Progress in Oceanography 136 (2015) 92–114

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic

Jacqueline M. Grebmeier [a,*], Bodil A. Bluhm [b,c], Lee W. Cooper [a], Seth L. Danielson [b], Kevin R. Arrigo [e], Arny L. Blanchard [b], Janet T. Clarke [f], Robert H. Day [g], Karen E. Frey [h], Rolf R. Gradinger [b,d], Monika Kędra [i], Brenda Konar [b], Kathy J. Kuletz [j], Sang H. Lee [k], James R. Lovvorn [l], Brenda L. Norcross [b], Stephen R. Okkonen [b]

[a] Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD 20688, USA
[b] School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK 99775, USA
[c] University of Tromsø, 9037 Tromsø, Norway
[d] Institute of Marine Research, 9294 Tromsø, Norway
[e] School of Earth Sciences, Stanford University, Stanford, CA 94305, USA
[f] Leidos, 4001 N. Fairfax Drive, Arlington, VA 22203, USA
[g] ABR, Inc.-Environmental Research & Services, Fairbanks, AK 99708, USA
[h] Graduate School of Geography, Clark University, Worcester, MA 01610, USA
[i] Institute of Oceanology, Polish Academy of Sciences, 81-712 Sopot, Poland
[j] US Fish and Wildlife Service, Alaska Region, Anchorage, AK 99503, USA
[k] Department of Oceanography, Pusan National University, Busan 609-735, Republic of Korea
[l] Department of Zoology and Center for Ecology, Southern Illinois University, Carbondale, IL 62901, USA

ARTICLE INFO

Article history:
Available online 22 May 2015

ABSTRACT

The northern Bering and Chukchi Seas are areas in the Pacific Arctic characterized by high northward advection of Pacific Ocean water, with seasonal variability in sea ice cover, water mass characteristics, and benthic processes. In this review, we evaluate the biological and environmental factors that support communities of benthic prey on the continental shelves, with a focus on four macrofaunal biomass "hotspots." For the purpose of this study, we define hotspots as macrofaunal benthic communities with high biomass that support a corresponding ecological guild of benthivorous seabird and marine mammal populations. These four benthic hotspots are regions within the influence of the St. Lawrence Island Polynya (SLIP), the Chirikov Basin between St. Lawrence Island and Bering Strait (Chirikov), north of Bering Strait in the southeast Chukchi Sea (SECS), and in the northeast Chukchi Sea (NECS). Detailed benthic macrofaunal sampling indicates that these hotspot regions have been persistent over four decades of sampling due to annual reoccurrence of seasonally consistent, moderate-to-high water column production with significant export of carbon to the underlying sediments. We also evaluate the usage of the four benthic hotspot regions by benthic prey consumers to illuminate predator–prey connectivity. In the SLIP hotspot, spectacled eiders and walruses are important winter consumers of infaunal bivalves and polychaetes, along with epibenthic gastropods and crabs. In the Chirikov hotspot, gray whales have historically been the largest summer consumers of benthic macrofauna, primarily feeding on ampeliscid amphipods in the summer, but they are also foraging further northward in the SECS and NECS hotspots. Areas of concentrated walrus foraging occur in the SLIP hotspot in winter and early spring, the NECS hotspot in summer, and the SECS hotspot in fall. Bottom up forcing by hydrography and food supply to the benthos influences persistence and composition of benthic prey that then influences the distributions of benthivorous upper trophic level populations.

* Corresponding author.
E-mail address: jgrebmei@umces.edu (J.M. Grebmeier).

http://dx.doi.org/10.1016/j.pocean.2015.05.006
0079-6611/

1. Introduction

The Pacific Arctic region, which extends from the northern Bering Sea to the Arctic Basin, is experiencing declining seasonal sea ice extent and earlier sea ice retreat along with increased ocean temperatures and freshwater content (Woodgate et al., 2012; Stroeve et al., 2014; Frey et al., 2014, 2015; Wood et al., 2015). These changes can drive shifts in marine species composition and carbon cycling (Grebmeier et al., 2006b; Bluhm and Gradinger, 2008; Nelson et al., 2014) and are in part tied to Pacific water advection into the Arctic, a key factor influencing hydrography, biogeochemical processes and associated ecosystem function (Carmack and Wassmann, 2006). A sea level elevation gradient drives this advection through the northward flow of Pacific water from the northern Bering Sea to the Chukchi Sea (Stigebrandt, 1984; Kinder et al., 1986; Danielson et al., 2014), despite the opposing prevailing northeasterly winds (Weingartner et al., 1999, 2013; Woodgate et al., 2005a,b). The resulting advection of heat, nutrients, organic carbon, and organisms supplies the shelves of the northern Bering and Chukchi Seas with large amounts of additional allochthonous material that adds substantially to seasonal *in situ* (autochthonous) production (Coachman et al., 1975; Sambrotto et al., 1984; Walsh et al., 1989).

Water from the Bering Sea shelf and slope flowing northward through Bering Strait crosses the Chukchi Sea along three main pathways following the regional bathymetry (Fig. 1; Winsor and Chapman, 2004; Spall, 2007). In the western Chukchi Sea, water flows northwesterly and exits mostly through Herald Canyon or turns eastward along the outer shelf. In the central Chukchi, the flow is northward through the Central Channel and then eastward, with branches wrapping around both the southern and northern flanks of Hanna Shoal. In the northeastern Chukchi, the flow follows the Alaska coast where it exits through Barrow Canyon, joining with the other Pacific-origin waters that have passed by Hanna Shoal (Weingartner et al., 2013). These inflowing pathways of Bering Sea water leave their imprint during seasonal sea ice retreat as embayments of water mass characteristics within the melting ice edge (Paquette and Bourke, 1981; Wood et al., 2015).

Benthic macrofaunal communities on the shallow continental shelves of the Pacific Arctic accumulate regionally high biomass in response to seasonally high levels of export pelagic production that is either being advected into the system from upstream primary production or produced *in situ* and deposited to the underlying sediments directly (Grebmeier et al., 2006a; Nelson et al., 2014). Benthic macrofaunal patterns have generally persisted in the Pacific Arctic from multiple years-to-decades (Grebmeier, 2012), although population composition and biomass vary regionally due to varying food supply and current structure that influences sediment grain size (Grebmeier and McRoy, 1989; Feder et al., 1994, 2006; Grebmeier et al., 2006a; Blanchard et al., 2013a; Blanchard and Feder, 2014; Schonberg et al., 2014). On these year-to decadal time scales, persistent seasonal *in situ* production and advected carbon from upstream sources, coincident with strong pelagic–benthic coupling processes, have maintained four major patches of relatively high, macrobenthic community biomass in the Pacific Arctic, which we refer here to as benthic "hotspots". These persistent hotspots occur on the continental shelf in the northern Bering Sea near the St. Lawrence Island Polynya (SLIP), in the Chirikov Basin south of Bering Strait (Chirikov), in the southeastern Chukchi Sea (SECS), and in the northeastern portion of the Chukchi Sea (NECS; Grebmeier et al., 2006a, 2010; Grebmeier, 2012). These four hotspots are associated with the annual, seasonal and spatially consistent reoccurrence of high chlorophyll *a* (chl *a*) content in the water column (Springer et al., 1996; Hill and Cota, 2005; Lee et al., 2007; Brown et al., 2011; Cooper et al., 2013). The benthic hotspots provide prey to mobile epibenthic and upper trophic level benthivores, particularly marine mammals and diving seabirds. Benthic predators include

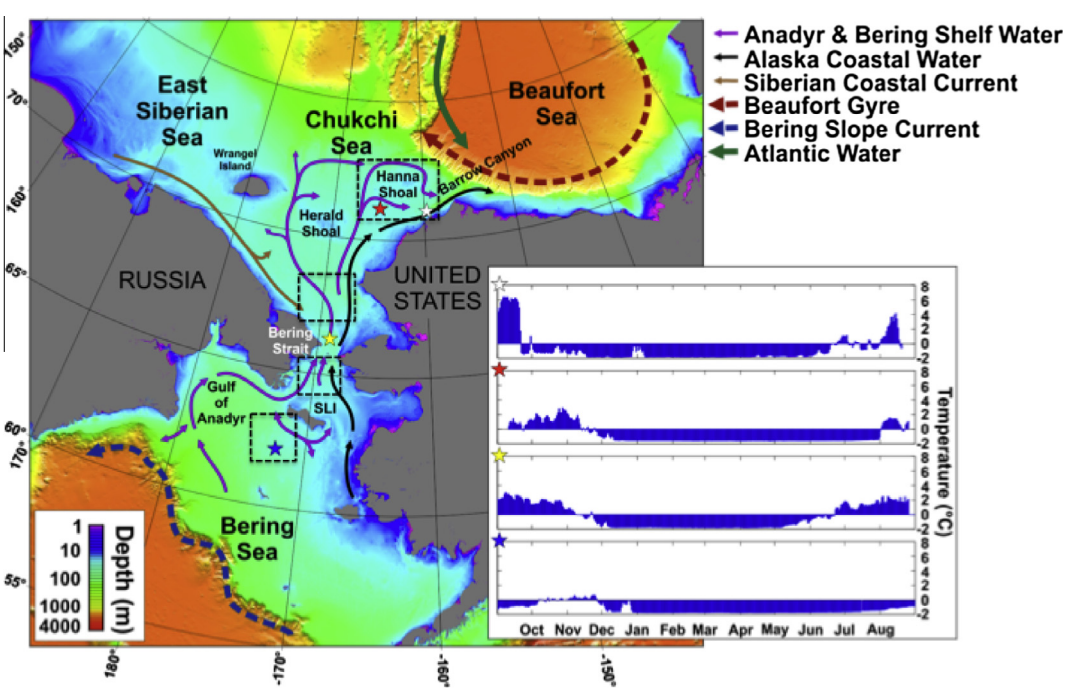

Fig. 1. Schematic of current flow patterns, water mass type, and bottom water temperatures at four moorings from the northern Bering Sea to the northeastern Chukchi Sea in relation to SOAR benthic hotspot sites (boxes). Key: Blue star = N55 mooring within the SLIP (St. Lawrence Island Polynya region) hotspot, Yellow star = A3 mooring between the Chirikov and SECS (Southeast Chukchi Sea) hotspots; Red star = S1 mooring within the NECS (Northeast Chukchi Sea) hotspot, and White star = upper Barrow Canyon mooring just at the eastern edge of the NECS hotspot; SLI = St. Lawrence Island. Data source: Danielson et al. (2014); also see footnote 1 in Table 1 for specific mooring data source locations.

gray whales, walruses, and bearded seals (Moore et al., 2003, 2014; Jay et al., 2012; Aerts et al., 2013), and in certain areas, benthivorous diving sea ducks (Lovvorn et al., 2009, 2015a).

We describe and evaluate the environmental and biological factors that create and maintain benthic hotspots in the Pacific Arctic region. Our approach in this review was to combine and synthesize available data in a descriptive way, both from published and unpublished sources, and to evaluate the ecosystem-forcing factors influencing four persistent hotspot regions in the northern Bering and Chukchi Seas. As such, we are evaluating spatial variability in benthic prey–predator hotspots and identifying specific factors that may support the persistence of these hotspots. We ask two overarching questions related to the persistence of these biological hotspots:

(1) What are the distinguishing characteristics of these persistent benthic biological hotspots in the Pacific Arctic region?
(2) What are the main environmental processes influencing these biological hotspots in the northern Bering and Chukchi Seas?

This paper is a contribution to the "Synthesis of Arctic Research" (SOAR) project, which aims to integrate knowledge concerning the relationships among environmental conditions and lower and upper trophic levels in the Pacific Arctic region (Moore and Stabeno, 2015). We provide a summary of distinguishing characteristic features of the four target areas by discipline, including physical oceanographic features and how they govern benthic biomass hotspot persistence, as well as the distribution of upper trophic level benthivores. Integrated conclusions and recommendations on future directions for ecosystem research follow.

2. General synthesis review format, methods, and data selection criteria

The four regions of interest were identified based on observations of persistently high macrofaunal benthic biomass of >20 g C m^{-2} compiled over periods up to four decades of sampling (Fig. 2; see also citations of data generators in the metadata file for Grebmeier and Cooper, 2014a). Bounding boxes were set to be inclusive of sampling stations supporting this level of biomass at

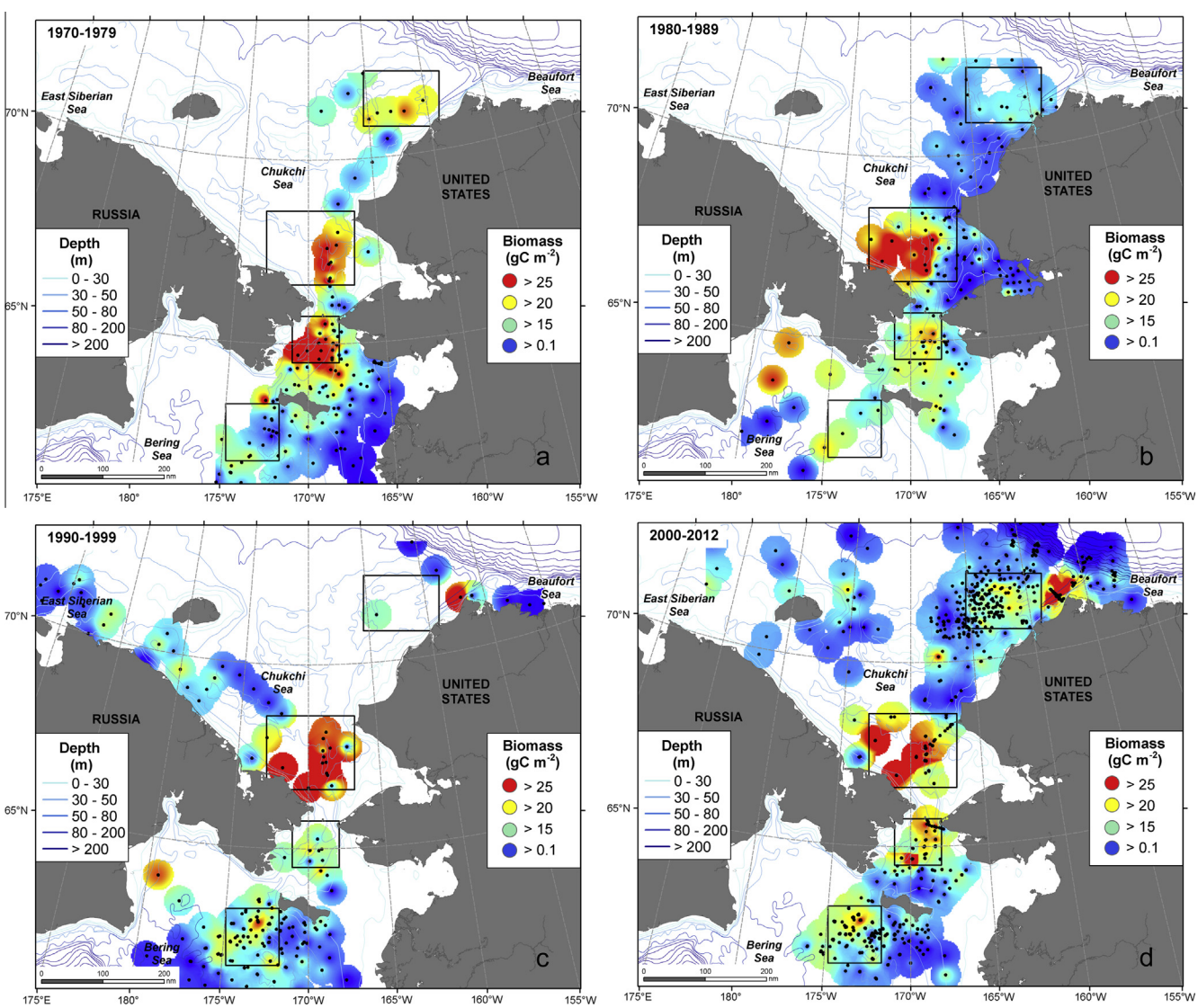

Fig. 2. Decadal distribution of macrofaunal benthic biomass in the northern Bering and Chukchi Seas for the time periods: (a) 1970–1979, (b) 1980–1989, (c) 1990–1999, (d) 2000–2012. Black boxes identify the four benthic bounding boxes used in our study with >20 g C m^{-2} station biomass that occurred during one or more of the decades in our study region. Specifically, these bounding boxes from south to north are: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and NECS (Northeast Chukchi Sea) hotspot. Data source: Grebmeier and Cooper (2014a).

some point over the four decades for which data were synthesized. Due to the patchiness of high macrobenthic biomass, each of the bounding boxes also includes some stations with <20 g C m^{-2} biomass (Grebmeier et al., 2006a; Grebmeier, 2012). Our goal in designating the bounding boxes was to provide for regional-level and ecosystem-level characterization of benthic hotspots in a comparative way.

The bounding boxes for the high benthic biomass hotspots were defined as follows:

- SLIP (St. Lawrence Island Polynya region), 61.75°N–63.37°N, 171.69°W–175.01°W.
- Chirikov (Chirikov Basin, northern Bering Sea), 64.49°N–65.76°N, 167.97°W–171.08°W.
- SECS (Southeast Chukchi Sea), 66.58°N–68.59°N, 166.59°W–173.12°W.
- NECS (Northeast Chukchi Sea), 70.62°N–72.37°N, 158.46°W–165.46°W.

For each of the four bounding boxes, we then compiled physical, hydrographic and biological data to describe relevant environmental forcing factors. Physical and hydrographic data included sea ice cover, including sea ice conditions, bottom water temperature and salinity, and current speed and direction. For each bounding box we also compiled biological data indicating food supply and its quality for the benthos, including nutrient concentrations, phytoplankton biomass (chl *a*) and production, surface sediment chl *a*, sediment total organic carbon (TOC) content, sediment grain size (specifically the silt and clay content), and sediment community oxygen consumption (SCOC). We also summarized data on both infaunal and epifaunal prey densities, biomass and dominant taxa for benthivorous birds and mammals as well as biomass of demersal fish. We then evaluated the distribution and/or areal use of these four hotspot regions by these upper trophic level benthivores. This exercise allowed a conceptual analysis of spatial, hydrographic and biogeochemical controls on benthic hotspots. This bottom-up approach to understanding trophic interactions is complementary to a parallel SOAR effort utilizing a top-down, higher-trophic level perspective (Kuletz et al., 2015).

3. General ecosystem processes and patterns at the hotspot regions

Each sub-section to follow begins with a short introduction to the theme, followed by a brief methods overview relating to the analyses presented, followed by results on a parameter-by-parameter basis. At the end of the section, we compare and contrast the findings for the four regions. A detailed description of disciplinary methods used for parameters analyzed in this synthesis is provided in Supplement A. Only summary methods for relevant components are included as part of the description of synthetic results below. Note that many raw summary data are archived at the open Pacific Marine Arctic Regional Synthesis (PacMARS) website (http://pacmars.eol.ucar.edu) and source files are indicated in both the table and figures in this section. We present the mean values in the text, with the standard deviations and range values for those means presented in the tables.

3.1. Currents and sediment grain size, bottom water temperature, salinity and inorganic nutrients, and sea ice cover

3.1.1. Currents and sediment grain size

Currents are strongest through the study areas' topographically controlled constrictions (Anadyr Strait, Bering Strait, Barrow Canyon) where the mean velocities can exceed 25 cm s^{-1} (Roach et al., 1995; Woodgate et al., 2005a,b). Elsewhere in the region the mean velocity is generally less than 10 cm s^{-1} (Fig. 1; Weingartner et al., 1999, 2005; Woodgate et al., 2005a; Danielson et al., 2006). From observations of locally elevated levels of nutrients, algal biomass and productivity, it can be inferred that the energetic flows in the straits promote mixing and locally enhanced nutrient flux into the euphotic zone (e.g., Walsh et al., 1989). Strong pelagic–benthic coupling is enabled just downstream of such features, where slower current speeds allow water column production to settle to the seafloor (Grebmeier and McRoy, 1989; c.f. Grebmeier et al., 2006a); this pattern is observed globally and is not restricted to the Arctic (De Leo et al., 2010). Recent studies in the northeast Chukchi Sea expand on this topic by addressing the concept of topographic control over water masses being associated with deposition of organic carbon to the benthos (Blanchard et al., 2013a). The SLIP, Chirikov, and SECS hotspots are bathymetrically level, but the NECS hotspot area described in Blanchard et al. (2013a) hosts a sub-region of more strongly sloped seafloor and thus more heterogeneous bathymetry.

