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ORIGINAL PAPER

Recent change in benthic macrofaunal community composition in relation to physical forcing in the Pacific Arctic

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Abstract

There is growing evidence that increased Pacific water transport into the Arctic affects the marine ecosystem. One of the theoretical predictions for a future Arctic characterized by such environmental change is that subarctic taxa will expand northward and invade the native Arctic ecosystem. This study focuses on variation in macrofaunal community composition and the influence of changing physical drivers at known benthic hotspots in the Pacific Arctic. The average number of macrofaunal family-level taxa has increased significantly south of St. Lawrence Island and in the Chirikov Basin, whereas the number of macrofaunal taxa in the southeastern Chukchi Sea showed no significant trend over the 2000–2013 time period. However, the Shannon–Weaver diversity index, based on abundance, did not mirror these regional changes in the number of macrofaunal taxa, indicating that the abundance of newly present taxa was negligible compared to the entire abundance already present. We also investigated temporal variations in meridional sea level gradient and local winds, which contribute 2/3 and 1/3 of the variation in northward volume transport at Bering Strait, respectively. There were significant increasing trends in the meridional sea level gradient and local winds, suggesting the increased northward seawater volume transports over the benthic hotspots could contribute to the expansion of subarctic taxa into these northern Arctic regions. Our data suggest an increase in macrofaunal taxa type with increasing current transport northward into the Pacific Arctic region that could have a strong influence in restructuring the benthic ecosystem in this region in the future.

Keywords Benthos · Macrofauna composition · Pacific arctic · Diversity · Volume transports

Introduction

The Bering Strait, characterized by a narrow (~ 85-km-wide) and shallow (~ 50-m-depth) channels between the northern Bering Sea and Chukchi Sea, is the only oceanic Pacific Arctic gateway. Although the currents transiting through the strait are modest in global term, the impact of the Bering Strait throughflow is substantial in the Arctic (Woodgate et al. 2015; Woodgate 2018). For instance, the heat flux through the Bering Strait acts as a trigger for sea ice retreat in the Chukchi and Beaufort Seas and a major subsurface source of heat to about half of the Arctic (Woodgate et al. 2010, 2012). In addition, the freshwater flux in the Bering Strait accounts for ~ 40% of the total freshwater input to the Arctic Ocean (Woodgate and Aagaard 2005). Beside its physical function, the Pacific water transiting through the Bering Strait plays a central role in the biogeochemical and biological environmental state in the Pacific Arctic (Giesbrecht et al. 2019). Water masses transiting through the Bering Strait include the relatively colder, saltier, and nutrient-rich water of the Anadyr Current in the west; warmer, fresher and nutrient-poor Alaskan Coastal Current in the east; and Bering Shelf water of intermediate properties in the middle (Pickart et al. 2010). The western areas in the region influenced by high nutrient concentrations in the Anadyr Current have comparatively higher standing stocks of phytoplankton, benthic macrofauna, and demersal fish (Grebmeier et al. 2015a, 2018).

Time series data obtained by a recent high-resolution mooring array indicate the Bering Strait throughflow increased ~ 50% from 2001 (~ 0.7 Sv) to 2013 (~ 1.1 Sv) (Woodgate et al. 2012; Woodgate 2018). The variation

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in northward flow through Bering Strait is set by the sea level gradient between the Bering and Chukchi Seas, and local wind (Woodgate et al. 2005, 2012; Woodgate 2018): the sea level gradient drives the northward flow through Bering Strait as background flow; the wind forcing drives strong but short-term fluctuation of the flow and often reverse the northward flow set by the sea level gradient (Coachman and Aagaard 1966). In fact, Danielson et al. (2014) reported that the northward transport through Bering Strait changes on inter-annual time scales in response to the meridional sea level gradient. They also described that synoptic to monthly time scale variations in shelf currents result from the local wind forcing as well as remotely generated continental shelf waves. Consequently, there is growing knowledge on the processes influencing recent variation in Pacific water transport through the Bering Strait to the Arctic.

Climate changes are affecting polar marine ecosystems faster and stronger than those in other regions (Doney et al. 2012), and hence assessing impacts of climate changes on species distribution is a major challenge in the Arctic Ocean (Mueter and Litzow 2008; Hollowed et al. 2013). One of the logical predictions for a future Arctic Ocean characterized by the increased northward volume transport through Bering Strait is that new taxa will expand their distribution northward and invade the Arctic ecosystem (Renaud et al. 2015). However, well-documented examples are still scarce due to the small number of time series measurements in the Arctic, particularly for benthic organisms (Renaud et al. 2015). Although benthic macrofauna are normally stationary and less mobile, benthic macrofauna with pelagic life stages will be less limited in their expansion abilities (Renaud et al. 2015). In addition, the dispersal distance of marine larvae in cold water are much greater than those in warmer water, because temperature is inversely related to larval duration (O'Connor et al. 2007). Non-native species with greater ecological generality and the capacity to tolerate more extreme abiotic conditions have the potential to seriously affect an ecosystem by outcompeting native species, resulting in disruptions of the existing biological interactions and food web dynamics (Sorte et al. 2010; Bates et al. 2013). Consequently, these facts suggest that benthic macrofaunal communities in the Arctic would be experiencing drastic variations in community composition as well as diversity in response to recent increased Pacific water transport. Since the Arctic, especially the Pacific Arctic, is an important foraging area for benthic feeding species (Grebmeier et al. 2006), variations in benthic macrofaunal community composition can propagate to upper trophic levels through trophic cascades (Grebmeier et al. 2010, 2015a). Thus, evaluating time series variations in benthic communities is crucial for better understanding of the Pacific Arctic ecosystem, because long-living benthic organisms are a valuable component for monitoring shifting environmental conditions (Grebmeier et al. 2018).

