Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change

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ABSTRACT

We examined quantitative catches of large medusae from summer bottom trawl surveys that sampled virtually the same grid station on the eastern Bering Sea shelf using the same methodology every year from 1979 to 1997. This series shows a gradual increase in biomass of medusae from 1979 to 1989, followed by a dramatic increase in the 1990s. The median biomass increased tenfold between the 1982–1989 and 1990–1997 periods. Most of this biomass was found within the Middle Shelf Domain ($50 < z < 100$ m). The greatest rate of increase occurred in the north-west portion of this domain. Whether this dramatic increase in biomass of gelatinous zooplankton has resulted from some anthropogenic perturbation of the Bering Sea environment or is a manifestation of natural ecosystem variability is unclear. However, several large-scale winter/spring atmospheric and oceanographic variables in the Bering Sea exhibited concomitant changes beginning around 1990, indicating that a possible regime change occurred at this time.

Key words: Bering Sea, ecosystem change, physical–biological coupling, scyphomedusae

INTRODUCTION

The Bering Sea, in common with many other ocean regions (Aebischer *et al.*, 1990; Rothschild, 1995; McGowan *et al.*, 1998), has undergone major changes in its environment and biota in recent decades (Francis *et al.*, 1998; Livingston *et al.*, 1999). The continental shelf of the eastern Bering Sea is the second largest in the world, and provides rich food resources for large populations of higher-level resident (pollock, flatfish and shellfish) and transient (Pacific salmon, seabirds and marine mammals) taxa (Springer, 1992; National Research Council, 1996; Loughlin *et al.*, 1999).

The broad (>500 km) south-eastern Bering Sea shelf consists of three distinct Domains characterized by contrasts in water column structure, currents and biota (Coachman, 1986; Schumacher and Stabeno, 1998). These Domains include the Coastal (<50 m deep with weak stratification), Middle Shelf (50–100 m deep with strong two-layered stratification), and Outer Shelf (100–200 m deep with mixed upper and lower layers separated by slowly increasing density). The Coastal and Middle Shelf Domains are separated by a structural front (width of order 10 km) while the Middle and Outer Shelf Domains are separated by a broad ($\approx$100 km) transition zone called the Middle front (Schumacher and Stabeno, 1998). At times stratification can extend landward from the Middle Shelf to coastal waters, depending on the balance between solar insolation and turbulent mixing (Overland *et al.*, 1999b). The Domains provide distinct habitats for biota. The zooplankton community in the two shallower Domains is composed primarily of the small copepods and euphausiids, whereas in the Outer Shelf Domain and in the Oceanic Regime large copepods dominate (Vidal and Smith, 1986).

The dominant physical features affecting primary production include timing and extent of sea ice, variability in storm activity, and transport of nutrients onto the shelf (Schumacher and Stabeno, 1998; Schumacher and Alexander, 1999). The Bering Sea is influenced by both regional and hemispheric-scale atmospheric forcing (Mantua *et al.*, 1997; Schumacher and Alexander, 1999). Productivity varies temporally

on annual and interannual time scales and spatially, with the highest levels occurring in the Outer Shelf Domain and slope region (the Green Belt: Springer *et al.*, 1996). Both chlorophyll *a* concentrations and mesozooplankton biomass have undergone year-to-year and longer-period fluctuations, but they have remained high compared with more oceanic regions of the Subarctic Pacific (Sugimoto and Tadokoro (1998).

Although the zooplankton fauna of the Bering Sea has been studied in some detail (reviews: Cooney (1981) and Coyle *et al.* (1996)), one group representing the largest zooplankton size fraction – the medusae – have been poorly studied despite their potential importance to the Bering Sea. The only detailed work to date specifically on medusae was done in the early 1980s (Hamner, 1983), although their presence has been reported in many studies. In this paper, we report on a major change in biomass of medusae in the Bering Sea that has occurred since the late 1970s. We then discuss possible causes and implications of this change.

METHODS

Our data on medusae come from quantitative bottom-trawl surveys of the eastern Bering Sea shelf conducted by the Resource Assessment and Conservation Engineering (RACE) Division of the Alaska Fisheries Science Center (AFSC). These surveys began in 1972 and have continued annually to the present. The early surveys (1972–1974, 1976–1977) were of limited extent on the south-eastern shelf. A larger-scale survey was first performed in 1975 during the late summer and fall. Since 1979, the beginning of the time series used here, a standard area encompassing 627 400 km^2 from inner Bristol Bay to the shelf edge and from Unimak Pass to St Matthew Island has been completed during the summer period of June to early August. A systematic grid (37 × 37 km) of ≈356 stations was occupied each year with 30 min tows using a modified flatfish trawl with a mouth opening of ≈17 m wide × 2.6 m high (Bakkala, 1993). Mesh sizes graded from 10 cm near the mouth to a codend liner of 3.8 cm to retain small animals. Although these demersal tows are most likely to catch gelatinous zooplankton during deployment and recovery of the trawl, the consistency of the sampling allows construction of an index of their biomass through time (Brodeur *et al.*, 1999). Also, the trawl used from 1979 to 1981 was slightly smaller than the standardized trawl used since, but we believe the data gathered during that time is sufficiently comparable to the

subsequent surveys to illustrate the trend. Temperature data were collected at each station using either an expendable bathythermograph or a trawl-mounted micro-bathythermograph.

