Abstract.—Microzooplankton retained by a 41-μm mesh was sampled along a 50-km transect in the Shelikof Strait between Kodiak Island and the Alaska Peninsula. We sampled once each year during spring (April–May) 1985–1989 using Niskin bottles closed at 10-m depth intervals. Sampling was conducted near the time and place of peak hatching of walleye pollock (*Theragra chalcogramma*) larvae. We examined horizontal and vertical patterns of abundance of potential prey organisms, especially copepod nauplii, and described these patterns with respect to the oceanography of the Strait. Hydrography, nutrients, chlorophyll-*a* and net zooplankton data also were collected and were used to help interpret the microzooplankton patterns. Copepod nauplii composed from 46 to 82% of all organisms in the formalin-preserved samples. Eggs (3–35%), rotifers (up to 14%) and loricate tintinnids (up to 11%) were the next most abundant taxa. The abundance of microzooplankton varied greatly across the Strait and, for copepod nauplii, had maxima associated with the Alaska Coastal Current. A mesoscale feature in the coastal current appeared to influence the distribution of microzooplankton and may affect feeding conditions for larval walleye pollock. Significant differences in abundance of copepod eggs and nauplii were detected between some transects. The integrated, 0-60 m depth, across-strait average abundance of copepod nauplii varied from a low of 5.8×10^3 m^{-2} (sampled in 1985) to a high of 17.6×10^3 m^{-2} (1987). The maximum concentration found in these same transects varied from 18 to 144 L^{-1}, respectively. Between 60 and 70% of the nauplii sampled were of a size (>125 μm total length) composing approximately 98% of the naupliar diet of larval walleye pollock in spring.

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Distribution and abundance of copepod nauplii and other small (40–300 μm) zooplankton during spring in Shelikof Strait, Alaska*

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The high mortality rate of marine fish larvae is attributed to high rates of predation (Moller, 1984; Bailey and Houde, 1989), sensitivity to feeding conditions (Theilacker and Watanabe, 1989) and interactions between these factors (Houde, 1987; Purcell and Grover, 1990). The larvae of temperate fishes often occur during spring, when planktonic production is in early stages of its annual cycle and is easily disrupted or delayed by adverse conditions. Also, larvae have small search volumes and generally small energy reserves (Bailey and Houde, 1989). Thus, a spatial or temporal "match" or "mismatch" between the demand for larval food and its availability seems intuitively likely and has been the subject of much research (e.g., Lasker, 1981; Buckley and Lough, 1987; Cushing, 1990). The quest to quantify feeding relationships has led to continuing efforts to reduce container effects in experimental studies (Gamble and Fuiman, 1987; McKenzie et al., 1990), to improve the sensitivity of physiological measurements (e.g., Buckley et al., 1990), to understand the small-scale distribution of prey in the field (Owen, 1989), and to understand the role of mixing in enhancing or retarding interactions between predator and prey (Rothschild and Osborne, 1988; Davis et al., 1991). In the ocean, feeding takes place in a complex spatial array of biological and physical conditions. Any study of rate-influencing processes that affect larvae must take into account the distribution of these conditions in order to understand effects at the population level.

In this paper we examine the springtime community of small zooplankton, primarily copepod nauplii, that may be prey for larval walleye pollock, *Theragra chalcogramma*, in Shelikof Strait, Alaska (Fig. 1), and we report on the distribution and abundance of these organisms with respect to oceanographic conditions. A large population of walleye pollock spawns in the Strait in late March and early April, forming dense aggregations of planktonic eggs in the deepest part of the sea valley between Kodiak Island and the Alaska Peninsula. Hatching occurs from middle or late April through early May (Kendall et al., 1987; Incze et al., 1989; Yoklavitch and Bailey, 1990). While the eggs remain mostly below 150 m, larvae

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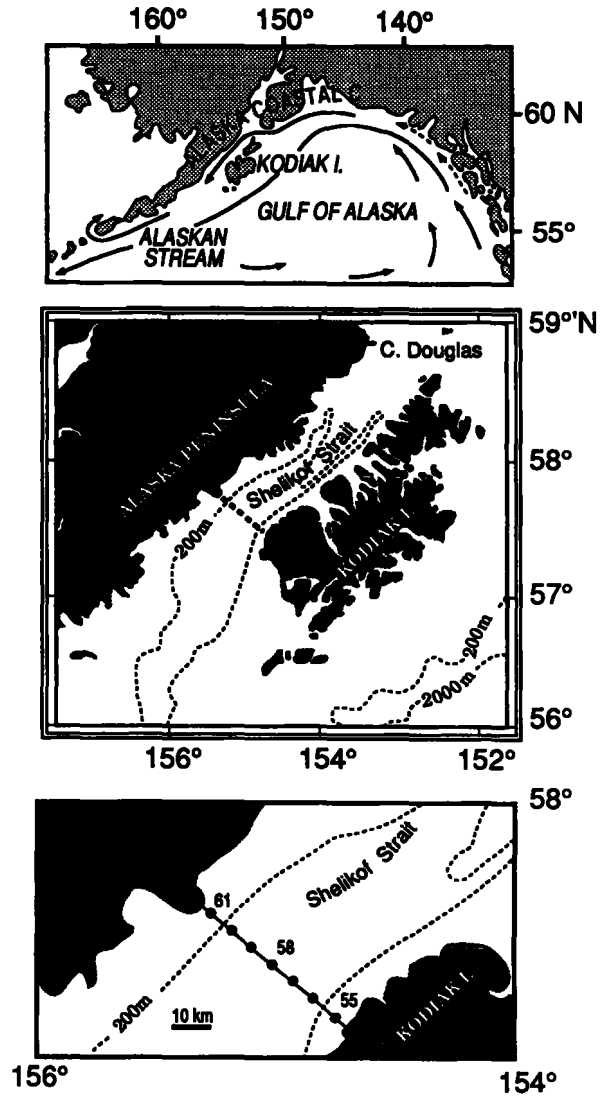

Figure 1

Top panel shows location of the study area and a generalized scheme of the surface circulation. Middle and bottom panels show Shelikof Strait and the sampling transect. Stations are numbered consecutively beginning with 55 near the Kodiak Island shore; only the end and middle stations are labeled.

are found primarily in the upper 50 m (Kendall et al., 1993[1]) and have been shown to prey heavily on copepod nauplii during the first several weeks of development (Dagg et al., 1984; Kendall et al., 1987; Canino et al., 1991).