We aimed to investigate potential influences of the northward volume transport on benthic community composition in the Pacific Arctic. In this study, temporal variations in the meridional sea level gradient and local wind were used as indices of the northward volume transport in the Pacific Arctic. Additionally, we examined the spatiotemporal variations in benthic macrofaunal biomass, number of macrofaunal taxa, and family-level diversity. These time series data have been observed at areas of notably high benthic biomass, termed benthic hotspots, by the international distributed biological observatory (DBO), which provide an observing framework for understanding changing Arctic ecosystems and expand on existing knowledge (Moore and Grebmeier 2018).

Materials and methods

Satellite altimetry data

Monthly mean gridded satellite altimetry data for 2000–2013 were downloaded from the Archiving, Validation, and Interpretation of Satellite Oceanographic (AVISO) data website (http://www.aviso.oceanobs.com/), which combines data from the TOPEX/Poseidon mission along with other satellites to generate global gridded sea surface height (SSH) anomalies. The merged data are mapped on a 1/3° global grid. Expected accuracy (<2 cm) is $<5\%$ of the signal variance for multi-satellite month-long averages, but variance increases in seasonally ice-covered waters therefore contain no usable data. The annual cycle was removed by subtracting each month's mean at each grid cell from original monthly data (Danielson et al. 2014).

Atmospheric reanalysis data

The National Centers for Environmental Prediction (NCEP) North American Regional Reanalysis (NARR) model (Mesinger et al. 2006) computes variable products containing temperatures, winds, moisture, soil data, and dozens of other parameters on a ~ 35 km grid. The data were obtained from the National Operational Model Archive & Distribution System (NOMADS) website (https://nomads.ncdc.noaa.gov/data/narr/) operated by the National Oceanic and Atmospheric Administration (NOAA) for 2000–2013, and used daily and monthly averaged values of 10-m-height wind vector components (u and v) for the region.

Benthic macrofaunal data

Benthic macrofaunal time series biomass, number of family-level taxa, and an abundance-based family-level Shannon–Weaver diversity index (SWI) were obtained from the public data archives (Grebmeier and Cooper 2018a, b). SWI is a commonly used diversity index that takes into account both the faunal type in a data set and evenness of abundance present in the community. The SWI index increases both when the number of faunal types (i.e., number of family taxa in our study) increases and when evenness of entities measured (i.e., abundance of each family taxa in our study) increases. The data were collected at 16 fixed stations (SLIP1–5, UTBS1–2, UTBS4–5, and UTN1–7) (Fig. 1; Table 1) in mid-July 2000–2013 (Table 2). These sampling stations are well known as benthic hotspots (Grebmeier et al. 2018). Note that data observed in 2009 were not used for our analysis because the sampling was limited and did not occur in July. Four replicate van Veen grabs were collected at each station. Sediments were sieved through 1 mm mesh screens, with the biological samples subsequently preserved with 10% buffered seawater formalin for post-cruise taxonomic identification and wet weight biomass determination. In this study, macrofaunal dry carbon biomass (using conversion values from wet mass, formalin-preserved samples) was used to reduce the bias of calcium carbonate on weight values (Grebmeier et al. 2015b). Detailed descriptions of methods used for determining macrofaunal biomass and conversion factors are provided in Grebmeier and Cooper (2018a, b).

Table 1 List of station names and locations of time series observation stations for benthic macrofaunal data in the benthic hotspots: south of St. Lawrence Island (SLI); Chirikov Basin (Chirikov); and southeastern Chukchi Sea (Chukchi)

Hotspot	Station	Latitude (°N)	Longitude (°W)
South of SLI	SLIP1	62.01	175.06
	SLIP2	62.05	175.21
	SLIP3	62.39	174.57
	SLIP5	62.56	173.55
	SLIP4	63.03	173.46
Chirikov	UT-BS5	64.67	169.92
	UT-BS2	64.68	169.10
	UT-BS4	64.96	169.89
	UT-BS1	64.99	169.14
Chukchi	UTN1	66.71	168.34
	UTN2	67.05	168.73
	UTN3	67.30	168.97
	UTN4	67.50	168.91
	UTN5	67.67	168.96
	UTN6	67.74	168.49
	UTN7	68.00	168.93

Results

Long-term variations in meridional sea level gradient and local winds

Figure 2a shows the difference in annual SSH between 2000 (SSH_{2000}) and 2013 (SSH_{2013}), suggesting a broad area of higher SSH in 2013 compared to 2000. Indeed,

