The vertical distribution of eggs and larvae of walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Gulf of Alaska*

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Abstract.—The vertical distribution of walleye pollock eggs and larvae in Shelikof Strait, Gulf of Alaska, was investigated by using data from 36 Multiple Opening-Closing Net and Environmental Sensing System (MOCNESS) tows taken in April and May, 1986–88. Most eggs were found below 150 m to near bottom (~300 m) but progressively shallower later in the season. Eggs in middle stages of development were found at shallower depths than were younger or older eggs. The vertical distribution of eggs was positively related to observed differences in seawater temperature but showed no relationship to density. Larvae hatch at incubation depth and quickly rise to the upper 50 m of the water column where they remain during larval development. Larger larvae (~7–10 mm standard length [SL]) undergo limited diel vertical migration within the upper 50 m. They are deepest during the day, shallowest at dusk, slightly deeper at night, and even deeper at dawn. Their mean depths of occurrence were between 21 and 37 m at all times. At these depths, prey (copepod nauplii) generally were at densities sufficient for larval pollock growth as determined in laboratory studies. Pronounced thermoclines and pycnoclines were present in the part of the water column inhabited by the larvae in late May. Larvae appear to remain below the upper mixed layer during periods of increased turbulence, but at depths during daytime where light was sufficient for feeding and where prey densities were adequate.

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The vertical distributions and movements of planktonic organisms must be studied to understand their population dynamics. Often individual populations undergo vertical migrations and inhabit different advective and thermal regimes on a daily cycle (e.g. Hardy, 1936; Enright, 1977). The entire planktonic community may migrate similarly, or different organisms may co-occur on a diel cycle. The reasons for diel vertical migrations of ichthyoplankton may be related to feeding-digestion cycles, enhanced predator avoidance, or directed transport (Norcross and Shaw, 1984; Lampert, 1989).

Planktonic eggs of most marine fishes occur in the upper water column, although there are exceptions (Ahlstrom, 1959; Coombs et al., 1981). Neilson and Perry (1990) reviewed literature on vertical migration in fishes, particularly larvae of marine fishes, and attempted to identify common patterns and underlying causal mechanisms. They concluded that changes in depth distribution of larvae, while possibly under endogenous control, seem to be mediated by a number of environmental factors. While light and gravity dominate, other factors such as hydrography, food, tidal currents, and turbulence may also be important (Neilson and Perry, 1990; Lough and Potter, 1993). Planktonic larvae of fishes are found generally at shallower depths at night than during the day (Kendall and Naplin, 1981) although the opposite pattern also occurs (Boehlert et al., 1985; Yamashita et al., 1985; Sogard et al., 1987). In some species inconsistent patterns have been found among studies, possibly indicating the confounding effects of several biotic and

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abiotic factors (Sclafani et al., 1993). Vertical migrations in ichthyoplankton usually take place within the upper water column and may be correlated with the vertical distribution of larval fish prey (Munk et al., 1989; Pritchett and Haldorson, 1989). In some species the vertical extent of diel migrations increases as larvae grow (Ellertson et al., 1981; Yamashita et al., 1985).

In early April a large population of walleye pollock, *Theragra chalcogramma*, spawns in a restricted region of Shelikof Strait, Gulf of Alaska. The resulting planktonic eggs and larvae can be found, often in large patches, through April and May. Recruitment variation of this population has been examined, particularly those factors affecting interannual fluctuations in egg and larval mortality (Schumacher and Kendall, 1991).

Previous studies of the vertical distribution of walleye pollock eggs and larvae in Shelikof Strait have relied upon unmonitored discrete depth sampling (Kendall et al., 1987; Kendall and Kim, 1989). They have suggested that eggs occur generally below 150 m, and systematically change depth during their ~14-day incubation. Most larvae in these studies were found in the upper water column between about 10 and 50 m, but they migrated vertically. They seemed to congregate near the upper part of this range around sunrise and sunset, were situated somewhat deeper during midday, and were distributed more uniformly at night. A similar pattern for larval walleye pollock has been observed in other parts of the North Pacific (Kamba, 1977; Pritchett and Haldorson, 1989; Walline[1]).

The present study describes the vertical distribution of walleye pollock eggs and larvae in relation to changing environmental factors, measured on several dates in Shelikof Strait. This study is based on the analysis of 36 MOCNESS tows (Multiple Opening-Closing Net and Environmental Sensing System; Weibe et al., 1976) made over a period of three years. We examine ontogenetic changes in vertical distribution of eggs and larvae, and relate observed patterns to estimated ambient light and to measured temperature, salinity, and seawater density. Effects of vertical distribution of larval prey and changes in mixed layer depth due to wind events are also considered.

Materials and methods

MOCNESS tows were made from the NOAA ship *Miller Freeman* during spring 1986, 1987, and 1988, in areas where high abundance of eggs or larvae were expected (Kendall and Picquelle, 1990) and had been detected by exploratory sampling. Details of sampling during these cruises are contained in Incze et al. (1987), Proctor (1989), and Lawrence et al. (1991). Some of the tows reported here (8–11 May 1986, series four) were also used in a study of the response of zooplankton to the passage of a storm (Incze et al., 1990). On each MOCNESS tow, seven or eight nets were deployed. The nets were towed obliquely at 0.8–1.0 m/second through selected depth intervals and opened and closed in sequence. Net depth, flowmeter readings, temperature, and salinity (1987 and 1988) were displayed in real-time and digitally recorded. The nets had a nominal mouth area of 1 m^2. Volumes filtered per tow ranged from 34 to 980 m^3 (mean=167 m^3). Net mesh was 0.153, 0.333, or 0.505 mm, depending on the size range of the larvae expected as well as other sampling objectives.

Depth intervals were based on previous studies indicating that the eggs occurred primarily below 150 m and the larvae primarily in the upper 50 m (Kendall et al., 1987; Kendall and Kim, 1989). Early in the season when eggs were predominant, we focussed on the lower water column (>150 m), which was subdivided into 20-m sampling strata. Later in the season, we subdivided the upper water column (<90 m) into 15-m sampling strata.

