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Ecological Characteristics of Walleye Pollock Eggs and Larvae in the Southeastern Bering Sea during the Late 1970s

Kyung-Mi Jung[1], Sukyung Kang[2]*, Suam Kim[3] and Arthur W. Kendall, Jr.[4]

[1]*E&C Technology Institute, Incheon, Kyunggi-Do 405-839, Korea*
[2]*Salmon Research Center, National Fisheries Research and Development Institute, Yangyang, Gangwon-Do 215-821, Korea*
[3]*Department of Marine Biology, Pukyong National University, Busan 608-737, Korea*
[4]*AJALA Enterprises, 635 Wanapum Drive, La Conner, WA 98257, U.S.A.*

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Walleye pollock (*Theragra chalcogramma*) is an ecologically and economically important groundfish in the eastern Bering Sea. Its population size fluctuates widely, driving and being driven by changes in other components of the ecosystem. It is becoming apparent that dramatic shifts in climate occur on a decadal scale, and these "regime shifts" strongly affect the biota. This paper examines quantitative collections of planktonic eggs and larvae of pollock from the southeastern Bering Sea during 1976–1979. Mortality, advection, and growth rates were estimated, and compared among the years encompassing the 1970s' regime shift. These data indicate that pollock spawning starts in late February over the basin north of Bogoslof Island. Over the shelf, most spawning occurs north of Unimak Island near the 100 m isobath in early or mid April. Pollock eggs are advected to the northwest from the main spawning area at 5–10 cm/sec. Larvae are found over the basin north of Bogoslof Island in April, and over the shelf between Unimak Island and the Priblof Islands in May. Compared to 1977, the spawning period appeared to be later in 1976 (a cold year) and earlier in 1978 (a warm year) in the study area. At the lower temperatures in 1976, egg duration would be longer and thus egg mortality would operate over a longer period than in the other years. Mean larval growth appeared to be lower in 1976 than in 1977 and 1979. Estimated egg mortality rate in 1977 was 0.6 in April and 0.3 in early May.

Keywords:
· Pollock eggs,
· pollock larvae,
· southeastern Bering Sea,
· regime shift,
· larval growth.

1. Introduction

Many marine teleosts spawn large numbers of pelagic eggs each year, and most eggs and larvae die due to starvation, predation, transport to unfavorable nursery areas, or intrinsic physiological weakness (Bailey and Houde, 1989). Fish eggs and larvae are generally distributed in the surface layer of the ocean where changes in climate and biological activities are most intense. Knowledge of the distribution and advection patterns of fish eggs and larvae near spawning or nursery grounds provides the context for studying mechanisms of survival and the recruitment process (Wooster *et al.*, 1983; Kendall and Kim, 1989; Niebauer and Quinn, 1995). For species with longer early life histories, the age of eggs and larvae needs to be determined to investigate parameters such as mortality, growth, and transport. Furthermore, information on interactions between biotic and abiotic components can be a basis for ecosystem management in the future.

The southeastern Bering Sea shelf sustains diverse and abundant wildlife and fisheries resources. Species totals residing there include 38 seabirds, 25 mammals, and over 300 fishes (Brodeur *et al.*, 1999; Loughlin *et al.*, 1999), and intensive fishing activity has been conducted for salmon, shrimp, crab, and groundfish species since the mid 20th century. Walleye pollock (*Theragra chalcogramma*, pollock hereafter), one of the groundfishes, is the most abundant species harvested in the Bering Sea, accounting for nearly 70% of the total groundfish biomass (Springer, 1992). Juvenile pollock are a nodal component of Bering Sea food webs, providing nourishment to piscivorous fishes, marine mammals, and sea birds (Napp *et al.*, 2000; Wespestad *et al.*, 2000).

* Corresponding author. E-mail: kangsk@momaf.go.kr

Besides its ecological importance, the pollock fishery is economically valuable. The pollock fishery alone was worth about 296 million US dollars in 2004 (www.afsc.noaa.gov/refm/stocks/assessments.htm).

Features of the physical environment of the eastern Bering Sea—including length of day, net short-wave radiation flux, wind fields, ice cover, on/off shelf transport, water column structure and temperature—exhibit strong seasonal, interannual, and interdecadal signals forced by climate (Stabeno *et al*., 2001). Such changes in climate are transmitted mechanistically and stochastically through the ocean to the biota (Bailey *et al*., 2005). As documented in the North Pacific, during the past five decades there have been three major climate changes: 1976/1977, 1988/1989, and 1998/1999 events (Hare and Mantua, 2000; PICES, 2004). The most prominent shift observed, in 1976/77, was called a climate regime shift, and, in comparison to the previous decade, there was a marked increase in air and sea surface temperature (SST), and a retreat of winter sea ice after 1976 (Hare and Mantua, 2000; Napp *et al*., 2000; Wespestad *et al*., 2000). For example, mean SST in the eastern Bering Sea during May was 1.23°C in 1976, but increased to 2.99°C, 3.63°C, and 3.71°C in 1977, 1978, and 1979, respectively (http://www.beringclimate.noaa.gov/data/index.php). These changes could affect both the structure of the marine food web and its productivity, and ultimately the distribution and abundance of upper trophic-level consumers (Hunt *et al*., 2002).