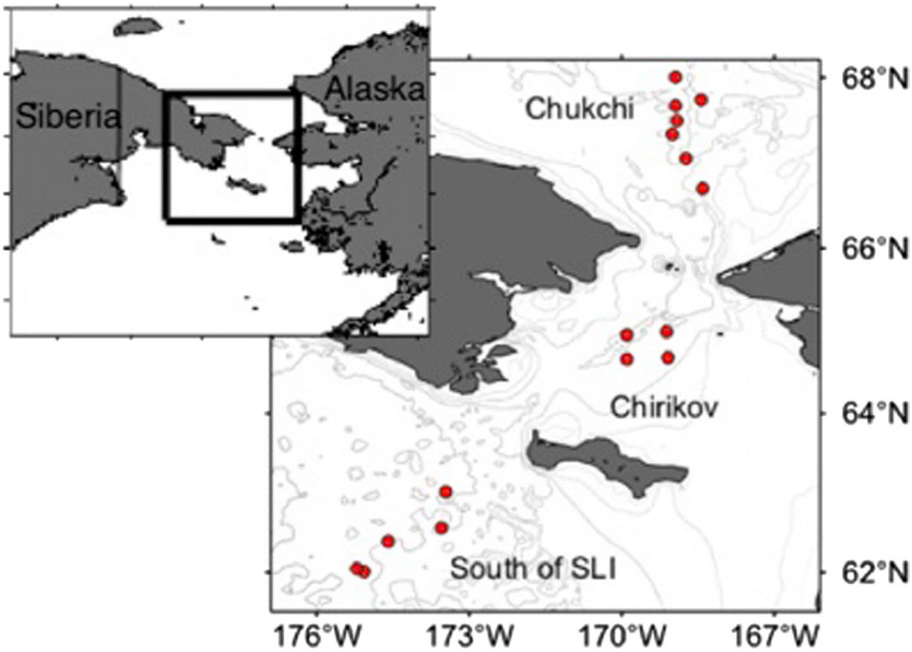

Fig. 1 Station locations at the benthic hotspots in the Pacific Arctic where time series benthic macrofaunal sampling were conducted in July 2000–2013, except 2009 (red circles). South of SLI, Chirikov, and Chukchi represent south of St. Lawrence Island (SLI), Chirikov Basin, and southeastern Chukchi Sea hotspots, respectively

Table 2 Cruise sampling dates, name, and number of benthic macrofaunal data sets (*N*) used in this study in the 3 hotspot regions collected in July 2000–2013

Date range	Cruise	*N*
19–23 Jul. 2000	SWL00	16
17–20 Jul. 2001	SWL01	16
15–18 Jul. 2002	SWL02	16
14–18 Jul. 2003	SWL03	16
15–19 Jul. 2004	SWL04	16
14–18 Jul. 2005	SWL05	16
12–17 Jul. 2006	SWL06	16
14–17 Jul. 2007	SWL07	16
16–21 Jul. 2008	SWL08	15
16–19 Jul. 2010	SWL10	16
15–18 Jul. 2011	SWL11	16
14–16 Jul. 2012	SWL12	16
13–20 Jul. 2013	SWL13	16

Note that data observed in 2009 were not used for our analysis because the sampling was limited and did not occur in July

temporal variation in SSH was significant (Mann–Kendall test, $p < 0.05$) in the Aleutian Basin, whereas the continental shelves extending from the northern Bering Sea to the Chukchi Sea exhibited insignificant trend over the period (Fig. 2b). Thus, we computed a temporal trend of a difference in SSH (ΔSSH) between the Aleutian Basin ($\mathrm{SSH_{AB}}$; 50°–55°N and 170°E–180°) and southwestern Chukchi Sea ($\mathrm{SSH_{CS}}$; 66°–70°N and 180°–170°W), which is as an index of the meridional sea level gradient between the Bering and Chukchi Seas, in accordance with a method proposed by Danielson et al. (2014). There was a significant increasing trend (Mann–Kendall test, $p < 0.05$) in ΔSSH due to the increased SSH in the Aleutian Basin with negligible trend in southwestern Chukchi Sea (Fig. 3). These variations in SSH represent an increasing trend in meridional sea level gradient with time, suggesting a greater annual mean northward volume transport from the Pacific to the Arctic oceans.

According to previous studies, there are slight differences in surface wind direction that gives the best correlation with the northward current (Woodgate et al. 2005; Danielson et al. 2012a, b, 2014). Hence, temporal variations in local wind headings 315°, 330°, and 0° were examined in three hotspot regions: south of St. Lawrence Island (SLI), Chirikov Basin (Chirikov), and southeastern Chukchi Sea (Chukchi), respectively (Woodgate et al. 2005; Danielson et al. 2012a, b). Comparing the local winds at each hotspot between 2000 and 2013, it was clear that both opposite (away from) and compatible winds (toward) acting on the best correlate directions declined and increased, respectively, more in 2013 than 2000 (Fig. 4). There were significant increasing local winds heading toward the best correlate directions within the three regions (Fig. 5).