The upper water column of Shelikof Strait consists of at least three distinct water types (Reed and Schumacher, 1989). A cold, slightly freshened, turbid coastal water band of narrow width (<10 km) remains near the Alaska Peninsula (northern) side of the Strait. This water receives its signature from glacial melt-waters draining into Cook Inlet at the northern end of the Strait and thus varies seasonally in volume. A second water type is encompassed in the Alaska Coastal Current (ACC), part of a baroclinic current running more or less continuously along 1000 km of the Alaskan south coast. The ACC flows from northeast to southwest in a band approximately 20 km wide through the middle portion of the Strait, but it has a highly variable current structure marked by numerous baroclinic instabilities (Mysak et al., 1981; Vastano et al., 1992). In the vertical, the southward flow of the ACC induces an opposite bottom flow of more saline, nutrient rich water that enters the sea valley at the shelf edge south of the study area (Fig. 1; see Reed et al., 1987). A third water type is made up of waters from a mixture of sources, including outer shelf and oceanic intrusions. Most of this water enters from the north and flows the length of the Strait along Kodiak Island, but current meter measurements and satellite imagery show that water sometimes enters from the south (Schumacher, 1991[2]).

The work reported here was undertaken as part of a multi-disciplinary program (Fisheries Oceanography Coordinated Investigations: FOCI) aimed at understanding the influence of environmental factors on the early life history of walleye pollock spawned in the Strait (Schumacher and Kendall, 1991). An extensive grid of sampling stations occupied in early May 1985, the first year of the program, showed that the spring bloom of large diatoms did not occur homogeneously throughout the Strait. Rather, in that year, large diatoms bloomed first in a band which occupied the longitudinal mid-portion of the Strait (Incze, unpubl. observ.). Hydrographic data show that this feature was in the ACC, which had at that time a shallower upper mixed layer than elsewhere in the Strait. It seemed likely, therefore, that conditions affecting the feeding and growth of larval walleye pollock would be subject to dynamics of the ACC and would differ across the Strait as well as through time. As part of the research program, a standard across-strait transect was established near the southern end of the Strait proper (about halfway up the sea valley: Fig. 1). This transect has been sampled with a CTD (Conductivity, Temperature, Depth) as often as ship and research schedules have permitted. Biological sam-

[1] A. W. Kendall Jr., L. S. Incze, P. B. Ortner, S. R. Cummings, and P. K. Brown. 1993. The vertical distribution of eggs and larvae of walleye pollock in Shelikof Strait, Gulf of Alaska. Submitted to Fish. Bull.

[2] J. Schumacher. 1991. Pacific Marine Environmental Laboratory, Seattle, WA, unpubl. data.

pling begins along this transect near the time of larval hatching each spring and proceeds down-current (westward) over time. In this paper we report on across-shelf patterns of abundance and vertical distribution of copepod nauplii and other small zooplankton from 1985 through 1989 and relate these patterns to hydrographic conditions, chlorophyll concentrations, and distributions of selected taxa of adult female copepods.

Materials and methods

For convenience, we use the term microzooplankton to refer to small zooplankton captured and preserved by methods described below. Hydrography, nutrients, and microzooplankton were sampled with a CTD and rosette sampler along a transect of stations across Shelikof Strait, Alaska, during spring from 1985 through 1989 (Fig. 1) (sampling dates are listed in Table 2). Hydrographic (CTD) data were obtained near bottom at 7 stations at 7–km intervals and were processed to give 1–m averaged data of salinity, temperature and density. Nutrients were sampled at five or more stations on the transect by removing water samples from 10–L Niskin bottles tripped at standard depths of 10, 20, 30, 50, 75, and 100 m; below this depth we sampled with lower resolution, generally at 50–m intervals, plus a sample near bottom. Nutrient concentrations were determined after the cruise by using standard autoanalyzer techniques on frozen samples (Whitledge et al., 1981[3]). Chlorophyll data were obtained from nutrient sampling depths in the upper 100 m in 1988 and 1989. Analyses were conducted on board the vessel following methods of Yentsch and Menzel (1963) as modified by Phinney and Yentsch (1985) with 0.45–μm Millipore HA acetate filters. Microzooplankton was sampled from Niskin bottles were tripped at 10–m intervals from 0 to 60 m in 1985 and from 10 to 60 m in other years. We used the same bottles as for nutrient and chlorophyll samples for those depths which were common to all. The number of stations sampled varied over the years, beginning in 1985 with stations 55, 58, and 61. In 1986 and 1987 we included station 60. In 1988 we sampled all seven stations along the transect, and in 1989 we sampled all except station 57.

Niskin bottles were sampled for nutrients and chlorophyll when called for; the remaining contents of the bottles were filtered through small (6 × 18 cm) conical nets made of 41–μm mesh nylon netting. Material retained on the netting was flushed into 4–ounce (120 mL) glass jars by using 0.45–μm filtered seawater and was preserved in a final solution of 5% formalin:seawater. Larger zooplankton was sampled at all seven stations by using 60–cm diameter bongo samplers equipped with 333–μm mesh nets and towed in double-oblique fashion from the surface to about 10 m off bottom. From 1986 onward, a 20–cm bongo sampler with 150–μm mesh nets was attached to the towing wire 1 m above the larger sampler to try to improve on the sampling of smaller copepods. Properties of each tow were monitored by time, wire angle from the towing block, mechanical flowmeters mounted across the mouth of each net, and a bathykymograph attached to the bridle of the large bongo.

