Summary, Conclusions, and Recommendations

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Much of the interest in dynamics in the Bering Sea, now and in the past, has been spurred by concerns over the stability and sustainability of its vast living resources. Particularly prominent today are depressed populations of several species of marine mammals, notably great whales, Steller sea lions, fur seals, harbor seals, and sea otters, and of additional species of considerable economic importance, such as king crabs, shrimp, and Pacific Ocean perch. The reason for the collapse of whales, shrimp, and Pacific Ocean perch is known—they were killed by commercial fisheries. The recent decline of sea otters in the Aleutian Islands is thought to have been caused by increased predation. The reasons for diminished populations of other species are not known, or at least not agreed upon, and have been the stuff of extensive, often rancorous debate. No less dramatic, however, have been spectacular increases of certain fishes, such as flatfishes, walleye pollock that grew in abundance by nearly an order of magnitude between the 1960s and 1980s, and Pacific salmon that provided record harvests across the northeastern North Pacific for many years in the 1980s and 1990s before collapsing in some regions, notably the Bering Sea, in 1997 and 1998.

This volume is the most recent in a growing series of publications devoted to the Bering Sea and is basically a report on certain advances that have been made in our understanding of the ecosystem—what it is and why it behaves as it does—primarily in regard to issues of interest to PICES. Thus, many of the papers presented here, as the general title indicates, address dynamics—dynamics of physical processes like meteorology and ocean circulation, and of ecosystem processes that are important to biomass yield at higher trophic levels in pelagic food webs. Others provide more descriptive information that will be useful in future dynamic contexts. My brief summary touches on some of the highlights of the foregoing chapters, but each must be read to fully appreciate the state of knowledge revealed in their pages.
Physical Dynamics

Studies of meteorology have broadened in recent years with (1) the recognition of teleconnections between the El Niño Southern Oscillation (ENSO) in the equatorial Pacific and meteorological variability over the North Pacific and Western Arctic and (2) a heightened awareness of the importance of meteorology to physical oceanographic conditions and the biological realm (Trenberth and Hurrell 1994; Roach et al. 1995; Mantua et al. 1997; Klyashtorin 1997; Springer 1998; Francis et al. 1998; Niebauer, in press; Niebauer et al., chapter 2; Schumacher and Alexander, chapter 6; Wyllie-Echeverria and Ohtani, chapter 21, this volume). Of particular interest are relationships between ENSO; fluctuations in the strength and position of the Aleutian Low pressure system between quasi-stable states with periods of decadal-scale proportions, otherwise known as regimes or the Pacific interDecadal Oscillation (PDO); oscillations in the Earth Rotation Velocity Index and the Atmospheric Circulation Index; and physical oceanographic variability in the subarctic North Pacific and Bering Sea. One significant example described here is the relationship between sea ice in the Bering Sea and the PDO (Niebauer et al., chapter 2; Niebauer, in press).

Good spatial descriptions of the physical seascape of the Bering Sea have existed for some time. The hydrographic domains across the eastern and northern shelf (inner, middle, outer) were elucidated in the 1970s and 1980s (Stabeno et al., chapter 1; McRoy, chapter 31; Hood, chapter 32) and are similar to domains in the western Bering Sea, with the exception that domain boundaries on the eastern shelf are comparatively stationary, whereas those on the narrow western shelf are dynamic and depend on the position of the Kamchatka Current (Khen, chapter 7). Another striking difference is that on the eastern shelf, the shallow inner domain is well mixed, a hallmark characteristic, whereas the inner domain of the western shelf is not.

Progress has been made in confirming earlier views about the general circulation of the Bering Sea and in discovering additional details about important broadscale and mesoscale processes and variability. Most attention has focused on volume transport and the trajectory of Alaskan Stream inflow through Aleutian Island passes, the generation and propagation of eddies over the basin and along the shelf edge, and characteristics of flow fields along the edge of the shelf and around the Pribilof Islands (Stabeno et al., chapter 1; Kowalik, chapter 4; Reed and Stabeno, chapter 8; Sapozhnikov, chapter 11). As a result, we now have a much improved understanding of dynamics. For example, transport variability in the Bering Sea gyre is >50% due to variations in wind-driven transport and inflow of Alaskan Stream waters through Aleutian Island passes, principally Near Strait (Stabeno et al., chapter 1), and transport of water out of the Bering Sea to the Arctic Ocean has apparently declined by 25-30% in the past 50 years (Roach et al. 1995; T. Weingartner, unpubl. data).
In contrast, little attention has been paid recently to the Alaska Coastal Current on the eastern shelf and it is hardly mentioned in any of the papers in this book. It originates on the southeastern shelf, contributes about 30% of the volume transport through Bering Strait, and can be traced well into the western Beaufort Sea (Coachman et al. 1975, Coachman 1993).