Regional differences in benthic macrofaunal community among the hotspots

Average macrofaunal biomass for 2000–2013 (Fig. 6a–c) had the highest value at the Chukchi hotspot (33.8 ± 12.5 gC $\mathrm{m^{-2}}$; mean ± 1SD), followed by the Chirikov hotspot (21.5 ± 4.8 gC $\mathrm{m^{-2}}$) and south of SLI hotspot (17.5 ± 3.1

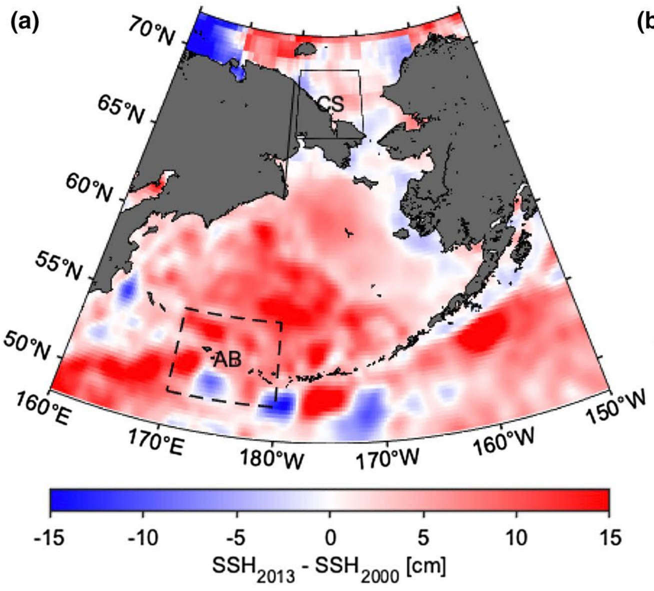

Fig. 2 Difference in annual sea surface height (SSH) between 2000 ($\mathrm{SSH_{2000}}$) and 2013 ($\mathrm{SSH_{2013}}$) (**a**), and temporal trend in annual SSH for 2000–2013 (**b**). White areas in **b** show the area with non-significant trend (Mann–Kendall test, $p \geq 0.05$). Dashed and solid boxes represent the areas integrated for deriving SSH difference between the Aleutian Basin (AB) and southwestern Chukchi Sea (CS)

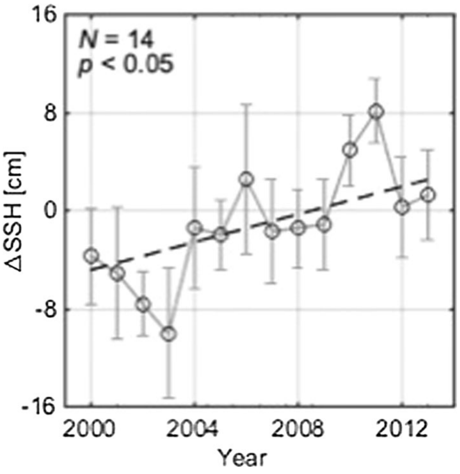

Fig. 3 Temporal trend in difference in sea surface height (ΔSSH) between the Aleutian Basin (SSH_{AB}; 50°–55°N and 170°E–180°) and the Chukchi Sea (SSH_{CS}; 66°–70°N and 180°–170°W) for 2000–2013 ($N = 14$). Dashed line represents Sen's median slope for ΔSSH time series that shows statistically significant trend (Mann–Kendall test for trend, $p < 0.05$). The areas integrated for deriving SSH_{AB} and SSH_{CS} are shown in Fig. 2. The standard deviations (±1SD) are denoted by the vertical bars

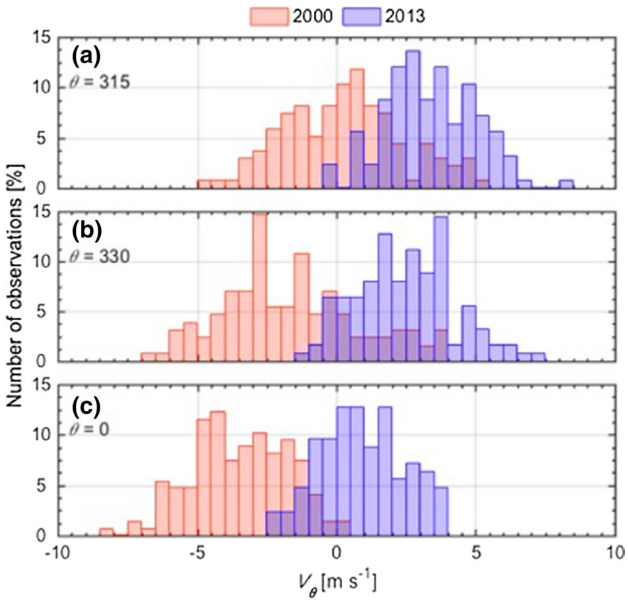

Fig. 4 Histograms of daily local wind velocities along best correlate directions (V_θ) the benthic hotspots. South of SLI, Chirikov, and Chukchi represent south of St. Lawrence Island (SLI), Chirikov Basin, and southeastern Chukchi Sea hotspots, respectively. θ were 315°, 330°, and 0° for south of SLI, Chirikov, and Chukchi. Red and blue bars represent winds in 2000 and 2013, respectively

gC m^{-2}). The Chirikov hotspot exhibited the largest average number of macrofaunal family taxa of 40 ± 6 no. taxa m^{-2}, whereas the region south of SLI hotspot and Chukchi hotspot were 38 ± 3 no. taxa m^{-2} and 35 ± 5 no. taxa m^{-2}, respectively (Fig. 6d–f). Furthermore, average SWI values (Fig. 6g–i) were the highest south of SLI (2.70 ± 0.22), with the intermediate SWI of 2.20 ± 0.41 in the Chirikov hotspot and the lowest SWI of 1.98 ± 0.53 in the Chukchi hotspot.

