

## **Interannual differences in growth and hatch date distributions of age-0 year walleye pollock *Theragra chalcogramma* (Pallas) sampled from the Shumagin Islands region of the Gulf of Alaska, 1985 – 2001**

A. B. DOUGHERTY\*, K. M. BAILEY AND K. L. MIER

*Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115, U.S.A.*

*(Received 13 December 2005, Accepted 30 March 2007)*

Daily increments of age-0 year walleye pollock *Theragra chalcogramma* otoliths from 1985 to 2001 were examined for interannual variability in growth and hatch dates. Fish were collected in summer and autumn surveys near the Shumagin Islands in the western Gulf of Alaska (GOA). Hatch date distributions of these fish were compared with hatch dates of larvae from spawning aggregations located in Shelikof Strait and the Shumagin Islands based on their spawning times. The hatch date distributions of age-0 year fish captured from the Shumagin Islands area were similar to those observed for larvae from the Shelikof Strait spawning group. Age-0 year fish whose hatch dates corresponded to the Shumagin Islands spawning, which occurred earlier in January and February, were not found. Sea surface temperature was associated with variability in hatch date distribution and growth. Journal compilation © 2007 The Fisheries Society of the British Isles

No claim to original US government works

Key words: growth; hatch date distributions; otoliths; *Theragra chalcogramma*.

### **INTRODUCTION**

Stock identity and productivity are important aspects of managing marine fisheries. Stock identity is certified by genotypic information, but because large effective population sizes of marine fishes limit genetic drift and potentially high dispersal rates promote mixing and genetic homogeneity (Hellberg *et al.*, 2002), phenotypic characteristics such as spawning time and growth characteristics are often used to infer population structure. Productivity of the stock reflects the balance of individual growth and the gain and loss of individuals through recruitment and mortality. Precise measurement of these population characteristics has been enabled by analysis of daily and annual growth increments on otoliths.

\*Author to whom correspondence should be addressed. Tel.: +1 206 526 6523; fax: +1 206 526 6723; email: [annette.dougherty@noaa.gov](mailto:annette.dougherty@noaa.gov)

The distribution of hatch dates of a sample of fishes can be determined from daily increment counts along with information on sampling dates. Differences in hatch date distributions of larval and juvenile fishes among geographical regions indicate differences in spawning times of discrete fish stocks (Begg & Marteinsdottir, 2000). This information can also be used to determine sources of juveniles. For example, young-of-the-year (YOY) juvenile (age-0 year) walleye pollock *Theragra chalcogramma* (Pallas) are found in the Shumagin Islands area in the Gulf of Alaska, but the origin of these fish is uncertain. There are several walleye pollock spawning aggregations in the Gulf of Alaska that may be potential sources of these juveniles, including spawners in the Shumagin Islands region itself and a larger up-current population spawning in Shelikof Strait (Fig. 1). The Shumagin Islands population is believed to spawn in late January and February (Dorn *et al.*, 2003; Guttormsen *et al.*, 2003), while walleye pollock spawn in Shelikof Strait in late March and early April (Kendall & Picquelle, 1990; Kendall *et al.*, 1996). Given the separation of spawning times, it should be possible to infer resident *v.* immigrant source of juveniles in the Shumagin region from their hatch dates.

Daily otolith increments are also used to determine growth rates, which in turn are used to assess both geographic and year-to-year variability in conditions that impact productivity. Juvenile walleye pollock show both geographical and interannual differences in growth (Bailey *et al.*, 1996a; Wilson, 2000; Wilson *et al.*, 2005), but the impact of environmental conditions on growth and subsequent effects of size-at-age on recruitment are largely unexamined.

In this study, age and standard length ( $L_S$ ) data of age-0 year walleye pollock from 1985 to 2001 were used to: 1) determine the stock of origin of juvenile fish caught in the Shumagin Islands region based on comparisons of their hatch date distributions to that of known spawning stocks and 2) to examine interannual variability in  $L_S$ -at-age and hatch-date distribution in relation to environmental conditions. This information is important, not only as background for management of the stock but also because juvenile walleye pollock in this area are a critical food resource to endangered marine mammals and seabirds (Springer, 1992; Brodeur & Wilson, 1996; Merrick *et al.*, 1997).

## MATERIALS AND METHODS

### FIELD SAMPLING AND DATA COLLECTION

Age-0 year walleye pollock samples were collected from the Shumagin Islands area (Fig. 1) in the Gulf of Alaska from 1985 to 2001. Gear type varied among years, but was chosen for each survey to best sample the estimated size range of the fish present during the time period of each cruise (Table I). The collection of age-0 year pollock was opportunistic in 1985–1988 when sampling locations were determined based on the presence of fish identified by hydroacoustics. Age-0 year walleye pollock from all other years were captured during grid surveys where the gear was fished at pre-determined locations within a sampling grid regardless of acoustic sign. Specimens collected for otolith analysis were either preserved in 95% ethanol or frozen until the otoliths could be removed for study. Sagittal otoliths from age-0 year walleye pollock were processed and aged following the procedures of Brown & Bailey (1992).

Briefly, the otoliths were mounted in resin in the sagittal plane, ground, and polished until the nucleus and surrounding daily increments were readable. Otoliths

