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Variation in annual production of copepods, euphausiids, and juvenile walleye pollock in the southeastern Bering Sea

Michael F. Sigler [a,*], Jeffrey M. Napp [b], Phyllis J. Stabeno [c], Ronald A. Heintz [a], Michael W. Lomas [d], George L. Hunt Jr. [e]

[a] *Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 17109 Pt. Lena Loop Rd., Juneau, AK 99801, USA*

[b] *Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115, USA*

[c] *Pacific Marine Environmental Laboratory, Oceans and Atmospheric Research, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, WA 98115, USA*

[d] *Bigelow Laboratory for Ocean Sciences, 60 Bigelow Drive, PO Box 380, East Boothbay, ME 04544, USA*

[e] *School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195, USA*

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ABSTRACT

We synthesize recent research on variation in annual production of copepods (*Calanus* spp.), euphausiids (*Thysanoessa* spp.), and juvenile walleye pollock (*Gadus chalcogrammus*) in the southeastern Bering Sea. We reach five conclusions: 1) the timing of the spring bloom is more important than the amount of annual primary production for the transfer of primary to secondary production (i.e., timing matters); 2) summer and fall, not just spring, matter: organisms must maximize energy intake devoted to somatic growth and storage of lipids and minimize energy expenditures during each season; 3) stored lipids are important for the overwinter survival of both zooplankton and age-0 walleye pollock; 4) variation in ice extent and timing of ice retreat affect the spatial distributions of phytoplankton, zooplankton, and age-0 walleye pollock; when these spatial distributions match in late-ice-retreat years, the annual production of copepods, euphausiids, and juvenile walleye pollock often increases (i.e., location matters); 5) if years with late ice retreat, which favor copepod, euphausiid, and juvenile walleye pollock production, occur in succession, top–down control increases. These conclusions help to explain annual variation in production of copepods, euphausiids and juvenile walleye pollock. Copepods and euphausiids often are more abundant in cold years with late ice retreat than in warm years with early ice retreat due to bloom timing and the availability of ice algae during years with late ice retreat. As a consequence, age-0 walleye pollock consume lipid-enriched prey in cold years, better preparing them for their first winter and their overwinter survival is greater. In addition, there is a spatial match of primary production, zooplankton, and age-0 walleye pollock in cold years and a mismatch in warm years.

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1. Introduction

For over 100 years, an intellectual challenge for biological and fisheries oceanographers has been to understand order-of-magnitude variation in annual production of zooplankton and fish (e.g., Cushing, 1982; Hjort, 1914). Annual production depends on: (1) the size of the mature population, (2) environmental variation leading to order-of-magnitude variation in abundance, and (3) the magnitude of top–down control (e.g., Bailey, 2000; Bakun, 1985; Hunt and McKinnell, 2006; Hunt et al., 2002; Hunt et al., 2011). Research in the North Pacific Ocean often has focused on spring (e.g., Dagg et al., 1984; Kendall and Duker, 1998) and the conditions that produce a strong spring phytoplankton bloom, and thus good feeding conditions for zooplankton and juvenile fish. The critical size that juvenile fish must reach to survive their first winter (critical size hypothesis, e.g., Beamish and Mahnken, 2001; Farley et al., 2009; Sogard and Olla, 2000) also has been repeatedly examined. Larger size confers reduced susceptibility to successful capture by gape-limited predators and enlarged energy reserves (Heintz and Vollenweider, 2010; Sogard, 1997). To understand variation in annual production of zooplankton and juvenile fish, a multi-factor hypothesis and integrated research approach is necessary (Hare, 2014).

* Corresponding author.
E-mail address: mike.sigler@noaa.gov (M.F. Sigler).

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In this paper, we synthesize recent integrated research on the annual production of copepods (*Calanus* spp.), euphausiids (*Thysanoessa* spp.), and juvenile walleye pollock (*Gadus chalcogrammus*) in the southeastern Bering Sea in relation to net primary production, and emphasize a bioenergetics perspective. In a strongly seasonal system, the nutritional energy available to zooplankton and juvenile fish strongly varies among seasons and among years. Further, the capacity of zooplankton and juvenile fish to store energy and bridge seasonal gaps in energy production may be limited depending on their life history stage and strategy. These organisms must obtain and maintain sufficient lipid stores each season; a full energy store only in spring is not enough (e.g., Sogard and Olla, 2000; Hurst, 2007). In addition, there may be a relationship between population size and recruitment that magnifies the impact of back-to-back years of poor or good recruitment.

