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

We used stomach content and stable δ^{13} C and δ^{15} N isotope analyses to investigate male 12 13 and female snow crab diets over a range of body sizes (30-130 mm carapace width) in five 14 regions of the Pacific Arctic (southern and northern Chukchi Sea, western, central, and Canadian 15 Beaufort Sea). Snow crab stomach contents from the southern Chukchi Sea were also compared 16 to available prey biomass and abundance. Snow crabs consumed four main prey taxa: 17 polychaetes, decapod crustaceans (crabs, amphipods), echinoderms (mainly ophiuroids), and 18 mollusks (bivalves, gastropods). Both approaches revealed regional differences. Crab diets in the 19 two Chukchi regions were similar to those in the western Beaufort (highest bivalve, amphipod, 20 and crustacean consumption). The Canadian Beaufort region was most unique in prey 21 composition and in stable isotope values. We also observed a trend of decreasing carbon stable 22 isotopes in crabs from the Chukchi to those in the Canadian Beaufort, likely reflecting the 23 increasing use of terrestrial carbon sources towards the eastern regions of the Beaufort Sea from 24 Mackenzie River influx. Cannibalism on snow crabs was higher in the Chukchi regions relative 25 to the Beaufort regions. We suggest that cannibalism may have an impact on recruitment in the 26 Chukchi Sea via reduction of cohort strength after settlement to the benthos, as known from the 27 Canadian Atlantic. Prey composition varied with crab size only in some size classes in the 28 southern Chukchi and central Beaufort, while stable isotope results showed no size-dependent 29 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.

Key words: Beaufort Sea, cannibalism, Chukchi Sea, diet, snow crab, stable isotopes

1. Introduction

Snow crabs (*Chionoecetes opilio*, O. Fabricius, 1788) 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). 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,b, 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, Lefebvre 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: Lefebvre 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 (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 well-documented "hot spots" of high primary production and tight benthic-pelagic coupling that

support high benthic standing stocks (Grebmeier et al. 1988, 2006a,b, 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 ~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 (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 δ^{13} C and δ^{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).

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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 the Chukchi and Beaufort seas?, (2) Does body size affect snow crab diets within and across study regions?, (3) Do trophic differences occur among some sex-age classes (male, immature female, mature female) within and across study regions?, and (4) Do snow crabs preferentially select for specific prey types or do they feed on prey in similar relative abundances to the prey's availability in the field?

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2. Methods

Snow crabs of sizes 30-130 mm CW were collected across five geographic regions during several cruises in the Chukchi and Beaufort seas from 2011 to 2013 (Table 1, Fig. 1). These regions were defined based on a combination of previous sampling schemes, hydrography and circulation, and sample size distribution: southern Chukchi Sea (bounding box: 66.05 to 70.00 °N, 164.14 to 168.50 °W), northern Chukchi Sea (70.50 to 73.00 °N, 157.18 to 168.51 °W), western Beaufort Sea (70.10 to 70.90 °N, 144.95 to 147.07 °W), central Beaufort Sea (70.50 to 71.30 °N, 147.28 to 151.34 °W), and Canadian Beaufort Sea (69.93 to 71.33 °N, 123.49 to 140.40 °W). The Alaska Chukchi Sea was divided into north and south regions at 70°N latitude to correspond with geographic terminology used in previous diet studies (e.g., Iken et al. 2010, Norcross et al. 2015). In addition, hydrographic conditions differ between the two regions: Water masses entering the southern Chukchi Sea through Bering Strait slow and allow advected particles to settle, leading to benthic hotspot regions (Grebmeier et al. 2015). Benthic communities in the northern Chukchi Sea are driven by the complex hydrography of water around Hanna Shoal, creating a mosaic of depositional and advective microhabitats (Blanchard et al. 2013b). The western and central Alaska Beaufort regions correspond with previous groundfish and benthic invertebrate sampling regions (Frost and Lowry 1983, Rand and Logerwell 2011, Divine et al. 2015). The western Beaufort also is under stronger influence and nutrient-rich particle advection from the Chukchi Sea than the central Beaufort Sea (Ashjian et al. 2005), serving as food source for benthic communities (Divine et al. 2015). The Canadian Beaufort region encompassed stations east of the U.S.-Canadian border. Chukchi Sea snow crabs were collected in July-August 2012 aboard the F/V Alaska Knight as part of the Arctic

Ecosystem Integrated Survey (Arctic Eis) using either an 83-112 eastern otter trawl (mesh size: 10.2 cm wings and body, 8.9 cm intermediate and codend, 3.2 cm codend liner, Goddard et al. 2014 for trawl operations) or a modified plumb staff beam trawl (PSBT-A, mesh size: 7 mm, 4 mm codend liner; Abookire and Rose 2005). We assume that any potential bias due to differences in sampling gears used in the Chukchi Sea was small and not relevant for the objectives of this study as we obtained a range of crab sizes representative of those observed previously in these regions. Crabs from the U.S. Beaufort Sea were collected in August-September aboard the R/V Norseman II during the 2011 BeauFish cruise and in August-September during the 2012 and 2013 U.S.-Canadian Transboundary cruises using the PSBT-A (for additional sampling details see Norcross et al. 2015, Ravelo et al. 2015). Snow crabs from the Canadian Beaufort Sea were collected in 2012 and 2013 aboard the R/V Frosti using a modified Atlantic Western IIA otter trawl (mesh size: 1.27 cm cod-end and intermediate liner, A. Majewski [DFO] pers. comm.) as part of the Beaufort Regional Environmental Assessment (Department of Fisheries and Oceans Canada). In all cases, stomachs were removed from crabs through incisions in the dorsal carapace and preserved in ethanol or 10% buffered formalin until analysis. A muscle sample for SIA was removed from a pereiopod of each crab and dried at 60°C for 24 h. In all cases, crabs were sexed and CW measured using digital calipers to the nearest 0.01 mm.

