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

Robert G. Campbell[a,*], Carin J. Ashjian[b], Evelyn B. Sherr[c], Barry F. Sherr[c], Michael W Lomas[d], Celia Ross[c], Philip Alatalo[b], Celia Gelfman[a], Donna Van Keuren[a]

[a] Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA
[b] Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
[c] College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA
[d] Bigelow Laboratory for Ocean Sciences, East Boothbay, ME 04544, USA

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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 μm), 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 4–30% 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 $26 \pm 48\%$ 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.

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; Ciannelli et al., 2004; Dwyer et al., 1987; Moore et al., 2002; Springer et al., 1989; Springer and Roseneau, 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,

* Corresponding author. Tel.: +1 401 874 6692.
E-mail address: campbell@gso.uri.edu (R.G. Campbell).

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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, with consequences during warm years for their fish predators that depend on them (Coyle et al., 2011; Heintz et al., 2013; Hunt et al., 2011; Sigler et al., 2013).

The southeastern Bering Sea shelf is differentiated into three, bathymetrically-fixed hydrographic regions; the Coastal or Inner Domain (shore-∼50 m water depth), the Middle Shelf Domain (50–100 m), and the Outer Shelf Domain (100–200 m) (Coachman, 1986; Iverson et al., 1979; Schumacher and Stabeno, 1998; Stabeno et al., 2001). Each of the three hydrographic domains contains characteristic mesozooplankton species (e.g., Cooney and Coyle, 1982; Coyle and Pinchuk, 2002; Dagg et al., 1982; Smith and Vidal, 1984, 1986; Springer et al., 1989; Smith, 1991; Stockwell et al., 2001; Vidal and Smith, 1986). Although, it is not clear if the domains maintain their integrity in the middle and northern Bering Sea, these same species are present there (e.g., Springer et al., 1989; Eisner et al., 2014). The outer domain is characterized by the oceanic copepod species *Neocalanus plumchrus, N. flemingeri*, *N. cristatus*, *Eucalanus bungii*, and *Metridia pacifica*, and the euphausiid *Thysanoessa inermis*. The middle shelf is dominated by *Calanus glacialis/marshallae* (two co-occurring species that are difficult to tell apart) and the euphausiid *T. raschii*, with the much smaller copepod species *Acartia longiremis* and *Pseudocalanus* spp. abundant, but not important to biomass at least during spring. The small copepod *Oithona similis* is present in both domains and is numerically dominant. The inner domain contains smaller, neritic copepods (e.g., *A. longiremis, Pseudocalanus* spp., *Eurytemora* spp.) and the euphausiid *T. raschii*. The two euphausiid species are relatively small with only the adults large enough, but just barely so, to be classified as macrozooplankton (20–200 mm). 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 (Fig. 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-m^2, 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

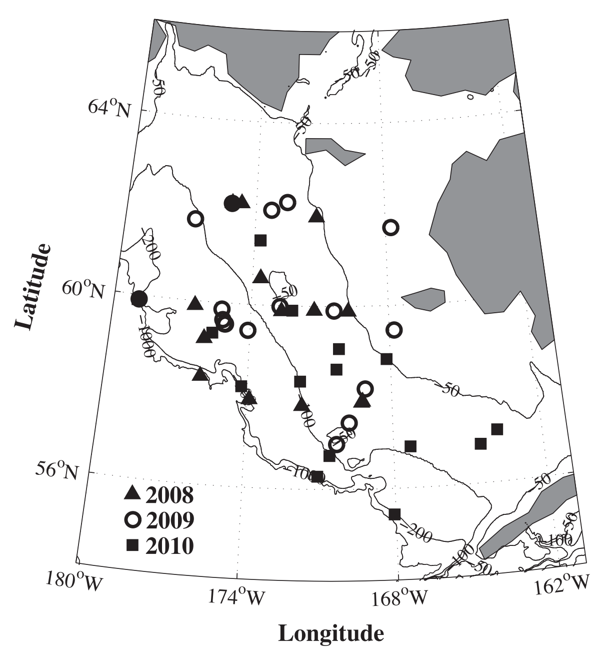

Fig. 1. Station locations of grazing experiments in the eastern Bering Sea during spring.