In the laboratory, each microzooplankton sample was filtered onto a 41–μm mesh sieve, stained overnight in Rose Bengal, transferred to a 10–mL scintillation vial and examined in approximately 2–mL aliquots. Microzooplankton was analyzed by using a stereo dissecting microscope equipped with an image analysis system consisting of a high-resolution video camera and computer software to make measurements and record data (Incze et al., 1990). The microscopist made identifications, placing each organism into one of thirteen categories (Table 1), and directed the orientation of measurements. Copepod nauplii were measured for total length (TL) and maximum width. Total length was the carapace length ("prosome"), plus the abdomen ("urosome") when present. The latter section often was curled beneath the carapace, necessitating measurement along a curved line. We measured the diameter of eggs and only the total body length of all other organisms. In most cases the entire sample was analyzed, but 25% of the original sample sometimes provided adequate counts, which we established as at least 50 nauplii per sample. Subsampling was done by increasing the stored sample volume to 200 mL, dividing as necessary, then recondensing the material for examination. Subsampling was checked for accuracy by completely analyzing both half-portions from 30 samples. Final counts of microzooplankton were corrected for the subsampling fraction and for differences in the original volume of water filtered and are presented as number of organisms per liter. Integrated abundances (No. m^{-2}) were estimated for the upper 60 m of the water column by using a trapezoidal algorithm.

Vertical and horizontal patterns of microzooplankton distribution were plotted by using an inverse distance gridding technique ("Surfer", Golden Software, Inc., Golden, CO) with a grid size

[3] Whitledge, T. E., S. C. Molloy, C. J. Patton, and C. D. Wirick. 1981. Automated nutrient analyses in seawater. Tech Rep. No. BNL-51398, Brookhaven Natl. Lab., Upton, NY.

Table 1

(A) Composition of microzooplankton in Shelikof Strait during spring, expressed as a percent of total organisms counted. Hyphens indicate values greater than zero but less than 2%; non-zero values shown are rounded to nearest whole number. Shed ovisacs are from *Oithona* spp.; "Other" includes infrequent and unidentified organisms. (B) Vertically integrated abundances of organisms are averaged across Shelikof Strait for each year; "All other" refers here to all categories from (A) combined except for those specifically listed.

A Percent composition

Category	1985	1986	1987	1988	1989
Copepod nauplii	50	46	54	82	76
Other nauplii	—	—	—	—	—
Invertebrate eggs	25	35	13	3	4
Ovisacs	3	—	—	2	—
Copepods	9	2	—	4	3
Euphausiids	—	0	—	0	0
Rotifers	—	7	14	—	4
Tinitinnids	2	—	11	—	—
Larvaceans	—	3	0	—	—
Polychaetes	—	—	—	—	—
Echinoderms	—	—	—	—	—
Foraminifera	—	—	—	—	—
Other	8	3	4	5	3

B Average integrated abundance (1000s m^{-2}) from 0–60 m

Copepod nauplii	5.8	13.9	17.6	9.4	9.6
Invertebrate eggs	3.0	10.4	3.6	0.4	0.6
All other	4.6	5.7	8.6	1.9	2.6
Total	13.3	30.0	29.8	11.8	12.8

set at 25 units in both the X and Y directions. The same technique was used for contouring CTD and nutrient data. A subset of contours from all three data types was compared by inspection to the original input data to look for artifacts caused by the contouring software. Integrated abundances of nauplii across the Strait were compared for the four years which had late April–early May sampling (1985, '86, '88, '89). Data were taken from those stations (#55, 58, 61) sampled every year in the series and were compared by using a non-parametric two-way analysis of variance (ANOVA) on ranks (also referred to as the Quade test: Conover, 1971). A multiple comparison based on ranks (Conover, 1971) was applied when the ANOVA showed statistically significant differences.

We used the estimated abundances of adult female copepods (No. m^{-2}) from the oblique bongo tows to consider possible sources of planktonic eggs and nauplii sampled in our study. Data are from a database being used to describe spatial and interannual patterns of major zooplankton taxa (FOCI Database, National Marine Fisheries Service, Seattle); subsampling and counting followed standard procedures and are detailed in a series of five reports (e.g., Siefert and Incze, 1991[4]). The relative contribution of each taxon to the standing stock of planktonic copepod eggs and early nauplii was estimated by using egg production rates reported in the literature or from unpublished data. This is simplistic, because it ignores changes in egg and naupliar concentrations as a function of birth rate, development time, and mortality, all of which may vary considerably. However, the calculations provide a rough evaluation of potential sources of nauplii in Shelikof Strait. Sizes of eggs and early nauplii (e.g., Nauplius I [NI]) were used when reports were found. We used the following information: *Calanus marshallae* (eggs 175–185 μm, fecundity 12 eggs d^{-1} [Runge, 1990[5]]; *Calanus pacificus* (eggs ca. 160 μm, fecundity 38 eggs d^{-1} [Runge, 1984]; NI ca. 220 μm CL [Fulton 1972]); *Metridia pacifica* (eggs 150 μm [Runge, 1990[6]]; fecundity 2.5 eggs d^{-1} [Batchelder and Miller, 1989]); *Pseudocalanus* spp. (eggs ca. 110–130 μm retained in ovisacs [Frost, 1987]; fecundity 4 eggs d^{-1} [Dagg et al., 1984; Paul et al., 1990]; NI ca. 180 μm CL [Fulton, 1972]). Jeffry Napp[7] and Kenric Osgood[8] both have found that *Metridia pacifica* held in the laboratory may produce eggs at higher rates, and they suggest that the population average at times may be several times greater than the rate given above.

Results

In this section we designate different transects by the year in which they were sampled but do not mean to imply that the differences necessarily were interannual. We address this distinction in the discussion section.

Nitrate concentrations in bottom waters were highest in 1985, 1988, and 1989 (>25 μg-at L^{-1} com-

[4] Siefert, D. L. W., and L. S. Incze. 1991. Zooplankton of Shelikof Strait, Alaska, April and May 1989: data from Fisheries Oceanography Coordinated Investigations (FOCI) cruises. Alaska Fish. Sci. Center, NOAA, Seattle, WA, 119 p.

[5] J. Runge. 1990. Insti. Maurice Lamontagne, Mont-Joli, Quebec, Canada, pers. commun. 1990.

[6] J. Runge. 1993. Inst. Maurice Lamontagne, Mont-Joli, Quebec, Canada, unpubl. data.

[7] Jeffry Napp, Nat. Mar. Fish. Serv., Alaska Fishereis Science Center, Seattle, WA, pers. commun. 1993.