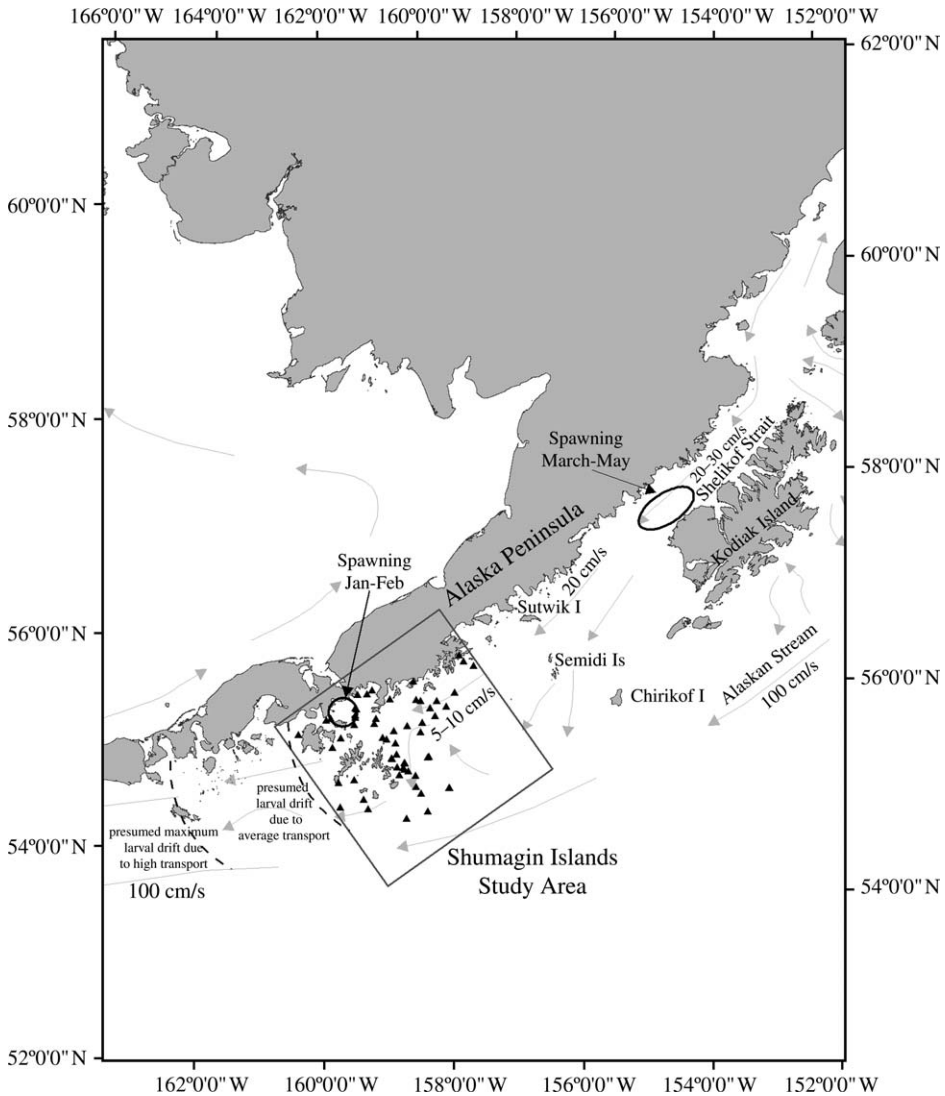


FIG. 1. Shumagin Islands study area (▲, sampled stations). Circled areas are known spawning grounds of walleye pollock in the Shumagin Islands and Shelikof Strait. ---, presumed larval drift of Shelikof Strait larvae due to average and high transport conditions.

were read using transmitted light at  $\times 400$  (for age-0 year daily increments outside the primary growth zone) and  $\times 1000$  (for larval daily increments) magnification using a Zeiss compound microscope. Daily increments for larval and age-0 year walleye pollock have been validated by Dell’Arciprete (1992) (2–3° C for yolk sac and early feeding larvae), Nishimura & Yamada (1984) (5–6° C) and Bailey & Stehr (1988) (8–9° C).

### GROWTH ESTIMATION

A non-linear Schnute (1981) model was fitted to an aggregated larval and juvenile data set from 1983 to 2001 to illustrate growth over all ages following the procedures

TABLE I. Collection information for age-0 year walleye pollock studied in the Shumagin Islands

| Year | Number of hauls aged | Haul dates               | Gear                       | Liner mesh (mm) | Number aged | $L_S$ range (mm) | Age range (days) |
|------|----------------------|--------------------------|----------------------------|-----------------|-------------|------------------|------------------|
| 1985 | 4                    | 30 August to 2 September | Shrimp trawl               | 3               | 60          | 44–75            | 104–135          |
| 1986 | 9                    | 3 to 9 September         | Shrimp trawl               | 3               | 53          | 42–79            | 96–146           |
| 1987 | 2                    | 25 to 27 August          | Shrimp trawl               | 3               | 43          | 47–71            | 95–129           |
| 1988 | 5                    | 18 to 30 August          | Shrimp trawl               | 3               | 56          | 46–85            | 99–145           |
| 1990 | 5                    | 11 to 13 September       | Anchovy trawl              | 3               | 46          | 49–85            | 112–143          |
| 1991 | 5                    | 25 to 29 July            | Method                     | 2 × 3           | 41          | 20–41            | 61–83            |
| 1993 | 3                    | 22 June to 5 July        | Issacs-Kidd midwater trawl | 4               | 55          | 15–32            | 48–73            |
| 1994 | 3                    | 18 to 19 July            | Issacs-Kidd midwater trawl | 4               | 11          | 38–48            | 79–89            |
| 1996 | 2                    | 1 to 4 July              | Issacs-Kidd midwater trawl | 4               | 54          | 16–30            | 58–90            |
| 1998 | 9                    | 20 to 21 June            | Method                     | 2 × 3           | 50          | 12–28            | 43–76            |
| 2000 | 4                    | 4 to 6 September         | Anchovy trawl              | 3               | 59          | 43–86            | 97–148           |
| 2001 | 7                    | 4 to 7 September         | Anchovy trawl              | 3               | 59          | 46–92            | 99–150           |

$L_S$ , standard length.

used in Brown & Bailey (1992). The larval data were from Bailey *et al.* (1996a) and more recently (1992–1997) from unpubl. data. The Schnute equation used was:

$$Y_t = \{Y_1^b + (Y_2^b - Y_1^b)[1 - e^{-a(t - \lambda_1)}][1 - e^{-a(\lambda_2 - \lambda_1)}]^{-1}\}^{b^{-1}}, \quad (1)$$

where  $t$  = time,  $Y_t$  = length at time  $t$  (in days) after hatching,  $\lambda_1$  and  $\lambda_2$  = two specified daily ages selected to represent upper and lower limits of the age range in the data,  $Y_1$  = predicted size-at-age  $\lambda_1$ ,  $Y_2$  = predicted size-at-age  $\lambda_2$ , and  $a$  and  $b$  are parameters of the curve. Non-linear least-squares regression (Wilkinson 1988) was used to estimate the parameters  $Y_1$ ,  $Y_2$ ,  $a$  and  $b$ . A ln transformation of the data was used to correct for multiplicative errors.

Although the growth of walleye pollock through several life stages is non-linear, growth has been well described by linear equations during segments of the life history. Size groups of late larval and age-0 year walleye pollock were defined by biological and statistical protocols in Brown *et al.* (2001). Briefly, to determine the  $L_S$  ranges for the growth changes observed on the Schnute model, a piecewise linear regression was fitted to the data and an iterative method was used to determine natural breakpoints in the regression. A breakpoint in the model at c. 40 mm  $L_S$ , corresponding to c. 90 days of age, was determined for age-0 year walleye pollock. This  $L_S$  corresponded to the size when walleye pollock are fully ossified and resemble small adults. Thus, for this study, group 1 (1991–1998) contained data with ages 30–90 days and group 2 (1985–1990, 2000 and 2001) contained data with ages 91–150 days. Coincidentally, these groups represented fish collected in June to July and August to September. Preserved  $L_S$  and age was used to calculate a least-squares linear growth equation for each year within a group. Residuals were randomly distributed indicating that linear models described the data adequately. Shrinkage in  $L_S$  due to preservation was not corrected for this part of the study so that the  $L_S$  would be comparable with past studies (Bailey *et al.*, 1996a). The linear regression equations for years within groups were compared using nested ANCOVAs and tested for interactions between year and age (except for 1994 which had a limited amount of data). A nested design was used with haul nested within year since  $L_S$  were not independent (fish within a haul were more similar than fish between hauls). Therefore, the sample size was the number of hauls, not the number of fish. Each ANCOVA was followed by pair-wise comparisons of slopes (growth rates) between years. Results were significant with  $P < 0.05$ .

Using the linear equation generated by each year's  $L_S$  and age data, a  $L_S$  for each year was backcalculated using age at 70 days for the small fish (group 1) and age at 120 days for the large fish (group 2) to compare years at a common age (Table II). These ages represented the approximate mean value for the data within each group. A parametric test using the  $t$ -statistic was used to determine if the estimated  $L_S$  at age 70 days for each year was different from the estimated  $L_S$  from all other years combined (Zar, 1984). The same test ( $L_S$ -at-age analysis) was applied to the age at 120 days for the applicable years. Growth anomalies for each year were determined as the difference of the predicted  $L_S$ -at-age (at either 70 or 120 days depending on the sampling dates for that year) and the within group mean  $L_S$ -at-age for all years but excluding that particular year. This result was compared to the average residual of each year calculated as the sum of the difference between observed  $L_S$ -at-age and the predicted  $L_S$  from the Schnute model divided by the number of observations. The mean residuals derived from each method were highly correlated ( $r^2 = 0.95$ ,  $n = 12$ ).

