THE FEEDING OF HERRING LARVAE AND THEIR ECOLOGY IN RELATION TO FEEDING

J. H. S. BLAXTER *
Marine Laboratory, Aberdeen, Scotland

INTRODUCTION

This contribution to the symposium consists of a review of published work and of new data obtained from recent experiments, some of which require confirmation. As material for study both dead larvae caught in plankton nets and live larvae reared in tanks have been used. It is difficult to catch live larvae by plankton net, but attempts to rear the Atlantic herring from the egg stage have met with more success than those on some other clupeoid species, thus providing interesting experimental material. Only brief consideration will be given to the feeding of herring larvae at the transition period from an internal yolk food supply to external sources and to concepts related to the "Critical Period" hypotheses, as this has been dealt with by Hempel in an earlier paper given to the symposium.

THE FEEDING PROCESS

Larvae up to a length of 30 mm or more catch their food by a darting movement produced by an S-shaped flexure of the body. Smaller larvae may follow active food organisms over short distances in the S-shaped position, presumably by movements of the pectorals or primordial fin. Smaller larvae appear to sight possible food organisms when they are about 5 mm away and make the forward dart with the food about 2 mm from the head. After ingestion the food may be seen to pass rapidly to the posterior end of the gut where digestion takes place.

NUMBERS OF FOOD ORGANISMS TAKEN

Feeding incidence: Herring larval surveys and analyses of gut contents have been especially done by European workers. The percentages of larvae caught with food organisms in the gut vary greatly. For instance Bowers and Williamson (1951) found values of 60–70%, whereas in other instances only small numbers or no larvae contained food (Lebour, 1921; Mielck, 1925; Marshall, Nicholls and Orr, 1937). Waldmann (1961) found that the incidence of feeding increased with size of larvae, but this might be deduced from the fact that older larvae have been presumably more successful at feeding and have a greater consumption. One reason for low percentages, apart from lack of suitable food, may be sampling at night. Hentschel (1950), for example, found that twenty times more larvae were found with food by day than by night. Another reason may be defecation under stress as Hardy (1924) observed in larvae kept in jars after capture. The present author saw larvae defecating under anaesthesis, but in tests to assess the effect of formalin on live larvae only about 10% of larvae were found to empty their guts during fixation.

Numbers: Some knowledge of numbers of food organisms taken is required to assess the food potential of an area and to estimate maintenance and growth requirements. The numbers found in those sea-caught larvae containing food vary greatly, depending on the size of the larvae and of the food organisms, quite apart from external factors such as time of day or artifacts such as the effect of capture. Hentschel (1950) gave the following average values:

Length of herring larvae	*Copepods/larva*	
	day	*night*
7–18 mm	0.72	0.21
18–30 mm	4.9	0.26
30–45 mm	5.9	0.41

Further values are summarized in Table 1. These are mainly instances of rather large numbers found in larvae which were feeding and not average values which may appear small due to a low incidence of feeding. The impression gained from the table, when comparing it with the percentage of larvae feeding and some instances of *average* number of organisms observed, is that herring larvae probably only rarely reach their capacity for ingestion. The feeding drive, the effect of satiation as studied in reared larvae and the concentration of food organisms in areas where larvae are caught are described in later sections.

SIZE OF FOOD ORGANISMS TAKEN

It is necessary to know something of the capacity to ingest large and small organisms in order to estimate the relevant biomass in the plankton. In the young stages very small food organisms may be taken, for example *Coscinodiscus* about 0.15 mm across (Hardy, 1924). Larvae up to 18 mm will take *Tintinnopsis*, measuring about 0.08 x 0.07 mm (Hentschel, 1950) or *Mytilus* trochophores about 0.1 mm long (Blaxter and Hempel, 1961). Larvae up to 40 mm in length will still feed on *Artemia* nauplii about 0.4 mm long (Blaxter, new data).

The average size of food taken depends on the size of the larvae as nearly all the workers have shown in general terms. Hentschel (1950) provided the following, more detailed data:

	Carapace length of copepods eaten in mm				
	0.3	*0.3–0.6*	*0.6–0.9*	*0.9–1.1*	*1.1*
9–18 mm	7%	61%	32%	0%	0%
18–40 mm	2%	18%	75%	2%	4%

* Present address: Natural History Department, Aberdeen University, Scotland.

TABLE 1

OBSERVATIONS ON AVERAGE AND ESPECIALLY HIGH NUMBERS OF FOOD ORGANISMS TAKEN BY HERRING LARVAE

Author	Length of larvae in mm	Organism	Number	Remarks
Bhattacharyya, 1957	14	*Limacina*	4.6/larva 62 in one larva	North Sea
Blaxter, 1962 new data	10–12 14–15	*Artemia; Balanus* nauplii Artemia	up to 10/larva up to 40/larva	Rearing experiments
Blaxter and Hempel, 1961	8–10 35	*Artemia* nauplii copepods	5–10/larva about 50 taken in 5 mins	Rearing experiments
Bowers and Williamson, 1951	6–10 10–15 >15	Gastropod larvae Gastropod larvae *Pseudocalanus* VI	4–10/larva 7/larva 3.6/larva	Irish Sea Irish Sea Irish Sea
Kurata, 1959*	<14	*Artemia* nauplii	5–11/larva 19 in one larva	Rearing experiments
Marshall, Nicholls and Orr, 1937	18.2 35	Crustacean eggs mixed copepodites	26.8/larva 69 in one larva + 26 other organisms	Clyde Clyde
Meyer, 1878			up to 20	Rearing experiments
Mielck, 1925	12–20	Small copepods?	up to 5	North Sea
Ogilvie, 1927	38, 41 35–40 —40–45 40+	*Pseudocalanus* VI Copepods Copepods Copepods	51 in each fish 27/fish 150/fish 479 in one fish	North Sea North Sea North Sea North Sea
Waldmann, 1961	16–25 26–35 36–45	"organisms" "organisms" "organisms"	2–3/larva 2–14/larva 2–60/fish	Baltic Baltic Baltic

* *Clupea pallasii*, all others *Clupea harengus*

The maximum sizes of food organisms taken for different lengths of larvae, as compiled from the various authors cited so far, are shown in Figure 1. As very few authors measured the food organisms they observed, the main dimensions (total length of the body, breadth including the antennae turned back) are mainly taken from Wiborg (1948), although it is appreciated that there may be differences in the size of a copepod species as a result of temperature (Raymont, 1963).

There are exceptional instances of large organisms being taken, for example adult *Pseudocalanus* by a 6 mm larva and adult *Calanus* by a 19 mm larva (Bowers and Williamson, 1951). Adult *Pseudocalanus* are taken normally at lengths from 12 mm onwards.

In his detailed work on the size of food of other clupeoid larvae Arthur (1956) found that those of *Sardinops caerulea* took food up to 0.08 mm at a length of 4 mm and up to 0.2 mm at 10 mm; those of *Engraulis mordax* could take food up to 0.05 mm greater at any given length of the larva.

