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Larval Herring Food Habits over Three Spawning Seasons (1974-76) in the Georges Bank-Nantucket Shoals Area

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Abstract

Larval herring (Clupea harengus L.) prey items and morphological condition measurements are summarized for over 7,000 larvae collected on 15 autumn-winter ICNAF survey cruises during the 1974, 1975, and 1976 spawning seasons in the Georges Bank-Nantucket Shoals area. Feeding incidence and prey selectivity are examined in relation to availability of prey over three contrasting seasons of larval production, growth, and survival. Production of larvae decreased in this area from the second highest level in the time series (1971-1978) in 1974 to a record low in 1976. At the same time, the spawning population centers shifted from northeastern Georges Bank to the Nantucket Shoals-western Georges Bank area.

During the first six months of life, herring larvae preyed on adults and developmental stages of the dominant species of copepods (in order of importance): Pseudocalanus sp., Paracalanus parvus, Centropages typicus, C. hamatus, Oithona spp., and Calanus finmarchicus. In 1974, Centropages spp., and Pseudocalanus sp. were major dietary components. In 1975 and 1976, Pseudocalanus sp. and Paracalanus parvus became the dominant prey items. Comparing the February surveys, there was a decline in abundance of Centropages spp. on Georges Bank from 1974 and 1975 to the 1976 season, which may account for their decreasing importance in the larval diet. Total prey densities over each spawning season ranged from 60-3800 organisms per m^3, which is relatively low compared to results from other investigations.

Larval feeding throughout the season was concentrated during the daylight hours with one peak shortly after sunrise, and a second peak 6-8 hours later in mid-afternoon. The mean prey length and width increased gradually with larval size over each spawning season. The prey in this study were much smaller in relation to larval size than predicted by Beyer's (1980) stochastic feeding model using Artemia nauplii as prey in laboratory experiments. Larvae in the Georges Bank-Nantucket Shoals area may satisfy their energy requirements by feeding on many small copepod prey as opposed to fewer numbers of large prey. Larvae of all lengths averaged 2-5 prey per gut over the spawning seasons.

The percentage of larvae with prey in their guts increased from 22-25% in 1974 and 1975 to 32% in the 1976 season. There was a corresponding increase in the body height/standard length condition factor ratios for the few larvae collected in the 1976 season indicating that these larvae were more robust for their size. The larval condition factor and food habits data are consistent with the greater mean size of larvae observed for each succeeding winter, as well as the increased survival rate estimated for these populations.

Proie et mesures de condition morphologique de hareng larvaire (Clupea harengus L.) sont résumé pour au delà de 7,000 larves rassemblées au cours de 15 campagnes de levée ICNAF automn-hiver pendant les saisons frayères de 1974, 1975, et 1976, dans l'aire du Banc George-Nantucket Shoals. Incidence alimentaire et sélectivité de proie sont examinés quant à la disponibilité de proie a travers trois saisons en contraste de production larvaire, croissance, et survivance. La production de larve dans cette aire décrue, de la deuxième hauteur dans la série temporel (1971-1978) en 1974 à un niveau le plus petit en 1976. A la fois, les centres de la population frayante ce déplacèrent du Banc George nord-est à l'aire de Nantucket Shoals-Banc George ouest.

Pendant les premiers six mois de vie, les larves de harengs s'acharnaient sur les adultes et les stades développementaux d'espèces dominants de copépodes (en disposition d'importance): Pseudocalanus sp., Paracalanus parvus, Centropages typicus, C. hamatus, Oithona spp., et Calanus finmarchicus. En 1974, Centropages spp., et Pseudocalanus sp. furent constituants alimentaire majeur. En 1975 et 1976, Pseudocalanus sp. et Paracalanus parvus devirent proies dominants. Comparant les levées de Février, il fut un déclin dans l'abondance de Centropages spp. sur le Banc George de 1974 et 1975 jusqu'à la saison de 1976, de quoi pourrait rendre compte de leur importance décroissante dans l'alimentation larvaire. La densité totale de proies pendant chaque saison frayère avait une portée de 60 à 3800 organisme par m^3, ceci est relativement bas comparé aux resultats d'autres enquètes.

D'un bout à l'autre de la saison l'alimentation larvaire fut concentré pendant le jour avec un summum bientôt après la lever du soleil, et un second summum 6 à 8 heures plus tard en mis-après midi. La longeur et largeur moyenne de la proie a augmenté graduellement avec la taille larvaire pendant chaque saison frayère. Les proies dans cette étude etaient plus petites par rapport a la taille larvaire prédit par le modèle d'alimentation stochastique de Beyer (1980) utilisant des nauplii d'Artemia comme proie dans des expériences au laboratoire. Les larves dans l'aire du Banc George-Nantucket Shoals pourraient satisfaire leurs réclamation d'énergie par se nourrissant de nombreux petits copépodes opposé à moins de grandes proies. Larves de toutes longeurs contenuent en moyenne 2 à 5 proies dans leurs intestins pendants les saisons frayères. Le pourcentage de larves avec proies dans leurs intestins accru de 22 à 25% en 1974 et 1975 à 32% dans la saison de 1976. Il y avait un accroissement correspondant dans les proportions de taille du corps/facteur standard de condition de longeur pour le petit nombre de larves rassembler pendant la saison de 1976 indiquant que ces larves étaient plus robuste pour leurs tailles. Le facteur de condition larvaire et les donneés de régime alimentaire sont en accord avec la plus grande taille moyenne de larves observées pour chaque hiver de suite, ainsi que le taux de survivance augmenté estimé pour ces populations.

Introduction

From 1971 through 1978, the Northeast Fisheries Center participated in a multinational study investigating the biological and physical factors controlling larval herring survival in the Georges Bank-Gulf of Maine region. The most complete sampling coverage for the eight spawning seasons was in the Georges Bank-Nantucket Shoals area. The major program objectives, rationale, and sampling methodology developed by ICNAF (International Commission for the Northwest Atlantic Fisheries) participants are summarized by Lough et al. (1981).

Our main objective here is to investigate the relationships among larval survival and feeding (through gut content analysis), morphological condition, and the distribution and abundance of available prey in this region during the first six months of larval life. Principal spawning grounds in the Georges Bank region are on the northeastern part of Georges Bank and on Nantucket Shoals. Most of the larvae hatch during October (September-December) and generally disperse in a southwesterly direction from the spawning sites reaching maximum areal coverage within the 100-m depth contour by December. The larvae grow at about 5-mm per month from a hatching length of 6-mm and may reach 50-55-mm by June when most are considered to have metamorphosed. Earlier evidence suggested that differential overwinter mortality of autumn-spawned herring larvae might be caused by starvation because zooplankton levels are at their lowest during this time of year (Sherman, 1971; Dubé et al., 1977; Lough et al., 1980; Graham and Davis, 1971; Chenoweth, 1970). Starvation and predation are generally thought to be the two major factors controlling larval survival (Hunter, 1976). Larval fish spawning and the production cycles of their zooplankton prey are closely linked (Cushing, 1967). Lasker and Zweifel (1978) further suggest that clupeoid larvae require patches of food organisms which are temporally and spatially stable for a sufficient amount of time in order to permit adequate feeding.

Larvae from the Georges Bank-Nantucket Shoals area were examined from surveys conducted during the 1974, 1975, and 1976 spawning seasons because preliminary examination of the data indicated significant differences in larval production, growth and mortality, and spawning sites, as well as the availability of zooplankton prey and environmental data for these years. In this paper we present a summary of our findings on the Georges Bank-Nantucket Shoals larval herring food habits which includes the following specific comparisons and contrasts over the three spawning seasons:

a. Seasonal feeding incidence and species composition.
b. Diel frequency of larval feeding and possible indication of feeding rates.
c. Size of prey in relation to larval size.
d. Frequency distribution of prey in guts by larval size class.
e. Morphological condition factors.
f. Prey densities and distribution based upon 0.165- and 0.333-mm samples
g. Relation to other studies on larval feeding and condition in this area.

Methods

I. Field Sampling

Survey curises were conducted approximately once a month, beginning in 1971, on a standard grid of stations 15-20 miles apart covering the Georges Bank-Gulf of Maine area from September through December, and since 1974, through February. The cruise tracks, survey dates, and participating vessels are included in a laboratory data report by Lough and Bolz (1980). The 15 surveys analyzed and referred to in this paper are listed below:

	Vessel Cruise No.	Cruise Dates
1.	Cryos 74-04	9/07 - 9/24/74
2.	Prognoz 74-01	10/18 - 10/30/74
3.	A. Dohrn 74-01	11/16 - 11/23/74
4.	Albatross IV 74-13	12/04 - 12/19/74
5.	Albatross IV 75-02	2/12 - 2/28/75
6.	Belogorsk 75-02	9/25 - 10/08/75
7.	Belogorsk 75-03	10/17 - 10/30/75
8.	A. Dohrn 75-187	11/01 - 11/18/75
9.	Albatross IV 75-14	12/05 - 12/17/75
10.	Albatross IV 76-01	2/10 - 2/25/76
11.	Wieczno 76-01	4/09 - 5/04/76
12.	Wieczno 76-03	10-14 - 11/03/76
13.	A. Dohrn 76-02	11/15 - 11/29/76
14.	Researcher 76-01	11/27 - 12/11/76
15.	Mt. Mitchell 77-01	2/13 - 2/24/77

Standard sampling gear consisted of a 61-cm mouth diameter bongo-net (0.333- and 0.505-mm mesh nets), and beginning in fall 1974, a 20-cm diameter bongo sampler (0.053- or 0.253-mm and 0.165-mm mesh nets) was added to the array (Posgay and Marak, 1980). At each station the sampling array was lowered at 50 m/min to a maximum depth of 100 m or to within 5 m of the bottom, and retrieved at 10 m/min in a double-oblique profile at a ship speed of 3.5 knots. During the 1974-1977 seasons, a 10-minute neuston haul (1x2-, or 0.5x1-m rectangular frame with a 0.505-mm mesh net) also was made simultaneously with the bongo haul.

II. Laboratory Procedures

A. Gut content

Numerous other investigators have studied the feeding habits of larval Atlantic herring, but only a few have focused on the Georges Bank area. In order to add any significant new information to these data, an extensive in-depth, systematic study was undertaken. Because of the low feeding incidence and the high variability of the morphological measurements observed in this study, a large number of larvae were processed. Gut content and morphological condition factor measurements were recorded from over 7,000 larvae from the 15 cruises over the 1974, 1975 and 1976 spawning seasons. More details of the larval food habits program rationale and laboratory methods are provided in Cohen and Lough (1979).

The herring larvae were sorted previously from 0.333- and 0.505-mm mesh bongo samples and vialed by station and cruise by the Plankton Sorting Center (Morski Instytut Rybacki) in Szczecin, Poland and the National Marine Fisheries Service, Northeast Fisheries Center. Larval dissections, measurements, and routine prey identifications were performed using a Wild M5 dissecting microscope. A Zeiss compound microscope was used to identify fragments and other unknown gut contents. The dominant prey items, developmental stages and adults of copepods, were identified from various sources in the literature compiled by Murphy and Cohen (1978).

B. Condition factor measurements of larvae

The following list of morphological measurements was made on all larvae examined for gut content according to procedures described in Cohen and Lough (1979):

1. Standard length

   Standard length was measured in order to group larvae into size (age) classes, calculate measures of condition, standardize data, and compare relative size of other body parts by length class over each season.

2. Skull width, maxillary length, mouth gape (maxillary length x $\sqrt{2}$ - Shirota, 1970)

   Skull width, maxillary length, and mouth gape were measured as indices of mouth size to correlate with prey size.

3. Eye height, head height, eye height/head height ratio

   Eye height remains relatively constant during starvation and can be a useful index with which to monitor the decrease in head height which occurs at this time. The ratio value is recommended for use as a condition factor for recently hatched herring larvae by Ehrlich *et al*. (1976).

4. Body height and body height/standard length ratio

   Ehrlich *et al*. (1976) also recommend this ratio for use as a condition factor although these authors as well as Blaxter (1971) agree that body height is not a sensitive measure of larval condition because of its increasing variability with age.

