

# The Bering Sea—A dynamic food web perspective

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## Abstract

The Bering Sea is a high-latitude, semi-enclosed sea that supports extensive fish, seabird, marine mammal, and invertebrate populations and some of the world's most productive fisheries. The region consists of several distinct biomes that have undergone wide-scale population variation, in part due to fisheries, but also in part due to the effects of interannual and decadal-scale climatic variation. While recent decades of ocean observation have highlighted possible links between climate and species fluctuations, mechanisms linking climate and population fluctuations are only beginning to be understood. Here, we examine the food webs of Bering Sea ecosystems with particular reference to some key shifts in widely distributed, abundant fish populations and their links with climate variation. Both climate variability and fisheries have substantially altered the Bering Sea ecosystem in the past, but their relative importance in shaping the current ecosystem state remains uncertain.

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## 1. Introduction

In this review, we examine some aspects of the variability in the climate and oceanography of the Bering Sea and how this variability affects biological dynamics. We pay specific attention to control mechanisms that vary in response to climate variability and to changes in the structure and flow of energy through key components for the Bering Sea food webs. While we review general oceanographic and biological patterns in the entire Bering Sea, when discussing climate forcing and ecosystem control we focus on changes observed over the last

25 years in the southeastern Bering Sea shelf because of the wealth of information available and our familiarity with the region.

## 2. Ecosystem description

### 2.1. Geography and circulation

Geographically, the Bering Sea consists of a deep central basin surrounded by continental shelves along the coasts of Alaska and Kamchatka. Two shelf ecosystems within this region have been defined as large marine ecosystems (Sherman et al., 1993): the eastern Bering Sea (EBS) and the western Bering Sea (WBS) (Fig. 1). The general circulation in the Bering Sea forms part of the North Pacific sub-Arctic gyre with water entering

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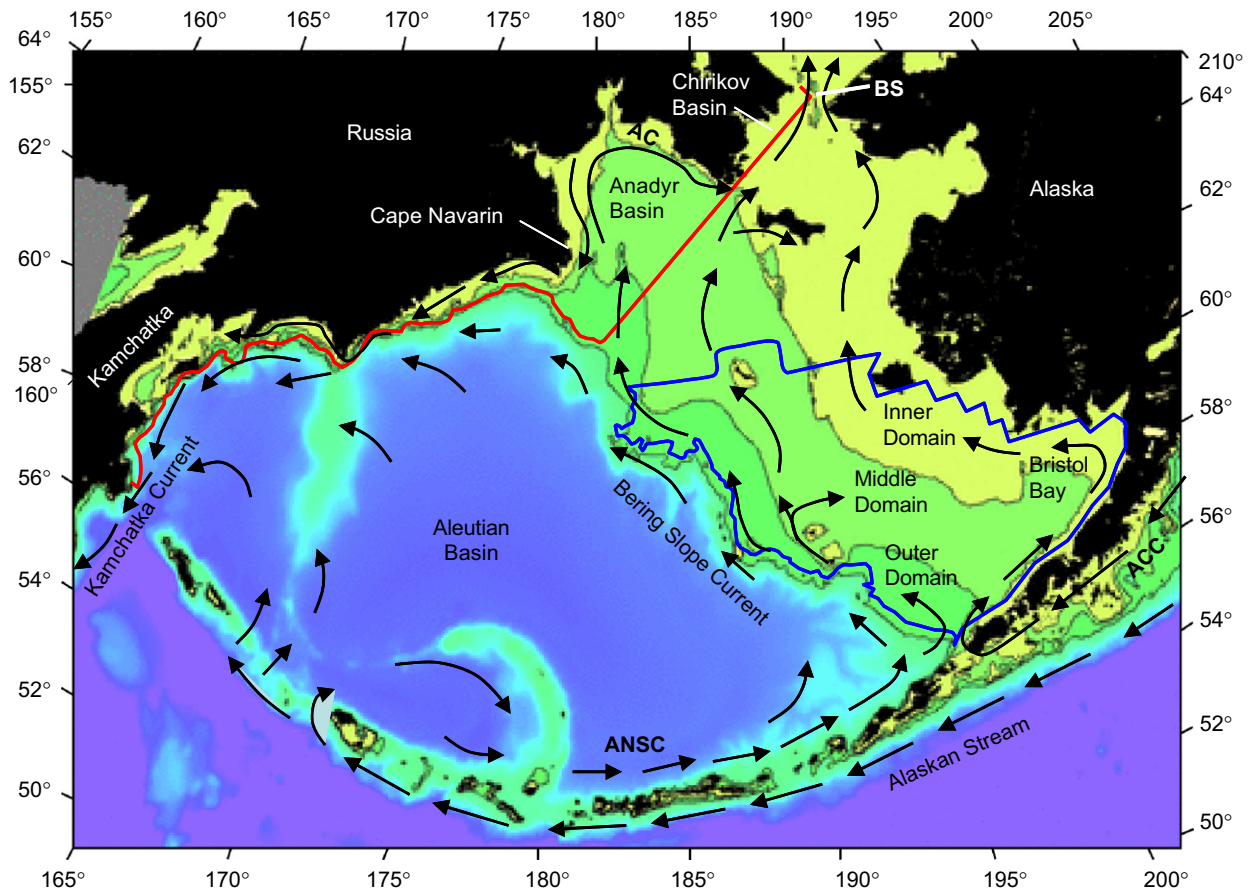


Fig. 1. The Bering Sea, with boundaries of the southeast Bering Sea shelf (EBS, blue line), and the western Bering Sea shelf (WBS, red line). Isobaths shown are 50 m (between inner and middle domains), 100 m (between middle and outer domains) and 200 m (between outer domain and slope/basin). Schematic of major currents based on Stabeno et al. (1999). AC: Anadyr Current, ACC: Alaska Coastal Current, ANSC: Aleutian North Slope Current, BS: Bering Strait.

from the Gulf of Alaska through several Aleutian passes, continuing anti-clockwise around the Bering Sea, and exiting through Kamchatka Strait. In addition there is a net outflow through the Bering Strait into the Arctic Ocean, which results in northward currents over the northern Bering Sea shelf. The cyclonic gyre in the Bering Sea comprises three major currents: the Aleutian North Slope Current flows eastward along the Aleutian Islands, continues northwestward as the Bering Slope Current, and finally turns into the swift, south-westward flowing Kamchatka Current, which exits through Kamchatka Strait (Stabeno et al., 1999).

The WBS includes a narrow shelf that covers less than 10% of the portion of the Bering Sea within the Russian exclusive economic zone (EEZ). South of Cape Navarin, the shelf (0–200 m) varies from less than 5–50 km in width (Fig. 1). North of Cape

Navarin, the shallow (50–100 m) Anadyr Basin and the most northern Chirikov Basin form northward extensions of the EBS shelf, but are included here as part of the WBS ecosystem. Water masses on the narrow shelf to the south can be divided into coastal, transitional and oceanic waters by temperature and salinity fronts. However, these divisions are not stationary and may vary interannually with the strength and east/west position of the Kamchatka Current (Khen, 1999). During the summer, both the coastal and transitional waters are thermally stratified, but the coastal area is characterized by lower salinities in the surface layer. Unlike in the EBS, waters inshore of 50 m are not vertically mixed due to relatively weak tidal currents in the WBS.

The EBS is characterized by a broad continental shelf (> 500 km) that can be divided into southeastern, central, and northeastern regions (Schumacher and

Stabeno, 1998). The eastern shelf is strongly influenced by the Pacific waters entering through Aleutian passes (Schumacher et al., 2003). Most of the shelf is characterized by diffuse flows to the north, which exit through Bering Strait into the Arctic Ocean (Schumacher and Stabeno, 1998). The southeastern region is the most studied and is separated into Inner, Middle, and Outer Domains separated by frontal structures associated with the 50 and 100 m isobaths (Fig. 1; Iverson et al., 1979; Coachman, 1986; Schumacher and Stabeno, 1998; Stabeno et al., 2001). During the summer, the Inner Domain is well mixed, while the Middle Shelf is a stratified system with a tidally mixed bottom layer and wind mixed surface layer. The Outer Domain consists of mixed upper and lower layers separated by a zone of gradually increasing density.

## 2.2. Climatology and ice

Climatically, the Bering Sea straddles a major Arctic/sub-Arctic atmospheric front and is therefore influenced by both Arctic and sub-Arctic weather patterns. Climatic variability in the Bering Sea is closely linked to the strength and position of the Aleutian Low and the Siberian High pressure systems. The gradient between these systems affects the path and intensity of storms across the Bering Sea (Overland, 1981), which have a major influence on the formation and distribution of ice, wind mixing, temperature conditions, and other oceanographic processes. The Aleutian Low and Siberian High, in turn, vary in response to decadal climate variability over the North Pacific and in the Arctic, and also responds to shorter-term variability in the tropical Pacific. This is evident in relationships between the strength and position of the Aleutian Low on the one hand and several indicators of large-scale climate variability on the other. The latter include the Pacific Decadal Oscillation (PDO), which is defined as the leading mode of sea-surface temperature variability in the North Pacific (Wallace et al., 1992), the Arctic Oscillation (AO), which is defined as the leading mode of sea-level pressure north of 20°N and represents the strength of the polar vortex (Thompson and Wallace, 1998), and the Southern Oscillation, which is defined as the difference between the normalized sea-level pressures for Tahiti and Darwin, Australia, and reflects El Niño variability (Niebauer, 1988; Fig. 2).

The North Pacific, including the Bering Sea, has experienced several relatively abrupt shifts in

climate conditions such as those observed around 1976/1977 and around 1988/1989 (Hare and Mantua, 2000). The 1976/1977 shift was characterized by an intensification of the Aleutian Low with a shift to warmer conditions in the EBS, whereas the main characteristic of the 1988/1989 shift was a strengthening of the polar vortex as indicated by a change in the sign of the AO index. These changes were associated with marked changes in numerous biological time series from the Bering Sea and throughout the northeast Pacific (Hare and Mantua, 2000). More recently, patterns in sea-level pressure and sea-surface temperature in the North Pacific have shifted to a new state (Bond et al., 2003) and conditions in the Bering Sea, particularly on the EBS shelf, have been characterized by persistent warm temperatures and a lack of sea ice (Overland and Stabeno, 2004; Grebmeier et al., 2006), although 2006 saw at least a temporary return to cooler conditions (Rodionov et al., 2006).

Winter ice coverage is one of the most important features of the Bering Sea and is both consequence and a source of extreme seasonal and interannual variability. The northern and northeastern portion of the continental shelf is generally covered by sea ice in the winter, whereas cover in the western and southeastern Bering Sea is highly variable (Walsh and Johnson, 1979). The seasonal advance and retreat of sea ice averages about 1700 km, larger than in any of the other sub-Arctic seas. In addition, both the spatial extent of ice cover and the timing of ice retreat vary considerably from year to year (Walsh and Johnson, 1979). At maximum ice extent, 20–56% of the Bering Sea is ice covered (Niebauer et al., 1999). Winter ice conditions, in turn, strongly influence temperature conditions during the following summer on both the eastern and western shelves (Khen, 1999; Overland et al., 1999), and may affect marine biota. In particular, ice formation over the EBS shelf results in the formation of a subsurface cold pool of water (<2 °C) that extends into the southeastern Middle Domain and persists into summer. The extent and persistence of the cold pool varies on interannual and decadal time scales, and affects the spatial distribution of fish stocks during summer (Wyllie-Echeverria and Wooster, 1998).

