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Current and Historical Role of Apex Predators in the Bering Sea Ecosystem

by

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Abstract

Marine mammals currently play a far less important role in the Bering Sea ecosystem than they did prior to their exploitation. Large population declines (>50%) since the mid-1970s in Bering Sea apex predator populations (Steller sea lions, northern fur seals, murre, and kittiwakes) may be an indication that major changes in this ecosystem's structure resulted from historical reductions in marine mammal (e.g., cetacean) populations there. Fishery surveys and diet analyses of these predators suggest that abundance of key prey (e.g., capelin, juvenile walleye pollock) has declined, due in part to changes in the oceanographic regime beginning ca. 1976-77. However, based on life-history theory natural fluctuations in prey availability should not have produced such large, chronic decreases in apex predator populations. At least two other factors may have significantly modified the Bering Sea's trophic structure--commercial fishing, and intense harvesting of whales, northern fur seals, and some fishes during 1960-75. Biomasses of adult groundfish are as high now as before the current apex predator declines, suggesting either that fishery effects (if any) are localized or that the current high adult groundfish biomass poorly predicts fishery effects. Zooplankton releases and reduced predation resulting from reductions in whale and fur seal numbers could have stimulated the five-fold increase in groundfish biomass during 1960-75, which with some fluctuation has remained high to the present. The resulting high abundance of piscivorous adult groundfish may be out competing mammalian and avian predators for their common prey. If the decline in marine mammal populations contributed to the current high biomass of gadids, flatfish, and salmonids, it suggests that whales and pinnipeds once (but no longer) exerted a structuring effect on the Bering Sea ecosystem. Moreover, the Bering Sea ecosystem's present trophic structure may impede the recovery of marine mammal and bird populations to historical levels.

Introduction

The role of marine mammals in structuring pelagic marine ecosystems remains largely unexplored except for limited theoretical considerations (e.g., Estes, 1979, 1994) or in the context of marine mammal-fishery interactions (Alaska Sea Grant, 1983; Harwood, 1983; Beddington et al., 1987; Northridge, 1991). Only in the Southern Ocean has the abundance of marine mammals

(i.e., large cetaceans) been documented to influence pelagic ecosystem structure. There the decline in whale stocks may have contributed to increases in seal and sea bird populations through the release of krill (Euphausia superba; Laws, 1985). Such a finding points out an unfortunate property of most contemporary marine ecosystems--they may be fundamentally altered from their historical state by reductions in marine mammal populations. As an example, Livingston (1994) calculated the "species richness" of the Bering Sea pelagic fish consumers guild to be around one because of the dominance of the pelagic ecosystem by walleye pollock (Theragra chalcogramma). Moreover, recent estimates suggest prey consumption by marine mammals is so small that they exert little effect on the Bering Sea ecosystem (Livingston, 1993; Perez and McAllister, 1993). Has the dominance of walleye pollock and subordination of marine mammals always been a feature of the Bering Sea or is this a result of the reduced marine mammal populations in the ecosystem? As marine ecosystem science matures it is incumbent upon us, marine scientists, to pursue the questions of how marine mammals may have shaped ecosystems historically, and how their absence may have produced the ecosystem states we are currently measuring.

TABLE 1

These questions appear crucial to the search for the cause of the declines of piscivorous marine mammals and birds in the Bering Sea, Aleutian Islands, and Gulf of Alaska (Table 1). Harvests of large cetaceans (blue, Balaenoptera musculus; fin, Balaenoptera physalus; sei, Balaenoptera borealis; humpback, Megaptera novaeangliae; northern right, Eubalaena glacialis; bowhead, Balaena mysticetus) so reduced their abundance that by 1976 all whaling was effectively terminated in the Bering Sea. Their populations have shown little recovery since then (Small and DeMaster, 1995), and all remain listed as endangered under the U.S. Endangered Species Act (ESA). The eastern Bering Sea population of northern fur seals (Callorhinus ursinus) began to decline in the mid-1960s due largely to harvests of adult females. The decline abated briefly in the mid-1970s but began again and continued through the early 1980s (NMFS, 1993). The population then is currently listed a depleted under the U.S. Marine Mammal Protection Act. Steller sea lion (Eumetopias jubatus) abundance remained high from the 1950s through the early 1970s, and then began a decline which has continued to the present (NMFS 1995). It is presently listed as threatened under the ESA, and the National Marine Fisheries Service (NMFS) is presently considering whether to list the western stock of the species as endangered. Harbor seals (Phoca vitulina) may also have declined since the 1970s in the Bering Sea and Aleutian Islands. Similar declines have been recorded for reg-legged kittiwakes (Larus brevitrostris), black-legged kittiwakes (Larus tridactyla), common murre (Uria aalge), and thick-billed murre (Uria lomvia) in the Bering Sea and eastern Aleutian Islands (Hatch, 1993; Piatt and Anderson, in press).

Although a variety of causes for the marine bird and mammal declines have been considered, the consensus appears to be that declines since the mid-1970s are a result of changes in the availability of preferred prey (Merrick et al, 1987; D. Calkins, ADF&G, 333 Raspberry Rd., Anchorage, AK, 99502, unpubl. data, 1988; Loughlin and Merrick, 1989; Alverson, 1991; Springer, 1992; Trites, 1992; Alaska Sea Grant, 1993; Decker et al., 1995; Merrick, 1995; Hunt et al., in press; Piatt and Anderson, in press). Dietary studies suggest that sea lions, harbor seals, fur seals, and piscivorous sea birds have historically relied on a variety of small (< 25 cm), schooling pelagic fish as prey (Pitcher, 1980, 1981; Sinclair et al., 1994; Decker et al., 1995; Hunt et al., in press; Merrick and Calkins, in press; Piatt and Anderson, in press; Sinclair et al., in

press). During the course of their declines their diet has become simplified and is now focused on a single prey (usually walleye pollock). Some prey (like capelin, *Mallotus villosus*) which were commonly consumed by most of these species prior to their declines disappeared from their diets in the late 1970s (D. Calkins, ADF&G, 333 Raspberry Rd., Anchorage, AK, 99502, unpubl. data, 1988; Decker et al., 1995; Piatt and Anderson, in press; Sinclair et al., in press). Areas or times where diets are more diverse appear to have more stable populations (Merrick, 1995; Merrick and Calkins, in press; Piatt and Anderson, in press). This suggests that many of these top predators need a variety of prey available, perhaps as a buffer to significant changes in abundance of any single prey.

