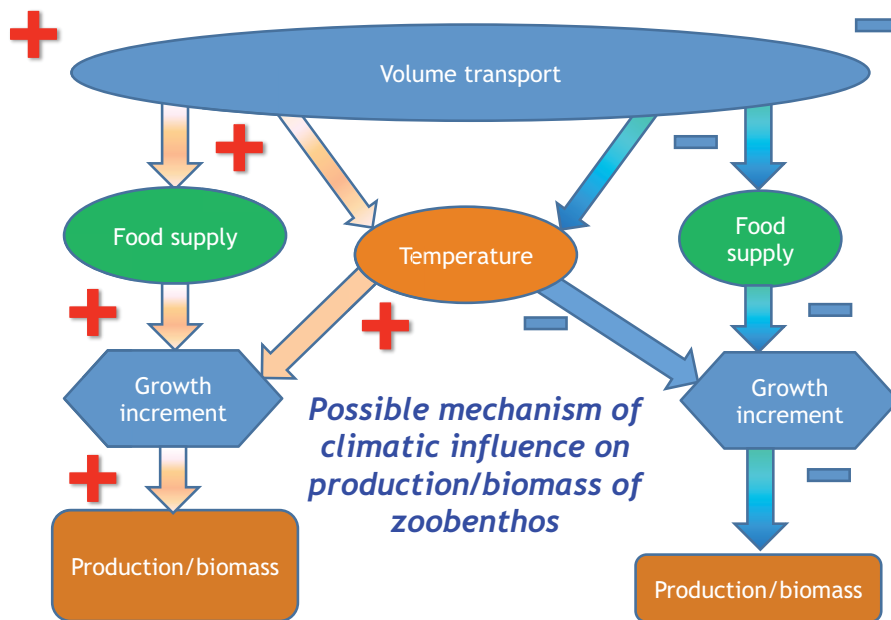


FIGURE 8. Schematic of possible mechanisms of climate influence on the production/biomass of benthic macrofauna. Increased transport through Bering Strait of Anadyr Water and associated nutrients would enhance production, food supply, macrofaunal growth increments, and overall production and biomass of benthic fauna. Increased seawater temperatures would also increase growth increments and associated benthic production and biomass. In comparison, decreased volume transport through Bering Strait would have a negative impact on food supply and, if temperatures were lower, would decrease benthic growth increments and reduce benthic production and biomass.

fauna, there were indications of a decline in epibenthic biomass since 2009 at some of the time-series sites. By comparison, the more sedentary macrofauna show a significant decline in biomass from 2004 to 2012, both for the composite time-series sites and at select sites located within Anadyr Water. Key drivers of both macrofaunal and epifaunal composition and biomass are known to include hydrographic factors, such as salinity and temperature, food supply as estimated by integrated chlorophyll *a* content, and sediment composition, all dependent on the advection of Pacific water entering the Chukchi Sea through Bering Strait. There is one notable difference in dependence on food availability, with food supply being a more directly influential factor for macrofaunal biomass and community structure than it is for epifaunal communities. The DBO international network, which encompasses many of the RUSALCA CS line time-series sites, will continue to enhance our understanding of ecosystem response to changing environmental conditions by providing seasonal and interannual tracking of physical, hydrographic, and biological factors in the region. While this periodic sampling is valuable, there is also a distinct need to increase process-level studies and modeling to track drivers of the

persistence of benthic fauna that are key prey for upper trophic benthivores in this highly productive region. These studies can also help to forecast future changes driven by advective forcing through Bering Strait that can have ramifications for overall ecosystem health and food web dynamics. ☒