5. Pectoral angle

   This measurement (also recommended by Ehrlich *et al*., 1976) decreases during starvation, but also decreases during the first 50 days of growth, and then increases.

6. Standard condition factor $\left(\frac{\text{Dry weight (mg) x } 10^3}{[\text{Standard length (mm)}]^3}\right)$

   The dry weight of individual larvae was not recorded in this study because of the large numbers of larvae processed. Instead, the dry weight was calculated from data in Chenoweth (1970) using the relationship: Log W = 5.73 + 4.66 Log L. This condition factor is common in the literature. It is highly dependent on length and increases with growth. The relative condition factor according to Erhlich *et al*. (1976) $\left[\frac{\text{Dry weight (mg) x } 10^5}{\text{Standard length (mm) x } 10^{4.571}}\right]$ would be a more appropriate measure of condition because it eliminates the dependence on length. However, this condition factor reduces to zero if the derived dry weights used here (Chenoweth, 1970) are substituted into the equation.

C. Zooplankton in the environment

Zooplankton from the 0.333-mm mesh 61-cm bongo samples were sorted and identified by the Polish Sorting Center. Selected 0.165-mm bongo samples were sorted by Northeast Fisheries Center personnel in Woods Hole. The 0.333-mm mesh data are used to infer general patterns of distribution and abundance of the major larval herring prey items and other zooplanktonic organisms. However, this mesh size retains copepods greater than 0.9 - 1.0 mm cephalothorax length (Davis, 1980), which includes only the adults of both species of *Centropages* and female *Pseudocalanus* sp.

Most of the 0.165-mm samples processed were located along a five station transect across central Georges Bank. This mesh size retains copepods whose cephalothorax lengths are equal to or greater than 0.26 mm, which includes all larval prey items enumerated except the first copepodite stages of Paracalanus parvus and both species of Centropages, the first three copepodite stages of Oithona spp., and most of the naupliar stages with the exception of those of Calanus finmarchicus (based upon measurements in Murphy and Cohen, 1978).

Results

The larval herring gut content and morphological condition data for the three spawning seasons are presented on an individual cruise basis broken down by larval length classes in the following tables and figures in a data report by Cohen et al. (1980):

A. Tables

1. Mean length and width of larval herring prey items by 5-mm length class.
2. Abundance of larval herring prey items by 5-mm length class.
3. Diel distribution (2-hourly) of feeding larval herring by 5-mm length class.
4. Mean values of larval herring condition factor measurements by 5-mm length class.

B. Figures (individual cruise plots)

1. Percentage of larval herring feeding per station.
2. Mean number of prey items per larval herring per station.
3. Mean value of larval herring eye height/head height ratios per station.
4. Mean value of larval herring body height/standard length ratios per station.

I. Prey Selection Based on Gut Content

The dominant prey items were developmental stages and adults of the following copepod species listed in general order of importance:

1. Pseudocalanus sp.
2. Paracalanus parvus
3. Centropages typicus
4. Centropages hamatus
5. Oithona spp.
6. Calanus finmarchicus

A. Prey species and seasonal feeding incidence

In 1974, Pseudocalanus sp. adults (19.7%), and Centropages typicus (14.2%) and C. hamatus (11.4%) copepodites were the dominant prey items (Table 1 and Figures 1 and 2). During 1975, Paracalanus parvus (18.3%), Pseudocalanus sp. (11.4%) and unidentified calanoid adults (27.5%), and copepod eggs (13.7%) were the most common food items. It should be noted that only a small number of larvae consumed a very large number of copepod eggs during the February 1976 survey and strongly biased these results. In 1976, Pseudocalanus sp. (33.7%), Paracalanus parvus (24.2%), and unidentified calanoid adults (35.9%) again predominated. In most cases the unidentified calanoids were thought to be Pseudo- or Paracalanus. The overall diversity of prey items decreased from 1974 and 1975 to 1976, and both species of Centropages became insignificant as prey in 1976. There was a shift from the smaller nauplii and copepodites early in the season to the adult stages and older copepodites of the larger species later in the season as the larvae increased in size. In 1976, when the larvae had a greater mean length on the average than the previous two seasons (Lough et al., 1980), no nauplii were found in the guts of early larvae (Figure 2). In 1976, the percentage of larvae feeding in December and February was high (42.9% and 48.9%, respectively) and increased over winter in contrast to the two previous years when it decreased (1974: 25.7% to 8.6% and 1975: 29.2% to 19.6%).

B. Diel feeding frequency

Herring are visual feeders and it is generally assumed in the literature that they feed only during the day (Noskov et al., 1979; Schnack, 1972; Bainbridge and Forsyth, 1971; Bhattaharyya, 1971; and others). In Figures 3A and B the percentage of larvae feeding over 24 hours versus the percentage feeding during daylight hours usually shows a substantial increase when calculated for daylight hours only. A plot of the percentage of larvae feeding over time for each season (Figure 4) shows feeding peaks shortly after sunrise and in mid-afternoon with only a few peaks during the night, possibly due to food from the previous day. The two peak feeding periods average about 6-8 hours apart and may represent the gut clearance time.

C. Prey size versus larval size

In most studies of prey size versus larval size the prey length is compared to the larval length or a measure of its mouth size. Prey width is a more meaningful measurement because it is commonly agreed that prey organisms are swallowed head first. In the present study both prey length and width were measured with a high correlation between the two measurements:

Season	Equation	Correlation Coef., r prey length vs. width
1974	L = 2.5013W + 0.0359	0.88
1975	L = 2.5953W + 0.0153	0.77
1976	L = 2.386W + 0.1551	0.91

L = Cephalothorax length (mm) for copepodites and adults, or total length for nauplii.
W = Maximum width (mm).

High correlation coefficients also result from a comparison of larval standard length with skull width (used to represent mouth width) and mouth gape:

eason	Equation	Correlation Coef., r Mouth gape vs. standard length	Equation	Correlation Coef., Skull width vs. standard length
1974	MG = 0.0921L - 0.0421	0.90	SW = 0.0454L + 0.2708	0.92
1975	MG = 0.3281L - 3.4625*	0.91	SW = 0.0533L + 0.1984	0.95
1976	MG = 0.1083L - 0.5810	0.97	SW = 0.0507L + 0.2181	0.98

MG = Mouth gape (mm), SW = Skull width (mm), L = Standard length (mm)
* Includes two different methods of measuring maxillary length.

Because of the high correlations between prey length and width, and standard length and mouth gape and skull width, these measurements can be used interchangeably for the purpose of comparisons between larval and prey size.

In Figure 5, it can be seen that prey length and width and their ranges generally increased over each spawning season, and with larval length. Beyer (1980) used literature data to generate two prey preference ratios:

1. 2 x prey width/larval standard length.
2. Prey width/mouth width (skull width used here).

Figures 6A and B present a comparison of these ratios based on Beyer's data and our data for the 1974, 1975 and 1976 seasons. The ratios in the 1975 season appear to be lower than the 1974 and 1976 seasons because of the large number of copepod eggs consumed by a few larvae in February 1976 as mentioned previously. Prey size, based on our data, is much smaller in relation to larval size than the optimal sizes predicted by Beyer. Most authors agree that copepod cephalothorax length and width are not affected by preservation in formalin except Christensen et al. (1980) who found shrinkage of *Artemia* nauplii in larval herring guts possibly due to preservation in formalin or to digestive processes. An additional complication is added by the problem of larval shrinkage during capture and preservation (Sameoto, 1972; Hay, 1979; Lockwood, 1973; and Theilacker , 1980). If larval standard lengths used to calculate the first ratio were corrected for shrinkage by increasing them, the resulting ratios would be even smaller.

D. Frequency distribution of prey items in larval gut

The mean number of prey per larval gut ranged from 1-9 and averaged 2-5 prey items for all size classes of larvae (Figure 7), but this range may be an underestimate because of the potential loss of gut content during capture and preservation (Lasker and Zweifel, 1978; Hay, 1979; Damkaer and Au, 1968; and Blaxter, 1965). Food was commonly concentrated in the hind gut.

E. Endoparasites

Incidence of larval gut parasites was low and occurred mainly during the winter months. In 1974, 5.5% of the larvae from the December survey were parasitized mostly by Bothriocephalus scorpii with a few Scolex pleuronectis present as well. In February 1975, 5.9% of the larvae were parasitized by Bothriocephalus. In December 1975, 0.6% of the larvae contained Bothriocephalus, and in February 1976, 4.8% of the larval guts had this species. In the 1976 season, 1.3% of the larvae examined from the October survey, 7.1% from the December survey, and 4.7% from February contained one or both species of parasite. (Identifications made by B. Hayden, NMFS, Woods Hole.)

II. Morphological Condition Factors

A breakdown of these data can be found in the summary tables and charts referred to previously in the data report by Cohen et al. (1980). The normalized (variable/standard length) measurements were analyzed with a factor analysis program (Nie et al., 1975) in order to select the most important variables which might serve as indices of condition. A step-wise discriminant analysis (Nie et al., 1975) also was attempted in order to separate healthy from starved larvae, on the basis of feeding versus non-feeding larvae, using the condition factor measurements. Both procedures produced inconclusive results to date.

The data in general showed very high variability (see data report for standard errors of measurements) and were difficult to interpret. However, body height/standard length ratios generally tended to increase from 1974 to 1976, when comparing similar larval length classes, indicating more robust larvae in 1976.

III. Zooplankton in the Larval Environment

A. 0.333-mm mesh bongo samples

A complete set of maps showing the distribution and abundance patterns for the dominant zooplankton prey and potential larval predators during these survey cruises will be forthcoming (Cohen and Lough, 1981a).

Because this mesh size does not quantitatively sample most of the larval herring prey, the results can only be used to infer information about the general patterns during each season. A major difference which emerged was the virtual disappearance of both species of Centropages from the eastern half of Georges Bank during February 1977 compared to February 1975 and 1976. Paracalanus parvus was very scarce in February of 1974 and 1976 and quite widespread but low in numbers during February 1975 (Figures 8-10).

B. 0.165-mm mesh bongo samples

An in-depth analysis of these samples will be available later this year (Davis, 1981).

There was very high variability from station to station, and total prey densities over all three seasons ranged between 60 organisms/m^3 to 3,800/m^3. Comparisons were made between the relative percentage of each prey species in the larval guts and that in the environment at each station where this information was available. There was usually good agreement except that Oithona spp. frequently appeared to be negatively selected.

Selectivity indices were calculated (Berg, 1979) for larvae at these stations but the results were inconsistent possibly for a number of reasons: a) low density of prey items, b) few feeding larvae at many of the stations, c) the patchy distribution of the zooplankton prey, and d) the integrated nature of the bongo hauls which masks any differences in vertical distribution of the organisms.

Discussion

I. Prey Selection

A. Species and size of prey

The major criteria for the initial selection of food by larval fish are size and density of prey, behavior of prey, and behavior of predator, or other species characteristics. Secondary selection may involve taste, texture, nutritional value, and eventually learning. Wankowski and Thorpe (1979) stated that there is an optimum particle size for maximum growth which represents a compromise of genetic background, behavioral and social factors, temperature, endocrine levels, and nutritional value of prey. Presumably the energy expended in prey capture represents the minimum amount required to obtain the maximum nutrition. The diet may consist of many small particles which are low in energy but easy to capture, or a few large particles which are high in energy but require more energy to capture depending on the environment (Eggers, 1977). In addition, the temporal and spatial structure of the prey organisms must remain stable long enough to allow larval feeding (Lasker and Zweifel, 1978).

