

Anomalous conditions in the south-eastern Bering Sea 1997: linkages among climate, weather, ocean, and Biology

JEFFREY M. NAPP^{1,*} AND
GEORGE L. HUNT, JR²

¹NOAA, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle, WA 98115–0070, USA

²Department of Ecology & Evolutionary Biology, University of California, Irvine, Irvine, CA 92697, USA

ABSTRACT

In 1997, the Bering Sea ecosystem, a productive, high-latitude marginal sea, demonstrated that it responds on very short time scales to atmospheric anomalies. That year, a combination of atmospheric mechanisms produced notable summer weather anomalies over the eastern Bering Sea. Calm winds, clear skies, and warm air temperatures resulted in a larger-than-normal transfer of heat to surface waters and the establishment of a shallow mixed layer. In spring, significant new production occurred below the shallow pycnocline over the Middle Shelf, depleting the subpycnocline nutrient reservoir that normally exists during summer. Following the depletion of nitrate and silicate from the system, a sustained (≥ 4 months) bloom of coccolithophores (*Emiliania huxleyi*) was observed – a phenomenon not previously documented in this region. Summer Middle Shelf Domain copepod concentrations were higher for some species in 1997 than in the early 1980s. Warmer surface water and lack of wind mixing also changed the basic distribution of hydrographic regimes on the south-eastern shelf and altered the strength and position of fronts or transition zones where apex predators seek elevated food concentrations. The Inner Front was well inshore of its normal

position, and adult euphausiids (the primary prey of short-tailed shearwaters, *Puffinus tenuirostris*) were unavailable at, and shoreward of, the front in autumn. High shearwater mortality rates followed the period of low euphausiid availability. Some, but not all, of these anomalous conditions re-occurred in 1998. These observations are another demonstration that the structure and function of marine ecosystems are intimately tied to forcing from the atmosphere. Alteration of climatological forcing functions, expressed as weather, can be expected to have large impacts on this ecosystem and its natural resources.

Key words: apex predators, Bering Sea, biogeochemical cycles, climate change, *Emiliania huxleyi*, food webs, marine ecosystems

INTRODUCTION

The Bering Sea is a high-latitude marginal sea that connects the North Pacific and Arctic Oceans. Its continental shelves, surrounding a central basin, are well known for their living marine resources (National Research Council, 1996). These resources are harvested by Pacific Rim countries in their Exclusive Economic Zones, and resources within the basin are taken by Pacific Rim countries and others engaged in high-seas fisheries. At present, about one-half of the US fish and shellfish harvest comes from the eastern Bering Sea. Income derived from the world's largest single-species fishery, walleye pollock (*Theragra chalcogramma*), has an ex-vessel value of about US\$ 210 million. The region is also a productive summer feeding ground for many resident and migratory seabird and marine mammal species (Lowry and Frost, 1985; Schneider and Shuntov, 1993). These resources, in total, also sustain the Native peoples living around the perimeter of the Bering Sea and are part of traditions that have existed for at least 1000 years (National Research Council, 1996). Thus living resources of the Bering Sea play an important role in the economy of regional nations and the lives of people that live on its margins.

Owing to its economic and ecological importance, the Bering Sea is also the focus of attention for

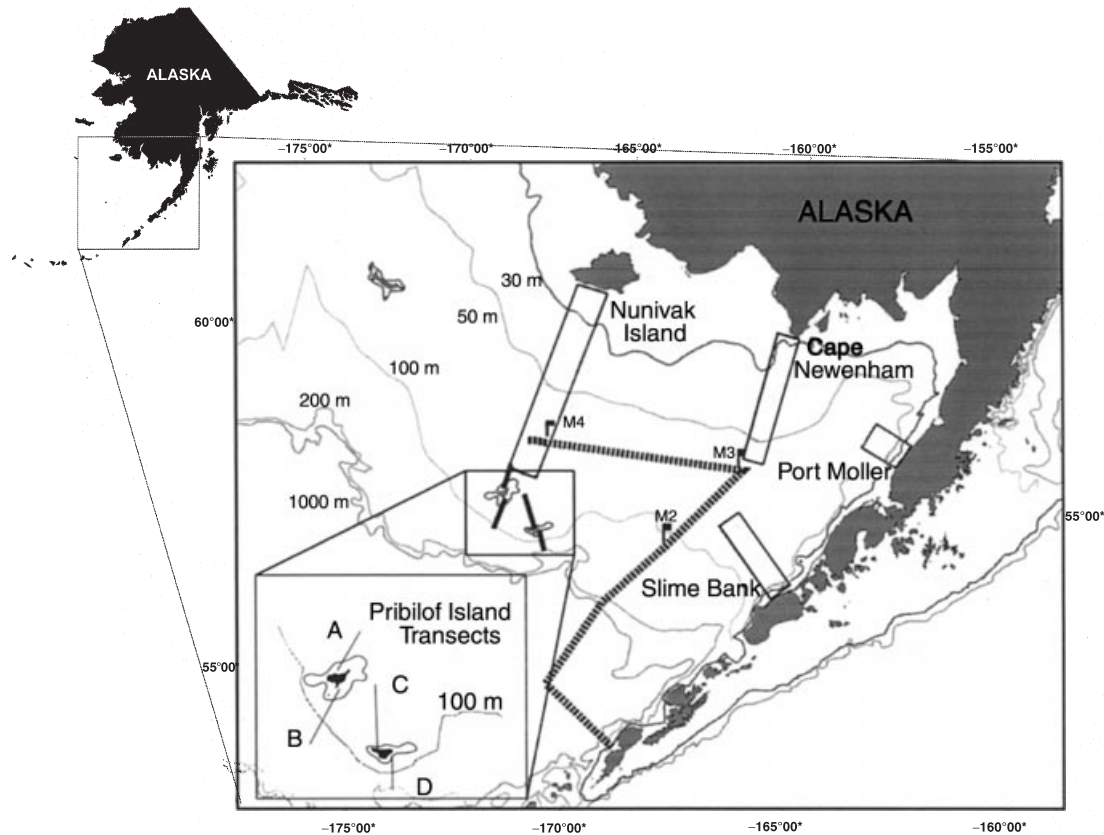
*Correspondence. e-mail: jeff.napp@noaa.gov

