

Abstract.—This study examines the early life history of a population of walleye pollock, *Theragra chalcogramma* (Pallas), that is found in Resurrection Bay, Alaska. Ichthyoplankton samples were taken at six stations in Resurrection Bay during early May and early June 1989 along with hydrographic data. Standard lengths of all walleye pollock were measured, and subsamples from two stations were aged by using otolith increments for growth rate and hatch date analysis. Abundances ranged from 60 to 575 larvae m^{-2} in May and from 0 to 10 larvae m^{-2} in June with densities of up to 12 larvae m^{-3} in May. The estimated growth rate was 0.18 mm/day. Back-calculated hatch dates ranged from late March until early May; the median hatch date was 22 April. Comparisons of abundance and growth rate to values from other habitats indicate that this deep fjord provides a suitable habitat for larval walleye pollock. Hydrographic data and larval size distribution suggest that advection plays a major role in determining the distribution of larvae in the fjord.

Distribution, abundance, and growth of larval walleye pollock, *Theragra chalcogramma*, in an Alaskan fjord

Franz-Josef Müter

Brenda L. Norcross

Institute of Marine Science, School of Fisheries and Ocean Sciences
University of Alaska Fairbanks
Fairbanks, AK 99775-1080

Fjords have long been recognized as nursery grounds for many commercially important fish species (De Silva, 1973; Lie, 1978; Carmo Lopes, 1979). Matthews and Heimdal (1980) in their review of food chains in fjords pointed out that many fjords along Scandinavian, Scottish, and North American coasts are highly productive areas. The productivity of fjords is often enhanced by hydrographic boundary conditions or land runoff that can increase nutrient levels (Matthews and Heimdal, 1980). Production in fjords may be further enhanced by upwelling conditions at their mouths. This is especially true for the southern coast of Alaska, where the relaxation of easterly winds in summer promotes coastal divergence and upwelling (Royer, 1982).

Rogers et al. (1987) described the nearshore zone of the Gulf of Alaska as an important spawning or rearing area, or both, for several commercially important fish species, including walleye pollock, *Theragra chalcogramma*. However, no work has been done to examine the dynamics of early life history stages of walleye pollock or other fishes in Alaskan fjords.

We chose walleye pollock for this study because it was more abundant than any other species in Resurrection Bay (Smith et al., 1991) and its development and early life history in other areas of the Gulf of

Alaska are well known (Dunn and Matarese, 1987; Kendall et al., 1987; Kim, 1989). Furthermore, it is very important commercially, with annual landings off Alaska exceeding one million metric tons (Lloyd and Davis, 1989), and the walleye pollock resource shows high fluctuations in year-class strength (Megrey, 1991), which creates a strong incentive to determine possible causes.

Most of the research on pollock in the Gulf of Alaska has been focused on the Shelikof Strait region (Schumacher and Kendall, 1991), while other areas along the Gulf, except for Auke Bay in Southeast Alaska (Haldorson et al. 1989, a and b), have received little attention. Although the Shelikof Strait spawning area is believed to be the most important in the Gulf of Alaska (Hinckley et al., 1991), substantial pollock spawning occurs in other areas of the Gulf (Müter, 1992; Norcross and Frandsen¹).

Resurrection Bay shares many features with other embayments along the southcentral coast of Alaska and can be considered representative of the area. This study used growth analysis together with

¹ Norcross, B. L., and M. Frandsen. Distribution and abundance of larval fishes in Prince William Sound, Alaska, during 1989 after the *Exxon Valdez* oil spill. EVOS Symposium Proceedings. Am. Fish Soc. Symposium. In review.

distribution and abundance data to evaluate the role of this northern Gulf of Alaska fjord in the early life history of walleye pollock. Specifically, the objectives of this study were 1) to determine the distribution and abundance of walleye pollock larvae in a glaciated fjord, 2) to quantify growth rates of larvae within this fjord and compare growth rates to literature values from other areas, and 3) to estimate hatch dates of the observed population.

Materials and methods

Resurrection Bay is a fjord approximately 32 km long and 4–8 km wide, located within the coastal mountain range on the Kenai Peninsula on the south-central coast of Alaska (Fig. 1). The fjord's bathymetry shows an inner basin with a maximum depth of 300 m, separated by a sill from the outer basin. The sill is located about 15 km from the fjord's mouth at the narrowest point, between our sampling stations RES 2.5 and RES 3 (Fig. 1), and rises to a depth of approximately 185 m. The outer basin is slightly shallower (265 m) than the inner basin and has an open connection with the shelf.

Six stations were sampled along the fjord axis (Fig. 1) during two cruises, 1–4 May 1989 and 7–9 June 1989. Ichthyoplankton samples for this study were collected from the RV *Little Dipper*, a 9-m aluminum boat. Horizontal plankton tows were taken at discrete depths by using a 1-m² Tucker trawl, rigged with two 505- μ mesh nets. Because no previous data

were available we took samples throughout the water column. We tried to obtain at least one sample from each of the following depth strata per station: 0–15 m, 15–30 m, 30–50 m, 50–80 m, 80–150 m, and 150-m to the bottom. Because of weather and time constraints, fewer samples were taken at some stations. Sample depths were initially estimated from wire angle and length of extended wire. Actual depths were recorded with an attached Seabird Seacat conducting-temperature-depth (CTD) (SBE 19) profiler and retrieved after completion of the cruise. The nets were rigged to a double tripper which allowed the second net to be opened and closed via a messenger from the surface. The net was towed for five minutes in the direction of tidal flow at a towing speed of 1.5 to 2.5 knots. Only daytime tows were made. Volume filtered during each tow was calculated from a TSK or General Oceanics flowmeter that was attached in a central position to the mouth of the net. Samples used for this analysis were immediately preserved in 50% isopropyl alcohol or 95% ethyl alcohol. The alcohol was renewed for each sample after 24 hours and after 2–3 days. Because differential shrinkage was observed between preservatives, only larvae preserved in isopropyl alcohol were used in size comparisons.

A Seabird CTD Profiler was attached to the net during most tows to record conductivity, temperature, and pressure throughout the tow. When no CTD data were recorded, depth was estimated from the wire angle and the length of extended wire. In addition, CTD data were taken at each station and along

cross-fjord transects through each station. Because of equipment failure, no temperature and salinity data were obtained during the June cruise. Additional CTD-profiles for RES 2.5 and GAK 1 were obtained from a cruise on 6 April of the same year.

