Mesozooplankton grazing during spring sea-ice conditions in the eastern Bering Sea

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Abstract

Mesozooplankton (copepods and euphausiids) grazing rates and prey preferences were determined during a series of three research cruises to the eastern Bering Sea in spring 2008, 2009, and 2010. Chlorophyll was dominated by large cells ($>5\ \mu\text{m}$), especially at bloom locations where they usually comprised greater than 90% of the total chlorophyll biomass. The relative importance of microzooplankton to the prey field biomass decreased with increasing chlorophyll concentration, and was less than 10% of the total prey biomass in ice-edge bloom regions. Overall, microzooplankton was the preferred prey of the mesozooplankton, although phytoplankton/ice algae were the dominant component of the diet because of their much greater biomass, especially during blooms. There were differences between mesozooplankton species in their prey preferences: *Metridia pacifica*, *Pseudocalanus* spp. and *Calanus* spp. had the strongest preference for microzooplankton prey, while euphausiids (*Thysanoessa* spp.) and *Neocalanus flemingeri/plumchrus* appeared to feed non-selectively on all prey items. Mesozooplankton exhibited a saturating feeding response to chlorophyll concentration (Holling's type II) that could be modeled by Michaelis-Menten equations. Taxa-specific maximum ingestion rates generally followed allometric theory, with smaller zooplankton having higher feeding rates than larger zooplankton, and ranged from about 4% to 30% body carbon day^{-1} . Trophic cascades during grazing experiments could result in a substantial underestimate of chlorophyll ingestion rates, especially for those taxa that had a strong preference for microzooplankton. Grazing impacts by mesozooplankton on the integrated chlorophyll biomass and primary production were 2.7 ± 4.4 and $26 \pm 48\% \text{ day}^{-1}$, respectively. Impacts increased significantly with increasing mesozooplankton biomass, which increased from early to late spring. However, grazing impacts

were extremely low in ice-edge bloom regions. Our findings suggest that even when grazing by microzooplankton is included in our grazing impact estimates, about 50% of the primary production in phytoplankton blooms during spring on the eastern Bering Sea shelf is not grazed and is available for direct export to the benthic community.

Keywords: Copepod, Euphausiid, Ingestion, Diets, Prey Selection, Grazing Impact, Spring Bloom

1. Introduction:

The eastern Bering Sea supports one of the richest fisheries in the world's oceans and provides almost half of the total U.S. fish catch annually (e.g. Sigler et al., 2010). This rich fishery can in part be attributed to the highly productive ice algal and phytoplankton spring blooms that occur as the sea ice retreats. These blooms, in turn, support a highly diverse planktonic food web of micro- and mesozooplankton grazers, many of which time their reproductive cycles to the spring bloom (e.g. Baier and Napp, 2003). The mesozooplankton, in particular, provide a rich prey supply for an array of upper trophic level predators, including fish (especially larval pollock), seabirds, and marine mammals (e.g., Bailey and Dunn, 1979; Brodeur et al., 2002; Cianelli et al., 2004; Dwyer et al., 1987; Moore et al., 2002; Springer et al., 1989; Springer and Roseaneau, 1985; Stabeno et al., 2012a, 2012b; Tynan, 2004; Tynan et al., 2001). The timing of these blooms also is important to life cycles of higher trophic levels since it can determine the productivity and energy pathways of the ecosystem. Hunt et al. (2002) hypothesized in their Oscillating Control Hypothesis (OCH), that during warm periods, the ice retreats earlier and the bloom occurs later in open, thermally stratified waters at warmer temperatures, while during cold periods, the ice retreats later and the bloom occurs earlier in association with the retreating ice edge and salinity stratified, colder water. During warm periods, much of the spring production is retained in the water column through higher, temperature-mediated grazing and production by zooplankton that then supports pelagic fish. In contrast, during cold periods temperature limits grazing and much of the production falls to the bottom, supporting the benthic communities. However, recent studies have suggested a slightly more complicated scenario in that some larger mesozooplankton (e.g. *Calanus*) are more productive during cold years, less so in warm years,

88 with consequences during warm years for their fish predators that depend on them (Coyle et al.,
89 2011; Heintz et al., 2013; Hunt et al., 2011; Sigler et al., 2014).
90
91 The southeastern Bering Sea shelf is differentiated into three, bathymetrically-fixed
92 hydrographic regions; the Coastal or Inner Domain (shore~50 m water depth), the Middle Shelf
93 Domain (50-100 m), and the Outer Shelf Domain (100-200 m) (Coachman, 1986; Iverson et al.,
94 1979; Schumacher and Stabeno, 1998; Stabeno et al., 2001). Each of the three hydrographic
95 domains contains characteristic mesozooplankton species (e.g., Cooney and Coyle 1982; Coyle
96 and Pinchuk, 2002; Dagget et al., 1982; Smith and Vidal 1984, 1986; Springer et al., 1989; Smith
97 1991; Stockwell et al., 2001; Vidal and Smith 1986). Although, it is not clear if the domains
98 maintain their integrity in the middle and northern Bering Sea, these same species are present
99 there (e.g., Springer et al., 1989; Eisner et al., 2014). The outer domain is characterized by the
100 oceanic copepod species *Neocalanus plumchrus*, *N. flemingeri*, *N. cristatus*, *Eucalanus bungii*,
101 and *Metridia pacifica*, and the euphausiid *Thysanoessa inermis*. The middle shelf is dominated
102 by *Calanus glacialis/marshallae* (two co-occurring species that are difficult to tell apart) and the
103 euphausiid *T. raschii*, with the much smaller copepod species *Acartia longiremis* and
104 *Pseudocalanus* spp. abundant, but not important to biomass at least during spring. The small
105 copepod *Oithona similis* is present in both domains and is numerically dominant. The inner
106 domain contains smaller, neritic copepods (e.g., *A. longiremis*, *Pseudocalanus* spp., *Eurytemora*
107 spp.) and the euphausiid *T. raschii*. The two euphausiid species are relatively small with only
108 the adults large enough, but just barely so, to be classified as macrozooplankton (20 - 200 μ m).
109 It has been shown that in recent years there are differences in community composition, in terms

of relative abundance, between the north and south regions and warm and cold regimes, especially in the middle domain (Eisner et al., 2014).

Most mesozooplankton previously believed to be herbivorous are now considered to be omnivorous, utilizing phytoplankton, ice algae, and microzooplankton depending on relative availability with preference changing seasonally as the dominant food supply changes (Campbell et al., 2009; Conover et al., 1986; Dagg 1993; Gifford 1993; Kleppel 1993; Landry 1993; Ohman and Runge 1994; Rivkin et al., 1996; Runge and Ingram 1988; Runge et al., 1991; Tourangeau and Runge 1991). To understand the potential impact of a reduced ice cover on the cycling of carbon in these ecosystems, it is critical to gain an understanding of the relative importance of ice algae, phytoplankton, and microzooplankton to the diet of the key mesozooplankton species, the grazing impact of these species on prey standing stocks, and how these preferences and impacts change under various conditions of ice cover and water column stability.

We present results from mesozooplankton grazing experiments conducted in the eastern Bering Sea in spring sea-ice conditions during three “cold years” as part of the Bering Sea Program. These studies were conducted in parallel with dilution assays to estimate microzooplankton grazing (Sherr et al. 2013) to gain a better understanding of the planktonic food web during spring. This study was guided by two overarching hypotheses: (1) Mesozooplankton are omnivorous; the importance of microzooplankton in the diet will depend on the prey preferences of individual mesozooplankton species and will be influenced by their relative abundance in the prey field. (2) Mesozooplankton grazing impacts will depend on total grazer biomass and phytoplankton biomass/productivity, which will vary across the shelf domains, latitudinal

regions, years, and bloom conditions. Here we describe the prey preferences, ingestion rates, and the grazing impacts on primary production and chlorophyll standing stock for the dominant mesozooplankton taxa.

2. Methods

Shipboard grazing experiments were conducted in spring (April–June) on the eastern Bering Sea shelf in 2008, 2009, and 2010 (Figure 1). The methods closely followed those outlined in Campbell et al., (2009). Mesozooplankton grazing experiments were conducted usually every other day at stations where a comprehensive suite of ecological measurements was performed, including determination of primary production and microzooplankton grazing (Lomas et al., 2012; Sherr et al., 2013). The mesozooplankton species/life stages that were dominant in terms of biomass at each location were selected for inclusion in the experiments. These included the copepods *Calanus glacialis/marshallae*, *Pseudocalanus* spp., *Metridia pacifica*, *Neocalanus flemingeri/plumchrus* (referred to here as *Neocalanus* spp.), *N. cristatus*, and *Eucalanus bungii*, among others, and euphausiids, primarily *Thysanoessa raschii* and *T. inermis*.

