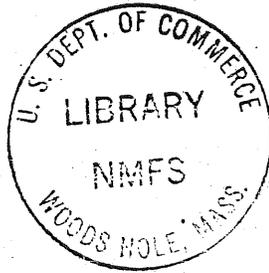


SAMPLER AND BEHAVIOR-RELATED VARIATION IN THE
CATCH OF LARVAL HERRING



John B. Colton, Jr. and John R. Green

National Marine Fisheries Service

Northeast Fisheries Center

Narragansett Laboratory, Narragansett, Rhode Island 02882

Laboratory Ref. No. 76-08
Northeast Fisheries Center
Woods Hole, Mass. 02543
5/10/76

ABSTRACT

In this paper the variation in the catch of larval herring collected with 61 cm bongo samplers is analyzed in reference to sampler selectivity and larval behavior and distribution. The most obvious discrepancies were the relatively high night/day abundance ratio (ca. 7/1) of yolk-sac larvae (4-6 mm) and fairly consistent night/day ratio (ca. 2/1) of larger larvae (7-30 mm). An attempt was made to rationalize the consistency of the night/day abundance ratios of larger larvae using an algebraic model involving reaction distance and escape velocity. The results indicated that 7 mm larvae could avoid the bongo sampler if their reaction distance was 8 m and that because escape velocities for nets detectable at 6 m or more are a small fraction of the towing speed, the increase in swimming speed with length is not sufficient to increase daytime avoidance. It was tentatively concluded that the relatively high night/day abundance ratio of yolk-sac larvae resulted from diel changes in their vertical distribution.

A comparison of 0.505 and 0.333 mm mesh catches and of maximum skull width measurements with mesh diagonal measurements indicated that the minimum length of full retention for 0.505 and 0.333 mm mesh nets were 12.0 and 7.5 mm respectively. Solely on a basis of skull width larvae as small as 8.5 mm could be retained by the 0.505 mm mesh and as small as 5.5 mm by the 0.333 mm mesh. To insure full retention of larvae smaller than 7 mm it would be necessary to use nets having a mesh aperture of 0.253 mm or less.

On a basis of this evaluation and in consideration of the sampling objectives, recommendations are made for future studies and for changes in sampling strategy to improve abundance estimates.

INTRODUCTION

In 1971 the International Commission for the Northwest Atlantic Fisheries (ICNAF) inaugurated a series of cooperative surveys of larval Atlantic herring (Clupea harengus harengus L.) in the Gulf of Maine-Georges Bank area. These surveys, incorporating standardized sampling methods and stations, have been continued on an annual basis since inception. Vessels from six countries have participated and 28 full-scale surveys have been completed as of June 1976. In addition, a number of supplementary coastal cruises of more limited scope have been undertaken in connection with this study.

The objectives of these surveys were to delimit the major spawning grounds and to obtain relative estimates of spawning stock size and information on larval drift and dispersal (ICNAF, 1971 and 1972). It was further agreed that, "The value of these surveys lies in the contribution they can make to estimation of adult stock size, to stock identification by following larval dispersion, and to understanding the factors influencing larval survival which will effect year-class size." (ICNAF, 1973)

In recent years considerable study has been made of the design and towing characteristics of plankton nets in an effort to improve their efficiency in capturing plankton, especially larval fishes. These studies have shown that net efficiency in respect to ichthyoplankton varies with net size (mouth area), filtering ratio (total mesh aperture area/mouth area), towing speed, and mesh size and also with length and species of larvae and time of day. The main causes of variation are escapement or extrusion of the smaller larvae through the meshes (Vannucci, 1968) and avoidance of the net by the larger larvae (Clutter and Anraku, 1968). In general there

is an increase in extrusion and a decrease in avoidance with increasing speed of tow and a decrease in avoidance during the night.

It is most important, therefore, that the sampling gear and method of tow be selected with a clear understanding of the research objectives and of the limitations the associated sampling variabilities impose. In this paper we attempt to evaluate on an a posteriori basis the effectiveness of the sampling techniques employed to furnish the quantitative estimates of abundance necessary to meet the objectives of the ICNAF larval herring surveys.

FIELD AND LABORATORY METHODS

Ichthyoplankton samples collected on one cruise of the Delaware II (U.S.A.), one cruise of the Anton Dohrn (Fed. Rep. of Ger.) and four cruises of the Albatross IV (U.S.A.) were used for this analysis. A total of 676 stations were occupied on these six cruises. The dates, station locations, and distribution of total herring larvae for each cruise are shown in Figure 1.

Fig. 1

At each station a 3.5 knot (6.5 km/hour), double-oblique tow was made using paired 61 cm bongo samplers (Posgay and Marak, 1976) fitted with 0.505 mm (port) and 0.333 mm (starboard) nylon mesh nets. The 0.505 mm and 0.333 mm mesh nets were used to sample ichthyoplankton and invertebrate plankton respectively. The sampler accessories (flowmeter, time-depth recorder, towing wire, and wire depressor) were rigged and of similar specifications as described by Posgay and Marak (1976). To date, all ichthyoplankton data generated from ICNAF larval herring surveys have been based on 0.505 mm mesh samples.

On Delaware II Cruise 71-4 the maximum depth of tow was 200 m or to within approximately 5 m off the bottom in shallower areas. The net was deployed at 50 m/min and retrieved at 20 m/min to 40 m depth. The upper 40 m of the water column was sampled in 20, 2 m interval steps of one-minute duration. On Albatross IV Cruise 71-7 the sampling procedure was similar except that the net was retrieved continuously at 10 m/min from 40 m to the surface. On all other cruises the maximum depth of tow was 100 m or to approximately 5 m off the bottom and the net was deployed at 50 m/min and retrieved at 10 m/min.

All samples used in this study were processed at the NMFS, Northeast Fisheries Center, Narragansett Laboratory. Fish eggs and larvae were sorted from the total 0.505 mm mesh samples and the larvae from each sample enumerated by species or to the lowest taxa possible. For species numbering less than 100, all larvae were measured for standard length to the nearest 0.1 mm. The larvae were later combined into 1 mm and 3 mm size groups. In samples containing greater numbers of larvae, a subsample of at least 100 specimens was taken for length determinations and the total length frequency determined by multiplying the number at each length interval by the reciprocal of the aliquot fraction.

Flowmeter calibration values (m^3 of water strained/revolution) were determined for each cruise by towing the nets with open cod ends a known distance, both with and against the current. The flowmeter readings for each tow were converted to m^3 of water filtered. These values for a given cruise were then plotted against the maximum tow depths and obvious discrepancies in volume values caused by windmilling, etc., were corrected on the basis of average tow depth-volume filtered values. Larval abundances in terms of numbers per unit of volume and

numbers per unit surface area ($\text{No}/\text{m}^3 \times \text{maximum depth sampled}$) were then determined for each tow.

The length frequency and abundance data were further allocated into day, night, and twilight categories. The times of sunrise and sunset for a given date and location were determined from Tide Tables, East Coast of North and South America published by the National Ocean Survey. Twilight was arbitrarily defined as the four-hour period, one hour before and after sunrise and sunset. The number of day, night, and twilight stations for each cruise are listed in Table 5.

RESULTS

The length frequencies and mean lengths of larvae for total, day, night, and twilight stations for individual and total cruises are given in Tables 1, 2, 3, and 4. Histograms of the total length frequencies based on 3 mm length intervals for all stations and for the three time periods are shown in Figure 2.

The length frequency distributions and mean lengths varied between cruises, but for a given cruise the degree of variation in mean length for the three time periods was unexpectedly low. However, due to the large number of observations an analysis of variance on length for the three time periods showed the small differences in mean length to be significant for Albatross IV Cruise 74-2 ($p=.05$) and highly significant ($p=.001$) for all other and total cruises. On the basis of previous field observations and theoretical studies of net avoidance in relation to time of day, we would expect to catch not only more, but appreciably larger larvae with decreasing light intensity. Our data show that the time period of maximum mean length of larval herring varied between cruises.

Tables
1-4

For total cruises, the mean length was greater during the day (15.5 mm) than at night and twilight (15.1 mm). The marked downward shift in modal length during twilight hours (Figure 2) reflects the high proportion of larvae from Anton Dohrn samples during this time period (54 percent of the total catch).

Fig. 2

The average abundance of 3 mm length group and total larval herring for the three time periods for individual and total cruises and the night/day and twilight/day ratios of abundance for total cruises are listed in Table 5. The average abundance values for the three time periods for total cruises are plotted in Figure 3. There was appreciable variation in the time period of maximum abundance between length groups and cruises. This is as would be expected from the contagious distribution of larval herring, which was more marked for individual length groups than for total herring (Figure 1). In addition, the percentage of total stations within a given time period in which herring were found did not vary significantly between day (45%), night (49%), and twilight (50%), indicating that if herring were present at any location they were caught, but not necessarily in proportion to their absolute numbers.