[8] Kenric Osgood, Dep. Oceanography, Univ. Washington, Seattle, WA, pers. commun. 1993.

pared to <20 μg-at L^{-1} in the other years); in surface waters they were lowest in 1987 (mostly <2 μg-at L^{-1}), followed by 1986 (<4 μg-at L^{-1}) and 1989 (<5 μg-at L^{-1}) (Fig. 2). Surface nitrate distributions generally reflected density structure. Isopleths of density (Fig. 2), salinity, and temperature show larger

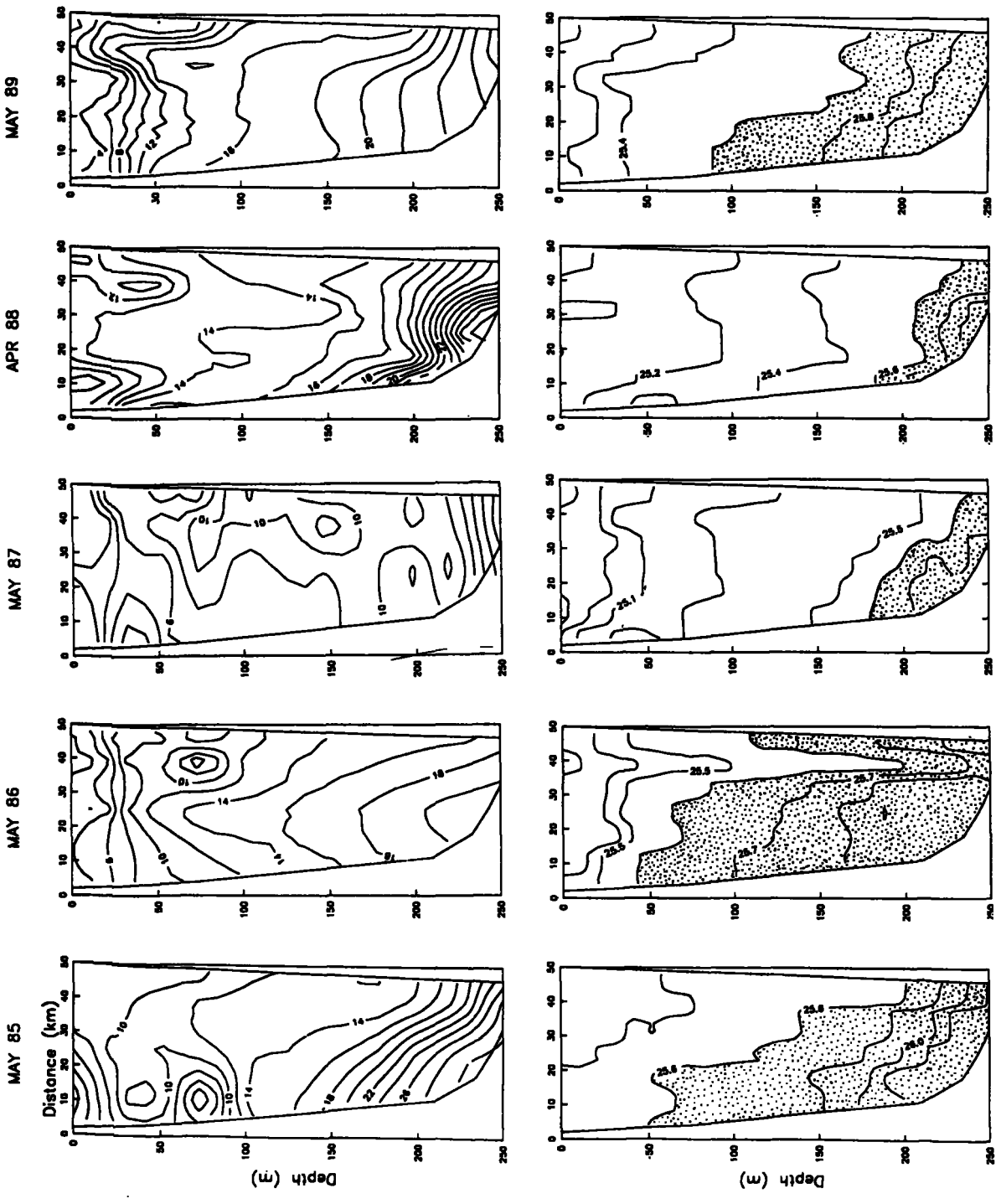

Figure 2

Profiles of nitrate (upper panel, μg-at L^{-1}) and density (lower panel, σ_t) across Shelikof Strait during spring, 1985–89. Water denser than σ_t=25.6 is shaded. The transect is viewed looking westward; distances are given from the Kodiak Island shore. Sampling dates are given in Table 2.

volumes of high density (high salinity) bottom water in 1985, 1986, and 1989 compared with other years. The upper mixed layer generally was deepest on the northern end of the transect, near the Alaska Peninsula, with a steeply sloping density gradient near the middle. The exception, in 1988, is discussed later. Averaged across the Strait, the upper mixed layer was deepest in 1985 and shallowest in 1986 and 1987.

Observations of phytoplankton clogging sampling nets during the cruises showed that the spring bloom of large diatoms occurred latest in 1985. By this approximation, what probably was the major spring bloom in the Strait began after the first week of May in 1985, whereas it already was well underway when we began sampling in early May 1986 and 1989 and late April 1988. A grid of sampling stations that extended to the northern end of the Strait in 1985 showed that the bloom in that year formed first in a band along the middle of the Strait for virtually its full length of 300 km. Our grid interval was not sufficiently fine to resolve the width of the bloom feature, but our findings are consistent with a diameter <25 km.

Our samples were dominated numerically by copepod nauplii, which composed from 46 to 82% of all organisms sampled along the transect over the five-year period (Table 1), followed in most years by copepods eggs, from 3.5 to 35%. Of the remaining taxonomic categories, only a few ever contributed more than 5% of the total organism count: small copepods (including copepodid stages), tintinnids, rotifers, and polychaete larvae. None of these ever exceeded 15% of the total count.