In this study it is possible to draw a number of conclusions about prey selection based on species availability, size, and prey density. The larvae examined fed on the dominant species of copepods present in the water column (*Pseudocalanus* sp., *Paracalanus parvus*, *Centropages typicus*, *Centropages hamatus*, *Oithona* spp., and *Calanus finmarchicus*). As they grew larger they selected older stages of the same prey species which may have been developing synchronously with the larvae. Herring larvae in the 1975 and 1976 seasons consumed very low numbers of *Centropages* spp. compared to 1974, reflecting a real change in these species' abundance in the environment, at least during 1976. In the Appendix a number of important larval herring feeding studies are summarized and compared with the present study. It can be seen that, in most cases, larvae select the most abundant prey available in a suitable size range. All these studies in which predator and prey size ranges are given correspond in their measurements. Bhattacharyya (1957), Blaxter (1965), and Marshall *et al.* (1937) recorded plant material in their larval gut contents. No plant material was found in our study except that ingested by the copepod prey, which is in agreement with other studies done in this area (Damkaer and Au, 1974; Noskov *et al.*, 1979; Sherman and Honey, 1971).

The larvae on Georges Bank fed on smaller particles than predicted by Beyer's (1980) model and so their strategy may be to feed on large numbers of small particles to meet their energy requirements. However, the larvae occasionally appeared to reject *Oithona* spp. as a suitable prey when it was abundant, which could be due to a number of reasons. *Oithona* may be: a) successfully avoiding the larvae, b) distasteful or of low nutritional value, c) too wide to swallow because the short antennae are held perpendicular to its long body axis, d) more transparent than the other copepods, or most likely, e) they are not really available to the larvae buy are at a different depth in the water column which is not detected by an integrated haul.

B. Diel feeding pattern

In our study two major peaks in feeding occurred shortly after sunrise and 6-8 hours later. Other investigators also have found feeding to be concentrated during the daylight hours. Peaks occurred which seemed related to sunrise and sunset in studies by Hempel (in Blaxter, 1965) and Bhattacharyya (1957). All of these peaks may reflect gut clearance rates and digestive times under the specific experimental conditions used in these studies. Rosenthal and Hempel (1970) recorded a passage time of 4-10 hours in their laboratory experiments. Gut clearance times depended on the initial amount of food in the guts, and digestion times depended on size and type of prey item. Blaxter (1965) estimated digestion time for from 4-8 hours, depending on temperature. Beyer and Laurence (1979) used a digestion time of 4 hours in their model of larval herring growth and mortality. So, our assumption that the 6-8 hour time interval between feeding incidence peaks may represent gut clearance time appears reasonable for Georges Bank-Nantucket Shoals larvae.

C. Number of prey consumed and position in gut

General descriptions of the feeding process have been published in numerous earlier studies (Blaxter, 1965; Beyer, 1980; Blaxter and Staines, 1969; Rosenthal, 1969; and others) and will not be repeated here.

There is a wide range of estimates of the number of organisms found in the larval guts. Schnack (1972) recorded an average of 4 items per gut in North Sea autumn-spawned larvae (14-17-mm) where the food supply was low. Spring-spawned larvae (19-24-mm) contained an average of 80 items/larvae at one station in the highly productive Schlei estuary. Schnack suggested that assimilation efficiency decreases when large numbers of prey are present in the gut, and therefore no additional energetic benefit would be derived from ingesting larger than optimum numbers of prey. Blaxter (1965) summarized (his Table 1) the number of prey per larva for 10 other studies, and the count ranged from 2-479 for 6-44-mm larvae. Sherman and Honey (1971) found a mean number ranging from 1.3-13.8 prey per larva, considering all size classes during the autumn, winter, and spring in central Maine coastal waters. Noskov et al. (1979) estimated 1.6, 2.4, and 2.0 prey per larva for small (5.0-7.9-mm), medium (8.0-12.9-mm), and large (13.0-17.9-mm) larvae, respectively. Beyer and Christensen (1980) found a value of 3.4 *Artemia* nauplii per larva in laboratory experiments. Our results showed mean values of from 2-5 prey per gut for all size ranges of larvae examined. One explanation for this variability in results has already been mentioned: the potential loss of gut content during capture and preservation. In addition, differences in larval size, prey size, plankton supply, and gut clearance time (temperature dependent) will all affect the number of prey counted in a larva at any one time. This variability is important to note because it will greatly affect estimates of daily ration used in models such as those already cited (Beyer, 1980; Beyer and Christensen, 1980; and Beyer and Laurence, 1979).

II. Morphological Condition Factors

Previous investigators have explored the use of histological (O'Connel, 1976; Ehrlich et al., 1976; and Theilacker, 1978) and biochemical (Buckley, 1979 and 1980; Balbontin, 1973; Ehrlich, 1974 and 1975) measurements in addition to the many studies of morphological condition (LeCren, 1951; Graham and Davis, 1971; Abbasov and Polyakov, 1978; Chenoweth, 1970; Ehrlich et al., 1976; Sameoto, 1972; Shelbourne, 1957; Blaxter, 1971; Vilela and Zijlstra, 1971; and others). There are numerous problems in the use of these measurements to evaluate larval health. One difficulty involves the shrinkage in dimensions caused by the effects of capture and preservation (see Cohen and Lough, 1979 for discussion, and Theilacker, 1980). Different species and sizes of larvae, as well as different body parts, shrink at different rates depending on the circumstances, and so no corrections were made in our study to account for this problem. Several authors note further that data obtained from laboratory-raised larvae cannot be used as standards with which to evaluate field data on the same species because body dimensions, growth patterns and other environmental factors are different for the two groups. Schnack (1972) hypothesized that the condition factor can only be used within a single population and size class as a measure of physiological condition.

LeCren (1951) suggests that sampling gear may create another problem by selecting fatter larvae. In contrast, Ehrlich (1975) cautions that the nets may collect mostly sick or moribund individuals.

Changes in morphology occur naturally with growth and may mask, accentuate or simulate the changes which result from starvation, disease, parasitism, predation, preservation, and sampling gear which are caused by osmoregulatory problems of larvae under stress. Most investigators, therefore, recommend recording several types of condition factor measurements to supplement each other.

With all these difficulties in mind, it is not surprising that our results were difficult to interpret. No consistent patterns in the distribution of two of the condition factors (eye height/head height and body height/standard length) were discernible (see Figures 31-60 in Cohen et al., 1980). However, one ratio, body height/standard length, seemed to be useful as an indication of more robust larvae during the 1976 season. Schnack (1972) speculated that when food supply is low, more weak larvae die and the survivors have a higher mean condition factor than a generally well-fed population, providing another possible interpretation for our results.

The factor and discriminant analyses were conducted on all the larvae collected over 24-hours. Discriminant analyses were performed on larvae collected during daytime only in order to eliminate any bias caused by the low incidence of larvae with gut content during the night, and on day- versus night-caught larvae in order to test for the possibility that healthy larvae can avoid the sampling gear more effectively during the day (see Lough et al., 1980). None of the procedures produced significant results.

III. Zooplankton Supply

The earlier section on prey selection described the general agreement between the species in the larval guts and the zooplankton supply based on the 0.333- and 0.165-mm mesh samples. However, because of the high station to station variability and the low number of sampling points per cruise in the 0.165-mm mesh series, it is difficult to draw conclusions about the density of prey available to the larvae each season. Feeding rate (Beyer and Christensen, 1980), feeding intensity (biomass ingested)(Schnack, 1972), and growth and survival (Werner and Blaxter, 1980) increase up to an optimum prey concentration; beyond this concentration, these parameters decline.

Schnack (1972) estimated that optimum prey density for 14-19-mm larvae was 200 "relevant food organisms" per liter. Rosenthal and Hempel (1970) reported that 10-11-mm larvae required 21-42 nauplii per liter and that 13-14-mm larvae needed 13-25 nauplii per liter, considerably lower than Schnack's estimate. Werner and Blaxter set the critical prey density for 4-12 week old larvae at 170 organisms per liter. In Beyer and Laurence's (1979) model, several estimates of larval growth and mortality are given based on different prey densities. A larva which hatches at 60 mg (8.9-mm) needs 800 nauplii per liter, but one hatching at 90 mg (9.8-mm) needs only 150 nauplii per liter. Other estimates by these authors predict that larvae of mean weight of 90 mg need at least 70 nauplii per liter to grow "at a positive rate." Larvae of 110 mg (>10-mm) need only 45 nauplii per liter. Optimum prey densities for first feeding larvae are set at 500 nauplii per liter.

Our estimates of prey density in the Georges Bank-Nantucket Shoals area range from 0.6-3.8 organisms per liter, which seem extremely low. As mentioned previously they represent the results of an integrated haul covering the entire water column and therefore obscure any patchiness which might provide the required densities. Also, the prey referred to in the literature are usually nauplii and our results represent mostly copepodites and adults. Fewer numbers of these larger organisms would be needed to meet the larval energy requirements. For this reason, it would be useful to compare the biomass ingested by different length groups of larvae and the biomass of available preferred prey items.

IV. Larval Feeding and Condition in Relation to Abundance, Distribution, and Survival

The patterns of our larval feeding and condition results are basically consistent with the abundance, distribution, and mortality patterns reported by Lough et al. (1980) for the 1974-1976 spawning seasons. They found that the production of herring larvae in the Georges Bank-Nantucket Shoals area was relatively high in 1974 (79 x 10^{12} larvae), intermediate in 1975 (21 x10^{12}) and extremely low in 1976 (<1 x 10^{12}). There was a shift in the spawning centers from the historic sites on Northeastern Georges Bank, where 86% of the total spawning occurred in 1974, to Nantucket Shoals in 1976, where 97% of the spawning took place. Spawning was divided between the two areas in 1975 with 66% occurring on Nantucket Shoals. Lough et al. (1980) discuss several reasons for this apparent shift in the herring fishery.

In 1974, larvae from the northeastern Georges Bank spawning sites were advected southwest across the bank, and by November, larvae were spread throughout the entire Georges Bank-Nantucket Shoals area within the 100-m contour (Lough et al., 1979). By December the larvae were concentrated into two large patches: one on central Georges and the other on southern Nantucket Shoals. During the 1975 season, larvae spawned on northeastern Georges Bank seemed to follow the expected southwesterly drift across Georges. However, a major portion of the larvae spawned on Nantucket Shoals appeared to be transported north into the Great South Channel by December. Nevertheless, by February 1976, larvae of the expected size were concentrated into three main patches within central Georges Bank and Nantucket Shoals. Production of larvae in 1976 was so low that after the initial spawning on Nantucket Shoals, only scattered occurrences of larvae were observed across the banks throughout the season. The winter of 1976-77 has been reported by Ingham (1979) to have produced unusually strong, persistent northwesterly winds in the Georges Bank and Middle Atlantic Bight region in January and February which produced southwesterly Ekman transport in the upper layers of the water column.

Age-specific mortality rates of the larvae estimated by Lough et al. (1981) for the autumn-winter periods indicated that in 1976 mortality was the lowest (2.2% per day), followed by the 1975 season (2.7% per day), and the highest in the 1974 season (3.2% per day). Concurrent with the trend of decreasing mortality (increasing survival) from 1974 to 1976, the mean larval length increased during each succeeding winter over the series, indicating that larval growth was increasing, or that larger larvae were surviving in proportionately greater numbers.

In the present study, we found a greater percentage of feeding larvae in the 1976 season. More specifically, the percentage of larvae feeding during the possibly critical winter period was high and increased from 42.9% in December to 48.9% in February. During 1974 it decreased from 25.7% to 8.6%, and in 1975 from 29.2% to 19.6%. It is interesting to note a shift in larval diet from 1974 to 1975 and 1976 in which both species of Centropages decreased in importance and Pseudocalanus sp. and Paracalanus parvus became dominant. This shift apparently reflects a significant decline in population levels of Centropages spp. on eastern Georges Bank in 1975 and 1976. The larvae collected in the 1976 season also appeared to be more robust for their size based upon one of the condition factor measurements (body height/standard length). Therefore, it is possible to speculate that the greater survival of herring larvae during the 1976 spawning season may have been a result of the increased population levels of the copepod prey Pseudo-Paracalanus.

V. Summary

A. Larval Atlantic herring in the Georges Bank-Nantucket Shoals area selected prey items on the basis of availability and size. In 1974, the dominant prey were Pseudocalanus sp. adults (19.7%), and Centropages typicus (14.2%) and C. hamatus (11.4%) copepodites. In 1975, Paracalanus parvus (19.3%), Pseudocalanus sp. (11.4%) and unidentified calanoid adults (27.5%), and copepod eggs (13.7%) dominated. In 1976, Pseudocalanus sp. (33.7%), Paracalanus parvus (24.2%) and unidentified calanoid adults (35.9%) again predominated.