REFERENCES

- Blanchard, A.L., C.L. Parris, A.L. Knowlton, and N.R. Wade. 2013a. Benthic ecology of the north-eastern Chukchi Sea: Part I. Environmental characteristics and macrofaunal community structure, 2008–2010. *Continental Shelf Research* 67:52–66, <http://dx.doi.org/10.1016/j.csr.2013.04.021>.
- Blanchard, A.L., C.L. Parris, A.L. Knowlton, and N.R. Wade. 2013. Benthic ecology of the north-eastern Chukchi Sea: Part II. Spatial variation of megafaunal community structure, 2009–2010. *Continental Shelf Research* 67:67–76, <http://dx.doi.org/10.1016/j.csr.2013.04.031>.
- Bloom, B.A., K. Iken, S. Mincks Hardy, B.I. Sirenko, and B.A. Holladay. 2009. Community structure of epibenthic megafauna in the Chukchi Sea. *Aquatic Biology* 7:269–293, <http://dx.doi.org/10.3354/ab00198>.
- CAFF (Conservation of Arctic Flora and Fauna). 2013. *Arctic Biodiversity Assessment: Report for Policy Makers*. CAFF, Akureyri, Iceland, 23 pp.
- Carmack, E., P. Winsor, and W. Williams. 2015. The contiguous panarctic Riverine Coastal Domain: A unifying concept. *Progress in Oceanography*, <http://dx.doi.org/10.1016/j.pocean.2015.07.014>.
- Clarke, K.R., and R.N. Gorely. 2006. PRIMER v. 6: User manual/tutorial, PRIMER-E, Plymouth, UK.
- Coachman, L.K. 1987. Advection and mixing on the Bering-Chukchi Shelves: Component A. Advection and mixing of coastal water on high latitude shelves. Pp. 1–42 in *ISHTAR Progress Report*, vol 1. Institute of Marine Science, University of Alaska Fairbanks.

- Cooper, L.W., J.M. Grebmeier, I.L. Larsen, V.G. Egorov, C. Theodorakis, H.P. Kelly, and J.R. Lovvorn. 2002. Seasonal variation in water column processes and sedimentation of organic materials in the St. Lawrence Island polynya region, Bering Sea. *Marine Ecology Progress Series* 226:13–26, <http://dx.doi.org/10.3354/meps226013>.
- Cooper, L.W., M.A. Janout, K.E. Frey, R. Pirtle-Levy, M.L. Guarinello, J.M. Grebmeier, J.R. Lovvorn. 2012. The relationship between sea ice break-up, water mass variation, chlorophyll biomass, and sedimentation in the northern Bering Sea. *Deep Sea Research Part II* 65:141–162, <http://dx.doi.org/10.1016/j.dsr2.2012.02.002>.
- Cooper, L.W., A.S. Savvichev, and J.M. Grebmeier. 2015. Abundance and production rates of heterotrophic bacterioplankton in the context of sediment and water column processes in the Chukchi Sea. *Oceanography* 28(3):84–99, <http://dx.doi.org/10.5670/oceanog.2015.59>.
- Coyle, K.O., B.A. Bluhm, B. Konar, A. Blanchard, and R.C. Highsmith. 2007. Amphipod prey of grey whales in the northern Bering Sea: Changes in biomass and distribution. *Deep Sea Research Part II* 54:2,906–2,918, <http://dx.doi.org/10.1016/j.dsr2.2007.08.026>.
- Denisenko, N.V., and J.M. Grebmeier. 2015. Spatial patterns of bryozoan fauna biodiversity and issues of biogeographic regionalization of the Chukchi Sea. *Oceanography* 28(3):134–145, <http://dx.doi.org/10.5670/oceanog.2015.62>.
- Denisenko, S.G., J.M. Grebmeier, and L.W. Cooper. 2015. Assessing bioresources and standing stock of zoobenthos (key species, high taxa, trophic groups) in the Chukchi Sea. *Oceanography* 28(3):146–157, <http://dx.doi.org/10.5670/oceanog.2015.63>.
- Doney, S.C., M. Ruckelshaus, J.E. Duffy, J.P. Barry, F. Chan, C.A. English, H.M. Galindo, J.M. Grebmeier, A.B. Hollowed, N. Knowlton, and others. 2012. Climate change impacts on marine ecosystems. *Annual Review of Marine Science* 4:11–37, <http://dx.doi.org/10.1146/annurev-marine-041911-111611>.

