Spatial and temporal patterns of walleye pollock (*Theragra chalcogramma*) spawning in the eastern Bering Sea inferred from egg and larval distributions

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ABSTRACT

Walleye pollock *Theragra chalcogramma* (pollock hereafter) is a key ecological and economic species in the eastern Bering Sea, yet detailed synthesis of the spatial and temporal patterns of pollock ichthyoplankton in this important region is lacking. This knowledge gap is particularly severe considering that egg and larval distribution are essential to reconstructing spawning locations and early life stages drift pathways. We used 19 yr of ichthyoplankton collections to determine the spatial and temporal patterns of egg and larval distribution. Generalized additive models (GAMs) identified two primary temporal pulses of pollock eggs, the first occurring from 20 February to 31 March and the second from 20 April to 20 May; larvae showed similar, but slightly lagged, pulses. Based on generalized cross-validation and information theory, a GAM model that allowed for different seasonal patterns in egg density within three unique areas outperformed a GAM that assumed a single fixed seasonal pattern across the entire eastern Bering Sea. This 'area-dependent' GAM predicted the highest densities of eggs (i.e., potential spawning locations) in three major areas of the eastern Bering Sea: near Bogoslof Island (February–April), north of Unimak Island and the Alaska Peninsula (March–April), and around the Pribilof Islands (April–August). Unique temporal patterns of egg density were observed for each area, suggesting that pollock spawning may be more spatially and temporally complex than previously assumed. Moreover, this work provides a valuable baseline of pollock spawning to which future changes, such as those resulting from climate variability, may be compared.

Key words: drift, spawning, stock structure, *Theragra chalcogramma*, walleye pollock

INTRODUCTION

Walleye pollock *Theragra chalcogramma* is a key fish species in ecosystems of the North Pacific Ocean. The geographic range of walleye pollock (pollock hereafter) is broad, extending from Japan northeast to the Bering Sea and Gulf of Alaska, and south to northern California. In the eastern Bering Sea, pollock is a central component of the food web, providing forage for myriad fish, marine mammals, and seabirds (Napp *et al.*, 2000; Wespestad *et al.*, 2000; Sinclair *et al.*, 2008). Pollock also feed upon a variety of planktonic, benthic, and pelagic crustaceans and fishes (Brodeur *et al.*, 2000; Ciannelli *et al.*, 2004). Declines of pollock have likely contributed to declines in Steller sea lion *Eumetopias jubatus* and sea bird populations (Merrick *et al.*, 1997). They are also important from an economic perspective; commercial catch of pollock in the eastern Bering Sea has averaged 1 billion kg since 1977 (Ianelli *et al.*, 2008), with an annual value of over US$600 million (Kinoshita *et al.*, 1998). Currently, pollock is the second largest single-species fishery in the world (FAO, 2007).

Pollock are generalists and occupy a wide range of habitats and environmental conditions. They are considered a subarctic species (Mueter and Litzow, 2008), inhabiting water temperatures ranging from 1 to 10°C. Pollock commonly associate with outer shelf and slope regions of oceanic waters, but can occupy a variety of habitats such as inshore seagrass beds, large estuaries, coastal embayments, and offshore oceanic waters (Bailey *et al.*, 1997). They are

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generally regarded as semidemersal, but can be exclusively pelagic in some environments (Bakkala, 1993). Maturity occurs at 3–4 yr of age, and individual females spawn millions of eggs each year (Hinckley, 1987).

Understanding the spatial and temporal patterns of pollock spawning is important because it sets the initial conditions in a series of events that eventually lead to year-class strength (Bailey and Spring, 1992; Bailey et al., 2005). Despite their considerable ecological and economic importance, a comprehensive investigation of the spawning locations of pollock in the eastern Bering Sea is lacking. Multiple spatially and temporally distinct spawning areas appear to exist for pollock in the eastern Bering Sea. For instance, based on 1 yr of commercial catches and maturity data, Hinckley (1987) proposed that three spawning locations were used by pollock in the eastern Bering Sea: one in the Aleutian Basin, one on the southeastern shelf and slope, and one northwest of the Pribilof Islands. Drawbacks of using commercial catch data are that it assumes fishers did not miss any spawning concentrations (which are often targeted by commercial fishers), and they are either fishing on spawning concentrations or there is no movement between the time of pre-spawning fishing activity and spawning. An alternative is to use fishery-independent sampling of ichthyoplankton to infer spawning distributions. Using 4 yr of ichthyoplankton data from the late 1970s, Jung et al. (2006) confirmed the southeastern Bering Sea shelf and slope spawning group, but could not address the other two locations found by Hinckley (1987) due to insufficient data.

The objective of our work was to describe the spatial and temporal patterns of pollock eggs and larvae in the eastern Bering Sea. Unlike previous studies, we used ichthyoplankton data collected over many years and seasons to draw general conclusions about the locations and timing of pollock spawning. This is the first study assembling pollock early life stages distribution in the Bering Sea with such a large geographic and temporal coverage. This retrospective analysis of early life stages allowed us to address various other aspects of the ecology of pollock, particularly drift pathways of eggs and larvae, ultimately leading to inferences about population structure and connectivity. In addition, our results provide a baseline of pollock spawning to which future potential changes may be compared, which is especially important given the scenario of a changing climate in the eastern Bering Sea (Overpeck et al., 1997; Grebmeier et al., 2006; Hunt et al., 2008).

METHODS

Eastern Bering Sea

The eastern Bering Sea is a large and dynamic ecosystem that supports some of the most productive and valuable fisheries in the USA. It is bordered on the east by mainland Alaska, on the south by the Aleutian Islands, on the west by the Aleutian Basin, and on the north by Siberia and the Bering Strait (Fig. 1). The physical oceanography of the eastern Bering Sea is a product of its expansive continental shelf, which is the largest of its kind outside the Arctic (Schumacher, 1984). The eastern Bering Sea shelf is commonly divided into four distinct regions that are separated by hydrographic fronts: the Coastal Domain (0–50 m deep), the Middle Domain (50–100 m deep), the Outer Domain (100–200 m deep), and the Slope (>200 m deep; Fig. 1). There is also evidence for a unique Pribilof Domain (Hunt et al., 2008). The extensive shelf allows for winter ice cover to create a pool of cold bottom water, which often persists well into the following summer due to strong thermal stratification (Hunt and Stabeno, 2002). The intensity and spatial extent of the 'cold pool' strongly influences the distribution of fish in the eastern Bering Sea (Wyllie-Echeverria and Wooster, 1998; Ciannelli and Bailey, 2005; Mueter and Litzow, 2008).

