

ON THE IMPORTANCE OF LARVAL SURVIVAL FOR THE POPULATION DYNAMICS OF MARINE FOOD FISH

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I. INTRODUCTION

Looking back at the first century of fisheries biology we see that each generation puts emphasis on a different aspect of the changes in abundance of exploited fish populations. The earliest publications stressed the point that fishing will reduce the spawning potential of a stock, and that this will lead to insufficient recruitment. The establishment of fish hatcheries to replenish the marine populations was the logical answer to these worries. Later, the influence of fishing on the composition of adult stocks in size and age was emphasized. Regulatory measures aimed at better yields were introduced. The influence of composition and density of the stock on the individual growth was discussed and models of the population dynamics of marine fish were developed. After the first "wave" of considerations of fishing effort versus yield, the detection of the fluctuation in year class strength and of changes in distribution forced the biologist to recognize fish stocks as ecological units dependent on changing environment rather than as a simple group of specimens which could be managed by man as he liked. At the present time, the biologists who stress mainly the effect of fishing and the other more fatalistic group who hold great stock in the idea of the overwhelming effect of the environment must face together the problem of recruitment. It is the common opinion of both groups that recruitment is one of the main factors determining the size of a heavily exploited fish population. During the last few years, the importance of recruitment to the exploitable stock gained world-wide interest, especially in those fisheries which are only based on one or two age-groups, mainly recruits.

The recruitment problem is now tackled from several angles. As in the old days, schemes of rearing of marine fish on a commercial scale have been set up with a new emphasis on improving the techniques in rearing, holding and feeding of fry (see Shelbourne in this volume). Theoretical contributions to the interrelationships between spawning stock and resultant recruits have been published (e.g., Ricker, 1954; Beverton and Holt, 1957; Murphy, 1961; Beverton, 1962). The distribution of fish larvae in the sea has been investigated for a very long time, but until now, data on the survival of larvae in the sea is scarce; some figures are, however, available on mackerel (Sette, 1942), Pacific sardine (Ahlstrom, 1954), smelt in the Elbe estuary (Lillelund, 1961), and Pacific herring (Stevenson, 1962). Extensive studies on larval plaice and herring are now under

way in British, Dutch and German laboratories. The need for simultaneous physiological work on marine fish larvae was realized eighty years ago (Meyer, 1878). Hempel and Blaxter (1963) described a program combining experimental rearing and an investigation of the distribution and survival of herring larvae in the sea in relation to changes in the environmental conditions from year to year and place to place.

My basic concept, in the framework of which I will examine the available evidence, is that in the course of its life a fish belongs successively to three or more populations; the larval populations, the population of young and adolescent fish, and the population of adults. Each of these phases has its own dynamics. Nevertheless, each depends on the survival in the foregoing phase. Theoretically there has to be also an influence of the terminal phase, the spawning stock on the initial phase of the next cycle, the number of eggs produced.

This paper will be mainly confined to the various approaches one might take to understand the interrelationship between survival of larvae and size of the adult stock. How greatly are the stocks of larval and juvenile fish dependent on the size of the parental stock?

II. DO ADULTS INHIBIT RECRUITMENT?

The simplest relationship would be that the adult stock simply decides on the number of recruits which it will accept every year in accordance with the carrying capacity of the habitat. According to Herrington (1948, see Ricker, 1954) this holds for haddock on the Georges bank where the adult stock determined directly from its own size, how many recruits were to be let in. Heavy competition for food between the adults and the pre-recruits resulted in a compensatory mortality of the pre-recruits. Radovich (1962) assumed that in the Pacific sardine very dense populations of adult fish have an adverse effect on the survival of the offspring due to competition for food.

Food competition between the adult stock and the young stages cannot be considered a general principle. In many species the utilization of food by larvae and adults differs both in size and in species composition. Adults and larvae may also occupy different geographical areas. More similarity is often found between the older stages of young fish (pre-recruits) and the adults. Nevertheless, year-class strength at this stage has normally already been fixed and the competition between old and young fish cannot be used as an explanation of the fluctuations.

In contrast to the results with crowded populations in small units of fresh water, studies of marine stocks indicate that the adult population does not take advantage of the whole carrying capacity of the habitat. There appears to be no quota for the acceptance of recruits in normal years. In populations such as the Norwegian herring and the North Sea haddock, the weight of the stock can increase several fold from one year to the next if a strong year class enters the stock. Those strong year classes do not, however, normally affect the growth and natural mortality as much as should be expected, if food and space were scarce. In addition, it may happen that after a year or two, another strong year class enters the stock just when the previous strong year class reaches its maximum biomass.

In most years recruitment is not sufficient to fill up the total number of vacant niches available for the adult stock. In regard to the food-niches, calculations by Petersen (1915), Thorson (1958) and Hardy (1959) showed that flatfish in the Kattegat used only one to two percent of the weight of available food. Invertebrate predators, chiefly starfish, ate the rest. Therefore, we may conclude that more fish could live in this area. The success of transplantation experiments into underpopulated areas is another hint. There is no reason why those stocks should not let in far more recruits if they were available.

III. SIZE AND COMPOSITION OF SPAWNING STOCK DETERMINES TOTAL EGG PRODUCTION

Another relationship is that the number of recruits directly depends on the number and weight of the female spawning stock. If the age and size-composition of the fish stock is constant, the number of eggs will fluctuate with the total biomass of the female stock. In the main species of marine food fish, we have no evidence that egg resorption or additional production of eggs occur to compensate for differences in the spawning potential.

As soon as the age composition of the stock changes, the spawning potential will be altered considerably. In most fish the number of eggs increases sharply with the body weight of the mother. As a modifying factor, age itself has a direct effect on the spawning potential of the fish, e.g., in Baltic herring, (Krivobok, 1961). A spawning population which consists mainly of young recruits will have a far lower total fecundity than a population of the same biomass but consisting of somewhat older fish.

