

**DISTRIBUTION, FEEDING, AND GROWTH OF LARVAL WALLEYE
POLLOCK, *Theragra chalcogramma*, FROM SHELIKOF STRAIT,
GULF OF ALASKA**

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ABSTRACT

Walleye pollock in the Gulf of Alaska have recently been found to form an intense spawning aggregation in late winter in Shelikof Strait. This produces a dense patch of planktonic eggs in early April, and later in spring a patch of larvae that can be followed as it drifts to the southwest. The density of larvae observed in 1981 indicated that density-dependent effects on feeding may be important for larval survival. In May 1983 we conducted a field study to investigate spatial and vertical distribution, feeding, and growth of larvae from this spawning. During this study we found, in an area of maximum concentration (~ 1 larva m^{-3}) located by an initial survey, larvae averaged 11.1 mm SL, and were similar in size to those found elsewhere. The larvae in 1983 were larger, and less abundant than at the same time in 1981. Larval growth was estimated from the number of otolith daily growth increments at size of larva and was similar in the area of maximum concentration and in other areas. Larvae were concentrated vertically between about 15 and 50 m and showed a crepuscular pattern of increased density at 14-28 m during twilight. Neither the vertical nor horizontal patterns of larval occurrences seemed closely associated with particular values of temperature or salinity. Most larvae were found in a temperature range of 7.0°-5.5°C and a salinity range of 31.5-32.2‰. Guts of larvae collected during darkness contained less food than those from daytime. Copepod nauplii were largely replaced by *Pseudocalanus* spp. copepodids in the diet of larvae larger than 14 mm. At the densities of walleye pollock larvae observed in this study, it appears that zooplankton production in the area did not impact larval growth, even in the area of maximum density.

A large spawning concentration of walleye pollock, *Theragra chalcogramma*, was discovered in 1980 in Shelikof Strait, and subsequently a 220,000 metric ton/year fishery developed. Shelikof Strait, a 50 by 200 km body of water in the northern Gulf of Alaska, between the Kodiak Archipelago and the Alaska Peninsula, is apparently the major spawning center for Gulf of Alaska walleye pollock. Ichthyoplankton surveys in 1981 and 1982 showed that spawning occurs primarily in a restricted area within Shelikof Strait and over a short period of time, producing a dense patch of eggs. Thereafter, larvae drift southwest with prevailing currents (Fig. 1). The

densities of walleye pollock eggs and early larvae found in Shelikof Strait in 1981 exceeded $50 m^{-3}$ (Dunn et al. 1984⁵), far greater than their densities in the Bering Sea (Kim and Kendall 1983⁶) or Funka Bay, Japan (Hayashi et al. 1968); moreover, these densities significantly exceed those reported for larvae of any other fish (Hempel 1979).

Energetic requirements of larvae in high densities may exceed production of food and possibly lead to density-dependent effects on larval growth and survival (Jones 1973). At larval densities frequently found (ca. $1 m^{-3}$), density-dependent effects are not considered important (McGowen and Miller 1980; Cushing 1983). Laboratory studies, however, have demonstrated effects of stocking

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⁵Dunn, J. R., A. W. Kendall, Jr., and R. D. Bates. 1984. Distribution and abundance patterns of eggs and larvae of walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. NWAFC Proc. Rep. 84-10, 66 p.

⁶Kim, S., and A. W. Kendall, Jr. 1983. The numbers and distribution of walleye pollock eggs and larvae in the southeastern Bering Sea. U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, NWAFC Proc. Rep. 83-22, 35 p.

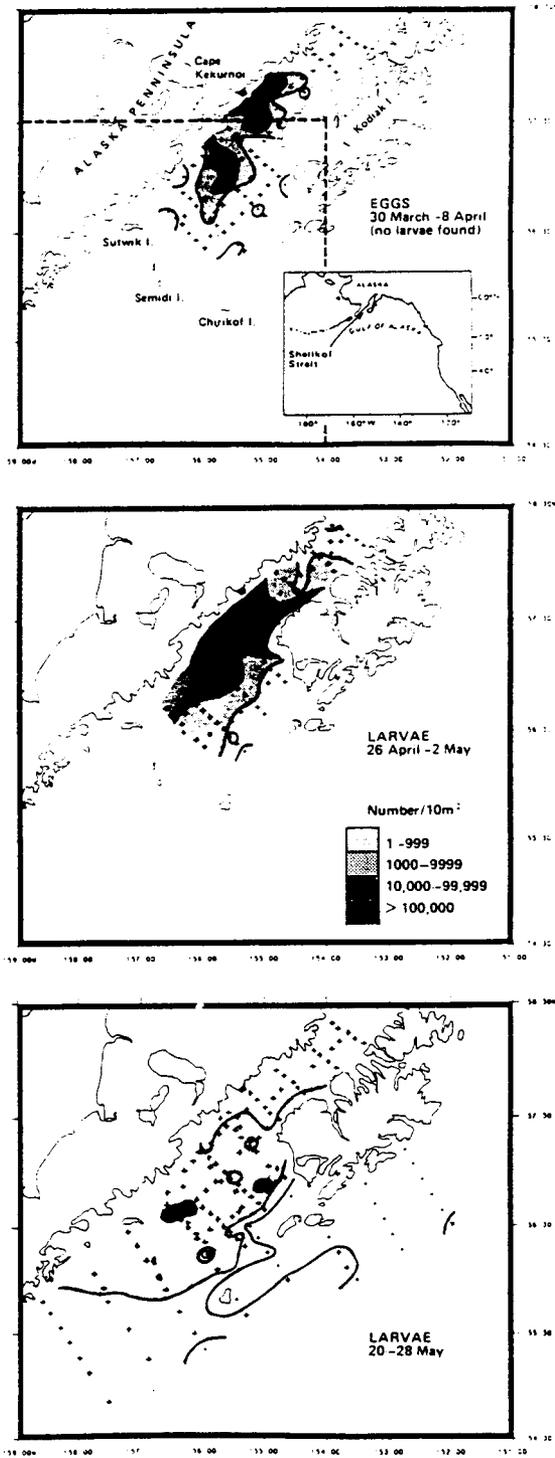


FIGURE 1.—Distribution and abundance of walleye pollock eggs and larvae, spring 1981. Based on Bates and Clark (text fn. 9). Cape Kekurnoi is blackened as a point of reference. Area shown in Figures 2 and 6 is outlined in upper panel.

density upon growth (O'Connell and Raymond 1970; Houde 1975), and recent studies on patches of larvae co-occurring with prey suggest that enhanced growth may be observed at high prey concentrations in the field (Govoni et al. 1985). Search volumes of 5 mm larvae morphologically similar to walleye pollock are about 10 L per day (Laurence 1982); thus with densities of 1 larva in 25 L found in Shelikof Strait in 1981, it is possible that density-dependence is important in larval feeding rate and growth.

Walleye pollock is widely distributed in the subarctic North Pacific. Larval feeding habit studies have been conducted in Uchiura Bay, Hokkaido, Japan (Kamba 1977) and in the southeastern Bering Sea (Clarke 1978) where the principal prey has been found to be copepod nauplii with *Pseudocalanus* spp. becoming increasingly important as the larvae grow. Larval growth in the same areas has been studied by Hayashi et al. (1968) and Nishimura and Yamada (1984) for Hokkaido and by Walline (1985) and Clarke (1984) for the Bering Sea. Growth rates in field collections and laboratory rearing studies have been shown to be quite variable, from about 0.16 to 0.37 mm d⁻¹ (Bailey and Stehr 1986).

We conducted a field study to investigate the ecology of larval walleye pollock in Shelikof Strait in May 1983 by locating and sampling the densest patch of larvae. Here we report on growth, feeding habits, and depth distribution of larval walleye pollock we collected.

METHODS AND MATERIALS

Field Collections

An ichthyoplankton survey of 63 stations on a 15 nmi (27.8 km) grid southwest of Kodiak Island, AK, was conducted aboard the NOAA ship *Chapman* from 21 to 28 May 1983 (Fig. 2). At each station a MARMAP double oblique bongo tow (Posgay and Marak 1980) was made from the surface to 200 m (as water depths permitted) with a 60 cm bongo net equipped with 505 μ m mesh nets. Flowmeters were mounted in the net mouths and a bathykymograph was used to determine the maximum tow depth and to evaluate the tow profile. A neuston net (Sameoto and Jaroszynski 1969) with 505 μ m mesh was also towed for 10 minutes at each station. The neuston net sample and one of the bongo net samples at each station were preserved in 5% sodium borate buffered formalin in seawater. Most walleye pollock larvae

from the other bongo net were rough sorted at sea and were immediately preserved in buffered 90% ethanol for otolith examination.

The results of the sorting of larvae at sea were used to choose a location of high larval density for the diel feeding/distribution study (Fig. 2). Another oblique tow, after this survey, confirmed the presence of high concentrations of larvae. Several preliminary tows with four 20 cm bongo nets on the towing wire fixed at 10 m depth intervals (between 5 and 91 m) were made to find depths of maximum larval concentrations. A tow was then taken every 4 hours for 48 hours during 28-30 May 1983 with 20 cm bongo nets equipped with 253 μ m mesh nets on one side and 333 μ m mesh nets on the other. Four nets were fished simultaneously for 10 minutes at a ship speed of approximately 100 cm/second. The nets were placed on the wire to fish at four depths within the region of larval abundance (nominally 20, 30, 40, and 50 m). Flowmeters were mounted in the mouths of the nets, and a bathykymograph was deployed with the deepest net to record actual tow depths. During setting and retrieving, the ship maintained reduced speed to minimize fishing outside the chosen depth strata. Thus, although no closing devices were used, nearly all of the water passing into the nets was at the chosen depth (Kendall and Naplin 1981). Tows were made at 1030, 1430, 1830, 2330, 0230, and 0630 local time (sunrise was at 0455 and sunset 2138 h). During the sampling of the stations at 1430 and 0230 on both days, a 1 m² mechanical Tucker trawl with 505 μ m mesh was fished for 10 minutes at 35 m to investigate escapement from the 20 cm bongo nets. Also during the second 24-h period a 60 cm bongo net with 505 μ m mesh was fished about 2 m below the deepest 20 cm bongo net to stabilize the wire and allow further catch comparisons.

Expendable bathythermograph (XBT) casts were done at each survey grid station and at the 1430 and 0230 vertical distribution study stations. Conductivity-temperature-depth (CTD) casts (Ocean Data Equipment Corporation⁷ Model 302) were made at 15 of the survey grid stations selected to provide three sections across the major southwesterly setting flow field in the area (Fig. 2).

