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Trophodynamics and organic matter assimilation pathways in the northeast Chukchi Sea, Alaska

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ABSTRACT

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We analyzed trophic linkages in the northeast Chukchi Sea shelf based on the stable carbon and nitrogen isotopic analysis of 39 species collected in 2009 and 2010. To decipher organic matter assimilation pathways, benthic fauna were first categorized into nine trophic guilds based on their physical location in the seabed (epibenthic, surface, or subsurface), feeding mode (suspension feeder, deposit feeder, predator, or scavenger), and food source (suspended particulate organic matter, phytoplankton, zooplankton, sediment, microflora, meiofauna, or macrofauna). A discriminant function analysis (DFA) determined that feeding modes were predicted by stable isotope values at an overall classification success rate of 42%, although classification success of each individual guild varied from 0 to 66%. In some instances, stable isotopes classified trophic guilds incorrectly more often than correctly, suggesting high trophic redundancy in the system. A striking pattern was observed where the δ^{13} C values of individuals in some trophic guilds, ranging from about -23 to -17%, were substantially more ¹³C-enriched than representative end-members, which includes phytoplankton (-24.0%), suspended particulate organic matter (-24.3%), and bulk sediment organic matter (-23.3%). In contrast, near-seafloor suspended particulate organic matter was significantly ¹³C-enriched compared to suspended particulate organic matter of near surface waters (p < 0.05), and bulk sedimentary organic matter was more ¹³C-enriched than overlying phytoplankton at seven of 10 stations. This suggests the presence of an unmeasured ¹³Cenriched end-member that is a product of biogeochemical alteration and reworking by the sediment microbial community. Although the microbial community is difficult to quantify using bulk stable isotope analytical techniques, these results indicate it cannot be overlooked as a critical component and avenue through which large amounts of reduced carbon are assimilated by a rich and diverse arctic shelf food web.

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1. Introduction

Recent declines in sea ice extent and duration (Perovich, 2011) are lengthening the open-water season for marine primary producers in arctic ecosystems (Arrigo et al., 2008). Typically, the retreating ice edge fosters an intense phytoplankton bloom in the Chukchi Sea that is largely ungrazed by a zooplankton population that is still low in abundance in early spring (Coyle and Cooney, 1988; Sakshaug and Slagstad, 1992). The earlier onset of open water with ice retreat over the past decade has led to contrasting projections for pelagic primary production. Kahru et al. (2011) and Saitoh et al. (2002) argued that phytoplankton blooms would occur earlier, potentially yielding less production due to lower light availability during the arctic spring compared to early summer. However, open-water blooms occurring later in the season are under increased grazing pressure by zooplankton (Coyle and Pinchuk, 2002). New evidence (Arrigo et al., 2012) suggests that thin (0.5–1.8 m) first-year sea ice permits sufficient light transmission to sustain intense phytoplankton blooms prior to open water events. The change in timing of the phytoplankton bloom is important since the productivity of benthic consumers is tightly coupled to pelagic primary production (Dunton et al., 2005; Dunton et al., 1989; Grebmeier et al., 1988, 1989; Iken et al., 2010).

Several studies have addressed the organic matter assimilation pathways in benthic food webs within high-latitude marine systems in the Alaskan Arctic (Dunton et al., 1989, 2012; Dunton and Schell, 1987; Feder et al., 2011; Iken et al., 2010; Lovvorn et al., 2005; McConnaughey and McRoy, 1979), but few detail the northeast Chukchi Sea, which is now an area of increased interest because of its enormous potential for offshore oil and natural gas exploration and production (Gautier et al., 2009). Tracing assimilation pathways from primary producers is essential to understand how high trophic level organisms (e.g., marine mammals, birds, fish), important for cultural and subsistence hunting

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practices of native Alaskan communities (Highsmith et al., 2006; Lovvorn et al., 2003), obtain their ultimate energy sources. The assimilation pathways that lead to apex predators are particularly of interest since their ultimate energy sources (primary producers) are heavily dependent on and regulated by sea ice dynamics. Although a multitude of studies relate climate change effects to primary producers in arctic ecosystems (Arrigo et al., 2008; Kahru et al., 2011; Wassmann and Reigstad, 2011), few approach the problem by addressing how organisms with different feeding modes may be affected (Sun et al., 2009).

