CHANGES IN CARBON FLOW TO TOP LEVELS IN THE BERING SEA SHELF ECOSYSTEM: TOP-DOWN EFFECTS OF CETACEANS

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Introduction

During the mid-1970s and early 1980s, when few whales were present in the Southeast Bering Sea, the food web of the middle shelf was primarily a benthic system, in which most of the primary production was largely ungrazed and sank to the seafloor (Walsh and McRoy, 1986). The abundance of pelagic grazers was low and the benthic biomass was high. The abundance and distribution of baleen whales during the late 1990s (Figures 1 and 2) however indicates that the pathway of carbon flow on the middle shelf has been altered. The summer distributions of migratory baleen whales typically reflect the productivity of their environment and indicate the location of predictably high concentrations of their prey. During the summer of 1999, 79% of the prey consumption by fin whales *Balaenoptera physalus* occurred in the central Middle Shelf Domain. This indicates that mid-water secondary production is now capable of supporting high whale biomass, and the middle shelf has shifted from a benthic to a more pelagic domain. The presence of foraging whales on the middle shelf (50-100 m isobaths) in the late 1990s also contrasts with the 1950s-1960s distribution during the whaling era, when the highest whale biomass was concentrated at the shelf edge (Figure 3) Green Belt region (Springer et al., 1996) (Figure 4).

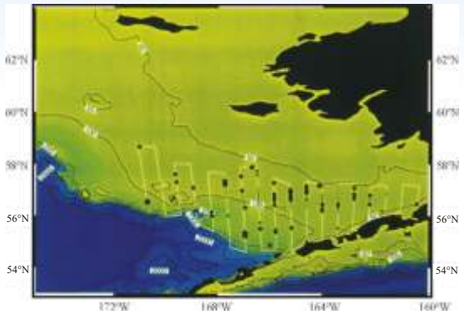

Figure 1. Distribution of 5 species of large whales in the southeast Bering Sea, July 17-August 5,1997, relative to a coccolithophore bloom (aqua lines): fin whale (★), humpback whale (●), right whale (+), minke whale (s), sei whale (■), fin or sei whale (†), and unidentified whale (◆).

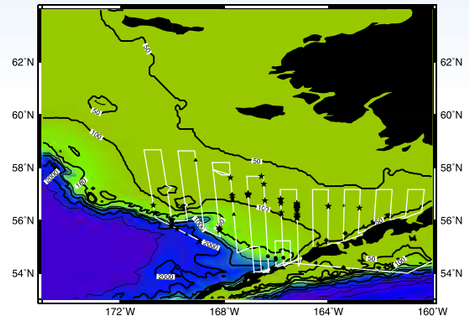

Figure 2. Distribution of large whales in the southeast Bering Sea, June 11-July 3,1999: fin whale (★), humpback whale (●), right whale (+), minke whale (s), and unidentified whale (◆).

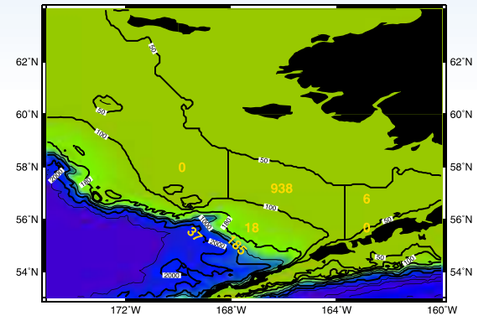

Figure 7. Fin whale abundance in the Southeast Bering Sea, stratified by shelf domain, June 14 - July 3, 1999.

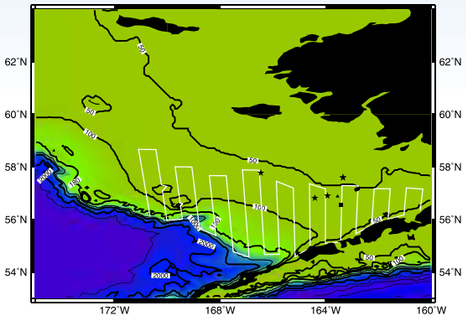

Figure 8. Distribution of opportunistic right whale sightings since 1985 (★) (Goddard and Rugh, 1998) and recent sightings during line-transect surveys on: July 20-21, 1997 (●), on June 14 (■), and July 31, 1999 (s).