⁷Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

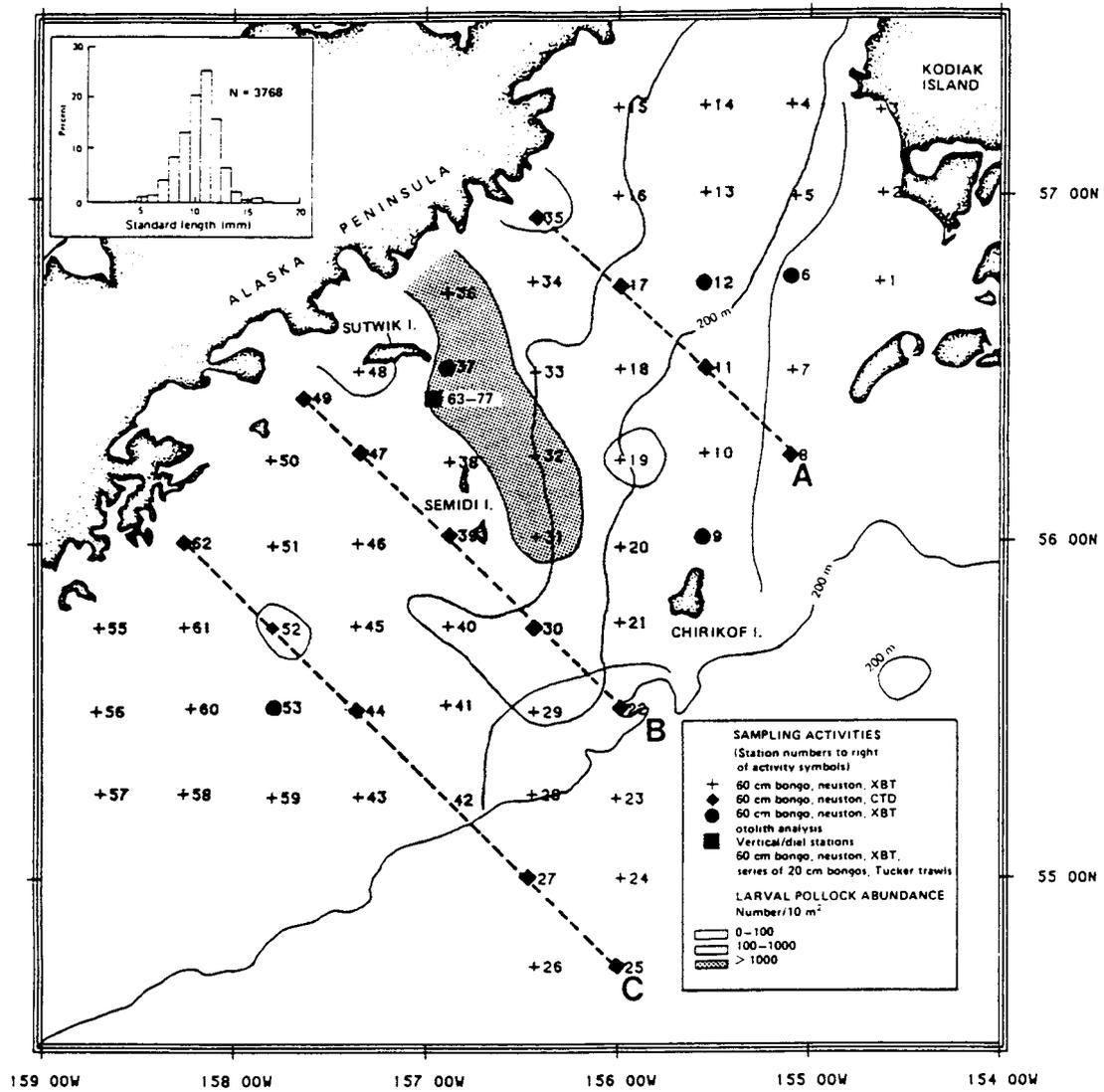


FIGURE 2.—Distribution, abundance (numbers per 10 m²) and lengths of walleye pollock larvae from 60 cm MARMAP bongo tows superimposed on sampling pattern used in the northern Gulf of Alaska, May 1983. Hydrographic sections are labelled A, B, C (see Figure 4).

Laboratory Procedures

Fish eggs and larvae were identified to the lowest taxon possible at the Polish Plankton Sorting Center in Szczecin, Poland. Fish larvae were measured to the nearest 0.1 mm standard length (SL); when more than 50 larvae of a taxon occurred in a sample, a random subsample of 50 was selected for measurement. Identifications were verified at the Northwest and Alaska Fisheries

Center. For distributional analysis of fish eggs and larvae from the survey, numbers per tow for each taxon were converted to numbers under 10 m² of water surface using volumes of water filtered and maximum tow depth (see Smith and Richardson 1977). To compare relative abundances of various taxa, an estimate of the total number of eggs or larvae of each taxon present in the entire survey area was derived by summing the catches at each station and multiplying by the

area of sea surface represented by that station (the Sette-Ahlstrom method, see Smith and Richardson 1977). This estimate was thought to make best use of all the available data.

A chi-square test analyzed differences in the numbers of walleye pollock larvae caught as a function of time of day and depth at the diel station. For this test, numbers of larvae in the two sides of the 20 cm bongo nets were combined. Also, catches at the same time and depth but on different days were combined when complete depth series were collected. Four out of six times two complete depth series were collected; at two times only one complete depth series was collected.

Zooplankton were sorted, identified, and enumerated from subsamples of collections made with the 253 μm mesh net. The subsample was chosen such that at least 500 organisms were sorted from each sample.

For larval feeding analysis, 20 walleye pollock larvae (or the total sample when <20 were caught) were selected to represent the size range in the total sample from each of the 333 μm mesh, 20 cm bongo net samples. The guts were dissected from the larvae, and all food items in the foregut, midgut, and hindgut were teased out, identified, and counted.

Lengths and greatest widths were measured for all food items in the larvae collected at 0630, 29 May. Lengths used were carapace length for copepod nauplii, metasome length for copepodids, and total length for all other prey. These measurements were used to estimate volumes of prey organisms, which were applied to the rest of the samples. Mensuration formulae were used to cal-

culate the volume of copepod eggs, copepod nauplii, copepodids of *Pseudocalanus* spp., *Acartia* spp., and *Oithona* spp. (Nishiyama and Hirano 1983; Table 1). *Pseudocalanus* spp. mensuration formulae were used to estimate the volumes of unidentified copepodids. The volumes of other food items were not estimated since their low abundance did not allow adequate measurement of body proportions.

Samples used for age and growth analysis were selected from one station within the area of highest larval density (Station 37, Fig. 2), and from four stations located outside of this dense patch. Standard lengths of larvae from as broad a size range as possible within each sample were measured to the nearest 0.1 mm using an ocular micrometer. Both sagittal otoliths were removed and cleaned using a pair of fine needles under a dissecting microscope fitted with polarizing filters. Whole otoliths were affixed to microscope slides with clear histological mounting medium and increments read in the sagittal plane under a compound microscope with transmitted light at 1000 \times magnification. Most of the otoliths had a distinct distal-proximal curvature and readability was enhanced when the otolith was mounted with the concave side up.

Increments were identified as a pair of adjacent light and dark bands, formed concentrically around the focus. A prominent dark band surrounding the focus was observed on each otolith (Fig. 3). Since mean otolith diameter at this band ($16.0 \pm 0.13 \mu\text{m}$ SE) was similar to the diameter of otoliths from 1-day-old, laboratory-reared larval pollock ($18.97 \pm 0.37 \mu\text{m}$, Nishimura and Yamada 1984; $16\text{--}20 \mu\text{m}$, Walline 1983; 15.3 ± 1.2

TABLE 1.—Mensuration formulae (Nishiyama and Hirano 1983),¹ length to width ratios, metasome to whole body ratios, metasomal lengths, mean lengths, and mean diameters used to calculate volumes of copepodids, copepod nauplii, and copepod eggs in guts of larval walleye pollock in Shelikof Strait.

Species	K	m	Lm
	Length:width (this study)	Metasome:whole body (Nishiyama and Hirano 1983)	Metasomal length (this study)
<i>Pseudocalanus</i> spp.	2.239	0.97	0.870
<i>Oithona</i> spp.	1.824	0.93	0.189
<i>Acartia</i> spp.	3.213	0.95	0.916
Unidentified copepodids	2.539	0.97	0.870

¹Mensuration formulae (Nishiyama and Hirano 1983):

Volume of copepodids = $(Lm/6 \cdot (Lm/K)^2 \pi) / m$.

Volume of copepod nauplii = $(\frac{\pi}{24} \text{carapace length}^3)$;
mean carapace length = 0.187.

Volume of copepod eggs = $(\frac{\pi}{6} \text{egg diameter}^3)$;
mean egg diameter = 0.110.

μm , Bailey and Stehr⁸), this band was presumed to be the hatching check and was counted as the first increment. Nishimura and Yamada (1984) found that increments were formed daily, beginning with the day of hatching, on the otoliths of laboratory-reared larval pollock. Similar observations have been made on larval walleye pollock otoliths viewed with both light and scanning electron microscopy by Bailey and Stehr (fn. 8). Increments were, therefore, considered to be deposited daily and increment counts were equated with the age of the fish in days after hatching.

The mean of two independent increment counts was used in growth rate analysis. Age-at-length data from each station were fitted separately with simple linear regressions. Analysis of covariance

⁸K. Bailey and C. Stehr, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, N.E., Seattle, WA 98115, pers. commun. 7 February 1985.

was used to compare growth rates and Dunnett's test of multiple comparisons identified significantly different rates (Zar 1974).

