

# Linking changes in eastern Bering Sea jellyfish populations to environmental factors via nonlinear time series models

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**ABSTRACT:** The Bering Sea ecosystem has experienced significant climatic and biological shifts over the past 3 decades, including temporal and spatial fluctuations of jellyfish biomass. Jellyfish are important predators and competitors of fish; thus, it is critical to understand the effects of environmental factors on their population dynamics. We explored the effects of ocean bottom temperatures and circulation on jellyfish populations using a non-parametric, nonlinear multiple time series analysis of a 23 yr dataset. The study area was divided into 3 subregions that reflected distinct jellyfish catches and distributions. Aggregations and the influence of temperature and circulation on jellyfish biomass were found to differ in each of the 3 subregions. The northern region biomass was affected by central biomass, mediated by the strength of advection from the central region. In both the northern and central regions, current-year biomass was associated with lag-1 biomass, but was mediated by local bottom temperatures (colder temperatures strengthened the relationship with lag-1 biomass). However, in the central region, this relationship held only for the period after 1997. Prior to 1997, advection from the southern region drove central region biomass, suggesting that the primary source of jellyfish biomass to the central eastern Bering Sea shelf changed, coming from the southern shelf before 1997 and from the central shelf after 1997. The southern jellyfish biomass was affected by only the lag-1 southern jellyfish biomass. Transport from the south may have seeded the central region in the early 1990s, but once established, jellyfish polyp populations near islands in the central region may have supplied the area with medusae in the late 1990s.

**KEY WORDS:** Scyphomedusae · Biophysical conditions · Climate change · Time series

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## INTRODUCTION

Jellyfish blooms are common occurrences in many marine habitats (Mills 1995, Purcell et al. 2007, Condon et al. 2012) and predation by jellyfish has important and complex effects on food webs in these systems (e.g. Purcell & Decker 2005, Møller & Riisgård

2007, Brodeur et al. 2008b, 2011). Jellyfish populations fluctuate over time and may be increasing in some regions (reviewed in Purcell et al. 2007, Purcell 2012). However, knowledge on the specific factors affecting jellyfish spatial and temporal dynamics is limited; thus, their impacts on zooplankton and fish populations are difficult to predict.

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Changes in jellyfish population sizes and distributions have been attributed to physical and biological processes. For example, ocean circulation processes, in coordination with vertical migration behavior, can influence the distribution and abundance of jellyfish (Graham 1993, 1994), and interannual variability in medusa distributions can be explained by advection and inflow events (Johnson et al. 2001, 2005, Barz et al. 2006). Environmental factors, such as temperature and prey availability, can have direct effects on the production of polyps, the benthic life stage present in many jellyfish species (Purcell 2007, Purcell et al. 2009, Han & Uye 2010), which in turn could dramatically influence the population sizes of medusae in a given year.

The eastern Bering Sea (EBS) shelf is a large region, extending over more than 8° of latitude. Consequently, important physical drivers of the ecosystem vary considerably from north to south (Stabeno et al. 2010). Oceanic flow on the shelf consists of a broad, slow mean flow towards the northwest (Kinder & Schumacher 1981), indicating that the flow of propagules between regions is likely to be from the southeast to the northwest. Consequently, it is important to examine regional differences in ecosystem variability. In addition, the EBS has experienced significant changes over the past 3 decades (Stabeno et al. 2001, 2007, 2012a), including large fluctuations in jellyfish biomass (Brodeur et al. 2008a). Because diet studies (Brodeur et al. 2002) indicate that EBS jellyfish are likely to be key predators and competitors of commercial fish in these important fishing grounds, it is critical to understand the processes influencing EBS jellyfish population dynamics and spatial patterns across the region.

We previously documented an apparent expansion of jellyfish habitat towards the northwestern EBS after 1990 (Liu et al. 2011). We also proposed that the increase of jellyfish biomass in the 1990s may have been driven by an interaction of stronger oceanic transport, which has enhanced advection of jellyfish from the southeastern shelf to the northwest, and warmer temperatures after 1990, which have increased jellyfish sexual and/or asexual production in the newly occupied regions.

Populations can have heterogeneous spatial structures, and exist as a mix of 2 or more subpopulations (Levin 1992, Fauchald et al. 2000). Depending on the level of degree to which organisms disperse among different aggregations (i.e. connectivity) and the spatial heterogeneity of forcing factors acting across an area, it is likely that separate subpopulations experience different temporal dynamics.

Multiple time series (MTS) analyses have been used to model the dynamics of multiple stocks within a single marine cod population (e.g. Fromentin et al. 1998, Stenseth et al. 1999a, Fromentin et al. 2001). However, many of these analytical approaches use a linear model framework, which cannot account for inherent nonlinearity and non-stationarity of organism–environment interactions. Also, these MTS approaches do not explicitly account for exchange of individuals due to passive transport among composing subpopulations.

