

# Prey Field of Larval Herring *Clupea harengus* on a Continental Shelf Spawning Area

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**ABSTRACT:** The predator-prey relationships of larval *Clupea harengus* L. were investigated on a continental shelf spawning area, Georges Bank-Nantucket Shoals, off the northeastern coast of the United States during 3 autumn-winter spawning seasons. Our observations are based on examination of the alimentary tracts (guts) of over 8,000 larval herring. Feeding was concentrated into 2 peaks during the daylight hours, and larvae averaged 1 to 7 prey (0.5 to 48  $\mu\text{g}$  dry weight) per gut. Larvae preyed on the synchronously developing juvenile and adult stages of the dominant copepods of this area (*Pseudocalanus* sp., *Paracalanus parvus*, *Centropages typicus*, *C. hamatus*, *Oithona* spp., and *Calanus finmarchicus*). During 1974, *Centropages* spp. and *Pseudocalanus* sp. dominated the larval diet; during 1975 and 1976, *Pseudocalanus* sp. and *Paracalanus parvus* were dominant. This shift in diet reflects a shift in zooplankton species distribution in the area. Larger, more robust larvae were collected in 1976 than in 1974 and 1975; survival was greater during this season, and a higher percentage of feeding larvae was observed.

## INTRODUCTION

In 1971 the International Commission for the North-west Atlantic Fisheries (ICNAF) initiated an investigation designed to measure major variations in larval herring production, growth and survival, and associated environmental conditions during the first 6 mo of life to determine the influence of larval mortality on the recruitment of new year-classes. Specific program objectives and larval abundance, distribution, and mortality patterns over the ICNAF time series are reported by Lough et al. (1980, 1981). The present study\* was conducted concurrently as part of the MARMAP (Marine Resource Monitoring, Assessment, and Prediction) program of the Northeast Fisheries Center (NEFC), which measures long-term variability of fish stock abundance off the northeastern United States (Sherman, 1980).

Fish spawning and the production cycles of the larval prey appear to be synchronous (Cushing, 1967). A secondary peak in zooplankton abundance off the coast of Maine was found to be synchronized with larval herring spawning by Sherman et al. (1976 and

1978) and Sherman (1980). 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 to permit adequate feeding. The 2 major causes of larval fish mortality are starvation and predation (Hunter, 1976). In the Georges Bank-Nantucket Shoals area 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 (Chenoweth, 1970; Graham and Davis, 1971; Sherman and Honey, 1971; Dubé et al., 1977; Lough et al., 1980). Our main objective was to investigate the relationship between larval herring survival and their feeding (through gut content analysis), morphological condition, and the distribution and abundance of their prey in this area during the first 6 mo of larval life. Larvae were examined from surveys conducted during the 1974, 1975, and 1976 spawning seasons (a spawning season referred to here extends from September through February) because preliminary examination of the data indicated differences in production, growth and mortality, and spawning sites, as well as zooplankton prey and environmental data for these years.

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## METHODS

### Sea Sampling

Larval herring survey cruises were conducted approximately once a month on a standard grid of stations 24 to 32 km (15 to 20 miles) apart covering the Georges Bank-Gulf of Maine region (Fig. 1) from September through February. The Georges Bank-Nantucket Shoals area represents our most complete sampling coverage over the seasons in this time series. The cruise tracks, survey dates, and participating vessels are included in a laboratory data report by Lough

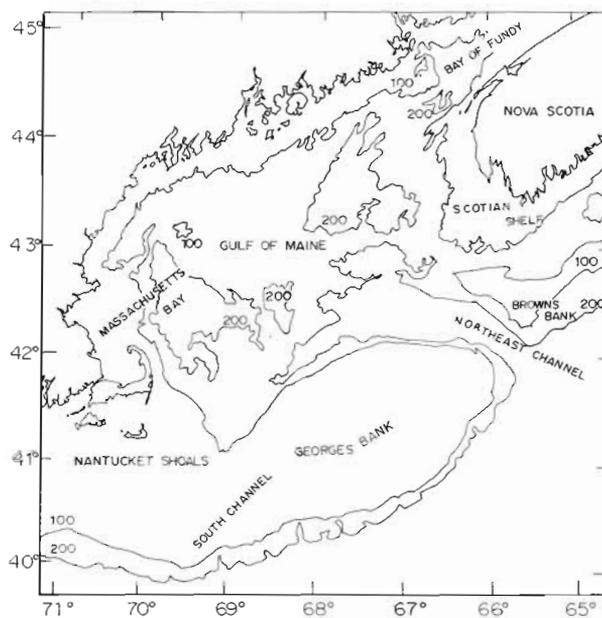


Fig. 1. Map of the Gulf of Maine-Georges Bank area

Table 1. Summary listing of survey cruises used in the larval herring food-habits study