IV. IS THE NUMBER OF RECRUITS INDEPENDENT OF SPAWNING POTENTIAL?

The linear relationship between the spawning stock and the number of offspring disappears normally during the early life-history of the fish. At the time of recruitment, the number of young fish is no longer correlated with the size of the parental stock. One may refer only to some of the most recent discussions

of the subject by Gulland (1962), Beverton (1961) and Hempel (1963). There are two ways of testing this independence; either to trace the origin of especially rich or poor year classes, or to examine long term records on stock size and recruitment.

The enormous year classes of Norwegian herring in 1904, 1950, 1959, and 1960 were not the results of very large parental stocks. In the Pacific sardine, medium sized spawning stocks produced the strongest year classes (Radovich, 1962). Ricker (1954), using data from Tester and Stevenson, even showed that in *Clupea pallasii* off Vancouver Island the below-average spawning stocks produced the strongest year classes and stronger spawning stocks produced poor year classes. (Any conclusions about the relationship between recruitment and parental stock derived from long-term series of data may be limited by differences in availability and by bias in sampling, especially if there is a segregation by age groups within the adult stock.) Beverton (1961) published one of the best series of observations. It does not show any correlation for a ten-fold range of parental stock size in plaice. In those populations however where population size and/or fecundity are very low, a positive relationship must be expected.

Why does the positive relationship between the size of the parental stock and the number of offspring hold for the egg stage and then disappear during the subsequent stages of early life? Is the fact that the year class-strength of the recruits is statistically not correlated with the number of their parents due to a true independence or due to masking effects and the lack of long-time series? In the following both alternatives will be considered. Although no decision in favor of one of the alternatives can be provided, it is worthwhile to discuss their biological implications and look for new approaches toward various parts of the problem.

IV. A. THE HYPOTHETICAL COMPENSATORY MORTALITY

A true independence between the number of recruits and the size of their parental stock may find its explanation in a compensatory mortality of the larvae or young fish; in other words, that the mortality rate following high egg production is more severe than that following low egg production. This explanation has been put forth several times, but proper proof is very difficult to achieve.

The compensation hypothesis envisages a "gate" somewhere in the early life history. It is narrow so as to permit passage of only a small number of fish toward the goal of recruitment. The width of this gate may change from year to year, and through this, the number of pre-recruits fluctuates. It may be assumed that the compensatory mortality works over a wide range of egg production. It will, however, fail to operate in very low stock-density, i.e., when the scarce stock of larvae does not occupy the entire carrying capacity of the habitat.

The compensation for high or low larval abundance may not be confined necessarily to a short specific

stage in the early life history, but the larvae and young fish may have to pass through several critical phases during which different density dependent factors level the annual abundance of recruits. In other words, it may happen that the corrections made by larval mortality are very crude, leaving the larval stock to vary within wide limits due to over- or under-compensation of primary larval abundance. After metamorphosis, further mortality with a density-dependent component may correct for those variations. Smelt (*Osmerus eperlanus*) in the mouth of the Elbe river showed indications of compensatory mortality after rather variable larval mortality (Lillelund, personal communication). In demersal fish, crowding at the first settling ground in coastal waters may have a regulatory effect. In pelagic fish, however, compensatory mechanisms of this kind are more difficult to imagine. Very little is known about the life history of most of our food fish in the phase between metamorphosis and the recruitment to the adult stock. Therefore, the considerations of this paper will be confined to the egg and larval phases only.

IV. A. 1. Are fertilization and egg mortality density-dependent?

In salmon and other species with an elaborate spawning behavior and special demands for spawning beds, high crowding on the spawning grounds disturbs spawning. No similar indications are at hand for the main marine food fishes. High percentages of unfertilized eggs are not reported. (It would be difficult, however, to trace this in species with pelagic eggs. Dead eggs sink rather quickly.) Rollefson (1931) discussed the optimum dilution of sperm for marine fish. Fertilization rate is low with very diluted dispersions of sperm but it remains constant at almost 100% over a wide range of sperm concentration. In species with demersal eggs, fertilization is not affected by multiple layering of the egg-masses. Most of the eggs seem to be fertilized just at the moment they sink to bottom.

In the open sea strong density dependent mortality of pelagic eggs is difficult to imagine. Even in very dense spawning, one will find only a few eggs per liter of surface water. The effect of dense shoals of cannibalistic, plankton-feeding parents (specially Clupeoids) has been mentioned several times (e.g., Radovich, 1962), but no proper data on their feeding intensity are available. Normally the daily mortality in the egg stage is rather low compared with the larval mortality. According to Sette (1942) the mackerel has a daily loss of 5% at the egg stage, but a loss of 10 to 14% of the larval stage. The intensity of egg production in species with demersal eggs may have a stronger influence on egg mortality than in species with floating eggs. In rearing experiments, herring eggs are very sensitive to dense compacting. In the sea, however, mortality is not very high in herring eggs, e.g., 12% in Norwegian waters (Runnstrøm, 1941) and up to 10% in British Columbian waters (Hart and Tester, 1934) where predation by birds plays a considerable role (Outram, 1958). For eggs deposited in littoral and uppermost sublittoral zones, also, desiccation

can be a significant detrimental factor (Hempel, unpubl.). Runnstrøm (1941) made a careful survey of the mortality of eggs deposited on rock or gravel. In contrast to Lea (1931), he found the sheets of spawn were rarely composed of more than 10 layers of eggs. The normal thickness was less than five layers. That is in agreement with the findings of Parrish, *et al.* (1959) on Clyde herring, where egg mortality was very low. In Norwegian egg-sheets, mortality increased during the incubation time, especially toward the end. It sometimes reached 97% in the lower egg-layers and 39% in the top layers. Neither Runnstrøm nor Parrish, *et al.* observed egg-sheets after hatching to check whether an additional mortality had occurred at about the time of hatching. According to Runnstrøm, high egg production by a large parental stock results in thicker layering rather than in extension of the spawning grounds. Runnstrøm stated, however, that there is little adverse effect of high egg production on the later recruitment, because even with high egg production, only very few of the sheets are detrimentally thick.