Fig. 1

Evidence suggests that key prey species (e.g., juvenile walleye pollock and capelin) are indeed less available now than prior to the declines. Juvenile walleye pollock abundance has been highly variable, but has generally shown a downward trend since the 1970s (Fig. 1). The feeding habits of pinnipeds and sea birds are such that either age-0 or age-1 pollock are consumed, and one good year-class may carry predators for more than one year. Still, periods would remain when few juvenile pollock were available which could effect predator survival. In addition to juvenile pollock many predators historically fed upon other small prey [e.g., capelin, Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea harengus*), and small demersal fish]. The available data, however, suggest that many of these species decreased in abundance from the late 1970s to the present. Eastern Bering Sea Pacific herring abundance was high in the early 1960s (1 mmt or greater), then declined to very low levels in the 1970s (< 0.1 mmt), rose in the early 1980s to around 0.6 mmt, and declined again to around 0.1 mmt in 1990 (Wespestad, 1991). Trawl data collected at Pavlof Bay (Alaska Peninsula) during 1972-92 indicated that the abundance of shrimp and some small forage and demersal fish species [e.g., capelin, Pacific sandfish (*Trichodon trichodon*)] decreased abruptly around 1978-82; similar changes have been found in a preliminary analysis of other areas of the Aleutian Islands and Gulf of Alaska (P. Anderson, NMFS, Kodiak, AK, 99615, pers. comm., 1994). Capelin abundance was high in the Bering Sea in the 1970s, but has since declined (V. Wespestad, NMFS, 7600 Sand Point Way N.E., Seattle, WA, 98115, pers. comm., 1994; A. Zolotov, Pacific Research Institute of Marine Fisheries and Oceanography, Vladivostok, Russia, pers. comm., 1994) and biomass of some other small prey species [e.g., eulachon (*Thaleichthys pacificus*), sculpins, and eelpouts (*Lycodes spp.*)] also appeared to decrease from the late 1970s to the mid-1980s (Bakkala, 1993; Fritz et al., 1993).

If the declines in apex predators have been induced by changes in abundance of their prey, then the forces which have induced these changes must be identified before effective management measures can be enacted to reverse the declines. In this review, I present the hypothesis that the decline in prey abundance is a result of a fundamental reordering of the Bering Sea trophic structure. That is, the current high population of groundfish (e.g., adult walleye pollock) is novel and has systematically reduced the abundance of marine mammal and sea bird prey. I discuss three hypotheses which further explain the low abundance of forage fish--effects of the 1976-77 oceanic regime shift, effects of commercial fisheries, and effects of a trophic cascade resulting from the depletion of large whales, fur seals, and some fin fish in the 1960s and 1970s.

The Groundfish Predation Hypothesis

Fig 2. A fundamental change in the trophic structure of the Bering Sea may have begun in the mid-1960s. Bakkala (1993) estimated the biomass of the eastern Bering Sea groundfish complex² increased from around 4.8 mmt in 1965 (when mammalian and avian predator numbers were high) to 15.2 mmt in 1984 (when their numbers were beginning to decline throughout Southwest Alaska). Most of the change in groundfish biomass was produced by increases in pollock, which grew from around 2 mmt in 1965 to 10-12 mmt in 1971 (Bakkala, 1993; Wespestad, NMFS, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. comm. 1995; Fig. 2). The initial increase in pollock biomass resulted from five above-average year-classes spawned during 1965-69; a feat which has not been repeated since then. A similar increase has been noted for the Gulf of Alaska (Alton et al., 1987). Adult pollock consume considerable amounts of fish, and in particular consume many of the same forage fish (e.g., juvenile pollock, herring) that marine mammals and sea birds eat (Livingston, 1991, 1993; Livingston et al., 1993). The five-fold increase in adult pollock biomass significantly increased the amount of fish consumed. The continued high abundance of groundfish through the present may then have resulted in a chronic depletion of prey available to mammalian and avian predators, and may be the major factor driving the declines of nonfish, apex predators in the Bering Sea. Assuming this to be the case, the question then is what produced this increase in groundfish abundance?

The Oceanic Regime Shift Hypothesis

Considerable attention is currently given to the hypothesis that regular changes in oceanic conditions occur in the north Pacific Ocean making it more or less hospitable to various mixes of vertebrate and invertebrate species. Shifts between warm and cool eras appear to occur on a decadal or greater (e.g., 18.6 yr) frequency in the North Pacific Ocean (Royer, 1989; Hollowed and Wooster, 1992; Royer, 1993; Trenberth and Harrell, 1995; Wooster and Hollowed, 1995). The most recent shift in the physical oceanography of the subarctic North Pacific Ocean (the Bering Sea, Aleutian Islands, and Gulf of Alaska) occurred around 1976-77 (Kerr, 1992; Francis and Hare, 1994; Trenberth and Harrell, 1995). This was manifested in increased sea surface temperatures (SST) and winds, which changed the mixed layer depth and intensified ocean transport (Royer, 1989; Tabata, 1989; Polovina et al., in press). The 1976-77 shift increased primary and secondary productivity in the North Pacific Ocean (Venrick et al., 1987; Venrick, 1995; Polovina et al., in press). Brodeur and Ware (1992) found that zooplankton production had doubled in the Gulf of Alaska between 1956-62 and 1980-89 either because 1) primary production increased from the increased Ekman pumping of nutrients into the upper mixed layer brought on by increased surface winds, or 2) winds decreased the mixed layer depth, slowed phytoplankton production, and allowed zooplankton to more efficiently graze the phytoplankton. This increased productivity also appears to have increased the biomass of a variety of nektonic fish and cephalopods (Beamish and Boullion, 1993; Beamish, 1994; Francis and Hare, 1994; Beamish and Boullion, 1995; Brodeur and Ware, 1995; Hare and Francis, 1995; Hollowed and Wooster, 1995; Polovina et al., in press). General relationships between oceanic SST (as a proxy for other physical factors) and year-class strength of fishes have been hypothesized for groundfish