The gape of the jaws may be related to the size of food taken. In Figure 2 the vertical gape (assuming an angle of 60° between upper and lower jaw) is shown for samples of herring larvae at various stages living on their yolk reserves before active feeding commenced (from 6–11 mm). Clear differences may be seen between different races, as a result of the size of the original egg.

In Figure 3 the gape for herring larvae of various races still living on their yolk reserves is given re-

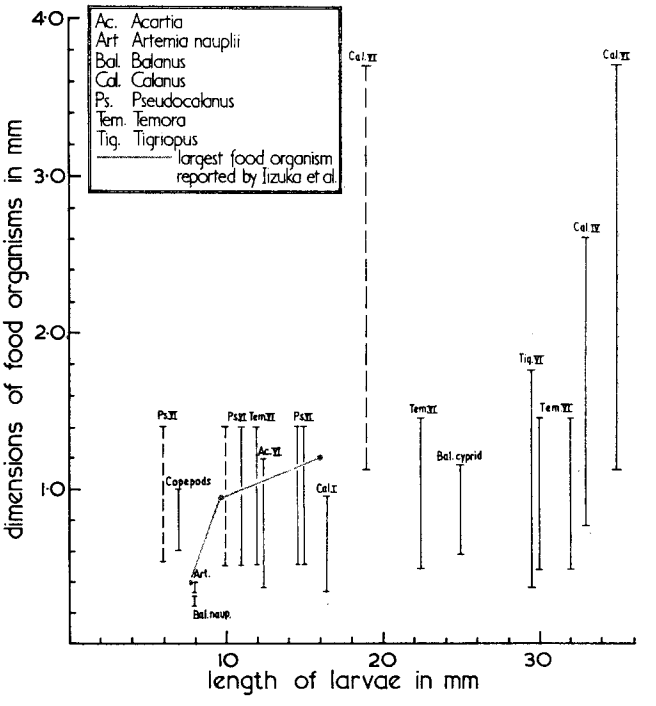

FIGURE 1. The dimensions of food organisms (total length and maximum breadth of body) reported by various authors to be taken by herring larvae.

– – – – normally taken

——— exceptional cases

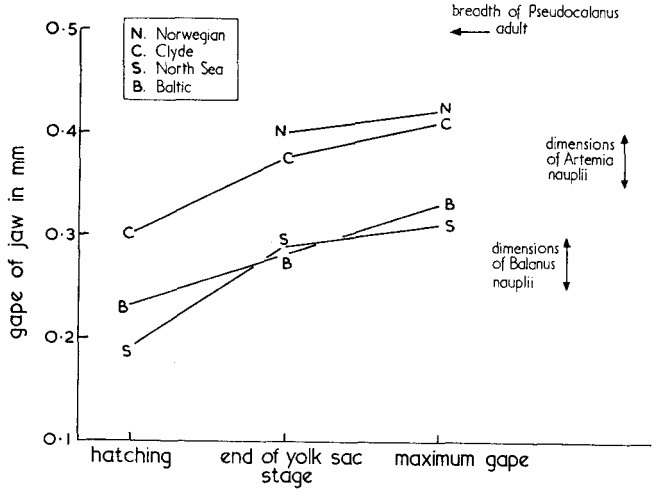

FIGURE 2. The vertical gape of the jaws of young herring larvae living on their yolk reserves, assuming an angle of 60° between the upper and lower jaw (using data from Blaxter and Hempel, 1963).

lated to length. In both figures the dimensions of the body (length and breadth) of *Artemia* and *Balanus* nauplii are given indicating that feeding on these sizes of organism might only just be possible. The racial differences in jaw gape could be of great significance. The reported cases of *Pseudocalanus* adults being taken at about 12 mm must mean that those organisms are taken "end on" and even then the gape would seem to be barely adequate. Recently Flüchter (1963) described an elastic ligament as the jaw articulation in herring larvae. This might enable large organisms to pass the restrictions of the articulation, but an instance has been found of a larva choked by taking too large a food organism.

Feeding is not only dependent on the size of the body of the food organism, but also on the nature of its appendages. Copepods are usually found taken with the antennae folded back along the body. This is probably not due to an intentional mode of feeding by the larvae. It is more likely that only organisms with their appendages folded in such a way

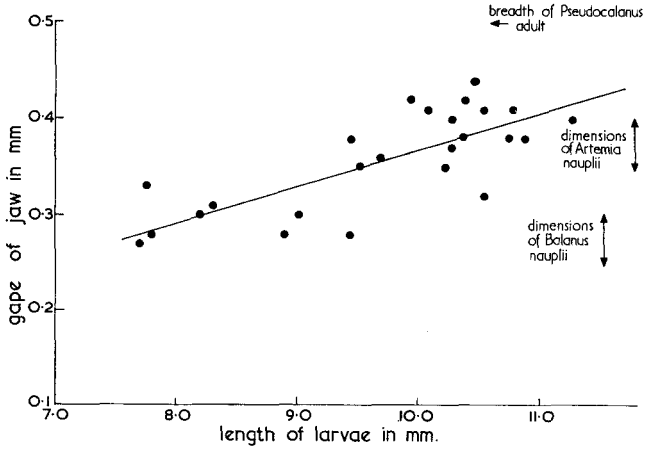

FIGURE 3. The vertical gape of the jaws of young herring larvae living on their yolk reserves related to length of the larvae (using data from Blaxter and Hempel, 1963).

during capture and approached from the right direction could be successfully fed on. Spiny organisms such as *Ceratium* might not pass through the mouth but presumably an ability to reject spiny objects might save the gut from being perforated.

SELECTION OF FOOD AND RATE OF FEEDING

Analyses of gut contents of herring larvae and also of the relevant zooplankton enable conclusions to be drawn about selection. The smaller larvae caught at sea most often contain copepod nauplii and eggs, mollusc larvae and some green food; at later stages copepodites and adult copepods, especially *Pseudocalanus* are found. Hardy (1924) inclined to the view that *Pseudocalanus* was selected and *Acartia* either ignored or rejected. Bowers and Williamson (1951) found that *Biddulphia sinensis* and *Ceratium* were not taken while *Arcatia* occurred rarely in the guts in relation to its frequency in the plankton. Hentschel (1950) also found few *Biddulphia* but many *Coscinodiscus* in the gut when both were plentiful externally. Nauplii were not taken though they comprised 50% of the plankton; adult copepods, however, were predominant in the gut though comprising numerically only 6% of the plankton. Waldmann (1961) found a preference for *Eurytemora* compared with *Acartia* and few nauplii in the guts. More *Acartia* were taken than *Eurytemora* only when the ratio was 15:1 or greater in the plankton. Lishev, Rannak and Lisivnenko (1961) found that Baltic herring only fed on Rotatoria when copepods were scarce.

