FEEDING OF LARVAL WALLEYE POLLOCK (*THERAGRA CHALCOGRAMMA*) IN THE OCEANIC DOMAIN OF THE BERING SEA

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# FEEDING OF LARVAL WALLEYE POLLOCK (*THERAGRA CHALCOGRAMMA*) IN THE OCEANIC DOMAIN OF THE BERING SEA

A

THESIS

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## ABSTRACT

Feeding of larval walleye pollock was examined with respect to abundance and distribution of prey at six depths in the oceanic domain of the Bering Sea in April 1992. Walleye pollock larvae and copepod nauplii distribution peaked at 30 m depth. Among copepod nauplii, walleye pollock larvae selected for *Metridia* sp. and *Microcalanus* sp., but against *Oithona similis*, even though the latter were the most abundant prey taxon. In addition, the larvae selected for larger nauplii and tended to consume stages I and II *Oithona similis* and stages III-V calanoid nauplii. Larvae at 30 m depth had the highest incidence of feeding and number of prey items ingested. Although the 30 m depth stratum provided best physical and foraging conditions, the overall low percentage of feeding larvae and low numbers of prey consumed, suggest that foraging conditions for larval walleye pollock at the time of sampling were below saturation feeding levels.

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# INTRODUCTION

Large fluctuations in the recruitment of commercially important marine fishes have been documented for many species. Often commercial fisheries are dependent on relatively few, exceptionally strong, year-classes. The relationship between food availability for first-feeding larval fishes and the magnitude of year classes was first suggested by Hjort (1914). This concept was expanded in the "match/mismatch hypothesis" (Cushing, 1975), wherein the success of recruitment is based on the synchrony of larval fish production with peak prey abundance. Survival of larval fish is regulated largely through predation and the effects of suboptimal food levels, such as starvation and reduced growth rates (Houde, 1987). Starvation is probably a direct source of mortality for only a short time after the onset of feeding. However, even small declines in growth rates will prolong the stage duration over which high mortality rates can operate. High and variable mortality rates during the larval stage constitute the potential of tenfold and greater differences in year class size (Houde, 1987). Therefore, the feeding ecology of larval fishes is an essential component in recruitment mechanisms and variability.

Walleye pollock (*Theragra chalcogramma*) is one of the most

abundant fish species in the Bering Sea, constituting nearly 70% of the total biomass of groundfish in the eastern Bering Sea and 85% in the western Bering Sea (Springer, 1992). In addition, walleye pollock currently supports the largest single-species fisheries in the world with an average annual harvest of 5.3 million tonnes since 1976 (Wespestad, 1993). Walleye pollock populations have high fluctuations in annual recruitment levels (Wespestad, 1993).

Prior to 1980 most walleye pollock harvests occurred inside the U.S. Exclusive Economic Zone (EEZ). Due to the expansion of domestic fisheries and the exclusion of foreign fleets from the EEZ, foreign fisheries was forced to exploit walleye pollock populations in the central oceanic basin of the Bering Sea ("donut hole"). In 1989 walleye pollock catches peaked in this area at 1.45 million tonnes, but have declined sharply since then (Wespestad, 1993). By 1991 the "donut hole" catches were 80 % less than in 1989.

Walleye pollock in the eastern Bering Sea are currently managed as one stock. However, there is controversy and some evidence for the existence of at least three spawning stocks: the Aleutian basin, the northwest continental slope and the southeast slope and northwest shelf population (Hinckley, 1987). As the linkage between on-shelf and off-shelf walleye pollock populations is not understood, the impact of the

extensive exploitation in the oceanic basin on US EEZ fisheries is largely unknown.

The southeastern Bering Sea is comprised of four hydrographic domains, the coastal, middle, outer shelves and oceanic domain (Kinder and Schumacher, 1981). The middle shelf frontal zone separates the outer shelf and oceanic domain from the middle shelf domain (Cooney and Coyle, 1982), effectively segregating the southeastern Bering Sea into two distinct production systems. The oceanic domain lacks a well-defined spring bloom. The large oceanic herbivorous copepods *Calanus christatus*, *C. plumchrus*, *Eucalanus bungii bungii*, and *Metridia pacifica* are the dominant species (Smith and Vidal, 1986). Also, *Oithona* sp. copepods had high abundances in the outer and oceanic domain (Clarke, 1984). However, grazing control on the small phytoplankton species is most likely due to a high standing stock of microheterotrophs that seem tightly coupled to primary production (Miller et al., 1991). In contrast, the middle shelf domain is dominated by smaller neritic copepod species (*Pseudocalanus* spp., *Acartia longiremis*, and *Oithona similis*) (Cooney and Coyle, 1982). Their grazing impact is insufficient to control the phytoplankton bloom; therefore, the middle shelf domain of the southeastern Bering Sea can be characterized as uncoupled with respect to the pelagic primary production. In this view, the Bering Sea

has two sharply different pelagic production systems, the oceanic and the middle shelf domain, separated by the middle shelf frontal zone.

First-feeding walleye pollock larvae prey predominantly on copepod nauplii (Clarke, 1984; Dagg et al., 1984; Nishiyama et al., 1986; Kendall et al., 1987; Sterritt, 1989; Pritchett, 1990; Canino et al., 1991; Kendall and Nakatani, 1992) and require up to 76 nauplii per day for metabolism and growth, depending on temperature and nauplii size (Yamashita and Bailey, 1990). Walleye pollock larvae in the laboratory feed at relatively low prey densities of 8 $l^{-1}$ (Paul, 1983). Saturation feeding *in vivo* occurs at densities as low as 20 nauplii $l^{-1}$ (Haldorson et al., 1989). On the major nursery ground of the Bering Sea shelf copepod nauplii concentrations are typically 5 - 15 $l^{-1}$ (Dagg et al., 1984). In Shelikof Strait, larval feeding and condition was found to depend on the geographical location of the larvae. Microzooplankton concentrations, larval feeding and RNA/DNA were higher inside a patch of high larval abundance than outside of it (Canino et al., 1991). In Funka Bay, Japan, walleye pollock larvae that hatched prior to the increase of copepod nauplii abundance suffered greater mortality than larvae that hatched synchronously with the nauplii production (Nakatani, 1991). Larval walleye pollock cohorts in Auke Bay hatching in synchrony with the herbivorous copepod maximum had higher growth rates than

earlier cohorts (Sterritt, 1989).

In the eastern Bering Sea, eggs of walleye pollock are spawned first in oceanic waters over the Aleutian Basin and continental slope, and later in the year over the shelf (Hinckley, 1987). Consequently, larvae from these eggs hatch into quite different production systems. Previous studies have focussed on the feeding ecology of walleye pollock larvae over the shelf in the neritic domain (Clarke, 1984; Dagg et al., 1984; Nishiyama et al., 1986; Grover, 1990). However, little is known about the feeding habits of walleye pollock larvae in the oceanic domain of the Bering Sea.

The goal of this thesis is to describe the trophic relationships of larval walleye pollock and their prey in the oceanic domain of the Bering Sea. The specific objectives are:

1. Examine the depth distribution of walleye pollock larvae and compare it with the depth and distribution of prey taxa.
2. Determine larval diet by depth and larval size class.
3. Compare prey eaten with prey available to determine if prey selection existed, based on taxa and size.
4. Determine if there were differences in larval dry weight and condition with depth.

## MATERIAL AND METHODS

### Field Methods

Samples were collected on board the NOAA R/V "Miller Freeman" in April 1992 at two stations in the southeastern Bering Sea (Table 1; Figure 1). The first station (55°1.09N, 168°19.96W) was sampled on April 20, 1992 in the deep water area off Bogoslof Island (1900 m bottom depth). The second station (54°46.06N, 168°57.97W) was sampled on April 24, 1992 over 2000 m deep water. At both stations sampling occurred during midday.

A Seabird CTD-system was used to record conductivity, temperature, and pressure from 0 to 90 m depth at both stations. Seven casts were performed prior to the ichthyoplankton sampling at station 1, five casts were done during the ichthyoplankton sampling at station 2.

Ichthyoplankton were collected at six discrete depths (10, 20, 30, 50, 70, and 90 m) using a 1 $m^2$ MOCNESS (Multiple Opening and Closing Net and Environmental Sensing System) (Wiebe et al., 1976), equipped with 505 µm mesh nets. The MOCNESS recorded elapsed time, temperature, salinity, sigma-t, net angle, horizontal and vertical velocity and volume filtered.

**Table 1.** Calendar dates, times, positions, depths and numbers of replicates sampled with MOCNESS. Time of sunrise 7:57 and 7:49, and of sunset 22:25 and 22:33 at station 1 and 2, respectively.

| Station 1 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Volume Filtered ($m^3$) Replicate$^{-1}$ | | | | | | | |
| Depth | 1 | 2 | 3 | Date | Time | Depth (m) | Latitude | Longitude |
| 10 | 527 | 527 | 537 | 4/20/92 | 14:58 | 1938 | 55'1.09 | 168'19.96 |
| 20 | 524 | 529 | 528 | | | | | |
| 30 | 536 | 537 | 536 | 4/20/92 | 12:56 | 1900 | 55'1.09 | 168'20.33 |
| 50 | 530 | 537 | 533 | | | | | |
| 70 | 537 | 534 | 536 | 4/20/92 | 10:46 | 1900 | 55'1.33 | 168'20.01 |
| 90 | 533 | 533 | 529 | | | | | |

| Station 2 | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Volume Filtered ($m^3$) Replicate$^{-1}$ | | | | | | | |
| Depth | 1 | 2 | 3 | Date | Time | Depth (m) | Latitude | Longitude |
| 10 | 520 | 509 | 514 | 4/24/91 | 15:57 | 2043 | 54'46.06 | 168'57.97 |
| 20 | 515 | 512 | 514 | | | | | |
| 30 | 510 | 515 | 520 | 4/24/91 | 13:51 | 2035 | 54'46.33 | 168'57.13 |
| 50 | 528 | 527 | 526 | | | | | |
| 70 | 535 | 530 | 536 | 4/24/91 | 11:12 | 2050 | 54'49.60 | 168'53.35 |
| 90 | 531 | 526 | 533 | | | | | |

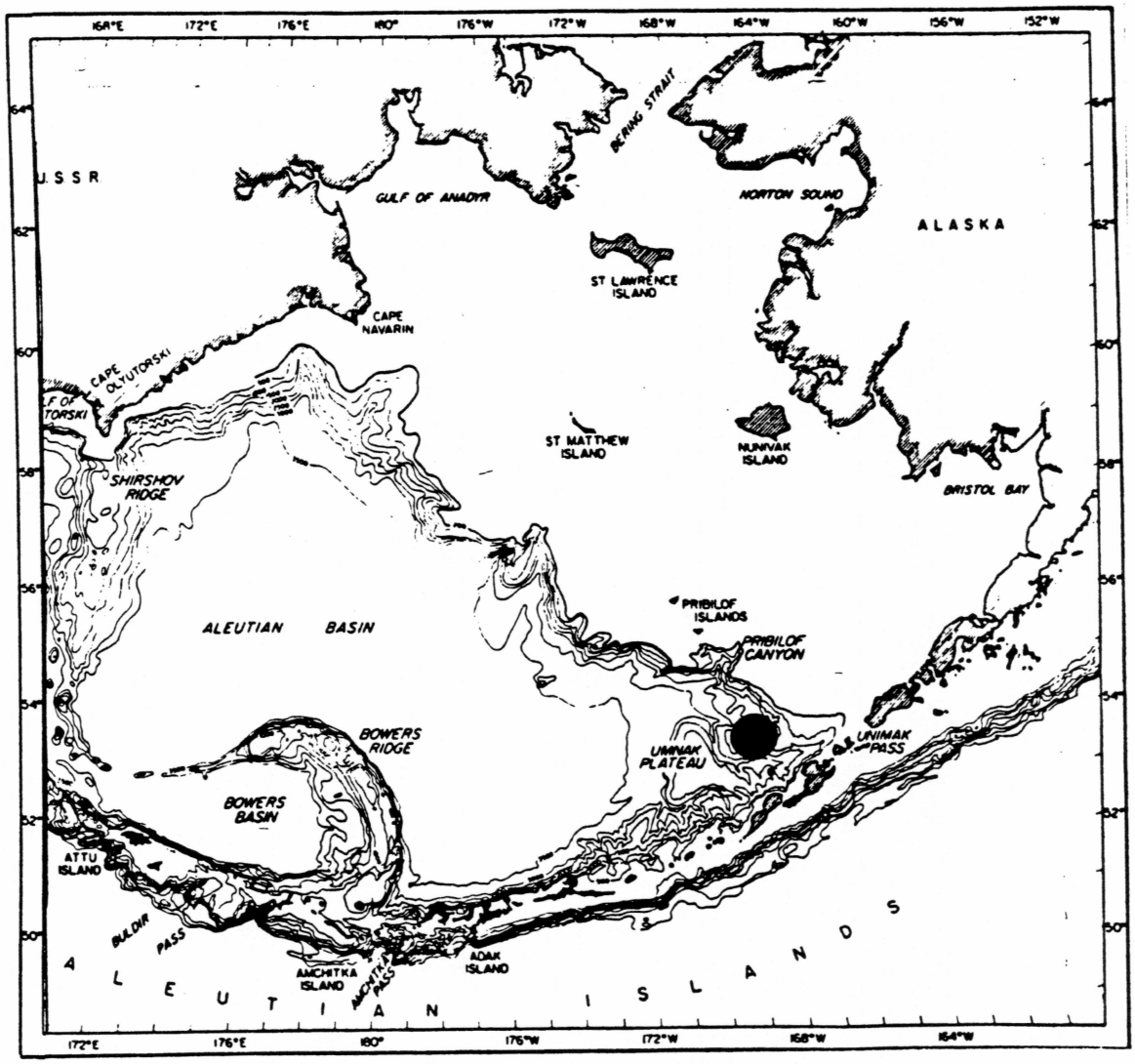


**Figure 1.** Location of sampling for station 1 and 2, April 20, 1992, in the oceanic domain of the Bering Sea.

Three replicates were collected at each depth, beginning with the deepest stratum and progressing sequentially to the shallowest. At each station three MOCNESS casts were taken, with two depths sampled per cast. The target volume of water filtered per replicate was 500 $m^3$. Upon retrieval of the gear the nets were thoroughly washed, codends detached and the samples rinsed through a 335 µm sieve. Concentrated samples were fixed in 10% buffered formalin-seawater solution.

Microzooplankton were collected using a rosette sampler equipped with 10 l Niskin bottles (A. J. Paul, pers. comm.). The sampler was connected to the CTD system described above and samples were taken simultaneously with the recording of the hydrographic data. Eight depths (5, 10, 20, 30, 40, 50, 70, and 90 m) with three replicates per depth were sampled. Water from the bottles was passed through a 64 µm bag net. The concentrated samples were preserved in 5% buffered formalin-seawater solution.

## Laboratory Methods

About four months after fixation, all fish larvae were removed from each sample under a dissecting microscope (10x), identified to species, and counted. Density of larvae was expressed as numbers 100 $m^{-3}$.

Length of larvae was measured to the nearest 0.1 mm using a BioQuant image analysis system with high resolution video system and a digitizer. No correction was made for larval shrinkage. The walleye pollock larvae were separated into 0.5 mm length classes and stored in 50% isopropyl alcohol.

Copepod nauplii from three replicates at each depth were measured to the nearest 10 µm with an ocular micrometer and identified to the lowest possible taxon. Counts of *Oithona similis* nauplii were provided by Dr. A. J. and J. M. Paul (pers. comm.). At station 1, the total lengths (total length = length of carapace and abdomen, excluding terminal spines) of 278 *Oithona similis* nauplii were measured at two depths, 30 m (replicate 1) and 70 m (replicate 1), respectively, and the naupliar stages were identified based on characteristics determined by Sazhina (1985). I counted and measured calanoid nauplii from six depths and three replicates per depth from samples provided by Dr. A. J. Paul. Total and carapace lengths were measured for calanoid nauplii, whenever possible. Stages were determined for *Metridia* sp. and *Pseudocalanus* sp. nauplii based on total length measurements and characteristic features identified by Ogilvie (1953). *Microcalanus* sp. nauplii were staged using total length (Ogilvie, 1953). Stages I and II of *Metridia* sp. and *Pseudocalanus* sp. nauplii could not be distinguished;

they were categorized as calanoids I/II. Calanoid nauplii that could not be identified were listed as calanoids. Naupliar density was expressed in numbers $l^{-1}$.