² This does not include the biomass of many of the fish and cephalopods which are prey for sea lions and other top-predators. For example, Pacific herring biomass was estimated to be around 1-1.2 mmt at the beginning of the 1960s (Wespestad 1991; Bakkala 1993).

by Hollowed and Wooster (1995) and for salmonids by Francis and Hare (1994; Hare and Francis, 1995). For example, strong year-classes of a number of Bering Sea fish stocks (e.g., walleye pollock, Pacific cod, Pacific herring) were spawned at the onset of the current warm regime in 1976-77 while declines were observed in stocks of some other finfish (e.g., capelin; P. Anderson, NMFS, Kodiak, AK, 99615, unpubl. data, 1994) and shellfish (e.g., pandalid shrimps, Albers and Anderson, 1985; king crab, Otto, 1989 and Kruse, 1993).

Marine mammal and sea bird declines began at approximately the same time (with a slight lag) as the 1976-77 shift in oceanic conditions suggesting that a linkage may exist to upper trophic levels. However, this may not be the only factor involved in these declines. Perhaps the strongest argument against normal decadal shifts in fish biomass producing large declines in marine mammal and sea bird populations lies in their life history characteristics. All have the features of classic "K-selected" species--slow development, delayed reproduction, few offspring, high parental investment in offspring, long lives, and long generation times. A species with such a life history is expected to maintain a relatively stable population size and to have evolved in a relatively stable environment (Cole, 1954; Pianka, 1970; Stearns, 1976; Estes, 1979). Such a species cannot rapidly recover from low population sizes and, while the population size is low, is vulnerable to extinction from a variety of factors (e.g., predation and disease). Moreover, most of the declining top predators are omnivorous indicating that they have adapted to an environment where prey abundance changes (at least at some time scale, decadal or otherwise). Omnivory allows them to switch as prey abundance changes. This decouples predator abundance from the abundance of any single prey and theoretically should allow the predators to maintain a relatively stable population size.

All this suggests that if the 1976-77 regime shift contributed to the declines of North Pacific marine top predators, then it reduced prey far below that encountered over the recent evolutionary history of the ecosystem. Pascual and Adkison (1994) concluded that the Steller sea lion declines were not induced by short-term environmental fluctuations, but by a long-term or catastrophic change in conditions. One cannot eliminate the possibility that the current carrying capacity is still natural but extremely rare (e.g., on the order of an ice age event). However, the probability of such an event occurring during our observational period seems unlikely. Moreover, the slight changes in ocean conditions (e.g., SST changed less than 2° C from the mean; Royer, 1989, 1993) would seem unlikely to produce such a dramatic change. If the regime shift was insufficient to elicit the major changes observed in marine mammal and bird populations then something else must have occurred.

The Commercial Fisheries Hypothesis

Present commercial fisheries target on adult forms of several of the most important prey species of Bering Sea top predators and consequently, have been considered by themselves to be a major cause for the decline in prey. However, other than temporal concordance, a strong, direct relationship between pollock removals and predator declines has not been substantiated. First, fisheries, marine mammals, and sea birds generally take different sizes of fish. Next, overall abundance of commercial-sized pollock was as high during the declines as before. Harvest

strategies have been quite conservative compared to past practices in the North Pacific and other areas of the world. The pollock exploitation rate in the eastern Bering Sea has been below 15% since the early 1980s (Table 2). Furthermore, analyses comparing changes in sea lion abundance with nearby fishery removals of pollock have produced inconclusive results (Loughlin and Merrick, 1989; Ferrero and Fritz, 1994). The lack of conclusive evidence from this research may, however, be due to the lack of appropriately scaled data on catch (Ferrero and Fritz, 1994). It has also been suggested that commercial pollock fisheries increase prey (e.g., juvenile pollock) because pollock are cannibalistic (Swartzman and Harr, 1983).

Low exploitation rates could, however, have allowed adult pollock and other groundfish species (e.g., flatfish) to maintain high biomasses to the detriment of both prey and competing, more heavily exploited species. Fisheries could also have reduced the abundance or availability of small prey by: 1) causing localized prey depletion, 2) disrupting fish behavior as nets pass through schools, and 3) bycatch of noncommercial prey species. Roe fisheries could have reduced the number of age-0 and age-1 pollock available to marine mammals and birds by reducing the number of spawners, by disrupting spawning behavior, and by removing a disproportionate number of female fish. Sampson (Oregon State Univ., Newport, OR 97365, unpubl. data, 1995) found that the winter roe fishery in the Bering Sea was significantly correlated to sea lion declines in the Aleutian Islands. These second-order fishery effects may have substantial impacts on North Pacific Ocean ecosystems and should be the subject of further research.