Spatio-temporal variations in benthic macrofaunal communities

Temporal trends in average macrofaunal biomass showed regional differences for the period 2000–2013: i.e., significant decreasing trend south of SLI (Mann–Kendall test, $p < 0.05$); no trend in the Chirikov hotspot (Mann–Kendall test, $p = 0.25$); and increasing trend observed in the Chukchi hotspot (Mann–Kendall test, $p < 0.05$). The average number of family-level taxa south of SLI and in the Chirikov hotspots showed a significant increasing trend over the period (Mann–Kendall test, $p < 0.05$), while that of Chukchi hotspot exhibited no significant increase or decrease (Mann–Kendall test, $p = 0.86$). The Chukchi hotspot was the only region that showed significant temporal variation in SWI for the 2000–2013 period (Mann–Kendall test, $p < 0.05$): temporal trend in SWI in the Chukchi hotspot showed significant decreasing trend, whereas the rest of hotspots exhibited no significant trends (Mann–Kendall test, $p = 0.63$ and 0.07 south of SLI and Chirikov hotspots, respectively).

Relationship between number of macrofaunal family and physical forcing

Direct comparisons between number of family-level taxa and the meridional sea level gradient showed significant positive relationships south of SLI and Chirikov hotspots (Fig. 7; Spearman's rank correlation test, $p < 0.05$), where the regions exhibited increasing trends in number of family taxa for 2000–2013 (Fig. 6). On the other hand, relationships between the number of family taxa at each hotspot and local winds at the regions were significant (Spearman's rank correlation test, $p < 0.05$) only south of SLI, and those of the other two hotspots were insignificant during the study period (Fig. 7; Spearman's rank correlation test, $p = 0.05$ and 0.62 in the Chirikov and Chukchi hotspots, respectively).

Discussion

The Aleutian Low is a semi-permanent low-pressure system located over the Bering Sea. Danielson et al. (2014) reported that eastward displacement of the Aleutian Low into the Gulf of Alaska from over the Bering Sea results in more northward volume transport at the Bering Strait owing to combination of two factors: increased sea level gradient between the Aleutian Basin and Chukchi Sea at inter-annual timescales, and increased southeasterly wind

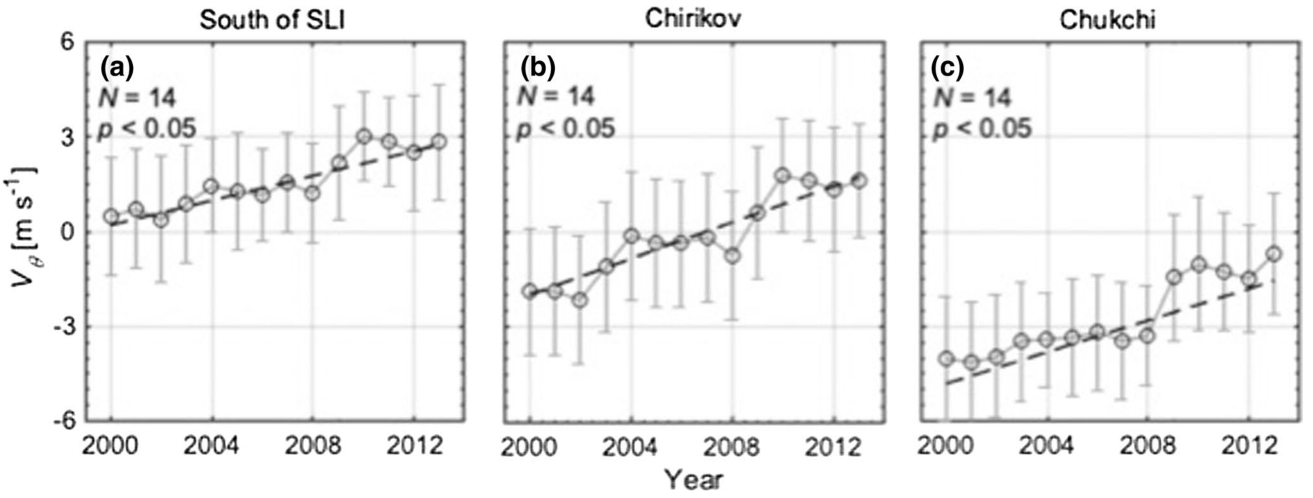

Fig. 5 Temporal trends in annual local wind velocities along best correlate directions (V_θ) the benthic hotspots for 2000–2013 ($N = 14$). South of SLI, Chirikov, and Chukchi represent south of St. Lawrence Island (SLI), Chirikov Basin, and southeastern Chukchi Sea hotspots, respectively. θ were 315°, 330°, and 0° for south of SLI, Chirikov, and Chukchi. Dashed lines represent Sen's median slopes for V_θ time series that show statistically significant trends (Mann–Kendall test for trend, $p < 0.05$). The standard deviations (±1SD) are denoted by the vertical bars