My observations show that herring larvae in tanks will take almost any kind of floating object ranging from their own faeces to bubbles on the surface, although they may rapidly adjust their initial selection after some experience of unfavorable food. Once an object is seized, secondary selection takes place within the mouth on the basis of taste and texture, as was shown in adult herring by Blaxter and Holliday (1958). For instance the larvae take fresh squid, but when it is soaked for 24 hours in sea water it is rejected. Live *Tigriopus* are retained but dead ones often rejected. Both live and dead *Daphnia* are also rejected, as are the eggs of herring, lemon sole and whiting, but not the connective tissue surrounding them.

The feeding drive may be weakened by experiencing unsuitable food, both at the initial selection and secondary selection stage. This drive also depends on the previous feeding history of the fish and weakens more rapidly with some types of food than others. In Figure 4 the number of pieces of squid flesh taken each minute by a group of eight larvae 22–40 mm long is shown after different periods without food. The effect of the time since last feeding is very variable but it seems that the first burst of feeding is at a high rate as long as the last feed was about five hours or more before. The rate drops rather rapidly with squid but picks up quickly if live *Tigriopus* are offered. The movement of *Tigriopus* seems to enhance the feeding drive as the number of organisms taken drops immediately when dead *Tigrio-*

pus are offered (Fig. 5). It should be remembered, however, that sea-caught larvae are often found with non-motile organisms, such as diatoms and copepod eggs, in the gut, so that movement of prey is far from essential to the feeding drive.

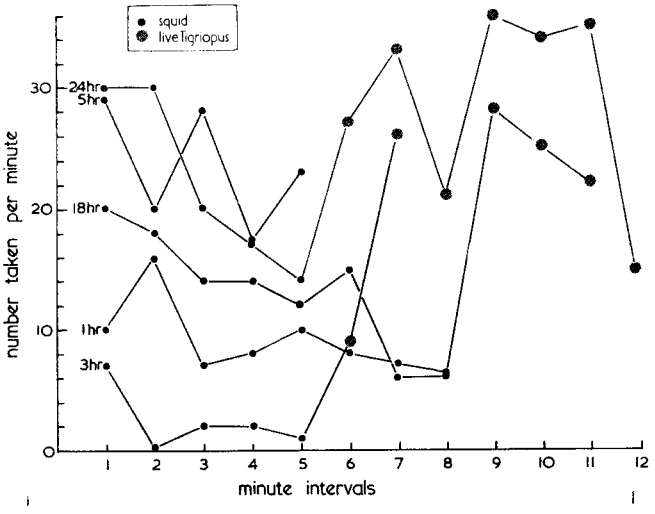

FIGURE 4. Number of pieces of squid flesh (weighing about 1.0 mg wet weight) and later live *Tigriopus* (wet weight about 0.5 mg) taken per minute by eight herring larvae 22–40 mm long after different periods without food at about 14° C. (new data)

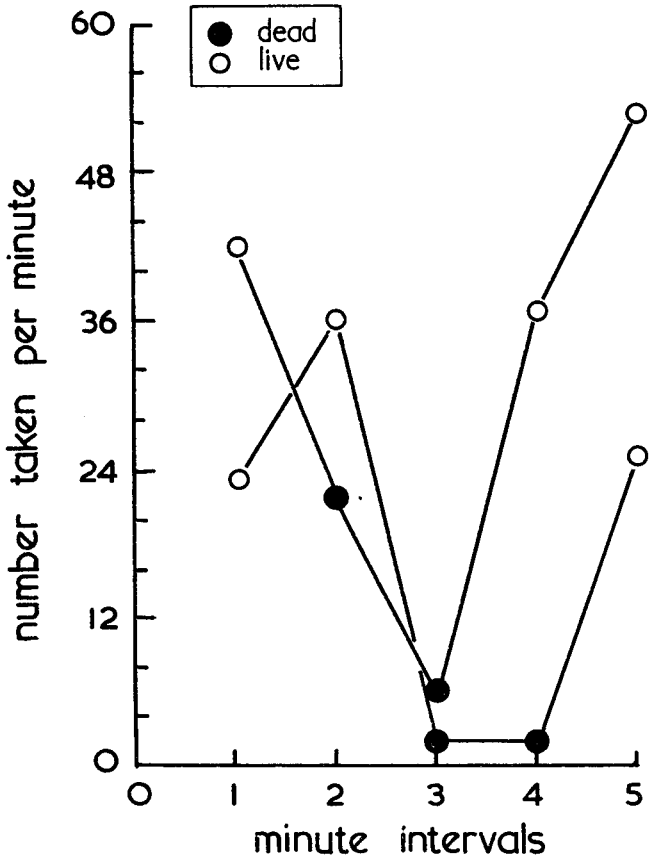

FIGURE 5. Number of live or dead Tigriopus (killed by drying, then soaked in sea water) taken per minute at a temperature of about 14° C (new data).

Arthur (1956), working on a restricted sample of *Sardinops caerulea* larvae, found that the distribution of food organisms in the guts was not random, but there were more larvae with a high number of food organisms than was expected by chance. He concluded that feeding might be enhanced in marginal food concentrations by the previous capture of an organism.

The rate of feeding may also be influenced by social factors. In rearing experiments size-hierarchy effects are apparent (Blaxter and Hempel, 1961; Blaxter, 1962). At the end of a period of two to three months after hatching the largest larva in a tank may be twice the length of the shortest, although abundant food has been offered and the larvae came from the same parents. While this may be partly due to differences in the ability to convert food, observations show that larvae may snap at each other, as well as compete actively for food.

DIGESTION

It has been suggested that digestion should be rapid in transparent larvae as an aid to remaining inconspicuous. The digestion time, defined as the time taken for the gut contents to become transparent, is given for different temperatures in Figure 6., based on tank observations and estimates from the study of gut contents of larvae caught at sea after dark. The time ranges from about 8 hours at 7°C to 4 hours at 15°C giving a Q_{10} of 2.4. Arthur (1956) working on *Sardinops caerulea* found times ranging from 11 hours in larvae 5.5 mm long to 3 hours when 10–25 mm long.

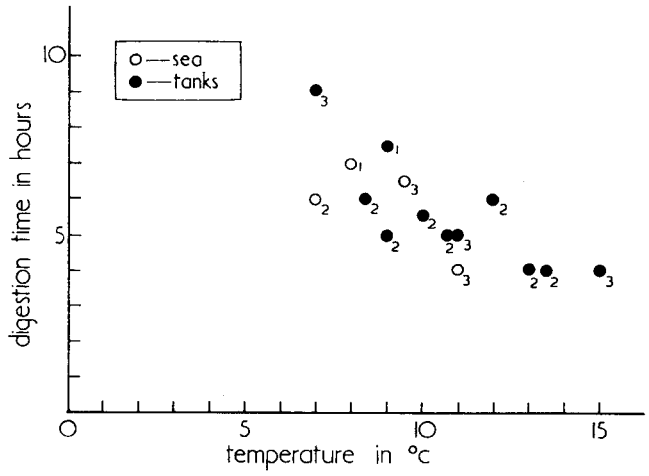

FIGURE 6. Time for digestion (taken as when gut contents become transparent) at different temperatures.
○ Sea: 1. Hentschel (1950), 2. Hempel (unpubl.), 3. Bhattacharyya (1957).
● Tank experiments: 1. Kurata (1957), 2. Blaxter and Hempel (1961), 3. Blaxter (1962).