RESULTS

Hydrographic Observations

Temperature in the survey area varied from just above 7°C at the surface at some stations to slightly <5°C in deeper shelf water (Fig. 4). Temperature gradually decreased with depth, and temperatures in the upper 50 m (where most of the walleye pollock larvae were found) were generally between 7.0° and 5.5°C. At the diel-vertical distribution station, temperatures were similar to those found throughout the area, although the temperature gradient was more uniform than elsewhere. In the upper 60 m at this station, tem-

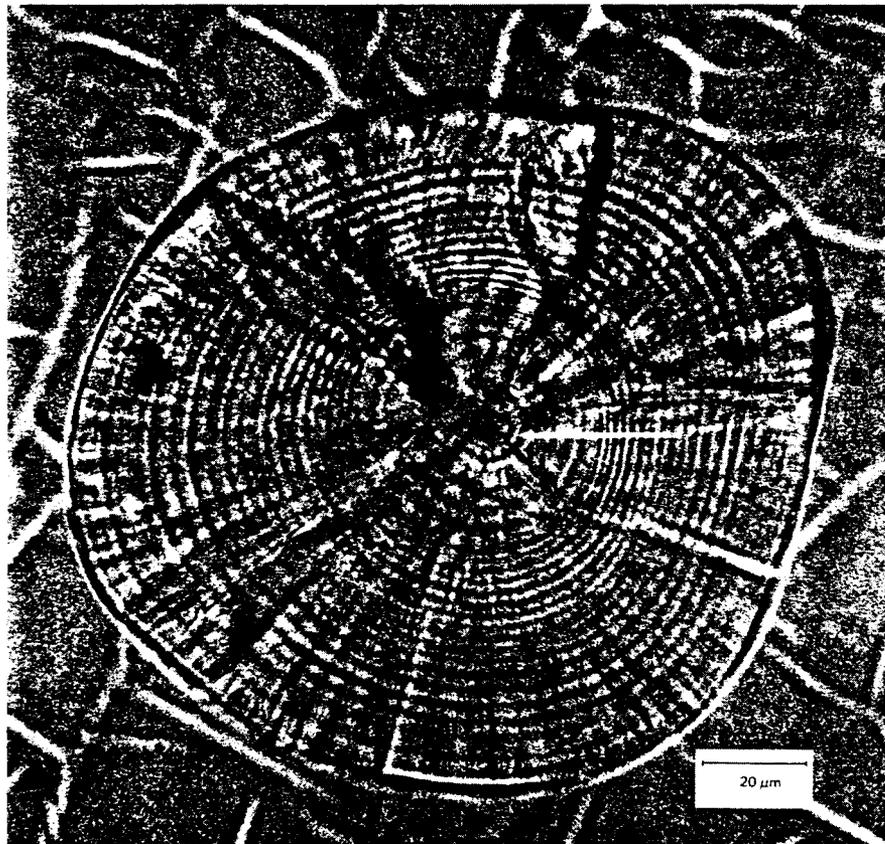


FIGURE 3.—Otolith from a 11.57 mm SL walleye pollock larva showing 27 daily growth increments. The arrow near the focus indicates the first increment. Scale bar indicates 20 μm .

STATION NUMBERS

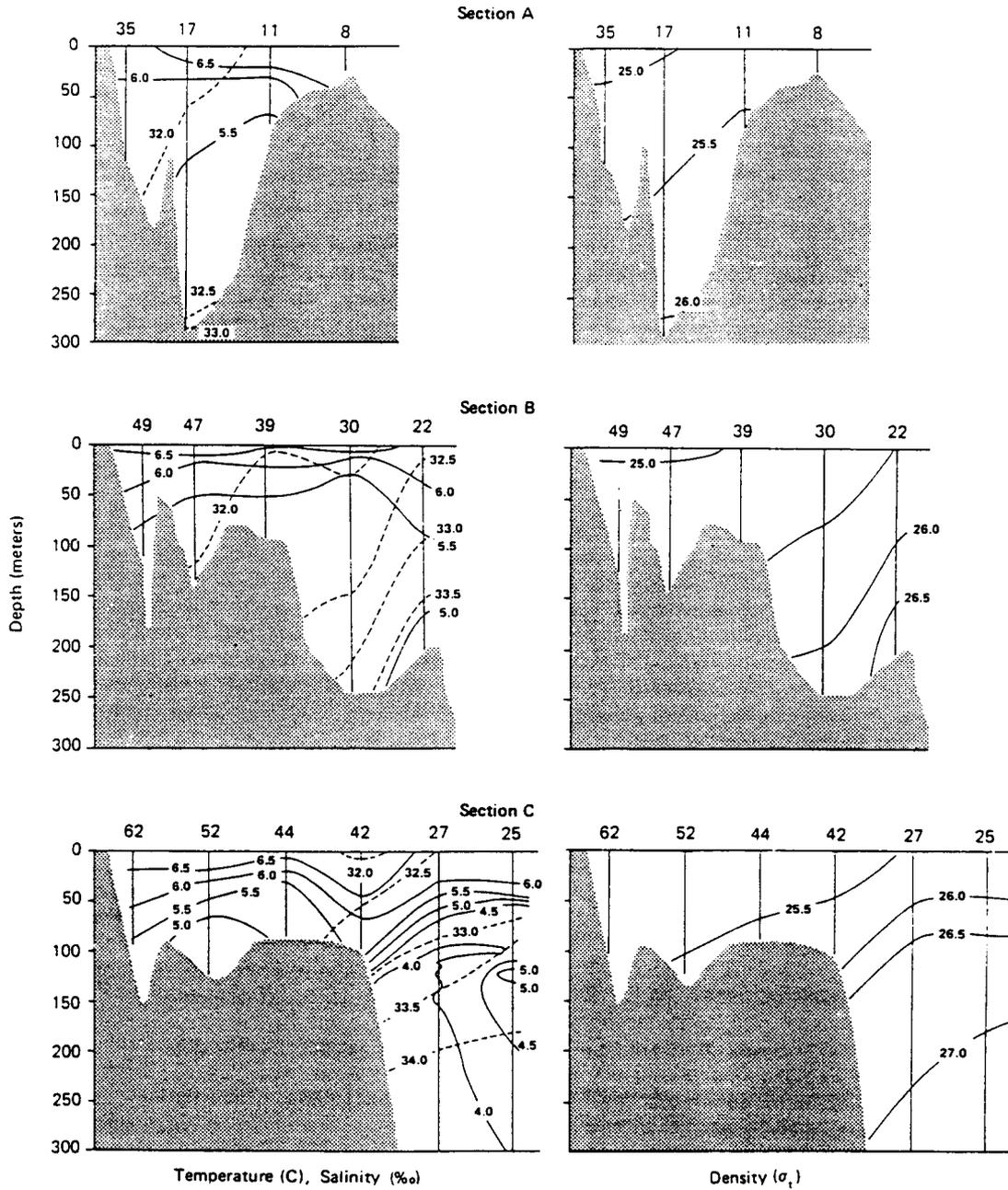


FIGURE 4.—Temperature (solid contours), salinity (broken contours), and density observed in three sections across the sampling area, May 1983. Station and section locations are shown in Figure 2.

perature steadily decreased from 6.9°C to 6.0°C, and at the bottom (120 m) the temperature dropped to 5.5°C. Among the four XBT casts (taken at 12-h intervals), the temperature at a given depth varied as much as 0.5°C: an isotherm depth varied vertically by as much as 50 m.

Salinity varied from 31.5 to >33.5‰ in the survey area. Lowest salinities were found at the surface toward the Alaska Peninsula, and high salinities were found offshore in deeper waters. Isohalines generally sloped from offshore to inshore. This slope was most pronounced at Section A, the one closest to Shelikof Strait. Most larvae were in water between 31.5 and 32.2‰. The salinity profile at the CTD station closest to the diel station showed a slight and steady increase in salinity with depth starting from a surface value of 31.8‰ and ending with a bottom (142 m) value of 32.1‰.

Density sections (σ_t) show the same sloping pattern as the salinity sections but are even more pronounced (Fig. 4). Values ranged from <25.0 at the surface near the Alaska Peninsula to >26.4 in deeper waters near the edge of the continental shelf. No sharp pycnocline was observed but rather a gradual increase in density with depth and distance from the Alaska Peninsula. Most walleye pollock larvae were in water with densities between 25.0 and 25.4 σ_t . The density profile observed near the diel station closely paralleled the salinity profile, with a gradual increase with depth from $\sigma_t = 24.9$ at the surface to $\sigma_t = 25.4$ at the bottom (142 m).

Relative Abundance of Eggs and Larvae

Neuston tows and bongo tows captured eggs of 13 and 14 taxa, respectively (Fig. 5). Rank orders of abundance, based on estimated total numbers of fish eggs in the neuston catches showed *Microstomus pacificus* (Dover sole) to be in greatest abundance, followed by *Glyptocephalus zachirus* (rex sole) and *Theragra chalcogramma*. In bongo catches, unidentified pleuronectid (righteye flounders) eggs were most abundant, followed by those of *M. pacificus*, *G. zachirus*, and *T. chalcogramma*.

Larvae of 29 and 42 taxa were identified in neuston and bongo catches. Rank order of abundance of fish larvae in neuston tows, based on estimated total numbers, showed *Ammodytes hexapterus* (Pacific sand lance) to be most abundant followed by *Hexagrammos decagrammus*

(kelp greenling), *Lyconectes aleutensis* (dwarf wrymouth), *Bathymaster* spp. (ronquils), and *T. chalcogramma*. In bongo catches *T. chalcogramma* larvae were most abundant followed by those of *Bathymaster* spp., *A. hexapterus*, *Hippoglossoides elassodon* (flathead sole), and unidentified gadids (codfishes).

Distribution and Abundance of Walleye Pollock Eggs and Larvae

Eggs of walleye pollock were taken in 26% of the bongo tows and in 27% of the neuston tows but in low abundance. Only 262 eggs were collected. Some early stage eggs were collected, indicating recent spawning, but older eggs were also present. Eggs were found mainly in water over the deeper part of Shelikof Strait, with decreasing abundance to the southwest (Fig. 6).

Larvae of walleye pollock were found in 89% of the bongo catches and 24% of the neuston catches. The center of larval concentration was near the middle of the survey pattern (Fig. 2). Mean standard length of the larvae throughout the survey was 10.63 mm (range 3.8-21.3 mm, SD = 1.81 mm), with no differences in mean length by area. At each of five stations near Sutwik Island and the Semidi Islands, more than 1,000 larvae/10 m² were encountered. At 44 of the 64 stations, more than 100 larvae/10 m² were found. A total of over 10¹² larvae was estimated to be present in the survey area.

Vertical Distribution of Walleye Pollock Larvae

In preliminary tows with the 20 cm bongo nets most larvae were caught above 60 m. During the vertical distribution study actual depths of sampling based on bathykymograph records covered the ranges of 14-20, 21-28, 28-38, and 39-47 m (Table 2).

The mean length of the larvae during our diel vertical distribution study was 11.1 mm SL. The range of mean lengths among the individual samples was 10.0-12.2 mm SL, and the range of standard deviations was 0.8-2.3 among hauls with more than 10 larvae. No patterns of size of larvae with depth or time of day were seen by visual inspection of the data, and since the range of mean lengths was so narrow, and the confidence intervals overlapped, no further analysis was performed.

