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High-latitude benthic bivalve biomass and recent climate change: Testing the power of live-dead discordance in the Pacific Arctic

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ABSTRACT

Time-averaged molluscan death assemblages sampled from tropical to temperate open continental shelves commonly disagree in species composition with local living communities only in areas that have changed in response to anthropogenic eutrophication and other locally intense human stresses, providing a means of recognizing shifted baselines. In contrast, the ability of live-dead discordance to resolve the spatially heterogeneous effects of human-induced climate change has not been tested in high-latitudes, where climate change entails substantial changes in nutrient cycling with consequences for benthic biomass and where cold waters are antagonistic to carbonate shell preservation. North Pacific Arctic and Subarctic seabeds offer ideal conditions for testing the resolving power of molluscan live-dead discordance, using well-documented ecologic changes in nutrient cycling and benthic biomass in response to reduced sea ice. Ecosystem monitoring since 1980 has established that the boundary between the Arctic and the Subarctic on the Bering Sea continental shelf, maintained by ice-influenced bottom water, shifted northward between 1998 and 2001. The benthic community in the transitioned area now experiences new pelagic predators, more variable quantity and quality of deposited food, and altered sediment grain size, and macrofaunal dominance has shifted from diverse communities of specialized suspension or deposit feeders to facultative deposit feeding guilds. We find that in habitats where either Subarctic or Arctic conditions have persisted, bivalve death assemblages agree closely with counterpart living communities in taxon and guild composition and are not subject to significant post-mortem bias. Significant live-dead discordance occurs only in areas with documented changes in carbon delivery, sediment grain size, and community composition over the last several decades; there, death assemblages are mixtures of shells from pre- and post-transition communities, as confirmed by monitoring data. This spatial pattern is robust to both numerical abundance- and biomass-based measures of community composition. In fact, biomass is especially powerful in revealing fine, station-level discordance that is strongly tied to known sites within habitats where new carbon deposition levels, grain size, or benthos have occurred since 1980. Live-dead discordance can thus reliably differentiate between stable and rapidly changing habitats in cold, high-latitude settings, relevant to evaluating climate change, and biomass-based currencies of community composition are as robust as numerical abundance data, and in fact, improve spatial resolution.

1. Introduction

Extensive field studies by geologists in temperate and tropical latitudes demonstrate that a time-averaged accumulation of empty mollusc shells on the seafloor—a "death assemblage"— sums input from communities over many decades, and thus has potential to register ecological changes over much longer periods than typically encompassed by biomonitoring and other observational data, which rarely start before the 1970s (for reviews, see Kidwell, 2013; Kidwell and Tomašových, 2013). Moreover, meta-analysis finds that significant live-dead discordance in molluscan species composition is associated only with recent human-driven change in the benthic community, not natural variability (Kidwell, 2007), confirmed by focused tests (e.g. Chiba and Sato, 2013; Ferguson, 2008; Gallmetzer et al., 2017; Gilad et al., 2018; Staff and Powell, 1999). Comparing the numerical abundances and diversity of species and functional groups in death assemblages with counterpart information from living assemblages in the same habitat thus allows an investigator to detect whether today's community is shifted from earlier states, and the longer the duration of time-averaged shell accumulation, the longer the ecological memory of the death

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assemblage.

The fidelity of death assemblages to living communities has, however, never been tested under the aggressive postmortem conditions of high-latitudes, where overlying water can be under-saturated with respect to calcium carbonate, at least seasonally (Jiang et al., 2015), and the ability of live-dead comparison to detect human-induced climate change has never been tested at any latitude, with the exception of Powell et al. (2017) that recently tested this change using several commercial mollusc species. Live-dead comparisons have also focused almost exclusively on species' presence-absence and numerical abundance data, rather than their biomass. Rare tests of biomass have been promising, showing that it can resolve past dominance (Powell et al., 2017; Staff et al., 1985).

Here, we use bivalve death assemblages from North Pacific and Arctic shelves to advance live-dead analysis and paleoecological reconstruction in these and other critical, high-latitude settings. In the few other Arctic assemblage studies, researchers have tested for unique taphonomic damage and whether enough material is preserved to yield meaningful results (Gordillo and Aitken, 2000). North Pacific Arctic waters pose a clear preservational challenge to biogenic carbonate. The low concentration of carbonate, the low temperature, and the intense activity of both microbial and macrobenthic communities can amplify processes leading to shell deterioration and loss (Bates et al., 2009; Mathis et al., 2014, 2015; Nelson et al., 2014; Nielsen, 2004). Notwithstanding these challenges, including low diversity even where shells are well-preserved, fully buried Arctic fossil assemblages can record significant paleoecologic changes such as deglaciation of the high Arctic Archipelago (Aitken, 1990; Cai, 2006; Gordillo and Aitken, 2000). In light of this promise, Arctic live-dead discordance deserves quantitative testing in modern seabeds to assess its ability to detect changes in the environment caused by humans and secular warming.

The amount of time represented by Arctic death assemblages is still largely unknown, but the previously mentioned preservational challenges suggest a short window of time averaging. The high density of biologic activity on the northern Bering and Chukchi shelves would contribute to postmortem shell loss, despite the continual addition of new skeletal debris to the death assemblage (Cooper and Grebmeier, 2018; Grebmeier et al., 2015a), particularly as the productivity of these marine shelves has the capacity to mix and irrigate to core-depths ≥18 cm despite moderately high sedimentation rates (median 0.12 cm/yr; Cooper and Grebmeier, 2018). The median postmortem age of a shell in an Arctic death assemblage is thus likely much younger than in counterpart temperate-shelf death assemblages, where median ages are 50–100 years (e.g. southern California Bight; Tomašových et al., 2014). Despite projected high rates of shell loss, a small subset of shells are likely to survive from previous millennia, much as they do elsewhere (e.g. maximum shell age ~8000 years in the southern North Sea (Flessa, 1998) and ~10,000 years on the southern California middle shelf (Tomašových et al., 2014); for review, see Kidwell (2013)). For now, we expect each hotspot to reflect a similar window of time-averaging, with median ages < 100 years and a centennial rather than millennial total duration; geologic age-dating is in progress.

Extensive observations in the North Pacific Arctic, conducted by a multi-institutional consortium across ~10 degrees of latitude, have established a known gradient of biotic reaction to climate change over recent decades, making it an ideal setting for testing the fidelity of high-latitude death assemblages and, in particular, the power of live-dead discordance to detect ecological change. The Distributed Biological Observatory (DBO) was established to monitor the response of ocean chemistry, circulation, seabed conditions (organic and nutrient flux, sediment grain size), and biological communities to climate change, particularly sea-ice retreat, focusing on several "hotspots" of persistently high macrobenthic biomass (Cheng et al., 2011; Moore and Grebmeier, 2018). These and other observations have established a strong coupling between physical oceanography, primary productivity, and the living infaunal community (Grebmeier, 2012; Grebmeier et al., 1988, 1989, 2015a). Regional response to the retreat of sea ice during the last 20 years has manifested as a "softening" and northward movement of the Arctic-Subarctic boundary, which was initially defined by extensive seasonal sea-ice cover and a very cold (< -1 °C) bottom water layer south of St. Lawrence Island (Grebmeier et al., 2006b).