Ichthyoplankton surveys for pollock in the Bering Sea began in 1955 by Japanese, followed by Soviet and USA scientists (Bulatov, 1982). The earlier surveys in the 1950s and 1960s were conducted in summer. Due to low spawning biomass as well as the unsuitable survey period, few pollock eggs were collected, and spawning grounds were not clearly identified. Since the 1970s several research cruises have revealed the major spawning areas and periods. Although information on stock composition in the eastern Bering Sea is not clear, Hinckley (1987) demonstrated that spawning occurred in the Aleutian Basin from January through March, in the southeastern Bering Sea from March through June, and northwest of the Pribilof Islands from June through August. Incze *et al*. (1984) reported that high egg concentrations usually occurred in the southeastern shelf in March–April. Spawning continued through early summer, but generally declined. Eggs were also released in the vicinity of the Pribilof Islands in April–May and south and west of St. Matthew Island in May–June (Springer, 1992). According to recent research in the southeastern Bering Sea (Kim *et al*., 1996), peak spawning intensity was found near the boundary between the outer and middle shelf between the Pribilof Islands and Unimak Island in April (Fig. 1).

Egg development rates are documented for pollock populations in Japan, the Gulf of Alaska, and the Bering Sea, and have been used to estimate early life history parameters such as egg production and mortality (Picquelle and Megrey, 1993; Brodeur *et al*., 1996), and distribution and abundance of eggs by age intervals (Nakatani, 1988; Kendall and Kim, 1989; Kendall and Picquelle, 1990; Kendall *et al*., 1994). The spawning ground of Bering Sea pollock is broad, and spawning varies temporally and spatially. Due to low seawater temperature, the incubation period of pollock eggs is longer (at about 3 weeks) in the Bering Sea than it is in the Gulf of Alaska or Asian coastal areas (Kim, 1992). Therefore, without staging the eggs, the exact spawning grounds of pollock in the eastern Bering Sea cannot be identified, nor can dispersion with time be estimated, if the eggs have drifted a long distance from the spawning area. In this paper we investigate the spawning characteristics of pollock using sampling data from the late 1970s. Distribution pattern, abundance, advection, and mortality of eggs and larvae and larval growth were estimated. More specifically, we identified the developmental stages of eggs and larvae and mapped their distribution to understand the influence of the 1970s' environmental changes due to the climate regime shift on egg production and larval growth.

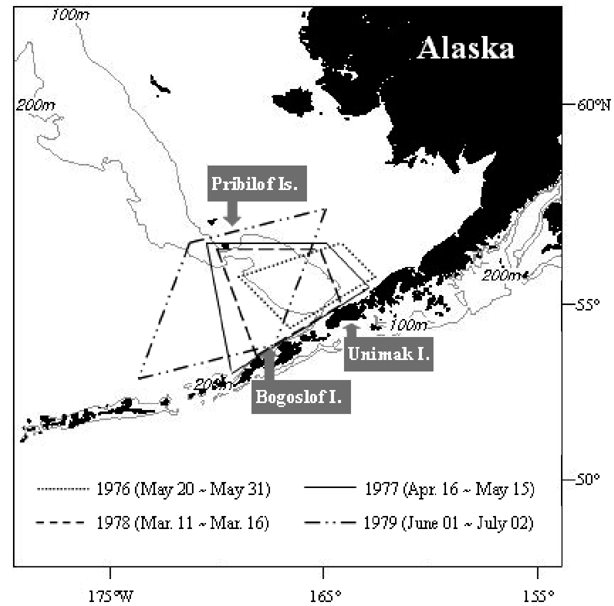


Fig. 1. Areas sampled during surveys from 1976 to 1979. Note that a limited area from the 1976 survey was selected for the analysis.

2. Methods and Assumptions

Ichthyoplankton surveys were conducted by US National Oceanic and Atmospheric Administration (NOAA) scientists using the R/V *Miller Freeman* in the southeastern Bering Sea: May 1976, April–May 1977, March 1978, and June–July 1979 (Table 1). For this study, we examined the eggs and larvae of pollock from these cruises, which were archived at the Alaska Fisheries Science Center (AFSC).

2.1 Collection of samples

A total of eight ichthyoplankton surveys were conducted in the major spawning grounds of pollock during 1976–1979 (Table 1, and Fig. 1). In 1976, two surveys were carried out northwest (16 stations during 26 April–12 May) and southeast (19 stations during 20–31 May) of the Pribilof Islands. In this paper, however, we only examined the data sets collected in the southeastern area because we limited our study area to the major spawning ground of pollock between the Pribilof Islands and Unimak Island. Intensive surveys were done in spring 1977 (16 April–15 May), when four repeated surveys at 127 stations were conducted. In 1978, a survey was done at 21 stations during 11–16 March, which was early in the spawning season. In 1979, two surveys were done at 9 stations during 1–7 June, and at 13 stations during 16 June–2 July; eggs were scarce, but larvae were abundant in these samples.

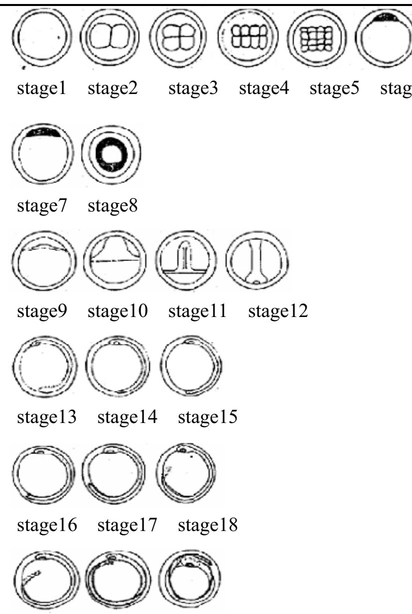
Fish eggs and larvae were collected using obliquely towed 60 cm bongo nets (0.505 and 0.303 mm mesh) from near bottom to the surface in the shelf area, or from a depth of 200 m to the surface in the slope area. Seawater temperatures were measured at all sampling stations during the surveys. Plankton was preserved in 5% formalin in the field. On shore, within a year of collection, fish eggs and larvae were separated from the remaining plankton and pollock eggs and larvae were identified and counted. Larval lengths were determined for a subset of the samples. After preservation in vials for more than two decades, pollock eggs and larvae were subjected to further analysis (egg staging, larval measurements) in laboratories of the Pukyong National University, Korea, and the AFSC in 2000–2001.