Vessel cruise No.		Cruise dates
1	Cryos 74-04	7-24 Sep. 74
2	Prognoz 74-01	10-30 Oct. 74
3	A. Dohrn 74-01	16-23 Nov. 74
4	Albatross IV 74-13	4-19 Dec. 74
5	Albatross IV 75-02	12-28 Feb. 75
6	Belogorsk 75-02	9 Sep.-8 Oct. 75
7	Belogorsk 75-03	17-30 Oct. 75
8	A. Dohrn 75-187	1-18 Nov. 75
9	Albatross IV 75-14	5-17 Dec. 75
10	Albatross IV 76-01	10-25 Feb. 76
11	Wieczno 76-01	9 Apr.-4 May 76
12	Wieczno 76-03	14 Oct.-3 Nov. 76
13	A. Dohrn 76-02	15-29 Nov. 76
14	Researcher 76-01	27 Nov.-11 Dec. 76
15	Mt. Mitchell 77-01	13-24 Feb. 77

and Bolz (1980). The 15 surveys analyzed and referred to in this paper are listed in Table 1. Standard sampling gear consisted of a 61-cm mouth diameter bongo frame (0.333- and 0.505-mm mesh nets), and a 20-cm diameter bongo frame (0.053- or 0.253-mm and 0.165-mm mesh nets) (Posgay and Marak, 1980). At each station the sampling array was lowered at 50 m min<sup>-1</sup> to a maximum depth of 100 m or to within 5 m of the bottom, and retrieved at 10 m min<sup>-1</sup> in a double-oblique profile at a ship speed of 3.5 knots. During the 1974-1976 seasons, a 10-min neuston haul (1 × 2, or 0.5 × 1-m rectangular frame with a 0.505-mm mesh net) also was made simultaneously with the bongo haul.

### Program Rationale and Laboratory Procedures

Numerous other investigators have studied the feeding habits of larval herring, but only a few have focused on the Georges Bank area. In order to add significant new information to these data (Damkaer and Au, 1974; Noskov et al., 1979) an extensive in depth, systematic study was undertaken with expanded temporal and spatial coverage of the area.

Gut content and morphological condition factor measurements were recorded from 8,598 larvae from 15 cruises over the 1974, 1975, and 1976 spawning seasons. Our initial efforts were concentrated on the winter surveys because previous studies by Lough et al. (1980) and Dubé et al. (1977) indicated that the differences which existed among the 3 spawning seasons in larval production, growth, mortality, potential food organisms, and environmental conditions were accentuated at this time of year. Up to 100 larvae per station were processed from these surveys because of the low incidence of prey in the guts and the variability of the condition factor measurements. Larval densities were greatly reduced by February (approximately 1 to 10 larvae at only one third of the standard survey stations) and so as many larvae as possible were processed to provide representative data.

Later in the study we processed larvae from the autumn surveys because conditions existing at those times could influence over-winter survival as well as winter conditions. Very high densities (> 100 per station) of larvae were collected in autumn and the number of larvae which could be processed had to be reduced to 30 per station at 5 high-density stations per cruise. Preliminary work did indicate that larvae of the same size consumed similar numbers of prey of the same size and species.

Herring larvae were sorted from the selected 0.333- and 0.505-mm mesh bongo samples and vialled in 4 % buffered formalin at the Polish Sorting Center in Szczecin, Poland and by NEFC personnel. Larvae for

this investigation were randomly chosen from these vials. Larval dissections, measurements, and routine prey identifications were performed using a Wild M5\* dissecting microscope, and a Zeiss\* compound microscope was used to identify fragments and other unknown gut contents. Standard length was measured from the tip of the upper jaw to the end of the notochord in preflex larvae, and to the end of the hypural plate in postflex larvae. Skull width was measured at the widest portion of the skull, just posterior to the orbital region. In order to calculate maximum potential mouth gape, the maxillary length (composing most of the upper jaw) was measured and multiplied by  $\sqrt{2}$  (Shirota, 1970). The cephalothorax length of adult copepods and copepodites was recorded as prey length, and the maximum width excluding appendages as prey width. Total length of copepod nauplii prey, excluding caudal armature, was measured.

Corresponding 0.333- and 0.165-mm mesh zooplankton bongo samples were aliquoted to 500 or 500–1000 organisms, respectively, and sorted and identified by the Polish Sorting Center and NEFC personnel. 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 zooplankton organisms (see Cohen and Lough, 1982, for station plots). However, this mesh size retains copepods greater than 0.9 to 1.0-mm cephalothorax length (Davis, 1980), most of which are adults of both species of *Centropages* and female *Pseudocalanus* sp. The 0.165-mm samples processed were located along a 5-station transect across central Georges Bank (see Davis, 1982). This mesh size retains copepods whose cephalothorax lengths are equal to or greater than  $0.26 \text{ mm} \pm 0.08 \text{ mm}$ , which included all larval prey items enumerated except the first copepodite stages of *Paracalanus parvus* and both species of *Centropages*, the first 3 copepodite stages of *Oithona* spp., and most of the naupliar stages except those of *Calanus finmarchicus*.

## RESULTS

### Prey Selection Based on Gut Content

The dominant prey items in larvae ranging in standard length from 5- to 45-mm were developmental stages and adults of the following copepod species listed in general order of importance: *Pseudocalanus* sp., *Paracalanus parvus*, *Centropages typicus*, *C. hamatus*, *Oithona* spp., and *Calanus finmarchicus*.