Walleye pollock larvae were subsampled from each size-class in each depth stratum. The subsample size was 10, unless fewer larvae were available (see Table 5; Appendix 3). Each larva was placed in distilled water for 1 min. It was then positioned on a microscope slide in a drop of distilled water and the standard length was measured with a dissecting microscope and ocular micrometer. The whole gut tract (alimentary canal) was removed and placed on a slide in a drop of glycerin. The gut was opened and the contents excised. Each item was measured with an ocular micrometer on a compound microscope to within 10 µm. The diameter of copepod eggs was measured. Copepod nauplii were identified as *Metridia* sp., *Pseudocalanus* sp., *Microcalanus* sp., calanoids I/II, calanoids, and *Oithona similis*. Carapace length and total length were measured, and the stages were determined, whenever possible.

In order to test the effect of the removal of the alimentary canal on the dry weight measurement, a subsample of 20 fish larvae of 5.0-5.9 mm size was selected. For 10 of the larvae the alimentary canal and the somatic tissue were weighed separately, meanwhile the remaining 10

larvae were weighted whole. The effect of the dry weight of the alimentary canal on the total dry weight of the larva was examined with the coefficient of variation. The coefficient of variation compares the relative amount of variation in populations with different means (Sokal and Rohlf, 1981). Since the removal of the larval gut resulted in a reduction of the coefficient of variation this method was used for the dry weight measurement.

After detachment of the alimentary canal, the remains of each fish larva was transferred to a pre-weighed aluminum pan and dried at 60 °C (Strickland and Parsons,1972). After 24 hours the aluminum pans were placed in a desiccator and allowed to cool before the dry weight was measured on a Cahn's electrobalance to within 0.001 mg .

## Statistical Methods

The average density (number 100 $m^{-3}$) of walleye pollock larvae was calculated for each depth. The null hypothesis that larvae were evenly distributed among depths was tested with single-factor analysis of variance (ANOVA), as was the null hypothesis that length did not differ with depth. If density or size differences were found among depths, Scheffé's and Tukey's multiple comparison procedures were conducted

to examine pairwise relationships (Sokal and Rohlf, 1981). Prior to statistical testing, data were checked for departure from assumptions of ANOVA. Normal probability plots were used to determine if data were normally distributed. Homoscedasticity was analyzed by plotting mean against variance. Departures from assumption of homoscedasticity were corrected with a log-transformation and the variates were coded by adding 1, because data to be transformed contained zeros ($\log_{10}(Y+1)$) (Sokal and Rohlf,1981).

The null hypothesis that copepod nauplii were evenly distributed by depth was tested with ANOVA. Data were transformed by $\log_{10}(Y+1)$ in order to meet the assumptions of ANOVA (Sokal and Rohlf, 1981). Scheffé's and Tukey's multiple comparison procedures were conducted to examine pairwise relationships.

Carapace length was regressed against total length in the three genera, *Metridia* sp., *Pseudocalanus* sp., and *Microcalanus* sp.. This allowed calculation of total length from carapace length for damaged calanoid nauplii in gut contents (Appendix 1).

Prey consumption by each 0.5 mm larval length class was described by percent frequency of occurrence, percent number, percent volume, and index of relative importance (Wallace, 1981, 1983). Volume of copepod nauplii was calculated from carapace length using

mensuration formulas (Nishiyama and Hirano, 1983).

The proportion of feeding larvae per depth and size-class was calculated. A chi-square test of independence was used to test the null hypothesis that feeding incidence was uniform with respect to depth or size-class.

The mean number of food items per larval gut was calculated for all guts that contained food items. The null hypothesis that the number and size of prey items per gut was evenly distributed with depth was tested with ANOVA. The counts were square-root transformed in order to meet the assumptions of ANOVA (Sokal and Rohlf, 1981). If differences were found, Scheffé's multiple comparison procedure was used to test for pairwise relationships. The data were examined for assumptions as described above and transformations were applied if necessary.

Food rations (D) ingested by larval walleye pollock at depth were estimated from gut contents using an equation modified by Canino et al. (1991)

$$D = \frac{A * T}{N}$$

A = Mean amount of prey items during feeding period

T = Feeding period in hours (approximately 14 hours at the time of

sampling)

N = Gut passage time in hours

The overall proportion of prey items and of developmental stages of prey taxa ingested was weighted by the proportion of the pollock population at each depth, so that the overall proportion of a given prey item ($O_j$) was:

$$O_j = \sum_{i=1}^{n} (f_{ij} * p_i)$$

$f_{ij}$ = prey item j at any given depth i.

$p_i$ = proportion of the population at depth i.

n = number of depths

Feeding selectivity was estimated using the natural log(L) of the Odds Ratio(O) as a measure of selectivity (Gabriel, 1978). L is symmetrically distributed around a mean of zero and ranges from zero to $+\infty$, in case of positive selection and zero to $-\infty$, in case of negative selection:

$$L = \log(O) = \log(\frac{p_1 * q_2}{p_2 * q_1})$$

A standard error of L can be calculated:

$$S.E. = \sqrt{\frac{1}{n_1 * p_1 * q_1} + \frac{1}{n_2 * p_2 * q_2}}$$

Since L has a lognormal distribution, the null hypothesis that an observed L is not significantly different from zero and prey therefore were consumed non-selectively, can be tested. The difference is expressed in terms of standard normal deviates (Z):

$$Z = \frac{L_{observed} - L_{expected}}{S.E.(L)}$$

where $L_{expected} = 0$;

$p_1$ = percentage of diet comprised by a given prey taxon.

$p_2$ = percentage of food item in environment comprised by a given taxon.

$q_1$ = percentage of diet comprised by all other prey taxa.

$q_2$ = percentage of food item in environment comprised by all other

taxa.

$n_1$ = total number of prey in diet sample

$n_2$ = total number of food organisms in environmental sample

Dry weight was regressed against standard length at the six depth strata. Diagnostics on the residuals were performed as described above. The null hypothesis that the slopes of the regression lines were uniform with respect to depth was tested with an analysis of covariance (ANCOVA) (Systat, 1992). Fulton's condition factor was calculated for each size-class by depth (McGurk, 1985):

$$Fulton's\ CF = \frac{W}{SL^3} * 100$$

W = dry weight of walleye pollock larva

SL = standard length of walleye pollock larva

The null hypothesis that the condition factor was uniform for a given size-class among depths was tested with ANOVA. If the null hypothesis was rejected, Tukey's multiple comparison procedure was conducted to identify significant differences between any two depths.

## RESULTS

Physical Environment

At station 1, temperature in the surface stratum was approximately 2.8°C and increased to 3.5°C at 90 m depth. At 20 m depth the temperature profile had a break (Figure 2). Salinity ranged from 32.4 ‰ in the surface to 32.7 ‰ at 90 m depth, gradually increasing with depth. The surface water of low temperature and salinity was probably due to ice melt. No seasonal thermocline was developed.

At station 2, the water column just prior to the ichthyoplankton sampling, between the first and second MOCNESS replicate, and between the second and the third MOCNESS haul had very different temperature regimes. In the first cast (Figure 3a) the water at 30 m depth was 3°C and increased at depth to 3.4°C. The water column during the second group of casts (Figure 3b) had a sharp stratification at 25 m depth. In the third set of casts (Figure 3c) the whole water column was about 3.8°C. The salinity profiles are indicative that cold, less saline water was replaced by warmer water with higher salinity.

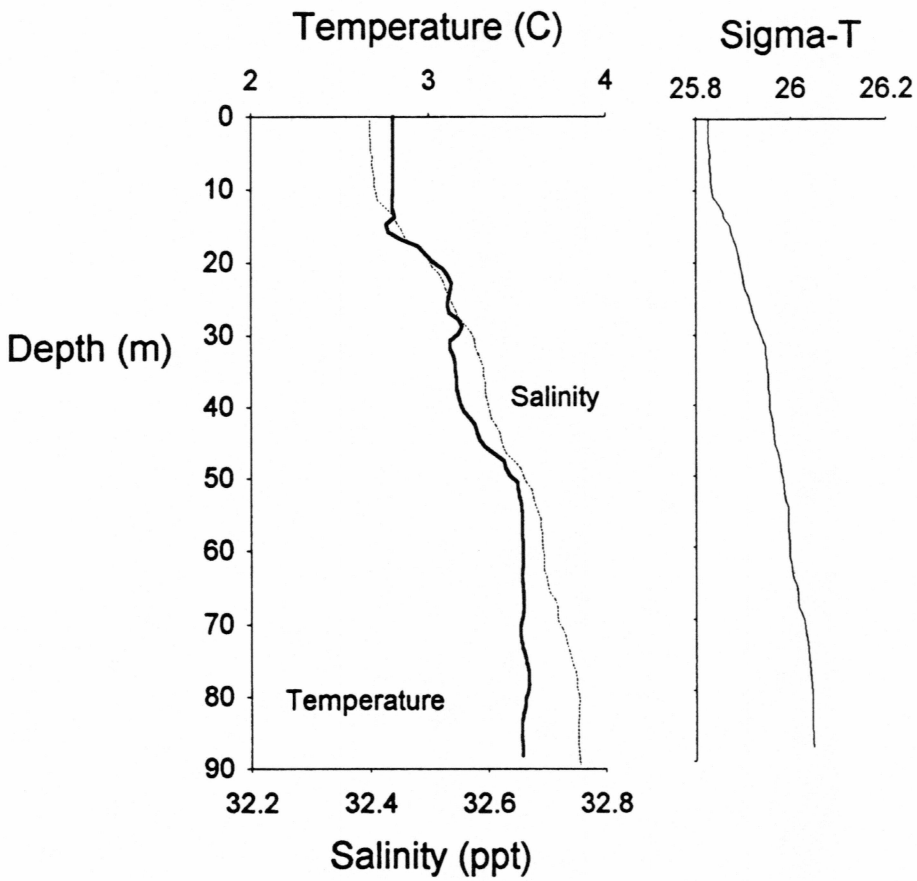


**Figure 2.** Temperature-salinity profile from station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

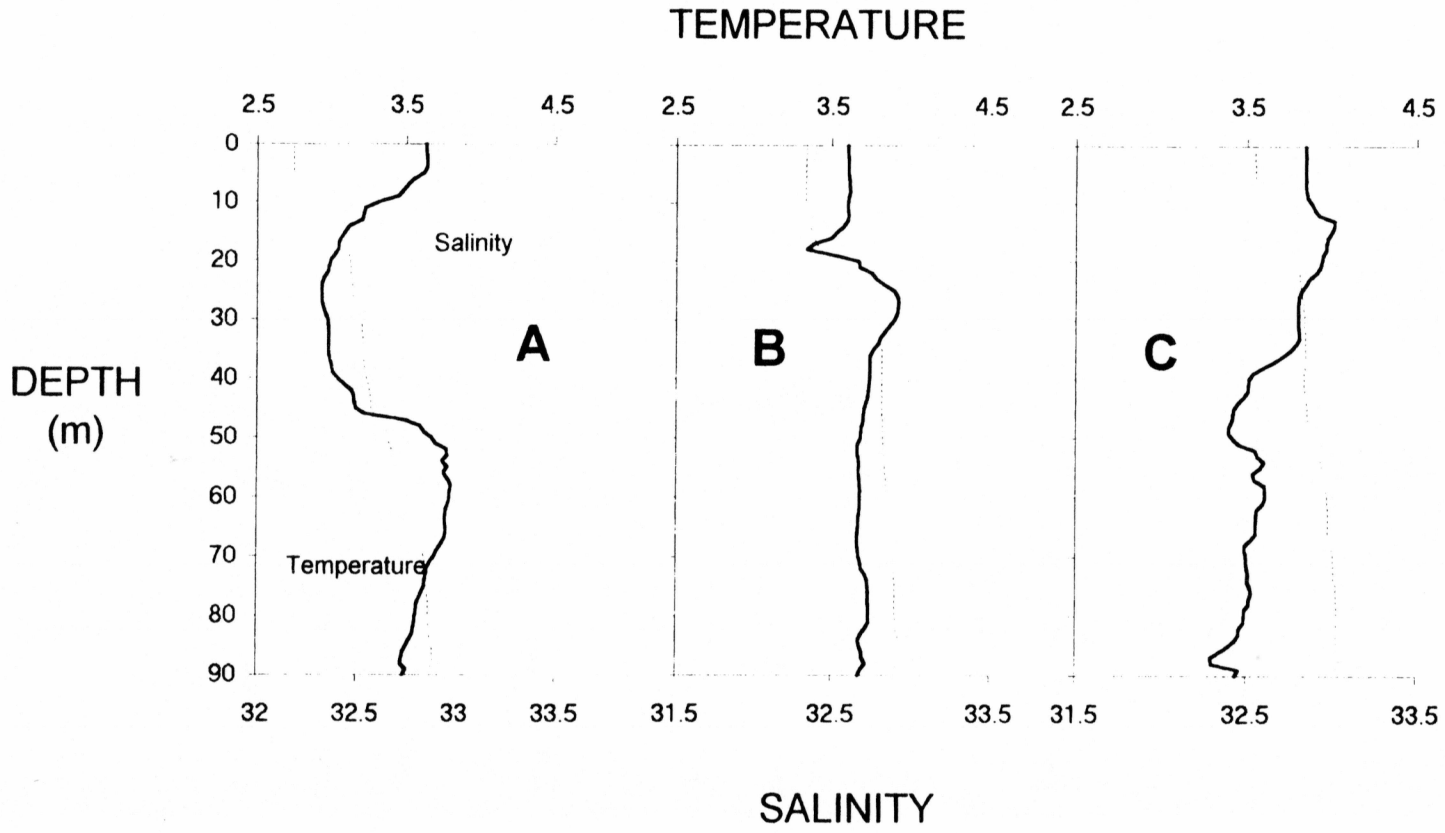


**Figure 3.** Temperature-salinity profile from station 2, April 20, 1992, in the oceanic domain of the Bering Sea

Larval Fish Abundance

Walleye pollock constituted 97% of the ichthyoplankton taxa at station 1, followed by Pacific Halibut (*Hippoglossoides stenolepis*) and *Atherestes* spp. (Table 2). *Atherestes* contains two species whose larvae are not readily distinguishable: arrowtooth flounder (*Atherestes stomias*) and kamtchatka flounder (*Atherestes evermanni*) (Matarese et al., 1989). Eight other taxa occurred but in negligible densities.

At station 2, the overall abundance of larval fish was only 4% of that at station 1 (Table 3). The most abundant taxa was *Atherestes* spp., constituting 38% of the larval fish. Walleye pollock larvae were relatively rare compared to the first sampling station. Walleye pollock, Pacific halibut, Rockfish (*Sebastes* sp.), and *Atherestes* spp. accounted for 93% of fish larvae. Three other taxa occurred in very reduced numbers.

Due to the low abundance of walleye pollock larvae at station 2, and because it seems doubtful that the same body of water was sampled in the replicate casts, all of the following analyses will be based on samples from station 1.

**Table 2.** Abundance of larval fish in number 100 $m^{-3}$ at station 1. Means are calculated from $\log_{10}(Y+1)$ transformed variates.

| Species | Depth | | | | | |
|---|---|---|---|---|---|---|
| | **10** | **20** | **30** | **50** | **70** | **90** |
| *Theragra chalcogramma* | 49.85 | 32.69 | 106.64 | 4.74 | 3.13 | 1.59 |
| (* = 95% CI) | *19.41<br>128.02 | *11.27<br>94.85 | *41.39<br>274.76 | *1.08<br>20.71 | *1.87<br>5.23 | *0.29<br>8.61 |
| *Atherestes* spp. | 0.00 | 0.00 | 0.30 | 1.69 | 0.18 | 0.00 |
| *Hippolgossoides stenolepis* | 0.00 | 0.06 | 0.43 | 1.24 | 0.42 | 0.06 |
| *Hemilepidotus* sp. | 0.44 | 0.23 | 0.00 | 0.00 | 0.00 | 0.00 |
| Stichaeidae | 0.12 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Ammodytes hexapterus* | 0.06 | 0.00 | 0.23 | 0.00 | 0.00 | 0.00 |
| *Sebastes* sp. | 0.00 | 0.00 | 0.06 | 0.06 | 0.00 | 0.00 |
| *Dasycottus setiger* | 0.00 | 0.00 | 0.00 | 0.06 | 0.00 | 0.00 |
| Macrouridae | 0.00 | 0.00 | 0.00 | 0.00 | 0.19 | 0.06 |
| *Leuroglossus schmidti* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.25 |
| *Protomyctophum thompsoni* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.06 |

**Table 3.** Abundance of larval fish in number 100 $m^{-3}$ at station 2. Means are calculated from $\log_{10}(Y+ 1)$ transformed variates.

| Depth | 10 | 20 | 30 | 50 | 70 | 90 |
|---|---|---|---|---|---|---|
| *Theragra chalcogramma* | 1.09 | 0.38 | 0.51 | 0.54 | 0.29 | 0.19 |
| *Atherestes* spp. | 0.00 | 0.13 | 1.74 | 1.64 | 0.00 | 0.18 |
| *Hippoglossoides stenolepis* | 0.00 | 0.06 | 0.77 | 0.50 | 0.00 | 0.00 |
| *Hemilepidotus* sp. | 0.24 | 0.13 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Radulinus* sp. | 0.00 | 0.12 | 0.00 | 0.00 | 0.00 | 0.00 |
| Stichaeidae | 0.00 | 0.00 | 0.18 | 0.00 | 0.00 | 0.00 |
| *Sebastes* sp. | 0.00 | 0.00 | 0.00 | 0.06 | 0.12 | 0.00 |

## Walleye Pollock Density And Size

Walleye pollock larvae were found at all depth strata sampled. Walleye pollock larvae were most abundant in the three strata nearest the surface, with a peak abundance of 106.6 $m^{-3}$ at 30 m depth (Figure 4). Mean abundance and variance at depth were positively correlated, therefore, data were transformed in order to meet the assumption of ANOVA. Differences in abundance among depths were significant ($F = 39.33$, $p \leq 0.0001$). The three shallowest and deepest strata formed two significantly distinct homogeneous groups (Tukey's *a posteriori*).