Current meter data from representative sites within/near the four hotspot regions for the period from late winter (March through May) and late summer (July through September) 2000–2012 are summarized in Table 1, with locations shown in Fig. 1. Not all moorings were deployed simultaneously, so the results must be interpreted with appropriate caution because interannual variability can be as large as seasonal variations. The velocity data have been tidally filtered and then subsampled to 6-hourly intervals. Further specifics on the raw data analyses are provided in Supplement A.

Regional currents are more energetic in the summer when the opposing winds are weaker and the buoyancy-driven Alaska Coastal Current is accelerated due to coastal discharge and warming in shallow waters. The upper 20 m of the water column is also sensitive to the direct effects of strong but seasonally varying wind forcing through Ekman transport, which tends to drive low salinity coastal waters westward (e.g., Danielson et al., 2006). Notably, for the records examined here, the mooring in Bering Strait (A3) (between the Chirikov and SECS hotspots) has a mean velocity magnitude of 34 cm s^{-1} in summer and 30 cm s^{-1} in winter; mooring BC2 in Barrow Canyon recorded 45 cm s^{-1} in summer and 16 cm s^{-1} in winter (Table 1). Weaker flows (mean velocity less than 5 cm s^{-1} in both seasons) were observed south of St Lawrence Island in the SLIP hotspot and at mooring S1 in the NECS hotspot. Within Bering Strait and Barrow Canyon in summer the standard deviation of the velocity components (*U* and *V*) are always smaller than the mean flow, indicating that the net flow dominates the flow field. In contrast, the records within SLIP and NECS have flows and associated standard deviations that are 1.5–10 times greater than the mean, suggesting a flow field that is also influenced by local variability in addition to net advection.

Sediment grain size, which is determined in part by the strength of the flow field, co-varies with sediment total organic carbon (TOC) content, benthic faunal community composition, and to a lesser degree benthic biomass (Grebmeier and Cooper, 1995; Grebmeier et al., 2006a; Blanchard et al., 2013a; Ravelo et al., 2014; Schonberg et al., 2014). In particular, sediment TOC is positively correlated with the smaller silt and clay ($\geqslant$5 phi[1]) grain particles (c.f. Grebmeier et al., 2006a), and those are predominant in low flow areas, and thus can be indicators of current speeds and deposition zones. Notably, in areas dominated by soft sediments we observe similar benthic macrofauna, leading to the conclusion that the heterogeneity of sediment grain size in association with TOC

[1] Unit based on Log 2 of sediment grain size diameter.

Table 1
Current flow indicators (cm s^{-1}) for the northern Bering and Chukchi Seas from 2008 to 2011 in late winter/spring (top of table) and summer/fall (bottom of table), with each mooring identified to the closest benthic hotspot region in Fig. 1. Mooring key: blue star within SLIP (St. Lawrence Island Polynya region) hotspot; yellow star between the Chirikov (Chirikov Basin) and SECS (Southeast Chukchi Sea) hotspots; red star within the NECS (Northeast Chukchi Sea) hotspot; and white star within BC (Barrow Canyon); *N* = number of observations during the date range of the deployment; *U* and *V* are the perpendicular current velocity vectors in cm s^{-1}, with *U* being the velocity toward east and *V* being the velocity toward north; std = standard deviation; min = minimum and max = maximum for current vectors. Maximum northward (*V*) velocity highlighted in bold for spring and summer. Raw data have had tides filtered and then subsampled to 6-hourly intervals (see Supplement A for further details). Data source: Danielson et al. (2014); also see footnote 1 below for actual data source location.

Mooring name (hotspot region)	Latitude (°N)	Longitude (°W)	Date range (Mo/Day/Year)	*N*	*U* mean	*V* mean	*U* std	*V* std	*U* min	*V* min	*U* max	*V* max
N55-blue star (SLIP)	61.96	171.97	3/1/–5/31/2009	368	0.59	−0.61	4.64	6.20	−13.07	−16.55	22.75	26.85
A3-yellow star (between Chirikov and SECS)	66.33	168.97	3/1–5/31/2009	368	−12.26	**26.87**	7.78	22.29	−28.96	−55.24	10.17	73.29
S1-red star (NECS)	71.00	165.00	3/1/–5/31/2009	368	4.70	2.55	9.86	4.91	−25.24	−7.28	38.08	25.34
BC2-white star	70.92	159.94	3/1–5/31/2011	368	15.65	1.48	31.89	11.41	−77.41	−40.08	61.26	21.79
N55-blue star (SLIP)	61.96	171.97	7/12/–9/30/2008	323	1.14	−1.80	3.21	3.35	−7.40	−8.56	9.31	13.03
A3-yellow star (between Chirikov and SECS)	66.33	168.97	7/1/–9/30/2008	368	-19.48	**28.04**	8.20	14.05	−33.63	−35.20	20.59	62.73
S1-red star (NECS)	71.00	165.00	9/10–9/30/2008 and 7/1/-8/26/2009	307	4.54	−1.20	7.06	6.89	−14.38	−18.96	21.74	25.83
BC2-white star	70.92	159.94	8/17/–9/30/2010 and 7/1/–8/16/2011	368	41.21	18.45	13.98	12.17	−20.53	−15.42	63.79	50.80

[1] = Mooring N55 was funded by NSF under the Bering Sea Ecosystem Study (BEST) Program, data archived at http://beringsea.eol.ucar.edu/. Mooring A3 data come from the APL Bering Strait archive http://psc.apl.washington.edu/HLD/Bstrait/bstrait. Mooring S1 data were provided by the Chukchi Sea Environmental Studies Program operated by Olgoonik Fairweather on behalf of ConocoPhillips, Shell Exploration and Production Company, and Statoil. The Barrow Canyon mooring BC2 was supported by ConocoPhillips, Shell, and DOI-BOEM, data archived at http://www.nodc.noaa.gov/.

are, therefore, important factors driving community composition (Grebmeier et al., 1989). C/N values in sediment can also be an indicator of the quality of organic carbon (Grebmeier et al., 1989, 2006a).

Within our review, sediment grain size was determined from surface sediment samples at individual stations during multiple cruises conducted in the northern Bering and Chukchi Seas from 2000 to 2012 and we used the fine silt/clay grain size as a proxy for current speed. Data on sediment grain size and TOC were summarized from the same interdisciplinary oceanographic cruises (see Supplement A and Table A1 for listing of cruises, associated projects, publications and weblinks for the project data). The full suite of all sediment parameters, including grain size components (silt/clay to sand and gravel), sediment TOC, chl *a*, and SCOC are available at the PacMARS EOL data portal (Grebmeier and Cooper, 2014b,c,d; http://pacmars.eol.ucar.edu).

Mean silt/clay and TOC content are highest in the SLIP and SECS hotspots (71–73% silt/clay and ~1% TOC; Table 2). The lowest mean silt/clay (~20% ⩾5 phi) and TOC (0.4%) content occurs in the Chirikov hotspot and are consistent with the predominantly sandy environment and high current flow in that region (Table 1). The second lowest mean silt/clay (~52% ⩾5 phi) and TOC (0.9%) content occurs in the NECS hotspot where the heterogeneous environment is composed of patches of mud interspersed with coarser sediment regimes (Blanchard et al., 2013a; Day et al., 2013). Mean C/N values of surface sediments in the SLIP, Chirikov and SECS hotspots ranged from 6.3 to 6.4 (wt./wt.), consistent with primarily marine input. By comparison, the mean C/N value was highest in the NECS hotspot 7.8 (wt./wt.), indicating more refractory, less labile organic carbon contributions from heterogeneous sediment recycling and/or terrigenous sources.

3.1.2. Bottom water temperature, salinity, and inorganic nutrients

Bottom water temperatures critically influence benthic communities because of their effect on metabolic rates, and therefore growth and nutrient recycling processes. Nutrient concentrations in part determine the capacity for productivity in a system. The Anadyr water mass carries elevated levels of nutrients across the western part of the Bering–Chukchi shelf ecosystem (Walsh et al., 1989; Codispoti et al., 2013). It is therefore possible to track Pacific waters originating near the Bering Sea shelf break transiting northward through Bering Strait and across the Chukchi Sea, with high nutrients also observable at depth on the slope of both the Chukchi and Beaufort seas (Codispoti et al., 2013).

An extensive set of CTD and bottom bottle cast data sampled within the four benthic hotspot regions from March to September 2000–2012 were obtained from various archives (Okkonen, 2014); these data were then subsequently processed to extract bottom water (BW) temperature and salinity values from each cast for the 2000–2012 period (Okkonen, 2014 CTD metadata file). These BW values were then combined with BW temperature

Table 2
Surface sediment silt/clay content (⩾5 phi), carbon/nitrogen ratio (C/N), total organic carbon (TOC), chlorophyll *a* (chl *a*), and sediment community oxygen consumption (SCOC) (mean ± standard deviation in bold print) for the four benthic hotspots from March–September 2000–2012 in the northern Bering and Chukchi Seas. Key: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and NECS (Northeast Chukchi Sea) hotspot; ± = standard deviation, number of samples in parentheses, and range of values in brackets. Date source: Grebmeier and Cooper (2014b,c,d).

Hotspot region	Months 2000–2012	Silt and clay grain size (⩾5 phi, %)	TOC (%)	C/N (wt./wt.)	Sediment chl *a* (mg m^{-2})	SCOC (mmol O_2 m^{-2} d^{-1})
SLIP	March–July	**73.19 ± 22.67** (203) [6.08–98.80]	**1.01 ± 0.45** (188) [0.18–2.60]	**6.42 ± 0.72** (188) [4.00–9.50]	**13.31 ± 6.51** (195) [0.12–37.95]	**9.86 ± 3.86** (137) [1.71–21.41]
Chirikov	May–August	**20.01 ± 6.99** (82) [7.18–41.25]	**0.42 ± 0.30** (89) [0.16–1.49]	**6.26 ± 0.82** (89) [4.21–8.85]	**15.74 ± 8.15** (74) [1.00–31.49]	**14.45 ± 7.43** (26) [2.03–29.66]
SECS	July–September	**71.74 ± 23.76** (124) [14.20–99.75]	**1.05 ± 0.51** (125) [0.08–2.45]	**6.35 ± 0.67** (124) [4.65–8.09]	**19.16 ± 9.80** (123) [0.11–44.29]	**22.35 ± 8.72** (63) [7.30–40.69]
NECS	May–September	**52.38 ± 23.40** (302) [1.87–98.58]	**0.85 ± 0.47** (277) [0.03–2.40]	**7.78 ± 1.72** (277) [3.00–28.00]	**12.74 ± 7.73** (57) [1.58–55.62]	**9.80 ± 3.33** (12) [5.42–16.97]

and salinity values obtained from all sites where benthic parameters were collected that did not overlap the previous archive results for the period March–September (Grebmeier and Cooper, 2014e; Table 3, Supplement Table A1).

In the SLIP hotspot, the mean BW temperature over the late winter to late summer (March–September) period are persistently low, as indicated both by bottle casts and mooring data (−1.6 °C; Table 3, Figs. 1 and 4). These cold bottom water temperatures are firstly a result of fall atmospheric cooling, and secondarily due to ice formation. In the northern part of the hotspot bounding box where a winter polynya forms, high salinity and cooling throughout the water column results from freezing processes. These temperature imprints persist in summer because of stratification and limited mixing (Fig. 1; c.f. Grebmeier and Barry, 2007; Cooper et al., 2012, 2013). In comparison, the mean BW temperature in the Chirikov hotspot during the same sampling period is much warmer (2.0 °C), with temperatures cooler in the spring and warming through the summer (Table 3, Figs. 1 and 4). The mean bottom water temperature in the SECS hotspot (2.2 °C) is only slightly warmer than in the Chirikov hotspot, with the caveat that the sampling period was July–September (Table 3, Figs. 1 and 4). These two regions are similar in BW temperatures because of stronger mixing in the area than in the SLIP hotspot. The mean bottom water temperature in the NECS hotspot (−0.7 °C) sampled from May to September was colder and more similar to the SLIP hotspot, although with greater seasonal variability (Figs. 1 and 4). Both areas have relatively weak mixing during summer (two layer structure), thus isolating the bottom water and allowing it to remain cold. Pacific-origin Winter Water is known not to be flushed out of the system until September (Weingartner et al., 2013). The variability around the means is indicative of the seasonality of the system at the scale of our study. By contrast, mean BW salinities were relatively similar (for biological communities) (32.2–32.5) across all four hotspots. However, the increasing salinity range from south to north hotspots could indicate a brine injection signature in the bottom waters from winter sea ice formation, as well as reflect each hotspot's contact with coastal waters (e.g., higher freshwater content in coastal waters in summer).

Nutrient concentrations are highest in the Anadyr water mass, which occurs offshore from the northern Bering Sea through the Chukchi Sea on the furthest western side of the study area (Codispoti et al., 2013). Mean concentrations of BW nitrate + nitrite (hereafter $NO_{3/2}$) and silica over the 2000–2012 period decline in a northerly direction from the SLIP hotspot ($NO_{3/2}$: 11.6 μM, Si: 35.1 μM) to the SECS hotspot ($NO_{3/2}$: 5.5 μM, Si: 15.1 μM), with slightly higher mean concentrations again in the NECS hotspot ($NO_{3/2}$: 6.9 μM, Si: 18.0 μM), indicating the biological uptake of nutrients in Pacific water from south to north (Grebmeier and Cooper, 2014f; Table 4). In contrast the mean concentrations of BW phosphate and ammonium are relatively constant at the four hotspots (PO_4: ~1.1–1.6 μM, ammonium: ~1.9–2.8 μM).

3.1.3. Sea ice cover

Sea ice characteristics in the study region vary between predominantly seasonal first-year ice in the northern Bering Sea to mixed first year/multi-year ice in the northern Chukchi Sea region (Grebmeier et al., 2010; Frey et al., 2014). Although summer sea ice extent has in general declined on a pan-Arctic scale, trends vary significantly on regional scales (Frey et al., 2014, 2015). Sea ice persistence affects the length of the vegetative season for primary production (Arrigo et al., 2008) and therefore potentially the food supply for benthic production, but also constrains or facilitates access by benthic detritivorous birds and marine mammals (Jay et al., 2012).

Multichannel Microwave Radiometer (SMMR) and Special Sensor Microwave/Imager (SSM/I) passive microwave instruments (Cavalieri et al., 2008) were used to investigate the variability in sea ice cover within the four defined hotspot boxes (also see Frey et al., 2015, for a broad scale analysis using the same

Table 3
Station depth, bottom water temperature and salinity (mean ± standard deviation in bold print) for the four benthic hotspot regions from March–September 2000–2012 in the northern Bering and Chukchi Seas. Key: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and the NECS (Northeast Chukchi Sea) hotspot; ± = standard deviation, number of samples in parentheses, and range of values in brackets. Data source: Grebmeier and Cooper (2014e) and Okkonen (2014).

Hotspot region	Months 2000–2012	Mean station depth (m)	Mean bottom water temperature (°C)	Mean bottom water salinity
SLIP	March–July	**65 ± 8** (234) [36–85]	**−1.64 ± 0.26** (232) [−1.81–0.13]	**32.47 ± 0.32** (232) [31.52–33.11]
Chirikov	May–August	**47 ± 6** (324) [17–62]	**2.01 ± 2.37** (308) [−1.69–10.50]	**32.20 ± 0.61** (308) [29.72–33.08]
SECS	July–September	**44 ± 8** (323) [23–60]	**2.20 ± 1.64** (316) [−1.78 to 8.84]	**32.36 ± 0.56** (316) [27.75–33.28]
NECS	May–September	**43 ± 9** (578) [19–89]	**−0.70 ± 1.54** (318) [−1.83 to 6.20]	**32.59 ± 0.84** (317) [23.20–34.42]

Table 4
Bottom water nutrient summary values for nitrate/nitrite, phosphate, silica and ammonium (mean ± standard deviation in bold print) for the four benthic hotspot regions in the northern Bering and Chukchi Seas from March–September 2000–2012. Key: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and the NECS (Northeast Chukchi Sea) hotspot; ± = standard deviation, number of samples in parentheses, and range of values in brackets. Data source: Grebmeier and Cooper (2014f).

Hotspot region	Months	Bottom water nutrients (μM)			
		Nitrate/nitrite	Phosphate	Silica	Ammonium
SLIP	March–July	**11.59 ± 4.78** (197) [1.32–23.90]	**1.64 ± 0.32** (197) [0.66–2.56]	**35.07 ± 10.11** (197) [9.88–81.25]	**2.61 ± 1.73** (197) [0.27–11.95]
Chirikov	May–August	**8.16 ± 7.08** (121) [0.10–44.90]	**1.13 ± 0.49** (125) [0.28–3.41]	**17.23 ± 11.58** (126) [1.40–40.51]	**1.88 ± 1.05** (110) [0.10–5.11]
SECS	July–September	**5.46 ± 4.59** (91) [0.05–16.00]	**1.33 ± 0.90** (93) [0.25–4.87]	**15.12 ± 13.24** (93) [0.48–51.72]	**2.79 ± 1.91** (85) [0.12–13.76]
NECS	May–September	**6.93 ± 5.30** (128) [0.15–20.98]	**1.50 ± 0.56** (128) [0.31–4.08]	**17.97 ± 12.48** (128) [3.90–50.51]	**2.81 ± 1.27** (128) [0.06–7.66]

methodology). We used a 15% ice concentration threshold to define the presence versus absence of sea ice cover for each pixel in the resulting daily time series. Annual sea ice persistence over the years 1979–2012 was assessed by summing the number of days that sea ice was present in a given year. The timing of sea ice breakup (formation) in each year was determined by recording the date on which at least one pixel registers two consecutive days below (above) a 15% sea ice concentration threshold, where we define the breakup period as 15 March–15 September and the freeze-up period as 15 September–15 March.

The sea ice time series for the four benthic hotspot sites demonstrates strong trends ($p < 0.1$) in sea ice persistence, the timing of sea ice breakup, and the timing of sea ice freeze-up over the 34-year record for the Chirikov, SECS and NECS hotspots (Fig. 3). No significant trends were observed for the SLIP hotspot. The Chirikov, SECS, and NECS hotspots all show declines in annual sea ice persistence, with a larger fraction of sea ice decline resulting from later dates in sea ice freeze-up and earlier dates of sea ice breakup. The NECS hotspot had the greatest mean sea ice changes with a decline in annual sea ice persistence (~30 days decade^{-1}), an earlier timing of sea ice breakup of (~13 days decade^{-1}), and a later timing of sea ice freeze-up (~15 days decade^{-1}). By comparison, the Chirikov and SECS hotspots show a similar, but more modest decline in annual sea ice persistence (~9–12 days decade^{-1}), an earlier timing of sea ice breakup of (~3–5 days decade^{-1}), and a later timing of sea ice freeze-up (~7–8 days decade^{-1}). Further details on the temporal and spatial aspects of the sea ice cover in the Pacific Arctic region are provided in Frey et al. (2015) and Wood et al. (2015).

3.1.4. Major similarities and differences in the four hotspots: currents and sediment grain size, bottom water temperature, salinity and inorganic nutrients, and sea ice cover

Temperature and salinity characteristics of near-bottom waters within each of the four hotspots reflect the interplay between local currents and constituent water masses. The Chirikov and SECS hotspots experience strong northward advection of cold, salty Anadyr Water, warm, fresh Alaska Coastal Water, and Bering Sea Water of intermediate properties (c.f. Spall, 2007). In contrast, the SLIP hotspot, and to a lesser extent the NECS hotspot, are characterized by weaker, less variable flow regimes that promote the retention of cold salinized waters derived from the production of sea ice. Current velocities are highest in/near Bering Strait and Barrow Canyon influencing sediment grain size patterns, with implications for the composition of the biological communities discussed below.

Sea ice thickness, duration and freeze-up, and bottom water nutrient concentrations exhibit a latitudinal gradient across the four hotspots, with ice cover increasing and nitrate + nitrite and silica concentrations mostly decreasing from south to north.