This series of manuscripts on recent events in the Bering Sea reflects Professor Michael Mullin's influence as Editor-in-Chief. He believed that ecosystem understanding required an integrative approach – that the whole presented in an integrated form would be more powerful than the sum of the individual parts. Thank you Michael for your support and teachings.

Received 15 March 1999

Revised version accepted 24 November 1999

Figure 1. Sampling coverage of the south-eastern Bering Sea shelf, 1997. Shown are the SEBSCC hydrographic lines (heavy dotted lines), moorings (flags), and Pribilof Islands hydroacoustic transects (inset), and the Inner Front cross-frontal survey areas (rectangles; Nunivak Is., Cape Newenham, Port Moller, and Slime Bank). The width of the rectangles represents multiple transects across the front, and the length represents offshore distance of the longest transect. Depth contour around the Pribilof Islands is the 30 m isobath.



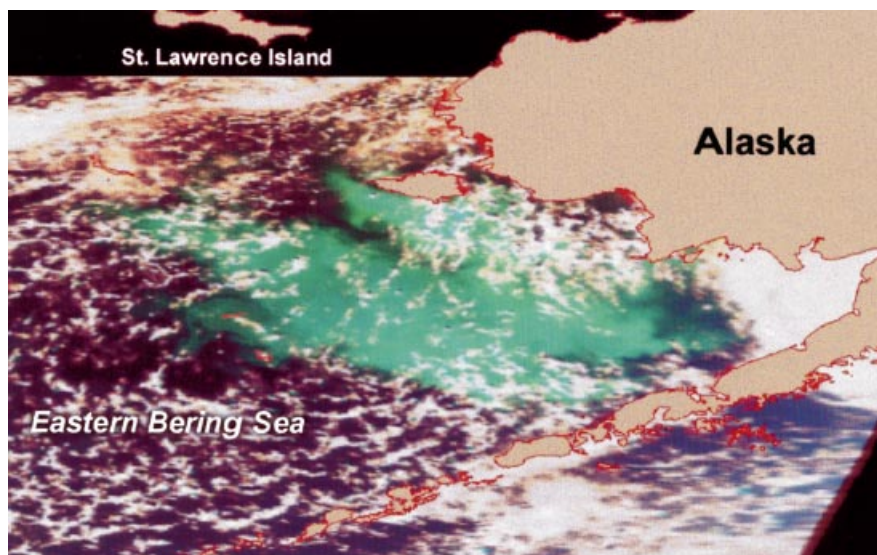
ecosystem research by many individual investigators as well as collaborative projects (e.g. PROBES – Walsh and McRoy, 1986; ISHTAR – McRoy, 1993; BS FOCI – Napp *et al.*, 2000). The present series of articles describes a collaboration between two research programmes: the NOAA, Coastal Ocean Program-funded ‘South-east Bering Sea Carrying Capacity (SEBSCC)’, and the NSF (Polar Programs)-supported ‘Study of Prolonged Production, Trophic Transfer, and Processes at the Bering Sea Inner Front’ (hereafter called ‘Inner Fronts’; Fig. 1). SEBSCC included modelling, monitoring, process, and retrospective studies to: (1) document the role of juvenile pollock (a nodal food web species) in the eastern Bering Sea ecosystem; (2) examine the factors that affect their survival; and (3) develop and test annual indices of prerecruit (age-1) abundance. Inner Fronts was designed to test the hypothesis that primary production in the vicinity of the south-eastern shelf inner front persists through summer, thereby providing food resources that support

apex predators (seabirds and marine mammals) longer there than in nonfrontal waters. The two programmes have four investigators in common, and both programmes were in the field in 1997, 1998 and 1999 when anomalous conditions were observed in the eastern Bering Sea. The following series of articles is a collaboration among scientists from the two programmes and a sharing of resources with the overall goal to provide a more complete description of the observed anomalies and their implications.