**Chemical Dynamics**

Chemical dynamics in the Bering Sea are forced by both physics and biology, and general principles of the dynamics of plant nutrients in particular have existed for some time (Whitledge and Luchin, chapter 10). Bottom waters in the basin are supplied by deep inflow from the North Pacific, are perhaps the oldest in the world, and contain the highest concentrations of naturally occurring macronutrients (e.g., nitrate, phosphate, silicate) in the world ocean (Coachman et al., chapter 13). Residence time for deep water displaced upward by bottom water flowing in from the North Pacific is 250-300 years. Over the shelf, nutrient concentrations are governed by rates of biological uptake and remineralization, by physical structural fronts that retard cross-shelf flow of nutrient-laden basin waters, and by countervailing physical features that distribute basin waters to the shelf. Interannual variability in nutrient flux over the shelf is related to the frequency of storms that force onwelling of basin waters laterally to impoverished middle and inner regions, as well as vertically to the euphotic zone by mixing of the water column. Such dynamics in turn have a large effect on the annual amount of primary production.

Currents also supply nutrients to regions that are otherwise limited. The most extreme example is on the northern shelf where the flow of Anadyr Water, which originates at depth along the shelf edge in the northwestern Bering Sea and is thus highly enriched in nutrients, creates a chemostat-like environment that fuels levels of primary production of world record proportions (McRoy et al. 1987, Springer and McRoy 1993). In the western Bering Sea, the strong Kamchatka Current likely plays a similar role in delivering nutrients to the narrow shelf there.

Eddies may also be important to nutrient budgets in the Bering Sea and thus to primary production. Sapozhnikov et al. (chapter 17) believe eddies off the Kamchatka Peninsula and in the Aleutian Basin have an important role in nutrient distributions (horizontal and vertical) and thus also in primary productivity. They cite as evidence depleted nitrate and supersaturated oxygen in eddies. This conforms to evidence of enhanced primary production in eddies along the shelf edge derived from remote sensing imagery (Eslinger 1994). Indeed, eddies may have further biological significance as described by Schumacher and Stabeno (1994) in the context of pollock survival and production.
Biological Dynamics

Phytoplankton

The oceanic domain over the basin, the largest domain of the Bering Sea, is characterized as high nutrient/low chlorophyll (HNLC); as in much of the open North Pacific, surface waters always have concentrations of macro-nutrients, particularly nitrogen, sufficient for phytoplankton growth, yet phytoplankton biomass is consistently low. The condition has been explained in terms of iron limitation of phytoplankton growth, phytoplankton uptake kinetics and competition for several forms of nitrogenous nutrients (nitrate, ammonia, urea), and grazing (Frost 1987, Martin and Fitzwater 1988, Miller 1993, Banse 1995). Here, Shiomoto (chapter 15) emphasizes phytoplankton size structure in the basin and controls that have to do with dynamics and standing stocks of nutrients, particularly nitrate, ammonia, silicate, and iron. Picoplankton (< 2 µm) numerically dominate the floral community in the basin, although nano- and microplankton can contribute substantially to biomass and production. Shiomoto subscribes to the model of ammonium inhibition of nitrate uptake as the explanation for the small size of phytoplankton and the HN condition. He believes that silicate might further limit the size of plankton, since diatoms, which are generally larger, need it, and he discounts iron as the reason for low primary production. But he presents no measurements of iron, which apparently do not exist, so this remains an unanswered question.

There are related questions about the actual level of primary production in the basin. Sapozhnikov et al. (chapter 17) contend, as does conventional wisdom, that it is low compared to the shelf. But Maita et al. (chapter 16) believe that primary production in the basin is much higher than previously thought, up to 250 g C per m² per yr compared to earlier estimates that average just 60 g C per m² per yr (Springer et al. 1996). They ascribe the high production to the occurrence of three blooms each year and a low grazing stress by mesozooplankton, primarily calanoid copepods.

An extension of this issue is the question of what accounts for the Green Belt along the shelf edge (Springer et al. 1996), where primary production is higher than over either the shelf or the basin, including even the higher estimates of Maita. Various possibilities have been considered, such as upwelling, stabilization of the water column by the shelf break front, and one that invokes nutrient dynamics. Whereas the basin is a HNLC region where primary production clearly is not limited by nitrate, the euphotic zone of the shelf is depleted of nitrate during most of the productive season and clearly is not iron limited. Thus, at the interface of basin and shelf waters at the shelf edge, each may contribute essential nutrients—nitrate from basin waters and iron from shelf waters—forming an “Iron Curtain” that leads to the Green Belt phenomenon (P. McRoy, pers. comm.).

Over the shelf, such things are better known and have to do primarily with a deterministic production regime that depends on light intensity,
water column stratification, and nutrient supply. The annual production cycle typically begins with an ice edge bloom in the low-salinity buoyant layer near the retreating ice front (McRoy and Goering 1974, Niebauer and Alexander 1985). Net production can be intense, up to at least 13 g C per m² per day, but growth is generally short-lived because of rapid nutrient depletion in the thin stratified layer or because winds break it down (Niebauer et al. 1995). Essentially all of the production at the ice edge is lost to pelagic food webs because there are no grazers present at that time (Coyle and Cooney 1988).

The ice edge bloom is succeeded in most years by a second, more prolific bloom following deeper thermal stratification of the water column that persists until nutrients are stripped from the euphotic zone. Sukhanova et al. (chapter 22) point out the magnitude of interannual variability in production over the middle shelf that is driven by storms, as previously described by Sambrotto et al. (1986). Storms can effectively resupply nutrients to the euphotic zone through onwelling of deep water laterally across the shelf and vertical mixing of the water column. Storms account for 10-50% of total production, an important proportion of which is new (nitrate) production, and are thus the most important factor influencing the annual production budget.