B. Two major peaks in feeding incidence occurred during the day: one shortly after sunrise, and the other 6-8 hours later in mid-afternoon. The time interval between peaks may represent gut clearance time and it is in agreement with literature values.

C. In this study, larvae commonly contained 2-5 prey items per gut. Comparisons are made with several other investigations. Food was concentrated in the hind gut.

D. Prey length and width increased gradully with larval length over each spawning season. Prey size in the Georges Bank-Nantucket Shoals area was significantly smaller in relation to larval size than predicted by Beyer's (1980) stochastic feeding model. Larvae in this area may satisfy their energy requirements by feeding on many small particles.

E. Several morphological condition factor measurements were recorded. One measurement, body height/standard length, apparently indicated that larvae in 1976 were more robust for their size than in 1974 and 1975.

F. There was a shift in zooplankton populations on eastern Georges Bank corresponding to the change in larval diet comparing February 1974 and 1975 to February 1976. Both species of Centropages greatly declined in numbers on Georges Bank during 1976, based upon the 0.333-mm mesh samples.

G. Prey densities ranged from 0.6 to 3.8 items per liter over all three spawning seasons based upon the 0.165-mm samples. This range is low compared to values cited in the literature, although most of the literature estimates apply to early larvae. Nevertheless, it appears that the greater mean size and survival of larvae reported for the 1976 season, particularly during the overwinter period, may be related to what was apparently an increase in the copepod prey Pseudocalanus sp. and Paracalanus parvus.

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Table 1. Percentage occurrence of prey in guts of larval herring processed from each of 15 cruises conducted during the 1974-1976 spawning seasons.

Species	Stage	Season: 1974-75 Cruise: Cryos 74-04	Prognoz 74-01	Dohrn 74-01	AlbIV 74-13	AlbIV 75-02	Year Total	Season: 1975-76 Cruise: Belogorsk 75-02	Belogorsk 75-03	Dohrn 75-187	AlbIV 75-14	AlbIV 76-01	*Wieczno 76-01	Yearly Total	Season: 1976-77 Cruise: Wieczno 76-03	Dohrn 76-02	Researcher 76-01	Mt. Mitchell 77-01	Yearly Total
		7-24 Sept	18-30 Oct	16-23Nov	4-19Dec	12-28Feb		25 Sep-8 Oct	17-30 Oct	1-18 Nov	5-17 Dec	10-25 Feb			14 Oct-3 Nov	15-29 Nov	27Nov-11Dec	13-24 Feb	
Pseudo-calanus sp.	nauplius	36.7	3.0		2.3		2.1		8.1	1.6				0.4					
	copepodite		6.1		0.5	3.1	1.4			4.9	1.7	0.8		1.7			37.5		3.3
	adult			2.2	5.2	56.1	19.7			2.5	10.8	16.3	27.7	11.4	12.1	42.9	37.5	47.7	33.7
Para-calanus parvus	nauplius				0.5		0.3												
	copepodite			2.2	2.6		1.8			13.1	7.6			5.4	3.0				
	adult		9.1	15.6	10.1	1.2	7.5			13.9	29.6	3.0	3.6	18.3	6.1	42.9	25.0	2.3	24.2
Pseudo-para	nauplius	3.3			2.0		1.4		13.5					0.4					
	copepodite		3.0		1.2		0.9		2.7	2.5	1.4	1.0		1.4	6.1				6.1
	adult				1.0	0.5	0.8				3.2	4.5	0.6	3.2	3.0				3.0
Centro-pages typicus	nauplius	26.7					0.4		2.7					0.08					
	copepodite		3.0	33.3	19.3	1.4	14.2			1.6	7.9	1.0	1.2	4.7	6.1				6.1
	adult			6.7	1.7	2.6	2.0				0.3	1.5	0.6	0.7		14.3			3.0
Centro-pages hamatus	nauplius																		
	copepodite				15.2	5.1	11.4												
	adult				5.1	10.8	6.5						1.8						
Centro-pages spp.	nauplius		3.0		0.08		0.1												
	copepodite				5.7	0.5	3.9			1.6				0.2	9.1				3.3
	adult				0.7	1.6	0.9												
Oithona spp.	nauplius		3.0				0.05												
	copepodite		3.0		1.8		1.2		5.4				3.6	0.2	12.1				4.3
	adult		9.1	2.2	5.2	0.7	3.8			4.1		4.3	3.0	1.8					
Calanus finmar-chicus	nauplius				0.3		0.2			4.1				0.7					
	copepodite											0.3	5.4	0.08					
	adult									0.8			10.2	0.08					
Unidenti-fied calanoid	nauplius	33.3	3.0	11.1	2.0		2.2		43.2	17.2				3.1					
	copepodite		39.4	13.3	3.6		3.3		5.4	8.9	4.0	0.8		3.4	9.1				3.3
	adult		9.0	13.3	6.5	14.3	8.9		10.8	23.8	31.1	24.3		27.5	33.3			50.0	35.9
Copepod eggs					2.8	1.7	2.3				0.2	41.3		13.7					
Invertebrate eggs					3.5		2.3		2.7		1.2	1.3	25.9	1.2					
Mollosc larvae					0.08		0.05		2.7		0.2			0.2					
Spiratella retroversa					0.2		0.1												
Mysids													7.2						
Euphausiids													7.8						
Hyperiids													0.6						
Fish larvae					0.2		0.2												
Candacia armata											0.2			0.08					
Acartia longiremis													0.6						
Unident. invertebrate					0.08	0.2	0.1		2.7		0.2			0.2					
# Stations		4	3	3	34	23	67	3	2	15	32	35	14	101	8	4	4	9	25
% Feeding by Day		5.9	16.7	43.3	25.7	8.6	22.6	0	23.3	13.8	29.2	19.6	57.1	24.6	14.8	14.3	42.9	48.9	32.1
Mean Length (mm) of Larvae		6.8	9.1	13.7	15.4	27.1		5.8	8.0	12.1	16.6	28.4	33.8		11.3	18.0	20.8	23.5	-

* Not included in yearly total.

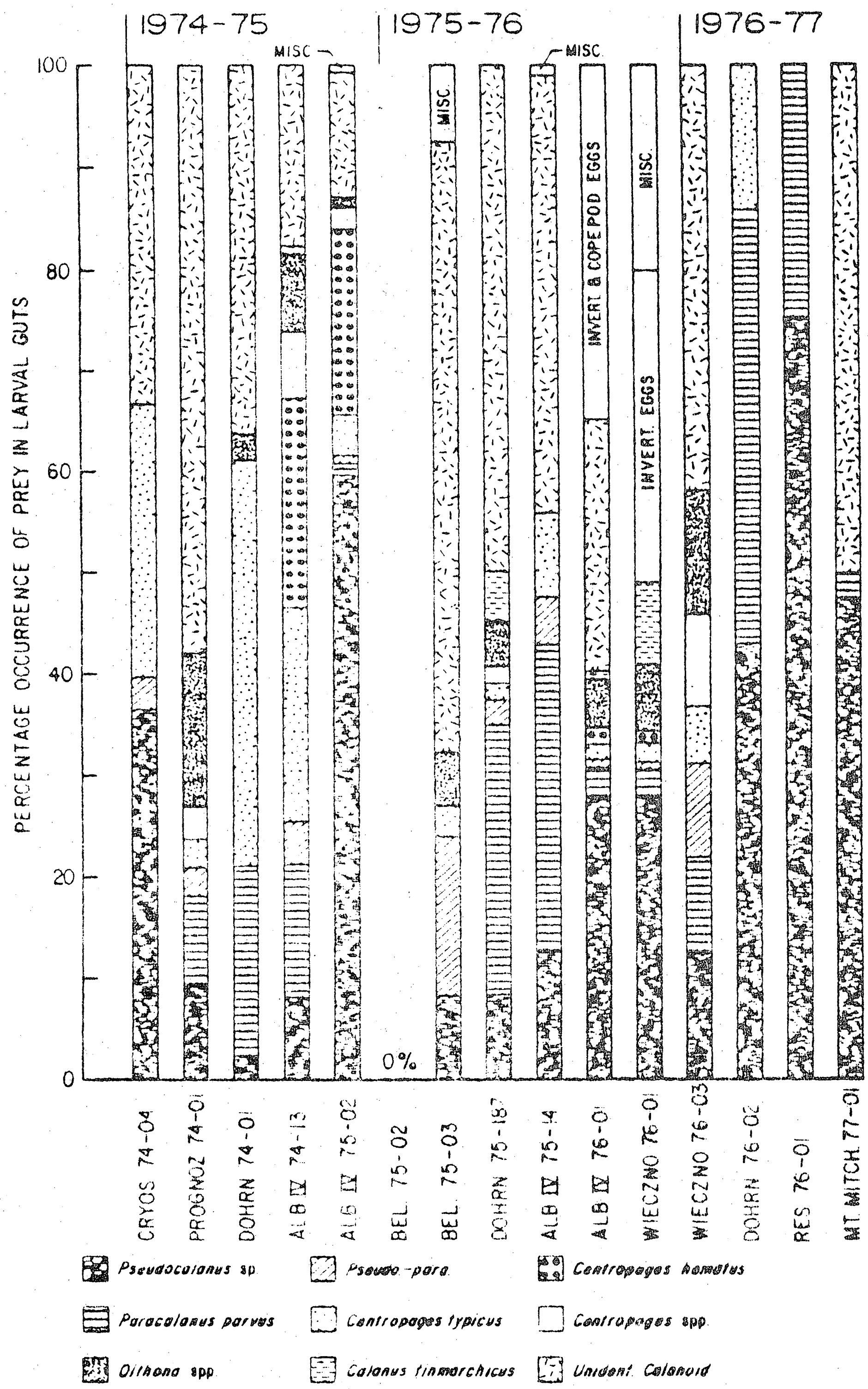

Figure 1. Percentage occurrence of copepod prey in autumn-spawned larval herring during 15 cruises over three spawning seasons (1974, 1975, and 1976) in Georges Bank-Nantucket Shoals area.