There were no diel differences in catch rates

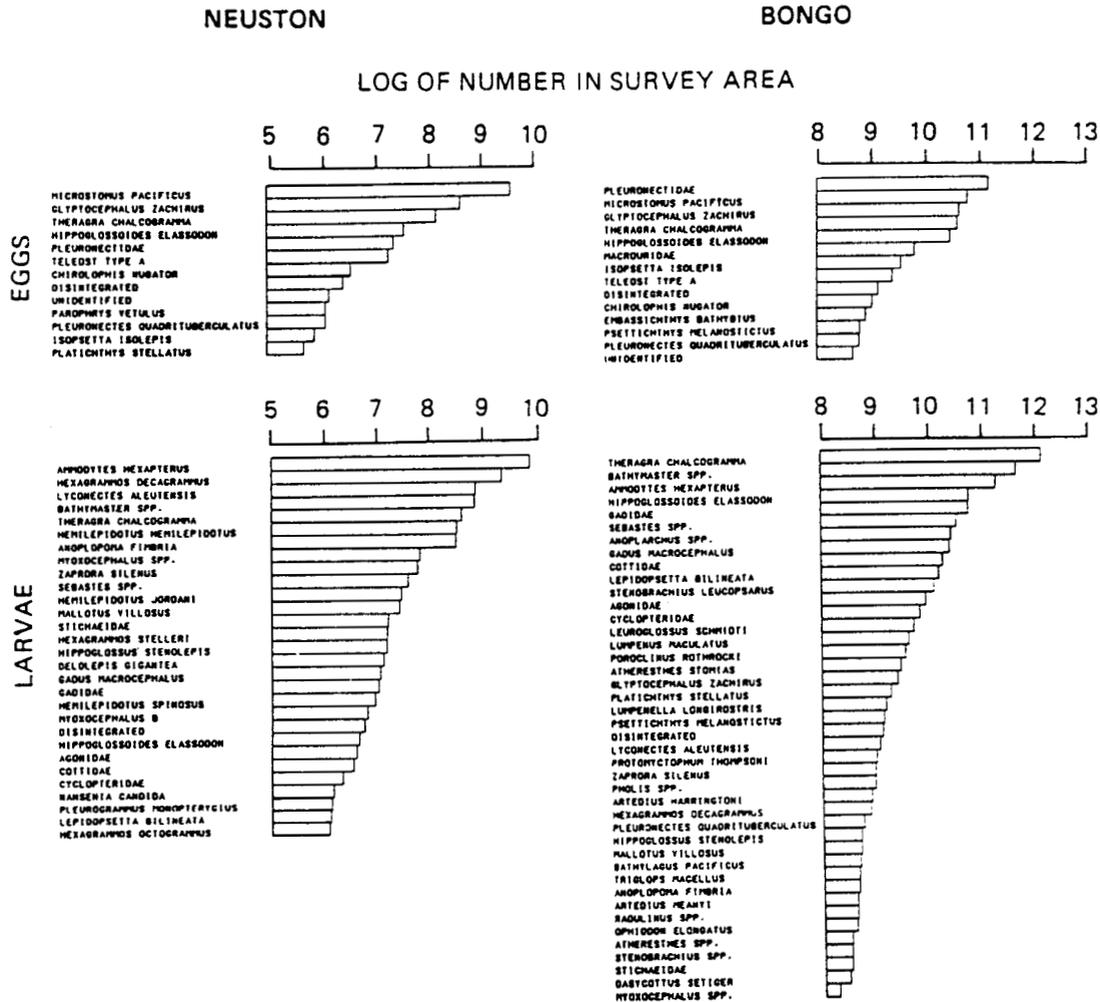


FIGURE 5.—Rank order abundance, as log of total numbers in the survey area, of fish eggs and larvae in neuston and bongo tows during the survey, May 1983.

TABLE 2.—Chi-square test of numbers of walleye pollock larvae with time and depth from the vertical distribution study, May 1983.

Depth (m)	Time											
	1840-1920		2235		0320-0238		0629-0635		1047		1432-1515	
	No. samples											
	16		8		16		16		8		16	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
14-19	76	(94)	98	(78)	133	(159)	100	(59)	61	(68)	37	(47)
21-28	76	(122)	138	(101)	202	(207)	68	(76)	108	(89)	65	(62)
28-38	110	(95)	11	(79)	201	(161)	46	(59)	87	(69)	56	(48)
39-47	136	(87)	83	(72)	140	(148)	35	(55)	33	(63)	43	(44)
Total	398		330		676		249		289		201	
χ^2	52.19		78.89		14.73		39.46		23.77		3.63	
Total $\chi^2 = 212.69$ (15 df, $P < 0.005$)												

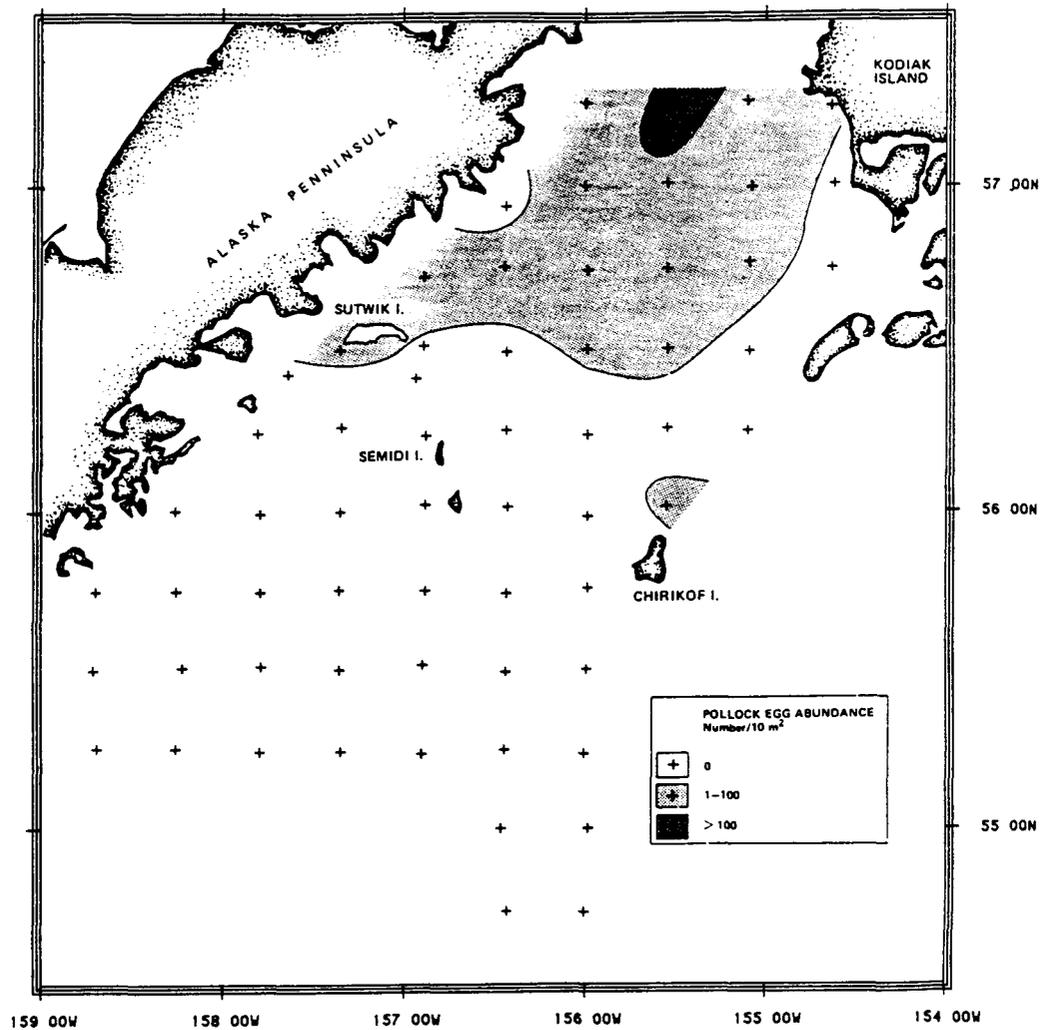


FIGURE 6.—Distribution and abundance of walleye pollock eggs, May 1983.

(Table 2). The means of the catch per 10 m^3 at each time-depth combination expressed as a percentage of the total catch at that time of day suggests a pattern of limited diel vertical migration (Fig. 7). The chi-square test was highly significant ($P < 0.005$) indicating that the null hypothesis, that the larvae were distributed at each depth in the same proportions among the different times, should be rejected. Examining the relative abundances within each time period, the larvae appeared to be concentrated above 20 m at 0630 h, and at 28-47 m by 1830 h (Fig. 7). They were most evenly distributed in the early afternoon and

most abundant in the 21-28 m stratum during darkness (2230 and 0230 h) and at 1030 h. The lowest percent abundance at each time period shows a complementary pattern, with relatively small catches at 39-47 m from 0230-1430 h. This pattern was observed on both days during the 48-h sampling.

In summary, it appears that some larvae gradually move up in the water column from a depth of 30-50 m in the evening to above 20 m in early morning. They gradually descend during daytime, and are most evenly distributed in the early afternoon.

PERCENTAGE OF LARVAE AT EACH DEPTH

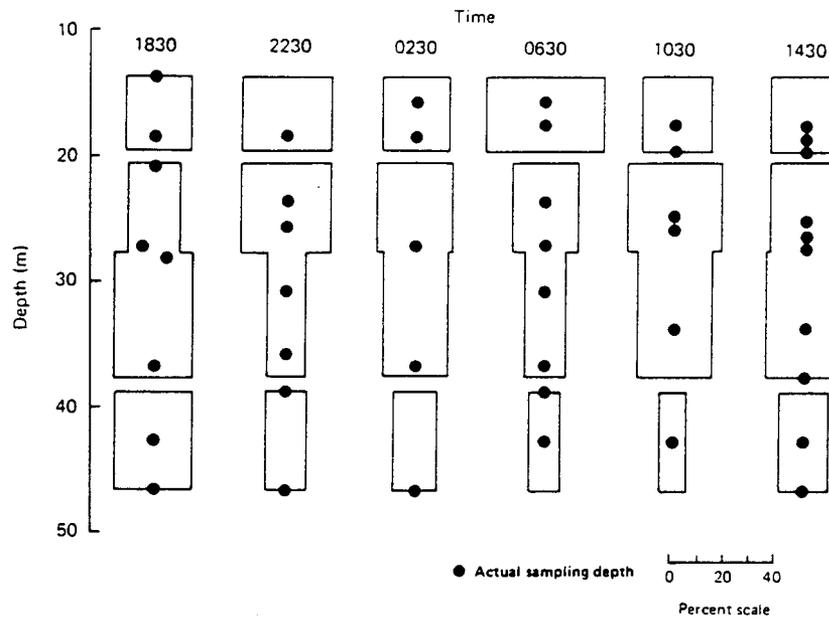


FIGURE 7.—Relative abundance as percent of larvae at each depth for each time interval, of walleye pollock larvae from the vertical distribution study, May 1983.

Comparison of Catches of Walleye Pollock Larvae by Different Gears

The sizes of larvae in the different bongo nets at the vertical distribution station were similar (Table 3). Mean lengths of larvae in the 20 cm bongo nets varied from 11.00 in the 333 μm mesh net to 11.10 mm in the 253 μm mesh net (SD = 1.76 and 1.69 mm respectively); mean length in the 60 cm bongo nets was 11.07 mm (SD = 1.77 mm). The Tucker trawl, however, caught larvae that had a mean length of 9.64 mm (SD = 1.67 mm). The overall mean abundance of larvae in the 20 cm bongo in the 28-38 m depth stratum nets (11.82 larvae/10 m^3) was similar to that in all the Tucker trawls (11.66 larvae/10 m^3) which were towed at 35 m. The mean of the catches in the 60 cm bongo nets, towed just below the deepest 20 cm bongo, was not notably different from the mean of those 20 cm bongo catches taken at the same times.

