

Effects of body size, gender, and prey availability on diets of snow crabs in the northern Bering Sea

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ABSTRACT : In efforts to maintain or restore populations of snow crabs *Chionoecetes opilio*, identifying important habitats requires knowing prey preferences and availability for different sexes and life stages. We analyzed the diets of juvenile, adolescent, and adult snow crabs of both sexes relative to available prey throughout a large area of the northern Bering Sea. Snow crabs of all sizes consumed a wide variety of prey including bivalves, gastropods, polychaetes, ophiuroids, and crustaceans. The proportions of different taxa in snow crab diets corresponded closely to the relative abundance of those taxa in different areas; thus, in this region, diets of respective sexes and ages can be predicted fairly accurately from the local abundance of different prey. The only apparent differences in diet between sexes were related to the larger and stronger claws of adult males. Larger crabs consumed larger prey that required greater handling ability and claw strength, such as harder-shelled bivalves and gastropods, larger polychaetes, and other snow crabs. Juvenile crabs consumed softer, more easily manipulated prey, such as amphipods and small bivalves with thin or incompletely calcified shells. Areas of high abundance of juvenile snow crabs, previously not recognized in designating essential habitat in this region, were characterized by high abundance of amphipods and small bivalves. Quality and importance of habitat for snow crabs appeared to depend jointly on several factors: hydrographic patterns that determine locations of larval settlement and subsequent ontogenetic migration, the combined abundance of all prey taxa, and ontogenetic capabilities for handling different sizes of prey.

KEY WORDS: Essential fish habitat · Decapod diets · Prey size selection · *Chionoecetes opilio* · Crustacean stomach contents · Benthic prey availability · Bering Sea

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INTRODUCTION

As the climate changes and fishing and other industries expand in northern regions, it is increasingly important to identify essential habitats for valued marine species (Beck et al. 2001, Pautzke 2005, Dew 2010, Brigham 2011). Snow crabs *Chionoecetes opilio* support circumpolar fisheries that are vulnerable to such effects. For example, in the southeast Bering

Sea, snow crab stocks declined precipitously in the early 1990s and remain depressed despite reduced harvests (Rugolo et al. 2006). Also, during a warm period in the early 2000s in the Bering Sea, the geographic range of mature snow crabs contracted northward from historical fishing grounds (Orensanz et al. 2004). Such trends, along with similar changes for groundfish, may encourage expansion of both crab and bottom trawl fishing into previously un-

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fished areas (cf. Perry et al. 2005). Anticipating these changes requires the identification of potential and existing habitats that are critical to snow crab populations, so that adequate protection can be provided (cf. Seitz et al. 2001, 2008, NMFS 2005).

In much of the northern Bering Sea, year-round bottom-water temperatures below -1°C are cold enough to prevent a positive energy balance in snow crabs fed ad libitum, and to suppress their growth and fecundity in the field (Thompson & Hawryluk 1990, Kolts 2012). Nevertheless, snow crabs are the most abundant macroinvertebrate predator in this region. Snow crab size and abundance vary geographically in the northern Bering Sea, largely due to physical oceanographic factors affecting planktonic dispersal, larval settlement and survival, and subsequent ontogenetic migrations (Kolts 2012). A key question is the degree to which the adequacy of benthic habitat for different life stages of snow crabs is limited by prey preferences or prey size constraints relative to prey availability. Resolving this uncertainty is important for identifying any bottlenecks in life history caused by habitat limitation of specific life stages (Lipcius et al. 2005).

Studies of snow crabs and other crab species have demonstrated highly variable diets that appear to reflect variations in total prey abundance, relative abundance among prey species, and different size classes of the crabs (Gotshall 1977, Feder & Jewett 1978, Paul et al. 1979, Laughlin 1982, Jewett & Feder 1983, Boulding & Hay 1984, Hines et al. 1990, Cerda & Wolff 1993). However, seldom has availability of the entire suite of potential prey been measured to assess the extent to which diets of different size classes of crabs can be predicted based solely on prey availability. Such insights might, for example, shift habitat conservation for crabs from an emphasis on prey community structure to total abundance of all potential prey, and facilitate models of the trophic role of crabs in different communities (Falk-Petersen 2004).

For snow crabs, the only studies that have compared diets with prey availability have been in the northwest Atlantic for snow crabs that are larger than those that occur in the northern Bering Sea. For example, in the southwest Gulf of St. Lawrence, Canada (Br thes et al. 1982), crustaceans were the most commonly consumed prey. However, neither crustaceans nor polychaetes were preferentially consumed, likely due to their high relative abundance (83 to 97% of available prey). In contrast, less abundant echinoderms and gastropods were selected, especially by larger crabs. Similarly, snow crabs in Bonne Bay, Newfoundland, Canada (Wieczorek &

Hooper 1995), fed randomly on abundant polychaete species, but selectively on less common taxa including poriferans, ophiuroids, small gastropods, and certain bivalve species.

The selectivity of diets in relation to prey abundance and distributions are unknown for snow crab populations in areas of the northern Bering Sea where fisheries could potentially expand due to climate change. In this paper, we characterize the diets of snow crabs of both sexes and of different sizes compared with variations in abundance and mass of available prey over this large region.

MATERIALS AND METHODS

Study system

We sampled stations between St. Matthew Island and Bering Strait on the shallow continental shelf of

