Deep-Sea Research II 65-70 (2012) 208–216

Contents lists available at SciVerse ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Do walleye pollock exhibit flexibility in where or when they spawn based on variability in water temperature?

Nathan M. Bacheler [a,*], Lorenzo Ciannelli [b], Kevin M. Bailey [c], Valerio Bartolino [d,e]

[a] Southeast Fisheries Science Center, National Marine Fisheries Service, 101 Pivers Island Road, Beaufort, NC 28516, USA
[b] College of Earth, Ocean and Atmospheric Sciences, 104 CEOAS Administration Building, Oregon State University, Corvallis, OR 97331, USA
[c] Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115, USA
[d] Swedish University of Agricultural Sciences, Department of Aquatic Resources, 45330 Lysekil, Sweden
[e] Department of Earth Sciences, University of Gothenburg, 40530 Gothenburg, Sweden

ARTICLE INFO

Available online 8 February 2012

Keywords:
Reproduction
Bering Sea
Ichthyoplankton
Generalized additive model
Sea surface temperature
Global climate change

ABSTRACT

Environmental variability is increasingly recognized as a primary determinant of year-class strength of marine fishes by directly or indirectly influencing egg and larval development, growth, and survival. Here we examined the role of annual water temperature variability in determining when and where walleye pollock (*Theragra chalcogramma*) spawn in the eastern Bering Sea. Walleye pollock spawning was examined using both long-term ichthyoplankton data ($N=19$ years), as well as with historical spatially explicit, foreign-reported, commercial catch data occurring during the primary walleye pollock spawning season (February–May) each year ($N=22$ years in total). We constructed variable-coefficient generalized additive models (GAMs) to relate the spatially explicit egg or adult catch-per-unit-effort (CPUE) to predictor variables including spawning stock biomass, season, position, and water temperature. The adjusted R^2 value was 63.1% for the egg CPUE model and 35.5% for the adult CPUE model.

Both egg and adult GAMs suggest that spawning progresses seasonally from Bogoslof Island in February and March to Outer Domain waters between the Pribilof and Unimak Islands by May. Most importantly, walleye pollock egg and adult CPUE was predicted to generally increase throughout the study area as mean annual water temperature increased. These results suggest low interannual variability in the spatial and temporal dynamics of walleye pollock spawning regardless of changes in environmental conditions, at least at the spatial scale examined in this study and within the time frame of decades.

Published by Elsevier Ltd.

1. Introduction

There is increasing appreciation for the importance of spatial effects on the temporal dynamics of marine fish populations (Cadrin and Secor, 2009; Ciannelli et al., 2007). In particular, it is recognized that where and when marine fish spawn sets the stage for egg and larval development, growth, and survival (Bailey et al., 2005; Cushing, 1990). The timing and location of spawning also affects the development of year-class strength through such processes as larval drift (Iles and Sinclair, 1982).

Abundance levels of walleye pollock (i.e., Alaska pollock, *Theragra chalcogramma*, hereafter referred to as 'pollock') are recognized to be highly dynamic and especially sensitive to the recruitment of new fish to the population (Bailey et al., 2005). Pollock are mostly associated with the outer continental shelf and slope of coastal waters of the North Pacific Ocean, but can also be found over very deep waters of the Aleutian Basin and nearshore in coastal embayments (Bailey et al., 1997). Generally they are found within a temperature range of 1–10 °C and closely associated with the bottom, but can be exclusively pelagic in some environments (Bakkala, 1993). Pollock aggregate to spawn during winter and spring, and an intense fishery for valuable roe develops prior to hydration and release of eggs. In deep basin waters, pollock may spawn as deep as 300–500 m, and over the continental shelf they aggregate closer to the bottom at depths of 100–300 m. Pollock mature around 3–4 years of age and are determinate batch spawners. In the laboratory individuals spawn over a period of a 2–3 weeks, and the spawning event is associated with pairing and an elaborate courtship behavior (Baird and Olla, 1991; Sakurai, 1982).

Several studies have examined the timing and locations of pollock spawning in the eastern Bering Sea. Hinckley (1987) used commercial catch data combined with observations of spawning fish to non-quantitatively assess the seasonal locations of spawning. She found three major spawning areas in the Aleutian Basin: an area near Bogoslof Island, an area north of Unimak Island, and the shelf region northwest of the Pribilof Islands (see Fig. 1). Bacheler et al. (2010) examined egg distributions from ichthyoplankton catches to

* Corresponding author. Tel.: +1 252 838 0825; fax: +1 252 728 8784.
E-mail addresses: nate.bacheler@noaa.gov (N.M. Bacheler), lciannelli@coas.oregonstate.edu (L. Ciannelli), kevin.bailey@noaa.gov (K.M. Bailey), valerio.bartolino@gmail.com (V. Bartolino).

0967-0645/$ - see front matter Published by Elsevier Ltd.
doi:10.1016/j.dsr2.2012.02.001

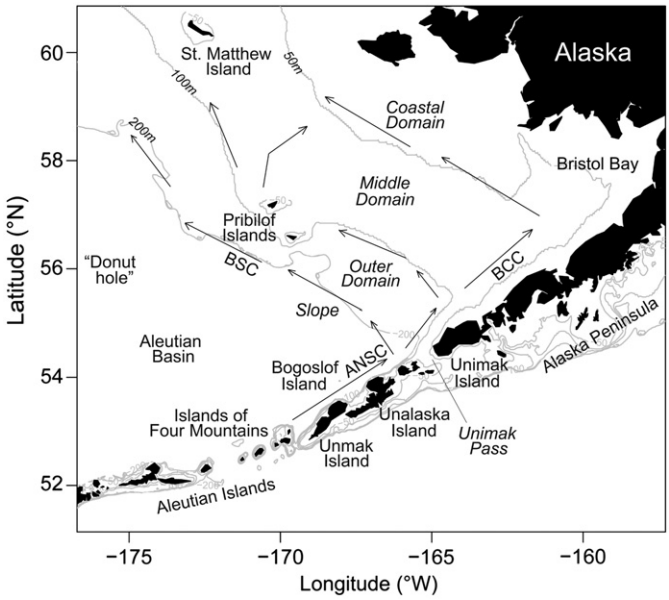

Fig. 1. The eastern Bering Sea showing depth contours (gray lines), domains (italics), major geographic features, and mean ocean circulation (arrows; ANSC=Aleutian North Slope Current; BCC=Bering Coastal Current; BSC=Bering Slope Current; Coachman, 1986).

further refine our understanding of the spatial and temporal dynamics of spawning in eastern Bering Sea. The next logical step is to quantify how environmental variability, specifically water temperature, affects where and when spawning occurs given the scenario of a changing climate in the eastern Bering Sea (Grebmeier et al., 2006; Overpeck et al., 1997).

Bacheler et al. (2009) examined the effects of climate and landscape on the spatial and temporal distribution of pollock eggs in the Shelikof Strait region of the Gulf of Alaska. They found a relatively minor effect of temperature on the spatial extent of spawning, suggesting that the location of spawning in the Gulf of Alaska is very consistent from year to year and may have a geographical orientation rather than a high degree of environmental lability. Alternatively, Smart et al. (2012) suggests that pollock spawning, as measured by egg and larval catches, can be influenced by water temperature. Some fish species may have populations where spawning is geographically fixed, and other populations where spawning location changes with environmental conditions (e.g. Pacific hake, *Merluccius productus*; Bailey et al., 2004). It is likely that population-level variability in spawning strategy is an important and highly selective trait. In the case of walleye pollock in the eastern Bering Sea, it is unknown if variability in the timing and location of spawning exists, and if so, whether such variability is related to environmental conditions.