The "Subarctic" Bering Sea ecosystem is characterized by seasonal ice cover in the middle-to-northern regions, variable primary production, and a high level of pelagic and demersal fish production and coincident pelagic predator levels. The Northern Bering Sea is a transition region between Subarctic-Arctic conditions, with the Northern Bering Sea supporting smaller bivalves of the F. Nuculidae (deposit feeder) and F. Tellinidae (facultative deposit feeder) (Grebmeier, 2012; Stoker, 1978) compared to larger bivalves (F. Tellinidae, F. Cardiidae, F. Astartidae) in the more Arctic Chukchi Sea to the north. In the Northern Bering Sea, the diving spectacled eider (*Somatera fuscgeri*) consume the smaller Nuculanidae and Tellinidae bivalves whereas walrus (*Odobenus rosmarus*) feed on larger Tellinidae and Cardiidae bivalves in the same region (Cooper et al., 2013; Grebmeier, 2012; Grebmeier et al., 2006b). In response to recent warming seawater conditions, the Subarctic ecosystem in the northern Bering Sea has expanded northward into the "Arctic" southern Chukchi Sea, creating a gradient of Subarctic to Arctic conditions through the Bering Strait to interface with the "Arctic proper" which has more extensive ice cover with later retreat, colder and more nutrient-rich water, and higher primary productivity carbon export to the sediments, all that support rich benthic faunal populations and benthivore predators (Grebmeier, 2012).

Environmental conditions and faunal composition have changed to different degrees in each hotspot across the Pacific Arctic region, often with change focused on single stations within each hotspot rather than pervasively throughout a hotspot (Goethel et al., 2017, 2018). In general, the Northern Bering Sea (DBO1) hotspot has been relatively productive, but shows changes in composition as well as declining biomass at some stations, with increasing but persistent Subarctic influence (Grebmeier et al., 2018). For example, the Spectacled Eider and their preferred bivalve prey (F. Nuculanidae) have been declining in the Northern Bering Sea with the increase in the smaller, less preferred small bivalve (F. Nuculidae) (Cooper et al., 2013; Grebmeier and Cooper, 2016b). In contrast, the northern DBO2 hotspot in the Chirikov Basin just south of Bering Strait and the DBO3 hotspot in the SE Chukchi Sea have each undergone varying levels of community transition from more Arctic to Subarctic conditions as sea ice retreats earlier coincident with warming seawater seasonally. The newly variable productivity and biomass in DBO2, DBO3, and even the NE Chukchi Sea DBO4 region are associated with increased current flow through the Bering Strait, increasing variability of carbon deposition in the Chukchi Sea over the last 10–20 years, and more northern movement of gray whales and other subarctic marine mammals (Blanchard, 2014; Grebmeier, 2012; Grebmeier et al., 2006a, 2015a; Schonberg et al., 2014).

This well-established framework of spatial and temporal variation in benthic communities suggests that (1) live-dead agreement in community composition and structure should be highest in the relatively stable hotspots (DBO1 and DBO3) and poorest – overall but particularly at a station-level – in the transitioned hotspots (DBO2 and DBO4). (2) Observed live-dead discordance should match known changes in community dominants (i.e. death assemblages should contain a mixture of dominants of past and present community states). (3) Given the potential for postmortem bias in species' preservation under aggressive high-latitude waters, live-dead agreement will not necessarily be 'perfect' even in hotspots or stations known to have experienced little ecological change; these sites will provide a benchmark for analytically correcting death-assemblage data from other sites for taphonomic bias. The availability of biomass data from variable DBO regions also permits (4) a novel taphonomic test of this ecological currency, moving beyond presence-absence and numerical abundance data and expanding live-dead analysis to ecosystem science.

Using DBO death assemblages, this study aims to answer the following questions:

(1) In cold water with potentially low rates of preservation, do death assemblages reliably reflect spatial patterns in the raw abundance and composition of living assemblages?
(2) Is biomass more sensitive than numerical abundance in using death assemblages to detect spatial and temporal variation in benthic communities?
(3) Can live-dead discordance detect known ecological shifts related to climate change?

2. Methods

2.1. Bivalve living and death assemblages

Living and death assemblages were acquired from benthic samples collected by the Arctic Research Group (ARG; Chesapeake Biological Laboratory/UMCES) during a summer 2014 cruise of the Canadian Coast Guard Ship *Sir Wilfrid Laurier* (SWL14). Sampling stations were distributed among four areas of known high benthic biomass (DBO hotspots; Fig. 1): five stations from DBO1 and ten from DBO3, which are areas with productive benthic communities that have been regionally stable over the past decade, but punctuated by intense station level changes; and four stations from DBO2 and six stations from DBO4, where the benthic community is less productive and more heterogeneous, and environmental conditions have changed significantly (Blanchard, 2014; Grebmeier, 2012; Grebmeier and Cooper, 2016a).

At each station (Fig. 1), two to five van Veen grabs (0.1 m^2) were used to collect sediment and infauna, with the sample sieved through a 1 mm screen with seawater and then preserved in 10% seawater-buffered formalin. The species composition of death and fossil assemblages can, like living assemblages, be sensitive to sieve size, but processing using a 1 mm sieve has been standard for the ARG monitoring effort, as it is for many agency surveys. A study by Pirtle-Levy (2006) at many of these benthic shelf hotspot sites found that, on average, 97% of the station macrofaunal biomass was caught on the 1 mm screen, compared to 3% remaining on the 0.5 mm screen, with more variable abundance levels on the combined screen size due to meiofauna and juvenile macrofauna. The collections on the 1 mm screen allow investigators to focus on adult individuals as opposed to juveniles and larvae, whose living abundance is more sensitive to the timing of a survey and whose dead shells are especially prone to post-mortem destruction (Kidwell, 2001, 2002; Kowalewski and Hoffmeister, 2003). In the Bering and Chukchi Seas, small-bodied taxa (1–2 mm) such as Thyasiridae are present both alive and dead, but comprise a very small proportion of bivalve biomass (see Results). Thus, for the analyses here focused on biomass and only one cruise's worth of data, the 1 mm sieve size was deemed sufficient to capture the composition of living and death bivalve assemblages.

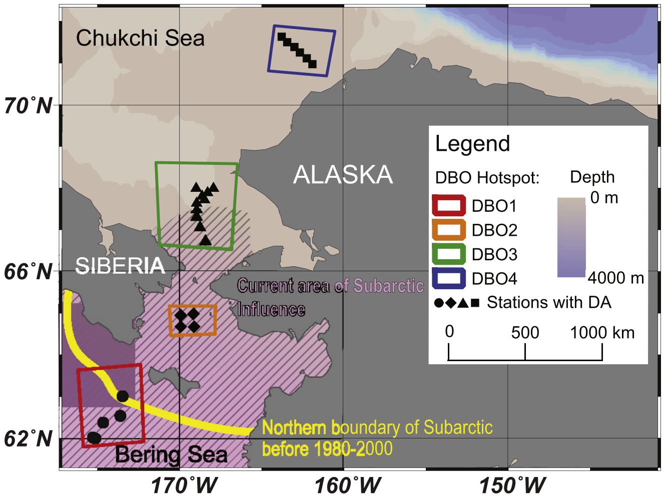

Fig. 1. Map of the Distributed Biologic Observatory (DBO) stations. Stations (black dots) sampled for bivalve live and dead assemblages during the summer 2014 CCGS *Sir Wilfrid Laurier* cruise. Analyses focus on data from four DBO 'hotspots' of high benthic biomass: the persistently subarctic northern Bering Sea (DBO1 = red box, circle stations), the persistently Arctic Chukchi Sea (DBO 4 = blue box, square stations), and areas in the Bering Strait and southern Chukchi Sea that began to transition from Arctic to subarctic conditions within the last ~10 years (DBO2 = orange box diamond stations, DBO3 = green box, triangle stations). All DBOs in water depths 35–81 m. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

The sampled living assemblage was sorted and identified to the family and species level by the ARG, and then archived in 50% propanol (Grebmeier and Cooper, 2018a). The remaining shell-rich residue from the sorting process was dried and identified at the University of Chicago. An empty bivalve shell or shell fragment was considered an individual if it was adult (body size > 1 mm) and retained ≥50% of the hinge line, as is standard in live-dead analysis (Kidwell, 2013). Each dead bivalve was identified to the lowest taxonomic level possible using print resources shared between the UMCES ARG and UChicago (Coan et al., 2000; Foster, 1991) and using two digital voucher collections (one created by the first author during visits to the ARG, and the other created by ARG collaborators to coordinate invertebrate researchers on the DBOs; (Kędra and Oleszczuk, 2017). With these resources, bivalve families and most species could be confidently identified using shell morphology. Each family represents a single guild, and thus family-level identification suffices to differentiate living communities among DBO hotspots, and even poorly preserved shells can be confidently identified to the family level.