The Trophic Cascade Hypothesis

If the change in the Bering Sea ecosystem began in the 1960s, then both the 1976-77 regime shift and current fisheries practices would have occurred after the change was initiated and thus by themselves would be insufficient to explain the change. I propose that the shift was initiated by the depletion of large whales and northern fur seals during 1955-75, with results cascading through the ecosystem and time up to the present. The regime shift and fishing may then have amplified the effects of the initial change. This hypothesis has the following elements (Table 2):

TABLE
2

- 1) Prior to the 1960s, North Pacific Ocean ecosystems were stabilized by the presence of K-selected species such as large whales, fur seals, and Pacific Ocean perch (Sebastes alutus). Populations of fish predators like walleye pollock were constrained by low juvenile survival resulting from competition with whales, herring and Pacific Ocean perch for zooplankton prey and by predation from fur seals, juvenile sea lions, harbor seals, and seabirds.
- 2) During the 1960s, many of the K-selected species were simultaneously reduced to low levels by exploitation. This released prey, reduced predation, and increased at least the Bering Sea's walleye pollock carrying capacity. The increased juvenile walleye pollock survival resulted in a series of strong pollock year classes in the Bering Sea during the late 1960s. Pacific herring populations (which were fed upon by marine mammals and competed with juvenile pollock for prey) were also heavily harvested in this period.
- 3) During the early 1970s, adult walleye pollock biomass increased due to the recruitment from the 1965-69 and 1972 year-classes. The biomass then declined, probably due to fisheries exploitation. Stock size remained higher than in the early 1960s, perhaps due to

the continued availability of extra zooplankton prey for adults (abundance of the whales, Pacific Ocean perch, and herring remained low). Some decline in abundance of forage fish may have occurred at this time due to pollock predation, and this may have contributed to the early 1970s decline of Steller sea lions in the eastern Aleutian Islands.

- 4) In the late 1970s and early 1980s the combination of favorable ocean conditions, continued zooplankton release, and low predation resulted in a series of strong pollock year-classes. Adult biomass again increased and remained high in the eastern Bering Sea (perhaps due to an effective fisheries management regime using light exploitation rates). Predatory Pacific cod (*Gadus macrocephalus*) and flatfish populations also increased. These high biomasses systematically cropped down small fish prey (e.g., such as capelin and sculpins). This, together with low juvenile pollock abundance, resulted in generally low prey biomasses which were insufficient to meet the dietary needs Steller sea lions.

The structural elements of this hypothesis (e.g., the simultaneous reduction of whale, herring, Pacific Ocean perch, and northern fur seals) and the potential linkages between the elements are well documented.

Initiation of the Trophic Shift: 1952-69

The strong pollock year-classes recruited from 1965-69 occurred in a period when ocean SST was mixed between cool and warm years. Thus, improved oceanic conditions do not provide a simple explanation for the increase in pollock recruitment. An additional effect was a combination of the:

- 1) Extensive harvests during 1955-1975 of some fish and marine mammal populations (which released prey and reduced predation),
- 2) Low adult pollock population size (which minimized cannibalism), and
- 3) Initial light fisheries exploitation of pollock.

A similar hypothesis has been considered previously by others (Bakkala et al., 1987; Alton et al., 1987), but has been discounted because releases of prey caused by reduced Pacific herring and Pacific Ocean perch populations would have been sufficient to account for the ultimate adult pollock biomass increase. However, Bakkala et al. (1987) did not consider that only juvenile pollock needed to benefit (adult pollock diets are more catholic and include a large amount of fish; Livingston, 1991; Livingston et al., 1993). They also did not consider that the substantial whale harvests during the period would also release juvenile pollock prey or that reductions in fur seal abundance would reduce predation on juvenile pollock. The life-history characteristics of pollock (an "r-selected" species) are such that they could rapidly exploit such an improvement in their environment.

Pelagic whaling of fin and sei whales in the North Pacific Ocean did not occur at significant levels until 1952. At that time, the Japanese resumed pelagic whaling and focused on fin whales in the eastern Bering Sea and Aleutian Islands. There was also a relatively small Soviet take of fin and humpback whales in the western Bering Sea-Kamchatka Peninsula area. Then in 1962, Soviet whalers shifted operations away from Kamchatka to the eastern Bering Sea and Gulf of Alaska, and increased their takes by an order of magnitude (Tønnessen and Johnson, 1982). Soon afterwards both nations increased their harvest of sei whales. The International Whaling

Fig 3

Commission ended the take of humpback whales in 1965, and harvests of fin and sei whales were effectively terminated in 1976. Between the 1950s and 1976, 77,603 whales (33,992 fin, 38,607 sei, 5,004 humpback) were removed (Fig. 3, D. Rice, NMFS, 7600 Sand Point Way N.E., Seattle, WA 98115, unpubl. data). Most of these whales came from the eastern Bering Sea, Aleutian Islands, Gulf of Alaska, and north Pacific Ocean waters immediately south of these areas. Fin and humpback whale takes would have most heavily influenced the eastern Bering Sea shelf, Aleutian Islands (which could have also influenced the eastern Bering Shelf through transport within the Bering Sea), and coastal waters of the Gulf of Alaska. Sei whales do not generally enter the Bering Sea or near shore waters, and as a result their removals would have most heavily influenced the central Subarctic Domain, and, in particular, the Alaska gyre.

Declines in Pacific herring (Fig. 3) and Pacific Ocean perch (Fig. 3) biomasses (due largely to harvesting by Japanese and Soviet fisheries) occurred simultaneous to the increase in fin and sei whale takes. Eastern Bering Sea Pacific adult (ages 3-9) herring biomass fell from 943,724 mt in 1960 to 106,206 mt in 1975 (Wespestad, 1991). Eastern Bering Sea adult (age 9+) Pacific Ocean perch biomass fell from 102,332 mt in 1960 to 47,157 mt in 1975, while in the Aleutian Islands biomass fell from 498,343 mt in 1960 to 93,956 in 1975 (Ito and Ianelli, 1994). As with the sei and fin whales, herring and perch harvests were heavily reduced or terminated by 1975-78, but populations of both fish and the whale species remain low (< 50% of the pre-exploitation levels) twenty years later.

The Eastern Bering Sea (Pribilof Islands) stock of northern fur seals was estimated at 2.1 million animals during 1949-51 (Kenyon et al., 1954). From 1956 to 1968 the stock was reduced by the killing of approximately 23,000 adult females annually. The population continued to decline until 1970, increased through 1976, declined again through 1981, and has since remained at stable but reduced levels (York and Hartley, 1981; NMFS, 1993). Stock size was estimated as 1.71 million animals in 1960, 1.14 million in 1970, and 1.26 million in 1975 (Fig. 3; NMFS/NMML, 7600 Sand Point Way N.E., Seattle, WA 98115, unpubl. data).