2.1. Experiments

Feeding rates were measured using natural particle assemblages or natural assemblages enriched with ice algae in on-deck incubations in a plankton wheel/water bath under ambient light and temperature conditions. Animals for experiments were collected in the pre-dawn hours with gentle, vertical hauls of a 1-m², 200-μm mesh plankton net equipped with a 4-l, non-filtering cod end. Upon reaching the surface, animals were immediately diluted into jars containing surface

water, placed in coolers and transported to an environmental chamber that was maintained at near the ambient surface seawater temperature (usually $\sim 1.8^{\circ}\text{C}$ due to the presence of sea ice). All sorting of animals and handling of water was done in the environmental chamber.

Water for the experiments was collected in 30-l Niskin bottles equipped with Viton o-rings and nylon coated steel springs, and attached to a CTD rosette with a fluorometer and photosynthetically available radiation (PAR) sensor. An initial cast was made to determine the water column profile from which the water collection depth was selected. Water was generally collected from the surface chlorophyll maximum. On occasion, when a deep chlorophyll maximum layer was present, water was collected from both the deep layer and the surface mixed layer. Upon retrieval, water was drained from the Niskin bottles into 50-l high-density polyethylene carboys (HDPE) using silicone tubing and immediately transferred to the environmental chamber. All water handling equipment was pre-cleaned in 10% HCL and rinsed with copious amounts of de-ionized water prior to use, and all procedures were performed using nitrile gloves. The initial nutrient concentrations were determined in the experimental water prior to the start of the experiments by the hydrography team. Nutrients (ammonium nitrate and sodium phosphate) were added as needed to the experimental water to bring concentrations to $5\text{ }\mu\text{M}$ N and $0.25\text{ }\mu\text{M}$ P to ensure that phytoplankton growth rates were not limited and were equivalent in control and experimental bottles. Experimental water was then siphoned using silicone tubing, while being gently mixed with a long-handled PVC plunger into experimental bottles (1- to 4-L polycarbonate bottles) in random order. The bottles were visually inspected and any large zooplankton that had been unintentionally added were removed by pipette.

At selected locations, a treatment enriched with an ice algal community was included in addition to the ambient treatment. Chunks of ice containing ice algae were obtained from ice cores provided by R. Gradinger or collected with long-handled dip nets from the stern of the ship. The ice was allowed to melt in filtered seawater, overnight, in the dark, while being maintained at near ambient temperature in the environmental chamber. The ice algal community was then added to a separate carboy collected from the same depth as the ambient treatment enriching the chlorophyll concentration by 5 to 10 $\mu\text{g l}^{-1}$. Handling of the enriched water was the same as for the ambient water treatment.

Animals for the experiments were generally sorted within an hour of collection. For copepods, sorting was performed with a large bore pipette and the aid of a dissecting microscope. Animals were sorted to genus/species and life stage. A double sort was employed to insure both proper identification and that the animals were active and in good condition. Euphausiids were sorted by eye from a dishpan with small plastic spoons. Again, great care was taken to make sure that they were in good condition. All experimental animals were kept in filtered seawater until the start of the experiment, generally about an hour.

For each treatment, three initial and three control treatments in 1- or 2-L bottles and three experimental bottles per target animal type, with the bottle size (1- to 4-L) dependent on the size of the animal type, were prepared by nearly filling each bottle with experimental seawater. A predetermined number of animals was added to each experimental bottle in a minimum amount of water so that the experimental particle concentration was unaltered. The number of animals was chosen so that ~25-30% of the water would be cleared by the animals during the 24-hr

202 incubation period based on similar grazing studies in Chukchi Sea (Campbell et al., 2009). For
203 example, depending on chlorophyll concentration, 20-40 adult female *Pseudocalanus*, 5-10 adult
204 female *Calanus*, and 2-4 large juvenile/adult euphausiids were added to 1, 2, and 4-L bottles,
205 respectively. All bottles were then topped off with make-up experimental water, sealed with
206 parafilm to ensure that no bubbles were present that might alter the feeding behavior, and capped.
207 The control and experimental bottles were then wrapped in colored plastic films to mimic the
208 light quality and intensity from depth that the water was collected. They were incubated on-deck
209 in a transparent polycarbonate 1-rpm plankton wheel enclosed in a water bath that was exposed
210 to natural light conditions and kept at ambient temperature with continuous flowing surface
211 seawater. Water bath temperatures during the experiments were monitored using submersed
212 HOBO temperature recorders (Onset Computers Inc.).

213
214 Chlorophyll (total and <5 μm) and microzooplankton samples were collected at the start of the
215 experiment from the initial bottles and at the termination from the control and experimental
216 bottles. Sampling from all bottles followed the same protocol. The bottles were gently inverted
217 by hand to mix the water. The water was then siphoned from the bottles into a beaker taking
218 care not to remove animals from the experimental bottles. If per chance animals were siphoned
219 from the bottles they were removed from the beaker by pipette and saved. The required volume
220 of water was then measured using a graduated cylinder and saved for each analysis. For
221 chlorophyll analysis, the <5 μm fraction was created by gently sieving water through 5- μm mesh.
222 The sample for the total size fraction was left unaltered. Triplicate samples of 50–500 ml,
223 depending on estimates of chlorophyll concentration, were filtered onto Whatman GF/F filters
224 and immediately extracted in 90% acetone at -20 °C for 18-24 hr. The chlorophyll *a*

concentration was determined with a Turner Designs fluorometer using the non-acidification method of Welschmeyer (1994). The non-acidification method was deemed justified for chlorophyll determination during the spring-bloom period, as degraded pigments should be at a minimum. To convert chlorophyll to carbon/nitrogen weight a POC or PON: Chl *a* ratio of 50 for carbon and 6.5 for nitrogen were used, which were determined from POC/N: Chl *a* relationships for these cruises (Lomas et al., 2012; M. Lomas unpublished.). Samples (125 ml) were also collected from each bottle for microzooplankton abundance and biomass and preserved in 5% acid-Lugol's solution in amber safety-coated glass bottles until analyzed by inverted microscopy (See Sherr et al., 2013 for complete details of counting and sizing methodology). In brief, between 15 and 50 ml of the sample was settled for 24 hr, and then counted and measured with a Nikon inverted microscope attached to computer digitizing system. From 60 to 400 cells were counted and sized in each sample. Cell measurements were converted to cell volume with appropriate equations, and the volume estimate converted to cell carbon. For dinoflagellates, cell carbon content was estimated from the equations of Menden-Deuer and Lessard (2000), and for ciliates, carbon was estimated using a value of 0.19 pg C μm^{-3} (Putt and Stoecker, 1989).

Following the water sampling, animals were collected from the experimental bottles and anesthetized with a solution of 0.6 g l⁻¹ of MS222 (3-aminobenzoic acid ethyl ester methanesulfonate salt) in filtered seawater. Under a dissecting microscope, each animal was identified, its relative condition determined, and an image taken with a high-resolution digital camera for later morphometric analysis. The animal then was transferred to a tin boat, dried at 60 °C, and stored over desiccant until analyzed for carbon and nitrogen content with a Carlo

Erba NA1500 elemental analyzer. Smaller animals (e.g. *Pseudocalanus* and *Acartia*) were grouped for carbon and nitrogen analysis.

2.2. Prey Preferences

For the analysis of prey preferences, we compared 1) the proportion of the prey types in the diet with those in the prey field and, 2) the clearance rates of different prey types. For the diet versus prey type comparisons all negative ingestion estimates were converted to 0. This did not likely bias the data set as both the chlorophyll and microzooplankton ingestion measurements had the same proportion of negative, mostly near 0, values (11.3%), and also the clearance rate comparisons gave very similar results. No corrections were made to the clearance rate comparisons. The electivity index D (Jacobs, 1974) was used to compare the preferences of different taxa:

$$D_i = (r_i - p_i) / (r_i + p_i - 2r_i p_i) \quad (1)$$

where D_i is the electivity index for prey type i , r_i is the proportion of prey type i in the prey field, and p_i is the proportion in the diet. The index values can range from -1 to 1, 0 indicates no selection and $D_i > 0$ and $D_i < 0$ indicate positive and negative selection, respectively. Because the data were usually not normally distributed and in many cases variances were unequal, all ANOVA and comparative statistical tests were non-parametric. All statistical analyses were performed with the Prism 5 statistical software package (GraphPad Software, Inc.).

2.3. Grazing Rates

Zooplankton clearance and ingestion rates were determined from the equations of Frost (1972) for each of the different chlorophyll size fractions and microzooplankton types (ciliates and dinoflagellates) and sizes on an individual and weight-specific basis (carbon and nitrogen for chlorophyll, carbon only for microzooplankton). The relationships between food concentration and ingestion followed a Holling's type 2 response, and so to describe the relationships Michaelis-Menten functions were fit to the data with curve fitting routines in the DeltaGraph 5 software program (Redrock Software):

$$I = (V_{max} * C) / (K_m + C) \quad (2)$$

where I is ingestion rate (individual or weight-specific), V_{max} is the maximum ingestion rate, K_m is the food concentration at which the ingestion rate is half of V_{max} , and C is food concentration in terms of chlorophyll a , nitrogen or carbon.