Figure 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).
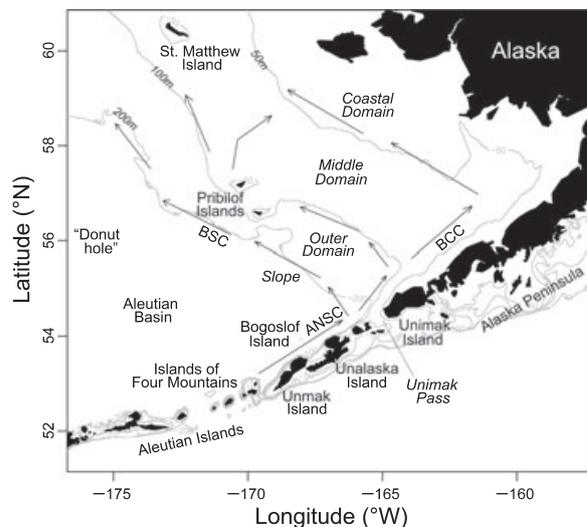
Field sampling protocol

Data analyzed in this study consisted of egg densities (numbers 1000 m^{-3}) collected during ichthyoplankton surveys conducted by the Alaska Fisheries Science Center (AFSC, Seattle, WA) in the eastern Bering Sea (Matarese *et al.*, 2003). Volume of water sampled was calculated as the area of the net opening multiplied by the distance the net was towed. Ichthyoplankton surveys used here were conducted in 1979, 1986, 1988, and 1991–2006 (Table 1). Overall, sampling took place in all months except November, December, and January (Table 1). The spatial and temporal coverage of the survey was somewhat variable over time, with more late winter samples occurring early in the time series, and more late summer samples occurring in later years (Fig. 2).

Three sampling gears were combined in this study, so that the spatial and temporal coverage of sampling was as broad as possible. Most sampling was conducted with obliquely towed 0.333-mm or 0.505-mm mesh bongo nets (90%) or Tucker nets (7%), towed from 10 m off the bottom to the surface in the shelf area or from a depth of 300 m to the surface in slope and basin areas. Comparative tows with these two net types and mesh sizes have generally indicated similar numbers and size distributions of pollock (Shima and Bailey, 1993). Both nets were towed at a speed to maintain a 45° wire angle at a retrieval rate of 20 m min^{-1}. The remaining sampling (3%) was conducted with a 1-m^2 multiple opening and closing net and environmental sampling system (MOCNESS; Wiebe *et al.*, 1976), which allowed for the collection of depth-discrete samples. We assumed that sampling differences between gears were minor compared to the spatial and temporal variability in pollock eggs and larvae. Eggs and larvae were preserved in 5% formalin and later sorted, identified to species, and measured [mm standard length (SL)] at the Plankton Sorting and Identification Center in Szczecin, Poland. Personnel from the AFSC later verified taxonomic identifications. Relative sampling effort by month was calculated as the total number of samples occurring in a particular month divided by the total number of samples taken across all months.

Data analysis

The locations and timing of pollock egg occurrences were used to define the spatial and temporal patterns of pollock spawning. Pollock larvae were analyzed separately within four length bins that represent important stages in ontogeny, generally following Brown *et al.* (2001). Larvae between 2.0–4.4 mm SL were classified as yolk-sac stage because hatching had occurred but exogenous feeding had not yet commenced. First-feeding larvae (4.5–6.9 mm SL) had

Table 1. Cruise information for ichthyoplankton surveys in the eastern Bering Sea used in this study. CR is the number of cruises taken within a year and *N* is total number of samples taken in the year.

Year	CR	*N*	Start date	End date	Minimum longitude	Maximum longitude	Minimum latitude	Maximum latitude
1979	1	132	06/01	07/23	165.26	178.88	52.09	60.91
1986	1	70	02/16	02/28	165.91	179.98	53.05	55.85
1988	2	111	03/17	05/08	161.30	179.90	53.85	58.94
1991	2	82	03/11	05/08	163.62	176.50	53.13	58.18
1992	2	81	04/16	07/14	165.17	171.57	53.82	55.04
1993	1	265	04/15	04/30	165.83	169.69	53.39	55.57
1994	4	216	04/15	09/21	163.49	179.60	53.51	62.37
1995	5	364	02/22	09/24	162.77	171.81	53.57	57.70
1996	6	170	03/06	09/13	160.99	173.04	53.10	63.08
1997	5	311	04/16	09/17	163.82	175.00	53.35	62.52
1998	3	63	04/07	09/14	156.78	170.97	54.59	57.72
1999	5	186	04/14	09/14	157.81	170.36	54.05	58.28
2000	5	75	02/17	09/22	162.77	170.21	54.30	58.06
2001	1	32	07/21	07/24	165.99	169.97	54.99	58.99
2002	5	274	05/13	10/06	161.00	179.73	52.32	65.00
2003	3	161	03/04	07/25	160.01	170.00	54.01	58.49
2004	4	86	07/28	10/02	163.88	176.02	54.41	62.32
2005	6	290	03/04	09/28	158.24	179.91	54.02	62.20
2006	2	202	05/09	06/25	160.00	170.00	53.37	58.00
Overall	63	3171	02/16	10/06	156.78	179.98	52.32	65.00