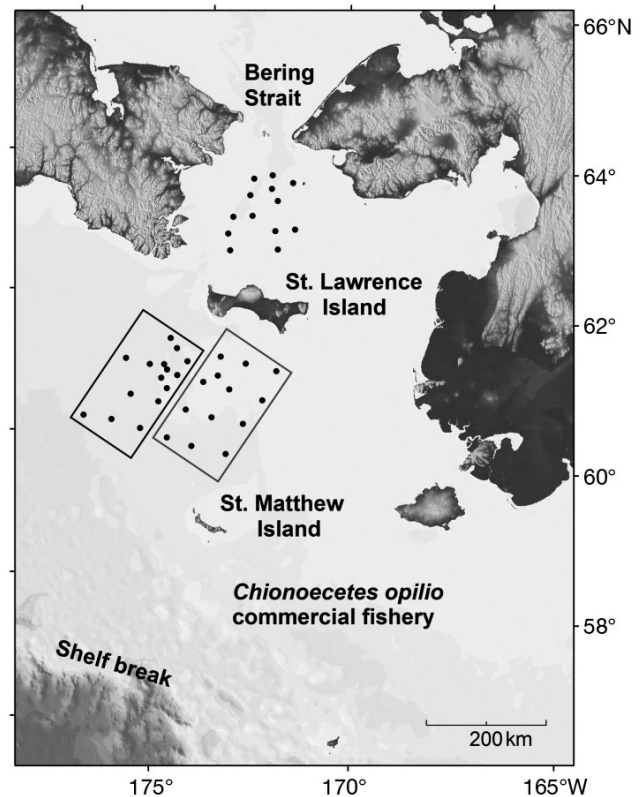


Fig. 1. Stations sampled for snow crab *Chionoecetes opilio* diets in the northern Bering Sea (St. Matthew Island to Bering Strait). The general area of the snow crab commercial fishery extends from south of our study area to beyond the lower (southern) edge of this map. The shelf break at about 200 m depth is also shown. Stations north of St. Lawrence Island (SLI) comprise the Chirikov Basin epibenthic assemblage. South of SLI, the rectangles separate East and West assemblage sectors

the northern Bering Sea (Fig. 1). Most of the study area south of St. Lawrence Island (SLI) is covered year round by a cold pool of bottom water $<1^{\circ}\text{C}$, which forms under sea ice during winter and persists through summer due to weak currents in this region of the shelf (Hu & Wang 2010). This mass of cold water excludes a number of snow crab predators that are common in the southeast Bering Sea, such as Pacific cod *Gadus macrocephalus* (cf. Alderdice & Forrester 1971, Orensanz et al. 2004). Cold temperatures also constrain the size structure of snow crabs in our study area, due to skipping of molts and ontogenetic migration toward warmer waters along the shelf break (Kolts 2012). Our study area is mostly north of the Bering Sea snow crab fishery (Fig. 1); the legal size (carapace width) for this fishery is >78 mm and marketable size is >100 mm, whereas all adult females we captured were <68 mm and all adult males <90 mm (Kolts 2012).

Distinct assemblages of epibenthic macrofauna occurred in separate regions of our study area. Cluster analysis separated stations north of SLI in the Chirikov Basin from those south of SLI, which were further differentiated into East and West sectors (Fig. 1, Kolts 2012; see the Supplement at www.int-res.com/articles/suppl/m483p209_supp.pdf). At 3 stations in the West sector, the total mass of benthic invertebrates and the abundance of some crab sizes were exceptionally high. However, that local area did not differ from the remaining West sector in either benthic prey composition or snow crab diets, and is not considered separately here. Station depths ranged from 35 to 52 m in the Chirikov Basin, and from 30 to 96 m south of SLI. For these cruises, maps of water temperature and salinity near the bottom, and grain size and total organic content of sediments, are given in the supplement to Cui et al. (2009). Bottom-water temperature did not vary among stations sampled south of SLI (all -1.7 to -1.8°C), and was 0 to -1.8°C at stations sampled in the Chirikov Basin.

Collection and measurement of crabs

We collected snow crabs and benthic prey at stations in the northern Bering Sea by trawling from the USCGC 'Healy'. In May and early June 2006, we collected 15 550 crabs from 59 trawls at 44 stations north and south of SLI using an otter trawl with a 7 m footrope and a 3.7 mm (1.5 in) stretched mesh. To provide a more constant area swept by the trawl for estimating crab density in a concurrent population study (Kolts 2012), in late May and June 2007 we used a 4 m beam trawl with the same mesh size to

collect 31 179 snow crabs from 89 trawls at 53 stations. Carapace width (CW) of crabs ranged from 5 to 90 mm, although less than 2% of crabs were over 60 mm CW (see Kolts 2012 for a map of all sampled stations and a size frequency histogram of all crabs collected). For diet studies, we selected 5 crabs of each sex in each instar-based size class from a subset of 42 stations covering the geographic range of our study area (this subset of all stations is shown in Fig. 1). Stations with the best representation of size classes of both sexes were chosen for diet analysis. This subsample of crabs analyzed for stomach contents (Fig. 2) ranged from Instars III to XII, although most crabs were Instars IV to X. As size-based differences in diet were not evident between crabs of adjacent instars, diets were analyzed across the 3 size classes that showed the greatest variation. These size classes were <20 mm CW (hereafter termed juveniles), 20 to 40 mm CW (immature and adolescents, the latter being males that are sexually but not morphometrically mature), and >40 mm CW (a mix of adolescent and morphometrically mature crabs).

For each crab, we measured fresh mass (including shells) to 0.1 g, CW, and height of the right chela (CH) in males (Jadamec et al. 1999). We distinguished mature from adolescent males by the ratio of CH to CW, using $\text{CH} = 0.191 \times \text{CW}$ as a dividing line (Kolts 2012). Maturity in females was determined from the size of the abdominal flap (Jadamec et al. 1999). All mature crabs were >40 mm CW.

Snow crab diets

The stomachs of nearly 10 000 crabs were removed through incisions in the dorsal region of the carapace and placed in 10% buffered formalin. Stomachs were allowed to fix for 4 to 7 d before being rinsed and stored in 70% ethanol. To avoid empty stomachs, at each station we chose the 'plumpest' stomachs available for each gender and size class for analysis. Based on this sample, we analyzed the stomach contents of 2928 snow crabs collected in May and June 2006 and 2007, including 1397 females ranging from 7 to 68 mm CW, and 1531 males from 10 to 90 mm CW (Fig. 2). Stomach contents were later removed and placed in a petri dish for visual inspection with a dissecting microscope (Olympus SZ-6045), and all contents within the stomach were identified to the lowest taxon possible. We calculated number of prey items and percent frequency of occurrence for all ingested taxa in each stomach as a percentage for all stomachs examined.