Samples were fixed in 4–5% formalin and shipped to the Polish Plankton Sorting Center in Szczecin, Poland, where fish eggs and larvae were separated, and walleye pollock eggs and larvae were identified and counted. Stage of development of eggs was determined in each tow taken early in the season according to Blood et al. (1994). When more than 100 eggs were present in a sample, a subsample of 100 was staged. The egg stage data then were compressed into six stage groups as in Kendall and Kim (1989). Standard length (SL) (to 0.1 mm) of the larvae in each sample was measured. A subsample of 50 larvae was measured when more than 50 larvae were present in a sample. Catches of eggs and larvae per depth interval are reported as numbers per 1,000 m^3 of water based on volume filtered as determined from digital flowmeter records and net-frame angle. Mean and standard deviations (SD) of numbers per 1,000 m^3 for each tow were computed from the weighted average of the numbers per 1,000 m^3 from each net within the tow, by using the length of the depth interval for each net as the weight. Estimation of egg and larval mean depth, larval mean length, and their standard deviations is based on cluster sampling where each tow represents a cluster, each net subsamples eggs and larvae from the cluster, and each egg or larva is an element within the cluster (Equations 8.1 and 8.2 in Scheaffer et al., 1986). The observation associated

[1] Walline, P D. 1981. Hatching dates of walleye pollock (*Theragra chalcogramma*) and vertical distribution of ichthyoplankton from the eastern Bering Sea, June–July 1979. NWAFC Processed Rep. 81-05. Northwest and Alaska Fish. Cent., NMFS, NOAA, Seattle, WA 98115-0070, 22 p.

with each egg or larva, used to estimate mean depth, is the depth of the net where it was collected. Additionally, observations of lengths of larvae in each net were used to estimate mean lengths. Gaussian statistics, including analysis of variance (ANOVA) and analysis of covariance (ANCOVA), were used to compare mean depths of eggs and larvae and stages of eggs, and lengths of larvae with various environmental variables: time of day, temperature, salinity, and depth.

Temperature and salinity data from vertical Seabird conductivity, temperature, and depth (CTD) casts made in conjunction with the MOCNESS tows in 1986 were processed at the Pacific Marine Environmental Laboratory, Seattle. CTD data were collected with Seabird sensors on the MOCNESS in 1987 and 1988 and were processed at the Atlantic Oceanographic and Meteorological Laboratory, Miami. CTD data were available at 1-m depth intervals. In comparing temperature and density (expressed as σ_t) with depths of occurrence of eggs and larvae among tows, the mean and standard deviation of temperature and density were calculated within the depth interval of +/– one standard deviation of the mean depth of eggs or larvae. Egg mean depth weighted by abundance was regressed on temperature. Meteorological data from the Kodiak airport for the sampling periods in April and May 1986, 1987, and 1988 were used to model hourly irradiance at depth in the area by using an attenuation coefficient of 0.16 (a mean value of 33 measurements [SD=0.103] made aboard ship in Shelikof Strait between 3 and 23 May 1991[2]).

[2] Davis, R. AFSC. Personal commun., April 1992.

Data from the 36 tows were grouped into nine "series" that were numbered sequentially based on calendar day without regard to year. The first time series included eggs sampled on 12–16 April, and the ninth series included larvae sampled on 23–25 May. Tows within a series were taken with the same rationale; i.e. in a fixed location or following a drogue, with similar depth schemes, and close to the same dates (Table 1). Each series was composed of one to eight tows taken in areas of high egg and/or larval concentrations except series six and seven, which were taken primarily for zooplankton studies (Fig. 1). Series eight, in mid-May, was taken about seven weeks after peak spawning, in the spawning area. Series four and nine had time series sufficient to investigate diel differences in vertical distribution. Tows during these two series were taken at local midnight (midway between sunset and sunrise), dawn (sun 20° above the horizon), local noon, and dusk (sun 20° above the horizon).

Results

Overall densities

Egg densities were highest in the first series of tows, taken between 12 and 16 April, when mean concentration in the water column based on all nets in the tows varied from 12,057 to 34,734 eggs/1,000 m^3 (SD ranged from 5,827 to 30,619). Egg densities were greater than 1,000/1,000 m^3 per tow in series two, and generally decreased as the season progressed (Table 2). Eggs were present during series three to eight through the middle of May, but in reduced con-

Table 1

Dates and tow depths for MOCNESS series used to investigate vertical distribution of walleye pollock, *Theragra chalcogramma,* eggs and larvae in the Shelikof Strait region.

					Depths (m)															
			Day of year		Net 1		Net 2		Net 3		Net 4		Net 5		Net 6		Net 7		Net 8	
Series	Date	No. tows	Start	End	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max
1	12–16 April 1987	3	102	106	1	50	50	100	100	150	150	170	170	190	190	210	210	230	230	250
2	21–27 April 1988	7	111	117	1	60	60	120	120	140	140	160	160	180	180	200	200	220	220	250
3	30 April–1 May 1988	3	120	121	1	20	20	40	40	60	60	80	80	100	100	150	150	200	200	255
4	8–11 May 1986	7	128	131	2	15	15	30	30	45	45	60	60	80	80	100	100	150	150	200
5	13–14 May 1986	3	133	134	2	15	15	30	30	45	45	60	60	80	80	100	100	150	150	180
6	15 May 1986	2	135	135	2	15	15	30	30	45	45	60	60	80	80	100	100	150	150	170
7	17–18 May 1986	2	137	138	1	15	15	30	30	45	45	60	60	80	80	100				
8	18 May 1986	1	138	138	1	15	15	30	30	45	45	60	60	80	80	100	100	150	150	195
9	23–25 May 1987	8	143	145	0	15	15	30	30	45	45	60	60	80	80	100	100	125	125	150
	Total tows	36																		

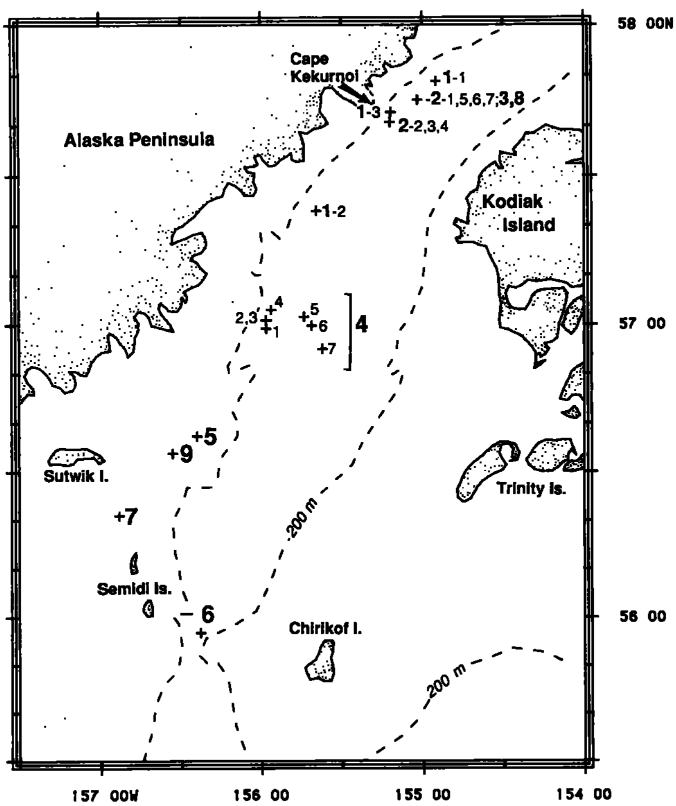

Figure 1

Locations of MOCNESS sampling series (large numbers) and tows (small numbers). Tows are shown only when there were substantial differences among their locations.

centrations, partially because sampling then was southwest of the main spawning area (Fig. 1), and partially because it was after peak spawning. The notable exception was the single tow of series eight taken in the area of maximum spawning. Although it was mid-May, egg densities were relatively high (139/1,000 m^3), indicating that some spawning had occurred within the previous two weeks.

