

# Phenological and geographical patterns of walleye pollock (*Theragra chalcogramma*) spawning in the western Gulf of Alaska

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**Abstract:** Over 20 years of egg sampling data were used to reconstruct the geographical and phenological patterns of walleye pollock (*Theragra chalcogramma*) spawning aggregations in the Gulf of Alaska (GOA). The analyzed time series (1972, 1978–1979, 1981–2000) included a documented event of climate change (i.e., 1988–1989) and the rise and fall of the GOA pollock population abundance and harvests. We compared results from two generalized additive model (GAM) formulations: one assuming no change of egg distribution and phenology over the examined time series (stationary) and the other admitting such changes (nonstationary) across an epoch determined from the data. Results from both model formulations corroborate the existence of a high egg concentration in Shelikof Strait, historically the primary spawning area of pollock in the GOA. However, model results also highlight the presence of other secondary, and possibly transitory, centers of egg distribution at various locations along the shelf and slope regions of the GOA. In addition, results from the nonstationary (and statistically superior) formulation indicate that the abundance of the non-Shelikof aggregations has increased over time, along with a tendency for earlier occurrence and displacement toward shallower areas of the high egg density regions.

**Résumé :** Nous avons utilisé des données d'échantillonnage des oeufs sur plus de 20 ans pour reconstituer les patrons géographiques et phénologiques des rassemblements de fraye de la goberge de l'Alaska (*Theragra chalcogramma*) dans le golfe de l'Alaska (« GOA »). Les séries chronologiques analysées (1972, 1978–1979, 1981–2000) incluent un épisode bien documenté de changement climatique (soit en 1988–1989), ainsi que la croissance et le déclin de l'abondance et des récoltes de goberges dans le GOA. Nous comparons les résultats provenant de deux formulations du modèle additif généralisé (« GAM »), l'une (stationnaire) qui ne présuppose aucun changement dans la répartition et la phénologie des oeufs dans la série chronologique examinée, alors que l'autre (non stationnaire) permet de tels changements sur une période déterminé à partir des données. Les résultats des deux formulations du modèle corroborent l'existence d'une forte concentration d'oeufs dans le détroit de Shelikof, qui est historiquement le principal site de fraye de la goberge dans le GOA. Cependant, les résultats du modèle soulignent aussi la présence d'autres centres secondaires, et peut-être transitoires, de répartition des oeufs à différents points dans les régions du plateau et du talus continentaux du GOA. De plus, les résultats de la formulation non stationnaire (plus robuste statistiquement) indique que l'abondance des rassemblements autres que celui de Shelikof a augmenté au cours des années, qu'il y a une tendance pour que ces rassemblements aient lieu plus tôt et qu'il y a un déplacement des régions de forte densité des oeufs vers des sites moins profonds.

[Traduit par la Rédaction]

## Introduction

Marine fish are for the most part oviparous with external fertilization, and to successfully reproduce, they depend on a series of reliable cues (timing) and clues (location) allowing them to gather in large numbers at the same site and time. The processes affecting the timing (phenology) and the location (geography) are scientifically intriguing and poorly un-

derstood (Cury 1994). Moreover, for commercial marine species, the spawning site is often the location where the harvests and assessment surveys occur, having critical management implications for understanding the phenology and geography of fish spawning habits.

The objective of this study is to characterize spawning aggregations of walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska (GOA, from Kodiak Island to

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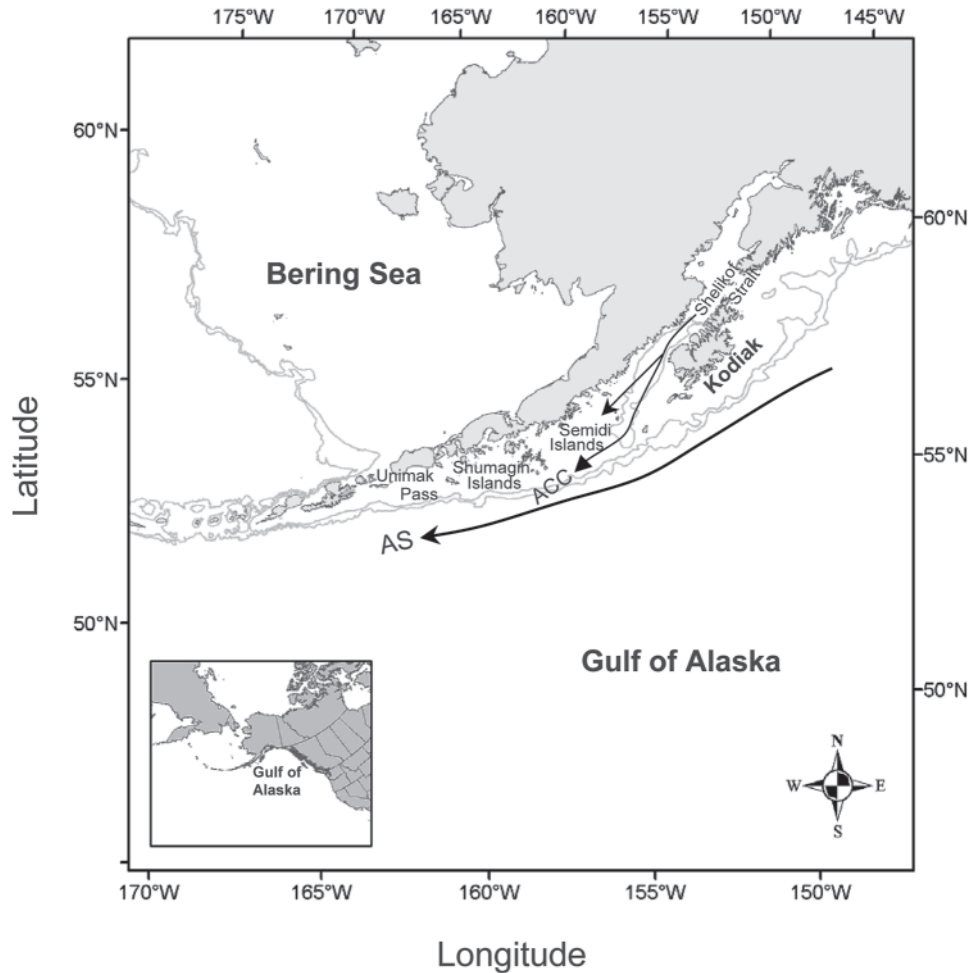
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**Fig. 1.** Gulf of Alaska (GOA) with the location of the Shelikof Strait, the primary walleye pollock (*Theragra chalcogramma*) spawning site in the GOA. Primary ocean currents are also marked (ACC, Alaska Coastal Current; AS, Alaska Stream). The bathymetry lines refer to 200 m and 1000 m.