Samples were sorted in the laboratory to isolate finfish larvae. Walleye pollock larvae were identified and measured to standard length (SL). Densities in larvae·m⁻³ were calculated and abundance in larvae·m⁻² at each station was estimated by integrating larval densities over the water column by using vertical distribution profiles. Density was set to zero at the surface and was assumed to change in a linear fashion between successive sampling depths. Be-

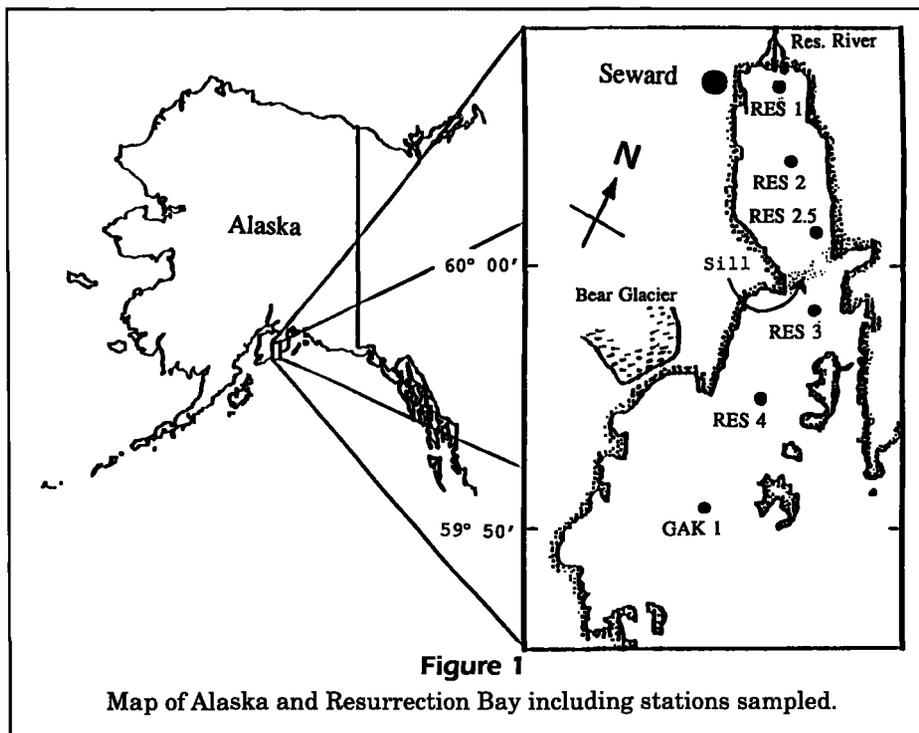


Figure 1

Map of Alaska and Resurrection Bay including stations sampled.

cause no replicate samples were taken, confidence limits could not be calculated.

A Student *t*-test (two-sample comparison) or a one-way ANOVA followed by a Tukey multiple comparison test (multiple samples) was employed to detect differences in mean standard length of larvae among different depths at the same station and among different stations. Nonparametric tests were employed in addition to parametric test procedures when the assumptions for parametric tests were violated. The nonparametric tests used were a Kruskal-Wallis test (nonparametric analysis of variance), a Mann-Whitney test (two-sample comparison), and a Tukey-type multiple comparison test (Zar, 1984).

Differences in larval length among stations were examined by using the most shallow samples from each station (<22 m), thus minimizing potential errors resulting from differences in size due to vertical distribution. In addition, pollock lengths from all depths were pooled for each station and the mean of the pooled data was compared between stations. For all between-station comparisons, larval mean SL was corrected for the date of sampling by using growth rates obtained during this study.

Ages of larvae were estimated from the number of otolith increments on sagittal otoliths as described in Kendall et al. (1987). Increments were independently counted a second time by the same reader. Readings were confirmed for a subsample of 20 otoliths by the Alaska Fisheries Science Center laboratory in Seattle, Washington. Only those independent readings that did not differ by more than one increment (in which case the higher count was used) were used for growth determination. Random subsamples of larvae from two stations, one in the inner basin (RES 2) and one in the outer basin (RES 4) were aged. Only larvae from these stations could be aged because otoliths from all other samples showed signs of erosion.

Larval growth rates were determined by fitting linear regression lines to length-at-age data. The linear regression equations describing growth were compared between stations to test for differences in regression coefficients. Slopes and elevations were compared by using Student's *t*-statistic (Zar, 1984). Hatch dates were estimated after correcting for mortality, because older fish in the sample experienced a higher cumulative mortality than larvae hatched closer to the date of sampling. Following Yoklavich and Bailey (1990), we created a stepped, size-specific mortality function with rates of 0.1, 0.08, 0.06, 0.03 per day for fish <7, 7.01–10.0, 10.01–15.0 and 15.01–20.0 mm SL, respectively. The range of ages corresponding to each size range was calculated from the growth

equation obtained in this study. The hatch date distribution was then estimated by backcalculating numbers of larvae at hatching for each daily cohort with the above mortality rates.

Results

Hydrography of the fjord

On 6 April 1989, temperatures at RES 2.5 (inner basin) and GAK 1 (mouth of fjord) increased with depth from approximately 4°C in the surface layer to almost 6°C below 200 m (Fig. 2). Between April and May 1989 the properties of the water masses inside and outside the fjord changed considerably. In April the upper 100 m were nearly homogenous, but a strong seasonal thermocline had developed between 10 and 20 m in early May. The surface temperature in May varied between 5.8°C at RES 2.5 and 7°C at RES 3 (Fig. 2). Temperature profiles in May showed a pronounced minimum of about 3.5°C to 4.5°C near 80 m. While temperatures in April in

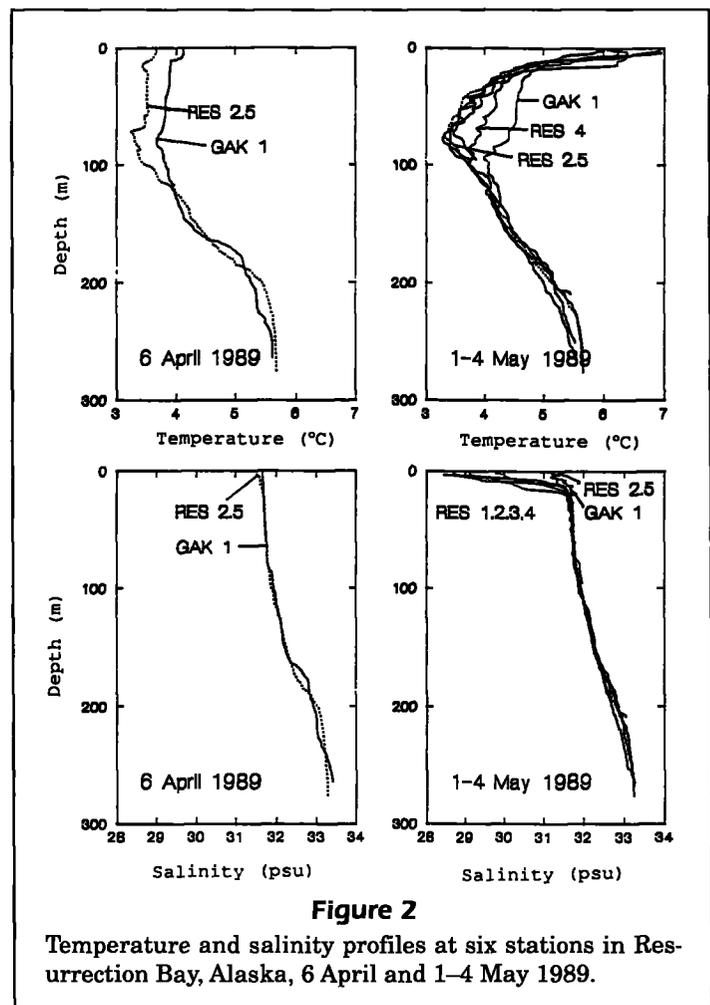


Figure 2
Temperature and salinity profiles at six stations in Resurrection Bay, Alaska, 6 April and 1–4 May 1989.

the upper 100 m did not differ by more than 0.5°C between RES 2.5 and GAK 1, the temperature difference in May was almost 1.5°C.

The water column was nearly isohaline in April: salinity increased approximately 1.5 psu (practical salinity unit) from surface to bottom. Salinity profiles in May show a well-developed low salinity surface layer at four of the stations (Fig. 2), resulting from river runoff and snow melt. The surface salinities were 2 to 4 psu lower than in April. However, at RES 2.5 and GAK 1 the freshwater lens was much less developed than at the other stations. The surface layer salinity was above 31 psu and almost identical at both stations. Below the halocline, salinities were very similar at all stations.