Mean length of walleye pollock larvae was greatest at 30 m depth with an average length of 5.3 mm and lowest at 90 m depth with 4.3 mm (Figure 5). Length differed significantly among depths ($F = 23.7$, $p \leq 0.0001$).

## Copepod Nauplii Density, Species, and Size Composition

Overall abundances of copepod nauplii were lowest at 10 m depth with 3.5 $l^{-1}$ and highest at 30 m depth with peak abundances of 26.3 $l^{-1}$ (Figure 6; Table 4). Differences in densities among depths were significant ($F = 7.677$, $p \leq 0.005$).

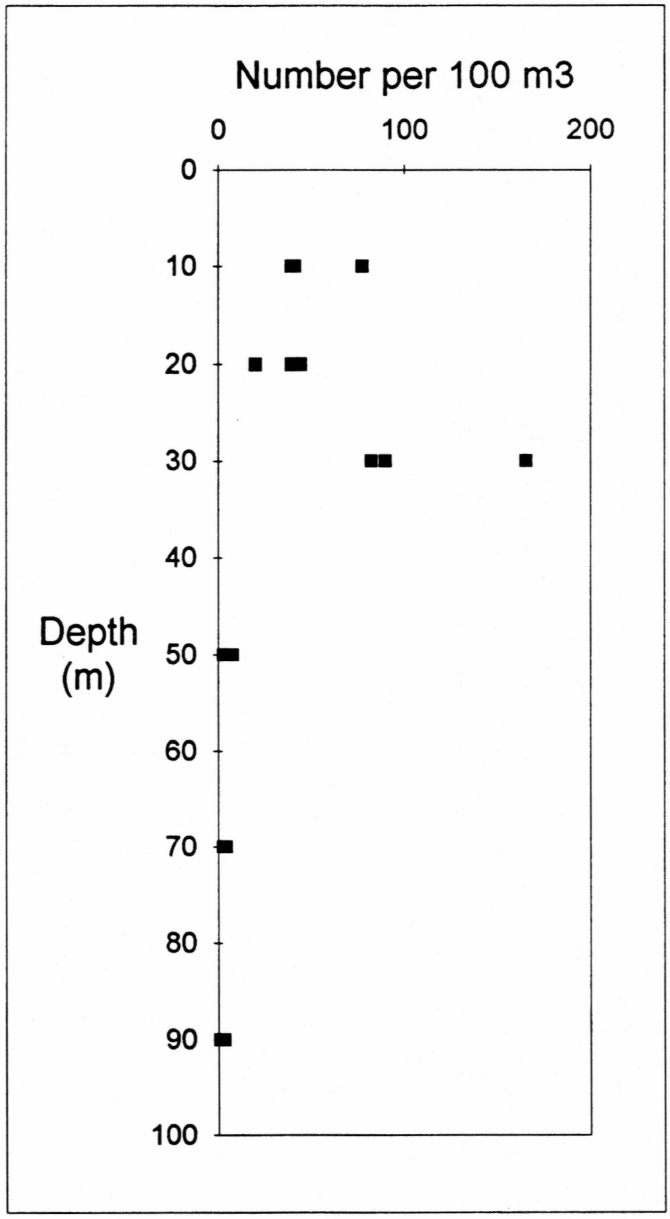


**Figure 4.** Abundance of walleye pollock larvae (100 $m^{-3}$) for three replicates per depth at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

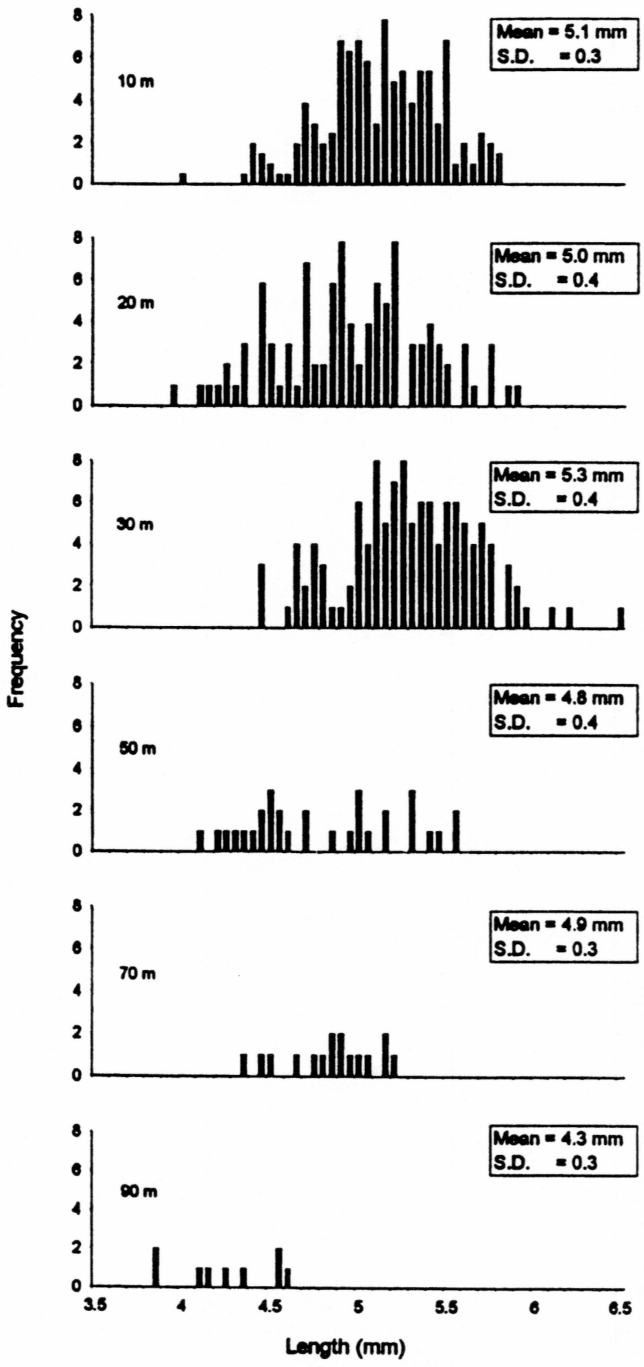


**Figure 5.** Length frequency distribution of larval walleye pollock at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

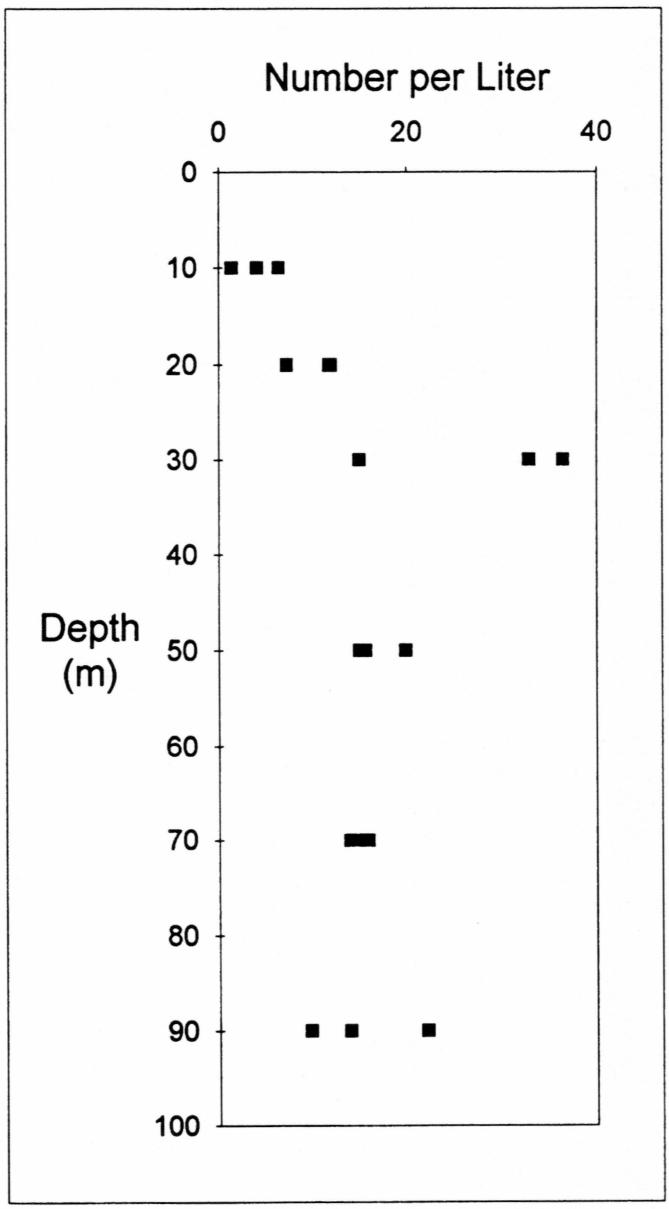


**Figure 6.** Overall abundance of copepod nauplii $l^{-1}$ for three replicates per depth at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

**Table 4.** Abundance of copepod nauplii $l^{-1}$ at station 1, April 20, 1992, in the oceanic domain of the Bering Sea. Means and 95% confidence interval were calculated from $\log_{10}(Y+1)$ transformed variates. Parentheses indicate 95% confidence interval.

| Depth (m) | *Metridia* sp. | *Pseudocalanus* sp. | *Microcalanus* sp. | *Oithona similis* | Total Calanoids | Total |
|---|---|---|---|---|---|---|
| 10 | 0.2 (0.0;1.2) | 0.4 (0.0;2.3) | 0.0 (0.0;0.0) | 3.0 (0.2;12.2) | 0.6 (0.0;3.5) | 3.5 (0.1;17.7) |
| 20 | 1.1 (0.8;1.4) | 1.3 (0.5;2.3) | 0.0 (0.0;0.2) | 7.3 (2.0;21.5) | 2.7 (1.9;3.7) | 10.2 (4.9;20.1) |
| 30 | 3.1 (1.3;6.2) | 0.4 (0.0;1.6) | 0.4 (0.0;2.6) | 21.5 (5.7;75.1) | 4.8 (1.9;10.7) | 26.3 (7.6;85.5) |
| 50 | 1.1 (0.0;3.7) | 0.5 (0.0;2.4) | 1.1 (0.0;10.9) | 12.7 (6.3;25.0) | 3.7 (1.3;8.6) | 16.7 (11.4;24.4) |
| 70 | 0.5 (0.0;2.2) | 0.3 (0.1;0.6) | 0.7 (0.0;11.2) | 12.9 (10.1;16.5) | 1.9 (0.0;8.6) | 15.1 (12.8;17.8) |
| 90 | 0.2 (0.0;0.3) | 0.1 (0.0;0.2) | 3.1 (1.8;5.0) | 10.4 (1.7;47.2) | 3.5 (1.8;6.2) | 14.5 (5.0;39.0) |

The most common nauplii (79%) were identified as *Oithona similis*, a cyclopoid species. The calanoid nauplii contained three genera: *Metridia* sp., *Pseudocalanus* sp., and *Microcalanus* sp.. The number of *Oithona similis* nauplii varied significantly among depths ($F = 5.36$, $p \leq 0.01$), reaching peak abundances at 30 m depth of 21.5 $l^{-1}$ (Figure 7a). The highest abundance of calanoid nauplii was observed at 30 m with 4.8 nauplii $l^{-1}$. *Metridia* sp. nauplii were most abundant at 30 m depth ($F = 12.02$, $p \leq 0.0001$) (Figure 7b).

The maximum density of 3.1 nauplii $l^{-1}$ was significantly different from other depths (Tukey's *a posteriori*). The density of *Pseudocalanus* sp. nauplii varied significantly with respect to depth ($F = 3.243$, $p \leq 0.05$) (Figure 7c). No *Microcalanus* sp. nauplii were found at 10 m depth. Significantly higher abundances of nauplii ( 3.1 $l^{-1}$) were found at 90 m ($F = 4.17$, $p \leq 0.05$) (Figure 7d).

Total length for calanoid nauplii in the environment was estimated with regression formulas (Appendix 1). Total length of *Metridia* sp., *Pseudocalanus* sp. nauplii averaged 260 µm and 280 µm, respectively, and showed no variation with depth. *Microcalanus* sp. nauplii total lengths varied significantly with depth ($F = 6.259$, $p \leq 0.0001$). The nauplii in the three deepest strata were significantly smaller than those at 30 m depth (Tukey's *a posteriori*). The mean length of *Microcalanus* sp.

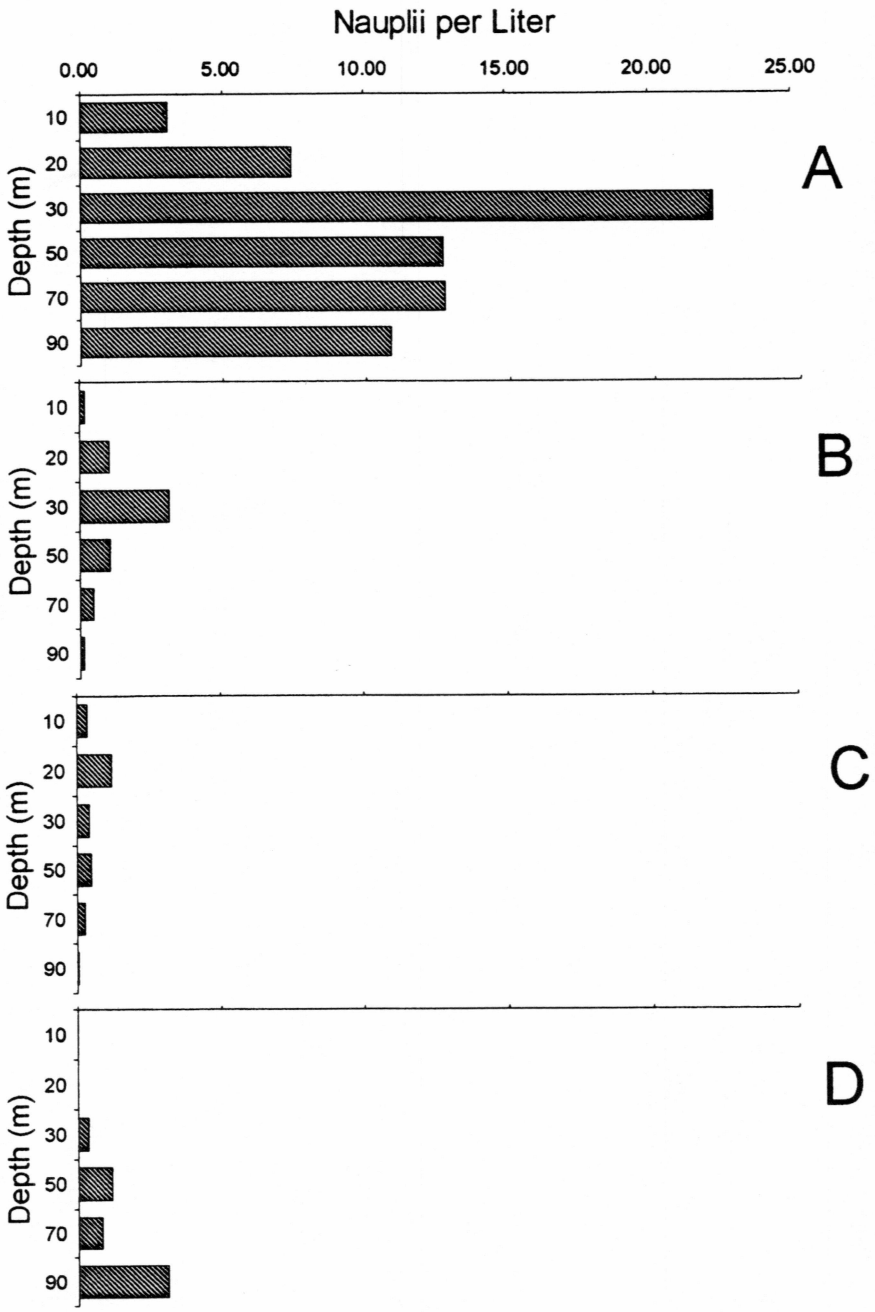


**Figure 7.** Abundance of copepod nauplii $l^{-1}$ at station 1, April 20, 1992, in the oceanic domain of the Bering Sea. Means calculated from $\log_{10}(Y+1)$ transformed data.

is 130 µm. Because of the trend in naupliar length with depth, the weighted average length, based on the number of nauplii ingested by larval walleye pollock at 20 to 70 m depth, was calculated, totalling 150 µm.