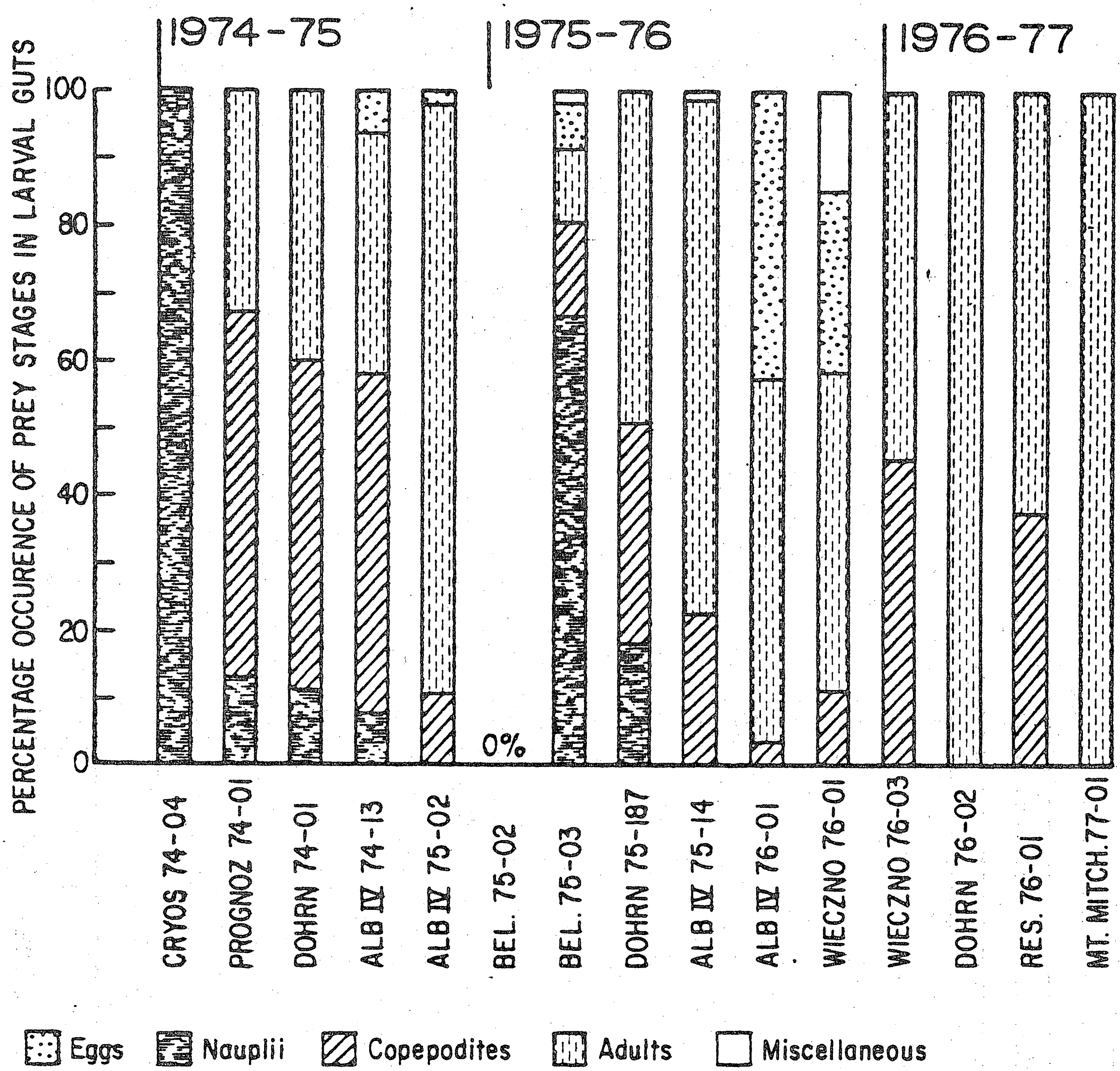

Figure 2. Percentage occurrence of the developmental stages of the copepod prey in autumn-spawned larval herring guts during 15 cruises over three spawning seasons (1974, 1975, and 1976) in the Georges Bank-Nantucket Shoals area.

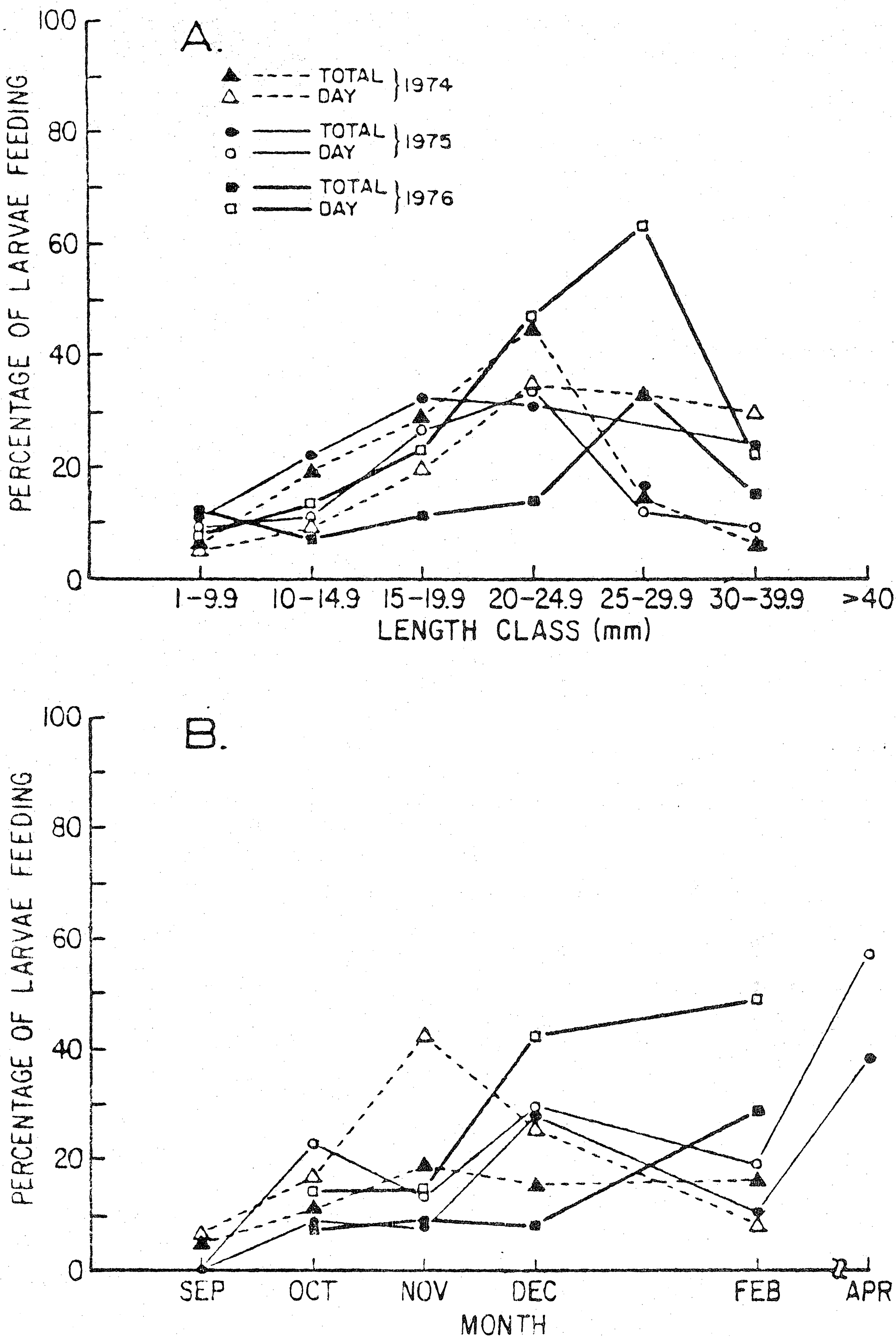

Figure 3. Percentage feeding of autumn-spawned herring larvae in the Georges Bank-Nantucket Shoals area over 24 hours compared to the percentage feeding during daylight hours only for the 1974, 1975, and 1976 spawning seasons plotted by: (A.) Larval length class, and (B.) Survey month.

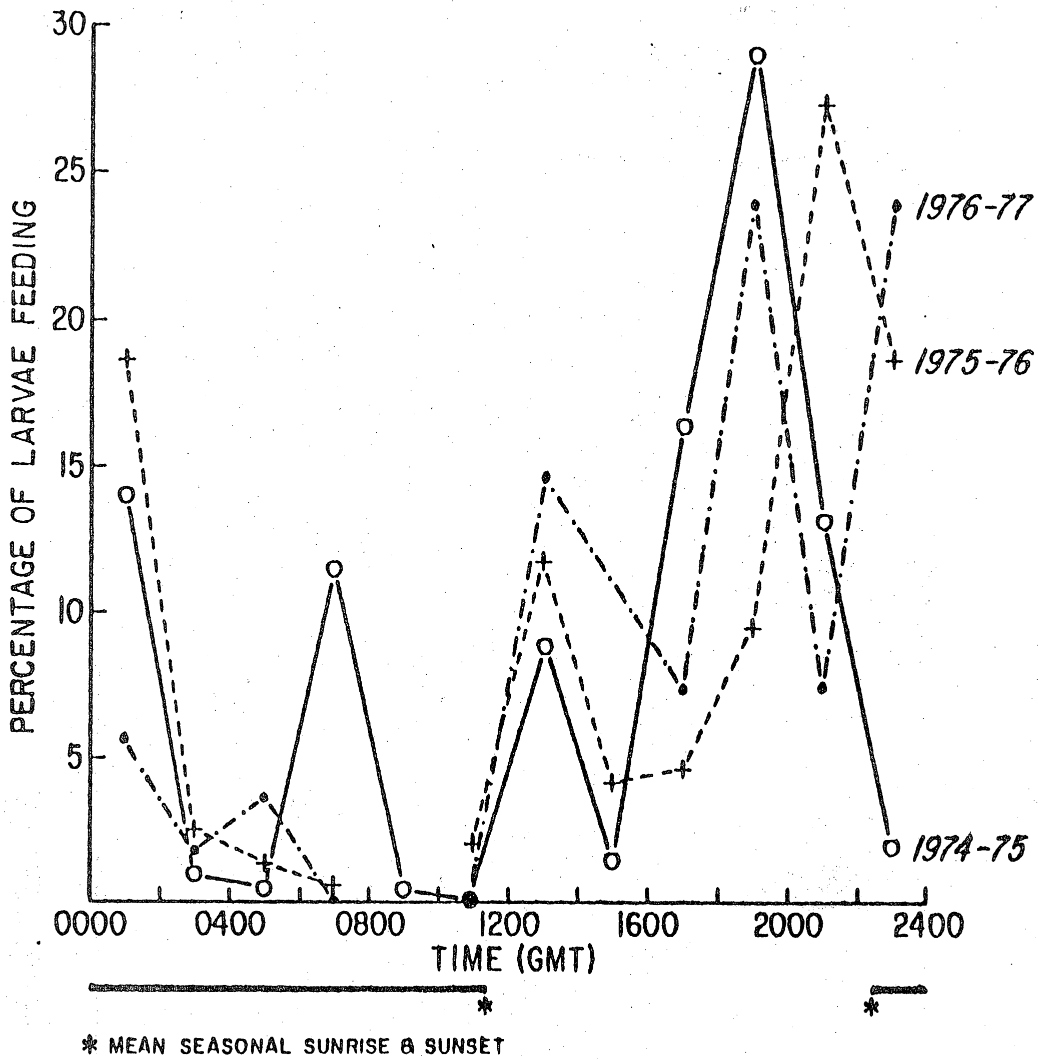

Figure 4. Percentage feeding of autumn-spawned herring larvae in the Georges Bank-Nantucket Shoals area during each spawning season (1974, 1975, and 1976) over a 24-hour period (GMT), with mean seasonal time of sunrise and sunset indicated.