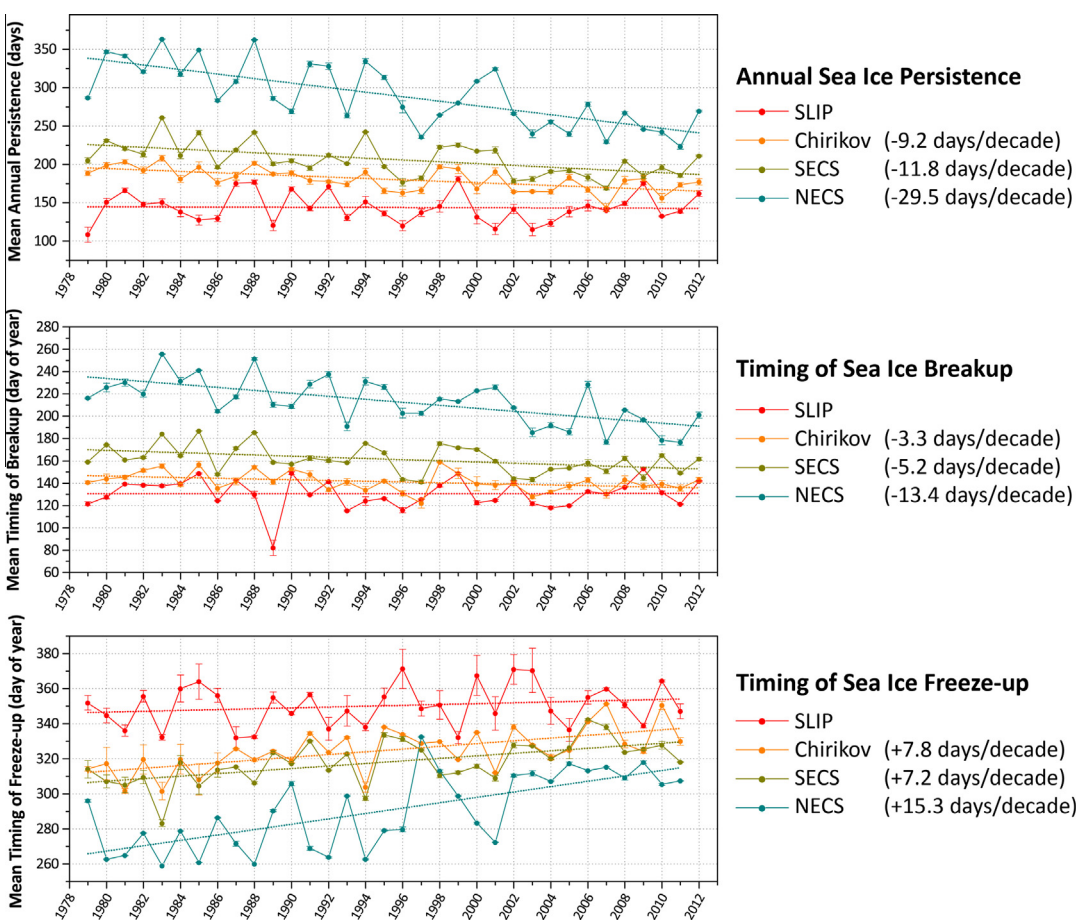

Fig. 3. Time series of annual sea ice persistence (top panel), break-up (middle panel), and sea ice-freeze up (bottom panel) for the study region from south to north: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and NECS (Northeast Chukchi Sea) hotspot. Values in parentheses are the changes in days per decade obtained through trend analysis (significance at $p < 0.1$) for each of the following parameters: top panel: negative value = reduced number of days for sea ice persistence, middle panel: negative value = earlier breakup of sea ice by days, and bottom panel: positive value is number of days of later sea ice freeze-up. The error bars for each annual value are standard deviation values. Data source: Sea ice concentration for data spanning the years 1979–2012 are derived from the Scanning Multichannel Microwave Radiometer (SMMR) and Special Sensor Microwave/Imager (SSM/I) passive microwave instruments (Cavalieri et al., 1996, 2008).

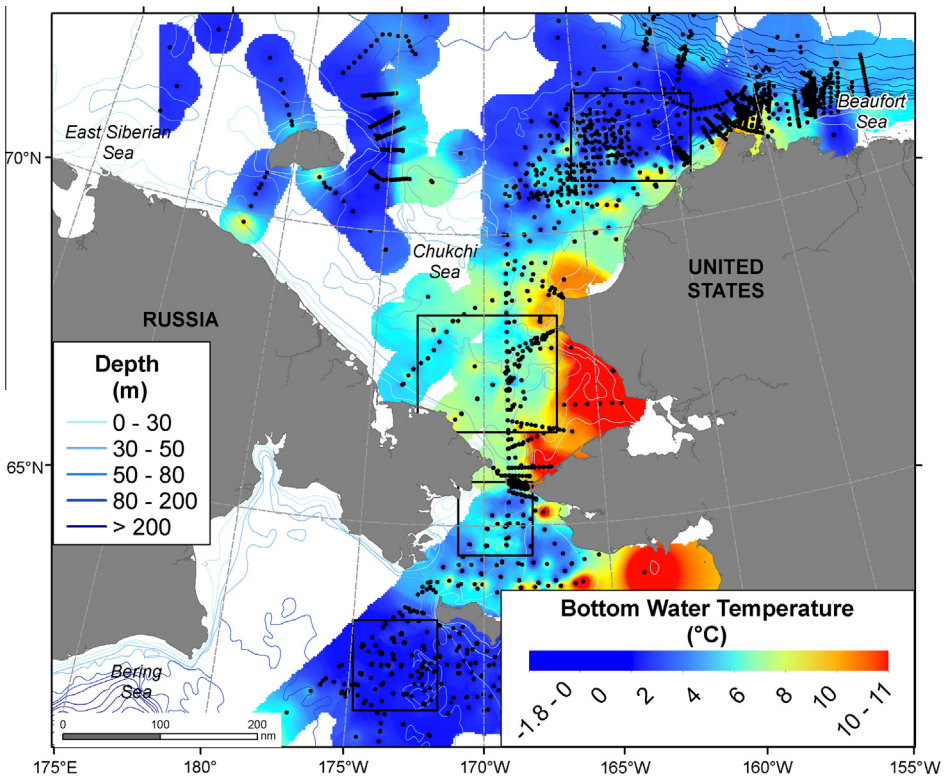

Fig. 4. Bottom water temperatures for the period March–September 2000–2012 in the northern Bering and Chukchi Seas. Black boxes are the location of the four benthic biomass bounding boxes from south to north used in our study: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and NECS (Northeast Chukchi Sea) hotspot. Data source: Grebmeier and Cooper (2014e) and Okkonen (2014).

Changes in sea ice cover over the past four decades are most extreme in the NECS hotspot and remained essentially stable in the SLIP.

The SLIP and NECS regions share consistently low mean BW temperatures throughout the summer (albeit the SLIP retains the coldest water longer through the season). However, these two sites differ in other respects, for example, SLIP has higher mean bottom water nutrients concentrations because it is closer to upwelled Anadyr Water, higher silt and clay and TOC content due to slower currents, and lower mean C/N ratios (more labile organic carbon) than the NECS hotspot, the latter site being more characteristic of an organic material recycling regime.

3.2. Primary production, sea ice algae and water column chl a, and pelagic–benthic coupling

The northward current flow from the northern Bering into the Chukchi Sea suggests that the additive effects of transporting live cells of surface and subsurface phytoplankton, along with phytodetritus, are important in maintaining downstream ecosystem structure (Grebmeier et al., 2006a,b; Grebmeier, 2012; Mathis et al., 2014; Nelson et al., 2014). Here, we focus on pelagic and ice algal primary production while recognizing that production by benthic microalgae also can be important in shallow Arctic waters (Glud et al., 2009; Woelfel et al., 2010; McTigue and Dunton, 2014). Little is known about benthic primary production in the Pacific Arctic, but because all four hotspots have a mean depth from 43 to 65 m we assume benthic primary production will be much less significant than pelagic and ice algal production due to light limitations. Concentrations of sediment chl *a*, however, are significant in some of these hotspots (Table 2) and reflect the aggregated algal biomass produced by pelagic, sympagic and perhaps benthic primary production.

3.2.1. Primary production

It is challenging to synthesize the patterns, especially the changes in primary production in the Arctic, into a coherent picture. The challenge arises from the strong seasonality of primary production, the inconsistency of recent results (derived with different methods), and the variable spatial coverage. Primary production on the northern Bering and Chukchi Sea shelves ranges from low rates in the winter months (<0.05 g C m^{-2} d^{-1}) to very high rates in the spring/early summer period (>1 g C m^{-2} d^{-1}) (Springer et al., 1996; Brown et al., 2011). In the northern Bering Sea, the highest values are related to the "Green Belt" on the outer shelf and slope and other areas regionally specific in the Bering Sea (Brown et al., 2011). By comparison, the lower to medium values are seasonally variable and the estimated lower primary production field measurements reported by Lee et al. (2012) may be due both to the measurements being made in less productive regions than the "Green Belt" and seasonal differences in the timing of sampling. The recent results by Lee et al. (2012), describing decreasing primary production over the recent decade in the northern Bering Sea, were obtained by measurements made in 2004–2008 compared to data from the 1980s in the same region. Satellite data used by Pabi et al. (2008) in the Bering Sea, in contrast, covered periods from 1998 to 2006 and showed some increasing trends in primary production, although over a broader area of study than Lee et al. (2012). In fact, Brown and Arrigo (2012, 2013) and Brown et al. (2011) indicate little or no change in net primary production in the Bering Sea from 1998 to 2010, and probably since the 1970s–1980s. Notably these findings are based on satellite data from the whole Bering Sea and not the smaller sub-regions of the northern Bering Sea as measured by Lee et al. (2012). Further field and satellite studies are needed at the same sites throughout the production season to evaluate seasonal and interannual changes.

In the Chukchi Sea, increased open water area and a longer ice-free season have led to conclusions that there has been increased net primary production for both the southern and northern regions (Arrigo et al., 2008, 2014; Pabi et al., 2008; Arrigo and van Dijken, 2015). However, seasonal field measurements in the SE Chukchi Sea during the ice-free, late season period, also provide evidence for a substantial decrease in recent primary production compared to earlier estimates in the 1980s (Lee et al., 2013), similar to findings in the northern Bering Sea. Notably a large part of the northern Chukchi Sea was previously ice-covered such that satellite observations were not possible, thus no ocean color and by extension, no biological activity were measured, although under ice-algal production could have been ongoing. Now that a large part of the northern Chukchi Sea is currently ice free in the spring and summer due to extensive ice retreat (Fig. 3), ocean color can be detected and thus some biological activity can be seen increasing in the region. Our findings indicate that the impacts of seasonal sea ice retreat on productivity remain equivocal depending on seasonal and regional sampling and the scale of evaluation.

A challenge to our synthesis effort was the variety of methodological approaches used to estimate productivity within the different bounding boxes (Supplement A). Also, uncertainties associated with each method are complex. *In situ* methods likely suffer from incubation artifacts but satellite imagery can also misidentify ocean color pigments related to runoff or colored dissolved organic matter as apparent surface production (Codispoti et al., 2013). Although we provide a summary synthesis of the seasonally varying primary production results for comparison at the four hot spot areas (Table 5), our analysis and hence conclusions are hampered in part by the differences in methodological approaches (Pabi et al., 2008; Lee et al., 2012, 2013; Yun et al., in press).

Seasonality is obviously critical to consider when evaluating pelagic production. Although we identify some seasonal patterns at the broad scale (Table 5), we are also cautious in extrapolating to annual production. For example, different seasonal patterns in mean daily carbon uptake rates (based on a 15-h photoperiod per day; Lee et al., 2007) were observed in the SLIP and SECS hotspots during 2007–2011. The mean daily carbon uptake rates in the SLIP hotspot were highest in May (1.2 mg C m^{-2} d^{-1}), and dropped by June (0.4 mg C m^{-2} d^{-1}) and July (0.2 ± mg C m^{-2} d^{-1}) (see Table 5 for citations). The maximum mean primary production estimated in May for the SLIP was also confirmed by Brown and Arrigo (2013) through satellite-derived estimates, with the actual timing of the peak of the bloom varying on the scale of weeks (within the month of May) depending on sea ice retreat timing each year. By comparison, the mean daily carbon uptake rates for the SECS hotspot for the June and July 2010–2011 period were an order of magnitude higher in June (12.9 mg C m^{-2} d^{-1}; Arrigo, unpubl. data) than in SLIP (Lee et al., 2012), declining in early August (1.6 mg C m^{-2} d^{-1}; Lee et al., 2013) and then decreased further toward late September (0.4 mg C m^{-2} d^{-1}, Lee et al., 2013; Table 5). Similar primary production maxima were observed from satellite platforms in late May to mid-June (http://neptune.gsfc.nasa.gov/csb/index.php?section=270) as the *in situ* measurements in the SECS, while lower *in situ* production measurements were observed late in the season (August–September; Lee et al., 2007, 2012). Notably, by mid-summer in the southern Chukchi Sea most production occurs at the deep subsurface chlorophyll maximum layer (Codispoti et al., 2013). Since satellite-derived estimates can miss this ongoing production it is complex to quantify seasonal primary production rates, although estimates of the magnitude of the error are relatively small for the area when evaluated over an annual cycle (Arrigo et al., 2011).

In the NECS hotspot, the daily carbon-uptake rate was low in May–June (~0.8 mg C m^{-2} $d^{-1;}$ Table 5; Lee et al., 2013) as well as in July and August (0.7 mg C m^{-2} d^{-1} in 2002–2004, Hill et al., 2005), similar to findings by Arrigo in July 2010 and 2011 (Table 5, Arrigo, unpubl. data). Notably, the highest carbon update value was observed in Barrow Canyon in spring (Hill et al., 2005; 8 mg C m^{-2} d^{-1}). The limited available data from Lee et al. (2012) and Arrigo et al. (2014 and unpubl. data) mean that it is not possible to characterize the seasonal variability in this hotspot in recent years. Notably Frey et al. (2015) used satellite observations to observe chl *a* concentrations and reported very high values near Point Barrow during June, and in the western Bering Strait during the June–August period, which is consistent with expectations of high nutrient upwelling. It is clear that there is a need for combined satellite and field data sampling throughout the open-water season to evaluate annual integrated chl *a* biomass and daily to annual primary production estimates and to reconcile the somewhat contradictory conclusions derived by the relatively limited available data and different methodologies used.

3.2.2. Sea ice algae and water column chl a

Sea ice algal blooms provide important early pulses of food to sympagic, pelagic and benthic food webs in Arctic systems (Sun et al., 2007; Søreide et al., 2010), although ice algal primary production typically contributes <10% of total annual algal production on Arctic shelves (e.g. Gradinger, 2009; Matrai and Apollonio,

Table 5
Net primary production measurements (mean ± standard deviation) for the four benthic hotspot regions in the northern Being and Chukchi Seas from March–September from 2002 to 2012. Key: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and the NECS (Northeast Chukchi Sea) hotspot; BC = Barrow Canyon; n.d. = no data; ± = standard deviation, number of samples in parentheses and range of values in brackets; * = NECS with BC data and ** = NECS without BC data. Bold print indicates maximum values. Data source: see citations in the table. ICESCAPE = Impacts of Climate on the Eco-Systems and Chemistry of the Arctic Pacific Environment project. Note for Lee et al. daily uptake rate = hourly uptake rate × 15 h day^{-1}.

Hotspot region	Date (Month, Year)	Mean net daily carbon uptake (mg C m^{-2} d^{-1})	Data source
SLIP	May 2007	**1.22 ± 0.77** (7)	Lee et al. (2012)
	June 2007	0.39 ± 0.33 (5)	Lee et al. (2012)
	July 2007	0.17 ± 0.10 (2)	Lee et al. (2012)
Chirikov	May 2007	**0.78 ± 0.34** (5)	Lee et al. (2012)
SECS	June 2010 and 2011	**12.90 ± 4.6** (2)	Arrigo ICESCAPE unpubl. data
	Early August 2007 and 2008	1.61 ± 1.11 (4)	Lee et al. (2013)
	mid-August 2004	0.74 ± 0.74 (4)	Lee et al. (2007)
	Early September 2012	0.72 ± 0.67 (5)	Lee et al. (2013)
	Late September 2009	0.40 ± 0.29 (7)	Lee et al. (2013)
NECS	May–June 2002 and 2004**	**0.78 ± (n.d.)**	Hill et al. (2005)
	July–August 2002 and 2004**	0.67 ± 0.08 (2)	Hill et al. (2005)
	July 2010 and 2011*	0.67 ± 0.08 (2)	Arrigo ICESCAPE unpubl. data
	August 2008**	0.31 ± 0.39 (5)	Lee et al. (2013)

2013). The seasonality of ice algal bloom and bloom composition are largely controlled by ice thickness, snow depth and under-ice surface water nutrient availability (e.g. Gradinger, 2009; Mundy et al., 2005, 2007).

The standing stock of ice algae was much higher in the thin sea ice of the SLIP hotspot than in the thicker ice of the NECS hotspot, although 2–3-fold less than annual mean integrated water column chl *a* values (Table 6). No sea ice cores and sea ice algal data are available from the Chirikov or SECS hotspots. Note that the mean integrated water column chl *a* values found in the four benthic hotspot regions are a composite of all sampling made over different seasons in that bounding box, so they do not conclusively show a latitudinal trend due to variability in temporal sampling (Table 6; Grebmeier and Cooper, 2014g).

3.2.3. Pelagic–benthic coupling

Cold water temperatures limit zooplankton growth during winter and spring in the Pacific Arctic, thus minimizing the overall capability of zooplankton to graze sedimenting particulate carbon early in the growing season (Coyle and Pinchuk, 2002). Low rates of early season grazing increase the amount of organic carbon that settles to the benthos (thus increased net carbon export) to support infaunal communities at the high benthic biomass hotspots (Grebmeier et al., 2006b; Grebmeier, 2012). The phenology and magnitude of primary production (Section 3.2.2), along with reduced grazing pressure early in the season, results in a proportionally higher export of organic carbon to shallow shelf sediments within the hotspots. In addition, the subsequent northward lateral advection of part of that carbon has a direct impact on the amount of organic carbon accumulating in the sediments to support extensive benthic macrofaunal communities (Grebmeier, 2012; Blanchard and Feder, 2014; Mathis et al., 2014). These factors contribute substantially to carbon recycling in the region. For surface sediment chl *a* and sediment SCOC results in this section we used data collected over the 2000–2012 period at the same sites as for other benthic parameters (Table 2; Grebmeier and Cooper, 2014c,d; Supplement A and Table A1).

An increasing level of export production, inferred from both the surface sediment chl *a* inventories and mean SCOC, both considered indicators of carbon supply to the benthos, is observed from the SLIP to the SECS hotspots (Table 2). There was an ~1.5-fold increase in sediment chl *a* concentrations and an ~2-fold increase in SCOC moving from the SLIP to the SECS hotspots (Table 2). By comparison, the values of both these parameters were similar between the NECS hotspot and the SLIP hotspot, which have similar cold BW temperatures (Table 3). The lower values of mean sediment chl *a* and SCOC at the NECS hotspot may be related to the known heterogeneous nature of the NE Chukchi Sea system (Blanchard et al., 2013a; Day et al., 2013). Another reason for this decline in carbon export to the benthos in the NECS may be that production farther south reduces the available productive capacity of the advective system, as reflected in the declining mean BW nitrate concentrations from south to north (Table 4).

3.2.4. Major similarities and differences in the four hotspots: primary production, sea ice algae, and pelagic–benthic coupling

The timing of sea ice retreat influences the seasonality of primary production across the four benthic hotspots. Mean daily primary production rates are highest in May in the SLIP and Chirikov benthic hotspot regions, then in June in the SECS hotspot, and variable from May–August at the northernmost hotspot in the NECS. Overall production values are highest in the SECS hotspot, with lower to medium values in the SLIP, Chirikov and NECS hotspots.

Sea ice algae, although the source of an important early season carbon pulse to the benthic system, provides a magnitude less algal biomass to the system than the mean integrated chl *a* standing stock during the open water season. Ice algal chl *a* was much higher in the thin sea ice of the SLIP hotspot than in the thicker ice of the NECS hotspot, but there are no sea ice cores from the Chirikov or SECS hotspots for comparisons. The mean integrated water column chl *a* values collected in the four benthic hotspot regions do not conclusively show a latitudinal trend in chlorophyll standing stock due to variability in temporal sampling, although the Chirikov hotspot had the highest mean integrated chl *a* for the four hotspot sites.

An increasing level of pelagic–benthic coupling, inferred from mean sediment chl *a* content and SCOC, was observed from the SLIP to the SECS hotspots, thus showing a strong latitudinal trend. By comparison, sediment chl *a* and SCOC were similar between the SLIP and NECS hotspots. The northward advection of organic carbon from the SLIP to the SECS hotspots, and likely northward to the more heterogenous NECS hotspot, demonstrates high connectivity among downstream benthic systems.