over the Bering shelf on synoptic storm timescales. Indeed, we found the increment of meridional sea level gradient in addition to reductions in the opposite wind (away from) and/or increases in the compatible wind (toward) acting on the northward currents at each hotspot. As nutrient-rich water of the Anadyr Current is one of the most crucial sources for high seasonal levels of primary production in the Pacific Arctic, these inter-annual patterns in sea level gradient and local winds increased lateral advection as well as in situ production of phytodetritus that impacts directly and/or indirectly the amount of organic carbon accumulating in the sediments (Blanchard and Feder 2014; Grebmeier et al. 2015a; Waga et al. 2019). Hence, the increased northward volume transport through the Bering Strait and subsequently increased amount of organic carbon content in the sediment could support increased macrofaunal biomass in the Chukchi hotspot (Grebmeier et al. 2018), because a stronger Bering Strait throughflow could represent a higher nutrient flux (Danielson et al. 2017). As macrofaunal composition in the Pacific Arctic is strongly linked with current flow that is a key driver for sedimentation patterns determining sediment grain size (Pisareva et al. 2015), these variations in recent current dynamics may affect not only biomass but also community composition of benthic macrofauna. Historically, macrofaunal community composition is quite different among hotspots: south of SLI hotspot has been dominated by mainly nuculid and nuculanid bivalves and sometime maldanid polychaetes; the dominant faunal taxa in the Chirikov hotspot were ampeliscid amphipods; the Chukchi hotspot was historically bivalve-dominated (Grebmeier et al. 2018). However, changes to sediment grain size have been simultaneously occurring south of SLI with an increased proportion of finer sediments, which coincided with the switch to dominance of polychaetes over bivalves (Grebmeier et al. 2015a). In addition, macrofaunal composition in station UT-BS5 (Table 1), which was dominated by ampeliscid amphipods in the 1980s–1990s, switched to polychaete dominance and sometime bivalves (Grebmeier et al. 2018). Consequently, changes in benthic macrofaunal biomass and community composition would be in part tied to the increased northward seawater volume transport (Grebmeier et al. 2015a).

Many benthic invertebrate species have a dispersive larval stage in their life cycles (Thorson 1950), and benthic organisms with pelagic life stages will be less limited in their expansion abilities (Renaud et al. 2015). Thus, pelagic dispersion of larvae would be able to bridge the barrier of the cold pool. We found significant relationships between the physical forcing controlling northward seawater volume transport and number of family-level taxa. These results suggest that the increased northward volume at each hotspot could promote northward expansion of subarctic taxa into the Pacific Arctic. In general, the cold pool south of SLI acts as a barrier to many temperate species that are intolerant of the low temperatures of ice-associated bottom water (Sigler et al. 2016), and therefore determines the boundary between arctic and subarctic communities (Wyllie-Echeverria and Wooster 1998; Grebmeier et al. 2006). However, there is evidence of increased heat flux through the Bering Strait over the last decade (e.g., Woodgate et al. 2015 and references therein; Woodgate 2018). Indeed, projected temperature increases in shallow (< 200 m) waters of many