Relationships were fit to the uncorrected ingestion data, and to data corrected for the experimental temperature and adjusted to 0 °C assuming a Q_{10} coefficient of 2.0. The temperature correction was made to determine if temperature differences between experiments had a significant effect on ingestion rate and the ingestion rate-chlorophyll relationships. It was also used to correct for differences in field temperatures when estimating grazing impacts by mesozooplankton at each station location.

In addition, in a subset of experiments where ingestion rates were determined for both chlorophyll *a* and microzooplankton prey, and paired dilution assays were conducted to estimate microzooplankton grazing rates, corrections were made to account for trophic cascades in the grazing jars following the recommendations of Nejstgaard et al., (2001) and using their general method. Because of the lack of mesozooplankton predation on microzooplankton in control jars, microzooplankton grazing pressure in the control jars can be significantly higher than in the experimental jars resulting in a lower apparent phytoplankton (chlorophyll) growth rate in the control jars relative to the experimental jars and an underestimate of grazing by mesozooplankton.

2.4. Grazing Impacts

Grazing impacts at each station were determined following Campbell et al. (2009) with several modifications. All life stages of the top ten copepod taxa in terms of biomass including: *Calanus* *glacialis/marshallae*, *Pseudocalanus* spp., *Metridia pacifica*, *Acartia longiremis*, *Neocalanus* *cristatus*, *N. flemingeri/plumchrus*, *Eucalanus bungii*, *Oithona similis*, *Microcalanus pygmaeus*, and *Oncaea borealis*, and all euphausiids were included in the estimates. Other taxa, including meroplanktonic larvae and appendicularians were not included in the estimates because we lacked ingestion rate measurements for them. However, this should not introduce a large error into the estimate, as they were not very abundant compared to the copepods at our sampling locations.

Ingestion rates at each location were determined using the chlorophyll-dependent grazing rate equations for each taxon and the maximum chlorophyll concentration at each location. For the small copepod species (*Acartia longiremis*, *Microcalanus pygmaeus*, *Oithona similis*, and *Oncaea borealis*) for which we did not have sufficient data to produce feeding relationships, we used the relationship for *Pseudocalanus* spp. This should not inject a serious error into the calculation as these species generally accounted for less than 10% of the total biomass. The rates were adjusted for 1) body size (stage) for each taxa, assuming rates are proportional to body weight ($Wt^{0.75}$; Kleiber 1947) and 2) mean field temperature (0-50 m) at each location assuming $Q_{10}=2.0$. Stage-specific body weights (carbon) were obtained from measurements of the carbon content from field-collected specimens. For missing weights of younger stages, an estimate was obtained from the ratio of the weight of the adult female to that of the missing stage from our data or from the literature.

The integrated grazing rates were determined from the product of the individual species/stage daily ingestion rates and their areal biomass estimates, and summed for all taxa. Zooplankton areal biomass was estimated from vertically integrated bongo net tows (150- μ m) from 100-m, or the bottom in shallower water, to the surface. Grazing impacts were expressed as the proportion of the total integrated chlorophyll or the total integrated primary production (Lomas et al., 2012) grazed at each station.

This method should provide an estimate of the maximum potential grazing impact of the mesozooplankton population. By estimating the ingestion rate at the highest chlorophyll concentration at the station we use the highest potential ingestion rate for that location. This

method assumes that all mesozooplankton in the upper 100 m are actively feeding and growing, they can move vertically to locate optimal feeding locations, and they don't need to remain in these optimal layers and continually feed to obtain their daily ration. The alternative approach, using clearance rates on the entire water column or just the mixed layer to estimate grazing impacts, would generally provide a much lower estimate.

3. Results

A total of 50 grazing experiments were conducted in spring over the course of the three-year study (2008–2010). There were 596 individual grazing estimates determined and samples from 304 of those experiments were enumerated to estimate grazing on microzooplankton. Grazing rates were determined for both the total and $>5\ \mu\text{m}$ chlorophyll *a* size fractions at those locations where the $<5\ \mu\text{m}$ size fraction exceeded about 5% of the total chlorophyll biomass. The locations spanned the entire shelf and included inner ($<50\ \text{m}$), middle (50–100 m) and outer ($>100\ \text{m}$) domains, but were predominantly from the outer and middle shelf domains (Figure 1).

3.1. Environmental Conditions

All three years were considered “cold” years, but environmental conditions still varied considerably between the cruises (Table 1). In 2008 and 2009, the research cruises were conducted from the icebreaker *USCGC Healy* from early April to early May, while in 2010, the cruise took place about a month later aboard the *R/V Thomas G. Thompson*. Since the *R/V Thompson* is not an icebreaker, experiments could not be conducted within the pack ice in 2010.

In 2008 and 2009 the incubation temperatures (similar to ambient surface water temperature) were about 3° C colder, on average, compared to the later cruise in 2010. The mean chlorophyll concentration and the microzooplankton biomass in the experimental water (taken from the chlorophyll maximum) were greatest in the later spring cruise in 2010 compared to the earlier spring cruises. The chlorophyll was dominated by larger cells, typical of a spring diatom bloom, in all three years.

The prey-field composition showed a consistent pattern with respect to the stage of the spring bloom (Figure 2). At bloom locations where chlorophyll concentrations exceeded about 2 µg chl *a* l⁻¹, the proportion of the chlorophyll in the >5 µm size class generally was 90% or greater. At pre-bloom locations, it was quite variable –ranging from 20–85%. The phytoplankton communities in the >5-µm size fraction were dominated by diatoms (Sherr et al. 2013), and were comprised mainly of centric diatoms including *Chaetoceros* spp., *Thalassiosira* spp. and *Cylindrotheca* spp. However, pennate diatoms, most likely of sea ice origin, *Fragilariopsis* spp., *Navicula* spp. and *Nitzschia* spp., could also be important in ice-covered regions. The proportion of microzooplankton biomass of the total prey field was inversely related to the phytoplankton biomass. In phytoplankton bloom conditions, the proportion of microzooplankton in the prey field was mostly less than 10% of the total prey field biomass, while in pre-bloom conditions, when chlorophyll was low and nutrient concentrations high, microzooplankton biomass could approach 50% of the total prey field biomass. It is interesting to note that the ice biota enriched treatments followed these same patterns: >90% of the chlorophyll was in the > 5 µm size-class, dominated by pennate diatoms, and microzooplankton amounted to less than 10% of the total prey field biomass.

3.2. Prey Preferences

Mesozooplankton showed a strong preference for ice algal/phytoplankton cells larger than 5- μ m (Figure 3, $p < 0.0001$, Wilcoxon Signed Ranks non-parametric test), as indicated by the higher proportion of large cells in the diet compared to the prey field (points falling above the 1:1 line). Similarly, mesozooplankton also preferred microzooplankton to chlorophyll (Figure 3; $p < 0.0001$, Wilcoxon Signed Ranks non-parametric test). Even though there was a strong overall preference for microzooplankton, the proportion of microzooplankton in the diet tended to decrease with increasing chlorophyll ingestion rate, although there is a great amount of variability in the data at low ingestion rates, indicating that it was a less important part of the diet when mesozooplankton were feeding at high rates in bloom conditions (Figure 4). Examples are shown for *Calanus* (adult females) and euphausiids (juveniles and adults) for which the most data are available. Other taxa exhibited a similar response.

There were differences in the preference shown for microzooplankton as a food source between taxa (Figure 5, Table 2). In particular, the copepods *Calanus* spp. and *Pseudocalanus* spp. typical of the middle shelf and *Metridia pacifica*, typical of the outer shelf and slope, consumed microzooplankton at about 2 to 7 times their relative proportions in the prey field. Other outer shelf/slope copepods, including, *Neocalanus* spp. (*N. flemingeri/plumchrus*) and *Eucalanus bungii*, and euphausiids (*Thysanoessa* spp.) fed readily on microzooplankton, but had much weaker preferences for them. *Calanus*, *Pseudocalanus*, and *Metridia*, were not significantly different from each other in their strong preference for microzooplankton prey, but they did have

a significantly stronger preference than *N. flemingeri/plumchrus*, *Eucalanus* sp. and *Thysanoessa* spp., which were not significantly different from each other. *Neocalanus cristatus* was not significantly different from either group. *Acartia* was not included in the comparisons because of small sample size (n=3), although microzooplankton were also preferentially ingested. The Electivity Index and the pairwise comparisons between the proportion of microzooplankton in the prey field and diet found the same patterns in preferences between the different taxa for the most part (Table 2). *Metridia*, *Pseudocalanus*, and *Calanus* had the strongest preferences for microzooplankton, while most copepods found in outer shelf/slope waters were much less selective. *Neocalanus flemingeri/plumchrus* had no preference and *Eucalanus bungii* a weak, but significant, preference for chlorophyll. Based on the prey field/diet comparisons, euphausiids showed no preference, but did have a significant preference for chlorophyll based on the electivity index. This result seems puzzling at first glance because the proportion of microzooplankton in the diet is greater than the prey field. However, diet variability was much higher than for other taxa and the statistical tests that were used were non-parametric, based on ranks, not absolute values, and therefore not as powerful.