## 2.3. Nutrient supply

The eastern and WBS shelves are characterized by high biological productivity, which is fueled by nutrient-rich waters supplied to the Bering Sea basin

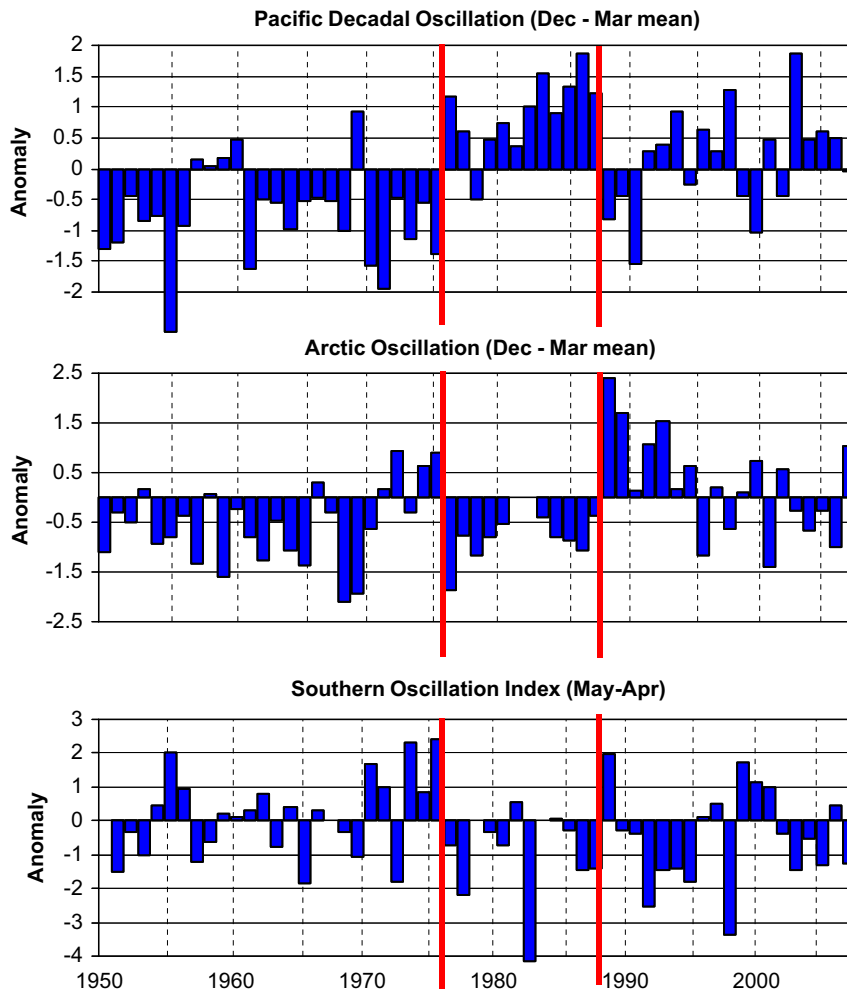


Fig. 2. Major climate drivers affecting the Bering Sea as indexed by the Pacific Decadal Oscillation, Arctic Oscillation, and Southern Oscillation index. Recognized regime shifts in 1976/1977 and 1988/1989 are highlighted.

via the global ocean “conveyor belt” (Broecker, 1991). Concentrations of nitrate, phosphate, and silicate in the deep waters of the Bering Sea basin are among the highest observed in the world’s oceans, and these nutrient-rich waters are the source for replenishing nutrients on the shelf (Whitledge and Luchin, 1999). Shelf-slope exchanges and cross-shelf fluxes are essential to supporting the high production observed on the shelf, but are poorly understood at present. In the well-mixed coastal areas and in the surface mixed layers on the shelf, nutrients are rapidly depleted during the spring phytoplankton bloom. Additional regenerated production is supported by the ammonium-dependent microbial loop, and additional new production may occur periodically or throughout the summer when nutrients are mixed into the surface layer through

wind and/or tidal mixing. A substantial portion of these nutrients may derive from regeneration in bottom sediments (Sambrotto et al., 1986). Nutrients on the shelf are ultimately replenished when nutrient-rich waters from the basin are advected or mixed onto the shelf. High primary productivity on the northern shelf is supported by the direct advection of nutrient-rich waters onto the shelf via the Anadyr Current and northward flows along the outer shelf.

#### 2.4. Primary production

Much of the high primary production in the Bering Sea is believed to be concentrated along the EBS and WBS shelf breaks and extends northward through the Bering Strait (“Green Belt”; Springer

et al., 1996). Total phytoplankton production for the southeastern Bering Sea has been estimated to range from highs of at least  $175\text{--}275\text{ g C m}^{-2}\text{ yr}^{-1}$  along the shelf break to lows of less than  $75\text{ g C m}^{-2}\text{ yr}^{-1}$  in the inner shelf region and in the oceanic domain (Springer et al., 1996). However, these estimates were based on new (nitrate) production and assumed  $f$ -ratios of 0.3–0.4; and more recent estimates based on carbon fixation suggest higher production in the inner domain, as well as a more uniform distribution across the shelf and slope regions (T. Whitledge, pers. comm.). Total primary production on the northern Bering Sea shelf is estimated to be substantially higher ( $350\text{--}750\text{ g C m}^{-2}\text{ yr}^{-1}$ ; Springer et al., 1996) than on the southeastern shelf, in part because the production season extends throughout the summer. Unlike the southeastern shelf, which depends on limited cross-shelf exchanges, high production on the northern shelf is supported by the direct and continuous advection of nutrient-rich waters onto the shelf via the Anadyr Current, as well as northward flows of nutrient-rich slope waters along the outer shelf and slope. Annual production on the northern shelf also exceeds that on the WBS ( $276\text{--}336\text{ g C m}^{-2}\text{ yr}^{-1}$ ; Sapozhnikov et al., 1995), but Shuntov and Dulepova (1995) concluded that the annual primary production in the WBS approaches  $420\text{ g C m}^{-2}\text{ yr}^{-1}$  when the contributions of macrophytes and periphyton are included. Because most of the WBS shelf region lies within the high production Green Belt, these values conform to the Springer et al. (1996) shelf-edge estimates.

Phytoplankton communities throughout the Bering Sea are a mix of large diatoms and microplankton, and differ between the shelf regions and the oceanic domain. On the continental shelves (inshore of the 200 m isobath), an ice-associated community, dominated by pennate diatoms of the genus *Fragilaria* and *Nitzschia*, can be distinguished from a shelf community dominated by centric diatoms such as *Thalassiosira* and *Chaetoceros* (Sukhanova et al., 1999). The oceanic community is dominated numerically by picophytoplankton ( $<3\text{ }\mu\text{m}$ ) and small flagellates, but a variety of oceanic and neritic species account for most of the biomass. Neritic species are transported into deep-water areas by mesoscale eddies that form along the slope on both sides of the Bering Sea (Sukhanova et al., 1999). Along the outer shelf and near the shelf break, the phytoplankton community is often dominated by the flagellate *Phaeocystis pouchetii*. On the EBS shelf, unusual blooms dominated by the

microphytoplankton coccolithophorid *Emiliania huxleyi* were observed between 1997 and 2001 (Napp and Hunt, 2001; Stockwell et al., 2001). The unusual blooms may have resulted from unusually light winds and anomalously warm, stratified water, which led to nutrient-poor conditions favoring this species (Stockwell et al., 2001).

The timing of ice retreat from the shelf plays an important role in the timing, amount, and fate of primary production over the shelf (Hunt and Stabeno, 2002). In general, an earlier ice melt results in lower phytoplankton biomass during the bloom (Saitoh et al., 2002). Melting ice stratifies the water column to form a shallow, low-salinity surface layer. An early, ice-associated phytoplankton bloom can occur in this layer, but only when the ice retreats after sufficient sunlight becomes available. If the ice retreats before the availability of sufficient sunlight, stratification from ice melt is eroded by frequent spring storms and a bloom on the middle shelf cannot develop until thermal stratification stabilizes the water column in late spring or early summer. The relative contribution of ice-associated blooms to annual primary production is therefore highly variable and may be substantial in years with extensive ice; moreover, as described below, bloom timing is hypothesized to affect the availability of ice-edge production to upper trophic levels.

Relative production of the EBS and WBS shelves may be linked through atmospheric forcing. Based on satellite chlorophyll measurements, Saitoh et al. (2002) describe a “seesaw” pattern of productivity between the eastern and WBS that appeared to be related to the position of the Aleutian Low. While this pattern is likely to affect productivity at all trophic levels, time series of productivity at higher trophic levels are not available to compare temporal patterns of variability between the eastern and WBS. Aydin et al. (2002) noted that, during the 1980s, the WBS shelf (shallower than 200 m) was more productive per unit area on trophic levels 1 and 2 than the EBS shelf, with nearly double the level of primary, secondary, and benthic production and higher standing stocks of epifaunal and infaunal invertebrate communities. This production difference was ascribed to a greater portion of the WBS’s narrower shelf lying both nearshore and near the highly productive shelf break, rather than to climatic forcing.

The advection of highly productive slope waters onto the northern Bering Sea shelf supports persistent “hot spots” of high benthic productivity



and a much larger benthic biomass on the northern shelf compared to the southeastern shelf (Alton, 1974; Grebmeier and Dunton, 2000; Cooper et al., 2002). These hot spots support populations of benthic-feeding seabirds and marine mammals (e.g., spectacled eider, *Somateria fischeri*, gray whales, *Eschrichtius robustus* and Pacific walrus, *Odobenus rosmarus divergens*). However, benthic productivity on the northern shelf has decreased over the last two decades (Moore et al., 2003; Grebmeier et al., 2006), a decrease that coincided with a reduction in northward flow through Bering Strait (Roach et al., 1995). Because of recent warming trends, the northern shelf region may be undergoing a transition from Arctic to more sub-Arctic conditions, associated with a reduction in benthic prey populations and an increase in fish populations (Overland and Stabenho, 2004; Grebmeier et al., 2006).

### 2.5. Secondary production

The most dominant taxa of meso- and macro-zooplankton on the both the EBS and WBS shelves are copepods (both *Calanus* and *Pseudocalanus* spp., with larger, oceanic *Neocalanus* spp. near the shelf break and dominant in the west), euphausiids (primarily *Thysanoessa raschii* and *T. inermis*), and chaetognaths such as *Sagitta elegans* (Cooney and Coyle, 1982; Vidal and Smith, 1986; Efimkin and Radchenko, 1991; Dulepova, 1993; Coyle et al., 1996). Amphipods and mysids are a smaller, but still significant component of zooplankton biomass on the shelves (Cooney, 1981; Efimkin and Radchenko, 1991). The oceanographic domain structure of the eastern shelf (Fig. 1) supports three distinct zooplankton communities (Cooney and Coyle, 1982); the inner shelf consists mainly of small *Pseudocalanus* spp. and *Acartia* spp. which are year-round residents; the middle shelf is dominated by the copepods *Calanus marshallae* and *Pseudocalanus* spp. and the euphausiid *T. raschii*; while the outer shelf is similar to the slope and basin and seasonally dominated by larger, oceanic copepod species (*Neocalanus* spp., *Eucalanus bungii*, *Metridia pacifica*) and the euphausiid *T. inermis* (Smith and Vidal, 1986; Napp et al., 2002). In addition to cross-shelf gradients in abundance, some species, such as *C. marshallae*, may be tied to fluctuations in climate and the presence of cold water and sea ice in the EBS (Baier and Napp, 2003).