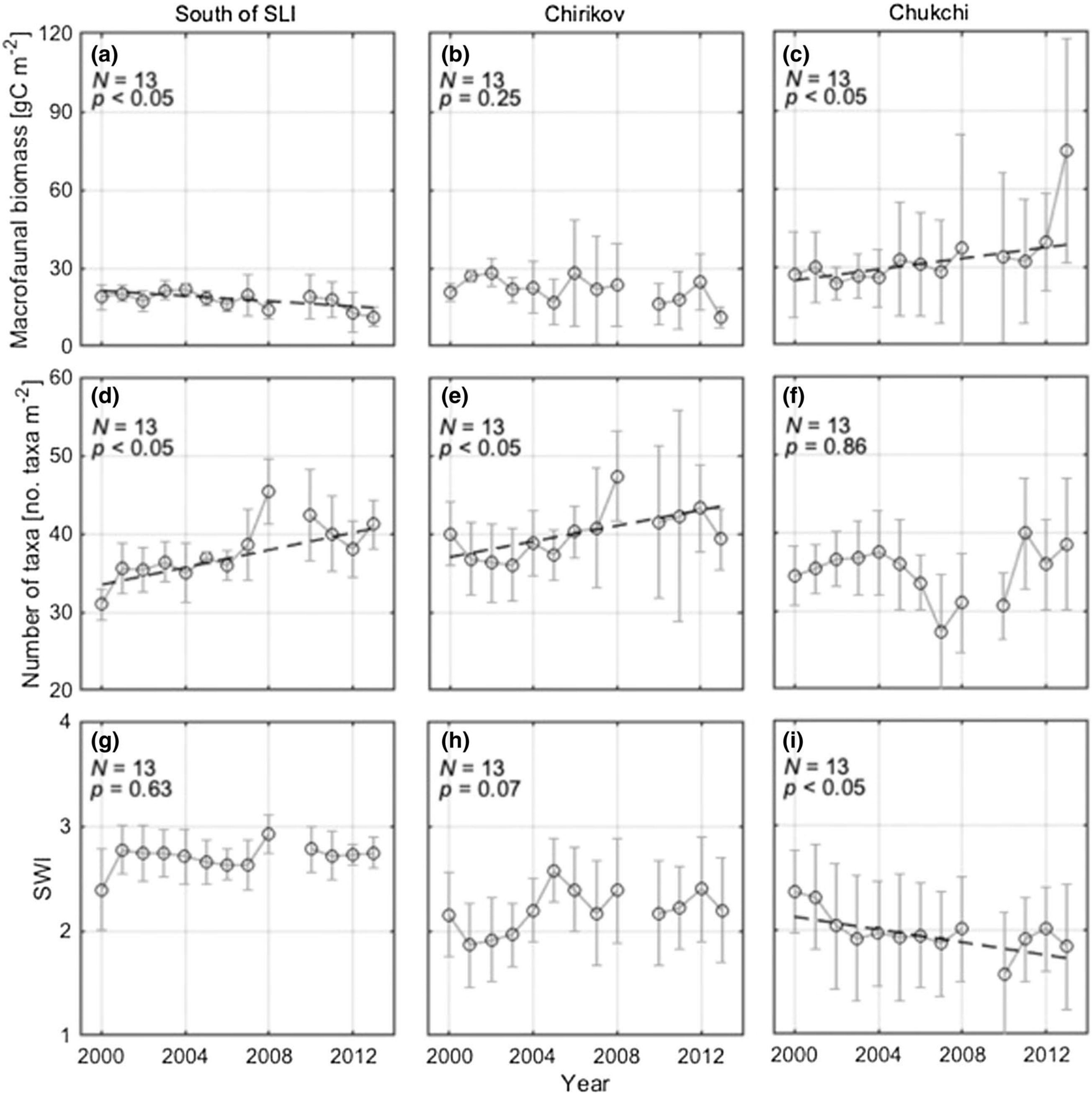

Fig. 6 Temporal trends in the averaged macrofaunal biomass (**a**–**c**), number of taxa (**d**–**f**), and Shannon–Weaver diversity index (SWI) (**g**–**i**) at the benthic hotspots during 2000–2013 ($N = 13$). South of SLI, Chirikov, and Chukchi represent south of St. Lawrence Island (SLI), Chirikov Basin, and southeastern Chukchi Sea hotspots, respectively. Sen's median slopes are shown only for those time series that show statistically significant trends (Mann–Kendall test, $p < 0.05$). The standard deviations (±1SD) are denoted by the vertical bars

Arctic marginal seas may exceed 2–3 °C by 2100 (Renaud et al. 2015). Since even small levels of ocean warming could reduce physiological barriers for subarctic taxa, warming of ocean temperatures in the future Arctic will have significant implications for northward expansion of subarctic taxa, not only benthic organisms with pelagic life stages but also other organisms such as demersal fishes (Mueter and Litzow 2008; Hollowed et al. 2013). Furthermore, Siddon and Zabor (2018) reported a reduction of a cold pool (remnant cold water at depth) that forms when the St. Lawrence Island polynya is functioning (Grebmeier et al. 2006). As northward movements of demersal fishes and other subarctic species were strongly restricted by the presence of the cold pool, the lack of the cold pool associated with less sea ice