For both living and death assemblages, bivalve abundances were reported as individuals per m^2 of seafloor and reflect pooling of all samples (replicates) collected at a given station in 2014. Assignment of bivalve taxa to guilds is based on both life habit (infaunal, epifaunal, nestling) and trophic group, following Todd (2000): chemosymbiont-bearing, obligate deposit-feeding, and facultative deposit-feeding infauna; suspension-feeding infauna, epifauna, and nestlers; and commensal. Predatory bivalves (e.g. cuspidariids) are not represented in the fauna.

Bivalve biomass (gC) was measured for living assemblages by the ARG using family level conversion factors developed by Stoker (1978) and Grebmeier (1987) that converted total wet mass to grams of organic (soft-tissue) carbon. To acquire comparable information on the biomass (B) of death assemblages, we used the conversion developed by Meadows (2019):

$$B = \frac{\alpha}{\beta}\frac{x}{\gamma}$$

where α is a conversion from total wet mass to organic carbon mass, β is a conversion from shell mass to total wet mass, x is the measured fossil mass, and γ is an estimate of the percent of the original shell preserved as the fossil, which also serves as an estimate of post mortem damage.

For bivalve shells showing evidence of intense postmortem dissolution (chalkiness) or other shell loss, we estimated biomass using a conventional method based on linear dimensions (e.g. Bradbury et al., 2005). Only bivalve shells that were sufficiently intact to be counted as individuals were used in the calculation of biomass. Both living and dead biomass are reported as g organic Carbon per m^2.

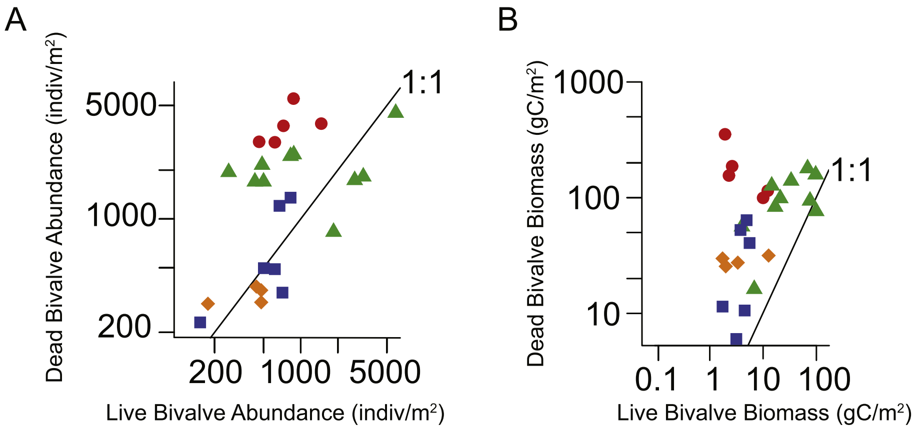

Fig. 2. Station biomass and abundance comparison. Comparison of live and dead bivalve biomass (density, gC/m^2) by station. Stations are color-coded according to the biomass hotspots as in Fig. 1 (DBO1 = red circles; DBO2 = orange diamonds; DBO3 = green triangles, DBO4 = blue squares). Although the time-averaged dead biomass is almost always greater than the standing live biomass at a station (above the black line representing unity), commonly by several orders of magnitude, the ranking of hotspots by live density is preserved. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2.2. Live-dead comparison

2.2.1. Death assemblage fidelity

The fidelity of death assemblages to living assemblages is assessed two ways: (1) comparing the amount of bivalve material preserved per station (Fig. 2), using both counts of individuals and biomass; this tests for the resolution of spatial patterns in secondary productivity on the seabed (Fig. 2); and (2) comparing the proportional biomass of guilds within each biomass hotspot (Fig. 3), a means of testing for differential preservation that might bias paleoecological inference.

2.2.2. Live-dead discordance

Live-dead discordance focuses on two measures of pairwise, live-dead similarity: (1) in taxon rank abundances, expressed as a correlation (Spearman's rho), and (2) in taxonomic similarity, that is presence-absence corrected for disparate sample sizes (Jaccard-Chao Index), following the widely used approach of Kidwell (2007). Rank-abundance correlation compares lists ordered by taxon abundance in the live and dead collections. A positive rho indicates that taxa that dominate the living assemblage are also highly ranked in the death assemblages and that taxa that are rare in one assemblage are also rare (or absent) in the other; a rho of 1 requires that taxa are ranked identically in both assemblages. The Jaccard-Chao (JC) index of taxonomic similarity expresses the proportion of taxa shared by two assemblages, using information on the numbers of singletons and doubletons to correct for ‘unseen taxa’ in the smaller sample (Chao et al., 2005). A JC index of 1 indicates that the live and the dead taxa lists are identical, that is all species are shared. Here, both JC and rho are calculated using bivalve families. The results are displayed on a cross-plot of JC versus rho, where stations falling in the upper-right quadrant have the least live-dead discordance (high proportion of shared species, with those species having similar relative abundances both alive and dead). This method has previously only been used with numerical abundance data, and originally only at the habitat level, i.e. after data from multiple stations had been pooled (Kidwell, 2007). Here, both numerical abundance and biomass data are used, and discordance is evaluated at the station level.

2.2.3. Canonical correspondence analysis (CCA)

Canonical correspondence analysis (CCA) was designed to identify environmental gradients within community data, based on the theory that species sort themselves among sites based on their realized niche and physiological optimum (Borcard et al., 2011; ter Braak, 1986; ter Braak and Verdonschot, 1995). With this theory as backing, CCA computes the χ^2 distances using the relative abundances of taxa among sites and taxa, to then find the relationships between environmental variables and the realized niches of the taxa sampled within the community at the sites (Fig. 1 in ter Braak and Verdonschot, 1995). This approach was chosen over non-metric multidimensional scaling (NMDS) and detrended correspondence analysis (DCA) because CCA allows both a comparison of the environment and the community and the calculation of a statistical correlation between the matrices in the constructed space (Borcard et al., 2011). The CCA space was constructed using family-level data on bivalve biomass, producing a live (circle) and a dead (squares) data point for each station. A multivariate