## CALCULATION OF HATCH DATE DISTRIBUTIONS

Before the age keys were applied to  $L_S$  frequencies to estimate hatch date distributions, the data were adjusted to account for sampling duration. For each year, the

TABLE II. Growth equation coefficients ( $a$ , intercept;  $b$ , slope) and statistical results for standard length ( $L_S$ )-at-age tests for Shumagin Islands age-0 year walleye pollock. Age group 1 is 30–90 days and age group 2 is 91–150 days. The  $L_S$ -at-age test for age group 1 was estimated at 70 days and age group 2 was estimated at 120 days (– or + represents small and larger-at-age respectively). Results are significant at  $P < 0.05$

| Year                      | Age group (years) | Growth coefficients* |      | $n$ | $r^2$ | $P$        |
|---------------------------|-------------------|----------------------|------|-----|-------|------------|
|                           |                   | $a$                  | $b$  |     |       |            |
| 1985                      | 2                 | –53.79               | 0.94 | 60  | 0.93  | 0.044 (–)  |
| All years<br>group 2-1985 |                   | –30.45               | 0.76 | 320 | 0.77  |            |
| 1986                      | 2                 | –30.39               | 0.71 | 53  | 0.89  | <0.001 (–) |
| All years<br>group 2-1986 |                   | –39.77               | 0.84 | 327 | 0.84  |            |
| 1987                      | 2                 | –7.27                | 0.59 | 43  | 0.68  | <0.001 (+) |
| All years<br>group 2-1987 |                   | –39.69               | 0.83 | 337 | 0.82  |            |
| 1988                      | 2                 | –54.30               | 0.96 | 56  | 0.89  | 0.144      |
| All years<br>group 2-1988 |                   | –29.71               | 0.75 | 324 | 0.77  |            |
| 1990                      | 2                 | –62.03               | 1.01 | 46  | 0.95  | 0.013 (–)  |
| All years<br>group 2-1990 |                   | –31.07               | 0.76 | 334 | 0.77  |            |
| 1991                      | 1                 | –24.49               | 0.71 | 41  | 0.87  | 0.383      |
| All years<br>group 1-1991 |                   | –6.08                | 0.45 | 170 | 0.54  |            |
| 1993                      | 1                 | –7.63                | 0.51 | 55  | 0.65  | <0.001 (+) |
| All years<br>group 1-1993 |                   | –13.92               | 0.56 | 156 | 0.69  |            |
| 1994                      | 1                 | –19.53               | 0.75 | 11  | 0.43  | <0.001 (+) |
| All years<br>group 1-1994 |                   | –5.70                | 0.44 | 200 | 0.68  |            |
| 1996                      | 1                 | –2.33                | 0.35 | 54  | 0.83  | <0.001 (–) |
| All years<br>group 1-1996 |                   | –15.56               | 0.62 | 157 | 0.85  |            |
| 1998                      | 1                 | –8.30                | 0.48 | 50  | 0.75  | 0.250      |
| All years<br>group 1-1998 |                   | –9.95                | 0.51 | 161 | 0.59  |            |
| 2000                      | 2                 | –45.37               | 0.87 | 59  | 0.85  | 0.005 (–)  |
| All years<br>group 2-2000 |                   | –31.39               | 0.77 | 321 | 0.78  |            |
| 2001                      | 2                 | –46.96               | 0.92 | 59  | 0.91  | <0.001 (+) |
| All years<br>group 2-2001 |                   | –29.78               | 0.75 | 321 | 0.78  |            |

\*Growth equation:  $L_S = a + bx$ , where  $x$  is age.

$L_S$  and age data were adjusted to the mean survey date (MSD) such that fish that were caught before or after the mean survey date would be ‘grown’ or ‘shrunk’ by the calculated growth rate of the cohort. For example, a fish that was sampled 1 day before the MSD would have to be increased in age by 1 day and its  $L_S$  increased by one unit of

growth derived from the growth equation for that group of fish. Adjustment to the mean survey date was preferred over using raw age- $L_S$  data or interpolating age from an age and  $L_S$  relationship (Hinckley *et al.*, 1993; Bailey *et al.*, 1996b). The equation used to calculate the  $L_S$  at MSD ( $L_{S\text{MSD}}$ ) from Bailey *et al.* (1996b) was:  $L_{S\text{MSD}} = L_{S\text{SSD}} + (\hat{L}_{S\text{MSD}} - \hat{L}_{S\text{SSD}})$ , where  $L_{S\text{SSD}}$  is the  $L_S$  at survey date (at day of capture),  $\hat{L}_{S\text{MSD}}$  is the predicted  $L_S$  at mean survey date and  $\hat{L}_{S\text{SSD}}$  is the predicted  $L_S$  at the survey date. The two predicted variables were calculated by applying the linear growth equation generated from the original  $L_S$  and age data with the ages altered for the adjustment to MSD and the original ages, respectively. All  $L_S$  were then standardized to fresh fork length ( $L_F$ ) using the preservation correction equations from Buchheister & Wilson (2005), since the length frequency data from 1985 to 1988 were recorded in fresh  $L_F$ . These corrections were necessary since different preservation methods (e.g. 95% ethanol, 10% formalin, frozen) were used in some years or the length frequency data were not recorded in  $L_S$ . The corrected lengths were then used to construct the age keys for each year. These corrections and adjustments were only used in the hatch date analysis.

To construct the age keys, MSD fresh  $L_S$  were placed into 10 mm intervals corresponding to lengths recorded at-sea. The age-key data were expanded across the length frequency data for each year to assign ages. Hatch dates were determined by subtracting the age of fish from the date of catch. Hatch dates were then summed into 5 day hatch groups and the total number of fish was calculated for each year. To determine the frequency percentage for each 5 day hatch group, the number in each hatch group was divided by the total number of fish and then multiplied by 100.

The age-0 year hatch date distributions were compared to the observed larval hatch date distributions from the Shelikof Strait and the estimated hatch dates from the Shumagin Islands spawning groups to determine the potential spawning origin of the fish. Larval hatch date distributions resulting from Shelikof Strait spawned fish were constructed from previously reported age and growth data (Bailey *et al.*, 1996a) and more recent data (1993, 1994 and 1996; unpubl. data). An estimated hatch date distribution for the Shumagin Islands area was constructed from the approximate spawning times, late January to February, as reported in Dorn *et al.*, 2003 and Guttormsen *et al.*, 2003. Average water temperature during the main spawning off Renshaw Point was estimated as 5–6° C. The hatching of the eggs was estimated to occur 14 days after fertilization for this temperature range based on egg development and temperature experiments (Blood *et al.*, 1994).

## ENVIRONMENTAL FACTORS AND RECRUITMENT

Sea surface temperature ( $T_{SS}$ ) data for 1985–2001 in the Shelikof and Shumagin areas were obtained from the Comprehensive Ocean Atmosphere Data Set (COADS) (A. Macklin & M. Spillane, unpubl. data). From these data, the mean  $T_{SS}$  for May through to July and May through to September for each year was calculated to compare to the overall mean for all years during the same period. Temperature anomalies were determined from either May to July or May to September mean temperatures depending on the sampling period for each year, representing the cumulative temperature that the cohort experienced prior to sampling (Table III). A wind mixing parameter was calculated as the wind speed cubed, from mean geotriptic winds calculated from atmospheric pressure differences in the sea valley between Kodiak Island and the Semidi Islands. The transport index ( $S_V$ ) south-westward through Shelikof Strait, below 100 m, from March to April was produced by the SPEM model as described by Hermann *et al.* (1996) (M. Spillane, unpubl. data). Recruitment was determined from the number of age-2 year walleye pollock returning to the western Gulf of Alaska population as defined from an age-structured stock assessment (Dorn *et al.*, 2003). Recruitment anomalies were calculated as the differences between annual values and the mean value across years.