Production over the eastern shelf is not especially high, with the bulk occurring during the spring bloom and little thereafter (Walsh and McRoy 1986). On the western shelf, however, Sapozhnikov et al. (chapter 17) estimate that post-bloom production amounts to 4-6 g C per m² per day, rates typical of growth during the bloom. They also note that it is fueled by ammonia and urea, i.e., recycled nitrogen, and thus does not contribute to export production.

So, which plants do all this growing? Sukhanova et al. (chapter 22) count 266 species among the planktonic flora of the Bering Sea. They say the high taxonomic diversity exists because of the great latitudinal expanse of the Bering Sea and its position sandwiched between the Arctic Ocean and temperate North Pacific. Patterns in distribution are related to both season and location (i.e., habitats): for example, picoplankton (diameter ≤2-2.5 µm) are more abundant by approximately an order of magnitude at most times over the outer shelf and basin than over the middle shelf and coastal zone. But they are small and contribute generally only a small to moderate amount (0.2-16%) to total biomass. Picoplankton might contribute more to standing stocks of phytoplankton if they were not grazed so efficiently by microheterotrophic protozoa. They are small and those that are not grazed sink very slowly so they contribute little to benthic production. Nevertheless, because they are grazed efficiently, their annual production is much higher than their biomass indicates, as might their contribution to the transfer of carbon and energy to higher trophic levels in the pelagic food web.

Issues of taxonomic composition of the phytoplankton community are major ones, since not all of the many species are of equal importance
in the scheme of food webs. During the PROBES studies in the 1970s it was proposed that as much as half of the annual primary production on the southeastern shelf was contributed by *Phaeocystis pouchetti*, a colonial haptophyte that is not efficiently grazed by herbivorous zooplankton (Kokur 1982). The other half was by diatoms that are among the favorite foods of grazers and were consumed almost completely. Temporal variability in production of various size classes of phytoplankton, or in the ratio of *Phaeocystis* to diatoms, therefore, could be expected to affect production at higher trophic levels. Data presented by Sugimoto and Tadokoro (1997) reveal considerable interannual and decadal variability in summer phytoplankton standing stocks in the Bering Sea, as well as intriguing patterns in the relationship of phytoplankton to zooplankton abundance that hint at changes in trophic dynamics of likely significance to food web structure and efficiency (Springer 1998).

**Zooplankton**

Unfortunately, there is not a chapter devoted to zooplankton, in spite of the crucial roles they play in marine food webs and the dynamic nature of their life histories and abundances at many time scales. It is not possible here to adequately cover such an important field but only to mention certain known or suspected facts about them.

Over the shelf, each of the domains has characteristic zooplankton communities and differential grazing stress is responsible for contrasting pathways of energy flow through regional food webs. The large calanoid copepods *Neocalanus cristatus*, *N. plumchrus*, *Eucalanus bungii*, and *Metridia pacifica* are efficient grazers but are restricted to the outer and oceanic domains because of physical fronts (Cooney 1981, Smith and Vidal 1984). Herbivorous zooplankton in the middle and inner domains are less efficient at harvesting phytoplankton of the spring bloom and a greater proportion of the production in these domains goes to the bottom than in the outer and oceanic domains (Cooney and Coyle 1982). Thus, benthic communities are much more developed in the middle domain than in the outer and oceanic domains, where pelagic food webs predominate (Walsh and McRoy 1986).

Zooplankton growth rates and biomass vary between years and over longer intervals (Vidal and Smith 1986, Sugimoto and Tadokoro 1997) as does the ratio of herbivorous to predatory species (Shuntov et al. 1996). The biomass of jellyfish on the eastern shelf has averaged an order of magnitude greater in the 1990s than in the 1980s (R. Brodeur, unpubl. data). Variability such as this is sufficiently great that it could be expected to influence production at other trophic levels.

Zooplankton biomass on the order of $2 \times 10^{12}$ g C per yr is advected annually from the Bering Sea to the Chukchi Sea, with roughly 70% of oceanic origin and the remainder from the shelf (Springer et al. 1989). Euphausiids and oceanic copepods transported in the flow support immense numbers of planktivorous seabirds on the northern shelf (Springer
The flux of zooplankton biomass is proportional to volume transport, as well as to seasonal standing stocks and annual production at the shelf edge, such that the long-term decline in transport through Bering Strait could be of significance to regional predators.

**Fishes**

Fishes have extremely high profiles because of their economic and ecosystem importance. They have been the focus of numerous major oceanographic research programs in the Bering Sea, beginning in the 1950s when Japan and Russia began exploring fishing grounds (e.g., Hokkaido University 1957-1970, Moiseev 1963-1970) and continuing with Processes and Resources of the Bering Sea Shelf (PROBES) in the 1970s and Fisheries Oceanography Coordinated Investigations (FOCI) and Southeast Bering Sea Carrying Capacity (SEBSCC) in the 1990s. As a result, the fisheries literature is large. A short list of recent examples with information on the Bering Sea includes the annual groundfish report of the National Marine Fisheries Service (e.g., NPFMC 1996), proceedings volumes of symposiums (e.g., Alaska Sea Grant 1989, 1997; Beamish 1995; Brodeur et al. 1996), and many journal articles cited here and in other papers in this volume.