The time for gut clearance depends much more on the feeding history of the larvae because feeding before or after a test feed can alter the rate of passage of food through the gut. Kurata (1959) gave the fol-

lowing figures for Pacific herring larvae 12 mm long held in tanks at 9°C.

Fed on 2–4 *Artemia*	12 h
Fed on 5–7 *Artemia*	15 h
Fed on 9–15 *Artemia*	19+ h

By feeding older larvae with squid flesh and using single feeds of *Tigriopus*, an orange copepod, as a marker, I found it possible to measure gut clearance by looking for the first signs of orange faeces. The time varied from 24–30 hours at 12°C if no food was given subsequent to the orange food.

SOME CONSIDERATION OF NUTRITION

Almost all authors who have studied the gut contents of herring have noted that food was taken before the yolk was resorbed. However, Schach (1939) found food in the gut only four days after resorption in rearing experiments. In the early stages green food remains have been reported by many authors (e.g. Hardy, 1924; Lebour, 1921, 1924; Ogilvie, 1927; Marshall *et al.*, 1937; Bhattacharyya, 1957) though it is not quite clear how often these are the results of secondary feeding, i.e. green food in the guts of zooplankton organisms taken as food. Schach (1939) and Blaxter and Hempel (1961) reared larvae to metamorphosis without green food being given while Soleim (1942) was of the opinion that green food was inadequate alone. The importance of dissolved organic matter (Pütter's Theory) has been discussed by Morris (1955), but evidence for the intake of such substances in marine fish larvae is still lacking.

Artemia nauplii have been used as a suitable food for rearing plaice larvae to metamorphosis (Shelbourne—this symposium) but Blaxter and Hempel (1961) were not successful in rearing larvae beyond a length of about 25 mm with *Artemia* alone; Artemia and wild plankton together produced better results. More recent experiments, given in Table 2, show a similar result.

TABLE 2

NUMBERS OF LARVAE REACHING DIFFERENT LENGTHS ON DIFFERENT DIETS (BLAXTER, NEW DATA)

Tank	Number hatched	Number* reaching 15 mm	20 mm	25 mm	30 mm
1 Fed on *Artemia*	3166	715	24	2	--
2 Fed on wild plankton	2676	682	127	44	23

* Corrected for larvae sacrificed.

Older larvae have been maintained, at least for a time, on chopped *Mytilus* (Dannevig, 1948) and squid (Blaxter—unpublished). No data are available on maintenance diets for herring larvae and their growth requirements, but experiments to determine these are in hand. The problems of making estimates when larvae cannot be kept singly in tanks, and when there is a fairly high, steady mortality, have to be solved.

IMPORTANCE OF VISION

The importance of vision in the life history of herring was reviewed by Blaxter and Holliday (1963). The feeding behavior of herring larvae and their prominent eyes stress the importance of vision in the early stages. This is supported by observations on the incidence of feeding in the sea by day and night (see later) and by preliminary experiments to measure the light intensity required for feeding in tanks. Larvae of 12–14 mm were dark-adapted in two black-walled tanks for at least two hours after a period of at least 12 hours without food. After dark-adaptation a given quantity of either *Artemia* or *Balanus* nauplii was put in the tanks. In one tank the overhead lighting was held at about 1000 lux while in the other the light was varied from experiment to experiment by means of neutral filters. The light intensity was measured at the surface, where the larvae feed, by a photo-multiplier unit (Craig and Lawrie, 1962) with a green filter giving a maximum sensitivity at about 510 mμ and calibrated against a standard light source in photopic lux. After one hour with food in the water a count was made in each tank to assess the proportion of larvae with food in the gut (this was easily seen as the guts are transparent). The proportion feeding after one hour in different light intensities was then expressed as a percentage of the proportion feeding in the control tank. The results are given in Figure 7, the threshold light intensity being taken when the proportion feeding in the experimental tank was half that in the control tank. The threshold using *Balanus* nauplii was 13 lux and for *Artemia* nauplii 0.3 lux; presumably the difference being due to the smaller size and greater transparency of the *Balanus* nauplii.

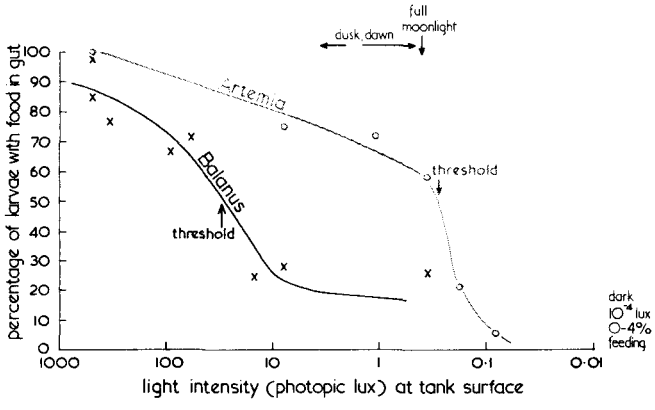

FIGURE 7. Percentage feeding on *Artemia* (o) and *Balanus* (x) nauplii fed at different light intensities in tanks (new data).

Initial studies of the histology of the eye of 8 mm and larger herring larvae (Jones and Blaxter—unpublished) show the presence of cones, but no rods have been demonstrated by the staining techniques to date. Their presence in larger larvae may be inferred from the density of nuclei in the "outer nuclear layer" (the layer containing the nuclei of the visual cells) which is much higher than the density of the cones. There are no signs of a foveal structure in the retina, al-

though there are some areas where the cones are especially dense. The size of the cones tends to increase with age of the larvae and the density decreases, as shown in Figure 8. The acuity of the eye, which is related to the reciprocal of the focal length and the density of cones (Tamura, 1957) will tend to be high in the young larvae as a result of the high density, but this will be offset by the small lens. In the older larvae the decrease in density and increase in size of the cones will tend to reduce the acuity, but this will probably be more than compensated for by the increase in size of the lens.

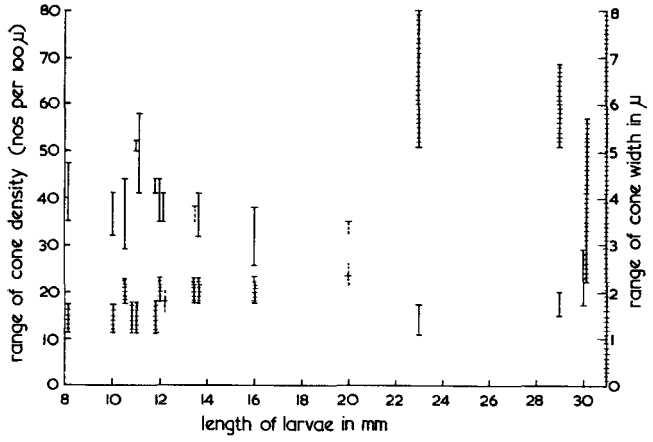

FIGURE 8. Density of cones (numbers/100μ section) and width of ellipsoids in μ for larvae of different length (Jones and Blaxter—new data).