In this study we analyzed two independent data sources using regression models to elucidate the spatial and temporal patterns of walleye pollock spawning in the eastern Bering Sea. Spawning distributions are described using both egg distributions from ichthyoplankton surveys and commercial fisheries data. We compare these two independent methods to make broad inferences about how water temperature influences the spawning dynamics of pollock in the eastern Bering Sea.

2. Material and methods

We employed two independent data sources to determine if pollock spawning is influenced by water temperature in the eastern Bering Sea. First, we used the locations and timing of pollock egg collections over space and time to define spawning aggregations. We considered the presence of pollock eggs to be the most direct, practical, and powerful approach to understand pollock spawning dynamics. Eggs serve as a record of the history of spawning over approximately the past month. However, the spatial and temporal coverage of ichthyoplankton surveys varied among years. Therefore, we developed an independent test of pollock spawning dynamics from ichthyoplankton data using long-term, foreign-reported commercial catch data of adult pollock. Adult catch data is advantageous because it is spatially and temporally extensive, but the disadvantage is that adult catches may not always reflect actual spawning locations because fishers historically targeted pre-spawning fish (Low and Ikeda, 1980). We consider the inclusion of commercial catch data as an independent validation of ichthyoplankton data; both data sources are described in detail below.

2.1. Ichthyoplankton data

The Alaska Fisheries Science Center (AFSC, Seattle, WA) has conducted ichthyoplankton surveys in the eastern Bering Sea for many years (see Fig. 1 for map of study area), and we used data on pollock egg abundance and distribution to make inferences about the spawning dynamics of the species. We initially examined 22 years of ichthyoplankton survey data (hereafter "ichthyoplankton data"), but sufficient sample sizes within the region of interest ($N>10$ tows) for this paper only occurred in 19 of these years: 1986, 1988, 1991–2000, 2002–2003, and 2005–2009. Sampling occurred in all months between February and September, but the temporal coverage of sampling was somewhat variable over time due to inconsistent availability of ship time and weather (Table 1).

Two sampling gears were used to sample pollock eggs in this study: bongo (93%) and Tucker (7%) nets. Each net type consisted of 0.333-mm or 0.505-mm mesh, and was towed obliquely from 10 m off the bottom to the surface in shelf areas or from a depth of 300 m to the surface in slope and basin areas. Pollock eggs have been captured in very similar numbers between these two net types (Shima and Bailey, 1993) and mesh sizes, suggesting that

Table 1
Cruise information for walleye pollock *Theragra chalcogramma* ichthyoplankton surveys in the eastern Bering Sea and used in this study. CR is the number of cruises taken within a year, and *N* is the total number of samples taken in the year. Information in the table only pertains to surveys conducted within the box in Fig. 2 occurring between 1 February and 31 May each year.

Year	CR	*N*	Start date	End date	Total eggs collected
1986	1	41	2/21	2/28	314673
1988	2	101	3/17	4/26	336341
1991	2	57	3/11	5/8	119140
1992	1	12	4/16	4/18	52
1993	1	211	4/15	4/30	2963
1994	1	97	4/15	4/30	27108
1995	5	263	2/22	5/21	228253
1996	3	20	4/23	5/20	1236
1997	2	54	4/16	5/13	57359
1998	1	16	4/9	4/12	5622
1999	2	84	4/14	5/20	235661
2000	1	13	5/7	5/11	19148
2002	1	67	5/13	5/21	5425
2003	2	117	3/4	5/24	13314
2005	3	160	3/4	5/22	10609
2006	1	114	5/9	5/18	2242
2007	3	172	4/11	5/18	135586
2008	4	130	2/18	5/21	9738
2009	3	126	2/26	5/18	4157
Total	39	1855	2/18	5/24	1528627

differences in catchability between these two gears or mesh sizes are minimal. An added benefit of analyzing data from two gear types is that the spatial and temporal coverage of ichthyoplankton data was as broad as possible. Both nets were towed at a speed to maintain a 45° wire angle at a retrieval rate of 20 m min^{-1}. Eggs were preserved in 5% formalin and later sorted and identified to species at the Plankton Sorting and Identification Center in Szczecin, Poland. AFSC scientists later verified a subsample for taxonomic identification accuracy.

Ichthyoplankton data analyzed in this study consisted of the number of eggs caught per standardized area sampled (numbers · 10 m^{-2}, hereafter referred to as "egg CPUE"). We used number of eggs per unit area instead of number per unit volume as the response variable because pollock egg density may decrease as the depth of the tow increases even when the true number of eggs in the water column is the same between shallow and deep sites. Therefore, we determined that number per unit area is more reflective of true abundance when comparing across depth zones. We ran models using both volumetric and area-based response variables; results were very similar between these two approaches, so only area-based results are provided. Tows with zero catch of pollock eggs (26% of tows) were excluded from the analysis. Since we were primarily interested in testing hypotheses about competing models rather than making predictions about spawning distribution, the removal of zero egg tows should not affect the results.

2.2. Foreign-reported commercial catch data collection

We used long-term foreign-reported, commercial catches of adult pollock (hereafter "commercial data") to independently validate observed patterns of pollock spawning dynamics from ichthyoplankton data. Foreign commercial fisheries began targeting adult pollock in the eastern Bering Sea in 1964 (Low and Ikeda, 1980). Foreign catches peaked in the early 1970s, but decreased after that time following bilateral agreements between the United States, Japan, and the former Soviet Union. By 1987, U. S. fishing vessels were able to take 99% of the quota (Ianelli et al., 2009), so foreign catches declined to nearly zero shortly after this time. We did not include any domestic observer data since 1987 in our analyses because of various spatial and temporal closures that have been enacted over time designed to protect spawning pollock, minimize bycatch, and enforce other restrictions; these closures would complicate our interpretations of the spawning dynamics of pollock when using commercial data.

Foreign commercial data in the eastern Bering Sea have been reported to the AFSC (1963–1991) and are used here as an independent validation of pollock spawning patterns observed from ichthyoplankton. The spatial and temporal resolution of the commercial data is not as high as the ichthyoplankton; total catch of pollock is provided for a number of 0.5° latitude by 1.0° longitude cells for each month and year of the time series. Total catch is low before 1965 and after 1987, so only 1965–1987 data are used here. Pollock were captured in a variety of fishing gears, but we limited our analysis to trawling in order to standardize catch-per-unit-effort (CPUE) to the greatest extent possible. The response variable was CPUE of pollock from commercial data (hereafter referred to as "adult CPUE"), computed as the total metric tons of pollock captured by trawling gear per hour trawled.

The spatial coverage of commercial data was much greater than that of ichthyoplankton data (Fig. 2). To standardize the spatial extent of the two data sources for comparative purposes, we analyzed ichthyoplankton and commercial data within a box extending from 53° to 58° latitude and 158° to 173° longitude (Fig. 2) that covered nearly all of the ichthyoplankton sampling over time. Furthermore, this box is consistent with previous analyses of ichthyoplankton data in the eastern Bering Sea (e.g., Bacheler et al., 2010).