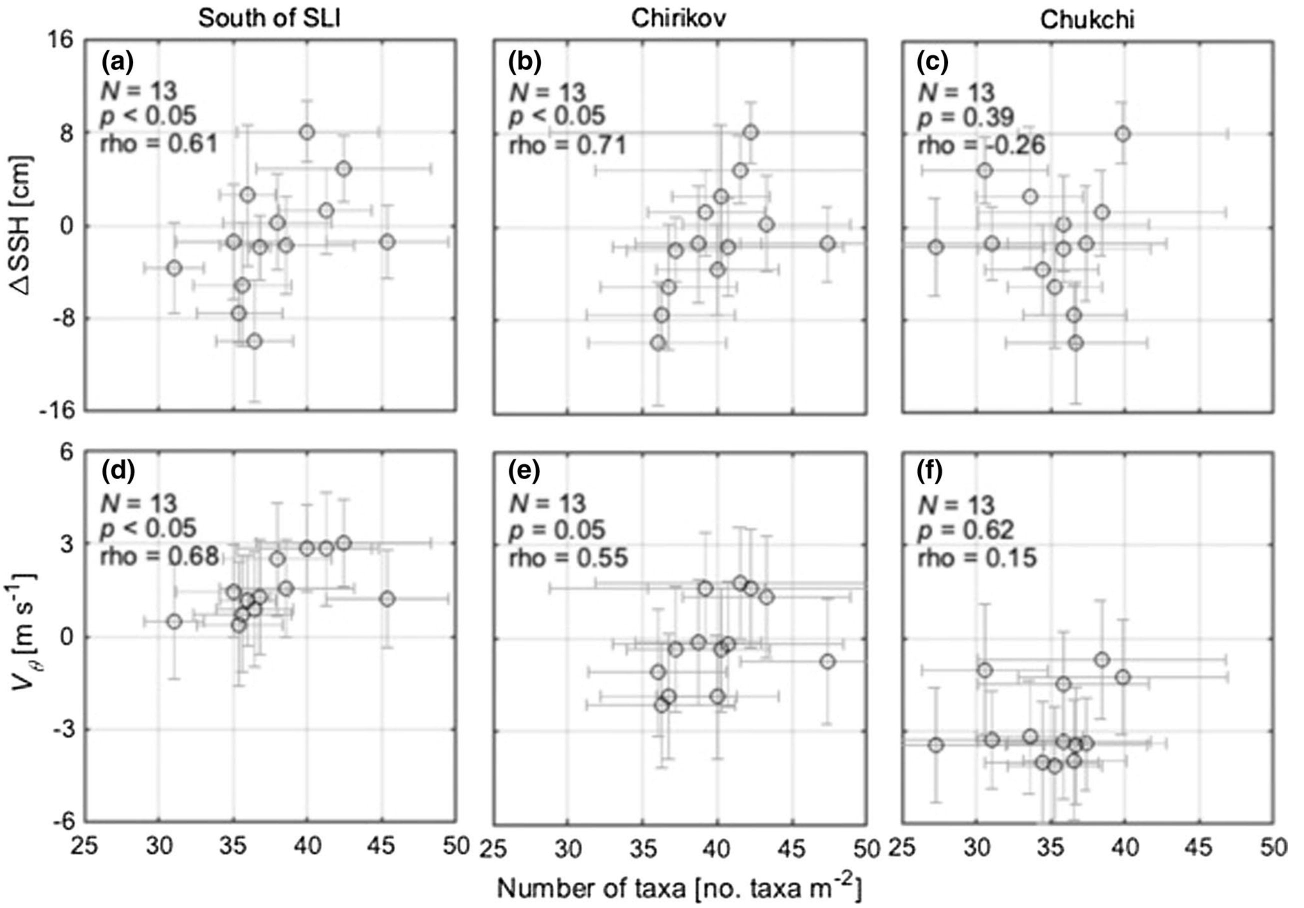

Fig. 7 Comparison results of number of taxa with difference in sea surface height between the Aleutian Basin and Chukchi Sea (ΔSSH) (**a**–**c**) and V_θ (**d**–**f**) at the benthic hotspots during 2000–2013 ($N = 13$), respectively. South of SLI, Chirikov, and Chukchi represent south of St. Lawrence Island (SLI), Chirikov Basin, and southeastern Chukchi Sea hotspots, respectively. Spearman's rank correlation coefficients are represented as rho. The standard deviations (± 1SD) are denoted by the vertical and horizontal bars

production would allow subarctic species to expand their distribution northward (Overland and Stabeno 2004). Overall, both reductions in the cold pool and warming of ocean temperature associated with increased northward volume transport would positively influence on northward dispersion and succession of colonization the Arctic by subarctic taxa, not only for benthic macrofauna but also other organisms (O'Connor et al. 2007; Ronowicz et al. 2015), because the poleward expansion of subarctic species is suggested to be largely related to thermal tolerance (Sunday et al. 2012).

Variations in SWI that represents abundance-based diversity in a macrofaunal community showed regional differences in our study, similar to the number of macrofaunal taxa. Despite the fact that the number of taxa in these hotspots has increased for 2000–2013, SWI south of SLI and in the Chirikov hotspots showed insignificant variation. These facts suggest the abundance of newly identified macrofaunal types into the regions seemed to be negligible compared with total macrofaunal population levels, resulting in quite little or no variation in evenness of abundance of each taxon. Additionally, these facts indicate that a decreased macrofaunal biomass south of SLI was caused by homogeneous decreases in biomass among the present taxa. Conversely, we observed a decreased SWI at the Chukchi hotspot for 2000–2013. Considering the facts that macrofaunal biomass and number of taxa showed increasing and negligible trends at the hotspot, respectively, the decrease in SWI would have been driven by a decrease in evenness of abundance in the macrofaunal community associated with an increased abundance of specific taxa. Grebmeier et al. (2018) found increasing bivalve populations in the Chukchi hotspot during our study period of 2000–2013, associated with high abundance of the tellinid bivalve *Macoma calcarea* as a result of hydrographic influences on food supply and sediment composition at this site (Goethel et al. 2019). Increased northward flow might enhance organic carbon loads in bottom waters, resulting in better feeding environment for suspension feeding organisms such as *M. calcarea* that can be both a suspension and deposit feeder (Goethel et al. 2019). Although this study has not examined a variation in abundance of individual family-level taxa, above facts would be reasonable evidences of decreased SWI. Overall, feeding strategy is likely to be important in deciding the winner of the race to secure supplies of foods and other resources (North et al. 2014). Therefore, not only in situ time series observations but also laboratory experiments evaluating differences among various feeding strategies would improve our understanding of ongoing ecosystem variations in benthic macrofaunal communities in the Pacific Arctic.

In summary, this study suggested that the different benthic hotspots from the northern Bering Sea to the southern Chukchi Sea are experiencing different changes in response to the increased northward volume transport in the Pacific Arctic: the number of macrofaunal taxa has increased significantly south of St. Lawrence Island and in the Chirikov Basin, whereas the number of macrofaunal taxa in the southeastern Chukchi Sea showed no significant trend over the 2000–2013 time period; meanwhile, SWI did not mirror these regional changes in the number of macrofaunal taxa, indicating that the abundance of newly present taxa was negligible compared to the entire abundance already present. These results imply that the benthic macrofaunal community in this region may be experiencing the beginning of community reconstruction from Arctic to subarctic faunal composition associated with the increased northward volume transport. Shifting species have the potential to seriously affect an ecosystem by outcompeting native species (Sunday et al. 2012), resulting in disruptions of the existing biological interactions and food web structure (Sorte et al. 2010). As subarctic species have higher habitat sensitivity and exposure to climate changes than Arctic taxa (Alabia et al. 2018), it is likely the future Pacific Arctic ecosystem will become closer in benthic community attributes to subarctic systems than what we see today.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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