Catches less than about 1150 kg were sorted and weighed completely. Larger catches were subsampled before processing. Biomass density for each taxon was expressed as kg ha^{-1} of area swept by the trawl (distance fished × net width). Biomass estimates for the jellyfish were made by expanding the mean density within each of six strata to the total area of the strata and summing over all areas. Even though medusae are most likely to be captured during deployment or retrieval (as expressed above), the use of density is believed to be appropriate for the index displayed. Most references to density of pelagic zooplankton are expressed in weight per 1000 m^3 of water filtered. For purposes of comparison an average tow would filter ≈124 000 m^3. However, the actual water filtered during deployment and retrieval is unknown and therefore the index concept is more appropriate for our purposes.

Sea surface temperature (SST) anomaly fields were taken from the National Centers for Environmental Prediction (NCEP) Reynolds analysis that is based on a blending of satellite and *in situ* data (Reynolds and Smith, 1995). Meteorological fields are from the NCEP reanalysis project (Kalnay *et al.*, 1996).

We obtained the position of the ice edge (1972–1994) from the compact disc produced by the National Ice Center, the Fleet Numerical Meteorology and Oceanography Detachment, and the National Climatic Data Center. This data set contains information on the ice concentration and thickness from weekly satellite images. Since 1994, data were digitized from the Alaska Regional Ice Charts that are produced by the Anchorage Forecast Office of the National Weather Service.

RESULTS

Biomass of medusae on the eastern Bering Sea shelf was relatively stable from 1979 to 1989, but beginning in 1990, there was a dramatic increase in biomass until 1994, dropping in the cold year of 1995 (Fig. 1). Biomass increased again in 1996–97 owing mainly to an increase in the north-west Middle Shelf Domain (50 m < z < 100 m), with the highest value of the time series occurring in 1997. The increase in medusa biomass during the 1980s was confined mainly to the Middle Shelf Domain between the 50 and 100 m isobaths near the Alaska Peninsula (Fig. 2a, Fig. 3). In the more recent period (1990–1997), the bulk of the

Figure 1. Biomass index of jellyfish caught in bottom-trawl surveys on the eastern Bering Sea shelf from 1979 to 1997. The total catch for all six sampling strata is shown by year as well as the catch for only the south-east and north-west regions of the Middle Shelf Domain (see inset for locations of these regions).
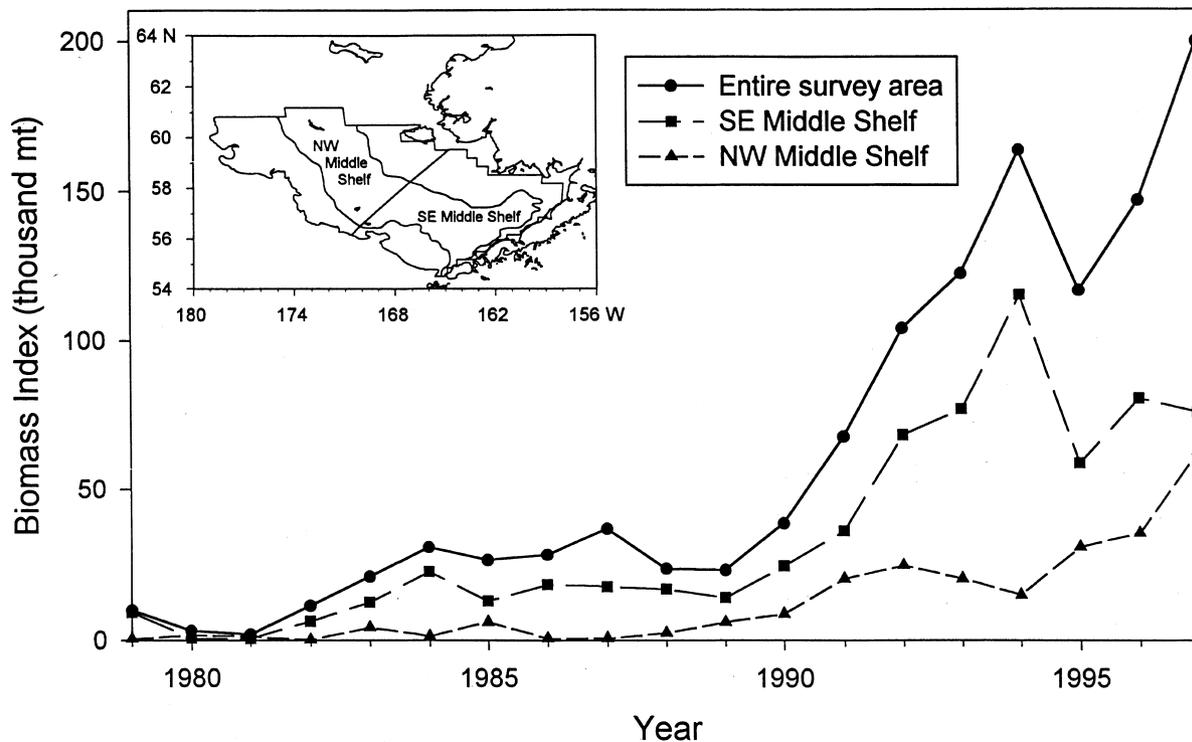