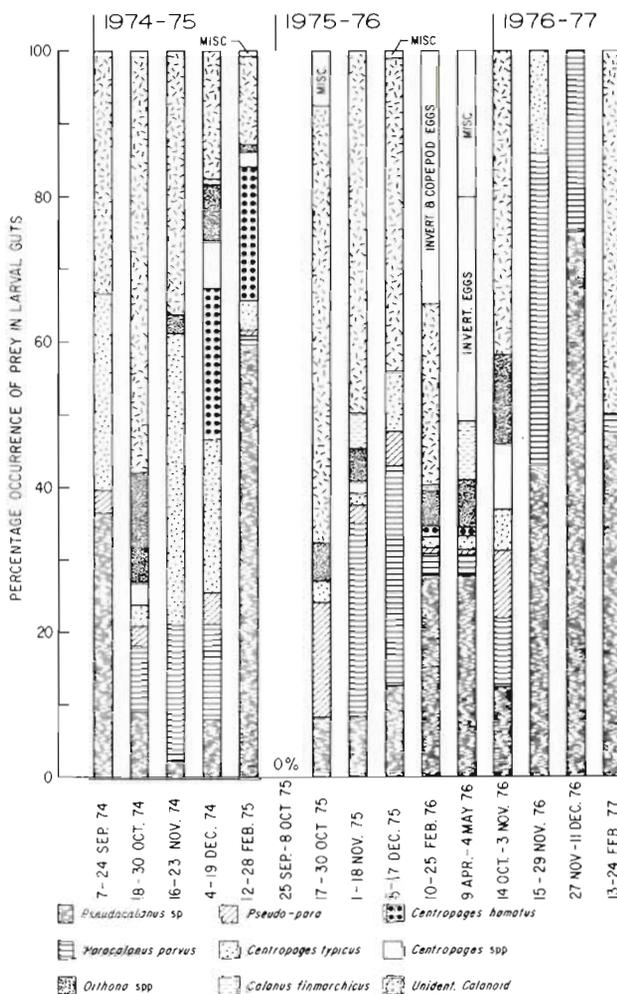


Fig. 2. Percentage occurrence of copepod prey in autumn-spawned larval herring during 15 cruises over 3 spawning seasons (1974, 1975, and 1976) in the Georges Bank-Nantucket Shoals area

In 1974, *Pseudocalanus* sp. adults (19.7%), and *Centropages typicus* (14.2%) and *C. hamatus* (11.4%) copepodites were the dominant prey items (Table 2 and Figs. 2 and 3). During 1975, *Paracalanus parvus* (18.3%), *Pseudocalanus* sp. (11.4%), 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 adult stages and older copepodites of

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

Table 2. 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				Season: 1975-76				Season: 1976-77					
		Cruise:		Cruise:		Cruise:		Cruise:		Cruise:		Cruise:			
		Cryos	Alb IV	Alb IV	Alb IV	Dohrn	Alb IV	Alb IV	Alb IV	Wiec-	Dohrn	Wiec-	Dohrn	Wiec-	Yearly
		74-04	74-01	74-13	75-02	75-03	75-14	75-14	76-01	76-01	76-03	76-02	76-01	76-01	total
<i>Pseudocalanus</i> sp.	Nauplius	7-24	18-30	16-23	4-19	12-28	1-18	5-17	10-25	9 Apr-	14 Oct-	15-29	27 Nov-	13-24	
	Copepodite	36.7	3.0	2.3	0.5	3.1	8.1	4.9	1.7	0.8	3.6	6.1	42.9	37.5	3.3
	Adult		6.1	5.2	56.1	19.7	2.5	10.8	16.3	27.7	11.4	12.1	42.9	37.5	33.7
<i>Paracalanus parvus</i>	Nauplius			0.5	0.3		13.1	7.6	3.0	3.6	3.0	6.1	42.9	25.0	2.3
	Copepodite		9.1	15.6	10.1	1.2	13.9	29.6	3.0	3.6	6.1	42.9	25.0	2.3	24.2
	Adult	3.3													
<i>Pseudo-para</i> sp.	Nauplius		3.0	2.0	1.4	1.4	2.5	1.4	1.0	1.4	6.1	6.1	6.1	6.1	6.1
	Copepodite		3.0	1.2	0.9	0.9	2.7	2.5	3.2	4.5	3.0	3.0	3.0	3.0	3.0
	Adult			1.0	0.5	0.8	2.7	2.5	3.2	4.5	3.0	3.0	3.0	3.0	3.0
<i>Centropages typicus</i>	Nauplius	26.7	3.0	33.3	19.3	1.4	1.6	7.9	1.0	1.2	6.1	6.1	6.1	6.1	6.1
	Copepodite		3.0	6.7	1.7	2.6	2.0	0.3	1.5	0.6	0.7	14.3	14.3	14.3	3.0
	Adult														
<i>Centropages hamatus</i>	Nauplius			15.2	5.1	11.4				1.8					
	Copepodite			5.1	10.8	6.5									
	Adult														
<i>Centropages</i> spp.	Nauplius		3.0	0.08	0.1	0.1	1.6	1.6	1.6	1.6	9.1	9.1	9.1	9.1	3.3
	Copepodite		3.0	5.7	0.5	3.9	0.7	0.5	0.9	0.9	0.2	0.2	0.2	0.2	0.2
	Adult			0.7	1.6	0.9									
<i>Oithona</i> spp.	Nauplius		3.0	1.8	1.2	0.05				0.05					
	Copepodite		3.0	9.1	2.2	0.7	3.8	5.4	4.3	3.0	1.8	12.1	12.1	12.1	4.3
	Adult		9.1	2.2	0.7	3.8	5.4	4.3	3.0	1.8	1.8	12.1	12.1	12.1	4.3
<i>Calanus finmarchicus</i>	Nauplius			0.3	0.2	0.2				0.2					
	Copepodite														
	Adult														
Unidentified calanoid	Nauplius	33.3	3.0	11.1	2.0	2.2	43.2	17.2	0.8	0.8	3.6	3.6	3.6	3.6	3.1
	Copepodite		39.4	13.3	3.6	3.3	5.4	8.9	4.0	0.8	3.0	3.0	3.0	3.0	3.4
	Adult		9.0	13.3	6.5	8.9	10.8	23.8	31.1	24.3	27.5	27.5	27.5	27.5	27.5
Copepod eggs	Invertebrate			2.8	1.7	2.3	2.7	2.7	0.2	41.3	13.7	13.7	13.7	13.7	13.7
	eggs			3.5	2.3	2.3	2.7	2.7	1.2	1.3	1.2	1.2	1.2	1.2	1.2
				0.08	0.2	0.1	2.7	2.7	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Mollusc larvae															
<i>Spiratella retroversa</i>															
Mysids															
Euphausiids															
Hyperiid															
Fish larvae															
<i>Candacia armata</i>															
<i>Acartia longiremis</i>															
Unident. invertebrate															
# Stations		4	3	3	34	23	3	15	32	35	14	101	4	4	9
	% Feeding by day	5.9	16.7	43.3	25.7	8.6	0	23.3	13.8	29.2	19.6	57.1	14.3	42.9	48.9
	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
# of larvae examined		312	150	150	3163	1230	16	150	776	1267	806	158	44	56	83