Copepods are a major prey for zooplanktivores, particularly larval and juvenile walleye pollock (*Theragra chalcogramma*; Napp et al., 2000; Cianelli et al., 2004a), and variation in their bloom timing may be critical to determining juvenile pollock survival, as described below. They are also an important dietary component for planktivorous seabirds such as the least auklet (*Aethia pusilla*) and crested auklet (*Aethia cristatella*), and right whales (*Eubalaena japonica*) that forage on dense aggregations of *C. marshallae* on the middle shelf (Tynan et al., 2001). Euphausiids are a major prey for many upper trophic level species, including juvenile and adult pollock, other forage and predatory fish, birds such as the short-tailed shearwater (*Puffinus tenuirostris*; Hunt et al., 2002b), and are less variable between successive summers than are copepods (Coyle and Pinchuk, 2002b). Moreover, euphausiids are relatively abundant in some fish diets throughout the summer, fall, and winter in the Bering Sea, and thus provide a more sustained source of energy for forage species than do copepods (Mito et al., 1999). Chaetognaths are abundant in both the east and west throughout the summer and fall, vary in relation to climate, and are a major predator on smaller copepods (Baier and Terazaki, 2005).

Previous conceptual models of the Bering Sea food web (e.g., Walsh and McRoy, 1986; Hood, 1999; Trites et al., 1999) show the transfer of energy from primary to secondary production dominated by flow between spring blooms of the large diatoms and crustacean zooplankton listed above. However, more recent research has emphasized the importance of microzooplankton, with a considerable density of dinoflagellates and ciliates providing a conduit between primary production and upper trophic levels (Olson and Strom, 2002). The unusual *E. huxleyi* blooms in the southeastern Bering Sea during the late 1990s emphasize the importance of interannual variation between microplankton and macrozooplankton energy pathways, and this variation may play a role in structuring upper trophic level communities (e.g., in affecting the availability of euphausiids to foraging seabirds; Hunt et al., 2002b).

### 2.6. Intermediate and upper trophic-level species

Fig. 3 illustrates the most detailed look at overall food web for the EBS to date, with biomass, production, and flow between 148 separate functional groups as calculated with data from the time

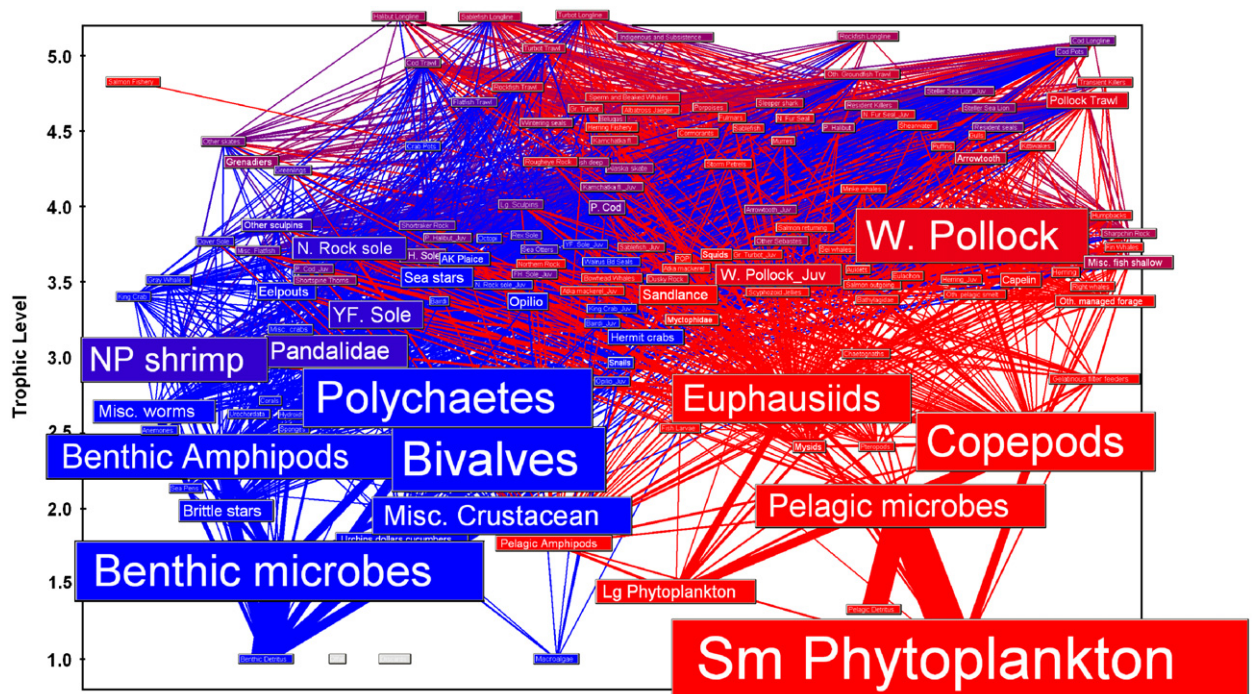


Fig. 3. The eastern Bering Sea (EBS) food web, with 148 distinct compartments, calculated using 1991–1994 data (Aydin et al., in press). Box size is proportional to biomass density ( $\text{t km}^{-2}$ ) and line width is proportional to flow volume ( $\text{t km}^{-2} \text{yr}^{-1}$ ). Coloring indicates pelagic (red) and benthic (blue) energy pathways, with mixed coloration in a box indicating the proportion of energy inflow from each pathway.

period 1991–1994 (Aydin et al., in press). The food webs of the eastern and WBS have been substantially analyzed in recent years, especially in reference to the effects of climate and fishing on species interactions (e.g., Trites et al., 1999; Aydin et al., 2002; Aydin et al., in press) and it is clear that the trophic structure differs not only between subregions of the Bering Sea, but over time within each subregion (e.g., Trites et al., 1999).

Here, we start by comparing production and consumption from trophic models for the food webs of the EBS and WBS shelf ecosystems constructed using data from the mid-1980s (after Aydin et al., 2002). We then examine food web changes in the EBS between the 1960s and the present and examine in detail some controlling mechanisms for walleye pollock and other groundfish, with reference to marine mammals, benthic communities, and the range of species which make up the ecosystems of the Bering Sea. For the purpose of comparison between the ecosystems, we define “intermediate” species as forage species that are generally prey for piscivores, lying between trophic levels 2.5 and 3.9 but excluding marine mammals. “Upper” trophic level species are trophic level 4+, but including the

intermediate trophic level marine mammals, such as baleen whales.

While the lower (planktonic) trophic levels of the WBS were more productive than those of the EBS, the intermediate and upper trophic levels were more similar in production between east and west, although production was spread across different species. In particular, the EBS has been dominated by walleye pollock since the early 1980s, while the WBS has been dominated by cephalopods and small forage fish (Fig. 4). Figs. 3 and 4 illustrate the central role of walleye pollock as an important mid-level (intermediate) predator (trophic level 3.7) and as prey for numerous upper trophic level consumers, including the trawl fishery. Pollock are cannibalistic in the Bering Sea (Dwyer et al., 1987; Livingston, 1993) and become demersal as they age, so juvenile pollock (age 0–1), an important forage group, are shown separately from adult pollock (age 2+), emphasizing their differing ecosystem role.

In addition to pollock, the EBS also has a much higher production (and biomass) of small flatfish and commercial crabs than the WBS, the EBS being characterized by a diverse community of intermediate benthic species; while the benthos of the WBS is

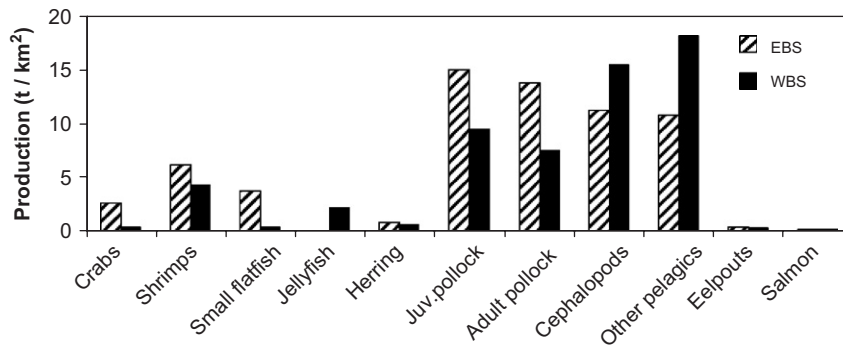


Fig. 4. Production ( $\text{t km}^{-2} \text{yr}^{-1}$ ) as calculated for the intermediate trophic level species (trophic levels 2.5–3.9 excluding marine mammals) for the eastern and western Bering Sea (EBS and WBS) regions. Values are based on trophic models constructed with data for the period 1980–1985 (Aydin et al., 2002).

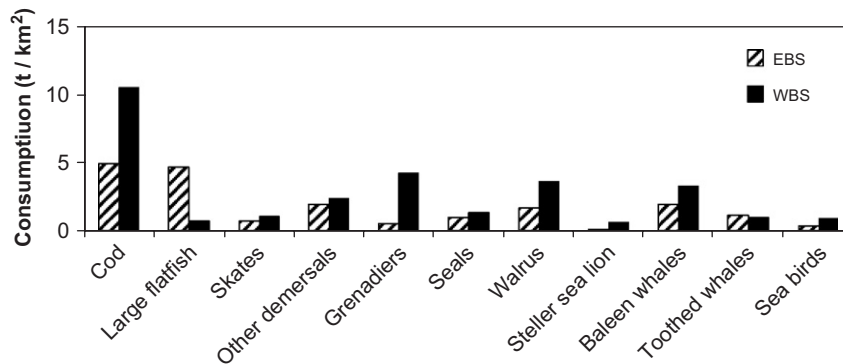


Fig. 5. Consumption by predators ( $\text{t km}^{-2} \text{yr}^{-1}$ ) of upper trophic level species (trophic level 4+, and all marine mammal species regardless of trophic level) as calculated for the eastern and western Bering Sea (EBS and WBS) regions. Values are based on trophic models constructed with data for the period 1980–1985 (Aydin et al., 2002).

dominated by lower trophic level epifauna (e.g., sea urchins and hermit crabs, not shown; Aydin et al., 2002). The diversity of the extensive intermediate benthic community in the EBS is also evident in the full food web shown in Fig. 3. Both the eastern and WBS, as well as the central basin, provide an important rearing area for many North American and Asian Pacific salmon (*Oncorhynchus* spp.) stocks, although due to their migratory nature this is not reflected as raw “production” within the ecosystem boundaries. Shrimp are an important forage species in both ecosystems, as evidenced primarily from groundfish diets (Aydin et al., 2002).

The impact of predation by jellyfish on the EBS ecosystem has been the cause for concern recently (Brodeur et al., 2002); therefore we examined estimated consumption rates for jellyfish in more detail. In the EBS, production of jellyfish was well below that of other predators in the ecosystem

(Fig. 4). Even the large increase in jellyfish biomass in the late 1990s (Brodeur et al., 1999) does not place jellyfish among the highest consumers overall, although at times and locations their concentration may increase to levels that may have an important local predatory impact.