In this study, we used jellyfish catch data spanning 3 decades to examine the linkages between current flow and jellyfish distribution and abundance, and determine the effects of variations in physical (temperature, currents) and biological (jellyfish biomass) conditions on temporal and spatial patterns of jellyfish in the EBS. Our approach combined statistical analysis with oceanographic circulation models, which are becoming increasingly common investigational tools in marine studies (e.g. Cowen & Sponaugle 2009). Oceanographic models have been used to estimate connectivity of planktonic marine organisms (e.g. Watson et al. 2010), but generally do not simultaneously account for organism–environment interactions. In this study, we explicitly accounted for potential connectivity of jellyfish aggregations between regions by including dispersal estimates from a circulation model. The term connectivity here is used to refer to exchange of individuals among the composing subunits of a population. As jellyfish are not capable of long-distance horizontal volitional swimming, the connectivity in our study case was passive and fueled by ocean currents. To account for the nonlinear relationship between jellyfish dynamics and intervening covariates, we used simple and threshold generalized additive models (GAMs) (Ciannelli et al. 2004, Liu et al. 2011). The inclusion of a threshold allowed us to test for potential nonstationary dynamics in jellyfish abundance.

Our analytical approach may be broadly applied to model the abundance of populations that are composed of different subunits, each affected by intrinsic (i.e. changes on demographic rates) and extrinsic (i.e. changes of immigration and emigration among composing subpopulations) dynamics. Thus, besides jellyfish, our modeling approach is also relevant for larval fish (e.g. Watson et al. 2011), quantifying connectivity within reserve networks (e.g. Mumby et al. 2011) and estimating the spread of marine pathogens in both space and time (e.g. McCallum et al. 2003).

## MATERIALS AND METHODS

### Jellyfish biomass and study regions

Jellyfish distribution and abundance data were obtained from quantitative bottom trawl surveys of the EBS shelf conducted by the Alaska Fisheries Science Center (AFSC). Since 1982, jellyfish have been collected annually during 22 May to 19 August. The survey of 356 to 376 stations arranged in a grid-like pattern (Fig. 1) required approximately 2 mo for 2 fishing vessels to complete. A 17 m wide trawl with graded mesh (10 cm at the mouth to 3.8 cm in the codend) was towed at a speed of  $1.54 \text{ m s}^{-1}$  (3 knots) on the bottom for 30 min at each station during daylight hours. Because jellyfish were distributed throughout the water column, their capture in the bottom trawl gear probably occurred during net retrieval. We assumed that these records, though not representative of the actual jellyfish abundance, accurately represented the temporal and spatial variation throughout the study region. Most of the biomass (>85%) consisted of one scyphomedusa, *Chrysaora melanaster* (Brodeur et al. 2002, Decker et al. 2014). Catches of large (bell diameters >50 mm) jellyfish were weighed

and standardized to catch per unit effort (CPUE in  $\text{kg ha}^{-1}$ , where  $1 \text{ ha} = 10\,000 \text{ m}^2$ ) (see Brodeur et al. 1999 for details). Jellyfish CPUE data were log-transformed and 20 data cases with extreme values in some covariates (i.e. bottom temperature  $>10^\circ\text{C}$ , bottom depth 200 m or sample date  $>240$ th day of the year) were excluded from the analysis, which resulted in 8147 observations over the period 1982 to 2004. Although jellyfish data extended to the present, the availability of circulation model output ended in 2004, limiting the time frame of our analysis.

We developed separate time series models for each of the following 3 regions: North (including St. Matthew Island), Central (including the Pribilof Islands) and South (near the Alaska Peninsula) (Fig. 1). The line dividing the North and Central regions intersects  $58.0^\circ\text{N}$ ,  $174.1^\circ\text{W}$  and  $60.7^\circ\text{N}$ ,  $169.4^\circ\text{W}$ , and the border of the Central and South regions intersects  $55.7^\circ\text{N}$ ,  $169.2^\circ\text{W}$  and  $59.1^\circ\text{N}$ ,  $163.0^\circ\text{W}$ . These 3 regions were delineated based on the spatial patterns of jellyfish (1982 to 2004), which showed 3 separate aggregations with differing temporal variability (Liu et al. 2011, Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m494p179\\_supp.pdf](http://www.int-res.com/articles/suppl/m494p179_supp.pdf)).

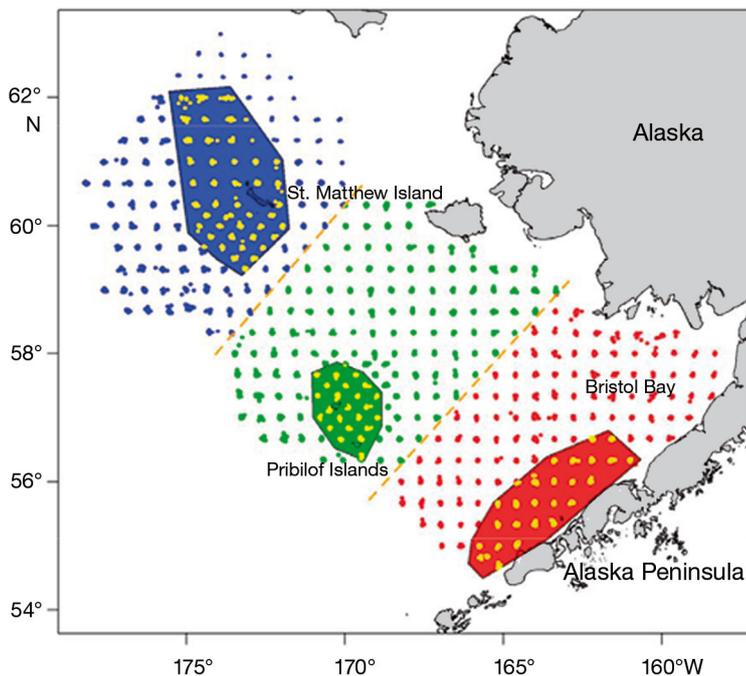


Fig. 1. Jellyfish sampling locations, with 3 regions indicated by color (blue is north, green is central and red is south). Stations within the 3 shaded sub-areas were used to estimate bottom temperature (BT) for each region (i.e. *BT.PENIN* near the Alaska Peninsula, *BT.PRIBS* surrounding the Pribilof Islands and *BT.NORTH* surrounding St. Matthew Island). Dots indicate station locations