Distribution and abundance

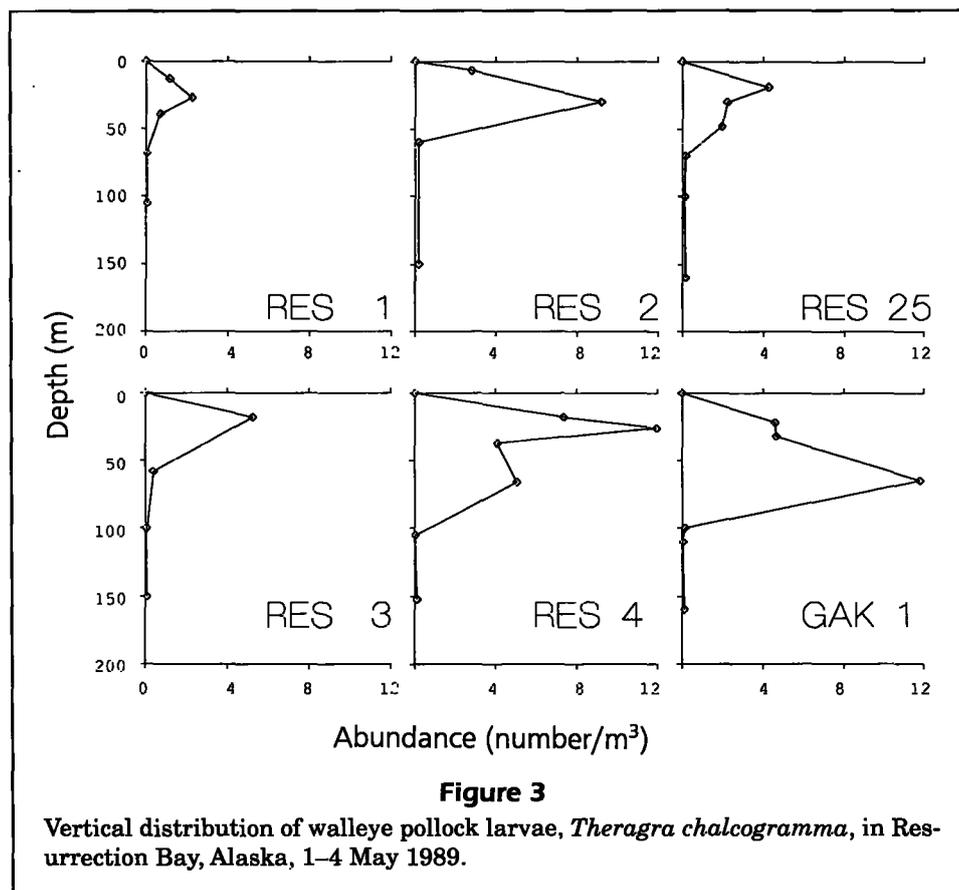
In early May, walleye pollock larvae were caught at all stations and sampled at all depths. A total of 16,950 pollock larvae were collected in 39 tows at depths between 7 and 280 m. Larval densities ranged from 0.03 larvae·m⁻³ (RES 4, 105 m) to a maximum of 11.9 larvae·m⁻³ (RES 4, 26 m). Larvae were generally concentrated in the upper 70 m (Fig. 3). Maximum densities occurred at depths between 18 and

30 m at all stations, except GAK 1, and ranged from 2.2 larvae·m⁻³ to 11.9 larvae·m⁻³. Pollock larvae were distributed deeper in the water column outside the sill, at stations RES 4 and GAK 1, than at stations inside the sill (Fig. 3).

Between May and June, larval densities decreased by two orders of magnitude and ranged from 0 to 0.4 larvae·m⁻³ in early June (Fig. 4). In June, a total of 420 walleye pollock larvae were collected in 45 tows at depths between 5 and 250 m. Only tows above 75 m caught pollock larvae. Vertically, the maximum in larval density occurred between 10 m (RES 1) and 58 m (RES 3). The vertical distribution in early June showed no apparent pattern in relation to station location (Fig. 4).

Using vertical distribution profiles, we estimated larval abundance at each station. In May, estimated abundances ranged from 60 larvae·m⁻² at RES 1 to 575 larvae·m⁻² at GAK 1 (Table 1). Abundances at the outer stations were much higher than in the inner basin owing to high larval densities below 50 m at RES 4 and GAK 1.

In June abundances ranged from 0.5 larvae·m⁻² at RES 1 to 10.3 larvae·m⁻² at RES 3. The estimated abundances were again higher at the outer stations. The highest abundance was found above the sill, as



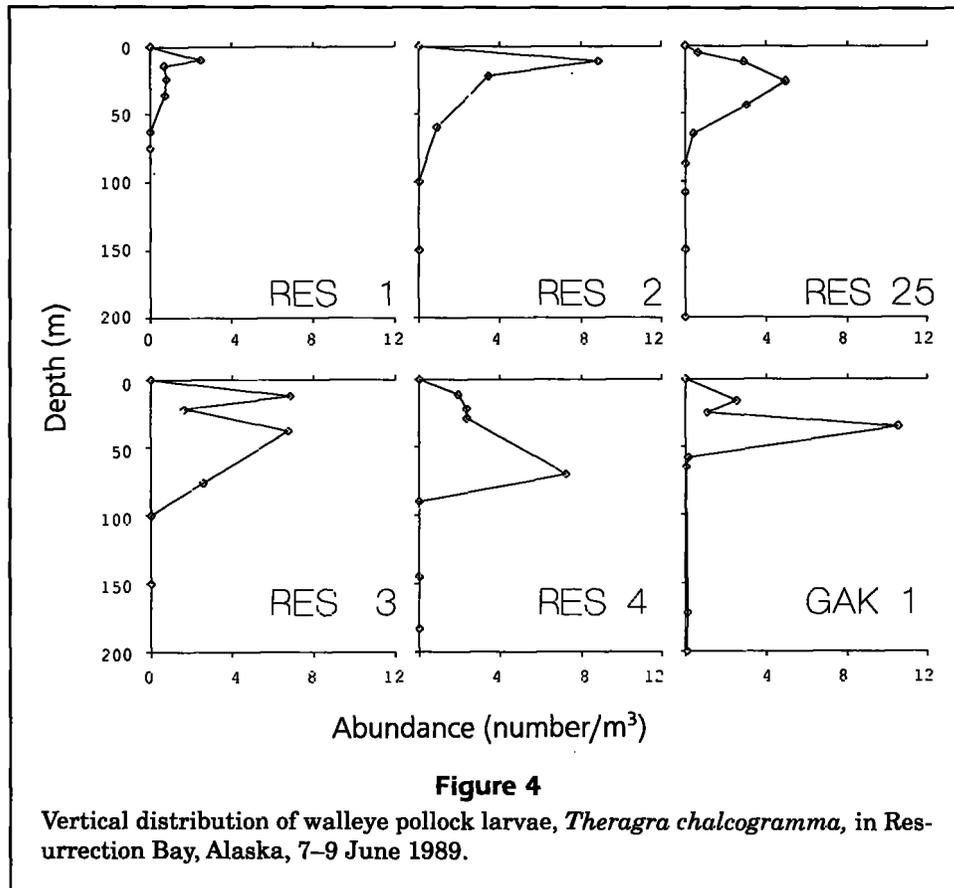


Figure 4

Vertical distribution of walleye pollock larvae, *Theragra chalcogramma*, in Resurrection Bay, Alaska, 7-9 June 1989.

the largest number of larvae was captured at RES 3 at 58 m. Abundance averaged across all stations decreased from 281 larvae·m⁻² in early May 1989 to 4.6 larvae·m⁻² five weeks later.

