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Trophodynamics of the Hanna Shoal Ecosystem (Chukchi Sea, Alaska): Connecting multiple end-members to a rich food web

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ABSTRACT

Predicting how alterations in sea ice-mediated primary production will impact Arctic food webs remains a challenge in forecasting ecological responses to climate change. One top-down approach to this challenge is to elucidate trophic roles of consumers as either specialists (i.e., consumers of predominantly one food resource) or generalists (i.e., consumers of multiple food resources) to categorize the dependence of consumers on each primary producer. At Hanna Shoal in the Chukchi Sea, Alaska, we used stable carbon and nitrogen isotope data to quantify trophic redundancy with standard ellipse areas at both the species and trophic guild levels. We also investigated species-level trophic plasticity by analyzing the varying extents that three end-members were assimilated by the food web using the mixing model *simmr* (Stable Isotope Mixing Model in R). Our results showed that ice algae, a combined phytoplankton and sediment organic matter composite (PSOM), and a hypothesized microphytobenthos (MPB) component were incorporated by consumers in the benthic food web, but their importance varied by species. Some primary consumers relied heavily on PSOM (e.g, the amphipods *Ampelisca* sp. and *Byblis* sp.; the copepod *Calanus* sp.), while others exhibited generalist feeding and obtained nutrition from multiple sources (e.g., the holothuroidean *Ocnus glacialis*, the gastropod *Tachyrhynchus* sp., the sipunculid *Golfingia margaritacea*, and the bivalves *Ennucula tenuis*, *Nuculana pernula*, *Macoma* sp., and *Yoldia hyperborea*). Most higher trophic level benthic predators, including the gastropods *Buccinum* sp., *Cryptonatica affinis,* and *Neptunea* sp, the seastar *Leptasterias groenlandica*, and the amphipod *Anonyx* sp. also exhibited trophic plasticity by coupling energy pathways from multiple primary producers including PSOM, ice algae, and MPB. Our stable isotope data indicate that consumers in the Hanna Shoal food web exhibit considerable trophic redundancy, while few species were specialists and assimilated only one end-member. Although most consumers were capable of obtaining nutrition from multiple food sources, the timing, quantity, and quality of ice-mediated primary production may still have pronounced effects on food web structure.

1. Introduction

Many recent Arctic food web studies have focused on how climate change-mediated alterations in sea ice extent and duration will impact benthic-cryopelagic linkages, notably with respect to the timing, quantity, and quality of ice algae and phytoplankton food resources to shallow shelf communities (McMahon et al., 2006; Bluhm and Gradinger, 2008; Søreide et al., 2010; Leu et al., 2011). There is clear evidence that primary production in the Arctic is mediated by sea ice cover (Sakshaug, 2004; Leu et al., 2011; Wassmann and Reigstad, 2011), which has steadily decreased in extent and volume over the past three decades (Arrigo and van Dijken, 2015; Simmonds, 2015). One argument is that with the earlier onset of open water, primary production might be reduced in response to ice-edge retreat occurring during lower light levels in the early spring (Saitoh et al., 2002; Kahru et al., 2011), but long-term observations have shown that the lengthening of the open water season by about 30 days coincides with increased annual net primary production (Arrigo and van Dijken, 2015). In addition, changes in the timing of peak biomass of autotrophs, which are rich in polyunsaturated fatty acids required for heterotrophic growth and reproduction, can cause a mismatch between reproductive cycles of consumers and these vital high-quality food sources (Søreide et al., 2010; Leu et al., 2011).

Increased pelagic primary production does not necessarily yield increased export to the seafloor or increased secondary production. The earlier onset of open water could reduce the magnitude and extent of the rapidly-sinking ice algae bloom, prevent water column stratification due to wind mixing, and cause later-occurring blooms that are

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dominated by phytoplankton (Bluhm and Gradinger, 2008). Later in the growing season, pelagic grazers that are not present in the early spring could efficiently reduce the quantity and quality of carbon that reaches the benthic food web on the seafloor (Carroll and Carroll, 2003). Although forecasting alterations to future primary production regimes is beyond the scope of this study, we track the assimilation of different carbon sources into the benthic food web and assess consumers' reliance on different organic matter sources. By assessing if consumers rely heavily on one organic matter source or exhibit flexibility in their diet, we can better predict how primary production regime shifts will impact the Chukchi Sea food web.