Measurements on the pigment layer surrounding the retina in larvae adapted to different light intensities have as yet shown no clear trace of a photomechanical response whereby the more sensitive rods might become free of pigment at low light intensities. This pigment migration occurs in the adult and its onset appears at a larval length of about 30 mm, at a time when the main pigmentation of the body begins to be laid down. The main movement of the retinal pigment is at intensities from 10–1 photopic lux.

The position of the eyes of the larvae suggests that there is a degree of binocular vision which should facilitate the estimation of distance when catching food organisms.

SUCCESS AND FAILURE IN FEEDING

Success and failure in feeding will depend on the searching power of the larvae, their ability to catch food and the abundance of suitable plankton.

Searching power: This may be defined as the distance covered by the larvae per day in search of food at times when the light is sufficient to make feeding possible. Light conditions are a limiting factor, for it has been shown that feeding does not occur at very low light intensities. This is confirmed by analyses of gut contents by day and night as shown in Figures 9a–d. Here the percentage of larvae with gut contents in three series of samples (Figs. 9a–c) is plotted against time of day, the hour of sunrise and sunset and the approximate time when the threshold light intensity (taken as 1 lux) is reached at the surface and bottom. In Figure 9d the results of a 2-day feeding experiment in natural light conditions (Kurata, 1959) are given. All show how feeding falls off in the dark hours and from this a measure of digestion time can be obtained (given earlier). Observations made on light intensity in three areas and seasons, where spawning occurs and larvae are caught show how the time for searching may vary quite widely, by as much as 5 hours in 24 (Table 3).

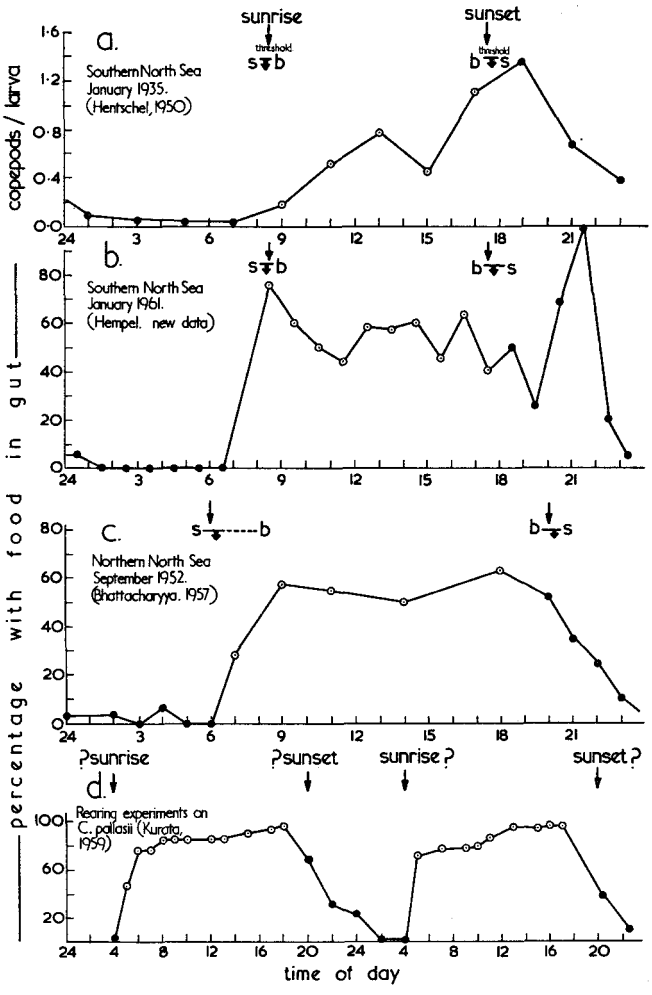

FIGURE 9a–d. Incidence of feeding at different times of day and night. a–c. sea caught larvae, d. rearing experiment. Times of sunrise and sunset are shown and related to the time when the threshold (taken as 1 lux) is reached at the bottom (B) and surface (S).

Presumably larger and stronger larvae will have greater powers of locomotion and be able to cover greater distances within the daylight period. Bishai (1960) found that herring larvae 6–8 mm long could sustain a water current of 0.58–1.03 cm/sec for at least one hour, perhaps giving them the possibility of swimming 20–30 m in one hour. At an average cruising speed of 1 cm/sec and with a perception distance of 5 mm, a small larvae could search about 3 liters of water per hour. Blaxter (1962) showed that the maximum speeds of herring larvae range from about 3

TABLE 3

TIME PER DAY FOR FEEDING OF HERRING LARVAE (10–20MM) BASED ON THRESHOLD LIGHT INTENSITY OF 1 LUX (BLAXTER, HEMPEL, NEW DATA)

Area	Month	Hours for feeding/day	
		Surface	Bottom
Southern North Sea	Mid-January	9.8	8.8*
Clyde	Mid-March	12.8	12.1
Northern North Sea	Mid-September	14.7	11.7†

* In some shallow turbid areas (e.g. Sandettie) the light is never above threshold on bottom.
† Measurements were probably made in an area more turbid than average.

cm/sec for 8 mm larvae to 30 cm/sec for 20 mm larvae with a rather sudden increase in their abilities at a length around 15 mm when the caudal fin is formed. No data are yet available on the activity of herring larvae, except those of Woodhead and Woodhead (1955), who found differences in activity of newly-hatched larvae in relation to light intensity, which they related to vertical migration.

While certain factors such as swimming ability may increase searching power and other factors such as temperature or light or the feeding drive may influence activity and swimming, all these will raise the metabolic rate and therefore the food demands of the larvae. Holliday, Blaxter and Lasker (1964) found that the metabolic rate may increase up to ten times from the resting rate during periods of intense activity. It seems that in darkness activity drops, at least in tanks, the larvae moving slowly or sinking gently, and in this way food reserves may be conserved.