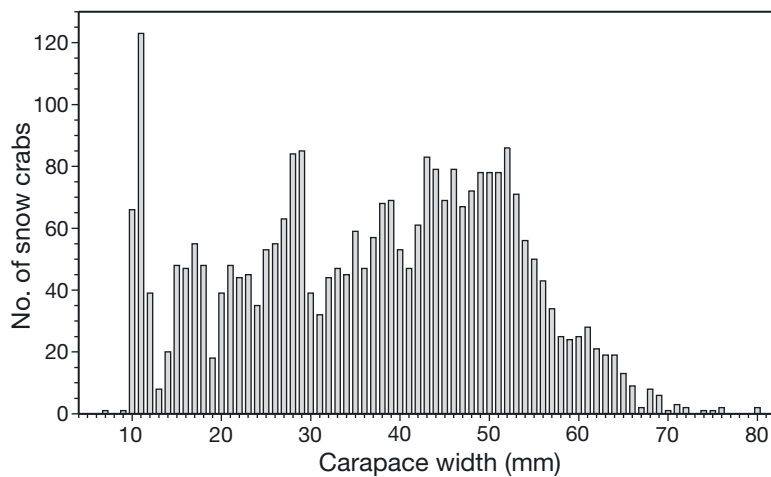


Fig. 2. *Chionoecetes opilio*. Size structure of snow crabs analyzed for stomach contents, collected in the northern Bering Sea in May and June 2006 and 2007. The legal size for the Bering Sea snow crab fishery is >78 mm carapace width (CW), and marketable size is >100 mm CW

Prey availability

Abundance (no. m⁻²) and carbon mass (gC m⁻²) of prey species were estimated from 4 pooled 0.1 m² van Veen grab samples collected in May and June 2006 at each station for which stomach contents were analyzed (prey availability data for 2007 were not available for these analyses). Grab samples were washed with sea water over a 1 mm sieve, and collected organisms were preserved in 10% buffered formalin for post-cruise analyses at the Chesapeake Biological Laboratory. Mean abundance and carbon mass (based on conversions from fresh mass of formalin-preserved animals to carbon mass in Stoker 1978) were calculated for prey taxa in the Chirikov Basin (N = 13 stations), East (N = 14), and West (N = 15) sectors of our study area (Fig. 1). Mean abundance indicates the frequency with which different prey taxa are encountered by snow crabs in their local habitat. Carbon mass, which excludes the substantial shell mass of bivalves and gastropods, indicates the prey mass available for assimilation by snow crabs. We also calculated abundance and carbon mass of prey taxa as proportions of the total available at each station.

Data analyses

We used Minitab version 15 and a significance level of 0.05 for all data analyses. We calculated approximate 95% confidence intervals for percent frequency of occurrence by the method of Agresti &

Coull (1998). We chose this approach over the more commonly used Wald method, which is inaccurate for small sample sizes or proportions near 0 or 1 (Whitlock & Schluter 2009); some dietary proportions we observed approached these levels. Proportions of specific prey taxa in the diets of different size classes or genders of snow crabs within the 3 sectors of our study area were considered different if their 95% confidence intervals did not overlap.

We used correlation analysis to evaluate the association of frequency of occurrence or proportion of prey items in the diet with prey availability for each of our 3 size classes of snow crabs in each sector. Juvenile crabs were absent at a number of stations in the Chirikov Basin and East sectors, so in those sectors only stations at which juvenile diets were examined were used to quantify available prey for crabs with CW <20 mm. We compared the number of prey items per stomach among the 3 size classes in each sector using 1-way ANOVA followed by Tukey comparisons. We used Student's *t*-tests to compare the number of prey items per stomach between males and females of the same size class within the same sectors.

We calculated an index of diet selection S_i as

$$S_i = D_i - E_i \quad (1)$$

where D_i is the relative frequency of occurrence of prey i in the diet, and E_i is the proportion of available prey composed of prey i at the sampled stations (Strauss 1979; relative frequency of occurrence was the frequency of occurrence of a given taxon expressed as a percentage of the sum of frequencies of occurrence of all taxa). This index ranges between -1 and +1, with negative values indicating avoidance or inaccessibility, positive values indicating preference, and values near zero indicating no preference in feeding. We calculated S_i using percent frequency of occurrence of taxa in diets as D_i . We used either proportion of total prey abundance or proportion of total carbon mass for E_i . We analyzed S_i separately for each snow crab size class in each sector of our study area.

RESULTS

All snow crab stomachs analyzed contained either recently consumed prey material or remnants from an earlier meal. Corners and folds in snow crab sto-

machs can retain small fragments of earlier meals. Thus, even stomachs that did not contain a full recent meal contained fragments of bivalve or gastropod shells or crustacean carapaces, or bits of polychaete or crustacean setae. All stomachs contained varying amounts of fine sediments, and often some unidentifiable soft tissue or detritus.

Diet differences by gender and maturity of crabs

There were no significant differences between the diets of male and female crabs <40 mm CW in any of the 3 sectors of our study area, or between sexes of any size class in the Chirikov Basin ($p > 0.05$). The only gender-based differences were for large females (>40 mm CW) eating some major prey taxa (smaller bivalves, gastropods, or ophiuroids) more often than similarly sized males in the same sectors (Table 1). By major taxa we mean the 5 broad taxonomic groups in Table 1: Bivalvia, Polychaeta, Crustacea, Ophiuroidea, and Gastropoda. South of SLI, diets differed little between mature and adolescent crabs within the same sex and size classes (overlap of 95% confidence intervals, Table 1). This maturity comparison was not possible in the Chirikov Basin because there were too few mature crabs. Given these minimal differences, both sexes and maturity categories were combined within size classes in subsequent analyses.

Table 1. *Chionoecetes opilio*. Number and percentage of stomachs containing at least 1 individual of the corresponding taxon, listed in decreasing frequency of occurrence for immature and mature female and male crabs >40 mm carapace width (CW), in the West and East sectors of our study area (Fig. 1). N = total number of snow crab stomachs examined. Lower and upper bounds of 95% confidence intervals (CI) were calculated using the method of Agresti & Coull (1998)