medusa biomass remained within the Middle Shelf Domain, but had spread to the north-west (Fig. 2b). Mean biomass (±SEM) was 0.54 (±0.07) kg ha^{-1} and 2.67 (±0.24) kg ha^{-1} for the periods 1982–1989 and 1990–1997, respectively. There was a significant (Mann–Whitney rank sum test; $P < 0.0001$) increase in median biomass (0.09–1.02 kg ha^{-1}) between these periods. A difference plot between the mean concentrations in the two time periods shows two regions of substantially increased biomass as well as several areas of decreased biomass in shallow coastal areas and over the slope (Fig. 4).

Jellyfish species were combined in the data because species composition data were not taken until 1994. Species commonly collected with the trawl in recent years include the scyphomedusae *Chrysaora melanaster* Brandt 1835, *Cyanea capillata* (Linnaeus 1758), *Phacellophora camtschatica* Brandt 1835, *Aurelia labiata* Chamisso & Eysenhardt 1821, and the very large hydromedusa *Aequorea aequorea* var. *albida* Bigelow, 1913. In most years, the medusae were probably primarily *C. melanaster* with fewer *C. capillata*. Many smaller species of hydromedusae are also present in the eastern Bering Sea during the summer (Cooney, 1981;

Hamner, 1983; Sugisaki *et al.*, 1998), but were not retained by the trawl gear.

The increased biomass of medusae may be related to changes in the general circulation of the atmosphere, which helps determine sea surface temperature (SST) and annual extent of sea ice. One way of quantifying these atmospheric circulation changes is through the use of teleconnection patterns. Teleconnection patterns are preferred spatial modes of variation in the atmosphere that may persist for months to decades. The dominant pattern over the Bering Sea in spring is referred to as the North Pacific (NP) index. This index has a north–south dipole in pressure, with higher pressure over the Bering Sea and lower pressure south of the Aleutian Islands in its positive phase and the opposite pattern (i.e. lower pressure over the Bering Sea) in its negative phase. The version of the NP index which we show was determined from the first rotated empirical orthogonal function (EOF) of the Northern Hemisphere 700 mb geopotential height field (Bell and Halpert, 1995). The yearly April–July mean value of the NP index is shown in Fig. 5(a); negative values of the index (blue) correspond to periods of lower 700 mb heights over the Bering Sea

Figure 2. Mean jellyfish catch per station for each grid station from the periods 1982–1989 (a) and 1990–1997 (b). Note that the greatest increase occurred mainly between the 50 and 100 m isobaths.
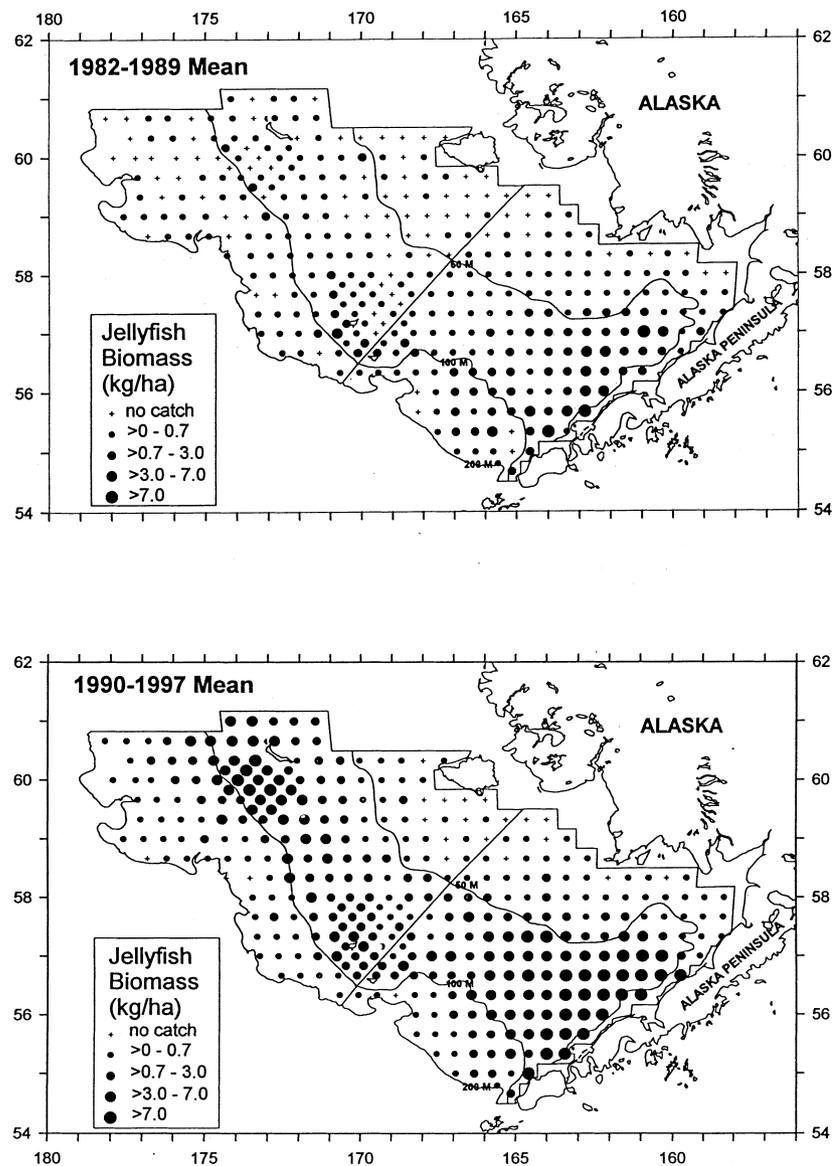