Stable isotopes are a valuable tool to track the assimilation of organic matter sources into a food web. The stable carbon and nitrogen isotope composition of consumer tissue is related to that of its assimilated food sources; therefore, if multiple basal food sources, also referred to here as ultimate organic matter resources or food web end-members, possess differing stable isotope signatures, then the contribution of those food sources to a consumer's diet can be discerned by using mixing models (Phillips et al., 2014). Stable nitrogen isotope ratios ($\delta^{15}N$) of consumers are generally more enriched than their food sources by 2 – 5‰, whereas stable carbon isotope ratios ($\delta^{13}C$) of consumers are only slightly more enriched than their food sources (0 – 1‰), although determining the appropriate trophic enrichment factors between trophic levels is a major source of uncertainty for using stable isotopes for food web studies (McCutchan et al., 2003; Jardine et al., 2006). But by using the appropriate trophic discrimination offsets for each respective stable isotope, consumers can be traced back to the basal food resources (e.g., primary producers, detritus, particulate organic matter) (Reid et al., 2008; Ben-David and Flaherty, 2012). Previous insights in applying stable isotopes to trophic ecology have developed the 'isotopic niche', which is quantified in bivariate $\delta^{13}C$ and $\delta^{15}N$ space, referred to as δ-space or isospace, of a species or population (Bearhop et al., 2004; Newsome et al., 2007). The isotopic niche is a measure of dietary niche width in that it allows the direct comparison of individuals or populations, combines information on richness and evenness of food resources, and allows the temporal integration of dietary information over different timescales (Bearhop et al., 2004). Therefore, it is possible to use isotopic niches to make inferences about the trophic roles of organisms in an ecosystem, i.e., to determine the importance of one food resource versus another, or which organisms couple multiple food resources to higher trophic levels (McMeans et al., 2015).

Several metrics can be used to quantify the character and size of a species, group, or population's isotopic niche, including the $\delta^{13}C$ and $\delta^{15}N$ ranges and the δ-space area of the convex hull (Layman et al., 2007). However, limitations exist in using stable isotopes to solve mixing models and quantify niche space. Two major limitations are the natural variation of stable isotope values exhibited by both consumers and end-members, and the uncertainty surrounding the use of appropriate trophic enrichment factors (TEFs) (McCutchan et al., 2003; Parnell et al., 2010, 2013). TEFs are typically assumed from broad ecosystem surveys (Vander Zanden and Rasmussen, 2001; Post, 2002) or classic lab studies that measured TEFs of several different organisms but only one marine invertebrate, *Artemia salina* (DeNiro and Epstein, 1978, 1981). These previous studies clearly showed that there is normally-distributed natural variation in TEFs, up to 4‰ for $\delta^{13}C$ and from -0.5 to 9.2‰ for $\delta^{15}N$, although the mean, median, and mode TEFs are ~1‰ and ~3.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Recent revelations suggest utilizing Bayesian inference to evade these limitations (Parnell et al., 2010, 2013; Jackson et al., 2011). This approach incorporates uncertainty surrounding assumptions of TEFs and variation of stable isotope values into the model, thereby generating potential solutions (e.g., of isotopic niche width or mixing model proportions) as true probability distributions, thus improving upon linear mixing equations that produce only one solution (Parnell et al., 2010).