Stable isotope analyses are used to identify the ultimate sources of carbon that are critical components of consumer diets and track the transfer of assimilated organic matter among organisms. Because of the consistent, stepwise fractionation or enrichment exhibited by carbon and nitrogen isotopes during biological processing, these analyses are reliable tools to investigate food web dynamics (Fry and Sherr, 1984). δ^{13} C values between source and consumer change approximately 0-2% per trophic step (DeNiro and Epstein, 1978, 1981; Post, 2002). Since ultimate sources of carbon often have distinct δ^{13} C signatures, and fractionation per trophic step is small, stable carbon isotopes can act as tracers of ultimate carbon sources from origin consumer. Stable nitrogen values (δ^{15} N) of organisms become enriched by 3–4‰ per trophic step (DeNiro and Epstein, 1981). Consequently, δ^{15} N values are used to model species' trophic position in a food web (Post, 2002; Vander Zanden and Rasmussen, 2001). Stable isotope analysis provides an advantageous tool for the Chukchi Sea system because it not only incorporates a long-term, integrated trophic position for organisms, but also distinguishes between food source assimilation versus ingestion as indicated by gut contents analysis. Moreover, organic matter assimilation pathways also represent the avenues that contaminants, like polycyclic aromatic hydrocarbons (PAHs) or heavy metals associated with oil and natural gas development, are transferred and biomagnified in the food web (Fox et al., 2014; Hoekstra et al., 2003; Rasmussen et al., 1990).

It is useful to explore the functional role of different organismal groups when investigating the biological processing of organic matter within an ecosystem. Studies that have used the trophic guild approach, in concert with stable isotope analyses, were able to describe organic matter assimilation pathways in food webs in the Mediterranean suprabenthos (Fanelli et al., 2009), tropical estuaries (Abrantes and Sheaves, 2009), temperate latitudes (Reum and Essington, 2008), arctic deep sea (Bergmann et al., 2009), and on the Antarctic shelf (Gillies et al., 2012; Mintenbeck et al., 2007). We grouped organisms, regardless of taxonomic lineage, into trophic guilds, or groups of organisms that exploit the same resource(s) in a similar manner (Root, 1967). By incorporating functional morphology (i.e., feeding mode), it is possible to elucidate the pathways by which organic matter is processed and passed to higher trophic levels. This approach is useful since marine food webs often represent a "trophic continuum" (i.e., a cascade of non-integer trophic levels) rather than a food web with discrete trophic levels (France et al., 1998).

The results presented here represent a subset of interdisciplinary studies conducted during the Chukchi Sea Offshore Monitoring in Drilling Area-Chemical and Benthos (COMIDA CAB) project that was designed to establish baseline chemical and biological characteristics for the northeast Chukchi Sea. The goal of this study was to determine major avenues of organic matter assimilation for the benthic food web. Specifically, we asked if stable isotope values of primary consumers in separate trophic guilds can discriminate major avenues of organic matter assimilation? We hypothesized that trophic guilds will exhibit high trophic redundancy, measured by isotopic niche overlap, if they assimilate organic matter resources from the same ultimate carbon and nitrogen sources.

2. Methods

2.1. Study area and sample collection

Our sampling stations in the COMIDA CAB study area in the northeastern Chukchi Sea were positioned between the Alaska coastline and 169°W, and from approximately $68.9^{\circ}N$ to $72.4^{\circ}N$ (Fig. 1). Samples were collected between 27 July and 12 August 2009 and 25 July and 16 August 2010 aboard the vessels *R*/*V Alpha Helix* and *R*/*V Moana Wave*, respectively. Stations were chosen



Fig. 1. Location of sampling stations in 2009 and 2010 with respect to the bathymetry of the northern Chukchi Sea.

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