2.3. Data analysis

We chose to construct relatively simple models to describe walleye pollock spawning dynamics because we were primarily interested in elucidating general patterns that were comparable among the different sources of data. We used generalized additive models (GAMs) to elucidate the spatial and temporal patterns of pollock spawning in relation to water temperature using egg and adult CPUE. A GAM is a nonparametric and nonlinear regression technique that does not require a priori specifications of the functional relationship between the response and predictor variables (Hastie and Tibshirani, 1990; Wood, 2006). GAMs replace the traditional least-squares estimate of multiple linear regression with a local smoother; here, we used the cubic spline smoother. We used a new formulation of a variable-coefficient GAM (Hastie and Tibshirani, 1993), which has the additional benefit of being able to identify specific locations where, in our case, pollock eggs or adult CPUE is expected to increase or decrease with changes in any of the predictor variables of the model (see Bacheler et al., 2009; Bartolino et al., 2011, for ecological examples of variable-coefficient GAM models). In our case, these spatially explicit models were used to determine the ways in which water temperature influenced the spatial and temporal dynamics of pollock spawning.

We constructed variable-coefficient GAMs with four predictor variables (hereafter referred to as "covariates"): (1) spawning stock biomass, to account for yearly changes in pollock egg abundance; (2) position (latitude and longitude), to account for changes in pollock spawning over space; (3) day of the year or month, to account for seasonal variability in pollock spawning; and (4) water temperature, to account for changes in pollock spawning dynamics at different water temperatures. Spawning stock biomass (*ssb*; Ianelli et al., 2009) was included in each model as a factor variable. Position was the latitude (ϕ) and longitude (λ) of either the individual ichthyoplankton sample or the center of the grid cell of the commercial adult CPUE. Day of the year was used in the ichthyoplankton dataset and month was used for the adult CPUE dataset because daily data were not available (both are referred to as time t below). Only data between 1 February and 31 May were analyzed in both datasets because this time interval encompasses most of the pollock spawning in the eastern Bering Sea (Bacheler et al., 2010; Hinckley, 1987; Jung et al., 2006) (Fig. 2).

We used average sea surface temperature (°C) between February and May as an annual index of water temperature in the eastern Bering Sea. Monthly temperatures for the eastern Bering Sea (55°N, 166°W) were acquired from NOAA's National Centers for Environmental Prediction (Earth System Research Laboratory, 2011). Although pollock spawn at depth, monthly sea surface temperature (*temp*) was used as a proxy for the water temperature experienced by spawning pollock because bottom temperatures were not available for most years of our study. This is a reasonable assumption because sea surface temperature is highly correlated with bottom temperature during spring months when most pollock spawning occurs (Bacheler et al., 2010; Hinckley, 1987). Generally, surface and bottom temperatures across the shelf are similar until late spring when the water column begins to stratify (Luchin et al., 1999), and interannual patterns in SST are coherent across the shelf (Niebauer, 1981). Even in summer, the mean annual surface temperature across the eastern Bering Sea shelf is correlated with bottom temperature (R^2=0.61 from 1982–2006; data from Buckley et al., 2009).

In our spatially explicit variable-coefficient GAM, we related the natural logarithm of pollock egg or adult CPUE, $x_{t,ssb,(\phi,\lambda)}$, to

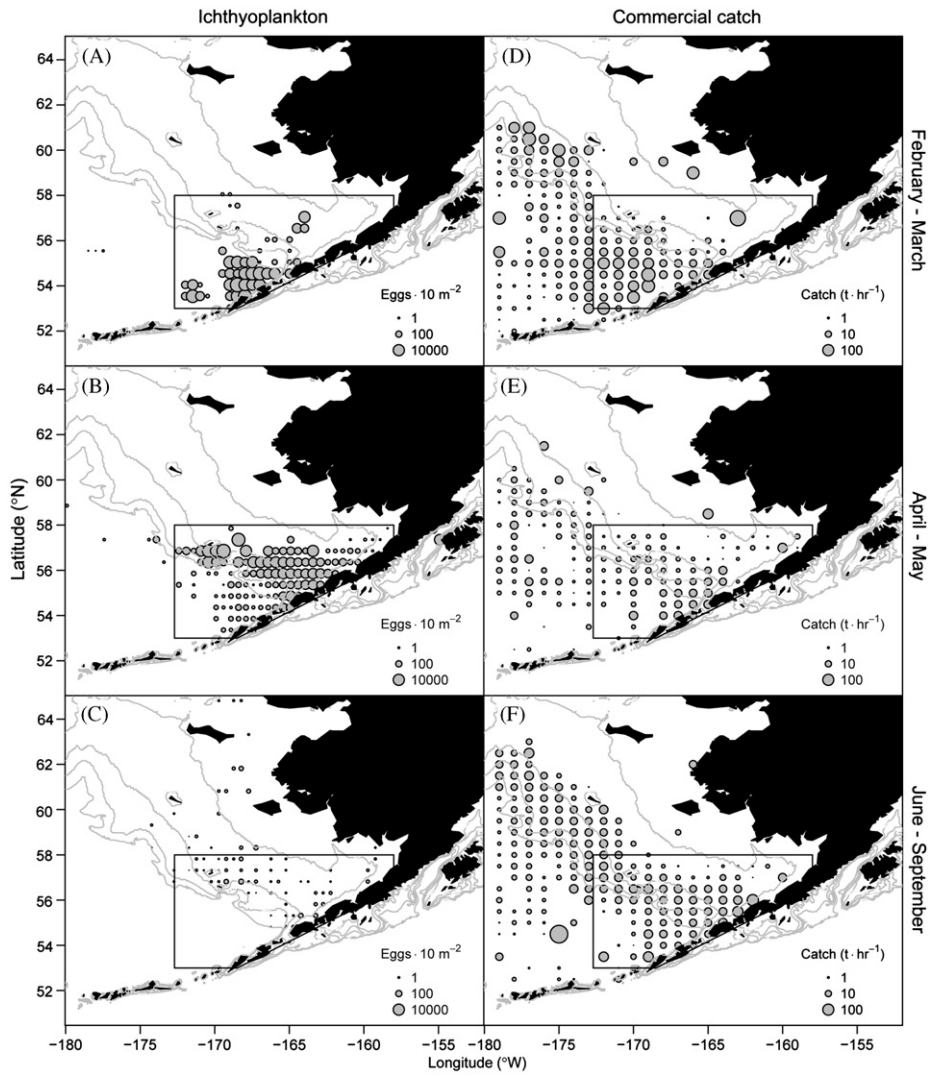

Fig. 2. Left column: mean walleye pollock *Theragra chalcogramma* egg catch-per-unit-effort (number of eggs · 10 m^{-2}) in (A) February–March, (B) April–May, and (C) June–September from surveys occurring in 1986, 1988, 1991–2000, 2002–2003, and 2005–2009. Right column: foreign-reported adult catch-per-unit-effort of walleye pollock (t per hour trawled) in the eastern Bering Sea in (D) February–March, (E) April–May, and (F) June–September in 1965–1987. Shown are mean egg or adult catch-per-unit-effort within each spatial cell averaged across all years of the study.

temporal, spatial, and temperature variables using the following model structure:

$$x_{t,ssb,(\phi,\lambda)} = a_{ssb} + g_1(\phi,\lambda) + g_2(\phi,\lambda)\cdot temp + g_3(\phi,\lambda)\cdot t + e_{t,ssb,(\phi,\lambda)} \quad (1)$$

where $x_{t,ssb,(\phi,\lambda)}$ is pollock egg or adult CPUE at time t, spawning stock biomass ssb, latitude ϕ, and longitude λ, a_{ssb} is the spawning stock biomass-specific intercept, $temp$ is spring water temperature, t is day of the year for the egg CPUE model or month for the adult CPUE model, g_{1-3} are nonparametric smoothing functions, and $e_{t,ssb,(\phi,\lambda)}$ is the random error assumed to be normally distributed (on a log scale) with a mean of zero and finite variance. The strength of the variable-coefficient GAM approach used here is the ability to predict specific areas where pollock egg or adult CPUE is expected to increase or decrease given changes in either water temperature or time.