Age, Sex, Sector	Taxon	No. of stomachs	Occurrence (%)	95% CI	
				Lower	Upper
Immature females, West sector (N = 329)	Bivalvia	261	79.3	74.6	83.4
	Polychaeta	233	70.8	65.7	75.5
	Crustacea	201	61.1	55.7	66.2
	Ophiuroidea	177	53.8	48.4	59.1
	Gastropoda	103	31.3	26.5	36.5
Immature males, West sector (N = 360)	Polychaeta	259	71.9	67.1	76.3
	Bivalvia	255	70.8	65.9	75.3
	Crustacea	224	62.2	57.1	67.1
	Ophiuroidea	171	47.5	42.4	52.7
	Gastropoda	48	13.3	10.2	17.3
Immature females, East sector (N = 200)	Crustacea	171	85.5	79.9	89.7
	Bivalvia	162	81.0	74.9	85.8
	Polychaeta	133	66.5	59.7	72.7
	Gastropoda	63	31.5	25.5	38.3
	Ophiuroidea	29	29.0	23.2	35.7
Immature males, East sector (N = 260)	Crustacea	217	83.5	78.4	87.5
	Polychaeta	180	69.2	63.4	74.5
	Bivalvia	179	68.9	63.0	74.2
	Ophiuroidea	58	22.3	17.7	27.8
	Gastropoda	48	18.5	14.2	23.7
Mature females, West sector (N = 68)	Bivalvia	50	73.5	61.9	82.6
	Polychaeta	44	64.7	52.8	75.0
	Crustacea	34	50.0	38.5	61.6
	Ophiuroidea	25	36.8	26.3	48.7
	Gastropoda	13	19.1	11.5	30.2
Mature males, West sector (N = 20)	Polychaeta	12	60.0	38.6	78.2
	Crustacea	9	45.0	25.9	65.8
	Bivalvia	5	25.0	11.0	47.5
	Ophiuroidea	4	20.0	7.7	42.3
	Gastropoda	1	5.0	0.0	25.7
Mature females, East sector (N = 35)	Bivalvia	28	80.0	63.7	90.2
	Crustacea	27	77.1	60.7	88.1
	Polychaeta	20	57.1	40.9	72.0
	Ophiuroidea	17	48.6	33.0	64.4
	Gastropoda	9	25.7	14.1	42.3
Mature males, East sector (N = 17)	Crustacea	14	82.4	58.0	94.4
	Polychaeta	11	64.7	41.1	82.7
	Bivalvia	10	58.8	36.0	78.3
	Ophiuroidea	2	11.8	2.3	35.9
	Gastropoda	1	5.9	0.0	29.3

Snow crab diets by area and crab size

Especially south of SLI, very few crabs contained only 1 or 2 prey taxa unless their stomachs were essentially empty, and some stomachs contained over 10 taxa. The same dominant species of each major taxonomic group of prey occurred in snow crab stomachs in all parts of our study area. *Macoma calca-*

rea, *Ennucula tenuis*, *Nuculana radiata*, and *Yoldia hyperborea* were by far the most common bivalves in snow crab stomachs (Fig. S1 in the supplement at www.int-res.com/articles/suppl/m483p209_supp.pdf). We were only rarely able to identify amphipods to species, as most had been broken into tiny fragments; other small crustaceans (including the cumacean family Leuconiidae and barnacles *Balanus* spp.)

were common at a few stations. Snow crabs composed almost all of the 'crab' prey category. The most common gastropods identified were naticids (mostly *Cryptonatica clausa* but also a few *Lunatia pallida*) and *Margarites olivaceus*. The colored film on the outside of naticid shells quickly delaminated in the stomachs of snow crabs, making it difficult to identify many gastropod fragments to species; however, we believe that most unidentified gastropods were *C. clausa*. The small shells and opercula commonly found in stomachs indicated that the gastropods eaten by snow crabs tended to be quite small, particularly in comparison to those collected in trawl samples. Except for *Pectinaria hyperborea*, we could not regularly identify polychaetes to species based on fragments of setae, cases, and mouthparts. Several families of Foraminifera (mostly Lituolidae) often occurred in the stomachs of all sizes of crabs, occasionally comprising the dominant taxa by volume. Foraminifera are thought to be ingested incidentally as a mixture of food and sediments eaten by snow crabs (Yasuda 1967).

South of SLI (West and East sectors), patterns of consumption of bivalves, polychaetes, and gastropods were similar at all stations. Bivalves were the most common prey of most size classes, while consumption of polychaetes was low by very small crabs but much higher by larger crabs (Fig. 3, Table 2, and Fig. S1 in the Supplement). Gastropods were eaten by most size classes in both sectors, but much less often than amphipods, bivalves, or polychaetes. Ophiuroids were surprisingly common in the diet in the West sector, with 40 to 50% occurrence in most crab size classes. Amphipods were eaten by all size classes, whereas crabs (almost entirely snow crabs) were more commonly eaten by larger snow crabs (Fig. 4).

In the Chirikov Basin, bivalves were replaced by polychaetes and crustaceans as the most common prey of all size classes (Fig. 3). Crustaceans were consumed much more frequently than polychaetes by crabs <40 mm CW, mainly due to high consumption of amphipods by these small crabs (Fig. 4). Polychaetes and crustaceans were equally common in crabs >40 mm CW, although these larger crabs consumed fewer amphipods and exhibited greater cannibalism than the smaller size classes (Fig. 4). Both ophiuroids and gastropods were uncommon in crab stomachs from the Chirikov Basin. Regardless of taxon, the mean number of prey items per individual crab was much lower ($p < 0.001$) in the Chirikov Basin (2.3 ± 1.5 SD) than in the East (4.7 ± 2.6) or West (4.4 ± 2.3) sectors.

Crab diets relative to prey availability

Based on grab samples, our entire study area generally had high abundance (no. m⁻²) of bivalves, crustaceans, and polychaetes, but much lower abundance of gastropods and ophiuroids (Fig. 5). Com-