Larval size distribution

Mean SL of larvae differed significantly with depth at all stations in early May (Table 2). Both a *t*-test and a Mann-Whitney test of differences between means showed highly significant differences between

the shallow and deep samples at RES 1, 2, 2.5, 3, and RES 4 ($P < 0.01$). An ANOVA for station GAK 1 suggested highly significant differences as well ($F = 42.33$; $P < 0.001$). Results from a Tukey HSD test showed significant differences in mean standard length between the samples from 22 m and 65 m at GAK 1 ($P = 0.01$). Differences between any of the remaining pairs at GAK 1 were not significant.

While significant differences in size with depth existed at all stations, the sign of the differences varied between stations. At the two innermost stations (RES 1 and RES 2) larval size decreased with depth, whereas at all other stations the opposite trend was found, i.e. larval size increased with depth, excluding the sample from 100 m at GAK 1. This sample showed a slight decrease in mean SL compared to shallower samples, but the difference was not significant.

To compare larval size between stations, mean SL was corrected for sample date by using observed growth rates. Since we sampled over a four-day period, the measured lengths differed because of growth during this period. Thus, standard length was corrected for date of sampling by using a growth rate of 0.18 mm/day, the overall growth rate of pollock larvae in Resurrection Bay (this study). Table 2 shows

Table 1

Abundance of larval walleye pollock, *Theragra chalcogramma*, in Resurrection Bay in early May and early June 1989.

Station	Abundance (larvae·m ⁻²)	
	May	June
RES 1	60	0.5
RES 2	285	4.0
RES 2.5	137	1.8
RES 3	168	10.3
RES 4	461	5.2
GAK 1	575	5.8

mean SL, variance, and corrected mean SL for all samples collected in the upper 100 m. The corrected mean SL will be hereafter referred to as mean SL.

A nonparametric ANOVA by ranks showed that mean SL differed significantly between the shallow samples from each station (Kruskal-Wallis test statistic=746.5, $P<0.001$). A Tukey type nonparametric multiple comparison (Zar, 1984) indicated significant differences ($P<0.05$) between the innermost station pair (RES 1 and RES 2) and each of the stations outside RES 2 (RES 2.5, 3, 4, GAK 1). Among the outside stations, the only significant difference was found between RES 3 and GAK 1 ($P=0.003$).

When samples from all depths were pooled and mean SL compared between stations, results were very similar. An ANOVA showed a highly significant difference in mean SL between the stations ($F=80.00$, $P<0.001$). A Tukey HSD multiple comparison again indicated that significant differences ($P<0.05$) exist between both of the two innermost stations and any one of the stations outside RES 2.

Larvae at stations RES 1 and RES 2 were significantly larger and older than those at stations outside RES 2. The observed size differences translate into an age difference of 8.5 days between the average at the two inner stations (RES 1 and RES 2) and that at the outer stations (RES 2.5, 3, 4, and GAK 1). Age was calculated by using growth equations obtained in this study. The average age of larvae collected at stations RES 1 and RES 2 was estimated at 15.1 days. The average age of larvae at the other four stations was estimated to be 6.6 days, relative to 2 May. Thus, the results of size and age comparisons suggest that the stations can be divided into two distinct groups on the basis of larval size.

Growth rates

Growth rates were determined for larvae collected 1–4 May 1989 at station RES 2 in the inner basin and at station RES 4 in the outer basin. At station RES 2, 62 larvae collected at 7 m on 4 May 1989 were measured and dissected to remove otoliths, of which 54 could be aged. The increment count ranged from 6 to 40 increments for larvae between 5.1 mm

Table 2

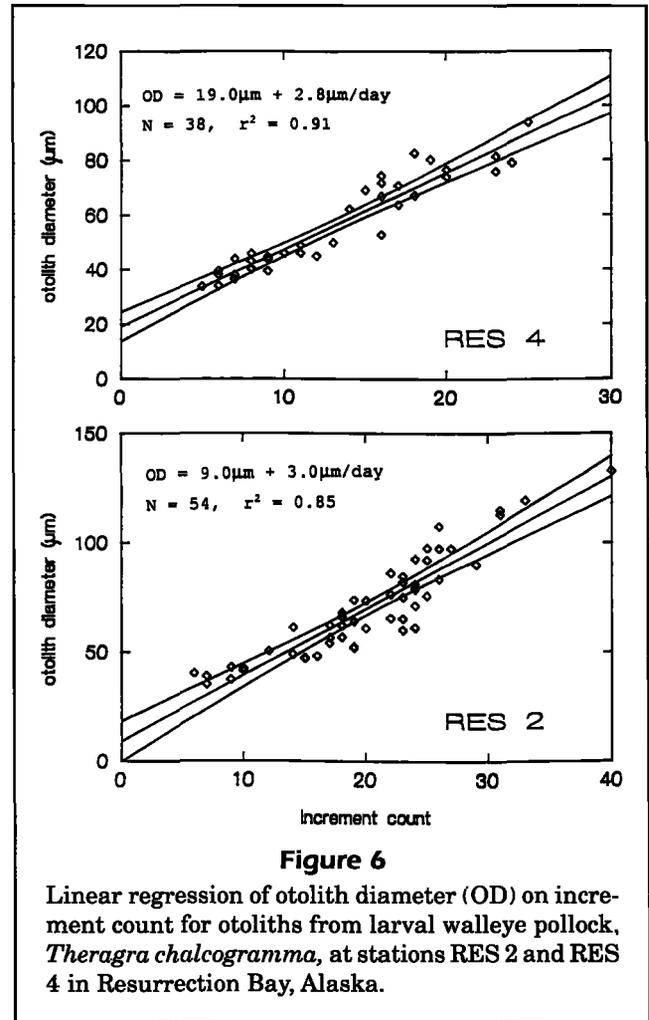
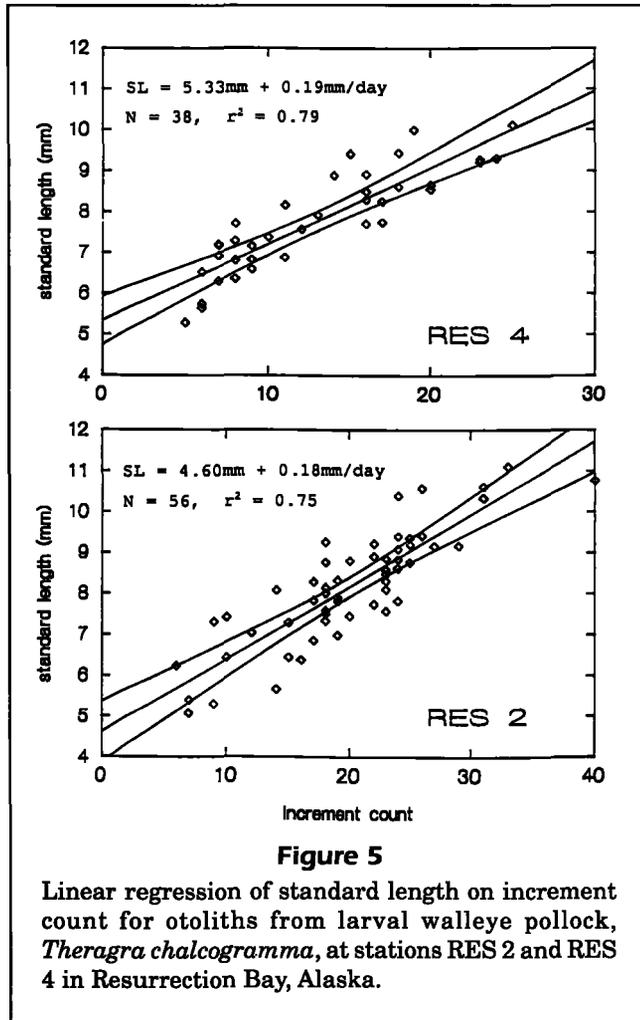
Range, mean, standard length (SL), variance, and mean SL corrected for date of sampling for larval walleye pollock, *Theragra chalcogramma*, collected in early May 1989 and preserved in isopropyl alcohol.