Larvae were abundant in all series except the first when they were absent (Table 2). Mean density of larvae among the tows in series two through nine ranged from 39 to 509/1,000 m^3 (SD ranged from 54 to 1,011/1,000 m^3). Series were not always in the expected area of maximum concentration of larvae and thus do not necessarily represent the seasonal trends in larval abundance (see Kendall and Picquelle, 1990).

Series four followed a surface drifter with a drogue at 30–35 m (Incze et al., 1990), whereas sampling during series nine was at a fixed geographic location. During the 2.5 days of series four, the buoy moved anticyclonically. Catches in these two series varied considerably; during series four the mean density among tows was 82–285 larvae/1,000 m^3, compared with 42–482 larvae/1,000 m^3 during series nine (Table 2). The coefficient of variation of density among tows for series four was 0.63 and for series nine it was 0.68, indicating that variability among tows using the two sampling strategies was similar.

Overall depth distributions

Mean depths of eggs decreased during the season. Multiple comparison tests of mean depths of eggs showed significant differences between series one, two, and three, when eggs were most abundant. Among the 10 tows in the first two series, the observed mean depth of eggs was between 153 and 206 m (Fig. 2). In series three through eight, the observed mean depth was less than 130 m, but the number of eggs was relatively small. The shallower towing schemes of series four through eight may have biased the mean depth of eggs, but the general trend is thought to be real.

During the second series, when only newly hatched larvae were present, their observed mean depths of occurrence were from 165 to 212 m among tows (Fig. 3). One standard deviation of mean depth was 27 to 73 m and generally increased during the series (Fig. 3). In the third series, when recently hatched larvae dominated, larval mean depths varied from 70 to 106 m (range of SD: 83–91 m). As opposed to series two and three, when larvae were mainly found below 100 m, mean depths of larvae during series four ranged from 24 to 58 m (range of SD=15–71 m)[3]. Mean depths of occurrence of larvae from series five through seven (13–18 May 1986) varied from 15 to 47 m (range of SD=8–36 m) (Table 3). In series eight, taken in mid-May in the spawning area, the larvae averaged 4.6 mm (SD: 0.18 mm) (Table 2), and their mean depth of occurrence was 21 m (SD = 18 m). During series nine in late May, mean depths of larvae among the tows ranged from 15 to 38 m (Table 3) and varied on a diel basis (see below).

[3] Larvae in the noon tow on the second day of sampling had a mean depth of 58 m (SD=71 m). This was due to an unusually large catch in the deepest net (607/1,000 m^3 [23% of all the larvae in the tow] at 150–200 m) of larvae with a mean length of 4.71 mm. This appeared to be larger than the overall mean of the larvae collected at this depth during this series (4.35 mm), indicating the catch was not all newly hatched larvae that had not moved to the upper water column. If we discount this net, the mean depth of larvae in this tow was 21.5 m, close to the value in the other tows of the series (Fig. 4).

Changes in depth distribution with ontogeny

There was considerable variation in the mean depths of occurrence and in the abundance of eggs of different stages among the 13 tows of series one, two, and three (Table 3). Stage groups one and six were significantly deeper than stage groups three, four, and five; stage group two was intermediate in depth (Fig. 5) (ANOVA, multiple comparisons test $P<0.05$).

Almost all of the larvae collected deeper than 100 m throughout the study were <5 mm, while the length of larvae in the upper part of the water column appeared to increase later in the season (Fig. 6). In several tows of series four through eight, a bimodal depth distribution was evident; most larvae were found in the upper 60 m, almost no larvae found between 60 and 100 m, and larvae again were present deeper than 100 m. Mean lengths of larvae in the nets of the tows of series nine ranged from 4.8 to 9.8 mm, with an overall mean of 7.8 mm. There was no indication of length stratification of larvae within the upper 100 m. The mean lengths of larvae among tows in series nine were relatively homogeneous (7.2–8.6 mm).

Table 2

Mean density (number/1,000 m^3) and standard deviation (SD) of density by tow of walleye pollock, *Theragra chalcogramma*, eggs and larvae, and mean and standard deviation of larval lengths (mm SL) from MOCNESS tows.

		Density (no./1,000 m^3)				Larval length (mm SL)	
		Eggs		Larvae			
Series	Tow	Mean	SD	Mean	SD	Mean	SD
1	1	19,994	14,317.2				
1	2	12,057	5,827.0				
1	3	34,734	30,618.6				
2	1	1,509	833.3	168	271.6	3.8	0.04
2	2	3,543	3,204.0	90	89.5	3.7	0.06
2	3	2,402	1,858.9	89	90.0	3.9	0.10
2	4	1,270	804.1	230	257.8	3.8	0.06
2	5	3,641	2,489.5	322	253.2	4.1	0.04
2	6	3,276	1,696.2	389	296.1	3.6	0.04
2	7	2,333	791.3	341	316.6	3.7	0.07
3	1	411	207.6	341	444.2	4.7	0.08
3	2	671	565.3	208	163.8	4.0	0.09
3	3	779	801.3	304	331.8	4.3	0.07
4	1	52	33.4	82	88.1	5.0	0.09
4	2	77	87.1	105	130.6	4.9	0.08
4	3	98	100.7	183	288.8	4.7	0.11
4	4	124	190.6	285	449.4	5.1	0.09
4	5	170	333.2	152	228.6	5.7	0.11
4	6	204	342.4	148	199.0	5.1	0.09
4	7	59	85.0	232	261.3	5.7	0.07
5	1	26	23.7	423	696.8	5.6	0.09
5	2	40	50.2	509	770.6	5.8	0.08
5	3	24	12.9	114	121.3	5.4	0.09
6	1	5	5.0	355	497.1	6.0	0.08
6	2	7	9.1	419	833.7	6.1	0.10
7	1	14	16.1	39	58.8	6.7	0.18
7	2	5	7.7	53	91.6	6.3	0.10
8	1	139	96.7	109	184.5	4.6	0.18
9	1			42	53.5	7.7	0.50
9	2			475	822.4	7.9	0.13
9	3			181	384.8	8.6	0.16
9	4			208	482.7	7.2	0.12
9	5			78	125.1	8.2	0.17
9	6			256	385.5	7.7	0.14
9	7			482	1,011.4	7.5	0.16
9	8			396	639.5	8.5	0.11

Relationship of depth distribution and hydrography

The temperature of the water column measured concurrently with the tows in series one through three increased with depth from about 4.0° to 5.0°C near the surface to 5.0° and 5.5°C at 150–250 m, where most of the eggs occurred (there is no hydrographic data from tows 3 and 5 of series two). Temperature at the mean depth of occurrence of eggs varied from 4.7° to 5.4°C among the tows in series one through three (Fig. 7A). Since temperature increased with depth, among the tows of series one through three there was a positive linear relationship between mean depth of occurrence of eggs and temperature ($P<0.001$, $r^2=0.7619$). The relationship between the depth distribution of eggs and water density among tows of series one through three was not significant ($P=0.632$) (Fig. 7B).

