



Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts

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ABSTRACT

A steep increase in jellyfish biomass, primarily *Chrysaora melanaster*, over the eastern Bering Sea shelf was documented throughout the 1990s. Their biomass peaked in summer 2000 and then declined precipitously, stabilizing at a moderate level after 2001. The onsets of the outburst and decline coincided with transitions between climatic regimes. Specifically, 1989 marked the beginning of a period of moderate temperatures in the eastern Bering Sea, after the warm conditions of the late 1970s through the 1980s. Very warm conditions came to the eastern Bering after 2000, as evidenced by decreased ice cover in winter and increased total heat content and surface water temperatures in summer. We examined the relationships between jellyfish biomass and temperature, ice cover, atmospheric variables, current patterns, zooplankton biomass, and associated fish biomass in two regions of the Middle Shelf Domain (SE and NW) by use of Generalized Additive Models (GAM). We found density-dependent interactions within and between jellyfish biomass in the two regions related to the flow regime, and demonstrated a linkage between biophysical indices and jellyfish biomass. In particular, ice cover (SE and NW), sea-surface temperature in spring (SE) and summer (NW), and wind mixing (SE) all influenced jellyfish biomass. In addition, the importance of juvenile pollock biomass (SE) and zooplankton biomass (NW) suggest that jellyfish biomass was sensitive to the availability of prey. Since most climate models suggest continued warming is likely in the Bering Sea, the jellyfish populations may remain at moderate levels there but will likely shift northward into the Arctic Ocean.

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1. Introduction

Evidence is accumulating that gelatinous zooplankton populations have increased recently in many regions of the world (Graham, 2001; Mills, 2001; Purcell et al., 2001; Link and Ford, 2006; Kawahara et al., 2006; Lynam et al., 2006). Jellyfish are generally detrimental to fisheries because they feed on zooplankton and ichthyoplankton, and so are both predators and potential competitors of fish (Purcell and Arai, 2001), and because they interfere with fishing directly (reviewed in Purcell et al., 2007). The effects of jellyfish population outbursts on ecosystems and the economies that depend on them can be profound (Purcell and Arai, 2001; Brodeur et al., 2002; Daskalov, 2002; Lynam et al., 2005b, 2006). Factors including climate change, overfishing, eutrophication, and species

introductions have been suggested to favor jellyfish populations (Shiganova, 1998; Arai, 2001; Parsons and Lalli, 2002; Purcell, 2005; Attrill et al., 2007; Purcell et al., 2007).

One of the most dramatic documented increases in jellyfish has been on the eastern Bering Sea shelf, where a substantial increase in jellyfish biomass was observed throughout the 1990s (Brodeur et al., 2002). In the relatively unpolluted Bering Sea, only climate variability and fishing are probable causes for changes in the jellyfish population. The southeast Bering Sea shelf was relatively warm between 1999 and 2005, with winter depth-averaged temperatures over the southeastern shelf ~ 3 °C warmer than in the 1990s. Winters since 2000–2001 have had sea ice coverage typically 30–80% less than the climatological average (1972–2000); the retreat of this ice in spring since 2001 was not only earlier, but also more rapid than average (Overland and Stabeno, 2004; Grebmeier et al., 2006). This anomalous warmth has been associated with below-normal sea level pressure (SLP) and

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below-normal winds from the north during winter, and hence a tendency for more mild maritime air and fewer outbreaks of frigid continental air. In addition, wind conditions have favored greater transports of relatively warm water from the south into the Bering Sea through Unimak Pass (Stabeno et al., 2007). The summers between 2000 and 2005 also were warm, averaging ca. 2 °C warmer than during the late 1990s. This summer warming appears to have been due to a carry-over of heat from the unusually warm winters combined with summer weather conditions, which have featured above-normal SLP, and hence reduced wind stress and anomalously strong solar heating of the water column. The sea-surface temperature (SST) on the southeast Bering Sea shelf during June through August of 2002–2005 was more than 0.7 °C warmer than any other 4-year period extending back to 1948, based on a record from the National Center for Environmental Prediction (NCEP).

During the last decade, the warm spring and summer sea-surface temperatures in the eastern Bering Sea have had significant impacts on the marine ecosystems. Massive blooms of the coccolithophorid, *Emiliana huxleyi*, have occurred in most summers since 1997, major shifts in the species composition and biomass of gelatinous and meso-zooplankton have occurred in summer, and populations of pinnipeds and several species of seabirds nesting at the Pribilof Islands have declined (Brodeur et al., 1999; Stockwell et al., 2001; Hunt and Stabeno, 2002; Napp et al., 2002; Schumacher et al., 2003; Coyle et al., in press).

Variations in climate, particularly temperature and salinity, have been linked to variations in jellyfish abundance in a number

of studies (Lynam et al., 2004, 2005a; reviewed in Purcell, 2005; Attrill et al., 2007). Jellyfish populations are opportunistic, responding quickly to changes in the physical and biological milieu, both by increasing production rates of young jellyfish from the benthic polyp stage, and by increased feeding, growth, and reproduction of medusae in good conditions. Our hypothesis is that climate-induced changes in ocean biotic and abiotic conditions caused variations in the jellyfish population in the Bering Sea by affecting the reproduction, survival, and growth of large jellyfish, primarily *Chrysaora melanaster*. Connections between environmental factors and abundance and survival of various terrestrial and aquatic organisms have been elucidated recently by use of Generalized Additive Models (GAM) (e.g., Guisan et al., 2002; Logerwell et al., 2003; Ciannelli et al., 2004). Herein, we use GAM to explore possible connections between the dramatic changes in jellyfish biomass over the past three decades and physical and biological conditions in the eastern Bering Sea.