Figure 2. Spatial and temporal aspects of the ichthyoplankton survey in the eastern Bering Sea. Samples that caught pollock eggs are shown by the colored circles (blue = Jan–Mar; green = Apr–Jun; red = Jul–Sep; gray = Oct–Dec), and samples failing to catch pollock eggs are shown by the gray 'X'.
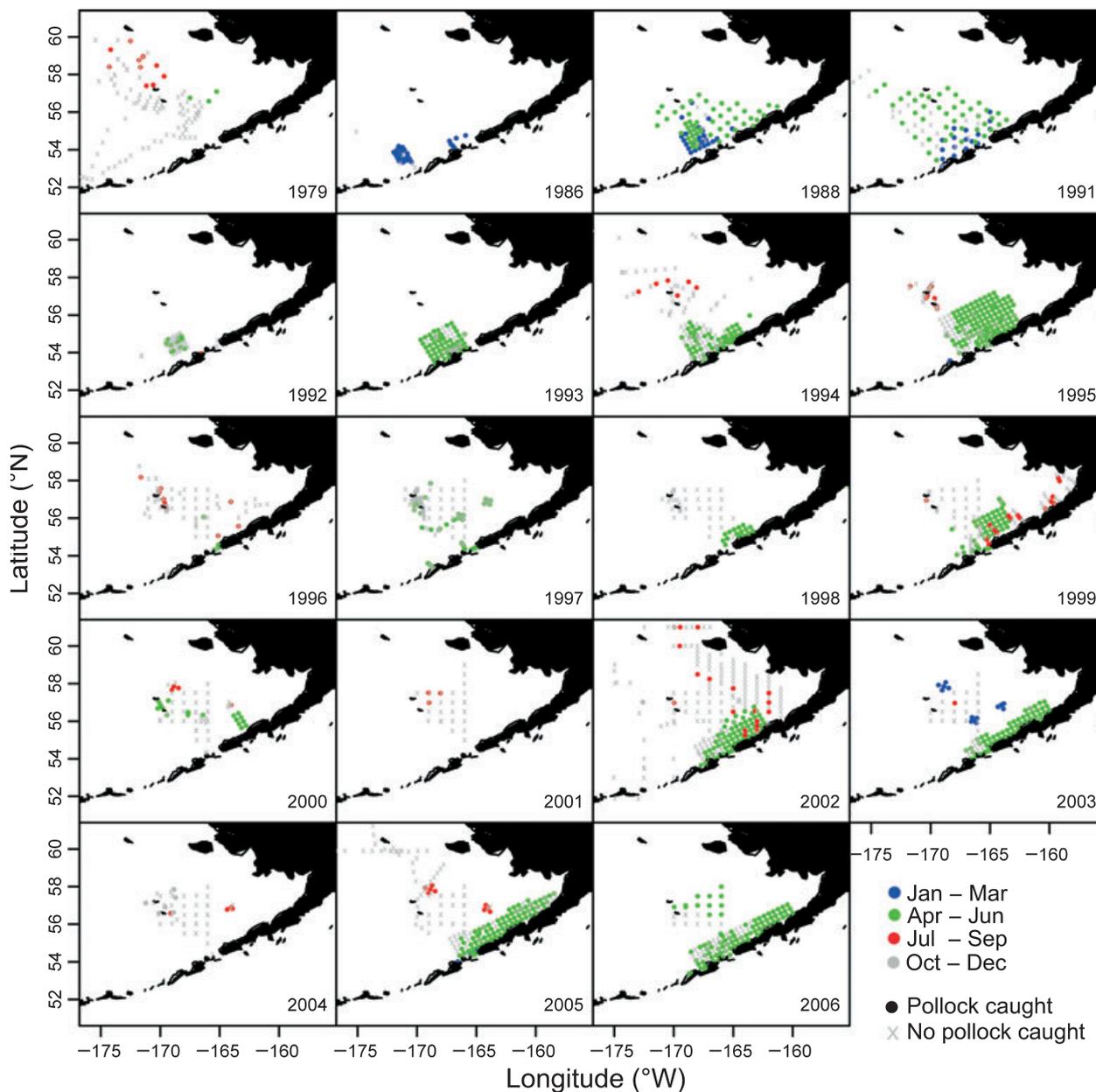
absorbed their yolk and begun exogenous feeding. Larger larvae were divided into pre-flexion (7.0–13.9 mm SL) and post-flexion (14.0–30.0 mm SL) stages due to differences in swimming ability and flexion of the notochord between these size groups. Larvae or juveniles larger than 30.0 mm SL were not considered in this study.

We used generalized additive models (GAMs) to relate the density of pollock eggs or larval stages to various predictor variables (covariates hereafter). A GAM is a nonlinear regression technique that does not require *a priori* specification of the functional relationship between the dependent and independent variables (Hastie and Tibshirani, 1990; Wood, 2006). A GAM can therefore fit nonlinear relationships between the response variable and covariates, which are common in ecological data. Only samples with positive catch were used in the analysis, and the

remaining density data were log-transformed to achieve normality and reduce heteroscedasticity. Covariates in the model included year, bottom depth, position of the sample in terms of latitude and longitude, and day of the year (DOY). Of particular importance for this analysis were the effects of DOY and position (degrees latitude and longitude), as they indicate the production phenology and spatial pattern, respectively. All models were coded and analyzed using the MGCV library (version 1.4-1; Wood, 2008) in R version 2.7.2 (R Development Team, 2008), using the Gaussian family model and identity link function. We also experimented with binomial data using presence and absence, and the Poisson distribution family using counts and logit link function, but as results were very similar, only the Gaussian models are presented. All GAM models presented in this paper met assumptions of constant variance and normal residuals using the gam.check function. There were no consistent patterns when the semivariance of the model residuals was plotted against the distance between sampling points on a yearly basis. The lack of pattern indicates minimal spatial autocorrelation in the residuals.

We compared two different GAM model formulations for each egg or larval stage: one assuming the same DOY relationship across all areas of the eastern Bering Sea ('area-independent' model), and one where three different areas were each uniquely related to DOY ('area-dependent' model). Only data from south of 58°N and east of 173°W were analyzed in this study due to few samples occurring outside this area. For the area-independent model, the natural logarithm of pollock egg or larval density x at DOY t, year y, latitude ϕ, and longitude λ was:

$$x_{t,y,(\phi,\lambda)} = a_y + g_1(\phi,\lambda) + g_2(b_{(\phi,\lambda)}) \\ + g_3(t_{(\phi,\lambda),y}) + e_{t,y,(\phi,\lambda)} \quad (1)$$

where a_y is the year-specific intercept, b is the log-transformed bottom depth, $e_{t,y,(\phi,\lambda)}$ is the random error assumed to be normally distributed (on a log scale) with a mean of zero and finite variance, and the g represents a nonparametric smoothing function for each term. This model assumes that pollock egg or larval density in a particular year, time of the year, and location is a function of position, bottom depth, and time of the year. In addition, any variability of the conditional mean observed at a given depth, location, and time of the year is assumed to be due to variation in yearly mean egg or larval density (e.g., Ciannelli *et al.*, 2007).