3.3. Benthic macrofauna, epifaunal invertebrates and demersal fish

3.3.1. Benthic macrofauna

Marine soft bottom macrofaunal communities are considered to be good indicators of long-term environmental conditions because they are composed of relatively immobile organisms that can be sampled quantitatively, and these organisms often have life spans from years to decades (Warwick, 1993). These characteristics also make benthic macrofaunal communities a useful tool for monitoring environmental variability of both natural and anthropogenic origin, especially in the context of climate change (Blanchard et al., 2010; Cloern et al., 2010; Grebmeier et al., 2010; Iken et al., 2013). With enhanced pelagic–benthic coupling in regions of the northern Bering and Chukchi Seas (Grebmeier and McRoy,

Table 6
Sea ice thickness, algal production, and integrated chlorophyll *a* (chl *a*) content (mean ± standard deviation; bold print indicates maximum values) for the four benthic hotspots in the northern Bering and Chukchi Seas from March–September 2004–2010. For comparative purposes the integrated water column chl *a* (mean ± standard deviation in bold) for the period 2000–2012 are included. Key: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and NECS (Northeast Chukchi Sea) hotspot; sample number in parentheses with range of values in brackets; ∗ = including Barrow Canyon for sea ice data only; n.d. = no data. Data source: Sea ice thickness and sea ice products and chl *a* content from Gradinger (2009) and unpubl. data; integrated water column chl *a* from Grebmeier and Cooper (2014g).

Hotspot region	Date (month/year) for sea ice data only	Mean sea ice thickness (cm)	Sea ice algal production (spring only) (g C m^{-2})	Mean integrated chlorophyll *a* in sea ice (mg m^{-2})	Mean integrated water column chlorophyll *a* for 2000–2012 (mg m^{-2}); [month; range]
SLIP	March–April 2008–2010	58.40 ± 23.34	n.d.	**10.50 ± 9.94**	**176.51 ± 212.04** (198) [March–July; range: 2.58–833.51]
Chirikov	2007	–	–	–	**286.49 ± 344.86** (143) [May–August; range: 1.69–1217.79]
SECS	–	–	–	–	**147.42 ± 187.82** (109) [July–September; range: 1.04–1133.94]
NECS*	May–June 2004	**134.61 ± 78.86**	2.0	0.55 ± 0.83	**130.36±172.56** (159) [July–September]; range: 3.20–1120.63]

1989; Grebmeier and Barry, 1991; Ambrose and Renaud, 1995; Piepenburg, 2005; Grebmeier et al., 2006a; Grebmeier, 2012; Mathis et al., 2014), benthic macrofaunal communities can locally achieve large biomass (Grebmeier et al., 2006a; Feder et al., 2007; Grebmeier, 2012). Thus, benthic macrofauna of the northern shallow seas in the Pacific Arctic region can be important prey items for seabirds and marine mammals (Lovvorn et al., 2003, 2014; Moore et al., 2003, 2014; Grebmeier et al., 2006a; Grebmeier, 2012; Hunt et al., 2013; Schonberg et al., 2014), and these benthic communities also contribute to carbon cycling and remineralization potential (Clough et al., 2005; Renaud et al., 2007; Mathis et al., 2014).

Macrofaunal data for this synthesis were summarized from cruises conducted from 2000 to 2012 and are listed in Supplement A, Table A1 and data are available (Grebmeier and Cooper, 2014a,h). Benthic populations usually were sampled with 3–4 replicates (<5% had 2 replicates) of either a single 0.1 m^2 van Veen grab (e.g., Grebmeier et al., 1988, 2006a,b) or double 0.1 m^2 van Veen grab (e.g., Blanchard et al., 2013a); the generated data include dominant macrofaunal composition, abundance and biomass. The biomass data are summarized both as formalin-preserved wet weight (gross wet weight) and as carbon dry weight (g C m^{-2}); the latter values were obtained with carbon conversion values determined by Stoker (1978, 1981) and also used by Grebmeier et al. (1989).

There is a northward latitudinal increase in mean benthic biomass at the three southern hotspots (Table 7, Fig. 2) that coincides with increasing export production inferred from sediment chl *a* and SCOC discussed previously (Table 2). Mean benthic macrofaunal biomass at the hotspots in the 2000–2012 period increased south to north from 16 g C m^{-2} at the SLIP hotspot to 23 g C m^{-2} in the Chirikov hotspot and up to 32 g C m^{-2} in the SECS hotspot (Table 7). By comparison, mean macrofaunal biomass decreased to 13 g C m^{-2} in the NECS hotspot. Note that there is a sub-region of upper Barrow Canyon that also has a locally high benthic biomass (Fig. 2).

Bivalves, polychaetes, crustaceans (primarily amphipods), and sipunculids dominate in the four benthic hotspots in differing proportions (Table 8, Fig. 5). Macrofaunal community composition, on large scales, corresponds to sediment grain size heterogeneity and food supply (as evident in TOC and sediment chl *a*) that both respond to hydrographic forcing described above. Both the SLIP and SECS hotspots have fine-grained, silty and clayey sediments with high organic content that are dominated by bivalves and polychaetes, although the SECS has the higher biomass of the two hotspots (Table 7). The macrobenthic community of the Chirikov hotspot, also under the influence of Anadyr water mixing with Bering Shelf water, occurs in sandy-mud sediments, and are dominated (by biomass) by amphipods that are a major prey source for gray whales, along with bivalves that are main prey taxa for walruses (Table 8, Fig. 5; see Sheffield and Grebmeier, 2009). In the offshore NECS hotspot, bivalves, polychaetes and sipunculids dominate the benthic macrofaunal biomass within a heterogenous array of sediment types under less productive water, with amphipods becoming more prevalent (by biomass) closer to shore off Alaska (Table 8, Fig. 5; Feder et al., 1994; Grebmeier et al., 2006a; Blanchard et al., 2013a; Schonberg et al., 2014).

3.3.2. Epifaunal invertebrates and demersal fish

Epibenthic communities contribute to organic carbon cycling and remineralization and – for mobile taxa – carbon redistribution (Ambrose et al., 2001), are prey for benthivorous marine mammals, and are long-term integrators of climatic conditions (Ambrose

Table 7
Benthic macrofaunal abundance and biomass (mean ± standard deviation in bold type) in the four hotspot regions in the northern Bering and Chukchi Seas from March–September 2000–2012 period. Key: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and NECS (Northeast Chukchi Sea) hotspot; number of samples in parentheses and range of values in brackets; gww = gram wet weight, gC = grams carbon dry weight. Data source: Grebmeier and Cooper (2014a, 2014h).

Hotspot region	Months	Abundance (individuals m^{-2})	Biomass (gww m^{-2})	Biomass (gC m^{-2})
SLIP	March–July	**3061 ± 1559** (173) [1,168–12,050]	**441.45 ± 231.56** (173) [45.50–1372.91]	**15.82 ± 7.32** (173) [1.79–42.74]
Chirikov	May–August	**6941 ± 5769** (74) [328–26,613]	**553.42 ± 344.63** (74) [38.68–1751.59]	**23.42 ± 14.89** (74) [1.91–106.09]
SECS	July–September	**7159 ± 5268** (104) [470–28,053]	**887.08 ± 778.04** (104) [106.06–5271.47]	**31.67 ± 26.30** (104) [5.05–186.67]
NECS	May–September	**2717 ± 2706** (290) [180–15,337]	**332.54 ± 190.04** (290) [1.06–1300.65]	**13.24 ± 6.64** (290) [0.04–41.60]

Table 8
Summary of dominant infaunal, epifaunal, and fish taxa, by biomass, along with the most species rich faunal type for each taxa group. Key: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and NECS (Northeast Chukchi Sea) hotspot. Data source: Data citations in Supplement Tables A1 and A2, with data available in Bluhm (2014a; Bluhm, 2014b) and Grebmeier and Cooper (2014h).

Hotspot region	Dominant infaunal taxa by biomass	Dominant epifaunal taxa by biomass	Dominant fish taxa by biomass	Most species rich infauna	Most species rich epifauna	Most species rich fish
SLIP	*Ennucula tenuis*, *Nuculuna radiata*, *Macoma calcarea*, *Nephtys caeca*, *Maldane sarsi*	*Ophiura sarsii*, Urochordata, *Chionoecetes opilio*	Liparidae, *Hippoglossoides robustus*, Stichaeidae, *Boreogadus saida*	Bivalves, polychaetes	Gastropods, decapods	flounders, cods
Chirikov	*Ampelisca macrocephala*, *Astarte borealis*, *Macoma calcarea*, *Ampharete* sp.	*Chionoecetes opilio*, Urochordata, Cnidaria	*Myoxocephalus scorpius*, *Lumpenus fabricii*, *Eleginus gracilis*	Amphipods, bivalves, polychaetes	Gastropods, decapods	Sculpins, cods
SECS	*Macoma calcarea*, *M. moesta*, *Ennucula tenuis*, *Nephtys caeca*, *Pontoporeia femorata*	*Chionoecectes opilio*, *Cryptonatica affinis*, *Leptasterias* spp.	*Lumpenus fabricii*, *Gymnocanthus tricuspis*, *Hippoglossoides robustus*, *Myoxocephalus scorpius*, *Boreogadus saida*	Bivalves, polychaetes, amphipods	Gastropods, crustaceans, echinoderms	Sculpins, eelpouts, flatfishes, prickle backs
NECS	*Macoma calcarea*, *Ennucula tenuis*, *Maldane glebifex*, *Golfingia margaritacea*	*Ophiura sarsii*, *Ocnus* sp., *Chionoecectes opilio*	*Boreogadus saida*, *Anisarchus medius*	Bivalves, polychaetes, sipunculids	Gastropods, crustaceans	Sculpins, eelpouts, prickle backs

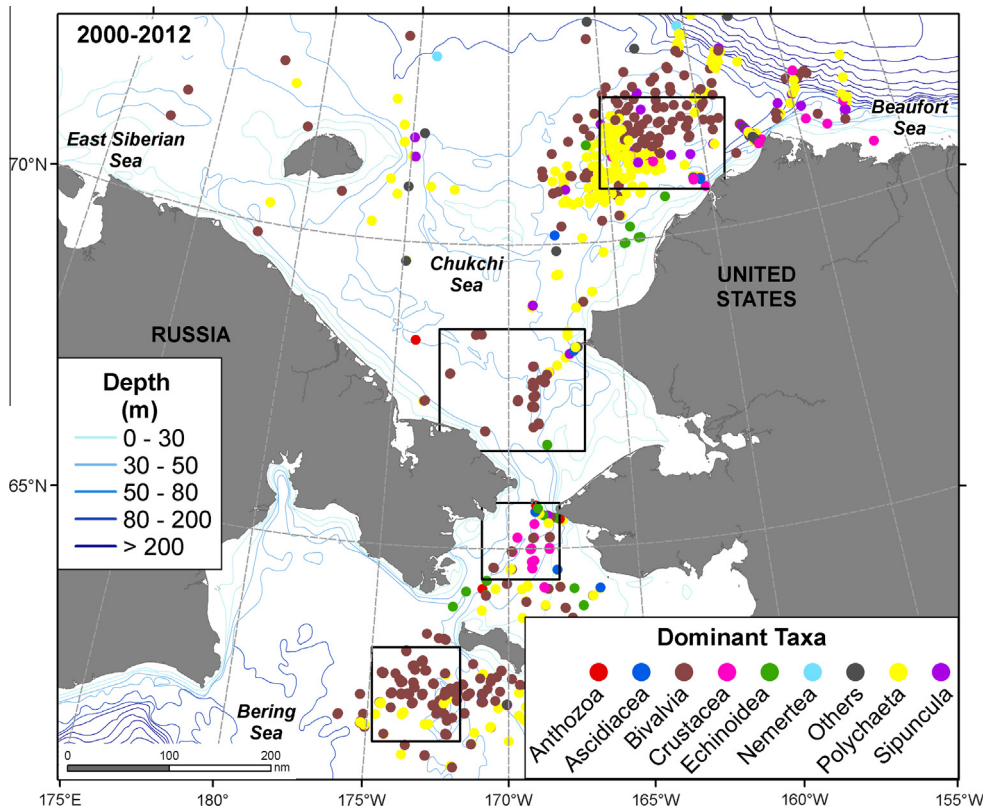

Fig. 5. Distribution of dominant macroinfauna taxa (by g C m^{-2} biomass) for benthic stations in the Pacific Arctic region during the 2000–2012 period. Black boxes are the location of the four benthic biomass bounding boxes from south to north used in our study: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and NECS (Northeast Chukchi Sea) hotspot. Data source: Grebmeier and Cooper (2014h).

et al., 2012). Epibenthic communities in the Pacific Arctic are typically dominated by echinoderms, crustaceans, and mollusks in varying proportions and their patchy biomass distribution result from a combination of hydrographic and substrate properties, food availability and quality, as well as trophic and other interactions (Bluhm et al., 2009; Iken et al., 2010; Ravelo et al., 2014; Konar et al., 2014). Fishes in these seafloor communities are dominated by small cods, sculpins, pricklebacks, flatfishes and eelpouts (Norcross et al., 2013). The numerically dominant Arctic cod occurs in all realms (Table 8; Gradinger and Bluhm, 2004; Logerwell et al., 2011; Hop and Gjøsaeter, 2013) and provides energy-rich prey for sea birds, seals, and whales (Whitehouse et al., 2014). Fish assemblages in the Pacific Arctic are structured primarily by hydrographic properties, water depth and sediment type (Cui et al., 2009; Norcross et al., 2010, 2013). Recently northward range shifts of some fish and epifaunal species and communities have been documented (Sirenko and Gagaev, 2007; Mueter and Litzow, 2008; Hollowed et al., 2013).

The abundance, biomass and species richness of both epifauna and demersal fish were estimated from area trawled (= net swath times distance towed) and standing stock was normalized to a standard area (see Supplement A for further details). Data included here were sampled during surveys conducted between 2004 and 2012; Supplement A and Table A2). Note that pelagic fishes were not included. Compositional dominant taxa were identified as those contributing the most to wet weight biomass in each benthic hotspot. Comparisons of epibenthic and fish communities among the four hotspots are somewhat biased by different trawl mesh sizes and trawl durations.

There is a clear pattern of higher epibenthic biomass than demersal fish biomass in all four hotspots (Tables 9 and 10, respectively), in contrast to the sub-Arctic southeastern Bering Sea and the Barents Sea where fish biomass dominates (Stevenson and Lauth, 2012; Hunt et al., 2013). Epibenthic biomass is higher and mean fish biomass lower at the SLIP hotspot that is characterized by very cold mean bottom waters compared to the warmer Chirikov hotspot (Table 3). Moving northward, the mean epibenthic biomass is higher in both the SECS and NECS hotspots compared to the two more southern SLIP and Chirikov hotspots; however, this difference is at least partly driven by the smaller trawl mesh size used in the SECS and NECS hotspot studies.

Demersal fish abundance and biomass are very low (although possibly gear-biased) in the consistently very cold SLIP hotspot, intermediate in the Chirikov hotspot, and highest in the SECS

Table 9
Epifaunal biomass (mean ± standard deviation in bold type), and the type of gear used for the sampling from May–September 2000–2012. Key: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and NECS (Northeast Chukchi Sea) hotspot; OT = Otter trawl, PSBT = plumb staff beam trawl, gww = gram wet weight. Number of samples in parentheses and range of values in brackets. *Results from two independent data sets presented for NECS. Data source: Supplement Table A2; Bluhm 2014a; Bluhm 2014b.

Hotspot region	Collection date 2000–2012	Epifaunal biomass (gww 1000 m^{-2})	Gear used (mesh size)
SLIP	May–June 2006, 2007	**27,200 ± 19,840** (17) [17,100–61,100]	OT, PSBT 19 mm (4 cod end)
Chirikov	May–June 2006, 2007	**2690 ± 2020** (10) [480–7220]	OT, PSBT 19 mm (4 cod end)
SECS	July–September 2004–2012	**65,475 ± 61,968** (21) [4077–217,023]	PSBT 7 mm (4 cod end)
NECS	July–August 2009, 2010 (2008–2010)	**86,000 ± 128,000** (31) [1000–644,000] (43,110 ± 56,218, n = 84)*	PSBT 7 mm (4 cod end)

Table 10
Fish abundance, biomass and species richness (mean ± standard deviation in bold type), along with gear and mesh size and citation/sources for the data. Sample size is in parentheses and range in brackets. *Note different mesh size: (19 mm) for beam trawl (BT) versus 7 mm for Plumb-staff beam trawl (PSBT) in other samples. Key: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and NECS (Northeast Chukchi Sea) hotspot. Data source: Citations for data provided in the table.

Hotspot region	Months	Demersal fish			Gear and mesh size	Citations
		Abundance (ind 1000 m^{-2})	Biomass (gww 1000 m^{-2})	Mean species richness		
SLIP*	May–June 2007	**5 ± 4** (28) [0–19]	**86 ± 90** (28) [0–333]	**2.7 ± 1.3** (28) [1–6]	BT: 19 mm stretch mesh (4 cod end)	Cui et al. (2009, 2012)
Chirikov*	May–September 2007	**5 ± 5** (9) [1–13]	**876 ± 1549** (9) [6–4767]	**1.7 ± 1.0** (9) [1–4]	BT: 19 mm (4 cod end)	Cui et al. (2009, 2012)
Chirikov	July–September 2004–2012	**235 ± 371** (6) [49–980]	**2185 ± 1964** (6) [88–4703]	**10.8 ± 3.8** (6) [8–18]	PSBT: 7 mm (4 cod end)	Norcross et al. (2010, 2013a); Holladay et al. (unpublished data)
SECS	July–September 2004–2012	**545 ± 554** (19) [62–1847	**3667 ± 4265** (19) [286–19,787]	**9.6 ± 3.9** 19) [5–21]	PSBT: 7 mm (4 cod end)	Norcross et al. (2010, 2013a); Holladay et al. (unpublished data)
NECS	July–August 2009–2010	**161 ± 161** (54) [8–812]	**446 ± 466** (54) [28–2365]	**7.5 ± 3.1** (54) [1–15]	PSBT: 7 mm (4 cod end)	Norcross et al. (2013); Norcross and Holladay (unpublished data)

hotspot where abundance was 3-fold and biomass 8-fold higher than in the NECS hotspot. The mean number of fish species per site decreases from the Chirikov to NECS hotspot (no comparable data are available in the SLIP area) (Table 10). These findings confirm earlier conclusions that low fish densities may be limited by very cold bottom temperatures (Hollowed et al., 2013), and that their low densities may remove predation pressure from epifaunal invertebrates (Feder et al., 2006).

Snow crabs and echinoderms dominate epifaunal biomass in virtually all hotspots. In addition, urochordates are common in the SLIP, along with cnidarians in the Chirikov hotspot, while moon snails dominate in the SECS hotspot (Bluhm et al., 2009; Table 8). Crabs and moon snails take advantage of the abundant bivalve and polychaete populations in the SECS hotspot (Table 8), based on the high occurrence of these prey in crab stomach contents from that region (Divine et al., pers. comm.) and the high occurrence of moon snail drill holes in the dominant tellinid bivalves in the region (Grebmeier, Bluhm, and Iken, pers. obs.). Gastropods contribute greatly to species richness in addition to crustaceans and echinoderms across the northern Bering and Chukchi Seas (Feder et al., 2006; Grebmeier et al., 2006a; Bluhm et al., 2009; Blanchard et al., 2013b; Ravelo et al., 2014). As for infauna, the variability of epibenthic community composition and diversity is a result of sediment grain size heterogeneity across the region, including some rocky substrate nearshore, or current flow (Bluhm et al., 2009; Ravelo et al., 2014).

Relationships of epifaunal biomass patterns to production regimes are less clear than for infauna, which is likely related to higher mobility of some taxa and interannual population changes in biomass-dominant snow crabs in the region (Bluhm, Iken, and Serratos, unpublished data). Arctic cod were biomass-dominant across all four hotspots but were most common in the NECS hotspot (Norcross et al., 2013; Table 8). Bering flounder was particularly common in the SLIP and SECS hotspots whereas sculpins were most abundant in the Chirikov and SECS hotspots (Cui et al., 2009; Norcross et al., 2010).

3.3.3. Major similarities and differences in the four hotspots: benthic macrofauna, epifaunal invertebrates and fish

There is a northward latitudinal increase in mean benthic macrofaunal biomass at the three southern hotspot regions. Notably the mean benthic biomass in the NECS hotspot was lower and more similar to that observed at the SLIP hotspot. Bivalves, polychaetes, amphipods, and sipunculids dominate in the four benthic hotspots in differing proportions that are influenced by advective processes that result in variable levels of sediment heterogeneity and food supply to the benthos. Dominant taxa, by biomass, within the hotspots include bivalves and polychaetes (SLIP and SECS), amphipods and bivalves (Chirikov), and bivalves, polychaetes and sipunculids (NECS).

There is a clear pattern of higher epibenthic biomass than demersal fish biomass in all four hotspots in contrast to the southeastern Bering Sea and Barents Sea where fish biomass dominates (Stevenson and Lauth, 2012; Hunt et al., 2013). The mean epibenthic biomass is higher in both the SECS and NECS hotspots in the Chukchi Sea compared to the two more southern SLIP and Chirikov hotspots in the northern Bering Sea. Snow crabs and echinoderms dominate epifaunal biomass in virtually all hotspots. Mean demersal fish abundance and biomass is very low in the consistently very cold SLIP hotspot, intermediate in the Chirikov hotspot, and highest in the SECS hotspot where abundance was 3-fold and biomass 8-fold higher than in the NECS. The mean number of fish species per site decreases from the Chirikov to NECS hotspots.