*Oithona similis* nauplii had a mean length of 140 µm, but varied significantly in length with respect to depth ($F = 6.429$, $p \leq 0.0001$). The mean total length weighted by the proportion of ingested *Oithona similis* nauplii was 170 µm.

Walleye Pollock Feeding

Of 330 larval walleye pollock guts examined, 187 (56.7%) contained food items. The highest incidence of feeding (97.5%) occurred at 30 m depth (Figure 8). At all other depth strata no more than 70% larvae were observed feeding. At 70 m the percentage of fish larvae with food in their guts was lowest with an average of 16%. No feeding was observed at 90 m depth. In addition, incidence of feeding at all depths was reduced in size classes 1 and 2 (Table 5). A chi-square test of independence revealed that feeding for all size classes varied significantly with respect to depth, in all cases highest incidence occurred at 30 m.

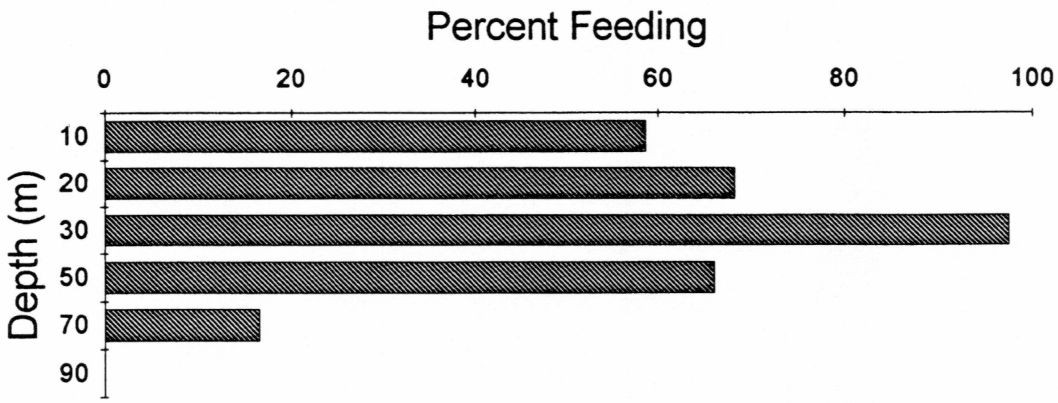


**Figure 8.** Observed proportion of feeding larval walleye pollock at station 1 at April 20, 1992 in the oceanic domain of the Bering Sea.

**Table 5.** Proportion of feeding larval walleye pollock (%) by depth and larval length at April 20, 1992 in the oceanic domain of the Bering Sea. The values in parentheses indicate the sample size N.

| Larval Length Class | | 1/2 | 3 | 4 | 5/6 |
|---|---|---|---|---|---|
| Length (mm) | | 3.5-4.49 | 4.5-4.99 | 5.0-5.49 | 5.5-6.49 |
| Depth (m) | 10 | 50.00 (6) | 45.45 (10) | 84.62 (11) | 61.11 (15) |
| | 20 | 50.00 (14) | 100.00 (10) | 90.91 (10) | 62.50 (11) |
| | 30 | 85.71 (7) | 100.00 (10) | 100.00 (10) | 100.00 (13) |
| | 50 | 43.75 (7) | 52.94 (11) | 93.33 (14) | 100.00 (5) |
| | 70 | 0.00 (0) | 30.00 (3) | 18.18 (4) | 0.00 (0) |

Larvae at 30 m depth had a mean of 4.6 food items ($F = 21.49$, $p \leq 0.0001$) (Figure 9), significantly more than larvae at all other depth strata (Scheffé's *a posteriori*).

Daily food rations for walleye pollock larvae ranged depending on water temperature and assumed gut passage time from a minimum of 2.89 nauplii $l^{-1}$ to 12.90 nauplii $l^{-1}$ (Table 6).

A total of 483 food items were identified. Weighted over all depths, *Metridia* sp. nauplii accounted for 28% of prey items ingested (Figure 10), followed by *Microcalanus* sp., *Oithona similis*, and copepod eggs, comprising 21, 18, and 17%, respectively. The lowest proportion consumed was constituted by *Pseudocalanus* sp. nauplii (5%).

Walleye pollock larvae, weighted over all depths, fed primarily on the older naupliar stages from *Metridia* sp. (IV), *Pseudocalanus* sp. (IV and V), and *Microcalanus* sp. (III, IV, and V), representing total lengths of 200-300 µm, 200-350 µm, and 130-210 µm, respectively (Figure 11, Appendix 2). However, *Oithona similis* nauplii in the larval diet were primarily stages I to III and therefore no larger than approximately 180 µm (Figure 11, Appendix 2).

Numerically, copepod nauplii were the most common food item consumed by larval walleye pollock at all depths (Figure 12, Appendix 3). The other item consistently found in the larval diet was copepod eggs.

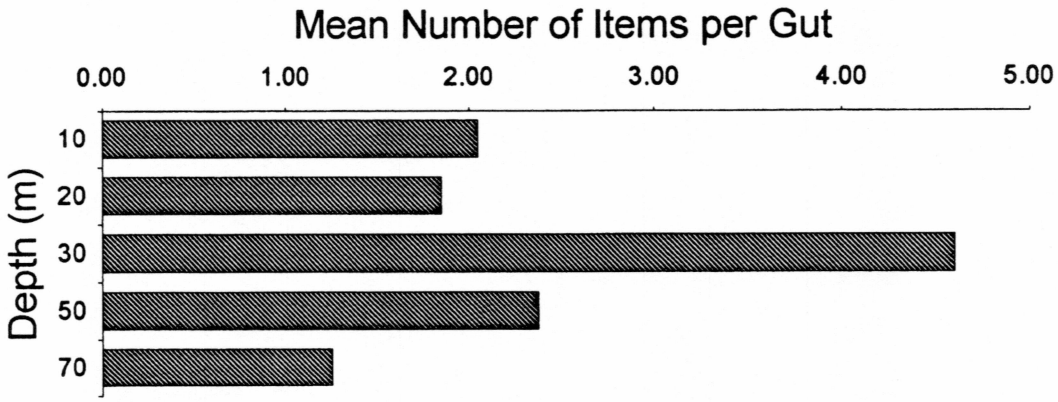


**Figure 9.** Mean number of prey items ingested by larval walleye pollock at April 20, 1992 in the oceanic domain of the Bering Sea. Averages are calculated based on square root-transformed variates.

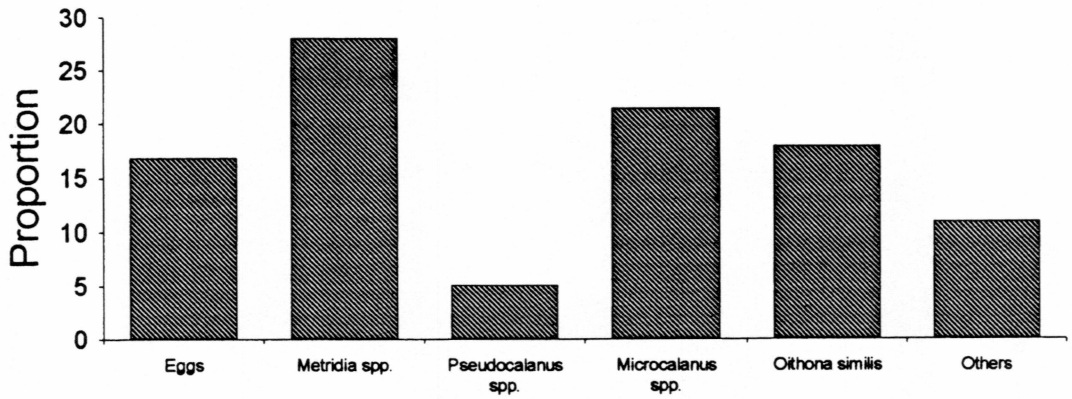


**Figure 10.** Overall proportions of prey taxa ingested by walleye pollock larvae at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

**Table 6.** Daily rations for walleye pollock larvae at depth at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

| Depth (m) | Mean no. prey $l^{-1}$ | Gut Passage Time (h) | | |
|---|---|---|---|---|
| | | 5.0* | 5.3** | 6.1*** |
| | | Daily Ration (D) (prey $larva^{-1}$ $d^{-1}$) | | |
| 10 | 2.1 | 5.75 | 5.42 | 4.71 |
| 20 | 1.9 | 5.19 | 4.90 | 4.26 |
| 30 | 4.6 | 12.90 | 12.17 | 10.57 |
| 50 | 2.4 | 6.66 | 6.28 | 5.46 |
| 70 | 1.3 | 3.53 | 3.33 | 2.89 |

* denotes water temperature of 5.5°C.
** denotes water temperature of 6.4°C and prey ration.
*** denotes water temperature of 6.4°C and low prey ration.

The number of copepod nauplii increased with depth. At 70 m only a total of 9 food items was found in 7 larval fish guts.

Copepod eggs were a consistent percentage of prey number in the larval diet at 10 and 20 m depth. However, at 30 and 50 m depths *Metridia* sp. and *Microcalanus* sp. increased in percentage. *Metridia* sp. nauplii accounted for 15.1%, 2.6%, 35.2%, and 22.5% of the larval diet at 10, 20, 30, and 50 m depth, respectively, and *Microcalanus* sp. for 2.8%, 8.3%, 25%, and 26.3%. *Pseudocalanus* sp. nauplii were rare in the larval diet (Figure 12; Appendix 3).

The volumetric percentage of copepod eggs was highest at 10 m depth (Figure 13; Appendix 3) and decreased with increasing depth. The volume of *Metridia* sp. increased with increasing depth. Even though high numbers of *Microcalanus* sp. nauplii were ingested, their volume was low because of their small size.

Calanoid nauplii were more frequently consumed than other prey items (Figure 14; Appendix 3). At 10 and 20 m depth copepod eggs were found in more than 40% of all walleye pollock larvae. However, at 30 and 50 m depth *Metridia* sp. and *Microcalanus* sp. nauplii were found more frequent.

At 10 and 20 m depth copepod eggs were the primary prey item for all size classes of larval walleye pollock (Figure 15; Appendix 3).

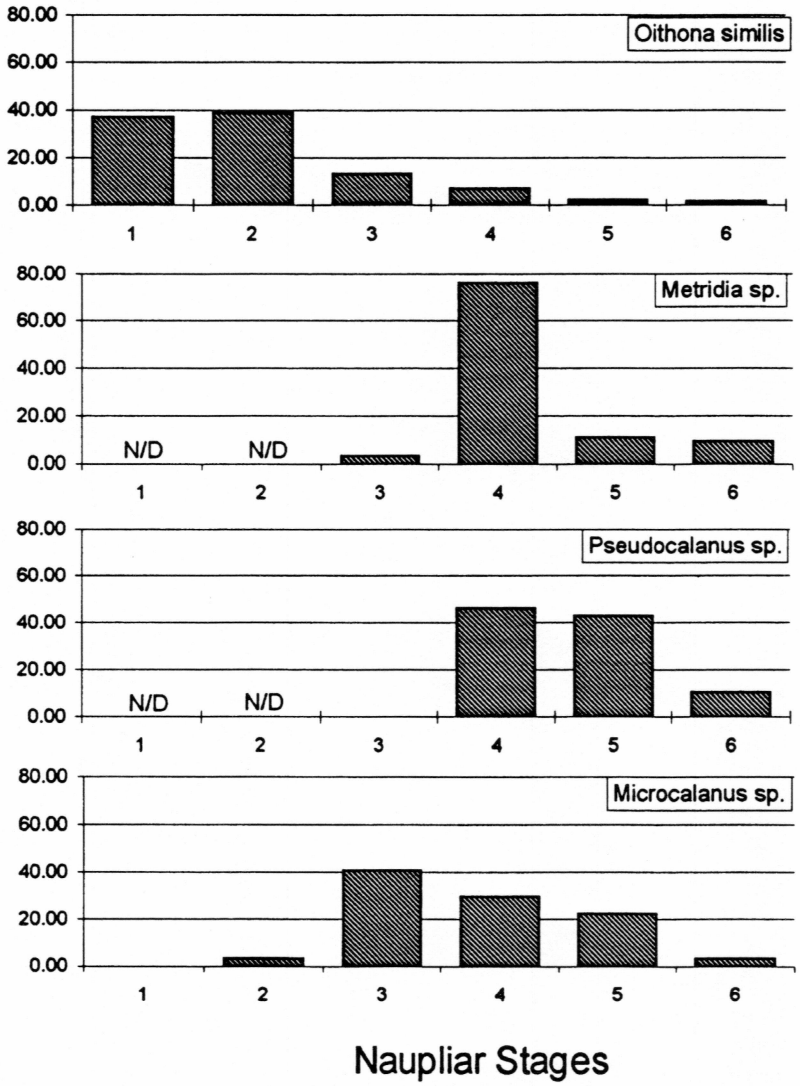


**Figure 11.** Overall proportion of naupliar stages ingested by walleye pollock larvae at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

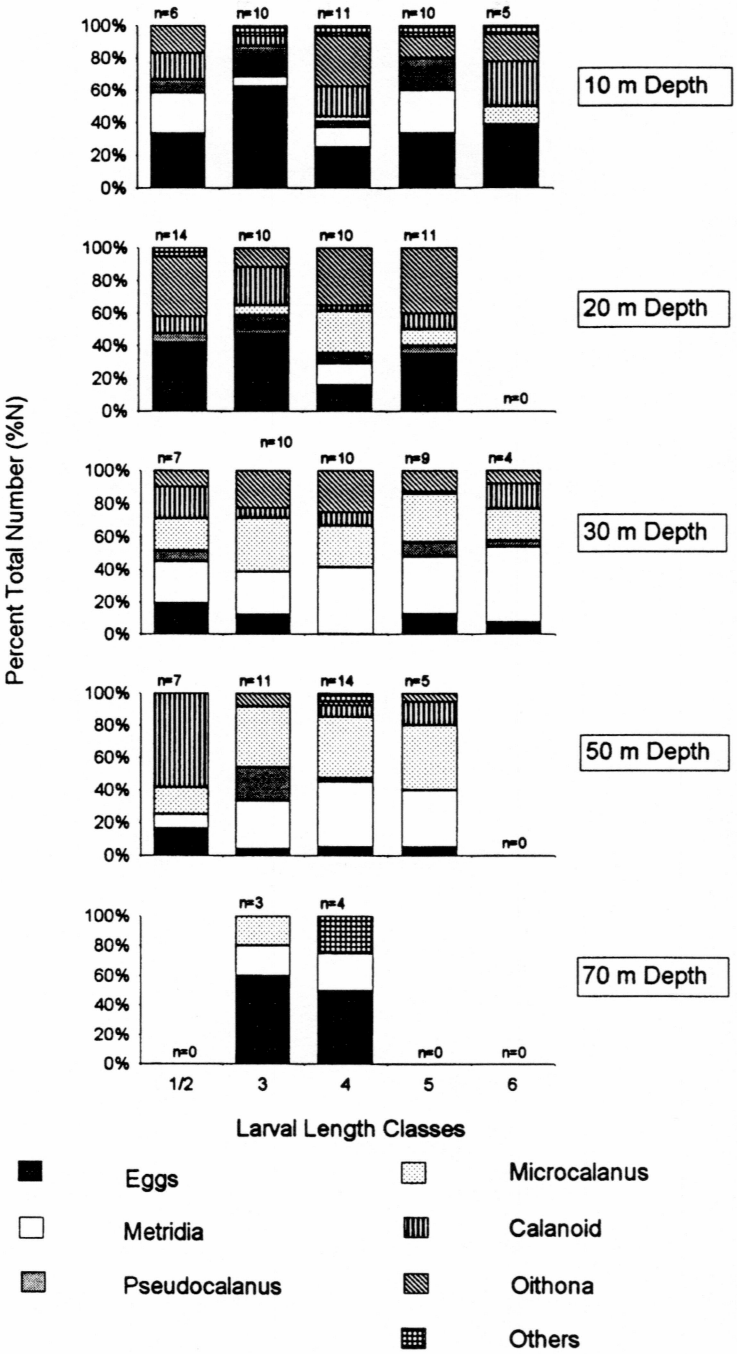


**Figure 12.** Percent total number of all prey items consumed by larval walleye pollock at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