- Duarte, C.M., S. Agustí, P. Wassmann, J.M. Arrieta, M. Alcaraz, A. Coello, and D. Vaqué. 2012. Tipping elements in the Arctic marine ecosystem. *Ambio* 41(1):44–55, <http://dx.doi.org/10.1007/s13280-011-0224-7>.
- Eleftheriou, A., and D. Moore. 2013. Macrofauna techniques. Chapter 5 in *Methods for the Study of Marine Benthos*, 4th ed. A. Eleftheriou, ed., John Wiley & Sons, Oxford, UK, <http://dx.doi.org/10.1002/9781118542392.ch5>.
- Ershova, E.A., R.R. Hopcroft, and K.N. Kosobokova. 2015. Inter-annual variability of summer mesozooplankton communities of the western Chukchi Sea: 2004–2012. *Polar Biology* 38:1,461–1,481, <http://dx.doi.org/10.1007/s00300-015-1709-9>.
- Feder, H.M., N.R. Foster, S.C. Jewett, T.J. Weingartner, and R. Baxter. 1994b. Mollusks in the northeastern Chukchi Sea. *Arctic* 47:145–161, <http://dx.doi.org/10.14430/arctic1285>.
- Feder, H.M., S.C. Jewett, and A.L. Blanchard. 2005. Southeastern Chukchi Sea (Alaska) epibenthos. *Polar Biology* 28:402–421, <http://dx.doi.org/10.1007/s00300-004-0683-4>.
- Feder, H.M., S.C. Jewett, and A.L. Blanchard. 2007. Southeastern Chukchi Sea (Alaska) macrobenthos. *Polar Biology* 30:261–275, <http://dx.doi.org/10.1007/s00300-006-0180-z>.
- Foyle, T., R. O'Dor, and R. Elner. 1989. Energetically defining the thermal limits of the snow crab. *Journal of Experimental Biology* 145:371–393.
- Frey, K.E., J.A. Maslanik, J. Clement Kinney, and W. Maslowski. 2014. Recent variability in sea ice cover, age, and thickness in the Pacific Arctic Region. Pp. 31–63 in *The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment*. J.M. Grebmeier and W. Maslowski, eds, Springer, Dordrecht.
- Frey, K.E., G.W.K. Moore, L.W. Cooper, and J.M. Grebmeier. 2015. Divergent patterns of recent sea ice cover across the Bering, Chukchi and Beaufort seas of the Pacific Arctic Region. *Progress in Oceanography* 136:32–49, <http://dx.doi.org/10.1016/j.pocean.2015.05.009>.
- Golikov, A. 1989. Arctic Ocean gastropod proboscians. Pp. 325–340 in *The Arctic Seas*. Y. Hermann, ed., Springer, http://dx.doi.org/10.1007/978-1-4613-0677-1_13.
- Grebmeier, J.M. 1992. Benthic processes on the shallow continental shelf. Pp. 243–251 in *Results of the Third Joint US–USSR Bering and Chukchi Seas Expedition (BERPAC): Summer 1988*. J.F. Turner and P.A. Nagel, eds, US Fish and Wildlife Service, Washington, DC.
- Grebmeier, J.M. 1993. Studies of pelagic–benthic coupling on the Soviet continental shelf in the northern Bering and Chukchi Seas. *Continental Shelf Research* 13:653–668, [http://dx.doi.org/10.1016/0278-4343\(93\)90098-I](http://dx.doi.org/10.1016/0278-4343(93)90098-I).
- Grebmeier, J.M. 2012. Shifting patterns of life in the Pacific Arctic and sub-Arctic Seas. *Annual Review of Marine Science* 4:63–78, <http://dx.doi.org/10.1146/annurev-marine-120710-100926>.
- Grebmeier, J.M., B.A. Bluhm, L.W. Cooper, S. Danielson, K.R. Arrigo, A.L. Blanchard, J.T. Clark, R.H. Day, K.E. Frey, R.R. Gradinger, and others. 2015. Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. *Progress in Oceanography* 136:92–114, <http://dx.doi.org/10.1016/j.pocean.2015.05.006>.
- Grebmeier, J.M., and L.W. Cooper. 1995. Influence of the St. Lawrence Island polynya on the Bering Sea benthos. *Journal of Geophysical Research* 100:4,439–4,460, <http://dx.doi.org/10.1029/94JC02198>.
- Grebmeier, J.M., L.W. Cooper, H.M. Feder, and B.I. Sirenko. 2006a. Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. *Progress in Oceanography* 71:331–361, <http://dx.doi.org/10.1016/j.pocean.2006.10.001>.
- Grebmeier, J.M., H.M. Feder, and C.P. McRoy. 1989. Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas: Part II. Benthic community structure. *Marine Ecology Progress Series* 51:253–268.
- Grebmeier, J.M., C.P. McRoy, and H.M. Feder. 1988. Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi seas: Part I. Food supply source and benthic biomass. *Marine Ecology Progress Series* 48:57–67.
- Grebmeier, J.M., S.E. Moore, J.E. Overland, K.E. Frey, and R. Gradinger. 2010. Biological response to recent Pacific Arctic sea ice retreats. *Eos, Transactions of the American Geophysical Union* 91(18):161–162, <http://dx.doi.org/10.1029/2010EO180001>.
- Grebmeier, J.M., J.E. Overland, S.E. Moore, E.V. Farley, E.C. Carmack, L.W. Cooper, K.E. Frey, J.H. Helle, F.A. McLaughlin, and S.L. McNutt. 2006b. A major ecosystem shift observed in the Northern Bering Sea. *Science* 311:1,461–1,464, <http://dx.doi.org/10.1126/science.1121365>.
- Iken, K., B.A. Bluhm, and K.H. Dunton. 2010. Benthic food-web structure under differing water mass properties in the southern Chukchi Sea. *Deep Sea Research Part II* 57:71–85, <http://dx.doi.org/10.1016/j.dsr2.2009.08.007>.