We included an additional quadratic term for the time variable in the egg CPUE model to relax the assumption of a linear relationship between the time of the year and egg CPUE. This model was formulated as

$$x_{t,ssb,(\phi,\lambda)} = a_{ssb} + g_1(\phi,\lambda) + g_2(\phi,\lambda)\cdot temp + g_3(\phi,\lambda)\cdot t + g_4(\phi,\lambda)\cdot t^2 + e_{t,ssb,(\phi,\lambda)}. \quad (2)$$

A quadratic term for month could not be included in the adult CPUE model because of the low number of monthly periods (four: February, March, April, and May) over which smoothing was not appropriate. Eq. (1) was considered the "base" model for adult CPUE and Eq. (2) was considered the "base" model for egg CPUE.

Traditional approaches to plotting the spatially explicit effects from variable-coefficient GAMs (e.g., Bacheler et al., 2009; Bartolino et al., 2011) were unavailable here because of the inclusion of the quadratic term for time in the egg CPUE model. Instead, we developed an alternative approach to visualizing the effects from the egg and adult CPUE models. Egg CPUE data were predicted for two seasonal periods (i.e., 15 March and 15 May) in a common year within each 0.5° by 0.5° degree cell over a grid encompassing our study area. We then plotted the difference in egg CPUE predictions for each grid cell as

$$x_{difference} = x_{15May} - x_{15March}. \quad (3)$$

Grid cells with a high positive effect occur where the predicted egg CPUE on 15 May far exceeds the predicted egg CPUE on 15 March, and high negative effects occur where predicted egg CPUE for 15 March far exceeds predicted egg CPUE on 15 May. The foreign-reported adult CPUE data were already provided in a

regular grid, so we predicted adult CPUE over the existing grid at a common year for both March and May, and the difference between the two was plotted for each grid cell in the same way as described above for the egg CPUE model.

The visualization of the effect of water temperature on egg and adult CPUE was developed the same way as the effect of time. Egg and adult CPUE were predicted over a grid at low (3 °C) and high springtime water temperatures (4 °C; see *3. Results* below), and the difference between these two predictions was plotted for each grid cell and each model.

We also noted that sample sizes within our study region for both ichthyoplankton and commercial data sources varied among grid cells. Therefore, we plotted the number of samples for each grid cell for both data sources; this figure assisted interpretations of the temporal and water temperature figures.

Egg and adult CPUE base models were compared to reduced models using generalized cross validation (GCV; a measure of the out-of-sample predicted mean squared error), Akaike information criterion (AIC; Burnham and Anderson, 2002), and standard model diagnostics. A variety of reduced models that had one covariate removed at a time were compared to each of the base models. Models with the lowest GCV and AIC scores were selected over models with higher scores, and the two measures selected the same overall best model for both ichthyoplankton and commercial data. Models were coded and analyzed using the mgcv library (version 1.6–2; Wood, 2004) in R version 2.11 (R Development Core Team, 2010) using the Gaussian family model and identity link function.

3. Results

Highest pollock egg CPUE occurred between February and May in the eastern Bering Sea; egg CPUE after May was much lower (Fig. 2), justifying our selection of February to May data to be analyzed in our study. Egg CPUE in February–March was highest in the Aleutian Basin around Bogoslof Island, but increased eastward in the Outer Domain in April–May. Adult CPUE from commercial data showed a similar pattern of being highest in the Aleutian Basin in February–March and highest in the Outer Domain in April–May (Fig. 2). The annual mean February–May water temperature ranged from a low of 2.0 °C in 2007 to 4.7 °C in 2003 (overall mean from 1965–2009 = 3.5 °C) (Fig. 3).

Within our study area (i.e., box shown in Fig. 2), ichthyoplankton data were collected in 1–5 cruises taken each year from 12 to 263 bongo or Tucker tow samples (Table 1). The fewest eggs were collected in 1992 (N=52) and the most were collected in 1988 (N=336,341); the total collected over all 19 years of the study was over 1.5 million (Table 1). The number of grid cells for which adult CPUE data was reported each year ranged from 1 in 1987 to 475 in 1981 (Table 2). The most adult pollock were reportedly caught in 1971 (2.2×10^5 t), but the highest adult CPUE occurred in 1967. Between 1965 and 1987, 1.3×10^6 t of pollock was reportedly caught from our study area, at an overall adult CPUE of 2.96 $t\cdot h^{-1}$ (Table 2).

The base models for egg and adult CPUE substantially outperformed any of the reduced models based on GCV and AIC scores (Table 3). The adjusted R^2 value was 63.1% for the egg CPUE model and 35.5% for the adult CPUE model (Table 3). Standard model diagnostics (using the gam.check function in R) suggested that both models fit the data very well. Therefore, all subsequent analyses are based upon the respective egg and adult CPUE base models only.

Spatially explicit sample sizes varied for the ichthyoplankton and commercial data sources (Fig. 4). Ichthyoplankton sample sizes were highest closest to the Alaska Peninsula and Aleutian Islands, particularly near Bogoslof Island and north of Unimak Island (Fig. 4A). In contrast, commercial data sample sizes were highest in the Outer Domain south of the Pribilof Islands (Fig. 4B). It is in these regions where our subsequent analyses of pollock spawning dynamics are likely to be most reliable.

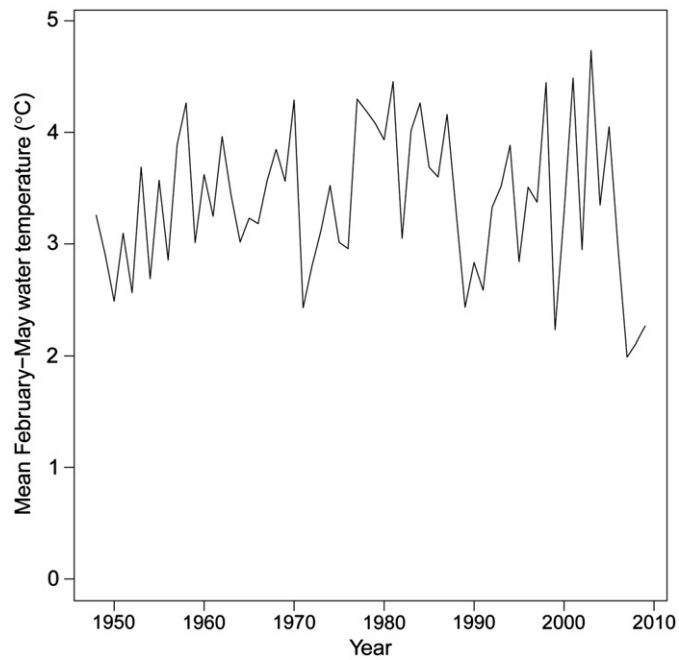

Fig. 3. Mean sea surface temperature (°C) from February to May in the eastern Bering Sea, 1950–2009. Data were provided by the Earth System Research Laboratory (2011).