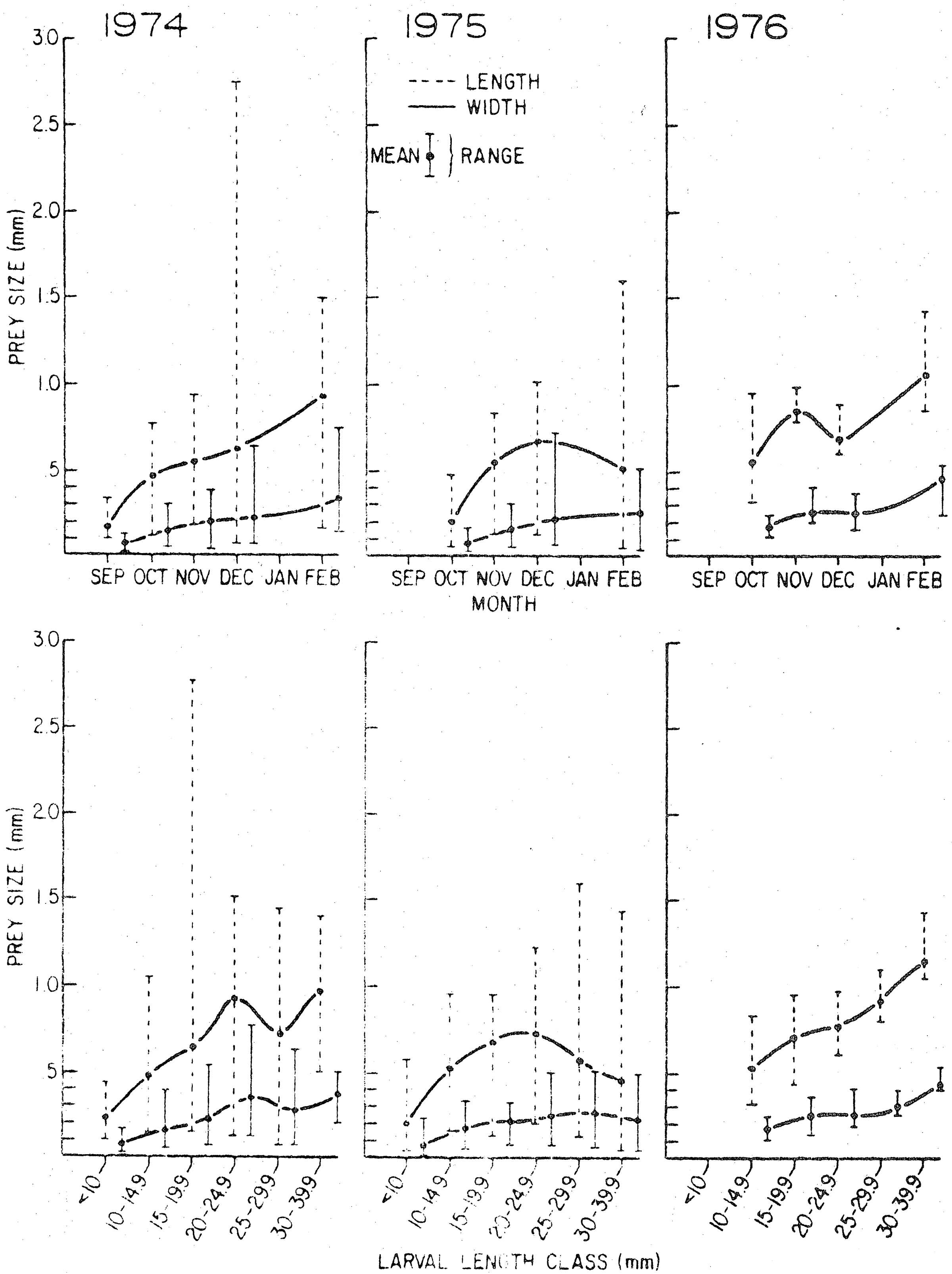

Figure 5. Mean prey length (mm) and width (mm) of autumn-spawned larval herring in the Georges Bank-Nantucket Shoals area over each spawning season (1974, 1975, and 1976) plotted by survey month and larval length class.

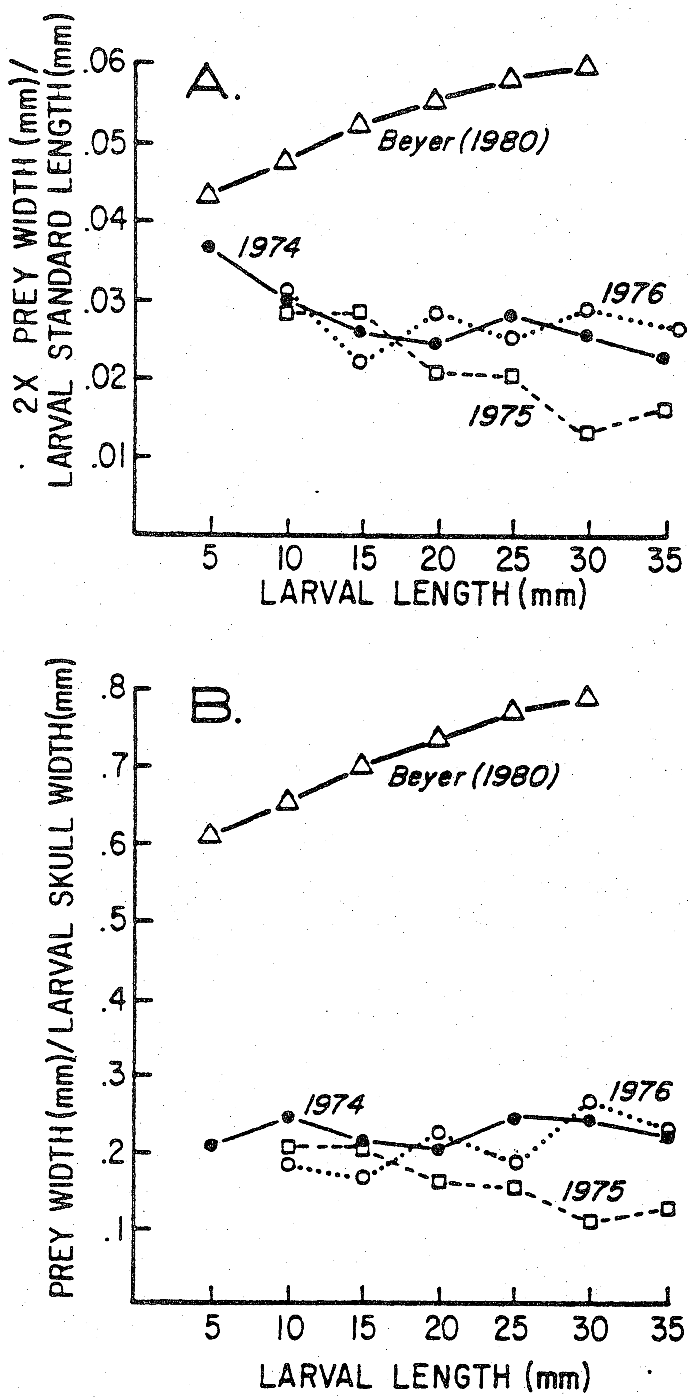

Figure 6. Comparison of (A.) 2 x prey width (mm)/larval standard length (mm) plotted by larval standard length and (B.) prey width (mm)/larval skull width (mm) plotted by larval standard length for autumn-spawned larval herring in the Georges Bank-Nantucket Shoals area over the 1974, 1975, and 1976 spawning seasons with the optimal values for these ratios predicted by the Beyer (1980) feeding model.

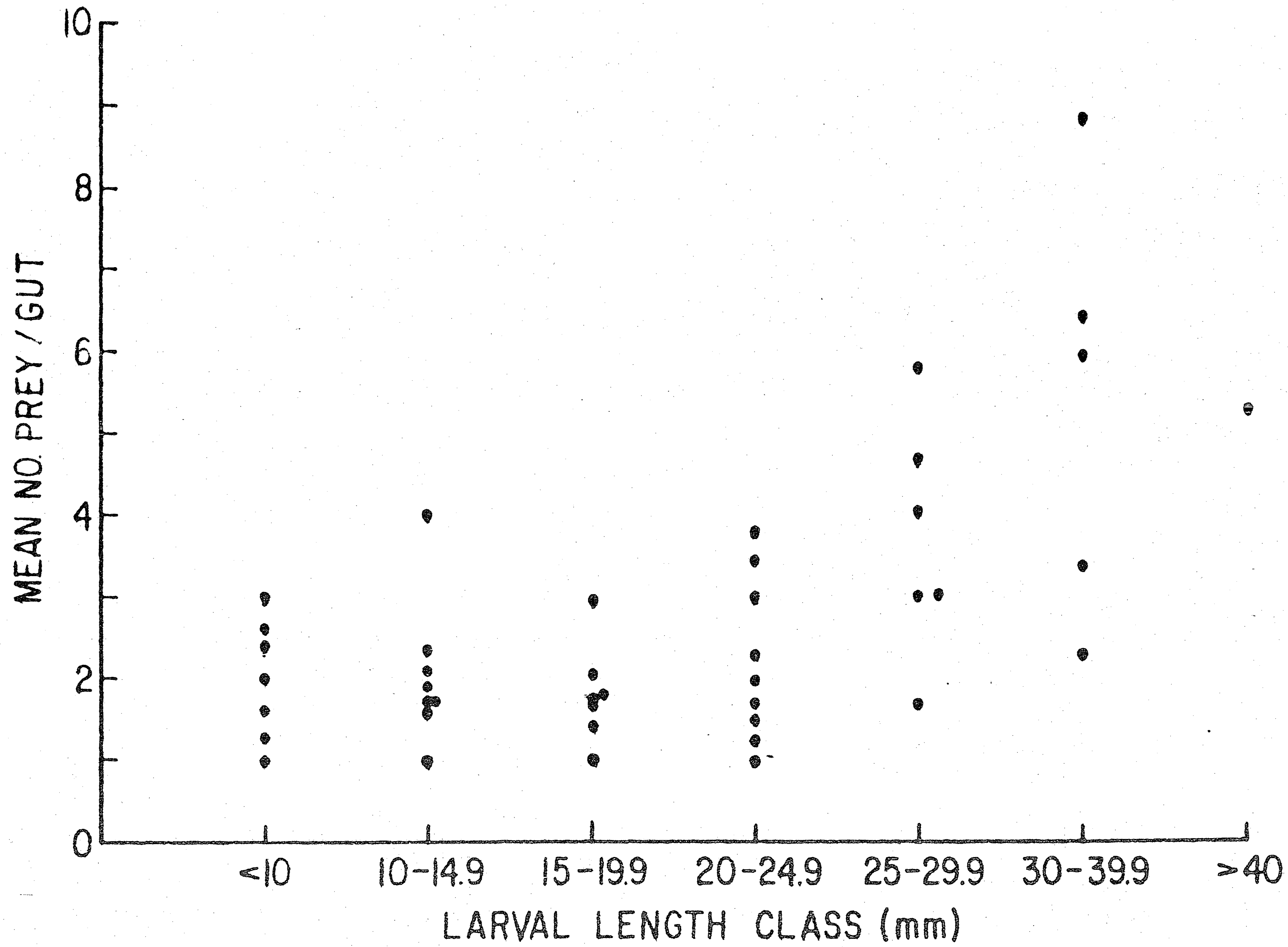

Figure 7. Mean number of prey items per larval herring gut plotted by larval length class for each of the 15 cruises during the 1974, 1975, and 1976 spawning seasons in the Georges Bank-Nantucket Shoals area.

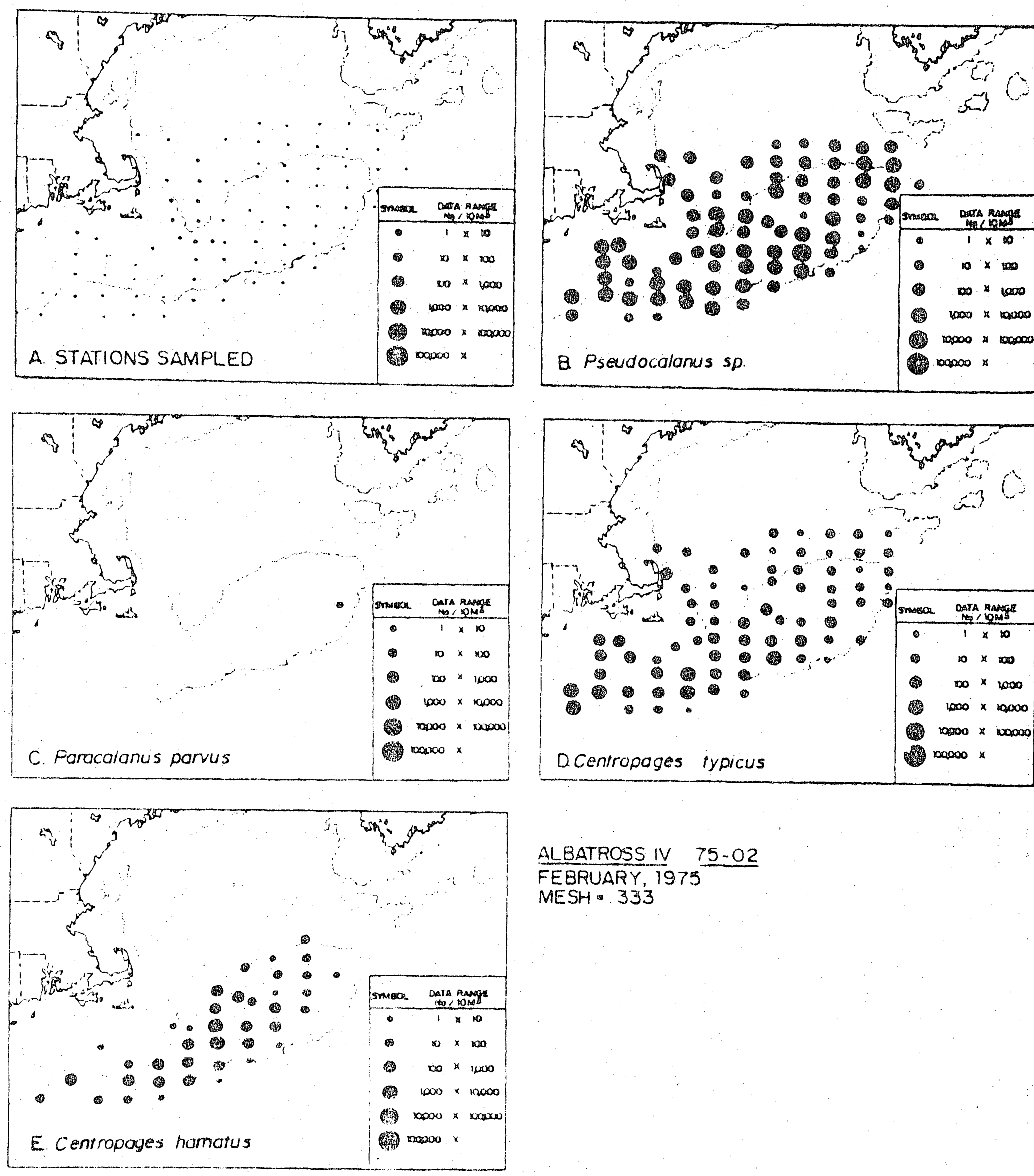

Figure 8. Distribution and abundance of the adults of 4 dominant copepod prey species of autumn-spawned larval herring in the Georges Bank-Nantucket Shoals area during February 1975, based on the 0.333-mm mesh sample series.

