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

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Supplement. Technical details of the nonlinear time series models

The supplement contains the following items:

- Fig. S1. Spatial distribution of jellyfish biomass on the Eastern Bering Sea
- Fig. S2. Day of sampling during annual bottom trawl surveys
- Fig. S3. Central Region air and bottom water temperatures
- Text S1. Scyphomedusan ephyra distributions
- Fig. S4. Distribution of scyphomedusan ephyrae in the eastern Bering Sea
- Fig. S5. Day and depth of occurrence of scyphomedusan ephyrae
- Text S2. Model selection procedure for varying coefficient models
- **Table S1.** Generalized cross-validation scores for the North model
- Table S2. Generalized cross-validation scores for the Central model
- Literature cited in the supplement

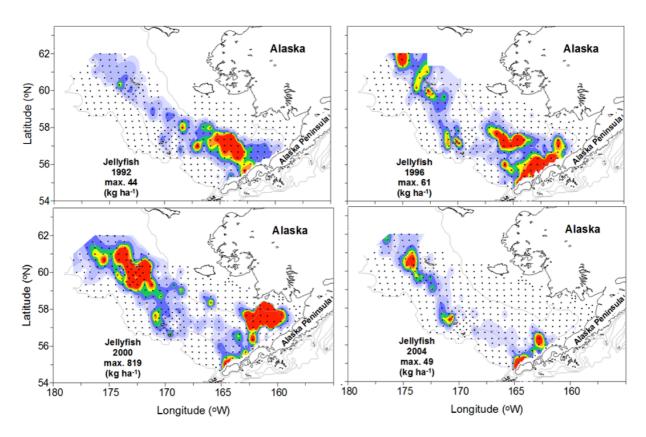


Fig. S1. Spatial distribution of jellyfish biomass (kg ha⁻¹) on the Eastern Bering Sea shelf during the summers of 1992, 1996, 2000 and 2004. Dots indicate sampling locations, and grey contour lines indicate bathymetry (from right to left: 50 m, 100 m and 200 m)

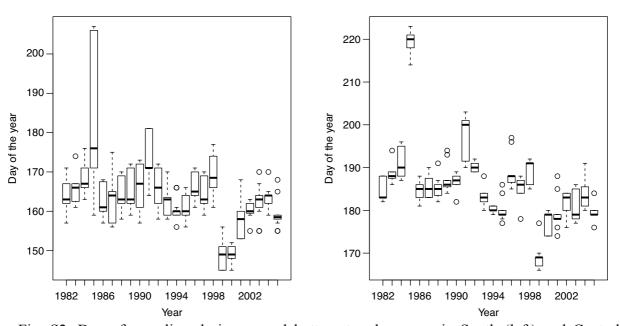


Fig. S2. Day of sampling during annual bottom trawl surveys in South (left) and Central (right) regions

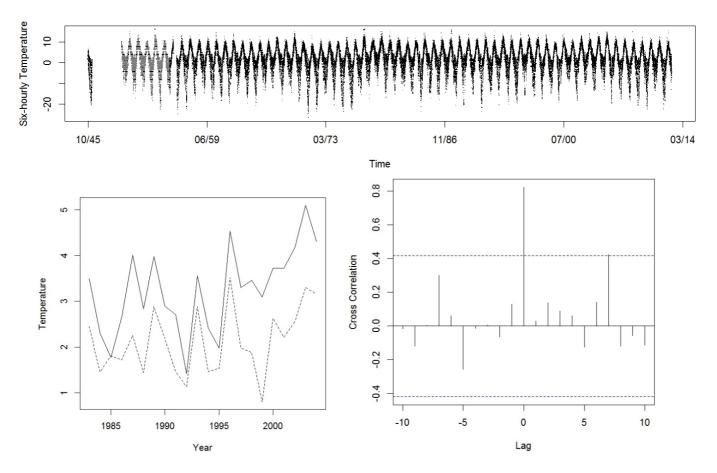


Fig. S3. Central region air and bottom water temperatures. The time plot of the 6-hourly temperature from the St. Paul airport is shown in the top panel. The bottom left panel shows the time plots of the 2 sets of temperature, solid line for bottom temperature around the Pribilof Islands, as obtained based on Eq. (1) in the main text, and dashed line the annual St. Paul temperature (averaged over data taken every 6 hours). These 2 sets of the annual temperature data track each other well (left panel). In addition, these datasets are correlated at lag 0 with correlation close to 0.8, but otherwise uncorrelated at other lags (sample cross correlation function in bottom right panel). These results provide strong support that the bottom temperatures as computed based on Eq. (1) are good proxies for the temperature conditions experienced by the jellyfish