Station	Depth (m)	Number of larvae	Range (mm)	Mean SL (mm)	Variance	Corrected mean SL
RES 1	13	188	4.81–10.20	7.75	1.15	7.39
	39	91	4.49–9.31	6.81	0.85	6.45
RES 2	7	481	4.07–15.03	7.61	2.01	7.25
	60	24	4.59–8.40	6.67	1.02	6.31
RES 2.5	19	678	2.65–9.69	5.76	1.17	5.58
	90–110	36	5.22–8.93	6.50	0.62	6.32
RES 3	18	919	3.37–10.68	6.27	1.18	6.09
	58	95	4.15–9.58	6.91	0.88	6.73
RES 4	18	730	3.78–9.15	5.85	0.86	5.85
	66	735	3.58–8.31	6.09	0.50	6.09
GAK 1	22	983	2.87–8.81	5.37	0.78	5.55
	32	299	3.62–7.88	5.45	0.71	5.63
	65	2534	3.80–8.61	5.90	0.40	6.08
	100	29	4.31–6.84	5.65	0.37	5.83

and 11.1 mm SL. A linear regression model relating mean SL and increment count yielded a growth rate of 0.18 ± 0.028 mm/day (95% CI) ($r^2=0.75$, Fig. 5), assuming each increment represents growth of one day. From a sample collected at RES 4, at 18 m on 2 May 1989, 38 larvae ranging in length from 5.3 mm to 10.1 mm were aged. The growth rate at this station was estimated to be 0.19 ± 0.016 mm/day ($r^2=0.79$, Fig. 5).

We compared the regression lines of standard length on increment count from RES 2 and RES 4 (Fig. 5) using the t -statistic according to Zar (1984) and found no significant difference between the slopes ($t=1.048$; $0.20<P<0.50$). This indicated that the growth rate was not different between the two stations. A common slope for both data sets was computed by using a weighted regression coefficient (Zar, 1984). The resulting combined growth rate for all walleye pollock larvae in Resurrection Bay was 0.18 mm/day.

In addition to length at age (increment count), we examined the relationships between otolith size and increment count and between otolith size and standard length. The regressions of otolith diameter on increment count resulted in a much tighter fit for both stations ($r^2=0.85$ for RES 2 and $r^2=0.91$ for RES 4; Fig. 6). Regressions of length on otolith size indicated a close relationship between body length and otolith diameter for the limited size range studied here ($r^2=0.83$ and $r^2=0.86$).



A comparison of elevations (y-intercept) of the two regression lines (Zar, 1984) also resulted in no significant difference ($t=1.797$; $0.05 < P < 0.10$). Since the two subsamples used for ageing came from different preservatives, no common regression equation was computed. The regression equations relating length and age for larvae preserved in isopropyl alcohol was

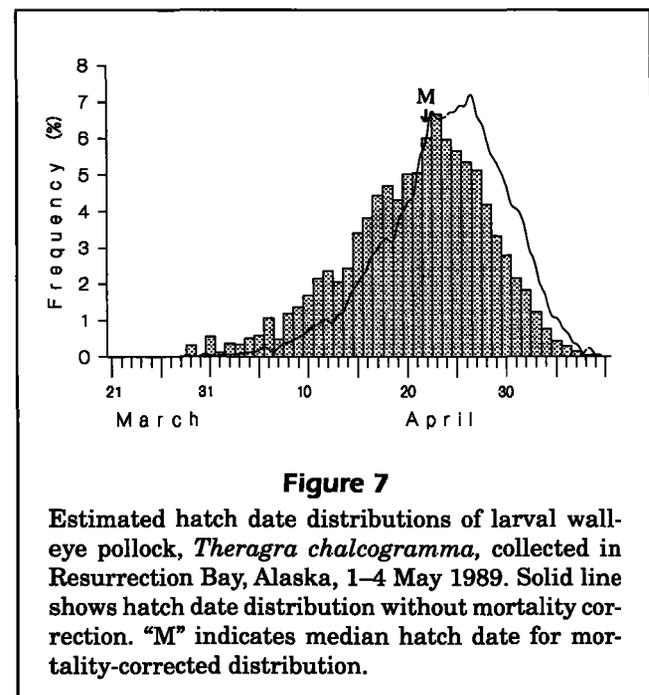
$$SL = 4.60 \text{ mm} + 0.18 \text{ mm/day} \times \text{age}(\text{days}).$$

Thus the following equation was used to convert length in isopropyl alcohol to ages:

$$\text{Age} = (SL - 4.60)/0.18.$$

Hatch dates

Estimated hatch dates for all larvae collected 1–4 May 1989 ranged from March 29 to May 9 with a median on 22 April (Fig. 7). Without mortality correction the median hatch date was 25 April.



Discussion

Distribution of pollock larvae in relation to hydrography

The vertical distribution of larval walleye pollock is influenced by behavioral responses to gravity, light, thermal stratification, turbidity, and turbulence (Olla and Davis, 1990). Even yolk-sac larvae are capable of oriented vertical movement. Olla and Davis (1990) found that larvae moved away from 3°C water in a vertical temperature gradient. Thus, temperature gradients may be reflected in the vertical distribution of walleye pollock larvae.

The results of this study show that the vertical distribution of walleye pollock larvae differed between the inner and the outer basin of Resurrection Bay in May 1989. Larvae at the outermost stations, RES 4 and GAK 1, were distributed deeper in the water column (Fig. 3). This is consistent with an upward migration of young larvae after hatching. Larvae are significantly younger at the outer stations and are distributed deeper in the water column and closer to the depth of hatching. Alternatively, larvae may select a preferred temperature by avoiding layers of cold water. Water temperatures below 40 m were about 1°C warmer at GAK 1 than at all stations inside the sill (Fig. 2). Temperatures at RES 4, located between GAK 1 and the sill, were intermediate. Cold water of less than 4°C below 40 m in the inner basin might prevent larvae from descending in the water column, resulting in the observed shallow distribution.

The horizontal distribution of larvae is largely determined by upper layer flow. Surface inflow of water into Resurrection Bay has been observed in acoustic doppler current profiler (ADCP) transects across the fjord, and average flow at 15 m depth at a mooring location above the sill was up-fjord between June and October 1989 (Weingartner²). If the water in this layer flowed up the fjord during April and May, it would provide a mechanism for advection of larvae into Resurrection Bay. Inflow of water at 15 m requires a compensating outflow. If the upper layer flow is divided in the horizontal plane with inflow on one side of the fjord and outflow on the other side, larvae may simply be transported through the fjord and their residence time could be very short. Alternatively, if surface inflow is compensated for by subsurface outflow or outflow in a shallow low-salinity surface layer, larvae could accumulate inside the fjord if they maintain their vertical position in the water column.

