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Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and δ^{13} C and δ^{15} N stable isotopes

Lauren M. Divine a,*, Bodil A. Bluhm a,b, Franz J. Mueter c, Katrin Iken a

- ^a University of Alaska Fairbanks, PO Box 757220, Fairbanks, AK 99775-7220, United States
- ^b Department of Arctic and Marine Biology, UiT- The Arctic University of Norway, 9037 Tromsø, Norway
- ^c University of Alaska Fairbanks, 17101 Point Lena Loop Rd., Juneau, AK 99801, United States

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ABSTRACT

We used stomach content and stable $\delta^{13}C$ and $\delta^{15}N$ isotope analyses to investigate male and female snow crab diets over a range of body sizes (30-130 mm carapace width) in five regions of the Pacific Arctic (southern and northern Chukchi Sea, western, central, and Canadian Beaufort Sea). Snow crab stomach contents from the southern Chukchi Sea were also compared to available prey biomass and abundance. Snow crabs consumed four main prey taxa: polychaetes, decapod crustaceans (crabs, amphipods), echinoderms (mainly ophiuroids), and mollusks (bivalves, gastropods). Both approaches revealed regional differences. Crab diets in the two Chukchi regions were similar to those in the western Beaufort (highest bivalve, amphipod, and crustacean consumption). The Canadian Beaufort region was most unique in prey composition and in stable isotope values. We also observed a trend of decreasing carbon stable isotopes in crabs from the Chukchi to those in the Canadian Beaufort, likely reflecting the increasing use of terrestrial carbon sources towards the eastern regions of the Beaufort Sea from Mackenzie River influx. Cannibalism on snow crabs was higher in the Chukchi regions relative to the Beaufort regions. We suggest that cannibalism may have an impact on recruitment in the Chukchi Sea via reduction of cohort strength after settlement to the benthos, as known from the Canadian Atlantic. Prey composition varied with crab size only in some size classes in the southern Chukchi and central Beaufort, while stable isotope results showed no size-dependent differences. Slightly although significantly higher mean carbon isotope values for males in the southern Chukchi may not be reflective of a gender-specific pattern but rather be driven by low sample size. Finally, the lack of prey selection relative to availability in crabs in the southern Chukchi suggests that crabs consume individual prey taxa in relative proportions to prey field abundances. The present study is the first to provide a baseline of the omnivorous role of snow crabs across the entire Pacific Arctic, as well as evidence for cannibalism in the Chukchi Sea. In light of climate change predictions for the Alaska Arctic, and the potential for future fisheries harvest of snow crabs in this region, continued monitoring of snow crabs, including population and trophic dynamics, is increasingly important to assess snow crab impacts on benthic communities and vice versa.

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1. Introduction

Snow crabs (*Chionoecetes opilio*) are widely distributed across subarctic and arctic regions of the northern parts of the North Pacific and North Atlantic Oceans (Armstrong et al., 2010), where they play important roles in benthic ecosystems. Since 2004, snow crabs have also established a non-native, but self-sustaining, population in the Barents Sea (Alvsvåg et al., 2009, Agnalt et al., 2011). Pacific Arctic snow crabs are considered a panmictic population across their geographic range (Albrecht et al., 2014).

* Corresponding author.

E-mail address: lmdivine@alaska.edu (L.M. Divine).

http://dx.doi.org/10.1016/j.dsr2.2015.11.009 0967-0645/© 2015 Elsevier Ltd. All rights reserved. They are a major contributor to epibenthic biomass across the Chukchi Sea shelf (Bluhm et al., 2009; Hardy et al., 2011; Blanchard et al., 2013a, 2013b, Ravelo et al., 2014) despite their generally small body sizes on the Chukchi shelf (Konar et al., 2014). Large individuals were recently found on the western Beaufort Sea shelf where they are also major contributors to biomass (Rand and Logerwell, 2011; Ravelo et al., 2015). While commercially fished snow crab populations have been extensively studied over decades (e.g., Tarverdieva, 1981; Lefébure and Brêthes, 1991; Lovrich and Sainte-Marie, 1997; Squires and Dawe, 2003), comparatively little is known about their biology, ecology and role in the non-harvested Pacific Arctic distribution range, including their diet and trophic role.