Unimak Pass), where the bulk of the entire Gulf pollock resides. This is accomplished by an analysis of the egg distribution data during a period (late 1970s to 2000) that included a documented event of climate change (i.e., 1988–1989; Hare and Mantua 2000) and the rise and fall of the GOA pollock population and harvest. Walleye pollock currently constitutes the second-largest single-species fishery in the world (State of World Fisheries and Aquaculture (SOFIA) 2004). Most of the landings come from the Okhotsk Sea and Bering Sea, but a large pollock stock, at present estimated to be slightly over 200 000 tonnes (spawning biomass), is present in the GOA (Dorn et al. 2002). In the past this fishery has supported harvests exceeding 300 000 tonnes.

Historically, pollock has spawned during a 2-week period at the end of March and the beginning of April in the Shelikof Strait, between Kodiak Island and the Alaska Peninsula (Fig. 1; Kendall et al. 1996). Through the last decade, however, spawning in the Shelikof Strait has greatly declined (Dorn et al. 2002). The decrease may in part be explained by an overall co-occurring decline of the pollock population. However, in other areas along the Alaska Peninsula (Dorn et al. 2002) and in coastal areas (Anderson and Piatt 1999), pollock biomass has actually increased, suggesting that

along with a decline of the Shelikof population, either a shift of adult distribution or changes in local population abundances may have occurred.

Pollock ichthyoplankton surveys in the GOA have taken place since the 1970s, and although the spatial and temporal coverage has not been consistent (see Discussion), these data offer a unique opportunity to reconstruct the spawning location of adult pollock during a period in which potential changes in spawning habits may have occurred. For the purpose of analyzing the pollock egg distribution, we developed an innovative model framework that allows for changes in spatial and temporal patterns of the density data. Such a framework could be readily applied to other systems in which the interaction between spatial and temporal dynamics is of interest or to detect changes in species distribution in relation to contrasting environmental regimes.

## Material and methods

### Data collection

The data analyzed in this study consist of pollock egg density (numbers·10 m<sup>-2</sup>), collected during the ichthyoplankton surveys of the Alaska Fisheries Science Center (AFSC, Seattle, Washington) in the GOA. We define spawning loca-

**Table 1.** List of nonzero sample size ( $N$ ), start and end date (month/day), and minimum and maximum longitude (degrees west) and latitude (degrees north) of the full egg data for each year included in the analysis of walleye pollock (*Theragra chalcogramma*) egg distribution.

Year	$N$	Start date	End date	Minimum longitude	Maximum longitude	Minimum latitude	Maximum latitude
1972	21	04/29	05/09	156.40	150.12	53.33	58.78
1978	24	03/31	04/16	155.42	150.62	55.95	58.96
1979	14	05/16	05/23	161.64	150.15	54.54	59.00
1981	297	03/18	05/28	162.25	151.50	54.05	58.33
1982	93	04/05	05/30	164.40	152.07	54.03	57.88
1983	16	05/21	05/25	157.35	154.63	56.01	57.26
1984	134	04/04	05/04	159.01	147.00	54.67	59.87
1985	324	03/18	05/28	157.99	148.62	55.32	59.21
1986	245	04/05	05/18	165.58	141.35	53.66	59.95
1987	171	04/04	04/27	165.08	147.75	53.66	59.67
1988	258	03/24	04/12	164.33	147.67	54.00	59.67
1989	302	04/06	05/16	157.48	152.06	55.78	58.64
1990	185	04/08	05/30	157.46	153.00	56.03	58.68
1991	328	04/02	05/25	158.55	147.84	54.48	59.78
1992	214	04/06	05/28	158.61	153.64	55.38	58.37
1993	201	04/06	05/30	157.93	153.09	55.06	58.47
1994	161	03/18	05/30	159.97	153.10	55.10	58.61
1995	53	05/21	05/28	163.51	154.78	54.25	57.71
1996	285	04/28	05/30	164.72	147.93	54.04	59.82
1997	38	05/24	05/30	158.60	153.50	55.57	58.34
1998	102	05/03	05/28	158.38	153.94	55.34	58.09
1999	65	05/22	05/30	164.72	154.59	54.17	57.73
2000	26	05/26	05/30	164.71	156.69	54.17	56.82