### Physical and biological covariates

Temperature profiles were taken at each survey station using an expendable bathythermograph or a Sea-Bird microbathythermograph attached to the headrope of the net. The shelf of the eastern Bering Sea is well mixed during the winter and strongly stratified during the summer (Kinder & Schumacher 1981, Ladd & Stabeno 2012). When the water column stratifies in the spring, bottom temperatures become isolated from further heat exchange with the atmosphere. Therefore, summer bottom temperatures measured by the survey are primarily representative of conditions during the previous winter and early spring (Stabeno et al. 2007).

We assumed that variability in bottom temperature primarily influences the production of jellyfish polyps (as opposed to medusae, which would experience a more variable temperature environment depending on their horizontal and vertical locations). Thus, we used bottom

temperatures averaged over smaller regions (Fig. 1; subsets of stations near the Alaska Peninsula and around the Pribilof and St. Matthew islands). These 3 areas were delineated around potential jellyfish source locations (i.e. shallow, rocky regions near land; see below for a description of bottom types), yet large enough to represent multiple bottom trawl locations and to characterize interannual variability. Because bottom trawl survey timing varies slightly from year to year (Fig. S2), we adjusted the bottom temperature (*BT*) to account for sampling date by fitting a GAM for each of the 3 sub-areas (i.e. *BT.PENIN* near the Alaska Peninsula, *BT.PRIBS* surrounding the Pribilof Islands and *BT.NORTH* surrounding St. Matthew Island; see Fig. 1):

$$\text{bot.temp}_{d,y,(\phi,\lambda)} = c_y + s(d) + s(\text{depth}_{(\phi,\lambda)}) + \varepsilon_{d,y,(\phi,\lambda)} \quad (1)$$

where *bot.temp* is the response variable bottom temperature, *y* is year, *d* is sampling day,  $(\phi,\lambda)$  is longitude and latitude of the survey station, *s* denotes an unknown smooth function to be estimated, and *depth* is water depth of the sampling site; *e*'s are independent and identically distributed error terms of zero mean and finite variance. We used the estimated intercept  $c_y$  as a proxy for average bottom temperature in each year. The annual mean temperature from the St. Paul airport (a proxy for the true annual bottom temperature around the Pribilof Islands) is strongly contemporaneously correlated with the bottom temperature around the Pribilof Islands (Fig. S3),

indicating that the bottom temperatures as computed based on Eq. (1) are good proxies for the temperature conditions experienced by the jellyfish.

To examine the influence of ocean circulation on the distribution and biomass of jellyfish, we used the Northeast Pacific Regional Ocean Modeling System (NEP ROMS) ocean circulation model (Haidvogel et al. 2000, Curchitser et al. 2005, Hermann et al. 2009), which has a grid resolution of ~10 km. The model configuration used here has output available from the start of the jellyfish biomass time series (1982) to 2004. Modeled currents were used to advect simulated jellyfish drifters. These drifters were released from the coastlines of the Alaska Peninsula and the Pribilof Islands on the EBS shelf (Fig. 2a)—areas determined by analysis of Bering Sea bottom types (National Oceanic and Atmospheric Administration 2010) to be 'hard and rocky' and, therefore, potential jellyfish polyp habitat. The occurrence of immature scyphomedusae (ephyrae; see Text S1 and Fig. S4 in the Supplement) matches well with the Alaska Peninsula initial drifter locations (Fig. 2a).

Studies of vertical distributions indicate that EBS jellyfish aggregate at approximately 30 to 40 m depth (Coyle & Cooney 1993, Brodeur et al. 2002) and ephyrae were found in the upper 40 m (Fig. S5). Thus, drifters (simulated jellyfish) were introduced at 3 depths in the model (20, 30 and 40 m). Model runs were initialized on 17 March each year, with a new set of drifters released every other day until