3.4. Upper trophic level seabirds and marine mammal benthivores

The Pacific Arctic is noted for large populations of resident and migratory populations of seabirds and marine mammals (CAFF, 2013), including benthic feeding or benthivorous species that are relevant to this synthesis. In the SLIP hotspot, spectacled eiders, walruses, and bearded seals are dominant benthivores, and collectively feed primarily on bivalves, polychaetes, epibenthic gastropods and crabs (Richman and Lovvorn, 2003; Jay et al., 2014; Lovvorn et al., 2014, 2015a; Moore et al., 2014), mostly during the winter and early spring when sea ice is present. In the Chirikov hotspot, gray whales historically have been the primary consumers of benthic infauna, primarily ampeliscid amphipods in the summer; however, there are indications that use of that area by gray whale may have declined between the 1980s and 2012 (Moore et al., 2003, 2014). Gray whales consistently use the SECS hotspot throughout the summer, and sightings during July appear to have increased over the last 30 years (Highsmith et al., 2006; Bluhm et al., 2007; Moore et al., 2003, 2014). In the NECS hotspot, gray whales are reliably seen from June to October shoreward of Barrow Canyon, whereas areas of aggregation offshore have changed over the last 30 years. Acoustic recordings now suggest that gray whales occur year-round in the NE Chukchi Sea (Stafford et al., 2007) where there are locally high benthic amphipod populations (Schonberg et al., 2014). Walruses radio-tagged predominantly in U.S. waters concentrated their foraging in summer in the NECS hotspot and in fall in the SE Chukchi Sea hotspot (Jay et al., 2012).

3.4.1. Benthivorous seabirds

The primary seabird group that forages on benthic marine organisms are sea ducks (Anseriformes: Anatidae, tribes

Aythyinae and Merginae). Globally, in some locations, sea ducks constitute a large portion of at-sea marine bird communities (e.g., Forsell and Gould, 1981; DeGange and Sanger, 1986; Savard, 1989; Vermeer and Morgan, 1992; Vermeer et al., 1992), where they can consume substantial quantities of benthic organisms (e.g., Lewis et al., 2008) and even affect the structure of benthic assemblages (Lacroix, 2001; Lewis et al., 2007). Within the Pacific Arctic, from December to April several hundred thousand spectacled eiders – virtually the entire world's population of the species – congregate in the St. Lawrence Island Polynya, primarily within the SLIP hotspot, but also in other areas south of there depending on ice conditions (Petersen et al., 1999; Lovvorn et al., 2009; Cooper et al., 2013). This single-species assemblage underscores the importance of the benthic biota to overwintering sea ducks in the SLIP. Interdisciplinary studies in the northern Bering Sea found that sea ice distribution, tied to winds and hydrographic conditions, sometimes limits the capability of spectacled eiders to access the best foraging areas south of St. Lawrence Island (Cooper et al., 2013; Lovvorn et al., 2009, 2014). Studies since the 1970s indicate decadal variations in bivalve prey for these diving sea ducks relative to overall macrobenthic biomass within the SLIP hotspot (Grebmeier, 2012; Grebmeier et al., 2006b; Lovvorn et al., 2009, 2014).

Seabird observations were synthesized from oceanographic cruises in the northern Bering Sea and Chukchi Seas from March through October over the years 2006–2012. Early season cruises sampled southern portions of the Pacific Arctic with cruises moving farther north in August–October, as the sea ice retreated. We binned all transects into 3-km segments to calculate the at-sea density (birds km^{-2}) of each species, focusing on benthivorous sea duck species. For this synthesis, we only used sea ducks on the water (assumed to be directly associated with the immediate area and possibly feeding) and separated out sea ducks in the air (presumably passing through the area but not feeding), and analyzed data only for those birds on the water. We estimated densities within each hotspot study area by averaging the densities of all 3-km segments within each hotspot. In March 2010, spectacled eiders were also counted in photographs taken during an aerial

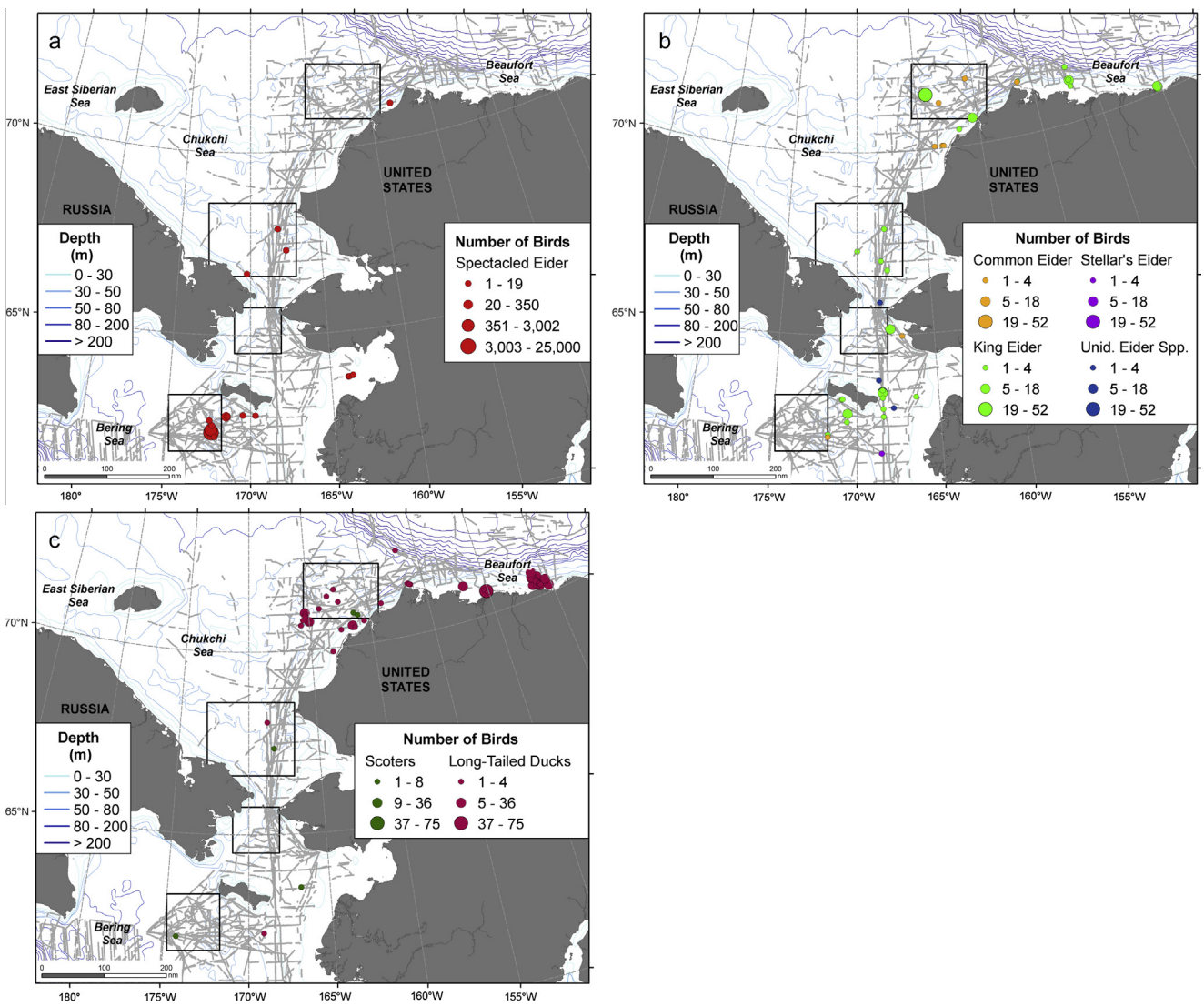

Fig. 6. Distribution of the sea ducks (number of birds per 3-km segment) that were on transect (on water or ice) during USFWS and ABR seabird surveys from 2006 to 2012, including (a) Spectacled Eiders, (b) Other eiders (Common Eiders, Steller's Eider, King Eider, and Unidentified Eider Species (Unid. Eider Spp.), and (c) Scoters and Long-tailed Ducks. Gray lines indicate survey effort. Circle size denotes relative abundance, with different scales among species. Black boxes are the location of the four benthic biomass bounding boxes from south to north used in our study: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, and NECS (Northeast Chukchi Sea) hotspot. Data source: U.S. Fish and Wildlife Service (USFWS, K.J. Kuletz) and ABR, Inc.—Environmental Research & Services (R.H. Day, A.E. Gall, and T.C. Morgan).

survey from a fixed-wing plane in March 2010 (Lovvorn et al., 2014). Further details are provided in Supplement A, Section 3.4.1.

Eiders appear to use only one of the four benthic hotspots in substantial numbers (Fig. 6a–c), with an estimated 370,000 birds counted in the SLIP region in March 2010 (Lovvorn et al., 2014). By comparison, use of the Chirikov, SECS, and NECS hotspots by sea ducks is minimal, based on the lack of birds on the water. Although sea ducks do not use the NECS hotspot, the nearshore zone (10–30 m depth) of the NE Chukchi Sea is very important to these birds during spring migration (Oppel et al., 2009; Lovvorn et al., 2015b), with over a half million sea ducks migrating through and staging there during late April and May (Quakenbush et al., 2009; Stehn et al., 2013).

The total mean density for sea ducks was highest in the SLIP hotspot (17.37 birds km^{-2}; data estimated from Lovvorn et al., 2014), followed in decreasing order by the Chirikov hotspot (~0.18 birds km^{-2}), the SECS hotspot (~0.11 birds km^{-2}), and the NECS hotspot (~0.09 birds km^{-2}; Table 11). Outside of the SLIP hotspot, the mean density of individual sea duck species on the water or ice for the other three hotspots never exceeded 0.08 birds km^{-2} (Table 11). The highest densities on individual 3-km segments were common eiders in the Chirikov hotspot, long-tailed ducks and spectacled eiders in the SECS hotspot, and long-tailed ducks and common and king eiders in the NECS hotspot (Fig. 6, Table 11). Thus, with the exception of the overwintering aggregation within the SLIP hotspot, seabird benthivores account for <1% of total marine birds recorded on mostly offshore transects in the study area during the open-water season (Kuletz, Day, Gall, and Morgan, unpubl. data).

Table 11
Benthic-foraging seabirds in the northern Bering and Chukchi Sea hotspot regions (excluding the St. Lawrence Island Polynya (SLIP) hotspot region) seen only on the water (i.e., flying birds removed from analysis). Mean, SD = standard deviation, and maximal densities (birds km^{-2}; corrected for detectability). Key: Chirikov (Chirikov Basin), SECS (Southeast Chukchi Sea), and NECS (Northeast Chukchi Sea) hotspots; BC = Barrow Canyon. Data source: U.S. Fish and Wildlife Service (K.J. Kuletz) and ABR, Inc.—Environmental Research & Services (R.H. Day, A.E. Gall, and T.C. Morgan). Seabirds in SLIP were sampled in spring and assessed from photographs, with the results only presented in the text of this paper.

Hotspot region	Seabird densities (number birds km^{-2})			Sampled area (km^2)
	Mean	SD	Maximum	
Chirikov				
Long-tailed Duck	0	0	0	563
Steller's Eider	0	0	0	563
Common Eider	0.07	1.28	25.04	563
King Eider	0.01	0.13	3.43	563
Spectacled Eider	0	0	0	563
Unidentified eider	0.08	1.42	30.32	563
White-winged Scoter	0.01	0.34	9.10	563
Surf Scoter	0	0	0	563
Black Scoter	0	0	0	563
Unidentified scoter	0.01	0.12	3.37	563
SECS				
Long-tailed Duck	0.04	0.67	17.01	945
Steller's Eider	0	0	0	945
Common Eider	0.02	0.41	9.07	945
King Eider	0.02	0.30	8.68	945
Spectacled Eider	0.03	0.63	18.94	945
Unidentified eider	0	0	0	945
White-winged Scoter	<0.01	0.11	3.48	945
Surf Scoter	0	0	0	945
Black Scoter	0	0	0	945
Unidentified scoter	0	0	0	945
NECS with/BC				
Long-tailed Duck	0.07	2.14	177.78	7869
Steller's Eider	<0.01	0.02	2.22	7869
Common Eider	0.01	0.87	70.37	7869
King Eider	0.01	0.62	57.78	7869
Spectacled Eider	<0.01	0.05	4.49	7869
Unidentified eider	<0.01	0.03	1.72	7869
White-winged Scoter	<0.01	0.06	3.33	7869
Surf Scoter	<0.01	0.09	8.85	7869
Black Scoter	0	0	0	7869
Unidentified scoter	0	0	0	7869

It is not clear why three benthic hotspots are essentially not used by sea ducks, although the timing of surveys may obscure this assessment and variation and concentration of benthic prey may be an underlying cause. Our surveys in the Chukchi Sea were mostly offshore starting in June, when sea ducks are already at terrestrial breeding sites (king and spectacled eiders, long-tailed ducks, scoters) or in shallow nearshore areas near nest sites (common eiders). During spring migration through the Chukchi Sea in April and May, open water is often restricted to nearshore polynyas, thus access to offshore hotspot regions are limited. However, sea ducks do use open marine waters during the fall migration. Water depths of the NECS hotspot (~43 m, Table 3) are considerably shallower than the depths at which spectacled eiders forage in the SLIP (~65 m; Day et al., 2013), so depth does not appear to be a limiting factor. It also is unclear why the Chirikov and SECS hotspots, in particular, are used so sparingly by sea ducks, considering the fact that hundreds of thousands sea ducks from both the American and Russian sides cross both hotspots while migrating to and from molting and wintering areas farther south and west (Fischer and Larned, 2004; Phillips et al., 2007; Oppel et al., 2009). A major wintering and migration area does occur to the west of the SECS hotspot along the Chukotka Coast (Petersen and Flint, 2002; Phillips et al., 2006). Notably we observed higher densities of sea ducks flying in the study area than on the water, but the locations of highest on-the-water seaduck density (40 × 40-km blocks) in the eastern Chukchi and western Beaufort seas showed that relatively few locations are used by sea ducks (compared with other seabird groups), and they were primarily coastal (Kuletz et al., 2015).

One possible reason for the lack of use of the benthic hotspot sites by benthivorous sea ducks north of the SLIP hotspot is that the bivalve prey base in those hotspots may not have the preferred taxa or size. The SLIP hotspot is dominated by small nuculid and nuculanid bivalves (Table 8; Grebmeier, 2012) of shell lengths preferred by spectacled eiders (e.g., mostly 12–30 mm, Lovvorn et al., 2003). By comparison, the sandy Chirikov hotspot is dominated numerically and by biomass with tube-dwelling ampeliscid amphipods (Table 8, Fig. 5) that are not preferred prey of diving sea ducks. Moving northward, the SECS hotspot is dominated by a higher percentage, by biomass, of larger tellinid bivalves that are generally too large for most sea duck species (Grebmeier, 2012; unpubl. data). However, these larger bivalves are suitable for king and common eiders (Frimer, 1997); smaller bivalves may be preferred by spectacled and common eiders (Bustnes and Erikstad, 1990; Richman and Lovvorn, 2003). The NECS hotspot is composed of lower overall biomass of smaller tellinid and nuculid clams, along with polychaetes, and sipunculids (Table 8, Fig. 5). Although the smaller nuculid bivalves can occur in high abundance in the NECS hotspot, they are not a preferred prey of spectacled eiders (Lovvorn et al., 2003).

Note that surface and other diving seabirds do use hotspots of pelagic prey abundance that are geographically consistent with the location of the four benthic hotspots in our study (see Kuletz et al., 2015). Thus, the benthic hotspots north of SLIP (Chirikov, SECS and NECS), while not used extensively by sea ducks, do appear to be important sites to seabird species foraging in the water column and at the surface.

3.4.2. Marine mammals

The Pacific Arctic region supports important benthic prey for gray whales, walruses, and bearded seals (Moore et al., 2000,

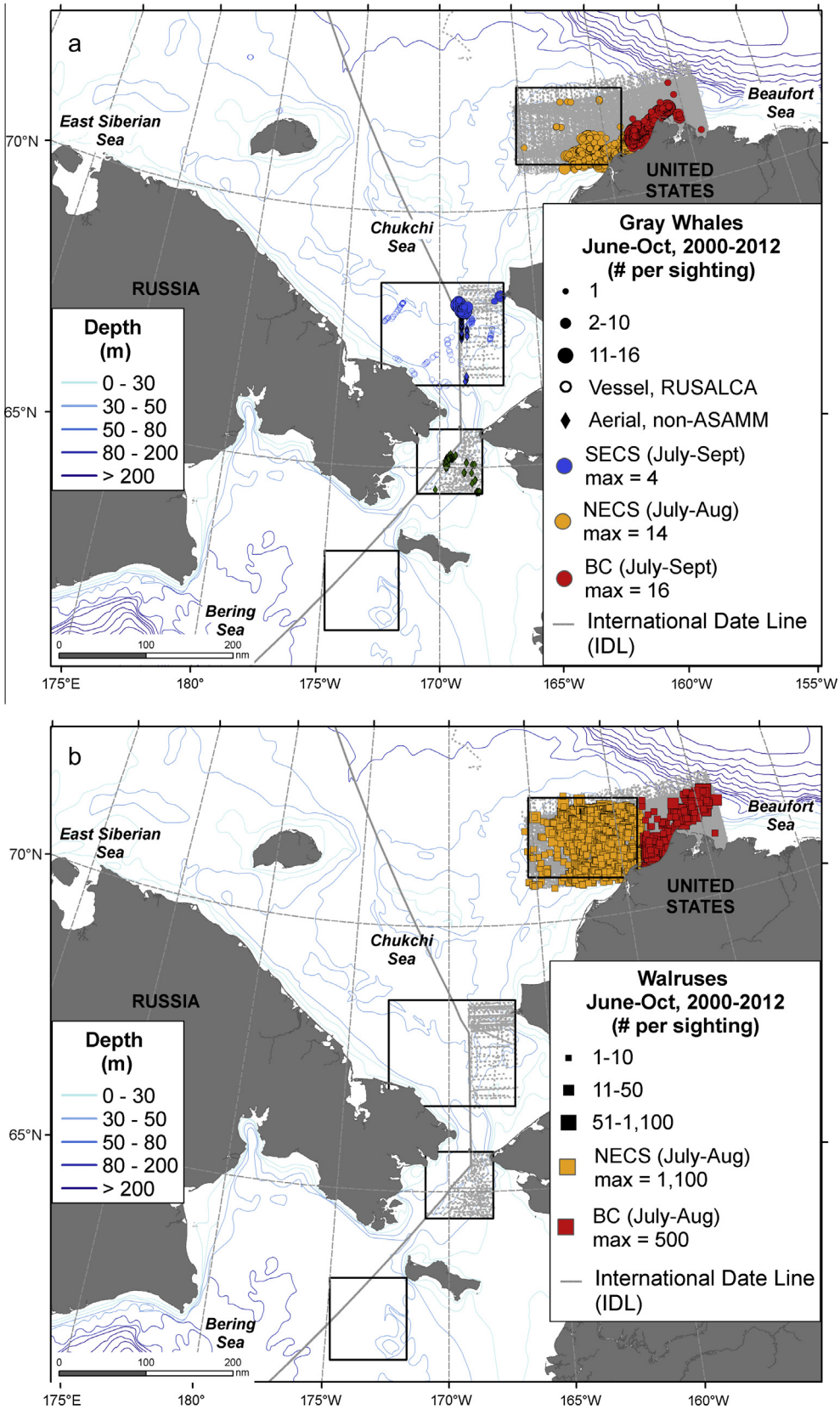

Fig. 7. Distribution of marine mammal sightings (# per sighting) for (a) gray whales and (b) walruses using Aerial Surveys of Arctic Marine Mammals (ASAMM) and Russian–American Long-Term Census of the Arctic (RUSALCA) data from June–October for the 2000–2012 period. Gray lines indicate aerial survey effort for ASAMM. Color-coding identifies the location and symbol size represents the maximum number of animals per sighting. Black boxes are the location of the four benthic bounding boxes from south to north used in our study: SLIP (St. Lawrence Island Polynya region) hotspot, Chirikov (Chirikov Basin) hotspot, SECS (Southeast Chukchi Sea) hotspot, NECS (Northeast Chukchi Sea) hotspot; in addition BC (Barrow Canyon) sightings for comparison. No data were collected in the SLIP area or on the Russian side of the international date line for ASAMM studies. Data source: Aerial Surveys of Arctic Marine Mammals (ASAMM) database, http://www.afsc.noaa.gov/NMML/cetacean/bwasp/.