Text S1. Scyphomedusan Ephyra Distributions

The life cycle of scyphozoan jellyfishes is complex and alternates between a pelagic (medusa) and a benthic (polyp) stage (Arai 1997). Scyphozoan polyps, which are the source of the medusae, tend to be perennial and asexually reproduce to form more polyps. Polyps, which are very small (a few mm in length), strobilate (i.e. undergo transverse fission) and release free-swimming juvenile medusae ('ephyrae', a few mm in diameter). Ephyrae grow quickly to sexually-mature medusae within months. Fertilized eggs develop into free-swimming planulae larvae, which within days to weeks settle on hard substrates (e.g. rocks, shells, Brewer & Feingold 1991, Pitt 2000, Holst & Jarms 2007) and metamorphose into polyps. Most of the current knowledge of jellyfish dynamics comes from the study of the pelagic medusae, while little is known of polyp distributions and their interannual dynamics since this life stage is so small and cryptic. This is a critical information gap, as the benthic polyps are clearly the source of the pelagic medusae

As for most scyphomedusan polyps, the location of polyps in the EBS is not known. However, for the circulation and connectivity studies, we assumed they are attached to rocky coastlines in shallow water. In order to corroborate this assumption for development of the circulation indices (see below), we obtained records of scyphomedusan ephyrae in plankton collections from K. Covle via the North Pacific Research Board's Bering Sea Integrated Ecosystem Research Program database. Ephyrae were sampled in zooplankton tows conducted with a 25-cm diameter CalVET system (CalCOFI Vertical Egg Tow) and with a 500 mm-mesh, 1-m² Multiple Opening/Closing Net and Environmental Sampling System (MOCNESS) as described in Coyle et al. (2008). Samples were collected on cruises in late spring (ca. 21 May-21 Jun) and late summer (ca. 22 Jul-11 Sep) in 1997-1999 and 2004. Scyphomedusan ephyrae were rare (19 ephyrae in 365 CalVET and 2144 MOCNESS samples), but present at nearshore stations along the Alaska Peninsula and the Southwest Alaskan coast (Fig. S4). Ephyrae were present from 23 May through 2 August (Fig. S5), indicating that scyphozoan strobilation occurs in the EBS from late spring though summer. Depth-discrete MOCNESS samples indicate that ephyrae occur in the upper 30-40 m (Fig. S5). Ephyrae were not found in the vicinity of the Pribilof Islands, which have rocky coastlines that are presumably suitable habitat for benthic polyps. However, sampling near these islands was done in 2004, a time at which the biomass of medusa had declined considerably (Fig. S1). Ephyrae may have been especially rare in 2004, and thus, may not have been detected by the limited plankton sampling near the Pribilof Islands.

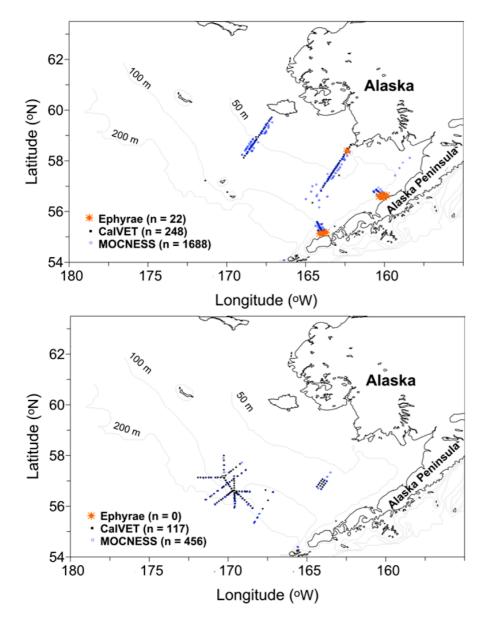


Fig. S4. Distribution of scyphomedusan ephyrae on the eastern Bering Sea shelf in summers of 1997-1998 (top) and (bottom). Samples were collected with a CalCOFI Vertical Tow Egg (CalVET) net and Multiple Opening/Closing Net and Environmental Sampling System (MOCNESS) by K. Coyle. Depth contours of 50, 100 and 200 m are indicated

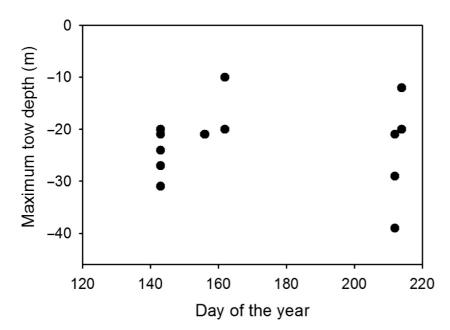


Fig. S5. Day and depth of occurrence of scyphomedusan ephyrae zooplankton tows collected on the eastern Bering Sea shelf. Samples were collected with a Multiple Opening/Closing Net and Environmental Sampling System (MOCNESS) on cruises in late spring (ca. 21 May-21 Jun) and late summer (ca. 22 Jul-11 Sep) in 1997-1999

Text S2. Model Selection Procedure for Varying Coefficient Models

North model

$$log(\mathit{CPUE}.N_t) = \beta_0^n + \beta_1^n(\mathit{CNDI}_t)log(\mathit{CPUE}.C_{t-1}) + \beta_2^n(\mathit{BT}.North_t)log(\mathit{CPUE}.N_{t-1}) + \varepsilon_t$$