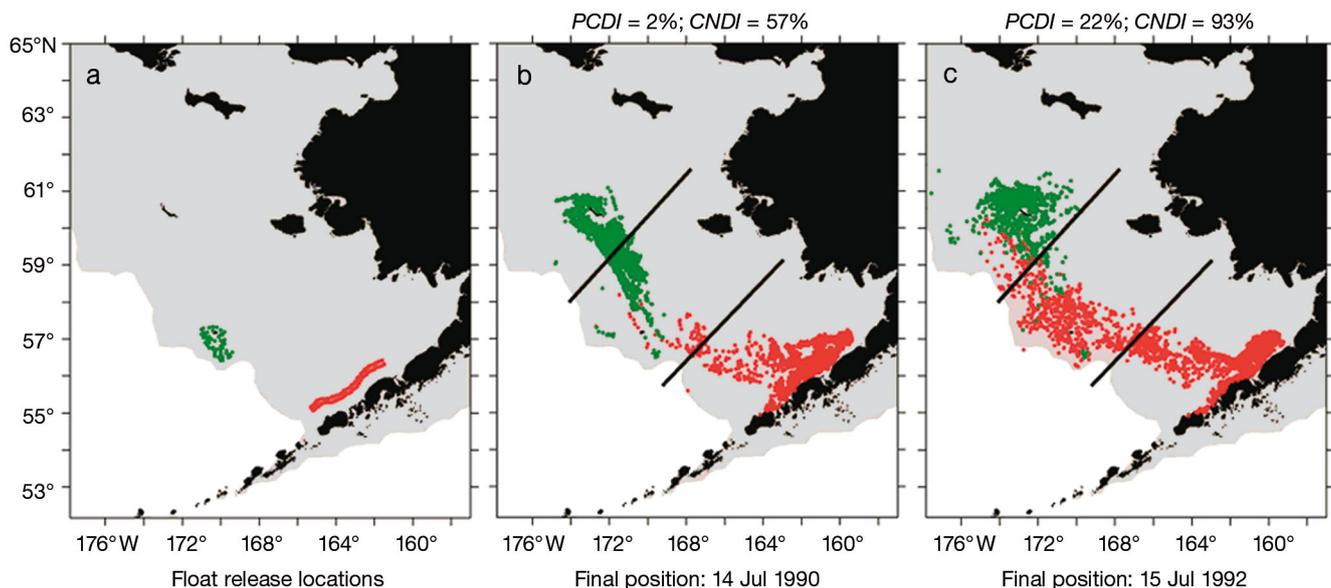


Fig. 2. (a) Initial locations of model drifters, (b) location of drifters on 15 July 1990 (a low Peninsula-to-Central Drift Index (*PCDI*) year), and (c) location of drifters on 15 July 1992 (a high *PCDI* year). Red denotes drifters initialized along the Alaskan Peninsula and green denotes drifters initialized near the Pribilof Islands. Gray shading denotes the shelf (shallower than 200 m) and the black lines delineate the 3 regions described in Fig. 1

3 April. Drifters were advected by the model currents until 15 July, which corresponds to the midpoint of the AFSC bottom trawl survey. Although polyps may continue to produce medusae through summer, (e.g. ephyrae occurred in August samples; Fig. S5), such newly released medusae would be too small to be collected by the trawl.

To assess interannual variability in drift patterns, we created 2 drift indices using output from the drifter advection model runs. The Peninsula-to-Central Drift Index (*PCDI*) is the proportion of drifters from the Alaska Peninsula source that drifted to the Central region (Fig. 1) by 15 July. The Central-to-North Drift Index (*CNDI*) is the proportion of drifters from the Pribilof Islands source that ended up in the North region (Fig. 1) on 15 July. These drift indices were calculated from 10 drifter releases (17 March to 3 April) and were used as covariates in the MTS models.

### Analytical approach

We used a nonlinear MTS modeling approach to examine the environmental conditions related to regional changes in EBS jellyfish distribution and biomass. The framework for each of the time series was that of a GAM, though we developed separate time series models for each of the 3 regions (North, Central and South; Fig. 1) and compiled jellyfish biomass data and related environmental conditions, specifically local bottom temperature, for each region. In addition, we used drift indices to examine connectivity between the regions via advection. The current-year jellyfish biomass is the response variable for each of the regional models (North, Central and South), and lag-1 and 'upstream' jellyfish biomass were considered as predictors in our models. The following variables were tested in the models: regional biomass of jellyfish in the current year,  $t$ , ( $CPUE.N_t$ ,  $CPUE.C_t$  and  $CPUE.S_t$ ), jellyfish biomass in the previous year ( $CPUE.N_{t-1}$ ,  $CPUE.C_{t-1}$  and  $CPUE.S_{t-1}$ ), drift indices ( $CNDI_t$ ,  $PCDI_t$ ) and trawl survey bottom temperature for the north and central regions ( $BT.NORTH_t$  and  $BT.PRIBS_t$ ). The south bottom temperature ( $BT.PENIN_t$ ) was also used, but was not found to be significant in our models. All covariates evaluated in the models are described in detail above and plotted in Fig. 3. Using these covariates, cross-regional comparisons were made between the North and Central regions and between the Central and South regions.