IV. A. 2. Is larval survival density-dependent?

Three main causes of mortality may be considered: (1) abiotic factors, (2) predation, and (3) starvation. I will discuss these factors first in relation to possible density-dependent effects.

(1) *Mortality from abiotic factors* has no compensations as long as the differences in the spawning potential do not create changes in the distribution of eggs in space and time.

(2) *Predation* has been regarded as the main cause of mortality in the Pacific sardine, but Murphy (1961) stated that this mortality by predation is independent of larval production because larvae make up only a minor part of the food supply for the marine predators. In general this is true. The larval stage is short (usually only a few weeks) in most marine fish populations; therefore, the larval population will not give rise to a build-up of great populations of predators.

(3) *Starvation* may be discussed in its relation to competition within the group of larvae. The extent of starvation due to competition within a group of larvae depends on several factors:

- (a) number of larvae per unit volume of water.
- (b) number and size of suitable organisms present per unit volume of water within the range (geographical area and depth zone) where the larvae live.
- (c) patchiness of distribution of the plankton.
- (d) "natural" population dynamics of the food organisms (other than grazing by the larvae), i.e., other sources of mortality, reproductive rate, individual growth, immigration, emigration.
- (e) number of organisms eaten daily per larva.
- (f) volume of water searched per day. This depends on the number of hours per day in which light

is sufficient for perception of food organisms in a given depth, the distance that larvae swim per day, their distance of perception, and their catching ability.

- (g) dispersion and migration of larvae in relation to the movement of the plankton.

Essential to the sufficient feeding of the larvae is a high absolute abundance of food organisms. Larvae with poor swimming performance and a small field of vision will be able to search only a small amount of water, in some cases only a few liters per day. In this amount of water, the larva must meet a considerable number of food organisms of proper size. A young sardine larva requires a concentration of about 20 copepod nauplii per liter (Nishimura, 1958; for rate of feeding see Lasker in this volume). The larvae will catch some of these organisms, others will be missed.

The next item to consider is the concentration of the larvae themselves; are they so concentrated that a considerable overlap of the individual feeding spaces occurs? Do the larvae stay for so long in the same mass of water that they deplete the plankton markedly? If there are only a couple of sardine larvae per cubic meter, and if each larva searches 5 liters per day, the grazing effect and the competition are insignificant. Survival depends merely on the abundance of food (not on the density of the larval stock). In larvae with better vision and better swimming performance, the volume of water searched every day is far greater. This involves an increasing probability of an overlap between the individual feeding spaces of neighboring larvae, which may finally result in serious competition during a period of low abundance of food.

A careful evaluation of the competition in larvae requires a combination of field work and laboratory experiments. A program of this kind (Hempel and Blaxter, 1963) is now established for various stocks of North Sea herring and Clyde herring which spawn in different seasons. The herring larvae are caught by the Gulf III sampler, the plankton by the Hardy plankton-recorder using narrow-meshed discs aiming for quantitative sampling of the smallest food organisms. In addition to this work at sea, which also includes investigations in the diet, in changes of the behavior of larvae and of their habitat, experiments on the feeding and the food-demand of herring larvae are in progress (Blaxter in this volume).

IV. A. 3. Indirect effects of stock size on larval survival

The size of the spawning stock and especially its age-composition often influences the spatial distribution of spawning and the duration of spawning time. It is this indirect effect of stock size which may result in density-dependent differences in larval survival. Changes in the size of the spawning stock may be connected with changes in the age-distributions; a decreasing stock may show a lack of old fish. The bigger stock often has a wider range of sizes than the smaller one, especially if this small stock is mainly confined to recruit-spawners. Extension of the spawning ground during years of strong spawning and prolongation of

the spawning period, however, have quite different effects on different stocks. In herring off Newfoundland, it endangers the stock (Olsen, 1961) but in arctic cod it results in strong year classes (Wiborg, 1954). A change of temperature is often connected with those shifts. In herring of the western Baltic, the spawning season is very long, lasting from the beginning of March to the beginning of June. In this period, the water temperature may rise from 4°C to 18°C. The effect of this shift in temperature on the biology of the larvae is very complex. It affects incubation time, duration of yolk sac stage, rate of growth, rate of resorption of the body reserves, swimming speed, digestion rate, food demand, etc. It also affects the abundance and species-composition of food plankton and predator populations. In rearing experiments, Blaxter and Hempel (1961 and 1963) analyzed some of the effects. Of special importance for the survival rate might be duration of the pre-feeding phase, i.e., the time from spawning until the larvae are capable of active feeding. This phase lasts only 10 days at 15°C but 30 days (or more) at 5°C. The span of time the larvae can live without food from hatching until death by starvation is 10 days at 15°C and 21 days at 5°C. The time from hatching to the "point of no return", i.e., the phase in which non-fed larvae become too weak to start feeding is twice as long at 5°C than at 15°C. In the Baltic herring also, young fish spawn late in the season.

A rejuvenation of the stock will therefore delay the average peakdate of spawning toward a season of higher average temperature. This will affect the very sensitive early stages of larvae. Changes in time and place of spawning may also have an influence on the transport of larvae to areas which are suitable for feeding or setting. One of the main effects, however, will be a change in the coincidence of the larval phase and the period of high production of small zooplankton. Beverton (1961) suggests that late-hatched plaice larvae may reach their feeding stage at a time when their older brothers have taken most of the baby food, the young *Oikopleura*. The older larvae are big enough to switch over to bigger food organisms but the young larvae will die. This would be a typical compensatory mortality for a great stock of plaice spawning over an extended period.