The timing of the marine mammal and fish removals bracketed the period in which pollock abundance increased and the removals are correlated with the pollock increase. For example, the cumulative fin whale removals and pollock increase are positively correlated (Pearson $r = 0.8639$, $DF = 13$, $P < 0.001$). Presumably, if actual whale abundance was known and declined in proportion to the take (Ohsumi and Wada, 1974), the sign of the correlation would have been negative as it was for a comparison of herring and pollock abundance for 1963-84 (Wespestad, 1991; Pearson $r = -0.5562$, $DF = 22$, $P = 0.007$). Fur seal abundance during 1963-75 was also correlated with pollock abundance (Pearson $r = -0.6736$, $DF = 12$, $P = 0.016$), but was not during 1976-84. A strong correlation existed between fur seal numbers and adult pollock abundance four years later (Pearson $r = -0.8582$, $DF = 12$, $P < 0.001$) suggesting that fur seals most heavily effect juvenile pollock abundance.

If there was a relationship between populations of pollock and other top predators then it dwells in the dietary overlap between whales, fish, and fur seals. Juvenile (and to a certain extent adult) pollock, herring, Pacific Ocean perch, and fin, sei, and humpback whales all rely on

euphausiids (*Thysanoessa* spp.) and calanoid copepods as their major prey in the north Pacific Ocean (Tomlin, 1957; Rumyantsev and Darda, 1970; Takahashi and Yamaguchi, 1972; Cooney et al., 1980; Smith, 1981; Gaskin, 1982; Walline, 1983; Dwyer et al., 1986; Livingston, 1991; Livingston et al., 1993). Northern fur seals, on the other hand, have traditionally fed heavily on walleye pollock in the eastern Bering Sea (Perez, 1986; Perez and Bigg, 1986; Sinclair et al., 1994, in press) and most of this consumption is either age-0 and age-1 pollock.

TABLE
3

How much walleye pollock could this have supported? A gross estimate of the scale of potential biomass release in the Bering Sea is shown in Table 3. By 1970, the reduction of fin whales, Pacific herring and Pacific Ocean perch in the Bering Sea and Aleutian Islands could have released 1.36 to 2.81 million mt of zooplankton prey a year. Wespestad (1994) estimated the size of an age-1 eastern Bering Sea pollock as 20.0 cm and 0.12 kg in 1994, and Livingston et al. (1993) estimated that the ration of small pollock was 0.011 kg per day for 240 days a year. Thus, an age-1 pollock would require around 0.32 kg of prey per year. The aforementioned release of prey (assuming complete diet overlap) would be sufficient to feed 4.3 to 8.9 billion age-1 pollock for a year. Assuming that 67% of the fur seal was pollock (Perez, 1994), 343,107 mt of the 492,100 mt of prey released by the reduced fur seal population would be pollock (mostly age-0 or age-1). If all were age-1 pollock, at 0.12 kg per fish, this could remove predation on 2.8 billion age-1 pollock.

Based on cohort analysis estimates of age-1 biomass from Wespestad (1994) and an average size for an age-1 fish of 0.12 kg, the average number of age-1 pollock in the eastern Bering Sea for 1979-1994 was 10.6 billion fish. Nine of the year-classes during the period were less than 11.7 billion fish. Thus, the released zooplankton and reduced predation pressure could have supported juvenile pollock year classes during 1965-69 at levels approaching recent recruitment. This is not to say that all this prey release would necessarily have been translated into pollock, but rather that the scale of the biomass release was similar to the increased juvenile pollock biomass (as were the timing of the release and the specific prey species released).

Two other factors also would have improved juvenile survival during 1965-70-- ocean conditions were warm in some years (which could have stimulated zooplankton production as discussed by Brodeur and Ware, 1992) and low amounts of pollock cannibalism. The spawner-recruit relationship for pollock suggests that the stronger year classes comes from years with lower adult biomass (Wespestad, 1994). At high adult population sizes, cannibalism on eggs, larvae, and juveniles reduces juvenile survival.

The Interim Period: 1970-75

During the late 1960s, the combination of increased zooplankton abundance and low cannibalism would have most benefitted juvenile pollock. As the 1965-69 year-classes recruited the larger adult biomass would have left less zooplankton for juveniles, and could have dampened further increases in juvenile biomass. Still, adults consume considerable amounts of fish as well as crustacea (Livingston, 1991; Livingston et al., 1993), and the increase in adult biomass must have increased the amount of fish consumed. This could have reduced the biomass of forage fish. Whether this occurred is unknown; however, it was during the 1970-75 period that the first

significant Steller sea lion declines were recorded (Braham et al., 1980). This occurred in the eastern Aleutian Islands, the area of sea lion habitat closest to the eastern Bering Sea. The impact on forage fish populations would have had a transient effect because the eastern Bering Sea pollock biomass increase was short lived; the pollock population began to decline almost immediately after reaching a peak in 1971. The eastern Aleutian Island sea lion decline appeared to abate soon after the Bering Sea pollock population began to decline. Thus, it is possible that competition with pollock may have exacerbated the eastern Aleutian Island sea lion declines induced by large incidental takes in the groundfish fishery (Perez and Loughlin, 1991).

Heavy fisheries exploitation of the stock during the 1970s (compared to the 1960s and 1980s) may explain the decline in pollock biomass (Fig. 2). Exploitation rates through the 1960s were 14% or less of the exploitable stock, but increased to as high as 25% in the 1970s. By the 1980s, the rate had returned to < 14%. It is notable, however, that the eastern Bering Sea pollock population never returned to the size (Fig. 2) estimated for the early 1960s (another hint that the carrying capacity has increased).