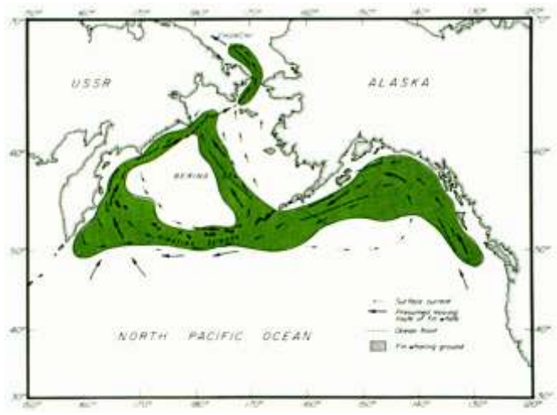

Figure 3. The whaling grounds for fin whales from 1952 to 1970 by Japanese whalers (from Nasu, 1974).

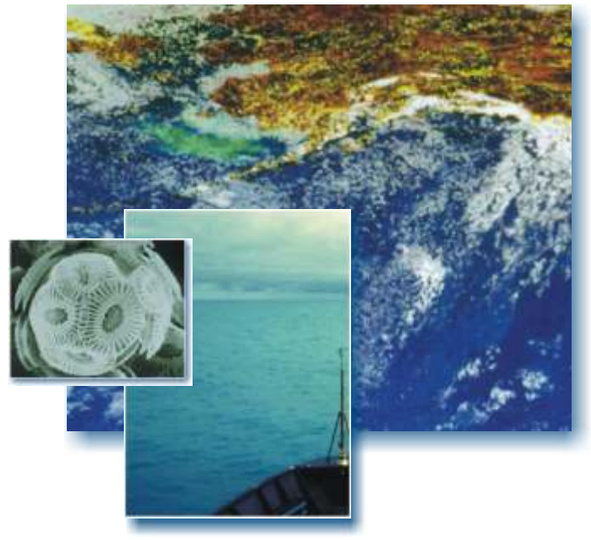

Figure 5. The aqua color of the coccolithophore bloom as seen at sea on July 24, 1997 and two months later from satellite by the Sea-viewing Wide Field-of-View Sensor (SeaWiFS) 8-day composite image for September 18-25, 1997. SeaWiFS imagery was provided courtesy of Gene Feldman, NASA. The species of coccolithophore, *Emiliana huxleyi* (from Ackleson *et al*., 19 88), responsible for the bloom.

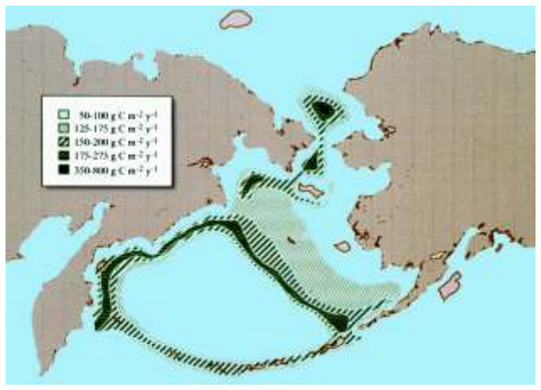

Figure 4. The distribution of primary production along the highly productive Green Belt (from Springer *et al.*, 1996).

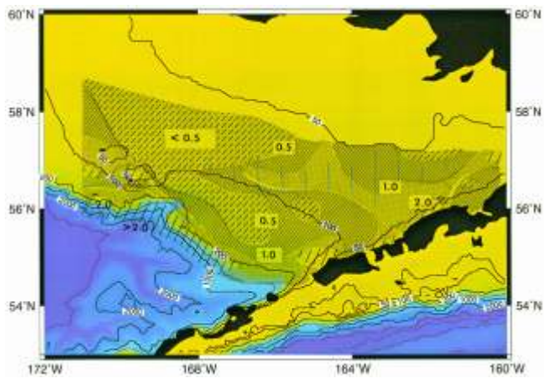

Figure 6. Distribution of chlorophyll *a* (µg/L) in the southeast Bering Sea, July 17-August 5, 1997, relative to an extensive coccolithophore bloom (aqua lines).