Estimated consumption rates ( $\text{t km}^{-2} \text{yr}^{-1}$ ) of upper trophic level species in both the EBS and WBS during the 1980s (Fig. 5) shows that groundfish, particularly Pacific cod (*Gadus macrocephalus*), were the dominant consumers in both systems. In the EBS, large flatfish, primarily arrowtooth flounder (*Atheresthes stomias*), Greenland turbot (*Reinhardtius hippoglossoides*), and Pacific halibut (*Hippoglossus stenolepis*), made up a substantial portion of the predator population. Other demersal species include sculpins (Cottidae), rockfish (Sebastidae), and sablefish (*Anoplopoma fimbria*). The WBS has a higher density of deep species such as



grenadiers (Macrouridae) in its area, due to its relatively narrow shelf. In addition, marine mammals, particularly baleen whales and pinnipeds, were important predators in both ecosystems.

### 3. Forcing functions and responses

#### 3.1. Human exploitation and climate effects

Bering Sea biota have been subject to substantial variation from both anthropogenic and natural sources, with non-subsistence anthropogenic impacts being documented for at least 200 years. Substantial northern fur seal (*Callorhinus ursinus*) and sea otter (*Enhydra lutris*) harvests have been recorded from the early 1700s (ACIA, 2004), bowhead populations were greatly reduced in the 1800s, and industrial whaling, which began in the 1940s, nearly drove whale populations to extinction by the 1960s (NRC, 1996). Pacific salmon have long been an important subsistence food on both sides of the Bering Sea, and became the subject of large commercial fisheries in the early 1900s. Fisheries for Pacific cod developed as early as the 1880s (NRC, 1996), and walleye pollock, which was listed as an important baitfish in the late 19th century, was being fished commercially by the 1930s. Large commercial fisheries for yellowfin sole (*Limanda aspera*) and other flatfishes on the shelf and for Pacific ocean perch (*Sebastes alutus*) and other rockfishes along the slope began in the late 1950s and peaked in the 1960s (NRC, 1996). As the abundance of Pacific Ocean perch decreased after the mid-1960s, presumably as a result of overfishing, walleye pollock and Pacific cod became the main target species (NRC, 1996). Catches of all harvested species, including gadids, flatfishes, rockfishes, crab, salmon, and Pacific herring (*Clupea pallasii*), have been closely monitored and quantified throughout the modern era, which began with the arrival of large industrial fleets in the 1950s.

Given this history of exploitation, understanding the combined effects of fishing and climate and separating natural from human-caused effects is a challenge. Climate clearly plays a role in fish population variability in the Bering Sea. For example, salmon populations have undergone large natural fluctuations due to variability in marine survival and have been at high levels of abundance throughout much of the North Pacific since the 1976/1977 regime shift (Francis and Hare, 1994). Similarly, large recruitment events for walleye

pollock in the late 1970s greatly increased the biomass of this species in the southeast Bering Sea. While these recruitment events are considered to be climate driven, it is not clear if the conditions which allowed for such events included the reduction of predation and/or competition through fisheries (e.g., Trites et al., 1999). For example, declines in Steller sea lion (*Eumetopias jubatus*) populations have been attributed variously to climate-induced variations in prey availability, competition with fisheries, direct human-induced mortality, and serial predation by killer whales following the reduction of baleen whales (NRC, 2003; Springer et al., 2003; DeMaster et al., 2006).

Against this uncertainty, a few common themes on the interaction between climate and marine populations have been generalized and mechanisms have been proposed that hold some explanatory power. Particularly, modern ocean observing and the extension and analysis of climatic time series have led to a new understanding of the importance of decadal and longer-scale climate patterns in influencing marine populations (Francis et al., 1998).

While broad climate indices, such as the AO or PDO (Fig. 2), point to large-scale decadal patterns as important drivers of climate variability, using these indices to predict changes in biological productivity presents at least two major difficulties. First, shifts in the dominant modes of climate variability imply that relationships between large-scale climate trends and local processes may change over time. For example, Bond et al. (2003) noted that the PDO has shown no clear “regime” style pattern since the late 1980s, while the second mode of variation, the “Victoria Pattern”, has recently dominated decadal-scale variability, with a shift in 1999. Thus, the biological responses to the PDO, such as increased pelagic and demersal productivity after the 1976/1977 shift (from negative to positive PDO values), failed to show a consistent response after the 1988/1989 reversal in the PDO (Mueter et al., in press). Second, biological variability responds in complex, nonlinear ways to changes in climate. For example, Hare and Mantua (2000) analyzed over 100 time series of physical and biological variation, and found that evidence for regime shifts in 1977 and 1989 appeared more clearly in biological than in physical time series, indicating that decadal changes in biological productivity may arise from more subtle mechanisms of climate influencing bottom-up or top-down control

within ecosystems, as complex (but generally linear) regime shifts in climatology may amplify into nonlinear and sudden “phase shifts” or threshold responses in biota (Hunt et al., 2002a; Duffy-Anderson et al., 2005).

### 3.2. Food web shifts in the late 1970s

Food webs are highly dynamic and the species composition of upper trophic levels in the Bering Sea has undergone substantial changes in the last several decades. Whereas food webs from the early 1980s provide a comparison of the relative importance of different taxa between the EBS and WBS for a single time period, consumption estimates based on food web models constructed by Trites et al. (1999) allow a comparison of the total consumption by intermediate and upper-level consumers in the EBS between the 1960s and 1980s (Fig. 6). These data are highly uncertain for the 1960s and based in part on the extrapolation of current ration estimates to historical biomass levels (Trites et al., 1999).

While pollock and demersal fish were important in both the 1960s and the 1980s, the overwhelming dominance of pollock as a consumer within the food web is a feature of the post-1970s time period. In the 1960s, pollock were responsible for 16% of the total prey consumption but this increased to 66% of the consumption in the 1980s. In contrast, the relative consumption by crabs declined from 27% to 4% between the 1960s and 1980s and consumption by Pacific herring and baleen whales each declined from 7% to 2%. While individual stocks of flatfish fluctuated greatly between the 1960s and 1980s, as described below, their total role as predators in the food web did not change greatly. The total consumption by all taxa in Fig. 6, which includes only taxa for which some method of abundance estimation exists in both time periods, appears to have increased approximately 30% between the 1960s and 1980s as assessed groundfish biomass increased, although this does not take into account differences in estimated rations that may arise through density dependence in consumption or changes in population age structure.

It is not known whether other taxa such as squid, shrimp, and small forage fish (e.g., capelin, *Mallotus villosus*) underwent a corresponding decrease as groundfish increased. Substantial decreases in shrimp and capelin were observed in the Gulf of Alaska, where they coincided with an increase in

gadids (including walleye pollock) and flatfish after the 1976/1977 regime shift (Piatt and Anderson, 1996). Recent groundfish diet estimates from the Gulf of Alaska, however, indicate that shrimp and capelin continue to play a substantial dietary role (Aydin et al., in press), so the observed decreases in the nearshore survey biomass of these species may represent a shift in the ecosystem from bottom-up to top-down control (e.g., Bailey, 2000; Ciannelli et al., 2004b): as a greater amount of their production is consumed by groundfish, the observed drop in survey biomass may arise from a redirection of energy into predators and not a drop in these species' overall gross production. The Gulf of Alaska case is of particular interest, as an interplay of factors (described below) may give rise to similar interactions and shifts in the Bering Sea.

### 3.3. Climate forcing and ecosystem control

Although in some cases species declines or shifts may be directly attributed to human activities (e.g., removal of baleen whales), “natural” variability plays a key role in biological processes in the region. In particular, fluctuations in salmon and groundfish populations of the Bering Sea are strongly associated with climatic and biological “regimes” of relatively stable production separated by episodes of rapid change (Hollowed and Wooster, 1995; Francis et al., 1998; Mueter et al., in press). While it is possible that these shifts are mediated or facilitated by human activities, uncovering the mechanisms linking climate to production is an important component of ecosystem studies.

For some species, there is evidence for a clear and direct link between climate shifts and production. For example, Wilderbuer et al. (2002) hypothesized that the larvae of winter-spawning flatfish in the EBS, specifically northern rock sole (*Lepidopsetta polyxystra*), flathead sole (*Hippoglossoides elassodon*), and arrowtooth flounder (*Atheresthes stomias*) are dependent on onshore advection from spawning areas near the southeast shelf break towards settling areas in Bristol Bay. The dominant direction of advection is associated with the Aleutian Low as indexed by the AO, which changed from predominantly negative to predominantly positive values after 1988 (Fig. 2). During the 1980s, advection was onto the shelf and favorable, leading to high recruitment, while during the 1990s, advection was along the shelf break and unfavorable. High recruitment of these species in the 1980s led to an

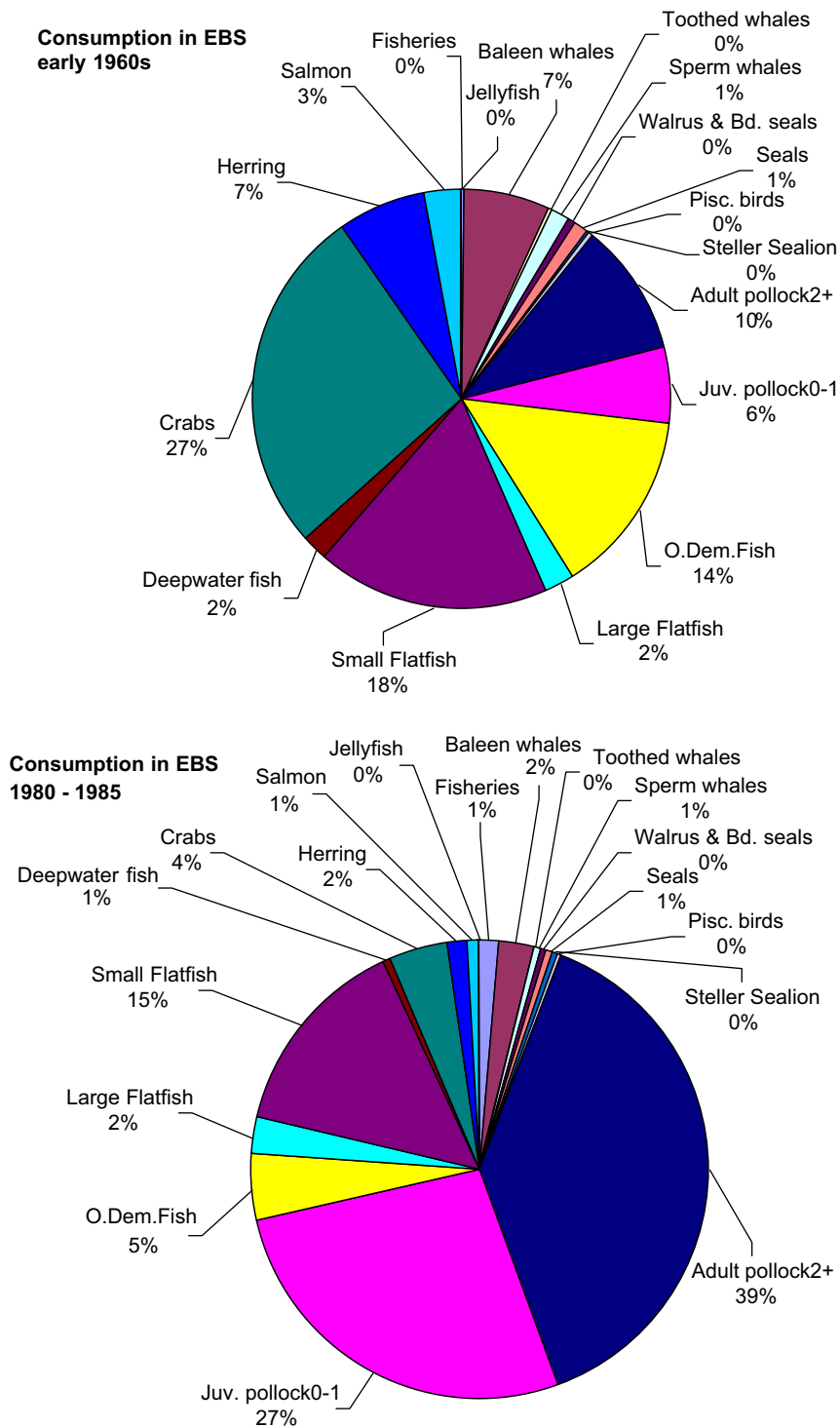


Fig. 6. Percent of intermediate and upper trophic level consumption attributed to each functional group within the eastern Bering Sea (EBS) shelf ecosystem in the 1960s (top figure) and in the 1980s (bottom figure) as reported by [Trites et al. \(1999\)](#). The total area of each circle is proportional to the total consumption pictured. Data from the 1960s is back-calculated from current conditions as described in [Trites et al. \(1999\)](#) and is highly uncertain.

increase in the adult populations, which have remained high to the present day. The available recruitment series do not extend far enough back in time to adequately resolve potential changes associated with the climate regime shift in 1976/1977.