The integrated (0–60 m depth) abundance of microzooplankton at the primary sampling stations increased across the Strait from south to north (see Fig. 3 for copepod nauplii). Average abundances of nauplii, eggs, and all other organisms were highest in 1986 and 1987. For copepod nauplii, abundance was lowest in 1985 and intermediate in 1988 and 1989 (Table 1). In 1985, near-surface concentrations averaged 86% of those at 10-m depth. Therefore, the assumption of uniform concentration of organisms in the upper 10 m may have introduced a small upward bias in the integrations from 1986 onward.

The 7-km resolution of microzooplankton obtained across the Strait in 1988 (Fig. 4) shows a more complex pattern of distribution than suggested by other transects. Specifically, comparatively large numbers of nauplii and other microzooplankton were found at stations 56 and 57, nearly equivalent to populations at the two northern stations. Both groups of stations were marked by waters of lower surface nitrate concentration (Fig. 2) associated with flow around a dynamic high in the middle of the Strait (Fig. 5). The two groups of stations differed from each other in the composition of planktonic eggs (greater concentrations at stations 60, 61) and other microzooplankton (greater at 56 and 57) and in temperature and salinity. The southern "limb" of the anticylconic feature was about 0.1° C warmer and 0.05 g kg^{-1} more saline than the northern limb. Chlorophyll data show high chlorophyll-*a* concentrations (up to 6 μg L^{-1}) and high integrated chlorophyll-*a* (140–180 mg m^{-2}, 0–100 m) in the two limbs of the ACC surrounding the anticyclonic feature; the lowest chlorophyll-*a* (10 mg m^{-2}) was found in the middle.

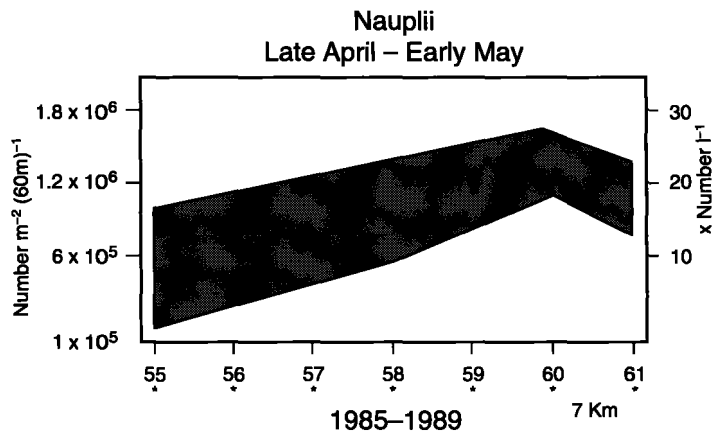

Figure 3

Across-strait patterns of integrated abundance (No. m^{-2}) and average concentration (no. L^{-1}) of copepod nauplii from surface to 60–m depth during spring at the primary time-series stations, marked with asterisks. Upper and lower lines describe the maximum and minimum values observed, 1985–89.

Copepod nauplii were found mostly in the upper 30 m, though they extended deeper at some stations in 1985 and 1988 (Fig. 6). Naupliar concentrations were greater in the northern half of the transect in 1985, 1986, and 1987; they were distinctly bipolar in 1988; and in 1989 maximum concentrations of both nauplii (Fig. 6) and chlorophyll-*a* (Fig. 7) occurred in the center of the Strait. Maximum naupliar concentrations encountered at any depth across the Strait per transect ranged from 18 L^{-1} in 1985 to 144 L^{-1} in 1987, both at 20 m depth at station 60. Planktonic copepod eggs also occurred mostly in the upper 30 m but exhibited a variety of across-shelf patterns that were

not always the same as those found for nauplii. Maximum egg concentrations ranged from 2.2 L^{-1} in 1988 (at 30 m depth) to 45 L^{-1} in 1986 (10 m depth), both at station 59. Most eggs and nauplii were in the upper mixed layer. Since sampling in 1987 occurred in late May, the relatively high abundance of nauplii may be attributed to time of year. Consequently, a statistical comparison between transects focussed on the other four years, which were sampled the last week of April and first week of May. This time period is close to the time of peak larval hatching. Abundance was statistically different among transects (Quade test $0.025 < P < 0.05$). The lowest (1985) and highest (1986) concentrations were significantly different at $\alpha = 0.05$; the intermediate concentrations of 1988 and 1989 differed from those in 1985 (but not 1986) at $\alpha = 0.10$ (Multiple comparisons of ranks).

The lengths of sampled nauplii showed positively skewed frequency distributions with peak abundance between 100 and 150 µm TL in all years and nearly identical cumulative distribution functions (Fig. 8). Median size differed by less than 15 µm among years and averaged 140 µm during the five–year period. The average length: width ratio of nauplii measured in this study was 2.2, with a standard deviation of 0.1 (n=1500). Consequently, our mesh, 41 µm on a side and 58 µm on the diagonal, should have retained some nauplii >90 µm long and all nauplii >128 µm. Our data showed a steep decline in frequency of nauplii with length <110 µm, between the above estimates, and width <50 µm, corresponding to the relationship 110/2.2 = 50. Most of the nauplii did not have urosomal segments, so total length and maximum width are equivalent to prosome length and width for most of our data.