Table 2
Commercial trawling catch of adult walleye pollock *Theragra chalcogramma*, as reported by foreign sources between February and May in 1965–1987 occurring within the box in Fig. 2 in the eastern Bering Sea. Catch data is reported in 0.5° latitude by 1.0° longitude cells for each month; *N* refers to the total number of spatial cells reporting positive pollock catch each year. Pollock caught is measured in metric tons (t), Hours trawled is the total number of hours trawling, and CPUE is the annual mean catch-per-unit-effort (t pollock caught per hour trawling) caught within the box in Fig. 2.

Year	*N*	Pollock caught (t)	Hours trawled	CPUE
1965	16	762	661	1.15
1966	31	3464	1592	2.18
1967	54	36399	5025	7.24
1968	282	62536	20962	2.98
1969	300	74761	17791	4.20
1970	303	143294	22166	6.46
1971	331	219582	32952	6.66
1972	306	162388	30499	5.32
1973	306	114783	21198	5.41
1974	264	61021	20182	3.02
1975	252	54274	22170	2.45
1976	246	82159	31416	2.62
1977	149	6219	10787	0.58
1978	270	15525	31441	0.49
1979	298	24826	27865	0.89
1980	361	45170	39016	1.16
1981	475	68921	39539	1.74
1982	416	39215	25609	1.53
1983	421	51824	27520	1.88
1984	203	33281	12421	2.68
1985	149	14732	6975	2.11
1986	81	15313	2250	6.80
1987	1	2	12	0.18
Total	5519	1330453	450078	2.96

Table 3
Model selection for the spatially explicit variable-coefficient generalized additive models for walleye pollock *Theragra chalcogramma* egg and adult CPUE models. Estimated degrees of freedom are provided for each term; na: covariate not applicable to that particular model; GCV: generalized cross validation score; AIC: Akaike information criterion; Adjusted R^2: adjusted coefficient of determination. Base is: $x_{t,ssb,(\phi,\lambda)}=a_{ssb}+g_1(\phi,\lambda)+g_2(\phi,\lambda)\cdot temp+g_3(\phi,\lambda)\cdot t+g_4(\phi,\lambda)\cdot t^2+e_{t,ssb,(\phi,\lambda)}$, where $x_{t,ssb(\phi,\lambda)}$ is pollock egg or adult CPUE at time t, spawning stock biomass ssb, latitude ϕ, and longitude λ, a_{ssb} is the spawning stock biomass-specific intercept, $temp$ is water temperature, t is day of the year for the egg CPUE model or month for the adult CPUE model, g_{1-4} are nonparametric smoothing functions, and $e_{t,ssb,(\phi,\lambda)}$ is the random error assumed to be normally distributed (on a log scale) with a mean of zero and finite variance.

Model	a_{ssb}	$g_1(\phi,\lambda)$	$g_2(\phi,\lambda)\cdot temp$	$g_3(\phi,\lambda)\cdot t$	$g4(\phi,\lambda)\cdot t^2$	GCV	AIC	Adjusted R^2
Egg CPUE model								
Base	18	20.8	17.5	30.0	29.9	2.950	6716	0.631
Base - $g_2(\phi,\lambda)\cdot temp$	18	22.6	na	30.0	29.4	3.033	6765	0.619
Base - $g_4(\phi,\lambda)\cdot t^2$	18	29.0	29.2	25.7	na	3.178	6845	0.598
Base - $g_3(\phi,\lambda)\cdot t$	18	28.0	24.6	na	27.9	3.196	6856	0.594
Base - $g_1(\phi,\lambda)$	18	na	21.3	30.0	27.3	3.222	6870	0.592
Base - a_{ssb}	na	21.3	19.8	30.0	27.4	3.651	7083	0.548
Adult CPUE model								
Base	22	22.6	7.4	22.2	na	0.745	14226	0.355
Base - $g_2(\phi,\lambda)\cdot temp$	22	23.5	na	22.1	na	0.747	14241	0.351
Base - $g_1(\phi,\lambda)$	22	na	23.0	23.2	na	0.754	14296	0.348
Base - a_{ssb}	na	21.5	13.0	21.2	na	0.774	14436	0.282
Base - $g_3(\phi,\lambda)\cdot t$	22	25.1	8.1	na	na	0.775	14444	0.280

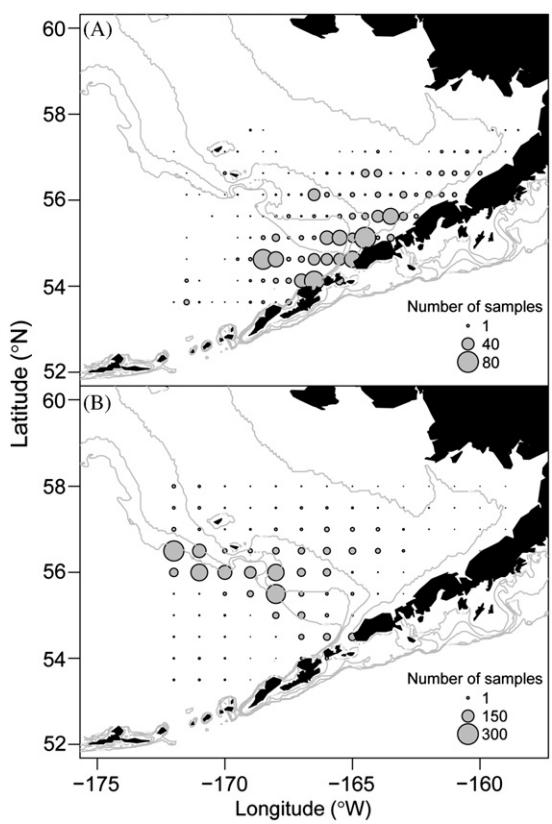

Fig. 4. Sample sizes of (A) ichthyoplankton surveys and (B) foreign-reported adult walleye pollock *Theragra chalcogramma* catch data in the eastern Bering Sea. The number of samples occurring within each grid cell was summed across all years of each survey (ichthyoplankton: 1986, 1988, 1991–2000, 2002–2003, and 2005–2009; foreign-reported data: 1965–1987).