2.2 Ageing eggs and larvae

The eggs collected at each sampling station were staged under a stereoscopic dissecting microscope according to the 21-stage scheme of Blood *et al.* (1994). When the number of eggs sampled was less than 100 at a station, all were staged. However, if it exceeded 100, egg staging was done on a randomly selected subsample of 100 eggs. A total of 6,345 eggs were staged, and each pollock egg that was assigned to a specific stage was then re-grouped into the 6 age groups as described by Kendall and Kim (1989): Stages 1–6 (age group 1: AG-1), stages 7–8 (AG-2), stages 9–12 (AG-3), stages 13–15 (AG-4), stages 16–18 (AG-5), and stages 19–21 (AG-6) (Fig. 2).

Table 1. Information on surveys conducted in the southeastern Bering Sea, 1976–1979.

	1976	1977				1978	1979	
	Survey	Survey 1	Survey 2	Survey 3	Survey 4	Survey	Survey 1	Survey 2
Sampling period	May 20–May 31	April 16–April 22	April 23–April 27	May 3–May 9	May 10–May 15	March 11–March 16	June 1–June 7	June 16–July 2
No. stations	19	33	33	32	29	21	9	13
Mean SST (°C)	1.09	3.25	3.49	4.38	4.31	—	—	—
Collection	Eggs/larvae	Eggs/larvae	Eggs/larvae	Eggs/larvae	Eggs/larvae	Eggs	Larvae	Larvae
Area ($\times 10^4$ km^2)	3.63	4.62	6.20	5.40	4.24	4.41	—	—



Age group	Developmental stage	Time after fertilization (hr) at 3.25°C	
		mid-time	end-time
1	stage1 stage2 stage3 stage4 stage5 stage6	16.0	31.9
2	stage7 stage8	62.8	93.7
3	stage9 stage10 stage11 stage12	127.8	161.8
4	stage13 stage14 stage15	189.6	217.3
5	stage16 stage17 stage18	268.0	318.7
6	stage19 stage20 stage21	411.1	503.6

Fig. 2. Developmental status of walleye pollock egg stage and developmental time after fertilization. Twenty-one developmental stages were re-grouped into six age groups (Kim, 1987).

Temperature-dependent egg developmental time from fertilization was calculated as described by Blood (2002). For example, if a pollock egg developed at 3.5°C, it would take about 20 days to hatch. AG-1 is the youngest group, which is about 1 day old and would occur near the spawning place. The equations used were

Stages 1–6 (AG-1)

$$\text{Age} = -10.6 + 19.167(\text{stage}) - 0.364(\text{stage})(\text{temperature}) - 5.129(\text{stage}^2) + 0.588(\text{stage}^3) - 0.011(\text{stage}^3)(\text{temperature}),$$

Stages 7–21 (AGs 2–6)

$$\text{Age} = -357.319 + 104.993(\text{stage}) - 6.946(\text{stage}^2) - 0.306(\text{stage}^2)(\text{temperature}) + 0.233(\text{stage}^3)$$

where age of egg and temperature are expressed in hours and in degrees Celsius, respectively.

For larval age, we could not use otoliths because the specimens were put in formalin when they were caught at sea, so the otoliths were partly dissolved. Instead, we measured standard length to estimate age using age-length keys. When fewer than 50 larvae were collected at a station, all were measured at 0.1 mm precision but if more than 50 were collected at a station, a randomly-chosen 50 larvae were measured. A total of 2,988 larvae were measured.

2.3 *Larval shrinkage*

We considered shrinkage rates because the larvae were preserved in formalin for approximately 20 years before they were measured in 2000–2001. We reviewed reports published soon after the cruises (Waldron and Favorite, 1977; Waldron and Vinter, 1978; Waldron, 1978; Walline, 1980; unpublished NOAA laboratory documents). Earlier reports recorded the range or mean standard length of larvae at each sampling station. We selected stations where one to three larvae were collected, to examine length differences (i.e., shrinkage due to long preservation in formalin) between 20-years ago and the present, and found 11 such stations from 1976 and 1977 cruises. The percent shrinkage (%) was estimated by the difference between the two measurements divided by the old measurement, i.e.,

Percent shrinkage = ((old measurement – new measurement)/old measurement) × 100.

2.4 *Analytical methods*

The total number of eggs (or larvae) present during each survey was calculated by the prism method (Kim, 1987). The sum of the volumes of all prisms within the survey area is the egg abundance during the survey, and mean egg density at each survey can be calculated from egg abundance divided by survey area. Egg abundance and mean density were calculated with respect to age groups. Daily Egg Production (DEP) indicates the trend of spawning intensity with time, and the sum of DEP in a spawning season is the total amount of eggs produced by the pollock stock in the study area. This is also fundamental data for estimating the location of the spawning ground and changes in spawning intensity with time. Because AG-1 eggs were about 1 day old, we could estimate DEP using the equation below:

$$\mathrm{DEP} = \frac{\text{Abundance of ' AG - 1'}}{\text{Development time }(\text{day})\text{ of ' AG - 1'}}.$$

To estimate advection and daily mortality rates of pollock eggs, patches of young eggs (i.e., AG-1, AG-2, and AG-3) were chosen from around the highest density area, north of Unimak Island. The advection rate of eggs was then calculated by regression analysis using the location of distributional centroids of age groups and differences in egg development time. The equation used for the calculation of centroids is given in Kim and Kendall (1989). The instantaneous coefficient (Z) of egg mortality over the three early age groups (AGs-1, 2, and 3) in each survey was also calculated from regression analysis assuming a constant rate of spawning in each survey and an exponential decrease in egg numbers with time. The slope of the regression line was the mortality rate during each survey. The data used were the egg abundances in unit time, i.e., egg abundance at each age group divided by age group duration, which was adjusted for seawater temperature during each survey. To visualize and analyze the density distribution, distributional centroids, and distance between stations, we used a GIS program (Marine Explorer, Environment Simulation Laboratory Inc., Japan).