Variations in overall catches in the 20 cm bongo nets at the vertical distribution stations seemed to reflect the patchy nature of the concen-

tration of larvae and not net avoidance related to time of day. The largest catches occurred during daylight, at 1030 h, while the smallest catches occurred during the time intervals immediately preceding (0630 h) and immediately following (1430 h) the largest catches. Since we sampled one geographic site rather than following a drogue, we probably sampled water with different concentrations of larvae as it drifted past us during the 48-h sampling. It appears that the larvae decreased from a concentration greater than 1 m^{-3} during the first 24 hours to $<0.5 \text{ m}^{-3}$ during the second 24 hours. The size of larvae did not change during the study again indicating that increased daytime net avoidance was not significant.

Hydrography in Relation to Distribution of Walleye Pollock Larvae

No obvious hydrographic features were associated with larval distributions. At the diel station, larvae were concentrated between 14 and 47 m where temperature within the upper 50 m was

TABLE 3.—Comparisons of catches and lengths (mm SL) of walleye pollock larvae with gear, time of day, and depth from the vertical distribution study, May 1983.

Depth (m)	mm SL (SD) number		mm SL (SD) number	
	333 μ m mesh		253 μ m mesh	
14-19	11.13 (1.80)	333	10.86 (1.77)	333
21-28	11.07 (1.74)	405	11.07 (1.87)	427
28-38	11.24 (1.68)	232	11.04 (1.73)	290
39-47	11.19 (1.60)	249	11.17 (1.46)	229
Time (local)				
1830	11.03 (1.67)	210	10.86 (1.65)	118
2230	10.98 (1.58)	189	10.76 (1.56)	185
0230	11.50 (1.83)	315	11.39 (1.75)	361
0630	11.12 (1.42)	133	11.31 (1.82)	116
1030	11.01 (1.75)	331	10.61 (1.81)	301
1430	10.73 (1.57)	183	11.13 (1.72)	182
Gear				
20 cm bongos, 253 μ m mesh	11.10 (1.69)	1,388		
20 cm bongos, 333 μ m mesh	11.00 (1.76)	1,381		
All 60 cm bongos	11.07 (1.77)	578		
All Tucker trawls	9.64 (1.67)	2,180		

stable at 6.90°-6.15°C (Fig. 8). Nearby, salinity and density showed a very gradual increase with depth.

The pattern of water movement in the survey area, derived from the temperature and salinity observations, indicated a general southwest flow of water at all depths. In the area of larval concentration, most of the flow tended southward, following the deep trough from Shelikof Strait across the continental shelf between the Semidi

Islands and Chirikof Islands (S. Kim⁹).

Diet and Feeding of Walleye Pollock Larvae

Eighteen different food items were identified in walleye pollock larvae sampled at the diel sta-

⁹S. Kim, School of Fisheries, University of Washington, Seattle, WA 98195, pers. commun. September 1985.

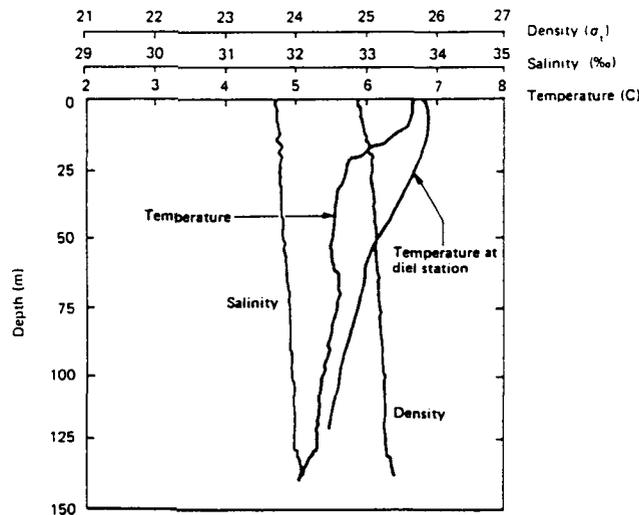


FIGURE 8.—Temperature, salinity, and sigma-t profiles at Station 47 with temperature profile from the diel station (Stations 63-77) shown for comparison. See Figure 2 for station locations.

tions. Copepod nauplii 90-600 μm in length and between 40 and 250 μm in width were the most abundant food item for larvae <14.0 mm (Fig. 9). The length- and width-frequency distributions of nauplii indicate that *Pseudocalanus* spp. and *Oithona* spp. are the likely prey taxa. Nauplii became numerically less important in diets of larger larvae. *Pseudocalanus* spp. copepodids, copepod eggs, and *Oithona* spp. copepodids made up a larger numerical portion of the food of these larger larvae (Fig. 10). The increased importance of *Pseudocalanus* spp. copepodids in the diet of larger larvae is evident in terms of gut volume (Fig. 10). Examination of the contribution of the copepod eggs to the diet indicates that while eggs increase numerically from 1.5% in the 8.0-8.9 mm size group to 55% in the 14.0-14.9 mm size group, their volume increases only from 0.5 to 3.6%.

The number of food organisms and mean prey volume per larva show a diel feeding pattern (Fig. 11). The maximum gut contents were observed during the afternoon. Collections at 2235, 0230, 0238, and 0629 have the lowest mean number of food items per larva, which suggests that feeding during darkness is reduced. The mean gut volumes show a similar pattern (Fig. 11). Although gut volume at 1047 h on 29 May was unusually low, it was not an indication of reduced feeding. Here the gut contents consisted of numerous copepod nauplii and few adult copepods. Thus the calculated prey volume is quite low, while the number of food items per gut is high.

Zooplankton Composition

Thirty-nine groups of zooplankters were identi-

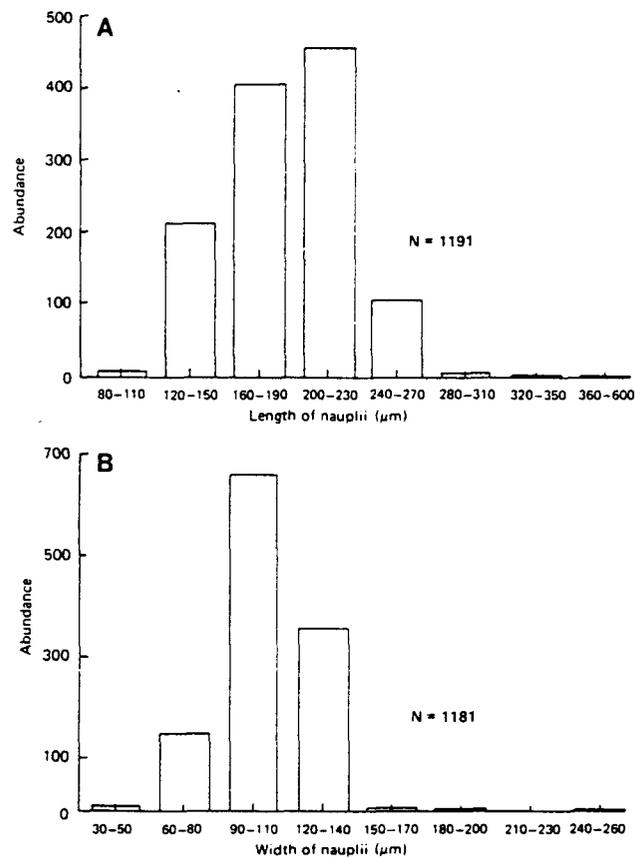


FIGURE 9.—Length (A) and width (B) size-frequency distribution of copepod nauplii from guts of walleye pollock larvae.

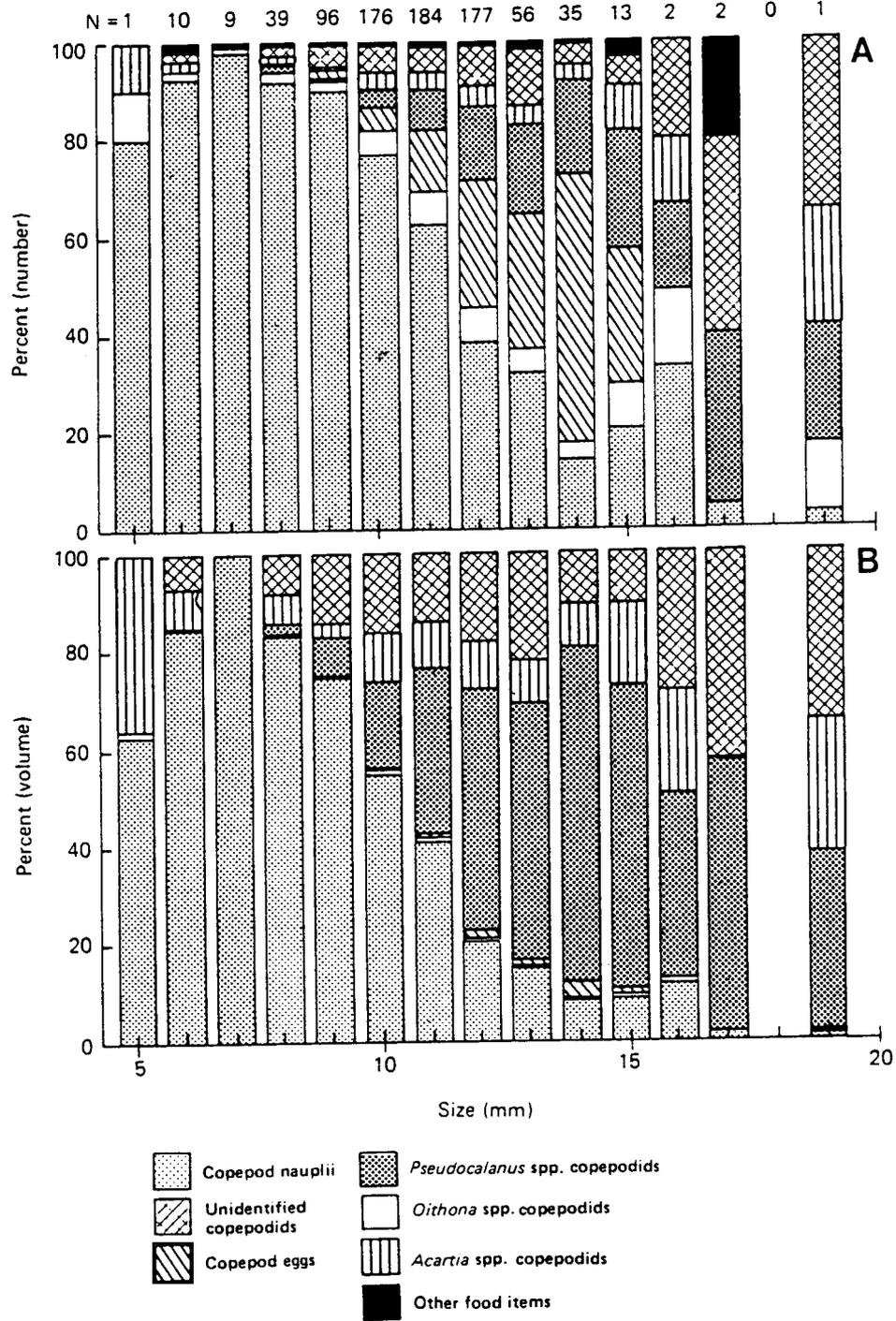


FIGURE 10.—Gut contents of walleye pollock larvae by 1 mm length intervals (5-20 mm) from northern Gulf of Alaska, May 1983. A—percent number; B—percent volume.