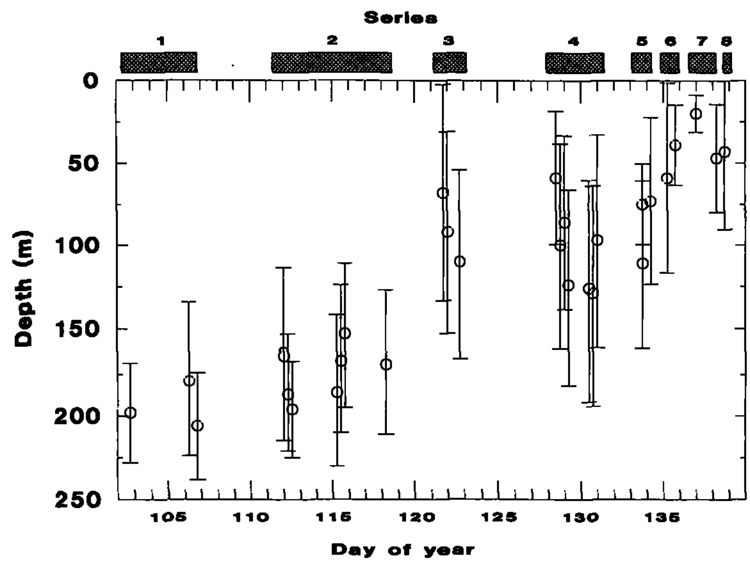

Figure 2

Eggs of walleye pollock, *Theragra chalcogramma*. Depth of occurrence by day of year and tow series number. Mean and standard deviation of the mean are shown for each tow.

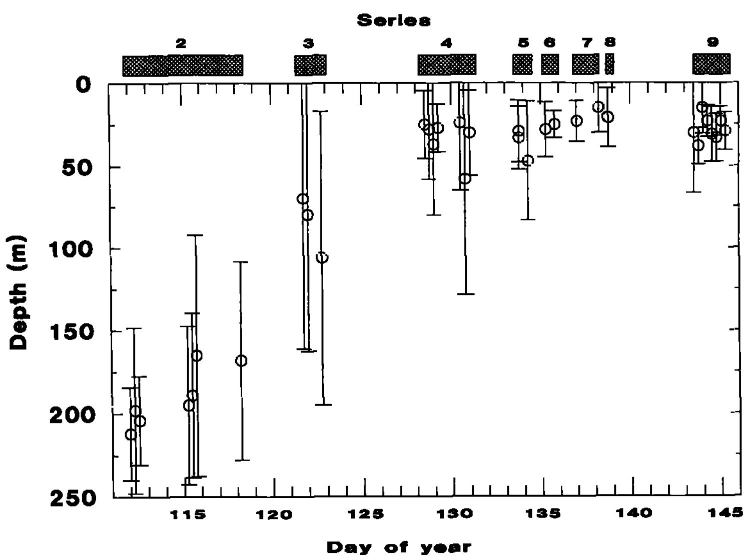

Figure 3

Larvae of walleye pollock, *Theragra chalcogramma*. Depth of occurrence by day of year and tow series number. Mean and standard deviation of the mean are shown for each tow.

When pollock larvae were first present in April as hatchlings in the lower part of the water column, they experienced temperatures of 4.9° to 5.3°C (Fig. 8). When the larvae first reached the upper part of the water column they experienced lower temperatures (~3.6°C during series four), but temperature at the mean depth of larval occurrence increased to about 5.7°C during series nine (Fig. 8).

Temperatures during series nine decreased with depth from about 6.2°C at the surface to just above

Table 3

Means and standard deviations (SD) of depths of walleye pollock, *Theragra chalcogramma*, eggs (total and by stage group) and larvae from MOCNESS tows.

				Eggs by stage group													
		Total eggs		Group 1		Group 2		Group 3		Group 4		Group 5		Group 6		Larvae	
Series	Tow	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	1	198	29.9	209	19.4	207	23.9	194	30.0	182	44.7	173	47.6	197	25.9		
1	2	179	44.8	180	31.0	174	45.6	174	51.9	183	51.2	196	51.7	200	44.9		
1	3	206	32.1	214	19.2	207	27.4	196	44.0	168	54.2	195	41.0	156	41.2		
2	1	164	50.5	161	33.2	158	48.5	156	59.6	155	54.1	158	45.7	199	42.3	212	27.9
2	2	187	33.9	179	22.4	182	27.6	193	35.1	191	36.1	184	36.5	200	35.4	198	49.8
2	3	196	28.9	196	16.9	189	24.1	191	34.7	198	31.1	199	30.1	203	30.1	204	26.6
2	4	186	44.1	177	21.9	181	25.3	163	52.0	140	65.1	177	49.2	210	33.5	195	47.6
2	5	167	43.0	206	14.2	167	36.2	143	28.8	127	38.8	144	39.4	193	34.0	189	49.5
2	6	153	42.0	193	23.2	158	47.1	145	37.3	146	37.4	143	39.7	187	40.6	165	72.7
2	7	169	42.0	184	24.9	167	31.1	159	32.6	166	49.8	159	40.1	186	46.7	168	59.7
3	1	68	65.5	144	54.6	95	66.9	54	73.3	37	40.0	56	43.6	101	77.0	70	91.1
3	2	92	60.9	133	33.4	68	52.4	84	67.8	76	46.9	92	49.1	77	67.7	80	82.7
3	3	110	55.7	84	68.8	129	56.1	94	65.5	90	47.6	102	44.8	130	51.7	106	88.9
4	1	59	40.4													25	20.5
4	2	100	61.7													28	30.1
4	3	86	52.7													37	48.3
4	4	124	57.9													27	14.5
4	5	126	65.6													24	40.9
4	6	129	65.2													58	70.5
4	7	97	64.2													30	25.7
5	1	75	24.7													29	18.6
5	2	111	50.4													33	19.0
5	3	73	50.6													47	36.2
6	1	59	57.6													28	16.5
6	2	39	24.3													25	8.0
7	1	20	11.2													23	12.3
7	2	47	32.7													15	14.8
8	1	43	47.2													21	17.7
9	1															30	36.4
9	2															38	10.9
9	3															15	15.4
9	4															23	9.6
9	5															31	16.6
9	6															33	14.3
9	7															23	8.8
9	8															29	11.3