In recent years, biologists have increasingly considered the effect of feeding condition and age of the spawners as an indirect effect of stock-size on the quality of eggs, and through this, an effect on the survival of the larvae and the extent of recruitment. This effect may take place through the age-structure of the population of breeding females and/or through the adequacy of nourishment of the females (which may be related to stock-density). This hypothesis requires careful experimentation. Nikolski (1961) refers to findings by Anokhina (1960) on White Sea herring which suggest that the fat content of the mother influences the variability in egg size, lean fish producing the wide range of egg-size which he considers favorable for survival of the biggest larvae. We could not detect this effect in North Sea herring.

Is there an effect of age and size of the mother on the survival of larvae? Eggs from Norwegian herring, partly from 4 to 5 year old recruits and partly from 10 to 14 year old fish, were reared separately under the same conditions. Eggs from the recruit-spawners were smaller than eggs from the older herring. After hatching, the larvae were starved. The larvae of the young mothers lived for 22 days, whereas the larvae from the older herring lived three days longer. This effect may considerably influence the survival rate of larvae in the sea; however, differences in spawning time of recruits and repeaters may counterbalance this. In those Norwegian herring the recruits spawn later during spring than the older herring. Thus, the larvae of these recruits hatch at higher temperatures and pass through the larval stage more rapidly. Also, the larvae of the recruits are smaller, and because of this, they are less capable of feeding; however, in spring these larvae will encounter more food than their brethren which were derived from older fish of the same race.

To summarize, there are indications of a proper density-dependent larval mortality (the "gate") only in special cases. *Direct* influences of stocksize on larval survival are very rare. *Indirect* effects due to shifts in spawning time and spawning season are probably more common.

V. THE HYPOTHESIS THAT EARLY MORTALITY IS INDEPENDENT OF STOCK-SIZE

The second hypothesis assumes that there is a correlation between parental stock size and subsequent recruitment, although being normally not detectable in the relatively short periods of observation and being masked by natural fluctuations. If this hypothesis is correct, we have to assume that compensatory effects in mortality of the early stages do not exist or do not counterbalance sufficiently changes in parental stock size. Consequently the stock will not be stable in number (or fluctuate above and below an average) but will show a long-term upward or downward trend. As a consequence of selection the trend would be in most cases upward until the carrying capacity of the habitat for the adults is filled up or the larval population is not anymore only a minor element of the plankton community. A breakdown of the population can only be expected if the environmental conditions deteriorate faster than adaptation of reproduction (see below) can take place. A serious decline may also happen if the parental population is so heavily fished that the positive effect of adaptation is canceled out.

V. A. PREDATION AND STARVATION AS NON-DENSITY-DEPENDENT PARAMETERS

Predation and starvation are the two main causes of larval mortality in many stocks of marine fish.

Their close relationship to the density of the larval stock was ruled out previously in this paper. We may assume that the rate of predatory mortality in a stock of fish larvae is mainly determined by the number of predators present, by their feeding capacity, and by

the ability of the larvae to avoid these predators. As long as the fish larvae comprise only a minor part of the total diet of the predators, the percentage of larvae which die by the predators will vary with the number of predators. In many cases, years of high predator abundance are also years of rich food abundance for the fish larvae and the food for larvae is often also the main food for the planktonic predators. For example, the early mass mortality in a population of larvae due to starvation might be relatively small in those years which have high predatory mortality. The inverse relationship between these two mortalities together with some compensatory mortality on later stages might be the reason why the fluctuations in year-class strength in some stocks of fish are far smaller than the fluctuations in the food organisms or the predators.

A factor not to be overlooked when considering starvation is the patchiness of food plankton and variations in the size and viability of the larvae which offers a chance of survival to at least a few larva, even if the "average" concentration of food and the searching effort of the "average" larva is far below the minimum level. Anokhina (1960) pointed to a higher variability in size of Baltic herring eggs in years of little food.

In a larval population suffering from early starvation, the survival curve will have the steep inflection typical of a "critical phase." If predation is the main cause of mortality, the curve might be more steady, with a constant or slowly decreasing instantaneous mortality. This mortality might bring the abundance of larvae down to the same low level as a "critical phase" caused by an abrupt starving period.

The adaptations of the larval production system which tend to alleviate mortality due to starvation are different than those which counteract predatory mortality. In order to meet deficiencies in food supply, the body of each larva should be equipped with a fair amount of energy reserve. Also, it should hatch at a stage of development where it will have a good swimming and feeding performance. If, however, predation is the main cause of mortality, the number of larvae should be as high as possible to keep the absolute number of larvae which survive on a sufficient level to ensure good recruitment. Because of the limit of reproduction in each female, both requirements conflict with each other. A compromise between size and number of eggs has to be achieved in order to cope with both kinds of mortality. It can be shown that this compromise is not uniform to all stocks of fish, but is closely related to the conditions larvae meet after hatching. An analysis of this phenomenon should be on an intraspecific level and based on very closely related stocks which differ mainly in spawning places and spawning season. The herring stocks of the northeastern Atlantic meet these requirements and offer a very good example.

V. B. ADAPTATION OF REPRODUCTION IN HERRING

Differences in egg size—There is no part of the neritic region of the northern Atlantic and its adja-

cent seas which is not occupied by one or several stocks of herring (*Clupea harengus* L.). Each stock has its specific spawning area, its fixed pattern of migration, and its typical spawning season although stocks may intermingle and shift their spawning areas slightly. In the northeastern Atlantic, three main tribes of herring are described. Each of them is split into various local populations. The *Atlanto-Scandian* tribe, a large-sized herring with an ocean-wide range of migrations, mainly spawns in the late winter off Norway. Other spawning areas of somewhat minor importance for this tribe are off Iceland, Faroe Islands, Shetlands and along the edge of the North Sea and the British shelf. Off Iceland, an isolated group spawns also in summer. The tribe of the small *Baltic* herring consists of various populations mainly spawning in spring and summer. Related groups also spawn outside of the Baltic in northern Russian waters and in the coastal region of the North Sea. The true *North Sea* herring (medium body-size) is confined to the shelf areas only. Its spawning season is mainly in the second half of the year. Relatives of the North Sea herring with similar spawning behavior live in the waters west of England and Scotland. The area of distribution of the three tribes overlaps somewhat, however, the nature of their spawning grounds differs. The *Atlanto-Scandian* herring spawns mainly in rather deep oceanic water (40-200 m), the *Baltic* herring chooses shallower, often inshore waters in the littoral or upper sublittoral zone. It resembles the *Pacific* herring (*Clupea pallasii* Val.). The *North Sea* herring spawns on banks, mostly off-shore at depths of 20 to 40 meters.