One thing about fish which is very well known is that many populations in the North Pacific and Bering Sea are highly dynamic. They fluctuate in abundance because of commercial fishing pressure, in relation to weather and climate, and perhaps for reasons that involve some combination of fishing, climate change, and predator/prey interactions, including cannibalism (Wakabayashi et al., cited in Bakkala 1981; Wespestad and Fried 1983; Francis and Hare 1994; Quinn and Niebauer 1995; Ito and Ianelli 1996; Anderson et al. 1997; Wespestad et al., in press).

Another well-known fact is that fishes are critical prey of many species of seabirds, marine mammals, and other fishes (Hunt et al. 1981, Springer et al. 1986, Perez and Bigg 1986, Livingston 1993, Merrick and Calkins 1996) including the very species that have experienced the greatest declines in the Bering Sea and Gulf of Alaska in the past two decades (Steller sea lions, fur seals, harbor seals, red-legged kittiwakes, and black-legged kittiwakes). It is believed that a lack of one or more species of forage fish is the cause of the declines (Alaska Sea Grant 1993).

In this volume, two papers show how water temperature is important to fish distributions on the continental shelf—certain species prefer colder temperatures, while others prefer warmer temperatures (Wyllie-Echeverria and Ohtani, chapter 21; Brodeur et al., chapter 24). Cold shelf bottom water temperature in winter drives most species to deeper, warmer waters at the shelf edge, increasing predator-prey interactions (Favorite and Laevastu 1981). Interannual and decadal variability in air temperatures, water temperatures, and sea ice extent alter patterns of distribution and abundance of several species of forage fishes that in turn likely change important predator-prey relationships.
Issues of trophic interactions among fishes are particularly prominent, since fishes are by far the greatest predators of each other (Livingston 1993). One potentially significant relationship not discussed here is that of pollock cannibalism, which is thought to be important to recruitment dynamics and may be proportional to wind-driven transport of surface waters on the southeastern shelf (Wespestad et al., in press). According to this model, interannual and longer-term variability in winds over the Bering Sea could be a significant factor affecting production dynamics of pollock.

An important variation on the theme of dynamics concerns stock structure and discreteness of abundant, widespread species. Bailey et al. (chapter 26) reviewed questions of pollock stock structure, migrations, spawning, harvesting, and management. They point out that years of strong recruitment in the Bering Sea were strong in all regions (stocks) and that intermittent recruitment events are important to fluctuations in stock biomass. The issue of panmictic or discrete stocks is critical to appropriate management discussions, since there is growing evidence of a rich pattern of pollock stock structure.

The chapter by Sinclair et al. (chapter 23) helps to fill the major gap in our knowledge of fishes in the basin of the Bering Sea, where biomass rivals that on the shelf. The biomass of the lanternfish *Stenobrachius leucopsarus* alone is estimated to be in the order of $10 \times 10^6$ t in just the western portion of the basin, making it perhaps the most abundant species of fish in the Bering Sea. Distribution and abundance of fishes vary between years in the basin, as they do on the shelf, with little known about driving forces in either region.

Mito et al. (chapter 25) review diets of numerous species and size classes of fishes. The information will be valuable in describing interspecific relationships, predator/prey interactions, and food web structure, and therefore to models of individual species and the ecosystem.

**Benthos**

Nothing was written about dynamics of benthic organisms or communities and the significance of variability in populations of several species to an understanding of the larger ecosystem of the Bering Sea. Two conspicuous examples are pink shrimp and red king crabs. Forty years ago, the pink shrimp stock of the eastern shelf region northwest of the Pribilof Islands was removed by an intense commercial fishery, and it has not recovered. The stock was not insignificant—it was distinguished by "... its huge area covering up to 120 miles in length and 20-30 miles in width," with winter test fishery catches reaching "... 100 q/hr [=10,000 k/h], which is probably a world record with respect to absolute size" (Ivanov 1970). More recently, the collapse of the red king crab stock on the southeastern shelf in the 1980s was a major economic loss to many people. The cause is not agreed upon, and the failure of crabs to recover has not been explained.
Another clear signal from the bottom of the sea of ecosystem dynamics has been the prolonged increase of several species of flatfishes resulting from strong to exceptional recruitment of year classes spawned in the 1980s (NPFMC 1996). The contrasting decline of one species, Greenland turbot, adds additional uncertainty about the processes at work.

**Seabirds**

The most extreme case of population dynamics of seabirds in the Bering Sea was that of the flightless cormorant, at one time abundant in the Commander Islands but exterminated by Russian explorers by the early 1800s (Stejneger 1885). However, numerous other nesting species were severely depleted in the two centuries following the discovery of the Aleutian Islands and the introduction of foxes and other terrestrial mammals to them (Murie 1959, Bailey and Kaiser 1993). And one migrant species, the short-tailed albatross, which was formerly very abundant in the Bering Sea, was decimated on its nesting grounds off Japan and has become an extreme economic concern to the fishing industry because of restrictions on take imposed by the U.S. Endangered Species Act.