Snow crabs generally occupy a predatory and scavenging role. Where diet studies have occurred, snow crabs consume a large variety of benthic prey including bivalves, gastropods, polychaetes, ophiuroids, and crustaceans (Bering Sea: Tarverdieva, 1981; Kolts et al., 2013a; Chukchi Sea: Feder and Jewett, 1978; Sea of Japan: Yasuda, 1967; Chuchukalo et al., 2011; western North Atlantic: Lefébure and Brêthes, 1991; Wieczorek and Hooper, 1995; Lovrich and Sainte-Marie, 1997; Squires and Dawe, 2003). In some regions, cannibalism on juveniles, combined with predation on other crab species, also is an important contribution to their diet (Lovrich and Sainte-Marie, 1997; Chuchukalo et al., 2011). However, the importance of cannibalism may vary by location and be related to the relative abundance of juveniles compared with abundance and size spectra of other available prey taxa. Ontogenetic diet shifts occur as crabs become larger and acquire larger chelae, allowing them to prey on larger prey items and harder-shelled mollusks and clams (Squires and Dawe, 2003; Kolts et al., 2013a).

Snow crabs support lucrative commercial fisheries in the northwest Atlantic (eastern Canada and western Greenland), the Sea of Japan, and the eastern Bering Sea. However, warming trends observed in the Bering Sea over the past three decades have resulted in a northward contraction of the commercially exploited stock out of historical fishing grounds in the southeastern portion (Zheng et al., 2001; Orensanz et al., 2004). The current center of distribution of snow crabs in the Bering Sea has shifted northward of 60°N (Orensanz et al., 2004; Mueter and Litzow, 2008). This northward contraction of snow crabs raises critical questions of dispersal and migration dynamics affecting commercial fishing in the eastern Bering Sea, as well as connectivity among populations in the northern Bering, Chukchi, and Beaufort seas. In addition to the decline of the exploitable snow crab stock in the southeastern Bering Sea, increased open waters of the Arctic due to reductions in sea ice associated with climate warming makes these Arctic regions potentially attractive to fishing (Hollowed et al., 2013). Although fisheries biomass removal is not currently permitted in the Alaska Arctic, the Arctic Fishery Management Plan lists snow crabs as a potential future fisheries target (North Pacific Fishery Management Council, NPFMC, 2009). In-depth knowledge of snow crab habitat requirements, including dietary preferences and prey availability, is therefore needed for effective fisheries management in this Arctic region.

Snow crabs occupy environmentally complex and disparate regions of the Chukchi and Beaufort seas. The Chukchi shelf is wide and shallow shelf with an average depth of 50 m, with welldocumented "hot spots" of high primary production and tight benthic-pelagic coupling that support high benthic standing stocks (Grebmeier et al. 1988, 2006a, 2006b, 2015). Variability in primary production across the shelf is related to the hydrography of several distinct overlying water masses (Walsh et al., 1989). Anadyr Water (AW) delivers high salinity, nutrient-rich waters to the western Chukchi, Alaska Coastal Water (ACW) is comparatively less saline with lower nutrient content in the eastern Chukchi, and the Bering Shelf Water (BSW) of intermediate water properties runs between the AW and ACW (Coachman, 1987). Distribution of epibenthic organisms in the Chukchi Sea is structured by sediment characteristics, water depth, and these water masses and their properties, which supply nutrients and carbon to the seafloor through pelagic-benthic coupling (Feder et al., 1994, 2005). Snow crabs on the Chukchi Sea shelf are members of the epibenthic communities that are typically dominated by crustaceans, echinoderms (mostly ophiuroids), and gastropods (Bluhm et al., 2009; Blanchard et al., 2013a; Ravelo et al., 2014). Snow crab abundance and biomass seem to vary regionally and interannually on the Chukchi shelf (Bluhm et al., 2009, 2015; Ravelo et al., 2014), and crabs occur even in areas where bottom temperatures are below

their experimentally defined lower thermal limit (≤ -1 °C, Foyle et al., 1989).