Due to the differences in spawning season, the larvae of each stock will meet rather different environmental conditions. It seemed worthwhile, therefore, to check whether differences in number and size of eggs were correlated with seasonal differences in the environmental pressure of temperature, drift, and especially predation and shortage of food. Data on the number of eggs produced by females of the same size but of different geographical origin were gathered from the literature. They showed in general that autumn-spawning herring have a higher fecundity than spring-spawning herring. This finding had to be related to the average size of the ripe eggs (Hempel and Blaxter, in preparation). Samples of 50-200 herring in spawning condition were collected from each of the main spawning groups. In some cases it was possible to repeat the sampling over two to three years. The dry-weight of 100 ripe, transparent eggs per herring gives a good average measure of the nutritive value of a herring egg, although the relative weight of the egg-shell which is of no nutritive value for the larvae, decreases slowly with increasing egg size. For young mothers, egg-size increases with age. The differences between egg sizes of the first and the second spawning are especially great. At greater ages, the size of the eggs remains constant or it drops slowly (in very old fish). A comparison between fish of different stock parentage and different growth pattern should be based on fish at the second or third spawning. These would be 4-year-olds in *Baltic* herring, 5-year-olds in *North Sea*

herring and 7-year-olds in *Atlanto-Scandian* herring. These fish, however, differ in their body-length. In order to allow for a possible direct relationship of egg-size to size of the mother's body, herring of the same size regardless of their age in relation to first maturity have also been compared. For this, 27.5 cm was chosen as a reference length. (Fish of this size are first-time spawners in Norwegian herring, but second-to-third-time spawners, or even older, in *North Sea* and *Baltic* herring.) Both sets of values are given in Table 1. Obviously, *Baltic* herring have considerably

TABLE 1
MEAN DRY WEIGHT OF RIPE EGGS IN DIFFERENT SPAWNING GROUPS OF HERRING

	recruit spawners			repeated spawners			mg at 27 cm total length
	age	mg	n	age	mg	n	
Oceanic herring (Atlanto-Scandian)							
Norway							
1961 + 1962	3-4	0.28	71	8-12+	0.35	128	0.26
Clyde 1962	2-4	0.32	54	(5-6	0.30	14)	0.32
Shelf herring							
Buchan 1961	3-4	0.16	15	5-7	0.16	33	0.15
Dogger 1961	3	0.26	54	5-10	0.28	18	(0.24)
Downs 1961	3	0.36	57	4-10	0.38	43	0.38
Dunmore 1962	2-3	0.31	13	4-10	0.36	43	0.38
Coastal herring							
western Baltic							
1961 + 1962	2	0.11	40	4-6	0.15	34	0.14

smaller eggs than Norwegian herring, although they do not differ greatly in spawning season (but rather in the living conditions for the fry, which find a very high abundance of food in the inshore waters of the *Baltic*). The difference between the two values for Norwegian herring results from the difference in age used in both sets. In *North Sea* herring, the mean weight of eggs varies considerably between spawning groups.

In the *North Sea* (Fig. 1) spawning occurs over a long period. The "autumn spawners" start in July at the Shetlands and continue in August-September off the Scottish coast. In September-October, they spawn in various places off the *North Sea* Coast of England and in the western part of the central *North Sea* (Doggerbank region). Some spawning of minor importance occurs at the same time, or a little later, at various locations further to the east. The southern group of *North Sea* herring (*Down-herring*) spawns in November-December in the entrance of the English Channel. It is uncertain whether the group of herring which spawn in January off the south coast of Ireland (*Dunmore herring*) is related to the *North Sea* herring.

Average values for complete samples, which cover the whole range of age-groups present in those populations (Fig. 2), emphasize that the summer-spawning *Buchan* herring have very low egg weights (0.1-0.2 mg dry matter per egg). These are similar to *Baltic* herring. In autumn-spawning herring of the *Dogger*

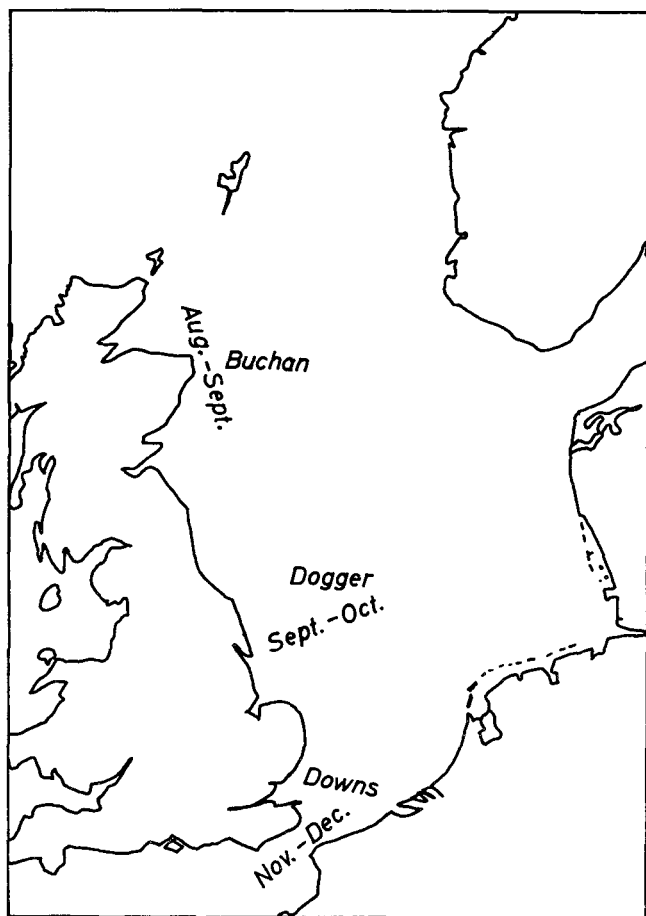


FIGURE 1. The main spawning communities of North Sea herring.