2. Methods

Trawl collections were made at each of 356 stations arranged in a grid pattern (36 km × 36 km) during daylight hours from June through August of each year by the Resource Assessment and Conservation Engineering (RACE) Division of the Alaska Fisheries Science Center (Brodeur et al., 1999, 2002). The trawl, which had a 26.5 m headrope and 34.1 m footrope with graded mesh (10 cm at the mouth to 3.8 cm in the codend), was towed on the bottom

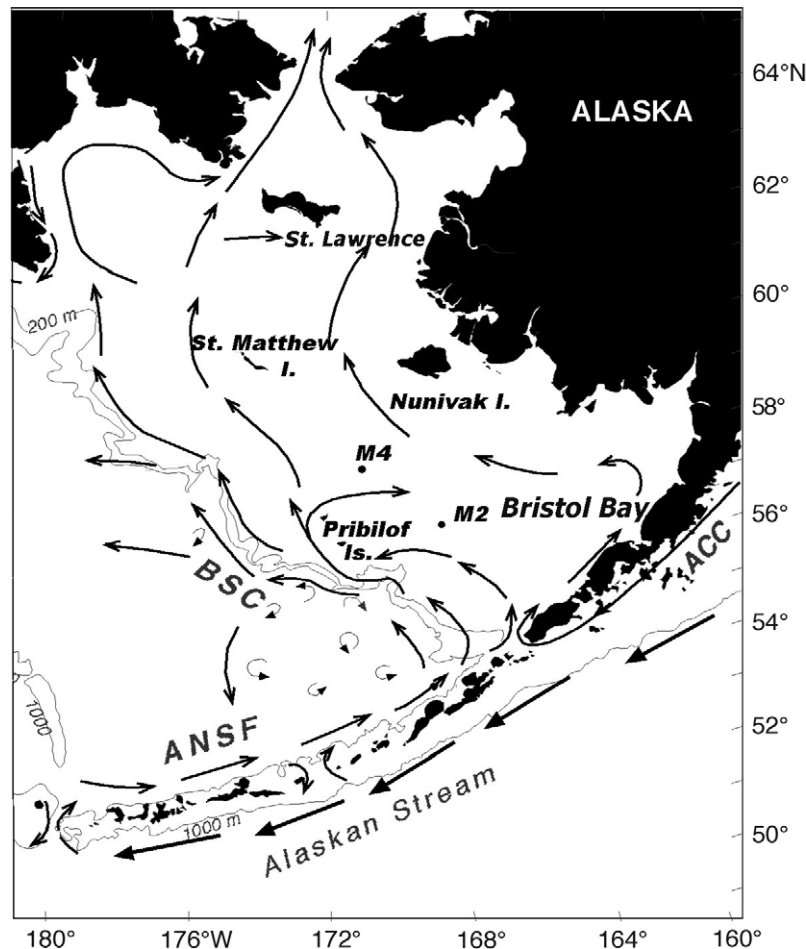


Fig. 1. Map of the eastern Bering Sea showing major currents, locations of the two moorings (M2 and M4) referred to in the text, and the 200, 500, and 1000 m isobaths. Also shown are the dominant coastal currents in the region including the Alaska Coastal Current (ACC), Aleutian North Slope Flow (ANSF), and Bering Slope Current (BSC).

for 30 min at 5.4 km h⁻¹ (Hoff, 2006). The net height was approximately 2.5 m above the bottom when fishing, but the trawl remained open and fished throughout the period of deployment and recovery. Catches of all large jellyfish (bell diameters >50 mm) were weighed at sea and standardized to kg ha⁻¹. Station depths ranged from 15 m in Bristol Bay (southeast corner of survey area) to nearly 200 m along the shelf break (western edge of survey area; Fig. 1). All tows were done during daylight. Since many of the jellyfish are distributed in the water column (30–40 m mean depth; Brodeur, 1998; Brodeur et al., 2002) above the headrope of the trawl, the biomass measurements presented here are considered an index of relative abundance that is comparable among stations and years.

The total biomass was estimated for six major geographic regions: inner, middle and outer shelf for the SE and NW regions. Two of these, the Southeast (SE) and the Northwest (NW) Middle Shelf domains accounted for, on average, 80%, and no less than 50%, of the total biomass over the 28-year period. Although taxonomic data were not collected on the jellyfish caught, species composition data from recent years suggest that most of the biomass (>90%) consisted of one species, *C. melanaster* (Brodeur et al., 2002; Acuna, unpublished data).

We looked for relationships in biomass changes within the two regions with region-specific physical and biological variables (Table 1; Fig. 2) using Generalized Additive Models (GAM). These are nonlinear regression techniques in which the relationships between the response variable and the forcing variables are modeled with nonparametric smooth functions (Hastie and Tibshirani, 1990; Wood, 2004, 2006). When using GAM, it is unnecessary to specify the type of relationship between the forcing and response variables *a priori*, because these are determined from the data. Specifically, given a response variable y and a set of m forcing variables x (covariates), the relationship between the two is established by

$$y_i = \alpha + \sum_{j=1}^m g_j(x_{ji}) + e_i.$$

The g_j are smooth nonparametric functions, typically natural cubic splines (Green and Silverman, 1994). ‘Smooth’ means that the function $g_j(x_{ji})$ is continuous (no jumps), and it has continuous first and second derivatives (no abrupt change of the slope). In the

case of cubic regression splines, each smooth is determined as an expansion of k basis functions and by the respective linear coefficients:

$$g(x) = \alpha + bx + \beta_1|x - x_1^*|^3 + \beta_2|x - x_2^*|^3 + \beta_3|x - x_3^*|^3 + \dots + \beta_k|x - x_k^*|^3.$$

The x^* are ‘knots’ located within the range of the x covariate. The number of the basis functions (k) is proportional to that of the knot locations ($k - 2$) and determines the level of roughness (i.e., ‘wiggliness’) of the resulting smooth, with a rougher fit corresponding to more basis functions and knots. In recent GAM applications, the degree of smoothness can be simultaneously and objectively estimated by minimizing the generalized cross validation (GCV), a measure of the leave-one-out mean predictive square error (Green and Silverman, 1994).