and a tendency for stormy weather. There is a shift toward more years with positive values of the NP (red) after the late 1980s, which implies reduced cloud cover and increased solar radiation at the sea surface. Figure 5(b, c) gives examples of the 700 mb geopotential height fields in years when the NP index is negative (1980, Fig. 5b) and positive (1997, Fig. 5c). Years with positive values of the NP tend to correspond to years with positive summer SST anomalies (Reynolds and Smith, 1995) owing to insolation, as seen in 1997 (Fig. 5d, e).

Using the time series of sea ice coverage, we constructed the difference between the mean spatial extent and duration (in weeks) of the eastern Bering Sea covered for the period 1990–1997 minus 1982–1989 (Fig. 6). Over the north-west Middle shelf, ice persisted from 0.5 to >3 weeks longer during the later period (associated with increasing jellyfish biomass) than during the earlier period (associated with low jellyfish biomass). Over the south-east Middle Shelf, the increase in duration was slightly less marked. Other changes in the temporal and spatial pattern of sea ice cover occurred between the two time periods. Between 1982 and 1997, ice arrived over the south-eastern middle shelf as early as the end of December and remained as late as the first week of May. The duration during a given year varied from a minimum of no ice (1987) to a maximum of 5 continuous weeks of

Figure 3. Mean catch of jellyfish by 50 m depth strata for the periods 1982–1989 and 1990–1997.
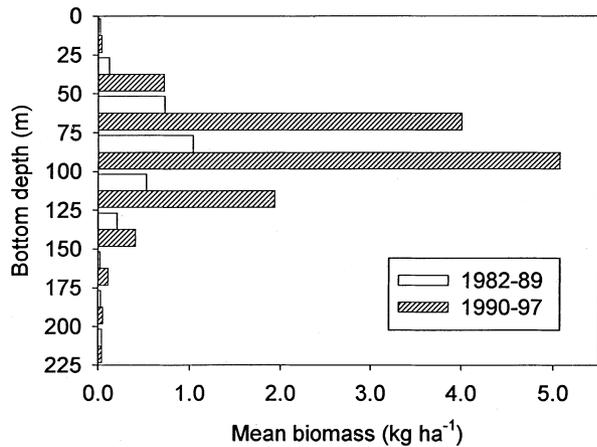
ice cover (1995). During the period between 1982 and 1988, three years had no ice, or it appeared and was gone in less than a week before mid-February. In the period 1990–1997, similar characteristics occurred only once (1996), and in six of the years ice persisted for several weeks after the beginning of March. Spatial changes in sea ice observed between 1982 and 1989 showed that sea ice generally (six of the eight years) did not extend west of 159°W and in 1987 ice was never present over the south-east Middle Shelf. From 1990 to 1997, ice generally (six of the eight years) extended west of 162°W.