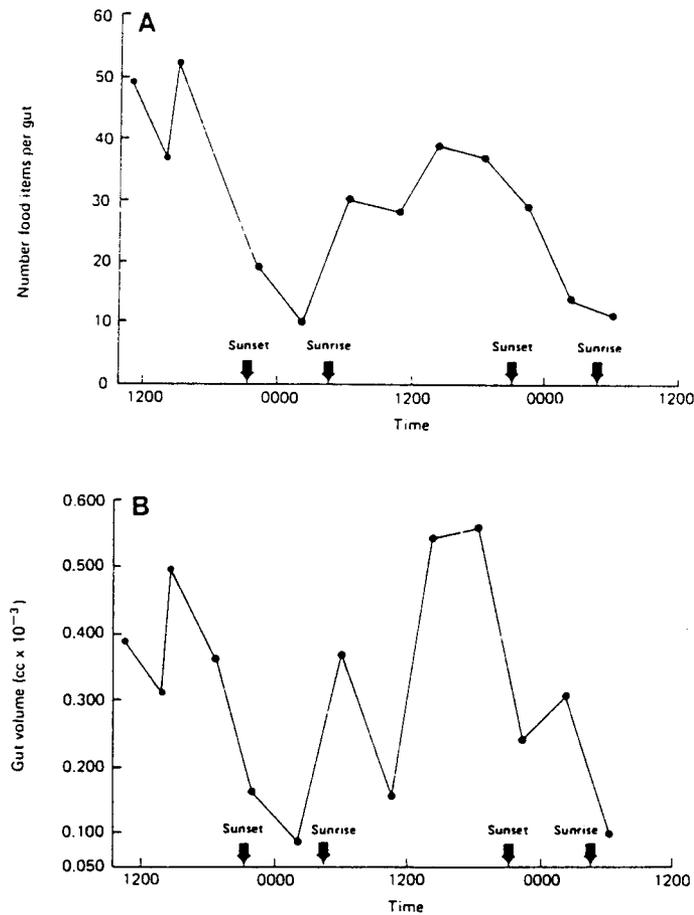


FIGURE 11.—Numbers of prey (A) and gut fullness (B) of walleye pollock larvae by time of day and depth from the vertical distribution stations, May 1983.

fied from samples taken with the 253 μm mesh net (Table 4). *Pseudocalanus* spp. were generally the most abundant taxon. Abundances of *Pseudocalanus* females ranged from 11 m^{-3} to a peak of 1,398 m^{-3} at 1515 h on the first day at a depth of 47 m. The overall mean abundance of *Pseudocalanus* females was 224 m^{-3} . These females comprised between 9 and 23% of the total zooplankton at all depth strata both during the daylight and darkness (Fig. 12). The highest percent contribution by this stage (22-23%) was during daylight hours at the two deepest strata. Peak abundances usually occurred at depth strata below 25 m. Copepodid stages of *Pseudocalanus* also reached a peak of 1,890 m^{-3} at the same station. These copepodids contributed the greatest percentage

(21-33%) of the total zooplankton at all depths and times. There were no obvious patterns associated with depth or time of day in either abundance or percent composition of the total zooplankton.

Oithona spp. were abundant in the samples even though they were not collected quantitatively in the 253 μm mesh net. The peak abundance observed was 1,323 m^{-3} . *Oithona* spp. were most abundant in the surface stratum comprising 18% of the total zooplankton during the day versus <10% of the zooplankton at deeper strata during the day and at all depths during the night (Fig. 12). *Acartia* spp., *Neocalanus* spp., and *Calanus* spp. were the only other abundant copepods. The *Neocalanus* spp. and *Calanus* spp. in-

TABLE 4.—Species composition of zooplankton samples from the vertical distribution stations.

Number (See Fig. 11)	Taxon		Maximum No./10 m ³	Minimum No./10 m ³	Mean No./10 m ³
		Name			
1		<i>Pseudocalanus</i> spp. adult female	13,981	118	2,245
2		<i>Pseudocalanus</i> spp. adult male	4,711	0	567
3		<i>Pseudocalanus</i> spp. copepodids 1-5	18,915	46	3,592
4		<i>Neocalanus</i> spp. and <i>Calanus</i> spp.	12,163	0	1,545
5		<i>Oithona</i> spp.	13,234	0	1,167
6		<i>Acartia</i> spp.	2,476	101	794
7		<i>Centropages</i> spp.	380	0	50
8		<i>Metridia</i> spp.	—	0	—
9		<i>Eucalanus bungii</i>	192	0	7
10		<i>Paracalanus</i> sp.	46	0	5
11		<i>Clausocalanus</i> sp.	25	0	1
12		<i>Tortanus</i> spp.	7	0	—
13		Unidentified calanoid	201	0	9
14		Euphausiid furcilia	3,431	0	511
15		Euphausiid calyptopsis	97	0	7
16		Euphausiid crytopsis	—	0	—
17		<i>Thysanoessa inermis</i> furcilia	1,307	0	517
18		<i>T. inermis</i> calyptopsis	—	0	—
19		<i>T. inermis</i> crytopsis	97	0	5
20		Euphausiid juveniles	—	0	—
21		<i>T. inermis</i> juvenile	73	0	5
22		Chaetognatha	592	0	94
23		Appendicularia	1,088	0	290
24		Hyperidae	183	0	31
25		Gastropoda	484	0	62
26		Decapoda	262	0	24
27		Balanidae	253	0	39
28		Gammandae	7	0	—
29		<i>Evadne</i> spp.	97	0	3
30		<i>Limacina</i> spp.	1,569	0	364
31		Pontellidae	19	0	—
32		Thecosomata	255	0	21
33		<i>Brachyura</i>	292	0	34
34		Gymnocomata	38	0	1
35		Echinodermata	1,511	0	117
36		Hydrozoa	311	0	18
37		Pelecypoda	28	0	1
38		Medusa	14	0	—
39		Siphonophore	8	0	—

cluded *N. plumchrus*, *C. pacificus*, and *C. marshallae*. Together these species contributed between 13 and 25% of the total zooplankton (Fig. 12).

Euphausiids were the only other abundant group of zooplankters; furcillae were the most abundant stage. The abundance of furcillae was generally <200 m⁻³; however, at 1047 h on 29 May, the numbers of furcillae exceeded 1,300 m⁻³.

Age and Growth

Ages were determined for 109 walleye pollock larvae, including 40 individuals collected from Station 37 within the area of highest larval abundance and 69 specimens from four stations well removed from this area. Standard lengths ranged from 6.0 to 14.6 mm and mean increment counts

(days since hatching) ranged from 7 to 45.5 (Table 5). The average growth rate varied from 0.12 to 0.25 mm/day among the five stations (Table 5). When compared pairwise with growth rates from all other stations, growth rates from all stations located outside the dense patch, ex-

TABLE 5.—Average growth rates, statistics on the linear regression, comparison lengths, and ages of larval walleye pollock used in growth analysis from five areas in the Shelikof Strait. Station 37 is in the area of highest larval density (Fig. 1).

Station	Y-intercept (mm)	b-growth (mm d ⁻¹)	r ²	N	No. of fish aged	Length range (mm)	Age range (days)
37	3.7	0.24	0.82	40	40	6.8-13.1	12-42
53	4.2	0.23	0.81	20	20	7.6-13.0	20-41
9	3.5	0.25	0.81	20	20	6.0-14.6	7-43
6	4.7	0.18	0.61	20	20	6.6-12.3	10.6-42.2
12	6.6	0.12	0.90	9	9	8.1-12.6	14-45.5