To guarantee that the model is identifiable (i.e., that there is a unique set of functions describing the relationships between forcing and response variables), each smooth estimate is constrained to average to 0 over the entire data set, i.e. $\sum_{i=1}^n g_j(x_{ji}) = 0$, where n is the sample size. Thus, to scale the model prediction back to the level of the response variable, an intercept term (α , typically equal to the mean of y) is added to the sum of all the smooth terms. The error terms e_i are generally assumed to be independent and identically distributed with zero mean and common variance.

The SE and NW regions were analyzed separately because the distribution maps clearly indicated the presence of two distinct centers of distribution (Fig. 4), and because the biomass of these two centers did not appear to fluctuate in concert across the middle shelf. Jellyfish biomass data were available for 1975 and 1979–2005, although statistical analysis and modeling was conducted only through 2004 due to lack of some environmental variables for 2005 (Fig. 2). To homogenize the variance and guarantee normality of the data, we log-transformed the dependent variable, jellyfish catch per unit effort (CPUE).

We applied a forward selection strategy to both the SE and the NW GAM regressions based on the minimization of the GCV, a measure of the model prediction error. Covariates were added one at a time in the model, in the order given in Table 1. The order in which covariates were included in the model reflected our prior knowledge of the variables affecting interannual variability of

Table 1
Names, descriptions and sources of the variables used in the Generalized Additive Modeling (GAM)

Variable name	Description and source
nwbiom sebiom	Catch per unit effort (CPUE) of jellyfish from quantitative bottom trawl surveys of the eastern Bering Sea conducted by the Alaska Fisheries Science Center (AFSC). Standardized jellyfish biomass (kg ha ⁻¹) calculated for the southeast and northwest regions of the Middle Shelf Domain
sesprtemp nwsprtemp	March–May sea-surface temperature at 57°N, 164°W (southeast region) and 59°N, 171°W (northwest region) derived from a National Centers for Environmental Prediction (NCEP) reanalysis. When ice is present, values represent the estimated temperature of the ice surface
sesumtemp nwsumtemp	June–August sea-surface temperature at 57°N, 164°W (southeast region) and 59°N, 171°W (northwest region) derived from a NCEP reanalysis
wstressna wstressmj	The along-peninsula component of the wind stress (N m ⁻²) at Unimak Pass (54°N, 165°W) for the periods November–April and May–June From the Bering Sea Climate website http://www.beringclimate.noaa.gov/index.html
wmixmay wmixjj	Wind mixing indices represent the average value of friction velocity u^3 for the period 1–31 May near St. Paul Island (57.1°N, 170.2°W) and for the period June–July at NOAA Mooring 2 (57°N, 164°W); from Bering Sea Climate website
currentlag	Distance (km) of the ending position from the center of the NW jellyfish aggregation (assumed to be 60°N, 172°W) that Ocean Surface CURrents Simulation (OSCURS) model drifters launched from the Unimak area (55°N 165°W) traveled from simulated launch (February 1) to retrieval (May 31); lagged by one year. Drifters ending south of the launch site were given negative values. From: http://las.pfeg.noaa.gov/las_oskurs/main.pl
icecover	Ice cover index constructed from a combination of ice-related parameters from multiple sources from Bering Sea Climate website which corresponds with the atmospheric forcing in winter and appears to be the primary factor controlling cold pool extent in summer
iceretreat	The day of ice retreat is defined as the number of days after 15 March for which sea ice coverage in the area 56–58° N, 163–165° W exceeds 10%. The date of ice retreat is most sensitive to the forcing in spring, and primarily impacts the nature and timing of the spring phytoplankton bloom on the shelf (Hunt and Staben, 2002). From Bering Sea Climate website
mszoop oszoop	Biomass (mg m ⁻³) of zooplankton on the Middle Shelf (mszoop) and the Outer Shelf (oszoop) based on summer sampling by Hokkaido University (HU) Research Vessel <i>Oshoro maru</i> . Provided by N. Shiga (HU) and J. Napp (AFSC)
nwpollock sepollock	Juvenile (<19 cm in length) walleye pollock biomass CPUE (kg ha ⁻¹) collected from the same surveys as the jellyfish in both middle shelf regions. Data provided by Dan Nichol (AFSC)
nwforage seforage	Forage fish complex (Pacific herring, eulachon, and capelin) biomass CPUE (kg ha ⁻¹) collected from the same surveys as the jellyfish in both middle shelf regions. Data provided by Dan Nichol (AFSC)