DISCUSSION

Evidence is accumulating that there was an abrupt change in atmospheric and oceanic conditions in the North Pacific beginning around 1989–90 (Beamish *et al.*, 1999; Overland *et al.*, 1999a; Watanabe and Nitta, 1999). The effects of this recent climate shift have begun to be observed in marine populations (Sugimoto and Tadokoro, 1998; Welch *et al.*, in press). An increase in the biomass of jellyfish that may also be related to climate changes has also been reported for the western Bering Sea in the early 1990s (Shuntov *et al.*, 1996). Whether this increase in biomass of gelatinous zooplankton is a result of changes in the physical regime, such as that seen in the Antarctic (Loeb *et al.*, 1997), or is a consequence of human intervention in the Bering Sea, perhaps related to overfishing (Parsons, 1992; Botsford *et al.*, 1997; Pauly *et al.*, 1998), is equivocal at this time. The walleye pollock fishery removes millions of tonnes of production from the eastern Bering Sea each year and these removals have likely affected the pelagic ecosystem to some undetermined extent. It is clear that jellyfish, with their rapid growth rates and turnover times, are highly opportunistic and can easily become a dominant component of perturbed pelagic ecosystems (Mills, 1995; Kovalev and Piontkovski, 1998).

Atmospheric forcing on time scales from individual storms to decadal and longer oscillations, together with oceanic thermodynamics, results in sea ice formation and distribution over the eastern Bering Sea,
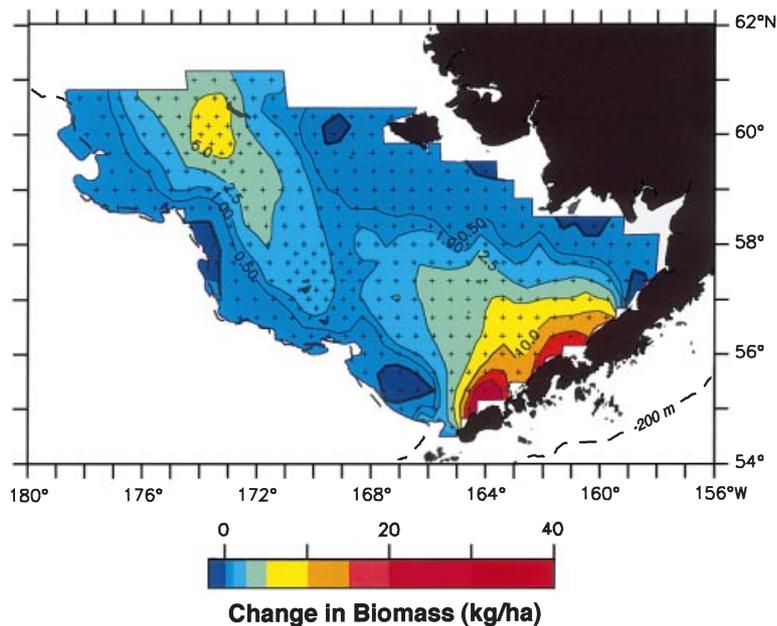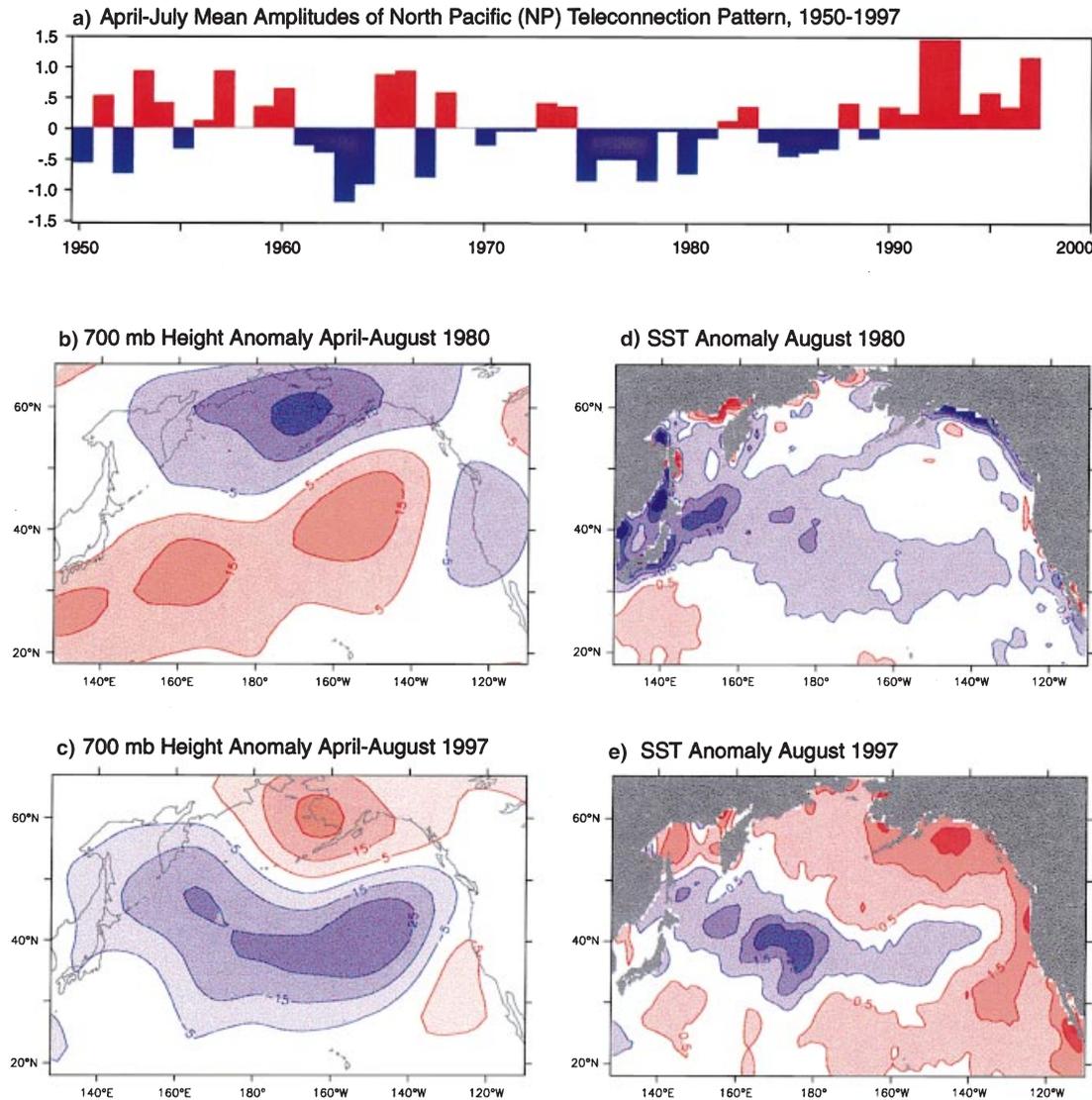