\* Not included in yearly total

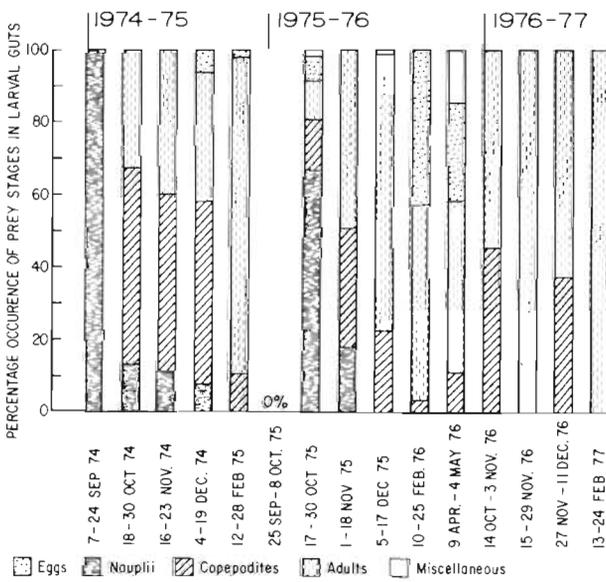


Fig. 3. Percentage occurrence of the developmental stages of the copepod prey in autumn-spawned larval herring guts during 15 cruises over 3 spawning seasons (1974, 1975, and 1976) in the Georges Bank-Nantucket Shoals area

the larger species later in the season as the larvae increased in size. In 1976, when the larvae had a greater mean length on average than the previous 2 seasons (Lough et al., 1980), no nauplii were found in the guts of larvae collected early in the spawning season (Fig. 3). The percentages of larvae feeding in

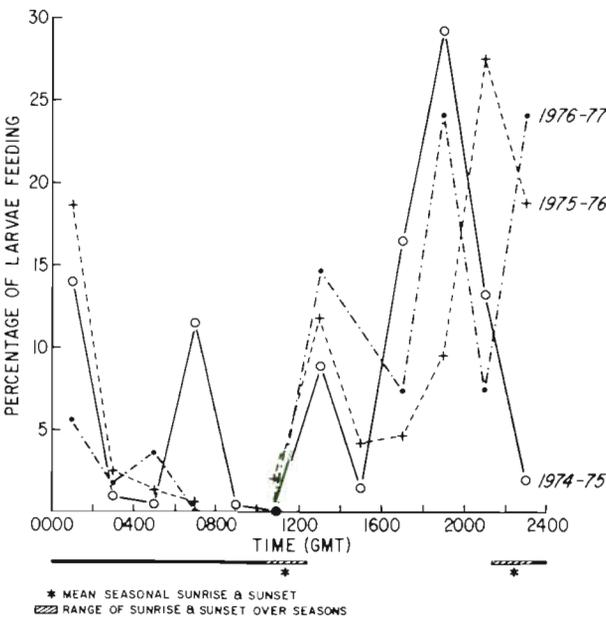


Fig. 4. Percentage of feeding of autumn-spawned herring larvae in the Georges Bank-Nantucket Shoals area during each spawning season (1974, 1975, and 1976) over a 24-h period (GMT), with mean seasonal time of sunrise and sunset indicated

December and February 1976 were high (42.9 % and 49.8 %, respectively) and increased over winter in contrast to the 2 previous years when they decreased (1974: 25.7 % to 8.6 % and 1975: 29.2 % to 19.6 %).

Herring are visual feeders and it is generally assumed in the literature that they feed only during the day (Bainbridge and Forsyth, 1971; Bhattacharyya, 1971; Schnack, 1972; Noskov et al., 1979; and others). A plot of the percentage of larvae feeding (larvae with food in their guts) over time for each season (Fig. 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 2 peak feeding periods average about 6 to 8 h apart and may represent the gut clearance time.