Detailed information on dynamics of seabirds in the Bering Sea does not begin until the 1970s, when colonies were first systematically censused. Populations monitored since then have experienced a variety of trends in abundance and productivity (e.g., Byrd et al. 1998). The chief concern has been dramatic declines of piscivorous red-legged and black-legged kittiwakes on the Pribilof Islands beginning in the mid-1970s in association with low productivity. This is particularly troubling in the case of red-legged kittiwakes due to their restricted numbers and breeding distribution: over 80% of the world population nests on St. George Island, where the decline was about 40% (Kildaw 1998). Other primarily piscivorous species on the Pribilof Islands, such as murres, the most abundant seabirds there, variously increased or decreased. Common murres on St. George Island were stable from the 1970s to the early 1990s and have increased by about 60% since then, while on St. Paul Island they declined by some 70% through the mid-1980s but have recovered by over 30% since. Thick-billed murres declined by about 30% on both islands through the mid-1980s, and may have increased by about 20% in the 1990s on St. George.

In contrast, these same four species all increased in the 1970s and 1980s in the western Aleutian Islands, indicating that conditions in that region of the Bering Sea were markedly different than on the eastern shelf near the Pribilof Islands. Hunt and Byrd (chapter 28) make this point, that seabird declines in the Bering Sea were unique to the Pribilofs, and they contend that the declines were precipitated by one or more large die-offs near the colonies. They further believe that a decline in carrying capacity of the Bering Sea has been limiting the populations by depressing reproductive output. In particular they cite a lack in diets of prey species with a high fat content, notably capelin.
Unfortunately, as the authors point out, there is no direct evidence of
die-offs of these seabirds of a magnitude that could cause such large de-
clines in abundance. For the population of red-legged kittiwakes on the
Pribilofs to have declined by half, some 75,000 birds would have to have
died. Likewise, a decline of 30% in numbers of thick-billed murres due to
die-offs would have required 500,000 deaths. These are very large num-
bers. Furthermore, it would be surprising if such a universal prey failure
occurred: the four afflicted species exploit a wide range of prey, including
myctophids and squid of the oceanic domain and pollock, capelin, sand
lance, and euphausiids of shelf domains. And, although kittiwakes are
restricted to foraging in surface waters, murres are capable of diving to
great depths. Still, the declines were abrupt and it is difficult to explain
them in terms other than high mortality of grown birds (adults and juve-
niles). Declining productivity alone appears to be inadequate, although as
Hunt and Byrd note, the appropriate population modeling has not been
done.

Another factor, which was discounted, is emigration. Seabirds gener-
ally are considered to be strongly philopatric, with low rates of emigration
and immigration. While this is true of adults, Divoky (1998) has shown
that juvenile black guillemots, a species closely related to murres, are
much more adventuresome. At Buldir Island in the western Aleutians, thick-
billed murres increased at a rate of 15% per year from 1991 to 1994 and
black-legged kittiwakes increased by 23% per year from 1975 to 1985.
These population growth rates apparently exceed those that can reason-
ably be accounted for by productivity alone (Nur and Ainley 1992). There-
fore, the increases at Buldir must have occurred in part from immigration.
The actual numerical increase of birds at Buldir does not equal the de-
crease at the Pribilof Islands, which allows for some mortality or immigra-
tion to other colonies in the Bering Sea where populations are not closely
monitored.

Information on planktivorous species, the auklets, is inadequate to
confidently conclude anything about trends in population abundance or
productivity (Hunt and Byrd, chapter 28). This is unfortunate, since these
birds are supported by the same species of mesozooplankton that are
critical links in the transfer of carbon and energy from phytoplankton to
most higher trophic levels in pelagic food webs, namely Neocalanus cris-
tatus, N. plumchrus, Calanus marshallae, and various species of euphausi-
ids. Elements of auklet breeding biology are very sensitive to fluctuations
in the prey availability (Roseneau et al. 1985, Springer et al. 1986) and as
a group they could provide an inexpensive, precise index of the abun-
dance of various species of zooplankton over a broad area of the Bering
Sea.

For the western Bering Sea, Shuntov (chapter 29) describes seasonal
abundances of seabirds and shows how numbers change. He believes that
fluctuations in abundance should be considered in time scales of 40-60
years, which correspond to broad changes in faunistic complexes. Shorter-
term climatic variability, including the scale of El Niño, is of little consequence by comparison. Yet, when time scales of change of murres and kittiwakes in the western Aleutian Islands and on the Pribilof Islands are examined, it would seem that certain shorter periods are highly relevant to dynamics. There, abundances have changed significantly (up and down) over periods of a decade or less. Indeed, if the hypothesis of Hunt and Byrd (chapter 28) is correct, interannual time scales may be quite significant.

**Marine Mammals**

Dynamics of marine mammal populations in the Bering Sea are considered in just one chapter. Loughlin et al. (chapter 27) describe movements of adult male fur seals out of Bering Sea in winter. In the North Pacific they generally follow the direction of surface circulation, which in the eastern subarctic takes them around the perimeter of the Alaska Gyre. The authors speculate that prey abundance is higher around the edge than in the center of the gyre, a view that is supported by a variety of other evidence (Springer et al., in press).