- Kędra, M., C. Moritz, E.S. Choy, C. David, R. Degen, S. Duerksen, I. Ellingsen, B. Górska, J.M. Grebmeier, D. Kirievskaya, and others. 2015. Status and trends in the structure of Arctic benthic food webs. *Polar Research* 34, 23775, <http://dx.doi.org/10.3402/polar.v34.23775>.
- Kolts, J.M., J.R. Lovvorn, C.A. North, J.M. Grebmeier, and L.W. Cooper. 2013. Effects of body size, gender, and prey availability on diets of snow crabs in the northern Bering Sea. *Marine Ecology Progress Series* 483:209–220, <http://dx.doi.org/10.3354/meps10292>.
- Jay, C.V., A.S. Fischbach, and A.A. Kochnev. 2012. Walrus areas of use in the Chukchi Sea during sparse sea ice cover. *Marine Ecology Progress Series* 468:1–13, <http://dx.doi.org/10.3354/meps10057>.
- Khim, B.K., D.E. Krantz, L.W. Cooper, and J.M. Grebmeier. 2003. Seasonal discharge of estuarine freshwater to the western Chukchi Sea shelf identified in stable isotope profiles of mollusk shells. *Journal of Geophysical Research: Oceans* 108, 3300, <http://dx.doi.org/10.1029/2003JC001816>.
- Lee, S.H., T.E. Whittedge, and S.H. Kang. 2007. Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. *Continental Shelf Research* 27:2,231–2,249, <http://dx.doi.org/10.1016/j.csr.2007.05.009>.
- Lee, S.H., M.S. Yun, B.K. Kim, S. Saitoh, C.K. Kang, S.H. Kang, and T.E. Whittedge. 2013. Latitudinal carbon productivity in the Bering and Chukchi Seas during the summer in 2007. *Continental Shelf Research* 59:28–36, <http://dx.doi.org/10.1016/j.csr.2013.04.004>.
- Mathis, J.T., J.M. Grebmeier, D.A. Hansell, R.R. Hopcroft, D.J. Kirchman, S.H. Lee, S.B. Moran, N.R. Bates, S. Van Laningham, J.N. Cross, and W.-J. Cai. 2014. Carbon biogeochemistry of the western Arctic: Primary production, carbon export and the controls on ocean acidification. Pp. 223–268 in *The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment*. J.M. Grebmeier and W. Maslowski, eds, Springer, Dordrecht.
- Moore, S.E., E. Logerwell, L. Eisner, E. Farley, L. Harwood, K. Kuletz, J. Lovvorn, J. Murphy, and L. Quakenbush. 2014. Marine fishes, birds and mammals as sentinels of ecosystem variability and reorganization in the Pacific Arctic region. Pp. 337–392 in *The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment*. J.M. Grebmeier and W. Maslowski, eds, Springer, Dordrecht.
- Moore, S.E., and P.J. Stabenro. 2015. Synthesis of Arctic Research (SOAR) in marine ecosystems of the Pacific Arctic. *Progress in Oceanography* 136:1–11, <http://dx.doi.org/10.1016/j.pocean.2015.05.017>.
- Mueter, F.J., and M.A. Litwiz. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecological Applications* 18:309–320, <http://dx.doi.org/10.1890/07-0564.1>.
- Münchow, A., T.J. Weingartner, and L.W. Cooper. 1999. The summer hydrography and surface circulation of the East Siberian shelf sea. *Journal of Physical Oceanography* 29: 2,167–2,182, [http://dx.doi.org/10.1175/1520-0485\(1999\)029<2167:TSHASC>2.0.CO;2](http://dx.doi.org/10.1175/1520-0485(1999)029<2167:TSHASC>2.0.CO;2).
- Orensanz, J.M., B. Ernst, and D.A. Armstrong. 2007. Variation of female size and stage at maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. *Journal of Crustacean Biology* 27:576–591, <http://dx.doi.org/10.1651/S-2790.1>.
- Petryashov, V., S. Vassilenko, A.Y. Voronkov, B. Sirenko, A. Smirnov, and I. Smirnov. 2013. Biogeographical analysis of the Chukchi Sea and adjacent waters based on fauna of some macrobenthos taxa. *Invertebrate Zoology* 10:49–68, <http://dx.doi.org/10.1134/S1063074009020011>.
- Pisareva, M.N., R.S. Pickart, K. Iken, E.A. Ershova, J.M. Grebmeier, L.W. Cooper, B.A. Bluhm, C. Nobre, R.R. Hopcroft, H. Hu, and others. 2015. The relationship between patterns of benthic fauna and zooplankton in the Chukchi Sea and physical forcing. *Oceanography* 28(3):68–83, <http://dx.doi.org/10.5670/oceanog.2015.58>.
- Rand, K., and E.A. Logerwell. 2011. The first demersal trawl survey of benthic fish and invertebrates in the Beaufort Sea since the late 1970s. *Polar Biology* 34(4):475–488, <http://dx.doi.org/10.1007/s00300-010-0900-2>.
- Ravelo, A.M., B. Konar, J.H. Trefry, and J.M. Grebmeier. 2014. Epibenthic community variability in the northeastern Chukchi Sea. *Deep Sea Research Part II* 102:119–131, <http://dx.doi.org/10.1016/j.dsr2.2013.07.017>.
- Schonberg, S.V., J.T. Clarke, and K.H. Dunton. 2014. Distribution, abundance, biomass and diversity of benthic infauna in the northeast Chukchi Sea, Alaska: Relation to environmental variables and marine mammals. *Deep Sea Research Part II* 102:144–163, <http://dx.doi.org/10.1016/j.dsr2.2013.11.004>.