TABLE III. Growth and sea surface temperature ( $T_{ss}$ ) data for age-0 year walleye pollock from 1985 to 2001

|   | 1985  | 1986  | 1987  | 1988    | 1990  | 1991    | 1993  | 1994  | 1996  | 1998    | 2000  | 2001  |
|---|-------|-------|-------|---------|-------|---------|-------|-------|-------|---------|-------|-------|
| Growth data                                 |       |       |       |         |       |         |       |       |       |         |       |       |
| Age-0 growth rates (mm day <sup>-1</sup> )  | 0.94  | 0.71  | 0.59  | 0.96    | 1.01  | 0.71    | 0.51  | 0.75  | 0.35  | 0.48    | 0.87  | 0.92  |
| $L_S$ at age 120 days (mm) group 2          | 59.0  | 54.8  | 63.5  | 60.9    | 59.2  |         |       |       |       |         | 59.0  | 63.4  |
| $L_S$ at age 120 all years (excluding year) | 60.8  | 61.0  | 59.9  | 60.3    | 60.1  |         |       |       |       |         | 61.0  | 60.2  |
| Comparison of size at age 120 days          | Small | Small | Large | Average | Small |         |       |       |       |         | Small | Large |
| $L_S$ at age 70 days (mm) group 1           |       |       |       |         |       | 25.21   | 28.1  | 33.0  | 22.2  | 25.30   |       |       |
| $L_S$ at age 70 all years (excluding year)  |       |       |       |         |       | 25.42   | 25.3  | 25.1  | 27.8  | 25.75   |       |       |
| Comparison of size at age 70 days           |       |       |       |         |       | Average | Large | Large | Small | Average |       |       |
| Growth anomaly                              | -1.74 | -6.22 | 3.62  | 0.69    | -0.96 | -0.21   | 2.79  | 7.87  | -5.67 | -0.45   | -1.98 | 3.22  |
| $T_{ss}$ (°C)                               |       |       |       |         |       |         |       |       |       |         |       |       |
| May to July mean                            | 6.37  | 6.20  | 7.40  | 7.73    | 7.30  | 6.97    | 7.70  | 7.43  | 7.13  | 7.53    | 7.00  | 7.97  |
| 1985-2001 May to July mean                  | 7.23  | 7.23  | 7.23  | 7.23    | 7.23  | 7.23    | 7.23  | 7.23  | 7.23  | 7.23    | 7.23  | 7.23  |
| May to July anomaly                         | -0.86 | -1.03 | 0.17  | 0.50    | 0.07  | -0.26   | 0.47  | 0.20  | -0.10 | 0.30    | -0.23 | 0.74  |
| May to September mean                       | 7.74  | 7.86  | 8.98  | 8.98    | 8.78  | 8.28    | 9.02  | 8.84  | 8.44  | 8.78    | 8.54  | 9.06  |
| 1985-2001 May to September mean             | 8.61  | 8.61  | 8.61  | 8.61    | 8.61  | 8.61    | 8.61  | 8.61  | 8.61  | 8.61    | 8.61  | 8.61  |
| May to September anomaly                    | -0.87 | -0.75 | 0.37  | 0.37    | 0.17  | -0.33   | 0.41  | 0.23  | -0.17 | 0.17    | -0.07 | 0.45  |

 $L_S$ , standard length.



## RESULTS

The combined larval and age-0 year data from 1983 to 2001 were used to construct a composite growth model to depict the overall growth dynamics during the early life history of walleye pollock (Fig. 2). The model demonstrated that combined early life-stage data for this species do not remain linear and hence the data must be broken down into age groups to compare the data interannually when sampling dates differ between years.

Examination of residuals around the lines determined from linear growth equations indicated that growth was well described by straight lines over the age intervals defining the groups (Fig. 3). The results from nested ANCOVAs on the linear growth equations demonstrated that there were significant differences in growth rates between some years. Due to limited data, 1994 was not included in the ANCOVA analyses. In group 1 (1991–1998), 1991 was identified as significantly different from all other years in the group, and 1996 was significantly different from 1998 (1996 had a lower growth rate). For group 2 (1985–1990, 2000 and 2001), 1986 and 1987 were significantly different (lower growth rates) from all other years in that group (Fig. 3). With the data assigned to age groups 1 or 2, the results from the  $L_S$ -at-age analyses (comparing points on two regression lines) identified which years were significantly different when  $L_S$ -at-age at 70 (group 1) or 120 (group 2) days was considered (Table II). Years in which the fish were determined to be significantly smaller-at-age by the  $L_S$ -at-age analyses were 1985, 1986, 1990, 1996 and 2000. Years in which

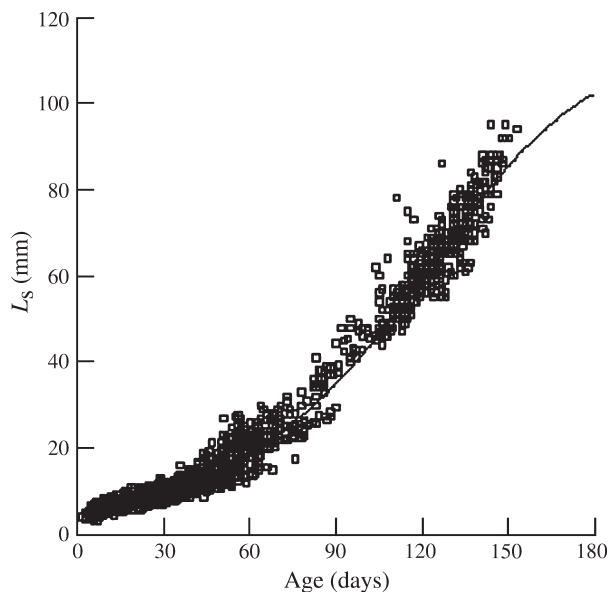


FIG. 2. Schnute growth model (equation 1) constructed from larval and age-0 year walleye pollock data for 1983–2001. Larval data are from 1983 to 1997 while the age-0 year data are from 1985 to 2001. The coefficients of the model for the equation 1 are  $Y_1 = 4.92$ ,  $Y_2 = 85.36$ ,  $a = 0.039$  and  $b = -1.72$ . The upper and lower limits chosen to represent the daily age range of the data were  $\lambda_1 = 0$  and  $\lambda_2 = 160$  days.