All larval lengths were adjusted by the shrinkage rates we determined, and larval abundance was allocated into eight length groups for our distribution and growth study (<5.0 mm, 5.0–6.9 mm, 7.0–8.9 mm, 9.0–12.9 mm, 13.0–16.9 mm, 17.0–21.9 mm, 22.0–26.9 mm, and >27.0 mm). We calculated larval abundance for each size group, and mean larval length for each cruise. Mean larval growth was estimated from the difference in weighted mean length between consecutive surveys. In 1976, only one survey was conducted in the study area, so only the weighted mean length could be calculated. In 1977, however, surveys were repeated four times, so growth rate was calculated by regression analysis between cruises.

Table 2. Abundance ($\times 10^{12}$) and mean density (eggs/m^2) of walleye pollock eggs in the southeastern Bering Sea by age group and sampling date.

Sampling date	Sampling area (km^2)	Age group						
		1	2	3	4	5	6	Total
1976/5/20–5/31	36280	0.122* (3.4)**	0.481 (13.3)	0.597 (16.4)	0.257 (7.1)	1.476 (40.7)	1.540 (42.4)	4.472 (123.3)
1977/4/16–4/22	46187	1.125 (24.4)	0.560 (12.1)	0.149 (3.2)	0.057 (1.2)	0.027 (0.6)	0.016 (0.3)	1.934 (41.9)
1977/4/23–4/27	62028	0.982 (15.8)	1.443 (23.3)	0.459 (7.4)	0.131 (2.1)	0.287 (4.6)	0.117 (1.9)	3.418 (55.1)
1977/5/03–5/09	53980	0.378 (7.0)	0.618 (11.5)	0.228 (4.2)	0.053 (1.0)	0.076 (1.4)	0.025 (0.5)	1.378 (25.5)
1977/5/10–5/15	42386	0.065 (1.5)	0.045 (1.1)	0.040 (0.9)	0.015 (0.4)	0.022 (0.5)	0.005 (0.1)	0.193 (4.6)
1978/3/11–3/16	44137	0.617 (14.0)	0.201 (4.5)	1.036 (23.5)	0.315 (7.1)	0.592 (13.4)	0.051 (1.2)	2.812 (63.7)

*Abundance; **Mean density.

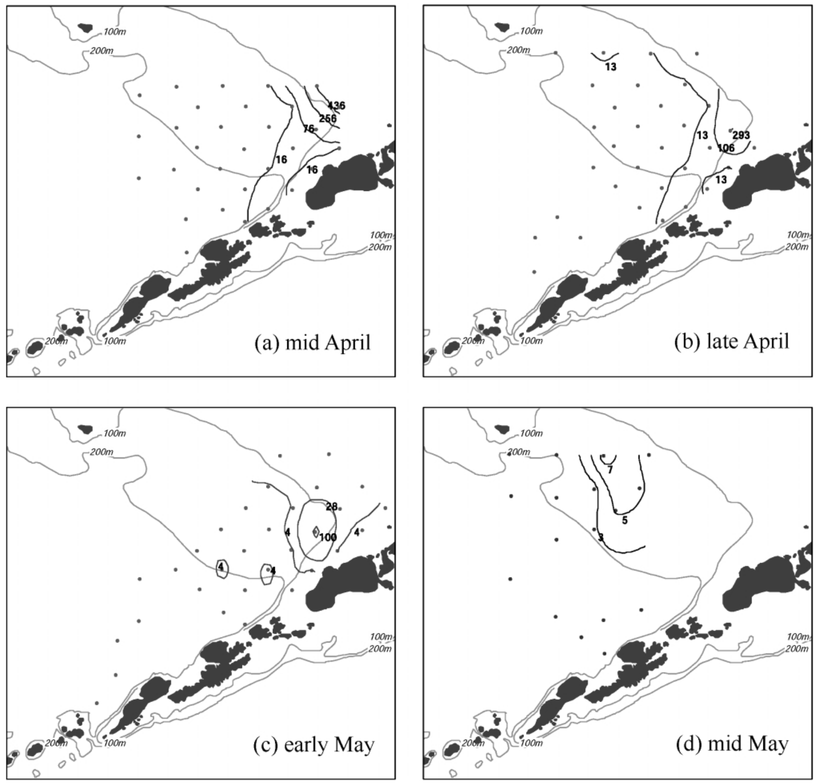


Fig. 3. Distribution and density of age group 1 walleye pollock eggs in the southeastern Bering Sea during mid April–mid May, 1977.

The slope of the regression line indicates the daily growth rate within the larval size ranges found. In 1979, two surveys were conducted, so the increment of mean larval length was divided by the time between the two cruises.

2.5 Assumptions

The following assumptions were made for the analysis.

(1) Ichthyoplankton surveys covered most major spawning grounds of pollock, and spawning locations were indicated by the presence of AG-1 eggs which are within 1 day after fertilization.

(2) Sampling was effective in collecting unbiased samples of pollock eggs and larvae, and the same group of spawners was responsible for all eggs and larvae sampled from the study area.

(3) No spatial heterogeneity in instantaneous egg mortality occurred within the survey area during each survey.

(4) There were no significant differences in spawning biomass during the 1976–1979 period, so the same numbers of eggs were produced each year (http://www.beringclimate.noaa.gov/data/index.php).

(5) Spawning intensity within a spawning season (late February–late May) followed a normal Gaussian distribution.

