Cyclic variability of eastern Bering Sea jellyfish relates to regional physical conditions

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ABSTRACT

Globally, there have been few long-term (>30 years), shelf-wide surveys of jellyfish that have allowed for the examination of how populations might respond to changing climatic and oceanographic conditions. One region where investigation of jellyfish responses to climate variability is possible is the eastern Bering Sea, where jellyfish biomass, primarily that of *Chrysaora melanaster*, has fluctuated dramatically since 1982, when systematic collections of these medusae began. Our previous investigations of a 27-year time series indicated that the timing of the jellyfish biomass increases and declines coincided with transitions between climatic regimes. In the current study, we used updated jellyfish catch and environmental data from 1982 to 2017 and reran our generalized additive model (GAM) analyses to determine if models using solely physical variables and lag of jellyfish biomass could describe accurately the increases and subsequent decreases observed in this jellyfish biomass index. GAMs hindcasting jellyfish biomass for the period 1982–2017 explained a large fraction of the variance, 92.3 % and 86.4 %, for the southeast (SE) and northwest (NW) portions of the survey area, respectively, using jellyfish biomass in the preceding year and physical variables (SE: ice retreat, sea-surface temperature, wind mixing, wind stress and current displacement; NW: sea-surface temperature, ice cover, wind stress and current displacement). We developed more parsimonious models by calculating the variance inflation factor for each term and dropping highly correlated terms from the models. The resulting GAMs continued to explain a significant portion of the variance in jellyfish biomass, i.e., 78.2 % and 73.5 %, in the southeast and northwest survey areas, respectively. Jellyfish biomass in the SE region was correlated with the jellyfish biomass in the preceding year and with wind mixing, wind stress and current displacement. In the NW region, jellyfish biomass was correlated with biomass from the preceding year, and with summer sea-surface temperature and current displacement. Jellyfish biomass in the eastern Bering Sea did not increase during warm periods, as has been speculated to occur elsewhere. Jellyfish, which are both predators and competitors of fish, appear to be responding to changes in physical conditions and are important indicators of ecosystem change in the eastern Bering Sea. The development of models that use physical parameters, as opposed to biological variables that are often not readily available, is key to predicting jellyfish abundance and their impacts on commercially important species.

1. Introduction

Jellyfish populations throughout the World's oceans fluctuate but the causes of these fluctuations are not well established (Condon et al. 2013). Some purported relationships among jellyfish abundance and environmental variables have been criticized as spurious because these studies examined only a portion of a longer-term jellyfish cycle (Pitt et al. 2018). Few scyphozoan abundance trends have been surveyed over

several decades and at broad spatial scales which could allow for examination of how populations might vary in response to changing climatic and oceanographic conditions. The eastern Bering Sea (EBS) is one marine ecosystem where such studies can be conducted due to an extensive systematic survey that has been conducted yearly since 1979 (Stephenson and Lauth, 2019).

The EBS is a productive and economically valuable ecosystem, supporting rich populations of zooplankton, forage fish, groundfish, crabs, marine birds, and mammals. Alaskan commercial fisheries are among the largest in the world, with combined annual landings of over 2.7 million metric tons valued at 1.8 billion $US (NMFS 2019). The highly productive EBS ecosystem also supports large populations of jellyfish (scyphomedusae, primarily *Chrysaora melanaster,* and hydromedusae), which have fluctuated substantially in biomass from estimates near zero to a high of 337,000 mt over the period 1979–2012 (Brodeur et al., 2008a; Decker et al., 2014). Jellyfish, which are both predators and competitors of fish, may respond quickly to changes in physical and biological conditions and thus, provide important clues to understanding ecosystem changes.

The eastern Bering Sea features a broad (~500 km wide), shallow (<200 m deep) shelf extending northwestward from the Alaska Peninsula to the eastern tip of Siberia. It is subject to ice cover whose average seasonal cycle in extent (including the Chukchi Sea to its north) is ~ 1700 km, the greatest of any Arctic or sub-Arctic region (Walsh and Johnson, 1979). The interannual variability in maximum sea ice extent is on the order of 400 km (e.g., Niebauer, 1983); the variability among years is large because the region can be dominated by air masses of either maritime or Arctic origin (Rodionov et al., 2007). The maximum ice extent and timing of ice retreat in spring represent the primary factors controlling physical conditions on the Bering Sea shelf throughout the year (Stabeno et al., 2001; Stabeno et al., 2012a; Sullivan et al., 2014), but weather conditions during the summer, especially the amount of storminess, wind-mixing and insolation (i.e., solar radiation that reaches the earth's surface) can also be important modifiers of the water properties and primary production (Bond and Overland, 2005).

The period of 2001 through 2018 has included strongly anomalous warm and cold periods on the Bering Sea shelf (Stabeno et al., 2017; Stabeno and Bell, 2019). The early portion (2001–2005) of this interval featured relatively mild winters and reduced sea ice (Stabeno et al., 2007) with pronounced impacts on lower-trophic levels and fish recruitment (Overland and Stabeno, 2004; Coyle et al., 2008; Stabeno et al., 2012a). A transition to colder conditions began in 2006 (Hunt et al., 2010). Between 2008 through 2013, ice cover on the southern portion of the shelf was comparable to that which occurred during the frigid period of the early 1970 s (Stabeno et al., 2017). A period of ocean warming and reduced sea ice cover began in 2014 and continued through 2019 (Stabeno et al., 2017; Stabeno and Bell, 2019). Changes in climate forcing and physical oceanography of the Bering Sea shelf are important in the present context due to linkages to lower-trophic level production and community structure, as elaborated below.

Sea ice is an important factor defining the interannual variability of the EBS shelf, influencing bottom temperatures throughout summer, cross-shelf transport, and timing of the spring phytoplankton bloom (Stabeno et al., 2012b; Stabeno et al., 2017). North of 60°N, ice usually covers the shelf for at least 98 % of March and April. Farther south (~57°N), the coverage averages < 10 % of the days in March and April (Stabeno et al., 2012b). Interannual variability in ice cover on the northern shelf was very small up to 2017/2018 (Stabeno and Bell, 2019), while the number of days ice has been present during March/April on the southern shelf up to 2016 has varied considerably (Hunt et al., 2022). Due largely to the influence of ice, the northern shelf has a low salinity surface lens and salty (31.8), cold (<-1.5 °C) bottom water (Stabeno et al., 2012b). Therefore, salinity contributes significantly to stratification on the northern shelf. Stratification of waters in the southern portion of the Middle Shelf Domain (depth 50 – 100 m) is driven primarily by solar heating of the surface layer in summer (Ladd and Stabeno, 2012). The differing drivers of stratification result in a sharp pycnocline in the south, while in the north, the pycnocline is more gradual, and often supports a subsurface bloom throughout the summer, a phenomenon rarely observed on the southern shelf (Stabeno et al., 2012b).

Changes in ice conditions and timing of the spring bloom affect Bering Sea zooplankton biomass (Hunt et al., 2002; Hunt et al., 2011; Sigler et al., 2016). In late winter/early spring, ice algae are a critical first food source for Bering Sea zooplankton (Wang et al., 2015a; Campbell et al., 2016; Pleuthner et al., 2016) and, in particular, are a driver of *Calanus glacialis/marshallae* (hereafter *Calanus* spp.) egg production (Baier and Napp, 2003; Durban and Casas, 2014; Daase et al., 2013). Later in spring, sea ice melting affects both the near-surface stratification by the release of freshwater, and the penetration of light into the water column. This increase in stratification and light can lead to an ice-associated phytoplankton bloom when the ice-melt comes late enough in the year to occur after the last of the big winter storms (Stabeno et al., 2001; Hunt et al., 2002). These ice-associated algae and phytoplankton appear to be important for the growth, metamorphosis and subsequent abundance of the dominant copepod and euphausiid taxa. (Campbell et al., 2016; Coyle et al., 2011; Eisner et al., 2020; Hunt et al., 2011, 2022; Kimmel et al., 2018). Observations from the Bering Sea show that the dominant middle shelf euphausiid, *Thysanoessa raschii,* forages on under-ice algae in spring (Lessard et al., 2010; Campbell et al., 2016). Additional evidence from the Barents Sea shows that *T. raschii* populations expand in cold periods and decline in warm periods (Drobysheva, 1994).

EBS jellyfish populations have fluctuated dramatically during the last four decades. A steep increase in jellyfish biomass was documented over the EBS shelf throughout the 1990 s (Brodeur et al., 2002). Biomass peaked in summer 2000 and then declined precipitously, stabilizing at a low to moderate level during 2001–2008 (Decker et al., 2014). The onset of the biomass increases during the 1990 s and the decline in 2000 coincided with transitions between climatic regimes: from a period of high interannual variability in sea ice extent and temperature to a period of consistently low penetration of sea ice coverage in the southeast and warm temperatures (Brodeur et al., 2008a). Jellyfish biomass on the EBS shelf exhibited a second steep increase beginning in 2009 to a second period of high biomass, which peaked in 2011–2012 (Decker et al., 2014).

Our previous investigations of a 27-year time series examined relationships between EBS jellyfish biomass and temperature, ice cover, atmospheric variables, current patterns, zooplankton biomass and associated fish biomass using Generalized Additive Models (GAM, Brodeur et al., 2008a). These analyses indicated that jellyfish increases during 1982–2004 were influenced regionally (northwest vs southeast) by interacting variables such as sea ice cover, sea surface temperature, currents, wind mixing, and food availability. In this paper, we use an updated time series, which included 13 additional years of environmental conditions and jellyfish biomass and spanned the period 1982–2017, to examine whether GAMs using solely physical parameters can accurately describe recent trends in Bering Sea jellyfish biomass. We focus on the use of physical parameters because they become available to researchers more quickly than biological data and thus, could be used to predict future levels of jellyfish biomass.

2. Material and methods

2.1. Jellyfish biomass and study regions

Jellyfish biomass data were obtained from annual quantitative bottom trawl surveys of the EBS shelf conducted by the NOAA Alaska Fisheries Science Center (AFSC). Collections were made at each of 356 stations arranged in a grid (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 AFSC (Brodeur et al.,

1999; Brodeur et al., 2002; Brodeur et al., 2008a; Decker et al., 2014). 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 for 30 min at 5.4 km h^{-1} (Lauth et al., 2019). 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. Since many jellyfish in the EBS 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 RACE survey indicates that most of the EBS jellyfish biomass (>85 %) consists of one scyphozoan species, *Chrysaora melanaster* (Brodeur et al., 2002; Decker et al., 2014). The remaining portion of the catch is comprised of the following species: *Aequorea* sp., *Aurelia* sp., *Cyanea capillata*, *Phacellophora camtschatica*, and *Staurophora mertensi*. Catches of all large jellyfish species are weighed, combined and standardized to catch per unit effort (CPUE in kg ha^{-1}, where 1 ha = 10,000 m^2; see Brodeur et al., 1999, for details). For our analyses, survey strata areas 10, 31, 32, and 50 were combined to create the southeast (SE) Middle Shelf area and strata 20, 41, 42, 43, 61, 62, 82, and 90 were combined to create the northwest NW Middle Shelf area (Lauth et al., 2019; Brodeur et al., 2008a; Fig. 1).