The area-dependent model was tested (1) based on previous studies indicating an area-specific phenology;

(2) exploratory plots suggesting that there are differences in the timing of spawning among major areas of the eastern Bering Sea; and (3) to account for the effects of variable sampling over space and time in the survey (Fig. 2). The area-dependent model was formulated slightly differently than the area-independent model. Three areas were selected based on natural divisions in the distribution of pollock eggs in the eastern Bering Sea, as well as unique temporal patterns within each area (see Fig. 3a for area delineations). Specifically, area A included the waters of the Aleutian Basin and Aleutian Islands, including the Islands of Four Mountains and Bogoslof Island. Areas from Unimak Pass eastward, including waters north of the Alaska Peninsula, were placed in area B. Finally, locations around the Pribilof Islands were included in area C. The area-dependent model was formulated as:

$$x_{t,y,(\phi,\lambda)}$$
$$= \begin{cases} a_y + g_1(\phi,\lambda) + g_2(b_{(\phi,\lambda)}) + g_3(t_{(\phi,\lambda),y}) + e_{t,y,(\phi,\lambda)} \\ \quad \text{if in area A,} \\ a_y + g_1(\phi,\lambda) + g_2(b_{(\phi,\lambda)}) + g_4(t_{(\phi,\lambda),y}) + e_{t,y,(\phi,\lambda)} \\ \quad \text{if in area B,} \\ a_y + g_1(\phi,\lambda) + g_2(b_{(\phi,\lambda)}) + g_5(t_{(\phi,\lambda),y}) + e_{t,y,(\phi,\lambda)} \\ \quad \text{if in area C.} \quad (2) \end{cases}$$

The area-dependent model differed from the area-independent model specifically because the function that linked egg or larval density with time of the year was allowed to vary by area. In models 1 and 2, thin plate splines were used for both one- and two-dimensional effects (Wood, 2006).

Two criteria were used to objectively compare the area-independent and area-dependent models, and both criteria were also used to evaluate which covariates were included in each model. First, we used the generalized cross-validation (GCV) score, which is a measure of the predictive squared error of the model (Wood, 2006). Secondly, we used Akaike's information criterion (AIC), which provides a trade-off between the number of parameters of a model and its likelihood (Akaike, 1973; Burnham and Anderson, 2002). Models with the lowest GCV and AIC scores were selected over models with higher scores, and in all cases these two criteria provided the same result.

RESULTS

Data from 63 cruises were included in our analyses, resulting in a total of 3171 samples over 19 yrs (Table 1). The number of samples taken annually
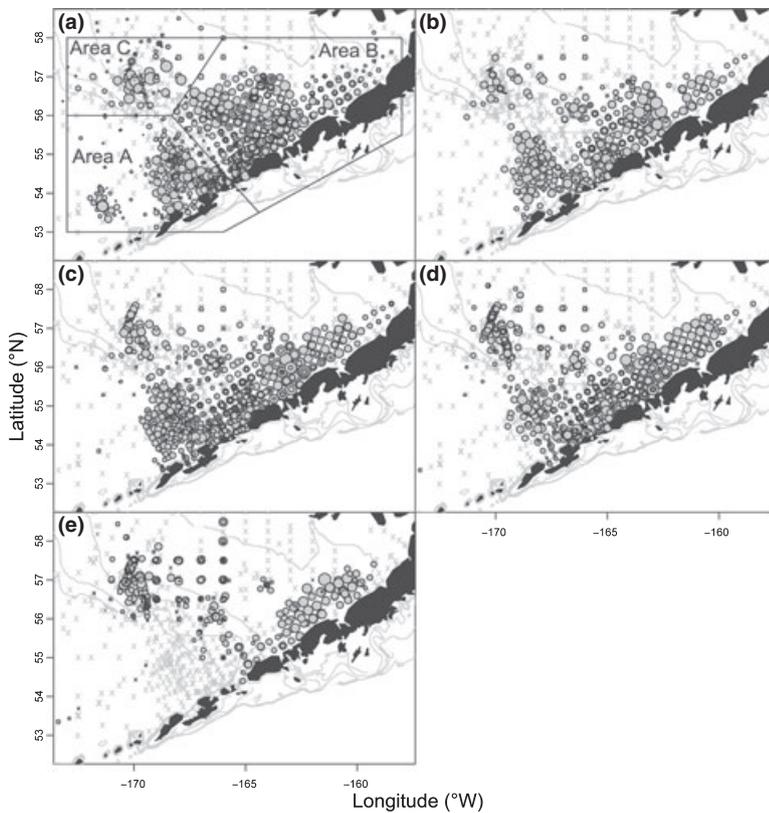
Figure 3. Log-transformed density of pollock eggs (a), yolk-sac larvae (b), first-feeding larvae (c), pre-flexion larvae (d), and post-flexion larvae (e) collected during 19 yr of sampling in the eastern Bering Sea. The size of the bubbles is scaled to the largest catch within each egg or larval stage, and locations of stations with zero catch are shown by the gray 'X'. Area polygons used in the area-dependent GAM analysis are provided in panel (a).

ranged from 32 in 2001 to 364 in 1995 (mean = 167; Table 1). Sampling occurred in all months from February through October, but was concentrated in April (28%), May (27%), July (17%), and September (13%; Table 2). The highest proportions of pollock eggs were caught in March and April (Fig. 2), whereas the highest proportions of yolk-sac, first-feeding, and pre-flexion larvae were caught in April and May (Table 2). In contrast, post-flexion larvae were caught most often in July. The lack of egg and larval catches in June was likely due to low sampling effort in that month (Table 2).

Pollock eggs and larvae were caught over a broad area in the eastern Bering Sea (Fig. 3). Generally, the

highest densities of pollock eggs and small larvae were observed north of Bogoslof Island, north of the Alaska Peninsula, and near the Pribilof Islands. Pre- and post-flexion larval densities varied somewhat from the distribution of eggs and smaller larvae by being less common off of Bogoslof Island and perhaps more dense near the Pribilof Islands (Fig. 3).

Pollock larvae increased in median length throughout the year (Fig. 4). Median length increased slowly from March (4 mm SL) to May (7 mm SL), but thereafter increased more rapidly throughout the summer months (Fig. 4). It did not appear, however, that only one cohort of pollock larvae was sampled in this study. Small pollock larvae (<5 mm SL) appeared

Month	Relative effort	Eggs	Yolk-sac larvae	First-feeding larvae	Pre-flexion larvae	Post-flexion larvae
February	0.02	0.23	0	0	0	0
March	0.03	0.27	0.20	0.14	0.02	0
April	0.28	0.38	0.53	0.52	0.36	0
May	0.27	0.12	0.27	0.32	0.37	0.08
June	0.03	<0.01	<0.01	<0.01	<0.01	0.01
July	0.17	<0.01	<0.01	0.02	0.24	0.87
August	0.05	<0.01	0	0	0.01	0.04
September	0.13	<0.01	<0.01	<0.01	0	0
October	0.01	<0.01	0	0	0	0

Table 2. Monthly proportion of total pollock eggs, larvae, and sampling effort occurring between February and October of the 19-yr time series in the eastern Bering Sea. Relative effort by month was calculated as the total number of samples occurring in a particular month divided by the total number of samples taken across all months.