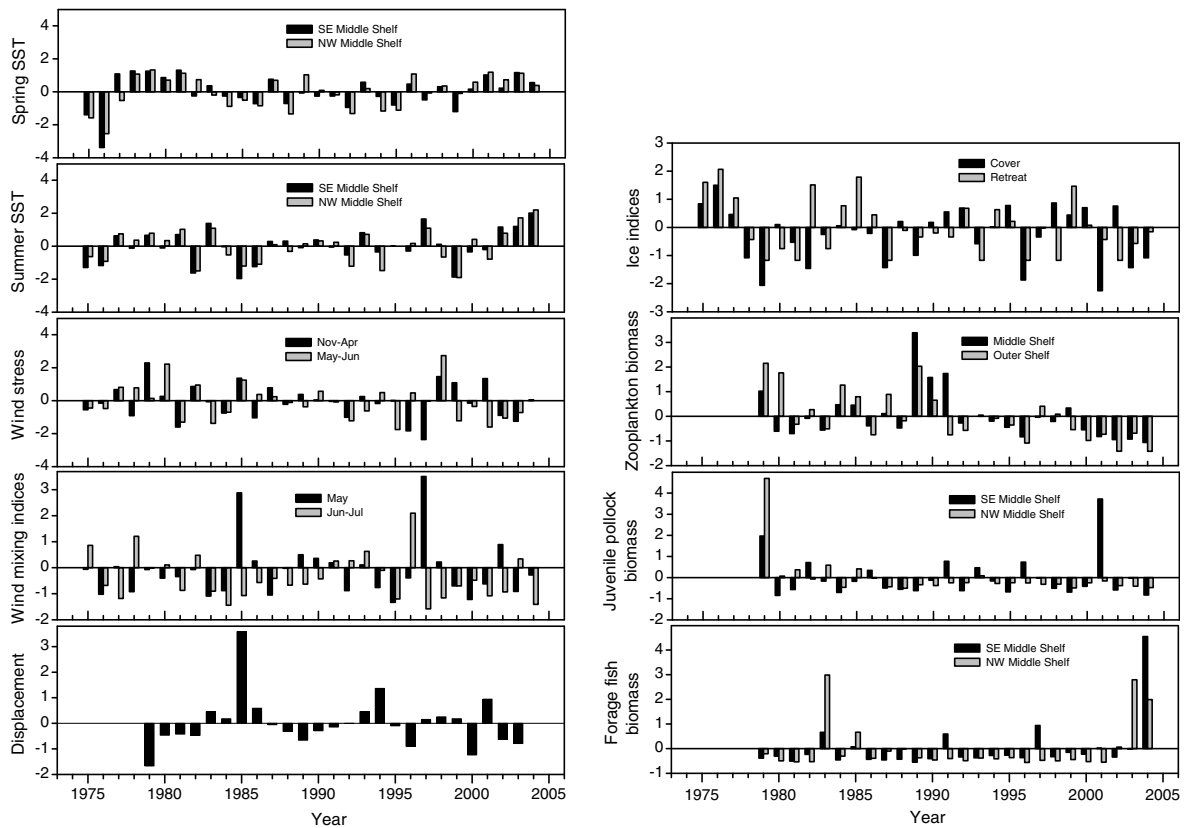


Fig. 2. Standardized anomalies of the physical and biological variables used in Generalized Additive Models (GAM) of jellyfish biomass in the Bering Sea. See Table 1 for a description of each variable and its source. (A) Spring (March–May) and (B) summer (June–August) sea-surface temperature anomalies based on climatological means from the period 1948–2004, (C) winter and spring wind stress, (D) wind mixing, (E) current displacement, (F) Bering Sea ice cover and ice retreat indices, (G) zooplankton biomass over the middle and outer shelf, (H) age-1 juvenile walleye pollock, and (I) combined forage fish abundance in trawl surveys over the continental shelf.

jellyfish biomass. A covariate was retained if it caused a decrease of the model GCV. Two covariates expressing the same physical or biological quantity, but in a different time of the year or units (e.g., spring and summer sea-surface temperature, ice cover and retreat) were never included simultaneously in the same model. To avoid excessive parameterization of the term smoothers, the degrees of freedom of each covariate term were limited to 4. If the addition of a covariate caused an increase of the significance term (i.e., p -value) of another covariate above 0.05, the latter term was dropped from the model if its removal caused a decrease of the model GCV.

To assess the goodness of fit of the final SE and NW jellyfish models, we simulated the entire time series of jellyfish biomass from the initial values and from the environmental forcing parameters used the GAM analysis. For example, in a year t , the SE jellyfish biomass was derived from the co-occurring (year t) observed environmental conditions and the predicted SE jellyfish biomass in the year $t - 1$. In the NW simulations, we used the predicted SE jellyfish biomass from the preceding year. In addition, the error of both models (i.e., residuals) was added to the predictions and the final results were the average of 500 replications.

3. Results

The catch of all medusae combined among all regions was less than 50×10^3 m each summer from 1975 to 1990 (Fig. 3). It rose quickly in the 1990s and averaged around 150×10^3 m. In 1999, the mean catch of 4.213 kg ha^{-1} ($SE = 0.359$) was about 20 times that in 1982. The catches nearly doubled again in 2000 due to seven unusually large catches primarily within shallow stations in

Bristol Bay, all of which exceeded the highest previous catch per station. The catch plummeted in 2001, and has remained at a moderate level during the subsequent four years (Fig. 3). In the early period of low jellyfish biomass (1982–1989), the largest biomass was mainly in the Southeast (SE) Middle Shelf Region (Fig. 4). In the escalating phase, jellyfish biomass increased in the Northwest (NW) Middle Shelf Region as well. At the peak (2000), biomass was high in both the SE and NW Middle Shelf Regions and extended into the SE Inner (<50 m depth) Shelf Region. In the declining phase, biomass was equally low in the SE and NW. Since 2001, jellyfish biomass has been greatest near the Alaska Peninsula and northwest of the Pribilof Islands, at the division between SE and NW regions (Fig. 4).

From a GAM analysis, we found that the SE jellyfish biomass was mainly correlated with the SE jellyfish biomass in the preceding year, with abiotic conditions in spring (i.e., ice cover, spring sea-surface temperature, wind mixing in May), and with biotic conditions in summer (i.e., juvenile walleye pollock, Fig. 5). The resulting SE model fit well with the data ($R^2 = 0.896$; Table 2). The relationship between juvenile pollock biomass and jellyfish in the SE was nonlinear with saturation toward high values of pollock biomass (Fig. 5). The possible saturation effect at the highest values of jellyfish biomass in the preceding year on the current jellyfish biomass suggests compensation, and an overall reduction in biomass growth as the overall biomass increased. Note that the biomass growth rate is proportional to the difference between two consecutive values of jellyfish biomass, and that negative density dependence or compensation is defined by a decrease of jellyfish biomass growth rates in spite of an increase of jellyfish biomass. Moderately cool to warm spring surface temperatures