tions and timing based on the spatial and temporal distribution of pollock eggs. Data on walleye pollock eggs were extracted from the Ichthyoplankton Cruise Database (IchBase), which encompasses a 30-year time series of ichthyoplankton data from cruises during 1972–2000 conducted by AFSC and partner institutions in the Gulf of Alaska (methods detailed in Matarese et al. 2003). In April and early May surveys, a 333 mesh on bongos and Tuckers was used to avoid extrusion of yolk-sac larvae, and in late May, a 505 mesh was used to avoid net clogging from algae. Use of these different meshes has no material impact on sampling of eggs because of their relatively large size and the hard chorion that prevents extrusion. All tows were quantitative and oblique, conducted in a standardized manner using flowmeters. If bottom depth was less than 200 m, then the tows were made up to 10 m off the bottom. Otherwise the tow was stopped at 200 m. Catches were preserved in 5% formalin and returned to the laboratory. They were sorted, identified to species, and measured at the Plankton Sorting and Identification Center, Szczecin, Poland. Ichthyoplankton identifications were verified by the taxonomic team at AFSC. The sampling grid spanned the entire shelf region of the western GOA, from Unimak Pass to the southwest and to the mouth of Cook Inlet to the northeast. However, because of the common belief that pollock spawning was consistently located in the Shelikof Strait, sampling has been more intense in this area.

Ichthyoplankton sampling in the GOA started in 1972 and continues to this day. However, in our analysis, we limit our study to the 1972–2000 period. Before 1981, only the following years were sampled: 1972, 1978, and

1979. After 2000, most of the sampling only occurred later in the year and was focused on larvae. In some years there was more than one survey. To allow a comparable temporal and depth coverage among years, we only included tows spanning from the 75th to the 150th Julian day and over depths of 33–403 m, the range that should largely include the bulk of pollock spawning activity in the GOA (Table 1).

In defining spawning locations from the full egg data, we implicitly assume that the diffusion and drift of eggs from the spawning event to the time of the catch are negligible. The Alaska Coastal Current (ACC) is primarily responsible for the drift of pollock eggs and larvae in this region. However, the ACC is a surface current (<60 m depth) and thus is not likely to generate a wide spatial displacement of eggs, which are located at greater depths, particularly during the very early stages (Kendall and Kim 1989).

#### Data analysis

We used generalized additive models (GAM) to inspect the patterns of pollock egg density in the GOA. Samples with no eggs (zero density) were removed from the analysis, and the remaining data were log-transformed to normalize the distribution and reduce heteroscedasticity. The independent variables (hereon covariates) were the position of the sampling defined by latitude and longitude, the natural logarithm of bottom depth in metres, and the Julian day of the catch. Bottom depth was log-transformed to allow a uniform distribution throughout the sampled depth range. The Julian day and the positional effects are also included to correct for differences in timing and location of sampling among years.

The analyzed egg data contained 3557 observations collected over 23 years, with an average number of 154 non-zero observations per year (Table 1).

We compared two different model formulations: one assuming no changes of egg distribution and timing over years (stationary spawning pattern and stationary model) and the other assuming a change in egg distribution and timing occurring during an epoch to be determined from the data (nonstationary spawning pattern and nonstationary model). Specifically, let  $x_{t,y,(\phi,\lambda)}$  be the natural logarithm of egg density at time  $t$  (time expressed in Julian day), year  $y$ , latitude  $\phi$ , and longitude  $\lambda$ . Let  $b_{(\phi,\lambda)}$  be the log-transformed bottom depth. The stationary model can be written as follows:

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

where  $e_{t,y,(\phi,\lambda)}$  is a random error assumed to be normally distributed with zero mean and finite variance,  $a_y$  is an intercept allowed to change for every year included in the analysis, and the  $g$ s are nonparametric smooth functions. In words, the model in eq. 1 assumes that the egg density at a given time of the year ( $t$ ), year ( $y$ ), and location ( $\phi,\lambda$ ) is a function of position, bottom depth, and time of the year. Furthermore, the model in eq. 1 assumes that these effects are constant throughout the sampling period, and any source of variability at a given location, depth, and time is solely due to the overall variation of yearly mean egg density (i.e., spawning output). The standard error estimates of the egg density predictions on a natural logarithmic scale are representative of the coefficient of variability (standard deviation over average) on the untransformed scale (Lewontin 1966). Thus, standard error estimates are here shown as an indication of the temporal variability of the spawning activity in the examined location.

The nonstationary model has the following formulation:

$$(2) \quad x_{t,y,(\phi,\lambda)} = \begin{cases} a_y + g_{1,1}(\phi,\lambda) + g_{2,1}(b_{(\phi,\lambda)}) + g_{3,1}(t) + e_{t,y,(\phi,\lambda)} & \text{if } y \leq y^* \\ a_y + g_{1,2}(\phi,\lambda) + g_{2,2}(b_{(\phi,\lambda)}) + g_{3,2}(t) + e_{t,y,(\phi,\lambda)} & \text{if } y > y^* \end{cases}$$

In contrast to the stationary model (eq. 1), in the nonstationary model the functions that link the egg density with location, bottom depth, and time of the year are allowed to change over two contrasting temporal periods. The two periods are separated by the year  $y^*$  to be determined from the data. It is important to note that given  $y^*$ , the model in eq. 2 becomes a fully additive formulation of the following type:

$$(3) \quad x_{t,y,(\phi,\lambda)} = a_y + g_{1,1}(\phi,\lambda)(1-u_y) + g_{2,1}(b_{(\phi,\lambda)})(1-u_y) + g_{3,1}(t)(1-u_y) + g_{1,2}(\phi,\lambda)u_y + g_{2,2}(b_{(\phi,\lambda)})u_y + g_{3,2}(t)u_y + e_{t,y,(\phi,\lambda)}$$

where  $u_y$  is an indicator variable with a value of either 0 or 1, depending on whether the year  $y$  is  $\leq$  or  $>$  than  $y^*$ , respectively. In both models 1 and 2, the one-dimensional effects ( $g_2$  and  $g_3$ ) are fitted by natural cubic splines (Wood 2004), whereas the two-dimensional effect ( $g_1$ ) is fitted with thin plate splines (Wood 2003).