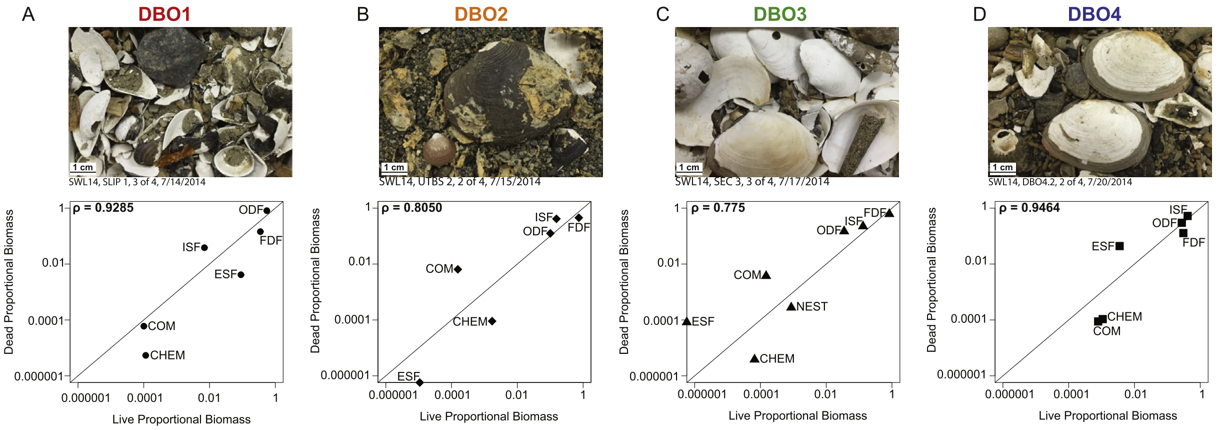

Fig. 3. Hotspot Bivalve Guild Comparison. Representative death assemblages (top row) and bivariate plots of the proportional biomasses of bivalve guilds in live and dead assemblages by DBO hotspot. Data points appearing on axes indicate the guild occurred live-only or dead-only because 0 cannot be displayed on a logarithmic scale. The black line denotes 1:1. ρ on each plot denotes the agreement between live and dead functional groups at the hotspot spatial-level. Feeding guilds abbreviated as follows; ODF = obligate deposit feeder, FDF = facultative deposit feeder, ISF = infaunal suspension feeder, ESF = epifaunal suspension feeder, COM = commensal, CHEM = chemosymbiotic, and NEST = nestling.

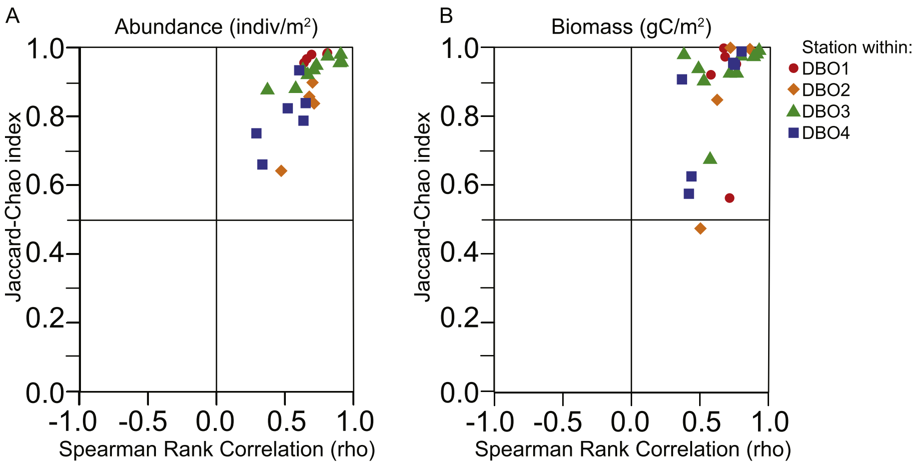

Fig. 4. Live-Dead Agreement. Comparing the live and dead taxonomic composition (shared taxa; Jaccard-Chao index) and relative abundance (rank correlation; Spearman rho), where taxa are ranked using (A) numerical abundance (number of individuals/m^2; left diagram) or (B) biomass (gC/m^2; right diagram). Each dot represents live-dead agreement at a single station, color-coded by DBO hotspot (DBO1 = red circles; DBO2 = orange diamonds; DBO3 = green triangles, DBO4 = blue squares), and is based on family-level data (22 total families). Stations with very low sample sizes (< 10 dead individuals) omitted; stations with identical live and dead assemblages would fall at the upper right corner of the cross-plot. (A) Stations exhibiting the highest live-dead agreement are from the highest-biomass portions of DBO1 and DBO3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

method, like CCA, is a necessary addition to live-dead comparison as the low diversity and uneven community structures in the DBO regions are likely to result in small changes in JC and rho, limiting the sensitivity of the traditional live-dead cross plots (described in section 2.2.2.).

Environmental data have been collected annually across the Bering and Chukchi Seas since 2010 as part of several multi-national efforts including the Distributed Biological Observatory (Cheng et al., 2011); longer time series begining in 1970 are available for many sites as part of the Pacific Marine Arctic Regional Synthesis (PacMARS; Grebmeier et al., 2015c). Here, in CCA, we consider the environmental parameters most important to benthic life and mediated by sea-ice cover and water circulation in the benthic zone: sediment grain size, specifically the weight-% of mud (< 0.062 mm, ≥5 phi); total organic carbon (TOC); total organic nitrogen (TON); and the carbon to nitrogen ratio (C:N), all based on surface sediment (top 1 cm of van Veen grab). However, because death assemblages sum bivalve communities over multiple years rather than a single year, we focus on *change* in environmental variables rather than single-season observations. To do this, for each station, the linear trend in a variable over the length of the measured time series (variable/yr) was found using the sediment variables gathered in the PacMARS between 1970 and 2012 (Grebmeier and Cooper, 2016a), SWL cruises in 2013–2014 (Grebmeier and Cooper, 2018b, c) and the Chukchi Sea Environmental Studies Program (CSESP) from 2007 to 2014 (Blanchard et al., 2013; Wisdom and System, 2014). Environmental change is displayed as arrows in the direction of the greatest positive trend in that variable. All spaces were constructed with the cca () function in the R vegan package (Oksanen et al., 2007).

3. Results

3.1. Comparison of bivalve abundances

In numerical abundance, dead-shell assemblages contain on average 3.2 individuals per live individual sampled, with per-station dead:live ratios ranging from 0.6 to 6.2. Death assemblages also contain more bivalve biomass except for one station, with an average of 18 g of organic-C biomass (extrapolated from preserved shell mass; Meadows, 2019); for every gram in the counterpart sample of the living assemblage (Fig. 2). Larger average body sizes are also found in the death assemblages than in living assemblages, as suggested by the representative photographs in Fig. 3. Death assemblage sample sizes from standard benthic grabs are thus sufficiently large to support confident analysis, containing three times more individuals and much more biomass than the standard minimum of 1 g/m^2 generally required for living biomass.

3.2. Comparison of bivalve guilds

With few exceptions, all seven guilds were found both dead and alive: in each DBO hotspot, the high functional diversity (6 or 7 guilds) observed in living assemblages is maintained in death assemblages (Fig. 3). Epifaunal suspension feeding bivalves were the only exception, occurring alive-only in one area (DBO2) and dead-only in another (DBO3), but occurring in such small numbers (singleton specimens) that intolerance of benthic conditions rather than sampling is the likely explanation. They occur in substantial numbers both alive and dead in the other two hotspots (Fig. 3).

Guilds also represent similar proportions of biomass in death and living assemblages in all hotspots (r^2 ranging from 0.775 to 0.9464; Fig. 3), even though the dominant guild varies among areas: obligate deposit feeders in DBO1, facultative deposit feeders in DBO1 and DBO3, and infaunal suspension feeders in DBO4 (Fig. 3). Chemosymbiotic taxa (Lucinidae and Thyasiridae) constitute a greater proportion of living than dead biomass in all four areas. This bias against dead chemosymbiotic taxa is likely due to their relatively small sizes (1–5 mm valve height): most dead shells and living individuals of other species are larger-bodied, suggesting that preservation under these cold-water conditions selects against small individuals and thus small-bodied species. No other consistent live-dead difference emerges among bivalve guilds.

3.3. Comparison of bivalve taxonomic composition

Using both numbers of individuals and biomass as currencies of abundance, death assemblages closely resemble counterpart living assemblages, with stations falling mostly within the upper right (high live-dead agreement) quadrant of the cross-plots of taxonomic similarity and rank-correlation in Fig. 4. A high proportion of families are shared between living and death assemblages at each station, and families that dominate (or are rare in) one assemblage also tend to dominate (or are rare in) the other.