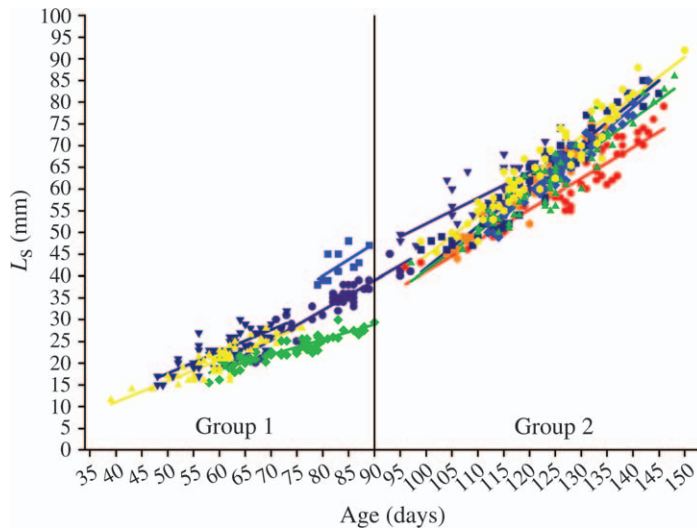


FIG. 3. Age and standard length ( $L_S$ ) data for 1985–2001 (group 1: ●, 1991; ▼, 1993; ■, 1994; ◆, 1996; ▲, 1998; group 2: ●, 1985; ●, 1986; ▼, 1987; ■, 1988; ◆, 1990; ▲, 2000; ●, 2001) for age-0 year walleye pollock. Fish were assigned to age group 1 or 2 to compare  $L_S$ -at-age of similarly aged fish in statistical tests (see Table II).

the fish were significantly larger-at-age were 1987, 1993, 1994 and 2001. The other years (1988, 1991 and 1998) were not significantly different and were considered to be average  $L_S$ -at-age (Table III). The mean  $L_S$ -at-age at 70 days was an extrapolation beyond the data in 1994, but inclusion was justified because the  $L_S$ -at-age is clearly higher than other years and the extrapolated value remains so. The predicted mean  $L_S$ -at-age fell within the data range for all other years.

Hatch date distributions for Shelikof Strait larvae, determined from surveys conducted in early and late May, were plotted to compare with the estimated Shumagin Islands region hatch date distribution (Fig. 4). The only overlap between these two geographically and chronologically distinct spawning stocks was at the end of March and a few days into April. The hatch date distributions determined for juveniles for all years from the Shumagin Islands region (Fig. 5) do not overlap with the estimated hatch date distribution of Shumagin Islands spawned fish, but did closely resemble the larval hatch date distributions from the Shelikof Strait spawning group. The within-year comparison between the Shelikof larvae and Shumagin age-0 year walleye pollock hatch dates were usually quite similar, such as 1985 and 1993 (Fig. 6).

Interannual variability in the mean hatch date in the Shumagin region was not related to either indices of March to April transport in Shelikof Strait (linear regression analysis,  $P > 0.05$ ) or to May winds in the Shelikof region ( $P > 0.05$ ), which potentially influences egg and larval transport (Table IV). Therefore, it was not apparent that the sampled span of the hatch date distribution was directly related to the variability in transport from the Shelikof spawning region. Assuming that the Shumagin age-0 year fish originated from Shelikof

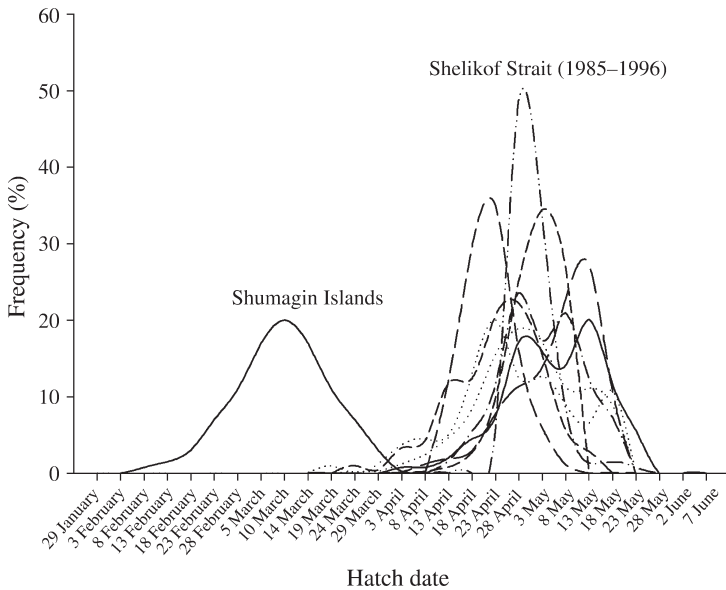


FIG. 4. Observed hatch date distributions of larval walleye pollock from the Shelikof Strait region from 1985 (.....), 1986 (-----), 1987 (-.-.-.-), 1988 (----), 1990 (-.-.-), 1991 (----), 1993 (—), 1994 (—), 1996 (-----) (only years in common with age-0 year data illustrated) and the presumed hatch date distribution of fish from the Shumagin Islands (—) spawning group based on observed spawning times and temperatures.

Strait spawning, mean hatch dates were significantly and negatively correlated with March to April  $T_{SS}$  (reflecting bottom temperatures prior to and during spawning and egg development assuming a well-mixed water column) in Shelikof Strait (Fig. 7;  $P < 0.05$ ). There was a significant positive relationship ( $P < 0.05$ ) between the interannual anomaly in  $L_S$ -at-age and the  $T_{SS}$  anomaly in the months prior to capture (Fig. 8). There was no significant relationship between the growth anomaly and recruitment anomaly data ( $P > 0.05$ ).

## DISCUSSION

Ocean currents in the western Gulf of Alaska are part of a vigorous and dynamic system that disperses eggs and larvae, and determines the subsequent distribution of juvenile walleye pollock. The Alaska Coastal Current (ACC) flows through Shelikof Strait in early spring at typical speeds of  $0.2\text{--}0.3\text{ m s}^{-1}$ , but sometimes exceeds  $0.5\text{ m s}^{-1}$  (Stabeno *et al.*, 2004). About half of the transport continues along the Alaska Peninsula at slower speeds of  $0.05\text{--}0.10\text{ m s}^{-1}$ , and the other half flows into the swifter Alaskan Stream with speeds of  $0.5\text{--}1\text{ m s}^{-1}$ . The potential drift zones of walleye pollock larvae spawned in Shelikof Strait based on average and high transport conditions are identified in Fig. 1. Current speed and direction towards the Shumagin Islands makes this a probable nursery area for the Shelikof Strait spawned fish that travel in the ACC along the Alaska Peninsula, as well as those swept into the Alaskan Stream and later meander back onto the shelf. Larvae that originated in

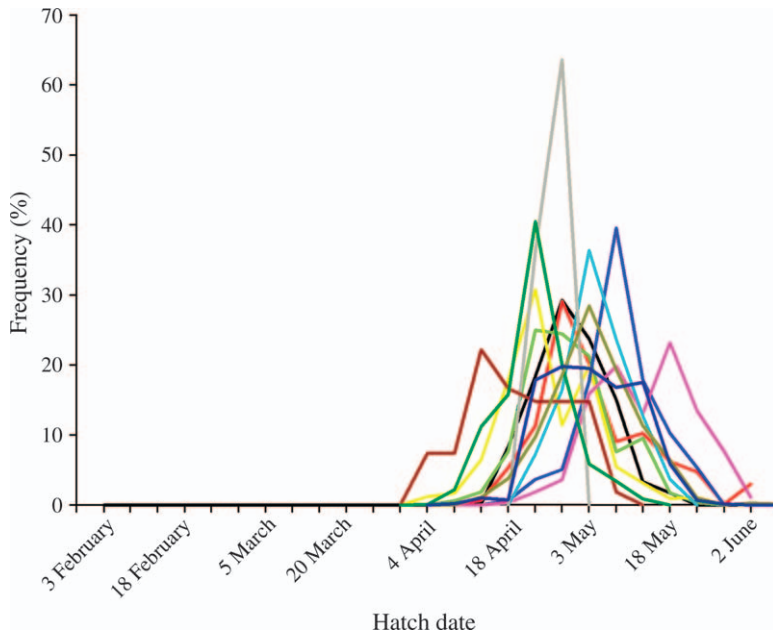


FIG. 5. Hatch date distributions of age-0 year pollock caught in the Shumagin Islands study area for 1985 (—), 1986 (—), 1987 (—), 1988 (—), 1990 (—), 1991 (—), 1993 (—), 1994 (—), 1996 (—), 1998 (—), 2000 (—) and 2001 (—). Intervals on the x-axis represent 5 day hatch intervals.