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2.1 Stomach content analysis

Stomach contents were removed and placed in a Petri dish for visual inspection under a dissecting microscope (Leica M165) outfitted with a Leica DFC420 camera. Each prey item was photo cataloged for taxonomic verification. Contents were identified to lowest taxonomic level possible and presence or absence of diet items was determined for each crab stomach. The frequency of occurrence (FO) for each prey item was determined as the percentage of all crab stomachs in which a diet item occurred within each region, body size, or sex-age class, depending on category of analysis. Hence, each prey item FO value ranged from 0-100% and was independent of the FO values for all other prey items (Brown et al. 2012). FO for each diet item was first averaged for all crabs within each region (regardless of size or sex-age class), and

we compared averages to determine regional differences in means. Then we partitioned crabs by size and sex-age classes and calculated FO for these groups, first by pooling across regions and then by comparing sizes and sex-ages within individual regions. The highly degraded state of many prey items as a result of grinding by the gastric mill in snow crab stomachs precluded enumerating prey items per stomach or measuring the dominant taxa by volume or mass.

2.2 Stable isotope analysis

- Samples for SIA from pereiopod muscle tissue were dried, and lipids were removed with 2:1 chloroform: methanol because lipids may be depleted in 13 C and thus may bias carbon values (Mintenbeck et al. 2007, Logan et al. 2008). Tissue samples were then re-dried at 60° C for 24 h. Samples were analyzed at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks on a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer with V-PDB and atmospheric N_2 as standards for carbon and nitrogen, respectively. Sample isotope ratios were expressed in the conventional δ notation as parts per thousand (‰) according to the following equation:
- $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) 1] \times 1000$
- where X is 13 C or 15 N of the crab tissue sample and *R* is the corresponding ratio 13 C/ 12 C or 15 N/ 14 N. Instrument error was < 0.2 ‰ for both δ^{13} C and δ^{15} N values.

2.3 In situ prey availability

To assess the degree of selectivity in snow crabs diets, we compared a subset of snow crab stomach contents to benthic prey availability. For this purpose, macro-invertebrate abundance (individuals m⁻²) and biomass data (g C m⁻²) generated from 0.1 m² van Veen grab samples rinsed over 1 mm mesh from the 2012 Russian-American Long-Term Census of the Arctic (RUSALCA) program were provided from five stations in the southern Chukchi Sea (CS17, CL1, CL3R, CS8R, CS12R) by J. Grebmeier and L. Cooper (both U. Maryland). These stations were chosen based on their close proximity to 2012 Arctic Eis stations where snow crabs were collected for stomach content analysis (see Fig. 1). No prey information was available for the other regions so that this analysis was only done for the southern Chukchi Sea region. Prey

taxa were grouped at the class level and ranked separately for abundance and biomass from 1 to 10 (1 being highest, 10 the lowest, 0 is absent) at each station (Table 2). Frequency of occurrence of prey taxa occurring in snow crab stomachs at the same stations in the southern Chukchi Sea were grouped by the same higher taxa as reported for prey biomass and abundance (see Table 2). Prey selectivity was compared only to macro-infaunal prey and not epifaunal prey as infauna comprised most snow crab diet items.

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2.4 Statistical analysis

We used permutational multivariate analysis of variance (PERMANOVA) at a significance level of α =0.05 for all statistical analyses (PRIMER v7 with PERMANOVA). We determined differences in SCA within and among regions, size groups, and sex-age classes based on presence/absence data analysis in a Jaccard Similarity Index resemblance matrix. For statistical analyses involving crab sizes, crabs were grouped into size classes of 10 mm CW (e.g., the 40 mm CW size class included all crabs with 40.0-49.9 mm CW) based on previous snow crab diet studies (Kolts et al. 2013a). Sex-age groups were male, mature female, and immature females. Males were not separated into immature and mature classes because there was high variability in the ratio of carapace width to chela height, a maturity metric used in other regions, which precluded our ability to confidently determine a CW break for immature versus mature male sizes. Maturity of females was determined based on the shape of the abdominal flap and presence or absence of an egg clutch. Immature and mature females overlapped in their size ranges. We treated region, CW, and sex-age class as fixed factors in the PERMANOVA for both SCA and SIA analyses. Post-hoc pairwise comparisons detailed the differences in diets across CW size classes among regions and within a region. Similarity of Percentages (SIMPER) analysis determined the prey taxa that contributed most to the differences in diets of the crab size classes within each region. We used non-metric multidimensional scaling (nMDS) plots to visualize the differences in diets of different size classes within those regions where significant differences occurred. Similarly, we investigated regional, size, and sex-age differences in snow crab $\delta^{13}C$ and $\delta^{15}N$ stable isotope values via PERMANOVA. Post-hoc pairwise comparisons were conducted across and within each region to explore which regions contributed to significant differences. Canadian Beaufort crabs were excluded from within-region comparisons because only males were collected in this region.

To rule out potential environmental influences on snow crab diets and stable isotope values that may confound SCA or SIA results, we correlated environmental variables (water depth, bottom-water temperature and salinity) with FO diet data and stable isotope values using the BIO-ENV routine in PRIMER. Ranked prey abundance and biomass data (Table 2) were compared with ranked snow crab stomach FO data to determine if crabs were selectively feeding on various prey taxa using non-parametric Mann-Whitney U-tests. Selectivity was defined as a significant difference between ranked prey abundance or biomass *in situ* and rank of prey FO in crab stomachs.