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, but prey width is a more meaningful measurement because 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 within each season (Table 3). The slopes of the 3 seasonal regression lines were significantly different from each other,

Table 3. Regression equations and correlation coefficients for width versus cephalothorax length of the copepod prey during 3 seasons (1974-1976)

Season	Number of larvae	Equation	Correlation coef., r, prey width vs. length
1974	1480	$W = 0.31L + 0.05$	0.88
1975	978	$W = 0.23L + 0.09$	0.77
1976	41	$W = 0.40L + 0.04$	0.93

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

reflecting the shifts in prey species and/or developmental stages consumed by the larvae, probably based on differences in prey size and availability and larval size among seasons. High correlation coefficients also resulted from a comparison of larval standard length with skull width (used to represent mouth width) and mouth gape (Table 4). 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. The slopes of the regression lines of skull width and mouth gape on standard length were significantly different based on a comparison of their confidence intervals (except for skull width-standard length regression lines slopes

Table 4. Regression equations and correlation coefficients between larval herring mouth gape vs. standard length and larval skull width vs. standard length for 3 spawning seasons (1974-1976)

Season	No. of larvae	Equation	Correlation coef., r, mouth gape* vs. standard length	No. of larvae	Equation	Correlation coef., r, skull width vs. standard length
1974	4036	$MG = 0.088L - 0.05$	0.92	4454	$SW = 0.048L + 0.18$	0.95
1975	2493	$MG = 0.315L - 3.01^{**}$	0.92	2692	$SW = 0.054L + 0.15$	0.94
1976	313	$MG = 0.099L - 0.40$	0.92	343	$SW = 0.054L + 0.11$	0.97

MG Mouth gape (mm); SW Skull width (mm); L Standard length (mm)  
 \* MG = Maxillary length  $\times \sqrt{2}$  (Shirota, 1970)  
 \*\* Includes 2 different methods of measuring maxillary length

between 1975 and 1976 seasons) possibly due to the differences in origin of spawning populations each season. These relationships also may change with larval stage of development, and the mean lengths and

growth rates differed somewhat among seasons (Lough et al., 1981).

Prey length and width and their ranges generally increased over each spawning season, and with larval

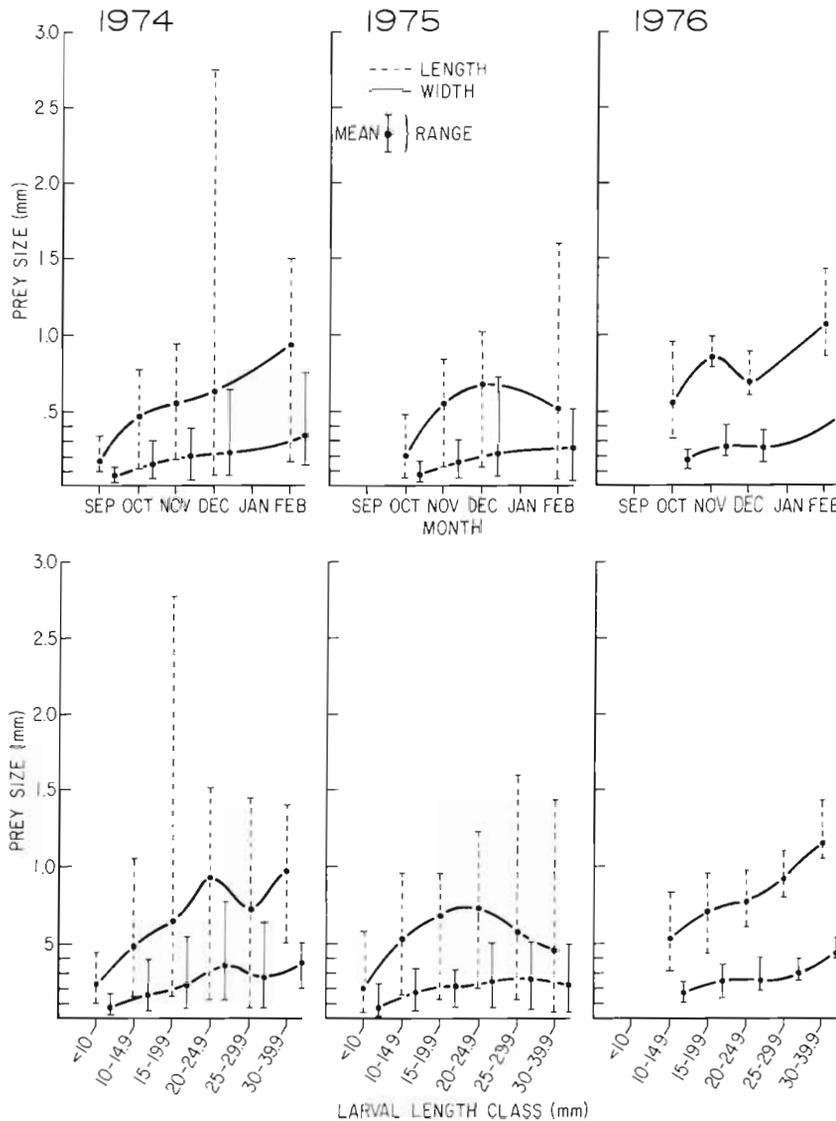


Fig. 5. Mean length (mm) and width (mm) of prey found in autumn-spawned larval herring in the Georges Bank-Nantucket Shoals area over each spawning season (1974, 1975, and 1976) plotted by survey month and larval length class

length (Fig. 5). Beyer (1980) used literature data to generate two prey preference ratios:

- (1)  $2 \times$  prey width/larval standard length.
- (2) Prey width/mouth width (skull width used here).