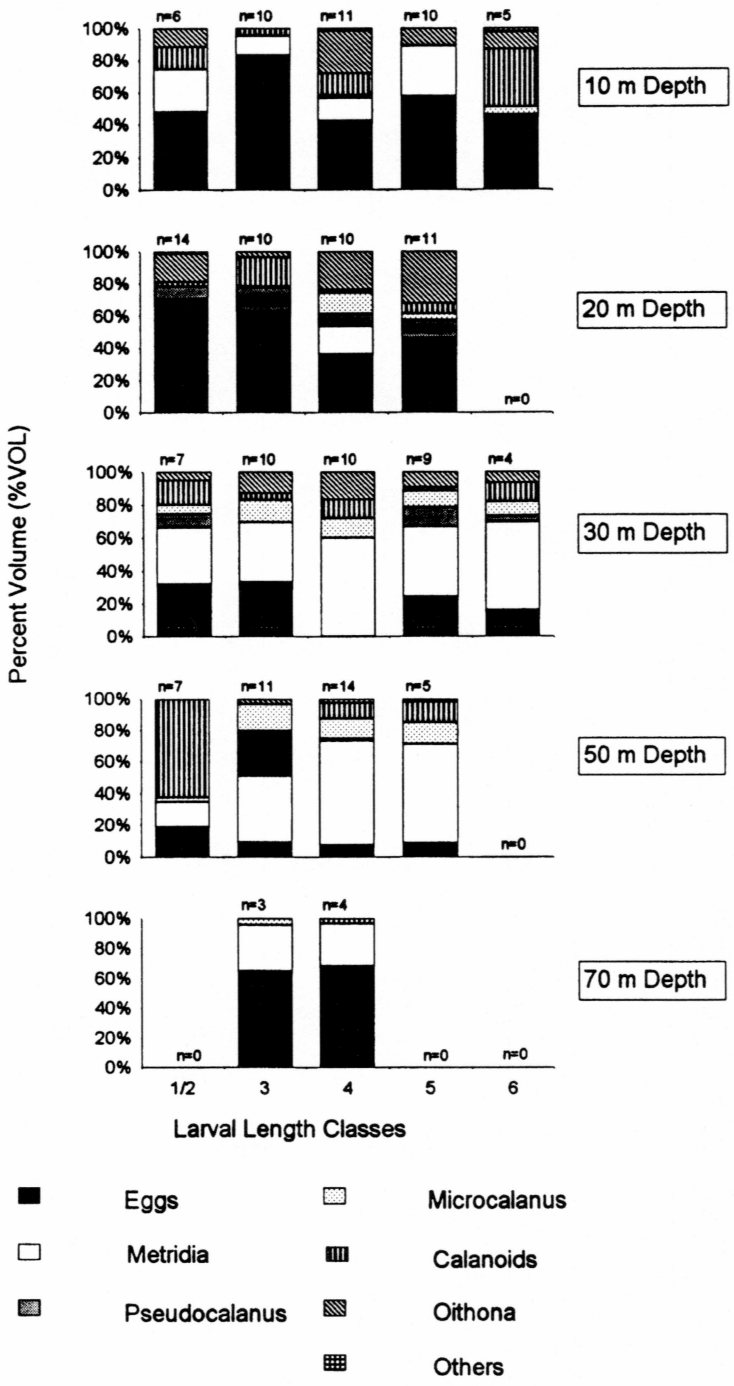


**Figure 13.** Percent total volume of all prey items consumed by larval walleye pollock at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

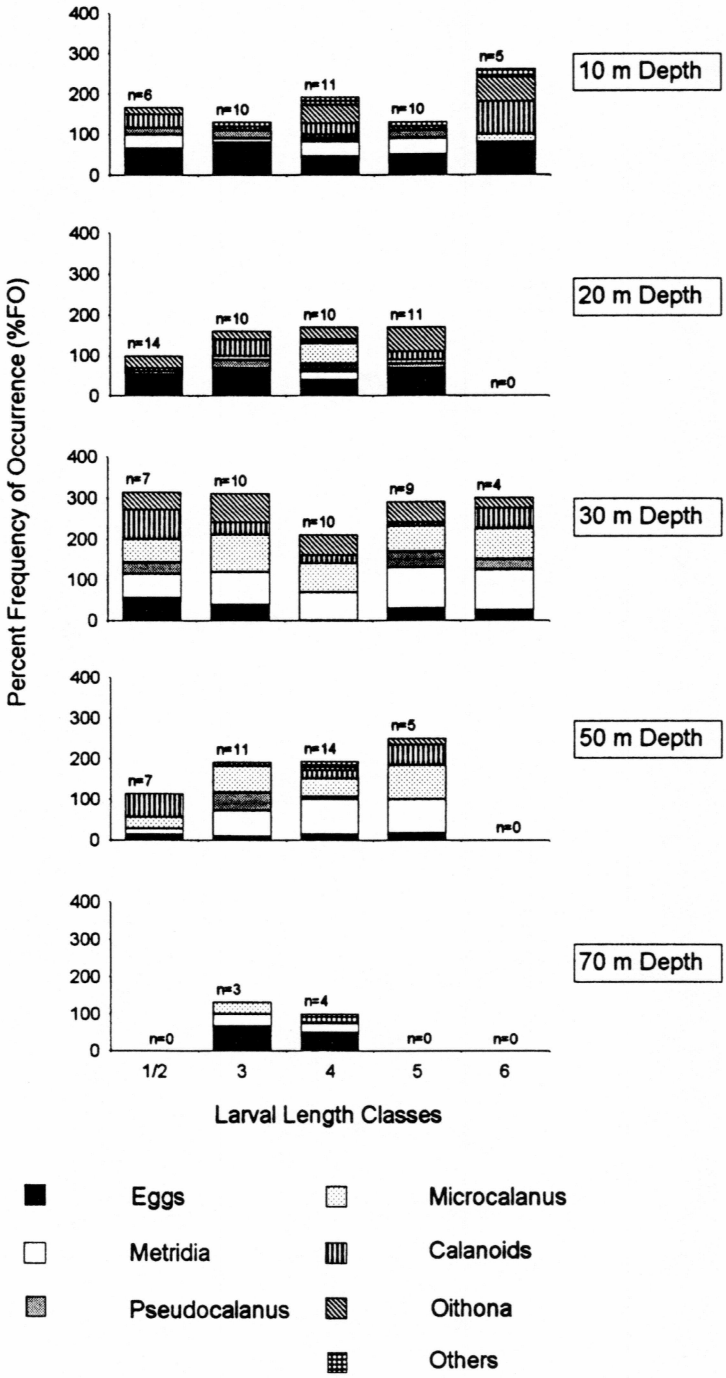


**Figure 14.** Percent frequency of occurrence of all prey items consumed by larval walleye pollock at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

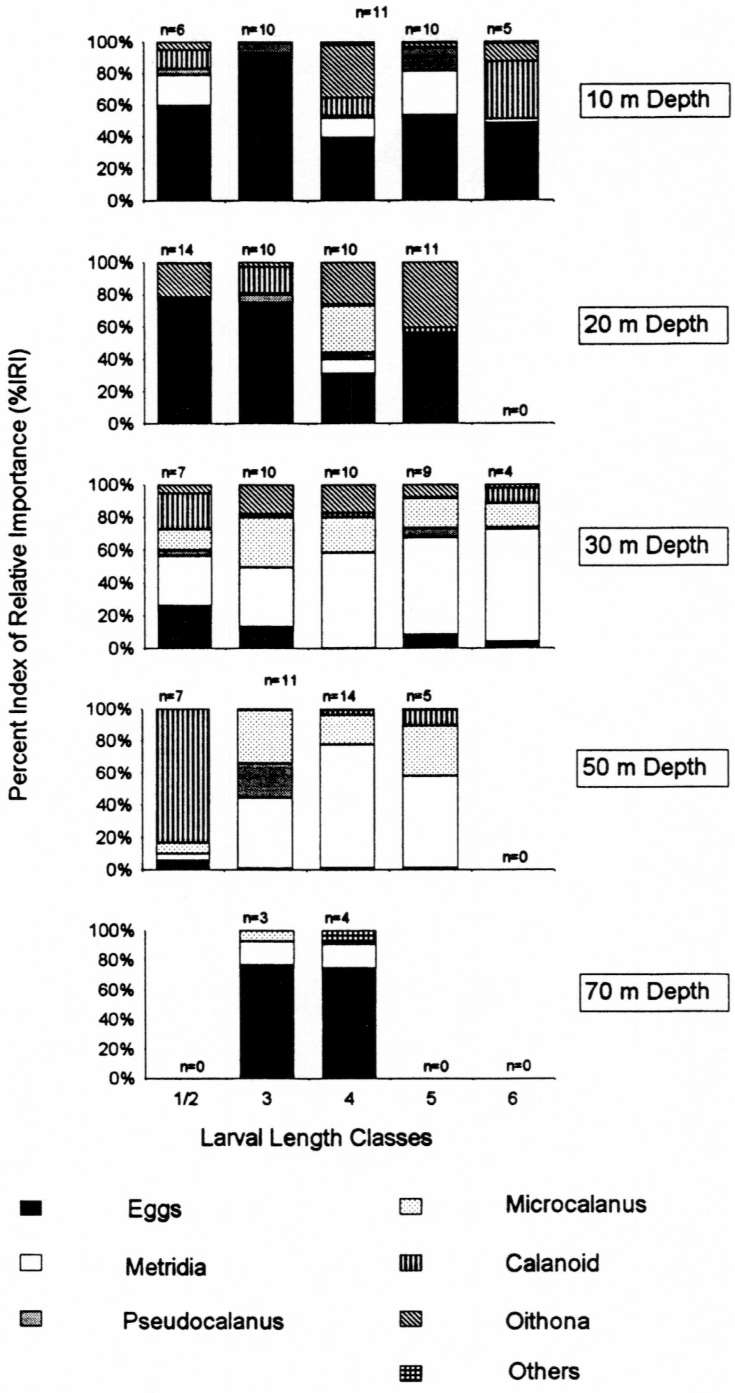


**Figure 15.** Percent index of relative importance of all prey items consumed by larval walleye pollock at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

At 30 and 50 m depth *Metridia* sp. predominated in the diet of pollock larvae, increasing in proportion with increasing larval length. *Microcalanus* sp. and *Pseudocalanus* sp. were second and third in importance as prey items. At 70 m depth copepod eggs predominated the larval diet.

The average total length of *Metridia* sp., *Pseudocalanus* sp., *Microcalanus* sp., and *Oithona similis* in the larval diet was 280 µm, 280 µm, 160 µm, and 150 µm, respectively. In each prey taxon there were no differences in mean length among depths.

Feeding Selectivity

Because only four food items of the categories tested were found at 70 m depths, no selectivity was calculated for this depth strata. Walleye pollock larvae selected significantly for calanoid nauplii and against *Oithona similis* nauplii at all depths (Table 7). In addition, there was positive selection at all depths for *Metridia* sp.. Walleye pollock larvae also positively selected for *Microcalanus* sp. nauplii at 30 and 50 m depths. No selectivity pattern could be established for *Pseudocalanus* sp. nauplii. Comparison of nauplii abundance and numbers of nauplii per gut support the selectivity results (Figure 16).

**Table 7.** Odds Ratio Analysis of selectivity for larval walleye pollock sampled April 20, 1992 in the oceanic domain of the Bering Sea.

| | Log (Odds Ratio) | | | |
|---|---|---|---|---|
| Depth (m) | *Metridia* sp. | *Pseudocalanus* sp. | *Microcalanus* sp. | *Oithona similis* |
| 10 | 1.41** | 0.25 | 27.01 | -2.45** |
| 20 | 1.36* | -3.35** | 1.03 | -4.82** |
| 30 | 1.59** | 1.03* | 3.28** | -3.79** |
| 50 | 1.98** | 1.47 | 6.69** | -8.23** |

* : $p \leq 0.05$
**: $p \leq 0.01$

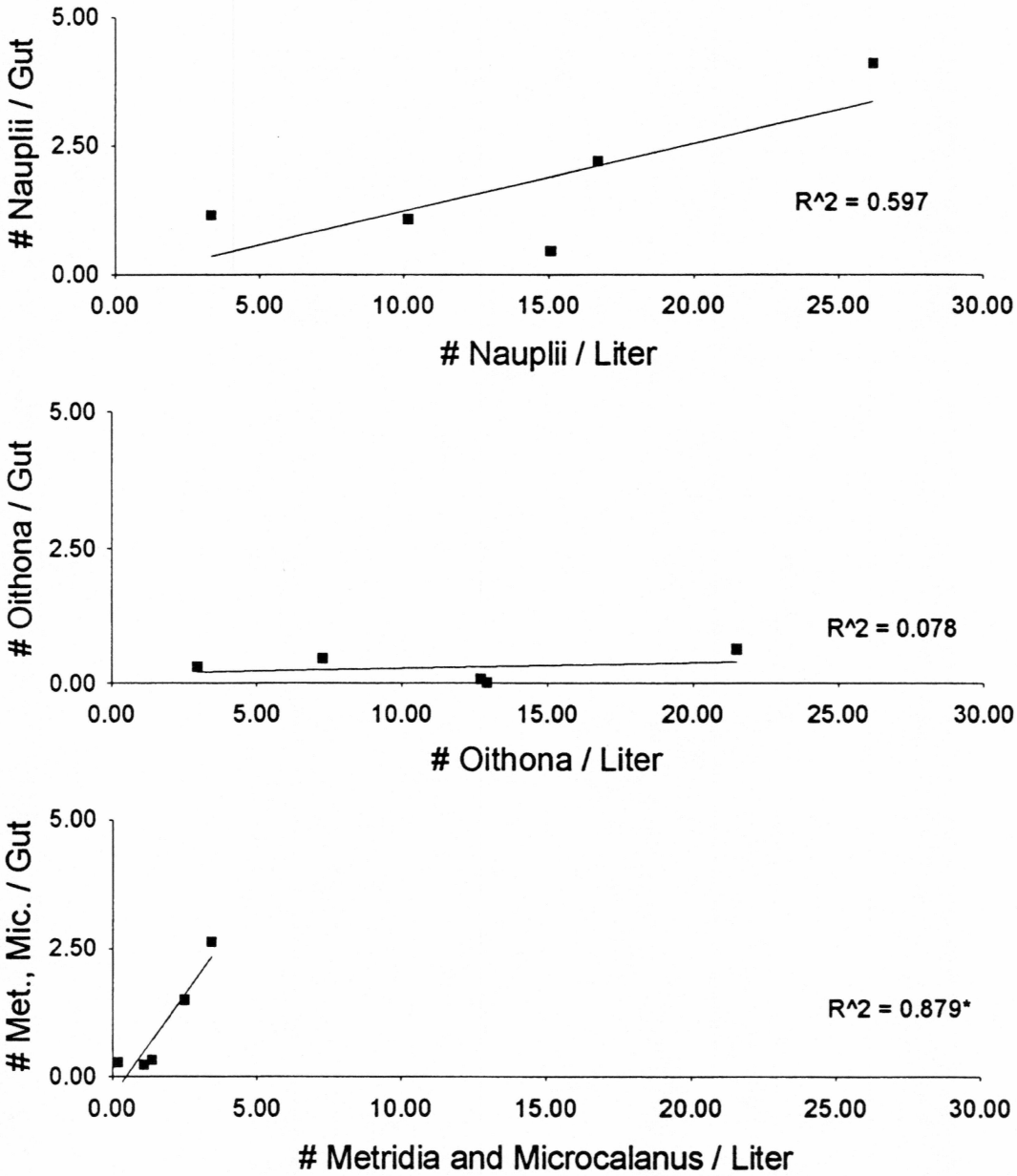


**Figure 16.** Functional response relationships between total nauplii ingested and in the water column, *Oithona similis* nauplii ingested and in the water column, and *Metridia* spp. and *Microcalanus* spp. nauplii ingested and in the water column at station 1, April 20, 1992, in the oceanic domain of the Bering Sea. The star designates significance at $p \leq 0.05$.

There is no relationship ($R^2$ = 0.078) between number of *Oithona similis* in the water column and in the larval guts. However, as the number of *Metridia* sp. and *Microcalanus* sp. increases, walleye pollock larvae consume considerably more of these nauplii (Figure 16).

The mean size of copepod nauplii in the larval diet was greater than that of nauplii in the environment. There was a significant difference between total length of nauplii in the diet and in the water column for *Metridia* sp., *Microcalanus* sp., and *Oithona similis* (Figure 17, Table 8) (T-test, $p<0.01$). No size differences were found for *Pseudocalanus* sp. nauplii (Figure 17).

Larval Dry Weight and Condition

A total of 209 larval dry weights, 166 at station 1 and 43 at station 2, were measured. The mean larval dry weight at station 1 increased with increasing larval length (Figure 18). Fulton's condition factor is a ratio and therefore correlated with its denominator (McGurk, 1985). This covariation with length precluded comparisons of condition between size classes (Frank and McRuer, 1989).