In contrast to the Chukchi shelf, the Beaufort shelf is a narrow, interior shelf receiving nutrient-rich water inflow from the Chukchi Sea in the west and more oligotrophic waters to the east (Dunton et al., 2006). Overall benthic biomass and abundance are lower in the Beaufort than the Chukchi Sea, reflecting generally lower primary production in the Beaufort Sea with some exceptions, such as the Cape Bathurst area or upwelling-induced algal blooms (Macdonald et al., 1989; Tremblay et al., 2011). Freshwater runoff and land fast ice limit the abundance and diversity of epifauna and infauna of the nearshore Beaufort Sea to \sim 25 m depth (Dunton et al., 2005; Ravelo et al., 2015). Epibenthic biomass is highest at the shelf break of the western Beaufort Sea (100-200 m; no deeper locations were sampled, Ravelo et al., 2015); snow crabs are most common at depths of 100-500 m along the western to central Beaufort slope (Rand and Logerwell, 2011), where they reach larger sizes than those in the Chukchi Sea including commercial-sized snow crabs (>78 mm carapace width [CW] defined for the Bering Sea stock) collected at depths of > 200 m on the Alaska Beaufort slope (Logerwell et al., 2011; Bluhm et al., 2015).

From other large-bodied crabs, such as red king crabs (Paralithodes camtschaticus), it is known that they can have substantial top-down influence on benthic community abundance and composition through their feeding activities (e.g., Jørgensen, 2005; Britayev et al., 2010). Vice versa, snow crabs are themselves can be prey, for example for some fish species (e.g., Livingston et al., 1993). Given the high abundance of snow crab in the Pacific Arctic (Paul et al., 1997; Bluhm et al., 2009; Ravelo et al., 2014; Kolts et al., 2015), their northward range shift (Orensanz et al., 2004), and the mandate to fill knowledge gaps in species of potential commercial interest (North Pacific Fishery Management Council, NPFMC, 2009), our goal was to study snow crab diet and trophic position in the Chukchi and Beaufort seas. Stomach content (SCA) and stable isotope (SIA) analyses are common and complementary methods to address diet composition. SCA can provide high taxonomic resolution and at times, depending on preservation state, size information of prey items that were recently consumed (Hyslop, 1980). SCA is a suitable tool to compare diets of crab species occupying similar or different habitats, investigate seasonal diet changes (e.g., Sundet et al., 2000), or ontogenetic shifts in diet composition (Stevens et al., 1982). However, soft bodied, easily digested, or crushed prey organisms are likely to be underestimated in importance (Hyslop, 1980) and SCA are snapshots of diet at a given time and location. These limitations of SCA can be at least partially overcome with the complementary use of SIA. Trophic studies based on SIA commonly use $\delta^{13}C$ and $\delta^{15}N$ ratios to identify primary carbon sources and trophic positions of species or higher taxa within a local or regional food web (Post, 2002). SIA indicates diet over a longer period, from weeks to months in polar invertebrates depending on turnover time of consumer tissues (Mintenbeck et al., 2007; Kaufman et al., 2008; Weems et al., 2012), and is not limited to recent feeding of the organism (Lovvorn et al., 2013). However, distinguishing relative proportions of specific prey in consumers that eat a variety of taxa that themselves have similar diets (and thus similar isotope values) is difficult using SIA. The combined use of SCA and SIA is a more powerful approach for diet studies than each individual method (e.g., Kolts et al., 2013b).

In the present study, we used the complimentary methods of SCA and SIA to provide insight into the diet composition of male and female snow crabs over a range of body sizes and different benthic environments in the Alaska Arctic. Specifically, we sought to address the following questions for the Chukchi and Beaufort seas: (1) Do regional differences occur in snow crab diets across

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