2003, 2014; Jay et al., 2012). Recent studies by Aerts et al. (2013), Blanchard et al. (2013a), Hannay et al. (2013) and Schonberg et al. (2014) show spatial overlap of high levels of benthic faunal abundance and biomass and area use by upper trophic level benthivores, specifically gray whales and walruses, which we focus on here, suggesting causal connections.

Aerial (and limited vessel) survey data for gray whales (Fig. 7a) and walruses (Fig. 7b) document sightings during the period 2000–2012. During June–October 2000–2012, gray whales were seen in 3 of the 4 benthic hotspots – Chirikov, SECS and NECS – as well as Barrow Canyon, and most appeared to be feeding. The lack of gray whale sightings in the SLIP hotspot is due, at least in part, to lack of systematic survey effort in that area. The distribution of gray whales in the SE Chukchi Sea was closely associated with the benthic hotspot there, with whales regularly observed near the International Date Line (169°W) during the 2000–2012 period (Fig. 7a; Bluhm et al., 2007). The more restricted distribution of gray whales in the Chirikov hotspot may be a consequence of the constrained ampeliscid amphipod prey base and biomass relative to earlier periods (Moore et al., 2003; Coyle et al., 2007).

In the NE Chukchi Sea, where aerial survey effort was most consistent from 2000 to 2012, the distribution of gray whales was primarily nearshore and partly outside the NECS hotspot. Most gray whales, but never in any great numbers, were seen in the shallow area between shore and Barrow Canyon, an area dominated by amphipods (Fig. 5; Schonberg et al., 2014). Gray whales have rarely been observed in the offshore areas of the NECS hotspot, a region dominated by bivalves (Figs. 5 and 7a). In the 1980s, gray whales were sometimes seen on southern Hanna Shoal in the NECS hotspot, although in small numbers (Moore et al., 2000). Gray whales were not seen south of Hanna Shoal during aerial surveys conducted in 2008–2012, although sightings were made during the Chukchi Sea Environmental Studies Program (CSESP) ship-board surveys (B. Day, pers. com.), suggesting gray whales still sometimes occur there.

Seasonal sea ice provides an important resting platform for walruses that use the SLIP and Chirikov hotspot regions in the spring as the ice retreats. Female walruses and their calves use the Chukchi Sea in the spring (Jay et al., 2012) and remain in the area throughout summer and fall. No walrus were observed during the very limited aerial survey effort during the summer months in 2000–2012 (Fig. 7b) when walrus by the thousands use the Chirikov hotspot site each year as they migrate north in the spring (Fay, 1982; Jay et al., 2012, 2014). Satellite tagging data for walrus indicate that few walruses would be expected in the Chirikov hotspot between June and October. By comparison, walrus sightings were more common in the NECS hotspot during the 2000–2012 period, which corresponded with greater survey effort (Fig. 7b). Walrus sighting distributions in the NECS and Barrow Canyon areas in 2000–2012 show a gap in sightings between the offshore area over Hanna Shoal, where large groups of walruses were observed in July and early August, and the nearshore area where many walruses were observed in late August and September prior to massing in on-shore haulouts (Jay et al., 2012). Recent walrus tagging data indicate little-to-no feeding in the nearshore region off Alaska nor in Barrow Canyon, suggesting these animals transit from shore to Hanna Shoal to feed.

Central walrus foraging areas derived from published Chukchi Sea monthly utilization distributions (or habitat use; Fig. 8; Jay et al., 2012) show that the NECS hotspot encompasses an area of high walrus foraging concentration, which peaks in July. Farther south, the SECS hotspot is another area of high walrus foraging concentration that peaks in October; however, tracking data in this region during July–September are limited. Although walruses occur in the Barrow Canyon area in low concentration (Jay et al., 2012; Hannay et al., 2013; Fig. 8), their limited foraging activity is mostly occurring in the upper canyon region.

There are insufficient telemetry data to evaluate the SLIP and Chirikov Basin benthic hotspots across decades, although it is known that walruses forage in these regions (Fay, 1982), particularly in the SLIP region in winter and early spring (Jay et al., 2014). The Chirikov Basin is occupied rather briefly as walruses migrate north in spring. Other areas of walrus aggregations in winter include the southeast Bering Sea and Anadyr Gulf in the northwestern Bering Sea (Fay, 1982), which presumably correspond to rich benthic feeding areas as well.

3.4.3. Major similarities and differences of the four benthic hotspots: upper trophic level seabirds and marine mammal benthivores

The two hotspots with the lowest bottom water temperatures, the SLIP and NECS hotspots, have the lowest mean benthic macrofaunal abundance and biomass, lower mean standing stocks of demersal fishes, sediment chl *a* concentrations, and export production (as indicated by SCOC) of the 4 hotspots. In contrast, the Chirikov and SECS hotspots, which are to a large degree influenced by high nutrient concentrations driving high productivity in Anadyr Water, have comparatively higher macrofaunal and demersal fish standing stocks, integrated and sediment chl *a* concentrations, and export production (SCOC). Epifaunal biomass varied in their standing stocks in the Chirikov and SECS hotspots in comparison to the above pattern for infauna. Dominant benthic prey items varied amongst hotspots, which may (in combination with ice cover and other factors), partly explain differences amongst hotspots in use and species composition of seabird and mammal predators.

Surprisingly, in spite of the high abundance and biomass of benthic infauna in these hotspots, three of the four hotspots (all except the SLIP) were unimportant to benthivorous sea ducks. All four

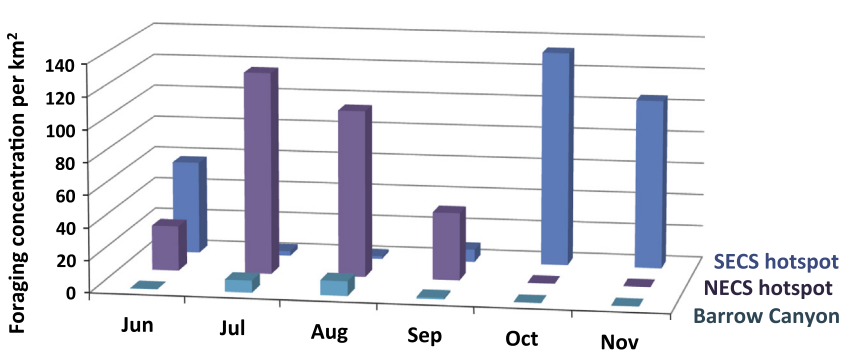

Fig. 8. Distribution of walrus foraging concentrations using tracking data within the two Chukchi Sea benthic hotspots: SECS (Southeast Chukchi Sea, blue) and NECS (Northeast Chukchi Sea, purple) for the months of June–November, 2008–2011. Values were also recorded for Barrow Canyon (aqua) for comparative purposes. Note that the SLIP and Chirikov hotspots did not have comparable tracking data for this type analysis. Data derived from Jay et al. (2012).

hotspots were shallow enough to be accessible to sea ducks, although the abundance of preferred prey varied among hotspots, at least partially explaining why most of the hotspots were unimportant to sea ducks. There is some indication that the SECS and southeast section of the NECS may now support more feeding gray whales than the Chirikov hotspot, a prime feeding area for gray whales in the early 1980s (Moore et al., 2000). Hanna Shoal is an important foraging area for walruses, regardless of the presence or absence of sea ice. Walruses normally use the NECS and SECS hotspots extensively in summer and autumn, respectively. Seasonal ice cover provides resting habitats and largely mediates benthic feeding and overall access to walruses to these regions (Jay et al., 2012). Comparative walrus foraging estimates in the Chirikov and SLIP regions are unavailable.

4. Summary and future directions

Understanding physical–biological interactions is key to evaluating the status and ongoing changes in the Pacific Arctic region and is especially pertinent to understanding key drivers for the persistence of benthic biomass hotspots. Hydrographic forcing and bathymetric steering of currents in some regions, along with associated water mass characteristics, such as nutrient flux, primary production, and carbon cycling, are all important processes that maintain hotspots. Advection, together with nutrients contributed in the various water masses, influence annual primary production, which in turn has a critical impact on benthic biomass and community composition, with the potential of long-term implications for persistence of these benthic hotspots (Grebmeier et al., 2006a,b, 2010; Blanchard et al., 2013a; Blanchard and Feder, 2014). Oceanographic processes that influence spatial patterns of food supply to the benthos and associated benthic faunal biomass and composition, sediment heterogeneity, carbon deposition patterns, and benthic predator–prey interactions, are critical to maintaining a productive benthic system in the northern Bering and Chukchi Sea hotspots.

Studies in the Pacific Arctic region indicate that northward nutrient supply via the Pacific water inflow, along with seasonal stratification, upwelling, and vertical mixing are all key factors influencing organic carbon cycling processes on the continental shelves (c.f. Grebmeier and Maslowski, 2014; Maslowski et al., 2014; Mathis et al., 2014; Williams et al., 2014). Water mass structure influences seasonal primary production, with the western nutrient-rich Anadyr and Bering Shelf Waters supporting higher seasonal production than the eastern, nutrient-poor Alaska Coastal Water (Walsh et al., 2005). The phenology of biological production cycles is tied to the annual cycle of light in high-latitude ecosystems that is then modulated by the period of seasonal ice cover (Fig. 3). Increasing light levels in spring and early summer as sea ice thins and retreats, combined with seasonally variable nutrient availability, results in a highly focused primary production peak in May–June in the northern Bering Sea (Table 5). Peak production advances northward in concert with the seasonal sea ice reduction so that it occurs in July–August in the Chukchi Sea. The annual peak in primary production, which varies with latitude and time, is followed by a delayed peak in secondary water column production somewhat later in the season due to early season colder water temperatures (Nelson et al., 2014). A strong degree of decoupling between the primary and secondary water column production compared to lower latitudes results in enhanced pelagic export to the underlying benthos in the early season of the bloom period.

Satellite and field observations indicate the seasonal reoccurrence of high concentrations of chl *a* at the benthic hotspot sites at different times of the year (Table 6), whereas annual shipboard sampling indicates the persistence of high densities and biomass of non-motile, macrofaunal organisms in patches on the shelf that benefit from the high levels of carbon export to the underlying benthos (Fig. 2, Table 7). These immobile benthic infauna respond to variable levels of annual export production, building up comparatively high biomass over multiple years-to-decades with abundant, persistent prey available in specific locations over at least the past four decades (Fig. 2; Grebmeier, 2012). These benthic biomass hotspots provide a concentrated prey base to mobile epibenthic animals and marine mammal and seabird benthivores.

Understanding biological hotspots within generally benthic-rich ecosystems, such as the Pacific Arctic region, is important for ecosystem evaluation. These sites can reflect the status and changes in physical forcing, sea ice retreat, and ecosystem response in a shallow water continental shelf system that is being stressed by both climate change and other anthropogenic impacts (e.g., oil development; also see Wassmann et al., 2011). Changes in hydrographic forcing and seasonal sea ice cover have the potential for reorganization of the ecosystem in the Pacific Arctic (c.f. Grebmeier et al., 1988, 1989, 2006a,b; Grebmeier and McRoy, 1989; Feder et al., 1994; Cloern et al., 2010; Blanchard et al., 2010, 2013a,b; Blanchard and Feder, 2014). Evaluation of benthic biomass and environmental factors can help differentiate the major factors maintaining such systems. Based on projections of continued sea-ice retreat, longer summer periods of wind forcing upon open waters subject to greater fetch and thus more wind-induced mixing will likely increase sediment resuspension over the shallow shelf.

If sea ice continues to retreat and opens up more surface area for sunlight, primary production could initially increase in the Pacific region (as it has, c.f. Arrigo et al., 2011; Arrigo and van Dijken, 2015) and enhance export production of phytodetritus to the benthos at the four hotspots. However, continued seawater warming and freshening could increase seawater stratification, leading to nutrient depletion, and thus reduce overall primary production and the level of export production of phytodetritus to the benthos (c.f. Grebmeier et al., 2006b). Similarly, warming earlier in the season would increase zooplankton abundance and grazing potential on phytoplankton standing stocks, thus also potentially limiting export potential of phytodetritus to the underlying benthos. Despite decadal-scale changes in Bering Strait transport, heat fluxes, and fresh water fluxes (Woodgate et al., 2012), we still anticipate seasonally high regional productivity will continue in the areas of highest nutrient loading, particularly at the Chirikov and SECS hotspots. However, continued changes in the timing and extent of sea ice retreat (Frey et al., 2014), potential changes in nutrient content, warming and freshening of Pacific water inflow earlier in the season will have complex and regionally variable impacts on phytoplankton production, the timing and development of zooplankton communities, and consequently on the strength of pelagic–benthic coupling, and benthic biomass of key prey for benthivores. Notably, any change in atmospheric forcing and current flow through Bering Strait, and changes in upstream productivity, could have a downstream impact via nutrient limitation on the Chukchi Sea ecosystem even with a reduction in sea ice cover seasonally. Finally, a warming Arctic troposphere and the associated increase in polar easterly winds (Wood et al., 2015) could result in more frequent upwelling events in Barrow Canyon (Pickart et al., 2013), and subsequently expand the footprint of the NECS benthic hotspot, depending on the timing of zooplankton grazing and life cycles, and on current transport.

A remaining general question is what currently maintains these benthic biomass hotspots? The SLIP hotspot is maintained by deposition of early season (May) primary production from either upstream or *in situ* production or a combination of the two, where carbon settles out within slower current velocities into very cold

bottom waters that are persistent throughout much of the year (Fig. 1; Grebmeier and Cooper, 1995; Grebmeier and Barry, 2007; Cooper et al., 2012, 2013). The Chirikov and SECS benthic hotspots, in contrast, are maintained in areas of higher annual pelagic production than in the SLIP, with variable advective flow patterns and differing sediment composition (Grebmeier et al., 2006a, 2010; Woodgate et al., 2012) and dominant faunal types between Chirikov and SECS hotspots. Despite higher flow rates and coarser sediments in the Chirikov versus the SECS hotspot, macrobenthic biomass reaches maxima in both areas where organic carbon is either carried in suspended loads and bound by filter-feeding and tube-building (sediment stabilizing) amphipods (Chirikov) or deposited when currents slow down (SECS) and thereby support persistent benthic deposit feeding bivalves and polychaetes. The NECS benthic hotspot is the most heterogenous, being maintained by variably bathymetric steering in cold bottom waters (Blanchard et al., 2013a; Blanchard and Feder, 2014) that allows both the transport of carbon in suspended load as well as periodic local to sub-regional scale deposition to the sediments as indicated by the variable sediment grain size and carbon content in the region.

Whether these various factors make one hotspot more or less vulnerable to changing environmental conditions is uncertain without a long enough time series for evaluation. Current time series range from <10 years in the NECS hotspot to >30 years in the SLIP hotspot. However, it can be hypothesized that benthic hotspots that are persistent under extremely cold temperatures may be more sensitive to future warming and changing sea ice conditions than those maintained by already warmer conditions (e.g., the Chirikov and SECS hotspots). Cold BW temperatures in both the SLIP and NECS reduce predation by fishes, resulting in predation primarily by predatory epibenthic invertebrates (Kolts et al., 2014), marine mammals (Frost and Lowry, 1986), and diving sea ducks (in the SLIP only; Lovvorn et al., 2009). Those benthic communities that persist under low temperatures could be more sensitive to local changes in heat, atmospheric forcing, and varying ice fields than the more advective Chirikov and SECS hotspots that may be more sensitive to larger scale impacts, such as upstream seawater warming and reduced ice cover.

Topographic control on water mass structure has been suggested as a mechanism for the small-scale ecological variations observed in the heterogeneous NE Chukchi Sea (Blanchard et al., 2013a,b), based on the varying depth in the region that drives circulation patterns (Weingartner et al., 2013). This complex bathymetry could have ecologically significant consequences on the variability in benthic communities. Notably the NECS hotspot has the largest depth range (19–89 m) of all the four hotspots resulting in a more complex environment, while the depth variance in the other three hotspots is smaller (SLIP, 36–85 m, Chirikov, 17–62 m, SECS 23–60 m). Interestingly, C/N values in surface sediments are less labile (mean ~7.8) in the NECS hotspot and more labile in the bathymetrically more homogeneous SLIP, Chirikov and SECS hotspots (mean ~6.4 for all). Perhaps the combination of later sea ice retreat, open water *in situ* primary and secondary production, and advection of nutrients and associated carbon products from upstream sites make the dominant processes influencing food supply to the benthos in the NECS hotspots different.

All of the benthic hotspots could indirectly be affected by a differential sea level change between the North Pacific and the Arctic. Associations between regional-scale climate variations and benthic communities have been suggested, both for the Pacific Arctic and elsewhere (Coyle et al., 2007; Blanchard et al., 2010; Cloern et al., 2010; Blanchard and Feder, 2014). Further analyses are needed to take the next step to identify mechanisms that would result in change to benthic hotspots and the overall benthic ecosystem in the Pacific Arctic. For example, if the western Arctic would experience a greater sea level rise relative to the North Pacific, there would presumably be a decrease in the Bering Strait through-flow and subsequent decrease in the nutrient delivery to the northern Bering and Chukchi shelves. Such a decrease in nutrient supply would likely cascade to a reduction in annual primary production and associated export of usable carbon to the benthos, and limit biomass of key macroinvertebrate prey base to upper trophic level benthivores. The alternative situation of an increase in northward Pacific transport, co-occurring with a continued reduction in seasonal sea ice, may open the Chukchi Sea to more sunlight, with increased seawater warming and stratification, primary production, and zooplankton grazing. The combined affect would reduce proportional export production to the benthos even if primary production increased. Thus, an important research need is for realistic coupled physical–biochemical modeling efforts, along with linked biological-trophic models, to evaluate potential system-level changes to this productive, but potentially vulnerable, Pacific Arctic ecosystem.

There are numerous knowledge gaps with respect to the mechanisms driving the development and persistence of benthic biomass hotspots. Based on this synthesis, we provide the following recommendations for future research relevant to the topic:

1. Although most benthic macrofauna have a wide-ranging distribution in the region (www.iobis.org), suggesting wide thermal tolerances, very few temperature-dependent rate measurements of benthic macrofauna have been made (but see Renaud et al., in press for thermal distribution types). The physiological capacity of benthic organisms to acclimate or adapt to warming or otherwise changing conditions is also woefully understudied (Poertner, 2010).
2. Time-series measurements, with simultaneous biological, biogeochemical and physical measurements undertaken in a coordinated fashion are needed to track (potential) ecosystem change, e.g. Distributed Biological Observatory (DBO) for the Pacific Arctic region (Grebmeier et al., 2010). Although we identify key processes in this synthesis that together facilitate and influence the persistence of the four major benthic hotspots we identified, we still lack consistent spatial and temporal coverage of process studies at the appropriate scales to develop nested models to evaluate rates of change.
3. Tracking vertebrate benthivore–prey interactions, and using these upper trophic level organisms as ecosystem sentinels at these key benthic-hotspot feeding sites, will help determine the processes that facilitate the persistence of prey biomass at specific locations and evaluate bottom up versus top down control. Currently we know very little about the magnitude of annual benthic biomass removal by higher-trophic level benthivores or the impacts of their changing populations on ecosystem function or vice versa.

In conclusion, benthic faunal biomass hotspots are ecologically important regions for higher trophic levels and for tracking ecosystem status and/or change in the Pacific Arctic. Thus, it is essential to understand variations in the interactions between water circulation, seafloor topography (aka bathymetry), benthic communities, and the benthivores that utilize these high biomass hotspots on the bottom of the ocean. A coordinated, multidisciplinary ecosystem approach over seasonal and interannual temporal and spatial scales is necessary to track the changes occurring in these benthic hotspots, and the continental shelves in general in the Pacific Arctic region. Development of conceptual and predictive models based on realistic experimental and field measurements are needed to determine the mechanistic drivers of persistent hotspots of benthic biomass in order to evaluate future change in this changing ecosystem.

Acknowledgements

We thank Katrin Iken, Brenda Holladay, Chadwick Jay, and Alexandra Ravelo for sharing data for this synthesis effort. Alynne Bayard, Tony Fischbach, and Elizabeth Labunski provided critical technical and graphical assistance, including use of geographical information system imagery. Chirk Chu provided essential macrofaunal computer analysis and statistical processing assistance. We also thank the multiple technicians and students that assisted with data analyses for the varied institutions of all co-authors, and Mette Kaufman, who assisted with editing the reference list. We thank three anonymous reviewers who helped improve an earlier version of the manuscript.