Abundance of food: Few estimates have been made of the food concentrations required for herring larvae and no correlations have been made between food available and larval mortalities, although Lishev *et al.* (1963) showed a relationship between relative numbers of Baltic herring "fry" (shortly after hatching) and the food supply from year to year. It seemed that larvae were four times more abundant in years when there were 20,000 food organisms/m^3 (copepod nauplii and copepodites) than when there were about 5500/m^3. Waldmann (1961), by counting the gut contents of Baltic herring larvae showed, for example, in 1958, that 68,000 larvae 5–15 mm long would be required to take the plankton during one feed in 1 m^3 in May, or 64 larvae 36–45 mm long the plankton in 1 m^3 in July. From this and other data he concluded the plankton was adequate, as such concentrations of larvae were not found. Nikitinskaya (1958), working on Pacific herring larvae hatched in tanks, estimated that densities of 22,000 organisms/m^3 or a biomass from 20–50 mg/m^3 (? wet weight) were required for newly-feeding larvae to find sufficient food. In 1955 in the Sakhalin area such quantities were rarely found. Dementeva (1958) was of the opinion that food supply was not limiting for larvae of the Sea of Azov anchovy and Murphy (1961), considering Arthur's (1956) data on *Sardinops caerulea* larvae, found little evidence which suggested that food supply was limiting. In 70% of all stations the standing crop of food organisms was 1000/m^3 or greater, and in 50%, 3000/m^3 or greater. Taking a particular station with a high density of larvae as a guide, and making certain other assumptions, this gave a ratio of larvae to food organisms of 1:500 in 70% of stations and 1:1500 in 50%, suggesting very little competition for food. The mean distances between food organisms, assuming a random distribution, are given in Table 4 based on the work of these authors. The table shows that in instances where estimates have been made food seems to be abundant. If the distance between food organisms is halved to give a measure of the distance between a larvae and a food organism, it can be seen that in these particular surveys larvae had only very short distances to swim in order to meet food, up to about 5 cm, a distance they could swim in about 5 seconds or less without extending themselves. There are clearly res-

TABLE 4

DISTANCES BETWEEN FOOD ORGANISMS

Author	Species of larvae	Species of food	Mean distance between food organisms (cm)	Remarks
Lishev *et al.* (1963)	Baltic herring	Copepod nauplii and copepodites	3-4 12–13	In years when larvae most abundant In years when larvae about ¼ as abundant
Waldmann (1961)	Baltic herring	nauplii *Eurytemora* *Acartia*	2–4.5 5+–16 5–7	Variations in years 1958–1959 between May and July— considered to be adequate
Nikitinskaya (1958)	Pacific herring	not given	3–4	Considered adequate density for newly-feeding larvae
Murphy (1961) using Arthur's (1956) data	*Sardinops caerulea*	nauplii	7 or less 10 or less	In 50% of stations ratio of larvae to food 1:1500 In 70% of stations ratio of larvae to food 1:500

ervations about these types of correlations (see Hempel in this symposium) but they are the best that can be done at the present time.

Clearly further quantitative estimates of this sort need to be made in many other areas where plankton may be scarcer in winter or early spring. This is now being attempted in the southern North Sea and Clyde by the present author and Hempel using the Hardy plankton indicator, in conjunction with the Scottish Marine Biological Association's Oceanographic Laboratory in Edinburgh.

Starvation in herring larvae and evidence for poor feeding conditions: Experimental evidence is now available on the time newly-hatched herring can survive on their yolk reserves (Blaxter and Hempel, 1963). This depends mainly on the original egg weight (and therefore larval size), and on temperature, and is dealt with by Hempel in this symposium. Slightly older feeding larvae have been kept in sea water at different temperatures after feeding on either *Balanus* or *Artemia* nauplii (see Fig. 10). Individual larvae lived from 1½–9 days depending to some extent on temperature, but especially on whether *Artemia* or *Balanus* nauplii were previously used as food; those larvae feeding on *Artemia* living up to twice as long.

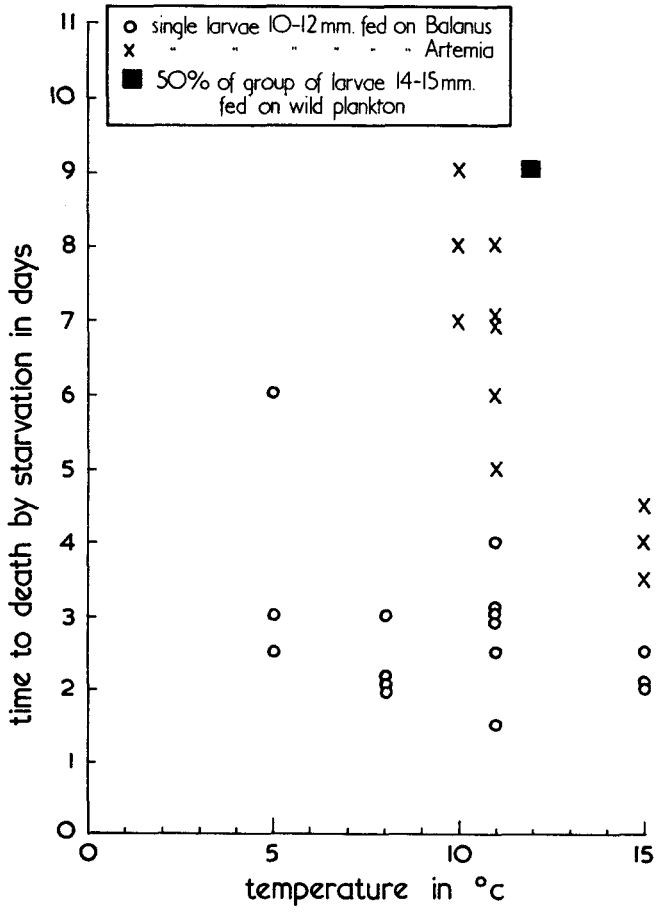

FIGURE 10. Survival time of herring larvae at different temperatures after feeding on various diets had ceased. (Blaxter, 1962 and new data).

A group of older larvae (14–15 mm long), reared on wild plankton, was found to survive for 9 days at 12°C when no food was offered (criterion for survival being 50% remaining alive). However, larvae in a weak state are less likely to feed and so a "point-of-no-return" needs to be measured, which is the point when starving larvae become incapable of feeding. The percentage of larvae (14–16 mm long) feeding after different periods without food is shown in Figure 11. The "point-of-no-return," when the percentage feeding is half the control percentage at the beginning of the experiment, appears to occur at 5–7 days, though confirmation is required of this.

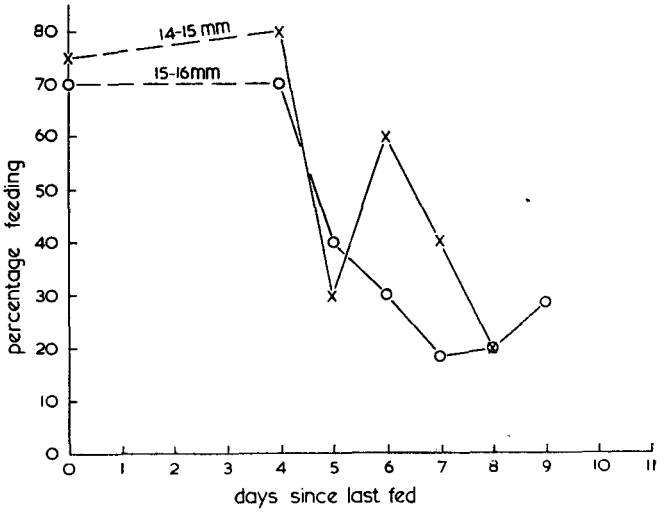

FIGURE 11. The ability of herring larvae to feed after different periods of time without food at 12° C (new data).