Figs. 6A and B present a comparison of these ratios based on Beyer's data and our data for the 1974, 1975,

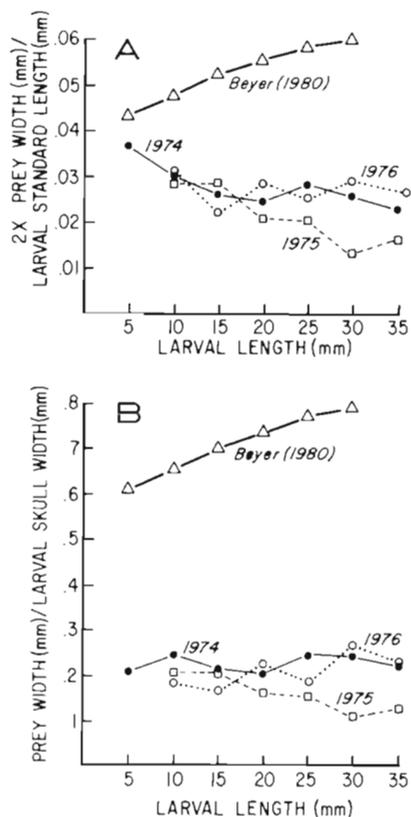


Fig. 6. Comparison of (A)  $2 \times$  prey width (mm)/larval standard length (mm) plotted by larval standard length and (B) prey width (mm)/larval skull width (mm) plotted by larval standard length of autumn-spawned larval herring in the Georges Bank-Nantucket Shoals area over the 1974, 1975, and 1976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

and 1976 seasons. The ratios in the 1975 season (for larvae greater than or equal to 20 mm) 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; Lockwood, 1973; Theilacker, 1980; and Hay, 1981). If larval standard lengths used to calculate the first ratio were corrected for shrinkage by increasing them, the resulting ratios would be even smaller.

The mean number and biomass ( $\mu\text{g}$  dry weight, calculated from equations summarized in Cohen and Lough, 1981) of prey items per larva of all size classes over each spawning season ranged from 1 to 7 (Fig. 7) and 0.5 to 48  $\mu\text{g}$  dry weight (Fig. 8), respectively. These

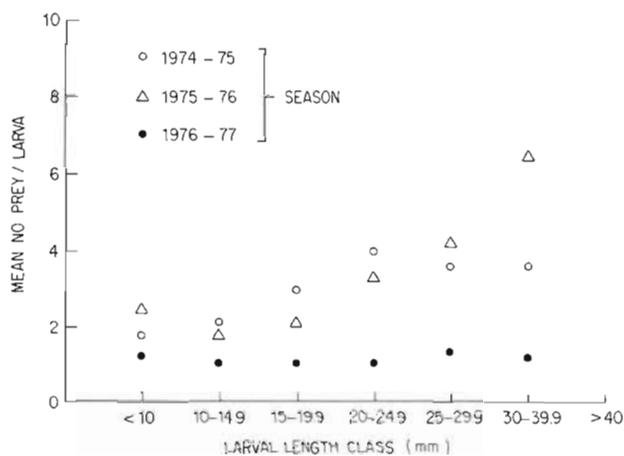


Fig. 7. Mean number of prey items per larval herring gut plotted by larval length class for each of the 15 cruises during the 1974, 1975, and 1976 spawning seasons in the Georges Bank-Nantucket Shoals area

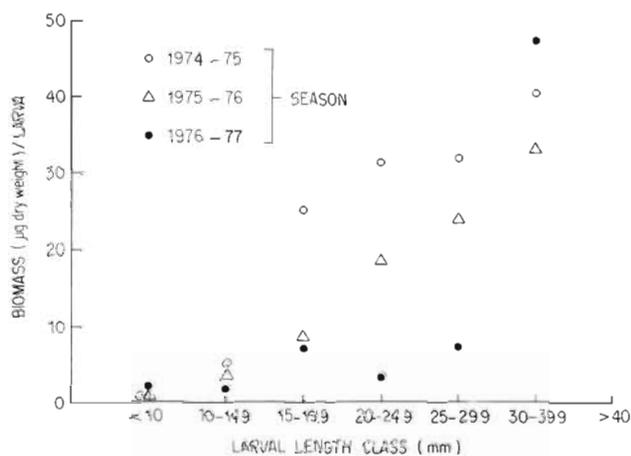


Fig. 8. Mean biomass ( $\mu\text{g}$  dry weight) of prey items per larval herring gut plotted by larval length class for each of the 15 cruises during the 1974, 1975, and 1976 spawning seasons in the Georges Bank-Nantucket Shoals area

ranges may be underestimated because of the possible loss of food (concentrated in the hind gut) during capture and preservation (Blaxter, 1965a; Damkaer and Au, 1968; Lasker and Zweifel, 1978; Colton et al., 1980; and Hay, 1981).

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 *B. scorpii*. In December 1975, 0.6 % of the larvae contained *B. scorpii* 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 Laboratory, Mass., USA.)

A further breakdown of the extensive statistical analyses performed on the gut content and condition factor data can be found in Cohen and Lough (1979) and in the summary tables and charts by Cohen et al. (1980). Since the analyses did not produce conclusive results, they will not be discussed further in this study. However, body height/standard length ratios (Erhlich et al., 1976) did appear to indicate that larvae were more robust for their size in the 1976 season than in 1974 or 1975.

### Zooplankton in the Larval Environment

A complete set of maps showing the distribution and abundance patterns of the dominant zooplankton prey and potential larval predators based on the 0.333-mm mesh bongo samples during these survey cruises was produced (Cohen and Lough, 1982). The results can only be used to infer information about the general patterns during each season because this mesh size does not quantitatively sample most of the larval herring prey. Adults of both species of *Centropages* virtually disappeared from the eastern half of Georges Bank during December 1975 and February 1977 compared to the same times during the other years. *Paracalanus parvus* was very scarce in February of 1974 and 1976 and quite widespread but low in numbers during February 1975.