To generate visualizations of jellyfish CPUE through time, we interpolated abundance between sampling locations. Specifically, we estimated the best fit model (matern, spherical, or gaussian) describing spatial autocorrelation within each sample time period, and then used kriging to interpolate between observed values (Gräler et al., 2016). We developed kriged maps for the observed regimes including high biomass periods, low biomass periods and transition periods.

2.2. Generalized Additive modeling

Brodeur et al. (2008a) examined interannual trends in jellyfish biomass for the period 1982–2004. They determined the environmental correlates associated with jellyfish population fluctuations using GAMs, a form of non-linear regression, in which nonparametric smooth functions are determined from the data (Hastie and Tibshirani, 1990; Wood,

2004; Wood, 2006). Brodeur et al. (2008a) constructed separate models for the southeast (SE) and northwest (NW) portions of the RACE bottom trawl surveyusing log jellyfish CPUE as the dependent variable and physical and biological parameters as the covariates. Other biophysical parameters were originally considered in the Brodeur et al. (2008a) analyses (e.g., wind stress, ice retreat, forage fish biomass), but they were not significant covariates in the 1982–2004 models. To be as consistent as possible with our earlier models, these parameters were not included in current analyses of the 1982–2017 data. While the jellyfish and physical data are available to the present date, some biological model covariates included in the Brodeur et al. (2008a) analysis, e.g., zooplankton biomass, were not available beyond 2009 due to a lack of comparable sampling (D. Kimmel, AFSC, Seattle, pers. comm.). For this reason, we included only readily available physical parameters and lagged jellyfish biomass (Table 1) in our current models so that we could examine covariates associated with the jellyfish biomass changes to 2017.

Using updated environmental data for the period 1982–2017 (Table 1), we reran the GAM analyses of Brodeur et al. (2008a) to determine the set of covariates that best explain the variance in jellyfish biomass on the southeast and northwest regions of the Bering Sea middle shelf. We used a forward stepwise selection strategy, limiting the degrees of freedom of each term to four. Variables were dropped if addition of subsequent variables resulted in an increase of the model Generalized Cross Validation (GCV), which is a measure of the model prediction error. We simplified our new models for the entire period 1982–2017 by identifying collinear predictors. A variance inflation factor (VIF) was calculated for each covariate. The terms with the highest VIFs were sequentially dropped until all parameters in the models fell below a VIF threshold value of 2.0 (HighstatLibV10.R, Highland Statistics ltd, 2020) in the R 3.5.3 software (Zuur et al., 2009).

To evaluate the relative contribution of each additive term included in the final GAM to the overall predictions, we obtained term-predictions over the entire time series. Term predictions are expressed as anomalies (i.e., deviations from the mean), resulting from the contribution of each covariate, given the value of the examined covariate at the target time point. To evaluate residual temporal correlation,
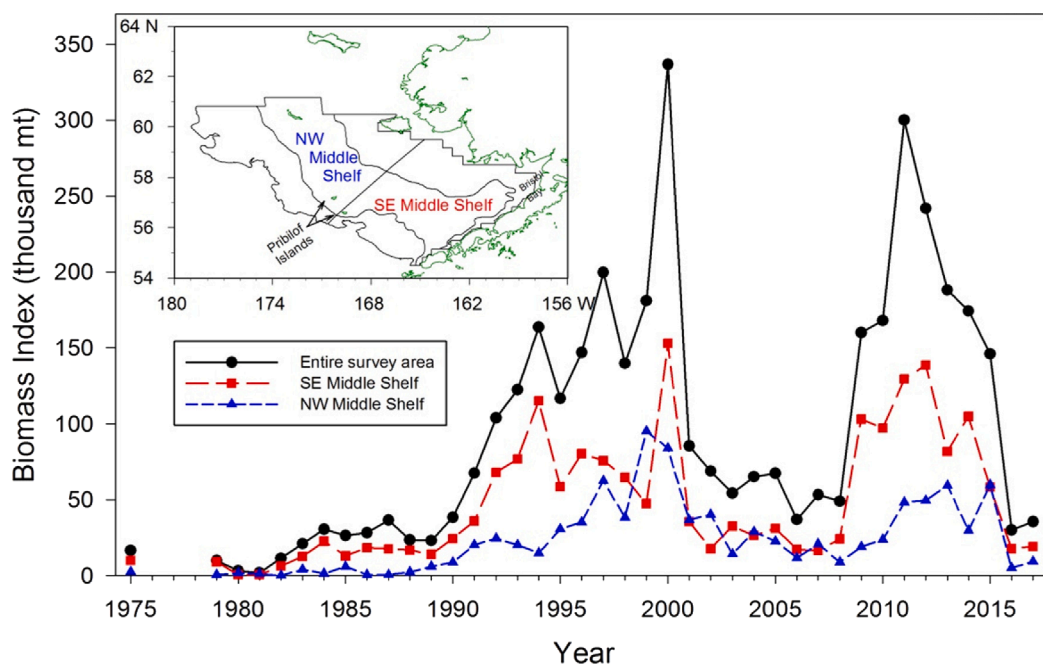

Fig. 1. Trend in jellyfish biomass from standardized bottom trawl surveys in the Bering Sea since 1975. Shown are the estimated total biomass (solid line) and subsets for the Southeast (SE, long dashed line) and Northwest, (NW, short dashed line) Middle Shelf Domains. The inset shows the sampling areas on the Bering Sea shelf.

Table 1

Model parameters used in Generalized Additive Modeling (GAM) analysis and descriptions, modified from Brodeur et al. (2008a).

Variable name	Description and source
current	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). Drifters ending south of the launch site were given negative values. From: https://oceanview.pfeg.noaa.gov/oscurs/.
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 wind forcing in spring, and primarily impacts the nature and timing of the spring phytoplankton bloom on the shelf (Hunt and Stabeno, 2002).
sebiomlag, nwbiomlag	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, lagged by 1 year.
sesprtemp	Mean March-April-May sea-surface temperature at 57°N, 164°W (southeast 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	Mean June-July-August sea-surface temperature at 57°N, 164°W (southeast region) derived from a NCEP reanalysis.
nwsprtemp	March–May sea-surface temperature at 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.
nwsumtemp	June-August sea-surface temperature at 59°N, 171°W (northwest region) derived from a NCEP reanalysis.
wmixjj	Wind mixing indices represent the average value of friction velocity u^3 for the period June–July at NOAA Mooring 2 (57°N, 164°W).
wmixmay	Wind mixing indices represents the average value of friction velocity u^3 for the period 1–31 May near St. Paul Island (57.1°N, 170.2°W).
wstressmj	The along-peninsula component of the wind stress (N m^{-2}) at Unimak Pass (54°N, 165°W) for the period May–June.
wstressna	The along-peninsula component of the wind stress (N m^{-2}) at Unimak Pass (54°N, 165°W) for the period November–April.

we used the *pacf* function in R. Finally, once we performed variable selection and model diagnostics, we simulated the entire time series of jellyfish biomass (log-transformed), based on the observed value of the covariates retained in the final model.

3. Results

The EBS bottom trawl survey indicates that EBS jellyfish populations have fluctuated widely over the last four decades; biomass reached a peak in 2000, declined rapidly to low levels during 2001–2005, a warm period (Hunt et al., 2022) and increased about eightfold to high levels in 2009–2014 (Fig. 1), a cold period (Hunt et al., 2022). With the return of warm conditions on the shelf beginning in 2015, jellyfish biomass declined once again to low levels (Fig. 1). Overall, the linear trend in jellyfish biomass showed a slight, but significant increase during the period 1979–2017 in both the SE (slope = 0.06, t = 4.15, p = 0.0002) and NW (slope = 0.10, t = 5.33, p < 0.0001) regions of the EBS.

The bottom trawl survey indicates that high jellyfish biomass levels occurred consistently in the southeastern survey region along the Alaska

Peninsula (Fig. 2). A second center of aggregation was located north of the Pribilof Islands to the west of St. Matthew Island at the northern extent of the survey (Fig. 2). Prior to 1991, EBS jellyfish biomass was distributed primarily in the southeastern portion of the survey (Fig. 2, Brodeur et al., 2008aLiu et al., 2011).

In the unconstrained models, SE jellyfish biomass in the preceding year was the strongest predictor of SE jellyfish biomass anomalies in the GAM analysis (Table S1). The following physical conditions also significantly contributed to the variation of jellyfish biomass: ice retreat, spring SE sea-surface temperature, wind mixing in May, wind mixing in Jun - Jul, wind stress in May - Jun, wind stress in Nov - Apr and current displacement (Fig. S1). The resulting SE model fit the data well (R^2_{adj} = 0.86, deviance explained = 92.3 %, GCV = 0.18, n = 36, Fig. S3).

Similarly, NW jellyfish biomass in the preceding year was the strongest predictor of NW jellyfish biomass anomalies in the unconstrained GAM analysis (Table S1) and with the following unconstrained physical conditions: summer and spring sea-surface temperature in the NW, ice cover, wind stress in Nov - Apr and current displacement (i.e., drifter displacement from the center of the NW jellyfish distribution) (Table S1, Fig. S2). The unconstrained NW model also fit the data well (R^2_{adj} = 0.79, deviance explained = 86.4 %, GCV = 0.86, n = 36, Fig. S3).

The unconstrained GAM analysis revealed that the relationships among jellyfish biomass and the environmental covariates were somewhat similar to those described by Brodeur et al. (2008a) (Figs. S1 and S2). We compared the contribution of each term included in the reparameterized model to the hindcasted value of jellyfish biomass (Fig. S4). The high jellyfish anomaly values estimated for both the SE and NW survey areas in 2009–2014 (Figs. S1 and S2) were mostly due to the positive effects of sea ice cover in the region (Fig. S4).