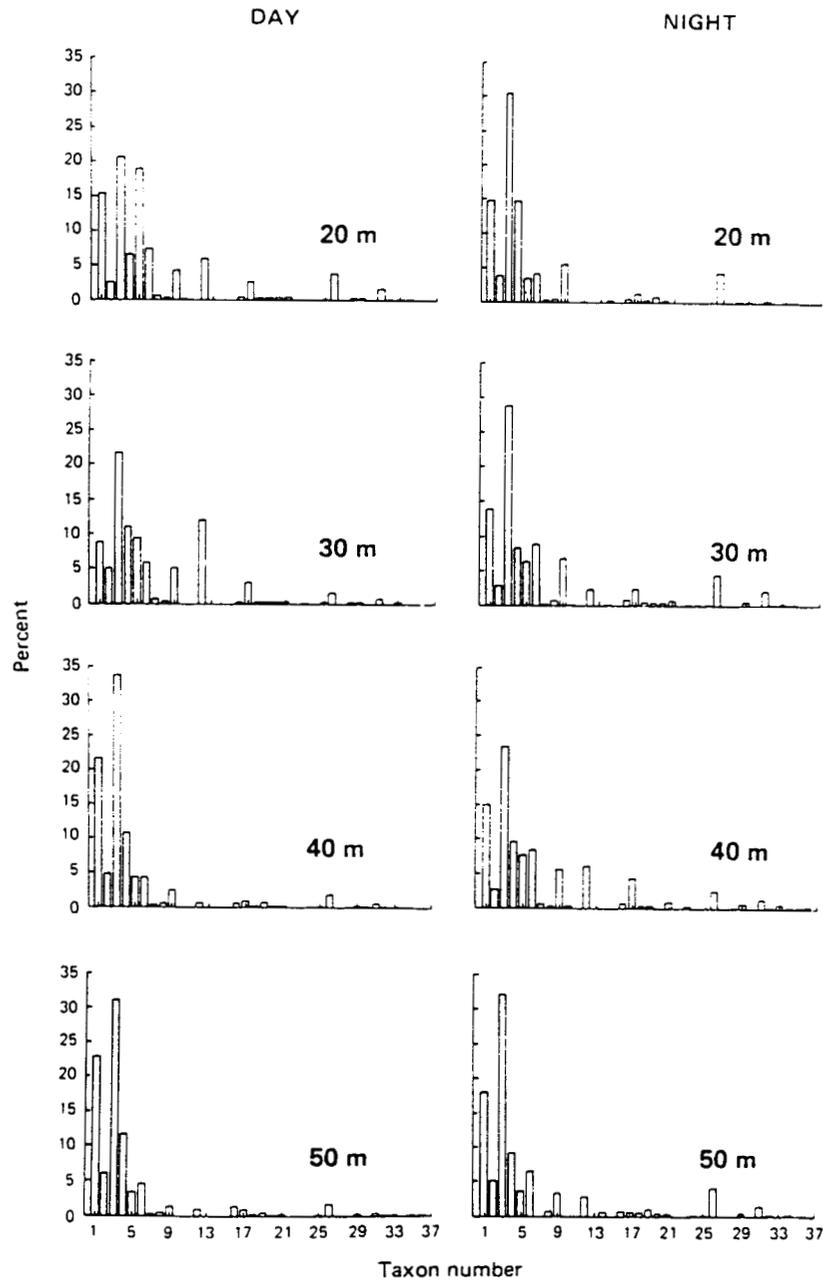


FIGURE 12.—Zooplankton distribution (percent total zooplankton) for day and night by depth from the vertical distribution stations, May 1983. Taxon numbers: 1: *Pseudocalanus* spp., adult female; 2: *Pseudocalanus* spp., adult male; 3: *Pseudocalanus* spp., copepodids 1-5; 4: *Neocalanus* spp. and *Calanus* spp.; 5: *Oithona* spp.; 6: *Acartia* spp.; 7: *Centropages* spp.; 8: *Metridia* spp.; 9: *Eucalanus bungii*; 10: *Paracalanus* sp.; 11: *Clausocalanus* sp.; 12: *Tortanus* spp.; 13: Unidentified calanoid; 14: Euphausiid furcilia; 15: Euphausiid calyptopsis; 16: Euphausiid crytopsis; 17: *Thysanoessa inermis* furcilia; 18: *T. inermis* calyptopsis; 19: *T. inermis* crytopsis; 20: Euphausiid juveniles; 21: *T. inermis* juvenile; 22: Chaetognatha; 23: Appendicularia; 24: Hyperidae; 25: Gastropoda; 26: Decapoda; 27: Balanidae; 28: Gammaridae; 29: *Evadne* spp.; 30: *Limacina* spp.; 31: Pontellidae; 32: Thecosomata; 33: Brachyura; 34: Gymnosomata; 35: Echinodermata; 36: Hydrozoa; and 37: Pelecypoda.

cept Station 12, were not statistically different from growth measured within the dense patch (Station 37). Larvae collected at adjacent Stations 6 and 12, located to the northeast of the densest area (Fig. 2), exhibited the lowest growth rates and were not statistically different from each other.

Estimated age-at-length data from all stations were combined to describe early growth in walleye pollock from the Shelikof Strait region as follows:

$$SL = 4.29 + 0.21 (\text{age, d}) \quad n = 109, r^2 = 0.75$$

where SL = standard length (Fig. 13). This relationship suggests a mean growth rate of 0.21 mm/day and an intercept of 4.29 mm, which corresponds with the known size of newly hatched larvae (Walline 1983; Nishimura and Yamada 1984).

The distribution of dates of hatching was estimated by back-calculating from the ages determined for larval walleye pollock in the Shelikof Strait. The median birthdates from all stations were similar and thus all 109 samples were combined (Fig. 14). The hatching period ranged from early April to mid-May with a mode in the last

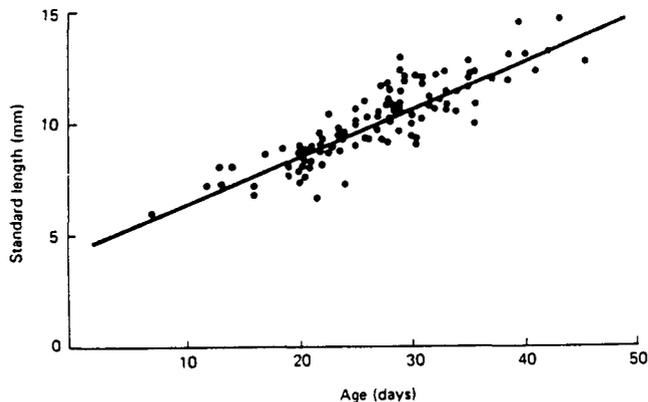


FIGURE 13.—Estimated age at length, fitted with linear regression, for all walleye pollock larvae analyzed from the northern Gulf of Alaska, May 1983.

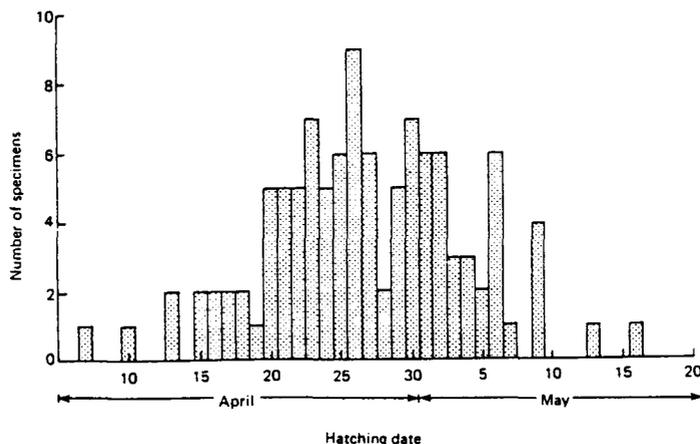


FIGURE 14.—Distribution of hatching dates for walleye pollock determined by back-calculation using age and date of collection.

week of April. Incubation time for walleye pollock eggs held at 5°-6°C in the laboratory is estimated to be 14 days (Haynes and Ignell 1983; Nakatani and Maeda 1984; Nishimura and Yamada 1984); spawning of walleye pollock occurs primarily in late March and early April in Shelikof Strait (Dunn et al. fn. 5), supporting our estimated hatching dates distribution.

DISCUSSION

Relative Abundance of Eggs and Larvae

Neuston collections in spring in the northern Gulf of Alaska have been reported only for 1978, mainly over the shelf, south and east of Kodiak Island, a month earlier than the present study (Kendall and Dunn 1985). Eggs of *Theragra chalcogramma* were most abundant; the rest of the identified eggs were of several pleuronectids. The greater abundance of *T. chalcogramma* in relation to the pleuronectids in the earlier cruise, when compared with the present data (Fig. 5), probably reflects the seasonal difference in spawning times. Pleuronectids spawn mainly in late spring and early summer in the Gulf of Alaska while *T. chalcogramma* is mainly a late winter-early spring spawner (Kendall and Dunn 1985).

Eggs have been reported from bongo catches from three other cruises in the northern Gulf of Alaska in May (Bates and Clark 1983¹⁰; Kendall and Dunn 1985); eggs of pleuronectids and those of *T. chalcogramma* were most abundant. However, the rank order of abundance of the various pleuronectids varied considerably among the cruises. Usually eggs of *Glyptocephalus zachirus*, *Hippoglossoides elassodon*, and *Microstomus pacificus* were among the five most abundant taxa.

Among larvae in the neuston tows during the present study, mainly spring spawning taxa (e.g., *Ammodytes hexapterus*, *Bathymaster* spp., *T. chalcogramma*) were represented; whereas larvae of fall-winter spawning taxa (e.g., three hexagrammids, and *Hemilepidotus* spp. [Irish lords]) were abundant during the earlier cruise (Kendall and Dunn 1985).

In bongo catches during other May cruises in

the area, larvae of *T. chalcogramma*, *Hippoglossoides elassodon*, *Bathymaster* spp., and *A. hexapterus* have always occurred frequently, as in the present study (Bates and Clark fn. 9; Kendall and Dunn 1985).

Distribution of Walleye Pollock Eggs

The few eggs collected during the present study represented a very late part of the spawning, which occurs in Shelikof Strait mainly in early April (Dunn et al. fn. 5) (Fig. 1). Recently hatched larvae (<5 mm SL), which were collected during our survey (Fig. 2), also indicate prolonged spawning but probably at a low level after mid-April. The eggs we found were mainly over the deep waters at the southwest end of Shelikof Strait, and it would be expected that they were also farther to the northeast. This is the same area of occurrence of eggs during the height of spawning (Dunn et al. fn. 5), indicating that the adults spawn mainly in Shelikof Strait throughout this period, although individual spawning fish probably migrate in and out of the area.

Comparisons of Distribution of Walleye Pollock Larvae

In 1981, several sequential cruises to Shelikof Strait mapped a large concentration of walleye pollock eggs in early April; and in late April and again in mid-May, a concentration of larvae was found progressively further to the southwest of the area where the eggs had been (Bates and Clark fn. 10) (Fig. 1). The size of the larvae in the concentration increased between the cruises.

Sampling in 1981 and 1982 for walleye pollock larvae was at the same area and time (24-28 May) as the present study (Dunn et al. fn. 5). Comparisons of distribution, abundance, and size of the larvae among these 3 years reveal remarkable differences (Table 6). Spawning time in 1981, based on ages of eggs caught in early April, and presence of newly hatched larvae in late April, centered around 5-8 April. In 1983, based on birthdate distributions presented here, modal spawning time was also in the second week of April. Sampling in subsequent years has shown a remarkable consistency in spawning place and time (Kendall unpubl. data). By 24-28 May the patch of larvae in 1981 and 1983 had drifted to the same area, just north of Sutwik Island (Figs.

¹⁰Bates, R. D., and J. Clark. 1983. Ichthyoplankton off Kodiak Island and the Alaska Peninsula during spring 1981. U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, NWAFC Proc. Rep. 83-09, 105 p.

TABLE 6.—Concentrations and lengths of pollock larvae collected 24-28 May 1981, 1982, and 1983 in the patch resulting from the Shelikof Strait spawning (1981 and 1982 data from Dunn et al. text fn. 5).

Year	Cruise	Date (May)	Stations	Larvae m ⁻²	Lengths (mm SL)	
					Mean	SD
1981	4MF81	24	73, 74	2,318	7.36	1.11
	3SH81	25	225	1,285 (mean = 2,040)	7.77	1.18
1982	2DA82	24-28	108, 115, 117, 123, 124, 126	14-38 (mean = 23)	7.74	1.10
			31, 32, 36, 37, 63	104-214 (mean = 151)	11.23	1.65

1, 2). However, the abundance of larvae in 1981 was about 2,000 m⁻² while in 1983 it was only about 150 m⁻². Mean length in 1981 was about 7.5 mm while in 1983 it was 11.2 mm. Since the spawning dates were the same, this would indicate a much slower growth rate (about 0.09 mm d⁻¹) in 1981 than in 1983 (0.21 mm d⁻¹). In 1982 there were fewer larvae (20 m⁻²) and they were distributed further southwest than in the other 2 years (Dunn et al. fn. 5). These larvae were not different in length from those in 1981 (7.7 mm). The position of the larvae in 1982 suggests a much faster drift than in 1981 and 1983.