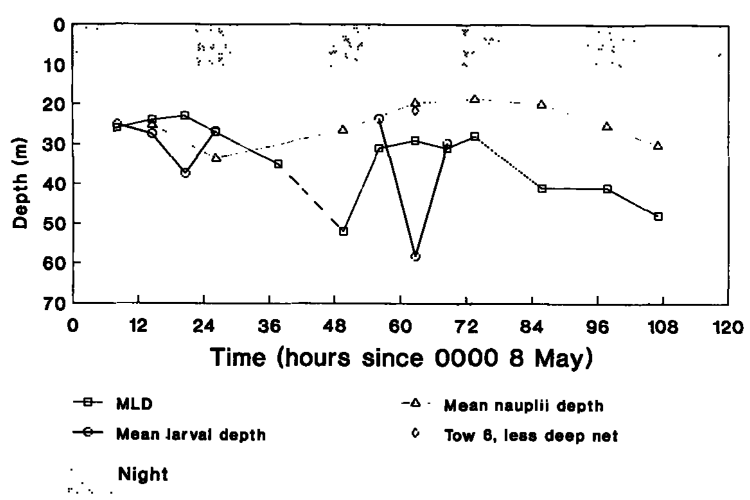

Figure 4
Time series of mixed layer depth, mean depth of copepod nauplii, and mean depth of walleye pollock, *Theragra chalcogramma*, larvae starting at 0000 hours, 8 May GMT. Mean depth of larvae excluding the catch in the deepest net of tow 6 also is plotted (see Results: overall depth distribution). Nighttime is shown by stippling near the top border.

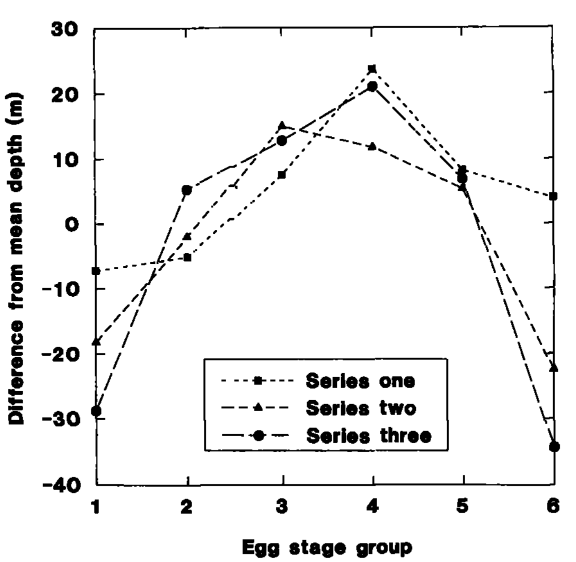

Figure 5
Vertical distribution of walleye pollock, *Theragra chalcogramma*, eggs by developmental stage group from series one, two, and three. Differences in mean depth of each stage group from mean depth of all eggs in a series are plotted.

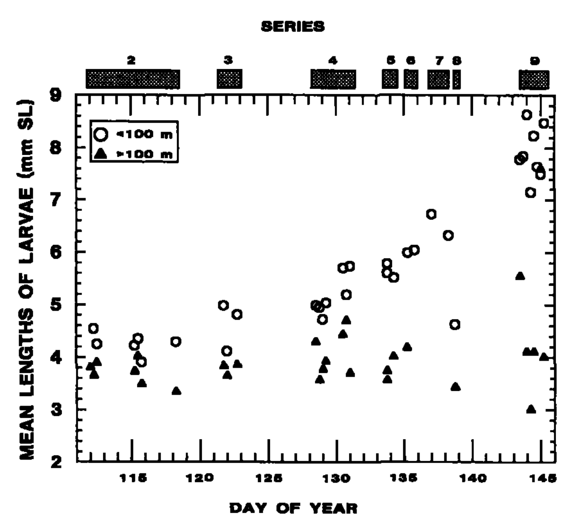

Figure 6
Standard lengths (SL) of walleye pollock, *Theragra chalcogramma*, larvae in tows above and below 100 m by day of year and tow series number.

5.0°C from about 60 m to the bottom (Fig. 9). There was a gradual thermocline between 10 and 40 m, and most of the larvae were present in or above this feature. Salinity during this series showed a gradual increase with depth from about 31.7 ppt at the surface to 32.2 ppt at 140 m. Density increased steadily from a σ_t of 24.85 at the surface to 25.25 at 60 m and 25.45 at 140 m (Fig. 9).

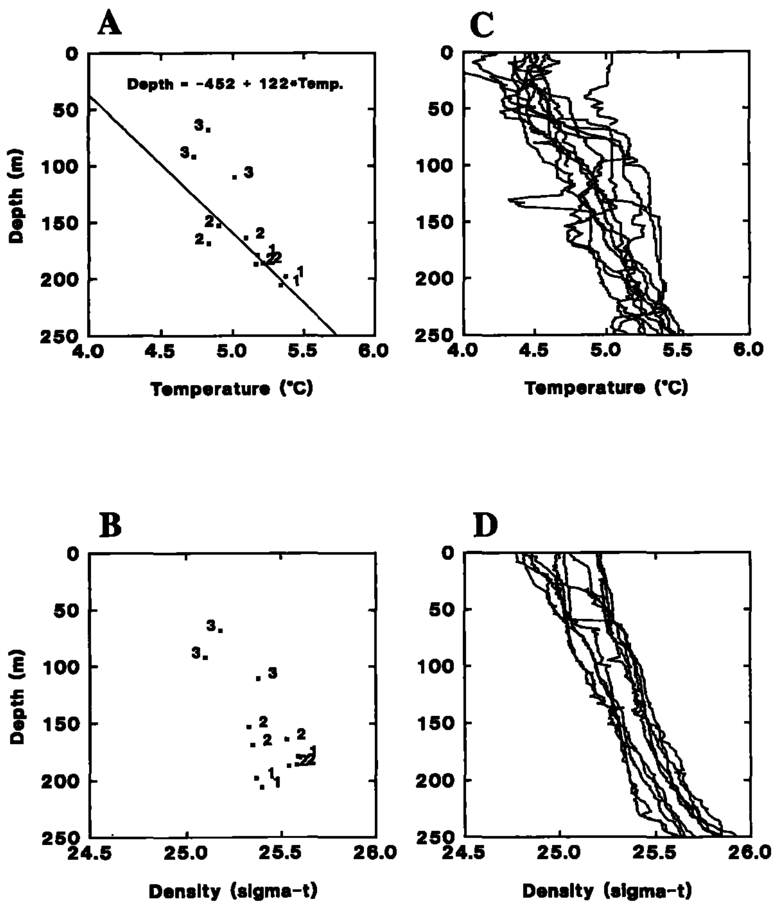

Figure 7

Mean depth of occurrence of walleye pollock, *Theragra chalcogramma*, eggs in series one, two, and three in relation to temperature (**A**) and density (**B**). Series numbers are indicated next to data points. Temperature (**C**) and density (**D**) profiles during series one, two, and three.