Population dynamics of marine mammals in the Bering Sea and greater North Pacific have been extreme in the past two centuries, mostly, or perhaps entirely as some would argue, due to the depravities of people. Steller sea cows were driven to extinction in the same period as was the flightless cormorant (Stejneger 1887). In the 1800s, bowhead and right whales were depleted by commercial whalers (Bockstoce and Botkin 1983) to the extent that bowheads have not yet reestablished a resident population in the Bering Sea and right whales remain one of the most endangered cetaceans in the world (Brownell et al. 1986). Polar bears were eliminated as a resident species in the Bering Sea when the last one was killed on St. Matthew Island in the 1890s (Hanna 1917). Others, notably fur seals, sea lions, walruses, and sea otters, have suffered intervals of heavy persecution with large swings in abundance as populations collapsed and then recovered (Kenyon 1962, 1969; Lander and Kajimura 1982; Fay et al. 1989). On the Pribilof Islands, walruses and vast numbers of sea otters were extirpated by humans and sea lions were greatly depleted. Since the end of World War II, other species of great whales—fin whales, sperm whales, and humpback whales—were nearly eliminated as well and are still at very low numbers.

Thus, the history of marine mammals in the Bering Sea is a sad one. And in some respects it has not improved in recent years. In the past two decades Steller sea lions have declined by approximately 80%, harbor seals appear to have declined by an undetermined but significant amount, fur seals are perhaps half to a third of their former abundance, and sea otter populations in the Aleutian Islands have collapsed (Lander and Kajimura 1982; York and Kozloff 1987; NMML 1994; Estes et al. 1998; NMFS, unpubl. data). The reasons for most of these recent declines are not known, and this has caused high anxiety over potential effects of commercial fisheries,
climate change, and historical changes in the ecosystem, e.g., the wholesale slaughter of whales. The classification of the bulk of the sea lion population as endangered in 1997 highlights the problem.

All is not doom and gloom, however. Bowhead whales have been recovering at a rate of 2% to 3% per year and the population numbered around 8,000 in 1993 (Zeh et al. 1995). Although none yet summer in the Bering Sea, as they did before exploitation, their summer range has apparently been expanding southward in the eastern Chukchi Sea from the Beaufort Sea where they found refuge from whalers in the nineteenth century (R. Suydam, pers. comm.). Gray whales have recovered (Buckland et al. 1993). Right whales have been sighted repeatedly in the southeastern Bering Sea during the past three summers, albeit in very small numbers (e.g., Goddard and Rugh 1998). Walruses have been abundant and seem to have been in equilibrium with carrying capacity since recovering from the most recent round of excessive commercial harvests from the 1930s to 1950s (Fay 1997). The status of populations of pagophilic seals—spotted, ribbon, ringed, and bearded—is not known, but at least there is no evidence of calamitous declines in numbers (L. Lowry, pers. comm.). It is not known if the decrease in sea ice extent in the Bering Sea during the past meteorological regime affected them.

**Humankind**

The book also stops short of considering dynamics of human populations in the Bering Sea, in spite of the fact that our heavy hand is known to have been responsible for many extreme changes and is suspected of causing or contributing to others. The invasions of explorers and pillagers from many nations since the 1700s left deep wounds, some of which have not yet healed. Commercial fisheries continue to alter habitats and populations in ways that are of concern to many people who find their livings and cultural identities in the sea or who wonder about unseen changes that may be accumulating in the ecosystem. Reassurances from fisheries managers have not allayed these fears.

**Modeling**

Francis et al. (chapter 20) tackle issues of ecosystem modeling and management. They make a strong case for paying close attention to scales of time and space when attempting to define ecosystems and understand how they work and why they vary. To do this, one must recognize patterns and use them as tools to identify scales—"... once patterns are detected and described, we can seek to discover the determinants of pattern, and the mechanisms that generate and maintain those patterns." They remind us that ecology has four dimensions—that time defines rates, and processes lose significance without reference to rates. Time has many scales and complex behavior will arise from the interaction of differently scaled processes.
For the Bering Sea, a final management strategy could range from single actions to a mix of actions combined with experimental manipulations (Francis et al., chapter 20). But this requires agreement that there is a problem with the current approach—if it isn't broken, don't fix it—and the resolve to try something new. It is likely that such an approach would lead to important new knowledge about individual species and the larger system, but it is less certain, as some argue, that it would be worth the economic disruption, political turmoil, or other probable consequences, especially if there is nothing inherently wrong with the status quo. And this comes back to our sense of pattern and scale—we are just beginning to know the magnitude of fluctuations in biomass over appropriate time and space scales. The work of Baumgartner et al. (1992) showed how greatly species vary naturally, i.e., not influenced by humans, yet we have limited knowledge about such things for the Bering Sea. We know only that in recent years of intense human involvement in the affairs of the Bering Sea ecosystem, there have been many big changes, some of which are disturbing.