Figure 4. Box plot of pollock larval lengths (mm SL) from March to September across all years of the study in the eastern Bering Sea.
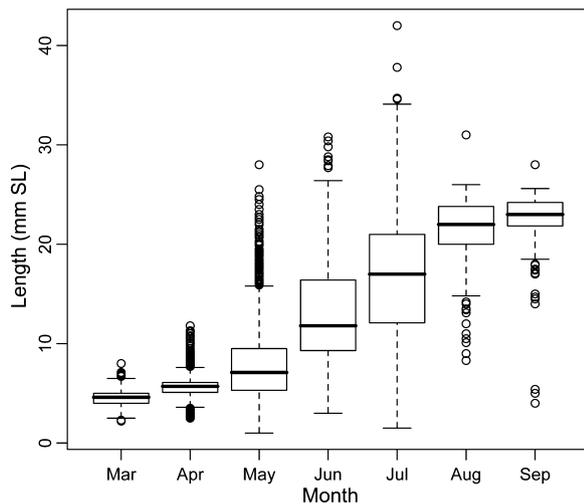
continuously in every month from March until September, with the possible exception of August (Fig. 4).

Based on both GCV and AIC scores, the area-dependent model was superior to the area-independent model for each egg and larval pollock stage (Table 3), suggesting that area-specific DOY relationships were important to accurately predict pollock ichthyoplankton densities. The deviance explained by the area-dependent models varied from 47% (yolk-sac larvae) to 74% (post-flexion larvae). All covariates

were retained in the egg and pre-flexion area-dependent models, but the best models for other larval classes excluded some of the covariates (Table 3).

To visualize the broad temporal patterns of pollock eggs and larvae throughout the entire eastern Bering Sea, the DOY relationships from the area-independent models are presented (Fig. 5); area-dependent models could not be used for this purpose because DOY relationships in these models were area-specific. The first and largest pulse of pollock eggs occurred between 20 February and 31 March (DOY 50–90), with the second pulse between 20 April and 20 May (DOY 110–140; Fig. 5). Temporal pulses of yolk-sac larvae occurred between 6 March and 10 April (DOY 65–100) and between 5 May and 30 May (DOY 125–150), followed closely by temporal pulses of first-feeding larvae [16 March–20 April (DOY 75–110) and 5 May–30 May (DOY 125–150)]. Pre- and post-flexion larvae had the highest concentrations much later than younger stages. The highest concentrations of pollock pre-flexion larvae occurred between 30 April and 4 June (DOY 120–155) and between 19 June and 19 July (DOY 170–200), and the timing of highest post-flexion concentrations was similar to pre-flexion larvae but lagged slightly [10 May–19 June (DOY 130–170) and 29 June–24 July (DOY 180–205); Fig. 5].

Next, we concentrated on further detailing the egg distribution models, as these are directly related to spawning location and phenology. The overall, absolute predicted egg densities from the area-dependent model were variable across both time and space in the southeastern Bering Sea (Fig. 6). During the first

Table 3. Results of two configurations of generalized additive models for various developmental stages of pollock ichthyoplankton for 19 yr in the eastern Bering Sea. 'NA' means the covariate was not applicable to that particular model, and 'ex' means the covariate was excluded from the model based on GCV and AIC scores.

Model	Tows with positive catch	GCV	AIC	Deviance explained	Lat./ Long.	Day of year, overall	Day of year, area A	Day of year, area B	Day of year, area C	Bottom depth
Area-independent										
Eggs	1575	2.655	6006.9	66%	<0.001	<0.001	NA	NA	NA	<0.001
Yolk-sac larvae	484	0.912	1327.3	46%	<0.001	<0.001	NA	NA	NA	ex
First-feeding larvae	1036	0.698	2566.3	48%	<0.001	<0.001	NA	NA	NA	<0.001
Pre-flexion larvae	851	0.733	2148.6	52%	<0.001	<0.001	NA	NA	NA	<0.001
Post-flexion larvae	503	0.492	1070.4	71%	0.03	<0.001	NA	NA	NA	<0.001
Area-dependent										
Eggs	1575	2.386	5837.8	70%	<0.001	NA	<0.001	<0.001	<0.001	<0.001
Yolk-sac larvae	484	0.903	1323.0	47%	<0.001	NA	ex	<0.001	ex	ex
First-feeding larvae	1036	0.661	2510.8	50%	<0.001	NA	ex	<0.001	ex	<0.001
Pre-flexion larvae	851	0.715	2126.8	54%	<0.001	NA	<0.001	<0.001	<0.001	<0.001
Post-flexion larvae	503	0.469	1045.0	74%	0.01	NA	<0.001	ex	<0.001	<0.001