² Weingartner, T. Institute of Marine Sciences, Univ. Alaska, Fairbanks, AK 99775-1080. Unpubl. data, 1989.

The available evidence suggests that the former mechanism, i.e. two-way surface flow, dominates in the outer fjord basin. The relatively high surface salinity at GAK 1 suggests that the water in the outer basin originates on the shelf. A salinity transect across GAK 1 shows relatively low salinities at both ends of the transect and higher salinities in the center. This does not imply, but is consistent with, an inflow of water along the east side of the outer fjord basin and an outflow along the western shore. Inflow of nearshore water along the eastern shore into Resurrection Bay can be seen in satellite images of the area (Royer³) and there is evidence from ADCP transects for a counterclockwise circulation in the outer basin (Weingartner⁴). Larvae that originate on the shelf thus may be carried counterclockwise through the outer basin. Larvae could be carried into the inner fjord by intrusions of surface water across the sill. We probably observed such an intrusion between 1 and 3 May 1989 (Müter, 1992).

It has been demonstrated for several fjords in Norway that water exchange processes can have a profound influence on the community structure within fjords (Lindahl and Perissinotto, 1987). Advective processes can even be the major factor regulating zooplankton biomass in a fjord (Lindahl and Hernroth, 1988). Advection of plankton into Resurrection Bay from the shelf is evidenced by the fact that in addition to resident nearshore species like *Pseudocalanus* spp., oceanic copepods (*Calanus* spp.) common in the Alaska Coastal Current, are found in high concentrations inside the fjord (Smith et al., 1991). Larval walleye pollock found inside Resurrection Bay could similarly originate on the shelf and enter the fjord as a result of advective processes. Plankton samples collected in 1991 suggest that larvae entered the fjord from outside (Müter, unpubl. data). However, acoustic surveys indicated the presence of adult walleye pollock inside Resurrection Bay in the spring of 1983 and at least some spawning may occur inside the fjord (Paul⁵).

Abundance

Our results indicate that walleye pollock larvae were abundant in Resurrection Bay and on the shelf outside Resurrection Bay, as represented by GAK 1. High densities of larval pollock up to 55 larvae·m⁻³ were

³ Royer, T. Institute of Marine Sciences, Univ. Alaska, Fairbanks, AK 99775-1080. Personal commun., 1992.

⁴ Weingartner, T. Institute of Marine Sciences, Univ. Alaska, Fairbanks, AK 99775-1080. Personal commun., 1992.

⁵ Paul, A. J. Seward Marine Center, Institute of Marine Sciences, Box 730, Seward, AK. Personal commun., 1992.

also observed in nearby Prince William Sound in May 1989 (Norcross and Frandsen¹). Larval concentrations inside the fjord in early May 1989 approached those found in the dense larval patch in Shelikof Strait in some years. In most years abundances of early larvae in Shelikof Strait range from 0 to 1,000 larvae·m⁻² (Kendall et al., 1987; Kendall and Picquelle, 1990), compared with 60–575 larvae·m⁻² in this study. However, in peak years, abundances in Shelikof Strait exceed the 1989 estimates for Resurrection Bay by one to two orders of magnitude, with 10,000 larvae·m⁻² in 1981 (Bates and Clark⁶). Larval concentrations in Funka Bay, Japan, decrease from >5,000 larvae·m⁻² at some stations in January to 200–400 larvae·m⁻² in early April (Nakatani, 1988). For the Bering Sea, typical abundance estimates range from 10 to 100 larvae·m⁻² distributed over a very large area (Incze et al., 1984). In Auke Bay, Alaska, the observed abundances were much lower with maximum densities of 3–15 larvae·m⁻² (Haldorson et al., 1989a).

In ichthyoplankton samples taken in Resurrection Bay in the upper 30 m in 1988, maximum densities ranged from 0.8 larvae·m⁻³ at RES 1 to 4.1 larvae·m⁻³ at RES 4 (Smith et al., 1991), translating into abundances per unit area of 24 larvae·m⁻² and 124 larvae·m⁻² respectively. However, these abundances may be underestimates, since only the upper 30 m were sampled by Smith et al. (1991), whereas our study found high abundances below 30 m, particularly in the outer basin of the fjord (Fig. 3). Additional samples were collected in Resurrection Bay in late April and early May 1991. Abundances were similar to those estimated for 1989 (Müter, unpubl. data). The available data from 1988 to 1991 suggest that larval walleye pollock are consistently found in Resurrection Bay. The observed abundances are close to those resulting from the dense spawn-

ing aggregations found in Shelikof Strait, Alaska, and Funka Bay, Japan (Kendall and Nakatani, 1992). Since the spatial extent of the spawning area in the vicinity of Resurrection Bay is unknown, total abundances cannot be compared at present.

Larval size and age distribution

Larvae from the shallowest samples at stations RES 1 and RES 2 were significantly larger and older than those at the other stations. Larvae from the shallowest tows may not be representative of the population as a whole because of changes in vertical distribution with age. Thus we also pooled larvae from all tows at each station for between-station comparisons. Some bias may remain because of inconsistencies in the depth sampling regime, but the results were almost identical to those obtained when only shallow samples are used. There is clearly a difference in size and age between larvae at stations RES 1 and RES 2 and larvae at all other stations. This observation is consistent with the hypothesis that larvae are transported into the fjord and accumulate inside the inner fjord basin. A length-frequency distribution for all larvae collected at each station (Fig. 8) shows a multimodal length distribution and

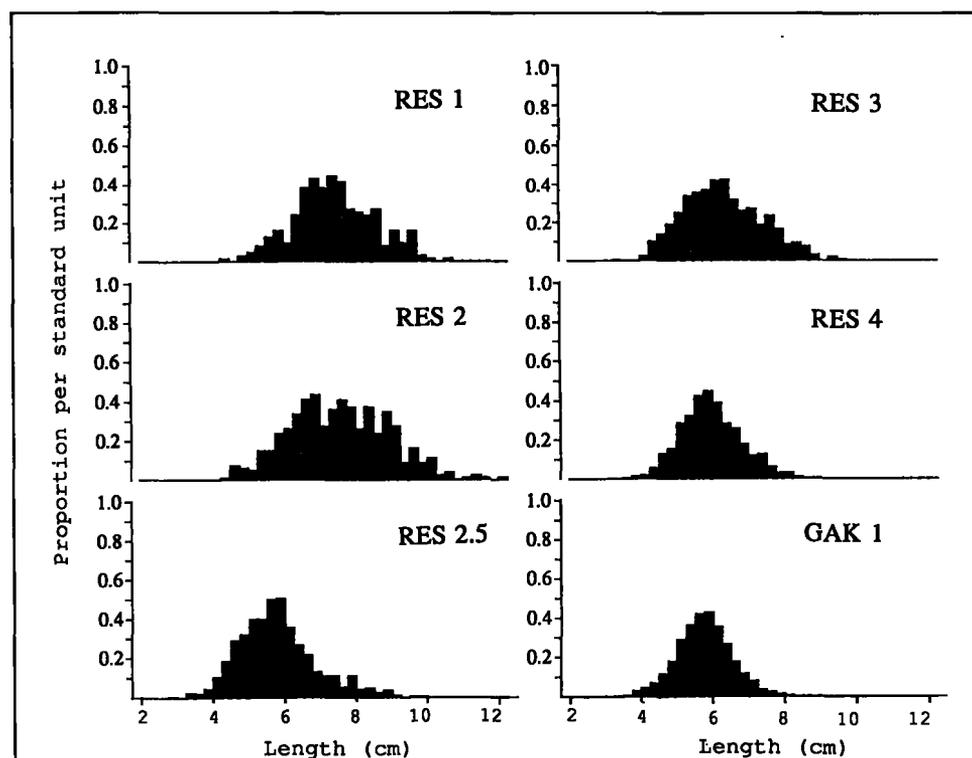


Figure 8

Length-frequency distributions of all larval walleye pollock, *Theragra chalcogramma*, captured at six stations in Resurrection Bay, Alaska, 1–4 May 1989.