3. Results

Egg and larval densities and abundances by age group revealed differences in temporal and spatial patterns of distribution. This information included spawning intensity with time (including peak spawning time), changes in spawning area within a season, total egg and larval abundances produced annually, and transport pathways from spawning areas to nursery grounds.

3.1 Temporal and spatial pattern of pollock spawning and egg distribution

In March 1978, eggs were abundant north of Bogoslof Island, near the deep basin and continental slope (figure not shown). They were rarely found over the continental shelf. Among the egg age groups, the density and abundance of AG-3 were the highest (mean density: 23.5 eggs/m^2, and abundance of AG-3: 1.036×10^{12}; Table 2). Comparing this amount with other age groups, this high abundance of AG-3 indicated that spawning activity started in the basin and slope areas early in the spawning season, and that spawning intensity was high north of

Table 3. Selected specimens for the calculation of shrinkage rate of pollock larvae.

Sampling year	Station (towing)	Old measurement		New measurement in 2001		Shrinkage rate (%)
		no. larvae	size range (mm)	no. larvae	size range (mm)	
1976	40	1	6.6	1	6.1	7.6
	42	1	5.0	1	4.3	14.0
	45	2	5.5–7.1	1	6.0	15.5
	mean					12.4
1977	11 (2)	1	4.0	1	3.7	7.5
	12 (1)	1	5.8	1	5.6	3.4
	16 (3)	1	7.7	1	6.8	11.7
	17 (2)	2	8.0	2	7.4–7.5	7.5, 6.3
	17 (3)	2	8.5–9.0	2	7.5–8.8	11.8, 2.2
	43 (1)	2	6.5–7.5	3	5.9, 6.2, 6.5	13.3, 9.2
	64 (2)	2	7.0–7.9	2	6.2–7.1	11.4, 10.1
	68 (1)	3	5.1	2	4.4–4.6	13.7, 9.8
	mean					9.1

Bogoslof Island 5–6 days earlier than the survey period (i.e., early March 1978).

The distribution of the youngest egg group (AG-1) indicated the location of spawning within the study area in 1977. Changes in spawning time and location were observed during the survey period: a high concentration f eggs occurred north of Unimak Island, particularly near he boundary (around the 100 m isobath) between the uter and middle shelf, and the highest density (517.6 ggs/m^2) of AG-1 was found in mid April. Eggs were arely found in the outer shelf and slope area (Fig. 3). igh egg concentrations persistently occurred north of nimak Island by early May, and moved toward the northwest (southeastern part of the Pribilof Islands) in mid May, hich demonstrates that pollock spawners moved toward he northwest late in the spawning season. The total umber of AG-1 eggs in the study area was the highest 1.125 × 10^{12}) in Survey 1 (mid April), decreasing to .982 × 10^{12}, 0.378 × 10^{12}, and 0.065 × 10^{12} in Survey 2 late April), Survey 3 (early May), and Survey 4 (mid ay), respectively (Table 2). This indicates that peak pawning probably occurred in early or mid April.

n late May 1976, eggs were distributed largely in he outer shelf and middle shelf areas. Whereas the mean ensity of AG-1 was as low as 3.4 eggs/m^2, the densities f AG-5 and AG-6 were comparatively high (40.7 ggs/m^2 and 42.4 eggs/m^2, respectively). Therefore, considering the high instantaneous mortality rate of fish eggs nd the long incubation period due to low seawater temperature (1.09°C) in May 1976, spawning seemed to be ctive until early May, and remained at a low level in the outheastern area in late May 1976. Actually, based on Blood (2002), the spawning dates of AG-5 and AG-6 eggs were roughly estimated as 20 days (i.e., early May) and 29 days (i.e., late April) before the sampling, respectively. Considering similar annual spawning biomasses during the 1976–1978 period, such a high abundance of eggs in late May implies the possibility of a delayed maturation or development in the shelf area due to the cold temperatures in 1976.

3.2 *Mortality rates of pollock eggs*

To estimate the instantaneous rate of daily egg mortality we used egg abundance per unit time and the developmental time of each age group from the 1977 samples in the area north of Unimak Island. Instantaneous daily mortality rates were calculated by regression analysis with AG-1 to AG-3 abundance information from Surveys 1–3. Survey 4 was excluded because spawning intensity was low and the survey did not fully cover the spawning ground. The instantaneous daily mortality rate was high early in the spawning season, i.e., 0.602 and 0.593 in mid April and late April, and then dropped substantially to 0.319 in early May (Table 4).

3.3 *Movement of pollock eggs and larvae*

Eggs were found over the basin area in March 1978, but were rarely found in the slope area in April. Most eggs were persistently present over the shelf in April 1976 and 1977. Spawners aggregated north of Unimak Island, forming a major spawning area in early–mid April, and spawned eggs drifted northwestward in accordance with the prevailing current pattern. If we examine the location of egg centroids by age groups, we can construct the tra-

Table 4. Information for estimating the rate of egg mortality, and calculated daily mortality rate during surveys from mid April to early May, 1977. Note that egg abundance was estimated from the area near the highest egg patch.