Walleye pollock has a central role in the Bering Sea food web, with a wide range of species feeding on this key forage species (Fig. 7). A number of mechanisms have been suggested for the control of walleye pollock in the EBS, but the available data do not clearly distinguish among the alternative hypotheses (Hunt and Drinkwater, 2005; Mueter et al., 2006). Hunt et al. (2002a) suggested the Oscillating Control Hypothesis (OCH), which states

that the walleye pollock population in the EBS shifts from bottom-up controls during cold regimes (e.g., pre-1976/1977) to top-down controls during warm regimes (post-1976/1977). Stock assessment results (Ianelli et al., 2005) show the dramatic increase in walleye pollock biomass following the 1976/1977 regime shift to warmer conditions (Fig. 8), which led to their dominance in the food web as evident in Figs. 3, 4 and 6. Over the last 40 years, fairly regularly spaced periods of high recruitment appear as “waves” in the percentage of the biomass attributable to different length classes of pollock with a high percentage of small, newly recruited pollock during periods of increasing

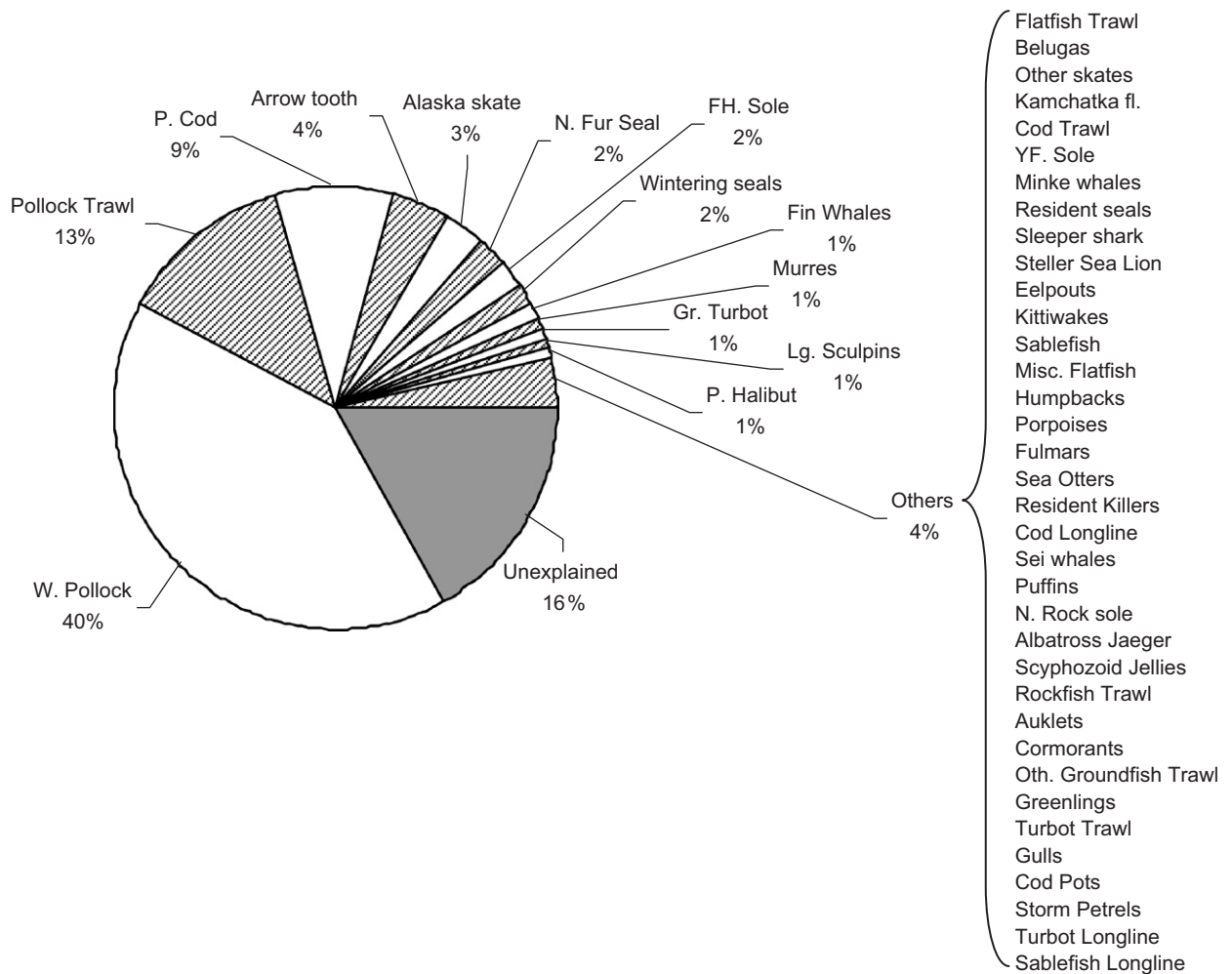


Fig. 7. Eastern Bering Sea Walleye pollock mortality sources (tons consumed/tons produced) as a percentage of total walleye pollock production averaged for the years 1991–1994. Individual (by species) mortality estimates are from Aydin et al. (in press) and have significant uncertainty associated with them. Total production is from Ianelli et al. (2005). “Unexplained” mortality is the difference between production and the sum of individual mortality components. No species in the “other” category causes more than 0.5% of the total mortality.



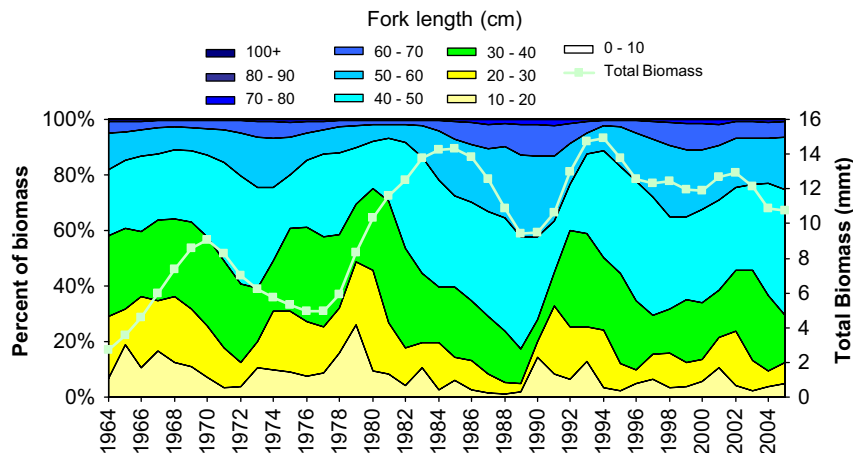


Fig. 8. Assessed biomass of walleye pollock (white line, from Ianelli et al., 2005) and percentage by weight in each 10 cm size class (based on fork length) in the population.

biomass and a high proportion of large pollock during periods of high or decreasing biomass (Fig. 8).

According to the OCH, warm climate conditions can trigger an increase in the abundance of pollock in the southeast Bering Sea by changing the timing of ice retreat and redirecting the flow of primary production (Hunt and Stabeno, 2002). When ice retreats late, as during a cold regime, an ice-edge bloom occurs in a cold-water column stratified by melting ice. Because copepod growth under these conditions is limited by cold temperatures (Coyle and Pinchuk, 2002a) much of the annual production may sink to the bottom, possibly benefiting benthic production and groundfish that consume benthic prey. During a warm regime, ice melt occurs prior to the availability of sufficient sunlight and an ice-edge bloom does not develop (Hunt and Stabeno, 2002). Instead, the first bloom is delayed until thermal stratification stabilizes the water column and can efficiently be grazed by copepods. The OCH proposes that these warm conditions favor walleye pollock growth and recruitment and lead to an increase in adult biomass.

EBS pollock, however, are cannibalistic and an increase in adult biomass exerts strong top-down controls on pollock recruitment. While both small and large pollock are primarily planktivorous, most of the natural mortality of juvenile pollock is due to cannibalism (Fig. 7). Therefore, in the “top-down” phase of the OCH, even favorable climate conditions do not lead to good recruitment because of the high rate of cannibalism. The top-down phase is hypothesized to end after a reversal to cold

conditions leads to poor recruitment (bottom-up control) and a gradual decrease in adult biomass.

Mueter et al. (2006) found some empirical evidence that support elements of the OCH, but additional cold/warm cycles are needed to confirm its predictions. As implied by the OCH, during periods with low adult biomass, the recruitment of walleye pollock is reduced in years with severe ice conditions and a late ice retreat. Moreover, when survival rates of juvenile pollock are low, the survival of yellowfin sole, which feed on benthic prey, is typically high (and vice versa). These observations are at least consistent with having different pathways of energy flow, favoring either the benthic or the pelagic system, in response to differences in bloom timing.

While the OCH speaks to the link between the spring bloom of copepods, juvenile pollock survival, and benthic production, it does not fully address some of the broader changes that have been observed in the southeastern Bering Sea forage community over the past 40 years. Production estimates (Fig. 4) suggest that other forage species such as capelin (a large component of “other forage” in Fig. 4) and shrimp are at times an important alternate pathway for energy in the EBS. Concurrent changes in pollock and small forage fishes have been described in the Gulf of Alaska, where a pronounced increase in groundfish (including pollock) in the early 1980s indicated a complete “community shift” from a shrimp and capelin-dominated system to a pollock-dominated system (Piatt and Anderson, 1996). Existing survey data, though limited, suggests that a similar shift to a

system dominated by pollock, cod, and flatfishes may have occurred in the EBS in the early 1980s (Conners et al., 2002).

It is not understood, however, how tightly linked the individual species in these “community shifts” are to each other. Does climate affect each species independently, resulting in independent “warm regime” and “cold regime” forage communities (as suggested in Hunt et al., 2002a) or does climate directly affect a single keystone species (e.g., pollock, as described in the OCH) with effects then propagating throughout the ecosystem? To clarify the potential effects of large fluctuations in walleye pollock biomass on other components of the EBS

system, we examined variability in forage fish abundance during one recent oscillation in pollock abundance. In particular, the increase in pollock biomass to its high values in 1983–1985 was followed by 3 years (1986–1988) of the highest recorded percentage of large adults in the pollock population and the lowest estimated levels of recruitment, which led to a sharp drop in pollock abundance from 1986 to 1991 (line in Fig. 8).