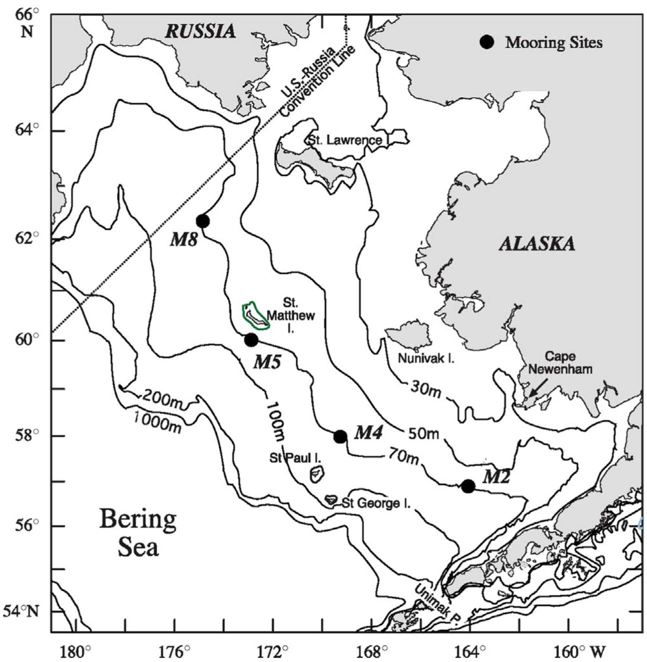

Fig. 1. Study area showing principal oceanographic moorings (in order from south to north, M2, M4, M5, M8). The three cross-shelf domains usually are defined by water depth (inner: 0–50 m; middle: 50–100 m; outer: 100–180 m) (Coachman, 1986) and the northern Bering Sea domain by latitude (60 °N) (Grebmeier et al., 2006; Sigler et al., 2011; Stabeno et al., 2012a).

The Bering Sea Project was a large, integrated ecosystem research program focused on the eastern Bering Sea shelf and the role of seasonal sea ice cover (Fig. 1) (Wiese et al., 2012). Sea ice consistently covers the northern Bering Sea each winter (Stabeno et al., 2012a), while ice extent and retreat timing vary annually in the southeastern Bering Sea (Stabeno et al., 2012b). The interaction of annual ice extent and the broad (500 km), nearly flat shelf makes the eastern Bering Sea spatially rich, with three cross-shelf domains (inner, middle, outer) (Coachman, 1986) and a distinct northern Bering Sea domain (Eisner et al., 2014; Grebmeier et al., 2006; Sigler et al., 2011; Stabeno et al., 2012a). The Bering Sea Project field years (2007–2010) occurred during a period of several cold years in succession when ice retreat was late in the southeastern Bering Sea (2006–2012), and followed a period of several warm years in succession when ice was absent or retreat occurred early (2001–2005) (Stabeno et al., 2012b) (Fig. 2). The abundances of copepods, euphausiids, and age-0 walleye pollock were low during the early-ice-retreat years and increased during the late-ice-retreat years (Fig. 2) (Coyle et al., 2011; Eisner et al., 2014; Hunt et al., 2011; Ohashi et al., 2013).

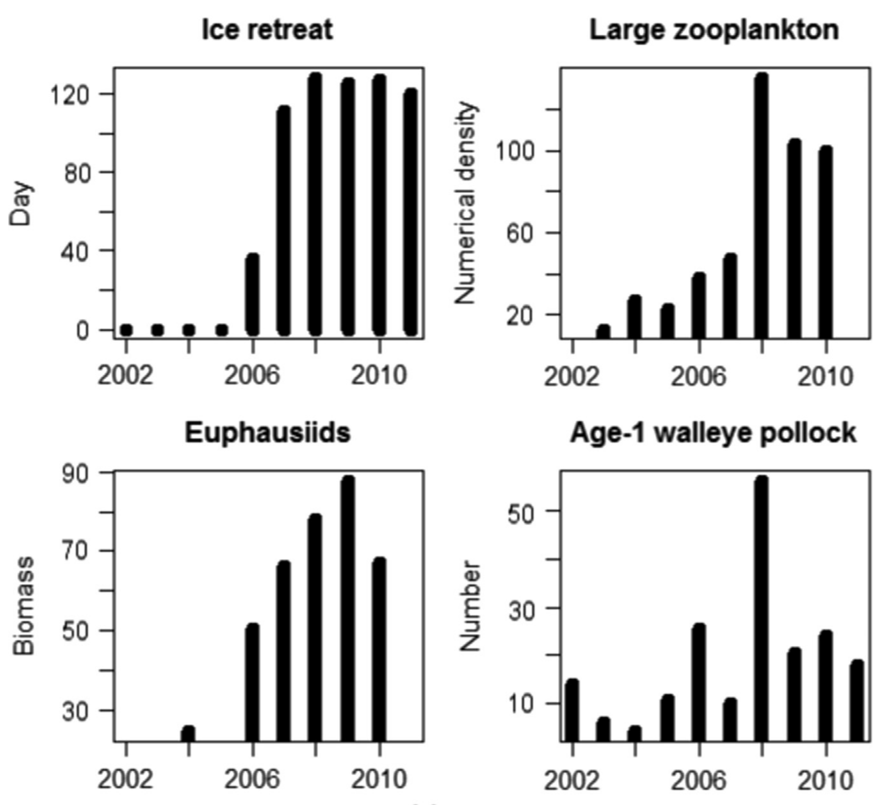

Fig. 2. Ice retreat day for the southernmost oceanographic mooring (M2) (if ice was absent that year, then ice retreat day is zero) (Sigler et al., 2014) and abundances of large crustacean zooplankton (mostly copepods) (number m^{-3}) (Eisner et al., 2014), euphausiids (mmt wet weight) (Ressler et al., 2014), and age-1 walleye pollock (billions of walleye pollock at age-1; in this case, year 0 is birth year) (Ianelli et al., 2014).