- Serrato, C. 2015. Spatial and temporal patterns of epibenthic community and food web structures in the Chukchi Sea between 2004–2012. MS thesis, University of Alaska Fairbanks, 44 pp.
- Sirenko, B., and S.Y. Gagaev. 2007. Unusual abundance of macrobenthos and biological invasions in the Chukchi Sea. *Russian Journal of Marine Biology* 33:355–364, <http://dx.doi.org/10.1134/S1063074007060016>.
- Sirenko, B.I., and V.M. Koltun. 1992. Characteristics of benthic biocenoses of the Chukchi and Bering seas. Pp. 251–261 in *Results of the Third Joint US–USSR Bering and Chukchi Seas Expedition (BERPAC): Summer 1988*. J.F. Turner and P.A. Nagel, eds, US Fish and Wildlife Service, Washington, DC.
- Stoker, S.W. 1978. Benthic invertebrate macrofauna of the eastern continental shelf of the Bering/Chukchi Seas. PhD thesis, University of Alaska Fairbanks, 253 pp.
- Walsh, J.J., C.P. McRoy, L.K. Coachman, J.J. Goering, J.J. Nihoul, T.E. Whittedge, T.H. Blackburn, P.L. Parker, C.D. Wirick, P.G. Shuert, and others. 1989. Carbon and nitrogen cycling within the Bering/Chukchi Seas: Source regions for organic matter affecting AOU demands of the Arctic Ocean. *Progress in Oceanography* 22:279–361, [http://dx.doi.org/10.1016/0079-6611\(89\)90006-2](http://dx.doi.org/10.1016/0079-6611(89)90006-2).
- Wassmann, P., K.N. Kosobokova, D. Slagstad, K.F. Drinkwater, R.R. Hopcroft, S.E. Moore, I. Ellingsen, R.J. Nelson, E. Carmack, E. Popova, and J. Berge. 2015. The contiguous domains of Arctic Ocean advection: Trails of life and death. *Progress in Oceanography*, <http://dx.doi.org/10.1016/j.pocean.2015.08.004>.
- Wassmann, P., C.M. Duarte, S. Agusti, and M.K. Sejr. 2011. Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology* 17:1,235–1,249, <http://dx.doi.org/10.1111/j.1365-2486.2010.02311.x>.
- Weingartner, T., K. Aagaard, R. Woodgate, S. Danielson, Y. Sasaki, and D. Cavalieri. 2005. Circulation on the north central Chukchi Sea shelf. *Deep Sea Research Part II* 52:3,150–3,174, <http://dx.doi.org/10.1016/j.dsr2.2005.10.015>.
- Woodgate, R.A., K.M. Stafford, and F.G. Prah. 2015. A synthesis of year-round interdisciplinary mooring measurements in the Bering Strait (1990–2014) and the RUSALCA years (2004–2011). *Oceanography* 28(3):46–67, <http://dx.doi.org/10.5670/oceanog.2015.57>.

