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A review of density-dependent and independent processes which may affect recruitment in herring stocks[1]

by

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The Production of Eggs

The production of ovarian follicles remains fixed for some fish species (Scott 1962; Woodhead and Woodhead 1965), while for others the number varies depending upon the food intake (Bagenal 1969; DeVlaming 1971; Tyler and Dunn 1976). The available evidence indicates that vitellogensis does not occur in all eggs produced, and the degree of vitellogensis depends on the food intake (Woodhead and Woodhead 1965; Tyler and Dunn 1976). Tyler and Dunn concluded that smaller ovaries related to a reduced ration of winter flounder *(Pseudopleuronectes americanus)* (Fig. 1) were due to less oocytes being produced and a reduction in vitellogensis. Herring *(Clupea harengus harengus)* are different; they seem to produce a constant number of oocytes for a particular length, but some of these eggs are reabsorbed during the process of maturation (Bowers and Holliday 1961). Hempel (1971) states that low fat content of pre-spawning females in Baltic herring effects fecundity, years of poor feeding not only causing retardation of growth but also a reduction in the number of eggs in a given size group. After a poor feeding season, egg production will, therefore, be particularly low. The atresia of eggs following poor feeding follows a sequence

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of yolk disappearance from the peripheral regions of the egg with the subsequent breakdown of the chorion and reabsorption through autolysis (Bowers and Holliday 1960). Annual variations in the relative fecundity, fecundity for a given length, have not been noted for a number of stocks; however, the Dogger (Zijlstra and Polder 1959) and Downs (Bridger 1961) stocks are notable exceptions. Furthermore, preliminary data on Gulf of St. Lawrence herring indicate that here too between 1967 and 1970 there has been a substantial increase in the relative fecundity.

The question arises that if herring do indeed have a mechanism for eliciting density-dependent fecundity (Bowers and Holliday 1960; Birjukov and Shapiro 1971), why is it not generally observable. The answer is two fold: first, herring produce benthic eggs which are not easily sampled, and second, there is no evidence of an adult herring stock ever illustrating density-dependent growth (Lett and Kohler 1976) although there is a substantial amount of evidence to support density-dependent growth in the juvenile stages (Iles 1967, 1973; Lett and Doubleday 1976; Lett and Kohler 1976). Thus, if changes in food intake must be environmentally induced, it is only rarely that egg production would be related to other factors than the reproductive biomass. Hempel (1971) supports this view when he states that there is a general positive relationship between adult stock biomass and egg production. Furthermore, density-dependent food intake or growth can only result in a negative correlation between biomass and egg production as Lett et al. (1973) have shown for cod. This relationship is due to a positive relationship between stock fecundity and production, and shift to the left of the maturity ogive with length (Fig. 2, 3). The clarity of any density-dependent relationship with biomass, however, would be masked by variations in population structure.

If the above arguments are true, the adjustment of fecundity by fish in response to food availability is a possible population control mechanism. Hypotheses such as this have been expostulated enumerable times (Bagenal 1966; Nikolsky 1969), but in some circles are considered overly dogmatized. It is true that the theory is still only partially supported by fact, and that the cybernetic importance of this type of mechanism is difficult to elucidate, given all the other factors operating. However, indirect evidence is available (Fig. 2, see Lett and Kohler 1976 Fig. 3).

It is well known that ration size and the growth rate of fish are related, and evidence has been presented here that gonadal growth rate and ration size are conjointly connected. Quite obviously then, somatic and gonadal growth are connected, and both are emergent properties of the events in the lives of fishes. Thus, the production of an adult fish stock, defined as $N\Delta W$, is a much better index of the spawning potential than biomass or egg production assuming a fixed fecundity-length relationship. Even for herring, variations in growth rate in response to the environment, would be reflected in the egg production although there may be no response to the adult stock size.

A considerable amount of information is available on factors determining incubation periods and survival rates in herring from laboratory experiments, but observations on the development of herring eggs under natural conditions in the sea are scarce. Although the spawning grounds of Atlantic herring can usually be quite accurately determined from the distribution of ripe herring and newly hatched larvae, the discrete spawning patches are often difficult to locate. These spawning grounds are usually small, ≈ 0.75 km^2, and egg layers are between 3 and 7. Runnstrøm (1942) found that the average number of layers for Norwegian herring was 5; however, he also noted that high egg production by a large parental stock results in thicker layering rather than an extension of the grounds. He concluded that there is little adverse effect of high egg production on later recruitment because even with high egg production, only a few sheets are detrimentally thick.