the Shumagin Islands were probably swept out of the survey area before the larvae and age-0 year fish from Shelikof Strait spawners were sampled around the Shumagin Islands. This may explain why age-0 year walleye pollock that were from the earlier Shumagin spawning group were not found even though the area was surveyed with different types of gear that were capable of catching the estimated size range for these fish (70–100 mm). These larvae may occupy downstream nurseries in the Aleutian Islands, or they are lost in the Alaskan Stream.

In order to collect as much age and  $L_S$  data as possible to construct a representative model of the age-0 year walleye pollock life history, samples collected from different age-0 year developmental periods were used so that a broad age and size range would be represented. The opportunistic nature of some sampling resulted in different fishing gears used throughout the age-0 year growth period (mid-June to late September).

The use of different gear types may have resulted in some of the smaller or larger members of the cohort not being sampled properly due to net avoidance (gear too slow or mesh too small) or escapement (mesh too large to retain smaller individuals). The gear used for surveys during this time period, however, should have captured fish of this size if they were present (Brodeur *et al.*, 1995). A size-selective effect due to the gear did not seem to be affecting the age range of age-0 year fish available for calculating the hatch date distributions.

By using both the growth rate (determined from linear growth equations fitted to the aggregated  $L_S$ -at-age at capture) and the estimated  $L_S$ -at-age from

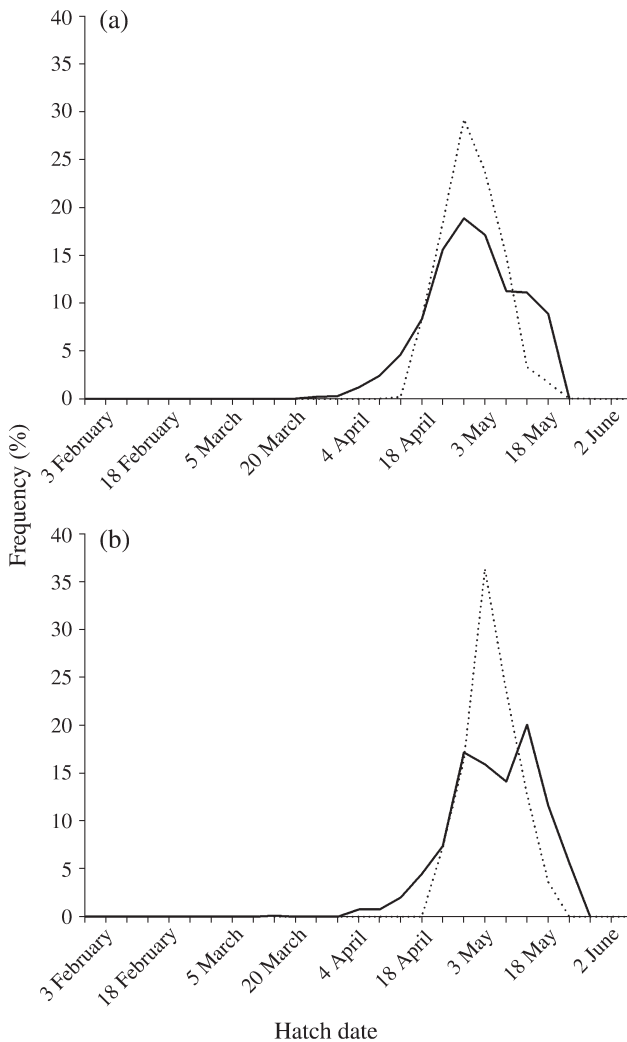


FIG. 6. Hatch date distributions of larvae from Shelikof Strait (—) compared to hatch date distributions of age-0 year walleye pollock sampled from the Shumagin Islands (.....) for (a) 1985 and (b) 1993.

the growth equations, it was possible to determine if there were growth differences at some point prior to capture. If only the growth equations had been examined, a difference between years in some cases would not have been detected. For example, the ANCOVA results for the comparison of growth equations for 1986 and 1987 indicated that growth rates were not significantly different. The estimated  $L_5$ -at-age at day 120 of the 1986 fish, however, were smaller than in 1987 even though the 'growth rate' for 1986 appeared to be slightly higher than 1987. Thus, fish were growing slower in 1986 prior to sampling and were smaller-at-age under sustained cooler water temperatures (below mean  $T_{SS}$  from the larval period to the early juvenile stage). Comparisons of growth rates based on slopes from regressions of  $L_5$  and age assume

TABLE IV. Environmental anomalies and regression results. Sea surface temperatures ( $T_{ss}$ ) are given in °C.  $T_{ss}$  anomaly is the May to September or May to July (1991–1998) deviation from the mean  $T_{ss}$  in the Shumagin region prior to sampling. Regression results are significant at  $P < 0.05$  (– or + represents a negative or positive relationship)

|   | 1985     | 1986  | 1987     | 1988     | 1990  | 1991   | 1993  | 1994     | 1996     | 1998     | 2000  | 2001  |
|---|----------|-------|----------|----------|-------|--------|-------|----------|----------|----------|-------|-------|
| Mean hatch date                             | 30-April | 4-May | 30-April | 25-April | 9-May | 13-May | 2-May | 26-April | 19-April | 23-April | 3-May | 3-May |
| Julian mean hatch date                      | 120      | 124   | 120      | 116      | 129   | 133    | 122   | 116      | 110      | 113      | 124   | 123   |
| March to April average $T_{ss}$ (Sheikof)   | 4.10     | 4.00  | 4.75     | 4.65     | 3.60  | 3.35   | 4.20  | 4.25     | 4.05     | 5.90     | 4.55  | 4.75  |
| March to April transport index ( $S_v$ )    | 0.57     | -0.04 | 0.29     | 1.01     | 0.26  | 0.40   | 0.47  | 0.33     | 0.29     | 0.43     | 0.41  | 0.58  |
| Mean May winds $m^3 s^{-3}$ (in thousands)  | 0.93     | 1.06  | 0.73     | 0.34     | 0.48  | 0.87   | 0.63  | 0.27     | 0.42     | 0.74     | 0.38  | 0.80  |
| Growth anomaly                              | -1.74    | -6.22 | 3.62     | 0.69     | -0.96 | -0.21  | 2.79  | 7.87     | -5.67    | -0.45    | -1.98 | 3.22  |
| $T_{ss}$ anomaly                            | -0.87    | -0.75 | 0.37     | 0.37     | 0.17  | -0.26  | 0.47  | 0.20     | -0.09    | 0.30     | -0.07 | 0.45  |
| Recruitment anomaly                         | 0.44     | -0.79 | 0.04     | 1.53     | 0.18  | -0.38  | -0.51 | 0.84     | -0.82    | -0.12    | 0.67  | -1.08 |
| Regression results                          | $n$      | $r^2$ | $P$      |          |       |        |       |          |          |          |       |       |
| March to April $T_{ss}$ and mean hatch date | 12       | 0.36  | 0.04 (-) |          |       |        |       |          |          |          |       |       |
| $S_v$ v. mean hatch date                    | 12       | 0.05  | 0.49     |          |       |        |       |          |          |          |       |       |
| May winds v. mean hatch date                | 12       | 0.14  | 0.23     |          |       |        |       |          |          |          |       |       |
| $T_{ss}$ anomaly v. growth anomaly          | 12       | 0.41  | 0.03 (+) |          |       |        |       |          |          |          |       |       |
| Growth anomaly v. recruitment anomaly       | 12       | 0.09  | 0.33     |          |       |        |       |          |          |          |       |       |