Preferences were found for different sizes and types of microzooplankton (Table 3). All mesozooplankton had higher clearance rates, a measure of selectivity, on large >40 μm cells. Only *Pseudocalanus* and *Eucalanus* did not have a significant preference for the larger cells. For most species, there was no significant preference for ciliates vs. dinoflagellates, with the exceptions of *Metridia pacifica* and euphausiids that both had a strong preference for ciliates. The euphausiid preference was surprising since they did not show a preference in terms of clearance rate for microzooplankton prey.

3.3. Ingestion Rates

Maximum weight-specific ingestion of chlorophyll as a function of chlorophyll concentration, in general, decreased with body size as would be predicted by allometric rules (Figure 6, Table 4), although the relationship was not significant. For example: *Pseudocalanus* spp. females and young *Calanus* spp. (C1-C4), the smallest taxa, had maximum ingestion rates of 20 to 30% body carbon day⁻¹; *Calanus* spp. (adult/C5) and *Neocalanus flemingeri/plumchrus* (C4/C5), similar in size, were on the order of 12% body carbon day⁻¹; *N. cristatus* (C5), the largest copepod, maximally fed at about 5% body carbon day⁻¹; and euphausiids, mainly *Thysanoessa raschii* and *T. inermis*, had maximum ingestion rates of only 4% body carbon day⁻¹. *Metridia pacifica*, a small copepod with low maximum ingestion rates was an exception. It had the strongest preference for microzooplankton and the poorest chlorophyll–ingestion rate relationships. Also, young copepodids of *Calanus* had much higher maximum rates than would be expected given their body weight. This might reflect higher relative food requirements of younger stages, as all of the other measurements represent adults or older copepodid stages.

Michaelis-Menten relationships were determined for both total chlorophyll and the >5 µm chlorophyll size fraction in terms of % body nitrogen and carbon for temperature-corrected and uncorrected ingestion rates (Table 4). In almost all cases the relationships were better (higher R²) for chlorophyll in the >5 µm size fraction than for total chlorophyll. Maximum nitrogen-specific rates (V_{max}) tended to be much lower than carbon-specific rates for most taxa. The rates were more similar for taxa with high C:N ratios that more closely approached those of the

454 phytoplankton/ice algae communities, such as *Neocalanus* spp. and young stages of *Calanus* spp.
455 The half-saturation concentrations (K_m), the chlorophyll concentration at which half of the
456 maximum ingestion rate is achieved, were generally similar for nitrogen and carbon based
457 ingestion rates. There were some large differences for some taxa, but no general pattern was
458 observed. Applying a temperature correction to bring all of the experimental rates to a constant
459 temperature of 0° C did not improve the fit (R^2) of the data to the model for most taxa.
460 Providing for larger temperature compensation by increasing the Q_{10} coefficient from 2 to 2.8
461 tended to further worsen the fit (not shown). However, temperature corrections did improve the
462 fit for *Metridia pacifica* and *Neocalanus* spp.
463
464 *Calanus* spp., *Pseudocalanus* spp. and euphausiids readily fed on ice algae when offered in
465 enriched treatments (Figure 7A, C, H). Quite often these ingestion rates were much higher than
466 those predicted by the equations, while at other times ingestion rates were much lower. This
467 might suggest that the quality of ice algae as a food source was highly variable. No enrichment
468 treatments were offered to the outer shelf copepods, *Neocalanus* and *Eucalanus*, because these
469 taxa were not encountered at locations where an ice algal bloom was present.
470
471 Corrections were made to account for trophic cascades in the grazing experiments that could
472 reduce the apparent mesozooplankton chlorophyll grazing rates because of the reduction of
473 microzooplankton grazing pressure in experimental relative to control jars (Nejstgaard et al.,
474 2001). These corrections could only be made for the subset of grazing experiments for which the
475 samples were enumerated for microzooplankton abundance/biomass and where paired dilution
476 assays to measure microzooplankton grazing were conducted. It is not surprising that the

correction had the greatest impact for the mid shelf copepods and *Metridia* because of their strong preference for microzooplankton (Table 5). The corrected grazing rates of mid shelf copepods were 26 to 44% higher, while the outer shelf/slope copepods, with the exception of *Metridia*, only increased by 3 to 15%, and euphausiids by 4%.

The total ingestion rate for this same sub-set of experiments was estimated by combining the corrected chlorophyll ingestion rates and the ingestion of microzooplankton (Table 5). Again, the mid shelf copepods and *Metridia* had the greatest proportional increase in total carbon ingestion relative to ingestion based on corrected chlorophyll alone. Including microzooplankton in the ingestion estimate further increased ingestion by 21 to 69% for mid shelf copepods and only 3 to 10% for outer shelf/slope copepods and euphausiids. Total ingestion estimates more than doubled relative to the uncorrected chlorophyll ingestion for *Pseudocalanus* spp. and *Acartia longiremis*. By comparison, euphausiid total ingestion was only enhanced by about 14%.

A comparison between the feeding rate responses predicted by the uncorrected versus corrected chlorophyll ingestion and the corrected chlorophyll versus total ingestion (chlorophyll and microzooplankton prey) were made for *Calanus* spp. C5-adults and euphausiids (Figure 8A-D). There were not enough experiments enumerated for microzooplankton for the other mesozooplankton taxa to produce reasonable functional relationships. The enhancement of ingestion rates, not surprisingly, was greatest for *Calanus* spp., since this taxon had a stronger preference for microzooplankton than euphausiids. Maximum ingestion rates ($V_{\max}$ with R^2 values in parentheses) were 14 (0.74), 17 (0.82), and 18.5 (0.83) % body carbon day⁻¹ for uncorrected chlorophyll, corrected chlorophyll, and total prey, respectively. In contrast, for

euphausiids, which were non-selective feeders, there were only marginal increases in their maximal ingestion rates, 3.1 (0.28), 3.3 (0.30), and 3.4 (0.30) % body carbon day⁻¹ for uncorrected chlorophyll, corrected chlorophyll, and total prey, respectively.

3.4. Grazing Impacts

The overall mean daily grazing impact on integrated chlorophyll biomass across all cruises and all experiments was only 2.7% ±4.4%, but an order of magnitude higher on integrated primary production, 26% ±48%. Uncorrected chlorophyll ingestion rates were used for these estimates because corrected ingestion relationships were not available for all taxa. Therefore, these estimates underestimate grazing impacts to some degree, likely more at inner and middle shelf regions than the outer shelf because of the higher preference for microzooplankton by the mesozooplankton community at those locations, and less at bloom than non-bloom locations because the microzooplankton were a less important part of the diet.

Grazing impacts of mesozooplankton on chlorophyll standing stock and primary production were compared between cruises, regions, domains, and bloom conditions (Table 6). Non-parametric tests were used for all comparisons because the variance was unequal in most cases and also the impact of outliers on the comparisons was reduced. Grazing impacts on chlorophyll standing stock were extremely low in all cases. The impacts on primary production were much higher than for chlorophyll standing stock. Mean grazing impacts on primary production in the South region was more than double that in the North, and impacts in the Outer domain were three times as high as those in the Inner and Middle domains, the latter appeared to be due to much higher

zooplankton biomass in the Outer domain. However, neither of the comparisons was significantly different because of the high variability of the measurements. Only the comparisons between bloom and non-bloom conditions were significantly different. In bloom conditions where primary production exceeded $1 \text{ gC m}^{-2} \text{ d}^{-1}$, grazing impacts were very low, on the order of $8 \pm 16\% \text{ d}^{-1}$.

The highest impacts occurred at locations where the chlorophyll biomass and primary productivity were low (Figure 9). During phytoplankton blooms the grazing impacts were relatively insignificant. Comparisons between years indicate that the grazing impact on chlorophyll standing stock was strongly correlated with the zooplankton biomass and the coincident higher grazing rates (Figure 9, Table 6). It was lowest in 2008 when the zooplankton biomass was lowest and highest in 2010 when the zooplankton biomass was more than three times as high as the earlier years (Table 6). The 2010 research cruise occurred about a month later than the 2008 and 2009 cruises, and the higher biomass likely reflects biomass accumulated during the spring. The mean grazing impact on the integrated primary production by cruise varied between 9 and 38% per day (Table 6). The high rates observed in 2008 were driven by a single outlier of 275% per day, where the measured primary production was extremely low. Removing the outlier would result in a mean value for the cruise of 16%, which is more similar to 2009 and a much stronger relationship between zooplankton biomass and the proportion of the primary production that was grazed (Figure 9).