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3. Results

3.1 Regional diet patterns

Together, SCA and SIA methods indicated Alaska Arctic snow crabs are omnivorous and consume a wide variety of benthic invertebrate prey across all study regions. The most frequently occurring diet items across all regions were the polychaete Cistenides hyperborea (59.5%), bivalves (57.1%), and 'other polychaete' worms (42.9%). Less frequent prey items included a variety of crustaceans including amphipods (27.2%) and crabs and shrimps (25.7%), ophiuroids (22.2%), and teleost fishes (7.4%). Other items included unidentifiable tissue parts and sediment particles. Regional differences occurred in snow crab diets as revealed in both SCA and SIA (p= 0.001 for both approaches, Table 3 and 4). Crabs in the southern Chukchi region most frequently fed on bivalves (FO= 61%), followed by C. hyperborea (FO= 47%) and amphipods (FO= 31%, Fig. 2). Compared with all other regions, crabs in the southern Chukchi had the highest FO for brachyuran crabs (possibly juvenile snow crabs, FO= 23%). Crabs in the northern Chukchi region had a similar diet composition to those in the southern Chukchi, including relative high FO for brachyuran crabs (possibly juvenile snow crabs, FO= 15%). In contrast, brachyuran crabs occurred in less than 5% of stomachs in any of the Beaufort regions (Fig. 2). Otherwise, snow crabs in the western Beaufort fed in similar proportions to those in the northern and southern Chukchi regions on bivalves (FO= 60%), 'other polychaetes' (FO= 28%),

and amphipods (FO=25%), but had a higher proportion of *C. hyperborea* (FO=70%) compared with Chukchi regions. Crabs in the central Beaufort region most frequently fed on *C. hyperborea* (FO=83%), with intermediate consumption frequency of 'other polychaetes', ophiuroids and bivalves (FO=39%, 29%, and 28%, respectively), and low consumption of teleost fishes and amphipods (FO=15% and 14%, respectively). Canadian Beaufort Sea crabs were quite different in their stomach contents compared with all other regions (PERMANOVA pair-wise comparison, p< 0.05 for all comparisons, Table 3), due mainly to high FO of 'other polychaetes' (FO=50%), low FO of *C. hyperborea* (FO=13%) and amphipods (FO=3%), and several common taxa in other regions being absent in the stomach contents of Canadian Beaufort crabs (e.g., brachyuran crabs, 'other crustaceans').

Stable δ^{13} C and δ^{15} N isotope values were also regionally different for snow crabs (PERMANOVA, p= 0.001, Table 4, Fig. 3). Across all regions, δ^{13} C ranged from -21.50 ‰ to -15.82 ‰ and δ^{15} N ranged from 11.71 ‰ to 17.27 ‰ in individual crabs. Canadian Beaufort male crabs (the only sex group sampled in that region) had the lowest δ^{13} C values and were statistically different from crabs in all other regions (PERMANOVA, p< 0.01 for all post-hoc comparisons, Table 4, Fig. 3). Crabs of all sex-age groups in the central Beaufort region were similar to each other in mean values of both isotopes, and were characterized by slightly lower δ^{13} C and higher δ^{15} N values compared with crabs from other regions (significant regional differences in all comparisons [p< 0.01], except with the northern Chukchi [p= 0.07]).

3.2 Effects of size on snow crab diets

Crab size was a significant factor for SCA only in the interaction between region and size class (PERMANOVA, p= 0.002, Table 3). These diets differences among size classes based on SCA only occurred within the southern Chukchi and central Beaufort regions (PERMANOVA pair-wise comparison, p= 0.001 and 0.007, respectively, Table 3, Fig. 4 and 5). In the southern Chukchi, the largest size class of snow crabs examined (80 mm CW) was different from all other size classes within that region (SIMPER analysis; average dissimilarity= 59.3%, Fig. 4, A.1) and most frequently consumed the polychaete *Cistenides hyperborea* (FO= 67%) and had higher FO of the bivalve *Yoldia hyperborea* (FO= 33%) and 'other polychaetes' (FO= 100%) than other

size classes. Small crabs (40-60 mm CW) more commonly consumed bivalve sp. 1, bivalve sp. 2, amphipods, and gastropods (Fig. 4A and B), as well as ophiuroids, which were absent from the diets of 80 mm CW crabs. Bivalve prey partitioning was seen among crab size classes in the southern Chukchi: *Ennucula tenuis* and bivalve sp. 1 were consumed equally among all size classes, while *Serripes groenlandicus* and 'other bivalves' (species others than those identified here) were consumed only by small crab size classes. *Yoldia hyperborea* was consumed most commonly by the smallest (40 mm CW) and largest (80 mm CW) size classes (17% and 33%, respectively).

In the central Beaufort, the two smallest size classes examined (50 mm and 60 mm CW) had significantly different stomach content composition compared with each other and most other size classes (PERMANOVA pair-wise comparisons p< 0.05, Table 3, Fig. 5).

Dissimilarities of the 50 mm CW class were driven, among other factors, by the lack of 'other polychaetes' and teleost fish parts in their diets (Fig. 5A) and low FO of detritus/sand/rocks (FO= 25%). Stomach contents within the 60 mm CW size class were characterized by high FO of ophiuroids (FO= 60%) and detritus/sand/rocks (FO= 100%), relatively low FO of 'other polychaetes' (FO= 20%), and the lack of *Yoldia hyperborea*, gastropods, and other prey taxa compared with other size classes (Fig. 5A and B). Several prey taxa were found only in intermediate size classes, such as the bivalve *Y. hyperborea*, gastropods, and teleost parts (Fig. 5A). In contrast to effects on SCA, body size was not a significant factor in stable isotope values of snow crabs (PERMANOVA, p= 0.72, Table 4).

3.3 Effects of sex-age on snow crab diets

SCA generally indicated similar diets for male, mature female, and immature female crabs across all study regions (PERMANOVA, p= 0.72, Table 3, Fig. 3). Within the southern Chukchi Sea, males were enriched in 13 C compared with immature and mature females (Fig. 3). SIA indicated sex-age differences in several regions (Table 4). Diet of most sex-age groups of the western Beaufort, northern and southern Chukchi Sea were relatively similar, except for slightly higher δ^{13} C and δ^{15} N values in southern Chukchi males (PERMANOVA, p< 0.01 for all post-hoc comparisons, Table 4, Fig. 3). Western Beaufort mature females were characterized by

distinctly lower δ^{15} N values than any other group (~1.0 % lower, Fig. 3) but were not statistically different (PERMANOVA, p= 0.06 for all post-hoc comparisons, Table 4).