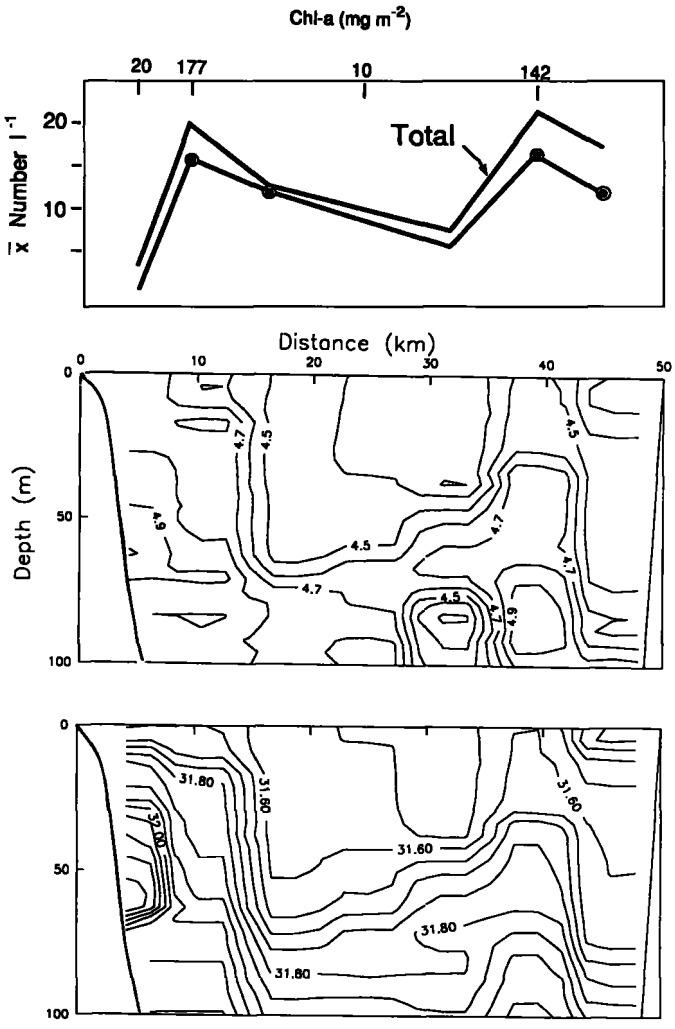

Figure 4

Mean number of nauplii and total microzooplankton per liter in the upper 60 m across the study transect in April 1988 (top panel), viewed looking westward. Numbers at the top of the panel show integrated (0–100 m) chlorophyll-a concentrations (mg m^{-2}). Temperature (°C) and salinity (g kg^{-1}) are shown in the middle and bottom panels, respectively. Data can be compared with nutrient distributions (Fig. 2), dynamic topography (Fig. 5), and depth distributions of nauplii (Fig. 6).

The abundance and size distribution of eggs differed substantially between years (Fig. 8). The greatest number (and smallest median size [ca. 75–µm diameter]) of planktonic eggs was present in 1986; the fewest eggs occurred in 1988, when median size was the largest (ca. 165 µm).

Abundances of potentially significant contributors to the standing stocks of copepod eggs and nauplii are given in Table 2. Among the taxa of interest, *Calanus pacificus* had low adult female numbers because most individuals were in copepodid stage 5 (C5) during spring. Other adult female copepods were broadly distributed across the Strait, but the maximum concentration of each taxon occurred in the northern half (among stations 58–61) in all but one instance. The across-Strait patterns of low and high abundances within species were similar from year to year and statistically significant (Spearman rank correlation test, P<0.05). The shift in mesh sizes for *Pseudocalanus* spp. collections limits the between-transect comparisons that can be made. (Note that there are interspecific differences within

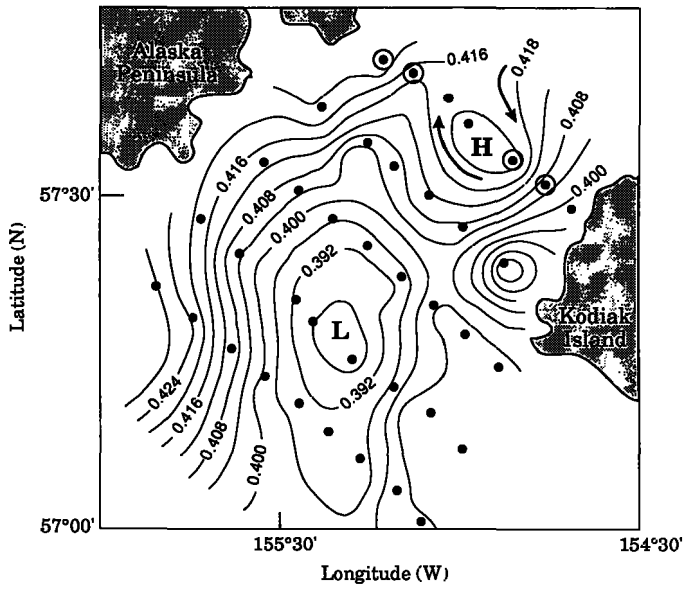

Figure 5

Contours of 0–150 m dynamic height in western Shelikof Strait during April 1988. Solid circles show locations of CTD stations. The study transect is the farthest northeast section. Open circles denote those transect stations with the highest microzooplankton standing stocks (cf. Figs. 4, 6). A dynamic high (H) and low (L) are labelled; arrows show inferred flow.

the genus that prohibit any simple correction for different mesh collections: see Frost, 1987.) Within these limitations, data for 1985 and 1986 (333 μm) were statistically different (Wilcoxon signed rank test, P=0.076), whereas the multi-year comparison for early spring samplings (1986, 1988, 1989: 150 μm mesh) showed no statistically significant differences (Quade test, α= 0.05). Among early spring values, there were no statistically significant differences in abundance of *Metridia* spp..

Discussion

The method of sampling and preservation used in this study under-represented smaller components of the microzooplankton (James, 1991) but was adequate to capture the majority of prey items of larval walleye pollock based on prey sizes reported from earlier studies of Clarke (1984: Bering Sea), Nishiyama and Hirano (1983, 1985: Bering Sea), Dagg et al. (1984: Bering Sea); and Kendall et al. (1987: Shelikof Strait). For small larvae of 5–10 mm standard length (SL) in those studies, copepod nauplii composed the majority of items found in larval stomachs. They also made up the bulk of estimated volume or carbon content of prey when these values were calculated (Incze et al., 1984; Nishiyama and Hirano, 1983). The 10–m vertical resolution of our sampling method almost certainly failed to detect the highest concentrations of prey available to larval walleye pollock under some conditions, such as in small patches (Owen, 1989), but probably reflects adequately the average abundances found at different depths in the water column, in different sections across the Strait and in different transects.

Size-frequency distributions of sampled nauplii and dimensions of the sampling mesh suggest that there was virtually complete retention of nauplii with total length ≥ 125 μm. In most cases these measurements were carapace ("prosome") lengths. Unpublished data from stomach content studies (Canino, 1992[9]) show that ca. 98% of the nauplii consumed by larval walleye pollock collected during our cruise in May 1989 had carapace length ≥ 125 μm. Between 60 and 70% of the nauplii in our samples were of this size (Fig. 8).