A Variance Inflation Factor analysis indicated that for the SE model, spring and summer temperatures (i.e., sesprtemp, sesumtemp), and ice conditions (i.e., icecover and iceretreat) exhibited multicollinearity with other variables remaining in the model. Similarly, for the NW model, springtime water temperature (i.e., nwsprtemp) and ice conditions (i.e., icecover and iceretreat) were correlated. Thus, these variables were omitted from our constrained analyses, resulting in the following simplified models for the SE and NW regions, respectively:

log(sejellybiom) ~ s(log(sebiomlag)) + s(wstressmj) + s(wmixmay) + s(wmixjj) + s(current).

log(nwjellybiom) ~ s(log(nwbiomlag)) + s(nwsumtemp) + s(current).

The GAM analysis on the constrained covariates (Table 2) determined that the SE jellyfish biomass in the preceding year caused the greatest variation of SE jellyfish biomass anomalies, and with the following physical conditions: wind mixing in May, wind mixing in Jun-Jul, wind stress in May - Jun, and current displacement (i.e., current, drifter displacement from the center of the SE jellyfish distribution) (Fig. 3). The resulting SE model had a high explained variance and fit the data without any specific pattern in the residuals (R^2_{adj} = 0.71, deviance explained = 78.2 %, GCV = 0.288, n = 36, Figs. 3, 4).

The NW jellyfish biomass in the preceding year caused the greatest variation in jellyfish biomass in the NW region, and with the following constrained physical conditions: summer sea-surface temperature in the NW, and current displacement (Table 2, Fig. 4). The constrained NW model also had a high explained variance and fit the data without any specific pattern in the residuals (R^2_{adj} = 0.68, deviance explained = 73.5 %, GCV = 1.01, n = 36, Figs. 4, 5).

These constrained GAMs estimating jellyfish biomass for the period 1982–2017 explained 78.2 % and 73.5 % of the time series variance for the southeast and northwest jellyfish models, respectively. The resulting models fit the data well (southeast R^2_{adj} = 0.71, n = 36, northwest R^2_{adj} = 0.68, n = 36, Fig. 4). We assessed the contribution of high jellyfish anomaly values estimated for the southeast and northwest regions during the recent biomass peak (i.e., 2009–2012, Fig. 4) and found that they were mostly due to the positive effect of the lag of the jellyfish biomass (Fig. 6). In addition, wind mixing in Jun - Jul was an important
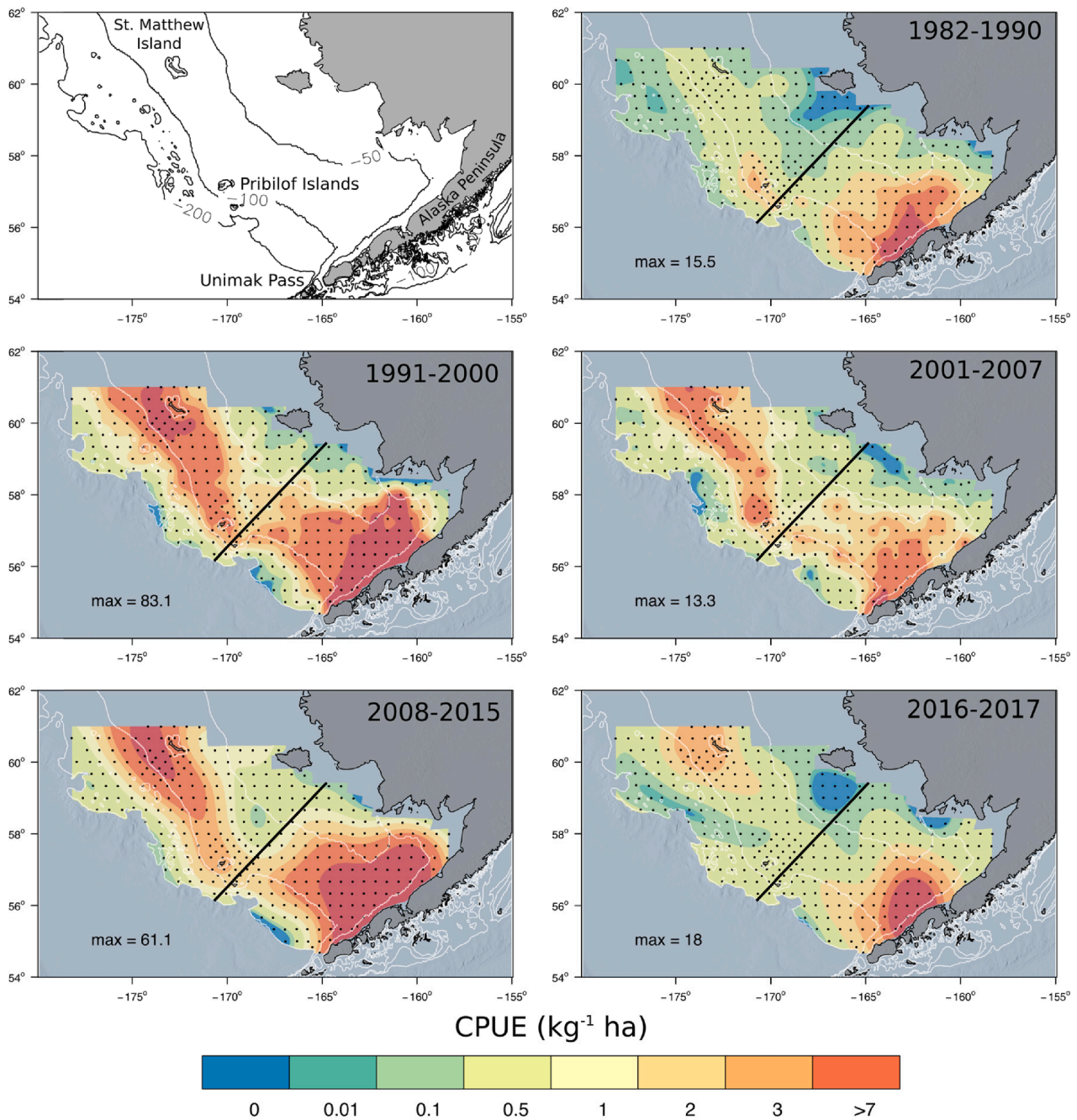
Fig. 2. (A) Study area and place names. The spatial distribution of jellyfish biomass (kg ha^{-1}) on the eastern Bering Sea shelf during the summer bottom trawl surveys, in (B)1982–1990, (C) 1991–2000, (D) 2001–2007, (E) 2008–2015, (F) 2016–2017. Contour lines indicate bathymetry (i.e., 50 m, 100 m and 200 m), dots indicate sampling locations and solid black lines bisecting the shelf indicate the division between the southeast and northwest regions.

covariate in the southeast model, particularly in the peak biomass year of 2011, and current displacement was a large contributor in the northwest model (Fig. 6).

The residuals of the resulting NW and SE models did not show any pattern of temporal autocorrelation, indicating that the intervening set of model covariates sufficiently addresses the observed temporal auto-correlation of the raw data. We did not check for spatial autocorrelation of the model residuals between the NW and SE regions because the two time series models were run independently of each other.

4. Discussion

Our examination of an additional 13 years of Eastern Bering Sea

jellyfish biomass surveys has demonstrated that jellyfish there continue to show fluctuations in biomass with a quasi-decadal cyclical pattern, resulting in a severalfold difference between the peak and low jellyfish abundance periods, and a northward shift in distribution. Although we found a slight increasing trend in biomass for the 1979–2017 period, this was most likely driven by the consistent period of low jellyfish biomass encountered at the start of this survey. Our constrained GAM analyses revealed that in both the SE and the NW Regions of the EBS, the greatest variation of jellyfish biomass anomalies was explained by jellyfish biomass in the preceding year. Additionally, in the SE Region abiotic conditions in spring (i.e., wind mixing, wind stress and current displacement), and summer (wind mixing) were important. In the NW region, summer sea-surface temperatures, and current displacement

Table 2

Results from all constrained 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. Bold models are those with the lowest generalized cross validation (GCV). Also shown is the percentage deviance explained (Dev.) for each model.

Region, terms	Dev.	GCV
SE		
sebiomlag, wstressmj, wmixmay, wmixjj, current	**78.2**	**0.288**
sebiomlag, wmixmay, wmixjj, current	78.3	0.302
sebiomlag, wmixmay, wmixjj	67.3	0.294
sebiomlag, nwsprtemp	64.1	0.291
NW		
nwbiomlag, nwsumtemp, wstressna, wstressmj, wmixmay, wmixjj, current	77.4	1.228
nwbiomlag, nwsumtemp, wstressna, wstressmj, wmixjj, current	77.4	1.137
nwbiomlag, nwsumtemp, wstressmj, wmixjj, current	75.5	1.090
nwbiomlag, nwsumtemp, wstressmj, current	74.8	1.026
nwbiomlag, nwsumtemp, current	**73.5**	**1.005**
nwbiomlag, current	64.7	1.129

were the most important physical variables, indicating that physical drivers of jellyfish biomass in the two regions differ.

The similarities between our modeling results and those of Brodeur et al. (2008a) suggest that the physical factors that control the explainable variance of jellyfish biomass have not changed in recent years, despite changes in environmental regimes. With a few exceptions (i.e., inclusion of additional wind variables and the omission of May sea-surface temperature in the southeast model) and the exclusion of collinear variables (i.e., temperature, ice), the terms in the updated models were the same physical variables that were found for the shorter time series of jellyfish biomass (1982–2004, Brodeur et al., 2008a).