Of the 54 length categories (9 length groups, 6 cruises) listed in Table 5, the catch of larvae was greatest in 55, 26, and 19 percent of these categories during the night, twilight, and daytime periods respectively. The total abundance was greatest at night on three cruises (Albatross IV Cruises 72-9, 73-9, and 74-2), greatest at twilight on two cruises (Delaware II Cruise 71-4 and Albatross IV Cruise 71-7), and approximately equal during night and twilight on one cruise (Anton Dohrn). For all cruises combined, the catch was greatest at night for all length groups except 13-15 mm larvae (twilight). The ratio of night/

twilight/day abundances of total larvae for all cruises was approximately 5/3/2.

Table 5
Fig. 3

The total night/day abundance ratios were greater than one for all length groups. The night/day ratio was appreciably greater for 4-6 mm larvae (ca. 7/1) than for the larger length categories (ca. 2/1). The relatively high night/day abundance ratio of 4-6 mm larvae could be due to sampling bias resulting from the small number of positive tows (5% of night and 4% of day tows), for a t-test (Snedecor and Cochran, 1967) of logarithmically transformed data for positive tows showed that the night/day differences in mean abundance values were not significant. The total twilight/day abundance ratios were greater than one for all length groups except 7-9 mm and 28-30 mm larvae. For these length groups day catches were slightly greater than twilight catches.

The total night/day abundance ratios for 1 mm length groups and linear regression lines based on these values and on night/day ratio values in the catch of Pacific sardine (Sardinops caerulea) larvae (Ahlstrom, 1954) are plotted in Figure 4. The Pacific sardine data are based on 626, 1.5 knot (2.8 km/hour), double-oblique, one-meter net (1.0 or 0.7 mm mesh) tows. The maximum sampling depth of these collections was approximately 100 m. The statistics of a linear regression line fitted to the Pacific sardine data show an increase in the night/day abundance ratio of 0.7 for each mm increase in length. Lenarz (1973) observed similar increases in the ratios of night to day catches of Pacific hake (Merluccius productus) and northern anchovy (Engraulis mordax). A linear regression line based on the Atlantic herring data showed no significant variation in the night/day abundance ratio values with length ($r=.2533$).

Fig. 4

To determine if there was any significant loss of herring larvae through the 0.505 mm mesh, we compared the 0.505 mm mesh and 0.333 mm mesh catches for Albatross IV Cruise 73-9. This comparison is summarized

in Figure 5. The total catch was slightly greater and the mean length slightly smaller for the 0.333 mm mesh due to the greater numbers of 7-12 mm larvae. The .333/.505 abundance ratios for 7-9 mm and 10-12 mm larvae were 1.7 and 1.4 respectively, although a t-test of logarithmically transformed data for positive tows showed that these differences in mean abundance values were not significant. For all other length groups the abundance values for the two mesh apertures did not differ appreciably (Table 6).

Fig. 5
Table 6

DISCUSSION

In reference to previous observations (e.g., Bridger, 1956), the two most obvious discrepancies in the larval herring data are the relatively high night/day abundance ratio (ca. 7/1) of yolk-sac larvae (4-6 mm) and the fairly consistent night/day ratios (ca. 2/1) of the larger larvae (7-30 mm). The observation that larval herring larger than 6 mm showed no appreciable variation in night/day abundance ratios with length suggests that all larvae above 6 mm are capable of avoiding the 61 cm bongo net to an equivalent degree and that this capability is dependent to a great extent on light conditions (visibility).

An algebraic model of net avoidance which takes into account the towing speed, net radius and the escape velocity, alarm or reaction distance, and the initial offset of the larvae has been developed by Barkely (1964) and further extended by Barkely (1972) and Murphy and Clutter (1972). As Barkely (1972) has pointed out, probabilities of certain capture can only be calculated for animals that react individually. Animals within a school react to each others behavior and thus a school is more effective than the sum of the individuals in detecting and responding

appropriately to the oncoming net. In an attempt to rationalize the consistency of the day/night abundance ratios, we determined theoretical minimum escape velocities for one meter interval reaction distances using equation (2) of Barkely (1972) in which:

$$u_e = \frac{U}{\sqrt{1 + \frac{x_0^2}{(R - r_0)^2}}}$$

- Where: u_e = minimum escape velocity (cm/sec)
 U = towing speed (cm/sec) = 180 cm/sec
 x_0 = reaction distance of larva (cm) = 100-1000 cm
 r_0 = initial offset of larva from net center (cm) = 0
 R = net radius (cm) = 30.5 cm

In these calculations we have assumed that:

1. Larva selects the shortest possible escape path (i.e., normal to direction of tow). It should be noted here that this ability to take well-directed evasive action may be dependent on light conditions.

2. Larva is located along the axis of tow (initial offset from dead center of net is zero).

3. Reaction distance is essentially constant for all size larvae under a given set of light conditions (specific time of day). This is probably a valid assumption, for in herring the visual cells are comprised of only cones in the larval stage and rods and associated retinomotor responses and schooling behavior do not develop until metamorphosis (Blaxter, 1965, 1966, and 1968; Blaxter and Jones, 1967; Rosenthal, 1968).

The calculated minimum escape velocities (u_e) are shown in Figure 6.

For reaction distances less than 5 m, swimming speed is highly critical (37.6 cm/sec increase in swimming speed required for a decrease in reaction distance from 4 to 1 m). For reaction distances greater than 5 m, swimming speed is not as critical (3.6 cm/sec increase in swimming speed required for a decrease in reaction distance from 10 to 6 m).

Fig. 6

Testing of avoidance theory requires some knowledge of escape velocities as a function of size. We are concerned here with darting or burst speeds sustainable over time periods of a few seconds and distances up to 100 cm or so. The literature on such quantified swimming ability for larval fishes is limited. Maximum swimming velocities of larval herring reported by Blaxter (1962) increased from 3 to 5 cm/sec in 8 mm larvae to 30 cm/sec in 20 mm larvae and fit well with the commonly used maximum swimming velocity of 10 body lengths/sec observed by Bainbridge (1960). For larval plaice (Pleuronectes platessa) having a mean length of 9.6 mm, Ryland (1963) obtained a mean darting speed of 10.0 cm/sec which corresponds to 10.4 body lengths/sec. Hunter (1972) observed maximum burst speeds of very short duration on anchovy (Engraulis mordax) as high as 28 body lengths/sec for 4.2 mm larvae and 25 lengths/sec for 12.1 mm larvae, but the typical average burst speeds were close to 15 lengths/sec. For larval lake whitefish (Coregonus clupeaformis) ranging in length from 15 to 28 mm, Hoagman (1974) observed maximum burst speeds of 4.4 and 8.2 body lengths/sec (mean, 7.6).

In Figure 6 we have plotted maximum swimming speeds of 5, 10, and 15 body lengths/sec for 1 mm length values to determine the minimum length at which escape is possible for reaction distances of 1 to 10 m. These minimum escape length values are listed in Table 7.

Table 7

Under the conditions of tow employed in the ICNAF larval herring surveys and within the range of maximum swimming speeds considered, none of the larvae within the size range sampled could escape at a reaction distance of 1 m. At a maximum swimming speed of 5 body lengths/sec and a reaction distance of 10 m, the minimum escape length is 11 mm. At maximum swimming speeds of 10 and 15 body lengths/sec, 7 mm larvae could avoid the 61 cm bongo net if their reaction distances were 8 and 5, respectively.

Considerable laboratory study has been made on the visual acuity of larval fishes, but these studies have been mainly concerned with their ability to find food. Woodhead (1966) has estimated the maximum sighting range of fishes under optimal conditions to be less than 15 m. Nichol (1963) concluded that in coastal waters (latitude 50°N) fish at 100 m depth could perceive objects from sunrise to sunset on the darkest winter day. Murphy and Clutter (1972) noted that the optical characteristics of sea water are such that objects become invisible through contrast attenuation rather than resolution attenuation. If this were so, large nets should be sighted at nearly the same distance as smaller nets resulting in a dramatic increase in catching efficiency with size of net. Their field data clearly show, however, that anchovy larvae reacted to the Isaacs-Kidd midwater trawl (IKMT) at considerably greater distances than to the 1 m net.

A reaction distance of 8 m during daylight hours appears to be reasonable and is similar to values determined by Barkely (1972) for anchovy larvae collected with a 10-foot IKMT ($u_e = 10 \text{ BL}$, $x_0 = 8.2 \text{ m}$). The credibility of this reaction distance estimate is enhanced when we consider that the avoidance reaction is most likely initiated

by a visual response to the whole bongo net array (including the wire depressor) rather than to the individual bongo samplers. Blaxter (1968) has suggested that because cones are the dominant mode of vision in larval fishes that they are better at perceiving movement than patterns or images. The speed of tow, tow configuration, and dimensions of the sampling gear and associated hardware would tend to augment this form of perception.