AN OVERVIEW OF 1997 ANOMALIES AND MECHANISMS

Prominent anomalies in the regional weather of the Bering Sea occurred in the spring and summer of 1997 owing to three factors operating on different time scales (Overland *et al.*, 2001). These factors include: a decadal trend towards higher warm-season atmospheric pressure over Alaska; a strong ridge of higher-

Figure 2. SeaWiFS composite true-colour image from 18 to 25 September 1997. The bloom covers most of the Middle Shelf and Coastal Domains and part of the Outer Shelf Domain. Area covered was estimated to be 2.1×10^5 km². Image courtesy of G. Feldman, NASA.



than-normal atmospheric pressure over the Gulf of Alaska during May (monthly); and a seasonal anomaly in the North Pacific atmospheric circulation in response to the El Niño of 1997/98. The May blocking ridge prevented most, but not all, weather systems from propagating over the eastern Bering Sea in 1997 (Overland *et al.*, 2001; Stabeno *et al.*, 2001). Together, these anomalies lowered the frequency and average strength of late spring and summer storms transiting the region, resulting in weaker wind mixing of the upper ocean and more calm, clear, summer days than is typical (Stabeno *et al.*, 2001). One exception to this was a late May storm that had a major impact on the system. The ocean responded to the lowered frequency and average June–July storm strength with a shallow mixed layer and anomalously high surface temperatures (4°C above the climatological mean). Light penetration below the pycnocline was initially high, and significant new production occurred at depth (Stockwell *et al.*, 2001). Sub-pycnocline primary production, coupled with decreased on-shelf transport of nutrient-rich slope water and a single strong storm in May (Stabeno *et al.*, 2001), resulted in exhaustion of phytoplankton macronutrients (nitrate and silicate) from below the pycnocline out to water depths of 70 m or more, a region that in summertime is normally a nutrient reservoir (Stockwell *et al.*, 2001). After nitrate and silicate became depleted from the surface waters, the coccolithophore *Emiliania huxleyi*, present in the water in May and June (Stockwell *et al.*, 2001), started a bloom in early July that persisted to at least

late October, covering 2.1×10^5 km² by September (Fig. 2; Sukhanova and Flint, 1998; Vance *et al.*, 1998). This was the first documented coccolithophore bloom in the Bering Sea (cf. Brown and Yoder, 1994) and was comparable in spatial extent and cell density to large-scale coccolithophore blooms in other parts of the world's oceans (Table 1). Note that the duration of the 1997 Bering Sea bloom was much longer than that of other *E. huxleyi* blooms of similar spatial extent.

Concurrent with the anomalous temperatures and the *E. huxleyi* bloom were elevated concentrations of some copepod species. In the Middle Shelf Domain, mean concentrations of *Acartia* spp., *Pseudocalanus* spp. and *Calanus marshallae* in 1997 were higher than in June 1981, during PROBES (Stockwell *et al.*, 2001). In the Inner Shelf Domain, *Acartia* spp. and *Pseudocalanus* spp. concentrations were higher in 1997 than in 1981, but there were no significant differences for *C. marshallae*, which normally is not abundant in that domain. Adult and juvenile euphausiid concentrations were low and not statistically different during the summers of 1997 and 1981.

Anomalous physical forcing also altered the position and geographical extent of particular hydrographic structures in the eastern Bering Sea. Ordinarily from April to September, the waters overlying the shelf can be divided into three hydrographic domains separated by transition or frontal zones (Coachman, 1986; Schumacher and Stabeno, 1998). Separating the stratified Middle Shelf Domain (between the 100 m

Table 1. Comparison of large-scale *Emiliania huxleyi* blooms.

Location	Size (km ²)	Duration of bloom (months)	Cell density (cells mL ⁻¹)	Lith density (liths mL ⁻¹)	Source
Coastal blooms	5–10 × 10 ⁴ 5 × 10 ⁵ 5 × 10 ⁵ 5 × 10 ⁵				Holligan <i>et al.</i> (1983) Balch <i>et al.</i> (1991) Brown and Yoder (1993) Brown and Podesta (1997)
Open ocean blooms	5 × 10 ⁵				Holligan <i>et al.</i> (1993)
Bering Sea	2.1 × 10 ⁵				This study
Gulf of Maine 1988		≈ 1	2.4 × 10 ³	1.3 × 10 ⁵	Townsend <i>et al.</i> (1994)
Gulf of Maine 1989		≈ 1	1.5 × 10 ³	3.0 × 10 ⁵	Townsend <i>et al.</i> (1994)
NE Atlantic 1991		1.1	1.0 × 10 ³	3.5 × 10 ⁵	Robertson <i>et al.</i> (1994)
Bering Sea 1997		4	3.1–4.7 × 10 ³	3–5 × 10 ⁵	This study

and 50 m isobaths) and the well-mixed Coastal Domain (< 50 m water depth) lies the Inner Front. Waters of the Coastal Domain are usually well mixed owing to a combination of wind mixing from above and tidal mixing from below (Coachman, 1986). In 1997, however, when wind energy was substantially lower than normal, the front moved shoreward of the 35 m isobath (Stabeno *et al.*, 2001). The front has been hypothesized to act analogously to structural fronts on the European shelf (Holligan, 1981) supporting enhanced, sustained primary production by continuous delivery of nutrients from below the stratified region to the surface (Hunt *et al.*, 1996). In 1997, this was not the case. By midsummer, dissolved inorganic nitrate and silicate were depleted below the pycnocline over the Middle Shelf from the surface to depths exceeding 70 m, and fluxes of nutrients to surface waters at the front were minimal (Stockwell *et al.*, 2001).