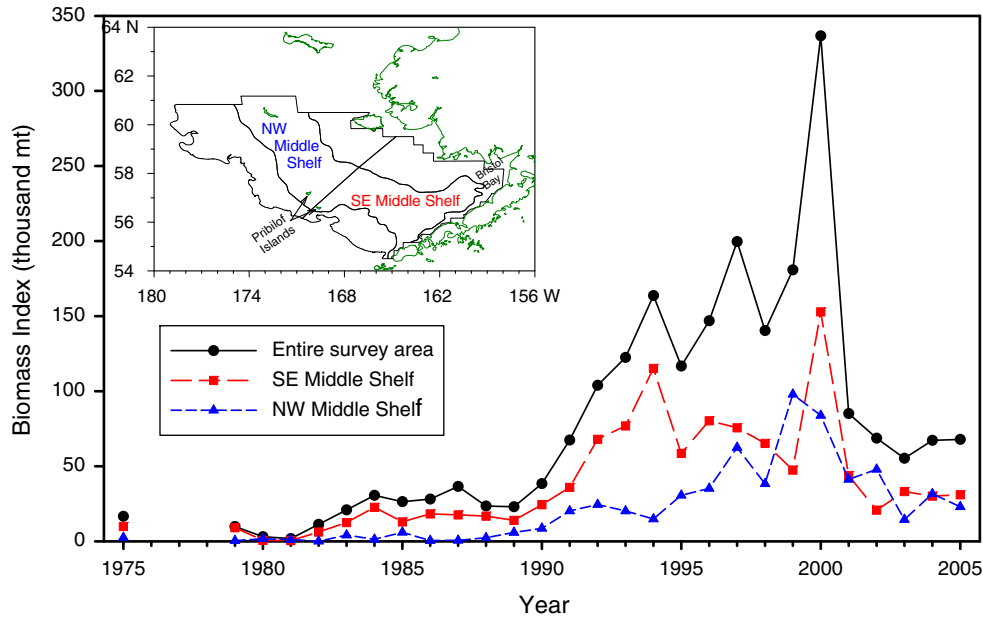


Fig. 3. Trend in jellyfish biomass from standardized trawl surveys in the Bering Sea since 1975. Shown are the total biomass (solid line) and subsets for the SE (long dashed line) and NW (short dashed line) Middle Shelf Domains. The inset shows the sampling areas on the Bering Sea shelf.

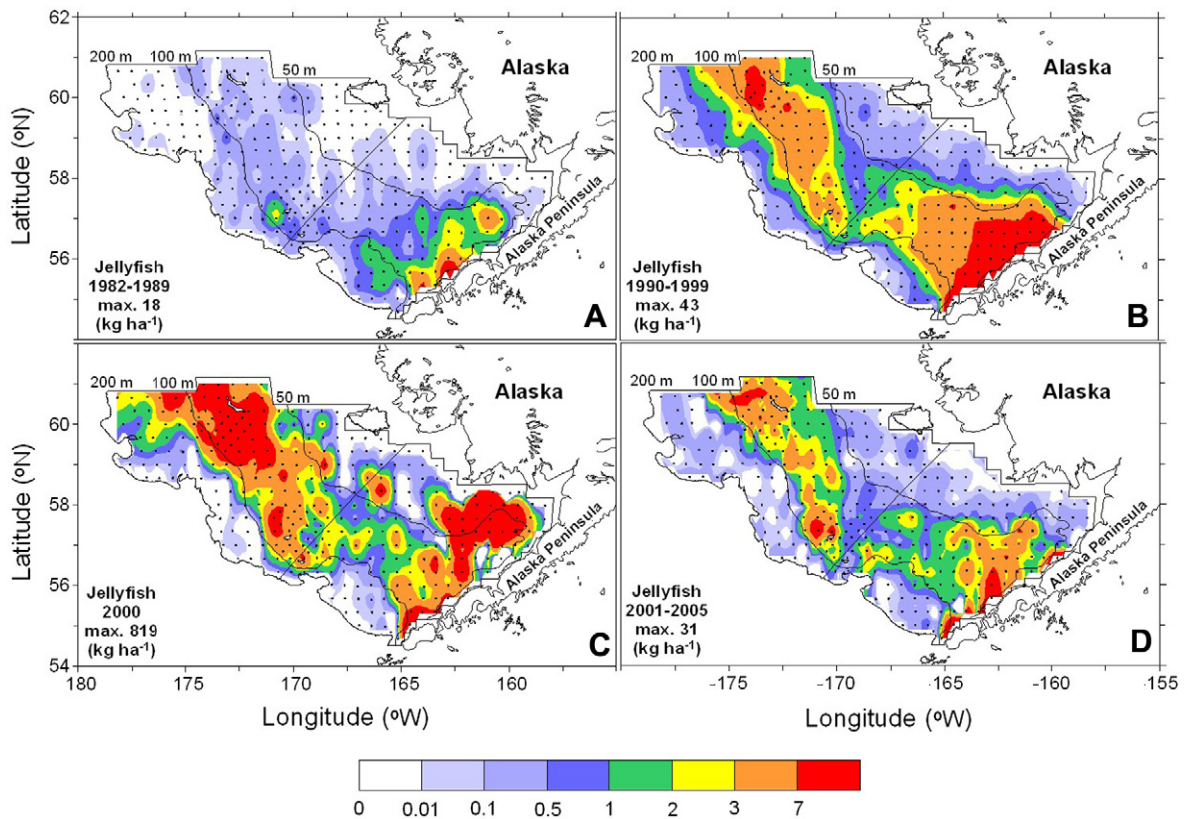


Fig. 4. Distribution of jellyfish biomass based on trawl surveys in the Bering Sea averaged over four periods (A) 1982–1989, (B) 1990–1999, (C) 2000, and (D) 2001–2004 identified in this paper as being oceanographically unique.

and low ice cover were associated with increased SE jellyfish biomass, and biomass anomalies were lowest at the warmest spring temperatures and in years when ice cover was unusually high. Wind mixing in May had a strong negative relationship with SE jellyfish biomass.