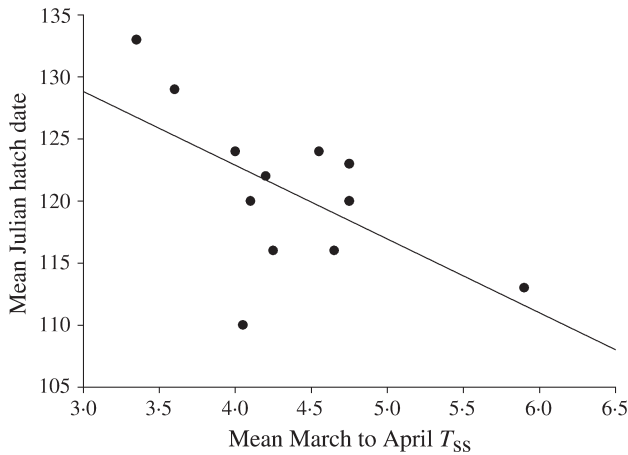


FIG. 7. Weighted mean Julian hatch dates for 1985–2001 calculated from age-0 year walleye pollock in relation to mean March to April sea surface temperature ( $T_{SS}$ ) in the Shelikof region. The curve was fitted by  $y = 146.65 - 5.94x$  (see Table IV).

that constant growth occurred for all ages prior to sampling, and thus need to be viewed with caution. Known violations of this assumption, such as seasonal variability in larval growth rates, justify the  $L_S$ -at-age analysis. In an exploratory analysis, variability was standardized around the linear equations by calculating the residuals (growth anomaly) and combining the residuals from the age groups. The result was essentially the same as estimating the mean residuals from the non-linear model due to the high correlation between residuals

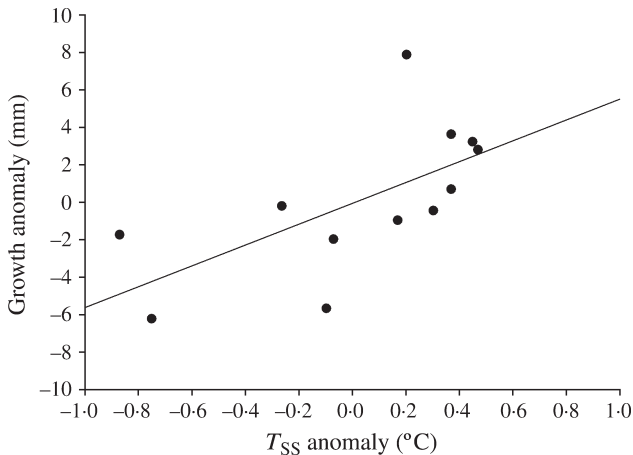


FIG. 8. Relationship of growth and sea surface temperature ( $T_{SS}$ ) for age-0 year walleye pollock from the Shumagin Islands study area. Growth and temperature anomalies were determined by the difference of annual values and the mean values across years. Growth anomalies were determined from standard length-at-age at either 70 or 120 days depending on the sampling dates in each year, and similarly their temperatures were either May to July or May to September, representing the cumulative temperature experienced by the cohort prior to sampling. The curve was fitted by  $y = -0.05 + 5.56x$  (see Table IV).

calculated using both methods ( $r^2 = 0.95$ ), but straight lines fit the data better over the observed age ranges.

The Shumagin Islands region is not necessarily the optimum location for fish growth when compared to other areas in the Gulf of Alaska. Brown & Bailey (1992) compared age and growth of the 1987 cohort of age-0 year walleye pollock from different areas. Fish from the Unimak Island area had similar growth and hatch dates to the fish caught upstream in the Shumagin Islands. Growth rates were significantly higher, however, in the Kodiak Island area compared to the fish sampled around the Shumagin Islands. The Kodiak-area fish were not only faster growing but they had also hatched earlier than the Shumagin-area fish. Wilson (2000) compared age-0 year walleye pollock size between geographic areas of the western GOA for 1985–1988 and showed that fish sampled around Kodiak Island were consistently larger than those around the Shumagin Islands and that the Unimak area age-0 year walleye pollock were similar in size to the fish sampled in the Shumagin Islands. Prey-rich areas in several of the bays on the east side of Kodiak Island were reported by Wilson *et al.* (2005), which along with higher temperatures, may explain the higher growth rates of age-0 year walleye pollock in bays.

When the age-0 year hatch date distributions for all years in this study were plotted together (Fig. 5), it demonstrated that the age-0 year walleye pollock surveyed in the Shumagin Islands hatched too late to have originated from the Shumagin Islands spawning group. Although the peak hatch date for the age-0 year fish shifted slightly from 1 year to the next (depending on temperature), the hatch date ranges were still similar to the observed hatch range of Shelikof Strait larvae. If it is assumed that the Shumagin-spawned fish had 60 days more growth than the Shelikof-spawned fish (with the same amount of size-selective mortality and similar growth rates as the Shelikof fish), then the expected  $L_S$  range for Shumagin-spawned fish in the first week of September would be *c.* 70–100 mm compared to the mean observed  $L_S$  range of 50–80 mm for age-0 year fish sampled from the Shumagin Islands.

Differences in the peak hatch-date distribution among years for the age-0 year walleye pollock may be the result of several different factors. For example, high early season mortality during the egg and larval stages would result in fewer fish represented at the start of the hatch date distribution. Numerous strong-wind events during the early larval development period could reduce the potential prey field or cause episodic advective losses of larval cohorts resulting in increased early larval mortality (Bailey & Macklin, 1994). Interannual variability in the annual mean hatch date of juveniles from the Shumagin region was not directly related to indices of transport, but it was negatively correlated with temperature; temperature may be an indirect signal of transport conditions. This negative correlation may also indicate a linkage with either earlier maturation of spawning fish or faster egg development and hatching.

By defining the hatch date distribution of the Shumagin Islands age-0 year walleye pollock, it was confirmed that some juveniles from the Shelikof Strait spawning use this area as a nursery ground. Although the feeding and growth conditions may be better in other areas in the Gulf of Alaska, the Shumagin Islands are a consistent habitat for age-0 year walleye pollock. Since the transport of the larvae to this area is dependent on the strength and direction of the



ACC, years with anomalous transport conditions will probably influence larval and age-0 year survival and hence future recruitment into the fishery. Interannual variability in temperature and feeding conditions may also affect the growth of the larvae and age-0 year fish and the overwintering potential of juveniles. The comparison of growth and recruitment information showed that the  $L_S$ -at-age anomaly was not linearly correlated with recruitment; years with relatively high recruitment may result from years with slow or fast growing age-0 year fish. Likewise, low recruitment years can arise from either fast or slow growing age-0 year fish. These results may reflect the complex balance between environmental conditions, enhanced survival of fast-growing individuals and density-dependence (Ciannelli *et al.*, 2004).