To determine if possibly the towing wire provided advanced warning of the approaching net, we made detailed wire profile calibrations in which time-depth recorders were placed on the towing wire at distances of 0, 10, and 20 m from the bongo array. A series of standard ICNAF oblique plankton tows were made to maximum depths of 50, 75, and 100 m and the wire depth at the three distance intervals determined both at the maximum depth of tow and at the midpoint of retrieval. The distance of the wire above the net was appreciably less at the midpoint of retrieval than at the maximum depth of tow (approximately 1/2), but in all tow situations the wire was well above the axis of tow (never less than 2.5 m above at 10 m distance and 5.5 m above at 20 m distance). It is unlikely that the towing wire provides cues enabling larval fishes to perform directed avoidance behavior (increasing reaction distance).

Because minimum escape velocities of nets detectable at 6 m or more are a small fraction of the towing speed, the increase in swimming speed with length is not sufficient to appreciably increase daytime avoidance. Reaction distance is more critical than swimming speed and we have concluded that this accounts for the fairly constant night/day abundance ratios observed for herring larger than 6 mm.

One rationale for the relatively high night/day abundance ratios of 4-6 mm larvae would be a significant increase in the night-time catch of invertebrate fauna resulting in increased clogging of the net meshes and reduced escapement or extrusion of the smaller herring larvae. To

check on this possibility, we determined total plankton displacement volumes for Albatross IV Cruise 73-9 samples. The night/day abundance ratio of 4-6 mm larvae collected on this cruise was 12.8 while the night/day ratio of displacement volumes was 1.3. It is improbable, therefore, that increased retention due to clogging accounts for the greater nighttime catch of the smaller larvae.

Another possible explanation would be an increase in active escapement (in contrast to passive escapement or extrusion) during the daylight hours associated with an increase in the visibility of the meshes. To our knowledge, no field or laboratory tests have been conducted to determine if in fact there are diel variations in the loss of organisms through the meshes of plankton nets, but our intuitive feeling is that at high filtration velocities vision plays only a minor role and that the loss of organisms is mainly due to extrusion.

The only other explanation we can think of for this anomaly is that the yolk-sac larvae are on or very near the bottom during the day and move up into the water column and above the maximum depth sampled by the bongo net during the night. To date there have been no published field observations in which closing nets were placed at small enough intervals to detect such small-scale vertical movements. There are some data from laboratory and field observations, however, regarding the vertical distribution of early stage herring larvae.

Blaxter (1973) monitored the movements of herring and plaice larvae of different ages from hatching to about eight weeks old in a vertical tube at varying natural and artificial light intensities. The critical natural light intensity for movement to occur was equivalent to that of Civil Twilight (0.14 mc). For both herring and plaice, 0-day old larvae exhibited the least vertical movement and activity, but herring larvae

from a fairly early stage undertook vertical migrations in response to day/night changes in light intensity.

Laboratory studies by Seliverstov (1974) showed that: (1) during the first 12 hours herring larvae do not respond to light or else have weak negative phototaxis; (2) 48 hours after hatching most larvae were able to remain in midwater and possessed strong positive phototaxis; (3) eight-day old larvae responded negatively to light by day, but weakly positive to light by night. Blaxter and Ehrlich (1974) observed that yolk-sac herring larvae have a high initial sinking rate and as yolk is absorbed with an accompanying increase in water content, the sinking rate decreases and the larvae require progressively less energy to maintain position in the water column.

The ICES Working Group on North Sea Herring Larval Surveys (Anonymous, 1971) recommended that yolk-sac larvae be omitted from estimates of larval abundance as they are normally restricted to a narrow depth stratum close to the bottom and not uniformly sampled due to considerable variation in the proximity to the bottom sampled by different countries. The restricted depth distribution of yolk-sac larvae has been further documented by Wood (1975) who showed that over a four-year period the most sizeable catches of yolk-sac herring in the central and northern North Sea were obtained during tows in which the sampling gear reached to within five meters of the sea bed.

Dive teams of the NMFS Northeast Fisheries Center's Manned Undersea Research and Technology (MUST) Investigation documented the presence of newly hatched herring larvae on the substrate on Jeffreys Ledge, Gulf of Maine during the daylight hours in October 1974 (Cooper, et al, 1975). Large numbers of yolk-sac larvae were observed amongst algal clumps in

diver-collected substrate samples from depths of 35-40 m. It was concluded that newly hatched larvae are retained for several days among algal branches during which time the yolk-sac is partially absorbed.

An examination of Albatross IV Cruise 73-9 maximum tow depth data for stations shoaler than 100 m showed that only 30 percent of the tows were made to within 5 m of the bottom and that these tows accounted for only four percent of the total catch of yolk-sac larvae. The average distance of the sampling gear from the bottom was 7.7 m (range: 5-11 m). The relatively high night-time catches of yolk-sac larvae were not due to diel variations in the maximum depth of tow. We still do not have, however, any direct evidence that yolk-sac larvae move off the bottom during the night.

The .0.333 mm and 0.505 mm mesh abundance values given in Figure 5 indicate that at a towing speed of 3.5 knots: (1) 4-6 mm herring larvae are not fully retained by either the 0.333 or 0.505 mm mesh; (2) 7-12 mm larvae are more fully retained by the 0.333 mm mesh; and (3) retention of larvae larger than 12 mm is similar for both mesh sizes.

Few quantitative studies have been made on the mesh retention of fish larvae by plankton gear. The laboratory and field studies of Saville (1959) and field observations of Smith, Counts and Clutter (1968) indicate that the maximum cross-sectional diameter of an organism must be greater than the mesh diagonal if it is to be fully retained. The degree of extrusion is strongly dependent on filtration velocity. Lenarz (1972) concluded that the mesh "diagonal rule" was too conservative for the case of Northern anchovy (Engraulis mordax) larvae sampled with slowly towed (1 1/2 knots) nylon nets. The rate of extrusion is also contingent on body shape (Vannucci, 1968), so that the loss of fusiform larval fish species is less than that of filiform species.

In studies of mesh retention of larval fishes, body depth at the insertion of the pectoral fin has frequently been used as the critical dimension to compare with the mesh diagonal. However, Wood (1972) suggested that for herring larvae maximum skull width is a more meaningful measurement as this is the first part of the body to ossify and thus less easily compressed or crushed. We measured maximum skull widths (excluding eye balls) and body depths at the base of the pectorals of 200 herring larvae ranging in length from 4.2 to 9.9 mm. The average body depth was 0.32 mm and the average skull width was 0.50 mm. With respect to mesh retention of larval herring within this size range, skull width is the significant dimension. It should be noted here that the maximum dimension of recently hatched larvae is the total depth (including the yolk-sac), but at a towing speed of 3.5 knots the yolk-sac is usually torn off or damaged.

In Figure 7 we have plotted maximum skull width values against standard lengths based on measurements made on 300 larvae ranging in length from 4.2 to 15.1 mm. There is a considerable range in skull width for larvae of a given length, but a comparison of skull width measurements with mesh diagonals indicates that the minimum lengths of complete retention for the 0.505 and 0.333 mm mesh nets are 12.0 and 7.5 mm respectively. We refer to this as a "minimum" retention length because at high filtration velocities there would be some extrusion of larvae larger than this due to the compressibility of the larvae and the flexibility of the meshes. These retention length values agree well with similar values estimated on a basis of a comparison of 0.505 and 0.333 mm mesh catches (Figure 5).

Fig. 7

Solely on a basis of skull width, larvae as small as 8.5 mm could be

retained by the 0.505 mm mesh and as small as 5.5 mm by the 0.333 mm mesh. These lengths should be considered as "maximum" retention lengths for obviously smaller larvae are in fact retained. In order to insure full retention of larvae smaller than 7 mm it would be necessary to use netting having a mesh diagonal of 0.36 mm or less (mesh aperture of 0.253 mm or less).

CONCLUSIONS

This study suggests that both avoidance and escapement or extrusion are a source of variation in larval herring abundance estimates based on samples obtained with the 61 cm bongo sampler fitted with a 0.505 mm mesh and towed at 3.5 knots. In addition, if in fact yolk-sac larvae are normally restricted to a narrow depth stratum close to the bottom, further bias results from the tow configuration employed in ICNAF surveys (double oblique tow to within 5 m of the bottom).