Egg and adult CPUE showed similar spatially explicit patterns based on the effect of time (Fig. 5). Egg CPUE increased between 15 March and 15 May most substantially in the Outer Domain between Unimak and the Pribilof Islands, and also west of the Pribilof Islands; it declined the most around Bogoslof Island and Bristol Bay (Fig. 5A). Similarly, adult CPUE increased the most in the Outer Domain between Unimak and the Pribilof Islands, and decreased the most around Bogoslof Island (Fig. 5B). In contrast, however, adult CPUE increased in Bristol Bay, but note that

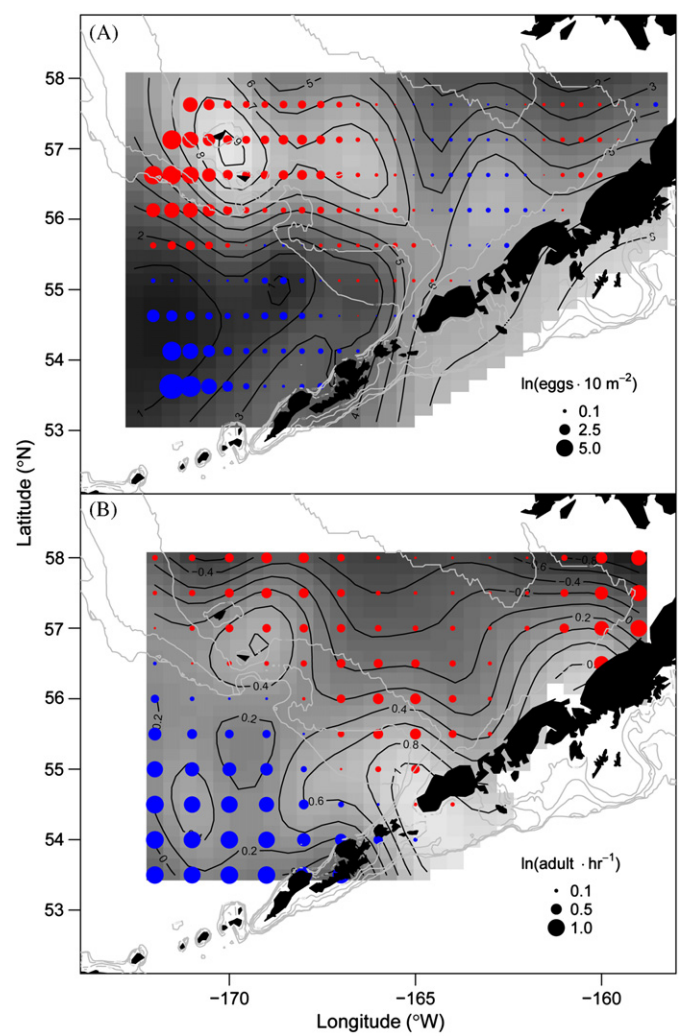

Fig. 5. Spatially explicit variable-coefficient generalized additive model plots for the effects of time on walleye pollock *Theragra chalcogramma* egg (A) or foreign-reported adult catch-per-unit-effort (B) in the eastern Bering Sea. Light gray grid cells denote highest overall predicted egg or adult CPUE and dark gray cells indicate the lowest. Overlaid on grid cells are red or blue bubbles, which indicate an expected increase or decrease, respectively, in log-transformed egg or adult pollock CPUE as time progressed from March to May, the core walleye pollock spawning season in the eastern Bering Sea.

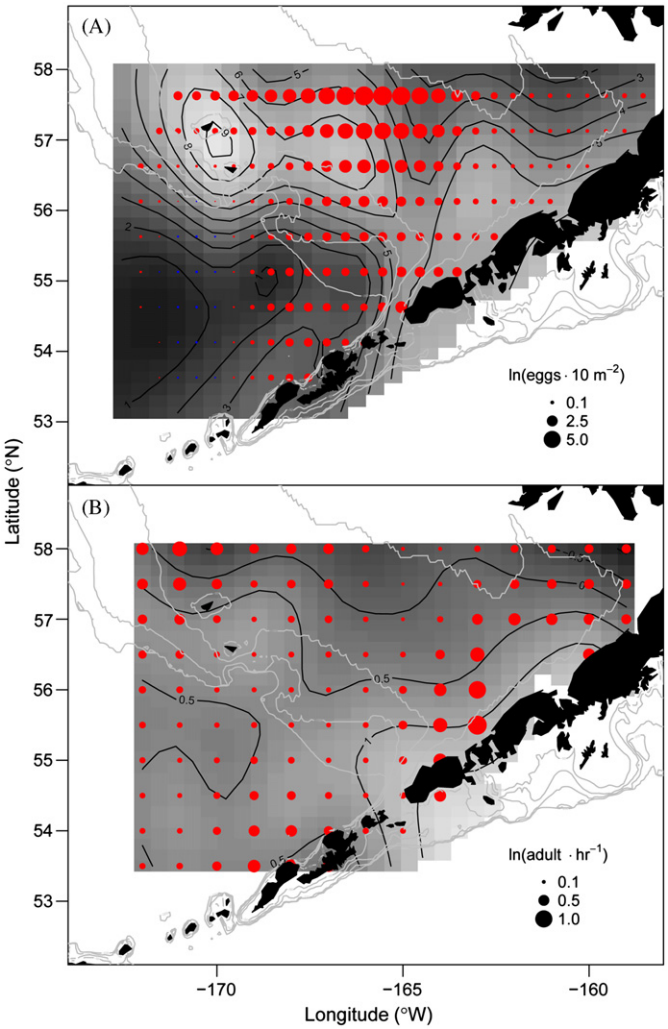

Fig. 6. Spatially explicit variable-coefficient generalized additive model plots for the effects of water temperature on walleye pollock *Theragra chalcogramma* egg (A) or foreign-reported adult catch-per-unit-effort (B) in the eastern Bering Sea. Light gray grid cells denote highest overall predicted egg or adult CPUE and dark gray cells indicate the lowest. Overlaid on grid cells are red or blue bubbles, which indicate an expected increase or decrease, respectively, in log-transformed egg or adult pollock CPUE as mean February to May sea surface temperature increased from 3 to 4° C.

commercial data sample sizes in this region were extremely low (Fig. 4B).

As water temperature increased from 3 to 4 °C, both pollock egg and adult CPUE increased throughout the study region (Fig. 6). Egg CPUE increased most substantially east of the Pribilof Islands in the Middle Domain, and least in Bristol Bay and basin waters north of Bogoslof Island (Fig. 6A). Adult CPUE increased the most near Unimak Island, the southern section of the Alaska Peninsula, and northwest of the Pribilof Islands (Fig. 6B).

4. Discussion

Understanding the degree to which the spawning spatial structure of marine populations is affected by environmental variability would enable us to infer the likelihood that species will shift their range or colonize new habitats. This is particularly relevant for subpolar regions where the effect of climate warming is more likely to cause shifts in population distributions (Mueter and Litzow, 2008). Over a long time period, it is reasonable to expect that marine populations may change their spawning distribution due to colonization of new and favorable habitats, especially during the early life stages (Iles and Sinclair, 1982). Spawning distribution can also change as a consequence of selective fishing removals (Opdal, 2010). However, on relatively shorter time scales of years to decades, the processes that affect spawning distribution are less clear. Do individuals conserve a memory of their previous or parental spawning locations (e.g., Corten, 2002; Cury, 1994) or do they exhibit flexibility in choosing their spawning sites (e.g., Bailey et al., 2004)? Can these two different strategies coexist, as is observed in Pacific hake, apparently with both geographically fixed and environmentally driven subpopulations (e.g., Bailey et al., 2004)?

Detection and monitoring of the spatial distribution of fish spawning requires high resolution data that are rarely available due to the short duration of spawning events, as well as harsh weather conditions during the spawning season (typically winter or late spring in temperate and subpolar stocks). Analytically, we face the challenge of detecting spatial patterns from limited time series and testing whether such patterns change over contrasting environmental regimes (Ciannelli et al., 2008).