Conclusions

The physical environment of the Bering Sea is intimately connected to the meteorology of the greater North Pacific Ocean and Western Arctic, which in turn has strong teleconnections with the El Niño Southern Oscillation over the equatorial Pacific. Interactions between the Aleutian Low and the Siberian High pressure systems complicate an understanding of ocean responses in the Bering Sea to atmospheric forcing. Nevertheless, there are clear indications that Bering Sea physics do adjust to state changes in atmospheric circulation over the North Pacific, e.g., regimes of sea ice that conform to meteorological regimes of the North Pacific. And just as the physical environment shifts between states, or more appropriately because of the shifts, the biosphere of the Bering Sea appears to shift between states as well. A strong case has been made in this regard for patterns in production of Pacific salmon and groundfish. Can this model be applied to other species and to the ecosystem as a whole? There is a variety of evidence that it can be (Francis et al. 1998, Springer 1998). However, past performance is no guarantee of future returns, and as the global climate continues to warm, predictions based on historical patterns may not be possible.

To improve on these models for the Bering Sea, however, a much broader net will need to be cast. For example, in most respects the basin of the Bering Sea continues to receive little scientific attention. The principal exception is that of circulation, which we now have a much improved understanding of and know to be much more dynamic than previously recognized. Circulation is highly variable between years and decades, and eddies are prominent features. They are thought to affect hydrography and nutrient distributions and deepwater renewal, primary production
and phytoplankton distributions, and in the shelf edge region might be important to pollock growth and survival. The formation of bottom water over the basin and the advection of bottom water into the basin from the North Pacific are important to oceanic circulation and nutrient budgets and may influence carbon and contaminant budgets as well.

Primary production over the basin may be higher than earlier estimates indicated. Higher production and an efficient biological pump would enhance the role of the basin in large-scale carbon budgets. Greater production over the basin would also help to balance carbon budgets for production at higher trophic levels there, e.g., by the apparently huge biomass of mesopelagic fishes and squids, as well as for walleye pollock that apparently must utilize shelf and basin regions to maintain a biomass as great as that to which it grew in the last decade.

Other questions remain about production in the basin. What limits primary production there and what accounts for the HNLC condition? Or, conversely, what accounts for the recent estimates of high production? What is the annual new (nitrate) production available for export? What are the roles of the several size classes of plankton, from picoplankton to mesoplankton, in food web dynamics? Likewise, we know very little about fishes and squids in the basin, primarily because there are relatively few commercially important species harvested there. If the estimated biomass of mesopelagic fishes in the western basin is applied to the entire basin, the resulting value would surpass that of any shelf species, including pollock. Does this apparently huge biomass of myctophids constrain secondary production and thus enhance primary productivity?

We still have only partial pictures of the overall distributions of many fishes, and much less knowledge of variability in distribution between years of contrasting physical conditions. The point was well made by Brodeur et al. (chapter 24) in their analysis of forage fish distributions between 1986, a cold year, and 1987, a warm year. The survey coverage they drew upon was not adequate to establish whether distribution, biomass, or a combination of the two was responsible for several of the interannual differences observed in the data. The reason for this is that standard surveys cover the region normally occupied by the bulk of the commercially important species and age classes, and excludes typically marginal habitat that is important in all years to some forage species (capelin, herring) and in some years to many or all age classes of others (pollock). A combination of economics and politics is responsible—broad-scale surveys are very expensive and the political climate between Russia and the United States has restricted the geographical coverage to territorial waters in most years. Even in the case of the broad Russian surveys, which were very revealing, important portions of the eastern inner shelf were omitted and thus species such as herring, capelin, and pollock still were not adequately sampled. This is not a minor detail, because we know that fishes do move around and fish abundance in particular areas is critical to
the success of predator populations. Yet in most cases we still do not know whether in years of low regional fish abundance it is because of diminished biomass, a change in distribution, or some combination.

The lack of comprehensive survey coverage also hampers our ability to answer questions posed by Bailey et al. (chapter 26) as revealed by their figures 4-6. In several cases an unknown, but possibly substantial, portion of the target group was outside the survey boundaries. It would seem that in the case of a species like pollock, which alone generates more than 1 × 10^9 $U.S. annually for the economies of the United States, Japan, Russia, Norway, and other nations, there could be proportional expenditures on such basic research elements as distribution and abundance and their relationship to a dynamic physical and biological environment.

We have made equally little progress toward an understanding of causes of population dynamics of species at higher trophic levels that may be initiated by fluctuations in abundance of species at the base of the food web or at intermediate levels. How do changes in the production base (phytoplankton and zooplankton community structure and production) influence rates and quantities of material and energy transferred to higher trophic levels? What are the magnitudes of fluctuations in these basic elements between years, between decades, and across space? Phytoplankton and zooplankton are sine qua non for most denizens of the oceans. Likewise, the biology of species at middle trophic levels is virtually unknown. These include the majority of forage species that are critical prey of many fishes, seabirds, and marine mammals, e.g., euphausiids, sand lance, capelin, herring, and myctophids, as well as species such as jellyfish that may play an important role in dynamics at higher and lower trophic levels.