The search for the threshold year ( $y^*$ ) is done by adopting the approach described in Ciannelli et al. (2004) and Stenseth et al. (2006). In brief, the model in eq. 3 is fit for as

many threshold years as there are years in the temporal range included in the analysis, except for those cases that resulted in having less than 10% of the data samples in each period. The final threshold year ( $y^*$ ) corresponds to that of the model with the lowest generalized cross-validation (GCV) score, a measure of the predictive squared error of the fitted model (Green and Silverman 1994).

The resulting nonstationary model is then compared with the stationary model (eq. 1) using the genuine CV score. Essentially, the CV measures the out-of-sample predictive error of the model and in the present application is determined as follows. A random sample of 200 observations (greater than the average of the sampled stations in each year) is excluded from the data set. The remaining observations are used to fit a stationary (eq. 1) or nonstationary (eq. 3) model with a variable threshold ( $y^*$ ) to be determined from the routine explained above. The so-found models are then used to predict the value of the out-of-sample 200 data cases and the relative mean squared prediction errors. This routine is repeated 500 times, with the final genuine CV of each model being the average of the 500 realizations. All the analyses were carried out in R, using the "tgam" library (developed by K.S. Chan).

### Corroborative analysis

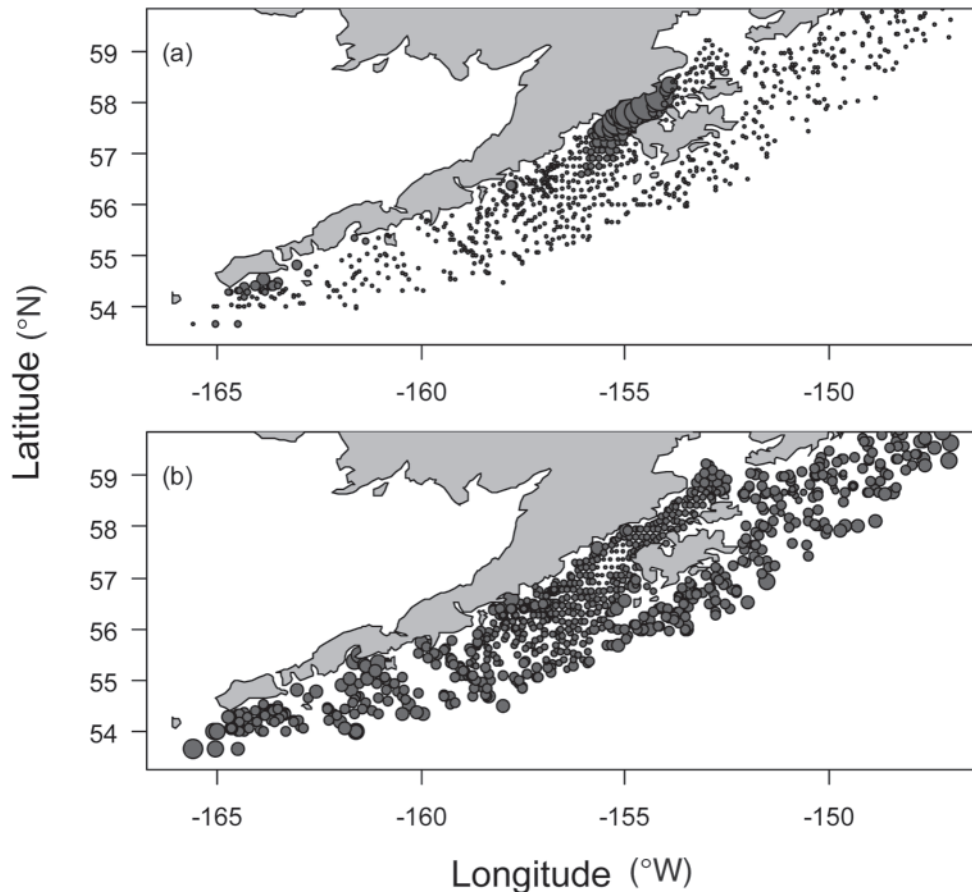
A potential problem of the egg distribution data was posed by the uneven temporal and spatial sampling coverage of the field data. In particular, in later years, sampling occurred primarily in the latter part of the year (i.e., after the end of April) and was focused in the Shelikof region (Table 1). Consequently, there were fewer samples available in the southwestern part of the Alaska Peninsula, particularly early in the year. To ensure that the results from the nonstationary model were not due to a change in sampling coverage, we performed a bootstrap analysis to assess the probability of detecting a nonstationary egg pattern from an underlying stationary egg distribution with uneven sampling coverage. The analysis was developed as follows. The estimated stationary egg model (eq. 1) was used to predict the egg density at the same time and locations of the full egg data. Within each year, scaled residuals from the nonstationary model were randomly added to these predictions. We refer to the newly predicted egg distribution as the simulated egg data to differentiate it from the full egg data derived from the field samples. Both the stationary (eq. 1) and nonstationary (eq. 2) models were fitted to the simulated egg data, and the difference between the two models' GCV (DGCV\*) was obtained. The same operation on the simulated egg data was repeated 1000 times to obtain 1000 DGCV\*. A similar difference was also obtained from the models fitted to the full egg data (DGCV). Finally, the probability of predicting a false nonstationary egg distribution pattern from an underlying stationary process was determined as the fractions of the DGCV\* being greater than the DGCV.