Figure 4. Contour of the difference (1990–1997 minus 1982–1989) in mean catch of jellyfish. The station locations are depicted as plus signs.

Figure 5. (a) The April–July mean value of the North Pacific (NP) index shown as the first-rotated empirical orthogonal function (EOF) of the 700 mb height field. A positive value corresponds to higher heights over the Bering Sea and lower heights for the region south of the Aleutian Islands. (b) and (c) The 700 mb height anomaly pattern (April–August) during a negative (1980) and positive (1997) phase of the North Pacific index. (d) and (e) The North Pacific sea surface temperature (SST) anomaly in August during the same two years. Areas of negative SST anomalies are shaded blue.

a) April-July Mean Amplitudes of North Pacific (NP) Teleconnection Pattern, 1950-1997

b) 700 mb Height Anomaly April-August 1980

d) SST Anomaly August 1980

c) 700 mb Height Anomaly April-August 1997

e) SST Anomaly August 1997

with persistence varying between extremes from less than a few weeks to more than five months (Schumacher and Stabeno, 1998). Associated with the presence of ice is a cold pool of water over the Middle Shelf Domain and the phytoplankton bloom associated with sea ice retreat can begin as early as March (Stabeno *et al.*, 1998). Given that there are sufficient hours of daylight, primary production occurs as the ice retreats (Niebauer *et al.*, 1995; Stabeno *et al.*, 1998). Time series observations show that chlorophyll *a* increases as temperature and salinity decrease (both

changes resulting from melting ice) throughout the water column (Stabeno *et al.*, 1998). Decreased density owing to cooling and stirring by ice motion can overcome the added buoyancy from ice melt. During years with early ice retreat, the spring bloom is set in May by solar heating. If ice persists into April, the sea ice can help stabilize the water column, resulting in an earlier bloom than normal (Alexander and Niebauer, 1981). The bloom associated with sea ice can account for a large fraction of the total annual phytoplankton production (Niebauer, 1991).
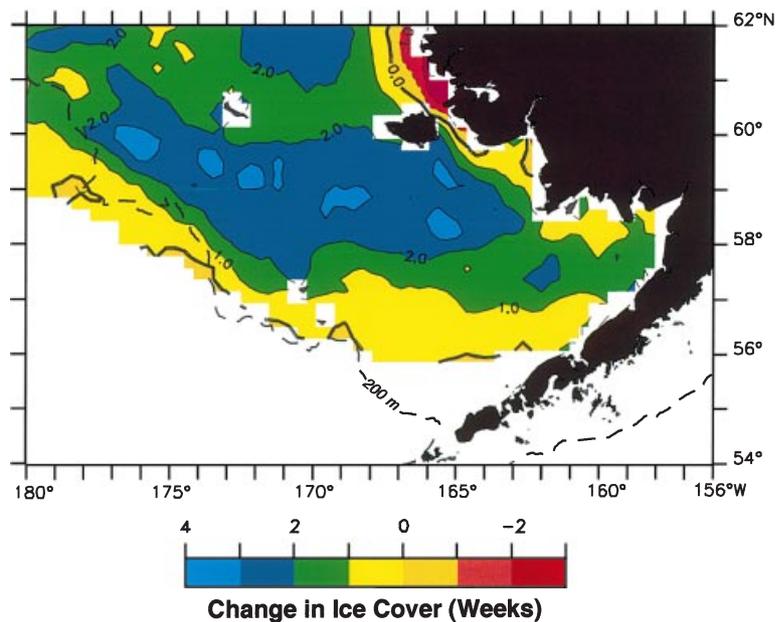
Figure 6. Contour of the difference (1990–97 minus 1982–89) in mean number of weeks that sea ice was present over the continental shelf. Contours are in weeks.