This study is part of the Synthesis of Arctic Research (SOAR) project and was funded in part by the U.S. Department of the Interior (DOI), Bureau of Ocean Energy Management (BOEM), Environmental Studies Program through Interagency Agreement No. M11PG00034 with the U.S. Department of Commerce, National Oceanic and Atmospheric Administration (NOAA), Office of Oceanic and Atmospheric Research (OAR), Pacific Marine Environmental Laboratory (PMEL). Additional support was provided to Bluhm, Cooper, Grebmeier, and Okkonen through the PacMARS (Pacific Marine Arctic Regional Synthesis) project funded by Shell Exploration and Production and ConocoPhillips, and administered and managed by the North Pacific Marine Research Institute (NPMRI Arctic Project A01) through the North Pacific Research Board, and with oversight from the National Science Foundation (NSF) Division of Polar Programs. Additional funding for this effort was provided to J. Grebmeier and L. Cooper by the NSF Division of Polar Programs (Grant ARC-1204082), NOAA Arctic Research Program CINAR A101053 (NA09OAR4320129), and BOEM funding through the COMIDA Hanna Shoal Project (UTA11-000872). Funding for Sang Lee was provided by the Korean Ministry of Oceans and Fisheries for the financial support to the K-PORT programs (PM13020 and PM14040). Funding for the fish data collected by B. Norcross was provided by CMI, CIFAR/RUSALCA, ConocoPhillips, Shell Exploration and Production Co., and Statoil USA E & P University of Alaska's Coastal Marine Institute Task Order M07AC13416 with funds from the BOEM/DOI. Catherine W. Mecklenburg is thanked for taxonomic assistance. K. Kuletz was funded through the NPRB (BSIERP Project B64), BOEM (Interagency Agreement M10PG00050), and US Fish and Wildlife Service, Migratory Bird Management. ABR seabird surveys were supported by ConocoPhillips, Shell, and Statoil USA. ASAMM surveys were funded by BOEM and co-managed by BOEM and NMFS. Various US national agencies, including BOEM, NASA, NOAA, NPRB, and NSF, along with ConocoPhillips, Shell, and Statoil USA, provided financial support to collect the data synthesized here by the co-authors of this manuscript. UMCES Contribution Number 5035.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2015.05.006.

References

Aerts, L.A.M., McFarland, A.E., Watts, B.H., Lomac-MacNair, K., Seiser, P.E., Wisdom, S.S., Kirk, A.V., Schudel, C.A., 2013. Marine mammal distribution and abundance in an offshore sub-region of the northeastern Chukchi Sea during the open-water season. Continental Shelf Research 67, 116–126.

Ambrose, W.G., Renaud, P.E., 1995. Benthic response to water column productivity patterns: evidence for benthic–pelagic coupling in the Northeast Water Polynya. Journal of Geophysical Research 100, 4411–4421.

Ambrose Jr., W.G., Clough, L.M., Tilney, P.R., Beer, L., 2001. Role of echinoderms in benthic remineralization in the Chukchi Sea. Marine Biology 139, 937–949.

Ambrose Jr., W.G., Renaud, P.E., Locke, W.L., Cottier, F.R., Berge, J., Carroll, M.L., Levin, B., Ryan, S., 2012. Growth line deposition and variability in growth of two circumpolar bivalves (*Serripes groenlandicus*, and *Clinocardium ciliatum*). Polar Biology 35, 345–354.

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

Arrigo, K.R., Dijken, G.Y., Pabi, S., 2008. Impact of a shrinking Arctic ice cover on marine primary production. Geophysical Research Letters 35, L19603. http://dx.doi.org/10.1029/2008GL035028.

Arrigo, K.R., Matrai, P.A., van Dijken, G.L., 2011. Primary productivity in the Arctic Ocean: impacts of complex optical properties and subsurface chlorophyll maxima on large-scale estimates. Journal of Geophysical Research: Oceans (1978–2012) 116 (C11).

Arrigo, K.R., Perovich, D.K., Pickart, R.S., Brown, Z.W., van Dijken, G.L., Lowry, K.E., Mills, M.M., Palmer, M.A., Balch, W.M., Bates, N.R., Benitez-Nelson, C.R., Brownlee, E., Frey, K.E., Laney, S.R., Mathis, J., Matsuoka, A., Mitchell, B.G., Moore, G.W.K., Reynolds, R.A., Sosik, H.M., Swift, J.H., 2014. Phytoplankton blooms beneath the sea ice in the Chukchi Sea. Deep Sea Research Part II: Topical Studies in Oceanography 105, 1–16. http://dx.doi.org/10.1016/j.dsr2.2014.03.018.

Blanchard, A.L., Feder, H.M., 2014. Interactions of habitat complexity and environmental characteristics with macrobenthic community structure at multiple spatial scales in the northeastern Chukchi Sea. Deep Sea Research Part II: Topical Studies in Oceanography 102, 132–143.

Blanchard, A.L., Feder, H.M., Hoberg, M.K., 2010. Temporal variability of benthic communities in an Alaskan glacial fjord, 1971–2007. Marine Environment Research 69, 95–107.

Blanchard, A.L., Parris, C.L., Knowlton, A.L., Wade, N.R., 2013a. Benthic ecology of the northeastern Chukchi Sea. Part I: Environmental characteristics and macrofaunal community structure, 2008–2010. Continental Shelf Research 67, 52–66.

Blanchard, A.L., Parris, C.L., Knowlton, A.L., Wade, N.R., 2013b. Megafaunal community structure, in the northeast Chukchi Sea and its association with environmental variables, 2009–2010. Continental Shelf Research 67, 67–76.

Bluhm, B., 2014a. WEBSEC-72 Trawl Data. doi: http://dx.doi.org/10.5065/D6QF8QW9.

Bluhm, B., 2014b. Epifauna Sampling Data. doi: http://dx.doi.org/10.5065/D67M05ZX.

Bluhm, B., Gradinger, R., 2008. Regional variability in food availability for Arctic marine mammals. Ecological Applications 18, 77–96.

Bluhm, B.A., Coyle, C.O., Konar, B., Highsmith, R.C., 2007. High gray whale densities at an oceanographic front in the south-central Chukchi Sea in 2003. Deep Sea Research Part II: Topical Studies in Oceanography 54, 2919–2933.

Bluhm, B., Iken, K., Hardy, S.M., Sirenko, B.I., Holladay, B.A., 2009. Community structure of epibenthic megafauna in the Chukchi Sea. Aquatic Biology 7, 269–293.

Brown, Z.W., Arrigo, K.R., 2012. Contrasting trends in sea ice and primary production in the Bering Sea and Arctic Ocean. ICES Journal of Marine Science 69, 1180–1193.

Brown, Z.W., Arrigo, K.R., 2013. Sea ice impacts on spring bloom dynamics and net primary production in the Eastern Bering Sea. Journal of Geophysical Research 118, 43–62.

Brown, Z., van Dijken, G.L., Arrigo, K.R., 2011. A reassessment of primary production and environmental change in the Bering Sea. Journal of Geophysical Research 116, C08014. http://dx.doi.org/10.1029/2010JC006766.

Bustnes, J.O., Erikstad, K.E., 1990. Size selection of common mussels, *Mytilus edulis*, by common eiders, *Somateria mollissima*: energy maximization or shell weight minimization? Canadian Journal of Zoology 68 (11), 2280–2283.

CAFF, 2013. Arctic Biodiversity Assessment. Status and Trends in Arctic Biodiversity: Synthesis. Conservation of Arctic Flora and Fauna, Akureyri, Iceland.

Carmack, E., Wassmann, P., 2006. Food webs and physical–biological coupling on pan-Arctic shelves: unifying concepts and comprehensive perspectives. Progress in Oceanography 71, 446–477.

Cavalieri, D., Parkinson, C., Gloersen, P., Zwally, H.J., 1996, updated yearly. Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data. NASA DAAC at the National Snow and Ice Data Center, Boulder, Colorado, USA.

Cavalieri, D., Parkinson, C., Gloersen, P., Zwally, H.J., 2008. Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I Passive Microwave Data. National Snow and Ice Data Center, Boulder, Colorado, USA. Digital Media.

Cloern, J.E., Hieb, K.A., Jacobson, T., Sansó, B., Di Lorenzo, E., Stacey, M.T., Largier, J.L., Meiring, W., Peterson, W.T., Powell, T.M., Winder, M., Jassby, A.D., 2010. Biological communities in San Francisco Bay track large-scale climate forcing over the North Pacific. Geophysical Research Letters 37 (21), L21602. http://dx.doi.org/10.1029/2010GL044774.

Clough, L.M., Renaud, P.E., Ambrose Jr., W.G., 2005. Impacts of water depth, sediment pigment concentration, and benthic macrofaunal biomass on sediment oxygen demand in the western Arctic Ocean. Canadian Journal of Fisheries and Aquatic Sciences 62, 1756–1765.

Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: The Regional Physical Oceanography. University of Washington Press, Seattle, p. 172.

Codispoti, L.A., Kelly, V., Thessen, A., Patrai, P., Suttles, S., Hill, V., Steele, M., Light, B., 2013. Synthesis of primary production in the Arctic Ocean: III. Nitrate and phosphate based estimates of net community production. Progress in Oceanography 110, 126–150.
Cooper, L.W., Janout, M., Frey, K.E., Pirtle-Levy, R., Guarinello, M., Grebmeier, J.M., Lovvorn, J.R., 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: Topical Studies in Oceanography 71–76, 5–15.
Cooper, L.W., Sexson, M.G., Grebmeier, J.M., Gradinger, R., Mordy, C.W., Lovvorn, J.R., 2013. Linkages between sea ice coverage, pelagic–benthic coupling and the distribution of spectacled eiders: observations in March 2008, 2009 and 2010 from the northern Bering Sea. Deep Sea Research Part II: Topical Studies in Oceanography 94, 31–43.
Coyle, K.O., Pinchuk, A.I., 2002. Climate-related differences in zooplankton density and growth on the inner shelf of the southeastern Bering Sea. Progress in Oceanography 55, 177–194.
Coyle, K.O., Konar, B., Blanchard, A., Highsmith, R.C., Carroll, J., Carroll, M., Denisenko, S.G., Sirenko, B.I., 2007. Potential effects of temperature on the benthic infaunal community on the southeastern Bering Sea shelf: possible impacts of climate change. Deep Sea Research Part II: Topical Studies in Oceanography 54, 2885–2905.
Cui, X., Grebmeier, J.M., Cooper, L.W., Lovvorn, J.R., North, C.A., Kolts, J.M., 2009. Spatial distributions of groundfish in the northern Bering Sea in relation to environmental variation. Marine Ecology Progress Series 393, 147–160.
Cui, X., Grebmeier, J.M., Cooper, L.W., 2012. Feeding ecology of dominant groundfish in the northern Bering Sea. Polar Biology 35, 1407–1419.
Danielson, S., Aagaard, K., Weingartner, T., Martin, S., Winsor, P., Gawarkiewicz, G., Quadfasel, D., 2006. The St. Lawrence Polynya and the Bering shelf circulation: new observations and a model comparison. Journal of Geophysical Research 111, C09023.
Danielson, S.L., Weingartner, T.W., Hedstrom, K., Aagaard, K., Woodgate, R., Curchitser, E., Stabeno, P., 2014. Coupled wind-forced controls of the Bering–Chukchi shelf circulation and the Bering Strait through-flow: Ekman transport, continental shelf waves, and variations of the Pacific-Arctic sea surface height gradient. Progress in Oceanography 125, 40–61.
Day, R.H., Weingartner, T.J., Hopcroft, R.R., Aerts, L.A.M., Blanchard, A.L., Gall, A.E., Gallaway, B.J., Hannay, D.E., Holladay, B.A., Mathis, J.T., Norcross, B.L., Questel, J.M., Wisdom, S.S., 2013. The offshore northeastern Chukchi Sea: a complex high-latitude system. Continental Shelf Research 67, 147–165. http://dx.doi.org/10.1016/j.csr.2013.02.002.
De Leo, F.C., Smith, C.R., Rowden, A.A., Bowden, D.A., Clark, M.R., 2010. Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. Proceedings of the Royal Society B 277, 2783–2792.
DeGange, A.R., Sanger, G.A., 1986. Marine birds. In: Hood, D.W., Zimmerman, S.T. (Eds.), The Gulf of Alaska: Physical Environment and Biological Resources. U.S. Department of Commerce and U.S. Department of the Interior, Anchorage, AK, pp. 479–524.
Fay, F.H., 1982. Ecology and Biology of the Pacific Walrus, *Odobenus rosmarus divergens*. North American Fauna 74, U.S. Fish and Wildlife Service, Washington, DC.
Feder, H.M., Naidu, A.S., Jewett, S.C., Hameedi, J.M., Johnson, W.R., Whitledge, T.E., 1994. The northeastern Chukchi Sea: benthos–environmental interactions. Marine Ecology Progress Series 111, 171–190.
Feder, H.M., Jewett, S.C., Blanchard, A., 2006. Southeastern Chukchi Sea (Alaska) epibenthos. Polar Biology 28, 402–421.
Feder, H.M., Jewett, S.C., Blanchard, A., 2007. Southeastern Chukchi Sea (Alaska) macrobenthos. Polar Biology 30, 261–275.
Fischer, J.B., Larned, W.W., 2004. Summer distribution of marine birds in the western Beaufort Sea. Arctic 57, 143–159.
Forsell, D.J., Gould, P.J., 1981. Distribution and Abundance of Marine Birds and Mammals Wintering in the Kodiak Area of Alaska. U.S. Fish and Wildlife Service, Office of Biological Services. Report No. FWS/OBS-81/13, Washington, DC.
Frey, K.E., Maslanik, J.A., Clement Kinney, J., Maslowski, W., 2014. Recent variability in sea ice cover, age, and thickness in the Pacific Arctic region. In: Grebmeier, J.M., Maslowski, W. (Eds.), The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment. Springer, Dordrecht, pp. 31–64.
Frey, K.E., Moore, G.W.K., Cooper, L.W., Grebmeier, J.M., 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.
Frimer, O., 1997. Diet of moulting king eiders *Somateria spectabilis* at Disko Island, West Greenland. Ornis Fennica 74, 187–194.
Frost, K.J., Lowry, L.F., 1986. Sizes of Walleye Pollock, *Theragra chalcogramma*, consumed by marine mammals in the Bering Sea. Fishery Bulletin 84, 192–197.
Glud, R.N., Woelfel, J., Karsten, U., Kühl, M., Rysgaard, S., 2009. Benthic microalgae production in the Arctic: applied methods and status of the current database. Botanica Marina 52, 559–571.
Gradinger, R., 2009. Sea-ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. Deep Sea Research Part II: Topical Studies in Oceanography 56, 1201–1212.
Gradinger, R.R., Bluhm, B.A., 2004. In situ observations on the distribution and behavior of amphipods and Arctic cod (*Boreogadus saida*) under the sea ice of the high Arctic Canadian Basin. Polar Biology 27, 595–603.
Grebmeier, J.M., 2012. Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. Annual Review of Marine Science 4, 63–78.
Grebmeier, J.M., Barry, J.P., 1991. The influence of oceanographic processes on pelagic–benthic coupling in polar regions: a benthic perspective. Journal of Marine Systems 2, 495–518.
Grebmeier, J.M., Barry, J.P., 2007. Benthic processes in polynyas. In: Elsevier Oceanography Series, vol. 74, pp. 363–390.
Grebmeier, J.M., Cooper, L.W., 1995. Influence of the St. Lawrence Island polynya on the Bering Sea benthos. Journal of Geophysical Research 100, 4439–4460.
Grebmeier, J., Cooper, L., 2014a. PacMARS Benthic Infaunal Parameters (1970–2012), Version 1.0. http://dx.doi.org/10.5065/D6H70CVR; available at the PacMARS EOL data archive site <http://pacmars.eol.ucar.edu>.
Grebmeier, J., Cooper, L., 2014b. PacMARS Surface Sediment Parameters, Version 1.0. http://dx.doi.org/10.5065/D6416V3G; available at the PacMARS EOL data archive site <http://pacmars.eol.ucar.edu>.
Grebmeier, J., Cooper, L., 2014c. PacMARS Sediment Chlorophyll-a, Version 1.0. http://dx.doi.org/10.5065/D6W9576K; available at the PacMARS EOL data archive site <http://pacmars.eol.ucar.edu>.
Grebmeier, J., Cooper, L., 2014d. PacMARS Sediment Community Oxygen Uptake, Version 1.0. http://dx.doi.org/10.5065/D600004Q; available at the PacMARS EOL data archive site <http://pacmars.eol.ucar.edu>.
Grebmeier, J., Cooper, L., 2014e. PacMARS Bottom Water Temperature and Salinity (2000–2012), Version 1.0. http://dx.doi.org/10.5065/D6VM49BM; available at the PacMARS EOL data archive site <http://pacmars.eol.ucar.edu>.
Grebmeier, J., Cooper, L., 2014f. PacMARS Bottom Water Nutrients (1988–2012), Version 1.0. http://dx.doi.org/10.5065/D6MW2F69; available at the PacMARS EOL data archive site <http://pacmars.eol.ucar.edu>.
Grebmeier, J., Cooper, L., 2014g. PacMARS Integrated Chlorophyll-a (1985–2012), Version 1.0. http://dx.doi.org/10.5065/D6F47M47; available at the PacMARS EOL data archive site <http://pacmars.eol.ucar.edu>.
Grebmeier, J., Cooper, L., 2014h. PacMARS Benthic Infaunal Parameters_dominant Fauna (2000–2012), Version 1.0. http://dx.doi.org/10.5065/D60C4SVZ; available at the PacMARS EOL data archive site <http://pacmars.eol.ucar.edu>.
Grebmeier, J.M., Maslowski, W., 2014. The Pacific Arctic region: ecosystem status and trends in a rapidly changing environment. In: Grebmeier, J.M., Maslowski, W. (Eds.), The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment. Springer, Dordrecht, pp. 1–16.
Grebmeier, J.M., McRoy, C.P., 1989. Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. Marine Ecology Progress Series 53, 79–91.
Grebmeier, J.M., McRoy, C.P., Feder, H.M., 1988. Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. Marine Ecology Progress Series 48, 57–67.
Grebmeier, J.M., Feder, H.M., McRoy, C.P., 1989. Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. II. Benthic community structure. Marine Ecology Progress Series 51, 253–268.
Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006a. Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi seas in the Amerasian Arctic. Progress in Oceanography 71, 331–361.
Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLoughlin, F.A., McNutt, L., 2006b. A major ecosystem shift observed in the northern Bering Sea. Science 311, 1461–1464.
Grebmeier, J.M., Moore, S.E., Overland, J.E., Frey, K.E., Gradinger, R., 2010. Biological response to recent Pacific Arctic sea ice retreats. Eos, Transactions American Geophysical Union 91, 161–168.
Hannay, D., Delarue, J., Mouy, X., Leary, D., Oswald, J., Vallarta, J., Martin, B., 2013. Marine mammal acoustic detections in the northeastern Chukchi Sea, September 2007–July 2011. Continental Shelf Research 67, 127–146.
Highsmith, R.C., Coyle, K.O., Bluhm, B.A., Konar, B., 2006. Gray whales in the Bering and Chukchi seas. In: Estes, J., DeMaster, D.P., Doak, D.F., Williams, T.M., Brownell, R.L. (Eds.), Whales, Whaling and Ocean Ecosystems. University of California Press, pp. 303–313.
Hill, V., Cota, G., 2005. Spatial patterns of primary production on the shelf, slope and basin of the western Arctic in 2002. Deep Sea Research Part II: Topical Studies in Oceanography 52, 3344–3354.
Hill, V., Cota, G.F., Stockwell, D., 2005. Spring and summer phytoplankton communities in the Chukchi and eastern Beaufort seas. Deep Sea Research Part II: Topical Studies in Oceanography 52, 3369–3385.
Hollowed, A.B., Planque, B., Loeng, H., 2013. Potential movement of fish and shellfish stocks from the sub-Arctic to the Arctic Ocean. Fisheries Oceanography 22, 355–370.
Hop, H., Gjøsaeter, H., 2013. Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. Marine Biology Research 9, 878–894.
Hunt Jr., G.L., Blanchard, A.L., Boveng, P., Dalpadado, P., Drinkwater, K.F., Eisner, L., Hopcroft, R.R., Kovacs, K.M., Norcross, B.L., Renaud, P., Reigstad, M., Renner, M., Skjoldal, H.R., Whitehouse, A., Woodgate, R.A., 2013. The Barents and Chukchi Seas: comparison of two Arctic shelf ecosystems. Journal of Marine Systems 109–110, 43–68.
Iken, K., Bluhm, B.A., Dunton, K., 2010. Benthic food web structure serves as indicator of water mass properties in the southern Chukchi Sea. Deep Sea Research Part II: Topical Studies in Oceanography 57, 71–85.
Iken, K., Bluhm, B.A., Søreide, J.E., 2013. Arctic Benthic Communities. Arctic Report Card Update 2013. <http://www.arctic.noaa.gov/reportcard/benthic communities.html>.
Jay, C.V., Fischbach, A.S., Kochnev, A.A., 2012. Walrus areas of use in the Chukchi Sea during sparse sea ice cover. Marine Ecology Progress Series 468, 1–13.