3.4 In situ prey availability (southern Chukchi region only)

Macro-infaunal prey taxa occurred at similar rank orders in snow crab stomach contents as they did *in situ* in the southern Chukchi Sea (p> 0.05), with the exception of Sipuncula (p= 0.02 for biomass and abundance) and Nemertea (p= 0.02 for biomass, Table 5). Sipuncula contributed a large fraction of *in situ* biomass and abundance at one station (ranked 1st in biomass and 6th in abundance, Table 2) but was absent in crab stomachs. Nemertea ranked 5th in biomass at one station but was also absent in crab stomachs.

4. Discussion

4.1 Regional diet trends

Together, data from SCA and SIA provided regional diet information that contributes to our understanding of snow crab ecology, trophic level, and resource partitioning on the Alaska Chukchi and Beaufort seas shelves. Overall, snow crabs mostly consumed four main invertebrate prey taxa including polychaetes, crustaceans, bivalves, and ophiuroids; in addition, fish were consumed in low frequencies. The range of main prey groups observed in the present study was consistent with previous diet studies of *Chionoecetes* crabs of similar size range in the Bering Sea (Feder and Jewett 1980, Kolts et al. 2013a), Gulf of Alaska (Jewett and Feder 1983), Cook Inlet (Paul et al. 1979), and Canadian North Atlantic (Wieczorek and Hooper 1995, Lovrich and Sainte-Marie 1997, Squires and Dawe 2003).

Snow crab diets included members of infaunal and epifaunal communities, both of which are patchily distributed throughout the study area as a consequence of varying combinations of hydrography, sediment properties, food supply and trophic interactions (Bluhm et al. 2009, Iken et al. 2010, Ravelo et al. 2014, 2015, Blanchard and Feder 2014, Whitehouse et al. 2014, Grebmeier et al. 2015). Infaunal abundance and biomass is typically dominated by polychaetes, bivalve mollusks, and amphipod crustaceans across the Chukchi and Beaufort seas (Bilyard and Carey 1979, Grebmeier et al. 2006a, Feder et al. 2007, Blanchard et al. 2013a). Our comparative

analysis of stomach contents with macro-infaunal prey in the southern Chukchi region showed that frequency of consumption of these groups as prey is closely related to their availability. This agrees with previous findings in the northern Bering Sea where *Chionoecetes* crabs tend to consume prey in relative proportions to prey abundance in the field (Kolts et al. 2013a). Some occasionally abundant taxa seemed to be consumed less frequently compared with their *in situ* abundance in our study, especially some soft-bodied taxa. We suggest, however, that the lack of Sipuncula and Nemertea in crab stomachs in the southern Chukchi Sea is likely based on the lack of identifiable hard parts in these taxa, which typically leads to underrepresentation in stomach content data (Warwick and Somerfield 2008).

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On the northeastern Chukchi shelf, polychaetes, bivalve mollusks, and crustaceans account for > 80% of total macro-infaunal abundance (Schonberg et al. 2014). Each of these taxa also had very high (> 50%) FO in crab stomachs from that region, again suggesting that the main prey items reflect local overall prey abundances. Macro-infaunal data for the Beaufort Sea are sparse and in part date back several decades (e.g., Wacasey et al. 1977, Bilyard and Carey 1979, Carey et al. 1984) or cover depths where snow crabs do not occur (e.g., < 10 m depth, Dunton et al. 2012). Thus, our ability to interpret snow crab diets in the context of prey availability is limited. The polychaete C. hyperborea was a particularly prominent prey item in crabs from the western and central Beaufort Sea, while other polychaetes were the most abundant prey item in crabs from the Canadian Beaufort Sea. Limited available data suggest that polychaete abundance in the central and eastern Beaufort Sea is highest at depths of 200 m along the outer continental shelf, and decreases sharply with increasing depth (Bilyard and Carey 1979, S.M. Hardy, UAF, unpublished data). This coincides well with the depth distribution of crabs on the Beaufort Sea shelf, which are most common along the shelf break and upper slope region (Logerwell et al. 2011). Across the Canadian Beaufort shelf, echinoderms (ophiuroids in particular) and bivalves comprise > 70% total macrofaunal biomass and polychaetes contribute up to ~40% biomass (g ww m⁻², Conlan et al. 2008, 2013, Roy et al. 2014). In summary, our results suggest that regional differences in snow crab stomach content observed in the present study likely reflect in situ community composition of prominent benthic macro-infaunal prey across the study region.

In addition to high consumption of infaunal prey taxa, snow crab also preyed on epibenthic fauna. Ophiuroids and crustaceans typically dominate abundance and biomass of epibenthic communities in varying proportions across both shelves (Chukchi Sea: Feder et al. 2005, Bluhm et al. 2009, Ravelo et al. 2014; Beaufort Sea: Roy et al. 2014, Ravelo et al. 2015). Ophiuroids account on average for > 40% biomass (g ww m⁻²) and > 60% abundance in the southeastern and northeastern Chukchi Sea, although with high spatial variability (Feder et al. 2005, Bluhm et al. 2009, Ravelo et al. 2014), and for > 40-90% in biomass (g ww m⁻²) and abundance on the Beaufort Sea shelf (Roy et al. 2014, Ravelo et al. 2015). Ophiuroids were common prey items and occurred at equal frequencies in snow crab stomachs in all regions. Despite the clear dominance of ophiuroids in epibenthic communities across the study regions, crabs in all regions consumed a variety of prey taxa, such as polychaetes, bivalves, and amphipods more frequently than ophiuroids. As these more common prey taxa are mostly infaunal, diet results from this current study may indicate that snow crab prey on epifauna taxa mostly opportunistically or that they are a less preferred food item due to their relatively low energy content (Hondolero et al. 2012).