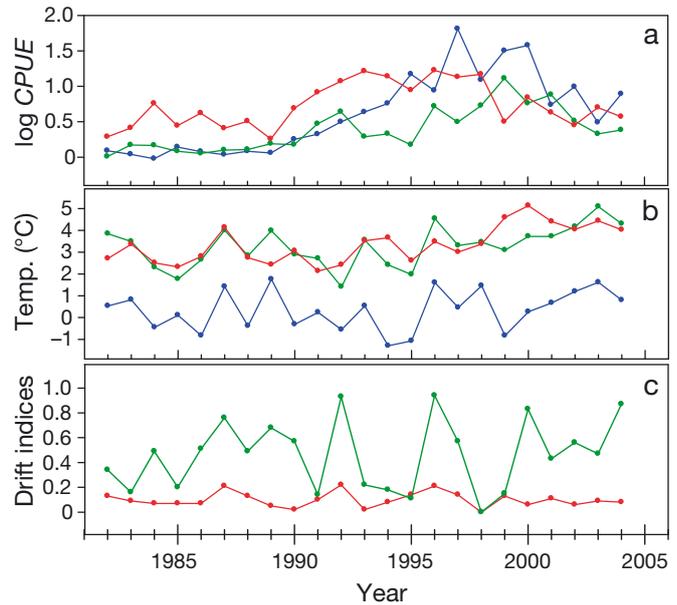


Fig. 3. Time series of the variables used in generalized additive models (GAMs) of jellyfish biomass in the Bering Sea. (a) Log of jellyfish biomass (catch per unit effort, *CPUE*) in the north (blue), central (green) and south (red) regions. (b) Summer (July to August) bottom temperature (adjusted for sampling day variation) in the north (blue), central (green) and south (red) regions. (c) Peninsula-to-Central Drift Index (green) and Central-to-North Drift Index (red). See Fig. 1 for description of regions

The basic statistical framework was that of a GAM with varying coefficients that relate the response  $y$  to the predictors via the following regression model:

$$y = \beta_0 + \beta_1(U_1) \times X_1 + \dots + \beta_p(U_p) \times X_p + \varepsilon \quad (2)$$

where  $X_1$  to  $X_p$  are the covariates, and  $\varepsilon$  is the error of zero mean and positive variance  $\sigma^2$ . Unlike traditional linear models, the regression coefficients are allowed to vary smoothly over the group stratified by variables  $U_1$  to  $U_p$ , represented by nonparametric smooth functions  $\beta_i$ ,  $i = 1, \dots, p$ , whose functional forms are estimated from the data using the gam function in the R package *mgcv* (see Wood 2006). The varying coefficient model can be used to explore complex nonlinear relationships between the response variable and the covariates, as well as their interactions. Note that the varying coefficient model reduces to an additive model if each  $X_i$  is identically equal to 1, so it generalizes the GAM. Thus, the varying coefficient model can include both additive and interactive covariate effects. As the generalization from GAM to the varying coefficient model is rather straightforward, even though it vastly extends the scope of applicability, the varying coefficient model is often simply referred to as a GAM; hence a

model of the form of Eq. (2) will be interchangeably called a varying coefficient model and GAM. Given the small sample size of our data, the function estimates of  $\beta_i$ ,  $i = 1, \dots, p$  are assumed to be natural cubic spline functions with maximum degrees of freedom equal to 3. Moreover, these functions are estimated by cubic regression splines with shrinkage, so that the function estimates can be automatically shrunken to linear functions or even zero function, as determined by the data (see Wood 2006 for details). This approach facilitates simpler model interpretation by promoting linearity in some coefficient functions and facilitating automatic variable selection, as a term will be automatically eliminated if its coefficient function estimate is completely shrunken to zero.

Adopting the varying coefficient model approach, we examined jellyfish dynamics in the South, Central and North regions between 1983 and 2004. Our modeling approach is ecologically based. First, for each region, under constant environmental conditions, the average (annual) jellyfish biomass may be modeled as a linear function of its lag-1 and the current or lag-1 jellyfish biomass in a potential source region (i.e. for the North (Central) region, the Central (South) region is a potential source, while the South is considered to admit no other source region). Second, the environmental effects probably alter the coefficients of the linear model, so we modeled the coefficients to be functions of 1 of 2 local environmental factors (ocean bottom temperature or drift indices). The models examined take the following general form:

$$\log(Y_t) = \beta_0 + \beta_1(E_{1,t}) \times \log(Y_{t-1}) + \beta_2(E_{2,t}) \times \log(X_t) + \varepsilon_t \quad (3)$$

where  $Y_t$  is a proxy for the jellyfish biomass in a study region as measured by the CPUE over that region in year  $t$ ,  $Y_{t-1}$  is its lag-1 and  $X_t$  is the proxy for the current-year jellyfish abundance in the source region. The second term on the right side of Eq. (3) models jellyfish production from the local polyp population that may be modulated by the environmental condition  $E_{1,t}$ , e.g. ocean bottom temperature around the study region, with the lag-1 of  $Y_t$  as a proxy for the abundance of medusae in the region. The third term models the direct contribution of jellyfish advected from the source region to the study region that is modulated by another environmental condition  $E_{2,t}$ , e.g. the drift index from the source region to the study region. However, jellyfish in the source region may render an indirect contribution by seeding the polyp community in the study region, in which case

$X_t$  in the third term is replaced by its lag-1. For each region, multiple ecological-based varying coefficient models were explored, and the final model was chosen based on p-values and the generalized cross validation (GCV). GCV is a measure of the out-of-sample predictive mean square error (hence, a model with a smaller GCV is preferable to another model with a larger GCV). Diagnostics (i.e. normality of the random errors and autocorrelation functions of the errors of each model) were evaluated to ensure validity of model assumptions. More details of the model selection procedure can be found in Text S2 and Tables S1 & S2 in the Supplement.