Many oceanographic fronts are loci for feeding activity by apex predators, either because of advection and concentration of prey, or because vertical flux of nutrients at the front supports enhanced production and associated food webs (Franks, 1992a, 1992b; Hunt *et al.*, 1999a). In the south-eastern Bering Sea, it is believed that a majority of short-tailed shearwaters have in the past foraged in the vicinity of the Inner Front (Schneider and Shuntov, 1993). During late summer 1997, abnormally high mortality of adult shearwaters was observed (11% of the surveyed population died; Baduini *et al.*, 2001). Starvation was the probable cause of death, because survivors were underweight. Between June and August, mean net body mass decreased by 19%, mean pectoral muscle mass decreased by 14%, and mean per cent body lipid decreased by 46% (Baduini *et al.*, 2001). By August 1997, their normal prey, adult euphausiids (*Thysanoessa raschii*), were scarce in the

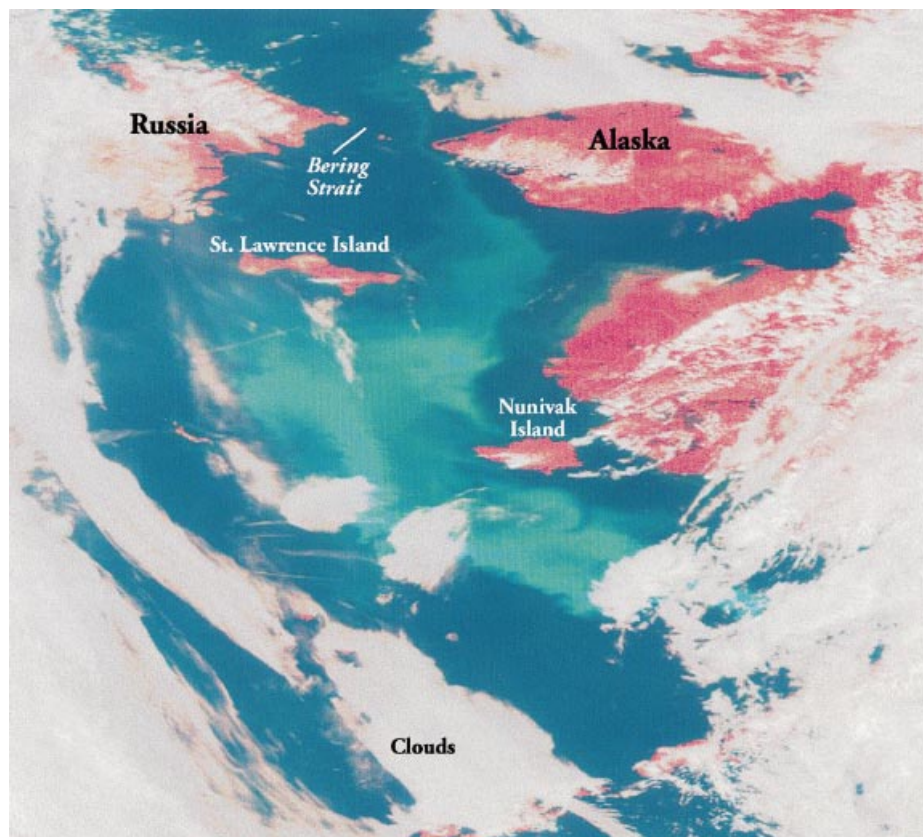
immediate foraging area (Baduini *et al.*, 2001; Stockwell *et al.*, 2001).

Coincident with our observations of starving sea-birds were lower-than-expected Pacific salmon runs in western Alaska (Kruse, 1998). Poor returns (by recent standards) of Bristol Bay sockeye salmon (*Oncorhynchus nerka*), Yukon River chinook salmon (*O. tshawytscha*), and summer chum salmon (*O. keta*) consisted of smaller-than-average fish. The runs, about one-half the expected number, caused severe economic and social hardships in western Alaska, as well as a request by the State for federal disaster relief.

Subsequent years – beyond 1997

A return to normal sea surface temperatures in the eastern Bering Sea began in November 1997 and was associated with frequent storms transiting the area (a strong Aleutian Low). Sea ice entered, then exited the south-east Bering Sea in February during a period of weak winds. Therefore sea ice had minimal influence on water column salt and heat content (Stabeno *et al.*, 2001). Summer anomalies in solar sea surface heating, which were strongly positive in 1997, were near zero in 1998. Thus 1998 summer sea surface temperatures were cooler than in 1997, but the average water column temperature was higher because sustained wind-driven mixing from winter until early June prevented isolation of cold water at the bottom (Stabeno *et al.*, 2001). Frequent storms during spring and summer 1998 resulted in stronger-than-average currents on the Middle Shelf and probably strong on-shelf transport of nutrients and salt. This is corroborated by observations of oceanic plankton just offshore of the inner front (K.O. Coyle, pers. comm.). The water column was also characterized by weak summer stratification over the middle shelf, and the inner front was more than 100 km further seaward than in 1997 (i.e. the coastal domain was much wider; Stabeno *et al.*, 2001).