4. Discussion

Mesozooplankton feeding ecology was investigated on three, 6-week cruises to the Bering Sea during which a large number of individual grazing determinations were conducted over a range of sea ice and phytoplankton bloom conditions, at multiple cross-shelf and along-shelf (northern vs. southern Bering Sea) locations and during both mid and late spring periods. This rich data set demonstrated that Bering Sea zooplankton show differences in prey preference and ingestion rate, that microzooplankton are preferred prey for several species, but that large phytoplankton (diatoms) comprise the largest portion of the mesozooplankton diet in spring simply because they are much more abundant than microzooplankton, that mesozooplankton readily ingest ice algae as prey, and that mesozooplankton in these ‘cold’ years did not graze a substantial proportion of the primary production or chlorophyll standing stock at most locations and particularly in phytoplankton bloom regions.

4.1. Mesozooplankton Feeding During Spring Sea-ice Conditions

In these experiments, we do not know with certainty the reason a particular prey type is chosen in preference to another. A prey type might be actively chosen or avoided because of many reasons including size, swimming speed or behavior, nutritional quality, or toxicity. Or, it could be that the zooplankter is incapable/inefficient at capturing a prey type because of many of the same reasons. Here we are measuring the apparent prey preference because of these uncertainties.

The types and proportions of prey in the diet of mesozooplankton depended on a combination of their apparent prey type preference, prey size preference, and the relative abundances of different

types and sizes in the ambient prey field. All mesozooplankton, including copepods and euphausiids, preferentially fed on larger ($>5\ \mu\text{m}$) phytoplankton/ice algal cells as opposed to smaller ($<5\ \mu\text{m}$) phytoplankton cells. These large cells were primarily diatoms, especially in the bloom regions (Moran et al. 2012; Sherr et al. 2013). The few occasions when there appeared to be a strong preference for smaller cells occurred at very low chlorophyll concentrations when grazing rates were low and variability in the grazing estimates were high. However, for the most part, even when smaller cells were relatively more abundant, larger cells were still preferred. This may simply reflect cell-capturing capability as opposed to preference, as particles less than about $5\text{-}\mu\text{m}$ are too small to be grazed efficiently by many mesozooplankton (Berggreen et al., 1988; Boyd et al., 1984; Fernandez, 1979; Nival and Nival, 1976).

Quite often many of the common mesozooplankton species, *Calanus* spp. for example, are referred to as herbivores, but that is a misnomer. It has been shown that many copepods are omnivorous, often preferring animal to plant food (Barthel, 1990, 1988; Campbell et al., 2009; Gifford 1993; Stoecker and Capuzzo, 1990). All of the mesozooplankton included in our grazing measurements were omnivorous to varying degrees, some such as the mid shelf copepods *Calanus* spp. and *Pseudocalanus* spp. and the outer shelf/slope species *Metridia pacifica*, strongly preferred microzooplankton, while the outer shelf/slope species *Neocalanus flemingeri/plumchrus* and *Eucalanus bungii* and the euphausiids readily fed on them, but were non-selective or preferred phytoplankton. In the Western Arctic Ocean, shelf copepods, especially *Pseudocalanus* spp., and the slope copepod *Metridia longa* were also found to have a strong preference for microzooplankton, while the Arctic Basin copepod *Calanus hyperboreus* fed non-selectively (Campbell et al., 2009). However, the dominant shelf species, *C.*

glacialis/marshallae, appeared to mostly feed non-selectively during spring, but strongly preferred microzooplankton during summer when they were more abundant and the phytoplankton was dominated by smaller cells (Hill et al., 2005). In the more oceanic regions of the subarctic Pacific Ocean as well as in the Gulf of Alaska, *Neocalanus* and *Eucalanus* appeared to have a stronger preference for microzooplankton than we found in the outer shelf regions of our study for these species (Gifford, 1993; Liu et al., 2005; Mackas and Tsuda, 1999). Thus, the degree of omnivory likely depends to a high degree on the food environment as well as the mesozooplankton taxa.

There were differences in the preferences for the size and type of microzooplankton prey. Most taxa significantly cleared larger microzooplankton at higher rates than small microzooplankton. If there was a preference shown for the type of microzooplankton prey, it was for ciliates as opposed to heterotrophic dinoflagellates, with both *M. pacifica* and euphausiids showing a strong preference for ciliates (and *Acartia longiremis* in single experiment). It was not surprising that *M. pacifica* had strong preferences for large microzooplankton and ciliates. This genus has very selective feeding behavior. It has been shown to be more predatory than *Calanus* spp. (e.g. Stevens et al., 2004) and has a highly variable, poorly predictable feeding response to chlorophyll concentration (this study, Campbell et al., 2009). Batchelder (1986) concluded that *M. pacifica* in the subarctic Pacific had a lower feeding rate on chlorophyll compared to similarly sized crustaceans, which also might suggest that other food sources, such as microzooplankton (including protists and small metazoans), must be an important component of the diet.

614 Prey composition (type, size, nutritional quality) plays an important role in determining the type
615 and quantity of prey consumed by the mesozooplankton at different locations and times (e.g.
616 Campbell et al. 2009; Gifford et al. 1981; Huntley et al. 1987; Klein Breteler et al., 1999;
617 Kleppel 1993; Langdon and Waldock 1981; Mullin, 1963; Nival and Nival 1976; Stoecker and
618 Capuzzo, 1990; Støttrup and Jensen 1990). Although many mesozooplankton taxa preferred
619 microzooplankton to phytoplankton, when the prey field was dominated by large phytoplankton
620 cells, the mesozooplankton diet would contain a larger proportion of phytoplankton because that
621 prey type was much more abundant than the microzooplankton. Consequently, large diatom
622 cells were the dominant food source for the mesozooplankton in spring simply because the large
623 diatoms dominated the prey field biomass in the characteristic spring phytoplankton and ice algal
624 blooms.

625

626 Ice algae are likely an important source of food for many Arctic and subarctic zooplankton taxa
627 during early spring. In the Arctic, pelagic copepods including, *Calanus glacialis* and
628 *Pseudocalanus* spp., have been observed migrating up to the ice/water interface to feed on ice
629 algae (Conover et al., 1986; Runge and Ingram 1991, 1988). During our cruises on ice station
630 deployments, euphausiids also were observed in close association with the ice and appeared to be
631 feeding (R. Gradinger pers. comm.). The enriched treatments to which ice algal communities
632 were added to the ambient water demonstrated that if ice algal communities were available they
633 were readily ingested, but they cannot be used to quantify their importance *in situ*. However, it
634 appears that ice algae are an important early season food source for most mesozooplankton
635 because they can provide an early, highly-concentrated food source when the water column food
636 supply is severely limited. They can also extend the very short growing season, which may be

critical for many species to complete their life cycles (e.g. Ji et al., 2012), and provide an energy source for early reproduction (e.g. Daase et al., 2013; Søreide et al., 2010;). It is critical then, that new methods be developed to quantify the importance of ice algae as a food source for mesozooplankton during the early spring to understand the food web dynamics of waters with seasonal sea ice. Promising new approaches include the quantification of prey DNA in gut contents of mesozooplankton (Durbin and Casas, 2014), and measurement of compound-specific, stable carbon isotopes that can distinguish between prey, including separating phytoplankton and ice algal food sources (Graham et al., 2014; Wang et al., 2013).

Estimating feeding rates from chlorophyll ingestion can provide a robust estimate of the energy intake for most mesozooplankton during spring blooms in high latitude regions because the majority of the ingested prey is chlorophyll based, in the form of phytoplankton or ice algae. During summer, ingestion based on chlorophyll provides a much poorer estimate of total food intake as smaller phytoplankton cells that are not grazed efficiently are more important and the microzooplankton are more abundant and a larger portion of the diet (Campbell et al., 2009). Ingestion estimates based on microscopic analysis can provide more information on the feeding capabilities and preferences, the types and sizes of the preferred prey, but at the cost of higher uncertainties in total prey consumption and much smaller number of ingestion estimates. By focusing a large part of this study's effort on estimating size-fractionated chlorophyll ingestion rates for as many of the dominant taxa as possible at each of the 50 process stations, 596 grazing estimates were obtained over the course of the 3 year study. This high number of estimates that covered a large range of chlorophyll concentrations allowed the determination of robust,

predictive functional relationships despite the high variability in food quality that can occur in natural assemblages compared with controlled laboratory studies.

It has been stated that trophic cascades in the experimental jars during grazing experiments can reduce the estimates of chlorophyll ingestion by the mesozooplankton grazers (Nejstgaard et al., 2001). This effect can be important when microzooplankton grazing-pressure is high and they are a strongly preferred prey item of the mesozooplankton. Nejstgaard et al., (2001) proposed a method to correct for trophic cascades in grazing experiments. To apply this correction, one has to enumerate the microzooplankton in the grazing experiments and conduct parallel dilution assays to estimate microzooplankton grazing on the same experimental water. This correction could be made for about half of our grazing estimates, 304 out of 596 measurements. The degree to which trophic cascades affected the grazing experiments depended on the strength of the preference for microzooplankton prey by the mesozooplankton taxa. Chlorophyll grazing rates, when corrected for trophic cascades, increased by over 40% for the strongly omnivorous *Pseudocalanus* spp. and *Metridia. pacifica*. The grazing rates were only enhanced by between 3 and 15% for the outer shelf copepods that were the biomass dominants, which overall did not have as strong a preference for microzooplankton prey. Likewise, average euphausiid grazing rates were only enhanced by 4% when trophic cascades were accounted for in their estimates. Without these corrections, grazing rates would likely be underestimated to a greater extent in summer, when the chlorophyll distribution is skewed to smaller sizes (Lomas et al., 2012), and the microzooplankton biomass is greater (Sherr et al., 2013; Stoecker et al., 2014).