One epifaunal prey group that showed strong regional differences in crab stomachs were brachyuran crabs, which were common prey items especially in Chukchi Sea crabs (FO= 23% and 15% in the southern and northern Chukchi Sea, respectively) but not in Beaufort Sea crabs (FO < 5% for all Beaufort regions). Brachyuran crabs, especially *C. opilio* and the lyre crab *Hyas coarctatus*, are common in the Chukchi Sea (Feder et al. 2005, Bluhm et al. 2009, Blanchard et al. 2013a, Ravelo et al. 2014). Although we could not fully confirm identity from the stomach content fractions, the appearance of fragments seemed to point to juvenile snow crabs as this prey category. This FO may indicate an appreciable amount of cannibalism in the Chukchi Sea. Cannibalistic feeding has been a common occurrence in laboratory studies of snow crabs, with 55% of crabs < 50 mm CW cannibalized by larger crabs (Dutil et al. 1997). Cannibalism has also been observed in populations in the northern Bering Sea (Kolts et al. 2013a), Newfoundland (Wieczorek and Hooper 1995, Squires and Dawe 2003), and the Sea of Japan (Chuchukalo et al. 2011). For example in the Sea of Japan, crabs were the main single prey item of snow crabs by FO (17.6%) and prey mass (18%, Chuchukalo et al. 2011). In the northern Bering Sea,

cannibalism on small juveniles (< 20 mm CW) occurred in localized regions and reached an FO of ~40% in snow crab stomachs (Kolts et al. 2013a). Potentially cannibalized crabs were found in the stomachs of Chukchi Sea crabs ranging from 30-80 mm CW, while we found little evidence of cannibalism in the larger crabs (90-130 mm CW) of the Beaufort Sea. In the St. Lawrence estuary, cannibalism was also more prominent in smaller snow crab < 50 mm CW than larger adults (Lovrich and Sainte-Marie 1997); thus, the lack of conspecific prey in larger crabs may be due to a prey shift to other larger, perhaps more nutritious, prey items. More likely, however, the regional differences in cannibalism we observed were not based on a sizedifference in the predatory crabs but result from there being very few small, juvenile crabs in the Beaufort Sea to serve as prey (Rand and Logerwell 2011, Ravelo et al. 2015), while small crabs are very common in the Chukchi Sea (Konar et al. 2014). In general, intraspecific predation may benefit adolescent snow crabs in the Chukchi Sea directly by increasing food supply and indirectly by reducing competition for resources. Severity of cannibalism is typically densitydependent, with smaller snow crabs at ~15-30 mm CW possibly the most susceptible to cannibalism (Lovrich and Sainte-Marie 1997). Cannibalism has been suggested to regulate recruitment and establish cohort strength during the early stages of snow crab ontogeny (Sainte-Marie et al. 1996, Lovrich and Sainte-Marie 1997) and is known as a significant source of mortality in other crab species (Hines and Ruiz 1995, Fernandez 1999). Cannibalism may be an important part of total mortality in the Chukchi Sea given the high abundances of snow crabs, including young stages (Konar et al. 2014), while it seems a negligible source of mortality in the Beaufort Sea. Cannibalism was not included in a previous assessment of snow crab mortality in the eastern Chukchi Sea (Whitehouse et al. 2014) but, based on results from the present study, should be considered in population dynamics and assessments of possible future snow crab fisheries in the Chukchi Sea.

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Regional differences in trophic structure also existed in the time-integrated measure of stable isotope analysis, despite overall high variability in the isotope data within each region. The main regional separation based on SIA was observed between the Chukchi Sea and the central and Canadian Beaufort Sea, similar to the regional diet differences we observed based on SCA. Most of this separation was along the carbon stable isotope axis, which represents differences in

basal food sources (DeNiro and Epstein 1978). Benthic food webs along the Alaska Beaufort Sea shelf and upper slope receive more marine carbon in the western Beaufort Sea versus stronger terrestrial carbon inputs in the central Beaufort Sea (Dunton et al. 2012, Divine et al. 2015, Bell 2015), which can be traced by the lighter $\delta^{13}C$ values of the terrestrial carbon sources (Wooller et al. 2007). Therefore, the depleted ^{13}C signal in central and Canadian Beaufort Sea crabs in the present study likely reflects the strong imprint of terrestrial source on the benthic food web in the western part of the Beaufort Sea.

4.2 Size and sex-age effects on snow crab diets

Generally, most size and sex-age classes within each region had similar diets with respect to both stomach contents and stable δ^{13} C and δ^{15} N isotopes. We found size effects only in SCA and sex-age effects only in SIA. Size-related differences in stomach contents were due to the unique diet composition of the largest size class (80 mm CW) relative to all other sizes for southern Chukchi crabs and diet compositions of the two smallest size classes (50 and 60 mm CW) in the central Beaufort Sea. Crabs > 80 mm CW in the southern Chukchi region did not consume several prey taxa that were common in smaller size classes (e.g., ophiuroids, bivalve sp. 1; both FO= 0%, A.1). Since > 80 mm CW was the largest size class of crabs encountered in the Chukchi regions, it is possible that we detected a shift in diets with increased body size, as has been observed in snow crabs in the northern Bering Sea (Kolts et al. 2013a). However, since size-based diet differences occurred only between a few size classes in two regions with no consistent patterns or trends across all regions, the size-based results may be artifacts of the low sample sizes or from binning crabs into 10 mm CW size classes. These factors may also explain the lack of detectable differences in SIA among size classes. Due to the overall narrow ranges of δ^{13} C and δ^{15} N isotope values among all crabs and high variability within any size grouping, larger sample sizes would be necessary to detect subtle differences.