While data for non-pollock forage species are limited and extremely noisy, catch-per-unit effort (CPUE) in Alaska Fisheries Science Center bottom trawl surveys since 1982 does show some distinct patterns (Fig. 9). In particular, pandalid shrimp,

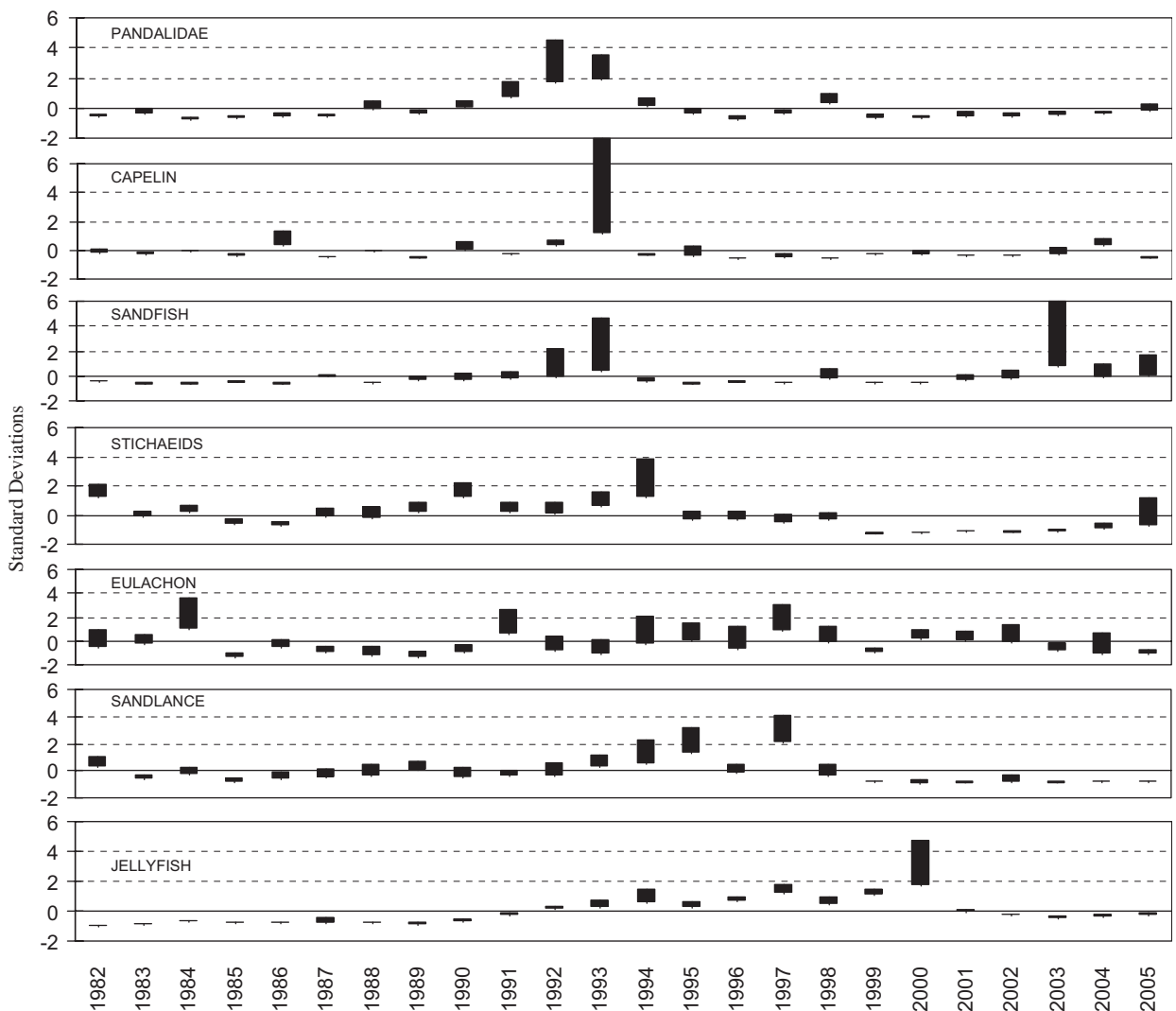


Fig. 9. Normalized trawl survey catch-per-unit-effort CPUE anomalies for selected forage fish in the eastern Bering Sea summer trawl surveys, 1982–2005 (Alaska Fisheries Science Center, March 2007, RACE Groundfish Survey Data: [www.afsc.noaa.gov](http://www.afsc.noaa.gov)). Due to the high variation in these surveys for forage fish, only the standard error range (bars) is shown.

capelin, Pacific sandfish (*Trichodon trichodon*), and stichaeids (pricklebacks) show anomalously high catch rates between 1991 and 1993, while sand lance and jellyfish biomass increased in the early to mid-1990s before declining abruptly in 1998 and 2001, respectively. Yang et al. (2005) showed anomalously high consumption of capelin by several groundfish predators during this time period, suggesting that this increase of their presence was not just an anomaly of the survey.

While the catch rates of these small species in surveys are extremely low, as the gear is not designed to target them, to assess the relative magnitude and role of these fluctuations, it is possible to make at least a back-of-the-envelope calculation of their importance in the ecosystem based on estimates of minimal consumption measured from the diets of large predators (Aydin et al., 2006; see Appendix A for scaling methods). This calculation “scales up” the CPUE of each forage species to an order of magnitude consistent with its predation level within the system (Fig. 10). Survey catchability was assumed constant throughout the time period so this scaling did not affect the interannual pattern in the observed trends. Using this scaling, it is clear that the rise of forage species during this time period represented a considerable, if temporary, shift in the biomass of the system, with a magnitude of fluctuation (bars in Fig. 10) greater than the preceding decline in pollock (line in Fig. 10).

A comparison of the observed trends in pollock biomass density and changes in forage fish abun-

dance (Fig. 10) suggests that the decreased pollock recruitment between 1986 and 1988 may have led to both a predatory and competitive release for other forage species as well as for juvenile pollock. Shrimp and capelin, for example, are both important competitors and prey of pollock: they feed on a similar range of zooplankton, and the main source of pandalid shrimp mortality is in fact pollock (Aydin et al., in press). Oscillations in pollock abundance, driven by climate and cannibalism, may therefore affect shrimp and other forage species.

To investigate this possibility further, we performed perturbation (sensitivity) analyses of the food web model shown in Fig. 3 following the methods described in Aydin et al. (2005); species were decreased individually in the model by lowering their survival and a “credible range” of resulting ecosystem states was simulated by performing this experiment over 100,000+ ecosystems drawn at random from the range of the food web data.

The results of this perturbation analysis are shown in Fig. 11. When copepods are decreased within the food web (Fig. 11A), juvenile and adult pollock both decrease; other forage species decrease but their decrease is much less and much more uncertain (error bars in Fig. 11A). On the other hand, when a euphausiid decrease is simulated, the resulting decrease in pollock is relatively small, but other forage species, including pandalids, capelin, sand lance, and other forage, all decrease significantly (Fig. 11B). Finally, when a decrease in

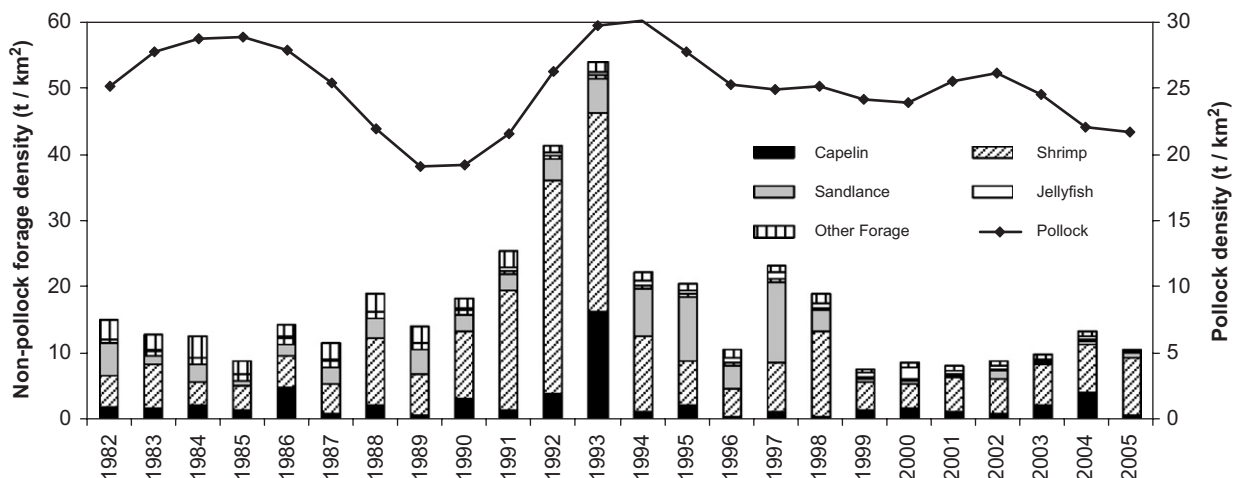


Fig. 10. Pollock biomass density (all ages,  $\text{t km}^{-2}$ ) from Ianelli et al. (2005) (line) and consumption-corrected biomass densities ( $\text{t km}^{-2}$ ) of other forage species from AFSC trawl survey data (bars). See Appendix A and Aydin et al. (in press) for consumption correction methods for biomass density.

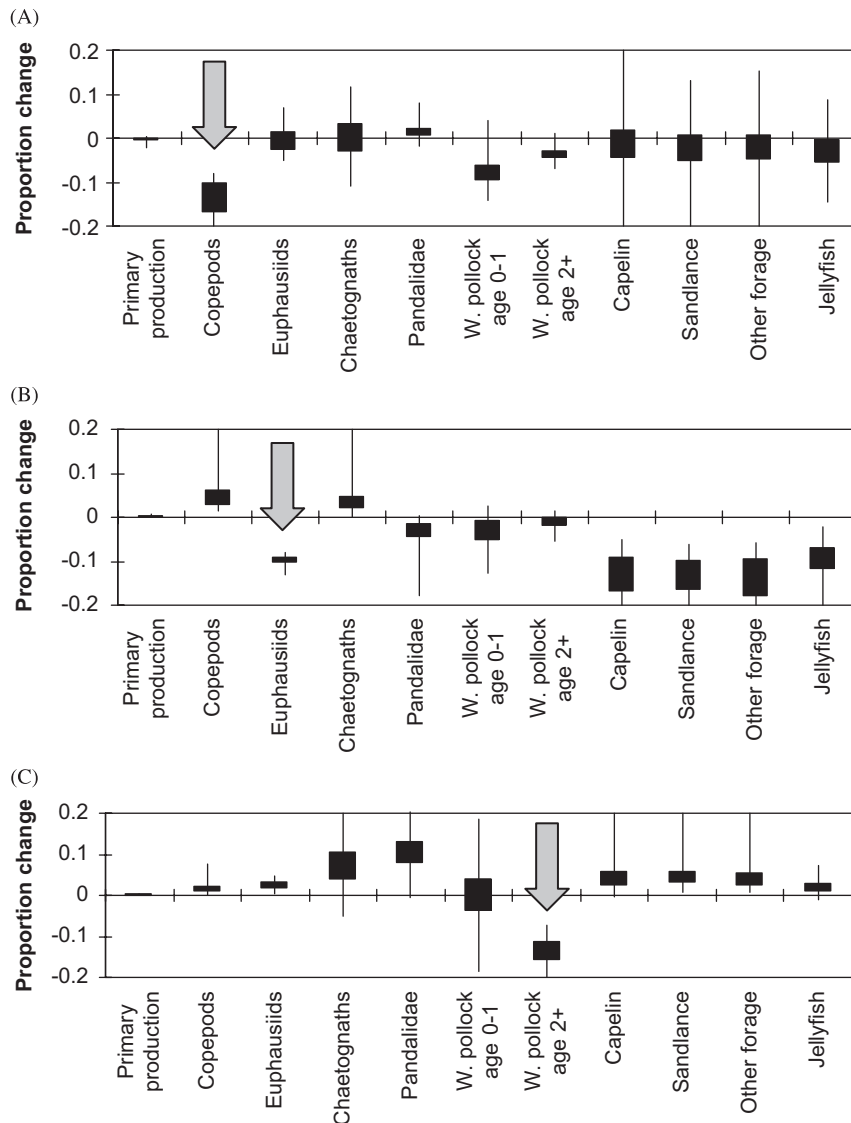


Fig. 11. Results of a sensitivity analysis of the eastern Bering Sea food web model described in Aydin et al. (in press) following the methods of Aydin et al. (2005). Perturbations modeled as indicated by arrows are the reduction of (A) copepod production by 10%; (B) euphausiid production by 10%; and (C) juvenile pollock recruitment by 10%. Each graph shows the corresponding modeled ecosystem response of selected species (shown as proportion change in biomass). Bars and lines show the range containing, respectively, 50% and 95% of the results out of 5000 simulated parameter sets.

pollock is simulated, an increase in forage species and plankton results (Fig. 11C). Note that juvenile pollock are strongly linked but uncertain (wide error bars), representing the uncertainty in the balance between increased spawning stock and accompanying cannibalism (density dependent mortality).