The varying coefficient model includes the potential effects for the North Model: 1) jellyfish biomass in the 'upstream' (Central) region in the previous (lag 1) or current year affects biomass in the North region, and is potentially mediated by oceanic transport (Central-to-North Drift Index, or *CNDI*) and 2) current year North biomass is affected by biomass in the same region in the previous year (lag 1), and is potentially mediated by local ocean bottom temperature. Generalized cross-validation scores (GCV) are used to select the model with the best prediction performance among candidate models with different covariates, which are summarized in Table S1. The covariates we considered only included relevant local environmental factors. For example, in the Central to North model, only the Central-to-North Drift Index (*CNDI*), bottom temperatures near Pribilof Islands in the Central region and near St. Matthew Island in the North region (i.e. areas with hard substrate that can support polyp colonies) were considered in the models for the North model.

We also explored non-stationarity by including time (i.e. year) as a threshold variable in the model, which allows the additive model to vary between the 2 regimes delineated by the threshold year. However, none of the threshold models explored were significant. Thus, the above varying coefficient model without a threshold effect is chosen as our final model with a GCV score of 0.107 (Table S1).

Central model

$$log(\mathit{CPUE}.C_t) = \begin{cases} \beta_0^c + \beta_{11}^c(\mathit{PCDI}_t)log(\mathit{CPUE}.S_{t-1}) + \varepsilon_t, & if \ t \leq 1997 \\ \beta_0^c + \beta_{12}^c(\mathit{BT}.\mathit{Pribs}_t)log(\mathit{CPUE}.C_{t-1}) + \varepsilon_t, & if \ t > 1997 \end{cases}$$

We implemented a similar model structure for the Central region as we did in the North region. We started with similar varying coefficient models without threshold effects. The GCVs are listed in Table S2. After including time as a threshold variable, the GCV was significantly reduced to 0.035 with regime shift occurring at year 1997 among several competing models with different covariates. As for the North model, only relevant local environmental factors were considered (e.g. *PCDI*, bottom temperature near Pribilof Islands and Alaska Peninsula). To confirm the finding of the threshold effects, we conducted a permutation test on the threshold effect as described in the manuscript and the p-value is 0.029. Therefore, the final South-to-Central model is found to be regime-varying and dependent upon different regression functions before and after 1997.

South model

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

We attempted to include bottom temperature and the *PCDI* in the model as additive terms, but both of them were eliminated by cubic regression spline with shrinkage. Varying coefficient models on lag-1 southern biomass also show no significant results.

Table S1. Generalized cross-validation scores (GCV) used to select the North model with the best prediction performance among candidate models with different covariates. The final model is indicated in **bold** text.

GCV	Temperature	Drift index	Biomass in adjacent region
0.107	North Current	CNDI Current	Central Lag-1
0.115	Pribilof Current	CNDI Current	Central Lag-1
0.113	North Current	CNDI Lag-1	Central Lag-1
0.113	North Current	CNDI Current	Central Current
0.113	North Current	CNDI Lag-1	Central Current
NA*	North Lag-1	CNDI Current	Central Lag-1

^{*}The models with lag-1 North sea bottom temperature as covariate tend to have numerical issues in model estimation.

Table S2. Generalized cross-validation scores (GCV) used to select the Central model with the best prediction performance among candidate models with different covariates. The final model is indicated in bold text.

GCV	Threshold	Temperature	Drift index	Biomass in adjacent region
0.035	Y	Pribilof Current	PCDI Current	South Lag-1
0.046	Y	Pribilof Current	PCDI Lag-1	South Lag-1
0.050	Y	Pribilof Lag-1	PCDI Current	South Lag-1
NA*	Y	Pribilof Current	PCDI Current	South Current
0.048	Y	Peninsula Current	PCDI Current	South Lag-1
0.054	N**	Pribilof Current	PCDI Current	South Lag-1
0.044	N**	Peninsula Current	PCDI Current	South Lag-1

^{*} The models with current southern biomass as covariate tend to have numerical issues in model estimation. ** No threshold effects in the model, so that the model formulation looks similar to the North Model

LITERATURE CITED

Arai MN (1997) A functional biology of Scyphozoa. Chapman & Hall, London

Brewer RH, Feingold JS (1991) The effect of temperature on the benthic stages of *Cyanea* (Cnidaria: Scyphozoa), and their seasonal distribution in the Niantic River estuary, Connecticut. J Exp Mar Biol Ecol 152:49–60

Coyle KO, Pinchuk AI, Eisner LB, Napp JM (2008) Zooplankton species composition, abundance and biomass on the eastern Bering Sea shelf during summer: the potential role of water column stability and nutrients in structuring the zooplankton community. Deep Sea Res II 55:1755–1791

Holst S, Jarms G (2007) Substrate choice and settlement preferences of planula larvae of five Scyphozoa (Cnidaria) from German Bight, North Sea. Mar Biol 151:863–871

Pitt KA (2000) Life history and settlement preferences of the edible jellyfish *Catostylus mosaicus* (Scyphozoa: Rhizostomeae). Mar Biol 136:269–280