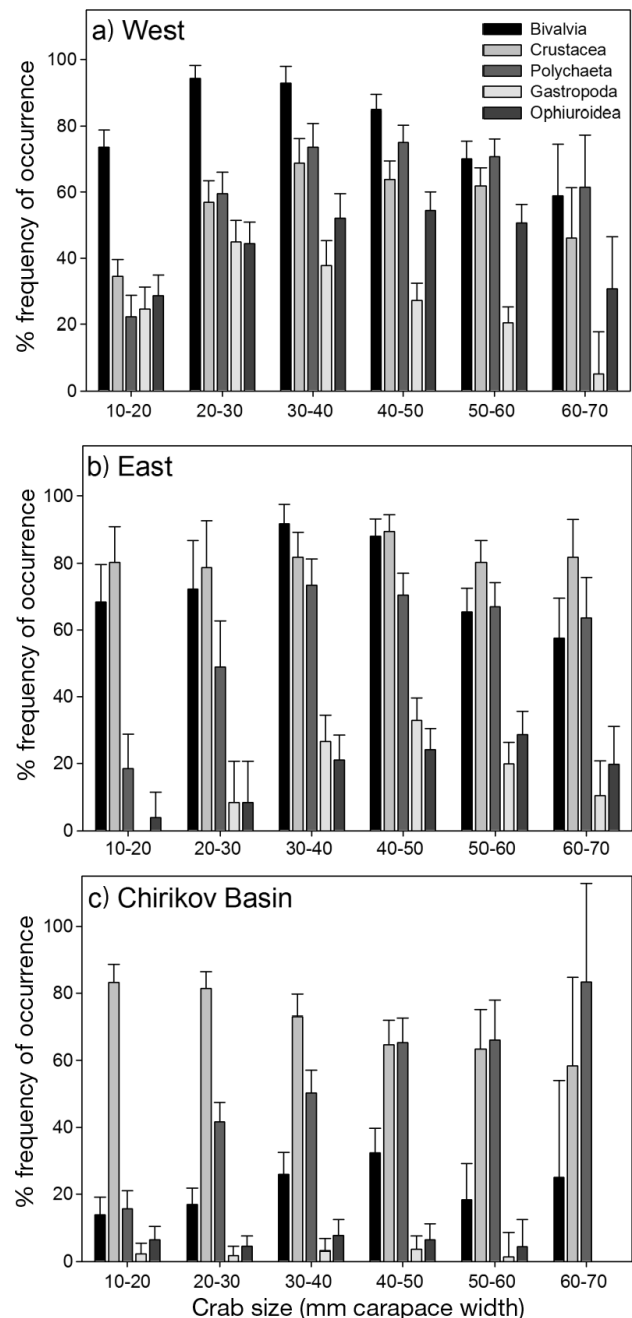


Fig. 3. Percent frequency of occurrence (with 95% CI) of bivalves, polychaetes, gastropods, and ophiuroids in stomachs of snow crabs from the (a) West, (b) East, and (c) Chirikov Basin sectors (Fig. 1) of the study area in the northern Bering Sea, May and June 2006 and 2007

Table 2. *Chionoecetes opilio*. Number and percentage of snow crab stomachs containing at least 1 individual of the corresponding prey taxon, listed in decreasing frequency of occurrence for each size class of snow crabs in the West, East, and Chirikov Basin sectors of our study area (Fig. 1). N = total number of snow crab stomachs examined. Lower and upper bounds of 95 % confidence intervals (CI) were calculated using the method of Agresti & Coull (1998). CW: carapace width

Sector, Size class	Taxon	No. of stomachs	Occurrence (%)	95 % CI	
				Lower	Upper
West sector, <20 mm CW (N = 172)	Bivalvia	127	73.8	66.8	79.8
	Crustacea	59	34.3	27.6	41.7
	Ophiuroidea	49	28.5	22.3	35.7
	Gastropoda	42	24.4	18.6	31.4
West sector, 20–40 mm CW (N = 392)	Polychaeta	38	22.1	16.5	28.9
	Bivalvia	367	93.6	90.7	95.7
	Polychaeta	257	65.6	60.7	70.1
	Crustacea	243	62.0	57.1	66.7
West sector, >40 mm CW (N = 689)	Ophiuroidea	187	47.7	42.8	52.7
	Gastropoda	164	41.8	37.1	46.8
	Bivalvia	516	74.9	71.5	78.0
	Polychaeta	492	71.4	67.9	74.7
East sector, <20 mm CW (N = 76)	Crustacea	425	61.7	58.0	65.2
	Ophiuroidea	348	50.5	46.8	54.2
	Gastropoda	151	21.9	19.0	25.2
	Crustacea	61	80.3	69.8	87.7
East sector, 20–40 mm CW, (N = 190)	Bivalvia	52	68.4	57.2	77.8
	Polychaeta	14	18.4	11.2	28.8
	Ophiuroidea	3	4.0	1.0	11.7
	Gastropoda	0	0.0	0.0	5.9
East sector, >40 mm CW (N = 460)	Bivalvia	165	86.8	81.2	91.0
	Crustacea	154	81.1	74.8	86.0
	Polychaeta	128	67.4	60.4	73.6
	Gastropoda	42	22.1	16.8	28.6
Chirikov sector, <20 mm CW (N = 226)	Ophiuroidea	34	17.9	13.1	24.0
	Crustacea	388	84.4	80.7	87.4
	Bivalvia	341	74.1	69.9	77.9
	Polychaeta	313	68.0	63.6	72.1
Chirikov sector, 20–40 mm CW (N = 476)	Ophiuroidea	116	25.2	21.5	29.4
	Gastropoda	111	24.1	20.5	28.3
	Crustacea	188	83.2	77.7	87.5
	Polychaeta	35	15.5	11.3	20.8
Chirikov sector, >40 mm CW (N = 247)	Bivalvia	31	13.7	9.8	18.9
	Ophiuroidea	13	5.8	4.3	8.7
	Gastropoda	5	2.2	0.0	6.2
	Crustacea	371	78.0	74.0	81.4
Chirikov sector, 20–40 mm CW (N = 476)	Polychaeta	215	45.3	40.7	49.7
	Bivalvia	98	20.6	17.2	24.5
	Ophiuroidea	27	5.7	3.9	8.2
	Gastropoda	11	2.3	1.3	4.2
Chirikov sector, >40 mm CW (N = 247)	Polychaeta	162	65.6	59.5	71.2
	Crustacea	159	64.4	58.2	70.1
	Bivalvia	70	28.3	23.1	34.3
	Ophiuroidea	14	5.7	3.4	9.4
	Gastropoda	7	2.8	1.3	5.9

binned abundance (mean \pm SD) of these 5 prey types was greater at stations in the Chirikov Basin (3841 ± 2954 ; ANOVA, $p = 0.047$) than in the West sector

(1895 ± 548), but did not differ between the East sector (3169 ± 2039) and the other sectors. Carbon mass (gC m^{-2}) per station, did not differ among the Chirikov Basin (17.2 ± 14.2), East (8.7 ± 4.9), or West (15.1 ± 6.5) sectors.

Percent frequency of occurrence was the percentage of stomachs containing at least one item of a particular taxon. Relative percent frequency of occurrence was the frequency of occurrence of a given taxon expressed as a percentage of the sum of frequencies of occurrence of all taxa. Relative percent frequency of occurrence of each of the 5 major prey taxa in snow crab stomachs was highly positively correlated with the relative percent abundance of those taxa among available prey ($r^2 = 0.71$, $p < 0.001$), but less correlated with their relative percentages of carbon mass of prey ($r^2 = 0.38$, $p < 0.001$). However, the percent frequency of occurrence of polychaetes in snow crab diets was correlated more closely with available carbon mass than with abundance, while the opposite was true for gastropods. We also calculated relative percent total number by counting the numbers of every different prey item (identified to lowest possible taxon) found in each stomach, and expressing the total number of each taxon summed across all stomachs as a percentage of the total number of all prey summed across all stomachs. Relative percent total number showed even higher positive correlation to relative prey abundance ($r^2 = 0.83$, $p < 0.01$; Table 3).