Figure 5. Predicted density anomalies (±95% confidence interval) of pollock eggs (a), yolk-sac larvae (b), first-feeding larvae (c), pre-flexion larvae (d), and post-flexion larvae (e) related to the day of the year in the eastern Bering Sea, as determined by area-independent generalized additive models using 19 yr of data.
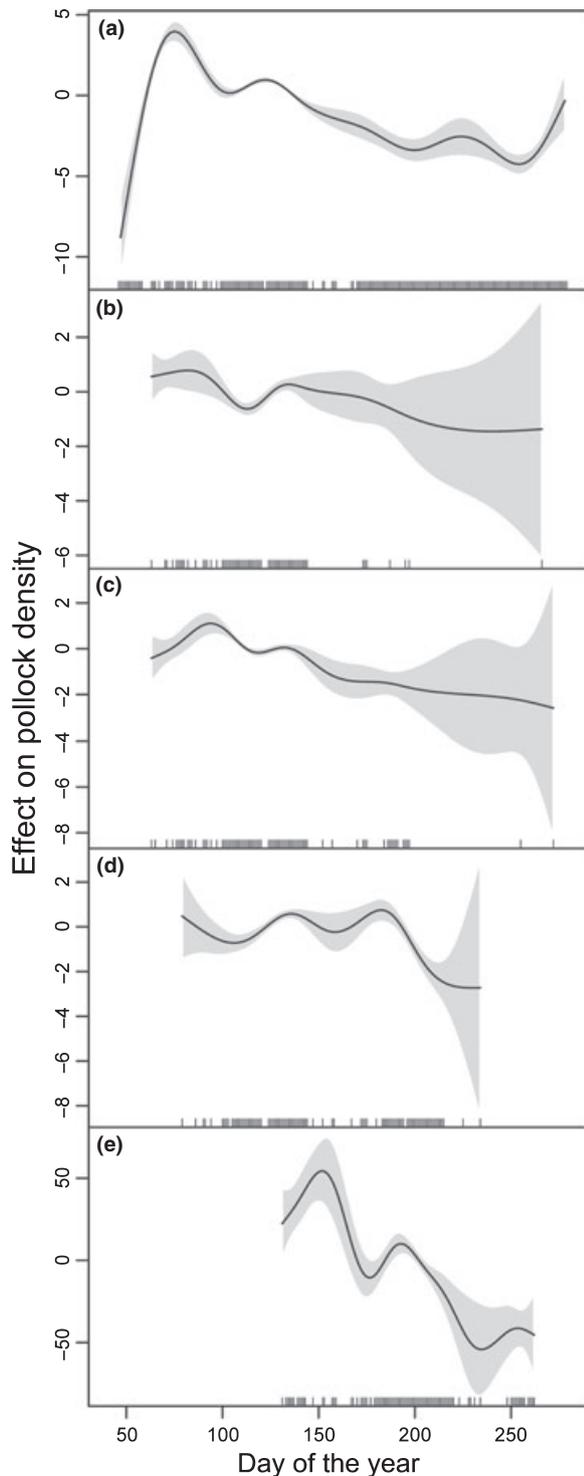
Figure 6. Predicted log-transformed pollock egg densities from the area-dependent generalized additive model, provided for three times of the year corresponding to the major temporal peaks of pollock eggs identified in Fig. 4: (a) 17 March (DOY 76), (b) 2 May (DOY 122), and (c) 23 August (DOY 235). Observed pollock egg densities are shown by the open circles ±10 days (a–b) or ±30 days (c) from the timing of predictions, which allows direct comparison of observed and predicted densities during each of the three time periods. Predictions are only shown for areas within 50 km of observations during each time period.
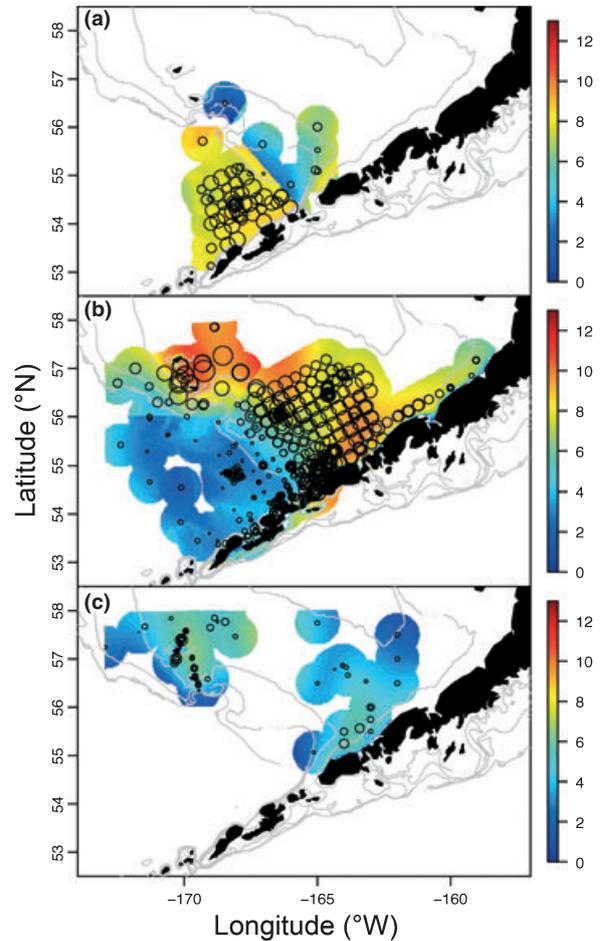
temporal pulse occurring on 17 March (DOY 76; see Fig. 5), the highest predicted egg density occurred in area A (Bogoslof Island and surrounding waters). Pollock density was highest in the Middle Domain (areas B & C) during the second temporal pulse (2 May; DOY 122), from the Alaska Peninsula northward to the Pribilof Islands (Fig. 6). In fact, the highest overall predicted egg densities in our study occurred around the Pribilof Islands during early May. Predicted pollock egg density during the late summer (23

August; DOY 235) was highest north of Unimak Island and around the Pribilof Islands (areas B & C), but absolute densities during this time period were low compared to the predicted densities from the first two temporal pulses.

Predicted log-transformed pollock egg density over time was also heterogeneous within each of the three areas examined in the area-dependent model (Fig. 7). In area A, temporal peaks were observed on 20 February (DOY 50) and 1 May (DOY 121), whereas peaks occurred on 15 March (DOY 74) and 10 May (DOY 130) in area B; both areas A and B had low predicted

Figure 7. Predicted log-transformed pollock egg densities (±95% confidence interval) in area A (a; waters of the Aleutian Basin and Aleutian Islands, including the Islands of Four Mountains and Bogoslof Island), area B (b; Unimak Pass eastward, including waters north of the Alaska Peninsula), and area C (c; waters around the Pribilof Islands) related to the day of the year, when all other covariates within the area are held constant.

egg density after 1 June (DOY 152; Fig. 7). We note that the eggs in the later peak in area A tend to be clustered farther inshore against the Aleutian Islands than in the earlier peak, when eggs were mostly over deep water. Mean predicted egg densities in Area C peaked on 20 April (DOY 110), 10 June (DOY 161), 20 August (DOY 232), and 1 October (DOY 274; Fig. 7) but there was substantial variation around the mean mostly as a consequence of the low sample size in this region and time of the year (Fig. 7).

DISCUSSION

Our analysis of 19 yr of ichthyoplankton data using generalized additive models showed that pollock eggs and larvae occurred in multiple spatially and temporally distinct concentrations in the eastern Bering Sea. Pollock eggs were the most spatially concentrated developmental stage, with centers of abundance occurring near Bogoslof Island, north of Unimak Island and along the Alaska Peninsula, and near the Pribilof Islands. More generally, our 'area-dependent' GAM approach may prove to be a valuable tool to understand the temporal and spatial patterns of spawning for marine fish in other systems.

Insight into pollock reproduction in the eastern Bering Sea can be obtained by assuming that the spatial and temporal distribution of pollock eggs represents actual spawning locations and timing. For instance, the addition of DOY as a covariate in our GAM models allowed for an examination of the temporal patterns of pollock spawning in the eastern Bering Sea, which broadly corroborates previous examinations of the timing of pollock spawning in the same area (e.g., Nishiyama and Haryu, 1981; Incze et al., 1984; Lynde, 1984; Hinckley, 1987; Dell'Arciprete, 1992; Jung et al., 2006). Two major temporal pulses of pollock eggs were observed, the first in February–March (DOY 50–90) and the second in April–May (DOY 110–140), but we also observed substantial fine-scale temporal variability in pollock egg density within each area of the eastern Bering Sea. Generally, spawning was initiated first at Bogoslof Island, then near Unimak Island, and finally around the Pribilof Islands.