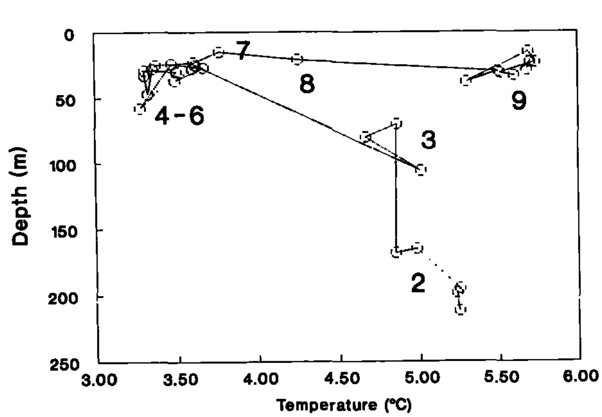

Figure 8

Mean depth of occurrence of walleye pollock, *Theragra chalcogramma*, larvae by tow in relation to temperature. Series numbers are near appropriate data points.

Diel changes in larval depth distribution

There was no clear diel pattern in the depth distribution of 5–6 mm larvae in series four (Fig. 4). During the first diel sampling period the mean depths varied from 25 to 37 m; the deepest mean depth occurred at dusk. During the second diel period, night was not sampled and an aberrant catch occurred during the noon sampling period (discussed above). The mean depths varied from 24 to 58 m, if the catch in the deep net of the noon tow is included, and from 21 to 30 m if that catch is excluded.

When proportions of larvae at each depth from series nine are examined, a clear pattern of vertical distribution emerges despite differences in overall density among tows. Although the deepest stratum sampled was 125–150 m, mean depths of occurrence of larvae were between 14.6 and 38.1 m (range of one SD=8.8–36.4 m), and fewer than 1% of all larvae were collected below 60 m. Within the upper 60 m, the larvae showed evidence of limited diel vertical migrations (Fig. 10). The observed mean depth of larvae was greater at noon than at other times (38 m and 33 m) and shallowest at dusk (15 m and 23 m). At night the larvae were found somewhat deeper (23 m and 29 m). Like the dusk sampling, the distribution at night appeared deeper during the second day compared with the first. At dawn the larvae were found between the night and noon depths (30 m and 31 m).

Although the same pattern of changes in vertical position of the larvae was observed during both 24-hour periods of series nine, differences in observed mean depths between various times of day were consistently greater on the first day than on the second (Fig. 10). The average difference in mean depth between sequential time periods on the first day was 13.2 m versus 6.2 m on the second (Table 4). The mean depths at dawn on the two days were within a meter of each other, but at the other sampling times there were differences of 4.8–8.4 m between mean depths on the two days at the same time of day. Differences were especially pronounced at dusk and night. Examination of standard deviations of mean depth and mean lengths of larvae among tows of series nine showed no consistent pattern of differences with any of the variables under consideration (time of day, depth, day).

Response of larvae to wind events and prey distributions

Increasing winds after 60 hours of sampling during series four prevented further MOCNESS tows, but other observations continued during the storm and documented the deepening of the mixed layer and subsequent changes in microzooplankton distribution (Incze et al., 1990). The path of the drogue, the sequence of CTD data obtained in the area, and limited satellite imagery suggested the presence of an anticyclonic eddy (Incze et al., 1990; Nieman[4]). The mixed layer depth during the first half of series four was variable, but during the last half it deepened, presumably in response to increased winds (Fig. 4). Copepod nauplii of length range 150–350 µm, which has been found to be the size range primarily eaten by 5–6 mm walleye pollock larvae (Paul et al., 1991), had mean depths between 20 and 34 m during series four (Fig. 4). Their observed mean depth increased during the storm, but their densities at some depth within the upper 45 m was always greater than 15 per liter. Excluding the deep net from the noon tow on day two, the mean depths of larvae in series four were at or 5–10 m below the mixed layer depth and the mean depth of 150–350 µm copepod nauplii.

Wind, measured hourly aboard the ship during series nine, increased from less than 8 m/second during the first six tows of this series to over 12 m/second by the end of the series. The mixed layer was about 25 m deep at the time of the last tow (night) in series nine as opposed to about 10 m during the previous seven tows (Fig. 9). The greater mean depths of larvae at dusk and night on the second day of sampling compared with the first day of sampling were possibly caused by increased turbulence and deepening of the mixed layer (Fig. 10).

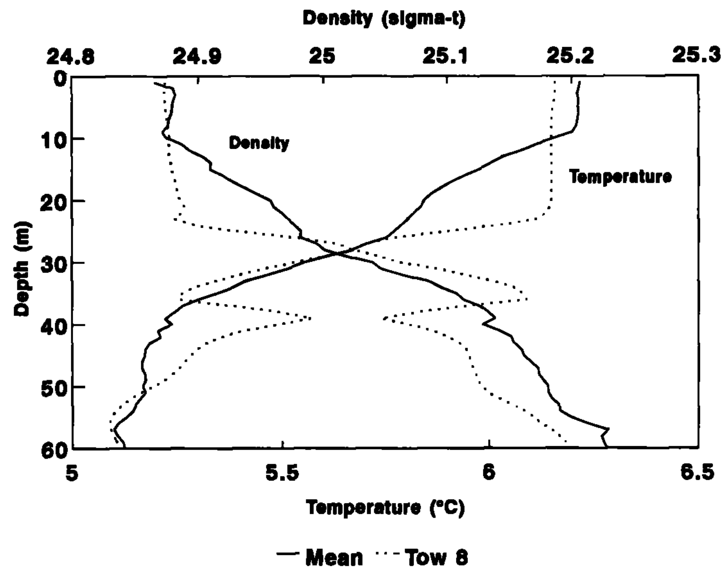

Figure 9

Temperature and density profiles from series nine. Profiles of means of all tows and from tow eight, showing deepening of the mixed layer (see Results: response of larvae to wind events and prey distributions), are plotted.

Table 4

Comparisons (means and standard deviations [SD]) of walleye pollock, *Theragra chalcogramma*, larvae by depth (m), length (mm SL) and density (no./1,000 m³) in series nine at four times of day (dawn, noon, dusk, and night).

		Depth (m)		Length (mm SL)		Density (no./1,000 m³)	
Tow	Time	Mean	SD	Mean	SD	Mean	SD
1	dawn	30	36.4	7.7	0.50	42	54
2	noon	38	10.9	7.9	0.13	475	822
3	dusk	15	15.4	8.6	0.16	181	385
4	night	23	9.6	7.2	0.12	208	483
5	dawn	31	16.6	8.2	0.17	78	125
6	noon	33	14.3	7.7	0.14	256	386
7	dusk	23	8.8	7.5	0.17	482	1,011
8	night	29	11.3	8.5	0.11	396	640
	dawn	30.6		8.06		33.6	
	noon	36.6		7.79		249.6	
	dusk	21.4		7.72		228.4	
	night	27.0		8.09		150.7	
	day 1	26.4		7.84		124.9	
	day 2	29.0		7.97		156.2	

Discussion

Most walleye pollock eggs in Shelikof Strait developed at depths between 150 and 200 m. However, there was considerable variation in the mean depth of eggs among the tows. Mean depth of eggs varied from 153 to 206 m in April (when egg densities were high) and from 20 to 129 m in

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May. Although many factors probably contributed to the distribution of eggs, their distribution was positively related to temperature, which increased with depth.