## Results

### Egg density and distribution

The stationary model (eq. 1) revealed significant effects from position, bottom depth, and time of the year on the dis-

**Fig. 2.** Predicted pollock (*Theragra chalcogramma*) egg density from (a) stationary (eq. 1) and (b) associate standard error estimates on the 100th Julian day. To improve clarity only a random subset of all available predictions is shown for the Shelikof region. Model predictions are scaled back to the actual units (i.e., number of eggs·10 m<sup>-2</sup>), whereas standard error estimates refer to the transformed logarithm units and approximately equal the coefficient of variation in the actual scale (i.e., standard deviation over mean; Lewontin 1966).



tribution of pollock eggs. The model explained 79.9% of the observed variance and had a genuine CV score of 1.736. The bulk of the egg density was predicted to occur in the Shelikof Strait region (Fig. 2). However, additional and secondary (in terms of density) centers of egg distribution were also identified in various locations along the Alaska Peninsula, e.g., Unimak Pass and the Shumagin and Semidi islands. Typically, the predictions in the Shelikof region had the lowest standard error, indicating a greater interannual stability of spawning activity, whereas around the Shumagin Islands and Unimak Pass and in various locations over the shelf break, the standard error was larger (Fig. 2). In line with previous studies on pollock spawning behavior, the timing of the egg density peaked between the 90th and the 110th day of the year (corresponding to 30 March – 19 April; Fig. 3), with an additional peak of minor intensity around the 140th day of the year (19 May). The bottom depth had a positive effect on egg density, with peaks at depths greater than 240 m (Fig. 3).

The GCV profile of the nonstationary egg model (eqs. 2 and 3) had a unique minimum between the years 1989–1990, indicating a change in egg distribution during that time (Fig. 4). Model predictions indicated that after 1989, the Shelikof Strait was no longer the only primary center of pollock egg density. In fact, comparable egg densities were

also predicted to occur along the Alaska Peninsula, particularly in the region of Unimak Pass (Fig. 5). The predicted effects of sampling day and depth also changed over these two periods. After 1989, egg densities increased earlier in the year and at shallower depths compared with pre-1989 estimates (Fig. 6). The described nonstationary model explained 82.4% of the observed variance in egg density and had a genuine CV of 1.556, a noticeable improvement over the stationary model.

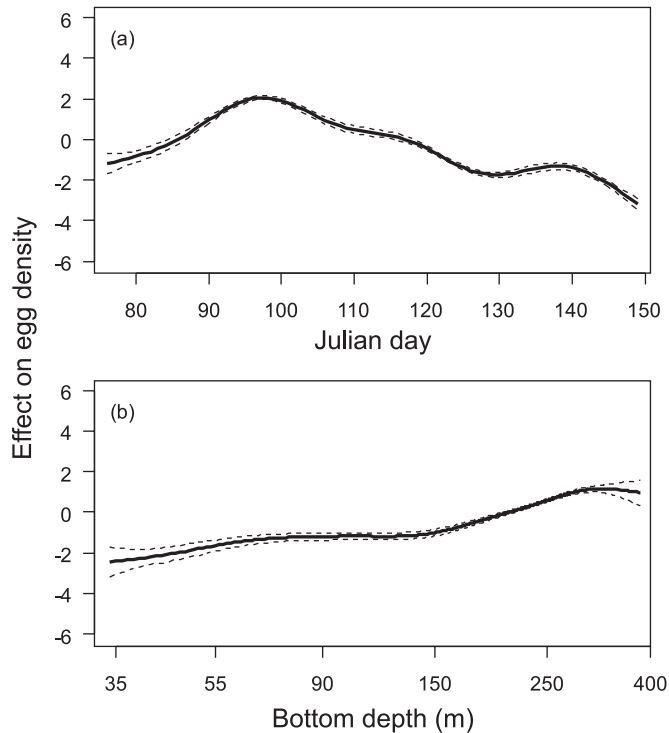
#### Corroborative analysis

The difference in GCV between the stationary and the nonstationary egg models (DGCV) was 0.201. The same difference averaged over 1000 realizations of the simulated egg data (DGCV\*) was -0.021. The probability of DGCV\* being greater than DGCV was <<0.001, indicating that the observed nonstationary egg pattern was not driven by the uneven sample distribution.

#### Discussion

While our analysis corroborates the existence of a high pollock egg concentration in Shelikof Strait, it furthermore highlights the presence of other secondary centers of egg distribution at various locations along the shelf and slope.