Even in spring when not yet very abundant, microzooplankton can contribute a significant portion of the diet for many taxa. For *M. pacifica* and the mid shelf copepod species including microzooplankton in the diet, on average, increased the total carbon ingested by about 20 to 40%, (69% in the single experiment with *A. longiremis*), despite microzooplankton being a small proportion of the prey field biomass. On average, the total ingested carbon was more than double than what was estimated based on uncorrected chlorophyll ingestion alone for *Pseudocalanus* spp. and *A. longiremis*. For the remaining outer shelf copepod species (*Neocalanus* spp., *E. bungii*), the enhancement was only between 3 and 10% and for euphausiids 7%, all very similar to the proportion that microzooplankton contributed to the prey field biomass. For *Calanus* and euphausiids there were enough experiments for which ingestion of microzooplankton were determined to allow us to fit ingestion relationships to the data. It was clear that not correcting for trophic cascades, and not including microzooplankton in the diet greatly underestimated the total carbon ingestion for *Calanus*. The maximum predicted chlorophyll ingestion rate was increased by 21% body carbon day⁻¹ for *Calanus*, but only 6% body carbon day⁻¹ for euphausiids. By including microzooplankton in the diet, the total carbon intake for *Calanus* increased over the uncorrected chlorophyll ingestion by 32% body carbon day⁻¹, while for euphausiids the increase was less than 10% body carbon day⁻¹. For the more strongly selective taxa it is important to both correct for trophic cascades and include the ingestion of microzooplankton in the diet to obtain an accurate estimate of total energy intake.

4.2. Mesozooplankton Grazing Impacts During Spring

The mesozooplankton grazing impacts during spring were generally very low. Mesozooplankton could crop a substantial portion of the chlorophyll biomass/production only when the chlorophyll biomass/production rates were low or when the mesozooplankton biomass was high, as occurred mainly for the late spring cruise in 2010. Overall, the mean copepod grazing impacts on integrated chlorophyll biomass was very low ($2.7 \pm 4.4\% \text{ d}^{-1}$); while that for integrated primary production was much higher ($26 \pm 48\% \text{ d}^{-1}$). However, for both impact measures the impacts were strongly skewed with high impacts only at the lowest chlorophyll biomass or primary production rates. During bloom conditions grazing impacts were on average very low: $< 8\%$ of the primary production was grazed. It should be emphasized that it is not the average grazing impacts during spring that are important for determining the strength of benthic-pelagic coupling, but rather the impacts during the ice-edge blooms where most of the spring production occurs.

Dagg et al. (1982) found that mesozooplankton grazing impacts on the southern Bering Sea shelf in May were similar in magnitude to our estimates; 18, 25, and 6% of the primary production was grazed in the outer, mid and coastal regions, respectively, despite encountering much warmer water temperatures of around 6°C . Their study also determined grazing rates from bottle incubations and mesozooplankton biomass from 60-cm Bongo net hauls. These grazing impacts, like ours, were likely underestimates because euphausiids are difficult to assess by any means and can avoid collection by nets (Hunt et al., this volume; Sameoto et al., 1993; Wiebe et al., 2013). Thus the euphausiid contribution to the grazing impacts was underestimated to some unknown degree in both studies.

Euphausiids only accounted for 12 to 15% of the mean, spring, mesozooplankton biomass and 3 to 6% of the grazing impacts in our study likely because their true biomass was severely underestimated. Hunt et al. (this volume) in a synthesis of net tow samples, acoustic data, and model output from recent years estimated the euphausiid biomass in the eastern Bering Sea for different regions and seasons. In spring, based on model output, mean biomass between 2004 and 2009 was 2,140 and 2,610 mg C m⁻² for the middle and outer domains, with a mean value of 2,475 mg C m⁻². In contrast, based on our bongo net samples we estimated mean krill biomass, on the shelf in spring, to be 47±83, 132±125, and 167±144 mg C m⁻² in 2008, 2009, and 2010, respectively, about 15 – 50 fold lower than Hunt et al.'s (this volume) mean estimate. If we assume that euphausiid biomass at all locations in spring was equal to the average value of Hunt et al. (this volume) then euphausiids would dominate the biomass of the mesozooplankton in spring (63-86% of total biomass across the three years). This is consistent with Vidal and Smith's (1986) findings for the middle domain in spring. Euphausiid grazing impacts, however, would increase to only 32 to 51% of the total impact across all years because of their lower weight-specific ingestion rates. With these new estimates, mesozooplankton grazing-impacts would increase to only 1 to 6% of the chlorophyll standing stock on average across all years. The grazing impacts on primary production would increase to between 12 to 84% (to only 41% if a single high outlier is excluded) on average across the years. However, the overall grazing impact on primary production in bloom regions still would only be 10% of the total production.

The eastern Bering Sea shelf can be characterized as having a benthic-dominated region in the north and a pelagic-dominated region in the south (Grebmeier et al., 2006). These two regions are separated by a transition zone occurring at about 60°N (Stabeno et al., 2012a, 2012b). In the

north region, permanently cold bottom waters on the middle shelf limits the northern distribution of demersal fish and invertebrate predators, which reduces predation and allows the benthic community to flourish (Grebmeier et al., 2006; Wyllie-Echeverria and Wooster, 1998). Earlier studies suggested that stronger benthic-pelagic coupling in the north compared to the south might also contribute to the higher benthic biomass in the north (Springer et al., 1989). However, the Oscillating Control Hypothesis suggested that at least for the southern region the connections are more complicated, with strong benthic-pelagic coupling in cold regimes and weaker coupling in warm regimes (Hunt et al., 2002). Here we directly determined the strength of benthic-pelagic coupling in spring by measuring the potential grazing impacts of the dominant mesozooplankton grazers across north and south regions for three consecutive spring seasons during a ‘cold’ period in the Bering Sea and did not find any significant differences between the regions. There appeared to be higher grazing impacts in the south, but these were not significantly different because of high variability. Furthermore, the grazing impacts were extremely low at all bloom locations where most of the spring production occurred. Benthic-pelagic coupling appears to be strong in spring across the entire shelf at least during cold periods. Whether or not benthic-pelagic coupling is weakened, with more of the production retained in the pelagial during warm periods, remains an open question. If the extremely high grazing impacts of microzooplankton measured during summer months, which often exceeded primary production (Stoecker et al., 2014), is an indication of the potential for warm spring periods then the strength of benthic-pelagic coupling in the south during warm periods could be much weaker.

On the eastern Bering Sea shelf, it appears that only about 50% of the primary production is grazed during spring blooms during ‘cold years’. Microzooplankton grazing accounted for about

40% of phytoplankton daily growth at bloom locations as measured in dilution assays that were paired with our experiments (Sherr et al., 2013), while our maximum estimates would suggest that only about 10% of the production is grazed by the mesozooplankton, including krill. Thus it would appear that in spring about half of the production would remain un-grazed and available for export to the benthic communities. This is consistent with estimates of *e*-ratios for the Bering Sea shelf in spring of about 50% (Moran et al., 2012). In contrast, during summer, microzooplankton grazing in the Bering Sea is much greater, exceeding phytoplankton growth in the inner and middle domains (Stoecker et al., 2014). Unfortunately, mesozooplankton grazing rates were not determined in summer as part of the Bering Sea project and so we do not know whether mesozooplankton might reduce microzooplankton grazing-pressure through top-down control given much higher mesozooplankton biomass in summer (Eisner et al., 2014; Vidal and Smith, 1986; see BEST MOCNESS net tow data sets at the EOL Data archive: <http://www.eol.ucar.edu/projects/best>) and strong preference for microzooplankton prey.

4.3. Summary

- Eastern Bering Sea mesozooplankton were omnivorous, with most preferring microzooplankton over chlorophyll (phytoplankton/ice algae). The strength of the preference was taxon-specific.
- Despite a strong preference for microzooplankton, phytoplankton comprised the dominant portion of the diet for all mesozooplankton taxa in spring blooms because its biomass was much greater than that of the microzooplankton.

- There were no significant differences in grazing impacts between regions or domains in spring: differences in trophic structure between the pelagically-dominated southern shelf and the benthically-dominated northern shelf could not be attributed to differences in planktonic grazing pressure at least for the three ‘cold years’ of this study.
- Grazing impacts were low in spring phytoplankton blooms during ‘cold years’. Only about 50% of the primary production in the blooms was grazed by the combined efforts of the micro- and mesozooplankton communities.

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Figure Captions

Figure 1. Station locations of grazing experiments in the eastern Bering Sea during spring.