Kendall and Kim (1989) developed a model, based on field collections and laboratory experiments, to describe the vertical distribution of walleye pollock eggs from Shelikof Strait in relation to water density. One of the model's assumptions was that the specific gravity of eggs does not vary interannually. Based on this assumption and their observations of the changes in egg buoyancy and depth distribution during development, eggs would rise to different depths in the middle stages of development depending on water density in particular years. The vertical distribution might then influence the horizontal distribution of eggs if there was a significant vertical shear in the water column. Like Kendall and Kim (1989), we found middle-stage pollock eggs at shallower depths than early or late stage eggs. Our data, however, suggest that the depth distribution of eggs changes during development regardless of water density. Pollock egg density appears to vary interannually—in the eight tows from which significant numbers of eggs were collected and for which concurrent hydrographic data are available, the mean depth of occurrence varied from 153 to 206 m, and the density varied from 25.31 σ_t to 25.63 σ_t. Among the four years for which Kendall and Kim (1989) present data (1977, 1981, 1985, 1986), density in the middle layer of the water column (162–216 m) varied interannually from 25.58 σ_t to 25.87 σ_t, and modelled depth distribution of middle-stage eggs varied from about 160 to 230 m. While the ranges of density and depth of eggs seen in the present study are similar to those modelled by Kendall and Kim (1989), the proposed relationship between depth of eggs and water density is not evident. A relationship might have been seen if a greater range of water densities had been found. The temperature and density of the water in which most of the eggs were found in the present study (1987 and 1988) most closely resembled the values reported for 1981 by Kendall and Kim (1989).

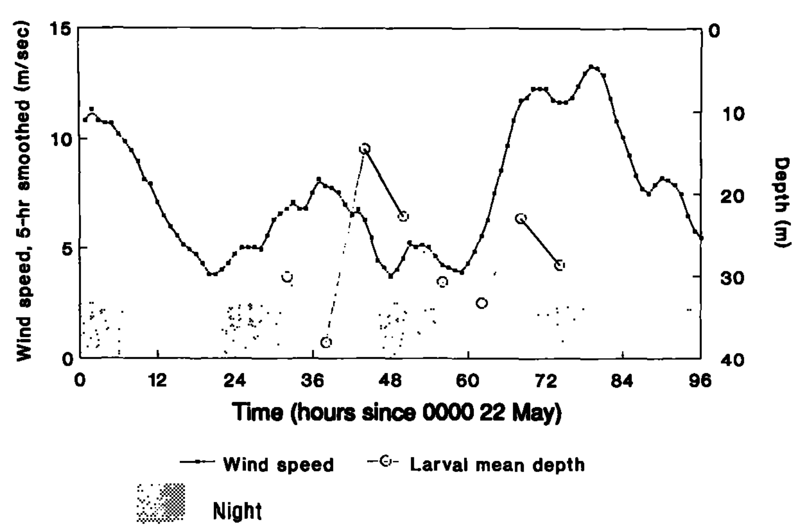

Figure 10
Mean depth of walleye pollock, *Theragra chalcogramma*, larvae and wind speed during series nine.

Ingraham et al. (1991) compared long-term annual means of water temperature, salinity, and density at 225 m depth in Shelikof Strait with values in individual years when circulation in the Gulf of Alaska was anomalous. They found high values for all three variables in 1985; this was a year when water on the continental slope did not include fresher, colder waters from the eastern Gulf of Alaska owing to reduced westward transport. Of the years considered here (1985–88), only 1985 was characterized by anomalous flow conditions that could have produced unusually warm, dense (>5.4°C, >26.2 σ_t) bottom water in Shelikof Strait (Ingraham et al., 1991). According to the model in Kendall and Kim (1989), the eggs should have risen closest to the surface in 1985. However, mean depth of eggs in the four tows in 1985 was 220 m, in the five tows in 1986 it was 211 m (Kendall and Kim, 1989), in the three tows of series one in 1987 it was 200 m, and in the seven tows of series two in 1988 it was 176 m.

In series three through eight, the mean depth of occurrence of eggs was less than 130 m. Given the low numbers of eggs and the sampling intervals designed mainly to sample larvae, these values are not robust. Kendall and Kim (1989) also found some eggs with significantly lower density than others in their specific gravity experiments. The data presented here confirm that some eggs have a low specific gravity value, but that these are infrequent and occur primarily later in the season after the majority of eggs have hatched.

Apparently after hatching, larvae move quickly to the upper part of the water column. Both eggs and larvae in series two had mean depths of occurrence between 153 and 212 m among the seven tows. The mean length of larvae in series two was 3.8 mm, which is within the range of size at hatching (Kendall et al., 1987). In series three, the mean depths of occurrence of eggs and larvae decreased to between 68 and 110 m, and the mean length of larvae increased to 4.4 mm, indicating that growth of some pollock larvae had occurred (SD of length was 0.18 in series three as opposed to 0.09 in series two). The standard deviations of depth of larval occurrence in series three (83 to 91 m) were larger than in any other series, suggesting that these larvae were in transition from the deep hatching environment to shallower levels. Although larvae respond positively to light within 24 hours of hatching, their negative geo/barotaxis may enable them to reach the upper layers since insufficient light for response penetrates to hatching depths (see Olla and Davis, 1990). The relatively shallow mean depth of eggs in series three also may account for the large variation in larval depth during that series. Older larvae from eggs at the depths observed during series two (>150 m) could have mixed with larvae hatching from eggs found at the depths observed during series three (<110 m). The larger standard deviation of larval length in series three compared with series two supports this explanation. In later series the mean depth of occurrence of the larvae was less than 60 m, and the standard deviation generally was less than 20 m. Once they reach the upper layers, vertical movements increase as larvae develop. No significant diel migrations were noted in series four, as opposed to the pattern seen in series nine. The mean length of larvae in series four was 5.3 mm; in series nine it was 7.9 mm. The larvae sampled by Kendall et al. (1987) in late May were 11.0 mm long and demonstrated a pattern of vertical distribution similar to the larvae collected here in series nine.

During series nine, larvae followed a diel (crepuscular) pattern of vertical movements in which they ranged deepest at noon, shallowest at dusk, and progressively deeper through the following noon. Although this pattern was observed on both days, the amplitude of movements were reduced on the second day. However, the wind had markedly increased by evening of the second day. Larvae may have been avoiding the turbulent surface on the second day when their mean depths were deeper. Olla and Davis (1990) found that pollock larvae avoid turbulence in the laboratory.