We examined preference of snow crabs for specific taxa with our selectivity index S_i (see Eq. 1), comparing relative frequency of occurrence with relative percent of total available prey abundance and carbon mass across all snow crab size classes and sectors (Fig. 6). Based on relative prey abundance, snow crabs showed little or no preference for or avoidance of any of the major prey taxa except for moderate avoidance of bivalves. However, relative to proportions of available carbon mass, snow crabs clearly selected for crustaceans and against bivalves.

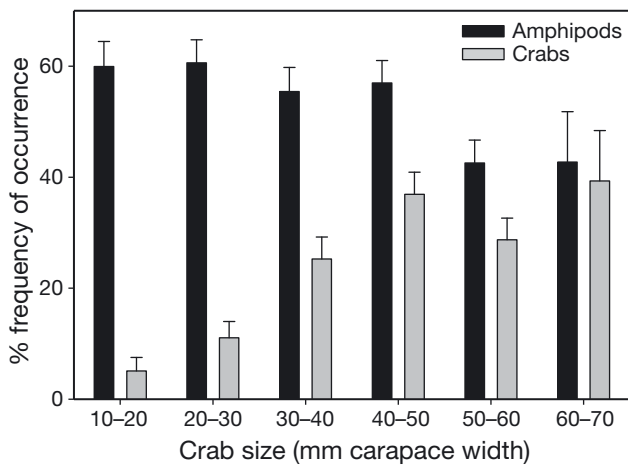


Fig. 4. Percent frequency of occurrence (with 95% CI) of amphipods and crabs (mostly snow crabs) in stomachs of snow crabs from the study area in the northern Bering Sea, May and June 2006 and 2007

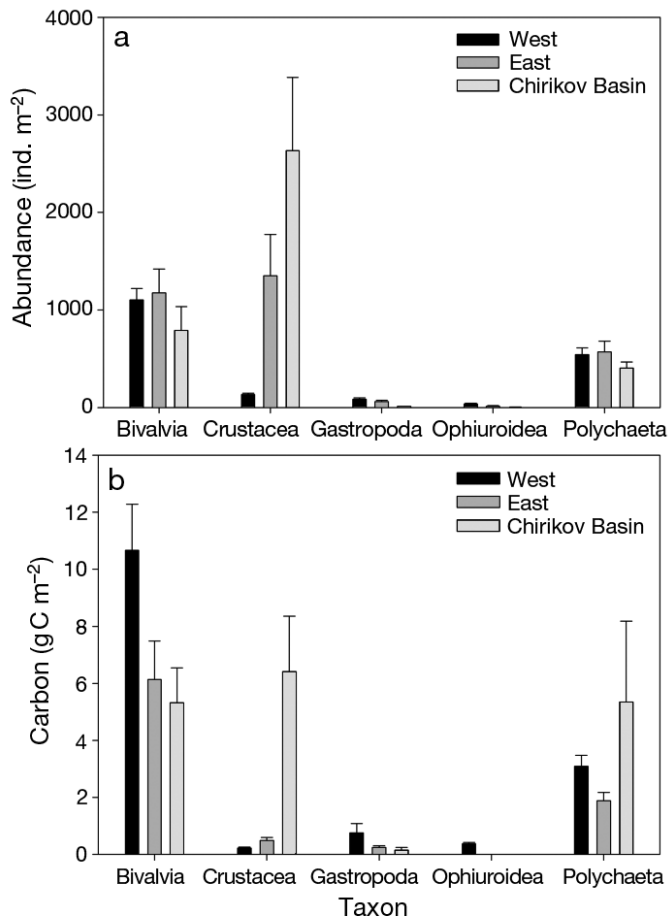


Fig. 5. Mean (\pm SE) (a) abundance (no. m⁻²) and (b) carbon mass (gC m⁻²) of bivalves, crustaceans, gastropods, ophiuroids, and polychaetes in each sector of the study area (Fig. 1), May and June 2006

Table 3. Correlations between relative percent total number of prey items in snow crab stomachs versus relative prey abundance and relative carbon mass across all size classes (<20 mm CW, 20–40 mm CW, >40 mm CW) and sectors (West, East, and Chirikov Basin) of our study area (Fig. 1). Relative percent total number was calculated by counting the numbers of every different prey item (identified to lowest possible taxon) found in each stomach, and expressing the total number of each taxon summed across all stomachs as a percentage of the total number of all prey summed across all stomachs. All correlations were positive ($r > 0$). N: respective number of taxa analyzed

Prey taxon	N	Prey abundance		Prey carbon mass	
		r ²	p-value	r ²	p-value
All taxa	45	0.83	<0.01	0.57	<0.01
Bivalvia	9	0.69	<0.01	0.90	<0.01
Crustacea	9	0.86	<0.01	0.85	<0.01
Gastropoda	9	0.81	<0.01	0.34	0.10
Ophiuroidea	9	0.87	<0.01	0.89	<0.01
Polychaeta	9	0.03	0.64	0.72	<0.01

DISCUSSION

Our large sample sizes (over 2900 snow crab stomachs), broad geographic range of sampling, and detailed data on prey availability allowed unique insights into diet variations by sex, size class, and geographic area. Overall, snow crabs of all sizes consumed most of the dominant prey available in each assemblage type, with bivalves, crustaceans,

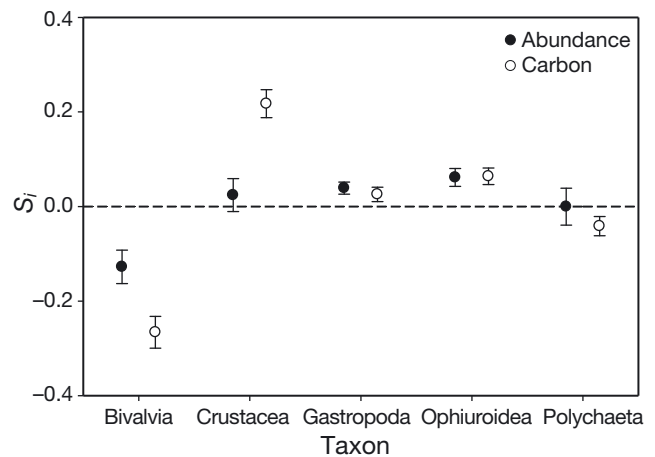


Fig. 6. Selectivity (S_i) of major prey taxa (bivalves, crustaceans, gastropods, ophiuroids, polychaetes) by snow crabs of all size classes combined in the northern Bering Sea according to relative percent frequency of occurrence compared with proportion of prey abundance and carbon mass for each of the major taxa of snow crab prey. Error bars represent 1 SE across snow crab size classes and sectors. Values of S_i near zero suggest no selection, positive values suggest selection for prey, and negative values indicate avoidance or inaccessibility of prey