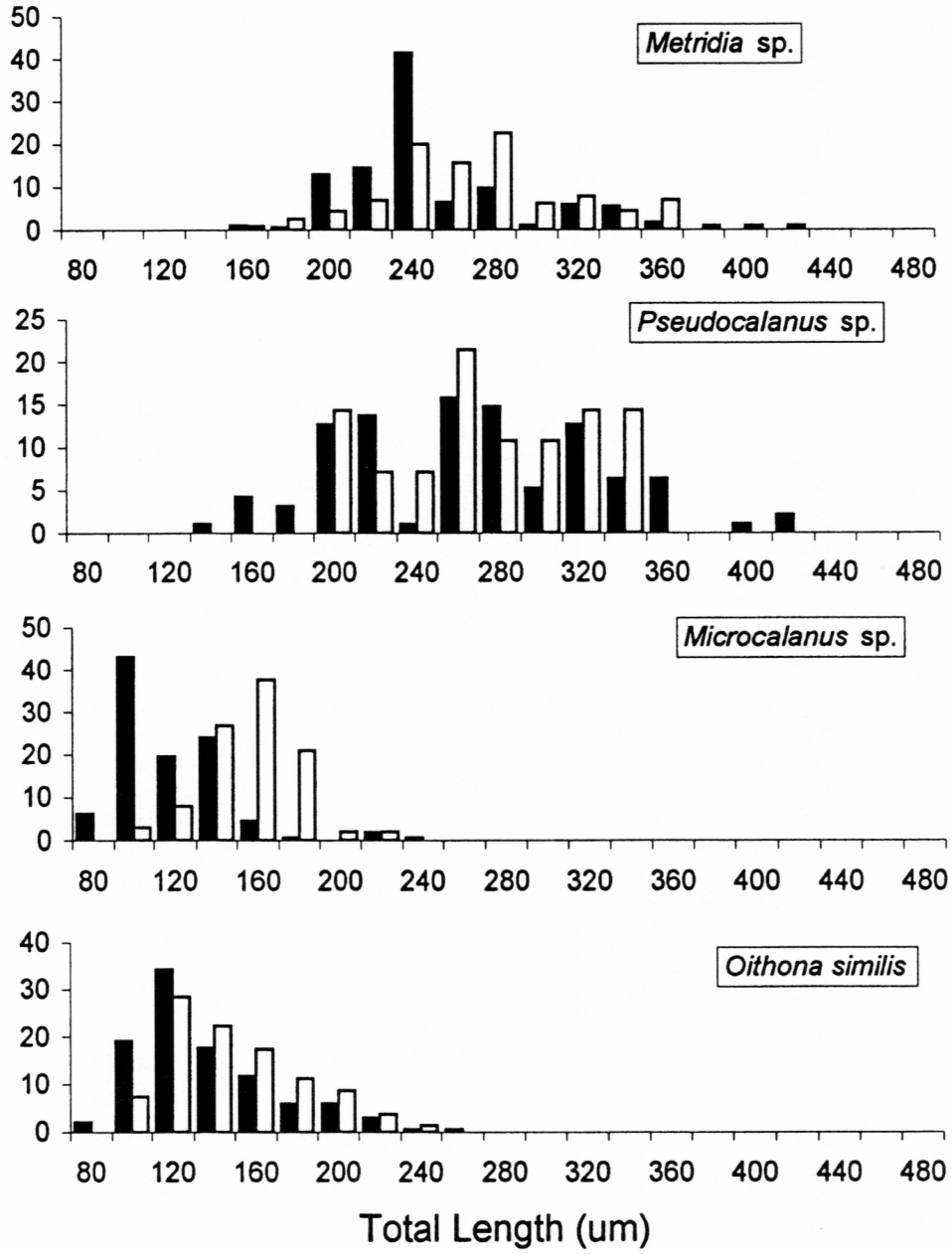


**Figure 17.** Comparisons of size frequency distributions in the diet of larval walleye pollock ( □ ) and in the environment ( ■ ) at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

**Table 8.** Comparison of mean length of copepod nauplii in the larval diet and in the environment at station 1, April 20, 1992, in the oceanic domain of the Bering Sea. Standard deviations are within parentheses.

| | *Metridia* spp. | *Pseudocalanus* spp. | *Microcalanus* spp. | *Oithona similis* |
|---|---|---|---|---|
| Environment | 258.97 (41.25) | 277.56 (62.53) | 130.44 (23.02) | 141.37 (33.36) |
| Range | (176;379) | (141;430) | (86;254) | (90;260) |
| Diet | 283.95 (48.92) | 284.22 (46.11) | 164.75 (22.25) | 154.44 (32.57) |
| Range | (162;433) | (213;358) | (109;221) | (100;250) |

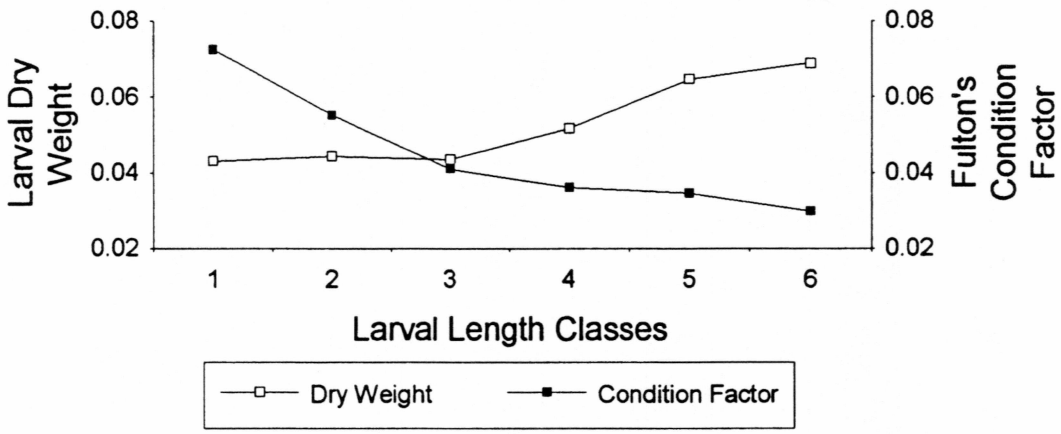


**Figure 18.** Mean larval dry weight and Fulton's condition factor by larval size class for station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

Pollock larvae at 30 m depth had the steepest increase of dry weight with increasing length, meanwhile larvae at 70 m revealed the weakest slope (Figure 19a). A comparison of regression slopes of standard length versus larval dry weight revealed that the slopes at 10 and 30 m depth were significantly steeper than at 70 m depths (ANCOVA, $p' \leq 0.015$).

Fulton's condition index decreased with increasing larval length at all depths (Figure 19b). The condition of larval length class 2 (4.0 - 4.49 mm) at all depths was approximately 0.055, except for larvae at 30 m depth (0.038). However, in length class 6 (6.0 - 6.49 mm) the condition of all larvae dropped to approximately 0.035, with the exception of larvae at 70 m depths (0.02).

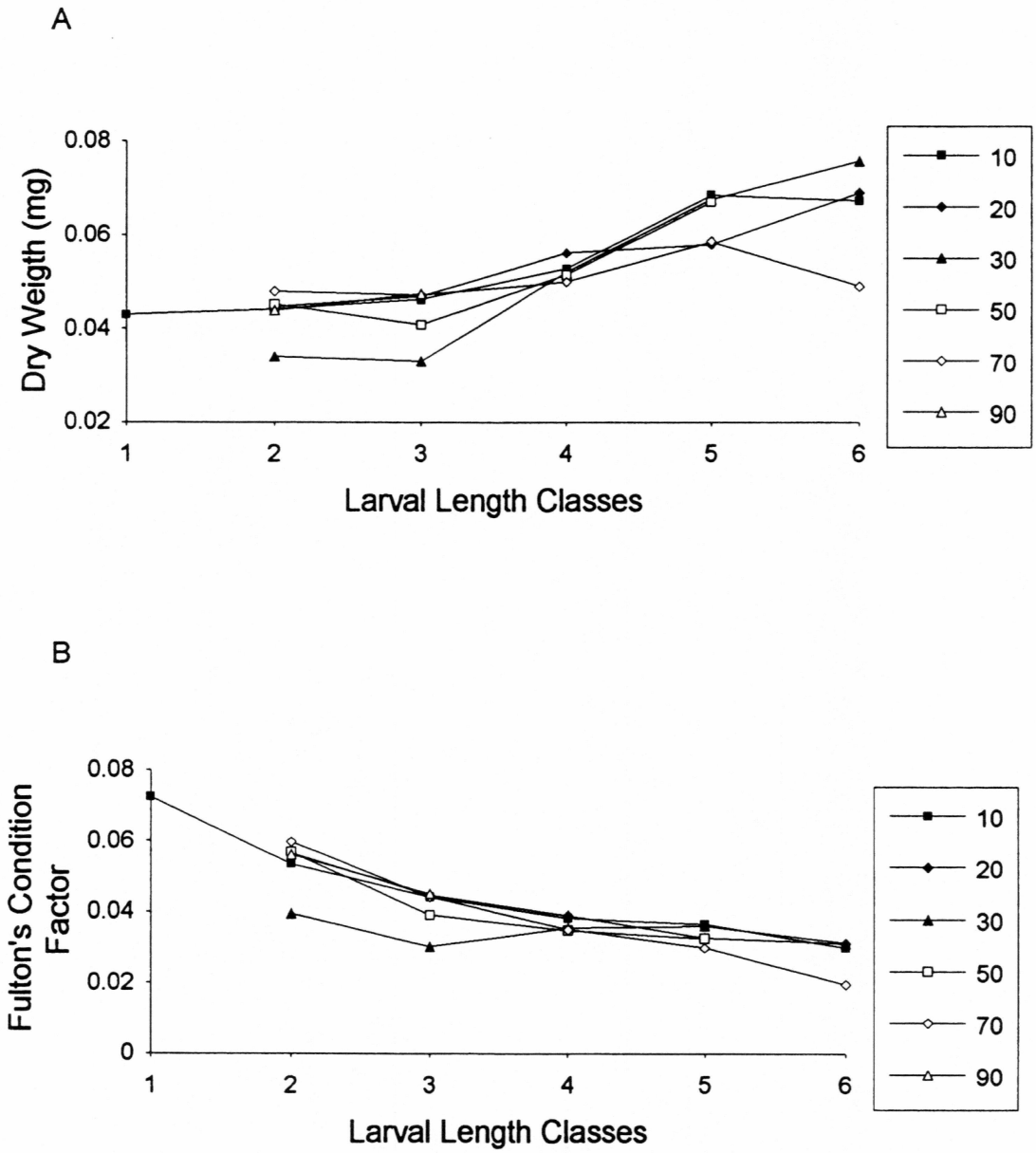


**Figure 19.** Larval dry weight and Fulton's condition factor by depth and size class at station 1, April 20, 1992 in the oceanic domain of the Bering Sea.

## DISCUSSION

Copepod nauplii are the most important prey item for walleye pollock larvae (Clarke, 1984; Dagg et al., 1984; Nishiyama et al., 1986; Kendall et al., 1987; Sterritt, 1989; Pritchett, 1990; Canino et al., 1991; Kendall and Nakatani, 1992). Dagg et al. (1984) found 93% of the larval prey in the Bering Sea to be copepod nauplii, and 6% copepod eggs. Copepod nauplii and eggs also comprised the bulk of the diet of larvae in Shelikof Strait, averaging 93% and 5.5% of the total prey, respectively (Canino et al., 1991). Copepod nauplii accounted for 64.6% of all the prey items consumed by larval walleye pollock in Auke Bay (Sterritt, 1989). In this study copepod nauplii and eggs were the most common food items comprising 78.7% and 19.5%, respectively. The importance of copepod nauplii increased with depth from 58.1% at 10 m depth to 91.7% at 50 m depth. Copepod eggs were a consistent prey item in larval diet at 10 and 20 m depth, accounting for 17% of prey items. However, there is controversy about the digestibility of copepod eggs by larval fish (Paul, pers. comm.).

The vertical distribution of larval fish has been hypothesized to ensure an optimal overlap with their prey (Lasker, 1978; Lafontaine and Gascon, 1989). In a vertically variable prey environment, the position of

the larvae in the water column will determine the prey concentrations they encounter. The aggregation of predators on patches where prey is more abundant might be explained by a behavioral pattern, in which capture success leads to apportionment of time to further feeding while failure leads to non-feeding, and thus, searching behavior. This behavior pattern has been termed the "numerical response" of predators to density of prey (Valiela, 1984).

In Auke Bay, Alaska, walleye pollock larvae frequently aggregated during the day at depths with highest prey concentrations (Pritchett and Haldorson et al., 1989). Vertical distribution of larval walleye pollock in the Bering Sea also coincided with naupliar distribution (Clarke, 1984; Dagg et al., 1984; Nishiyama et al., 1986). In the present study the highest observed density of larval walleye pollock and copepod nauplii coincided at 30 m depths. Overall densities of copepod nauplii ranged from 3.7 $l^{-1}$ at 10 m to 27.2 $l^{-1}$ at 30 m and were consistent with densities reported from other studies. For example, Dagg et al. (1984) found peak densities of 15 - 20 nauplii $l^{-1}$ in the southeastern Bering Sea (mean = 7.5 nauplii $l^{-1}$) and Clarke observed maximum abundances of 41.17 nauplii $l^{-1}$ (mean (1980) = 6.6; mean (1981) = 6.9 nauplii $l^{-1}$). In the Gulf of Alaska prey was available at concentrations of 12.5 to 26 nauplii $l^{-1}$ (Canino et al., 1991) and exceeding 30 nauplii $l^{-1}$ (Incze et al., 1990).

However, nauplii abundance and taxa composition change over time (Clarke 1984; Paul et al., 1991). In Auke Bay, nauplii concentrations were 5 - 15 $l^{-1}$ during April but were frequently above 20 $l^{-1}$ in May and June (Paul et al., 1991). In the eastern Bering Sea, Clarke (1984) found a similar trend, namely an increase in nauplii abundance between April and June in all hydrographic domains. In the present study, sampling occurred in mid-April prior to spring stratification. It is likely that prey abundance and taxonomic composition changed with progression of the annual production cycle.

However, at the time and location of sampling, the 30 m depth stratum seemed to provide the best physiological and ecological conditions for walleye pollock larvae. Nishiyama et al. (1986) defined that portion of the water column most advantageous for survival and growth of the early larvae as the "nursery layer".

Successful feeding by walleye pollock larvae is a function of factors such as temperature, light and prey abundance (Paul, 1983). Water temperature had a marked effect on the feeding incidence in pollock larvae (Paul, 1983); larvae in colder water were less successful in capturing prey. In the laboratory, walleye pollock larvae avoided cold water and larvae entrained in cold water below the thermocline became immediately torpid (Olla and Davis, 1990). At station 1, water in the

upper 20 m was homogeneously cold. Below 20 m, the temperature increased with increasing depth. Walleye pollock larvae below 20 m depth, therefore, encountered better thermal conditions than those larvae in shallower depths. Walleye pollock larvae are visual feeders with a luminance threshold for feeding of about 0.4 lux (Paul, 1983). In the southeastern Bering Sea this light level is available to approximately 30 m depth (Olla and Davis, 1990).

Pollock larvae in the present study were highly concentrated in the upper 30 m of the water column. Larval abundance peaked significantly at 30 m depth. At this depth stratum larvae experienced optimal conditions with warmer water, light levels sufficient for feeding success, and the peak of prey concentration.

The average length of preserved larval walleye pollock changed with respect to sampling depth, larvae being significantly smallest at 90 m (4.3 mm) and largest at 30 m (5.3 mm) depth. Nishiyama et al. (1986) observed the same decrease in larval length with increasing depth. The size of newly hatched, net-caught, unpreserved walleye pollock larvae is around 4.0 mm (Clarke, 1984; Kendall et al., 1987; Kim, 1988). In Shelikof Strait larvae hatch at mid-depth (150 - 250 m) and float toward the surface (Kim, 1988). Thus, the small fish at 90 m depth might represent freshly hatched larvae. However, no larvae with more than

residual yolk were observed. Therefore, it might be concluded that the walleye pollock larvae at the deeper depth strata did not successfully initiate feeding and were sinking out of the water column. Walleye pollock larvae are negatively buoyant and therefore need to actively swim to remain at one depth in the water column (Davis and Olla, 1992). Walleye pollock larvae fed on lipid-deficient prey had reduced growth, gas-bladder size, and survival (Davis and Olla, 1992). These underfed larvae sank in a head-down orientation, which probably increased their sinking speeds. In the present study larval dry weight increased with increasing length at all depths, except for larvae at 70 m. In addition, larvae at 70 m depth seemed to have a lower condition factor in the highest larval length classes. These observations support the theory that underfed pollock larvae slowly sank out of the "nursery layer" of the water column.