From this type of tank experiment it is possible also to measure the condition factor of larvae during starvation

$$\frac{(\text{mean dry weight of a fixed sample in mg} \times 1000)}{(\text{mean fixed standard length}^3)}$$

as a measure of the body reserves. The height of the body (excluding the gut) is another measure of emaciation. Decreasing values of condition factor and body height for newly-hatched and older larvae which were not feeding are given in Figure 12. The tendency for irregularity in the condition factor or body height as time passes is due to sampling errors and the possibility of somewhat larger larvae surviving better in such experiments. For Clyde larvae reared in tanks the condition factor and body height at a point near starvation may be taken as:

10–11 mm Condition factor 0.09; Body height 0.39 mm.
14–15 mm Condition factor 0.134; Body height 0.78 mm.

Data of this sort enable the condition of larvae in the sea to be assessed. There are various reports of dead herring larvae being taken in plankton hauls (Soleim, 1942). Arthur (1956) considered that dead or moribund larvae of *Sardinops caerulea* might be often taken, whereas, active, healthy larvae are less liable to capture. This does not seem likely to be a

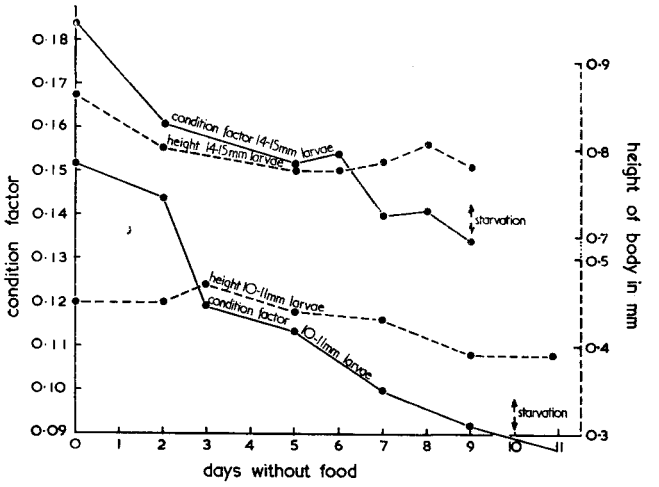

FIGURE 12. The condition factor and body height of herring larvae held in sea water tanks without adding food. Larvae of 10–11 mm had been living on yolk reserves, larvae of 14–15 mm had been feeding on *Artemia* and *Balanus* nauplii (from Blaxter and Hempel, 1963 and new data).

serious source of error in larval surveys for moribund larvae will quickly sink to the bottom. The condition factor and body height of some samples of herring larvae taken in the Clyde from 1959–1961 are shown in Figure 13 a and b. (Hempel and Blaxter, 1963 and new data). Also shown are the condition factor and body heights of larvae near starvation in tanks. The condition factors are much higher in the early stages up to 10 mm, presumably due to remnants of yolk reserves within the body (larvae with yolk sacs were not used), but they fall to a lower level between 10 and 15 mm and then rise again as a result of allometric growth and the formation of skeletal structures. Thus comparisons of condition factor, and of height, from year to year, need to be made within restricted length ranges. If this is done it can be seen that there is a tendency for the 1959 condition factor to be low and those of 1960 to be higher. What is of interest is that both in terms of condition factor and height the 10–11 mm larvae seem to be rather near the starvation point. At 14–15 mm they appear to be in very poor condition—unless the growth of larvae in tanks is abnormal giving high condition factors and body heights at starvation. Obviously this work, which is only in progress, requires confirmation. Data over a series of years are especially required, covering both the condition of the larvae and the available plankton. Further measurements are also needed on larvae reared in tanks and spurious factors in the measurement of condition factor and body height, such as shrinkage and differences in water content, need to be allowed for.

From the foregoing it would seem that in some areas covered, such as the Clyde (and also the southern North Sea), studies on the larvae and knowledge of the plankton suggest a fairly strong influence of availability of food on larval survival. Not only is the plankton scarcer but the hours for feeding are also less. The somewhat greater size of the winter-

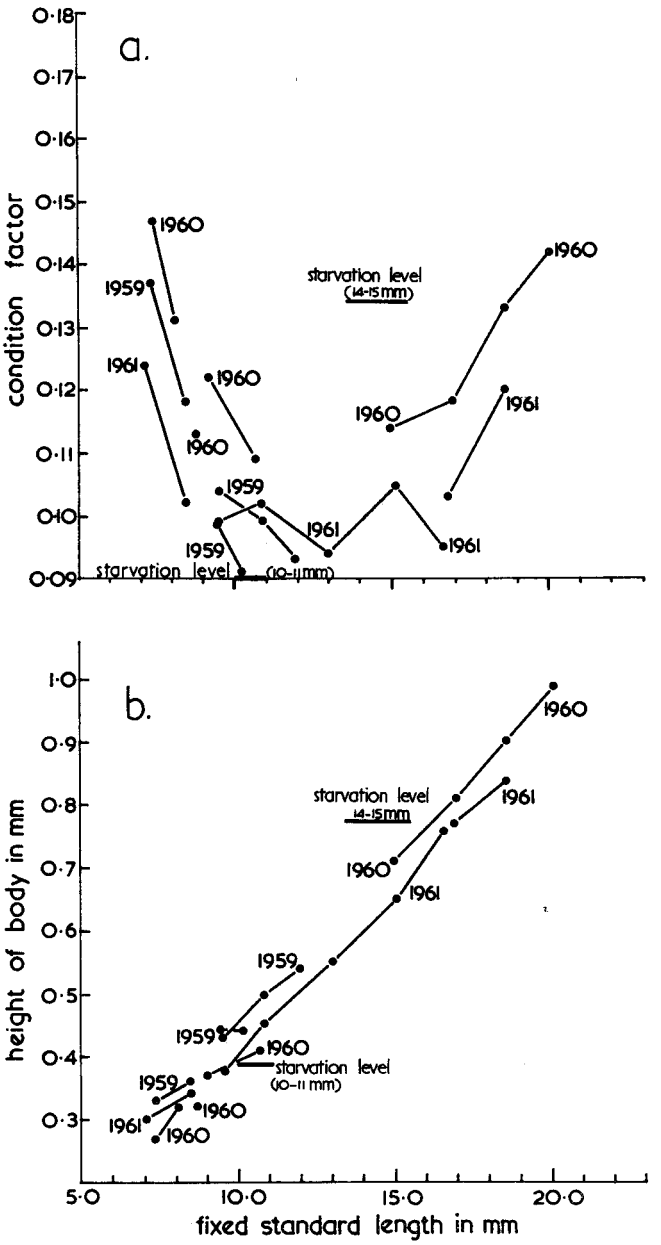

FIGURE 13. a. Condition factor; b. body height of herring larvae of different length caught in the Clyde in the spring 1959–1961 with estimated values at starvation (from Hempel and Blaxter, 1963 and new data).

and spring-spawned larvae may well have considerable adaptive significance. In the Baltic, at a later season, food might be less limiting (Waldmann, 1961) and here the larvae are smaller at hatching.