Our results from the analysis of the ichthyoplankton data refine previous work on the spatial distribution of pollock spawning in the eastern Bering Sea obtained from other data sources (e.g., adult catches). For instance, Hinckley (1987) suggested that three spawning groups exist in the southeastern Bering Sea: the first in the Aleutian Basin, the second on the southeastern continental shelf and slope, and the third
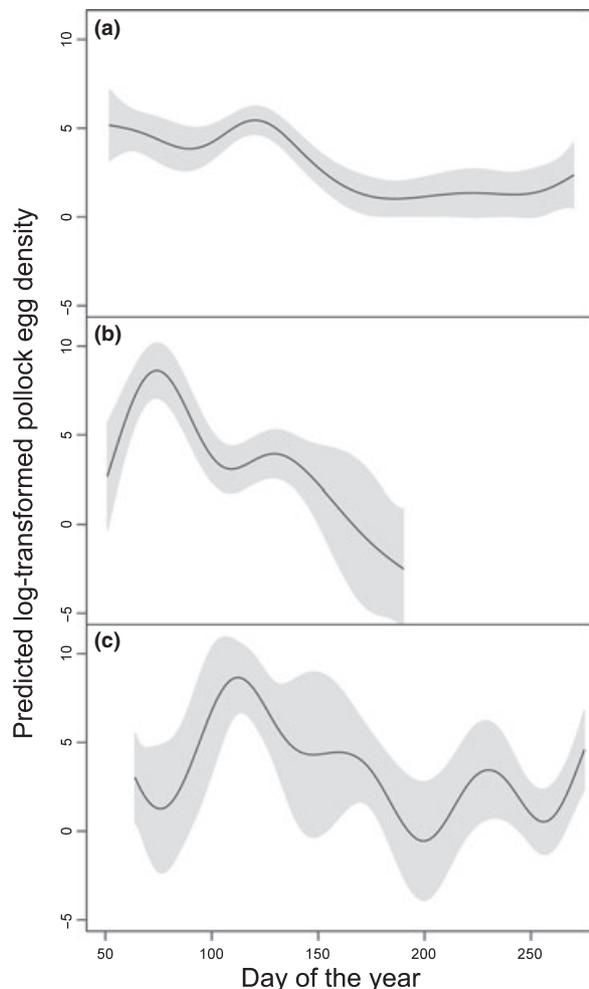
northwest of the Pribilof Islands. It appears that the main egg concentrations found in our study correspond primarily to her first and second groups, but our work also suggests that substantial fine-scale spatial structure of pollock spawning may exist within each of the broad groups defined by Hinckley (1987). Our results support previous work that found spawning concentrations of pollock eggs near Bogoslof and Unimak Islands (Nishiyama and Haryu, 1981; Lynde, 1984; Dell'Arciprete, 1992; Kim *et al.*, 1996; Jung *et al.*, 2006), but we also documented an additional spawning concentration around and slightly east of the Pribilof Islands. Two temporal peaks in egg distribution in the Aleutian Basin region may indicate two separate spawning populations there. It is notable that the first peak was associated with eggs over deep water in the Basin, and the second peak was formed from eggs found inshore near the Aleutian Islands. There is a possibility that eggs found near Bogoslof Island drifted toward Unimak Island and were part of the same spawning event. However, the hypothesis of a series of unique spawning events in each area is more plausible given the depth of eggs in the Basin (>300 m; Dell'Arciprete, 1992), the sluggish currents at those depths (about 1 cm s^{-1} or about 0.9 km day^{-1} transport; Cokelet and Stabeno, 1997), the break in egg distribution between these two aggregations (about 500 km in 1986; Fig. 3), and the higher density of eggs found downstream in area B (Fig. 6). Spawning schools have been observed in each area in acoustic surveys.

Density plots of raw pollock egg data showed a group of eggs north of the Islands of Four Mountains in area A, but this concentration disappeared in our GAM predictions. Further investigation determined that these eggs were caught during a single cruise on 21–26 February 1986 in a concentrated area. Given the limited samples collected in this region during February, it is difficult to draw conclusions about the importance of this potential spawning location of pollock. However, winter acoustic surveys indicate this is a region of consistent pollock aggregation (Honkalehto *et al.*, 2005). Future studies should attempt to determine the importance of this possible spawning location.

The fate of pollock eggs spawned near the Islands of Four Mountains and in the Bogoslof Island region remains unclear. The major temporal pulses of yolk-sac larvae corresponded well to the temporal pulses of eggs, assuming a time lag to account for assumed growth rates of pollock larvae in the eastern Bering Sea (Walline, 1985; Dell'Arciprete, 1992). Likewise, pollock first-feeding larvae showed slightly delayed

temporal pulses compared to yolk-sac larvae, also consistent with known growth rates. However, the first temporal pulse observed for eggs and smaller larvae, which corresponds to individuals caught around the Islands of Four Mountains or Bogoslof Island, was not observed for pre- and post-flexion larval stages. There are three potential explanations for this discrepancy. First, the spatial and temporal sampling effort in our study may have simply missed larger larval stages in this region. For instance, later-stage larvae may be advected in the strong Bering Slope Current to regions that have been historically under-sampled, such as northwest of the Pribilof Islands along the Bering Slope. Secondly, the single survey that sampled near the Islands of Four Mountains and Bogoslof Island may have terminated before the larvae spawned in this area had a chance to reach pre- or post-flexion stages. A third explanation is that larvae spawned in this area may have been spawned in an area unsuitable for good survival or advected into the Aleutian Basin or similar unfavorable habitats, where they might experience high mortality (Dell'Arciprete, 1992; Bailey *et al.*, 1997). Finally, they might have been advected onto the shelf where they would be diluted and difficult to sample, and their numbers overwhelmed by the much more abundant larvae from the shelf stock. Additional research or analyses are needed to elucidate the fate of pre- and post-flexion larvae originating from the Islands of Four Mountains and Bogoslof Island.

Analysis of the Aleutian Basin populations is more difficult now because these populations have been decimated. Reported harvests in the 'Donut Hole' region (located in international waters in the Aleutian Basin) totaled 1.4 million metric tons (mt) in 1987, but have been non-existent since 1994. In the Bogoslof area, catches peaked at 337 thousand tons in 1987 and the fishery stopped in 2004. In 2008, 8 tons were harvested (Ianelli *et al.*, 2008). Given the geographic discreteness of these areas, it seems likely they were once separate and important spawning areas but, due to lack of adults, larvae have not been captured by more recent ichthyoplankton surveys.