In general, all sex-age groups consumed similar diets in the present study. Previous gender-specific SCA studies among similar-sized males and females have produced mixed results at different spatial scales in some regions. For example, no differences were found in the diets of male and female snow crabs of similar sizes in Bonne Bay, Newfoundland (Wieczorek and Hooper 1995), but differences between male and female feeding habits occurred at a larger

scale across the northeast Newfoundland shelf (Squires and Dawe 2003). In that area, males consumed more ophiuroids, fish, polychaetes, and clams (considered harder to capture prey items), while females preyed more on easily accessible prey items such as shrimp, gastropods, crabs and sea urchins. In the northern Bering Sea, diets were identical for males and females of similar sizes and in general reflected *in situ* prey availability (Kolts et al. 2013a). Additionally, Lovrich and Sainte-Marie (1997) found males were more likely to engage in cannibalism in the laboratory, but the present study found both males and females consumed smaller snow crabs.

Stable isotope analysis revealed subtle gender-specific diet differences in several regions, despite the lack in gender differences of diets from SCA. Males in the southern Chukchi were enriched in 13 C compared with mature and immature females within the same region, but given that the mean δ^{13} C value for males was within 1 ‰ (considered the range of natural variation, DeNiro and Epstein 1978) of mean δ^{13} C values for females in the same region, we suggest that these differences are likely of minor biological importance. Differences in mean isotope values were more variable between sexes in the Beaufort Sea, although not significant because of high variability in a low number of replicates.

4.3 Conclusions

Snow crab prey items in the Chukchi and Beaufort seas included common benthic taxa that occur across the study region. Frequency of occurrence of prey taxa differed regionally, with most separation of diets observed between the central and Canadian Beaufort regions. Neither size nor gender was a consistent factor explaining diet differences, and the few differences we found may need to be investigated further with larger sample sizes. Cannibalism was pronounced in the Chukchi Sea but not elsewhere, a pattern that may result from the locally high densities of small snow crabs in the Chukchi Sea relative to the Beaufort Sea. As suggested for other regions (Lovrich and Sainte-Marie 1997), we hypothesize that cannibalism may contribute to regulating recruitment in the Chukchi Sea via intraspecific predation that reduces cohort strength after settlement to the benthos. It may be more important than previously considered for fisheries managers to incorporate this source of mortality into assessments of snow crab population dynamics and estimations of sustainable yields for the Arctic Chukchi Sea population (NPFMC 2009). Given that no prey selectivity was apparent in the southern Chukchi Sea (where

statistically tested), the present population of snow crabs seems to impact benthic prey fields equally. Should strong range shifts of large (> 80 mm CW) crabs or substantial increases of snow crab populations occur in the southern Chukchi Sea as some evidence suggests (Feder et al. 2005, Mueter and Litzow 2008, Bluhm et al. 2009), they would likely exert increased top down pressure and have the potential to restructure benthic food webs (e.g., Falk-Petersen et al. 2011, Dvoretsky and Dvoretsky 2015). Thus, continued monitoring of snow crab life history and population dynamics in the Pacific Arctic region is essential to detect future potential increases in snow crab abundances that may impact the benthic prey communities, and subsequently benthic food web structure. More detailed work on establishing relationships between snow crab diets and prey availability across the entire Alaska Arctic will allow a better assessment of how potential increases in snow crab populations in the Arctic may impact benthic communities. Conversely, changes in benthic community composition, as predicted with continued climate changes (Grebmeier 2012), may impact snow crabs as a potentially valuable commercial resource in the future.

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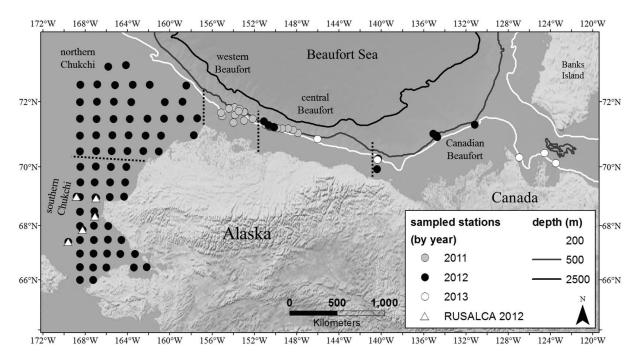


Figure 1. Map of station locations in the Chukchi and Beaufort seas where snow crab collections occurred. Stations are shaded by year of collections. White triangles represent RUSALCA stations where macrofauna were collected for prey availability analysis. Regions are delineated by black dotted lines.

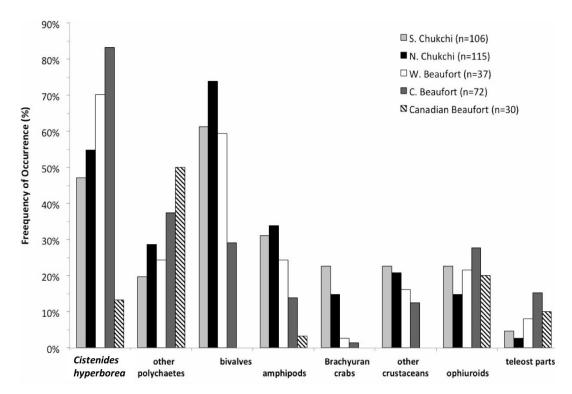


Figure 2. Frequency of occurrence (%) data for the most common prey taxa categories by regions in the Chukchi and Beaufort Seas. Sample sizes for each region are indicated in parentheses in the legend.