There was very high station-to-station variability in the 0.165-mm mesh bongo samples, and total prey densities over all 3 seasons ranged between 60 and 3800 organisms  $m^{-3}$ . Comparisons were made between the relative percentage of each prey species in the larval guts and that in the environment at each station where both kinds of data were available with limited correlation, though there was general broad scale agreement between these abundances. Selectivity indices were calculated (Berg, 1979) for larvae at these stations but the results were inconclusive, possibly for a number of reasons: (a) low density of prey items, (b)

few feeding larvae at many of the stations, (c) patchy distribution of the zooplankton prey, (d) the integrated nature of the bongo hauls masking any differences in vertical distribution of the organisms, and (e) the poor match among 0.165-mm mesh zooplankton stations sorted and stations at which larval feeding was examined. Comparisons between the biomass (mg dry weight) of the available prey supply and the biomass of prey consumed ( $\mu g$  dry weight) were made at a number of stations, using equations in Cohen and Lough (1981), but no consistent relationship emerged. The 0.165-mm mesh data base (Davis, 1982) was not extensive enough to show yearly changes in species abundances (as the 0.333-mm data base did) but it did show seasonal patterns of occurrence of the major prey species consistent with those found previously (Sherman and Jones, 1980). Seasonal feeding patterns of the larval herring corresponded to species availability patterns fairly well: *Centropages* spp. and *Paracalanus parvus* are fed on more heavily in the autumn when they are most abundant (contributing to the secondary zooplankton peak referred to previously) and *Pseudocalanus* sp. is consumed in larger numbers in the late winter and spring when it is dominant (along with *Calanus* contributing to the primary zooplankton peak) (Table 2).

## DISCUSSION

### Prey Selection

A number of conclusions about prey selection based on species availability, size, and prey density can be drawn from this study. General descriptions of the feeding process have been published elsewhere (Blaxter, 1965a; Blaxter and Staines, 1969; Rosenthal, 1969; Beyer, 1980; and others) and will not be repeated here. The larvae examined fed on the dominant species of copepods present in the water column which were the same for the whole Georges Bank-Nantucket Shoals area. As they grew larger, they selected older stages of the same prey species 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 change in these species' abundance in the field, at least during 1976.

A comparison of our results with a number of important larval herring feeding studies (Marshall et al., 1937; Bowers and Williamson, 1951; Bhattacharyya, 1957; Blaxter, 1965a; Bainbridge and Forsyth, 1971; Bjorke, 1971; Rudakova, 1971; Sherman and Honey, 1971; Schnack, 1972; Gosheva and Slonova, 1976; Noskov et al., 1979; and Last, 1980) shows that larvae generally select the most abundant prey of a suitable

size range. All the studies in which predator and prey size ranges are given correspond in their measurements. Several authors (Marshall et al., 1937; Bhattacharyya, 1957; Blaxter, 1965a) have recorded plant material in the guts of larvae, usually under 10 mm. No plant material was found in our study except material ingested by copepod prey, although few larvae under 10 mm were examined, which is in agreement with other studies done in this area (Sherman and Honey, 1971; Damkaer and Au, 1974; Noskov et al., 1979; Colton et al., 1980). Colton et al. (1980) did examine larvae under 10 mm and also found no plant material in their diet. Bjorke (1978) found an unusually high proportion of copepod eggs in the diet of larvae 6.4 to 12.4 mm in length.

The larvae on Georges Bank fed on smaller particles than predicted by Beyer's (1980) model. Perhaps their strategy is to feed on larger numbers of small particles to meet their energy requirements. The larvae did not prey extensively on the small cyclopoid, *Oithona*, 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 the long body axis, (d) more transparent than the other copepods, or (e) they are not really available to the larvae but are at a different depth in the water column (not detected by the integrated haul). Zooplankton samples collected by towing opening/closing nets at discrete depths are currently under analysis and will help answer this question.

In our study 2 major feeding peaks occurred: one shortly after sunrise and another 6 to 8 h 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 Bhattacharyya (1957), Hempel (in Blaxter, 1965a), Bjorke (1978), and Last (1980). All of these peaks may reflect gut clearance rates and digestive times under the specific experimental conditions of these studies. Rosenthal and Hempel (1970) recorded a passage time of 4 to 10 h 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 (1965a) estimated digestion time as 4 to 8 h, depending on temperature. Beyer and Laurence (1981) used a digestion time of 4 h in their model of larval herring growth and mortality.