The retention of smaller larvae is necessary for the delimitation of spawning areas and for better estimates of spawning biomass, while the capture of larger larvae is essential to the assessment of dispersal and to the prediction of recruitment. A dilemma exists regarding future sampling strategies for opposing tactics are required to increase retention and reduce avoidance. To insure retention of yolk-sac larvae (4-6 mm) would require the use of nets having a mesh aperture of 0.253 mm or less. But with nets of this mesh diameter it would be necessary to reduce the towing speed to maintain an adequate filtration efficiency. In addition, because yolk-sac larvae appear to be restricted to a narrow depth stratum close to the bottom it would be necessary to use conductor cable and a

pressure transducer to insure that sampling was carried out to a uniform and minimum distance above the sea-bed. Considering the amount of data already collected and the complications involved in using conductor cable and associated electronic equipment, it would seem more reasonable to omit yolk-sac larvae from estimates of abundance as is done in the case of the ICES surveys.

The paired 61 cm bongo samplers are about the maximum size of gear that can be handled efficiently from most research vessels, so that the only way to reduce avoidance would be to increase the towing speed. Taking into consideration the generation of acceleration fronts due to net drag and the increased extrusion and damage resulting from the additional filtration pressure on the larvae, it would appear that 5 knots is about the maximum speed at which the 0.505 mm mesh bongo sampler can be towed effectively. However, at a towing speed of 5 knots avoidance would remain a major factor in determining sampler selectivity and it would still be necessary to correct samples by size and time-of-day so that all information could be used in estimating abundance.

On a basis of the data analyzed to date and considering the possibilities outlined above for changes in sampling techniques, we feel that effort should be directed towards improving the biomass estimates of the smaller larvae (7-12 mm). An initial step in this direction would be to utilize the 0.333 mm mesh samples for ichthyoplankton abundance estimates. These samples are currently being processed at the Plankton Sorting Center in Szczecin, Poland. Before optimum sampling and data reduction techniques can be ascertained, considerable effort must be expended in the analysis of all data collected to date on ICNAF larval herring surveys and in conducting special studies of size-specific retention, avoidance, and availability rates.

ACKNOWLEDGMENTS

The larval fishes used in this study were sorted and identified by the staff of the Ichthyoplankton Investigation, NMFS Northeast Fisheries Center, Narragansett Laboratory. Ruth Byron supervised the sorting and identification, Susan Senerchia was responsible for the initial tabulation of the cruise data, and Lianne Armstrong drew the figures. We thank Judith Hoskins and Greg Lough for advice regarding statistical analysis of the data and Kenneth Sherman for critical reading of the manuscript.

LITERATURE CITED

- Ahlstrom, E. H.
1954. Distribution and abundance of egg and larval populations of the Pacific sardine. U.S. Fish and Wildl. Ser., Fish. Bull. 56: 83-140.
- Anonymous.
1971. Report of the Working Group on North Sea Herring Larval Surveys. ICES, C.M. 1971/H:10, pp. 1-4 (Mimeo).
- Bainbridge, R.
1960. Speed and stamina in three fish. J. Exp. Biol. 37: 129-153.
- Barkely, R. A.
1964. The theoretical effectiveness of towed-net samplers as related to sampler size and to swimming speed of organisms. J. Cons. 29: 146-157.
- Barkely, R. A.
1972. Selectivity of towed-net samplers. Fish. Bull., U.S. 70: 799-820.
- Blaxter, J. H. S.
1962. Herring rearing IV. Rearing beyond the yolk-sac stage. Marine Res. Scotland. No. 1: 1-18.
- Blaxter, J. H. S.
1965. The feeding of herring larvae and their ecology in relation to feeding. Rep. Calif. Coop. Oceanic Fish. Invest. 10: 79-88.
- Blaxter, J. H. S.
1966. The effect of light intensity on the feeding ecology of herring. Symp. Br. Ecol. Soc. 6: 393-409.
- Blaxter, J. H. S.
1968. Visual thresholds and spectral sensitivity of herring larvae. J. Exp. Biol. 48: 39-53.
- Blaxter, J. H. S.
1973. Monitoring the vertical movements and light responses of herring and plaice larvae. J. Mar. Biol. Ass. U.K. 53: 635-647.
- Blaxter, J. H. S. and K. F. Emrlich.
1974. Changes in behaviour during starvation of herring and plaice larvae. In "The Early Life History of Fish." (J. H. S. Blaxter, Ed.), pp. 575-588. Springer-Verlag, New York.
- Blaxter, J. H. S. and M. P. Jones.
1967. The development of the retina and retina-motor responses in herring. J. Mar. Biol. Ass. U.K. 47: 677-697.
- Bridger, J. P.
1956. On day and night variations in catches of fish larvae. J. Cons. 22: 42-57.

Clutter, R. I. and M. Anraku.

1968. Avoidance of samplers. In "Reviews on zooplankton sampling methods, Part I" (D. J. Tranter, Ed.), pp. 57-76. UNESCO, Monogr. Oceanogr. Methodol. 2, Zooplankton Sampling.

Cooper, R. A., J. R. Uzmann, R. A. Clifford, and K. J. Pecci.

1975. Direct observations of herring (Clupea harengus harengus L.) egg beds on Jeffreys Ledge, Gulf of Maine in 1974. Int. Comm. Northwest Atl. Fish. Res. Doc. 75/93 (Mimeo).

Hoagman, W. J.

1974. Vital activity parameters as related to the early life history of larval and post-larval lake whitefish (Coregonus clupeaformis). In "The Early Life History of Fish." (J. H. S. Blaxter, Ed.) pp. 547-558. Springer-Verlag, New York.

Hunter, J. R.

1972. Swimming and feeding behavior of larval anchovy, Engraulis mordax. Fish. Bull., U.S. 70: 821-838.

ICNAF.

1971. Report of standing committee on research and statistics. App. I. Int. Comm. Northw. Atl. Fish. Redbook 1971, Part I: 21-63.

ICNAF.

1972. Report of standing committee on research and statistics. App. II. Int. Comm. Northw. Atl. Fish. Redbook 1972, Part I: 43-66.

ICNAF.

1973. Report of standing committee on research and statistics. App. II. Int. Comm. Northw. Atl. Fish. Redbook 1973, Part I: 31-49.

Lenarz, W. H.

1972. Mesh retention of Sardinops caerulea and Engraulis mordax by plankton nets. Fish. Bull. U.S. 70: 839-848.

Lenarz, W. H.

1973. Dependence of catch rates on size of fish larvae. Rapp. Proc. Verb. 164: 270-275.

Murphy, G. I. and R. I. Clutter.

1972. Sampling anchovy larvae with a plankton purse seine. Fish. Bull. U.S. 70: 789-798.

Nichol, J. A. C.

1963. Some aspects of photoreception and vision in fishes. Advanc. Mar. Biol. 1: 171-208.

Posgay, J. A. and R. R. Marak.

1976. The MARMAP bongo zooplankton samplers. J. Cons. (in press).

Rosenthal, H.

1968. Beobachtungen über die entwicklung des schwarmverhaltens bei den larven des herings, Clupea harengus. Mar. Biol. 2: 73-76.

Ryland, J. S.

1963. The swimming speeds of plaice larvae. J. Exp. Biol.
40: 285-299.

Saville, A.

1959. Mesh selection of plankton nets. J. Cons. 23: 192-201.

Snedecor, G. W. and W. G. Cochran.

1967. Statistical Methods. 6th Ed. Iowa State University Press,
Ames, Iowa.

Seliverstov, A. S.

1974. Vertical migrations of larvae of the Atlanto-Scandian herring
(Clupea harenqus L.). In "The Early Life History of Fish." (J. H. S.
Blaxter, Ed.), pp. 253-265. Springer-Verlag, New York.

Smith, P. E., R. C. Counts, and R. I. Clutter.

1968. Changes in filtering efficiency of plankton nets due to
clogging under tow. J. Cons. 32: 232-248.

Vannucci, M.

1968. Loss of organisms through the meshes. In "Reviews on Zooplankton
Sampling Methods, Part I." (D. J. Tranter, Ed.), pp. 77-86. UNESCO,
Monogr. Oceanogr. Methodol. 2, Zooplankton Sampling.

Wood, R. J.

1972. On the loss of herring larvae through nylon nets in a standard
high-speed plankton sampler. ICES, C. M. 1972/H:14, pp. 1-10 (Mimeo).

Wood, R. J.

1975. On catches of small herring larvae. ICES, C. M. 1975/H:23,
pp. 1-6 (Mimeo).

Woodhead, P. M. J.

1966. The behaviour of fish in relation to light in the sea. In
"Oceanogr. Mar. Biol. Ann. Rev." (H. Barnes, Ed.), pp. 337-340.
George Allen and Unwin Ltd., London.

Table 1. Length frequencies and mean lengths of larval herring, total stations.