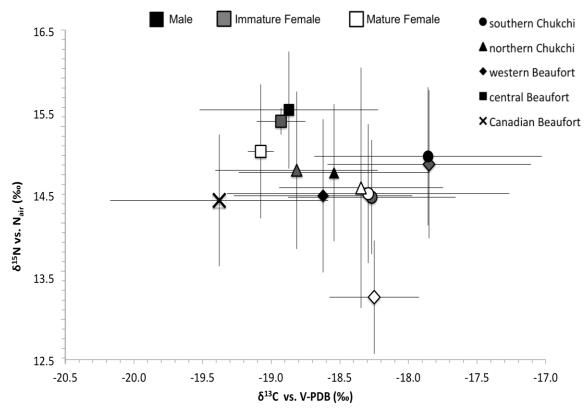
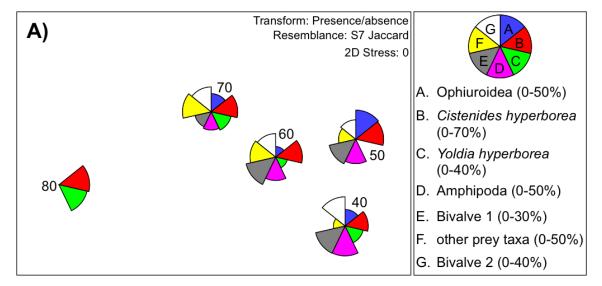


Figure 3. Mean δ^{13} C and δ^{15} N stable isotope values for males and immature and mature females for five regions: southern and northern Chukchi Sea and western, central, and Canadian Beaufort Sea. Error bars are ± 1 S.D.



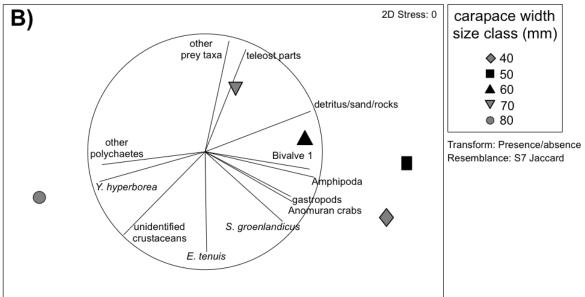
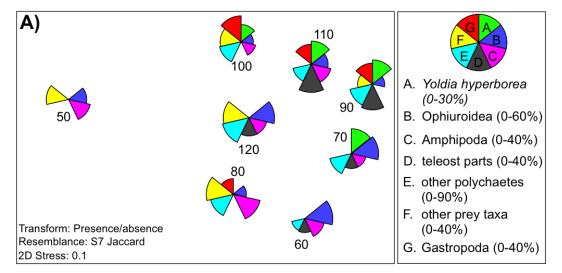


Figure 4. MDS plots for snow crabs in the southern Chukchi Sea showing A) seven prey taxa contributing to differences among size classes (carapace width size classes are represented numerically) and their frequency of occurrence (FO) within diets for each size class (FO minimum to maximum range indicated in parentheses). Pie pieces are proportional within each specified taxa to the range of FO occurring among size classes. B) Prey taxa that contributed to dissimilarities in the diets among various carapace width size classes as indicated in SIMPER analysis. Distances among data points are proportional to the degree of dissimilarity among size classes and overlaid directional lines indicate prey taxa that contribute to these dissimilarities.



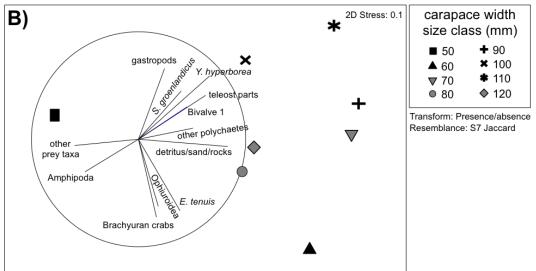


Figure 5. MDS plots for snow crabs in the central Beaufort Sea showing A) seven prey taxa contributing to differences among size classes (carapace width size classes are represented numerically) and their frequency of occurrence (FO) within diets for each size class (FO minimum to maximum range indicated in parentheses). Pie pieces of each specified taxa are proportional to the range of FO occurring among size classes. B) Prey taxa that contributed to dissimilarities in the diets among various carapace width size classes as indicated in SIMPER analysis. Distances among data points are proportional to the degree of dissimilarity among size classes and overlaid directional lines indicate prey taxa that contribute to these dissimilarities.

- 1 Table 1. Overall carapace width (CW) size ranges and number of stomachs analyzed for
- 2 males, immature females, and mature females for each of the five study regions.

Region southern Chukchi southern Chukchi	Sex class	Size range	No. of	No. Isotope	
Region	Sex class	(mm CW)	Stomachs	samples	
southern Chukchi	males	40-80	78	79	
southern Chukchi	immature females	40-50	24	26	
southern Chukchi	mature females	30-60	NA	33	
northern Chukchi	males	40-80	101	79	
northern Chukchi	immature females	40-50	10	10	
northern Chukchi	mature females	30-60	NA	32	
western Beaufort	males	30-70	26	24	
western Beaufort	immature females	30-50	5	5	
western Beaufort	mature females	30-60	3	3	
central Beaufort	males	50-120	64	33	
central Beaufort	immature females	60-70	3	3	
central Beaufort	mature females	60	2	2	
Canadian Beaufort	males	80-130	22	28	

Table 2. Ranked biomass and abundance prey taxa for five stations from the 2012 RUSALCA cruise and for five carapace width (CW)

2 size classes of snow crabs collected at close-by stations to the 2012 Arctic EIS cruise to the southern Chukchi Sea (see Fig. 1 for

3 station locations) "—" indicates that prey taxa were absent at a station.