Furthermore, given that the spatial distribution of the jellyfish in the EBS changed after 1990 (Liu et al. 2011), we also explored potential nonstationarity (threshold effects) in the jellyfish dynamics over the 23 yr. A threshold GAM (TGAM) with year as the threshold variable was used to detect and characterize possible threshold effects of environmental conditions on jellyfish biomass (Ciannelli et al. 2004). Specifically, we checked whether a regression function (including varying coefficient function) changed from one form over the years before the threshold year  $\tau$  (the pre- $\tau$  period) to another form in the post- $\tau$  period. Here,  $\tau$  was evaluated for each year between 1983 and 2004 to find the threshold year that minimizes the GCV for the 2 varying coefficient models. We required that each of the 2 periods had at least 5 yr to ensure adequate data for estimating the sub-models in each period (regime). Note that the threshold year need not coincide with that of the jellyfish spatial distribution as the underlying dynamical changes may continue unabated for a longer period even after the spatial distribution of the jellyfish has shifted to a new pattern.

The evidence of nonstationarity (presence of a threshold year) was assessed by a permutation test (see Liu et al. 2011 for a relevant discussion). Essentially, under the hypothesis of no changes in the regression function, we could (1) shuffle the data by randomly permuting the year label, (2) fit a threshold model with the randomly shuffled data, (3) compute the minimum GCV of the threshold model to be denoted by  $T^*$ , (4) repeat (1) to (3)  $B$  times to get a baseline distribution of  $T^*$  ( $B = 1000$  for all numerical works reported below) and (5) compute the p-value of the permutation test for threshold nonstationarity as the fraction of  $T^*$  greater than the minimum GCV of the threshold model fitted with the original data. A threshold model was deemed spurious if its p-value was larger than 5%.

## RESULTS

### North model

Using the modeling approach outlined above, the Central to North dynamics was found to be given by the following model:

$$\log(CPUE.N_t) = \beta_0^n + \beta_1^n(CNDI_t) \times \log(CPUE.C_{t-1}) + \beta_2^n(BT.North_t) \times \log(CPUE.N_{t-1}) + \varepsilon_t \quad (4)$$

Jellyfish biomass in the North region depended on its lag-1 biomass, with the coefficient being a function of ocean bottom temperature in the north region ( $p < 0.001$ ). The (autoregressive) coefficient ranged from about 0.5 to 1.0, and was a decreasing function of local bottom temperature, although the autoregressive coefficient was always positive. Thus, lower bottom temperature was found to increase density dependence. The North biomass was also found to be positively associated with the lag-1 of Central biomass, with the coefficient found to be an increasing function of  $CNDI$  ( $p = 0.028$ , indicating overall significance of the function even though the individual 95% confidence band is somewhat wide and apparently contains the zero function, as shown in Fig. 4). No significant threshold effects were found for the north model using the proposed model selection procedure and permutation test.

### Central model

The South-to-Central jellyfish dynamics were found to be nonstationary, as depicted by the following threshold GAM (TGAM) model:

$$\log(CPUE.C_t) = \begin{cases} \beta_0^c + \beta_{11}^c(PCDI_t) \times \log(CPUE.S_{t-1}) + \varepsilon_t, & \text{if } t \leq 1997 \\ \beta_0^c + \beta_{12}^c(BT.Pribs_t) \times \log(CPUE.C_{t-1}) + \varepsilon_t, & \text{if } t > 1997 \end{cases} \quad (5)$$

The function estimates are displayed in Fig. 5. We performed a permutation test with 1000 replications and the threshold effect was found to be statistically significant ( $p = 0.029$ ). In the first regime (1983 to 1997), the Central jellyfish biomass depended positively on the lag-1 of the South biomass, with the coefficient being an increasing function of  $PCDI$ —the index quantifying advection from the South to the Central region ( $p = 0.027$ ). From 1997 to 2004, the dynamics switched into a new phase characterized by the dependence of the central jellyfish biomass on its lag-1, with the coefficient being a positive,

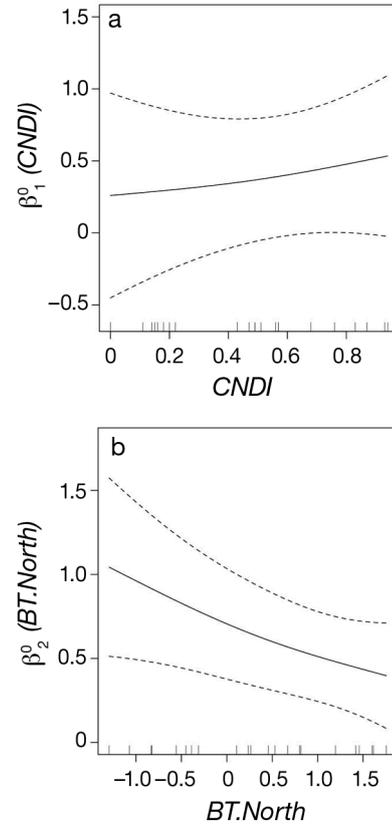


Fig. 4. Estimated nonparametric varying coefficients in the north model. (a) Coefficient of lag-1 central biomass as a function of Central-to-North Drifting Index ( $CNDI$ ). (b) Coefficient of lag-1 north (local) biomass as a function of bottom temperature ( $BT$ ) in the north region. Dashed lines denote the 95% pointwise confidence bands

decreasing function of bottom temperature near the Pribilof Islands ( $p < 0.001$ ). Thus, the fitted model reveals the emergence of density dependence after 1997 and, similar to the North model, lower bottom temperature was found to be associated with increased density dependence.