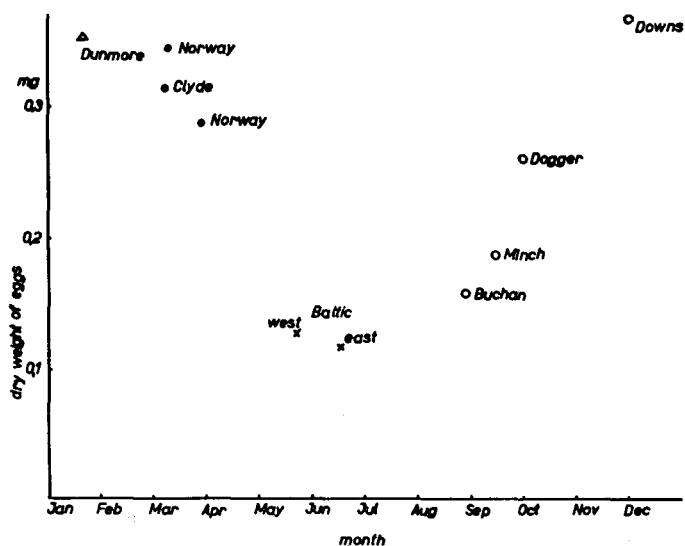


FIGURE 2. Mean dry weight of ripe herring eggs in relation to the spawning season. ● Atlanto-Scandian herring, × Baltic herring, ○ North Sea Shelf herring, △ Irish Shelf herring.

region, the mean weight of ripe eggs is significantly higher, and is higher still in Downs herring which spawn in early winter. In this southern group, egg-size (0.30–0.35 mg dry matter per egg) is about the same as in later winter-spawners off the coasts of Norway and western Scotland (Clyde).

Comparing fish of equal size, the individual energy-drain due to reproduction is of the same order in the different tribes of herring, although some minor differences are noteworthy. In Norwegian herring, the burden for reproduction is lower relative to body weight than in other groups of herring. This might be related to the greater longevity in this tribe than in other groups of herring. Within one tribe, the burden may vary in accordance with the spawning season (see below). The amount of organic matter put into the spawning products increases at a higher rate than the body-weight increases. Only in very old females does the weight of the gonad (calculated as the mean weight of the eggs times average number of eggs recorded in a female of a given length) seem to be reduced.

The Ecological Value of Egg-Size

The biological value of the size of the egg would be indicated best by percentage survival of the offspring in the sea. Measurement of this is difficult to achieve and the resultant data are open to some criticism.

In order to get some tentative indication of the quantitative relationship between rate of survival and egg-size we started rearing experiments. Eggs of different size and different origin were incubated under similar conditions (on glass plates in tanks or jars) mainly at 8° and at 12°C in 15‰ salinity, but with additional experiments at 5° and 14°C. and at different salinities varying from 5 to 50‰. After hatching, some of the larvae were sacrificed at various stages of development for measurements of the dry weight of larval body and yolk sac. Others were kept under constant conditions without food to see how long herring larvae developing from eggs of different size (and content of yolk) could survive on their body reserves. Fifty larvae of each female were transferred into jars with 1 to 2 liters of sea water. Every day the dead larvae were counted and removed. Normally, mortality started suddenly a few days after the resorption of the yolk sac. It was obvious that this mass mortality was due to starvation. Still other larvae were used for feeding and respiration experiments (Blaxter in this volume and Holliday, Blaxter and Lasker, 1964).

The results of the rearing experiments will be reviewed only briefly here (details in Blaxter and Hempel, 1963). Eggs of the following spawning groups were used: Norwegian herring, Clyde herring (west of Scotland), Kiel (western Baltic), North Sea herring from the Buchan, Dogger and Downs spawning grounds. For the different races, the average absorption of yolk was followed by daily (or every other day) weighing of samples of dried larvae. The mean weight of the unfertilized eggs of the mother used for the rearing experiments was known and

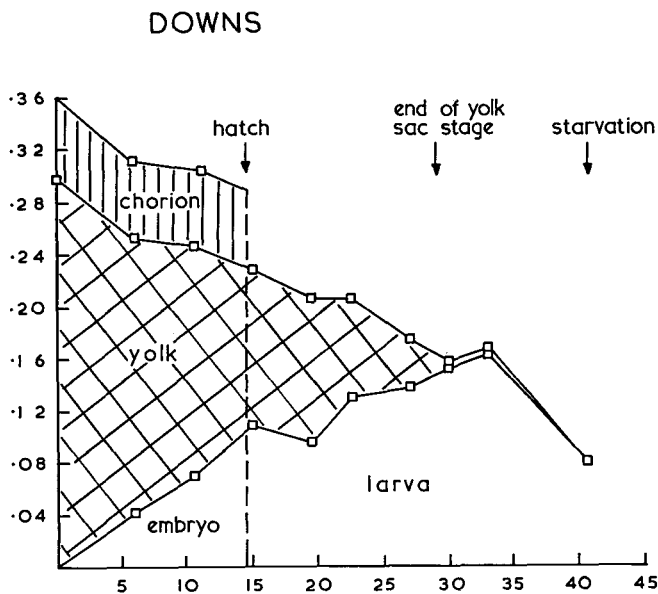
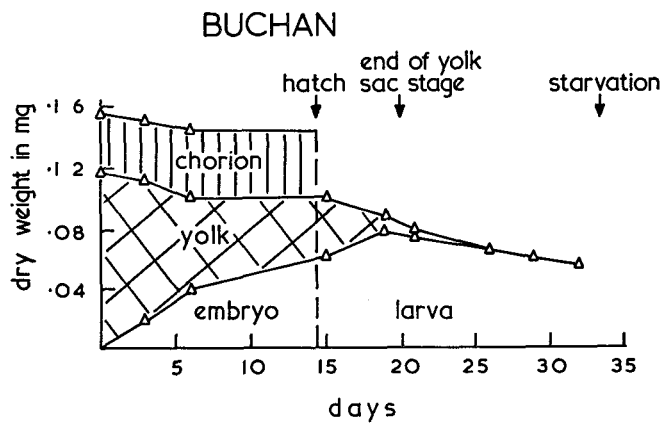