Length mm	<u>Del. II</u> 71-4	<u>Alb. IV</u> 71-7	<u>Anton</u> <u>Dohrn</u>	<u>Alb. IV</u> 72-9	<u>Alb. IV</u> 73-9	<u>Alb. IV</u> 74-2	Total	
4	-	-	3	10	9	-	22	
5	-	-	21	12	113	1	147	402
6	-	1	32	20	179	1	233	
7	2	-	84	9	103	-	198	
8	4	2	471	7	113	-	597	1751
9	1	8	811	13	123	-	956	
10	3	19	1152	33	102	2	1311	
11	9	16	284	118	86	-	513	2524
12	16	34	336	158	156	-	700	
13	6	58	635	109	211	1	1020	
14	10	65	725	77	256	-	1133	3232
15	10	64	491	78	435	1	1079	
16	6	143	260	123	697	5	1234	
17	5	255	183	134	609	13	1199	3639
18	-	281	176	130	612	7	1206	
19	-	253	145	117	516	11	1042	
20	-	173	157	96	716	17	1159	2967
21	-	124	48	87	486	21	766	
22	-	66	33	67	319	29	514	
23	-	39	29	52	153	14	287	960
24	-	27	6	21	68	37	159	
25	1	7	6	18	10	29	71	
26	-	2	1	15	14	25	57	167
27	-	4	5	5	11	14	39	
28	-	2	-	5	12	16	35	
29	-	1	-	2	9	16	28	81
30	-	3	-	1	2	12	18	
31	-	1	1	2	-	1	5	
32	-	-	-	2	-	2	4	15
33	-	-	-	-	2	4	6	
Total	73	1648	6095	1521	6122	279	15738	
Mean	13.0	18.0	12.4	16.2	16.6	23.6	15.2	

Table 2. Length frequencies and mean lengths of larval herring, day stations.

Length mm	<u>Del. II</u> 71-4	<u>Alb. IV</u> 71-7	<u>Anton</u> <u>Dohrn</u>	<u>Alb. IV</u> 72-9	<u>Alb. IV</u> 73-9	<u>Alb. IV</u> 74-2	Total
4	-	-	-	-	2	-	2
5	-	-	6	-	2	-	8
6	-	1	11	3	5	-	20
7	-	-	29	4	6	-	39
8	-	2	96	2	8	-	108
9	1	8	115	2	7	-	133
10	-	17	107	1	24	1	150
11	4	11	40	8	22	-	85
12	-	21	48	6	59	-	134
13	-	10	72	18	63	-	163
14	4	4	97	12	55	-	172
15	6	10	88	12	128	-	244
16	5	16	55	22	148	-	244
17	5	22	26	44	186	3	286
18	-	33	22	50	148	-	253
19	-	34	14	50	96	4	198
20	-	16	22	25	78	3	144
21	-	15	3	21	46	1	86
22	-	12	-	10	25	2	49
23	-	4	-	13	33	1	51
24	-	5	-	7	24	10	46
25	-	2	-	3	2	11	18
26	-	-	-	3	7	7	17
27	-	-	-	1	-	1	2
28	-	-	-	2	2	4	8
29	-	-	-	1	-	6	7
30	-	-	-	-	-	3	3
31	-	-	-	-	-	1	1
32	-	-	-	2	-	1	3
33	-	-	-	-	-	2	2
Total	25	243	849	322	1176	61	2676
Mean	14.6	16.5	12.1	17.8	16.7	24.8	15.5

Table 3. Length frequencies and mean lengths of larval herring, night stations.

Length mm	<u>Del. II</u> 71-4	<u>Alb. IV</u> 71-7	<u>Anton</u> <u>Dohrn</u>	<u>Alb. IV</u> 72-9	<u>Alb. IV</u> 73-9	<u>Alb. IV</u> 74-2	Total
4	-	-	3	10	5	-	18
5	-	-	12	12	108	1	133
6	-	-	13	17	175	1	206
7	2	-	48	4	95	-	149
8	4	-	369	3	99	-	475
9	-	-	661	8	107	-	776
10	1	3	936	29	68	1	1038
11	-	4	187	27	53	-	341
12	1	6	246	131	85	-	469
13	1	41	353	83	115	1	594
14	-	54	345	48	138	-	585
15	1	48	202	49	225	1	526
16	-	108	120	74	473	4	779
17	-	174	90	66	370	9	710
18	-	190	107	58	419	6	780
19	-	167	95	50	393	4	714
20	-	124	102	57	628	12	923
21	-	77	44	51	434	15	621
22	-	39	31	47	293	22	432
23	-	25	29	32	117	10	213
24	-	17	6	12	42	20	97
25	-	5	6	12	7	10	40
26	-	2	1	12	8	15	38
27	-	4	4	4	11	12	35
28	-	1	-	2	10	9	22
29	-	1	-	1	9	7	18
30	-	2	-	1	2	8	13
31	-	1	-	2	-	-	3
32	-	-	-	-	-	1	1
33	-	-	-	-	2	2	4
Total	10	1093	4010	972	4497	171	10753
Mean	9.6	18.1	12.0	15.7	16.7	23.1	15.1

Table 4. Length frequencies and mean lengths of larval herring, twilight stations.

Length mm	<u>Del. II</u> 71-4	<u>Alb. IV</u> 71-7	<u>Anton</u> <u>Dohrn</u>	<u>Alb. IV</u> 72-9	<u>Alb. IV</u> 73-9	<u>Alb. IV</u> 74-2	Total
4	-	-	-	-	2	-	2
5	-	-	2	-	4	-	6
6	-	-	13	-	-	-	13
7	-	-	31	1	2	-	34
8	-	-	17	2	6	-	25
9	-	-	35	3	10	-	48
10	2	-	95	3	10	-	110
11	5	1	59	12	11	-	88
12	15	7	46	21	12	-	101
13	5	7	207	8	33	-	260
14	6	7	276	17	64	-	370
15	3	5	199	17	73	-	297
16	1	19	87	27	77	1	212
17	-	57	63	24	53	1	198
18	-	58	40	22	46	1	167
19	-	52	31	17	23	3	126
20	-	33	31	14	11	2	91
21	-	32	1	15	7	5	60
22	-	15	1	10	2	5	33
23	-	10	-	7	4	3	24
24	-	5	-	2	2	7	16
25	1	-	-	3	-	8	12
26	-	-	-	-	-	3	3
27	-	-	1	-	-	1	2
28	-	1	-	1	-	3	5
29	-	-	-	-	-	3	3
30	-	1	-	-	-	1	2
31	-	-	1	-	-	-	1
32	-	-	-	-	-	-	-
33	-	-	-	-	-	-	-
Total	38	310	1236	226	452	47	2309
Mean	12.9	18.5	13.7	16.6	15.3	23.5	15.1

TABLE 5. Average abundance (No./1000m³) of larval herring by day, night, and twilight for individual and total cruises and total night/day and twilight/day abundance ratios.

Cruise	Time Period	No. Sta.'s	Length (mm)									Total
			4-6	7-9	10-12	13-15	16-18	19-21	22-24	25-27	28-30	
<u>Del. II</u> 71-4	Day	54	0	0.02	0.08	0.21	0.21	0	0	0	0	0.51
	Night	46	0	0.14	0.04	0.04	0	0	0	0	0	0.22
	Twi.	22	0	0	1.23	0.78	0.06	0	0	0.06	0	2.12
<u>Alb. IV</u> 71-7	Day	45	0.03	0.38	1.86	0.90	2.70	2.46	0.80	0.07	0	9.22
	Night	80	0	0	0.28	3.08	10.16	7.92	1.74	0.24	0.09	23.51
	Twi.	23	0	0	0.78	1.84	12.92	11.29	2.88	0	0.20	29.89
<u>Anton</u> <u>Dohrn</u>	Day	31	0.84	11.87	9.65	12.87	5.00	1.93	0	0	0	42.01
	Night	62	0.67	25.96	32.98	21.64	7.64	5.82	1.60	0.27	0	96.58
	Twi.	21	1.17	6.50	15.66	53.42	14.89	4.93	0.08	0.08	0	96.81
<u>Alb. IV</u> 72-9	Day	34	0.17	0.46	0.84	2.38	6.53	5.40	1.69	0.40	0.17	18.14
	Night	73	0.96	0.38	6.40	4.40	4.91	3.93	2.27	0.69	0.11	24.12
	Twi.	18	0	0.62	3.72	4.34	7.56	4.77	1.97	0.32	0.11	23.37
<u>Alb. IV</u> 73-9	Day	29	0.55	1.27	6.41	15.08	24.92	13.43	5.01	0.55	0.12	71.84
	Night	66	7.04	7.40	5.07	11.71	31.04	35.90	11.09	0.63	0.52	110.44
	Twi.	16	0.71	2.10	3.83	19.76	20.45	4.76	0.93	0	0	52.51
<u>Alb. IV</u> 74-2	Day	15	0	0	0.18	0	0.53	1.40	2.29	3.34	2.29	10.71
	Night	30	0.14	0	0.06	0.14	1.26	2.06	3.39	2.46	1.60	11.38
	Twi.	11	0	0	0	0	0.43	1.45	2.17	2.03	0.72	6.81
Total Cruises	Day	208	0.22	2.08	2.73	4.30	5.81	3.17	1.08	0.28	0.14	19.83
	Night	357	1.56	6.18	8.16	7.49	10.00	10.00	3.27	0.51	0.24	47.41
	Twi.	111	0.32	1.61	4.51	13.99	8.71	4.19	1.11	0.29	0.12	34.84
	N/D Ratio		7.09	2.97	2.99	1.74	1.72	3.15	3.03	1.82	1.71	2.39
	T/D Ratio		1.45	0.77	1.65	3.25	1.50	1.32	1.03	1.04	0.86	1.76

Table 6. Average abundance (No./1000m³) of larval herring for 0.505mm and 0.333mm mesh nets and 0.333mm mesh/0.505mm mesh abundance ratios, Albatross IV Cruise 73-9.