	Survey 1	Survey 2	Survey 3
Mid-cruise	19 April	25 April	6 May
Sea surface temperature (℃)	3.25	3.49	4.38
Stage duration (hr)			
age group 1	32	31	27
age group 2	62	58	45
age group 3	68	62	40
Abundance ($\times10^{11}$ inds.)			
(Abundance per unit time ($\times10^{11}$ inds./hr))			
age group 1	9.722 (0.304)	6.612 (0.213)	3.207 (0.119)
age group 2	4.863 (0.078)	9.182 (0.158)	5.819 (0.129)
age group 3	1.229 (0.018)	1.081 (0.017)	1.755 (0.044)
Instantaneous rate of daily egg mortality	0.602	0.593	0.319

jectory of flow of the cohorts of eggs. Thus, we mapped the centroids of AGs-1, 2 and 3 from the 1977 samples. Each survey of 1977 was conducted at an interval of approximately one week, and this duration is roughly equivalent to the developmental time from fertilization to AG-3. Distributional centroids of eggs occurred around the 100 m isobath north of Unimak Island, and eggs were advected to the northwest as they developed (Fig. 4). Because eggs have no swimming ability, they were advected to the northwest by the slow current over the 100 m isobath. Advection rates were 7.2 cm/sec, 9.9 cm/sec, and 4.7 cm/sec in Surveys 1, 2, and 3, respectively. Due to the distinct depression of spawning activity in the area during Survey 4, it was excluded from the estimation of advection rate.

Larval shrinkage was evident (Table 3). The percent shrinkage seemed to be distributed randomly, regardless of larval length. Shrinkage rates estimated were 12.4% and 9.1% for the 1976 and 1977 samples, respectively. To reveal larval distribution and growth, all larval lengths measured in 2000–2001 were adjusted by the mean of these ratios. We examined the distribution of larvae and their dispersal as they grew. Note that pollock larvae were found in basin and slope areas from early April 1977 (figure not shown). The larval cohort that hatched in mid April 1977 (Survey 1) grew 0.1–0.2 mm per day (see later section of this paper), so they grew to size classes 5.0–6.9 mm, 7.0–8.9 mm, and 7.0–8.9 mm in late April (Survey 2), early May (Survey 3), mid May (Survey 4), respectively (Fig. 5). Most larvae were distributed over the deep basin and continental slope in April, and they moved progressively to the east toward the outer shelf in early May. Then, as shown with the eggs, the larvae were also advected to the northwest, conspicuously in outer shelf and slope areas after mid May. Larval transport rate is not considered in this paper, because of the large variance in larval distribution.

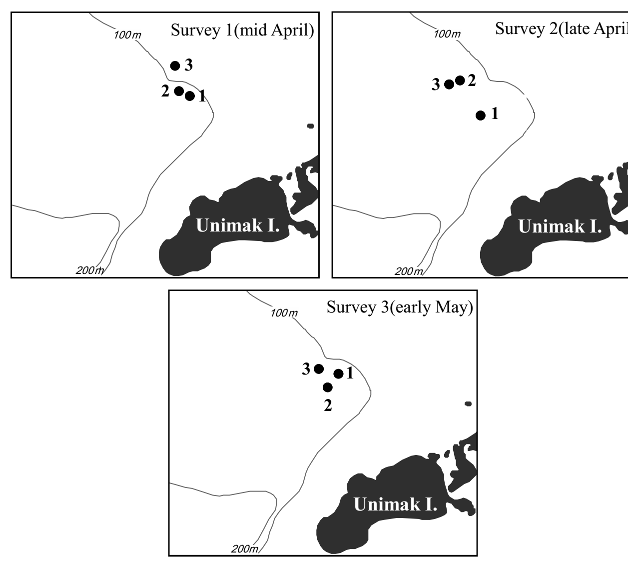


Fig. 4. Location of distributional centroids of age groups 1–3 of walleye pollock eggs from the surveys in 1977.

3.4 *Influence of annual temperature differences on pollock spawning and larval growth*

Seawater temperatures may have a significant influence on migratory pathway/spawning schedule. We used the Daily Egg Production (DEP) to examine temporal change in spawning intensity among years. The spawning intensity curve based on four repeated surveys in 1977 was drawn assuming normal distribution-type spawning activity (Fig. 6). With this curve, we derived the follow-

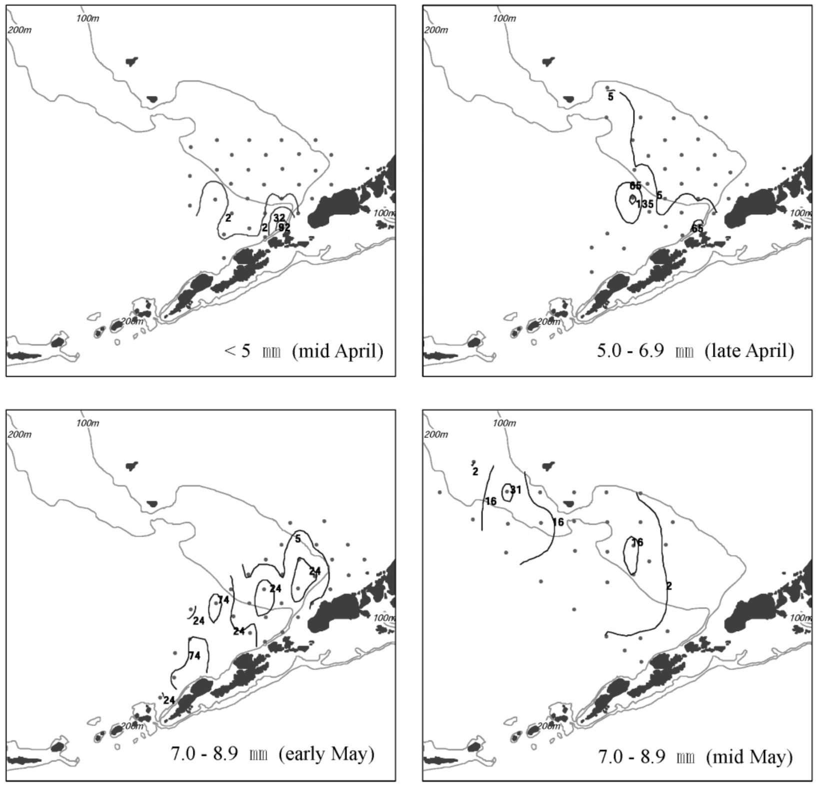


Fig. 5. Movement of a larval cohort of walleye pollock hatched in mid April through spring 1977. Numbers denote the larval density (inds./m^2).

ing pattern of spawning activity: spawning started in late February, peaked in early–mid April, and finished in late May. Assuming that there were no differences in spawning biomass of pollock during the 1976–1978 period, and that pollock has a same spawning behavior each year, egg production of other years might fall on this expected normal curve. Interestingly, when we added the DEPs of 1976 and 1978 surveys, those values fell above the normal spawning curve from 1977. Consequently, the timing of peak spawning could shift either earlier (in 1978) or later (in 1976) depending on climate conditions: spawning of pollock in 1978, which was a warmer-than-normal year, might have occurred earlier, while spawning in 1976, which was a colder-than-normal year, occurred later than in 1977.