The Eastern Bering Sea is a notable example of a system that experiences low-frequency temporal oscillations in jellyfish biomass depending on variations in environmental conditions (Condon et al., 2012; Condon et al., 2013). The increases occurring in colder periods with extensive sea ice and the reductions during extended warm periods with little sea ice and are likely tied to the availability of large crustacean zooplankton on which the jellyfish forage (see below). Within the present time series, it is apparent that once jellyfish populations are
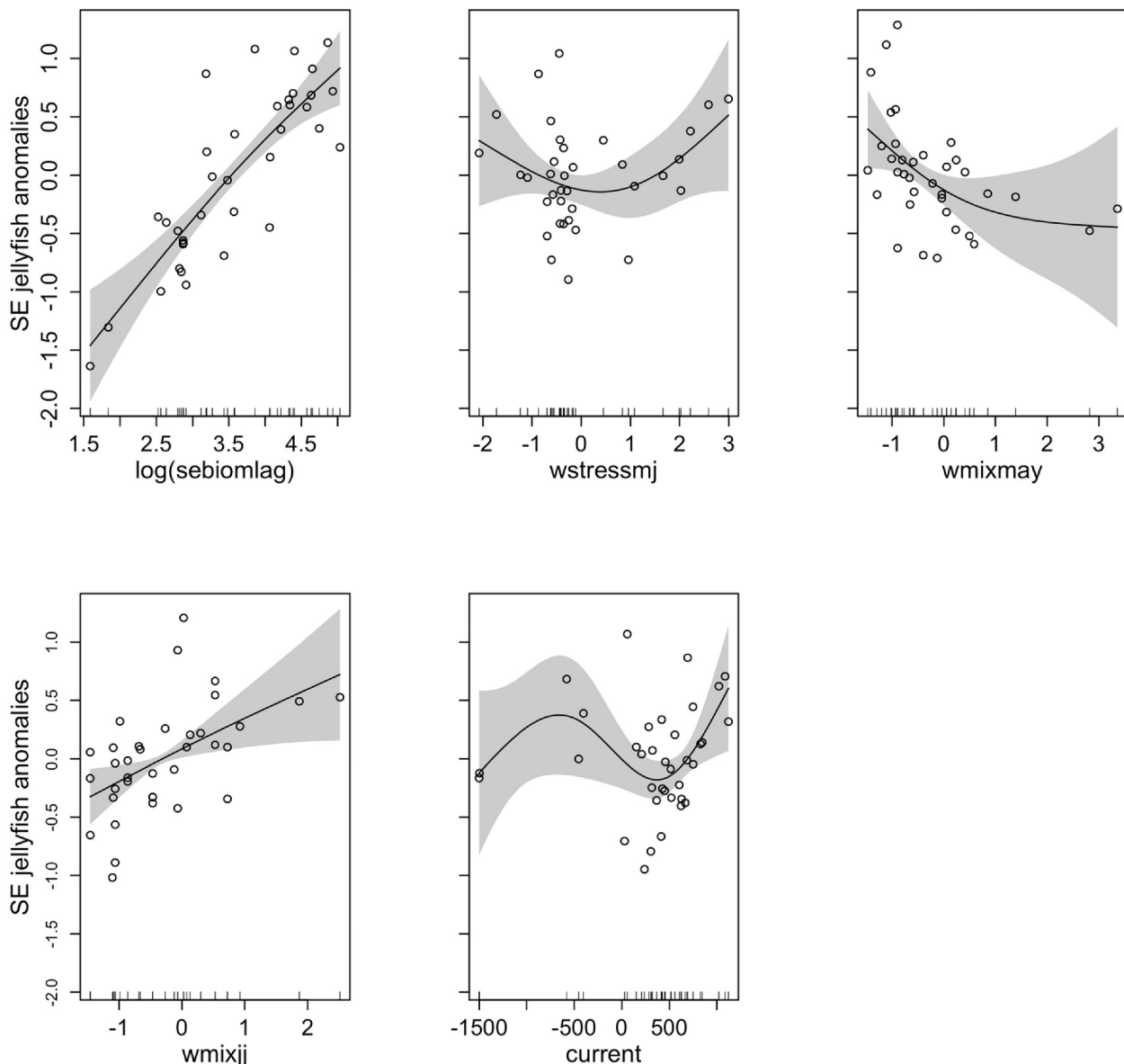

Fig. 3. Additive effects of the significant covariates included in the simplified southeast jellyfish biomass model (correlated variables dropped). Grey areas indicate 95% confidence limits. Axis labels are variable names, which are defined in Table 1.
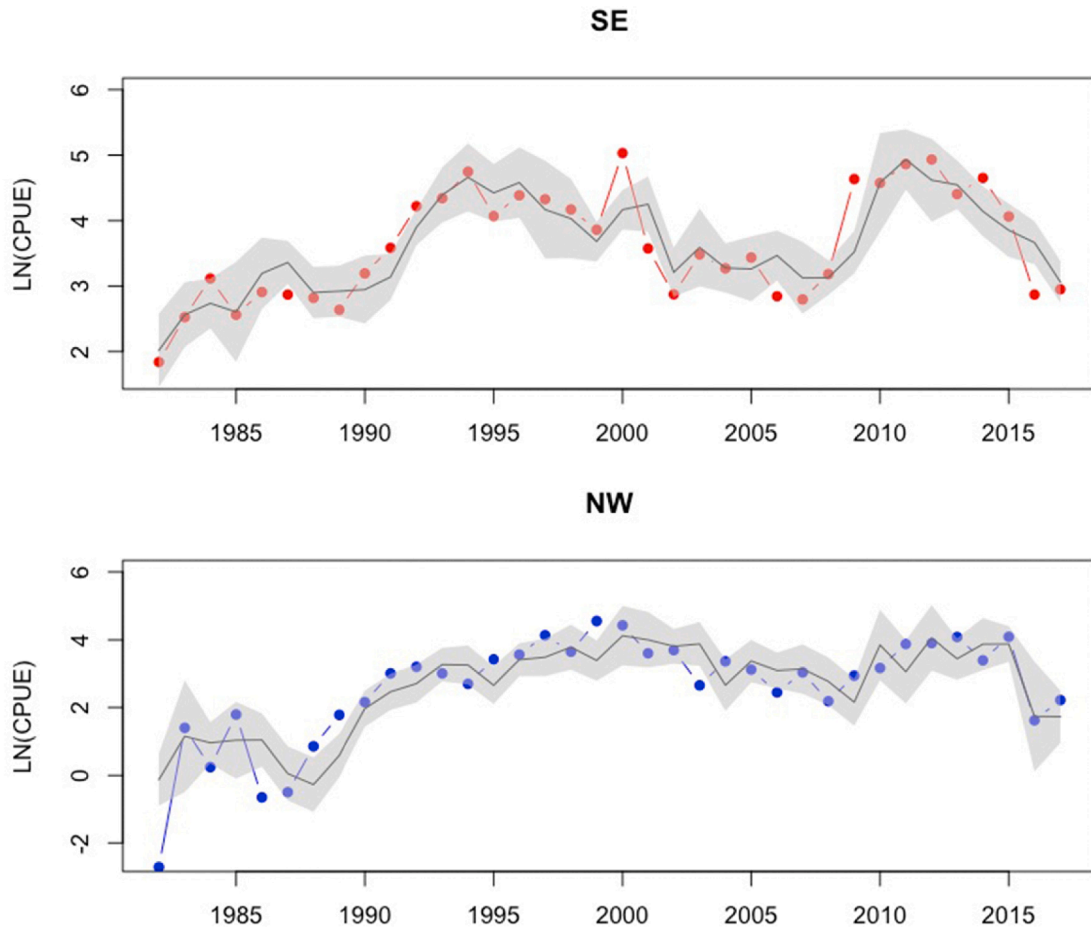
Fig. 4. GAM results (correlated variables dropped) for the two regions of the eastern Bering Sea shelf showing observed (dots) and hindcasted (solid line) jellyfish biomass CPUE (ln[kg ha^{-1}]) for the southeast middle shelf (top) and northwest middle shelf (bottom). Grey areas are the 95% confidence limits of the model fit.
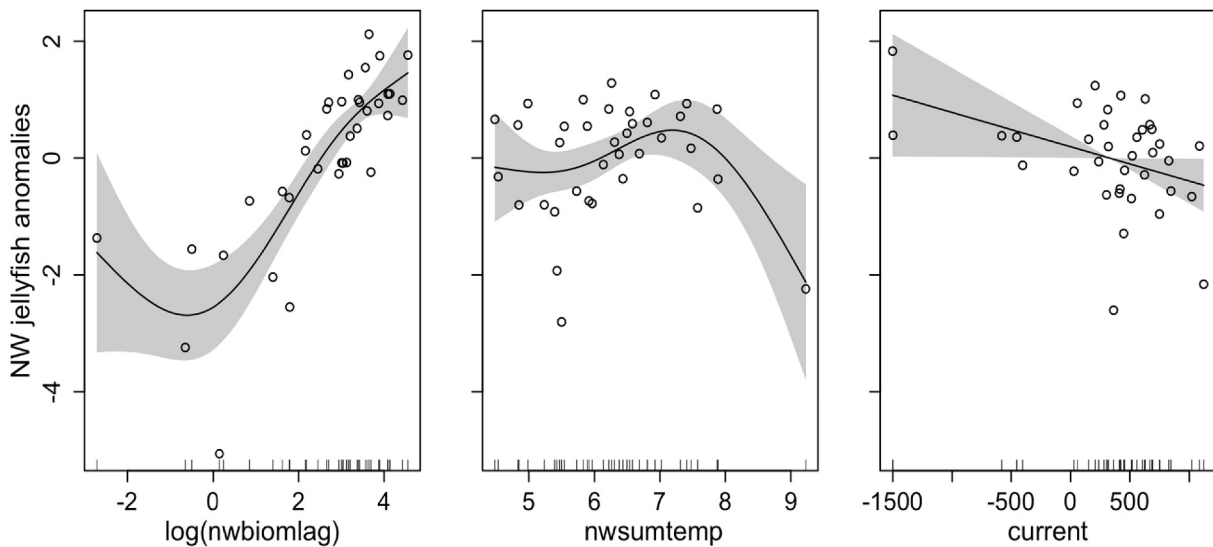

Fig. 5. Additive effects of the significant covariates included in the simplified northwest jellyfish biomass model (correlated variables dropped). Grey areas indicate 95% confidence limits. Axis labels are variable names, which are defined in Table 1.

severely reduced, it takes a series of years with favorable conditions for their populations to rebound.