Figure 2. Prey field. The proportion of chlorophyll *a* >5 μm (left) and proportion of microzooplankton carbon of the total carbon in the prey field (right) vs. chlorophyll *a* concentration in the experimental water.

Figure 3. Diet vs. prey field comparisons for all mesozooplankton species combined. (Left) The proportion of chlorophyll *a* (>5 μm) in the diet vs. the prey field, and (Right) the proportion of microzooplankton biomass in the diet vs. the prey field, with diet proportions corrected for trophic cascades. Dashed lines indicate the 1:1 relationship or no preference.

Figure 4. Importance of microzooplankton in the diet as it relates to chlorophyll ingestion rate. The proportion of microzooplankton in the diet vs. chlorophyll ingestion rate is shown for (Left) *Calanus glacialis/marshallae* adult females and (Right) all euphausiids (juveniles and adults). Values corrected for trophic cascades.

Figure 5. Diet and prey field comparison for different taxa. The proportion of microzooplankton in the prey field and diet are compared for each taxon. Asterisks indicate statistically significant differences between prey field and diet. Statistical comparisons are provided in Table 2. Values corrected for trophic cascades.

Figure 6. Maximum ingestion rate versus body size. The maximum ingestion rate (V_{max}) from the carbon ingestion rate vs. total chlorophyll relationships is plotted against the mean carbon content for the 8 species/stage groupings in Table 4. Values not corrected for trophic cascades. Each point is labeled by the species initials and dominant stage (f = female; c = copepodid). The value for all euphausiids (Krill) is shown, not *Thysanoessa raschii* only.

Figure 7. Ingestion rate relationships. The mean ingestion rates for each experiment as a function of the initial chlorophyll *a* ($>5 \mu m$) concentration for ambient and enriched treatments are shown for A) *Calanus* spp. (C5-adult), B) *Calanus* spp. (C1-C4), C) *Pseudocalanus* spp. (adult female), D) *Metridia pacifica* (adult female), E) *Neocalanus flemingeri/plumchrus* (C4, C5), F) *Neocalanus cristatus* (C5), G) *Eucalanus bungii* (C5, adult female), and H) *Thysanoessa* spp. (Juvenile, adult). Relationships for Michaelis-Menten equations were fit to the ambient values only. Parameter estimates are given in Table 4. Values not corrected for trophic cascades.

Figure 8. Ingestion rate comparisons. Ingestion rates (percent body carbon) as a function of the initial chlorophyll *a* or prey field carbon concentration for the subset of experiments where chlorophyll and microzooplankton ingestion rates were determined for *Calanus* spp. (C5-adult, A, C) and *Thysanoessa* spp. (juvenile and adult, B, D). Uncorrected chlorophyll and corrected chlorophyll (Nejstgaard et al. (2001) correction for trophic cascades) ingestion rates are shown in A and B. Corrected chlorophyll and total carbon ingestion (corrected chlorophyll and microzooplankton) are shown in C and D. Michaelis-Menten curve fits are shown for each data set.

1177 Figure 9. Grazing Impacts. A, B) The proportion of chlorophyll *a* standing stock and primary
1178 production grazed in terms of the integrated chlorophyll and primary production. C, D) The
1179 proportion of chlorophyll *a* standing stock and primary production grazed in terms of
1180 zooplankton biomass. Linear regressions for the proportion of chlorophyll ($R^2=0.75$; $p<0.0001$)
1181 and primary production ($R^2=0.36$; $p<0.0001$), excluding the outlier of 275%, grazed vs.
1182 zooplankton biomass are shown. Values not corrected for trophic cascades.

Figure 1.

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Figure 5.

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Figure 9.

Table 1. Environmental conditions and prey field concentrations. The mean ($\pm$ sd) experimental conditions during each cruise are shown, including incubation temperature, chlorophyll concentration, proportion of chlorophyll $>5\ \mu\text{m}$, and the carbon biomass of chlorophyll a and microzooplankton in the experimental water.

Cruise	Dates	Exps. n	Temp $^{\circ}\text{C}$	Chl a $\mu\text{g Chl } a\ \text{l}^{-1}$	Chl a , >5 Proportion	Chl a Biomass $\mu\text{g C l}^{-1}$	μzp Biomass $\mu\text{g C l}^{-1}$
HLY0802	4/2/08 – 5/1/08	14	-1.2 ± 0.9	4.6 ± 5.8	0.76 ± 0.23	230 ± 290	18.6 ± 16.6
HLY0902	4/6/09 – 5/8/09	18	-0.9 ± 0.5	7.0 ± 11.4	0.64 ± 0.30	350 ± 570	33.7 ± 33.6
TN249	5/12/10–6/11/10	18	1.9 ± 1.1	9.9 ± 8.8	0.82 ± 0.21	495 ± 440	45.0 ± 19.0

Table 2. Prey field vs. diet comparisons. The proportion of microzooplankton biomass (carbon) in the prey field and diet (mean $\pm$ sd values shown) are compared for each taxon with the significance level based on the non-parametric Wilcoxon Matched-Pairs Signed Ranks Test (p). The electivity indices (D) within each taxon, positive values indicating preference for microzooplankton and negative values a preference for chlorophyll, are compared using the non-parametric Wilcoxon Signed Ranks Test (p). Electivity index (D) comparisons between taxa were significant ($p < 0.0001$) based on the non-parametric Kruskal-Wallis One-Way ANOVA. Dunn's Multiple Comparisons test was used in post-hoc comparisons with letters (a, b) indicating groupings ($p < 0.05$). The sample size for *Acartia* was too small to perform the test. Chlorophyll ingestion rates used in the diet proportion estimates were corrected for trophic cascades (see Methods for details).

	Microzooplankton Preferences					
	n	Microzooplankton Proportion			Electivity Index	
		Prey Field	Diet	p	D	p
Mid Shelf copepods						
<i>Acartia longiremis</i>	3	0.18	0.41±0.05		0.52±0.07	
<i>Calanus</i> spp.	74	0.13±0.13	0.28±0.26	<0.0001	0.39±0.36 ^a	<0.0001
<i>Pseudocalanus</i> spp.	23	0.11±0.08	0.38±0.28	<0.0001	0.53±0.46 ^a	0.0006
Outer shelf/slope copepods						
<i>Eucalanus bungii</i>	9	0.10±.07	0.04±0.05	0.0078	-0.52±0.39 ^b	0.0177
<i>Metridia pacifica</i>	32	0.06±0.03	0.33±0.31	<0.0001	0.58±0.37 ^a	<0.0001
<i>Neocalanus cristatus</i>	15	0.08±0.06	0.16±0.09	0.0009	0.32±0.37 ^{a,b}	0.0043
<i>Neocalanus</i> spp.	21	0.07±0.03	0.05±0.05	ns	-0.20±0.54 ^b	ns
Euphausiids						
<i>Thysanoessa</i> spp.	87	0.08±0.08	0.17±0.29	ns	-0.14±0.64 ^b	0.004

Table 3. Clearance of microzooplankton by size and type. The comparisons between clearance rates for large and small microzooplankton and for ciliates and dinoflagellates are shown for each taxon. The level of significance (p) is shown for the non-parametric Matched-Pairs Signed Ranks Test for each comparison. The sample size for *Acartia* was too small to perform the test.

	n	Clearance of microzooplankton, ml $\mu\text{gC}^{-1} \text{ day}^{-1}$					
		Size		p	Type		p
		<40 μm	>40 μm			Ciliate	
Mid shelf copepods							
<i>Acartia longiremis</i>	3	0.90±1.11	2.19±0.36		7.39±2.79	1.27±0.29	
<i>Calanus</i> spp.	74	0.31±0.75	1.57±1.44	<0.0001	0.92±0.94	1.04±0.94	ns
<i>Pseudocalanus</i> spp.	23	1.54±1.29	2.51±2.35	ns	1.96±2.84	2.24±1.11	ns
Outer shelf/slope copepods							
<i>Eucalanus bungii</i>	9	-0.02±0.15	0.20±0.30	ns	-0.02±0.15	0.07±0.15	ns
<i>Metridia pacifica</i>	32	0.34±0.3	1.14±0.77	<0.0001	1.01±0.51	0.67±0.54	0.0008
<i>Neocalanus cristatus</i>	15	0.06±0.17	0.18±0.29	0.0181	0.11±0.22	0.12±0.19	ns
<i>Neocalanus</i> spp.	21	0.09±0.14	0.24±0.19	0.037	0.14±0.16	0.17±0.20	ns
Euphausiids							
<i>Thysanoessa</i> spp.	87	0.05±0.09	0.08±0.17	0.0058	0.12±0.19	0.03±0.08	<0.0001