The Current Regime: 1976 to the Present

Now we come to 1976-77 and the oceanic regime shift. In many ways conditions were similar to those during 1965-69--whale abundance was so low that fin and sei stocks were designated as protected in 1976, Pacific herring and Pacific Ocean perch had just reached their lowest biomass levels since 1960 (Wespestad, 1991; Ito and Ianelli, 1994; Heifetz et al., 1994), and fur seal populations had rebounded somewhat but were still low (NMFS, 1993). Adult pollock populations were moderately low, so that cannibalism was reduced. With these conditions overlaid on the template of favorable ocean conditions the result was the strong 1977-84 year-classes. First, pollock and cod and later flatfish increased to record or near-record levels. Alaskan salmon stocks also began to build to record levels³.

Despite these increases in the biomass of some fishes, conditions still appeared to deteriorate for top predators. Preferred prey began to disappear in a serial (not simultaneous) fashion. First, between 1976 and 1981, capelin and some small demersal fish (e.g., sculpins, Pacific sandfish and pricklebacks) which were common in marine mammals and sea bird diets in the 1970s all but disappeared both from diets and from resource surveys between 1976 and 1981 (D. Calkins, ADF&G, 333 Raspberry Rd., Anchorage, AK, 99502, unpubl. data, 1988; Fritz et al., 1993; P. Anderson, NMFS, Kodiak, AK, 99615, unpubl. data 1994; Hunt et al., in press; Piatt and Anderson, in press). Next, Pacific herring in the eastern Bering Sea, which had increased in the early 1980s due to strong year-classes in 1976-77, returned to the low 1970s level (Fritz et al., 1993). Perhaps herring (which require large numbers of spawners to produce large year-classes) could not capitalize on favorable conditions because the spawning biomass had been reduced by over exploitation and predation by pollock (Wespestad and Fried, 1983). Finally, juvenile

³ Hare and Francis (1995) found that Alaska pink (*Oncorhynchus gorbusha*) and sockeye (*Oncorhynchus nerka*) salmon stocks grew to levels greater than existed during the earlier period (pre-1950s) of peak salmon production. It is possible that these higher levels of salmonid production could have been stimulated by both the improved oceanic conditions that existed after 1976-77 and the release of zooplankton from sei whale removals in the Central Subarctic Domain.

pollock abundance declined to progressively lower levels (Fig. 1). Rice (1995) predicts that cohort strengths will become highly variable when survivorship increases as a result of increased food availability to sub-adult stages. He also notes that time lags between changes in prey and changes in predator would become common in this situation.

Thus, the availability of the preferred prey of marine mammals and sea birds fell progressively lower through the 1980s. This was not the case for adult groundfish as their biomass remained relatively high through the 1980s and 1990s. Eastern Bering Sea groundfish exploitable biomass was 13.7 mmt in 1980, 12.6 mmt in 1986, and 13.5 mmt in 1993 (NMFS, 1987; NPFMC, 1992; Bakkala, 1993). A considerable amount of fish would need to be consumed to maintain the high stock sizes of piscivorous fish such as pollock and arrowtooth flounder (*Atheresthes stomias*). Both pollock and arrowtooth flounder are semi-demersal as adults and would be ideally located to prey upon small fishes associated with the bottom like capelin and sculpins as well as pelagic fishes like juvenile pollock and herring (Wespestad and Fried, 1983; Livingston, 1991, 1994; Livingston et al., 1993).

It has also been proposed that the high biomass of groundfish has contributed to the depressed shellfish stocks in Alaska. The reduction in pandalid shrimps stocks in the Gulf of Alaska has been attributed to predation by Pacific cod (Albers and Anderson, 1985). Similarly, stocks of crabs may have been reduced by predation by small-mouthed flatfish (e.g., yellowfin sole, *Limanda aspera*) on juvenile crab, and Pacific cod on adult crab (B. Otto, NMFS, Kodiak, AK, 99625, pers. comm., 1995).

This hypothesis is not without parallels in other marine ecosystems. A similar hypothesis has been proposed to explain the Arctic cod (*Gadus morua*), seal, and sea bird declines which occurred in the Barents Sea in the late 1980s (Hamre, 1994). Herring was overexploited from the early 1970s onwards, and this appeared to create an imbalance in predator (cod) - prey (herring/capelin) relationships. However, in the 1970s and early 1980s the imbalance was not obvious because cod (at relatively low stock sizes) could feed on capelin (which was then abundant). In the mid- 1980s favorable recruitment conditions existed for both cod and herring. Herring stocks were not sufficiently large to capitalize on conditions. Cod, whose recruitment is not dependent on adult stock size, produced three strong year-classes. With a lack of juvenile herring as prey, the rapidly growing cod stock grazed down other available prey species, including its own offspring. This was followed by the crash of cod, capelin, sea bird, and seal populations, and, of course, the cod and capelin fisheries. Similar conditions may have occurred in the eastern Bering Sea with the exception that the predator (pollock and arrowtooth flounder) populations have not collapsed. The essential difference may be the availability of zooplankton (released by the reduction in whale populations) to supplement fin fish consumption.

Implications of the Decline in Prey Availability to Recovery of Marine Mammal and Bird Populations

If progress is to be made towards rebuilding populations of marine mammals and birds, serious consideration must be given to the hypothesis that the current high biomass of groundfish

may be incompatible with historical populations of nonfish apex predators. Acceptance of this hypothesis requires an acknowledgment that:

- 1) Marine ecosystems are hierarchically organized. Within this hierarchy overall stability is maintained by homeostatic mechanics exerted by higher levels dampening the large variations inherent in the lower levels (Dickie, 1973; O'Neill et al., 1986).
- 2) K-selected species, through competition and predation, structure marine ecosystems, although abiotic processes may constrain total productivity (Margalef, 1975; Estes, 1979; Ray, 1981).
- 3) Removal of these species as a functioning component of ecosystems removes the homeostatic controls and resets ecosystems to a novel state. Conditions thereafter would be highly unpredictable (Allen, 1985; Rice, 1995). As a result, current marine ecosystem research cannot be completely relevant to understanding how marine ecosystems function because they usually ignore how K-species structured these ecosystems over their evolutionary history. Unfortunately, most marine ecosystem research in the North Pacific Ocean began after the system's structure had already been perturbed by human actions.