However, no correction was made for larval shrinkage due to net capture and preservation. The amount of shrinkage is dependent on the time in the net, size of the larva, and type of preservative used (Theilacker and Porter, 1993). In the present study, walleye pollock larvae were collected from six depths, sampling two depths per cast and starting with the deeper stratum. Larvae sampled from the first depth of each cast were smaller than those from the second depth of the same

cast, suggesting that the longer time spent in the net resulted in higher shrinkage in length.

Fish larvae discriminate among prey organisms and actively select their prey from among a wide variety of items they encounter (Peterson and Ausubel, 1984; Jenkins, 1987; Pryor and Epifanio, 1993). Selectivity may be influenced by encounter rates, prey visibility, capturability, fine-scale distribution of predator and prey, and preferences of predator (Jenkins, 1987). Visibility characteristics of the prey could include size, shape, contrast, color, and movement (Jenkins, 1987; Pryor and Epifanio, 1993). Larvae of Atlantic mackerel (*Scomber scombrus*) selected copepod nauplii by species and fed predominately on *Temora longicornis* nauplii (Peterson and Ausubel, 1984). *T. longicornis* may be more visible due to a pair of long caudal spines even though length and width of the three most common nauplii species were approximately equal. In addition, *T. longicornis* nauplii are much more active than other occurring species therefore attracting the predators attention more readily. Larval weakfish (C*ynoscion regalis*) in laboratory experiments displayed feeding selectivity that was influenced by prey size, swimming speed and characteristics, and prey abundance; the selectivity patterns changed ontogenetically (Pryor and Epifanio, 1993).

Previous studies on the feeding of first-feeding larval walleye

pollock have not directly enumerated individual prey taxa and stages. Indirect evidence has been used to determine the species composition of the prey field but no direct identification of the copepod nauplii was undertaken. In the Gulf of Alaska the length- and width-frequency distribution of nauplii indicated that *Pseudocalanus* spp. and *Oithona* spp. were the most likely prey taxa present in guts (Kendall et al., 1987). Clarke (1984) observed that the increase of *Pseudocalanus* spp. copepodite biomass matched that of the nauplii biomass and concluded that *Pseudocalanus* spp. were a likely source of the prey field for walleye pollock larvae in the Bering Sea. In this investigation, copepod nauplii were identified to the lowest possible taxa. *Oithona similis* was the most abundant taxon, constituting 79% of the microzooplankton. Both *Oithona similis* and *Metridia* sp. had maximum abundances at 30 m depths of 21.5 nauplii $l^{-1}$ and 3.1 nauplii $l^{-1}$, respectively. *Microcalanus* sp. were found at highest abundances of 3.1 nauplii $l^{-1}$ at 90 m depths. *Pseudocalanus* spp. nauplii occurred at low abundances at all depths sampled .

In this study, walleye pollock larvae significantly selected for and against certain copepod taxa and stages. The most abundant prey items in the larval diet were copepod nauplii of *Metridia* sp. and *Microcalanus* sp.; positive selection occurred for both species. *Oithona similis* nauplii

were by far the most abundant species in the environment. However, they did not predominate in the diet of walleye pollock larvae. *Pseudocalanus* sp. nauplii occurred at all depths at less than 1 $l^{-1}$, except for 20 m (1.3 $l^{-1}$) in the water column. No selectivity pattern could be established, probably due to their low abundance.

Cyclopoid copepods like *Oithona similis* are known to have different swimming behaviors than calanoid copepods. Cyclopoids tend to swim in a jerky fashion due to the movement of their cephalic appendages, while calanoid copepods swim in a smoother pattern (Pryor and Epifanio, 1993). The irregular swimming pattern of cyclopoids may serve as a visual attractant for some foraging fish larvae (Govoni et al., 1983). However, in this study calanoid copepods were chosen over cyclopoids. The smooth swimming style of calanoid copepods may be more predictable, thereby facilitating their capture.

Within the group of calanoid copepods walleye pollock larvae preferred *Metridia* sp. and *Microcalanus* sp. nauplii over *Pseudocalanus* sp. nauplii. Body length and width of *Metridia* sp. and *Pseudocalanus* sp. nauplii were approximately equal, so size can be excluded as a distinguishing characteristic. However, *Pseudocalanus* sp. nauplii have extremely vigorous escape responses that might prevent their successful capture (Peterson and Ausubel, 1984). In addition, enhanced prey

motion increases the reactive distance of visual predators. Both, *Pseudocalanus* sp. (Peterson and Ausubel, 1984) and *Oithona similis* (Buskey et al., 1993) nauplii appear to be relatively inactive organisms with long periods of non-swimming activity that therefore might not be spotted as readily.

Both *Microcalanus* sp. and *Metridia* sp. are calanoid copepods. However, *Metridia* sp. nauplii range in size from ca. 150 µm to 400 µm total length, meanwhile *Microcalanus* sp. nauplii are distinctly smaller, reaching approximately 80 - 250 µm total length. Thus, prey size cannot be the common selectivity characteristic for *Metridia* sp. and *Microcalanus* sp. nauplii.

The mean size of *Metridia* sp., *Microcalanus* sp. and *Oithona similis* nauplii in the larval diet was significantly greater than those present in the water column. Since, pollock larvae are visual predators, for any given visual acuity, larger prey will be detected at further distances, resulting in the consumption of proportionately more large than small prey (Valiela, 1984).

Both *Microcalanus* sp. and *Oithona similis* nauplii in the water column revealed trends in length with depth, being smaller at deeper depths. *Microcalanus* sp. nauplii had a weighted mean length of 150 µm, that was still smaller than their mean length of 160 µm in the larval

diet. Thus, even though foraging walleye pollock larvae in the upper 50 m of the water column probably encountered relatively more larger *Microcalanus* spp. nauplii, they still selected for larger sizes. The weighted mean length for *Oithona similis* nauplii in the environment was 170 µm and therefore higher than the mean size in the larval diet.

However, prey size does not explain the selection for *Metridia* spp. and *Microcalanus* spp. nauplii. In previous studies fish larvae selected strongly for prey size, but consumed prey of similar size relatively indiscriminantly (Theilacker and Dorsey, 1980). In the present study I found the opposite, namely that fish larvae selected for prey size if the prey taxon was suitable.

Suboptimal food levels may regulate survival of larval fish through reduced growth rates and prolonged stage duration, affecting especially first-feeding larvae (Houde, 1987). High densities of prey organisms, on the other hand, may enhance growth rates and increase survival of larval fish. Clarke (1984) suggested that differences in larval pollock growth rates in the Bering Sea were related to differences in food abundance. In Shelikof Strait, gut fullness and RNA/DNA values of walleye pollock larvae were positively related to copepod nauplii density (Canino et al., 1991). In early spring, optimal feeding conditions occurred in a large patch of walleye pollock larvae.

In the present study, larval dry weight increased with increasing larval length at all depth strata, with exception of 70 m depth. Fulton's condition factor was used to describe the nutritional status of larval walleye pollock at depth. This factor typically covaries with standard length, thereby preventing comparison of condition between different-sized larvae (Koslow et al., 1985). In addition, the assumption of isometric growth (b = 3) may be incorrect, as the weight-length exponent in larval fishes is often closer to 4 (McGurk, 1985). In contrast, Frank and McRuer (1989) demonstrated that an empirically derived exponent b for field-caught haddock (*Melanogrammus aeglefinus*) larvae was very close to 3. However, larval walleye pollock in the present study occurred in a very narrow size range from 3.5 to 6.5 mm. Fulton' s condition factor decreased with increasing larval length up to 4.9 mm (larval length class 3). This initial decline of the condition factor might be explained by an increase in larval length based only on yolk protein. For larval length classes 3 to 6 (5.0 to 6.5 mm) the condition stayed approximately constant at all depth strata. Walleye pollock larvae are shown to vertically migrate (Haldorson et al, 1990), so that long-term responses, such as larval dry weight and condition, should not vary with respect to their vertical position. However, the condition factor for larvae at 70 m depth was lower in the higher length classes than for the according larval

length classes at all other depth strata, indicating that walleye pollock larvae at 70 m may no longer be able to ascend to shallower depths. Those larvae might represent underfed fish that slowly sank out of the water column. This hypothesis is supported by the negative growth in dry weight for larvae at 70 m depth.

In the present study, I analyzed vertical patchiness. Feeding intensity and concentration of copepod nauplii were depth dependent and highest at 30 m depths. Feeding incidence of walleye pollock larvae peaked at 30 m depth (97.5%). At all other depths no more than 70% of larvae were observed feeding. The overall percentage of larvae feeding was only 56.7 % and was therefore far below values observed in other studies. For example, Nishiyama et al. (1986) observed 77 - 98% feeding walleye pollock larvae. In the southeastern Bering Sea, 95% of the larval walleye pollock had food in their guts (Dagg et al., 1984; Clarke, 1984).

The numbers of prey items ingested ranged from 2 items in the surface stratum to a peak value of 4.6 items per larval gut at 30 m depth. This value is somewhat below that of other studies. Nishiyama et al. (1986) observed 4.2 - 6.7 food items in 3.5 - 5.5 mm larvae and Clarke (1984) found 6.1 items per gut. In the Gulf of Alaska, the mean number of prey per walleye pollock larvae ranged from 2.25 to 9.32 (Canino et

al., 1991). In Auke Bay the mean number of prey items for larvae hatched prior to the herbivorous copepod maximum was 3.7, and 7.0 for larvae that occurred simultaneously with maximum densities of herbivorous copepods, respectively (Sterritt, 1989).

The estimates of daily ration for walleye pollock larvae at 30 m depth were considerably higher than for larvae at all other depths, ranging from 12.9 prey items $d^{-1}$ with a gut passage time of 5 h at 5.5°C to 10.57 prey items $d^{-1}$ with a gut passage time of 6.1 h at 6.4°C. For the temperature range encountered at station 1, no gut passage time estimates were available. However, due to the low temperature at station 1, the gut passage time might be longer and the daily ration estimates still too high. Also, the daily rations might be overestimated because copepod eggs, in spite of the controversy about their energetic value, were included in the calculation. However, the estimates for daily ration in this study were far below values from other studies. Dagg et al. (1984) reported that each walleye pollock larvae in the southeastern Bering Sea was estimated to ingest 18.3 nauplii $d^{-1}$. In Shelikof Strait, larval walleye pollock in late April had food rations of 16.9 (inside a larval patch) and 7.2 (out of the larval patch) nauplii $d^{-1}$ (Canino et al., 1991), and of approximately 27 $d^{-1}$ in mid-May. These food ration estimates are considerably lower than estimates derived from bioenergetic rates

measured in the laboratory. Yamashita and Bailey (1989) calculated that walleye pollock larvae require up to 76 nauplii $d^{-1}$ for metabolism and growth.

In summary, I found that the 30 m depth stratum was the most advantageous vertical position for pollock larvae. However, overall feeding incidence, numbers of items ingested, and estimated daily rations suggest poor foraging success compared to previous studies conducted on larval pollock feeding ecology (Clarke, 1984; Nishiyama et al., 1986; Sterritt, 1989).

In addition, the larvae in this study represented first-feeding larvae that are very sensitive to prey deprivation. Poor foraging success may result in mortality due to starvation or increased vulnerability to predation. Based on the condition factor and dry weight, the larvae that were found at 70 and 90 m depths may represent starving larvae that were sinking out of the "nursery layer". Walleye pollock larvae in the present study seemed to experience poor foraging conditions at a developmental stage that has low resistance to suboptimal feeding.

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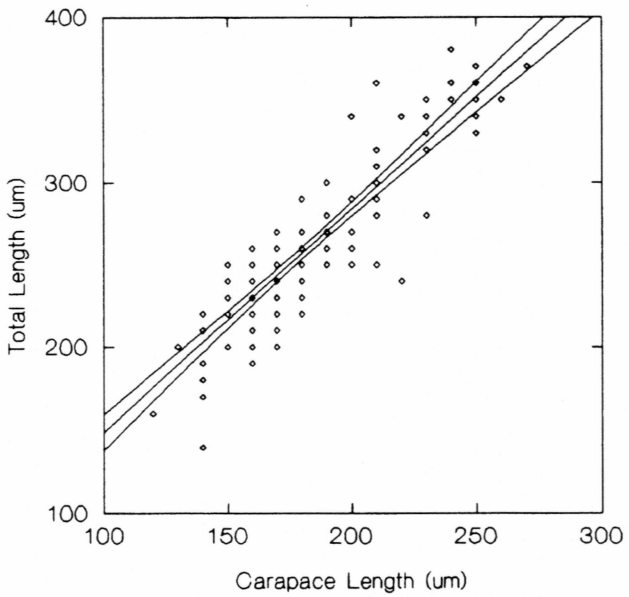
## APPENDIX

**Appendix 1.** Conversion equation for *Metridia* spp, *Pseudocalanus* spp., and *Microcalanus* spp. nauplii total length

Regression of total length on carapace length for *Metridia* spp. with 95% confidence interval:



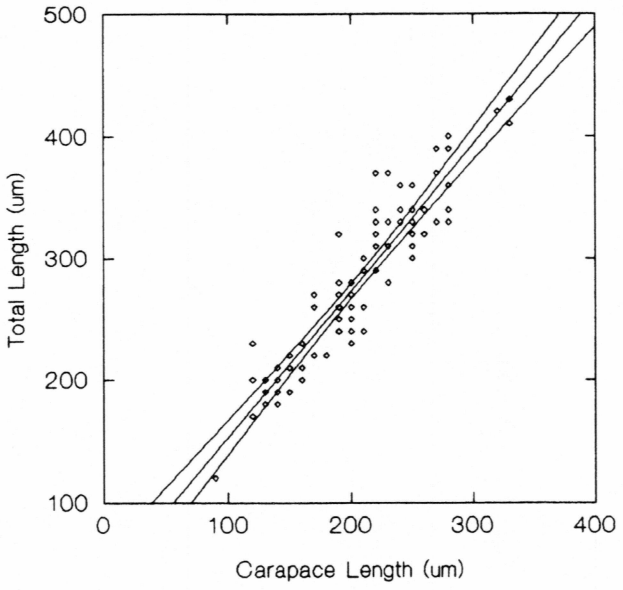

$R^2 = 0.805$

The model for the linear regression is:

$$TL = 13.666 + 1.352 * CL$$

**Appendix 1 (contd.).**

Regression of total length on carapace length for *Pseudocalanus* spp. nauplii with 95% confidence interval:



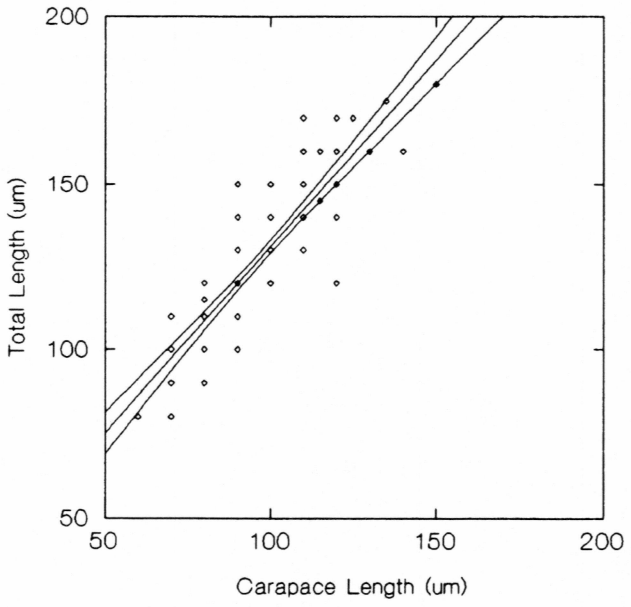

$R^2 = 0.872$

The model for the linear regression is:

$$TL = 32.454 + 1.204 * CL$$

**Appendix 1 (contd.).**

Regression of total length on carapace length for *Microcalanus* spp. nauplii with 95% confidence interval (after removal of four outlier variates):