⁶ Bates, R. D., and J. Clark. 1983. Ichthyoplankton off Kodiak Island and the Alaskan Peninsula during spring 1981. NWAFC Proc. Rep. 83–89. Northwest and Alaska Fisheries Sci. Center, NMFS, NOAA, Seattle, WA, 105 p.

a wide range of measured lengths at both RES 1 and RES 2, whereas at all other stations they show a more narrow, unimodal distribution. This distribution could be the result of several intrusions of surface water and larvae into the inner fjord.

Growth

The growth rates in Resurrection Bay were close to those reported for larvae from other geographic areas (Table 3), including Shelikof Strait and Auke Bay, which are located in the Gulf of Alaska at latitudes similar to Resurrection Bay. Temperatures in the upper layer in Resurrection Bay were slightly lower in early May 1989 than those observed in Shelikof Strait and Auke Bay at the same time of year (Kendall et al., 1987; Pritchett and Haldorson, 1989; Fig. 2). The low temperatures in the inner basin in May reflect delayed warming of the upper water column relative to the shelf outside the fjord. Thus, it may seem that the fjord in early spring provides less favorable conditions for growth than the shelf, considering the lower temperatures inside the fjord. However, salinities also differ between the shelf and the fjord, resulting in a more pronounced stratification inside Resurrection Bay. Stratification of the water column will reduce vertical mixing and can result in an earlier onset of phytoplankton and zooplankton blooms. In spite of differences in temperature, stratification, and vertical distribution (Kim, 1989; Pritchett and Haldorson, 1989), growth rates are very similar in Shelikof Strait, Auke Bay, and Resurrection Bay.

We detected no difference in growth rate between stations RES 2 and RES 4 in Resurrection Bay. This result is not surprising, given the proximity of the stations and the similarity in water properties. The growth rates, especially at the outer station, may be biased because only fish from the shallowest samples

were aged. Larvae from the upper layer may not adequately represent the whole population. More samples would be needed to accurately test for differences in growth between stations. To test for interannual differences, data from additional years are needed. Differences in growth rates are most commonly attributed to variations in water temperature and prey concentration. The primary prey of first feeding walleye pollock are copepod nauplii ranging in length from 100 to 300 μm (Kamba, 1977; Clarke, 1978). Smith et al. (1991) found over 20 copepod nauplii (150–350 μm length) per liter throughout May 1988 in Resurrection Bay with numbers exceeding 100 per liter in mid-May. These prey concentrations are sufficient for successful feeding of larval walleye pollock (Paul, 1983; Haldorson et al., 1989b). Under these conditions growth of larvae in Resurrection Bay is not food limited. Growth rates in Resurrection Bay were also similar to those observed in the laboratory under optimal feeding conditions and at a higher temperature (Bailey and Stehr, 1988), further suggesting that growth was not food or temperature limited.

Many studies have documented the effects of water temperature on growth of fish larvae (Houde, 1989). Laboratory studies have shown that first-feeding walleye pollock larvae reared at 5.5°C are more successful at capturing prey than larvae reared at 3°C (Paul, 1983). Brown and Bailey (1992) found geographical differences in growth for juvenile walleye pollock that could be attributed to differences in temperature as well as nutrient levels. In our study, temperatures in the larval environment ranged from 3.5 to 6.3°C and growth rates fall well within the observed range of growth in other habitats.

Hatching and spawning

Hatch dates in Resurrection Bay fall well within the range of observed hatch dates in other parts of the

Table 3
Laboratory and field-estimated growth rates of larval walleye pollock, *Theragra chalcogramma*.

Year	Location	Size range (mm)	Temperature range (°C)	Growth rate (mm/day)	Reference
1981	Shelikof Strait	3–13	no data	0.17	Kim and Gunderson (1989)
1983	Shelikof Strait	6–15	5.5–7	0.21	Kendall et al. (1987)
1986	Auke Bay	4–13	6–7	0.23	Haldorson et al. (1989a)
1987	Auke Bay	5–11	5.5–7	0.16	Haldorson et al. (1989a)
1988	Auke Bay	5–11	6–7	0.22	Haldorson et al. (1989a)
1989	Auke Bay	5–12	4–6.5	0.18	Haldorson et al. (1989a)
	Laboratory	4–11	9.3±0.5	0.20	Bailey and Stehr (1986)
	Laboratory	4–10	8–9	0.18	Bailey and Stehr (1988)
	Resurrection Bay	3–15	3.5–6.3	0.18	This study

Table 4

Median hatch dates of larval walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska.

Year	Location	Hatch date	Reference
1983	Shelikof Strait	23 April	Yoklavich and Bailey (1990)
1985	Shelikof Strait	23 April	Yoklavich and Bailey (1990)
1986	Shelikof Strait	29 April	Yoklavich and Bailey (1990)
1987	Shelikof Strait	2 May	Yoklavich and Bailey (1990)
1987	Auke Bay	28 April	Haldorson et al. (1989a)
1989	Resurrection Bay	22 April	This study

Gulf of Alaska (Table 4). The median hatch date is remarkably consistent among different parts of the Gulf and among different years which would require a common, underlying mechanism to trigger spawning over such a broad geographical range. The values from Shelikof Strait suggest a trend towards later spawning dates between 1983 and 1987. More data are needed to determine if a similar trend exists in other areas of the Gulf and to identify parameters responsible for the timing of spawning.

Conclusions

The high abundances and growth rates of larvae in Resurrection Bay indicate that the fjord provides a suitable environment for the successful growth of larval walleye pollock. The hydrography of the region and larval size distributions support the hypothesis that larvae recruit to the fjord from outside by advection into the outer basin of Resurrection Bay and across the sill. These observations and the high abundances of pollock larvae in nearby Prince William Sound during the same year (Norcross and Frandsen¹) suggest that a large spawning population of walleye pollock exists in the region and that not all walleye pollock in the northern Gulf of Alaska spawn in Shelikof Strait. Larval walleye pollock are also abundant in the bays of Southeast Alaska (Haldorson et al., 1989, a and b). Thus, it is likely that many embayments along the Gulf of Alaska are utilized by this species.

Future work is needed to determine the extent of spawning in the vicinity of Resurrection Bay and Prince William Sound and to test whether the area is consistently used by larval walleye pollock or whether abundances observed in 1989 were unusual. Also, the residence time of larvae in the area is not known. While larval pollock were found in Resurrection Bay in all three years for which data are available, there has been only one report of juvenile walleye pollock in the fjord (Feder et al., 1979).