The analyses in Fig. 11 show the net of both direct and indirect effects in the food web. Pollock are both a major predator on pandalids and a major

consumer of euphausiids and copepods; therefore the predicted increase in pandalids after a decrease in pollock (Fig. 11C) is a result of both lowered predation and increased prey supply. For other forage fish such as capelin in Fig. 11C, pollock do not cause a substantial portion of the mortality, so the primary mechanism is competitive release. While diet data for non-pollock forage are limited, the diet of capelin in the Bering Sea appears to be dominated by euphausiids (Aydin, unpublished



data), similar to the better-studied capelin collected in Shelikof Strait in the Gulf of Alaska (Wilson et al., 2006). It may be that juvenile pollock (age-1 and age-2) are superior competitors, possibly better able to gain recruitment benefits from copepod blooms in warm years and thereafter dominate feeding on euphausiids outside the spring season, such that capelin distributions are limited or shifted to less productive waters when juvenile pollock are present. This competitive effect may be confounded with or augmented by direct temperature preferences of the individual species.

The existence of this apparent tight coupling seen in the respective time series gives rise to three considerations. First, it provides evidence that both top-down and bottom-up forces are continually important in the EBS, and we hypothesize that the release of top-down pressure on euphausiids from pollock has in the past led to increases in other forage species, and that this interaction is apparent in the early 1990s. For some species, other predators may play a role (e.g., cod consumption of capelin; Ciannelli and Bailey, 2005). However, the increased capelin CPUE in the trawl surveys corresponds with the increased presence of capelin in the diet of predators (Yang et al., 2005), suggesting that a prey release of zooplankton increased the forage fish, resulting in their increased consumption by piscivorous predators.

An alternative explanation is that oceanographic conditions alternately favor copepods versus euphausiids and thus alternatively favor pollock versus other forage; however, the lag-response in Fig. 10, while not conclusive, is more consistent with the top-down explanation, and Coyle and Pinchuk (2002b) did not find significant interannual differences in euphausiid biomass within the inner domain, although more recent data suggest that significant interannual has occurred in these euphausiid populations (G. Hunt, pers. comm.).

Overall, the importance of competitive release in the above sensitivity analyses suggests that competition for zooplankton among forage fish is in fact a limiting factor in ecosystem production in the EBS, as evidenced during the period of competitive release in the early 1990s. Finally, it is worth asking if this release in top-down control was a regular part of the climate-driven OCH controlling pollock production, or whether the time near 1992–1994 was a “potential” regime switch—in other words, a period in which the scramble for resources as described in Rice (2001) could have been won by species other than pollock.

### 3.4. Multiple shifts and recent history

One danger of any mechanistic explanation of the relationships among species within large marine ecosystems is that just when a mechanism is uncovered, climate changes or other changes affecting the ecosystem may modify the rules again in unexpected ways. In the EBS, predation on larger (“adult”) pollock has changed in recent years due to changes in the community composition of major pollock predators. Each of the main predator species of walleye pollock in Fig. 7 shows a foraging preference for a different size range of pollock. Length frequencies of pollock in the stomachs of groundfish predators (Fig. 12) show that small flatfish and pollock primarily target small (age 0–1) pollock, while larger predators such as Pacific halibut (*Hippoglossus stenolepis*), Pacific cod, Greenland turbot (*Reinhardtius hippoglossoides*), and Alaska skate (*Bathyraja parmifera*) primarily target larger pollock. Arrowtooth flounder are unique in targeting primarily mid-sized (age 2) pollock.

Recent changes in relative abundance of the major predators on pollock may have led to a considerable shift in the impact of non-cannibalistic predation in terms of the age classes most affected. For example, Pacific cod decreased from a high biomass in the 1980s, while arrowtooth flounder biomass has increased (lines in Fig. 13B,C). Overall, the total non-pollock groundfish predator biomass has gone down in the Bering Sea according to current stock assessments, with the drop of Pacific cod in the 1980s exceeding the rise of arrowtooth flounder in terms of biomass. The increasing population of arrowtooth flounder in the Bering Sea implies a shift in the age of pollock consumed, with arrowtooth flounder taking primarily age-2 pollock, while Pacific cod primarily consume larger pollock, according to length frequencies in summer diet data (Fig. 12). Moreover, the populations of arrowtooth flounder and other large groundfish predators have matured and are currently dominated by large individuals capable of consuming large adult pollock (dark blue shading in Fig. 13B), a shift that is also evident in predator diets. Prior to 1992, it was rare to see pollock greater than 30 cm in arrowtooth flounder stomachs, whereas since 1992 predation on pollock between 30 and 50 cm has not been uncommon (Fig. 14). A large increase of arrowtooth flounder also has been observed in the Gulf of Alaska, where these flatfish currently

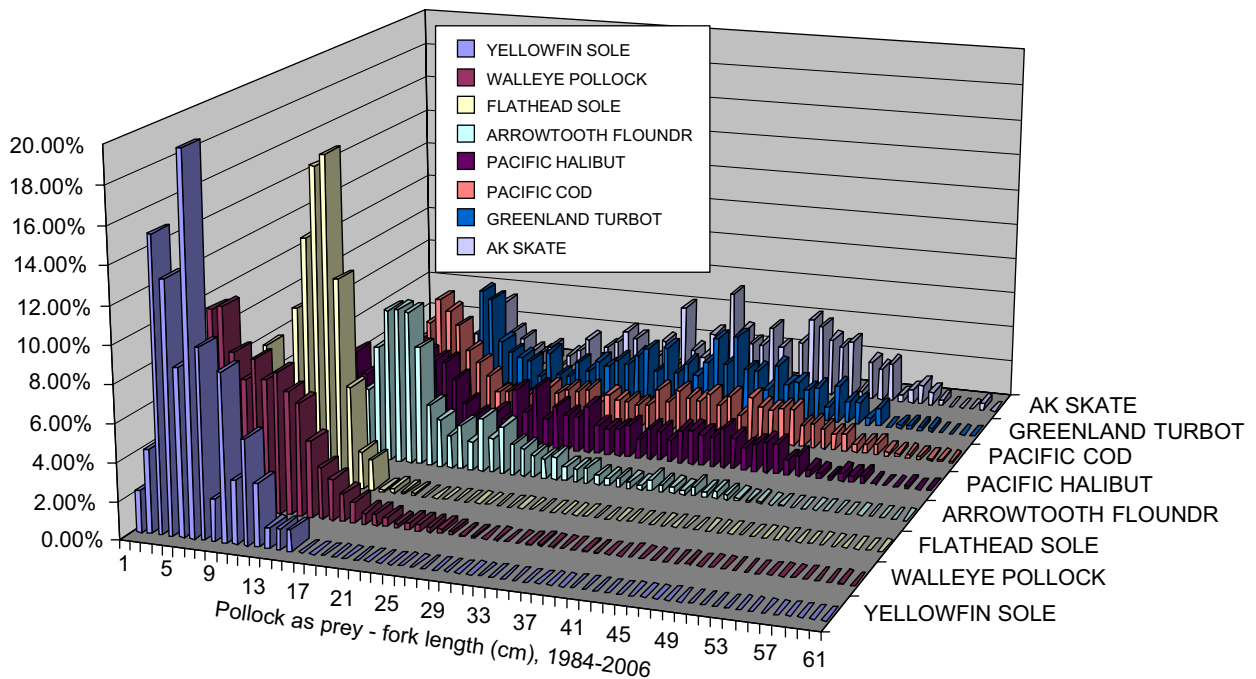


Fig. 12. Length frequency of pollock found in stomachs, from groundfish food habits collected from 1984 to 2006 on AFSC summer trawl surveys in the eastern Bering Sea. Predators are sorted by median prey length of pollock in their stomachs. All lengths of predators are combined.

dominate groundfish biomass and cause severe predation mortality on walleye pollock.

Thus, while the OCH in itself explains a climate-driven cycle between bottom-up and top-down control of a pollock population, the top-down component may have been further moderated in recent years with the longer period (possibly AO-moderated) flatfish cycle described above. It remains to be seen if increased predation on adult pollock modifies the OCH cycle. In any case, it may be worth extending the hypothesis to a Multiple Life-History Control Hypothesis (MLCH). Under MLCH, intermediate cycles (pollock control of its own recruitment via OCH) interact with cycles in longer-lived species such as arrowtooth flounder (recruitment variation associated with the AO), so that primary control of pollock populations shifts from cannibalism to other predators. A similar shift in recruitment control has been hypothesized for pollock and arrowtooth flounder in the Gulf of Alaska (Bailey, 2000; Ciannelli et al., 2004b), although it is not clear if the Gulf of Alaska shift represents a cycle or a unidirectional trend. If MLCH holds in the EBS, the rise of large predators, in response to both longer term climate variation and available prey, occurs on a longer time scale

than we have observed between the late 1970s and the present day.