### South model

The modeling strategy outlined above and the flexibility of the estimation procedure yielded the following simple linear model for the jellyfish dynamics in the South region:

$$\log(CPUE.S_t) = \beta_0^s + \beta_1^s \times \log(CPUE.S_{t-1}) + \varepsilon_t \quad (6)$$

The lag-1 South biomass has a positive linear effect on  $CPUE.S_t$ , with the slope estimated to be 0.60 with standard error (SE) 0.17, and intercept 0.31 with SE 0.13. Thus, jellyfish in the South region follow a

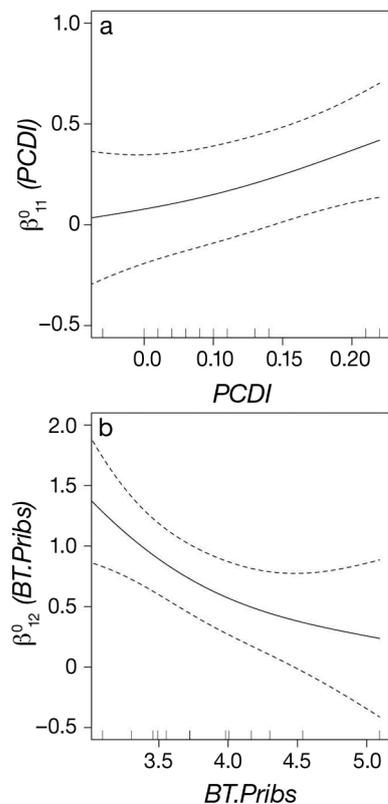


Fig. 5. Estimated nonparametric varying coefficients in the central model. (a) Coefficient of lag-1 south biomass as a function of Peninsula-to-Central Drift Index (*PCDI*) in the pre-1997 regime. (b) Coefficient of lag-1 central (local) biomass as a function of bottom temperature (*BT*) near the Pribilof Islands in the post-1997 regime. Dashed lines denote the 95% pointwise confidence bands

stationary AR(1) model (autoregressive model of order 1). This is consistent with the temporal pattern of the South jellyfish (Fig. 3), which indicates that South jellyfish biomass was elevated during the mid-to late 1990s, but otherwise fluctuated stably. By contrast, the Central jellyfish biomass time series model appears to be nonstationary.

## DISCUSSION

MTS analyses indicated that bottom temperatures and advection by currents influenced EBS jellyfish populations. In addition, we showed that these factors vary by region and over time. Earlier analyses (Brodeur et al. 2008a) examined the effects of environmental factors on jellyfish biomass on very broad, shelf-wide scales. By contrast, here we used MTS analyses to examine regional parameters, such as temperature and currents, on smaller scales and at depth to understand conditions that might affect

local production and transport of medusae from jellyfish polyps. The existence of different dynamics for each of the sub-regions examined in our analysis indicates a previously unexplored level of population spatial structure, which is further discussed below.

## Regional differences

### North

Jellyfish biomass in the North region of our study site (Fig. 1) is dependent on multiple factors. Northern jellyfish biomass in the previous year positively influenced the current year's biomass, reflecting an overall increase in population size through the time series. The link between current- and previous-year biomass is mediated by local bottom temperature with a stronger link at colder temperatures. Central jellyfish biomass in the previous year was positively associated with current-year North biomass and the association became stronger as *CNDI* increased, suggesting that the biomass increase in the North region was in response to both local factors and transport from the Central region.

Regional bottom temperature significantly influenced the strength of association between northern current and lag-1 jellyfish biomass. Although ice cover was not used as a predictor to minimize the number of covarying parameters used in the model, cold summertime bottom temperatures (i.e. the 'cold pool' created by seasonal ice) are a proxy for the presence of sea ice in winter (Stabeno et al. 2001). EBS sea ice varies greatly in both horizontal extent (i.e. maximum southern location) and duration (i.e. persistence) (Stabeno et al. 2012b). North of St. Matthew Island, sea ice is present almost every day during March and April, but to the south, the amount of sea ice varies greatly between warm and cold years and can influence hydrography and primary production (Stabeno et al. 2012b). Thus, the positive association between cold bottom temperatures and northern jellyfish biomass suggests that heavy ice cover may have promoted medusa winter survival in this region after 1995, as hypothesized by Brodeur et al. (2008a).

### Central

Jellyfish biomass in the Central region is dependent on multiple factors, and these effects change through time. From 1983 until 1997, Southern jellyfish biomass in the previous year positively influ-

enced the current year's Central biomass, with the strength of the influence mediated by advection from the South to the Central region (*PCDI*). This suggests that the South population was the source for the current year's medusae. This could be due to survival of adult medusae through winter, as well as the production and successful settlement of sexually produced larvae in the previous year. This was also consistent with the result that the *PCDI* was a factor; thus, variability in transport from the Alaskan Peninsula influenced variability in the Central jellyfish population.