1327 Table 4. Michaelis-Menten relationships. Parameter estimates for relationships for ingestion rate as a function of initial chlorophyll *a*
1328 concentration (total and >5 µm) are given. Parameter estimates for V_{max} and K_m, and R² values are provided for uncorrected rates
1329 and temperature corrected rates set to 0°C, assuming a Q₁₀ coefficient of 2, for both nitrogen- and carbon-specific ingestion rates for
1330 each taxon grouping. In addition, the stages included in the grouping, their mean (±sd) weight (N and C), C:N ratio, and the total
1331 number of experiments and samples included in the relationship are given. Ingestion rates were not corrected for trophic cascades.
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Taxon	Stages	N wt (µg)	C wt (µg)	C:N	Exp. n	Sample n	Chl <i>a</i> fraction	Temp. corr. to 0° C	Nitrogen (% Body wt/day vs. Chl <i>a</i> , µg/l)			Carbon (% Body wt/day vs. Chl <i>a</i> , µg/l)		
									V _{max}	K _m	R ²	V _{max}	K _m	R ²
<i>Calanus spp.</i>	C5-Adult	60±14	252±65	4.20	42	128	Total	None	6.47	2.89	0.67	12.44	3.09	0.70
							Total	Q10=2	6.08	2.30	0.66	11.79	2.53	0.69
							>5 µm	None	6.23	1.89	0.72	11.95	2.05	0.75
							>5 µm	Q10=2	5.92	1.53	0.73	11.43	1.68	0.75
<i>Calanus spp.</i>	C1-C4	10±7	72±61	7.20	7	21	Total	None	23.30	3.41	0.50	32.13	5.20	0.58
							Total	Q10=2	21.44	3.39	0.46	28.41	4.77	0.57
							>5 µm	None	22.28	2.12	0.58	28.28	2.84	0.68
							>5 µm	Q10=2	20.67	2.21	0.54	25.70	2.81	0.68
<i>Pseudocalanus spp.</i>	Adult Female	2.4±0.6	10.4±3.7	4.33	23	69	Total	None	12.40	1.89	0.37	21.29	1.89	0.41
							Total	Q10=2	11.81	1.57	0.36	20.26	1.57	0.40
							>5 µm	None	12.64	1.40	0.43	21.68	1.39	0.48
							>5 µm	Q10=2	12.12	1.19	0.42	20.77	1.18	0.47
<i>Metridia pacifica</i>	Adult Female	20±4	81±17	4.05	18	54	Total	None	3.24	7.59	0.10	6.32	7.37	0.10
							Total	Q10=2	3.42	5.19	0.21	6.68	4.97	0.21

							>5 µm	None	2.73	4.08	0.07	5.29	3.84	0.07
							>5 µm	Q10=2	3.02	2.81	0.17	5.91	2.71	0.18
<i>Eucalanus bungii</i>	C5,Female	71±20	286±89	4.03	6	18	Total	None	7.08	7.63	0.95	11.71	4.67	0.85
							Total	Q10=2	6.31	5.60	0.91	11.12	3.92	0.79
							>5 µm	None	6.37	5.00	0.99	10.53	2.63	0.94
							>5 µm	Q10=2	5.64	3.39	0.98	10.17	2.15	0.89
<i>Neocalanus cristatus</i>	C5	172±60	894±484	5.20	6	14	Total	None	2.17	4.58	0.72	5.38	9.60	0.95
							Total	Q10=2	1.71	3.71	0.63	3.97	7.08	0.84
							>5 µm	None	1.95	2.61	0.75	4.48	5.61	0.97
							>5 µm	Q10=2	1.64	2.55	0.70	3.59	4.66	0.89
<i>Neocalanus spp.</i> (<i>flemingeri/plumchrus</i>)	C4,C5	50±22	450±241	9.00	12	36	Total	None	14.04	7.31	0.45	13.28	8.11	0.45
							Total	Q10=2	12.64	6.96	0.51	12.00	7.76	0.52
							>5 µm	None	13.81	5.86	0.46	13.06	6.63	0.50
							>5 µm	Q10=2	12.55	5.77	0.58	11.91	6.54	0.62
<i>Thysanoessa raschii</i>	Juv/Adult	1301±1010	5719±4833	4.40	44	128	Total	None	2.30	6.05	0.62	3.94	4.77	0.54
							Total	Q10=2	2.20	5.31	0.56	3.87	4.29	0.48
							>5 µm	None	2.25	5.06	0.64	3.88	4.04	0.57
							>5 µm	Q10=2	2.17	4.51	0.58	3.82	3.67	0.51
Euphausiid (All) <i>T. raschii</i> , <i>T. inermis</i> ,	Juv/Adult	1269±979	5731±4775	4.52	55	159	Total	None	2.16	6.50	0.52	3.60	4.83	0.46
							Total	Q10=2	2.03	5.40	0.47	3.52	4.21	0.40

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>5 μm	None	2.18	5.83	0.57	3.67	4.43	0.51
>5 μm	Q10=2	2.06	4.81	0.53	3.59	3.84	0.46

Table 5. Ingestion measurement comparisons. The mean ($\pm$ sd) values for ingestion of chlorophyll *a*, corrected chlorophyll *a* (Nejstgaard et al. (2001) correction for trophic cascades in experimental jars applied), and total carbon (corrected chlorophyll *a* and microzooplankton) for the subset of experiments where chlorophyll *a* and microzooplankton ingestion rates were determined are shown for each taxon. In addition, mean values are given for the proportional increase in ingestion rate for the corrected chlorophyll *a* relative to uncorrected chlorophyll *a*, and total carbon relative to corrected chlorophyll *a*. Data are not temperature corrected.

		Ingestion, %Body Carbon day ⁻¹			Proportional Increase	
	n	Chl <i>a</i>	Chl <i>a</i> corr.	Total	Chl <i>a</i> corr.	Total
Mid shelf copepods						
<i>Acartia longiremis</i>	3	11.5±3.0	15.3±3.2	25.9±4.4	0.33	0.69
<i>Calanus</i> spp.	74	7.7±7.7	9.7±10.3	11.8±11.8	0.26	0.21
<i>Pseudocalanus</i> spp.	23	9.9±9.2	14.2±11.8	20.0±13.0	0.44	0.41
Outer shelf/slope copepods						
<i>Eucalanus bungii</i>	9	6.0±4.3	6.1±4.5	6.3±4.6	0.03	0.03
<i>Metridia pacifica</i>	32	4.2±4.4	6.0±4.7	7.5±4.8	0.41	0.26
<i>Neocalanus cristatus</i>	15	3.5±5.0	4.1±5.1	4.5±5.2	0.15	0.10
<i>Neocalanus</i> spp.	21	6.5±3.3	7.2±3.9	7.5±4.2	0.10	0.06
Euphausiids						
<i>Thysanoessa</i> spp.	87	2.2±1.8	2.3±1.8	2.5±1.9	0.04	0.07

Table 6. Grazing Impacts by cruise, region (< or > 59.8° N), domain (< or > 100 m), and bloom conditions (primary production < or > 1 gC m⁻² d⁻¹). Mean values (±sd) are provided for integrated mesozooplankton biomass, integrated chlorophyll *a*, integrated primary production, integrated mesozooplankton grazing rates, and the proportions of the chlorophyll *a* standing stock and primary production that were grazed each day. Statistical comparisons were made to test for differences in the proportion of primary production grazed within each grouping. The non-parametric Kruskal-Wallis one-way ANOVA was used to test for differences between cruises and the non-parametric Mann-Whitney test for the remaining paired comparisons. Only the proportion of primary production grazed between non-bloom and bloom conditions was significantly different (* p=0.0006). Grazing impact estimates not corrected for trophic cascades.

	Zoop. Biomass mgC m ⁻²	Int. Chl a mgChla m ⁻²	Int. Prim. Prod. mgC m ⁻² d ⁻¹	Zoop. Graz. mgChla m ⁻² d ⁻¹	Proportion Chl a Grazed	Proportion Prim. Prod. Grazed
Cruises						
2008	472 ±307	132 ±156	871 ±1253	0.64 ±0.66	0.01 ±0.002	0.38 ±0.78
2009	1075 ±759	220 ±317	2093 ±2850	1.29 ±1.66	0.02 ±0.02	0.09 ±0.10
2010	3218 ±4259	139 ±149	3319 ±6922	4.31 ±5.19	0.05 ±0.06	0.34 ±0.39
Region						
South	1817 ±2461	221 ±243	2585 ±3047	2.54 ±2.74	0.03 ±0.04	0.34 ±0.62
North	1549 ±3338	81 ±155	1802 ±6028	1.81 ±4.62	0.03 ±0.05	0.16 ±0.17
Domain						
Inner/Middle	631 ±569	70 ±93	1050 ±2248	0.79 ±0.93	0.02 ±0.03	0.14 ±0.16
Outer	3393 ±4008	304 ±279	3901 ±6387	4.49 ±5.01	0.04 ±0.06	0.42 ±0.69
Bloom Conditions						
Non Bloom	1385 ±2223	75 ±110	247 ±275	1.28 ±2.29	0.03 ±0.04	0.37 ±0.57
Bloom	2417 ±3730	317 ±272	5308 ±6295	4.03 ±4.85	0.03 ±0.05	0.08* ±0.16