Using egg and adult CPUE in a regression framework explicitly developed for testing variability of spatial patterns (e.g., Bacheler et al., 2009), we have documented that there are consistent seasonal patterns of pollock spawning locations in the eastern Bering Sea. Seasonally, we show that peak spawning occurs early in the year (March) in the Bogoslof and Islands of Four Mountains regions and progresses toward the slope area and around the Pribilof Islands by May. We interpret these seasonal patterns as a manifestation of spawning activities from multiple subpopulations (Bacheler et al., 2010; Bailey et al., 2000; Hinckley, 1987). Water temperature also caused changes in both egg and adult CPUE, but the effect of water temperature was less spatially heterogeneous compared to that of seasons. Locally, the magnitude of the effect caused by a 1 °C variation in water temperature is similar to that caused by a seasonal progression (March to May), albeit a much more spatially homogeneous effect. Thus, temperature does not appear to drastically change the spatial patterns of spawning locations, but primarily the magnitude. Within the time frame examined here (1965–2009), we have observed temperature variations of up to 3 °C, indicating that locally the effect of interannual changes of temperature over the time series may exceed that of seasons, within each sampled year.

Despite the socioeconomic and ecological importance of pollock in the Bering Sea, there have been relatively few studies that characterize their spawning geography and phenology, and none to date that have addressed spawning variability over time. Our study is in agreement with previous studies that have examined pollock spawning geography (Hinckley, 1987) and phenology (Bacheler et al., 2010) in the Bering Sea. We build upon these studies by examining the ways in which interannual variability in spawning is linked to environmental variability. We estimate that the effect of water temperature warming on pollock spawning activity is locally strong, but more spatially homogeneous than the effect of season. Thus we contend that there is persistence in pollock spawning locations with respect to changes in thermal conditions (Cury, 1994), at least at the spatial scale examined in this study (hundreds of km) and within the time frame of decades. A similar analysis conducted on pollock eggs in the Shelikof Strait region of the Gulf of Alaska also found a limited effect of water temperature on egg spatial patterns (Bacheler et al., 2009).

Our results indicate that pollock spawning locations in the Bering Sea may have undergone interannual changes, as evidenced by the combined patterns of the egg and catch data. However, these changes appear more linked to variability of

recruitment events between stocks or substocks; the role of fishing on the spatial variability in spawning over time undoubtedly played a significant role for the Aleutian basin spawning aggregations, particularly as large recruitment events ceased in this region (Ianelli et al., 2009). Specifically, adult CPUE data between March and May show the largest change of spatial patterns as a decline of CPUE in the Bogoslof and Islands of Four Mountains regions. The egg data show a similar spatial decline in the Island of Four Mountains, albeit the magnitude is much reduced. The foreign-reported adult CPUE data used in our analyses ended in 1987, while the egg CPUE data analyzed here started in 1986. Thus, the two data sets cover different time periods. It is then reasonable to assume that the seasonal decline of spawning activity in the Islands of Four Mountains region has been accompanied by an overall progressive decline of spawning activity over time in that region. This observation is consistent with what we know about the collapse of the pollock stock from the Aleutian Basin, where the Islands of Four Mountains region was a prominent spawning area. After the early 1990s, pollock catches from that region had declined by 80% compared to the peak catches of the mid and late 1980s (Ianelli et al., 2009). This does not imply that similar effects are occurring now, rather that future analyses of spawning distribution patterns may want to consider including fishery removals.

We consider the egg abundance data as the most reliable source of information for pollock spawning activity. We did not score eggs based on their maturity stage, thus egg distribution patterns may reflect some drift activity (Wespestad et al., 2000). However, given that pollock tend to spawn in relatively deep regions of the water column (>200 m) where currents are typically sluggish, and that previous analyses on yolk-sac larval distribution compared to egg distribution showed a modest amount of drift between these two stages (Bacheler et al., 2010), we expect that the effect of drift on eggs is minimal compared to the spatial resolution of the sampling. The main problem that we see in the egg CPUE data is its spatial and temporal coverage. Hence, we also included adult CPUE data in our analyses, but acknowledge that commercial CPUE data can be problematic because of differences in their abilities (e.g., skipper skills or technologies) to catch fish (Hilborn and Walters, 1992). Overall we found strong agreement in the ways in which pollock spawning varied in relation to season or water temperature observed from these two very different datasets. The main differences were found with respect to seasonal patterns, particularly in the Bristol Bay region where the sample sizes were small and uncertainty was large.

Declining fish stocks are often reflected in a contraction of their spawning distribution (Atkinson et al., 1997; McFarlane et al., 2002; Watanabe et al., 1997). It follows that documenting changes in spawning location and extent is of particular relevance to fisheries management as an indicator of changes in population abundance. During their spawning migrations, fish are typically subject to a high degree of site-specific associations (Cury, 1994), and many marine fish species exhibit philopatry (e.g., Brophy et al., 2006; Rooker et al., 2008). If there are multiple subunits within a population, the spawning geography is very heterogeneous (e.g., Iles and Sinclair, 1982). Thus, the spatial structure during the spawning phase also reflects the population genetic and ecological structure, and its monitoring over time has important implications for conservation and management (Schindler et al., 2010).

Acknowledgments

This research was supported by the Bering Sea Integrated Ecosystem Research Program (BSIERP) of the North Pacific Research Board. This research is contribution EcoFOCI-0771 to NOAA's Fisheries-Oceanography Coordinated Investigations, BEST-BSIERP Publication No. 52, and NPRB Publication No. 338. We thank S. Barbeaux and A. Hollowed for data acquisition, T. Smart and J. Duffy-Anderson for discussions about pollock spawning, and A. Chester, B. Degan, T. Kellison, P. Marraro, P. Rudershausen, and M. Sigler, and three anonymous reviewers for their comments on previous versions of this manuscript.

References

Atkinson, D.B., Rose, G.A., Murphy, E.F., Bishop, C.A., 1997. Distribution changes and abundance of northern cod (*Gadus morhua*), 1981–1993. Can. J. Fish. Aquat. Sci. 54 (Suppl. 1), 132–138.

Bacheler, N.M., Bailey, K.M., Ciannelli, L., Bartolino, V., Chan, K.S., 2009. Density-dependent, landscape, and climate effects on spawning distribution of walleye pollock *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 391, 1–12.

Bacheler, N.M., Ciannelli, L., Bailey, K.M., Duffy-Anderson, J.T., 2010. Spatial and temporal patterns of walleye pollock (*Theragra chalcogramma*) spawning in the eastern Bering Sea inferred from egg and larval distributions. Fish. Oceanogr. 19, 107–120.

Bailey, K.M., Ciannelli, L., Bond, N.A., Belgrano, A., Stenseth, N.C., 2005. Recruitment of walleye pollock in a physically and biologically complex ecosystem: a new perspective. Prog. Oceanogr. 67, 24–42.

Bailey, K.M., Hollowed, A.B., Wooster, W.S., 2004. Complexity in marine fisheries dynamics and climate interactions in the Northeast Pacific Ocean. In: Stenseth, N.C., Ottersen, G., Hurrel, J.W., Belgrano, A. (Eds.), Marine Ecosystems and Climate Variation. Oxford University Press, pp. 147–152.

Bailey, K.M., Stabeno, P.J., Powers, D.A., 1997. The role of larval retention and transport features in mortality and potential gene flow of walleye pollock. J. Fish. Biol. 51 (Suppl. A), 135–154.

Bailey, K.M., Quinn, T.J., Bentzen, P., Grant, W.S., 2000. Population structure and dynamics of walleye pollock, *Theragra chalcogramma*. Adv. Mar. Biol. 37, 179–255.