Jellyfish biomass in the NW region was highly correlated ($R^2 = 0.938$; Table 2) with SE jellyfish biomass the preceding year, summer sea-surface temperature, ice cover, zooplankton biomass on the middle shelf, and displacement (currentlag, i.e., drifter displacement from the center of the NW jellyfish distribution lagged

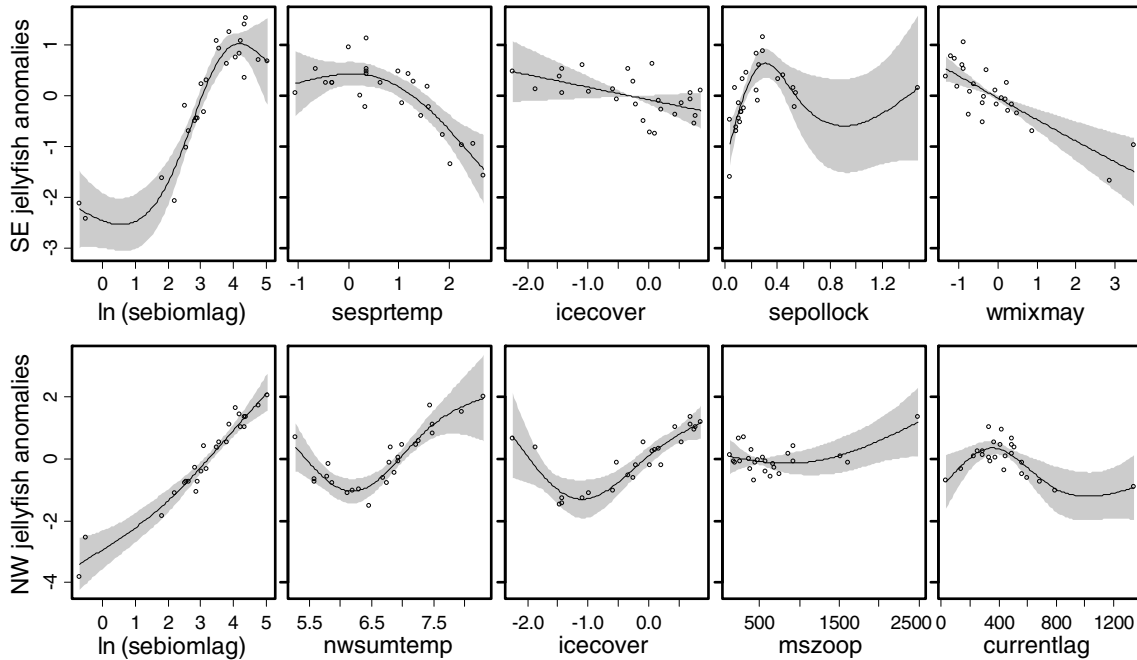


Fig. 5. Additive effects of the significant covariates included in the SE (top row) and in the NW (bottom row) jellyfish biomass models. Grey areas indicate 95% confidence limits. Axis labels are defined in Table 1.

Table 2
Results from all models fitted in the GAM analysis of the southeast (SE) and northwest (NW) jellyfish biomass in the Bering Sea. The degrees of freedom of each term were limited to 4

Region, terms	R ² (%)	GCV
<i>SE</i>		
sebiomlag	59.0	0.853
nwbiomlag	51.5	1.086
nwbiom	45.5	1.112
sebiomlag, sesprtemp	68.9	0.756
sebiomlag, sessumtemp	57.6	0.922
sebiomlag, sesprtemp, iceretreat	68.6	0.827
sebiomlag, sesprtemp, icecover	66.9	0.787
sebiomlag, sesprtemp, oszoop	75.2	0.620
sebiomlag, sesprtemp, mszoop	67.4	0.833
sebiomlag, sesprtemp, oszoop, wmixmay	77.2	0.606
sebiomlag, sesprtemp, oszoop, wmixj	76.2	0.626
sebiomlag, sesprtemp, oszoop, wmixmay, seforage	75.9	0.677
sebiomlag, sesprtemp, oszoop, wmixmay, sepollock	88.3	0.414
sebiomlag, sesprtemp, wmixmay, sepollock	89.2	0.361
sebiomlag, sesprtemp, wmixmay, sepollock, wstressna	89.0	0.389
sebiomlag, sesprtemp, wmixmay, sepollock, wstressmj	91.0	0.370
sebiomlag, sesprtemp, wmixmay, sepollock, icecover	89.6	0.356
<i>NW</i>		
nwbiomlag	65.2	1.419
sebiomlag	68.6	1.281
sebiom	65.1	1.469
sebiomlag, nwsprrtemp	67.5	1.288
sebiomlag, nwssumtemp	76.9	1.012
sebiomlag, nwssumtemp, icecover	84.1	0.777
sebiomlag, nwssumtemp, iceretreat	74.1	1.162
sebiomlag, nwssumtemp, icecover, oszoop	83.1	0.869
sebiomlag, nwssumtemp, icecover, mszoop	92.9	0.493
sebiomlag, nwssumtemp, icecover, mszoop, current	91.9	0.592
sebiomlag, nwssumtemp, icecover, mszoop, currentlag	93.8	0.463
sebiomlag, nwssumtemp, icecover, currentlag	91.1	0.536
sebiomlag, nwssumtemp, icecover, mszoop, currentlag, wmixmay	93.3	0.531
sebiomlag, nwssumtemp, icecover, mszoop, currentlag, wmixj	93.3	0.508
sebiomlag, nwssumtemp, icecover, mszoop, currentlag, nwforage	93.0	0.552
sebiomlag, nwssumtemp, icecover, mszoop, currentlag, nwpollock	93.6	0.506

Bold models are those with the lowest generalized cross validation (GCV).

by one year). Displacement had a more positive contribution toward low rather than high distances (Fig. 5). Summer temperature and ice cover were nonlinearly related to jellyfish biomass in the NW, with a minimum toward intermediate values (Fig. 5). The 1-year lagged SE jellyfish biomass had a strong positive relationship with the NW jellyfish biomass. A model using the potential effect of SE jellyfish biomass on NW jellyfish biomass without a lag did not yield a good fit, indicating that the relationship of the SE jellyfish in the NW was more likely driven by transport than a set of co-occurring and beneficial survival events. Lagged NW biomass in the SE model also did not yield a good fit, indicating that the process worked only in the direction of the prevailing current (SE toward NW) (Table 2). Residuals from both the NW and the SE GAM models were not autocorrelated and, from a visual assessment, none of the residual patterns from the inspected models presented signs of heteroscedasticity or had strong departure from normality. Forward simulations of the best SE and NW models fit the data extremely well in both regions (Fig. 6).