Station	Polychaeta	Bivalvia	Crustacea	Sipuncula	Ophiuroidea	Echinoidea	Anthozoa	Ascidiacea	Nemertea	Others
Biomass	$(g C m^{-2})$									
CS8R	3	1	2	7	4	_	6	_	8	5
CS12R	4	1	2	_	_	_	3	_	5	6
CS17	4	2	6	5	7	10	9	3	8	1
CL1	1	2	4	8	5	7	_	_	6	3
CL3R	2	3	4	1	6	7	_	_	_	5
Abundan	ce (individual	$(s m^{-2})$								
CS8R	3	2	1	8	5	_	6	_	7	4
CS12R	3	2	1	_	_	_	4	_	6	5
CS17	1	6	2	5	3	9	_	7	8	4
CL1	2	1	3	7	4	6	_	_	_	5
CL3R	2	1	3	6	5	6	_	_	_	4
Snow Cre	ab CW size cl	ass								
40 mm	3	1	2	_	4	_	_	_	_	5
50 mm	1	2	3	_	4	_	_	_	_	5
60 mm	2	1	3	_	5	_	_	_	_	4
70 mm	1	2	2	_	_	_	_	_	_	3
80 mm	1	2	3	_	_	_	_	_	_	

1 Table 3. PERMANOVA results comparing carapace width size classes (CW) and sex-age

- 2 classes within study regions in the Chukchi and Beaufort Seas. Results shown indicate
- 3 variance components explained by region, body size, and sex-age class for stomach
- 4 contents analysis, as well as F-statistics and significance. Post-hoc comparisons are
- 5 provided at the among-region and individual region level. Statistical details for
- 6 differences among CW size classes (SIMPER analysis) in the southern Chukchi and
- 7 central Beaufort Seas are provided in Appendix 1.

Source of variation	df	SS	MS	Pseudo -F	P (based on 999 permutations)	
Stomach Contents Analysis-						
Region, CW, Sex-age as fixed variables						
Among regions	3	20333.0	6777.7	2.8	0.001	
Among CW	9	27793.0	3088.2	1.3	0.056	
Among Sex-age	1	1680.3	1680.3	0.7	0.718	
Region*CW	13	42935.0	3302.7	1.4	0.002	
Region*Sex-age	3	9085.7	3028.6	1.2	0.182	
CW*Sex-age	4	10605.0	2651.2	1.1	0.344	
Region*CW*Sex-age	2	3123.7	1561.9	0.6	0.874	
Stomach Contents Analysis- post-hoc						
pairwise regions						
southern Chukchi- northern Ch					0.208	
southern Chukchi- western Beaufort					0.281	
southern Chukchi- central Beaufort					0.001	
southern Chukchi- Canadian Beaufort					0.025	
northern Chukchi- western Beaufort					0.338	
northern Chukchi- central Beaufort					0.001	
northern Chukchi- Canadian Beaufort					0.008	
western Beaufort- central Beaufort					0.655	
western Beaufort- Canadian Beaufort					0.013	
central Beaufort- Canadian Beaufort					0.001	
Stomach Contents Analysis-						
Individual region CW groups						
southern Chukchi	4	24572.0	6143.1	2.2	0.001	
northern Chukchi	4	10109	2527.4	1.0	0.473	
central Beaufort	7	21653.0	3093.3	1.7	0.007	
western Beaufort	4	9717.5	2429.4	1.1	0.305	
Canadian Beaufort	4	10150	2537.6	0.8	0.656	

- 1 Table 4. PERMANOVA results for stable isotope analysis (SIA) comparing carapace width size
- 2 classes (CW) and sex-age classes within study regions in the Chukchi and Beaufort Seas. Results
- 3 shown indicate variance components explained by region, body size, and sex-age class, as well
- 4 as F-statistics and significance. Post-hoc comparisons are provided at the regional and the sex-
- 5 age levels.

Source of variation	df	SS	MS	Pseudo- F	P (based on 999 permutations)
SIA-Region, CW,					
Sex-age as fixed variables					
Among regions	4	0.61	0.15	7.1	0.001
Among CW	9	0.13	0.01	0.7	0.722
Among Sex-age	2	0.15	0.10	4.7	0.034
Region*CW	14	0.25	0.02	0.8	0.654
Region*Sex-age	6	0.24	0.04	1.9	0.056
Region*CW*Sex-age	4	0.06	0.02	0.7	0.658
SIA- post-hoc pairwise regions					
southern Chukchi-northern Chu	ıkchi				0.064
southern Chukchi-western Beau	ufort				0.084
southern Chukchi-central Beaufort					0.009
southern Chukchi-Canadian Bea	0.001				
northern Chukchi-western Beau	ıfort				0.137
northern Chukchi-central Beau	fort				0.073
northern Chukchi-Canadian Bea	0.002				
western Beaufort-central Beaufort					0.002
western Beaufort-Canadian Beaufort					0.013
central Beaufort-Canadian Beaufort					0.001
SIA-post-hoc pairwise within region	on				
southern Chukchi					
male-immature female					0.001
male-mature female					0.005
immature female-mature female					0.981
northern Chukchi					
male-immature female					0.848
male-mature female					0.547
immature female-mature female					0.724
western Beaufort					
male-immature female					0.140
male-mature female					0.055
immature female-mature female					0.056
central Beaufort					
male-immature female					0.937

male-mature female	0.064
immature female-mature female	0.094

- 1 Table 5. Mann-Whitney U-tests comparing ranked prey biomass and abundance in situ to
- 2 ranked importance (based on frequency of occurrence [%]) of snow crabs within the
- 3 southern Chukchi Sea.

Source of variation	df	U	P-value
Polychaeta (biomass)	1	2.32	0.13
Polychaeta (abundance)	1	1.22	0.27
Bivalvia (biomass)	1	0.12	0.73
Bivalvia (abundance)	1	0.12	0.73
Crustacea (biomass)	1	0.97	0.32
Crustacea (abundance)	1	1.04	0.31
Ophiuroidea (biomass)	1	0.05	0.83
Ophiuroidea (abundance)	1	0.29	0.59
Echinoidea (biomass)	1	3.75	0.05
Echinoidea (abundance)	1	3.75	0.53
Anthozoa (biomass)	1	3.71	0.05
Anthozoa (abundance)	1	2.22	0.14
Ascidiacea (biomass)	1	1.00	0.32
Ascidacea (abundance)	1	1.00	0.32
Sipuncula (biomass)	1	5.53	0.02
Sipuncula (abundance)	1	5.54	0.02
Nemertea (biomass)	1	5.58	0.02
Nemertea (abundance)	1	3.72	0.05
Other prey (biomass)	1	0.20	0.67
Other prey (abundance)	1	0.20	0.66