We wish to thank K. Chumbley (National Marine Mammal Laboratory, Alaska Fisheries Science Center) and the crew of the NOAA ship *Miller Freeman* for their generous help with specimen collections. We also thank S. Porter and M. Wilson for comments on the manuscript. This research is contribution FOCI-0565 to NOAA'S Fisheries Oceanography Coordinated Investigations. Reference to tradenames does not imply endorsement by NMFS-NOAA.

### References

- Bailey, K. M. & Macklin, S. A. (1994). Analysis of patterns in larval walleye pollock *Theragra chalcogramma* survival and wind mixing events in Shelikof Strait, Gulf of Alaska. *Marine Ecology Progress Series* **113**, 1–12.
- Bailey, K. M. & Stehr, C. L. (1988). The effects of feeding periodicity and ration on the rate of increment formation in otoliths of larval walleye pollock *Theragra chalcogramma* (Pallas). *Journal of Experimental Marine Biology and Ecology* **122**, 147–161.
- Bailey, K. M., Brown, A. L., Yoklavich, M. M. & Mier, K. L. (1996a). Interannual variability in growth of larval and juvenile walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska, 1983–91. *Fisheries Oceanography* **5** (Suppl. 1), 137–147.
- Bailey, K. M., Picquelle, S. J. & Spring, S. M. (1996b). Mortality of larval walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska, 1988–1991. *Fisheries Oceanography* **5** (Suppl. 1), 124–136.
- Begg, G. A. & Marteinsdottir, G. (2000). Spawning origins of pelagic juvenile cod *Gadus morhua* inferred from spatially explicit age distributions: potential influences on year-class strength and recruitment. *Marine Ecology Progress Series* **202**, 193–217.
- Blood, D. M., Matarese, A. C. & Yoklavich, M. M. (1994). Embryonic development of walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. *Fishery Bulletin* **92**, 207–222.
- Brodeur, R. D. & Wilson, M. T. (1996). A review of the distribution, ecology and population dynamics of age-0 walleye pollock in the Gulf of Alaska. *Fisheries Oceanography* **5** (Suppl. 1), 148–166.
- Brodeur, R. D., Busby, M. S. & Wilson, M. T. (1995). Summer distribution of early life stages of walleye pollock, *Theragra chalcogramma*, and associated species in the western Gulf of Alaska. *Fishery Bulletin* **93**, 603–618.
- Brown, A. L. & Bailey, K. M. (1992). Otolith analysis of juvenile walleye pollock (*Theragra chalcogramma*) from the western Gulf of Alaska. *Marine Biology* **112**, 23–30.
- Brown, A. L., Busby, M. S. & Mier, K. L. (2001). Walleye pollock *Theragra chalcogramma* during transformation from the larval to juvenile stage: otolith and osteological development. *Marine Biology* **139**, 845–851.

- Buchheister, A. & Wilson, M. T. (2005). Shrinkage correction and length conversion equations for *Theragra chalcogramma*, *Mallotus villosus*, and *Thaleichthys pacificus*. *Journal of Fish Biology* **67**, 541–548. doi: 10.1111/j.1095-8649.2005.00741.x
- Ciannelli, L., Chan, K. S., Bailey, K. M. & Stenseth, N. C. (2004). Non-additive effects of environmental variables on the survival of a large marine fish population. *Ecology* **85**, 3418–3427.
- Dell'Arciprete, O. P. (1992). Growth, mortality, and transport of walleye pollock larvae (*Theragra chalcogramma*) in the eastern Bering Sea. MS Thesis, University of Washington, Seattle, WA.
- Dorn, M., Barbeaux, S., Guttormsen, M., Megrey, B., Hollowed, A., Wilkins, M. & Spalinger, K. (2003). Assessment of walleye pollock in the Gulf of Alaska. In *North Pacific Groundfish Stock Assessment and Fishery Evaluation Report*, Section 2, pp. 33–148. Anchorage, AK: North Pacific Fishery Management Council.
- Guttormsen, M. A., Wilson, C. D. & Stienessen, S. (2003). Results of the February and March 2003 echo integration-trawl surveys of walleye pollock (*Theragra chalcogramma*) conducted in the Gulf of Alaska, Cruises MF2003-01 and MF2003-05 (Appendix D). In *North Pacific Groundfish Stock Assessment and Fishery Evaluation Report*, Section 2, pp. 799–843. Anchorage, AK: North Pacific Fishery Management Council.
- Hellberg, M. E., Burton, R. S., Neigel, J. E. & Palumbi S. R. (2002). Genetic assessment of connectivity among marine populations. *Bulletin of Marine Science* **70** (Suppl. 1), 273–290.
- Hermann, A. J., Rugen, W. C., Stabeno, P. J. & Bond, N. A. (1996). Physical transport of young pollock larvae (*Theragra chalcogramma*) near Shelikof Strait as inferred from a hydrodynamic model. *Fisheries Oceanography* **5** (Suppl. 1), 58–70.
- Hinckley, S., Bailey, K., Picquelle, S., Yoklavich, M. & Stabeno, P. (1993). Age-specific mortality and transport of larval walleye pollock *Theragra chalcogramma* in the western Gulf of Alaska. *Marine Ecology Progress Series* **98**, 17–29.
- Kendall, A. W. Jr & Picquelle, S. J. (1990). Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. *Fishery Bulletin* **88**, 133–154.
- Kendall, A. W. Jr, Schumacher, J. D. & Kim, S. (1996). Walleye pollock recruitment in Shelikof Strait: applied fisheries oceanography. *Fisheries Oceanography* **5** (Suppl. 1), 4–18.
- Merrick, R. L., Chumbley, M. K. & Byrd, G. V. (1997). Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. *Canadian Journal of Fisheries and Aquatic Sciences* **54**, 1342–1348.
- Nishimura, A. & Yamada, J. (1984). Age and growth of larval and juvenile walleye pollock, *Theragra chalcogramma* (Pallas), as determined by otolith daily growth increments. *Journal of Experimental Marine Biology and Ecology* **82**, 191–205.
- Schnute, J. (1981). A versatile growth model with statistically stable parameters. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1128–1140.
- Springer, A. M. (1992). A review: walleye pollock in the North Pacific – how much difference do they really make? *Fisheries Oceanography* **1**, 80–96.
- Stabeno, P. J., Bond, N. A., Hermann, A. J., Kachel, N. B., Mordy, C. W. & Overland, J. E. (2004). Meteorology and oceanography of the Northern Gulf of Alaska. *Continental Shelf Research* **24**, 859–897.
- Wilkinson, L. (1988). *SYSTAT: The System for Statistics*. Evanston, IL: SYSTAT, Inc.
- Wilson, M. T. (2000). Effects of year and region on the abundance and size of age-0 walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska, 1985–1988. *Fishery Bulletin* **98**, 823–834.
- Wilson, M. T., Brown, A. L. & Mier, K. L. (2005). Geographic variation among age-0 walleye pollock (*Theragra chalcogramma*): evidence of mesoscale variation in nursery quality? *Fishery Bulletin* **103**, 207–218.
- Zar, J. H. (1984). *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall, Inc.