and polychaetes being by far the most frequent prey (Fig. 3 and Fig. S1 in the Supplement). A high positive correlation between relative percent total number of all major prey taxa in snow crab diets versus their relative abundance among available prey ($r^2 = 0.83$, $p < 0.01$; Table 3) suggests that consumption of different prey was in almost direct proportion to their relative abundance in the study area. Any selective feeding by snow crabs appeared to be driven by size and handling requirements. Small crabs focused on prey requiring lower handling ability, while larger crabs used their greater claw strength and mobility to eat larger prey. These results suggest that in the northern Bering Sea, diets of snow crabs in different areas and at different times can be predicted fairly accurately from the relative abundance of potential prey taxa. Moreover, food web models can assume that when prey community structure changes, the diet of snow crabs will also shift accordingly.

Diets compared to prey availability

As noted above, the relative occurrence of each major prey taxon in the diets of all size classes of snow crabs was highly positively correlated with their relative abundance among prey. The only exception was polychaetes, whose consumption was independent of abundance, but increased strongly with increasing carbon mass of these prey (Table 3). In fact, relative occurrence of prey in crab diets was well correlated with proportions of prey carbon mass for all taxa except gastropods.

We investigated the lack of correlation between occurrence of polychaetes in crab diets and their relative abundance among available prey by calculating selectivity by sector and size class. These analyses suggested that juvenile crabs (<20 mm CW) selected against polychaetes, while crabs >40 mm tended to select for polychaetes. This finding is reasonable, as most polychaetes we encountered were much too large for juvenile crabs to handle easily, and larger crabs tended to eat fewer but larger items. Also, the body of the main polychaete consumed, *Pectinaria hyperborea*, is covered by a conical shell of sand and mucus which may resist attacks by small crabs. Snow crabs in the Chirikov Basin sector, where polychaetes composed only $18.5 \pm 14.6\%$ (SD) of available prey, tended to select for polychaetes; however, crabs in the West sector south of SLI, where polychaetes composed $30.0 \pm 10.9\%$ of available prey, tended to select against polychaetes. This pattern probably occurred because polychaetes were

the main large prey for larger crabs in the Chirikov Basin, where prey were dominated by small amphipods and bivalve abundance was lower than south of SLI. Although polychaetes had higher abundance and composed a greater fraction of available prey in the West sector than in the Chirikov Basin sector, the other large prey (gastropods, ophiuroids, and larger bivalves) were also more abundant in the West sector and were consumed in the same proportions.

As gastropods were the only prey taxon in which relative occurrence in the snow crab diet was not correlated with proportion of prey carbon mass, we also used selectivity analyses to investigate this lack of agreement. However, no selection for or against gastropods was evident for snow crabs of any size class in any sector of our study area. Because relative prey abundance was highly positively correlated with relative percent total number in diets ($r^2 = 0.81$, $p < 0.01$; Table 3), and as most snails found in crab stomachs were quite small, the most important factor influencing gastropod consumption was likely the density of small gastropods. Relative carbon mass depended more on gastropod size than did relative abundance, and was therefore a poorer predictor of gastropod consumption as large snails were not common snow crab prey.

Our selectivity index indicated no preference for or against gastropods, ophiuroids, or polychaetes with regard to abundance or carbon mass (Fig. 6). In contrast, the index suggested that bivalves were selected against and crustaceans were selected for, especially in terms of carbon mass. We believe these preferences were based on handling costs associated with different prey sizes relative to the generally small size of crabs in our study area. Potential crustacean prey were quite abundant in parts of our study area (Fig. 5), but most of these crustaceans were small, easily handled amphipods. Many of the bivalves appearing in van Veen grab samples were much larger than the generally smaller, younger individuals of the same species found in snow crab stomachs, particularly in crabs <40 mm CW. The smaller size of available crustaceans resulted in low carbon mass relative to their abundance, compared with the same index in bivalves (Fig 5). These larger clams with thicker, harder shells were either avoided or not available as prey to many of the crabs we sampled, while the small amphipods were easily consumed by most size classes of crabs. Although there was little preference shown for or against bivalves or crustaceans based on abundance, this size discrepancy is manifested as greater selection against bivalves and for crustaceans in terms of carbon mass (Fig. 6).

Note that total energy obtained from prey will be more closely associated with carbon mass than with abundance.

Comparisons with diets in other studies

In Cook Inlet, Alaska, congeneric Tanner crabs *Chionoecetes bairdi* consumed a variety of prey dominated by the same 5 major taxa (bivalves, crustaceans, gastropods, polychaetes, and ophiuroids) that dominated the prey of snow crabs in our study (Paul et al. 1979). As for snow crabs in our study, diets of Tanner crabs in Cook Inlet varied among stations and typically reflected the most common prey. Major prey in the Tanner crab stomachs were small clams, hermit crabs, barnacles, and crangonid shrimps. While small clams were also a dominant prey in our study, we found that snow crabs only rarely consumed hermit crabs, barnacles, or crangonid shrimps. Barnacles, however, were extremely common in snow crab stomachs at our few stations where they were abundant.

Near Kodiak Island, Alaska, the Tanner crab diet was similar to that of Tanner crabs in Cook Inlet and of snow crabs in our study, with bivalves, decapods, crustaceans, and polychaetes among the dominant prey groups (Jewett & Feder 1983). While fish were of greater importance to Tanner crabs near Kodiak Island than to snow crabs in our study, sediments were found in most stomachs in both areas. These sediments might have been ingested incidentally, or obtained from the digestive tracts of consumed crustaceans. However, the sediments might also have had nutritional value owing to associated biofilm (Jewett & Feder 1983).