A. Stations sampled
B. Pseudocalanus sp.
C. Paracalanus parvus
D. Centropages typicus
E. Centropages hamatus

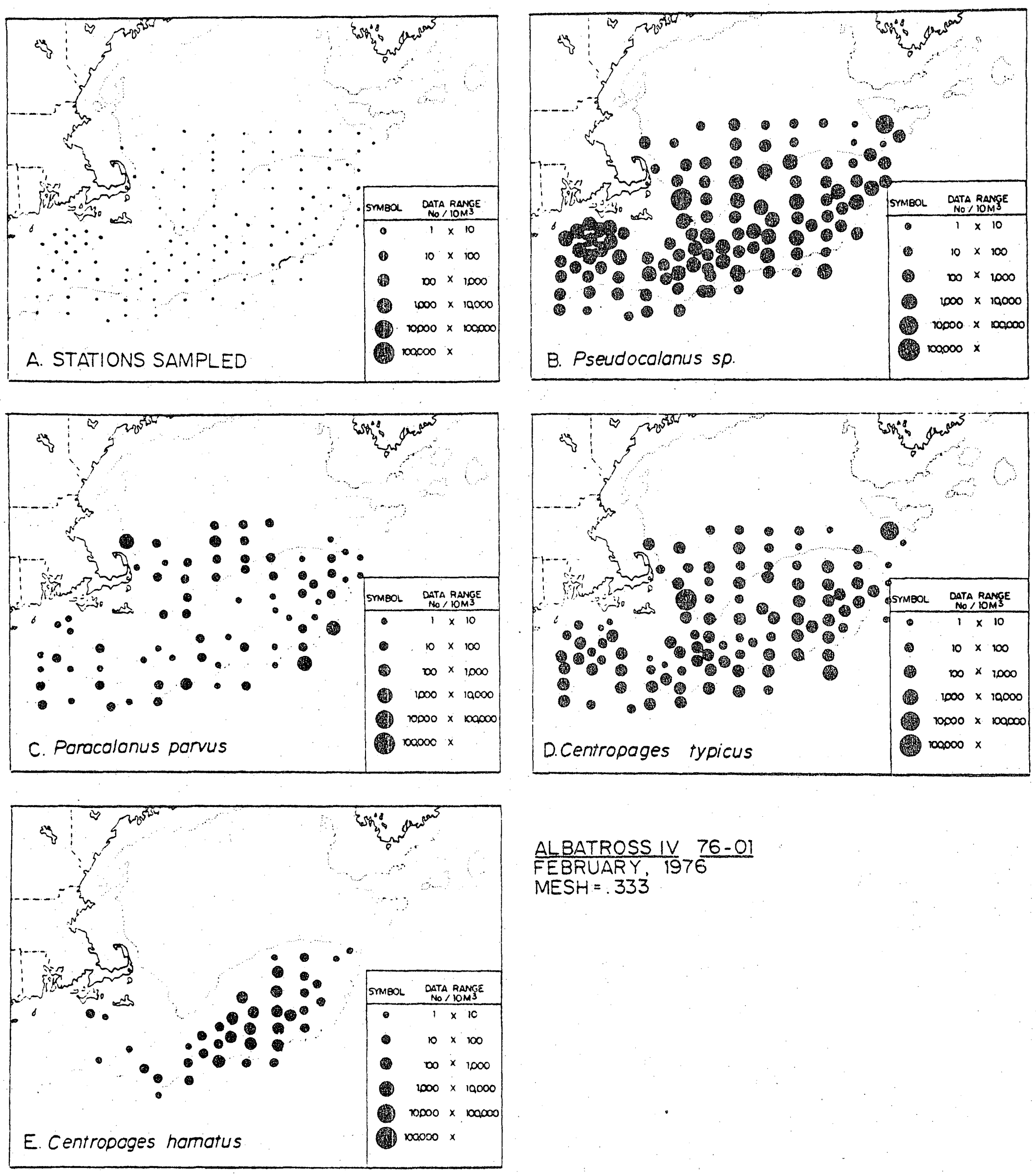

Figure 9. Distribution and abundance of the adults of 4 dominant copepod prey species of autumn-spawned larval herring in the Georges Bank-Nantucket Shoals area during February 1976, based on the 0.333-mm mesh sample series.

A. Stations sampled
B. Pseudocalanus sp.
C. Paracalanus parvus
D. Centropages typicus
E. Centropages hamatus

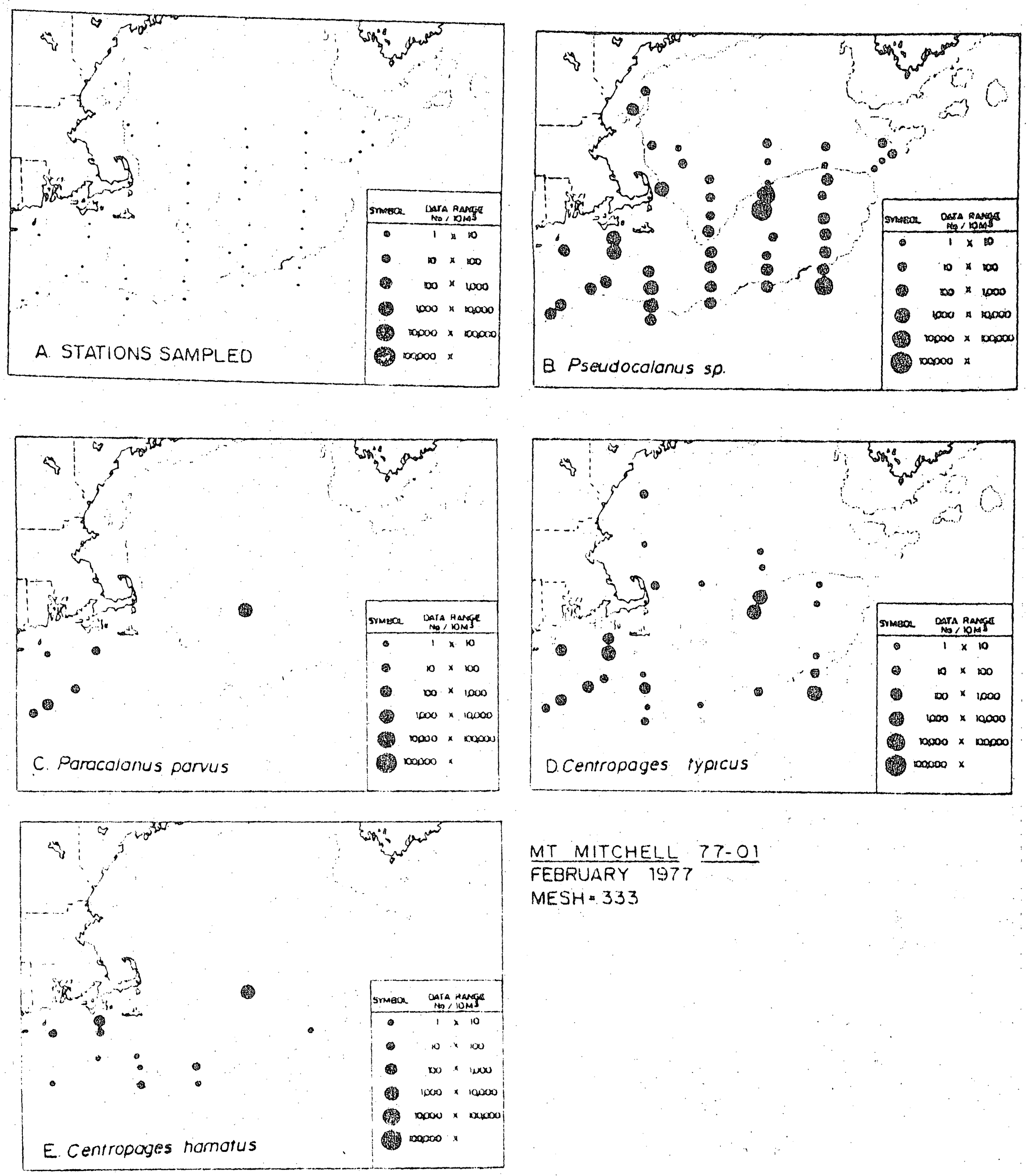

Figure 10. Distribution and abundance of the adults of 4 dominant copepod prey species of autumn-spawned larval herring in the Georges Bank-Nantucket Shoals area during February 1977, based on the 0.333-mm mesh sample series.

A. Stations sampled
B. <u>Pseudocalanus</u> sp.
C. <u>Paracalanus parvus</u>
D. <u>Centropages typicus</u>
E. <u>Centropages hamatus</u>

APPENDIX - Summary of the results of this study of larval herring feeding on Georges Bank compared with other important feeding studies of clupeoid larvae (Clupea harengus L. except where noted).