	Length (mm)								TOTAL
	4 - 6	7 - 9	10 - 12	13 - 15	16 - 18	19 - 21	22 - 24	25 - 27	
.505 mm Mesh	4.49	5.06	5.13	13.46	28.61	25.63	8.06	0.52	91.33
.333 mm Mesh	3.95	8.62	7.25	15.17	27.81	25.25	8.53	0.54	97.22
.333/.505 Ratio	0.88	1.70	1.41	1.13	0.97	0.99	1.06	1.04	1.06

TABLE 7. Minimum escape length (mm) for various swimming speeds (BL/sec) and reaction distances (m).

		Reaction Distance									
		1	2	3	4	5	6	7	8	9	10
5 BL	-	--	--		27.5	22.0	18.0	16.0	14.0	12.0	11.0
10 BL	-	27.0	18.0	13.5	11.0	9.0	8.0	7.0	6.0	5.5	
15 BL	-	18.0	12.0	9.0	7.5	6.0	5.0	4.5	4.0	3.5	

LIST OF FIGURES

- Figure 1. -- Dates, station locations, and distribution of total herring, Albatross IV, Deleware II, and Anton Dohrn cruises.
- Figure 2. -- Length frequency of larval herring for total, day, night, and twilight stations (* = less than one). Data are combined in 3 mm size groups.
- Figure 3. -- Average abundance (total cruises) of 3 mm length group and total herring by day, night, and twilight.
- Figure 4. -- Relationship between average night/day abundance ratio and standard length. The lines are least square regressions.
- Figure 5. -- Total catch, mean length, length frequency (3 mm size groups), and average abundance (1 mm size groups) of larval herring for 0.333 and 0.505 mm mesh nets, Albatross IV Cruise 73-9 (* = less than one).
- Figure 6. -- Relationships between reaction distance (x_0) and minimum escape velocity (u_e) and between larval length and maximum swimming speed for velocity values of 5, 10, and 15 body lengths (BL)/sec. Values of u_e for one meter intervals of x_0 are indicated by vertical dashed lines.
- Figure 7. -- Relationship between standard length and maximum skull width for larval herring. The horizontal dashed lines indicate the mesh diagonal of 0.505, 0.333, and 0.253 mm nets.

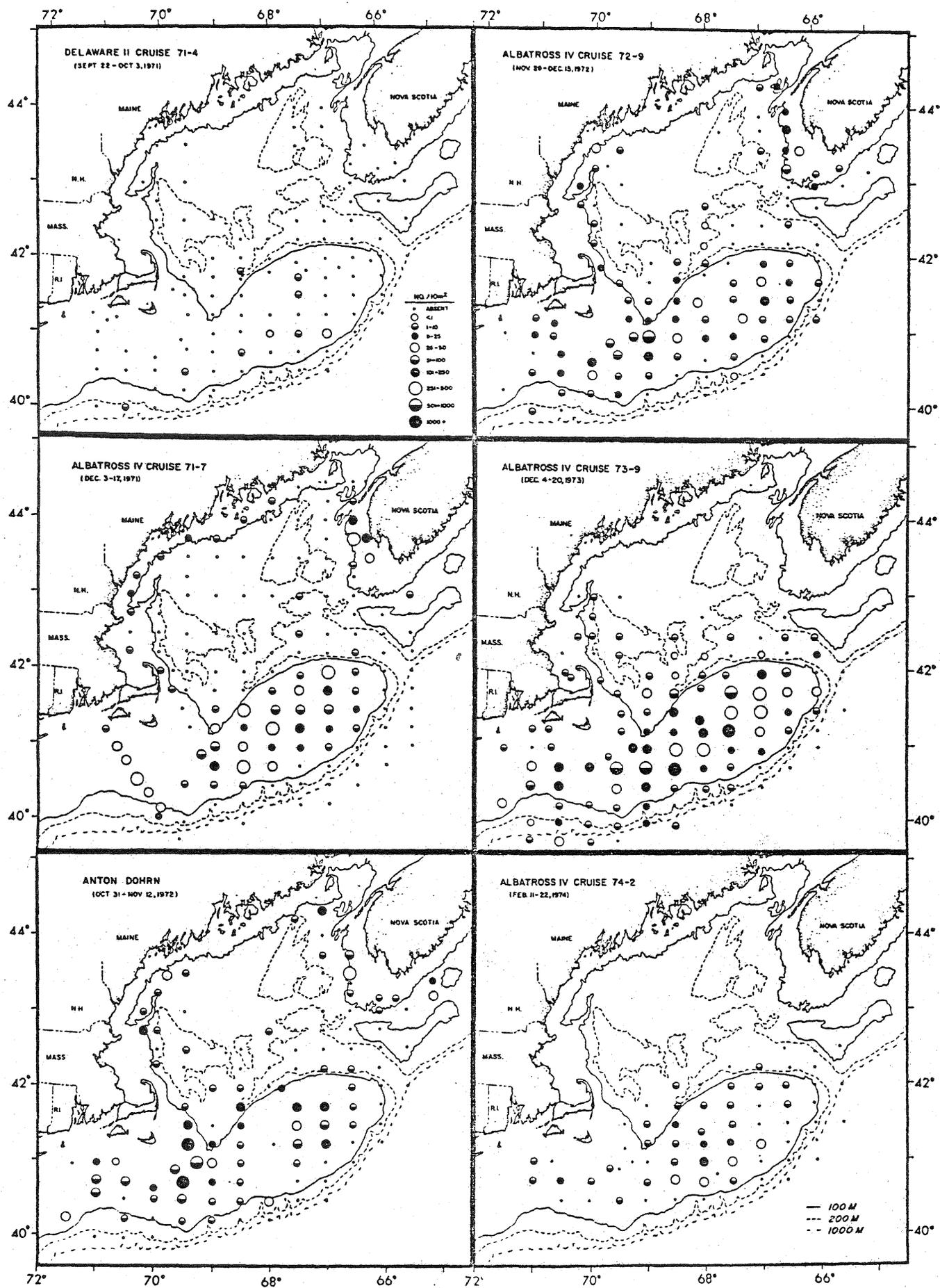
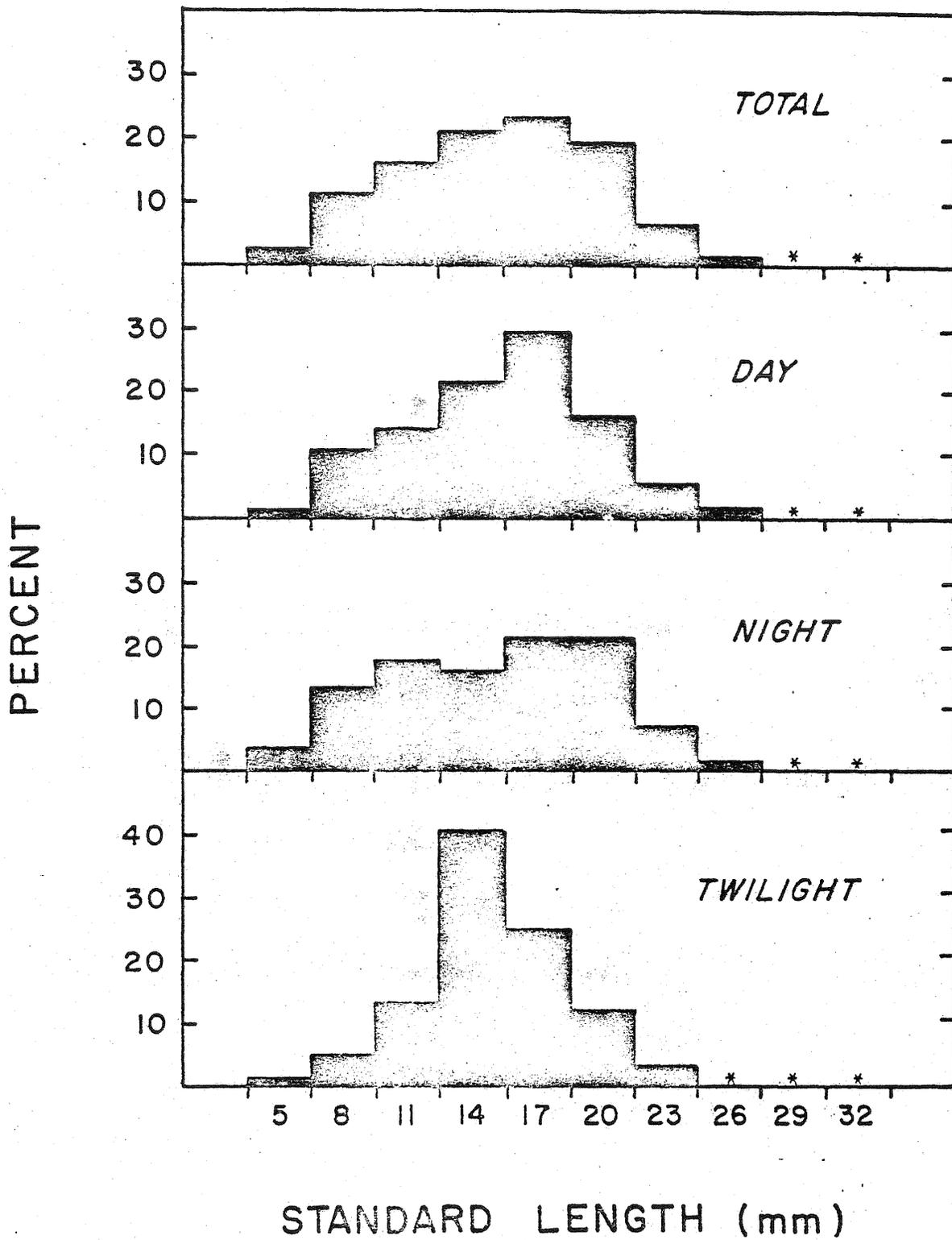