Prey taxa important to snow crabs in the northern Bering Sea were very similar to those reported from other studies in Alaska and Atlantic Canada (Feder & Jewett 1978, Jewett & Feder 1983, their Table 8 and references therein). In Bonne Bay, Newfoundland, snow crabs opportunistically consumed a number of abundant species without selection (Wieczorek & Hooper 1995). However, some less abundant prey (ophiuroids, and small bivalves and gastropods) that were commonly eaten but not preferred in our study were selected for by snow crabs in Newfoundland. The Newfoundland snow crabs also selected for poriferans, which did not occur in crabs we sampled. In waters near our study area (Norton Sound, south-eastern Chukchi Sea, Kotzebue Sound), crustaceans, bivalves, and polychaetes were the most common taxa in snow crab diets (Feder & Jewett 1978), as they were in our study. Also, taxa that were less common

(gastropods, ophiuroids) or spatially patchy (barnacles) in snow crab diets in our study followed similar patterns in these nearby areas.

In the northern Bering Sea, the diets of snow crabs basically corresponded to prey availability; any selective feeding appeared to result from the greater claw strength and mobility of larger crabs that allowed them to eat larger prey. Analogous to our findings, the diets of larger juvenile and adult blue crabs *Callinectes sapidus* included a greater proportion of gastropods, (larger) bivalves, other blue crabs, and fish, whereas smaller juveniles focused more on soft-bodied or less-mobile polychaetes, small crustaceans, plant matter, and detritus (Lipcius et al. 2007). Efforts to identify essential fish habitat for juvenile crabs of a range of species should consider these size-related differences in diet.

Defining important habitats for snow crabs

Snow crabs occurred at high densities throughout our study area, despite bottom-water temperatures low enough to prevent small snow crabs from achieving positive energy balance in the laboratory, even when fed ad libitum (Thompson & Hawryluk 1990). High densities of crabs are sustained in this very cold region by hydrographic transport into localized areas of planktonic crab larvae and water of suitable settling temperatures (Kolts 2012). However, prey availability is important to subsequent growth and development.

As feeding by snow crabs was largely opportunistic, much of habitat adequacy appeared to depend on overall prey abundance, regardless of prey taxa. However, there were subtle but important differences among snow crab size classes. The Chirikov Basin and East sectors were the 2 areas where juvenile snow crabs occurred at extremely high densities (Kolts 2012). In those areas, bivalves and crustaceans composed 87 and 91%, respectively, of prey items in juvenile crab stomachs, and 85 and 77%, respectively, of available prey. In the West sector, juveniles occurred only at low densities. There, bivalves and crustaceans (mostly amphipods) composed only 69% of prey consumed by juvenile crabs, as amphipods occurred at very low densities. Although substantially more juveniles in the West sector consumed gastropods and ophiuroids than those in the other sectors, 28% of juvenile crabs there consumed neither those taxa nor polychaetes. Thus, juvenile crabs were most abundant where their amphipod and small bivalve prey were abundant and composed a large fraction of the crabs' diet.

Essential fish habitat for 'late juvenile' (adolescent or immature) and adult crabs, and for egg production (based on mature female distributions), has been identified for both the Bering and Chukchi Seas (NMFS 2005). However, due to insufficient data, these designations do not consider habitats essential to settling larval and juvenile crabs, and for the Bering Sea include only a few stations in our study area north of St. Matthew Island (see Fig. 1). Discrete areas of extremely high juvenile abundance occurred just south of the eastern end of SLI and south of Bering Strait in the Chirikov Basin (Kolts 2012). Abundant juveniles in these areas appear to result from advection and deposition of snow crab larvae from the south by currents, which also bring warmer water into regions that might otherwise be too cold for stenothermic, early snow crab instars (see Dionne et al. 2003, Parada et al. 2010). Also, these areas of high juvenile abundance appear to be important sources of recruits to adjacent areas of essential habitat for snow crabs, due to ontogenetic migration by the crabs (Kolts 2012). Adolescent crabs in the Chirikov Basin appear to migrate into the Chukchi Sea, while crabs south of SLI migrate in a southward direction toward deeper waters of the shelf break both before and after molting to maturity.

As both areas of high juvenile concentrations had especially high abundances of amphipods and small bivalves, it is not clear whether such high densities of juveniles could persist in other areas where such prey are not so abundant. It is also unclear if the currents that deposit snow crab larvae are also responsible for high abundance of their preferred prey, and whether climate-forced changes in those currents might alter both deposition of snow crabs and the distributions of prey important to their early life stages. Regardless of causation, these areas clearly represent important habitat for juveniles, and (as a precondition) either high settlement or high subsequent survival of snow crab larvae. South of SLI, the region of high juvenile abundance likely contributes substantial numbers of recruits to the main location of reproducing crabs south of our study area (Kolts 2012). Thus, protecting the prey base in these source regions from adverse disturbances should be a key priority for snow crab management.

CONCLUSIONS

Snow crab diets included most of the dominant prey available in each region of our study area in the northern Bering Sea. Occurrence of prey in crab

diets depended mainly on relative availability of prey taxa, and any dietary preference appeared to be controlled by prey size and handling requirements relative to crab size. Small snow crabs focused on softer, more easily manipulated prey such as amphipods or small bivalves with thin shells. Larger crabs ate larger prey such as harder-shelled bivalves, polychaetes, and other crabs that required greater handling ability and claw strength. Differences in the diets of male and female crabs of similar size were negligible.

Selectivity for prey in our study was lower than that reported for snow crabs in Northwest Atlantic waters. This difference may result from (1) very high overall prey densities throughout our study area, (2) dominance of the prey base by amphipods and small bivalves, and (3) predominance of small crabs in our area, owing to very cold temperatures and ontogenetic emigration. Changes in these factors might decrease the high correlation between snow crab diets and relative abundances of different prey taxa. In the northern Bering Sea, the best habitat for snow crabs of different ages appeared to depend jointly on several factors: hydrographic patterns that determine locations of larval settlement and subsequent ontogenetic migration, combined total abundance of all prey taxa, and ontogenetic capabilities for handling prey of different sizes.

Acknowledgements. We thank the officers and crew of the USCGC 'Healy' for invaluable help in the field, and L. Rugolo (Alaska Fisheries Science Center, NOAA Fisheries) and M. Hoberg (School of Fisheries and Ocean Sciences, University of Alaska, Fairbanks) for critical help with taxonomic methods. H. Julien, M. Foster, A. Roe, E. Anderson, and X. Cui helped with ship-board sampling, and H. Julien processed many crabs in the laboratory. Funding was provided by the US National Science Foundation, Office of Polar Programs grant ARC-0454454 to J.R.L., J. Grebmeier, and L. Cooper, and North Pacific Research Board grant no. 713 to J.R.L. (this is NPRB Publication no. 392).

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