Baird, T.A., Olla, B.L., 1991. Social and reproductive behavior of a captive group of walleye pollock, *Theragra chalcogramma*. Environ. Biol. Fish. 30, 295–301.

Bakkala, R.G., 1993. Structure and Historical Changes in the Groundfish Complex of the Eastern Bering Sea. U.S. Department of Commerce, NOAA Technical Report, vol. 114, 91 pp.

Bartolino, V., Ciannelli, L., Bacheler, N.M., Chan, K.S., 2011. Ontogenetic and sex-specific differences in density-dependent habitat selection of a marine fish population. Ecology 92, 198–200.

Brophy, D., Daliowicz, B.S., King, P.A., 2006. Spawning season fidelity in sympatric populations of Atlantic herring (*Clupea harengus*). Can. J. Fish. Aquat. Sci. 63, 607–616.

Buckley, T.W., Greig, A., Boldt, J.L., 2009. Describing Summer Pelagic Habitat Over the Continental Shelf in the Eastern Bering Sea, 1982–2006. NOAA Technical Memo. NMFS-AFSC196, pp. 1–49.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second ed. Springer, New York.

Cadrin, S.X., Secor, D.H., 2009. Accounting for spatial population structure in stock assessment: past, present, and future. In: Beamish, R.J., Rothschild, B.J. (Eds.), The Future of Fisheries Science in North America. Springer, New York, pp. 405–426.

Ciannelli, L., Dingsør, G.E., Bogstad, B., Ottersen, F., Chan, K.S., Gjøsæter, H., Stiansen, J.E., Stenseth, N.C., 2007. Spatial anatomy of species survival: effects of predation and climate-driven environmental variability. Ecology 88, 635–646.

Ciannelli, L., Fauchald, P., Chan, K.S., Agostini, V.N., Dingsør, G.E., 2008. Spatial fisheries ecology: recent progress and future prospects. J. Mar. Syst. 71, 223–236.

Coachman, L.K., 1986. Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. Continent. Shelf Res. 5, 23–108.

Corten, A., 2002. The role of 'conservatism' in herring migrations. Rev. Fish. Biol. Fish 11, 39–361.

Cury, P., 1994. Obstinate nature: an ecology of individuals: thoughts on reproductive behavior and biodiversity. Can. J. Fish. Aquat. Sci. 51, 1664–1673.

Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26, 249–293.

Earth System Research Laboratory, 2011. Physical Sciences Division of the Earth System Research Laboratory. 〈http://www.esrl.noaa.gov/psd/〉 (last accessed: 7 March 2011).

Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., McNutt, S.L., 2006. A major ecosystem shift in the northern Bering Sea. Science 311, 1461–1464.

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

Hastie, T., Tibshirani, R., 1993. Varying-coefficient models. J. Roy. Stat. Soc. B 55, 757–796.

Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty. Kluwer Academic Publishers, Boston, MA.

Hinckley, S., 1987. The reproductive biology of walleye pollock, *Theragra chalcogramma*, in the Bering Sea, with reference to spawning stock structure. Fish. Bull. 85, 481–498.

Ianelli, J.N., Barbeaux, S., Honkalehto, T., Kotwicki, S., Aydin, K., Williamson, N., 2009. Assessment of the Walleye Pollock Stock in the Eastern Bering Sea. Stock Assessment and Fisheries Evaluation Report. North Pacific Fisheries Management Council, 605 W. 4th Ave., Anchorage, Alaska 99501.

Iles, T.D., Sinclair, M., 1982. Atlantic herring—stock discreteness and abundance. Science 215, 27–633.

Jung, K.-M., Kang, S., Kim, S., Kendall Jr, A.W., 2006. Ecological characteristics of walleye pollock eggs and larvae in the southeastern Bering Sea during the late 1970s. J. Oceanogr. 62, 859–871.

Low, L.L., Ikeda, I., 1980. Average Density Index for Walleye Pollock (*Theragra chalcogramma*) in the Bering Sea. NOAA Technical Memo. SFRF743.

Luchin, V.A., Menovshchikov, V.A., Lavrentiev, V.M., Reed, R., 1999. Thermohaline structure and water masses in the Bering Sea. In: Loughlin, T.R., Ohtani, K. (Eds.), Dyanmics of the Bering Sea.. University of Alaska Sea Grant, Anchorage, pp. 61–92.

McFarlane, G.A., Smith, P.E., Baumgartner, T.R., Hunter, J.R., 2002. Climate variability and Pacific sardine populations and fisheries. Am. Fish. Soc. Symp. 32, 195–214.

Mueter, F.J., Litzow, M.A., 2008. Sea ice alters the biogeography of the Bering Sea continental shelf. Ecol. Appl. 18, 309–320.

Niebauer, H.J., 1981. Recent short-period wintertime climatic fluctuations and their effect on sea-surface temperatures in the eastern Bering Sea. In: Hood, D.W., Calder, J.A. (Eds.), The Eastern Bering Sea Shelf: Oceanography and Resources, vol. 1. University of Washington Press, Seattle, pp. 23–30.

Opdal, A.F., 2010. Fisheries change spawning ground distribution of northeast Arctic cod. Biol. Lett. 6, 261–264.

Overpeck, J., Hughen, K., Hardy, D., Bradley, R., Case, R., Douglas, M., Finney, B., Gajewski, K., Jacoby, G., Jennings, A., Lamoureux, S., Lasca, A., MacDonald, G., Moore, G., Retelle, M., Smith, S., Wolfe, A., Zielinski, G., 1997. Arctic environmental change of the last four centuries. Science 278, 1251–1256.

R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rooker, J.R., Secor, D.H., De Metrio, G., Schloesser, R., Block, B.A., Neilson, J.D., 2008. Natal homing and connectivity in Atlantic bluefin tuna populations. Science 322, 742–744.

Sakurai, Y., 1982. Reproductive Ecology of Walleye Pollock *Theragra chalcogramma* (Pallas). Ph.D. Thesis, Faculty of Fisheries, Hokkaido University, Hakodate (translated from Japanese).

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., Webster, M.S., 2010. Population diversity and the portfolio effect in an exploited species. Nature 465, 609–612.

Shima, M., Bailey, K.M., 1993. Comparative analysis of ichthyoplankton sampling gear for early life history stages of walleye pollock (*Theragra chalcogramma*). Fish. Oceanogr 3, 50–59.

Smart, T.I., Duffy-Anderson, J.T., Horne, J.K., Farley, E.V., Wilson, C.D., Napp, J.M., 2012. Influence of environment on walleye pollock eggs, larvae, and juveniles in the southeastern Bering Sea. Deep Sea Res. II 65–70, 196–207.

Watanabe, Y., Zenitani, H., Kimura, R., 1997. Variations in spawning ground area and egg density of the Japanese sardine in Pacific coastal and oceanic waters. Fish. Oceanogr. 6, 5–40.

Wespestad, V.G., Fritz, L.W., Ingraham, W.J., Megrey, B.A., 2000. On relationships between cannibalism, climate variability, physical transport, and recruitment success of Bering Sea walleye pollock, *Theragra chalcogramma*. ICES J. Mar. Sci. 57, 272–278.

Wood, S.N., 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. J. Amer. Stat. Assoc. 99, 673–686.

Wood, S.N., 2006. Generalized additive models: an introduction with. R Chapman and Hall/CRC, Boca Raton, FL.