Concentrations and integrated abundances of nauplii differed across Shelikof Strait in patterns that appear to be related to circulation features. Our data indicated that standing stocks and maximum concentrations of copepod nauplii in spring were greatest in the ACC, which is also where greatest chlorophyll-*a* concentrations occurred (latter data for 1988, 1989; cf. Figs. 4, 6, 7). The lowest naupliar concentrations of the early spring samplings occurred in 1985, which had the weakest stratification. In general, nauplii were most abundant at 20-m depth except in 1988, when maximum concentrations occurred at 30-m depth in the deeper mixed perimeter of the anticyclonic feature. The lowest standing stock of nauplii coincided with the latest apparent phytoplankton bloom in 1985, but we cannot determine if lower individual copepod egg production rates or lower standing stocks of copepods were responsible because we lack adequate collections (150–μm mesh) of *Pseudocalanus* spp. in 1985. Alternatively, the low naupliar standing stocks could have been due to higher predation, but our data show that springtime populations of predators were generally low and were similar among years.

Our data suggest that the distribution of copepod nauplii and some other microzooplankton across

[9] M. Canino. 1992. Natl. Mar. Fish. Serv., Alaska Fisheries Science Center, Seattle, WA, unpubl. data.

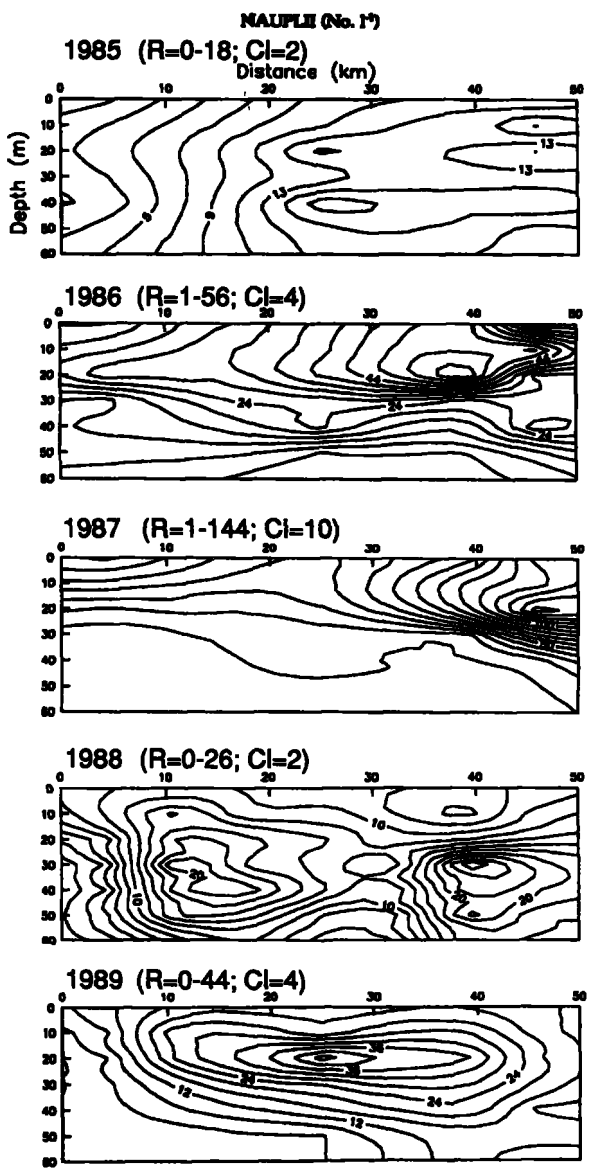

Figure 6

Contour plots of naupliar concentrations (no. L^{-1}) across Shelikof Strait during spring. Numbers in parentheses after the year (upper left of each plot) show the range (R) of data and the contour interval (CI) used in plotting. Transects are viewed looking westward.

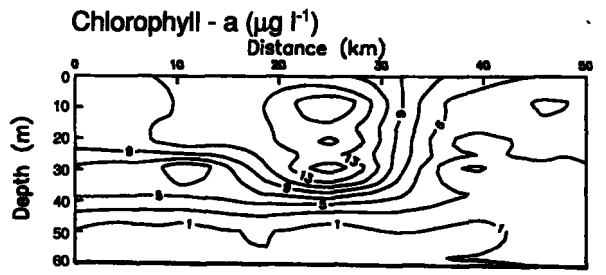

Figure 7

Chlorophyll-*a* distributions across Shelikof Strait, May 1989, looking westward (data may be compared with nutrient and hydrographic structure in Fig. 2 and naupliar concentrations in Fig. 6).

Shelikof Strait were subject to the influence of baroclinic instabilities. The timing and rotational sense of these instabilities therefore may have a large influence not only on the distribution of walleye pollock larvae themselves (Reed et al., 1989; Incze et al., 1990; Vastano et al., 1992), but also on the feeding conditions they experience. For example, the feature sampled in 1988 covered a substantial portion of the main spawning and hatching area. Although we do not have extended observations of this feature, Vastano et al. (1992) showed that eddy-like features may remain near the hatching area for as long as two weeks, a substantial portion of the hatching period (Yoklavitch and Bailey, 1990). If walleye pollock larvae migrate vertically into the center of a dynamic high after hatching, then the amount of time that passes before they are advected into better feeding conditions (in this case at the periphery of the high) may be important to early larval feeding and growth.

The average integrated abundance of copepod nauplii across the Strait was different for the various transects. The maximum values that were seen in 1987 probably can be attributed to the comparatively late sampling of that year. However, among the four years with similar timing of transect sampling, there remained statistically significant differences that may have been important to hatching walleye pollock larvae (see Canino et al., 1991, for feeding conditions and larval RNA/DNA ratios). Since hatching takes place over a relatively short time period (Yoklavitch and Bailey, 1990), the phasing of hatching and upper layer conditions may play an important role in establishing the larval year class. Unfortunately, we do not know how long the observed conditions persisted in each year relative to the population hatching time or to other requirements of the early feeding period in larval development. Advection (Incze et al., 1989) and short-term fluctuations in mesoscale circulation (Vastano et al., 1992) may cause conditions in the Strait to change quickly, requiring more frequent sampling and improved techniques to rapidly assess prey distributions.