Results

During the late 1990s anomalous oceanographic conditions and ecological response occurred over the southeast Bering Sea shelf. During the summer of 1997, an El Niño year, sea surface temperature was up to 3ºC above normal in June.We encountered an extensive coccolithophore bloom of *Emiliana huxleyi* (Figure 5) on the middle shelf domain (Figure 5). The bloom was first observed on July 19 during a northerly transect along 161º 34.6¹ W. The western edge of the bloom was observed on July 29 along 167º 40.35¹ W, suggesting that the coccolithophore bloom was at least 200 km wide by late July. By September, the first SeaWiFS satellite imagery of the feature revealed a 700 km wide bloom over much of the eastern Bering Sea shelf (Figure 5). Since 1997, coccolithophore blooms have become predicatable features of the eastern shelf ecosystem.

During 1997, the highest chlorophyll *a* concentrations on the shelf (1-2 µg/L) occurred in the Middle Shelf Domain, a region that included the coccolithophore bloom (Figure 6). The shelf-edge region of the Green Belt was still the most productive water (2-33 µg/L).

WHALES. During 1997, the highest densities of large whales, including fin *Balaenoptera physalus*, humpback *Megaptera novaeangliae,* sei *B. borealis*, minke *B. acutorostrata*, and right whales *Eubalaena glacialis*, occurred south of the 50 m isobath and in or near the coccolithophore bloom of the middle shelf (Figure 1). During June, 1999, the highest whale biomass again occurred in the middle shelf domain (Figure 2). During both 1997 and 1999 fin whales were the dominant species of large whale in the southeast Bering Sea and were most numerous in the Middle Shelf Domain (Figure 7).

During the late 1990s, a small number of right whales predictably returned to the middle shelf domain during summer (Figure 8) to forage on the Calanoid copepod *Calanus marshallae* (Figure 9). The remnant population of right whales appears to have shifted their preferred foraging ground and prey species since the whaling era. Right whales appear to have moved from deeper waters beyond the shelf-edge, where they foraged historically on the large oceanic species *Calanus cristatus* (Omura et al., 1969), to the Middle Shelf Domain.

ZOOPLANKTON PRODUCTION. Whales rely on critical thresholds of prey density to make their foraging energetically worthwhile. That fin whales and right whales return to the middle shelf to forage, suggests that whales are attracted to a region of predictably high prey density. Concentrations of *C. marshallae*, collected near right whales in 1997 and 1999 (333 µm mesh net), were an order of magnitude higher than during the early 1980s (Figure 9).

CONSUMPTION ESTIMATES. Fin whale consumption of prey by 938 whales (54% CV) (Figure 7) on the central Middle Shelf accounted for 79% of all prey consumed by fin whales in the entire Southeast Bering Sea. Fin whales consumed 315 x 10^6 kg C of prey over 4 months of foraging on the middle shelf. The prey of fin whales may have consisted of euphausiids, copepods, or schooling fish.

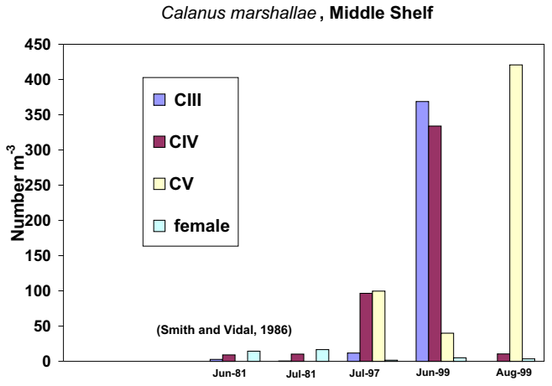

Figure 9. Concentration (number m^{-3}) of copepodite stages and adults of *Calanus marshallae* on the middle shelf of the southeast Bering Sea during June and July 1981 (Smith and Vidal, 1986) compared to those near right whales on July 20, 1997, June 14 and August 1, 1999.

Conclusions

Results of the 1997 and 1999 cetacean surveys contradict the historical pattern, in which the majority of whale biomass was associated with the Green Belt of the shelf edge. During summer, large whales now forage in the Middle Shelf Domain, suggesting that conditions on the middle shelf provide predictably productive foraging for cetaceans and their prey.

The distribution of large whales on the middle shelf indicates a long-term shift in regional secondary productivity and altered structure and function of the Bering Sea ecosystem. The middle shelf appears to have shifted from a benthic to a more pelagic system, where high secondary production is now capable of supporting high whale biomass. This pattern also suggests that less carbon is available to the benthos.

It is important to examine the relative production of pelagic versus benthic production in the Bering Sea and to determine whether similar shifts in shelf ecosystems are occurring in other subpolar seas.

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