Figure 3. SeaWiFS false-colour image from 24 July 1998 (S.I. Zeeman, pers. comm.). Note the filament of bloom-affected water heading towards the Bering Strait.



The coccolithophore bloom returned to the Bering Sea in 1998 (Hunt *et al.*, 1999b), 1999, and 2000, covering large portions of the south-eastern shelf by late summer. Aquamarine waters were observed earlier in 1998 than in 1997 (April rather than July), and a July 1998 SeaWiFS image showed a filament from the bloom extending northward along the Coastal Domain to Bering Strait (Fig. 3). In February of 1999, *E. huxleyi* was found in the south-eastern shelf nanoplankton, albeit in low numbers (S. Zeeman, pers. comm.).

In 1998, shearwater mean net body mass was almost the same as in 1997, but there were few observations of floating or beachcast carcasses. Although there appeared to be a decrease in shearwater abundance between 1997 and 1998, the densities were not different from estimates between 1975 and 1981 (Baduini *et al.*, 2001).

Bristol Bay sockeye salmon returns were also well below expectation in 1998, although the number of fish returning was still higher than historically low returns in the previous decadal regime (prior to 1978). In 1999, the sockeye salmon return was 39 million fish, about double that of the previous two years.

IMPLICATIONS

Ecologists and resource managers are attentive to two types of natural or anthropogenic forcing: oscillatory and secular. The Northern Pacific Ocean and Bering Sea are well known for atmospherically forced decadal oscillations in community structure and biomass ('regime shifts', e.g. Brodeur and Ware, 1992; Mantua *et al.*, 1997; Sugimoto and Tadokoro, 1997; Francis *et al.*, 1998). In addition, global climate models predict that global warming will have its largest impact at high latitudes (Cattle and Crossley, 1995). Already there are reports of alterations in the thickness and extent of Bering Sea and Arctic Ocean sea ice (Wadhams, 1995). Because of the interactions among the current decadal trend, ENSO events and interannual and intraseasonal atmospheric variability, more extreme oceanographic conditions may result in the future over the North Pacific (Overland *et al.*, 2001).

It is too early to determine if the anomalies observed in 1997 and 1998 were a harbinger for either class of system perturbation (a regime shift or global warming), although many of the observed anomalous

features were predicted to result from global warming (U.S. GLOBEC, 1996). Our observations, however, demonstrate the speed and magnitude with which parts of the Bering Sea ecosystem respond to alterations in atmospheric forcing.

The atmosphere drives upper ocean circulation, determining to a large extent the degree of nutrient transport or replenishment from the Bering Sea basin to the shelf. During 1997, weaker-than-average winds resulted in a decrease in nutrient flux from the continental slope to the shelf. The opposite occurred in 1998. Annual new production, however, was higher in 1997 and 1998 than during the late 1970s to early 1980s because phytoplankton had access to new nitrogen normally sequestered below the pycnocline (Stockwell *et al.*, 2001). If, in the future, transport onto the shelf were to decrease or be below the long-term average, then total primary production over the shelf would eventually be affected. This, in turn, would be expected to affect other ecosystem components.

Anomalous atmospheric forcing also had a noticeable impact on the structure and function of the Inner Front. In 1997, the front was weakened and spatially distant from a source of inorganic nutrients. If this becomes a recurring scenario, primary production at the front will decrease and foraging conditions for fish and seabirds may be less advantageous than at present.

The coccolithophore bloom was the most visually noticeable anomalous feature, and the only anomaly to occur in multiple years (1997–2000). Attenuation and scattering of light by whole cells and detached coccoliths alter submarine light fields (Voss *et al.*, 1998), thereby influencing competition among phytoplankton species and affecting the quality and quantity of light for subsurface visual predators (e.g. diving seabirds). Secchi disk depths inside bloom-affected waters were 2 m compared with 6 m outside the bloom. Coccolithophore blooms also dramatically alter water column reflectance. Thus, special algorithms are required for synoptic remote sensing of chlorophyll concentration (Balch *et al.*, 1989). Dense concentrations of coccolithophores alter regional biogeochemical cycles, making large positive contributions to calcite and dimethylsulphide production (Matrai and Keller, 1993; Brown and Podesta, 1997). In 1998, export of calcite and dimethylsulphide from the Bering Sea to the Arctic Ocean likely occurred, as evidenced by the filament of aquamarine water in Bering Strait in July (Fig. 3). Coccolithophore-dominated communities also alter marine food webs, sometimes favouring microzooplankton communities and longer pathways

for primary production to reach the prey of planktivorous fishes, seabirds and marine mammals (Nejstgaard *et al.*, 1997).