Differences do appear between hotspots and among stations within hotspots (Fig. 4). Regional trends among DBOs are most apparent in numerical abundance (Fig. 4A), the standard currency for live-dead comparison. Regionally, stations in DBO1 and DBO3, which are both highly productive and relatively stable (Grebmeier, 2012), all exhibit very high live-dead agreement and plot closely to one another in the upper right corner (Fig. 4A). In contrast, stations in DBO2 and DBO4, which are more spatially heterogeneous (Grebmeier, 2012), exhibit lower live-dead agreement and greater between-station differences (Fig. 4A).

Live-dead agreement is also very high for biomass data, except for five stations (Fig. 4B). These five stations – SLIP3 from DBO1, UTBS4

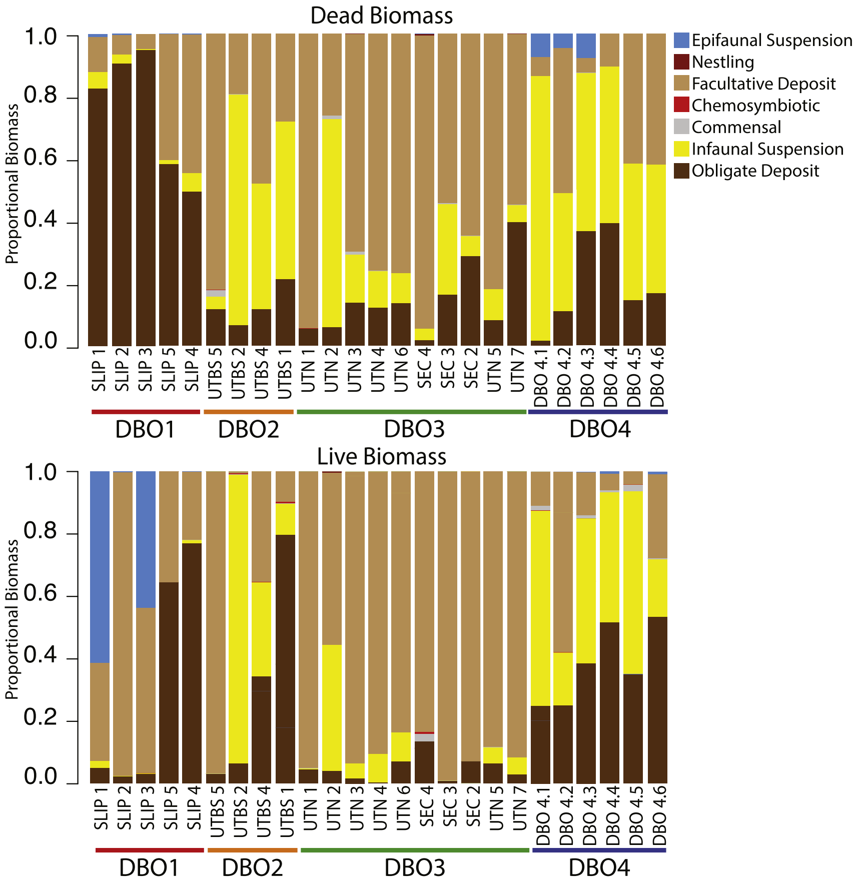

Fig. 5. Biomass of bivalve guilds by DBO Station. Dead (top) and live assemblages (bottom) by station and by guild in proportional biomass. By guild, obligate deposit feeders are much more abundant dead than live in the DBO 1 and 3 stations, in DBO3 and at specific stations throughout the region. Facultative deposit feeders are most dominant in the 2014 live.

from DBO2, SEC3 from DBO3, and DBO4.4 and DBO4.2 – are all being monitored for either biotic or environmental change because they are among the stations positioned in transition zones between water masses (Cooper et al., 1997; Grebmeier, 1987; Grebmeier and Cooper, 2016b; Stoker, 1978).

The proportional biomass of guilds at the station level also shows large discordances (Fig. 5). In general, facultative deposit feeders (Tellinidae) are more abundant in living than in counterpart death assemblages, which tend to contain a greater diversity of guilds.

3.4. Variation in bivalves with the environment

Canonical Correspondence Analysis (CCA) indicates that live-dead differences in family composition are associated significantly with large net changes in environmental parameters (Fig. 6; p-value = 0.027). This association preserves known changes in the most highly variable and heterogeneous DBO regions. For example, the DBO2 and DBO4 hotspots (gold and blue icons in Fig. 6) comprise benthic communities known to have changed significantly in past decades, and the environment there has become muddier and more carbon-rich, in general. The stations in the DBO2 and DBO4 hotspots exhibiting large distances between living and death assemblages are aligned with stations experiencing increasing mud and TOC (Fig. 6) (Grebmeier, 2012; Grebmeier et al., 2015b; Grebmeier and Cooper, 2016a). In addition, the five stations exhibiting high live-dead discordance in Fig. 4 maintain large separations between living and death assemblages in this CCA space (icons with black outlines, Fig. 6).

The relationship between changes in the environment and live-dead discordance can be seen most clearly within DBO1, which is regionally stable but has recently undergone large station-level shifts (red icons in Fig. 6). In DBO1, death assemblages fall in the lower left quadrant of CCA space, associated with the obligate deposit-feeder Nuculanidae, relatively high nutrients, and coarser grain size. In contrast, living assemblages of DBO1 are in the upper right quadrant, associated with the facultative deposit-feeder Tellinidae, which are common alive in all four hotspots, and with fewer nutrients and finer grain sizes. Assemblages from other DBO hotspots show a similar but less strong live-dead separation, generally with a more trophically diverse death assemblage and a living assemblage dominated by a single family common throughout the region (usually Tellinidae). These environmental gradients do not align precisely with a change in a single environmental variable, instead align weakly with a change in both sediment TOC and TON content and with grain size composition (Fig. 6).

4. Discussion

4.1. Ecologic fidelity of high-latitude death assemblages

Despite cold waters that present challenging conditions for shell preservation, expected to lead to low ecological fidelity, we found strong positive and statistically robust relationships between living and death assemblages in hotspots known to have relatively stable environmental conditions and community compositions. Live-dead *discordance* was encountered only in hotspots known to have transitioned in recent decades, and that discordance was of the type predicted by known changes in the benthic community. Both results indicate that these high-latitude death assemblages are useful ecological records of local conditions over at least decadal scales.

Live-Dead discordance was not focused in one hotspot or habitat. Each of the five stations exhibiting live-dead discordance in biomass – SLIP3 (DBO1), UTBS4 (DBO2), SEC3 (DBO3), DBO4.2 and DBO4.4 – has different dominant water masses and grain sizes, and each station represents a known ecologic shift in the benthic community (see section 4.2). Taphonomically, death assemblages from these five stations range