The coupled atmosphere–ocean–sea ice system and its attendant phenomena play an important role in the temporal and spatial characteristics of secondary production and help to determine the distribution of higher trophic level species (Wyllie-Echeverria and Wooster, 1998; Wyllie-Echeverria and Ohtani, 1999). If survival of early life stages of jellyfish depends on ice-associated phytoplankton blooms and the attendant secondary production, then in terms of both its persistence and spatial extent, more favourable conditions have existed since 1990.

Comparison of the fauna in the late 1990s with that first reported for the Bering Sea by Bigelow (1913) shows no major change in species composition. Increases in biomass were therefore assumed to be intrinsic to the ecosystem rather than due to invasion by a new species, as exemplified in the Black Sea earlier this decade by the dramatic increase of the ctenophore *Mnemiopsis leidyi*. This species competed with larval and juvenile fishes for food and ultimately contributed to the demise of several pelagic fisheries (Zaitzev, 1992; Shiganova, 1998).

Most scyphomedusae have an annual cycle, with young medusae asexually reproduced from benthic polyps in the spring (Arai, 1997). In temperate waters, the medusae usually persist in the water column into late fall. It is possible that benthic conditions affecting release of medusae from the polyps are important in the increase of jellyfish biomass reported here, yet nothing is known about the ecology of scyphozoan polyps in the Bering Sea. Therefore, the increase in

medusae biomass could have its origin in either the benthic or pelagic portions of their life cycle, or both.

The population increase over many years reported here could happen in several different ways. Increased settling success of embryos would yield greater numbers of benthic polyps, as would conditions that allow for greater asexual reproduction of polyps (which can create additional polyps as well as medusae) on the bottom, and could also increase the benthic population over time. In the water column, good feeding conditions could enable greater spring survival of young medusae, leading to more medusae collected later in the year. An increase in food or temperature would also result in even the same number of medusae showing faster individual growth rates and reaching a larger terminal size in the 1990s, thus increasing overall biomass. Our temperature data collected at the time of trawling show a slight though not significant increase in mean SST between our two time periods [6.73 (±0.12)°C to 6.91 (±0.14)°C for the periods 1982–1989 and 1990–1997, respectively]. However, the bottom temperatures actually decreased slightly [2.55 (±0.07)°C to 2.47 (±0.09)°C], possibly owing to colder initial water column temperatures in the spring from later ice melting. Temperature changes in the critical early development during spring could be more important than summer temperatures; however, we lack long time series of spring water column temperatures in the Bering Sea.

Gelatinous zooplankton may affect fisheries resources in ways that are both beneficial and dele-