Fig. 1



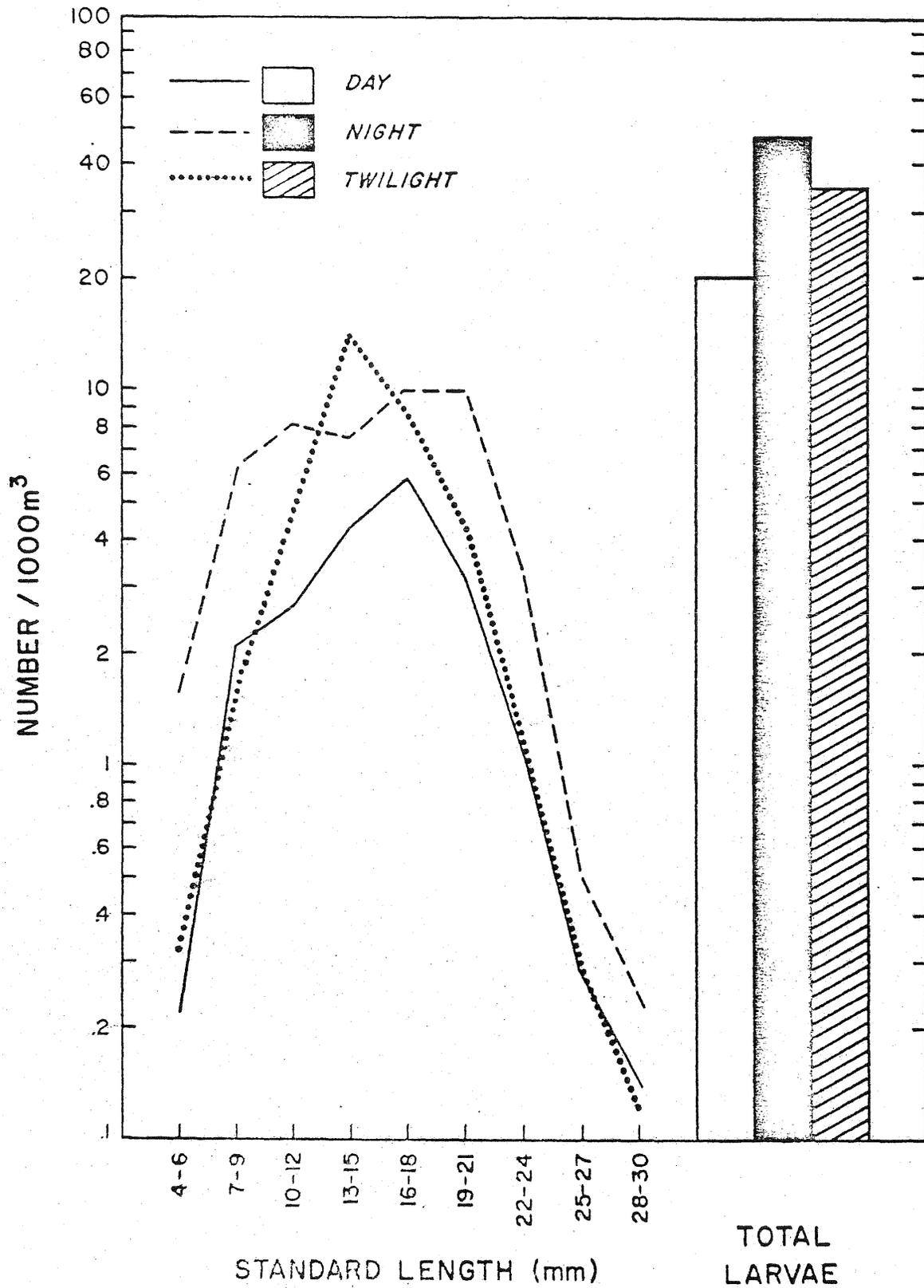


FIG. 3

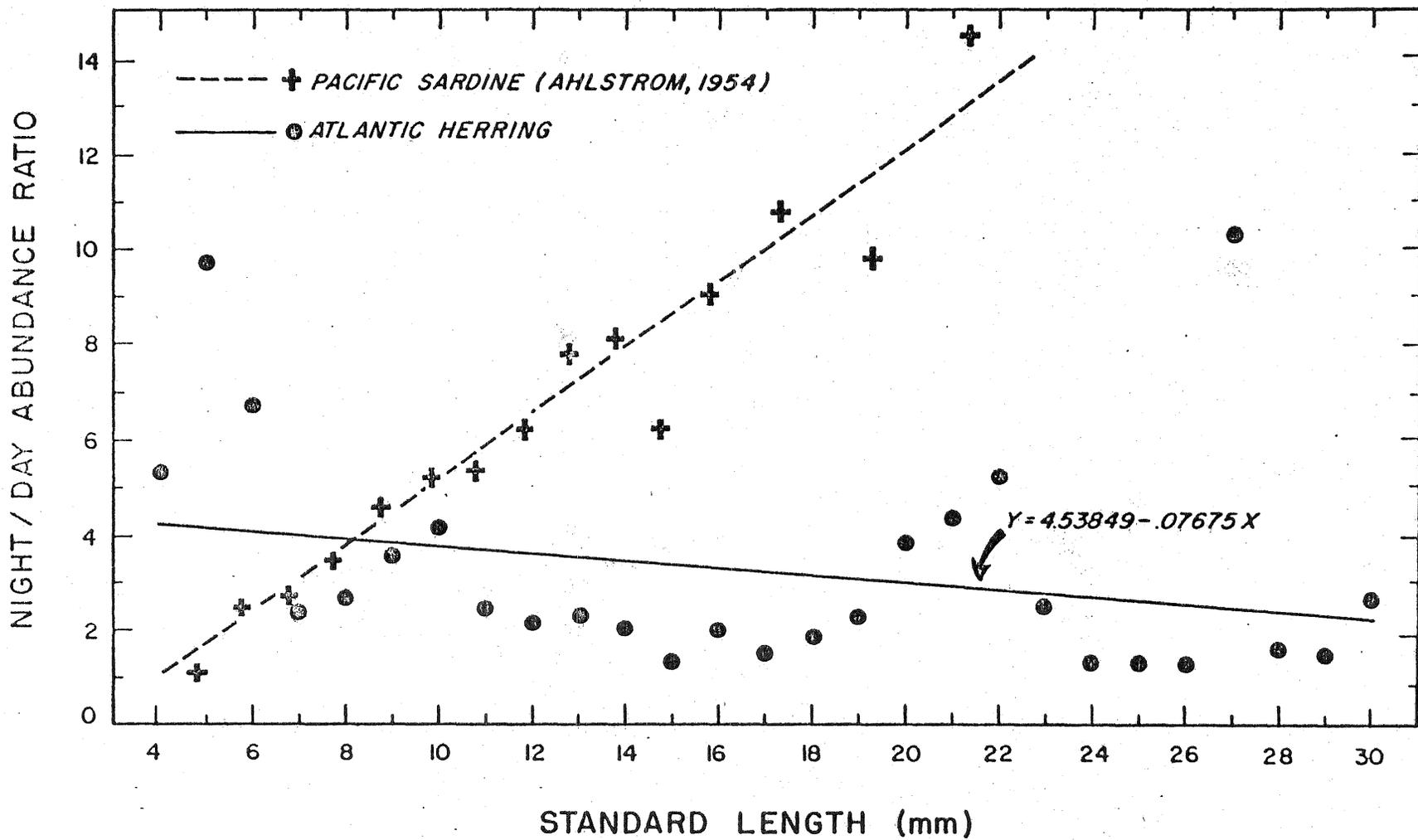