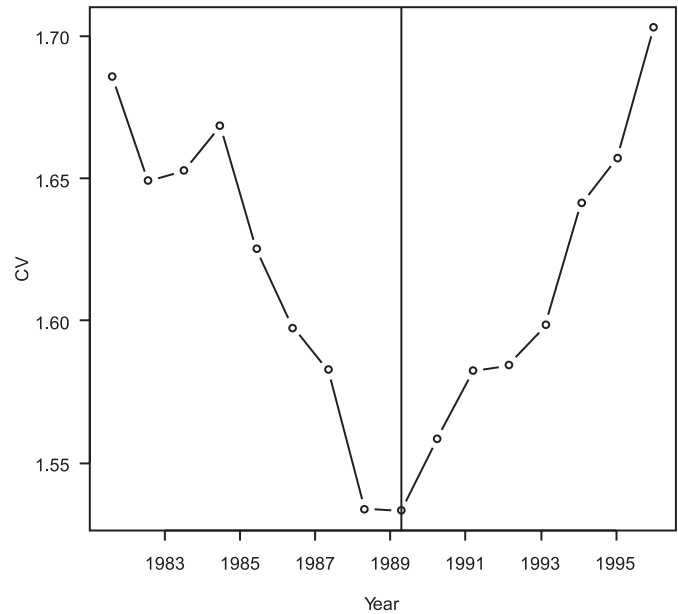
**Fig. 3.** Effects of (a) Julian day and (b) bottom depth on pollock (*Theragra chalcogramma*) egg density, as predicted from the stationary model. Values on the y axis indicate the effect of the x-axis covariate on the egg densities anomalies (i.e., egg density minus mean). Model predicted values are given by the sum, at corresponding locations, of all covariate effects with the yearly intercept (see eq. 1). The broken lines indicate the point-wise 95% confidence interval.



These may be viewed as ephemeral or less stable spawning areas owing to the large error estimates. The presence of multiple centers of egg distribution also suggests the presence of multiple spawning locations and ultimately some degree of structure within the pollock spawning populations in the GOA. While the importance of the Shelikof spawning locations has been consistent over time, that of the secondary locations has become more apparent only in recent years. The geographical lability of the secondary spawning locations compared with the consistency of the Shelikof location indicates that the pollock populations of the GOA use different clues to determine where to spawn. Some of these clues must be consistent over time, like those in Shelikof, whereas others may be more ephemeral, like those corresponding to secondary spawning locations.

Several gadoid populations have complex spawning geography. Pacific hake (*Merluccius productus*) is one of them, with offshore populations that shift spawning location with environmental conditions and genetically distinct nearshore populations that spawn in fixed locations (Bailey et al. 2004). Atlantic cod (*Gadus morhua*) stocks along the Norwegian coast are another example, being comprised of genetically distinct offshore and coastal spawning populations, with the latter being more consistent in their spawning habits (Knutsen et al. 2007). Therefore, like hake and cod, offshore spawning stocks of pollock, such as those sometimes observed in deep troughs offshore from Kodiak Island or over

**Fig. 4.** The genuine cross-validation (CV) profile resulting from the application of the nonstationary egg distribution model. The vertical line indicates the year at which the CV reached the minimum value, corresponding the predicted year of change in pollock (*Theragra chalcogramma*) egg distribution.

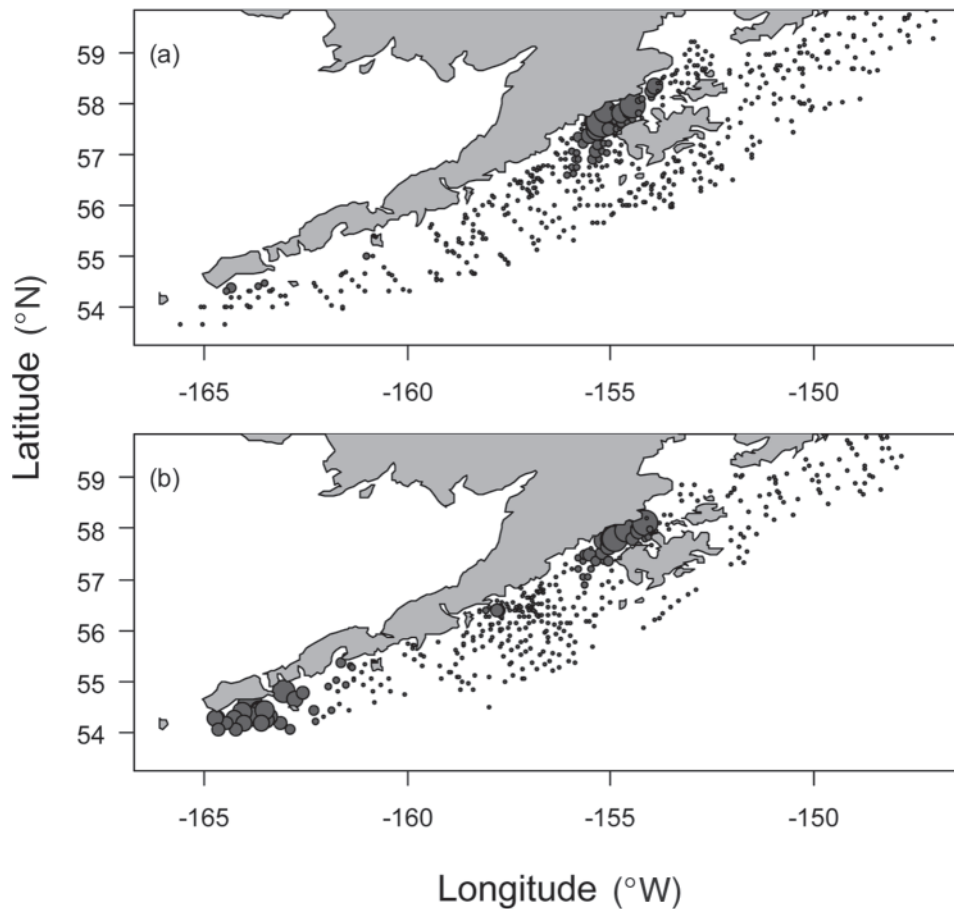


deep oceanic water, may be “environmentally fixated” and coastal spawning populations may be “geographically fixated”, thus demonstrating remarkable behavioral flexibility within a species.