Figure 7. Estimated mean numbers (±SEM) of age 1 fish caught in the bottom-trawl survey as an indicator of the size of the previous year's year class (data from J. Ianelli, AFSC, NMFS) and mean mesozooplankton biomass on south-east Bering Sea shelf from Japanese surveys (from Hokkaido University data reports – see Sugimoto and Tadokoro, 1998, for explanation of sampling methods). Dashed lines indicate overall mean of the time series.
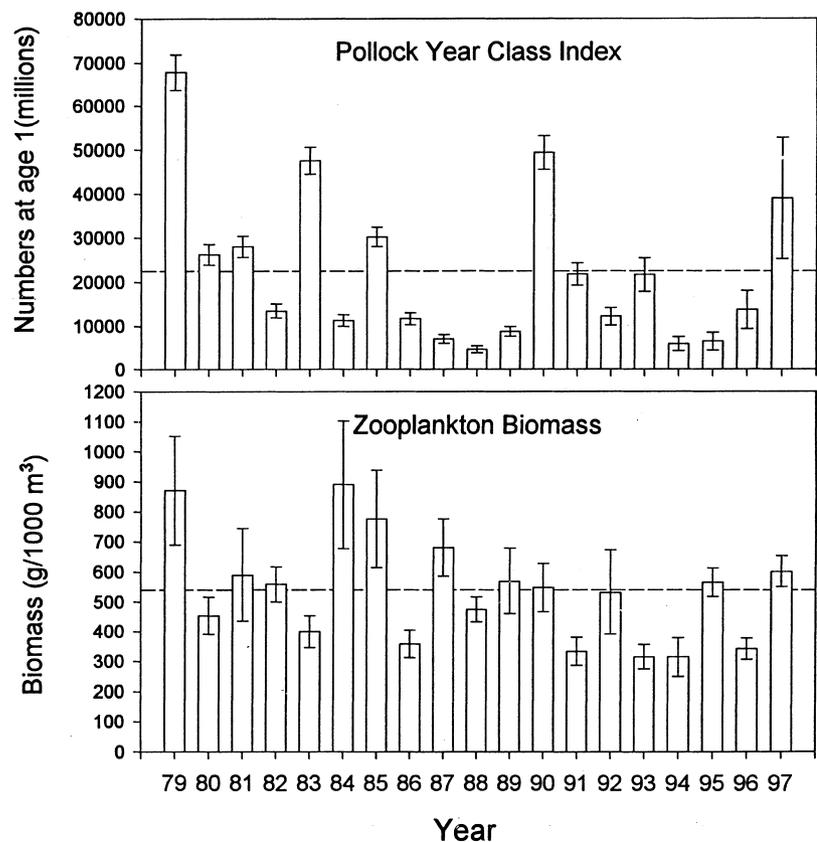
terious (Arai, 1988). Potential negative impacts include competition for limited resources with, or direct predation on, early life stages of fishes (Möller, 1984a, 1984b; Purcell, 1985). Our trawl collection methods precluded quantitative gut content analysis, but based on collections from fall cruises using midwater nets, some stomachs of our dominant species, *C. melanaster*, were found to contain juvenile walleye pollock (R. Brodeur, personal observation). Moreover, the $\delta^{13}C$ trophic level of *C. melanaster* was significantly higher than that of other small jellies and macrozooplankton and was similar to that of adult pollock, which implies that this species preys on young pollock and carnivorous zooplankton (H. Sugisaki, Tohoku National Fisheries Laboratory, Shiogam, Japan, pers. comm.). A congener that occurs in Chesapeake Bay, *Chrysaora quinquecirrha* (Desor), has been well studied in recent years; its diet includes copepods, cladocerans, fish eggs and larvae, ctenophores and hydromedusae (Larson, 1986; Purcell, 1992; Purcell *et al.*, 1994; Purcell and Cowan, 1995). However, this species is known to select fish eggs and larvae over other available prey (Purcell, 1997). It is probable that *C. melanaster* has a similar diet, as the available data suggest that scyphomedu-

san diets are fairly consistent at the genus level (summarized in Arai, 1997). *Cyanea capillata* is also known to have a varied diet consisting mainly of crustacean and gelatinous zooplankton (Fancett, 1988; Brewer, 1989; Båmstedt *et al.*, 1997).

Although scyphomedusae in the eastern Bering Sea have increased substantially in biomass over the past decade, no concomitant precipitous decline in the recruitment of any fish species has been observed in the Bering Sea (National Research Council, 1996). It should be noted, however, that one of the dominant fish species in the Bering Sea, walleye pollock, has had only one strong year class since 1989, although most of the year classes spawned in the 1990s were around the same magnitude as those of the 1980s (Fig. 7a). Summer zooplankton biomass on the south-east Bering Sea shelf has declined slightly in the 1990s (Fig. 7b), but it is difficult to ascribe this change either to predation by medusae or to climate change.

On the other hand, some fish species may benefit from the increase in large medusae. The juvenile stages of some fish species (Arai, 1988; Kingsford, 1993), including walleye pollock (van Hyning and Cooney, 1974; Hamner, 1983; Brodeur, 1998), are found associated with medusae and may utilize them as

shelter sites from intensive predation in the pelagic realm. It is too early to know how, if at all, the recent increase in large medusae will affect fish production in the Bering Sea, but continual monitoring and study of the ecology, including reproduction, feeding habits, and predators of this group is clearly warranted. Although jellyfish are fed upon by some sea birds in the Bering Sea (Harrison, 1984), few other predators on these large medusae have been identified, and they are generally excluded from food webs leading to commercially utilized species (Verity and Smetacek, 1996). Thus, we suggest that this biomass may represent a vast unavailable reservoir of carbon in this system which may contribute a substantial carbon flux to the benthos in the winter when they die and sink to the bottom.

CONCLUSIONS

Both physical and biological aspects of Arctic ecosystems are beginning to show the effects of climate change (Martin *et al.*, 1997; Tynan and DeMaster, 1997), and may show amplification of these effects relative to low-latitude systems (Walsh *et al.*, 1996; Thompson and Wallace, 1998). Model results (Shindell *et al.*, 1999) suggest that such an amplification may persist as a consequence of increased greenhouse gases. Based on quantitative trawl data collected in a consistent manner, we conclude that the biomass of large jellyfish has increased dramatically in the 1990s compared with the previous decade. Changes in atmospheric pressure patterns, translated to the Bering Sea through changes in extent and persistence of sea ice cover, are concurrent with the increase in jellyfish biomass, but the direct mechanisms linking the two remain unclear. Although we cannot rule out anthropogenic causes for the ecosystem perturbations we observed, our results provide an example of how climate change might influence an Arctic ecosystem, though we are not able to identify the underlying processes that transferred the physical changes through the ecosystem resulting in the observed increase of medusae biomass.

ACKNOWLEDGEMENTS

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