The horizontal spatial distribution of jellyfish biomass also has also not been consistent since the start of the survey in 1982. After 1990, an increased proportion of jellyfish biomass was found in the northern

portion of the bottom trawl survey area, which contributed to two distinct centers of distribution, i.e., one in the southeastern portion of the survey and one to the northwest near St. Matthew Island (Brodeur et al., 2008a; Liu et al., 2011, Fig. 2). Recent surveys of the northern Bering Sea indicate a large (400 %) increase in jellyfish biomass in 2017,
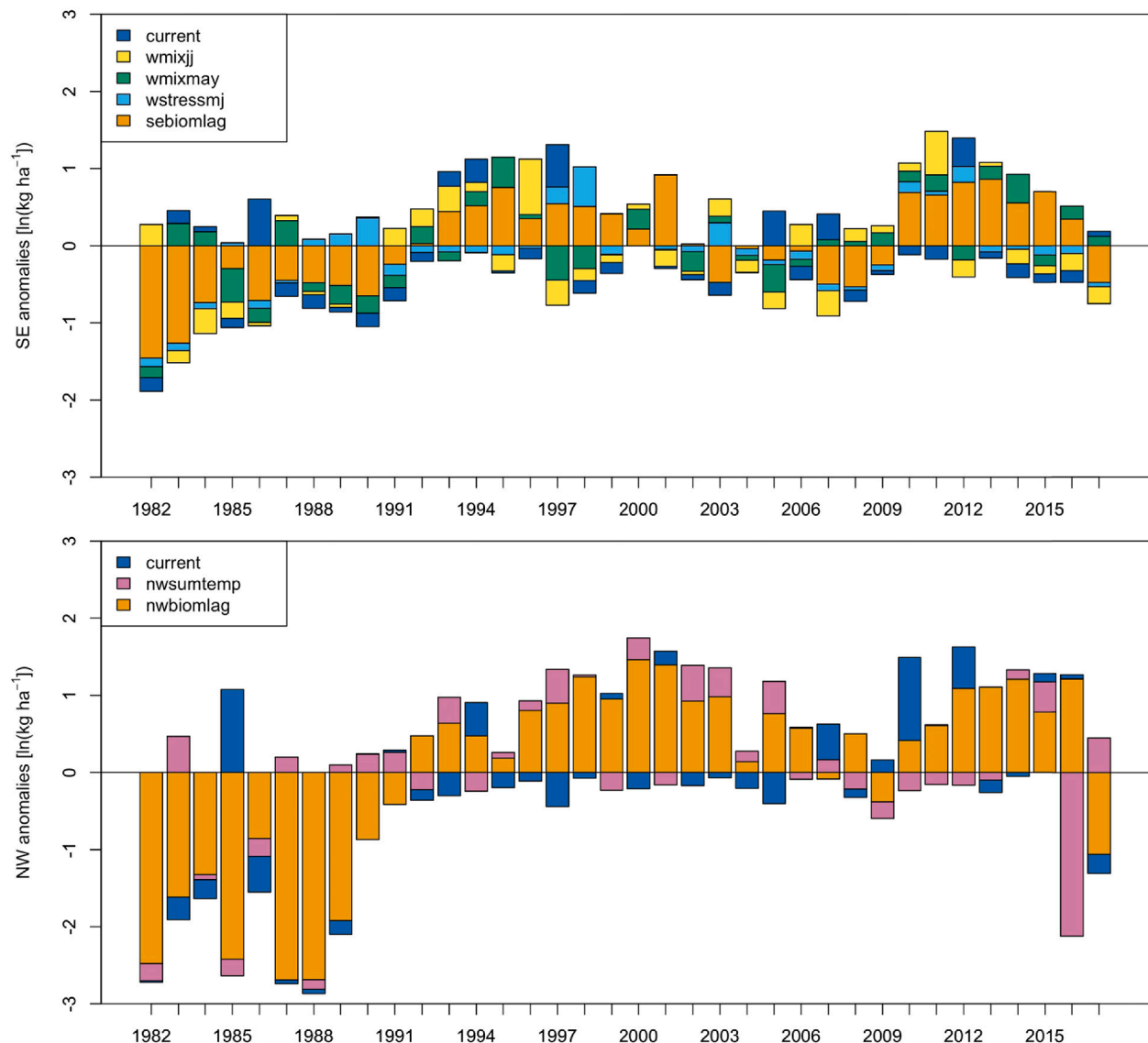
Fig. 6. Jellyfish biomass partial effect over the predicted mean in the southeast (top panel) and northwest (bottom panel) regions of the Bering Sea shelf during 1982–2017. The partial effect of each covariate can be positive or negative, depending on the value of the covariate. For the SE Jellyfish biomass (bottom panel) in 1982 for example, wmixjj had a positive effect of 0.3 units, meaning that it was positively contributing to the jellyfish biomass. However, the remaining covariates, and especially the lagged SE jellyfish biomass all had a negative effect, with cumulative impacts summing to about −1.8, which exceeded the positive effect caused by the wind mixing. Thus, the overall biomass of jellyfish in 1982 was below the mean value by about −1.5 units (on a log scale). The hindcasted mean value of jellyfish was 3.63 ln[kg ha^{-1}] in the southeast region and 2.59 ln[kg ha^{-1}] in the northwest region. The color-coding of the bars represents the contribution to the overall anomaly value of each term included in the simplified southeast jellyfish model (see Table 1 for variable descriptions).

a warm year, in comparison to 2010, a cool year (Lauth et al. 2019, Stevenson and Lauth, 2019). Thus, in some warm years, it is likely that the standard survey area has not encompassed the entire distribution of the jellyfish due to a northward shift beyond the northernmost latitude sampled.

Our previous analyses (Brodeur et al., 2008a) suggest that cold periods of high zooplankton biomass, when large copepod species predominate, contribute to favorable conditions for EBS jellyfish, whereas jellyfish are not favored in warm periods when smaller crustacean species predominate. Populations of large *Calanus* spp. on the eastern Bering Sea shelf remained at low to intermediate levels during the period when interannual variability in temperature and sea ice dominated, such as during 1995–99 (Stabeno et al., 2012a). By contrast, series of consecutive years with warm conditions and early ice retreat, such as, that which occurred in 2001–2005, appears to have been detrimental to the large, crustacean zooplankton (Eisner et al., 2014).

Specifically, *Calanus* spp. and the shelf euphausiid *T. raschii* were scarce during this period and this was related to the lack of sea ice or elevated water temperatures and unusually strong summer stratification of Middle Domain waters (Coyle et al., 2008; Hunt et al., 2008).

It is notable that wind mixing in May is negatively related to the SE biomass, but wind mixing in June-July is positively related. We suggest that enhanced wind mixing in May results in a reduced spring bloom (Sambrotto et al., 1986; Saitoh et al., 2002), while, conversely, more wind mixing in June-July could result in greater primary production once the water column becomes stratified (Stabeno et al., 2001; Stabeno et al. 2010), and thus, ultimately providing more phytoplankton for the large copepods. Eisner et al. (2016) have shown the correspondence between wind mixing and late summer primary production and how this relates to increased abundance of copepods in late summer. The positive response of the SE biomass to current values that are both large (i.e., drifters that ended well to the south of the NW jellyfish aggregation) and

negative (i.e., drifters were displaced to the south of the launch site; Table 1) may represent reduced displacement of jellyfish from their likely benthic sources along the Alaska Peninsula, resulting in retention of jellyfish in the SE region. We interpret the inverse relationship between the NW biomass and current to indicate that when displacement along the shelf is low, jellyfish are retained in the NW region.

The physical covariates included in the constrained models of jellyfish biomass may not be mechanistic drivers of jellyfish biomass, but instead may be proxies for the regional influence of climate that is known to affect the EBS ecosystem. Atmospheric forcing is the primary driver of sea ice dynamics in the Bering Sea (Stabeno et al., 2012a). Sea ice cover affects water temperature as well as the presence of ice-associated phytoplankton blooms (Sigler et al., 2014), both of which influence secondary production and zooplankton community composition on the shelf (Eisner et al., 2018).

Recent ecosystem studies indicate that with cooling during 2006–2014, populations of large, lipid-rich crustacean zooplankton (i.e., *Calanus* spp. and euphausiids) have increased (Coyle et al., 2011; Hunt et al., 2011; Ressler et al., 2012; Stabeno et al., 2012a; Eisner et al., 2018). Large zooplankton species may provide the secondary production necessary for an increase in jellyfish populations. *Chrysaora* spp. are known to ingest copepods and the eggs and early life stages of euphausiids among other prey (Brodeur et al., 2002; Suchman et al., 2008; Ruzicka et al., 2012; Ruzicka et al., 2020). A period of high biomass of large copepods began in 2008 (Eisner et al. 2020), which preceded the start of the second peak in jellyfish biomass in 2009 by one year (Fig. 1). During cool periods (e.g., 2007–2013, Stabeno et al. 2017), jellyfish may be responding to the increase in large zooplankton, such as *Calanus* spp. and euphausiids, or to some factor(s) that covary with this increase (Hunt et al., 2011).

Both *T. raschii* and *Calanus* spp. store lipids to carry them through winter in near-bottom shelf waters (Falk-Petersen et al., 2000; Coyle et al., 2011). After several years with little ice and warm summers, these bottom waters warm from −1.5 °C to 3–4 °C, which increases the metabolism of overwintering zooplankton and may challenge their ability to have sufficient lipid reserves the following winter/spring to produce a strong cohort (Coyle et al., 2011; Hunt et al., 2011; Sigler et al., 2016). Extended periods with warm years with little sea ice, such as occurred in 2001–2005 and 2014–2016, result in low populations of *Calanus* spp., and *T. raschii*, whereas moderately cold (2006) and extremely cold years (2007–2010) result in increasing abundances of these large, lipid-rich crustacean zooplankton (Coyle et al., 2011; Hunt et al., 2011; Hunt et al., 2018; Ressler et al., 2012). Year-class strength of walleye pollock (*Gadus chalcogrammus*), the dominant pelagic fish in the EBS, has also been shown to be related to sea ice extent and duration in spring (Hunt et al., 2022).

The late winter/early spring period may be a critical bottleneck for jellyfish production with favorable conditions leading to higher production and survival of early life stages. Ephyra (i.e., juvenile medusa) production and growth increase when scyphozoan polyps are experimentally provided with more food (Ishii and Watanabe, 2003; Wang and Li, 2015; Wang et al., 2015b; Hubot et al., 2017), suggesting that increased prey availability could stimulate a rapid increase in jellyfish populations. In addition, scyphozoan polyps, which ensure the long-term persistence of jellyfish populations during periods of unfavorable environmental conditions (Lucas et al., 2012), increase their rates of asexual reproduction in response to prey availability, though responses are species-specific (Hubot et al., 2017). Direct studies on *C. melanaster* polyps have not been conducted to our knowledge, however, it appears that this dominant jellyfish species in the EBS is responding to changes in food availability during warm and cold periods, thereby responding indirectly to changes in physical conditions via their crustacean zooplankton prey. Thus, jellyfish may be an important indicator of ecosystem changes in the eastern Bering Sea.

The bifurcating flow through Unimak Pass, which travels more strongly to the northwest along the 100 m isobath in winter and more strongly eastward along the Alaska Peninsula in summer (Stabeno et al., 2002), may be, in part, responsible for the observed spatial patterns of jellyfish in the survey area. The benthic, overwintering phase of the jellyfish life cycle (polyps) require hard substrates to settle upon, which are scarce on the EBS shelf. We suggest that benthic jellyfish polyps, likely located along the rocky shorelines of Unimak Pass and the Alaska Peninsula, release juvenile medusae, which would be advected eastward along the Alaska Peninsula and on the middle shelf to the northwest by the predominant flow patterns. This explanation is supported by Huo et al. (2021) who found distinct horizontal distribution patterns of *C. melanaster* related to the deep-water intrusion from Bering Canyon that influenced coastal circulation patterns in the region. The source of medusae for the northern aggregation may be the rocky subtidal coast of the Pribilof Islands, and the northwestern flow along the shelf in this region may contribute to the observed spatial pattern of jellyfish to the north. Drift simulations are in agreement with these hypotheses (Decker et al., 2013). However, it is not known how climate change and large-scale ocean variability will influence these locations where medusa sources are likely to occur in the EBS, and how such changes will affect the cross-shelf advection and retention of *C. melanaster*.