The climate regime shift of the late 1970s resulted in warmer temperatures in subsequent years as well as shorter pollock eggs development times. During late May 1976, and the mean SST in the southeastern Bering Sea was 1.09°C. At this temperature, egg development time from fertilization to hatching requires about 33 days, according to Blood (2002), and such a delayed hatching might result in high mortality during the egg period. A climate regime shift occurred in late 1976, and mean SST was higher in early 1977 than in previous years. During 16 April–15 May 1977, mean SSTs during four repeated surveys were 3.25°C, 3.49°C, 4.38°C, and 4.31°C, and egg development time was about 21, 20, 15, and 15 days, respectively. Decreased development time might produce more larvae due to a decrease in time for egg mortality to occur.

The climate change of late 1970s influenced not only pollock spawning but also mean larval growth. We examined mean growth in terms of body length of larvae collected in 1976, 1977, and 1979 (Fig. 7). We regressed average larval size from the four cruises from mid April to mid May 1977, and mean larval growth was determined to be 0.12 mm/day within the larval size range observed. In 1979, there were two cruises during May–June, and larval growth was 0.23 mm/day. However, the difference in growth cannot be compared directly, because the larval size ranges in 1977 and 1979 were quite different. Visual examination of Fig. 7 indicates that growth of larvae in both years did not seem to be very different. In contrast, the average larval size was 7.0 mm in mid May 1976. This was very small for that time of year, compared to larval size in 1977 and 1979. Larvae of this size appeared approximately 30 days earlier in 1977, i.e., in

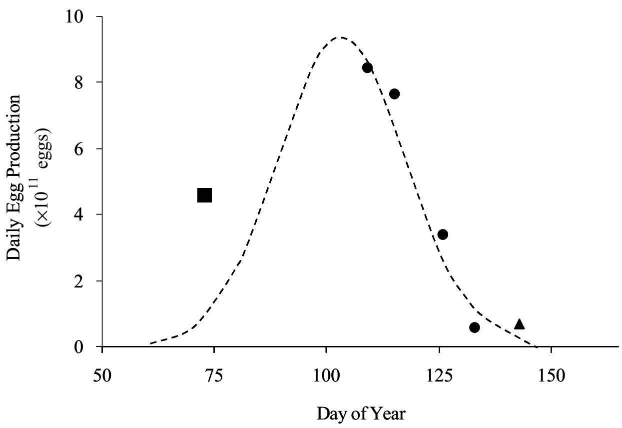


Fig. 6. Spawning intensity curve of walleye pollock over the daily time scale, based on daily egg production in 1977 (●). Daily Egg Productions from other years (1976 (▲) and 1978 (■)) are shown for comparison.

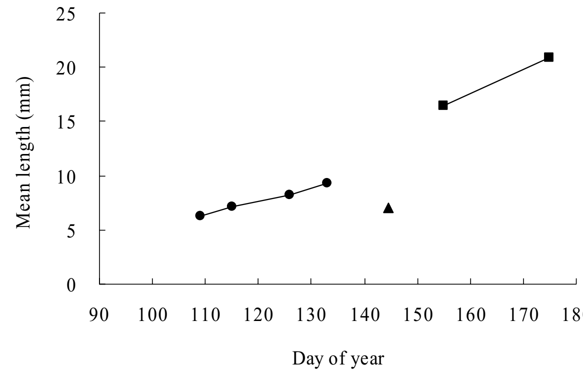


Fig. 7. Larval growth of walleye pollock in terms of body length in the southeastern Bering Sea in 1976 (▲), 1977 (●), and 1979 (■).

mid April. Considering the seawater temperature difference in 1976 (a cold year) and 1977 (a transitional year), spawning activity would occur later and/or larval growth would be slower in 1976 than in 1977.

4. Discussion

4.1 Spawning of pollock in the southeastern Bering Sea

Based on distributions of the youngest age group of eggs collected during the intensive surveys in 1977, the spatial and temporal patterns of spawning activity of pollock in the southeastern Bering Sea were clearly observed in April through May. Comparing our results with other studies, ours mostly agree concerning the major spawning ground, egg distribution patterns, and the movement of spawning toward the northwest (Serobaba, 1974; Hinckley, 1987; Springer, 1992). Based on monthly pollock catches from foreign commercial fisheries in 1983–1984, Hinckley (1987) suggested three separate spawning stocks within the Bering Sea: (1) in the Aleutian Basin, (2) over the southeastern continental shelf and slope and northwest shelf area, (3) over the continental slope northwest of the Pribilof Islands. The eggs and larvae used in this study belong to the second group of pollock stocks, and pollock spawners might have an onshore spawning migration from offshore to the southeastern Bering Sea shelf, assuming the same spawning group produced eggs and larvae in the survey areas.

Although our research showed direct evidence of spawning based on the distribution of AG-1 eggs, it also has a weakness in respect to determining spawning area. The highest egg densities occurred persistently at the easternmost stations during a period of about one month. This means that sampling did not cover the whole spawning area, and there is a possibility that another high spawning concentration could occur northeast of the survey area. Consequently we may have underestimated egg abundance, and introduced a bias in our estimates of egg mortality and advection rates.