Although most of the spawning occurs in the deep trench (>200 m) in Shelikof Strait, the larvae are in the upper part of the water column. Southwest of Shelikof Strait the trench runs south between the Semidi Islands and Chirikof Island (Fig. 2). Early larvae drift in the Alaska Coastal Current which flows southwest, parallel to the Alaska Peninsula (Schumacher and Reed 1980). At the time of our surveys in May 1981 and 1983, larvae had drifted to the area between Sutwik Island and the Semidi Islands. In 1982 they were further to the southwest in water over the deeper trough and the continental shelf.

Vertical Distribution of Walleye Pollock Larvae

Vertical distribution of walleye pollock larvae has been addressed in detail in several other studies (Kamba 1977; Cooney et al. 1978; Walline 1981¹¹; Dagg et al. 1984). Although the areas of

¹¹Walline, P. D. 1981. Hatching dates of walleye pollock (*Theragra chalcogramma*) and vertical distribution of ichthyoplankton from the eastern Bering Sea, June-July 1979. U.S.

study, procedures, and gear have varied, a consistent pattern of diel-vertical distribution emerges from these studies and is supported by the present study. Haryu (1980) summarized his and earlier work by stating "larvae inhabit the mid-layer rather than the surface layer and perform diurnal vertical migration in search of food." Most larvae have been found between 10 and 60 m, and within this depth range, some larvae generally move to shallower depths at night. Vertical movement is not pronounced in any of the studies but is evident by comparing proportions of larvae at various sampling depths at different times of day. In general it appears that larvae <15 mm are most concentrated vertically at 10-15 m at twilight, both in the evening and morning. During nighttime and daytime the larvae are more dispersed vertically, and during daytime their distribution is deeper than at night. Samples confined to day and night periods do not show the crepuscular nature of the distribution. This pattern is seen in the present study but is less pronounced than in some others, possibly because we conducted our sampling only in the vertical range of high concentration. Larvae larger than about 15 mm appear able to avoid plankton nets to some extent, particularly during daytime. The available data, however, suggest that these larger larvae remain concentrated in a shallow depth stratum (5-15 m) except at night when they are more dispersed vertically and may rise closer to the surface (Walline fn. 11).

Fish larvae of most other species that have been studied also migrate upward in the water column at night (Kendall and Naplin 1981). Some species undergo a much more pronounced vertical migration than is apparent with walleye pollock larvae and may cross much greater temperature gradients than observed here. Similar to walleye pollock, larvae of other fish species are visual feeders, and their vertical movements are probably associated with a diel feeding periodicity. Walleye pollock larvae may move to shallower depths at night to allow more feeding in reduced light. They then may spread downward in the water column during daytime in response to increased light penetration and the distribution of their prey. Too little is known about predation on fish larvae to assess the importance of vertical movements on predator avoidance (see Incze et al. 1984).

Dep. Commer., Natl. Mar. Fish. Serv., NOAA, NWAFC Proc. Rep. 81-05, 12 p.

Feeding of Walleye Pollock Larvae

The diet composition of larval walleye pollock in Shelikof Strait is similar to that described for walleye pollock larvae collected in the southeastern Bering Sea (Clarke 1978) and Uchiura Bay, Hokkaido, Japan (Kamba 1977). Copepod nauplii and copepodids of *Pseudocalanus* spp. were the dominant food items in the guts of 6-20 mm larvae in all these studies. As in this study, copepod eggs were also abundant food items. It is difficult in any of these studies to judge if the eggs were captured as individual food items or along with adult female copepods.

Feeding by larvae in the Gulf of Alaska is highest during daylight hours, as observed in other studies (Kamba 1977; Clarke 1978). Clarke (1978) reported that the few collections made at sunrise had larvae with the lowest feeding incidences. Kamba (1977) also reported that the lowest feeding incidences and the lowest abundance of food in the gut occurred near sunrise.

The high densities of larvae in the Shelikof Strait seem to have little effect on their food habits. *Oithona* spp. are abundant in the Bering Sea, Gulf of Alaska, and Uchiura Bay, Japan, and are intermediate in size between *Pseudocalanus* spp. copepodids and copepod nauplii. *Oithona* are an important component of the diet of pollock larvae in the Bering Sea, accounting for more than 25% of the total number of food items for larvae between 11.8 and 17.7 mm (Clarke 1978), but are rare in guts of larvae collected near Hokkaido (Kamba 1977), and represent <16% of the food items for all size groups in the present study. Kamba (1977) cited the low incidence of occurrence of this food item in larvae collected in Uchiura Bay as evidence of selective feeding by walleye pollock larvae.

The zooplankton species composition in the oceanic and outer shelf regions of the Bering Sea (Cooney and Coyle 1981; Smith and Vidal 1984) is similar to that described for the northern Gulf of Alaska and Ocean Station P (Le Brasseur 1965; Damkaer 1977; Fulton 1983; Miller et al. 1984). The Shelikof Strait species composition is similar to these areas. Our zooplankton sampling did not include copepod nauplii so we cannot assess their abundance. The size distribution of copepod nauplii ingested, however, indicates that *Pseudocalanus* spp. and *Oithona* spp. are the probable sources of the copepod nauplii ingested by larval walleye pollock in Shelikof Strait.

Daily production of copepod nauplii at a single station in the Bering Sea has been estimated to be 27,094 m⁻², of which more than 95% was *Pseudocalanus* spp. (Dagg et al. 1984). The abundance of *Pseudocalanus* females ranged from 9.9 to 258.9 m⁻³ (\bar{x} = 87.7). The mean abundance of *Pseudocalanus* females in Shelikof Strait was 244 m⁻³, or 2.6 times greater than the mean abundance in the Bering Sea. Assuming the same rate of daily production, about 69,000 nauplii m⁻² would be produced in Shelikof Strait. Mean abundance of walleye pollock larvae where Dagg et al. (1984) performed their study was 6.3 larvae m⁻², whereas at the diet station in Shelikof Strait the abundance was 156 m⁻², about 25 times greater than in the Bering Sea study. If these larvae ate nauplii at the same rate as those in the Bering Sea, 18.3 per day, they would eat about 24% of the production, as opposed to the <1% in the Bering Sea. Other factors such as the relationship between size of larvae and daily ration need to be investigated before more precise estimates of the impact of larval feeding and the possibility of food limitation can be made. It appears that enough nauplii were being produced to preclude density dependent food restrictions at the larval densities observed in the present study.

Growth of Walleye Pollock Larvae

Growth rates were similar in areas of both high and low density (Table 5, Fig. 13). It cannot be determined from our study whether density-dependent factors modified larval growth; growth variations could be produced by patchy distributions of prey. Walleye pollock larvae have been shown to grow faster in the laboratory at higher food densities (Bailey and Stehr 1986), further, where lower or constant larval densities interact with variable prey density, field studies have shown variability in growth (Govoni et al. 1985). Without knowledge of prey availability at each location, however, it is difficult to discern if high densities of prey coincide with dense patches of larvae. The relatively low growth rates found at two adjacent stations outside the patch (Stations 6, 12; Table 6) might indicate an area of less than adequate prey availability.

Growth rates for fishes can be influenced by environmental factors such as temperature, as well as availability of adequate food supplies (Boehlert and Yoklavich 1983). Within species,

growth rates are usually positively correlated with temperature over the normal temperature range. Growth rate for larval walleye pollock in the Gulf of Alaska (0.21 mm d^{-1}) is considerably lower than that determined for larvae of the same size range (4-25 mm SL) collected in the southeastern Bering Sea in June-July 1979 (0.35 mm d^{-1} , Walline 1985). Water temperatures were similar in both studies (about $6^{\circ}\text{-}8^{\circ}\text{C}$). Maximum growth determined for larvae collected in the Bering Sea in March-June 1980 while water temperature was much cooler ($2^{\circ}\text{-}6^{\circ}\text{C}$), was 0.22 mm d^{-1} (Clarke 1984). Thus differences in growth rates of larval walleye pollock in the Bering Sea could be due to differences in water temperature, food availability, or a variety of other factors which may affect growth in larvae (Bailey and Stehr 1986). Future research on growth variability in the field should take into account prey availability, temperature, and size-specific mortality rates.

SUMMARY

1. Walleye pollock in the Gulf of Alaska form an intense spawning aggregation in Shelikof Strait in late winter that produces a dense patch of planktonic eggs in early April. Larvae from this spawning can be followed as they develop and are carried by currents to the southwest during spring.
2. In late May 1981, the density of larvae in this patch ($>10 \text{ m}^{-3}$) suggested that density-dependent effects on growth and survival might be expected. A field study of larvae in late May 1983 found maximum densities of only 1 larva m^{-3} , and investigated growth and vertical distribution, and feeding in the patch.
3. The larvae were concentrated vertically between about 15 and 50 m, and tended to be in the upper part of this range during night and early morning, whereas they were deeper during the afternoon and evening.
4. Larvae $<10 \text{ mm}$ fed primarily on copepod nauplii, with copepodids becoming more important in larvae up to 20 mm. Copepodids of *Pseudocalanus* spp. made up a large fraction of the diet of larvae $>10 \text{ mm}$. Most feeding occurred during daylight.
5. The copepods *Pseudocalanus* spp., *Neocalanus* spp., *Calanus* spp., *Oithona* spp., and *Acartia* spp. dominated the net zooplankton samples ($253 \mu\text{m}$ mesh net).
6. Growth, based on otolith increments counted on 109 larvae (6.0-14.6 mm) was linear (0.21 mm/day , intercept = 4.29 mm, $r^2 = 0.75$). Growth rates in the area of high abundance were generally not significantly different from those elsewhere.
7. While at the larval densities observed in 1981, density-dependent effects are possible, at the lower densities we observed in 1983 no such effects were expected or indicated in growth rates or diet. Future studies should include direct measurement of copepod naupliar production rates in the areas inhabited by the larvae.

ACKNOWLEDGMENTS

We wish to thank the officers, crew, and scientific staff aboard the NOAA ship *Chapman* for making the field work associated with this study both pleasant and productive. We thank Beverly Vinter, Jay Clark, and Darlene Blythe of NWAFC for their help in various stages of this study: converting animals in vials to data in the computer and our scribbles into typescript. Suam Kim, University of Washington, kindly helped analyze the hydrographic data. J. J. Govoni, NMFS Beaufort, NC; R. T. Cooney, University of Alaska, Fairbanks; and A. J. Paul, University of Alaska, Seward, provided excellent, thought-provoking reviews of an earlier draft of this paper.

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