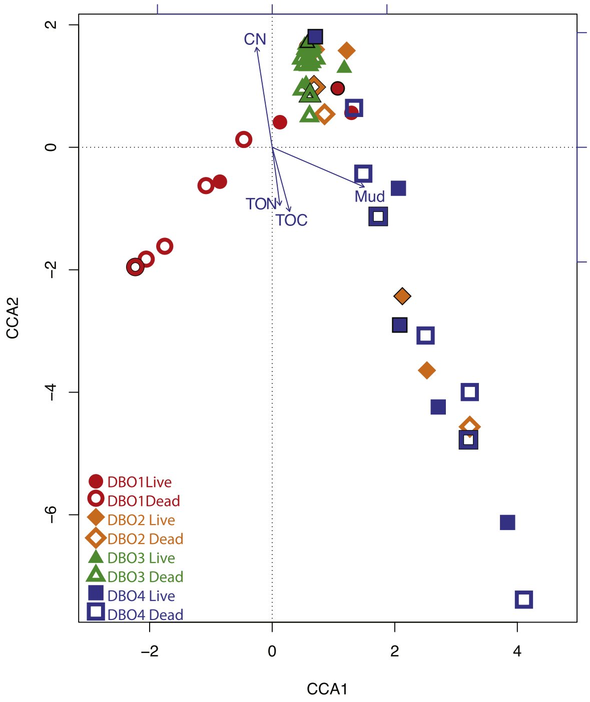

Fig. 6. Canonical correspondence analysis of Live and Dead assemblages. CCA based on family biomass. Each point represents a live (closed shape) or dead (open shape) assemblage from a single station, which are color-coded by DBO hotspot (DBO1 = red circles; DBO2 = orange diamonds; DBO3 = green triangles, DBO4 = blue squares). The five points outlined in black fell outside the main group in Fig. 3B (DBO 4.4 (blue), DBO 4.2 (blue), SEC 3 (green), UTBS 4 (orange), and SLIP 3 (Red)). Blue arrows denote the direction of increase in the annual value of an environmental variable: (C/N = carbon:nitrogen, TON = total organic nitrogen, TOC = total organic carbon, weight-percent mud) over the duration of in situ observations. The arrangement of these stations with these environmental variables is slightly significant according to Anova test (p-value = 0.027). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

from high (> 500 individuals; SLIP3 and SEC3, DBO 4.2) to low (100-50 individuals; UTBS4, DBO4.4) abundance and biomass. Overall, the DBO housed relatively small numbers of dead shells – a dead:live ratio of ~3, compared with a global median of 8 for tropical and temperate settings (Kidwell, 2013) – is consistent with a high rate of post-mortem shell loss and a short window of time-averaging. However, the range of sample sizes and habitats in both well-agreed and poorly-agreed stations argues against a consistent preservational bias, as does the spatial matching of discordance to observed temporal changes mentioned above. Live-dead discordance thus most likely reflects ecologic change in hotspots rather than preservational bias. Thus, although Arctic death assemblages are less abundant and less diverse than their temperate and tropical counterparts (Tomašových et al., 2014), the dense secondary productivity of the Alaskan shelf still supplies sufficient material to assess ecologic change using death assemblages, especially with biomass as an added paleoecologic currency (Fig. 2).

The largest-bodied taxa include Tellinidae (maximum valve height > 45 mm), Cardiidae (60 mm), and Astartidae (a few > 34 mm). However, other smaller-bodied taxa are regularly collected near their maximum recorded size (e.g. Nuculanidae > 15 mm shell height; pers. comm. David Jablonski, 2017). All taxa are represented by a broad range of individual sizes, from the minimum of 1–2 mm to the larger sizes listed previously. Small and large body sizes are found throughout the region with no apparent bias based on the hotspot. Areas with coarser grain sizes (muddy sand in select stations in DBO4 and DBO2) contained more shell fragments and fewer small dead individuals, but these stations still contained suitable sample sizes (> 30 individuals) and the grain size had no clear correlation with high or low live-dead agreement. Fossil assemblages of all ages commonly contain few specimens of ontogenetically young individuals, regardless of adult body size and despite the high mortality expected among young individuals, suggesting that shell loss is not a simple function of shell size (Kidwell, 2013). In death assemblages from our study area, few specimens are smaller than 5 mm in length, regardless of species, and maximum shell sizes are larger than are observed in counterpart living assemblages.

Larger bodied individuals are also more abundant in death than living assemblages in the study area, which may arise from three possibilities, not mutually exclusive. First, large shells might be preserved more readily than small shells, which is both expected and observed for fossil assemblages in general (Cooper et al., 2006; Cummins et al., 1986; Kidwell and Bosence, 1991; Valentine et al., 2006). Second, finding larger body sizes in past generations is consistent with anecdotal evidence that bivalves in the region have been getting smaller since the 1970s (Feder et al., 1994; Goethel et al., 2017; Munroe et al., 2013; Stoker, 1978). Third, van Veen grab gear is less effective in sampling larger bodied and thus deeper burrowing living individuals, making them appear to be proportionally more abundant dead than alive (Powell and Mann, 2016). To test for such an artifact, we re-ran our JC and rho analyses omitting large dead shells (> 30 mm height and > 0.42 g valve mass) and found that overall live-dead agreement decreased slightly but remained high in both abundance and biomass and the five stations with lower biomass live-dead agreement maintained their discordance (stations identified in section 3.3).

A secular reduction in adult body size might have several drivers, including increased mortality from pre-mortem dissolution and bioerosion heightened by ocean acidification (Goethel et al., 2017) or a decrease in body size due to increasing bottom water temperature (Mann et al., 2013; Munroe et al., 2013). For example, stations within DBO3 and DBO4 are known to have bottom waters that are undersaturated in aragonite today (Goethel et al., 2017; Mathis et al., 2015; Pickart and Grebmeier, 2017). Ocean acidification in this region is progressing more rapidly and over a more extended period than is increasing bottom water temperature, which has remained relatively stable until recently (Stabeno et al., 2018; Woodgate, 2018). In late 2018, after the SWL14 survey, bottom water temperatures increased above 0 °C in DBO1 for the first time (bottom water anomalies ~ +2 °C; (Grebmeier et al., 2018; Stabeno et al., 2018). Whether this new temperature anomaly in DBO continues into 2019 and onwards is uncertain, and whether it will start affecting bivalve physiology on the Bering Sea Shelf, as well as allowing more demersal and pelagic predators access to the seafloor communities requires further study (Goethel et al., 2018; Grebmeier et al., 2006b, 2018; Stabeno et al., 2018).

As stated in Nielsen (2004), Arctic shells must persist through (1) bioerosion and dissolution while still alive, (2) bioerosion and microbial maceration after death, (3) abrasion, disarticulation, and fragmentation that increase reactive surface area, and (4) postmortem dissolution occurring at or just below the sediment-water interface (Alexandersson, 1979; Freiwald, 1998), although antagonistic porewaters are possible at any latitude (e.g. (Aller, 1982). These stages of shell loss can leave different signatures as a function of shell microstructure and life habit (Nielsen, 2004). However, in general, one expects a preferential loss of shells with high-organic microstructures, shells constructed of crystallites having a high surface area to volume ratios, and small-bodied or very thin-shelled individuals (Glover and Kidwell, 1993). Despite these limits, the “taphonomically vulnerable” families of Mytilidae, Nuculidae, and Nuculanidae with reactive microstructure are all abundant in death assemblages and their rank abundances are similar to that in living assemblages. Members of Tellinidae, characterized by especially thin aragonitic shells, exhibit the same pattern (Fig. 3). The similar proportional abundances of these “vulnerable” taxa in both living and death assemblages in areas of little ecological change suggests the persistence of their populations over the duration of time-averaging, counter-balancing preservational biases that should favor other groups with relatively thick shells. Preservational conditions are arguably extremely difficult for all shell types, but families do differ strongly in preservation potential.

Preservational caveats related to shell type and body size are thus essential to consider when interpreting Arctic death assemblages. However, in this system, they do not appear to be a barrier to confident paleoecological inference at the habitat level: every life habit represented in the living assemblage in a DBO is also found in the death assemblage there (Fig. 3). Exceptionally, chemosymbiotic bivalves (Lucinidae, Thraciidae) were proportionally more abundant alive than dead, even if they remained a small part of the overall bivalve assemblage biomass (Figs. 3 and 4). While evidence suggests that freshwater inputs, anoxic muds, and increasing temperatures allow chemosymbiotic bivalves to increase in number in Arctic ecosystems (Herder et al., 2017), the sample sizes examined here were too small to identify such a pattern. Future work will be aimed to examine the living and death bivalve assemblages for more small size fraction bias in Arctic death assemblages and possible recent changes in chemosymbiotic bivalve abundance within the DBOs.