There is a wide range of estimates of the number of organisms found in the larval guts (Table 5). Our results showed mean values of 1 to 7 prey per gut for all size ranges of larvae examined. Differences in larval size, prey size, plankton supply, gut clearance time (temperature dependent), and loss of gut content during capture will affect the number of prey counted per larva at any given time. This variability is important to note because it will influence estimates of daily ration used in models such as those already cited (Beyer, 1980; Beyer and Christensen, 1980; Beyer and Laurence, 1981). For example, the daily ration (individual prey biomass  $\times$  mean number of prey gut<sup>-1</sup>  $\times$  number of gut fillings d<sup>-1</sup>) of 15-mm herring larvae is 62.1  $\mu$ g dry weight, calculated using data from Beyer and Christensen (1980), Christensen et al. (1980), and Beyer and Laurence (1981). Our data (for a 15-mm larva feeding on *Pseudocalanus* sp.) yields a daily ration of 19.6  $\mu$ g dry weight, a little less than a third of the literature estimate. This discrepancy is due to the different estimates of the mean number of items per gut and the number of gut fillings. The number of gut

Table 5. Several recorded estimates of the mean number of food particles per larval herring gut

Author	Larval length (mm) and/or weight (mg)	No. of particles per gut	Remarks
Blaxter (1965) (his Table 1 summarizes 10 other studies)	6-44	2-479	See original text for details
Sherman and Honey (1971)	All size classes collected	1.3-13.8	Central Maine coastal waters; autumn, winter, and spring collections
Schnack (1972)	14-17	4	North Sea; autumn- spawned larvae
	19-24	80	North Sea; Schlei estuary; spring-spawned larvae
Noskov et al. (1979)	5.0- 7.9	1.6	Georges Bank; autumn- spawned larvae
	8.0-12.9	2.4	
	13.0-17.9	2.0	
Beyer and Christensen (1980)	Mean: 15.1	3.4	Laboratory data

fillings is dependent on digestion rate which is determined by mean size, prey type, predator size, and previous feeding history (Fänge and Grove, 1979). Feeding behaviour also depends on the number of hours of light at or above the threshold intensity required by larvae for feeding (Blaxter, 1965b).

### Zooplankton Composition

The preceding sections on prey selection describe the general agreement between the species in the larval guts and the zooplankton composition based on the 0.333- and 0.165-mm mesh samples. However, because of the high station-to-station variability and

### Larval Feeding and Condition in Relation to Abundance, Distribution, and Survival

The patterns of larval feeding and condition described in this study 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 ( $79 \times 10^{12}$  larvae), intermediate in 1975 ( $21 \times 10^{12}$ ) and extremely low in 1976 ( $< 1 \times 10^{12}$ ). 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

Table 6. Several recorded estimates of prey densities required by larval herring for growth and survival

Author	Larval length (mm) and/or dry weight and/or age	Concentration of prey required
Rosenthal and Hempel (1970)	10–11 mm 13–14 mm	21–42 nauplii l <sup>-1</sup> 13–25 nauplii l <sup>-1</sup> } for 'optimum feeding'
Schnack (1972)	14–19 mm	200 'relevant food organisms' l <sup>-1</sup>
Beyer and Laurence (1979) (model predictions)	8.9 mm (60 mg) 9.8 mm (90 mg) 9.8 mm (90 mg)	800 nauplii l <sup>-1</sup> 150 nauplii l <sup>-1</sup> Minimum of 70 nauplii l <sup>-1</sup> to grow at a positive rate
	≥ 10 mm (110 mg) First feeding larvae	45 nauplii l <sup>-1</sup> Optimum density ≅ 500 nauplii l <sup>-1</sup>
Werner and Blaxter (1980)	4–12 wk old	170 organisms l <sup>-1</sup>

\* 'Optimum feeding' = 'continuous filling of gut during daylight hours'

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 with increasing prey numbers up to an optimum concentration; beyond this concentration, these parameters decline. Table 6 summarizes the results of several studies on the prey concentrations required by herring larvae of different lengths. Our estimates of prey density, based on the 0.165-mm mesh samples, in the Georges Bank-Nantucket Shoals area range from 0.06 to 3.8 organisms l<sup>-1</sup>, 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. However, the water column is isothermal during the autumn and winter in this area.

spawning took place. Spawning was divided between the two areas in 1975 with 66 % occurring on Nantucket Shoals. Lough et al. (1980) and Anthony and Waring (1980) discuss several reasons for this apparent shift in the herring fishery.

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 % d<sup>-1</sup>), followed by the 1975 season (2.7 % d<sup>-1</sup>), and the highest in the 1974 season (3.2 % d<sup>-1</sup>). There was a trend of decreasing mortality (increasing survival) from 1974 to 1976, and 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. No recruitment data are available for the Georges Bank area to compare to larval herring survival over the 1974–1976 spawning seasons.

In the present study, we found a greater percentage of feeding larvae (with generally lower prey numbers

and biomass per larva) in the 1976 season, especially during the possibly critical winter period. It is interesting to note a shift in larval diet from the 1974 season to the 1975 and 1976 seasons 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. There is no evidence that consistent differences exist in larval prey field between Nantucket Shoals and Georges Bank. The larvae collected in the 1976 season also appear to be more robust for their size based upon one of the condition factor measurements (body height/standard length ratio). *Pseudocalanus* and *Paracalanus* may have more nutritional value than *Centropages* spp. and other prey items which were consumed in larger numbers (and biomass) during the 1974 and 1975 seasons when growth rates were lower and mortality rates were higher than in 1976. However, Laurence (1976) found that there were no significant differences in calories per gram ash-free dry weight among *Pseudocalanus minutus* and both *Centropages* species, based on formalin-preserved specimens of unspecified size.

Alternatively, these larvae may have increased their daily ration by filling their guts more frequently with the small prey items. This change would not be detected by our sampling methods. Because relatively few larvae were examined during the 1976 season, the low numbers of prey per gut could also be due to inadequate sample size. Nevertheless, it is still possible to speculate that the greater survival of herring larvae during the 1976 spawning season resulted from the increase in relative population levels of the copepod prey *Pseudocalanus* and *Paracalanus*.

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