Nauplii that were most abundant in the diet of larval pollock must have come from copepods large enough to be retained by mesh sizes used on the

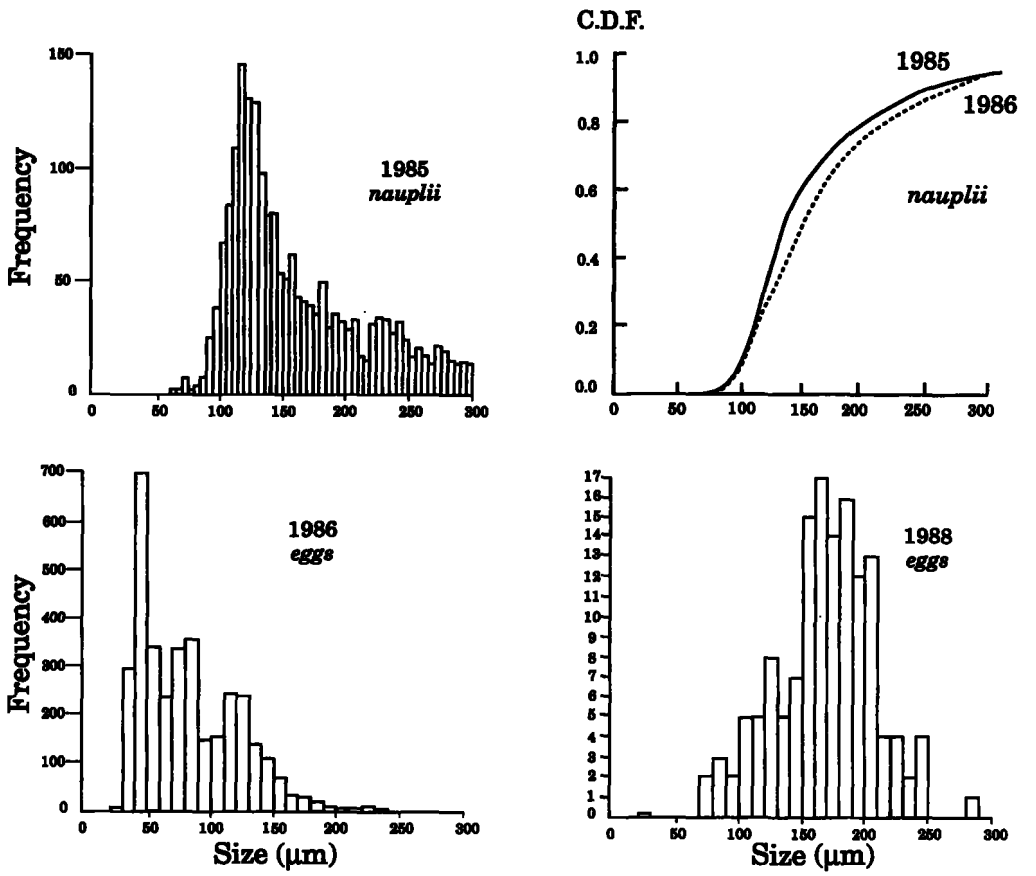

Figure 8

Size-frequency distribution of nauplii and eggs. Graph in upper left shows size frequency of nauplii from 1985. Graph in upper right shows the full range of size distributions of nauplii by comparing the cumulative distribution functions (CDF) for the two extremes, 1985 and 1986. Size distributions of eggs are shown in the two lower graphs for years with the smallest (1986) and largest (1988) eggs. Note changes in frequencies shown on the various ordinates.

bongo samplers (Table 2). Based on the average abundance and fecundity (see Methods) of adult female copepods, the approximate contribution of each species to the daily production of NI would be: *Pseudocalanus* spp., >75%; *Metridia pacifica*, 18%; *Calanus marshallae*, 4%; and *Calanus pacificus*, <1%. These percentages are useful only for the relative scaling they permit; many factors may influence copepod reproduction rates, and rates of development and mortality will influence further the total standing stock of nauplii contributed by each species. These results agree with those of Dagg et al. (1984) with respect to the importance of *Pseudocalanus* spp. naupliar production for larval walleye pollock feeding. Our results differ in the greater inferred role of *Metridia* spp., probably because of the deep waters of the Shelikof sea valley compared with the Bering Sea shelf where Dagg and his coauthors worked. The numerous small nauplii <120 μm that we sampled are from unknown sources. The abundance and fecundity of *M. pacifica* suggest that they were significant contributors to populations of planktonic eggs and that *Calanus marshallae* plays a lesser role. A large number of small planktonic eggs <150–μm diameter are not accounted for by the adult female copepods retained by our nets.

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Table 2

Abundance (no. m^{-2}) of adult female copepods on a transect across western Shelikof Strait during spring. Data are listed vertically showing mean, (standard deviation) and range. *Metridia pacifica* is *Metridia pacifica*/*M. lucens*; unidentified *Metridia* spp. are not included in this tally. Hyphens indicate absence of data.

	Year and day				
Taxon and mesh size	1985 (3 May)	1986 (3 May)	1987 (19 May)	1988 (27 Apr)	1989 (10 May)
Pseudocalanus spp.	—	14,183	41,058	13,634	8,450
150 μm		(6,523)	(25,527)	(4,128)	(4,026)
		6,758–18,994	6,108–78,976	7,846–20,316	2,870–12,563
Pseudocalanus spp.	9,119	16,232	33,098	—	—
333 μm	(4,767)	(8,295)	(19,398)		
	2,509–16,110	7,848–30,573	6,273–51,729		
Calanus marshallae	130	82	610	125	618*
333 μm	(146)	(72)	(532)	(93)	(786)
	0–431	0–211	0–1,343	0–238	0–2,196
Metridia pacifica	5,082	3,168	9,537	3,211	2,713
333 μm	(4,128)	(1,956)	(5,570)	(1,626)	(2,549)
	68–11,899	24–6,340	288–5,715	288–5,715	0–6,945
Calanus pacificus	15	2	0	28	133
333 μm	(27)	(4)		(61)	(228)
	0–73	0–9		0–164	0–521

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