There are emerging issues of inter-ecosystem interactions in the Bering Sea of potentially great significance that are not discussed here. One case is the dynamic benthic ecology on the eastern shelf and its relationship to pelagic production processes and variability. The rapid growth of most flatfish populations and continued low production of red king crabs and shrimp are conspicuous signs of broad state changes of importance to food web production and commercial interests. What is their connection, if any, to pelagic production processes and food web dynamics?

Another case in point is the collapse of sea otters in the Aleutian Islands (Estes et al. 1998). Sea otters are members of the kelp forest ecosystem, yet might interact at times in critical ways with members of the pelagic ecosystem. Changes in predator-prey relationships at numerous trophic levels form connections between the two ecosystems. As an extension of this notion, one can ask if there are emergent properties of the Bering Sea ecosystem as suggested by Francis et al. (chapter 20), such as inherent stability and resistance to external perturbations (e.g., climate shifts) by virtue of diverse and abundant long-lived species at high trophic levels. Was that compromised by the depletions of certain whales and fishes?
The effect of top-down interactions, originating with marine mammals, in structuring ecosystems in the Bering Sea is conspicuous in some cases (e.g., sea otter effects on kelp forests, and walrus and gray whale effects on benthic communities), but here and elsewhere in the open ocean it is poorly understood (Bowen 1997). If, for instance, killer whales are responsible for the collapse of sea otter populations in the Aleutian Islands and the cascade of effects in the nearshore ecosystem, what might have been their role in the earlier declines of sea lions and harbor seals, or their role in the recovery, or lack thereof, of these species? Killer whales are the apex predators in the Bering Sea and should not be ignored as a possible factor in dynamics of prey populations. What was the effect on trophic linkages in Bering Sea food webs of the rapid removal of most of the great whales in the 1950s to 1970s? Further development of multispecies models for the Bering Sea, e.g., Trites et al. (1999), may help answer such questions.

Much complementary information on features of the Bering Sea ecosystem obtained by scientists from several countries has not been integrated into a single body of knowledge. The various data sets cover a large amount of geography and a growing length of time. Understandably, much has been reported in national outlets in native languages and is thus not widely utilizable to scientists outside the individual countries. One of the notable examples is trophic dependencies of groundfishes: the paper by Mito et al. (chapter 25) summarizes much of the Japanese data and refers it in some degree to U.S. data but hardly to Russian data. One message from this overview is that there remains a need to integrate disparate data sets to see what knowledge might emerge on spatial and temporal variability in components of the ecosystem that are particularly important to present scientific, economic, and conservation concerns. One must bear in mind, however, that such analyses might show only the futility in attempting comparisons between data sets for a variety of reasons. If so there might yet be a silver lining to the exercise—it might provide an avenue for cooperation in designing sampling strategies and methods of data reduction for future studies that would allow comparisons to be made in a dynamic context, rather than only the descriptive ways now possible. A nice example where this has begun is presented in the paper by Sinclair et al. (chapter 23) in the compilation of Japanese, Russian, and U.S. data on mesopelagic fishes and squids.

**Recommendations**

- Do not think of the Bering Sea as pristine, or of the same ecological maturity as it was before being so greatly disturbed by people in the past two centuries. The history of excessive exploitation must be borne in mind when developing ecosystem models and when planning long-range conservation and management strategies.
Keep a broad view of spatial scales when thinking about the Bering Sea. It is characterized by a variety of habitats over the shelf and basin, each with particular dimensions. At the same time, the Bering Sea is but a small embayment of the North Pacific and tractable as a study area at this scale given innovative approaches.

Improve our limited knowledge of dynamics of important food web organisms, particularly phytoplankton and zooplankton, the base of the food web that determines in large measure biomass production at higher trophic levels, and forage species at intermediate levels that are critical prey of many fishes, seabirds, and marine mammals.

Give the basin a little respect—it is an integral part of the larger ecosystem but is virtually ignored.

Ensure that, in the continuing search for clues to ecosystem processes over interannual time scales, the information will be useful in identifying patterns over decadal and longer time scales.

Expand efforts to meld data on the Bering Sea held by Pacific Rim nations and to pool their financial and intellectual resources to more efficiently devise and undertake research of interest and value to all. This should include a much greater emphasis on translations of national literature so it can be entered into the collective knowledge pool.

Seek greater financial and in-kind participation by the commercial fishing industry in Bering Sea research.

Implement a multinational, long-term monitoring strategy for key ecosystem components. This could include, for example, expanding the boundaries of annual groundfish surveys; improving sampling of noncommercial forage species such as capelin, sand lance, myctophids, and squids; tracking primary and secondary production and the composition of phytoplankton and zooplankton assemblages across domains over time; initiating a dedicated whale censusing program; and making better use of existing databases to investigate change in distributions and abundance of species in both time and space.

The biodiversity of the Bering Sea is by many measures much reduced from former times—two species are extinct and a third nearly so, others have been locally or regionally extirpated, and still others exist at diminished abundances. There are many fewer examples of population increases, although these are dramatic. Thus, in a comparative sense the Bering Sea does not “team with wildlife” as in the past. Many of the changes were caused by people directly, while others may have been exacerbated by our actions. To the extent that changes in exploitation rates and practices might improve this situation, every opportunity
should be taken to test innovative management approaches that could benefit a broad spectrum of inhabitants and users.

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