4. Discussion

Our 28-year time series of jellyfish catches extended through two major regime shifts in the Bering Sea, one beginning in 1989 and another in 1999 (Hare and Mantua, 2000; Hunt and Stabeno, 2002; Bond et al., 2003). Environmental conditions and jellyfish biomass in the Bering Sea changed dramatically with each regime shift (Table 3). Between 2001 and 2005, there were decreases in ice cover (2002 was an exception) and increases in sea-surface temperature (Overland and Stabeno, 2004) (Fig. 2), and total heat content in summer. There have been substantial decreases in summer zooplankton biomass since 2001 relative to the 1990s (J. Napp, Alaska Fisheries Science Center, personal communication), which may have decreased the food available for medusae. The SE jellyfish biomass was most sensitive to summertime biological conditions (the juvenile pollock biomass) and to spring physical conditions (temperature and ice cover). In contrast, the NW bio-

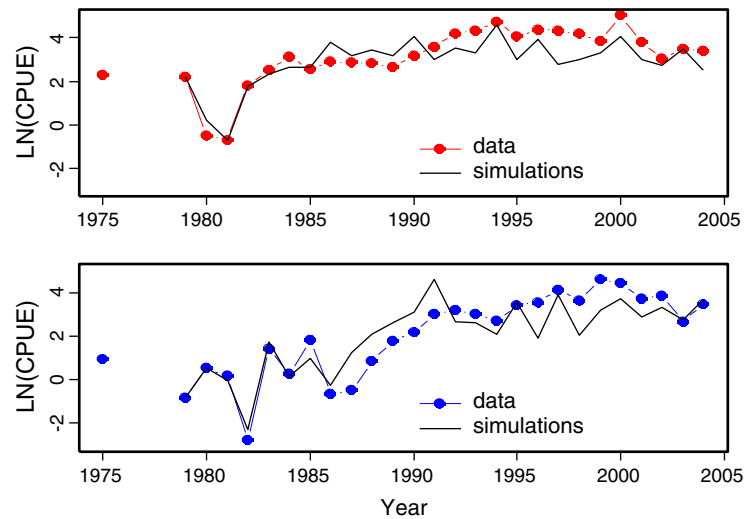


Fig. 6. Forward simulations of the best-fit model for jellyfish biomass in the SE (top) and NW (bottom) shelf regions of the Bering Sea.

Table 3

Summary of prevailing conditions in the Southeast (SE) and Northwest (NW) Bering Sea Middle Shelf (MS) regions in relation to jellyfish biomass fluctuations during 1975–2004

Period	Jellyfish biomass	Location of maximum biomass	Sea-surface temperature	Sea ice cover	Large zooplankton biomass	Age-0 pollock biomass
1975–1989	Low	SE MS	Cool, then warm	High, then low	Moderate ^a to high	Moderate to high
1990–1999	Increasing	SE & NW MS	Moderate	Moderate	Moderate to low	Moderate
2000	Peak	SE & NW MS	Moderate	Moderate	Low	Moderate
2001–2004	Moderate	SE & NW MS	Very warm	Low	Low	Very high, then moderate

^a Where “moderate” is defined as close to the long-term average.

mass was related most strongly to physical variables in the summer; however, a marked improvement in the NW model resulted from inclusion of the lagged SE jellyfish biomass. Our results demonstrate that the dynamics of the jellyfish population in the Bering Sea were different in distinct oceanographic regions, similar to regional differences among jellyfish populations in the North Sea (Lynam et al., 2005a), and may need to be examined on finer geographic scales than the analyses presented here.

Local biotic and abiotic factors are important for the success of both the benthic and planktonic stages. Temperature and salinity have been shown in species other than *C. melanaster* to affect asexual production of jellyfish from the polyps (reviewed in Purcell, 2005, 2007) and growth of the young pelagic jellyfish (ephyrae) (Widmer, 2005). Unfortunately, nothing is known about the location or conditions for strobilation of *C. melanaster* polyps. Because the polyps must live on hard surfaces, and much of the eastern Bering Sea shelf seabed is composed of sand or mud and is not suitable as polyp habitat, we assume that their major substrates in our study region are the Alaskan Peninsula and the Aleutian and Pribilof islands. Jellyfish distributions in summers of moderate abundance (before 1989 and after 2001) show concentrations in these areas (Fig. 4). High SE jellyfish biomass in years with moderate spring temperatures (Fig. 2) suggests that high temperatures may not promote ephyrae production. Interpretation of the relationships of biotic variables with jellyfish biomass is confounded by abiotic effects on the many components of the food web and their interactions. Nevertheless, it is likely that climatic factors also would affect jellyfish biomass through effects on lower trophic-level productivity, which would affect the entire food web (Behrenfeld et al., 2006). Thus, high jellyfish biomass would result from environmental conditions that favor production and survival of the ephyrae and their zooplankton prey.

We have developed a conceptual model (Fig. 7) that may enhance understanding of the effects of biophysical forcing on

jellyfish biomass during the different regimes. During early ice retreat and warm water conditions, seasonal stratification of the water column is delayed until May, leading to a relatively late spring bloom in warm water, and moderate production of mostly very small copepod genera such as *Pseudocalanus* and *Acartia* (Hunt and Stabeno, 2002). This outcome would be expected to set up unfavorable feeding and survival conditions for adult jellyfish. In the periods of low-moderate jellyfish biomass before 1989 and after 2001, we hypothesize that production of new medusae was in balance with export (transport and mortality). Between 1990 and 1999 when jellyfish biomass was increasing, an early spring bloom led to high production of zooplankton food (Hunt and Stabeno, 2002; Napp et al., 2002), which likely resulted in good survival and growth of ephyrae leading to high jellyfish biomass. The extremely high jellyfish populations in 2000, in combination with high numbers of other zooplanktivores, may have reduced the available standing stocks of zooplankton and triggered a negative feedback loop (dashed line in Fig. 7) that resulted in lower zooplankton overwintering survival and a decline in jellyfish in subsequent years. Alternatively, high overwintering mortality or changes in transport between sampling in 2000 and 2001 could have reduced the adult jellyfish population markedly. Unfortunately, data are lacking to test these alternative hypotheses.