Fisheries managers need to accept that while the large increases in groundfish biomass in the eastern Bering Sea after the early 1960s were good for commercial groundfish fisheries, the increases may have been to the detriment of other members of the ecosystem.

A reduction in K-selected species abundance coupled with an increase in abundance of r-selected species (e.g., pollock) may shift ecosystem stability toward greater uncertainty in population sizes and greater variability. In a practical sense, this makes fishery stocks "progressively less amenable to conventional management and progressively more vulnerable to the uncontrollable and largely unpredictable forces of the environment" (Apollonio, 1994, p. 165). This is essentially what may have occurred in the North Pacific Ocean since the 1950s. Prior to exploitation, a suite of K-selected species (large whales, fur seals, sea lions, harbor seals, ice seals, sea birds, some fish) may have exerted considerable control over the ecosystems. Consumption of zooplankton and predation on groundfish by these species kept juvenile groundfish abundance at low levels, which restricted the possible stock size of adult groundfish. This then limited the impacts of groundfish on other fish populations. Reductions in the populations of some K-species during the 1960s triggered a sequence of events which required two decades to impact unharvested K-selected species (e.g., sea lions and sea birds). If pollock in the eastern Bering Sea have occupied the niche formerly filled by whales, then recovery of whale (and other mammalian and avian) populations will remain extremely slow. It may be that the current condition of these ecosystems will not allow them to recover to historical levels.

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Table 1.--Recent changes in abundance and current management status of selected Bering Sea apex predators. Cetacean and pinniped information from Small and DeMaster (1995) and sea bird data from Hatch (1993) and Piatt and Anderson (in press).

Species	Area	Population trend	Listing status
Cetaceans			
Blue whale	NPO	Low and trend unknown	Endangered
Fin whale	NPO	Low and trend unknown	Endangered
Sei whale	NPO	Low and trend unknown	Endangered
Humpback whale	NPO	Low but increasing	Endangered
Northern right whale	NPO	< 5% of historical; trend unknown	Endangered
Bowhead whale	B.S.	< 20% of historical; increasing	Endangered
Pinnipeds			
Steller sea lions	B.S./AI/GOA	< 20% of historical; declining	Threatened
Pacific harbor seals	B.S./AI/GOA	Low GOA; B.S./AI unknown	Not listed
Northern fur seals	B.S.	< 50% of historical; stable	Depleted
Sea birds			
Red-legged kittiwakes	B.S.	Reduced and declining	Candidate
Black-legged kittiwakes	B.S.	Reduced and declining	Not listed
Common murres	B.S./AI/GOA	Declines in all areas	Not listed
Thick-billed murres	B.S.	Declining	Not listed

Table 2.--Matrix of elements related to recent trophic changes in the Bering Sea. Walleye pollock data from Wespestad (1994), and all other data as cited in text.

Element	1960-64	1965-69	1970-74	1975-79	1980-84	1985-89	1990-94
Pollock exploitation rates	0-0.11	0.09-0.14	0.14-0.25	0.20-0.23	0.08-0.24	0.06-0.14	0.14-0.17
Adult biomass	Low (< 2.5 mmt)	Low, but increasing (2.5- 9mmt)	Peak in 1971, then down (9 to 11 to < 7 mmt)	Stable (< 7 to > 5 mmt)	Increasing (> 5 to 13 mmt)	High, beginning to decline (13 to 15 to 11 mmt)	Declining (11 to 7 mmt)
Juvenile biomass	Low	Strong in 1965-69	Most weak except 1972	Strong in 1977-78	1982 and 1984 strong	Most weak except 1989	All Weak
Whale abundance	Declining	Declining	Declining	Low, stable	Low, stable	Low, stable	Low, stable
Fur seal abundance	Declining	Declining	Increasing	Declining	Low, stable	Low, stable	Low, stable
Herring abundance	High	Declining	Declining	Low, stable	Increasing	Declining	Low
Other forage fish abundance	?	?	Capelin high?	Capelin, and others down	Capelin, and others down	Capelin, and others down	Capelin, and others down
Ocean regime	Warm	Mixed	Cool	Mixed	Warm	Cool	Cool

Table 3--Predator biomass removals and annual prey biomass release from harvests of fin whales, Pacific herring, Pacific Ocean perch, and northern fur seals through 1970. BW indicates feeding rate as equal to body weight for year. Northern fur seal and fin whale estimates of feeding from Perez (1994).

Species	Area	Stock reduction		Feeding rate (kg/day) (B)	Days feeding in area (C)	Biomass release (mt) (A*B*C)
		Number (A)	Biomass (mt)			
Fin whale	EBS	4,000	196,000	1,265	120	607,200
	EBS/AI	11,000	539,000	1,265	120	1,669,800
Northern fur seal	EBS	569,000	24,467	5	180	512,100
Pacific herring	EBS	-	721,000	BW	240	721,000
Pacific Ocean perch	EBS	-	35,300	BW	240	35,300
	EBS/AI	-	419,300	BW	240	419,300
Minimum - EBS only			976,767		1,875,600	
Maximum - EBS/AI			1,703,767		3,322,200	