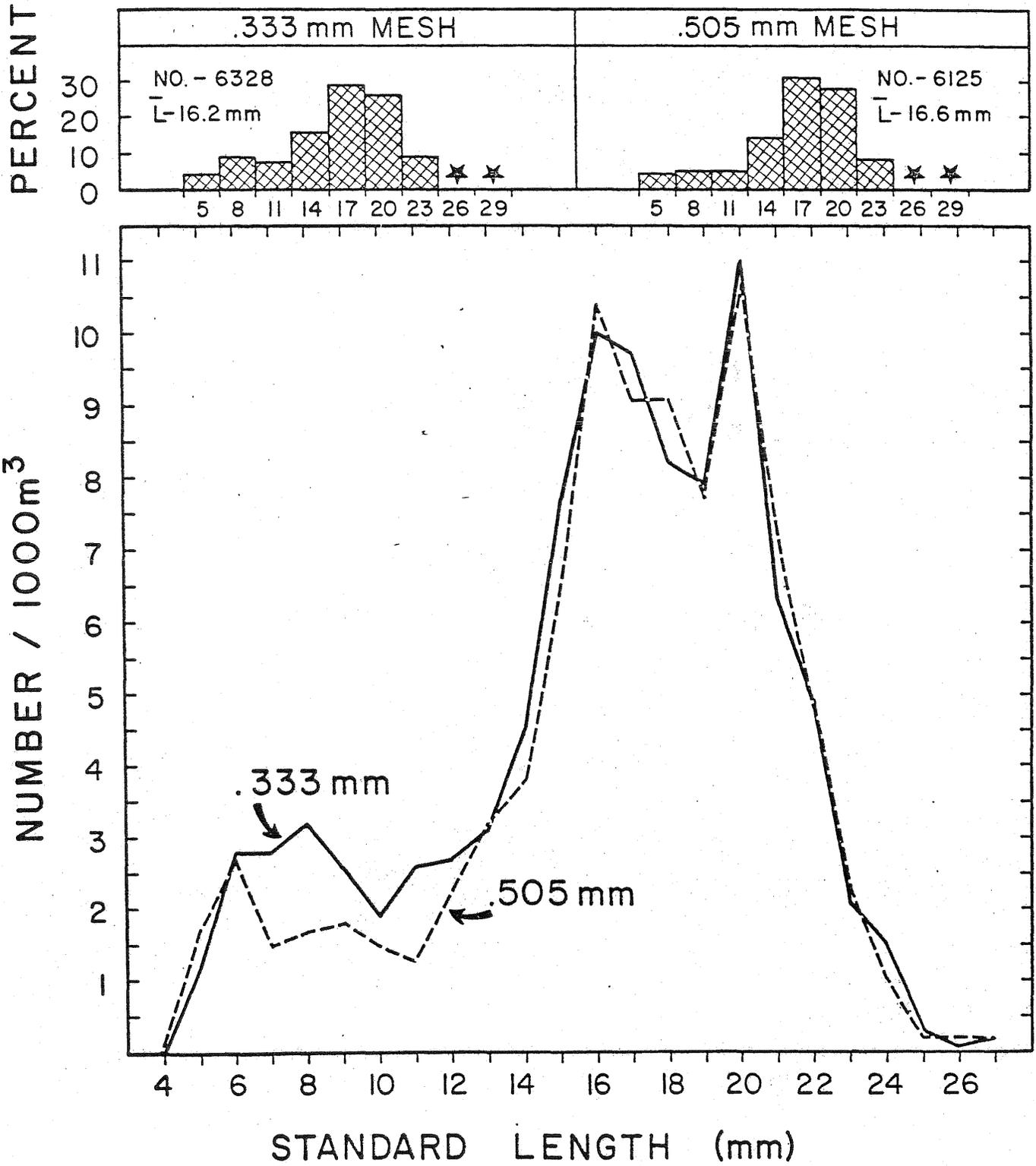


Fig 4



REACTION DISTANCE (X_0 [m])

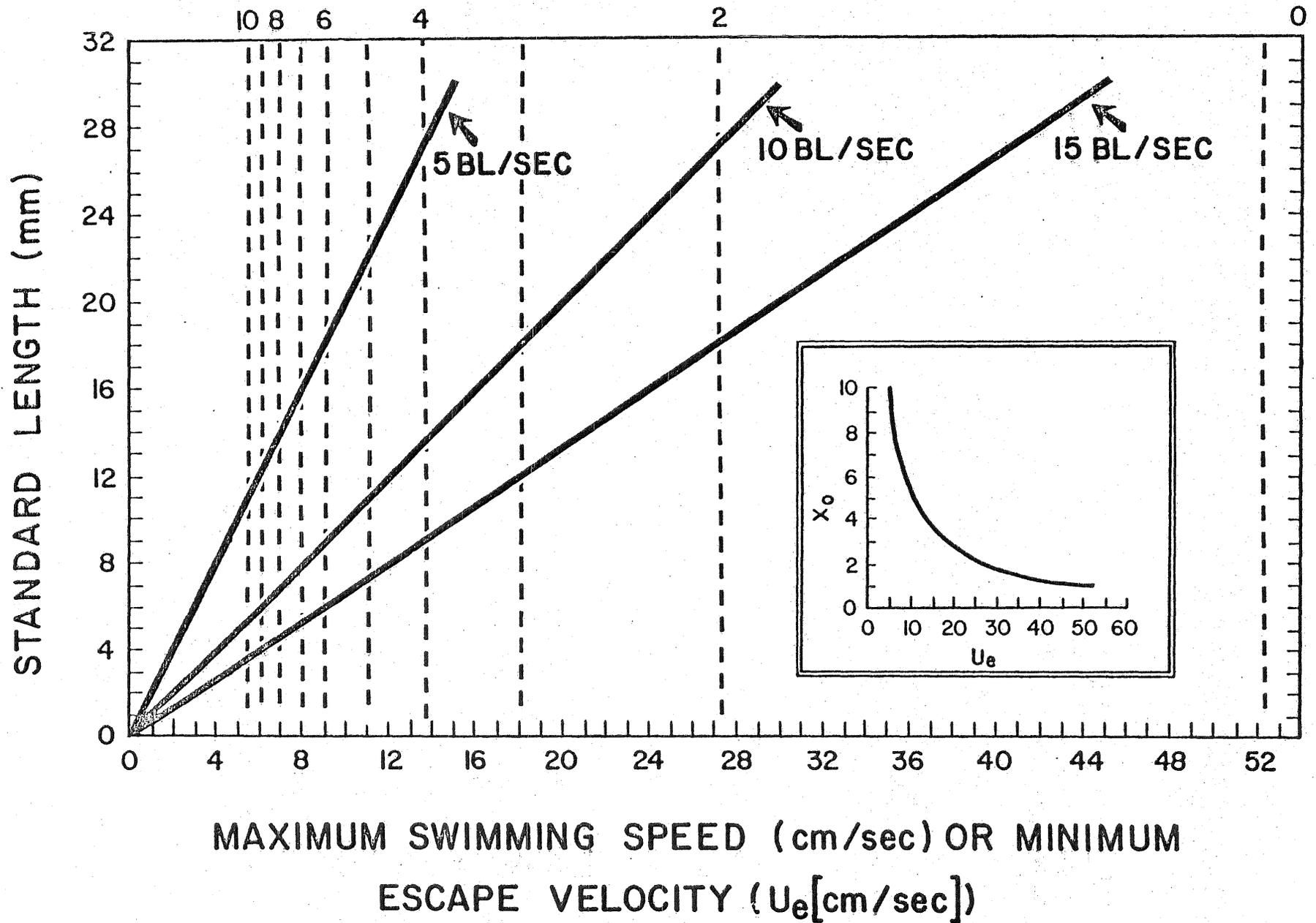


Fig. 6