For those salmon species that remain over the eastern Bering Sea shelf while at sea (i.e. chinook and chum salmon, Kruse, 1998) or forage there during migrations (Nishiyama, 1974), the diminished runs and smaller fish suggest that the Bering Sea's carrying capacity has decreased. The observed high surface temperatures in 1997 may also have negatively affected outmigrating juvenile Bristol Bay sockeye salmon that began their oceanic phase in abnormally warm water (Welch *et al.*, 1998). These fish began to return to their natal streams in 2000.

Die-offs of shearwaters are thought to be infrequent in the south-eastern Bering Sea, but for the few times they have been observed they were usually associated with warm water events such as El Niño (Baduini *et al.*, 2001). Overland *et al.* (2001) hypothesize that because of interactions among the current decadal trend in atmospheric pressure, ENSO events, and interannual and intraseasonal atmospheric variability, oceanographic anomalies may be more extreme than in the recent past. If this is the case, then years of high mortality may dominate the population dynamics of this seabird.

Since the mid 1970s, the ability of the south-eastern Bering Sea shelf to support apex predators may have declined. Evidence for a decline includes fewer birds breeding on the Pribilof Islands (Hunt and Byrd, 1999) and recent decreases in the average size of adult salmon in western Alaska (Kruse, 1998). As the numbers of planktivorous marine mammals on the Bering Sea shelf continue to rebound from decades of whaling (Baretta and Hunt, 1994; Tynan, 1998) and biomass of another plankton predator (Scyphomedusae) remains high after recent rapid increases (Brodeur *et al.*, 1999), food may become a limiting resource for established populations such as walleye pollock (i.e. the opposite of the cascade hypothesis; Merrick, 1995, 1997; National Research Council, 1996). If this happens, then atmospherically-forced ecosystem perturbations that affect the production of zooplankton and their availability to apex predators may have an even greater effect on the structure of trophic webs than was observed in 1997.

In the following papers, we trace the origin and fate of the anomalies seen in 1997 from the regional atmospheric forcing conditions (Overland *et al.*, 2001), the effect of local weather on the physical structure and function of the shelf ecosystem (Stabeno *et al.*, 2001), the effects of the physical regime on the distribution and abundance of nutrients, primary

production and zooplankton (Stockwell *et al.*, 2001), to the impact that these anomalies in the ecosystem had on the trophic ecology and survival of an apex predator, the short-tailed shearwater (Baduini *et al.*, 2001). These papers focus on events in 1997 and refer to time series and historical time point measurements from previous studies to put the events of 1997 in context. In some instances, the papers include data from 1998. Conditions in 1998 were also anomalous, but in ways quite different from those encountered in 1997. Future publications will fully document the conditions encountered in 1998, and will integrate the full suite of data from 1997, 1998 and 1999.

ACKNOWLEDGEMENTS

Our research was supported by grants from the NOAA Coastal Ocean Program through Southeast Bering Sea Carrying Capacity (JMN) and the NSF Office of Polar Programs (GLH; OPP-9617287). We gratefully acknowledge their support. We thank our colleagues in the SEBSCC and Inner Front programmes for allowing us to write this synthesis to accompany their primary research articles. Reviews by N. Bond, R. Brodeur, A. Kendall Jr, K. Morgan, S. Stabeno and one anonymous reviewer improved the manuscript. This is Contribution Number S-354 to NOAA's Fisheries-Oceanography Coordinated Investigations (FOCI).