The final outcome of such an “extended” (MLCH) cycle is uncertain, as are its possible interactions with fisheries. For example, in the Bering Sea (unlike the Gulf of Alaska), large pollock actually prey on small arrowtooth flounder (Ianelli et al., 2006). The predation by large pollock on small arrowtooth flounder suggests that pollock may “cultivate” (i.e., protect) its offspring by preying on a species that would eat and compete with its young. Under this “cultivation/depensation” hypothesis (Walters and Kitchell, 2001), the removal of large pollock through fishing could lead to an accelerated decline of pollock, as the control exerted on predators of its own recruits is removed—this has been cited as a cause for a decline of cod in the Baltic Sea in the presence of herring feeding on young cod (Walters and Kitchell, 2001). In situations like this, it is possible that predator culling (e.g., removing arrowtooth) may not have a strong effect towards controlling predation compared to applying additional caution to pollock harvest and thus preserving this natural control. At the moment, this concern for Bering Sea pollock is qualitative and the complex interaction

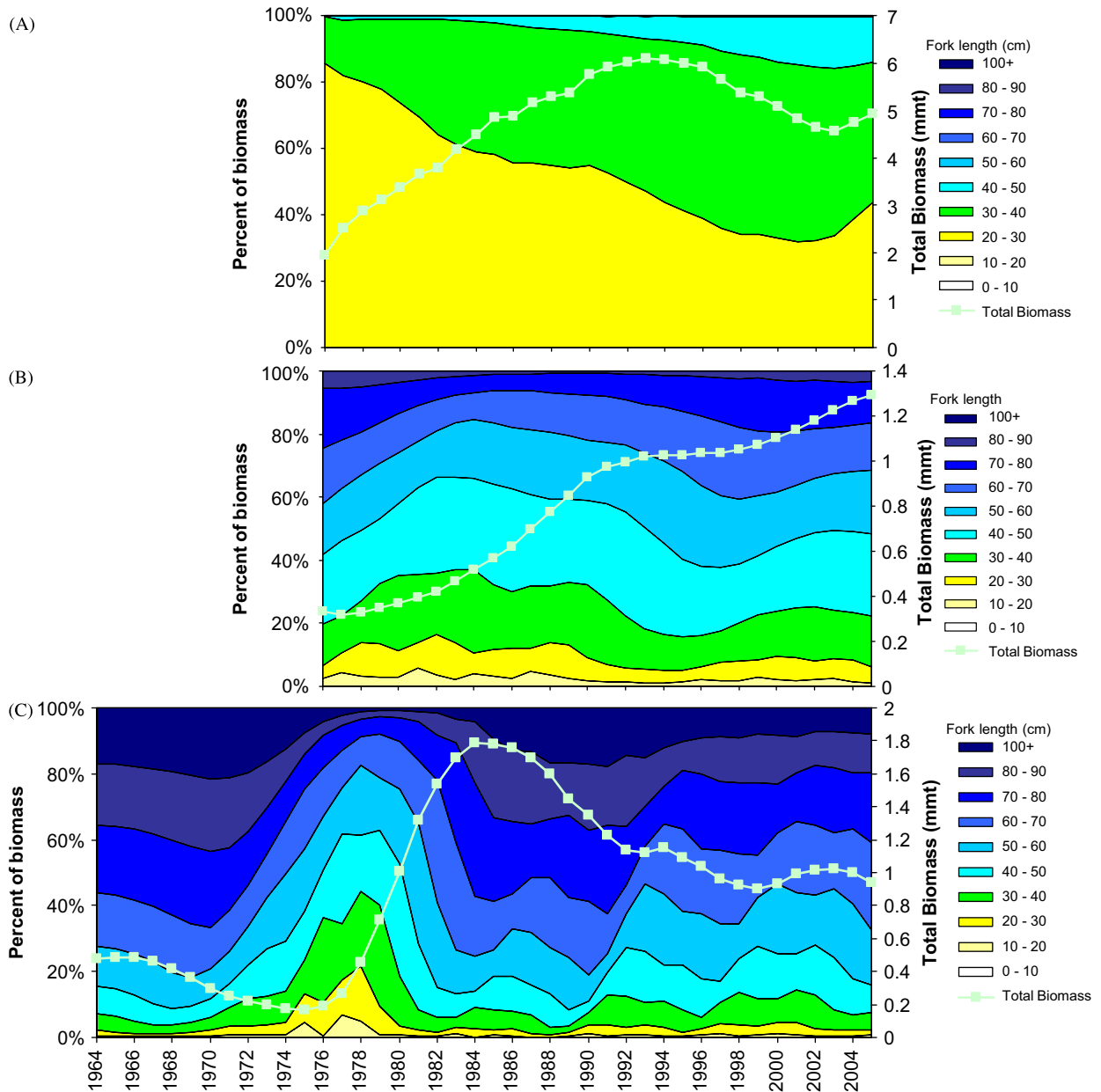


Fig. 13. Assessed EBS biomass (white lines) of (A) combined rock sole (Wilderbuer and Nichol, 2005a), yellowfin sole (Wilderbuer and Nichol, 2005b), and flathead sole (Stockhausen et al., 2005) populations; (B) arrowtooth flounder (Wilderbuer and Nichol, 2005c); and (C) Pacific cod (Thompson et al., 2005) and percentage by weight in each 10 cm size class (based on fork length) in each population.

between pollock and arrowtooth are the subject of active investigations (e.g., Jurado-Molina et al., 2005).

Finally, it is important to note that an overall warming trend has been observed in the Bering Sea since 2000, particularly with regard to the dramatic loss of sea ice on the EBS shelf in recent years (Overland and Stabenro, 2004). This trend, if it

continues, may have profound effects on ecosystem structure and function. It may affect local production and species composition through changes in productivity, redirection of energy flows, and spatial shifts in distribution. There is increasing evidence that such changes are already occurring. Northward shifts of snow crab have been related to retreating cold water while at the same time, the increase in

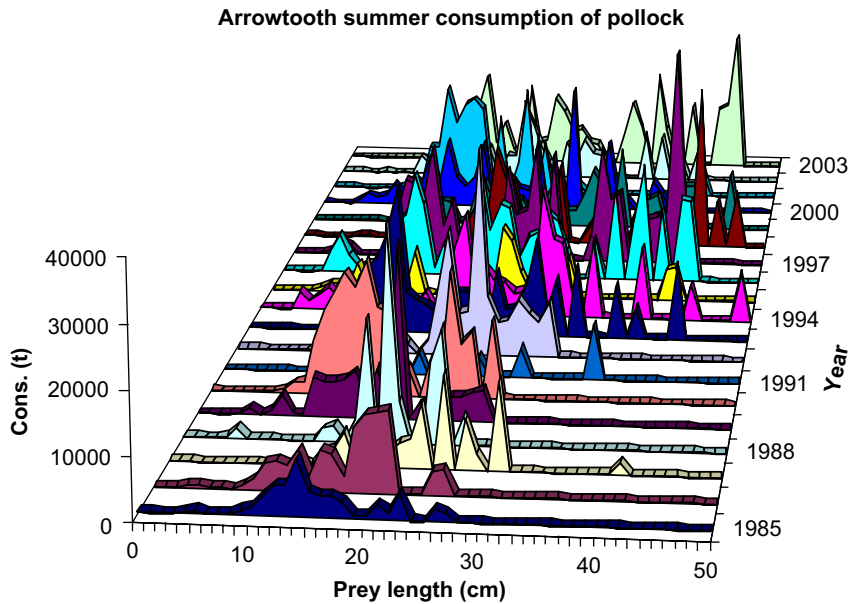


Fig. 14. Summer consumption of EBS walleye pollock by arrowtooth flounder, binned by prey length classes (1 cm fork length intervals), 1985–2003. Estimation method is described in [Lang et al. \(2005\)](#).

sub-Arctic predators such as Pacific cod may prevent snow crab from resettling in more southern areas during short-term cooling events ([Orensanz et al., 2004](#)). Other sub-Arctic species, such as salmon and juvenile pollock, are increasingly colonizing the northern Bering Sea shelf ([Grebmeier et al., 2006](#)). Changes in productivity also may have occurred on the southeastern Bering Sea shelf as suggested by a decrease in the summer standing stock of zooplankton since 1998 ([Napp and Shiga, 2006](#)). This is consistent with results shown in [Fig. 10](#); forage CPUE in the bottom trawl surveys has been at a consistently low level since 1999. While the Bering Sea ecosystems have remained productive throughout the climate oscillations of the last 100+ years, recent changes are outside the range of previously observed variability and may lead, or may have led to, ecosystem changes that will take years to untangle and understand.

#### 4. Summary

The Bering Sea shelf supports an extraordinary diversity and abundance of marine life that forms the basis of important commercial fisheries, as well as important subsistence harvests by Alaska Natives. Marine fish, seabird, and marine mammal populations have undergone large changes in the

past in response to both harvesting and changes in climate.

However, while both climate variability and fisheries have substantially altered the Bering Sea ecosystem in the past, their relative importance in shaping the current ecosystem state remains uncertain. Several direct links between climate, fishing and specific fish populations have been previously hypothesized as described in this paper; for example, the connection between the AO and winter-spawning flatfish, and the connection between ice-retreat timing, copepod blooms, and pollock production (OCH). As these primary and direct links between climate and particular species are uncovered and understood, we gain significant insight; yet these direct correlations and relationships may give rise to “secondary” or indirect effects (e.g., top-down control of forage by pollock, or the MLCH hypothesis) which ultimately switch modes of control or relationships. Such surprises will become more common, but also more understood, as our time window of observations is extended.

Finally, the location of the EBS at the transition point between the sub-Arctic and the Arctic may make the region particularly sensitive to climatic changes. In particular, changes in the extent and timing of ice retreat may have profound effects on the flow of energy through the system, benthic vs.



pelagic pathways, and the structure of the community. There are indications that the region is currently undergoing a transition from Arctic to sub-Arctic conditions related to recent warming trends (Overland and Stabeno, 2004; Grebmeier et al., 2006). If warming trends continue as predicted (IPCC, 2001), profound changes in the structure and functioning of the EBS ecosystem are likely to occur. However, the cascading effects of continued warming on the ecology of the EBS cannot be predicted with any certainty based on our current understanding of system dynamics.

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### Appendix A. Calculating survey catchability for forage species using minimal consumption estimates

Forage species are not sampled well by current gear in the Bering Sea; however, relative biomass (CPUE) from Alaska Fisheries Science Center bottom trawl surveys is reported with annual CVs less than interannual variation, implying that CPUE may be useful as an index. To sum these indices to a measure of total forage fish, a standard assumption on catchability is necessary. Calculating the minimum biomass required to support measured groundfish consumption is one possibility, with a method described in Aydin et al. (2006) as follows:

The biomass ( $B$ ), ration (Ration), and diet composition (DC, % wet weight) are calculated for groundfish predators within a reference (base) year, using groundfish food habits data and rations described in Lang et al. (2005). In this case, the base year used was 1991, due to the extended sampling during that year. Minimum required biomass of prey is then calculated as the sum of consumption by its predators as a fraction of its mortality as follows:

$$\hat{B}_{\text{cons},f}^{1991} = \frac{\sum_{\text{pred}} (B_{\text{pred}}^{1991} \text{Ration}_{\text{pred}}^{1991} \text{DC}_{\text{pred},f}^{1991})}{0.8Z_f^{1991}}. \quad (\text{A.1})$$

Here,  $Z$  is the mortality (equilibrium production rate) of the forage species, generally taken from single-species estimates from literature review (Aydin et al., in press). The constant 0.8 is a “default minimal” assumption that 20% of the forage fish production is “unexplained” (attributed to  $M_0$ ). After biomass for the reference year is calculated, the catchability  $q$  of the survey for the forage species is calculated by

$$\hat{q}_{\text{cons},f}^{\text{survey}} = \frac{\text{CPUE}_{\text{survey},f}^{1991}}{\hat{B}_{\text{cons},f}^{1991}}. \quad (\text{A.2})$$

Then, for years other than the reference year, survey CPUE may be converted to biomass using the conversion

$$\hat{B}_{\text{cons},f}^{\text{year}} = \frac{\text{CPUE}_{\text{survey},f}^{\text{year}}}{\hat{q}_{\text{cons},f}^{\text{survey}}}. \quad (\text{A.3})$$

A future improvement will be to specifically estimate  $q$  over multiple years of diet and mortality data to evaluate the stability of  $q$ .

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