FIGURE 3. Changes in dry weight of chorion, yolk, embryo and larvae during the early development of herring.
a) small eggs of a Buchanan summer spawner
b) large eggs of a Downs winter spawner
The larvae were not fed and died by starvation (from Blaxter and Hempel, 1963).

also the ratio between egg shell and yolk in the egg. The pattern of yolk utilization and the ratio between yolk sac and larval body at any given time depends on the egg-size. It was found, however, that larvae from eggs of the same size but from different races did not differ in these characters. Thus, we can consider Norwegian, Clyde and Downs larvae as a group of "big larvae," Buchan and Kiel larvae as "small larvae," whereas the larvae of Dogger-spawners belong to the group of the "medium-sized-larvae."

How do the "big larvae" compare with the "small larvae"? In Figure 3, typical examples for the progression of yolk-absorption are given for these two groups. In newly hatched Clyde larvae, dry weight of the yolk is far greater than the dry weight of the larval body although *incubation time* is the same as in small eggs. The larvae of the Kiel herring lack an

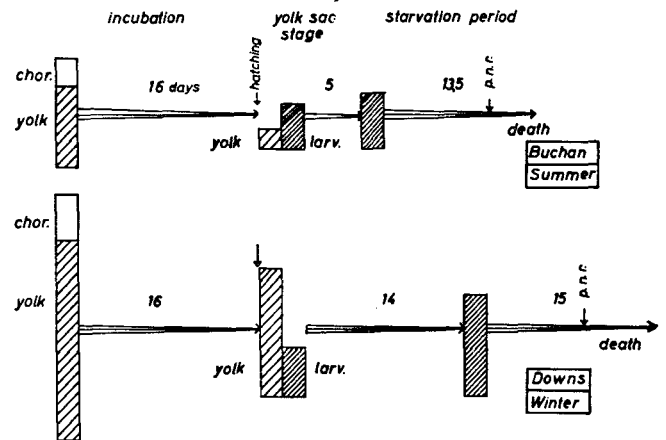


FIGURE 4. Different development of larvae of summer and winter spawners, due to difference in egg size. Development in days at 8°C. Larvae not fed. p.n.r. = point of no return. The vertical bars indicate the dry weight of a) yolk and chorion at fertilization, b) of yolk and larval body at hatching and c) of the larval body at the end of the yolk sac stage. The figures refer to the duration of incubation, yolk sac stage and starvation period (after resorption of the yolk).

appreciable yolk sac; most of the yolk content of the egg is used up in the course of incubation, partly for building the larval body and partly for respiration. In accordance with the size of the yolk sac, a considerable difference in the *duration of the yolk sac stage* has been recorded. While the yolk sac in Kiel larvae last only for three days, it remains for 10 to 14 days in Norwegian, Clyde and Downs larvae. Concerning the total "life span" of non-fed larvae we have to expect that larvae with great yolk reserves can endure starvation longer than can larvae with small yolk sacs. Under similar conditions, larvae of Norwegian herring lived 24 days after hatching while Kiel larvae survived for only 12 days. (Figure 4)

From the ecological point of view, the period of life up to the point when larvae become too weak to start feeding is of greater importance than the total "life span" which includes the final period of irreversible starvation between the "point-of-no-return" and the death. This point-of-no-return has been traced by Blaxter (this volume) in the course of feeding experiments at various stages of development. It is normally reached after the second third of the total life of unfed larvae.

Under the natural temperature conditions which both groups encounter in the sea, this difference will be even more striking. The average water temperature in the region where Norwegian herring spend their first month of life is about 6°C. Kiel larvae encounter up to 18°C. Kiel larvae reach the point-of-no-return about a week after hatching, whereas Norwegian herring will last for about three weeks. Among the habitats of the three groups of North Sea herring, water temperatures at spawning time are rather similar, ranging from 10–12°C, but it cools off in the southern region in mid-winter during the early larval stage of the Downs herring.

Differences in egg size also influence *length* and *breadth* of larvae at hatching. When leaving the egg shell, larvae hatched from big eggs are longer and broader than those from small eggs. The average length of larvae of Norwegian, Clyde and Downs herring was 8mm at hatching and that of larvae from small Baltic and Buchan eggs was 6.5mm. Beyond this point, the difference increased considerably due to the longer yolk sac period of the "big larvae". Norwegian larvae grew to a length of 11mm before the yolk was gone, while the larvae of small eggs reached only about 8mm body length by means of their yolk reserves. These differences in body size influence the size of the mouth aperture and the swimming speed of the larvae. At the stage when the larvae first become capable of feeding (during the second half of the yolk-sac stage), larvae hatched from big eggs may be able to take larger food organisms because they may swim faster and because they have wider mouth openings (details in Blaxter, in this volume).

The greater amount of yolk present in bigger eggs is used for two purposes: for a prolongation of the period that the larvae can last without food after hatching and also for increase in body size and hence, feeding performance. The relative contribution of the surplus yolk among these two purposes is similar in larvae of different tribes. Larvae of the Dogger herring, which has medium sized eggs, are in all characters intermediate between the larvae of big eggs and those of small eggs.