Kim *et al.* (1996) used the same 1977 cruise data to illustrate temporal and spatial patterns of pollock spawning and egg distribution. However, eggs were not staged in their research, so precise analysis could not be carried out. One of the new findings from the present study is the correction in peak spawning time. Because the highest egg abundance calculated with unstaged egg information appeared in the second survey (i.e., late April) in the southeastern Bering Sea shelf area, Kim *et al.* (1996) concluded that the peak spawning of pollock occurred in late April. Our present analysis based on AG-1 eggs, however, revealed that the highest egg abundance of AG-1 was in the first survey (i.e., mid April), and AG-1 abundance in the second survey was less than that in the first one. Therefore peak spawning happened in early/mid April in 1977. It is recommended that when a long incubation period occurs research on spawning intensity and early life ecology should use staged egg information.

4.2 Transport of eggs and larvae

Advection of eggs was estimated from centroid distributions of the young age groups collected during three sequential cruises in 1977. We found that eggs were spawned near the 100 m isobath north of Unimak Island, and drifted to the northwest at between 4.7 and 9.9 cm/sec. This is in close agreement with the mean circulation pattern found in this part of the Bering Sea. Based on CTD observations in the southeast Bering Sea during spring 1979–1981, Reed (1998) reported a northwestward flow of 4–6 cm/sec offshore of 100 m.

The distribution and movement of larvae was analyzed by mapping the distribution of larval length groups through the season. Larval lengths were adjusted by shrinkage, and our shrinkage rates (12.4% and 9.1% for 1976 and 1977 samples, respectively) were not very different from Porter *et al.* (2001) who reported 10% shrinkage after one month in formalin. Small larvae were first found in April over the deep basin and slope. These larvae probably resulted from the spawning north of Bogoslof Island in March. These larvae moved east toward the outer shelf as they grew. However, north of Unimak Island, small larvae first appeared in mid April samples, which were then advected to the northwest in the outer shelf and slope areas, toward the Pribilof Islands, where most age-0 juveniles are found in summer (Swartzman *et al.*, 2005). In contrast to this distribution pattern of age-0 pollock, Coyle and Pinchuk (2002) observed high densities on the inner shelf during August and September in the late 1990s. The oceanic processes that contributed to this difference in age-0 distributions between these two periods were not investigated.

4.3 Changes in mortality through spawning season

Based on temperature-dependent development rates, egg mortality in a specific survey was estimated with staged eggs collected near the highest egg patch. For example, there were four repeated surveys in spring 1977, and the time difference between mid-cruise of Survey 1 and Survey 2 was only 6 days. Therefore, due to the short interval between surveys, AG-1 eggs collected in Survey 1 would have reached AG-3 by the time of Survey 2. This assumes that the same population of eggs was sampled in both cruises. If we apply the daily egg mortality rate of 0.602 to the AG-1 abundance per unit time (i.e., 9.722×10^{11} inds./32 hrs = 0.304×10^{11} inds./hr) in Survey 1, AG-3 in Survey 2 (i.e., 4.7 days later) would be 0.018×10^{11} inds./hr in an exponential decreasing model. Actually, our calculation of AG-3 in Survey 2 indicates 0.017×10^{11} inds./hr (Table 4), showing the validity of our mortality estimate.

We found that egg mortality decreased during the season (i.e., 0.602, 0.593, and 0.319 in mid April, late April, and early May). This was similar to results reported from the Gulf of Alaska where mortality also decreased during the season (i.e., 0.433, 0.386, 0.115, and 0.091 in mid March, late March, late April, and late May 1981, respectively (Kim, 1989)). In the Gulf of Alaska, pollock eggs are located mostly below 200 m in the main spawning area where warm water usually exists (Kim, 1987). In contrast, however, the eggs in the eastern Bering Sea are distributed in the upper layer of the water column, where harsh environmental conditions such as strong winds and cold temperatures exist. Furthermore, more diverse and abundant predatory organisms reside in the surface layer, resulting in a higher chance of predatory mortality in the Bering Sea compared to the Gulf.

4.4 The influences of climate change

In this study, mean larval lengths and daily growth rates of pollock larvae in 1976, 1977, and 1979 were estimated (Fig. 7). The results showed that warm temperature might contribute to a higher growth rate in 1979 (0.23 mm/day), which was the warmest among the study years. In contrast, in 1976, which was the coldest year, larval length in mid May seemed to be much shorter than it was in the other years. Our growth rates (0.12 and 0.23 mm/day) were estimated in April–May 1977 and May–June 1979, respectively. In the Bering Sea, growth rates of individual pollock larvae as determined by otoliths in June–July 1979 were about 0.20 mm/day and 0.35 mm/day for yolk-sac and post-yolk larvae, respectively (Walline, 1983), and a growth rate of about 0.20–0.22 mm/day has been generally accepted in spring. The growth rate (0.17–0.23 mm/day) observed in April and May 1980 and 1981 by Clarke (1984) seems to be similar to our estimates of larval growth.

Dramatic interannual changes in SST in the Bering Sea can indicate regime shifts and other climate changes. North Pacific ecosystems have experienced climate regime shifts in 1976/1977, 1989 and 1998/1999 (PICES, 2004), and related changes in SST have significantly reformed the ecosystem structure and function of the Bering Sea. Changes in spawning behavior, recruitment, and survival and growth of early life stages of pollock are related to these ecosystem changes. Because early life stages of pollock are located in the upper 50 m of the water column in the southeastern Bering Sea shelf (Nishiyama *et al.*, 1986), larval growth and survival is related to changes in SST and possibly food availability.

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