REFERENCES

Arthur, D. K. 1956. The particulate food and the food resources of the larvae of three pelagic fishes, especially the Pacific sardine, *Sardinops caerulea*. Ph.D. Thesis, University of California, Scripps Institution of Oceanography,: 231 (Typewritten).

Bhattacharyya, R. N. 1957. The food and feeding habits of larval and post-larval herring in the northern North Sea. Mar. Res. Scot. No. 3: 14 pp.

Bishai, H. M. 1960. The effect of water currents on the survival and distribution of fish larvae. *J. Cons. int. Explor. Mer*, 25 : 134–46.

Blaxter, J. H. S. 1962. Herring Rearing—IV. Rearing beyond the yolk sac stage. *Mar. Res. Scot.*, No. 1: 18 pp.

Blaxter, J. H. S. and G. Hempel 1961. Biologische Beobachtungen bei der Aufzucht von Heringsbrut. *Helgoländ. Wiss. Meeresunters.*, 7: 260–83.

Blaxter, J. H. S. and G. Hempel 1963. The influence of egg size on herring larvae, *J. Cons. int. Explor. Mer*, 28 :211–40.

Blaxter, J. H. S. and F. G. T. Holliday 1958. Herring (*Clupea harengus L.*) in aquaria.—II. feeding. *Mar. Res. Scot.*, No. 6 : 22 pp.

Blaxter, J. H. S. and F. G. T. Holliday 1963. The behaviour and physiology of the herring and other clupeoids. In "Advances in Marine Biolgy" Vol. 1, Ed. F. S. Russell. Academic Press, London and New York: 410 pp.

Bowers, A. B. and D. I. Williamson 1951. Food of larval and early post-larval stages of autumn spawned herring in Manx waters. *Rep. mar. biol. Stat. Pt. Erin*, 63 : 17–26.

Craig, R. E. and R. G. Lawrie 1962. An underwater light intensity meter. *Limnol. Oceanogr.*, 7 : 259–61.

Dannevig, A. 1948. Rearing experiments at the Flødevigen sea fish hatchery 1943–1946. *J. Cons. int. Explor. Mer*, 15 : 277–83.

Dementeva, T. F. 1958. Methods of studying the effect of environmental factors on the fluctuations in abundance of the Azov anchovy. *Trudy V.N.I.R.O.*, 34 : 30–62.

Flüchter, J. 1962. Funktionsanatomische Untersuchungen am Kieferapparat der Heringslarven. *Kurz. Mitt. Inst. Fischereibiol. Hamburg*, 12 : 1–12.

Hardy, A. C. 1924. The herring in relation to its animate environment. Pt. I. The food and feeding habits of the herring with special reference to the east coast of England. *Fish. Invest. Lond., Ser II*, 7 (3) : 53 pp.

Hempel, G. and J. H. S. Blaxter 1963. On the condition of herring larvae. *Rapp. Cons. Explor. Mer*, 154 : 35–40.

Hentschel, E. 1950. Die Nahrung der Heringslarven. *Helgoländ. Wiss. Meeresunters.*, 3 : 59–81.

Holliday, F. G. T., J. H. S. Blaxter and R. Lasker 1964. Oxygen uptake of developing eggs and larvae of the herring (*Clupea harengus* L.) *J. mar. biol. Ass. U.K.*, 44 :711–23.

Iizuka, A., S. Mikami and M. Tamura 1962. Studies on the early life history of herring *Clupea pallasi*. 2. On the growth and survival of larvae in Akkeshi Bay, Hokkaido. *Bull. Hokkaido Reg. Fish. Res. Lab.*, 25 : 1–10.

Kurata, H. 1959. Preliminary report on the rearing of the herring larvae. *Bull. Hokkaido Reg. Fish. Res. Lab.*, 20: 117–38.

Lebour, M. V. 1921. The food of young clupeoids. *J. mar. biol. Ass. U.K.*, 12 : 458–67.

Lebour, M. V. 1924. The food of young herring. *J. mar. biol. Ass. U.K.*, 13 : 325–30.

Lishev, M. N., L. A. Rannak and L. N. Lisivnenko 1961. Condition of the Baltic herring stock in north-eastern Baltic and Gulf of Riga. *I.C.E.S. Baltic-Belt Sea Committ*, Paper No. 124 (mimeo).

Marshall, S. M., A. G. Nicholls and A. P. Orr 1937. On the growth and feeding of the larval and post-larval stages of the Clyde herring. *J. mar. biol. Ass. U.K.*, 22 : 245–67.

Mielck, W. 1925. Heringslarven, Eier und Larven anderer Fische und Nahrung der Larven in der westlichen Nordsee im Oktober 1922. *Ber. dtsch. Komm. Meeresforsch.*, 1: 209–46.

Morris, R. W. 1955. Some considerations regarding the nutrition of marine fish larvae. *J. Cons. int. Explor. Mer*, 20: 255–65.

Murphy, G. I. 1961. Oceanography and variations in the Pacific sardine population. *California Cooperative Oceanic Fisheries Investigations*, 8 : 55–64.

Nikitinskaya, I. V. 1958. On the onset of active feeding of the larvae of *Clupea harengus pallasii* Val. (In Russian) *Zool. Zh.*, 37 : 1568–71.

Ogilvie, H. S. 1927. Observations on the food of post-larval herring from the Scottish Coast. *Rep. Fish. Bd. Scot.*, No. 1 : 10 pp.

Raymont, J. E. G. 1963. "Plankton and productivity in the oceans." Pergamon Press, London and New York: 660 pp.

Schach, H. 1939. Die künstliche Aufzucht von *Clupea harengus*. *Helgoländ. Wiss. Meeresunters.*, 1: 359–72.

Soleim, P. A. 1942. Årsaker til rike og fattige årganger av Sild. *Fiskervidir. Skr. Havundersøk.*, 7(2) : 39 pp.

Tamura, T. 1957. A study of visual perception in fish, especially on resolving power and accommodation. *Bull. Jap. Soc. Sci. Fish.*, 22 : 536–57.

Verheijen, F. J. 1959. A peculiar nystagmus and a corresponding foveal structure in the eye of the herring (*Clupea harengus* L.), *Experientia*, 15 :443–4.

Waldmann, J. 1961. Untersuchungen an Heringslarven und Zooplankton des Greifswalder Boddens in den Jahren 1958 und 1959. *Zeit. Fisch. Hilfswiss.*, 10 : 523–36.

Wiborg, K. F. 1948. Experiments with the Clarke-Bumpus plankton sampler and with a plankton pump in the Lofoten area in northern Norway. *Fiskeridir. Skr. Havundersøk.*, 9 (2) : 32 pp.

Woodhead, P. M. J. and A. D. Woodhead 1955. The reactions of herring larvae to light; a mechanism of vertical migration. *Nature, Lond.*, 176 : 349–50.