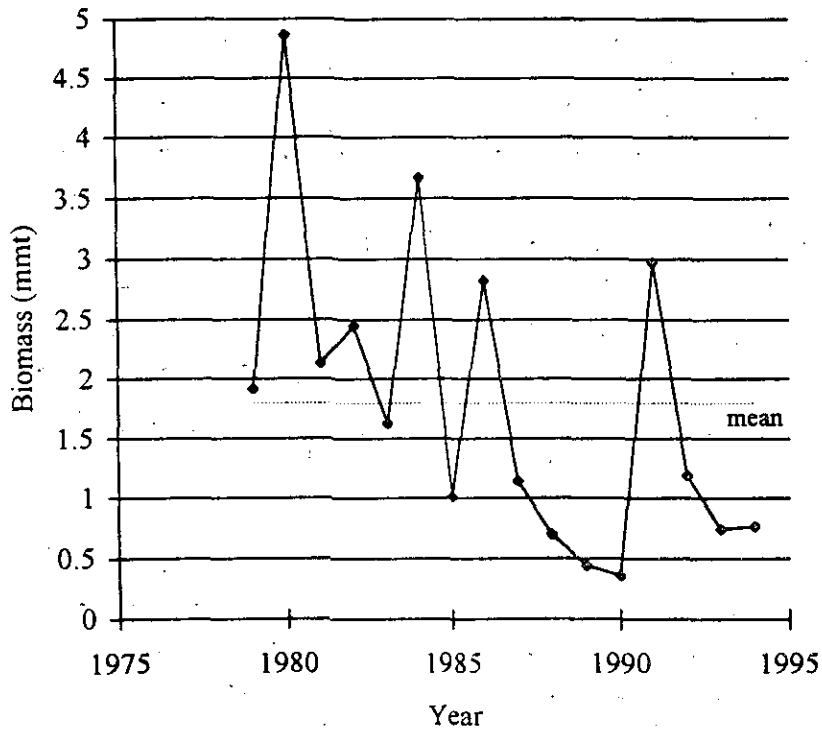


Figure 1. Age-1 walleye pollock biomass by survey year for 1979 to 1994. Data from Wespestad (1994).

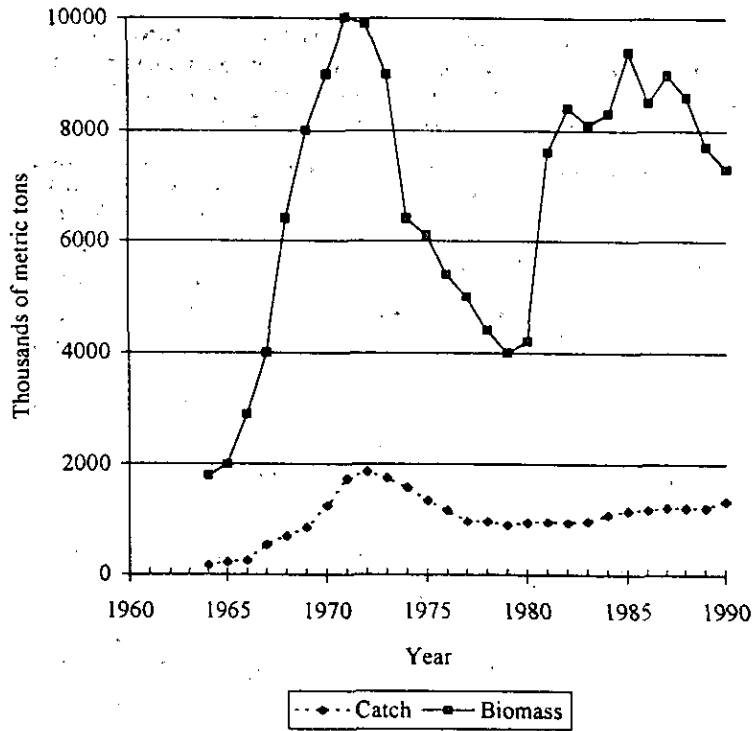


Figure 2. Eastern Bering Sea adult and age-1 walleye pollock biomass, and adult pollock catch: 1960-90. Data from Wespestad (1994).

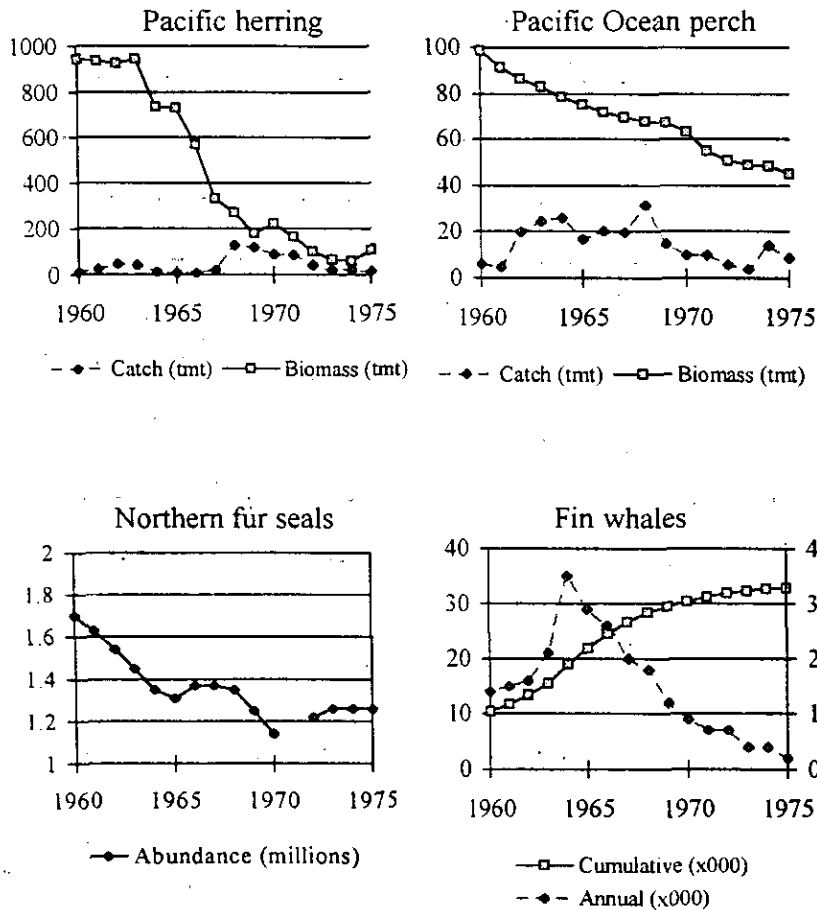


Figure 3. Harvests or biomass of Pacific herring, Pacific Ocean perch, northern fur seals, and fin whales from the North Pacific Ocean (eastern Bering Sea) from 1960 to 1975. Sources of data as described in text.