Although a number of physical parameters were related to the variability of *Chrysaora* biomass in both regions, the biomass in the previous year's survey was a strong predictor of biomass in a given year, especially in the NW region (Fig. 6). The cause of this correlation is not discernable from our surveys which take place only once a year in summer. One hypothesis is that although most large scyphomedusae are considered an annual species, occurring in the pelagic zone only from spring through early winter, it is possible that some members of the population may overwinter and contribute to the following year biomass. Large adult *C. melanaster* were observed at the ice edge in the southern Bering Sea (i.e., near moorings M2 and M4, (Brodeur et al., 2008a) and below sea ice in the Chukchi Sea, situated just north of the Bering Sea, during May and June in several years (Purcell et al., 2017). However, due to the prevailing currents in this region, it is unlikely that a large number of adults would be retained in this region of the southern Bering Sea for over a year. Almost all the adults collected during our surveys fall within a limited size range and we do not see a pronounced bimodal distribution in the population during the late summer (Brodeur, 1998; Brodeur et al., 2002). We suggest instead that the high population correlation between years likely results from high numbers of adults producing many planulae, which settle as benthic scyphistoma, and then strobilate to produce high numbers of the free-swimming ephyra stage the following spring, with the inverse happening during low abundance periods. Only during the transition years between the high and low abundance levels (i.e., rapid increases or declines in abundance), does the physical forcing apparently override this recruitment mechanism.

Jellyfish are important zooplankton consumers and have the potential to restructure food webs when their abundance is high (Condon et al., 2011). Jellyfish and forage fish distributions often overlap (Brodeur et al., 2008b; Decker et al., 2018) and thus jellyfish can negatively impact fisheries because they compete with zooplanktivorous fish (Schnedler-Meyer et al., 2016; Opdal et al., 2019), feed on early life stages of fish, and divert lower trophic level production away from upper trophic levels (Purcell and Sturdevant, 2001; Lynam et al., 2005a; Lynam et al., 2005b; Brodeur et al., 2008b; Brodeur et al., 2011; Robinson et al., 2015; Ruzicka et al., 2020). Gelatinous zooplankton can substantially alter the carbon cycle in systems where they are abundant (Condon et al., 2011).

5. Conclusions

An important conclusion from our work is that increasing ocean temperatures associated with climate change may not necessarily lead to a higher biomass of jellyfish in all ecosystems (e.g., Long et al., 2021), and that a suite of physical and biological factors may be responsible for changes in jellyfish populations observed in the world's oceans (Mills,

2001; Purcell, 2005; Purcell et al., 2007; Richardson et al., 2009). Laboratory studies of temperate *Chrysaora* congeners have shown increased asexual reproduction at warm temperatures (e.g., Thein et al., 2013; Treible and Condon, 2019). However, our results indicate that the links between climate and jellyfish biomass are complex, probably involving direct effects on the production, survival and dispersal of all jellyfish life stages (i.e., medusae, polyps, ephyrae, and planulae), as well as the indirect effects of climate on the production and availability of jellyfish prey.

Our updated models hindcast levels of jellyfish biomass during 2005–2017 in the two geographic regions with high degrees of accuracy. These results provide some confidence that our models have value as tools to predict future levels of jellyfish biomass. Furthermore, it is promising that our models predict jellyfish biomass without biological parameters, other than the lag of jellyfish biomass. In comparison to physical parameters, which become available to researchers quickly, zooplankton samples can take years to process. Models that include only physical predictors can be used when biological sampling cannot be conducted. However, recent unprecedented warm temperatures on the Eastern Bering Sea shelf and negligible winter sea ice extent well beyond the historical record (Duffy-Anderson et al., 2017, Duffy-Anderson et al., 2019, Huntington et al., 2020) may pose a challenge for future extrapolations of our model. Indeed, recent observations of jellyfish biomass from the bottom trawl survey (Britt, 2021) indicate both high (2019) and low (2021) jellyfish biomass levels despite elevated temperatures throughout this period. Jellyfish, due to their short lifespan and ability to respond quickly to changing ocean conditions (Richardson et al., 2009), may be a key indicator species in this highly productive ecosystem.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2022.102923.

References

Baier, C.T., Napp, J.M., 2003. Climate-induced variability in *Calanus marshallae* populations. Journal Plankton Research 25, 771–782. https://doi.org/10.1093/plankt/25.7.771.

Bond, N.A., Overland, J.E., 2005. The importance of episodic weather events to the ecosystem of the Bering Sea shelf. Fish. Oceanogr. 14, 97–111. https://doi.org/10.1111/j.1365-2419.2004.00321.x.

Britt, L., 2021. Jellyfishes - Eastern Bering Sea Shelf. In: Siddon, E. (Ed.), Ecosystem Status Report 2021: Eastern Bering Sea, Stock Assessment and Fishery Evaluation Report, North Pacific Fishery Management Council, 1007 West Third, Suite 400, Anchorage, Alaska, pp. 104-105.

Brodeur, R.D., 1998. *In situ* observations of the associations of juvenile fishes and scyphomedusae in the eastern Bering Sea. Mar. Ecol. Prog. Ser. 163, 11–20. https://doi.org/10.3354/meps163011.

Brodeur, R.D., Mills, C.E., Overland, J.E., Walters, G.E., Schumacher, J.D., 1999. Substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fish. Oceanogr. 8, 296–306. https://doi.org/10.1046/j.1365-2419.1999.00115.x.

Brodeur, R.D., Sugisaki, H., Hunt Jr., G.L., 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. Mar. Ecol. Prog. Ser. 233, 89–103. https://doi.org/10.3354/meps233089.

Brodeur, R.D., Decker, M.B., Ciannelli, L., Purcell, J.E., Bond, N.A., Stabeno, P.J., Acuna, E., Hunt Jr., G.L., 2008a. Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. Prog. Oceanogr. 77, 103–111. https://doi.org/10.1016/j.pocean.2008.03.017.

Brodeur, R.D., Suchman, C.L., Reese, D.C., Miller, T.W., Daly, E.A., 2008b. Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. Mar. Biol. 154, 649–659. https://doi.org/10.1007/s00227-008-0958-3.

Brodeur, R.D., Ruzicka, J.J., Steele, J.H., 2011. Investigating alternate trophic pathways through gelatinous zooplankton and planktivorous fishes in an upwelling ecosystem using end-to-end models. In: Omori, K., Guo, X., Yoshie, N., Fujii, N., Handoh, I.C., Isobe, A., Tanabe, S. (Eds.), Interdisciplinary Studies on Environmental Chemistry: Marine Environmental Modeling and Analysis. TERRAPUB, Tokyo, pp. 57–63.

Campbell, R.G., Ashjian, C.J., Sherr, E.B., Sherr, B.F., Lomas, M.W., Ross, C., Alatalo, P., Gelfman, C., Van Keuren, D., 2016. Mesozooplankton grazing during spring sea-ice conditions in the eastern Bering Sea. Deep-Sea Res. II 134, 157–172. https://doi.org/10.1016/j.dsr2.2015.11.003.

Condon, R.H., Duarte, C.M., Pitt, K.A., Robinson, K.L., Lucas, C.H., Sutherland, K.R., Mianzan, H.W., Bogeberg, M., Purcell, J.E., Decker, M.B., Uye, S.I., Madin, L.P., Brodeur R.D., Haddock, S.H.D., Malej, A., Parry, G.D., Eriksen, E., Quiñones, J., Acha, M., Harvey, M., Arthur, J.M., Graham, W.M., 2013. Recurrent jellyfish blooms are a consequence of global oscillations. Proceedings of the National Academy of Sciences, 110,1000-1005, doi: 10.1073/pnas.1210920110.

Condon, R.H., Steinberg, D.K., del Giorgio, P.A., Bouvier, T.C., Bronk, D.A., Graham, W. M., Ducklow, H.W., 2011. Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. Proc. Natl. Acad. Sci. 108, 10225–10230. https://doi.org/10.1073/pnas.1015782108.

Condon, R.H., Graham, W.H., Duarte, C.M., Pitt, K.A., Lucas, C.H., Haddock, S.H.D., Sutherland, K.R., Robinson, K.L., Dawson, M.N., Decker, M.B., Mills, C.E., Purcell, J. E., Malej, A., Mianzan, H., Uye, S., Gelcich, S., Madin, L.P., 2012. Questioning the rise of gelatinous zooplankton in the world's oceans. Bioscience 62, 160–169. https://doi.org/10.1525/bio.2012.62.2.9.

Coyle, K.O., Pinchuk, A.I., Eisner, L.B., Napp, J.M., 2008. Zooplankton species composition, abundance and biomass on the southeastern Bering Sea shelf during summer: the potential role of water column stability in structuring the zooplankton community. Deep-Sea Res. II 55, 1775–1791. https://doi.org/10.1016/j.dsr2.2008.04.029.

Coyle, K.O., Eisner, L.B., Mueter, F.J., Pinchuk, A.I., Janout, M.A., Cieciel, K.D., Farley, E. V., Andrews, A.G., 2011. Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the Oscillating Control Hypothesis. Fish. Oceanogr. 20, 139–156. https://doi.org/10.1111/j.1365-2419.2011.00574.x.

Daase, M., Falk-Petersen, S., Varpe, Ø., Darnis, G., Søreide, J. E., Wold, A., Leu., E., Berge, J., Philippe, B., Fortier, L., 2013. Timing of reproductive events in the marine copepod *Calanus glacialis*: a pan-Arctic perspective. Canadian Journal of Fisheries and Aquatic Sciences, 70, 871-884, doi: 10.1139/cjfas-2012-0401.

Decker, M.B., Cieciel, K., Zavolokin, A., Lauth, R.R., Brodeur, R.D., Coyle, K.O., 2014. Population fluctuations of jellyfish in the Bering Sea and their ecological role in this productive shelf ecosystem. In: Pitt, K.A., Lucas, C.H. (Eds.), Jellyfish Blooms. Springer, Dordrecht, pp. 153-183, doi: 10.1007/978-94-007-7015-7_7.

Decker, M.B., Liu, H., Ciannelli, L., Ladd, C., Cheng, W., Chan, K.S., 2013. Linking changes in eastern Bering Sea jellyfish populations to environmental factors via nonlinear time series models. Mar. Ecol. Prog. Ser. 494, 179–189. https://doi.org/10.3354/meps10545.