REFERENCES

- Baduini, C.L., Hunt, G.L. Jr, Hyrenbach, K.D., Coyle, K.O., Pinchuk, A. and Mendenhall, V. (2001) Die-off and starvation of short-tailed shearwaters due to an apparent lack of available euphausiids in the eastern Bering Sea during summer 1997. *Fish. Oceanogr.* **10**:117–130.
- Balch, W.M., Abbott, M., Eppley, R.W. and Reid, F.M.H. (1989) Bias in satellite-derived pigment measurements due to coccolithophorids and dinoflagellates. *J. Plankton Res.* **11**:575–581.
- Balch, W.M., Holligan, P.M., Ackleson, S.G. and Voss, K.J. (1991) Biological and optical properties of mesoscale coccolithophore blooms in the Gulf of Maine. *Limnol. Oceanogr.* **36**:629–643.
- Baretta, L. and Hunt, G.L. Jr (1994) Changes in the numbers of cetaceans near the Pribilof Islands, Bering Sea, between 1975–78 and 1987–89. *Arctic* **47**:321–326.
- Brodeur, R.D. and Ware, D.M. (1992) Interannual and interdecadal changes in zooplankton biomass in the subarctic Pacific Ocean. *Fish. Oceanogr.* **1**:32–38.
- Brodeur, R.D., Mills, C.E., Overland, J.E., Walters, G.E. and Schumacher, J.D. (1999) Evidence for a substantial increase in jellyfish biomass in the Bering Sea, with possible links to climate change. *Fish. Oceanogr.* **8**:296–306.
- Brown, C.W. and Podesta, G.P. (1997) Remote sensing of coccolithophore blooms in the western South Atlantic Ocean. *Remote Sens. Environ.* **60**:83–91.
- Brown, C.W. and Yoder, J.A. (1993) Blooms of *Emiliania huxleyi* (Prymnesiophyceae) in surface waters of the Nova Scotian shelf and the Grand Bank. *J. Plankton Res.* **15**:1429–1438.
- Brown, C.W. and Yoder, J.A. (1994) Coccolithophoroid blooms in the global ocean. *J. Geophys. Res.* **99**(C4):7467–7482.
- Cattle, H. and Crossley, J. (1995) Modelling Arctic climate change. *Phil. Trans. R. Soc. Lond. A* **352**:201–213.
- Coachman, L.K. (1986) Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. *Cont. Shelf Res.* **5**:23–108.
- Francis, R.C., Hare, S.H., Hollowed, A.B. and Wooster, W.S. (1998) Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. *Fish. Oceanogr.* **7**:1–21.
- Franks, P.J.S. (1992a) Sink or swim: accumulation of biomass at fronts. *Mar. Ecol. Progr. Ser.* **82**:1–12.
- Franks, P.J.S. (1992b) Phytoplankton blooms at fronts: patterns, scales and physical forcing mechanisms. *Rev. Aquat. Sci.* **6**:121–137.
- Holligan, P.M. (1981) Biological implications of fronts on the northwest European continental shelf. *Phil. Trans. R. Soc. Lond. A* **302**:547–562.
- Holligan, P.M., Viollier, M., Harbour, D.S., Camus, P. and Champagne-Philippe, M. (1983) Satellite and ship studies of coccolithophore production along a continental shelf edge. *Nature* **304**:339–342.
- Holligan, P.M., Fernandez, E., Aiken, J., Balch, W.M., Boyd, P., Burkill, P.H., Finch, M., Groom, S.B., Malin, G., Muller, K., Purdie, D.A., Robinson, C., Trees, C.C., Turner, S.M. and van der Wall, P. (1993) A biogeochemical study of the coccolithophore, *Emiliania huxleyi*, in the North Atlantic. *Global Geochem. Cycles* **7**:879–900.
- Hunt, G.L. Jr and Byrd, G.V. Jr (1999) Marine bird populations and carrying capacity of the eastern Bering Sea. In: *Dynamics of the Bering Sea*. T.R. Loughlin and K. Ohtani (eds). Alaska Sea Grant Press, AK-SG-99-03, Fairbanks, AK, pp. 631–650.
- Hunt, G.L. Jr, Coyle, K.O., Hoffman, S., Decker, M.B. and Flint, E.N. (1996) Foraging ecology of short-tailed shearwaters near the Pribilof Islands, Bering Sea. *Mar. Ecol. Progr. Ser.* **141**:1–11.
- Hunt, G.L. Jr, Baduini, C.L., Brodeur, R.D., Coyle, K.O., Kachel, N.B., Napp, J.M., Salo, S.A., Schumacher, J.D., Stabeno, P.J., Stockwell, D.A., Whitledge, T.E. and Zeeman, S.I. (1999b) The Bering Sea in 1998: the second consecutive year of extreme weather-forced anomalies. *EOS Trans. Am. Geophys. Union* **80**:561 and 565–566.
- Hunt, G.L. Jr, Mehlum, F., Russell, R.W., Irons, D., Decker, M.B. and Becker, P.H. (1999a) Physical processes, prey abundance, and the foraging ecology of seabirds. In: *Proc. 22nd International Ornithological Congress, Durban, South Africa*. N.J. Adams and R.H. Slotow (eds). Johannesburg: Bird Life South Africa, pp. 2040–2056.
- Kruse, G.H. (1998) Salmon run failures in 1997–98: a link to anomalous ocean conditions? *Alaska Fish. Res. Bull.* **5**:55–63.
- Lowry, L.F. and Frost, K.J. (1985) Biological interactions between marine mammals and commercial fisheries in the bering sea. In: *Marine Mammals and Fisheries*. J.R. Beddington, R.J.H. Beverton and D.M. Lavigne (eds). London: George Allen & Unwin, pp. 41–61.
- McRoy, C.P. (1993) ISHTAR, the project: an overview of Inner Shelf Transfer and Recycling in the Bering and Chukchi seas. *Cont. Shelf Res.* **13**:473–479.

- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. and Francis, R.C. (1997) A Pacific interdecadal oscillation with impacts on salmon production. *Bull. Am. Meteor. Soc.* **78**:1069–1079.
- Matrai, P.A. and Keller, M.D. (1993) Dimethylsulfide in a large-scale coccolithophore bloom in the Gulf of Maine. *Cont. Shelf Res.* **13**:831–843.
- Merrick, R.L. (1995) *The relationship of the foraging ecology of Steller's sea lions (Eumetopias jubatus) to their population decline in Alaska*. Ph.D. diss., Univ. Washington, Seattle, 172 pp.
- Merrick, R.L. (1997) Current and historical roles of apex predators in the Bering Sea ecosystem. *J. Northwest Atl. Fish. Sci.* **22**:343–355.
- Napp, J.M., Kendall, A.W. Jr and Schumacher, J.D. (2000) A synthesis of biological and physical processes affecting the feeding environment of larval walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. *Fish. Oceanogr.* **9**:147–162.
- National Research Council (1996) *The Bering Sea Ecosystem: Report of the Committee on the Bering Sea Ecosystem*. Washington, DC: Nat. Acad. Press, 324 pp
- Nejstgaard, J.C., Gismervik, I. and Solberg, P.T. (1997) Feeding and reproduction by *Calanus finmarchicus*, and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore *Emiliana huxleyi*. *Mar. Ecol. Progr. Ser.* **147**:197–217.
- Nishiyama, T. (1974) Energy requirement of Bristol Bay sockeye salmon in the central Bering sea and Bristol Bay. In: *Oceanography of the Bering Sea with Emphasis on Renewable Resources*. D.W. Hood and E.J. Kelly (eds). Fairbanks: University of Alaska, *Inst. Mar. Sci. Occ. Publ.* **2**:321–343.
- Overland, J.E., Bond, N.A. and Adams, J.M. (2001) North Pacific atmosphere and SST anomalies in 1997: links to ENSO? *Fish. Oceanogr.* **10**:69–80.
- Robertson, J.E., Robinson, C., Turner, D.R., Holligan, P., Watson, A.J., Boyd, P., Fernandez, E. and Finch, M. (1994) The impact of a coccolithophore bloom on oceanic carbon uptake in the northeast Atlantic during summer 1991. *Deep-Sea Res.* **41**:297–314.
- Schneider, D.C. and Shuntov, V.P. (1993) The trophic organization of the marine bird community in the Bering Sea. *Rev. Fish. Sci.* **1**:311–335.
- Schumacher, J.D. and Stabeno, P.J. (1998) Continental shelf of the Bering Sea. In: *The Sea*, Vol. 11. A.R. Robinson and K.H. Brink (eds). New York: J. Wiley & Sons, pp. 789–822.
- Stabeno, P.J., Bond, N.A., Kachel, N.J., Salo, S.A. and Schumacher, J.D. (2001) On the temporal variability of the physical environment over the southeastern Bering Sea shelf. *Fish. Oceanogr.* **10**:81–98.
- Stockwell, D.A., Whitledge, T.E., Zeeman, S.I., Coyle, K.O., Napp, J.M., Brodeur, R.D., Pinchuk, A.I. and Hunt, G.L. Jr (2001) Anomalous conditions in the southeastern Bering Sea: nutrients, phytoplankton, and zooplankton. *Fish. Oceanogr.* **10**:99–106.
- Sugimoto, T. and Tadokoro, K. (1997) Interannual–interdecadal variations in zooplankton biomass, chlorophyll concentration and physical environment in the subarctic Pacific and Bering Sea. *Fish. Oceanogr.* **6**:74–93.
- Sukhanova, I.N. and Flint, M.V. (1998) Anomalous blooming of coccolithophorids over the eastern Bering Sea shelf. *Oceanology* **38**:502–505. (translated from *Okeanologiya* **38**:557–560).
- Townsend, D.W., Keller, M.D., Holligan, P.M., Ackleson, S.G. and Balch, W.M. (1994) Blooms of the coccolithophore *Emiliana huxleyi* with respect to hydrography in the Gulf of Maine. *Cont. Shelf Res.* **14**:979–1000.
- Tynan, C.T. (1998) Coherence between whale distributions, chlorophyll concentration, and oceanographic conditions on the southeast Bering Sea shelf during a coccolithophore bloom, July–August, 1997. *EOS, Trans. Am. Geophys. Union* **79**:127.
- U.S. GLOBEC (1996) *Report on Climate Change and Carrying Capacity of the North Pacific Ecosystem*. Berkeley, CA: University of California. U.S. GLOBEC Rep. No. 15. 95 pp.
- Vance, T.C., Baier, C.T., Brodeur, R.D., Coyle, K.O., Decker, M.B., Hunt, G.L. Jr, Napp, J.M., Schumacher, J.D., Stabeno, P.J., Stockwell, D., Tynan, C.T., Whitledge, T.E., Wyllie-Echeverria, T. and Zeeman, S. (1998) Aquamarine waters recorded for first time in eastern Bering Sea. *EOS, Trans. Am. Geophys. Union* **79**:121 and 126.
- Voss, K.J., Balch, W.M. and Kilpatrick, K.A. (1998) Scattering and attenuation properties of *Emiliana huxleyi* cells and their detached coccoliths. *Limnol. Oceanogr.* **43**:870–876.
- Wadhams, P. (1995) Arctic sea ice extent and thickness. *Phil. Trans. R. Soc. Lond. A* **352**:301–319.
- Walsh, J.J. and McRoy, C.P. (1986) Ecosystem analysis in the southeastern Bering Sea. *Cont. Shelf Res.* **5**:259–288.
- Welch, D.W., Ishida, Y. and Nagasawa, K. (1998) Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming. *Can. J. Fish. Aquat. Sci.* **55**:937–948.