Our findings raise the interesting question as to what caused the change in relative egg abundance between Shelikof and non-Shelikof spawning sites. Several hypotheses are being discussed. At the end of the 1980s, in the North Pacific, there was an overall cooling of the sea surface temperature (Hare and Mantua 2000). The change of climate was short-lived, reversing to pre-existing conditions within 3–4 years (Bond et al. 2004). The temporal coincidence of the change in pollock egg distribution with the climate change suggests that pollock may have altered their homing habits in response to the changed environmental conditions. However, such a hypothesis does not explain why pollock has not reverted to the original spawning habits once the climate condition reversed. Thus, although a portion of the entire pollock stock residing in the western GOA may change spawning location according to environmental clues, another, and probably greater portion, may orient on different clues.

Homing strategies based on behavioral and social interactions (e.g., McQuinn 1997; Corten 2002) are other likely mechanisms to explain the observed change of pollock egg distribution in the GOA. In the early 1980s, pollock catches reached record levels, particularly in the Shelikof Strait, owing to the development of a pollock roe fishery. In those years, the fishery was mainly targeting the very strong cohorts of the late 1970s (e.g., the very strong 1978 year class was age 6 in 1984 and age 7 in 1985 and formed the bulk of the 1984–1985 catches). Expectedly, estimates of the returning mature individuals (>age 6) in the Shelikof area dropped dramatically after 1984–1985, and with them also the “tradi-

**Fig. 5.** Predicted pollock (*Theragra chalcogramma*) egg density from the nonstationary model (a) before and (b) after 1989, the estimated year of change in egg distribution. To improve clarity, only a random subset of all available predictions is shown for the Shelikof region. All model predictions are scaled back to the actual units (i.e., number of eggs·10 m<sup>-2</sup>) and were referred to the 100th Julian day.



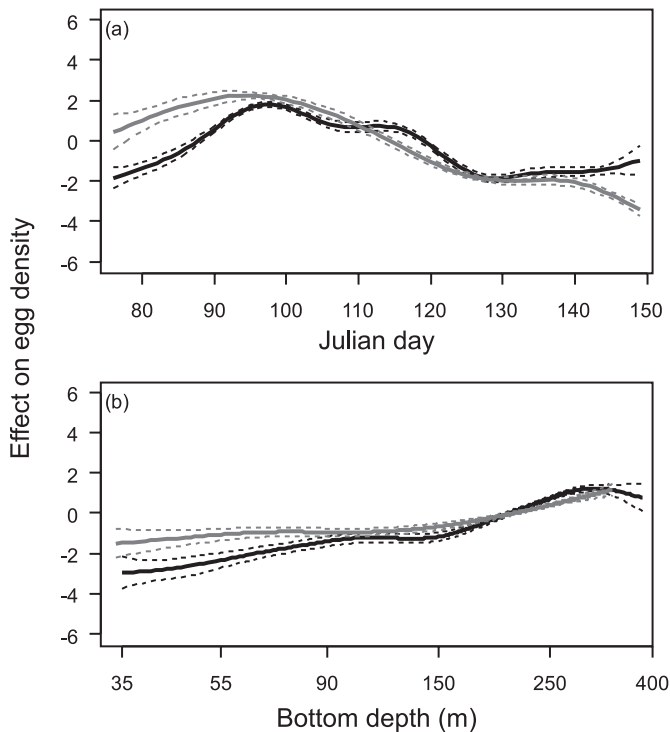
tion” to home in Shelikof may have been severely reduced. Thus adult pollock from other spawning regions may have entrained newly matured individuals toward other spawning locations. Although appealing, the described hypothesis is not definitively supported by our data and does not exclude the existence of other mechanisms (e.g., loss of genetic diversity).

An alteration in the relative abundance of various genetically distinct subpopulations is also likely to explain changes of spawning patterns. Indeed, loss of the genetic memory of a population driven to extinction would result in the loss of that spawning population over any practical sense of time. A genetically fixed homing strategy, coupled with the presence of multiple spawning locations, also implies the existence of several genetically distinct stocks, strong natal homing, and the existence of larval retention areas that limit the extent of larval drift and mixing among stocks (MacLean and Evans 1981; Iles and Sinclair 1982). The evidence gathered so far on pollock is conflicting about whether genetically distinct populations occur in the GOA (Bailey et al. 1999; O’Reilly et al. 2004). Also, no genetic stock analysis has been done on fish from the Shumagin and Unimak areas. The flow pattern of the Alaska Coastal Current supports the persistence of temporally consistent and predictable larval retention areas (Bailey et al. 1997). Eddies and fronts in the

Shelikof region tend to locally retain larvae. On the other hand, eggs spawned in the Shumagin Island region are apparently not retained in the local area (Dougherty et al. 2007). Otolith microchemistry analyses on the GOA pollock have indicated that larval pollock experience different water masses during their early ontogeny (Fitzgerald et al. 2004), further corroborating the existence of multiple spawning aggregations. Indeed, more genetic and otolith analyses on samples from different regions within the GOA during various life stages would be instrumental to better understand the interplay between population structure and spawning aggregations in this area.