Decker, M.B., Robinson, K.L., Dorji, S., Cieciel, K.D., Barceló, C., Ruzicka, J.J., Brodeur, R.D., 2018. Jellyfish and forage fish spatial overlap on the eastern Bering Sea shelf during periods of high and low jellyfish biomass. Mar. Ecol. Prog. Ser. 591, 57–69. https://doi.org/10.3354/meps12273.

Drobysheva, S.S., 1994. The Barents Sea euphausiids and their role in the formation of fishing biological production. Murmansk: PINRO Press, 1994. 139 p. (in Russian).

Duffy-Anderson, J.T., Stabeno, P.J., Siddon, E.C., Andrews, A.G., Cooper, D.W., Eisner, L. B., Farley, E.V., Harpold, C.E., Heintz, R.A., Kimmel, D.G., Sewall, F.F., 2017. Return of warm conditions in the southeastern Bering Sea: Phytoplankton - Fish. PLoS One 12 (6), e0178955.

Duffy-Anderson, J.T., Stabeno, P., Andrews, A.G., Cieciel, K., Deary, A., Farley, E., Fugate, C., Harpold, C., Heintz, R., Kimmel, D., Kuletz, K., 2019. Responses of the northern Bering Sea and southeastern Bering Sea pelagic ecosystems following record-breaking low winter sea ice. Geophys. Res. Lett. 46, 9833–9842. https://doi.org/10.1029/2019GL083396.

Durban, E.G., Casas, M.C., 2014. Early reproduction by *Calanus glacialis* in the northern Bering Sea: the role of ice algae as revealed by molecular analysis. J. Plankton Res. 36, 1–19. https://doi.org/10.1093/plankt/fbt121.

Eisner, L.B., Napp, J.M., Mier, K.L., Pinchuk, A.I., Andrews, A.G., 2014. Climate-mediated changes in zooplankton community structure for the eastern Bering Sea. Deep Sea Res., Part II 109, 157–171. https://doi.org/10.1016/j.dsr2.2014.03.004.

Eisner, L.B., Gann, J.C., Ladd, C., Cieciel, K.D., Mordy, C.W., 2016. Late summer/early fall phytoplankton biomass (chlorophyll a) in the eastern Bering Sea: spatial and temporal variations and factors affecting chlorophyll a concentrations. Deep Sea Res. Part II 134, 100–114. https://doi.org/10.1016/j.dsr2.2015.07.012.

Eisner, L.B., Pinchuk, A.I., Kimmel, D.G., Mier, K.L., Harpold, C.E., Siddon, E.C., 2018. Seasonal, interannual, and spatial patterns of community composition over the eastern Bering Sea shelf in cold years. Part I: zooplankton. ICES J. Mar. Sci. 75, 72–86. https://doi.org/10.1093/icesjms/fsx156.

Eisner, L.B., Yasumiishi, E.M., Andrews, A.A., O'Leary, C.A., 2020. Large copepods as leading indicators of walleye pollock recruitment in the southeastern Bering Sea: Sample-based and spatio-temporal model (VAST) results. Fish. Res. 232, 105720 https://doi.org/10.1016/j.fishres.2020.105720.

Falk-Petersen, S., Hagen, W., Kattner, G., Clarke, A., Sargent, J., 2000. Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. Canadian Journal of Fisheries and Aquatic Science 57, 178–191. https://doi.org/10.1139/f00-194.

Gräler, B., Pebesma, E., Heuvelink, G., 2016. Spatio-Temporal Interpolation using gstat. The R Journal 8, 204–218.

Hastie, T., Tibshirani, R., 1990. Generalized Additive Models. Chapman and Hall, London.

Highland Statistics Ltd., 2020. Corvif function. Available from: http://www.highstat.com/Books/Book2/HighstatLibV10.R.

Hubot, N., Lucas, C.H., Piraino, S., 2017. Environmental control of asexual reproduction and somatic growth of *Aurelia* spp. (Cnidaria, Scyphozoa) polyps from the Adriatic sea. PLoS ONE, 12(6):e0178482, doi: 10.1371/journal.pone.0178482.

Hunt Jr., G.L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R.D., Napp, J.M., Bond, N.A., 2002. Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep Sea Research II 49, 5821–5853. https://doi.org/10.1016/S0967-0645(02)00321-1.

Hunt Jr., G.L., Stabeno, P.J., Strom, S., Napp, J.M., 2008. Patterns of spatial and temporal variation in the marine ecosystem of the southeastern Bering Sea, with special reference to the Pribilof Domain. Deep-Sea Res. II 55, 1919–1944. https://doi.org/10.1016/j.dsr2.2008.04.032.

Hunt Jr., G.L., Allen, B.M., Angliss, R.P., Baker, T., Bond, N., Buck, G., Byrd, G.V., Coyle, K.O., Devol, A., Eggers, D.M., Eisner, L., Feely, R.A., Fitzgerald, S., Fritz, L.W., Gritsay, E.V., Ladd, C., Lewis, W., Mathis, J., Mordy, C.W., Mueter, F., Napp, J., Sherr, E., Shull, D., Stabeno, P., Stepanenko, M.A., Strom, S., Whitledge, T.E., 2010. Status and trends of the Bering Sea region, 2003–2008. In: McKinnell, S.M., Dagg, M.J. (Eds.), Marine Ecosystems of the North Pacific Ocean, 2003–2008, PICES Special Publication 4. North Pacific Marine Science Organization, Sidney, BC, pp. 196–267.

Hunt Jr., G.L., Coyle, K.O., Eisner, L.B., Farley, E.V., Heintz, R.A., Mueter, F., Napp, J.M., Overland, J.E., Ressler, P.H., Salo, S., Stabeno, P.J., 2011. Climate impacts on eastern Bering Sea foodwebs: a synthesis of new data and an assessment of the Oscillating Control Hypothesis. ICES J. Mar. Sci. 68, 1230–1243. https://doi.org/10.1093/icesjms/fsr036.

Hunt Jr., G.L., Renner, M., Kuletz, K.J., Salo, S., Eisner, L., Ressler, P.H., Ladd, C., Santora, J.A., 2018. Timing of sea-ice-retreat affects the distribution of seabirds and their prey in the southeastern Bering Sea. Mar. Ecol. Prog. Ser. 593, 209–230. https://doi.org/10.3354/meps12383.

Hunt Jr., G.L., Yasumiishi, E.M., Eisner, L.B., Stabeno, P.J., Decker, M.B., 2022. Climate warming and the loss of sea ice: the impact of sea-ice variability on the southeastern Bering Sea pelagic ecosystem. ICES J. Mar. Sci. 79 (937), 953. https://doi.org/10.1093/icesjms/fsaa206.

Huntington, H.P., Danielson, S.L., Wiese, F.K., Baker, M., Boveng, P., Citta, J.J., De Robertis, A., Dickson, D., Farley, E., George, J.C., Iken, K., 2020. Evidence suggests potential transformation of the Pacific Arctic ecosystem is underway. Nat. Clim. Chang. 10, 342–348. https://doi.org/10.1038/s41558-020-0695-2.

Huo, Y., Decker, M.B., Wang, L., Zhao, J., Lemoine, H., Lankowicz, K., Bi, H., 2021. The influence of a deep-water intrusion on the distribution of *Chrysaora melanaster* in the southeastern Bering Sea. J. Geophys. Res. Oceans 126. https://doi.org/10.1029/2020JC016867.

Ishii, H., Watanabe, T., 2003. Experimental study of growth and asexual reproduction in *Aurelia aurita* polyps. Sessile Organisms 20, 69–73. https://doi.org/10.4282/sosj.20.69.

Kimmel, D.G., Eisner, L.B., Wilson, M.T., Duffy-Anderson, J.T., 2018. Copepod dynamics across warm and cold periods in the eastern Bering Sea: Implications for walleye pollock (*Gadus chalcogrammus*) and the Oscillating Control Hypothesis. Fish. Oceanogr. 27, 143–158. https://doi.org/10.1111/fog.12241.

Ladd, C., Stabeno, P.J., 2012. Stratification on the eastern Bering Sea shelf revisited. Deep-Sea Res. II 65–70, 72–83. https://doi.org/10.1016/j.dsr2.2012.02.009.

Lauth, R. R., Dawson, E. J., Conner, J., 2019. Results of the 2017 eastern and northern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate fauna. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-396, 260 p.

Lessard, E.J., Shaw, C.T., Bernhardt, M., Engel, V.L., Foy, M.S., 2010. Euphausiid feeding and growth in the eastern Bering Sea, Eos Transactions of the American geophysical Union, 91(26), Ocean Sciences Meeting Supplement, Abstract IT356-01.

Liu, H., Ciannelli, L., Decker, M.B., Ladd, C., Chan, K.S., 2011. Nonparametric threshold model of zero-inflated spatio-temporal data with application to shifts in jellyfish distribution. J. Agric. Biol. Environ. Stat. 16, 185–201. https://doi.org/10.1007/s13253-010-0044-4.

Long, A.P., Haberlin, D., Lyashevska, O., Brophy, D., O' Hea, B., O'Donnell, C., Scarrott, R.G., Lawton, C., Doyle, T.K., 2021. Interannual variability of gelatinous mesozooplankton in a temperate shelf sea: greater abundance coincides with cooler sea surface temperatures. ICES J. Mar. Sci. 78, 1372–1385, doi:10.1093/icesjms/fsab030.

Lucas, C.H., Graham, W.M., Widmer, C., 2012. Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. Adv. Mar. Biol. 63, 133–196. https://doi.org/10.1016/B978-0-12-394282-1.00003-X.

Lynam, C.P., Hay, S.J., Brierley, A.S., 2005a. Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. J. Mar. Biol. Assoc. U.K., 85, 435-450, doi: 10.1017/S0025315405011380.

Lynam, C.P., Heath, M.R., Hay, S.J., Brierley, A.S., 2005b. Evidence for impacts by jellyfish on North Sea herring recruitment. Mar. Ecol. Prog. Ser. 298, 157–167. https://doi.org/10.3354/meps298157.

Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451, 55–68. https://doi.org/10.1023/A:1011888006302.

Niebauer, H.J., 1983. Multiyear sea ice variability in the eastern Bering Sea: An update. J. Geophys. Res. 88, 2733–2742. https://doi.org/10.1029/JC088iC05p02733.

National Marine Fisheries Service (NMFS), 2019. Annual Commercial Landing Statistics. http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html Accessed February 20, 2022.

Opdal, A.F., Brodeur, R.D., Cieciel, K., Daskalov, G.M., Mihneva, V., Ruzicka, J.J., Verheye, H.M., Aksnes, D.L., 2019. Unclear associations between pelagic fish and jellyfish in several major marine ecosystems. Nat. Sci. Rep. 9 (2997), 1–12. https://doi.org/10.1038/s41598-019-39351-7.