The northeast Chukchi Sea is a unique location to conduct food web studies. It has been identified as a benthic 'hotspot' due to its persistent, seasonally intense primary production, which is efficiently exported to the benthos to support high macrofaunal biomass (Grebmeier et al., 2015). The northeast Chukchi Sea, particularly near Hanna Shoal, hosts multiple end-members that can supply nutrition to the benthic food web. The nutrient rich waters in the Chukchi Sea support some of the highest water column primary production and organic carbon flux to the seafloor in the Arctic (Sakshaug, 2004; Moran et al., 2005). Due to its unique hydrology, Hanna Shoal receives northward-advected, nutrient-rich Pacific Ocean water (Weingartner et al., 2013). Sea ice is retained in the region (oftentimes into late summer) and provides an ice algae subsidy to the benthos. Sea ice algae can have a wide range of $\delta^{13}C$ values, greatly depending on algal health, from -24 to -14‰ (Søreide et al., 2006; Tremblay et al., 2006; Gradinger, 2009). Conversely, phytoplankton and particulate organic matter (POM) are typically between $\delta^{13}C$ values of -25 and -22‰ (Iken et al., 2010; McTigue and Dunton, 2014), so ice- and water column-derived organic matter can potentially be isotopically disparate. Sediment organic matter (SOM), the feeding substrate for deposit feeders, is usually isotopically similar to overlying POM, which demonstrates the tight pelagic-benthic coupling on the Arctic shelf (Iken et al., 2010; McTigue and Dunton, 2014; Tu et al., 2015).

Another organic matter source has been posited as a benthic end-member that would produce a ^{13}C-enriched signal in the benthic food web: benthic microalgae (Glud et al., 2009; Wulff et al., 2009; McTigue and Dunton, 2014; Tu et al., 2015). Benthic microalgae have eluded stable isotope analysis in the Chukchi Sea, but they have been identified in other systems as ^{13}C-enriched primary producers relative to phytoplankton (France, 1995; Dubois et al., 2007) (see Table 1). Benthic microalgae typically exhibit $\delta^{13}C$ values that fit within the range of an end-member that would explain the ^{13}C-enriched benthic consumers in the Bering and Chukchi Seas (Lovvorn et al., 2005; McTigue and Dunton, 2014; North et al., 2014; Tu et al., 2015).

An alternative to benthic microalgae that could provide a ^{13}C-enriched OM source for benthic consumers is microbially-degraded OM, first hypothesized by McConnaughey and McRoy (1979) as a ^{13}C-enriched OM source for the Bering Sea benthic food web. Since microalgae have been observed to pass through a consumer's gut undigested (Hansen and Josefson, 2004), it is plausible that microalgae are not bioavailable to some consumers until they have entered the phytodetritus pool via microbial re-working (North et al., 2014), which occurs readily to recently deposited microalgae in Arctic sediments (Sun et al., 2009). Microbial re-working of a carbon pool should preferentially release ^{13}C-depleted CO_2, causing ^{13}C-enrichment of the remaining substrate (Macko and Estep, 1984; Coffin et al., 1990). Bolstering this hypothesis, there is a relationship between sedimentary biomarkers of degraded microalgae and enriched $\delta^{13}C$ values of benthic consumers (McTigue et al., 2015). Moreover, bacteria themselves are a ^{13}C-enriched food source available to benthic food web deposit feeders (Oakes et al., 2016).

Regardless of the true identity of the 'missing' carbon source (Dunton et al., 2014), the $\delta^{13}C$ values of benthic fauna in the Arctic provide convincing evidence that a ^{13}C-enriched organic matter source is assimilated into the food web that cannot be explained by POM, SOM, or ice algae alone (Lovvorn et al., 2005; Lalande et al., 2007; McTigue and Dunton, 2014; North et al., 2014). Since the underlying goal of this research is to apply stable isotope mixing models to elucidate diet proportions of consumers and since mixing models require inclusion of all potential end-members in analysis (Phillips et al., 2014), we included a hypothetical ^{13}C-enriched end-member in our food web. Hereafter, this source is referred to as microphytobenthos (MPB), which is defined by the literature-derived values of benthic microalgae (Table 1). But this ^{13}C-enriched source could also include microbially-degraded phytocarbon or bacteria themselves since these assemblages would overlap in isospace with MPB and cannot not be distinguished using stable isotopes. We emphasize that the actual identity of this end-

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