The relationships of larval fish feeding, growth, and survival to storms and turbulence have been the subject of numerous studies (e.g. see Sundby and Fossum, 1990; Maillet and Checkley, 1991). Both positive and negative effects have been postulated and observed. Positive effects of increased turbulence include hypothesized enhanced encounter rates between larvae and their prey (Rothschild and Osborn, 1988), and enhanced primary production after mixing has ceased owing to infusion of nutrients from below the photic zone. Negative impacts include dilution of vertically enriched layers of prey to levels below successful feeding thresholds and reduced naupliar production in lower phytoplankton concentrations (Lasker, 1978). There is evidence that in Shelikof Strait, below-average walleye pollock production may result if strong wind events occur when larvae are at the first-feeding stage.[5] Incze et al. (1990) found that naupliar concentrations remained above feeding threshold levels during the passage of a storm, but this was a relatively transient phenomenon. The present study indicates that larvae may avoid upper layer turbulence by moving deeper in the water column. If so, they might experience prey densities or light levels too low for optimal feeding.

In a 24-hour study of the vertical distribution of pollock larvae in Auke Bay, Alaska (average depth 60 m), Pritchett and Haldorson (1989) found larvae congregated at 10 m at noon, at 5 m at dawn and afternoon, and at 15–20 m at night. At twilight (0.3 hour before sunrise, 1.5 hours before sunset), larvae were more dispersed, seen mostly at 10 m near sunrise and at 15 m near sunset. The vertical extent of diel migration increased with larval length. In the present study, depths of occurrence were greater at all times than those reported by Pritchett and Haldorson (1989), and noon depths of larger larvae were greater than the night depths. However, in both studies, larvae were found to be deeper at noon than at dawn and dusk, and a relationship between vertical migration and larval length was seen. The depth distribution of copepod nauplii in Auke Bay usually centered around 5–10 m (Paul et al., 1991). Inzce et al. (1990) reported maximum densities of copepod nauplii in the upper 30 m of Shelikof Strait when pollock larvae are abundant. Since nauplii are the primary prey for pollock larvae, the larvae may well adjust their daytime feeding depths to correspond to those of the nauplii. Alternatively, the greater daytime depth of pollock larvae in Shelikof Strait may be related to the greater depth of light penetration in Shelikof Strait compared with Auke Bay (Zeimann et al., 1990).

Light is frequently cited as a factor controlling the depth of occurrence for fish larvae. Larvae of some species follow the common trend of rising toward the surface at night and of remaining deeper during the day (Smith et al., 1978; Kendall and Naplin, 1981; Davis et al., 1990). Other species follow an opposite pattern, ranging deeper at night than by day (Boeh-

[5] Bailey, K. M., AFSC, and S. A. Macklin, Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE., Seattle, Washington 98115-0070. Personal commun., February 1993.

lert et al., 1985; Yamashita et al., 1985; Sogard et al., 1987; Davis et al., 1990). Fewer studies have examined the vertical distribution of fish larvae during crepuscular periods. The present study has shown that larger larval pollock range deeper during the day than at night and that, at dawn and dusk, they are present at shallower depths in the water column than at midday. We hypothesize that these changes in vertical position allow pollock larvae to extend the length of their daily feeding period.

In the laboratory, first-feeding pollock larvae could not feed at light levels below 0.006 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Paul, 1983). Except at night, light levels are brighter than those at the depths where we found feeding-stage larvae. In studies of behavioral responses of walleye pollock larvae (4–8 mm SL) to light in the laboratory, Olla and Davis (1990) found reduced activity and orientation in a nonfeeding mode at light levels <0.01 and avoidance of light at levels >13 $\mu mol \cdot m^{-2} \cdot s^{-1}$. In the dark, larvae migrated upward and remained in the upper part of the chambers, demonstrating negative geotaxis or barotaxis, or both. Light levels between 0.01 and 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ are estimated to have occurred between about 25 and 60 m during our sampling in Shelikof Strait. The mean depths of feeding larvae were typically in the upper part of this range (Fig. 11). Larvae longer than 7 mm seemed to adjust their vertical position on a diel cycle to stay at light levels similar to those "preferred" in the laboratory. At night these larvae were present at depths where light had been greater than 10 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during the day.

The relationship of vertical distribution of larval fish to vertical temperature structure of the water column varies among species (Kendall and Naplin, 1981; Sogard et al., 1987). Hypothetically, there are metabolic advantages to diel descents into cooler waters (Lampert, 1989). Larvae that stay nearer the surface (at higher temperatures) at night when they are digesting their food may accrue such advantages (Wurtsburgh and Neverman, 1988). However, given the small differences in temperature with depth observed here (~1°C), energetic advantages are almost certainly insignificant compared with the advantages of feeding at optimal light levels and at depths of maximum prey abundance. An alternative advantage of residing deeper, and thus at lower light levels during daytime, may be to avoid visual predators.

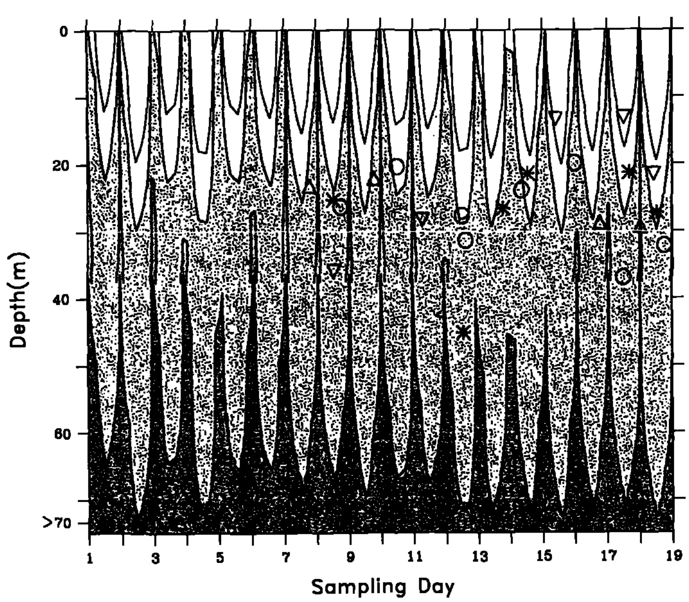

Figure 11

Predicted light levels at depth on days of sampling and mean depths of walleye pollock, *Theragra chalcogramma*, larvae in MOCNESS tows (indicated by circles for daytime tows, triangles pointed down for dusk tows, asterisks for night tows, and triangles pointed up for dawn tows). Depths of three light levels are plotted: 50, 10 and 0.01 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Light levels above 50 are clear, those 10–50 are light gray, those 0.01–10 are medium gray, and those less than 0.01 $\mu mol \cdot m^{-2} \cdot s^{-1}$ are dark gray. Light levels are based on incident light at the Kodiak airport during the sampling periods with an extinction coefficient of 0.16.

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