The importance of large size and greater feeding ability is probably greatest during winter when food is scarce, and especially when a sufficient supply of very small larvae of zooplankton is lacking. In winter there is a more restricted period of the day during which light intensity is sufficient for larvae to detect and snap up food. Light readings in the English Channel and the Straits of Dover in January showed that the maximum duration of daylight in the surface zone occupied by the larvae is 9 hours. At the spawning grounds of Sandettié, which is an area of high turbidity, the light intensity at the sea floor in thirty meters depth did not reach the threshold value for visibility of food at any time during an overcast winter day. Therefore, the area searched is rather small. This is balanced by more days of potential feeding before starvation, by a higher swimming speed, by better vision, by faster and more precise snapping and by the ability to swallow large organisms. The big eggs of winter-spawning herring provide their larvae with these advantages.

It may be bigger egg size alone which allows these populations to spawn in the most adverse season (from the standpoint of the feeding of the youngest larvae). The principle that under adverse conditions fish with low fecundity but well developed larvae have the best chance of survival seems to hold for all herring populations inspected thus far.

Winter is not an entirely adverse season for spawning. It has two advantages over summer: (1) Herring

can use the whole period from spring to autumn for feeding. That may be the reason why the individual gonad weight increases within the tribe of North Sea herring from 5g dry matter in summer spawning Buchan herring to over 6.1g in autumn spawning Dogger herring and to 7.3g in winter spawning Downs herring (among herring only of 27.5 cm total length). (2) The relatively low abundance of predatory plankton organisms in winter, whereas in the summer the larvae meet more predators. In many cases the larvae ascending to the surface must pass through a layer of medusae. In summer, high abundance of larvae seems most essential. Summer larvae, however, do not need highly developed feeding abilities because food organisms are abundant and the searching day is long. In the northern North Sea Buchan larvae which hatch in September find 14 hours of daylight. Kiel larvae have even a longer daily period in which they are able to see their food.

We have seen that herring can establish several distinct populations even in such narrow areas as the North Seas, the Irish Sea and the Baltic. These stocks living side by side differ mainly in their spawning time. This segregation was made possible only by adaptation of reproduction to the differential predation on and feeding by the larvae.

One might speculate on how the adaptation of reproduction to different conditions takes place. While effects of temperature and feeding conditions during the maturation of eggs may play a role, the main factor will, however, be selection. Slight differences in survival due to differences in the number-to-size ratio will have a considerable selective value. Through this, the optimal relationship will be achieved rather rapidly after a population has invaded a new area. Perhaps in herring, the number-to-size ratio of eggs is more variable than in other fishes and thus, the herring is in the position to occupy several different habitats.

If any increase in parental stock-size results in a wider range in spawning time and in spawning area, a portion of the larvae will find themselves under food/predator conditions for which they are not adapted. Before a new adaptation can take place, the stock will decrease due to higher initial mortality. This might be a mechanism by which an increase in population (which has been postulated to be a consequence of any form of positive relationship between spawning potential and recruitment) will be stopped.

In this paper I did not attempt to explain even tentatively why, in many stocks of marine fish, the number of recruits is the limiting factor for a steep increase in abundance and productivity. Experimental stocking and careful studies of the larvae and young fish in their natural environment might yield a better understanding of this question. One might guess that the answer would be along the line of a permanent sub-optimal adaptation of egg-number and egg-size to a continually changing environment.

SUMMARY

(1) In the course of its life a fish belongs successively to several populations (e.g. larvae, young fish, adult fish). This paper deals with the inter-relationship between the larval stock and the adult stock.

In most years recruitment is not sufficient to fill up the total number of vacant niches in the adult stock. Recruitment to the adult stock seems to vary independently from parental stock while the number of eggs spawned per season depends directly on the size and average age of the parental stock.

(2) This might be explained in two alternative ways:

First hypothesis: The number of recruits is determined by a "gate" which permits only a given number (from year to year somewhat changing) of offspring to pass through. This hypothesis implies a regulatory mortality which compensates for differences in the number of eggs. Very little evidence is available for a density-dependent mortality of eggs and larvae. The following effects of the parental stock on larval survival are discussed, although they have rarely been shown to be serious in marine fish. Negative effects may be due to a low average age (e.g., in a heavily fished stock) and/or poor feeding conditions of the mother (by adverse environmental conditions, overcrowded feeding grounds).

Second hypothesis: There is a correlation between the parental stock size and recruitment, although it is normally not detectable in the relatively short periods of observation, being masked by bias in sampling and especially by natural fluctuations. In a completely stable environment and in case of constancy of spawning place and time, adaptation by selection would result in a decreasing larval mortality and by this in increasing stock size toward the complete filling up of the carrying capacity of the habitat. Most changes in the hydrographical regime, however, will have adverse effects on the survival of the larvae, until a new adaptation takes place.

(3) Although starvation and predation are not related to the abundance of larvae, they change considerably with time and place of spawning. The first and second hypothesis meet in this relationship. With increasing of the adult stock size spawning time and spawning area may change. These will adversely influence survival of larvae and act as regulatory mechanisms against a further increase of recruitment and stock size. The ratio of egg size to egg number in herring has been studied as an example of the adjustment of reproduction to the given environmental conditions of the early larval phase. The ratio differs between the spawning groups according to their differences in spawning time. Under low pressure of predation but under unfavorable feeding conditions (winter-larvae), a population of few but big and vigorous larvae may give a higher number of survivors than a dense population of small larvae.

Experiments with herring eggs and larvae are described. Compared with the larvae of the summer spawners, larvae from big eggs are longer at hatching and have a bigger yolk sac, which lasts over a longer period. These larvae start feeding at a far more advanced stage which gives them a better chance for getting more and bigger food organisms.

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