Discrete genetic stocks of pollock have not been observed to date within the eastern Bering Sea, implying some degree of historical mixing due to larval drift or migration and interbreeding of juveniles and adults among stock components (Shields and Gust, 1995; Bailey *et al.*, 1999; Olsen *et al.*, 2002). However, based on genetics, otolith microchemistry, and parasite studies, there is evidence for distinct spawning aggregations across broad geographic regions (e.g., Gulf of Alaska and the Bering Sea; eastern and western Bering Sea). Some aspects of the ecology of

pollock argue for limited genetic mixing between populations. For instance, histological evidence suggests that individual pollock have partially synchronous reproduction, bringing one discrete group of oocytes to maturation and spawning in successive batches over a period of days to weeks (Sakurai, 1982; Hinckley, 1987; Merati, 1993). Therefore, it is unlikely that pollock spawn in more than one area annually (Hinckley, 1987). It has been suggested that pollock are philopatric, showing fidelity to particular spawning grounds, despite broad movements of adults away from spawning grounds after reproduction (Dawson, 1994). Furthermore, meristic and morphometric measurements have indicated considerable fine-scale population structure in the eastern Bering Sea (Hinckley, 1987; Dawson, 1994) and elsewhere throughout their range (Iwata and Hamai, 1972; Koyachi and Hashimoto, 1977; Janusz, 1994). Our results suggest that, even though pollock spawn in discrete locations in space and time, some mixing may occur during the larval stage. Therefore, gene flow resulting from larval drift and mixing may be high enough to homogenize at least partially the genetic structure of pollock populations across the eastern Bering Sea, although subsequent natal homing may also counter such effects. Alternatively, the large contemporary population sizes of pollock may retard the effects of genetic drift in regions colonized, as the last major glaciations and the duration of stock separation may not be sufficiently long for significant genetic divergence to develop.

Pollock ichthyoplankton drift patterns were geographically variable and appear to be related to prevailing circulation patterns of the eastern Bering Sea. Larval drift towards the north or northwest was observed for pollock spawned near Bogoslof Island, likely because they became entrained in the Bering Slope Current that flows northwestward along the Shelf Slope (Dell'Arciprete, 1992; Stabeno *et al.*, 1999). Larvae spawned north of Unimak Island and in the southeastern Middle Domain appeared to be much more locally retained, drifting only very slowly eastward in the coastal current adjacent to the Alaska Peninsula (Bering Coastal Current) and northward in the weak currents over the middle shelf (Stabeno *et al.*, 1999). These results suggest that if larval drift is indeed the primary mechanism by which pollock genetic structure is homogenized, genetic stock structure may be more likely to exist where local retention of larvae appears to be more likely, such as around the Pribilof Islands (Stabeno *et al.*, 2008). Some eggs and larvae may be advected into the Bering Sea through Unimak Pass, a potential conduit for exchange

between the Gulf of Alaska and the Bering Sea (Lanksbury *et al.*, 2007; Duffy-Anderson *et al.*, in press). Water originating from the Gulf of Alaska and flowing through Unimak Pass moves northwards in winter and early spring, following the 100- and 200-m isobaths towards the Pribilof Islands. In late spring, however, flow through Unimak Pass is primarily deflected eastward along the 50-m idobath, becoming entrained in the seasonally established Bering Coastal Current (Kachel *et al.*, 2002). As such, some mixing of Gulf-spawned and Bering-spawned pollock larvae could occur, particularly over the Middle and Outer Domains, although the influx would be extremely low relative to larvae of Bering Sea origin.

Our conclusions depend on several key assumptions. First, we assume that the sizes and number of pollock eggs and larvae caught were similar across the three sampling gears employed in this study. Generally, sampling differences among these gears appear to be relatively minor for pollock eggs and larvae (Shima and Bailey, 1993) and should not strongly influence our conclusions. Secondly, we assume that the location and timing of egg collections can be used to infer spawning in space and time. Increased resolution of pollock spawning concentrations would have occurred if eggs had been staged and only the earliest egg stages had been used to define spawning concentrations (e.g., Jung *et al.*, 2006). However, given moderate mortality rates (0.2 day^{-1}) for pollock eggs, 82% of the eggs in the water column would be expected to be 3 days old or less, and 99% would be younger than 7 days old. Thirdly, we assume that sampling has occurred at all major spawning areas in the eastern Bering Sea, which is likely the case given the considerable number of samples taken throughout the eastern Bering Sea over the course of this study. Fourthly, we assume that the removal of samples with zero catch did not bias our GAM results. Zero values may include both 'true zeros', where eggs or larvae are absent, and 'false zeros', where eggs or larvae were present but missed by the sampling gear. Our particular study appeared robust to the exclusion of zero data, given that a binomial model built upon the presence–absence of pollock egg data produced very similar results as our model that excluded zero catches. Lastly, by combining data across 19 yr, we assume that interannual differences in the timing and locations of spawning are negligible. If interannual differences in spawning did exist, they would tend to obscure overall trends in spatial and temporal concentrations.

High-latitude ecosystems like the Bering Sea respond to climate variability on both short-term and long-term time scales (Overland and Stabeno, 2004;

Grebmeier *et al.*, 2006; Stabeno *et al.*, 2007). Although we are beginning to understand how environmental variability affects the broad-scale distribution patterns of fish in the eastern Bering Sea (e.g., Wyllie-Echeverria and Wooster, 1998; Mueter and Litzow, 2008), very little is known about its effects on the spatial and temporal patterns of fish spawning. This is unfortunate because spawning geography and phenology are important indicators of the health of a stock. Well-recognized stock collapses around the world have been anticipated by dramatic shrinkages of spawning distribution (Atkinson *et al.*, 1997; McFarlane *et al.*, 2002). Also, spawning distribution can reveal the degree of structure within a stock and the starting locations of drift pathways. Ciannelli *et al.* (2007) showed that pollock spawning in the nearby Shelikof Strait, Gulf of Alaska, occurred earlier and towards shallower water after the late 1980s. Furthermore, Ciannelli *et al.* (2007) noted concomitant increases in egg densities in secondary spawning areas along the shelf and slope west of the Shelikof Strait. It is unclear whether these changes were the result of intense harvesting on primary spawning locations or the result of environmental variability. Likewise, understanding the geography and phenology of pollock spawning in the eastern Bering Sea and its changes through various harvesting and environmental regimes will be an important topic as attempts are made to manage this ecologically and economically valuable species in the face of environmental change.

ACKNOWLEDGEMENTS

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