ACKNOWLEDGMENTS

We would like to thank the many people who assisted with field collections, including Boris Sirenko, Sergey Gagaev, and Petr Strelkov of the Zoological Institute, St. Petersburg, Russia, and Alexander Bosin and Alexander Kolesnik of the Pacific Institute of Oceanology in Vladivostok, Russia. Arianne Balsom (2004) and Betty Carvellas (2009 and 2012) facilitated macrobenthos and sediment field collections for the Grebmeier/Cooper component. We thank Sarah Hardy and Jared Weems (2009) and Lauren Bell (2012) for field assistance for the epibenthic component. We appreciate the time and effort of Terry Whittedge (University of Alaska Fairbanks) as Chief Scientist for the RUSALCA 2004, 2009, and 2012 expeditions as well as the CTD hydrography team under the supervision of Robert Pickart (WHOI). We thank Kathy Crane of the National Oceanic and Atmospheric Administration (NOAA) for continued support of the RUSALCA program, Marshall Swartz and Robert Pickart for providing physical oceanographic data, Terry Whittedge for providing water

column chlorophyll values, and the crew and scientists of *R/V Professor Khromov* for various logistical support. Financial support was provided by the NOAA Arctic Office to Pls Grebmeier and Cooper (2004: NOAA-CIFAR 10-067, 2004-2005), 2009 and 2012 (NA08OAR4310608), along with the RUSALCA synthesis award (NOAA Cooperative Agreement #NA09OAR4320129: WHOI CINAR #19930.00 UMCES). This publication is the result in part of research support to K. Iken and B. Bluhm sponsored by the Cooperative Institute for Alaska Research with funds from NOAA under cooperative agreements NA13OAR4320056 and NA08OAR4320870 with the University of Alaska. In addition, MS student C. Serratos was in part supported by a student award of the Center for Global Change and Arctic System Research. The Russian Foundation for Basic Research provided financial support of this research effort by Russian collaborators.

AUTHORS

Jacqueline M. Grebmeier (jgrebmei@umces.edu) is Research Professor, Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD, USA. **Bodil A. Bluhm** is Affiliate Faculty, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA, and Professor, Department of Arctic and Marine Biology, UiT-The Arctic University of Norway, Tromsø, Norway. **Lee W. Cooper** is Research Professor, Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD, USA. **Stanislav G. Denisenko** is Professor, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia. **Katrin Iken** is Professor, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA. **Monika Kędra** is Research Scientist, Institute of Oceanology, Polish Academy of Sciences, Sopot, Poland. **Carlos Serratos** is an MS student, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK, USA.

ARTICLE CITATION

Grebmeier, J.M., B.A. Bluhm, L.W. Cooper, S.G. Denisenko, K. Iken, M. Kędra, and C. Serratos. 2015. Time-series benthic community composition and biomass and associated environmental characteristics in the Chukchi Sea during the RUSALCA 2004–2012 Program. *Oceanography* 28(3):116–133, <http://dx.doi.org/10.5670/oceanog.2015.61>.