Jay, C.V., Grebmeier, J.M., Fischbach, A.S., McDonald, T.L., Cooper, L.W., Hornsby, F., 2014. Pacific Walrus (*Odobenus rosmarus divergens*) resource selection in the northern Bering Sea. PLoS One 9 (4), e93035. http://dx.doi.org/10.1371/journal.pone.0093035.

Kinder, T.H., Chapman, D.C., Whitehead Jr., J.A., 1986. Westward intensification of the mean circulation on the Bering Sea shelf. Physical Oceanography 16, 1217–1229.

Kolts, J.M., Lovvorn, J.R., North, C.A., Janout, M.A., 2014. Oceanographic and demographic mechanisms affecting population structure of snow crabs (*Chionoecetes opilio*) in cold waters of the northern Bering Sea. Marine Ecology Progress Series 518, 193–208.

Konar, B., Ravelo, A.M., Grebmeier, J.M., Trefry, J.H., 2014. Size frequency distributions of key epibenthic organisms in the eastern Chukchi Sea and their correlations with environmental parameters. Deep Sea Research Part II: Topical Studies in Oceanography 102, 107–118.

Kuletz, K.J., Ferguson, M.C., Hurley, B., Gall, A.E., Labunski, E.A., Morgan, T.C., 2015. Seasonal spatial patterns in seabird and marine mammal distribution in the eastern Chukchi and western Beaufort seas: identifying biologically important pelagic areas. Progress in Oceanography 136, 175–200. http://dx.doi.org/10.1016/j.pocean.2015.05.012.

Lacroix, D.L., 2001. Foraging Impacts and Patterns of Wintering Surf Scoters Feeding on Bay Mussels in Coastal Strait of Georgia, British Columbia. MS Thesis, Simon Frasier University, Burnaby, BC, Canada.

Lee, S.H., Whitledge, T.E., Kang, S.H., 2007. Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. Continental Shelf Research 27, 2231–2249.

Lee, S.H., Joo, H.-M., Yun, M.S., Whitledge, T.E., 2012. Recent phytoplankton productivity of the northern Bering Sea during early summer in 2007. Polar Biology 35, 83–98.

Lee, S.H., Yun, M.S., Kim, B.K., Saitoh, S., Kang, C.K., Kang, S.H., Whitledge, T.E., 2013. Latitudinal carbon productivity in the Bering and Chukchi seas during the summer in 2007. Continental Shelf Research 59, 28–36.

Lewis, T.L., Esler, D., Boyd, W.S., 2007. Effects of predation by sea ducks on clam abundance in soft-bottom intertidal habitats. Marine Ecology Progress Series 329, 131–144.

Lewis, T.L., Esler, D., Boyd, W.S., 2008. Foraging behavior of surf scoters (*Melanitta perspicillata*) and white-winged scoters (*M. fusca*) in relation to clam density: inferring food availability and habitat quality. Auk 125, 149–157.

Logerwell, E., Rand, K., Weingartner, T.J., 2011. Oceanographic characteristics of the habitat of benthic fish and invertebrates in the Beaufort Sea. Polar Biology 34, 1783–1796.

Lovvorn, J.R., Richman, S.E., Grebmeier, J.M., Cooper, L.W., 2003. Diet and body condition of spectacled eiders wintering in pack ice of the Bering Sea. Polar Biology 26, 259–267.

Lovvorn, J.R., Grebmeier, J.M., Cooper, L.W., Bump, J.K., Richman, S.E., 2009. Modeling marine protected areas for threatened eiders in a climatically changing Bering Sea. Ecological Applications 19, 1596–1613.

Lovvorn, J.R., Anderson, E.M., Rocha, A.R., Larned, W.W., Grebmeier, J.M., Cooper, L.W., Kolts, J.M., North, C.A., 2014. Variable wind, pack ice, and prey dispersion affect the long-term adequacy of protected areas for an Arctic sea duck. Ecological Applications 24, 396–412.

Lovvorn, J.R., Jacob, U., North, C.A., Kolts, J.M., Grebmeier, J.M., Cooper, L.W., Cui, X., 2015a. Modeling spatial patterns of limits to production of deposit-feeders and ectothermic predators in the northern Bering Sea. Estuarine, Coastal and Shelf Science 154, 19–29.

Lovvorn, J.R., Rocha, A.R., Jewett, S.C., Dasher, D., Oppel, S., Powell, A.N., 2015b. Limits to benthic feeding by eiders in a vital Arctic migration corridor due to localized prey and changing sea ice. Progress in Oceanography 136, 162–174. http://dx.doi.org/10.1016/j.pocean.2015.05.014.

Maslowski, W., Clement Kinney, J., Okkonen, S.R., Osinski, R., Roberts, A.F., Williams, W., 2014. The large scale ocean circulation and physical processes controlling Pacific–Arctic interaction. In: Grebmeier, J.M., Maslowski, W. (Eds.), The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment. Springer, Dordrecht, pp. 101–132.

Mathis, J.T., Grebmeier, J.M., Hansell, D.A., Hopcroft, R.R., Kirchman, D.L., Lee, S.H., Moran, S.B., Bates, N.R., Van Laningham, S., Cross, J.N., Cai, W.-J., 2014. Carbon biogeochemistry of the western Arctic: primary production, carbon export and the controls on ocean acidification. In: Grebmeier, J.M., Maslowski, W. (Eds.), The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment. Springer, Dordrecht, pp. 223–268.

Matrai, P., Apollonio, S., 2013. New estimates of microalgae production based upon nitrate reductions under sea ice in Canadian shelf seas and the Canada Basin of the Arctic Ocean. Marine Biology 160, 1297–1309.

McTigue, N.D., Dunton, K.H., 2014. Trophodynamics and organic matter assimilation pathways in the northeast Chukchi Sea, Alaska. Deep Sea Research Part II: Topical Studies in Oceanography 102, 84–96.

Moore, S.E., Stabeno, P., 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.

Moore, S.E., DeMaster, D.P., Dayton, P.K., 2000. Cetacean habitat selection in the Alaskan Arctic during summer and autumn. Arctic 53, 432–447.

Moore, S.E., Grebmeier, J.M., Davies, J.R., 2003. Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. Canadian Journal of Zoology 81, 734–742.

Moore, S.E., Logerwell, E., Eisner, L., Farley, E., Harwood, L., Kuletz, K., Lovvorn, J., Murphy, J., Quakenbush, L., 2014. Marine fishes, birds and mammals as sentinels of ecosystem variability and reorganization in the Pacific Arctic region. In: Grebmeier, J.M., Maslowski, W. (Eds.), The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment. Springer, Dordrecht, pp. 337–392 (Chapter 11).

Mueter, F.J., Litzow, M.A., 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecological Applications 18, 309–320.

Mundy, C.J., Barber, D., Michel, C., 2005. Variability of snow and ice thermal, physical and optical properties pertinent to sea ice algae during spring. Journal of Marine Systems 58, 107–120.

Mundy, C.J., Ehn, J.K., Barber, D.G., Michel, C., 2007. Influence of snow cover and algae on the spectral dependence of transmitted irradiance through Arctic landfast first-year sea ice. Journal of Geophysical Research 112. http://dx.doi.org/10.1029/2006JC003683.

Nelson, R.J., Ashjian, C., Bluhm, B., Conlan, K., Gradinger, R., Grebmeier, J., Hill, V., Hopcroft, R., Hunt, B., Joo, H., Kirchman, D., Kosobokova, K., Lee, S., Li, W.K.W., Lovejoy, C., Poulin, M., Sherr, E., Young, K., 2014. Biodiversity and biogeography of the lower trophic taxa of the Pacific Arctic region: sensitivities to climate change. In: Grebmeier, J.M., Maslowski, W. (Eds.), The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment. Springer, Dordrecht, pp. 269–336.

Norcross, B.L., Holladay, B.A., Busby, M.S., Mier, K.L., 2010. Demersal and larval fish assemblages in the Chukchi Sea. Deep Sea Research Part II: Topical Studies in Oceanography 57, 57–70.

Norcross, B.L., Raborn, S.W., Holladay, B.A., Gallaway, B.J., Crawford, S.T., Priest, J.T., Edenfield, L.E., Meyer, R., 2013. Northeastern Chukchi Sea demersal fishes and associated environmental characteristics, 2009–2010. Continental Shelf Research 67, 77–95.

Okkonen, S.R., 2014. CTD Summary Data. doi: http://dx.doi.org/10.5065/D6DB7ZVJ; available at the PacMARS EOL data archive site <http://pacmars.eol.ucar.edu>.

Oppel, S., Dickson, D.L., Powell, A.N., 2009. International importance of the eastern Chukchi Sea as a staging area for migrating king eiders. Polar Biology 32, 775–783.

Pabi, S., van Dijken, G.L., Arrigo, K.R., 2008. Primary production in the Arctic Ocean, 1998–2006. Journal of Geophysical Research 113, C08005. http://dx.doi.org/10.1029/2007jc004578.

Paquette, R.G., Bourke, R.H., 1981. Ocean circulation and fronts as related to ice melt-back in the Chukchi Sea. Journal of Geophysical Research 86. http://dx.doi.org/10.1029/JC086iC05p04215.

Petersen, M.R., Flint, P.L., 2002. Population structure of Pacific Common Eiders breeding in Alaska. Condor 104, 780–787.

Petersen, M.R., Larned, W.W., Douglas, D.C., 1999. At-sea distribution of spectacled eiders: a 120-year-old mystery resolved. Auk 116, 1009–1020.

Phillips, L.M., Powell, A.N., Rexstad, E.A., 2006. Large-scale movements and habitat characteristics of king eiders throughout the nonbreeding period. Condor 108, 887–900.

Phillips, L.M., Powell, A.N., Taylor, E.J., Rexstad, E.A., 2007. Use of the Beaufort Sea by king eiders breeding on the North Slope of Alaska. J Wildlife Manage 71 (6), 1892–1898.

Pickart, R.S., Spall, M.A., Mathis, J.T., 2013. Dynamics of upwelling in the Alaskan Beaufort Sea and associated shelf-basin fluxes. Deep-Sea Research Part I 76, 35–51.

Piepenburg, D., 2005. Recent research on Arctic benthos: common notions need to be revised. Polar Biology 28, 733–755.

Poertner, H.O., 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. Journal of Experimental Biology 213, 881–893.

Quakenbush, L.T., Suydam, R.S., Acker, R., Knoche, M., Citta, J., 2009. Migration of King and Common Eiders Past Point Barrow, Alaska, During Summer/Fall 2002 through Spring 2004: Population Trends and Effects of Wind. Final Rep, OCS Study MMS 2009-036, Fairbanks, AK.

Ravelo, A.M., Konar, B.H., Trefry, J.H., Grebmeier, J.M., 2014. Epibenthic community variability in the northeastern Chukchi Sea continental shelf. Deep Sea Research Part II: Topical Studies in Oceanography 102, 119–131.

Renaud, P.E., Morata, N., Ambrose Jr., W.G., Bowie, J.J., Chiuchiolo, A., 2007. Carbon cycling by seafloor communities on the eastern Beaufort Sea shelf. Journal of Experimental Marine Biology and Ecology 349, 248–260.

Renaud, P.E., Sejr, M.K., Bluhm, B.A., Sirenko, B., Ellingsen, I.H., 2015. The future of Arctic benthos: expansion, invasion, and biodiversity. Progress in Oceanography (special issue) (in press).

Richman, S.E., Lovvorn, J.R., 2003. Effects of clam species dominance on nutrient and energy acquisition by spectacled eiders in the Bering Sea. Marine Ecology Progress Series 261, 283–297.

Roach, A.T., Aagaard, K., Pease, C.H., Salo, S.A., Weingartner, T., Pavlov, V., Kulakov, M., 1995. Direct measurements of transport and water properties through the Bering Strait. Journal of Geophysical Research 100 (C9), 18443–18457.

Sambrotto, R.N., Goering, J.J., McRoy, C.P., 1984. Large yearly production of phytoplankton in the western Bering Strait. Science 225, 1147–1150.

Savard, J.-P., 1989. Birds of the rocky coastlines and pelagic waters in the Strait of Georgia. In: Vermeer, K., Butler, R.W. (Eds.), The Ecology and Status of Marine and Shoreline Birds in the Strait of Georgia, British Columbia. Canadian Wildlife Service, Special Publication, pp. 132–141.

Schonberg, S.V., Clarke, J.T., Dunton, K.H., 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: Topical Studies in Oceanography 102, 144–163.

Sheffield, G.S., Grebmeier, J.M., 2009. Pacific walrus (*Odobenus rosmarus divergens*): differential prey digestion and diet. Marine Mammal Science 25. http://dx.doi.org/10.1111/j.1748-7692.2009.00316.

Sirenko, B.I., Gagaev, S.Y., 2007. Unusual abundance of macrobenthos and biological invasions in the Chukchi Sea. Russian Journal of Marine Biology 33, 355–364.

Søreide, J.E., Leu, E., Berge, J., Graeve, M., Falk-Petersen, S., 2010. Timing in blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. Global Change Biology 16, 3154–3163.

Spall, M.A., 2007. Circulation and water mass transformation in a model of the Chukchi Sea. Journal of Geophysical Research: Oceans (1978–2012) 112 (C5).

Springer, A.M., McRoy, C.P., Flint, M.V., 1996. The Bering Sea Green Belt: shelf-edge processes and ecosystem production. Fisheries Oceanography 5, 205–223.

Stafford, K.M., Moore, S.E., Spillane, M., Wiggins, S., 2007. Gray whale calls recorded near Barrow, Alaska throughout the winter of 2003–2004. Arctic 60, 167–172.

Stehn, R.A., Larned, W.W., Platte, R.M., 2013. Analysis of Aerial Survey Indices Monitoring the Waterbird Populations of the Arctic Coastal Plain, Alaska, 1986–2012. US Fish and Wildlife Service, Anchorage, AK.

Stevenson, D.E., Lauth, R.R., 2012. Latitudinal trends and temporal shifts in the seafloor ecosystem of the eastern Bering Sea shelf and southeastern Chukchi Sea. Deep Sea Research Part II: Topical Studies in Oceanography 65–70, 251–259.

Stigebrandt, A., 1984. The North Pacific: a global-scale estuary. Journal of Physical Oceanography 14, 464–470. http://dx.doi.org/10.1175/1520 0485(1984)014 <0464:TNPAGS>2.0.CO;2.

Stoker, S.W., 1978. Benthic Invertebrate Macrofauna of the Eastern Continental Shelf of the Bering/Chukchi Seas. Dissertation, University of Alaska Fairbanks.

Stroeve, J.C., Markus, T., Boisvert, L., Miller, J., Barrett, A., 2014. Changes in Arctic melt season and implications for sea ice loss. Geophysical Research Letters 41. http://dx.doi.org/10.1002/2013GL058951.

Sun, M., Carroll, M.L., Ambrose, W.G., Clough, L.M., Zou, L., Lopez, G.R., 2007. Rapid consumption of phytoplankton and ice algae by Arctic soft-sediment benthic communities: evidence using natural and C-13-labeled food materials. Journal of Marine Research 65 (4), 561–588.

Vermeer, K., Morgan, K.H., 1992. Marine bird populations and habitat use in a fjord on the west coast of Vancouver Island. In: Vermeer, K., Butler, R.W., Morgan, K.H. (Eds.), The Ecology, Status, and Conservation of Marine and Shoreline Birds on the West Coast of Vancouver Island. Canadian Wildlife Service, Occasional Paper No. 75, pp. 86–96.

Vermeer, K., Morgan, K.H., Dorst, A., Whittington, B., 1992. Bird populations of estuaries on the southwest coast of Vancouver Island. In: Vermeer, K., Butler, R.W., Morgan, K.H. (Eds.), The Ecology, status, and Conservation of Marine and Shoreline Birds on the West Coast of Vancouver. Canadian Wildlife Service, Occasional Paper No. 75, pp. 97–108.

Walsh, J.J., McRoy, C.P., Coachman, L.K., Goering, J.J., Nihoul, J.J., Whitledge, T.E., Blackburn, T.H., Parker, P.L., Wirick, C.D., Shuert, P.G., Grebmeier, J.M., Springer, A.M., Tripp, R.D., Hansell, D.A., Djenidi, S., Deleersnijder, E., Henricksen, K., Lund, B.A., Andersen, P., Müller-Karger, F.E., Dean, K., 1989. Carbon and nitrogen cycling within the Bering/Chukchi Seas: source regions for organic matter effecting AOU demands of the Arctic Ocean. Progress in Oceanography 22, 277–359.

Walsh, J.J., Dieterle, D.A., Maslowski, W., Grebmeier, J.M., Whitledge, T.E., Flint, M., Sukhanova, I.N., Bates, N., Cota, C.F., Stockwell, D., Moran, S.B., Hansell, D.A., McRoy, C.P., 2005. A numerical model of seasonal primary production within the Chukchi/Beaufort seas. Deep Sea Research Part II: Topical Studies in Oceanography 52, 3541–3570.

Warwick, R.M., 1993. Environmental impact studies on marine communities: pragmatical considerations. Australian Journal of Ecology 18, 63–80.

Wassmann, P., Duarte, C.M., Agusti, S., Sejr, M.K., 2011. Footprints of climate change in the Arctic marine ecosystem. Global Change Biology 17, 1235–1249.

Weingartner, T.J., Danielson, S., Sasaki, Y., Pavlov, V., Kulakov, M., 1999. The Siberian Coastal Current: a wind and buoyancy-forced arctic coastal current. Journal of Geophysical Research 104, 29697–29713.

Weingartner, T.J., Danielson, S.L., Royer, T.C., 2005. Freshwater variability and predictability in the Alaska Coastal Current. Deep Sea Research Part II: Topical Studies in Oceanography 52, 169–191.

Weingartner, T., Dobbins, E., Danielson, S., Winsor, P., Potter, R., Statscewich, H., 2013. Hydrographic variability over the northeastern Chukchi Sea shelf in summer–fall 2008–2010. Continental Shelf Research 67, 5–22.

Whitehouse, G.A., Aydin, K., Essington, T.E., Hunt Jr., G.L., 2014. A trophic mass balance model of the eastern Chukchi Sea with comparisons to other high-latitude systems. Polar Biology 37, 911–939.

Williams, W., Shroyer, E., Clement Kinney, J., Itoh, M., Maslowski, W., 2014. Shelf-break exchange in the Bering, Chukchi and Beaufort seas. In: Grebmeier, J.M., Maslowski, W. (Eds.), The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment. Springer, Dordrecht, pp. 133–166 (Chapter 6).

Winsor, P., Chapman, D.C., 2004. Pathways of Pacific water across the Chukchi Sea: a numerical model study. Journal of Geophysical Research: Oceans 109, C03002. http://dx.doi.org/10.1029/2003JC001962.

Woelfel, J., Schumann, R., Peine, F., Flohr, A., Kruss, A., Tegowski, J., Blondel, P., Wiencke, C., Karsten, U., 2010. Microphytobenthos of Arctic Kongsfjorden (Svalbard, Norway): biomass and potential primary production along the shore line. Polar Biology 33, 1239–1253.

Wood, K.R., Bond, N.A., Danielson, S.L., Overland, J.E., Salo, S.A., Stabeno, P.J., Whitefield, J., 2015. A decade of environmental change in the Pacific Arctic region. Progress in Oceanography 136, 12–31. http://dx.doi.org/10.1016/j.pocean.2015.05.005.

Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2005a. Monthly temperature, salinity, and transport variability of the Bering Strait through flow. Geophysical Research Letters 32, L04601. http://dx.doi.org/10.1029/2004GL021880.

Woodgate, R.A., Aagaard, K., Weingartner, T.J., 2005b. A year in the physical oceanography of the Chukchi Sea: moored measurements from autumn 1990–1991. Deep Sea Research Part II: Topical Studies in Oceanography 52, 3116–3149.

Woodgate, R.A., Weingartner, T.J., Lindsay, R., 2012. Observed increases in Bering Strait oceanic fluxes from the Pacific to the Arctic from 2001 to 2011 and their impacts on the Arctic Ocean water column. Geophysical Research Letters 39 (24).

Yun, M.S., Kim, B.K., Joo, H.T., Eun Jin Yang, E.J., Nishino, S., Chung, K.H., Kang, S.-H., Lee, S.H., in press. Regional productivity of phytoplankton in the western Arctic Ocean during summer in 2010. *Deep Sea Research Part II: Topical Studies in Oceanography*. http://dx.doi.org/10.1016/j.dsr2.2014.11.023.