After 1997 (i.e. from 1998 to 2004), during a period of warming, bottom temperatures near the Pribilof Islands modulated the influence of lag-1 central biomass on the current-year biomass, with an overall positive effect, but stronger influence at colder temperatures. The Southern jellyfish biomass and the *PCDI* no longer influenced the Central jellyfish biomass suggesting that polyps near the Pribilof Islands were an important source to the local jellyfish during this time period. The observed threshold at 1997 may be related to changes that occurred in the temperature time series around that year. Before the mid-90s, interannual variability dominated the bottom temperature record, whereas after the mid-90s, bottom temperatures exhibited an increasing trend. Thus, multiyear periods of warmth may be required to enhance polyp production. The 1997 threshold suggests that in the earlier regime, the South region was the primary source for the Central region, while after 1997, a local source was more important. These findings partially support the hypothesis of Liu et al. (2011) that the presence of stronger oceanic transport after 1990 enhanced advection of jellyfish from south to north. That is, transport from the south may have been important for seeding the central region in the early 1990s, but once established, polyps near the rocky Pribilof Islands (in the central region) may have supplied the area with medusae in the late 1990s. However, there are no direct observations of scyphomedusae polyps in the Bering Sea (as is true for most systems) and further work is needed to verify these interpretations of our results.

### South

In contrast to the North and Central regions, where jellyfish biomass is influenced by multiple factors, the Southern jellyfish biomass was affected by only the lag-1 Southern jellyfish biomass, and this effect did not change through time. We were not able to look at other potential sources of medusae to the southeast-

ern Bering Sea, i.e. from the North Pacific through Unimak Pass, owing to the lack of medusa data. Thus, other regions may have been important source locations, but we were not able to evaluate this in the present study.

### Environmental variability and connectivity between regions

The Bering Sea shelf is a dynamic system, forced by variable climatic conditions (Stabeno et al. 2001, Bond & Adams 2002, Aydin & Mueter 2007). Changes in ice conditions and timing of the spring bloom have been hypothesized to affect zooplankton biomass on the shelf (Hunt et al. 2011), and recent ecosystem studies indicate that climatic variability and changes in ice cover influence the abundance of large zooplankton species, such as *Calanus marshallae* and euphausiids (Coyle et al. 2011, Hunt et al. 2011). Jellyfish biomass in the EBS also appears to respond to climate fluctuations (Brodeur et al. 2008a, this study). Our results indicate that jellyfish biomass in the South and North regions increased through the mid-1990s (Fig. 3). By contrast, the statistical properties of the Central jellyfish time series changed over time (i.e. were nonstationary). These regional differences may be indicative of characteristic physical processes acting within an area. For example, the Central region is influenced by the extent and timing of sea ice, which is highly variable. In contrast, the South rarely sees heavy ice cover, whereas, sea ice occurs in the North region every winter.

The MTS approach reveals new insights on the hypotheses proposed by Liu et al. (2011) on a regional basis. Stronger oceanic transport from the Alaska Peninsula to the Central region enhanced advection of jellyfish up to 1997, indicating that the Central and Southern jellyfish aggregations are linked via current flow. Our results suggest that polyp production in the North and Central regions may have been enhanced by changes in bottom temperature during the time series and that the North and Central aggregations were connected by ocean transport, as predicted by Liu et al. (2011). This is a further indication of connectivity between these 2 regions, and that changes in transport and climate interact to influence the jellyfish spatial distributions.

EBS jellyfish, which are both predators and competitors of fish, appear to be responding to physical conditions and may be providing keys to understanding ecosystem changes. Results from this study suggest that management of EBS living resources should

be carried out on a regional basis and also indicate the complex nature of the ecological effects of climate change. Our findings could lead to the development of models that can predict jellyfish blooms (Decker et al. 2007), which are key to understanding ecosystem changes.

The methodologies used in our study are widely applicable to other systems and organisms. For example, Chen et al. (2005) examined the interconnectivity among 3 Atlantic cod *Gadus morhua* L. populations in the North Sea and the Skagerrak and Kattegat straits and accounted for environmental effects using a GAM. They found strong statistical evidence of migration of adults between regions, but found no indication of egg and larval transport. Similarly, Stenseth et al. (1999b) conducted parametric, nonlinear time series analyses of Canadian lynx density and showed that the nonlinear lynx dynamics was structured into 3 broad regions across Canada, each with a discrete genetic signature (Rueness et al. 2003). This geographical structuring is influenced by differential lynx–hare interactions due to large-scale climatic factors (Stenseth et al. 2004). These studies, as well as the present study, collectively indicate that nonlinear organism–environment interactions, coupled with models that simulate dispersal, can be important investigational tools for understanding the dynamics of species that are structured over space.

*Acknowledgements.* We are grateful to the survey participants and support teams from the AFSC, and the captains and crew from the various research vessels, for diligently collecting the jellyfish biomass and environmental data during their trawl surveys. We are also grateful to K. Hedstrom and E. Curchitser, who were instrumental in creating the NEP ROMS circulation model, A. Hermann for discussions of circulation model results, and to K. Coyle, who provided records of scyphomedusan ephyra occurrence. We acknowledge the following funding sources: National Science Foundation Collaboration in Mathematical Geosciences Grants (0620789 and 0934617 to K.S.C., 0621153 and 0934961 to L.C., 0620493 and 0934727 to M.B.D.) and North Pacific Research Board (NPRB) project number 606. This is contribution 3721 from NOAA's Pacific Marine Environmental Laboratory, 2184 from the Joint Institute for the Study of the Atmosphere and Oceans, University of Washington, and EcoFOCI-0768 from NOAA's Fisheries-Oceanography Coordinated Investigations (EcoFOCI).

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