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Literature cited

- Bailey, K. M., and C. L. Stehr.**
1986. Laboratory studies on the early life history of the walleye pollock, *Theragra chalcogramma* (Pallas). *J. exp. Mar. Biol. Ecol.* 99:233–246.
- 1988.** The effects of feeding periodicity and ration on the rate of increment formation in otolith of larval walleye pollock, *Theragra chalcogramma*, Pallas. *J. exp. Mar. Biol. Ecol.* 122:147–161.
- Brown, A.L., and K. M. Bailey.**
1992. Otolith analysis of juvenile walleye pollock *Theragra chalcogramma* from the western Gulf of Alaska. *Mar. Biol.* 112:23–30.
- Carmo Lopes, P. do.**
1979. Eggs and larvae of *Maurolicus muelleri* (Gonostomatidae) and other fish eggs and larvae from two fjords in western Norway. *Sarsia* 64:199–210.
- Clarke, M. E.**
1978. Some aspects of the feeding biology of larval pollock, *Theragra chalcogramma* (Pallas), in the southeastern Bering Sea. M.S. thesis, Univ. of Alaska, Fairbanks, Alaska, 44 p.
- De Silva, S. S.**
1973. Abundance, structure, growth and origin of inshore clupeid populations of the west coast of Scotland. *J. exp. Mar. Biol. Ecol.* 12:119–144.
- Dunn, J. R., and A. C. Matarese.**
1987. A review of the early life history of northeast Pacific gadoid fishes. *Fish. Res.* 5:163–184.
- Feder, H. M., A. J. Paul, and J. McDonald.**
1979. A preliminary survey of the benthos of Resurrection Bay and Aialik Bay, Alaska. Sea Grant Report 79-9. Alaska Sea Grant Program, Fairbanks, Alaska, 53 p.
- Haldorson, L., A. J. Paul, D. Sterritt, and J. Watts.**
1989a. Annual and seasonal variation in growth of larval walleye pollock and flathead sole in a southeastern Alaskan bay. *Rapp. P.-v. Reun. Cons. int. Explor. Mer* 191:220–225.
- Haldorson, L., J. Watts, D. Sterritt, and M. Pritchett.**
1989b. Seasonal abundance of larval walleye pollock in Auke Bay, Alaska, relative to physical factors, primary production, and production of zoo-

- plankton prey. *In* Alaska Sea Grant Report 89-1, p. 159-172.
- Hinckley, S., K. M. Bailey, S. J. Picquelle, J. D. Schumacher, and P. J. Stabeno.**
1991. Transport, distribution, and abundance of larval and juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. *Can. J. Fish. Aquat. Sci.* 48:91-98.
- Houde, E. D.**
1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fish. Bull.* 87:471-495.
- Incze, L. S., M. E. Clarke, J. J. Goering, T. Nishiyama, and A. J. Paul.**
1984. Eggs and larvae of walleye pollock and relationships to the planktonic environment. *In* D. H. Ito (ed.), *Proceedings of the workshop on walleye pollock and its ecosystem in the eastern Bering Sea*, p. 109-159. NOAA Tech. Memo. NMFS F/NWC-62.
- Kamba, M.**
1977. Feeding habits and vertical distribution of walleye pollock, *Theragra chalcogramma* (Pallas), in early life stage in Uchiura Bay. *Res. Inst. N. Pac. Fish., Hokkaido Univ., Spec. Vol.*, p. 175-197.
- Kendall, A. W., Jr., and S. J. Picquelle.**
1990. Egg and larval distributions of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. *Fish. Bull.* 88:133-154.
- Kendall, A. W., Jr., and T. Nakatani.**
1992. Comparisons of early-life-history characteristics of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska, and Funka Bay, Hokkaido, Japan. *Fish. Bull.* 90:129-138.
- Kendall, A. W., Jr., M. E. Clarke, M. M. Yoklavich, and G. W. Boehlert.**
1987. Distribution, feeding and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. *Fish. Bull.* 85:499-521.
- Kim, S.**
1989. Early life history of walleye pollock, *Theragra chalcogramma*, in the Gulf of Alaska. *In* Alaska Sea Grant Report 89-1, p. 117-139.
- Kim, S., and D. R. Gunderson.**
1989. Cohort dynamics of walleye pollock in Shelikof Strait, Gulf of Alaska, during egg and larval periods. *Trans. Am. Fish. Soc.* 118:264-273.
- Lie, U.**
1978. Eggs and larvae of fish from Lindaspollene. *Sarsia* 63(3):163-167.
- Lindahl, O., and R. Perissinotto.**
1987. Short-term variations in the zooplankton community related to water exchange processes in the Gullmar Fjord, Sweden. *J. Plankton Res.* 9:1113-1132.
- Lindahl, O., and L. Hernroth.**
1988. Large-scale and long-term variations in the zooplankton community of the Gullmar Fjord, Sweden, in relation to advective processes. *Mar. Ecol. Prog. Ser.* 43:161-171.
- Lloyd, D. S., and S. K. Davis.**
1989. Biological information required for improved management of walleye pollock. *In* Alaska Sea Grant Report 89-1, p. 9-31.
- Matthews, J. B. L., and B. R. Heimdal.**
1980. Pelagic productivity and food chains in fjord systems. *In* H. J. Freeland, D. M. Farmer, and C. D. Levings (eds.), *Fjord oceanography*. Plenum Press, New York, p. 377-397.
- Megrey, B. A.**
1991. Population dynamics and management of walleye pollock *Theragra chalcogramma* in the Gulf of Alaska, 1976-1986. *Fish. Res.* 11:321-354.
- Müter, F. J.**
1992. Distribution, abundance, and growth of larval walleye pollock (*Theragra chalcogramma*) in an Alaskan fjord. M.S. thesis, Univ. Alaska Fairbanks, 91 p.
- Nakatani, T.**
1988. Studies on the early life history of walleye pollock in Funka Bay and vicinity, Hokkaido. *Mem. Fac. Fish., Hokkaido Univ.* 35:1-46.
- Olla, B. L., and M. W. Davis.**
1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. *Mar. Ecol. Prog. Ser.* 63:105-112.
- Paul, A. J.**
1983. Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae *Theragra chalcogramma*. *Mar. Ecol. Prog. Ser.* 13:175-179.
- Pritchett, M., and L. Haldorson.**
1989. Depth distribution and vertical migration of larval walleye pollock (*Theragra chalcogramma*). *In* Alaska Sea Grant Report 89-1, p. 173-183.
- Rogers, D. E., B. J. Rogers, and R. J. Rosenthal.**
1987. The nearshore fishes. *In* D. W. Hood and S. T. Zimmerman (eds.), *The Gulf of Alaska, physical environment and biological resources*. Mineral Management Service OCS study MMS 86-0095, p. 399-416.
- Royer, T. C.**
1982. Coastal freshwater discharge in the northeast Pacific. *J. Geophys. Res.* 87:2017-2021.
- Schumacher, J. D., and A. W. Kendall Jr.**
1991. Some interactions between young walleye pollock and their environment in the western Gulf of Alaska. *CalCOFI Rep.*, Vol. 32, p. 22-40.
- Smith, R. L., A. J. Paul, and J. M. Paul.**
1991. Timing and abundance of herring and other fish larvae in an Alaskan glaciated fjord. *In* Proc. int. herring symposium Oct. 1990, Anchorage, Alaska. Alaska Sea Grant Report 91-01.
- Yoklavich, M. M., and K. M. Bailey.**
1990. Hatching period, growth and survival of young walleye pollock *Theragra chalcogramma* as determined from otolith analysis. *Mar. Ecol. Prog. Ser.* 64:13-23.
- Zar, J. H.**
1984. Biostatistical analysis. Prentice-Hall, New Jersey, 718 p.