Reference	Location	Season	Feeding Period	% Larvae Feeding	Length or Age of Larvae	Prey Size Range (Length)	Dominant Prey	Available Prey
Cohen & Lough (This Study)	Georges Bank	1974-Fall & Winter	Day	22.6	1974 <10 mm 10-14.9 15-19.9 20-24.9 25-29.9 30-39.9	.1 - .44 mm .12 - 1.06 .12 - 2.78 .08 - 1.44 .16 - 1.50 .5 - 1.40	1974 Pseudocalanus sp. adults - 19.7% Centropages typicus copepodites - 14.2% C. hamatus copepodites - 11.4%	.165 and .333 mm mesh bongos Both Centropages spp. and Paracalanus parvus = abundant in fall. Pseudocalanus sp. = more abundant in late winter and spring. Oithona spp. = fairly high numbers in fall, winter and spring. In 1974 Centropages was more numerous than in 1975 and 1976 on Georges Bank.
		1975-Fall, Winter, Spring	Day	24.6	1975 <10 10-14.9 15-19.9 20-24.9 25-29.9 30-39.9	.04 - .58 .16 - .96 .12 - .96 .20 - 1.24 .14 - 1.6 .05 - 1.44	1975 Pseudocalanus sp. adults - 11.4% Paracalanus parvus adults - 18.3% Unidentified calanoid adults 27.5% Copepod eggs - 13.7%	
		1976-Fall & Winter	Day	32.1	1976 10-14.9 15-19.9 20-24.9 25-29.9 30-39.9	.32 - .84 .44 - .96 .60 - .96 .82 - 1.10 1.04 - 1.44	1976 Pseudocalanus sp. adults - 33.7% Paracalanus parvus adults - 24.2% Unidentified calanoid adults - 35.9%	

Reference	Location	Season	Feeding Period	% Larvae Feeding	Length or Age of Larvae	Prey Size Range (Length)	Dominant Prey	Available Prey
Bainbridge & Forsyth (1971)	Firth of Clyde Ballantree Bank area	Apr. & May 1962, 1963, 1964	Day Night (before sun-rise)	70% 0%	10-11 mm 12-15 mm 16-17 mm	$\leq$ 0.6 mm $\leq$ 1.0 mm $\leq$ 1.2 mm	nauplii & copepodites of dominant copepods	1962: Para-Pseudocalanus, Temora, Acartia, Centropages hamatus more abundant than 1963; nauplii and copepodites relatively scarce. 1963: Para-Pseudocalanus, Calanus; larval cirripedes, molluscs, and polychaetes more abundant than 1962 or 1964
Bhattacharyya, R.N. (1957)	Moray Firth Cromarty Firth & Fair Isle area of North Sea	Apr. & Aug.-Nov., 1952		11% Highest in morning & right before sunset - 35.5% overall = 35.2%	6-9 mm 9-35 mm		Coccinodiscus, Nauplii of Pseudocalanus copepod eggs, adults & juvenile copepods, lamellibranch larvae, gastropod larvae, centric diatoms, tintinnids, dinoflagellates. Oithona and Pseudocalanus = dominant copepods; "green patch"	

Reference	Location	Season	Feeding Period	% Larvae Feeding	Length or Age of Larvae	Prey Size Length (Length)	Dominant Prey	Available Prey
Bjorke, H. (1971)	Møre, Norway	Spring, 1967 (4-10 Apr.)	Noon Midnight	76% 32% overall = 51%			Calanus finmarchicus eggs = 94%; C. finmarchicus nauplii = 3%; copepodites & adults of Microsetella norvegica = 1%; other organisms = 2% copepods = 4% of gut contents	90% of copepod eggs were Calanus finmarchicus; 80% of copepod nauplii were Calanus finmarchicus; Oithona similis was common; Totals: 64% copepodites; 25% copepod nauplii; 1% Microsetella sp. Copepods = 43% of plankton samples
Blaxter, J.H.S. (1965a) [from Hentschel (1950) & own data]					9-18 mm 18-40 mm	Carapace length of copepods: 0.3 - 0.9 mm 0.3 - 1.1 mm	smaller larvae select copepod eggs & nauplii, mollusc larvae, green food; larger larvae select copepodites and adults especially Pseudocalanus	
Bowers, A.B. & D.I. Williamson (1951)	Southeast of Isle of Man	Sept.-Dec., 1949		28% 70% 60%	Larvae (up to yolk sac resorption - 10 mm) Post Larvae 10-15 mm 15-25 mm		mollusc larvae more important; copepods more important; Pseudocalanus most important species of prey for larvae ≥15 mm	Sept./Oct. - mostly Pseudocalanus and Paracalanus (combined here) (300/m^3 in Sept.), Acartia clausi (80/m^3 in Sept.), Oithona similis (30/m^3 in Sept.), Calanus finmarchicus (up to 10/m^3); eggs & nauplii; Nov./Dec. - all decreased; lamellibranch & gastropod larvae common in all months but missed by their sampler.

Reference	Location	Season	Feeding Period	% Larvae Feeding	Length or Age of Larvae	Prey Size Range (Length)	Dominant Prey	Available Prey
Gosheva, T.D. and S.A. Slonova (1976) (*Clupea harengus pallasi maris-albi*)	Onega Bay (White Sea)	Spring. 1967-1972		20-40%	6-8.9 mm		Onega Bay small zooplankton; juvenile calanoids, mollusc larvae rotifers & their eggs.	Onega Bay - 6.6-19.1x10^3 organisms/m^3. *Synchaeta* sp. and all stages of calanoids. Also lamellibranch and *L. helicinia* larvae, *Tintinnopsis meuner*; few juvenile cladocerans & polychaetes
					>9 mm		Same but with larger proportion of calanoids varied yr. to yr.	
	Duina Bay (Un'ya Bay)	Spring, 1968-1972		46.6-62%	6-8.9 mm >9 mm		Un'ya Bay nauplii & copepodites of calanoids, older calanoids. Also some lamellibranch & polychaete larvae & *Limacina helicina* juveniles	Un'ya Bay - 3.4-10.7x10^3 organisms/m^3; mainly calanoids & their young, (2.9-9.2x10^3/m^3) also lamellibranch larvae (in low numbers - 38-40 larvae/m^3).
	Mezen Bay	Spring, 1968-1972			6-11.9 mm		Mezen Bay *Tintinnopsis* sp. most important, lamellibranch larvae, calanoids of all stages. All areas varied from yr. to yr.	Mezen Bay - 315-1953 organisms/m^3; polychaeta & *Balanus* larvae most abundant; some calanoids, *T. meuneri*, and lamellibranch larvae.

Reference	Location	Season	Feeding Period	% Larvae Feeding	Length or Age of Larvae	Prey Size Range (Length)	Dominant Prey	Available Prey
Last, J.M. (1980)	West-central North Sea	Feb. to Nov., 1980	24 hr. period	23.7% overall				Not available here
				0%	5-6.9		None	
				16%	7-7.9	0.10	67% tintinnids 33% copepod nauplii	
				15%	8-8.9	0.20	67% copepod nauplii 33% Paracalanus parvus copepodites	
				14%	9-9.9	0.25	50% copepod nauplii 50% Paracalanus parvus copepodites	
				35%	10-10.9	0.33	16% copepod nauplii 51% Oithona helgolandica copepdites 27% Paracalanus parvus copepodites	
				38%	11-11.9	0.30	26% copepod nauplii 31% Oithona helgolandica copepodites 31% Paracalanus parvus copepodites	

Reference	Location	Season	Feeding Period	% Larvae Feeding	Length or Age of Larvae (mm)	Prey Size Range Length (mm)	Dominant Prey	Available Prey
Last, J.M. (1980) (continued)				29%	12-12.9	0.32	31% copepod nauplii 14% Oithona helgolandica copepodites 38% Paracalanus parvus copepodites	
				14%	13-13.9		33% Oithona helgolandica copepodites 33% Paracalanus parvus copedites 13% Temora longicornis copepodites	
				4%	14-14.9		100% copepod nauplii	
				27%	15-15.9		44% copepod nauplii 33% Oithona helgolandica copepodites 23% Temora longicornis copepodites	
				29%	16-16.9		20% copepod nauplii 20% Oithona helgolandica copepodites 50% Paracalanus parvus copepodites	

Reference	Location	Season	Feeding Period	% Larvae Feeding	Length or Age of Larvae (mm)	Prey Size Range (length mm)	Dominant Prey	Available Prey
Last, J.M. (1980) (continued)				50%	17-17.9		67% *Oithona helgolandica* copepodites 33% *Paracalanus parvus* copepodites	

Reference	Location	Season	Feeding Period	% Larvae Feeding	Length or Age of Larvae	Prey Size Range (Length)	Dominant Prey	Available Prey
Marshall, S.M. et al. (1937)	Clyde Sea area	Spring 1934, 1935		Low	yolk-sac larvae, larger larvae		"green mush," developmental & adult stages of copepods, Apr. 1935: Pseudocalanus, Microcalanus, Oithona May: Centropages, Temora, Acartia varied from station to station over time; also consumed Pseudocalanus and/or Calanus eggs in large numbers; Cladocerans	Microcalanus, Pseudocalanus, Calanus, Centropages, Oithona, Acartia, Temora, and developmental stages predominated
Noskov, A.S. et al. (1979)	Georges Bank (Northwest Atlantic)	Fall-October, 1965-1975	Day	1966 3% = minimum 1972 66% = maximum Average = 21% 11% 28% 33%	All Lengths 5.0-7.9 mm 8.0-12.9 mm 13.0-17.9 mm	 0.10-0.75 mm 0.15-1.10 mm 0.10-1.50 mm	5.0-7.9 mm larvae copepod eggs & nauplii 8.0-12.9 mm Small stages of Oithona spp., Centropages spp., and Paracalanus spp. 13.0-17.9 mm Larger stages of Paracalanus spp., Pseudocalanus spp., and Calanus finmarchicus	Varied greatly yr. to yr. Oithona spp., Centropages spp., and copepod nauplii were dominant; high numbers of zooplankton in 1969-1970 due to large increase in Oithona spp.; concentrations were $4\text{-}16 \times 10^3$ organisms/m^3

References	Location	Season	Feeding Period	% Larvae Feeding	Length or Age of Larvae	Prey Size Range (Length)	Dominant Prey	Available Prey
Rudakova, V.A. (1971)	Norwegian Coast & Faroe Archipelago	Mar. 1966-1967	Largest numbers fed in morning & early evening	Norwegian Shoals 1966-5.1% 1967-13.6%			Norwegian Shoals 1966: copepod eggs-81.7%, nauplii & copepodites-19.2% 1967: copepod eggs-80.9%, nauplii & copepodites-21.1%	
			See paper for details of % feeding at different depths & times	Lofoten Area 1966-6.0% 1967-0%	5-16 mm		Lofoten Area Copepod eggs - 44.4%, nauplii & copepodites - 51.9%	1966 - juvenile copepod dominated 1967 - more copepod eggs
				Faroe Area 1966-25% 1967-34.6%			Faroe Area Juvenile plankton organisms, diatoms	
Schnack, D. (1972)	North Sea	Autumn		50%	14-17 mm	0.1-0.9 mm	North Sea copepod nauplii-39%; Acartia copepodites, mollusc larvae = major prey; some adult Acartia & Oithona	North Sea 10-meter depth: copepod nauplii = 37% by weigth, Acartia copepodites - 38%, Oithona - 25%; mid-depth: nauplii largest numbers, + 10 groups copepodites (Acartia), bivalve larvae, Acartia adults, Oithona, Temora, Pseudo-Paracalanus, copepod eggs, gastropod larvae, harpacticoids; deepest level: larger % copepodites, adult Acartia & Pseudocalanus, decrease in nauplii

Reference	Location	Season	Feeding Period	% Larvae Feeding	Length or Age of Larvae	Prey Size Range (Length)	Dominant Prey	Available Prey
Schnack, D. (1972) (continued)	Schlei (coastal Baltic Sea)	Spring		70-100%	Mainly 14 & 19 mm some 8 mm & 20 mm larvae	Mean Length 0.19-0.58 mm	Apr.-May Schlei 14 mm larvae - nauplii & Eurytemora copepodites & adults some harpacticoids, Oithona, & Podon 19 mm larvae - nauplii = rare; Acartia, Pseudocalanus, and mainly Eurytemora; (copepodite stages most common)	Schlei very variable-changing frequencies of Pseudocalanus, Acartia, Eurytemora, calanoid copepodites & nauplii, cirripede and polychaeta larvae, cladocerans, & harpacticoids, Brachionus, Filina (rotifers)
					19-24 mm		June adult copepods, Brachionus, Filina, gastropods	Different proportions of same groups - consult original paper for details
Sherman, K. and K.A. Honey (1971)	Coastal Gulf of Maine	Autumn, Winter & Spring of 1967-68; Spring 1965, 1966		1965-1968 Autumn 57.3%	Autumn 1-10 11-20	Autumn 0.20-0.62 0.16-0.86	Autumn 7-10 mm larvae eat nauplii & copepodites	Increase in standing crop in spring; larger variety consumed in spring
				Winter 51.0%	Winter 11-20 21-30 31-40	Winter 0.39-0.74 0.09-0.64 0.45-2.15	Winter copepods are dominant	
				Spring 61.2%	Spring 21-30 31-40 41-50	Spring 0.06-1.73 0.19-1.60 0.34-0.80	Spring cirripede larvae, crustacean eggs, & tintinnids; larger larvae eat Pseudocalanus	

Reference	Location	Season	Feeding Period	% Larvae Feeding	Length or Age of Larvae	Prey Size Range (Length)	Dominant Prey	Available Prey
Sherman, K and K.A. Honey (1971) (continued)							<u>Spring</u> (cont'd) *minutus* & *Oithona* sp. in spring also harpacticoids	