$R^2 = 0.752$

The model for the linear regression is:

$$TL = 19.169 + 1.119 * CL$$

**Appendix 2.** Counts of naupliar stages in larval diet by depth and taxa at station 1, April 20, 1994, in the oceanic domain of the Bering Sea

| **Stages** | **1** | **2** | **3** | **4** | **5** | **6** |
|---|---|---|---|---|---|---|
| **Depth** | *Metridia* spp. | | | | | |
| 10 | N/D | N/D | 1 | 8 | 0 | 2 |
| 20 | N/D | N/D | 0 | 4 | 0 | 0 |
| 30 | N/D | N/D | 2 | 52 | 8 | 6 |
| 50 | N/D | N/D | 1 | 15 | 9 | 6 |
| 70 | N/D | N/D | 0 | 1 | 0 | 1 |
| | *Pseudocalanus* spp. | | | | | |
| 10 | N/D | N/D | 0 | 0 | 7 | 1 |
| 20 | N/D | N/D | 0 | 4 | 2 | 0 |
| 30 | N/D | N/D | 0 | 5 | 2 | 1 |
| 50 | N/D | N/D | 0 | 4 | 2 | 0 |
| 70 | N/D | N/D | 0 | 0 | 0 | 0 |
| | *Microcalanus* spp. | | | | | |
| 10 | 0 | 0 | 1 | 0 | 2 | 0 |
| 20 | 0 | 0 | 3 | 5 | 3 | 0 |
| 30 | 0 | 2 | 22 | 15 | 11 | 2 |
| 50 | 0 | 1 | 9 | 17 | 7 | 0 |
| 70 | 0 | 0 | 0 | 1 | 0 | 0 |
| | *Oithona similis* | | | | | |
| 10 | 0 | 7 | 5 | 3 | 4 | 0 |
| 20 | 5 | 8 | 7 | 5 | 1 | 0 |
| 30 | 5 | 11 | 13 | 3 | 1 | 1 |
| 50 | 1 | 2 | 1 | 0 | 0 | 0 |
| 70 | 0 | 0 | 0 | 0 | 0 | 0 |

(N/D = not distinguishable)

| 10 m Depth: | % FO | | | | | | %N | | | | | | %VOL | | | | | | %IRI | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Size Classes | 1/2 | 3 | 4 | 5 | 6 | Total | 1/2 | 3 | 4 | 5 | 6 | Total | 1/2 | 3 | 4 | 5 | 6 | Total | 1/2 | 3 | 4 | 5 | 6 | Total |
| N | 6 | 10 | 11 | 10 | 5 | 42 | 6 | 10 | 11 | 10 | 5 | 42 | 6 | 10 | 11 | 10 | 5 | 42 | 6 | 10 | 11 | 10 | 5 | 42 |
| Invertebrate Eggs | 66.7 | 80.0 | 45.5 | 50.0 | 80.0 | 61.9 | 40.0 | 62.5 | 25.0 | 33.3 | 38.9 | 36.6 | 42.4 | 70.4 | 41.3 | 39.7 | 46.0 | 48.5 | 59.6 | 91.3 | 39.4 | 53.1 | 48.4 | 68.3 |
| Metridia spp. | 33.3 | 10.0 | 36.4 | 40.0 | 0.0 | 26.2 | 30.0 | 6.3 | 12.5 | 26.7 | 0.0 | 12.9 | 23.3 | 10.2 | 13.3 | 21.7 | 0.0 | 13.0 | 19.3 | 1.4 | 12.3 | 28.1 | 0.0 | 8.8 |
| Pseudocalanus spp. | 16.7 | 20.0 | 9.1 | 20.0 | 0.0 | 14.3 | 10.0 | 18.8 | 3.1 | 20.0 | 0.0 | 8.6 | 11.4 | 15.4 | 3.3 | 30.8 | 0.0 | 12.0 | 3.9 | 5.9 | 0.8 | 14.8 | 0.0 | 3.8 |
| Microcalanus spp. | 0.0 | 0.0 | 9.1 | 0.0 | 20.0 | 4.8 | 0.0 | 0.0 | 3.1 | 0.0 | 11.1 | 3.2 | 0.0 | 0.0 | 1.5 | 0.0 | 4.7 | 1.3 | 0.0 | 0.0 | 0.6 | 0.0 | 2.3 | 0.3 |
| Unid. Calanoids | 33.3 | 10.0 | 27.3 | 0.0 | 80.0 | 23.8 | 20.0 | 6.3 | 18.8 | 0.0 | 27.8 | 15.1 | 12.7 | 4.0 | 13.4 | 0.0 | 36.3 | 12.4 | 11.8 | 0.9 | 11.5 | 0.0 | 36.5 | 8.5 |
| Oithona similis | 16.7 | 0.0 | 45.5 | 10.0 | 60.0 | 23.8 | 20.0 | 0.0 | 31.3 | 13.3 | 16.7 | 18.3 | 10.1 | 0.0 | 25.4 | 7.7 | 10.5 | 11.9 | 5.4 | 0.0 | 33.7 | 3.1 | 11.6 | 9.3 |
| Others | 0.0 | 10.0 | 18.2 | 10.0 | 20.0 | 11.9 | 0.0 | 6.3 | 6.3 | 6.7 | 5.6 | 5.4 | 0.0 | 0.1 | 1.8 | 0.0 | 2.5 | 1.0 | 0.0 | 0.5 | 1.9 | 1.0 | 1.2 | 1.0 |
| 20 m Depth: | | | | | | | | | | | | | | | | | | | | | | | | |
| N | 14 | 10 | 10 | 11 | 0 | 45 | 14 | 10 | 10 | 11 | 0 | 45 | 14 | 10 | 10 | 11 | 0 | 45 | 14 | 10 | 10 | 11 | 0 | 45.0 |
| Invertebrate Eggs | 53.8 | 70.0 | 40.0 | 70.0 | 0.0 | 53.3 | 42.1 | 47.1 | 16.1 | 35.0 | 0.0 | 32.2 | 71.1 | 62.9 | 36.4 | 46.1 | 0.0 | 53.7 | 76.1 | 75.0 | 31.0 | 53.4 | 0.0 | 63.9 |
| Metridia spp. | 0.0 | 0.0 | 20.0 | 0.0 | 0.0 | 4.4 | 0.0 | 0.0 | 12.9 | 0.0 | 0.0 | 4.6 | 0.0 | 0.0 | 17.4 | 0.0 | 0.0 | 4.3 | 0.0 | 0.0 | 9.0 | 0.0 | 0.0 | 0.6 |
| Pseudocalanus spp. | 7.7 | 20.0 | 20.0 | 10.0 | 0.0 | 13.3 | 5.3 | 11.8 | 6.5 | 5.0 | 0.0 | 6.9 | 7.2 | 14.3 | 7.3 | 10.9 | 0.0 | 9.8 | 1.2 | 5.1 | 4.1 | 1.5 | 0.0 | 3.1 |
| Microcalanus spp. | 0.0 | 10.0 | 50.0 | 10.0 | 0.0 | 15.6 | 0.0 | 5.9 | 25.8 | 10.0 | 0.0 | 12.6 | 0.0 | 1.2 | 13.3 | 4.2 | 0.0 | 4.7 | 0.0 | 0.7 | 28.9 | 1.3 | 0.0 | 3.8 |
| Unid. Calanoids | 7.7 | 40.0 | 10.0 | 20.0 | 0.0 | 17.8 | 10.5 | 23.5 | 3.2 | 10.0 | 0.0 | 10.3 | 3.0 | 18.0 | 1.8 | 6.7 | 0.0 | 6.8 | 1.3 | 16.2 | 0.7 | 3.1 | 0.0 | 4.3 |
| Oithona similis | 30.8 | 20.0 | 30.0 | 60.0 | 0.0 | 33.3 | 36.8 | 11.8 | 35.5 | 40.0 | 0.0 | 32.2 | 17.2 | 3.6 | 23.8 | 32.1 | 0.0 | 20.3 | 20.8 | 3.0 | 26.3 | 40.7 | 0.0 | 24.4 |
| Others | 7.7 | 0.0 | 0.0 | 0.0 | 0.0 | 2.2 | 5.3 | 0.0 | 0.0 | 0.0 | 0.0 | 1.1 | 1.4 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 30 m Depth: | | | | | | | | | | | | | | | | | | | | | | | | |
| N | 7 | 10 | 10 | 9 | 4 | 40 | 7 | 10 | 10 | 9 | 4 | 40 | 7 | 10 | 10 | 9 | 4 | 40 | 7 | 10 | 10 | 9 | 4 | 40.0 |
| Invertebrate Eggs | 57.1 | 40.0 | 0.0 | 30.0 | 25.0 | 30.0 | 19.4 | 12.2 | 0.0 | 12.5 | 7.7 | 10.6 | 32.3 | 33.5 | 0.0 | 22.2 | 16.3 | 21.6 | 26.2 | 13.3 | 0.0 | 8.2 | 4.1 | 8.0 |
| Metridia spp. | 57.1 | 80.0 | 70.0 | 100 | 100 | 82.5 | 25.8 | 26.5 | 41.7 | 35.7 | 46.2 | 34.3 | 34.2 | 35.9 | 60.0 | 39.3 | 53.2 | 44.0 | 30.4 | 36.3 | 58.5 | 59.1 | 66.5 | 53.5 |
| Pseudocalanus spp. | 28.6 | 0.0 | 0.0 | 40.0 | 25.0 | 17.5 | 6.5 | 0.0 | 0.0 | 8.9 | 3.8 | 4.0 | 8.1 | 0.0 | 0.0 | 10.6 | 3.7 | 6.9 | 3.7 | 0.0 | 0.0 | 6.1 | 1.3 | 1.6 |
| Microcalanus spp. | 57.1 | 90.0 | 70.0 | 60.0 | 75.0 | 72.5 | 19.4 | 32.7 | 25.0 | 26.6 | 19.2 | 26.3 | 5.5 | 13.5 | 11.9 | 9.1 | 8.3 | 9.7 | 12.6 | 30.2 | 21.2 | 17.8 | 14.2 | 21.6 |
| Unid. Calanoids | 71.4 | 30.0 | 20.0 | 10.0 | 50.0 | 52.5 | 19.4 | 6.1 | 8.3 | 1.8 | 15.4 | 16.2 | 14.8 | 4.4 | 11.4 | 2.0 | 12.0 | 7.8 | 21.6 | 2.3 | 3.2 | 0.3 | 9.4 | 10.4 |
| Oithona similis | 42.9 | 70.0 | 50.0 | 50.0 | 25.0 | 32.5 | 9.7 | 22.4 | 25.0 | 12.5 | 7.7 | 8.6 | 5.2 | 12.7 | 16.7 | 8.7 | 6.5 | 10.0 | 5.6 | 17.9 | 17.1 | 8.4 | 2.4 | 5.0 |
| Others | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 50 m Depth: | | | | | | | | | | | | | | | | | | | | | | | | |
| N | 7 | 11 | 14 | 5 | 0 | 37 | 7 | 11 | 14 | 5 | 0 | 37 | 7 | 11 | 14 | 5 | 0 | 37 | 7 | 11 | 14 | 5 | 0 | 37.0 |
| Invertebrate Eggs | 14.3 | 9.1 | 14.3 | 16.7 | 0.0 | 13.5 | 16.7 | 4.2 | 5.0 | 5.0 | 0.0 | 6.3 | 18.9 | 9.1 | 7.6 | 8.7 | 0.0 | 10.2 | 6.1 | 1.2 | 1.5 | 1.6 | 0.0 | 2.4 |
| Metridia spp. | 14.3 | 63.6 | 85.7 | 83.3 | 0.0 | 67.6 | 8.3 | 29.2 | 40.0 | 35.0 | 0.0 | 32.3 | 15.8 | 41.9 | 65.3 | 62.4 | 0.0 | 50.4 | 4.1 | 43.2 | 76.0 | 56.5 | 0.0 | 60.8 |
| Pseudocalanus spp. | 0.0 | 45.5 | 7.1 | 0.0 | 0.0 | 16.2 | 0.0 | 20.8 | 2.5 | 0.0 | 0.0 | 6.3 | 0.0 | 28.8 | 1.9 | 0.0 | 0.0 | 7.3 | 0.0 | 21.6 | 0.3 | 0.0 | 0.0 | 2.4 |
| Microcalanus spp. | 28.6 | 63.6 | 42.9 | 83.3 | 0.0 | 54.1 | 16.7 | 37.5 | 37.5 | 40.0 | 0.0 | 35.4 | 2.7 | 16.9 | 12.3 | 13.8 | 0.0 | 11.9 | 6.7 | 33.1 | 18.0 | 31.3 | 0.0 | 27.8 |
| Unid. Calanoids | 57.1 | 0.0 | 21.4 | 50.0 | 0.0 | 8.1 | 58.3 | 0.0 | 7.5 | 15.0 | 0.0 | 4.2 | 62.6 | 0.0 | 10.1 | 13.3 | 0.0 | 18.0 | 83.1 | 0.0 | 3.2 | 9.9 | 0.0 | 2.0 |
| Oithona similis | 0.0 | 9.1 | 7.1 | 16.7 | 0.0 | 27.0 | 0.0 | 8.3 | 2.5 | 5.0 | 0.0 | 13.5 | 0.0 | 3.3 | 0.7 | 1.7 | 0.0 | 1.4 | 0.0 | 1.0 | 0.2 | 0.8 | 0.0 | 4.4 |
| Others | 0.0 | 0.0 | 14.3 | 0.0 | 0.0 | 5.4 | 0.0 | 0.0 | 5.0 | 0.0 | 0.0 | 2.1 | 0.0 | 0.0 | 2.1 | 0.0 | 0.0 | 0.8 | 0.0 | 0.0 | 0.8 | 0.0 | 0.0 | 0.2 |
| 70 m Depth: | | | | | | | | | | | | | | | | | | | | | | | | |
| N | 0 | 3 | 4 | 0 | 0 | 7 | 0 | 3 | 4 | 0 | 0 | 7 | 0 | 3 | 4 | 0 | 0 | 7 | 0 | 3 | 4 | 0 | 0 | 7.0 |
| Invertebrate Eggs | 0.0 | 66.7 | 50.0 | 0.0 | 0.0 | 57.1 | 0.0 | 60.0 | 50.0 | 0.0 | 0.0 | 55.6 | 0.0 | 65.1 | 66.4 | 0.0 | 0.0 | 66.1 | 0.0 | 76.9 | 74.4 | 0.0 | 0.0 | 78.9 |
| Metridia spp. | 0.0 | 33.3 | 25.0 | 0.0 | 0.0 | 28.6 | 0.0 | 20.0 | 25.0 | 0.0 | 0.0 | 22.2 | 0.0 | 30.4 | 28.0 | 0.0 | 0.0 | 29.7 | 0.0 | 15.5 | 16.7 | 0.0 | 0.0 | 16.8 |
| Pseudocalanus spp. | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Microcalanus spp. | 0.0 | 33.3 | 0.0 | 0.0 | 0.0 | 14.3 | 0.0 | 20.0 | 0.0 | 0.0 | 0.0 | 11.1 | 0.0 | 4.5 | 0.0 | 0.0 | 0.0 | 3.1 | 0.0 | 7.5 | 0.0 | 0.0 | 0.0 | 2.3 |
| Unid. Calanoids | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Oithona similis | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Others | 0.0 | 0.0 | 25.0 | 0.0 | 0.0 | 14.3 | 0.0 | 0.0 | 25.0 | 0.0 | 0.0 | 11.1 | 0.0 | 0.0 | 3.5 | 0.0 | 0.0 | 1.1 | 0.0 | 0.0 | 9.0 | 0.0 | 0.0 | 2.0 |

**Appendix 3.** Percent frequency of occurrence (%FO), number (%N), volume (%VOL), and index of relative importance (%IRI) of all prey items consumed by larval walleye pollock at station 1, April 20, 1992, in the oceanic domain of the Bering Sea.

**Appendix 4.** Means and standard deviations of numbers of items per larval gut at station 1, April 20, 1994, in the oceanic domain of the Bering Sea. Statistics based on raw counts

| | Eggs | *Metridia* sp. | *Pseudocalanus* sp. | *Microcalanus* sp. | Unidentified Calanoids | *Oithona similis* | Others | Total |
|---|---|---|---|---|---|---|---|---|
| 10 m | | | | | | | | |
| Mean | 0.81 | 0.29 | 0.19 | 0.07 | 0.33 | 0.40 | 0.12 | 2.21 |
| S.D. | 0.80 | 0.51 | 0.51 | 0.34 | 0.75 | 0.83 | 0.33 | 1.42 |
| 20 m | | | | | | | | |
| Mean | 0.65 | 0.09 | 0.14 | 0.26 | 0.21 | 0.65 | 0.02 | 2.02 |
| S.D. | 0.65 | 0.48 | 0.35 | 0.73 | 0.47 | 1.38 | 0.15 | 1.65 |
| 30 m | | | | | | | | |
| Mean | 0.51 | 1.66 | 0.20 | 1.27 | 0.41 | 0.78 | 0.00 | 4.83 |
| S.D. | 0.93 | 1.44 | 0.46 | 1.38 | 0.67 | 0.96 | 0.00 | 2.30 |
| 50 m | | | | | | | | |
| Mean | 0.16 | 0.82 | 0.16 | 0.89 | 0.34 | 0.11 | 0.05 | 2.53 |
| S.D. | 0.44 | 0.73 | 0.37 | 1.29 | 0.75 | 0.39 | 0.23 | 1.41 |
| 70 m | | | | | | | | |
| Mean | 0.71 | 0.29 | 0.00 | 0.14 | 0.00 | 0.00 | 0.14 | 1.29 |
| S.D. | 0.76 | 0.49 | 0.00 | 0.38 | 0.00 | 0.00 | 0.38 | 0.49 |