During the dramatic increase of medusa biomass in the 1990s, we hypothesize that new production of medusae was much greater than export. Conditions may have been more favorable than those in the pre- and post-bloom periods for production of new medusae (more polyps, buds, more strobilation, higher survival), retention of adult medusae (low transport, low mortality), or both. Baier and Napp (2003) found that a large copepod (*Calanus marshallae*), which dominates the meso-zooplankton of the eastern Bering Sea middle shelf, showed better survival during cool years with more southerly sea ice extent. Increased *C. marshallae* biomass may result in better survival and higher

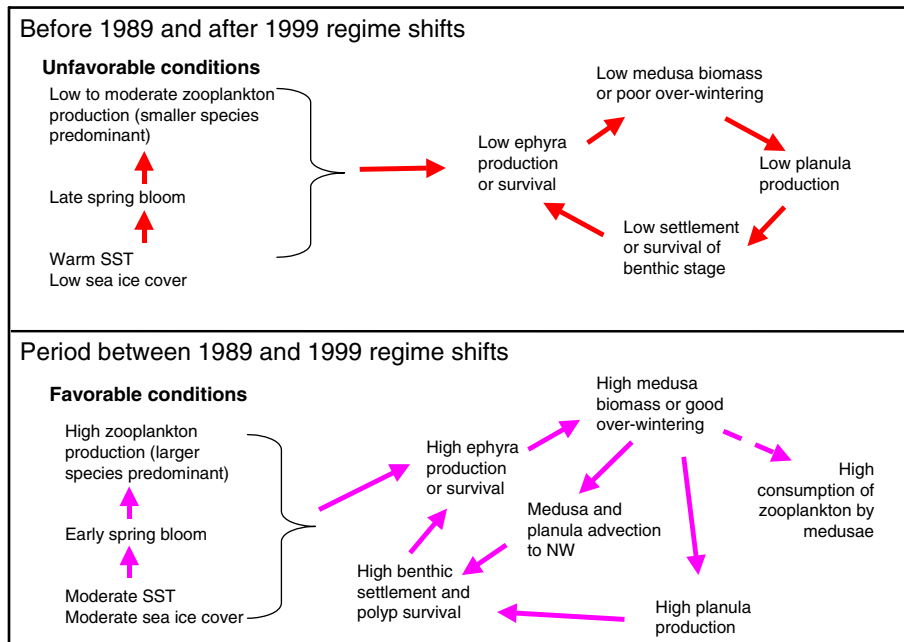


Fig. 7. Conceptual model of linkages between the biomass of medusae and their physical and biological environment in the warm periods (top) and cool periods (bottom). Figure was adapted from the model of [Lynam et al. \(2004\)](#).

jellyfish biomass in the SE, with subsequent advection to the NW. With flourishing adult populations, sexual reproduction would be great and lead to increased polyp populations. In addition, conditions during this period may have been favorable for survival of adult jellyfish through the winter. Previous reports of large *C. melanaster* in ice-free waters during spring ([Brodeur et al., 2002](#)) lend support to this possibility. Additionally, in May, 2006, large jellyfish were seen at the ice edge, and caught at depth north of moorings M2 and M4 in the Bering Sea ([Hunt and Hyrenbach](#), personal communication). Other species over-winter in some locations; for example in Norwegian fjords, jellyfish may live multiple years ([Jarms et al., 1999](#)).

We recognize that although our sampling grid is fixed in space each year, the distribution of jellyfish is fluid and can extend to the northern Bering Sea beyond our sampling region during warm years, as observed with some pelagic fish distributions in recent years ([Grebmeier et al., 2006](#)). A northward shift in the distribution of jellyfish would be expected during warming ocean conditions and *C. melanaster* is known to be abundant in the Arctic Ocean, well north of our study area ([Raskoff et al., 2005](#), JEP pers. obs.). Production of ephyrae along the Aleutian Peninsula might have been reduced by recent unusually warm temperatures and increased in cooler rocky habitats farther north (e.g., St. Matthew and St. Lawrence islands). It also is possible that there was an increase in the northward advection of jellyfish, but we have no data indicating a significant change in northward flows on the shelf starting in 2001.

Important conclusions from our work are that increasing ocean temperatures associated with global warming may not necessarily lead to a higher biomass of gelatinous macrozooplankton in all ecosystems, and that a suite of biophysical factors probably is responsible for jellyfish changes observed in the world's oceans ([Mills, 2001](#); [Purcell, 2005](#); [Purcell et al., 2007](#)). Also, our analysis indicates that the links between climate and jellyfish biomass are complex, probably involving the survival and dispersal of life-stages that are not easily sampled (i.e., polyps, ephyrae, and planulae). Most species studied to date have been temperate and have shown increased production in the laboratory at warm temperatures. Species living near the upper limits of their temperature

ranges may not increase in abundance with further warming ([Purcell, 2005](#); [Purcell et al., 2007](#)).

Although many physical variables display a linear response to climate change, the behavior of most biological components of large marine ecosystems has been shown to be nonlinear ([Hsieh et al., 2005](#)). Lower trophic-level organisms in the Pacific Ocean, including most zooplankton taxa, show more sensitivity to changing climate conditions than higher trophic-level species ([Benson and Trites, 2002](#)), and may be more likely to express nonlinear responses ([Hays et al., 2005](#)). Given the abundant fisheries resources available in boreal systems such as the Bering Sea ([Connors et al., 2002](#); [Hunt et al., 2002](#); [Schumacher et al., 2003](#)) and the potential for competition with or predation upon these resources by gelatinous zooplankton ([Purcell and Arai, 2001](#); [Brodeur et al., 2002](#); [Lynam et al., 2005b](#)), relatively minor changes in jellyfish biomass may have profound effects on the ecosystem and fisheries. Additionally, due to their conspicuous presence, jellyfish can serve as key sentinel species for monitoring changes in this highly productive, subarctic ecosystem and elsewhere in the world's oceans ([Hays et al., 2005](#); [Hay, 2006](#)).

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