Using the same metrics as used for live-dead comparisons, 'live-live' comparisons among stations in the DBO4 hotspot reveal more spatial heterogeneity than do live-dead comparisons (using biomass data, an average live-live Jaccard-Chao of 0.78 and average Spearman rho of 0.54, compared to an average live-dead JC of 0.83 and rho of 0.58). This spatial heterogeneity is confirmed by current benthic monitoring (Blanchard, 2014; Blanchard et al., 2013; Grebmeier et al., 2015a, 2018). Live-live discordance is only slightly larger than live-dead discordance, however, still falling in the upper-right, well-agreed corner of Fig. 4. The low diversity and uneven community structures in the Arctic thus have little effect on taxonomic composition and rank abundance measures, and these measures should be paired with multivariate analysis to increase sensitivity. Multivariate analysis of proportional biomass data also reveals greater dispersion among living assemblages than death assemblages in DBO4, but it is again very slight (Fig. 6). Therefore, death assemblages are capturing the spatial heterogeneity in this region despite being time-averaged recorders of ecology, indicating that the time averaging window may be short due to the preservational caveats listed in this section.

This study was somewhat challenged by small sample sizes, especially of the living assemblages. Typically, DBO benthic surveys are conducted over an entire summer, revisiting stations on as many as three cruises per season, and trends are compiled over multiple years of such summer sampling (e.g. Grebmeier et al., 2015b). Here, however, we acquired death assemblages from only a single cruise in order not to overwhelm the shipboard protocol, and thus we considered only the living assemblage from those same samples, as is standard in live-dead analysis. Despite using these considerably smaller total numbers of individuals than is typical in live-dead studies, and only a fraction of the information ordinarily available to biologists on these living bivalve communities, significant patterns emerged.

4.2. Power of live-dead discordance to detect benthic response to climate change

Given preservational concerns and small samples, the results presented here probably represent a conservative estimate of the ability of live-dead discordance to detect changes in the benthic ecosystem in the last 10–20 years. These results are thus very encouraging for using death assemblages and live-dead comparison in other high-latitude and cold-water settings. Death assemblages from additional years and seasons would likely yield similar results, as most bivalve taxa in this region have long lives and thus experience multiple seasons. Although live-dead discordance does not identify all stations that are being monitored for ecological changes, the five stations exhibiting relatively high live-dead discordance (Fig. 4B) are representative of three types of benthic transitions recognized from biomonitoring of the DBO regions:

(1) A shift from a more diverse bivalve community toward dominance by Tellinidae. This change is exemplified by live-dead discordance at SLIP3 (DBO1) and SEC3 (DBO3) but occurs at stations in each DBO region (Fig. 4B; Fig. 6). The Tellinidae shift is related to an increase in either sediment TOC to the benthos or decrease in sediment grain size, which have been mediated by sea-ice retreat altering bottom-water circulation in the Northern Bering and Chukchi Seas (Goethel et al., 2017; Grebmeier, 2012; Lovvorn et al., 2018; Woodgate, 2018). The Tellinidae shift seems to be associated with a shift in hydrography and not necessarily the direction of that change. For example, within DBO1, a recent increase in Tellinidae is correlated with an increase in surface sediment TOC and a decrease in grain size, owing to the likely slowing of the Anadyr stream or variable seasonal current flow in the region. The community is so altered at these stations that it is now most similar to samples taken much farther north in DBO3, which has also seen a rise in Tellinidae biomass since 2004 (Goethel et al., 2017; Grebmeier, 2012; Grebmeier and Dunton, 2000; Sirenko and Gagaev, 2007). As freshwater inputs and temperature continue to increase across the shelf, this new dominance of Tellinidae is likely to be accompanied by an increase in the abundance of chemosymbiotic bivalves (Lucinidae and Thraciidae), such as already seen in estuaries and bays in the Arctic (Herder et al., 2017). This shift towards Tellinidae, which are proportionally more abundant alive than dead, is unlikely to arise from taphonomic bias because the stations undergoing this transition contain abundant and diverse death assemblages (> 500 individuals and > 7 families). These death assemblages contain many other families with low preservation potential (e.g. Nuculanidae at SLIP3, Cardiidae at SEC3). In addition, Tellinidae maintain high ranks (1st or 2nd in DBO3) in the proportional biomass in death assemblages (Fig. 5). The discordance here results from Tellinidae of live assemblages unevenly dominating the community, resulting in a much less diverse living assemblage (e.g. 54% Tellinidae in Dead SEC3 to 99% in Live SEC3; Fig. 5).

(2) A shift in dominance among groups within the same trophic guild, exemplified by live-dead discordance throughout DBO2 and especially at UTBS4. Monitoring data show that DBO2 once hosted abundant amphipods in a gray whale feeding ground, but amphipod dominance has waned since the 2000s and been replaced by polychaetes and, in some cases, facultative deposit-feeding and suspension-feeding bivalves (Grebmeier, 2012). This change was not accompanied by large shifts in functional diversity among bivalves (see Fig. 5). However, associated with this decline in amphipods, the dominant bivalve families have shifted within a functional group. For example, within the suspension feeding functional group, the family Cardiidae was found only in death assemblages at UTBS4 and the family Astartidae was found only in living assemblages at UTBS4, resulting in little discernible difference between proportional biomass of live and dead infaunal suspension feeders at that station (Fig. 5) but considerable live-dead discordance in the family composition (Fig. 4). This shift in dominance is unlikely to be the result of taphonomic bias because taxa shift in dominance within a feeding guild and do not follow expected bias for shell preservation (i.e. thinner/organic-rich mereologies are not always found more in death assemblages). Particularly in the examples provided from UTBS4, families with thinner shells (Yoldiidae and Cardiidae) are found in death assemblages in higher proportional abundance than more robust shells (Nuculidae and Astartidae).

(3) A decline in the abundance of "Alaskan taxa" such as the infaunal suspension-feeding Astartidae, obligate deposit-feeder Yoldiidae, and epifaunal suspension-feeder Mytilidae (all more abundant dead than alive) is responsible for live-dead discordance at DBO4.2 and DBO4.4. At these two stations, the reduced proportional biomass of

these taxa is compensated for by slightly higher abundances of Cardiidae, Nuculidae, and Tellinindae. The population decline observed in the 2000s of these once-dominant Alaskan taxa may be due to a combination of a recent increase in organic carbon and a more prolonged decline in aragonite saturation of bottom waters, beginning in 1975–1985 (Cross et al., 2018; Goethel et al., 2017; Pickart and Grebmeier, 2017). DBO 4.2 and 4.4 experienced possible ocean acidification conditions in summer 2017, (post-dating our 2014 live-dead data), with evidence of shell dissolution on living bivalves collected in 2017 (e.g. chalky mineral where periostracum absent, personal observation). In the past, ocean acidification in the Chukchi Sea was associated with discrete upwelling events, but now corrosive, low aragonite saturation waters form and persist on the shelf for the majority of the year (Cross et al., 2018). This prolonged exposure has the potential to alter the bivalve community through failed settlement and other early mortality of select taxa, particularly at the interface between the Alaskan Coastal water and rapidly moving shelf waters, such as those at DBO4. Bivalves collected in 2014 and 2015 were examined and subjected to ocean acidification (OA) experiments to determine the effect of these new chemical conditions in DBO3 and DBO4 (Goethel et al., 2017). The "Alaskan taxa" known to be in decline here, however, proved to be relatively resilient to OA conditions in the lab, whereas open shelf associated taxa such as Cardiidae, Nuculidae, and Tellinidae that increase in proportional abundance alive were more sensitive. In other DBO regions with less extensive OA, Tellinidae and at fewer stations Cardiidae and Nuculidae have continued to dominate the living community, contrasting with DBO4, where these taxa have shifted into top ranks, but the bivalve community structure has remained relatively even. Loss of the "Alaskan taxa" in DBO4 may be related to a combination of oceanic parameters and because of the region's heterogeneity, examining live-dead agreement in 2015 could show if the Alaskan taxa regained their dominance after longer exposure to ocean acidification (Blanchard, 2014; Goethel et al., 2017). This shift away from "Alaskan taxa" is unlikely to be the result of taphonomic bias because both "Alaskan taxa" and the open shelf associated bivalves (Cardiidae, Nuculidae, and Tellinidae) are present in high abundances in living and death assemblages (e.g. typically > 75 dead individuals per station) but in varying proportions in no apparent relationship to their size or shell mineralogy (e.g. Alaskan: Mytilidae with calcite and high-organic nacre found in death assemblages and not live at DBO4.2).

