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

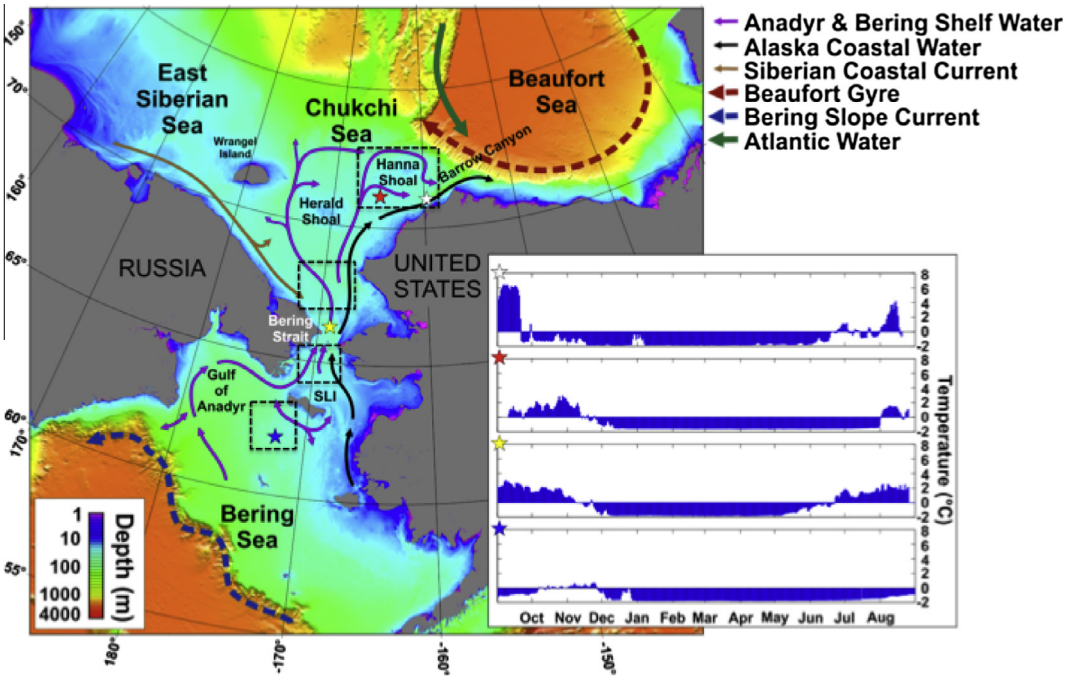

Fig. 1. Schematic of current flow patterns, water mass type, and bottom water temperatures at four moorings from the northern Bering Sea to the northeastern Chukchi Sea in relation to SOAR benthic hotspot sites (boxes). Key: Blue star = N55 mooring within the SLIP (St. Lawrence Island Polynya region) 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.