Overland, J.E., Stabeno, P.J., 2004. Is the climate of the Bering Sea warming and affecting the ecosystem? Eos Trans. AGU 85 (33), 309–312. https://doi.org/10.1029/2004EO330001.

Pitt, K.A., Lucas, C.H., Condon, R.H., Duarte, C.M., Stewart-Koster, B., 2018. Claims that anthropogenic stressors facilitate jellyfish blooms have been amplified beyond the available evidence: a systematic review. Front. Mar. Sci. 5, 451. https://doi.org/10.3389/fmars.2018.00451.

Pleuthner, R.L., Shaw, T.C., Bernhardt, M.S., Lessard, E.J., Harvey, H.R., 2016. Individual lipid markers of diet history and their retention in the Bering Sea euphausiid *Thysanoessa raschii*. Deep-Sea Res. II 134, 190–203. https://doi.org/10.1016/j.dsr2.2015.08.003.

Purcell, J.E., 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. J. Mar. Biol. Assoc. U. K. 85, 461–476.

Purcell, J.E., Uye, S.I., Lo, W.T., 2007. Anthropogenic causes of jellyfish blooms and direct consequences for humans: a review. Mar. Ecol. Prog. Ser. 350, 153–174. https://doi.org/10.3354/meps07093.

Purcell, J.E., Juhl, A.R., Mańko, M.K., Aumack, C.F., 2017. Overwintering of gelatinous zooplankton in the coastal Arctic Ocean. Mar. Ecol. Prog. Ser. 591, 281–286. https://doi.org/10.3354/meps12289.

Purcell, J.E., Sturdevant, M.V., 2001. Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser. 210, 67–83. https://doi.org/10.3354/meps210067.

Ressler, P.H., De Robertis, A., Warren, J.D., Smith, J.N., Kotwicki, S., 2012. Developing an acoustic survey of euphausiids to understand trophic interactions in the Bering Sea ecosystem. Deep-Sea Res. II 65, 184–195. https://doi.org/10.1016/j.dsr2.2012.02.015.

Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol. Evol. 24, 312–322. https://doi.org/10.1016/j.tree.2009.01.010.

Robinson, K.L., Ruzicka, J.J., Hernandez, F.J., Graham, W.M., Decker, M.B., Brodeur, R.D., Sutor, M., 2015. Evaluating energy flows through jellyfish and gulf menhaden (*Brevoortia patronus*) and the effects of fishing on the northern Gulf of Mexico ecosystem. ICES J. Mar. Sci. 72, 2301–2312. https://doi.org/10.1093/icesjms/fsv088.

Rodionov, S.N., Bond, N.A., Overland, J.E., 2007. The Aleutian low, storm tracks, and winter climate variability in the Bering Sea. Deep-Sea Res. II 54, 2560–2577. https://doi.org/10.1016/j.dsr2.2007.08.002.

Ruzicka, J.J., Brodeur, R.D., Emmett, R.L., Steele, J.H., Zamon, J.E., Morgan, C.A., Thomas, A.C., Wainwright, T.C., 2012. Interannual variability in the Northern California Current food web structure: changes in energy flow pathways and the role of forage fish, euphausiids, and jellyfish. Prog. Oceanogr. 102, 19–41. https://doi.org/10.1016/j.pocean.2012.02.002.

Ruzicka, J.J., Brodeur, R.D., Cieciel, K., Decker, M.B., 2020. Examining the ecological role of jellyfish in the Eastern Bering Sea ecosystem. ICES J. Mar. Sci. 77, 791–802. https://doi.org/10.1093/icesjms/fsz244.

Saitoh, S.I., Iida, T., Sasaoka, K., 2002. A description of temporal and spatial variability in the Bering Sea spring phytoplankton blooms (1997–1999) using satellite multi-sensor remote sensing. Prog. Oceanogr. 55, 131–146. https://doi.org/10.1016/S0079-6611(02)00074-5.

Sambrotto, R.N., Niebauer, H.J., Goering, J.J., Iverson, R.L., 1986. Relationships among vertical mixing, nitrate uptake, and phytoplankton growth during the spring bloom in the southeast Bering Sea middle shelf. Cont. Shelf Res. 5, 161–198. https://doi.org/10.1016/0278-4343(86)90014-2.

Schnedler-Meyer, N.A., Mariani, P., Kiørboe, T., 2016. The global susceptibility of coastal forage fish to competition by large jellyfish. Proc. R. Soc. B 283, 20161931. https://doi.org/10.1098/rspb.2016.1931.

Sigler, M.F., Stabeno, P.J., Eisner, L.B., Napp, J.M., Mueter, F.J., 2014. Spring and fall phytoplankton blooms in a productive subarctic ecosystem, the eastern Bering Sea,

during 1995–2011. Deep Sea Research II 109, 71–83. https://doi.org/10.1016/j.dsr2.2013.12.007.

Sigler, M.F., Napp, J.M., Stabeno, P.J., Heintz, R.A., Lomas, M.W., Hunt Jr., G.L., 2016. Variation in annual production of copepods, euphausiids, and juvenile walleye pollock in the southeastern Bering Sea. Deep-Sea Res. II 134, 223–234. https://doi.org/10.1016/j.dsr2.2016.01.003.

Stabeno, P.J., Bell, S.W., 2019. Extreme conditions in the Bering Sea (2017–2018): Record-breaking low sea-ice extent. Geophys. Res. Lett. 46, 8952–8959. https://doi.org/10.1029/2019GL083816.

Stabeno, P.J., Bond, N.A., Kachel, N.B., Salo, S.A., Schumacher, J.D., 2001. On the temporal variability of the physical environment over the southeastern Bering Sea. Fish. Oceanogr. 10, 81–98. https://doi.org/10.1046/j.1365-2419.2001.00157.x.

Stabeno, P.J., Bond, N.A., Salo, S.A., 2007. On the recent warming of the southeastern Bering Sea Shelf. Deep-Sea Res. II 54, 2599–2618. https://doi.org/10.1016/j.dsr2.2007.08.023.

Stabeno, P.J., Farley, E.V., Kachel, N.B., Moore, S., Mordy, C.W., Napp, J.M., Overland, J. E., Pinchuk, A.I., Sigler, M.F., 2012a. A comparison of the physics of the northern and southern shelves of the eastern Bering Sea and some implications for the ecosystem. Deep-Sea Res. II 65, 14–30. https://doi.org/10.1016/j.dsr2.2012.02.019.

Stabeno, P.J., Kachel, N.B., Moore, S.E., Napp, J.M., Sigler, M., Yamaguchi, A., Zerbini, A.N., 2012b. Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep Sea Res. II 65, 31–45. https://doi.org/10.1016/j.dsr2.2012.02.020.

Stabeno, P.J., Duffy-Anderson, J.T., Eisner, L.B., Farley, E.V., Heintz, R.A., Mordy, C.W., 2017. Return of warm conditions in the southeastern Bering Sea: Physics to fluorescence. PLoS One 12 (9), e0185464.

Stabeno, P., Napp, J., Mordy, C., Whitledge, T., 2010. Factors influencing physical structure and lower trophic levels of the eastern Bering Sea shelf in 2005: Sea ice, tides and winds. Prog. Oceanogr. 85, 180–196. https://doi.org/10.1016/j.pocean.2010.02.010.

Stabeno, P.J., Reed, R.K., Napp, J.M., 2002. Transport through Unimak Pass, Alaska. Deep-Sea Res. II 49, 5919–5930. https://doi.org/10.1016/S0967-0645(02)00326-0.

Stevenson, D.E., Lauth, R.R., 2019. Bottom trawl surveys in the northern Bering Sea indicate recent shifts in the distribution of marine species. Polar Biol. 42, 207–421. https://doi.org/10.1007/s00300-018-2431-1.

Suchman, C.L., Daly, E.A., Keister, J.E., Peterson, W.T., Brodeur, R.D., 2008. Feeding patterns and predation potential of scyphomedusae in a highly productive upwelling region. Mar. Ecol. Prog. Ser. 358, 161–172. https://doi.org/10.3354/meps07313.

Sullivan, M.E., Kachel, N.B., Mordy, C.W., Salo, S.A., Stabeno, P.J., 2014. Sea ice and water column structure on the eastern Bering Sea shelf. Deep Sea Res. Part II 109, 39–56. https://doi.org/10.1016/j.dsr2.2014.05.009.

Thein, H., Ikeda, H., Uye, S.I., 2013. Ecophysiological characteristics of podocysts in *Chrysaora pacifica* (Goette) and *Cyanea nozakii* Kishinouye (Cnidaria: Scyphozoa: Semaeostomeae): effects of environmental factors on their production, dormancy and excystment. J. Exp. Mar. Biol. Ecol. 446, 151–158. https://doi.org/10.1016/j.jembe.2013.05.013.

Treible, L.M., Condon, R.H., 2019. Temperature-driven asexual reproduction and strobilation in three scyphozoan jellyfish polyps. J. Exp. Mar. Biol. Ecol. 520, 151204 https://doi.org/10.1016/j.jembe.2019.151204.

Walsh, J.E., Johnson, C.M., 1979. An analysis of Arctic sea ice fluctuations, 1953–77. J. Phys. Oceanogr. 9, 580–591. https://doi.org/10.1175/1520-0485(1979)009<0580:AAOASI>2.0.CO;2.

Wang, S.W., Budge, S.M., Iken, K., Gradenger, R.R., Springer, A.M., Wooler, M.J., 2015a. Importance of sympagic production to Bering Sea zooplankton as revealed from fatty acid-carbon stable isotope analyses. Mar. Ecol. Prog. Ser. 518, 31–50. https://doi.org/10.3354/meps11076.

Wang, N., Li, C., 2015. The effect of temperature and food supply on the growth and ontogeny of *Aurelia* sp. 1 ephyrae. Hydrobiologia 754, 157–167. https://doi.org/10.1007/s10750-014-1981-7.

Wang, N., Li, C., Liang, Y., Shi, Y., Lu, J., 2015b. Prey concentration and temperature effect on budding and strobilation of *Aurelia* sp. 1 polyps. Hydrobiologia 754, 125–134. https://doi.org/10.1007/s10750-014-1978-2.

Wood, S.N., 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. J. Am. Stat. Assoc. 99, 637–686. https://doi.org/10.1198/016214504000000980.

Wood, S.N., 2006. Generalized additive models: an introduction with R. Chapman and Hall, London, doi: 10.1201/9781420010404.

Zuur, A.F, Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer, New York, doi: 10.1007/978-0-387-87458-6.