Each of these ecologic shifts inferred from live-dead discordance is a documented ecologic change from macrobenthic time series started in the 1980s. Live-dead discordance is thus able to detect regional and local changes in the benthic bivalve community related to sea ice retreat in the last 10 years.

4.3. Biomass as a paleoecologic currency

Live-dead comparison based on biomass data can reveal spatially finer, station-level discordances than can numerical abundance data alone and is moreover linked more directly to changes in the hydrographic variables. Previous live-dead studies performed with biomass found similar spatial benefits and, allow the paleoecologist to work with a greater proportion of the total community because molluscs are so much larger-bodied than numerically dominant polychaetes (Meadows, 2019; Powell et al., 1985; Staff et al., 1985). Live-dead analysis has previously been performed almost exclusively using numerical abundance data (Kidwell and Tomašových, 2013). Here, however, we wanted to bring paleoecological insights to the recent history of organic carbon biomass, linking to the 40-year record of benthic ecosystem monitoring of the Pacific Arctic (Grebmeier, 1987, 2012; Grebmeier et al., 2015a; Stoker, 1978). This long time-series of observations is rare in ecology and has established connections between physical processes, such as sea-ice loss, and primary and secondary productivity through pelagic-benthic coupling (Cooper et al., 2013; Grebmeier et al., 1988, 1989).

To take full advantage of our finding of robust live-dead agreement in Arctic waters, further work is needed to establish the amount of time represented in these time-averaged death assemblages and, in particular, the geologic age-range of specimens from species that are more abundant dead than alive. Such temporal calibration of changes within the last century can be accomplished by individually dating shells, as used to such ends elsewhere (Kowalewski et al., 2018; Tomašových and Kidwell, 2017); using radiocarbon-calibrated amino-acid racemization, decadal (< 50 year) resolution of shell ages should be possible. Despite these caveats, biomass-based live-dead analysis shows the ability of death assemblages to capture both regional shifts in dominance (Fig. 5) and station-level community reactions to changes in the physical environment (Fig. 6).

5. Conclusions

Bivalve death assemblages from a single cruise (SWL14) demonstrate that an immense amount of ecologic information is often discarded at the end of processing benthic samples for living animals. The fidelity of dead skeletal debris was tested here by comparing live-dead discordance to known changes in the Pacific Arctic ecosystem. Here we use stations as a test of the spatial resolution of death assemblages and find that, regardless of ecologic currency, all stations show live-dead agreement of the expected kind – good where conditions have been stable, and poorer where they have transitioned – showing that stations represent a reasonable scale of spatial resolution for death assemblages on this productive shelf. The opportunity to use biomass and the station spatial scale allowed access to the large amount of data gathered by the DBO and other similar missions at these stations in the last 40 years. This view of the past can be used to test the strength of ecosystem linkages today, such as those emerging within the N Bering Sea between community composition and sediment organic carbon content (Lovvorn et al., 2018). Death assemblages constitute a valuable and new kind of historical data that can add temporal depth to existing directly-observed Arctic time series, providing information on the community that lived in a station sometime before the time of benthic sampling.

This study sought to test the reliability of high-latitude death assemblages in general, the power of biomass in particular as a new currency in live-dead analysis, and the ability of live-dead analysis to capture known shifts in ecology related to climate change. We found positive results on all three fronts: (1) death assemblages are reliable averages of past community structure; (2) biomass data helped reveal live-dead discordance at stations that have undergone ecologic change, differentiating areas that have changed from those that have been stable and with station-level resolution; and (3) live-dead discordance was not detected at every station that has undergone an ecological shift, but never exists where conditions have been stable, making live-dead discordance a conservative guide, as found in other, lower-latitude settings (Kidwell, 2007). Regional and station-level variation in shell abundance is almost certainly a function of the net effects of locally high benthic production and the composition of bottom- and pore-water, a rich topic for future analysis. Quantifying the ages of shells in these death assemblages (work in progress) will determine the full scale of time-averaging of the assemblage and thus its historical reach, the better to determine the timing of changes in species' ranges and population sizes and to understand the dynamics of post-mortem shell loss.

This promising test of the ecological fidelity of high-latitude death assemblages, despite taphonomic challenges, indicates that they should be more fully exploited in high-latitude settings, expanding into areas without long records of biophysical monitoring, to gain information about previously unknown Arctic ecologic baselines.

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Appendices

A: Stations and grabs from SWL14 used in analysis.

Appendix A

Table A1
Stations and grabs from SWL14 used in analysis. Table of site information including the Cruise ID (CruiseID), Station Names (StationNme), what DBO box the station lies within (DBOregion), Date collected (DataDate, Year_Month_Day), the location and depth (Latitude, Longitude, Depth (m)), and number of grabs used to gather death assemblage (# Reps).

CruiseID	StationNme	DBOregion	DataDate	Latitude	Longitude	Depth (m)	# Reps
SWL2014	SLIP-1	DBO1	20140714	62.0113	−175.0592	81	3
SWL2014	SLIP-2	DBO1	20140714	62.0498	−175.2086	84	3
SWL2014	SLIP-3	DBO1	20140714	62.3904	−174.5699	71	3
SWL2014	SLIP-5	DBO1	20140714	62.56	−173.5493	65	3
SWL2014	SLIP-4	DBO1	20140715	63.0301	−173.4595	71	3
SWL2014	UTBS-5	DBO2	20140715	64.6707	−169.9202	47	3
SWL2014	UTBS-2	DBO2	20140716	64.6815	−169.1	45	3
SWL2014	UTBS-4	DBO2	20140716	64.9603	−169.8909	49	3
SWL2014	UTBS-1	DBO2	20140716	64.9906	−169.1408	48	3
SWL2014	UTN-1	DBO3	20140717	66.7115	−168.3986	35	2
SWL2014	UTN-2	DBO3	20140717	67.0501	−168.7291	47	2
SWL2014	UTN-3	DBO3	20140717	67.3297	−168.9093	50	3
SWL2014	UTN-4	DBO3	20140717	67.5014	−168.9042	50	4
SWL2014	UTN5 = SEC1	DBO3	20140718	67.6705	−168.9087	50	2
SWL2014	UTN-6	DBO3	20140717	67.7413	−168.4397	50	4
SWL2014	SEC-2	DBO3	20140718	67.7828	−168.6009	50	3
SWL2014	SEC-3	DBO3	20140718	67.8979	−168.2345	59	3
SWL2014	UTN-7	DBO3	20140719	68.0002	−168.9308	57	4
SWL2014	SEC-4	DBO3	20140718	68.0124	−167.8693	53	3
SWL2014	DBO4.1	DBO4	20140720	70.9728	−161.9012	45	3
SWL2014	DBO4.2	DBO4	20140720	71.1036	−162.264	47	4
SWL2014	DBO4.3	DBO4	20140720	71.2326	−162.635	46	3
SWL2014	DBO4.4	DBO4	20140721	71.3618	−163.0082	46	4
SWL2014	DBO4.5	DBO4	20140721	71.4898	−163.3882	43	2
SWL2014	DBO4.6	DBO4	20140721	71.6182	−163.7711	42	4

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