Some discussion of the data limitation is appropriate. Over time the egg survey has shifted somewhat to primarily occur in the later part of the year (after mid-April). Thus we cannot completely rule out the possibility that the reported transition of egg distribution was caused by the uneven sampling scheme. However, the result of the corroborative analysis poses more evidence toward a real shift in egg distribution rather than an outcome of the sampling scheme. Furthermore, field data on adult individuals also corroborates the occurrence of a real change in spawning patterns. For example, although the GOA acoustic survey detected a sharp decline of adult pollock in the Shelikof Strait, the catches from the coastal surveys of the Alaska Department

**Fig. 6.** Effects of (a) Julian day and (b) bottom depth on pollock (*Theragra chalcogramma*) egg density, as predicted from the nonstationary model. In each panel, the black line indicates the effect before 1989, whereas the shaded line indicates the effect after 1989. Values on the y axis indicate the effect of the x-axis covariate on the egg densities anomalies (i.e., egg density minus mean). Model predicted values are given by the sum, at corresponding locations, of all covariate effects with the yearly intercept (see eq. 3). The broken lines indicate the point-wise 95% confidence interval.



of Fish and Game have remained fairly constant (Dorn et al. 2002). Similarly, since the end of the 1980s, the small mesh survey conducted by the AFSC detected an increase of pollock biomass in coastal areas (Anderson and Piatt 1999) — an increase that persists. Finally, it is important to realize that the reported shift of egg distribution was not only the result of a change in the spatial pattern, but also in the timing of egg abundance. It is hard to imagine how a progressive delay of the survey could have caused earlier peaks of egg density in more recent years. Thus, it is more likely that the uneven sampling coverage has hampered the full detection of the shift in egg distribution, rather than generating it.

This data set, as typical of many other marine and terrestrial sampling data sets, is characterized by an inflation of zero counts (zero-inflated counts), which are hard to categorize within the available statistical distribution families and may also bias variance estimates and inferences (Welsh et al. 1996). In our analysis, we only modelled the nonzero counts for two reasons. First, we were mainly interested in locating “centers” of pollock egg abundance, i.e., locations where egg density is higher than the average background value. In such circumstances, the removal of zero egg tows (located primarily in areas or times of the year of consistently scarce eggs) should not affect the end results. Second, because of

the protocol adopted to sort the ichthyoplankton samples, our data set is comprised of egg density values rather than egg counts. Thus we could not use exponential distribution families that allow overdispersion (e.g., Poisson, negative binomial). A typical approach used to model zero-inflated data, also known as two-step approach or conditional modeling, is to first model the presence-absence using a binomial distribution and then to model the abundance conditional on the presence using, for example, a truncated Poisson or negative binomial distribution (Welsh et al. 1996). Fox et al. (2000), among others, used the two-step approach to model distribution of fish eggs. Although the two-step approach retains the information carried by the zero counts and produces unbiased predictions, it makes inference rather complicated as there are two sets of environmental effects to consider, those from the presence-absence and those from the abundance model, often with contradictory results (Barry and Welsh 2002). In our specific case, the use of a binomial distribution family for modelling the presence-absence of pollock egg limits our ability to detect shifts in centers of egg pollock distribution. In fact, the likelihood of finding eggs in a high density region may change little over time, whereas the abundance may change substantially. In spite of these considerations, it is still recommendable that a method be developed to model zero-inflated counts in future applications. Ideally, such a method should be continuous (i.e., applicable to noncount data), nonlinear, and nonadditive. The recent work by Rigby and Stasinopoulos (2004) extends the GAM to the so-called GAMLSS (generalized additive models for location, scale, and shape) that allows these more general conditional response distributions. An advantage of the GAMLSS is that, unlike the popular two-stage estimation strategy that uses the zero and the non-zero data separately, it facilitates a coherent inference with the entirety of the zero-inflated data.

Regardless of the ecological mechanisms that caused a change of pollock egg distribution in the GOA, its occurrence can have repercussions on the survival of the early life stages and on recruitment success. For example, the consistency of spawning activity in the Shelikof region is the result of locally and consistently favorable physical and biological features. In contrast, the probability of survival success of pollock eggs spawned in non-Shelikof regions may be more dependent on ephemeral environmental conditions and may represent a bet-hedging strategy of the species. In the Shelikof Strait, favorable features include a deep trench (the Sea Valley) that cuts into the shelf and extends to the Strait and the presence of the nutrient-laden southwestward-drifting ACC. The presence of the deep trench allows pollock embryos to reside in relatively deep waters where they can find favorable thermal and density environments (Kendall and Kim 1989). The presence of the ACC favors egg and nonfeeding larval advection towards productive nursery areas along the Alaska Peninsula (Hinckley et al. 2001).

Unfortunately, the interplay of harvest strategies with population structure and spawning geography in marine fish is largely neglected from the management arenas (Rowe and Hutchings 2003). For example, the harvest of many marine schooling fish is focused on older individuals gathering in spawning or feeding locations. Although such practice may favor a delay in the age of maturation over short evolution-



ary time scales (Heino and Godø 2002), it may also cause a larger proportion of the surviving population to spawn in secondary and probably suboptimal locations or lead to loss of genetic diversity as the result of inbreeding (Hoarau et al. 2005). These mechanisms can lead to a rapid population decline, particularly at low densities (i.e., Allee effect), if indeed the environmental benefits of spawning in secondary locations are marginal. Behaviorally mediated effects can magnify the speed of the decline, as has been proposed to explain the alternation in abundance of anchovy and sardine (i.e., “school trap hypothesis”; Bakun and Cury 1999). Currently the harvest of walleye pollock, although substantially reduced from the 1980s, is still focused in the Shelikof Strait region (Dorn et al. 2002). If the scenario of behaviorally controlled spawning-site philopatry is correct, the impact of such harvests on the recovery and recruitment of the Shelikof spawning aggregation should be critically examined.

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