Blaxter (1971) studied the development of eggs in the different layers and noted that it is not uniform throughout the egg layer; the greater the number of layers the greater the variability in development. In addition, the pattern of development within the egg layers changes during the survey period. In early samples the eggs in the lower layers are at higher stages of development than those in the upper layers, while in later samples the eggs in the surface layers are generally at a more advanced stage. Both he and Runnstrøm agreed that mortality amount eggs was low but rose from 1-2% when spawning first occurred to about 12% when the eggs hatched 17-18 days later. Furthermore, egg mortality was greater on the bottom than on the surface of the egg sheets.

One factor which contributes greatly to the mortality of eggs which is not included in the above estimates is predation, principally by haddock (Hempel and Hempel 1971). In general, Hempel (1971) estimated that one haddock ate the spawn of one herring each day, and therefore concluded this must be one of the principal sources of herring egg mortality.

Environmental effects on egg survival

Environmental effects on egg survival have been investigated by a number of individuals. Holliday (1965) was particularily concerned about the effect of salinity on the osmoregulation of teleost eggs. He states that the ability of an organism to survive extremes in salinity is based on the tolerance of the embryonic tissues to change in water content, coupled with the ability of the developing organisms to regulate to some extent, the osmotic concentrations of tissue and tissue fluid. Immediately following spawning the egg is freely permeable, giving no protection against osmotic withdrawal. Following their release they become isotonic with sea water, so that in low salinities eggs are larger, while in high they are smaller. Once the blastopore is closed the eggs become much more tolerant to changes in salinity since it is following gastrulation that herring eggs can begin to regulate ionic concentration. The response to salinity is quadratic (Fig. 4) since both extremes of salinity are damaging to eggs.

The rate at which salinity acts on the hatching success of herring eggs is modified by temperature (Alderdice and Velsen 1971) since temperature alters the ionic balance of the yolk and perivitelline fluid of the eggs. Both Blaxter (1956) and Alderdice and Velsen (1971) found temperature (Fig. 5) like salinity perpetrated a quadratic response of egg survival. There is then a conjoin optimal salinity and temperature for maximum egg survival.

The size of eggs varies among stocks (Hempel 1965) (Fig. 6) and seasonally within stocks. For example, Hislop (1975) has shown the egg size declines as the spawning season progresses so that hatching larvae will be the optimal size to take advantage of their position in the annual production cycle. Ware (1975) illustrates an inverse exponential relationship between egg diameter and temperature, low temperatures being affiliated with extremely large eggs (3 mm). Ware (1975) follows the holistic paradigm of Sheldon et al. (1972) that smaller particles experience a much higher mortality rate, thus if incubation is prolonged in cool temperatures, it is an advantage to be larger. Strictly from the point of view of predation, if an egg is larger, the number of organisms which can consume it decreases exponentially. Hempel (1965), having made the same observation, argues its consequences from a different point of view. Larger eggs are usually the result of an increase in the amount of yolk (Fig. 7) (Blaxter and Hempel 1963) so that there can be a prolongation of the period that the larvae can last without food after hatching and also for increase in body size, hence feeding performance. The importance of larger size and greater feeding ability is probably greatest during the cold of winter when food is scarce and especially when a sufficient supply of very small larvae of zooplankton is lacking. In addition, bigger larvae have larger eyes which increases the reactive volume in which they can detect prey. Smaller larvae, resulting from smaller eggs, are usually hatched during the warmer summer months when small food items are much more abundant, and there is no need for a prolonged yolksac stage. Furthermore, the volume search per meal is substantially reduced because of the greater density of food items. Many more small larvae must be produced in the summer months as opposed to winter since there is also a high incidence of predatory plankton.

Larval energetics

Some insight into larval bioenergetics and feeding is essential to understand their behavior and general ecology. One aspect which is extremely important to larval survival is their ability to search. Bishai (1960) found larval herring 6-8 mm long could sustain swimming speeds of 0.58-1.03 cm/sec or 20-20 m/hr. At an average cruising speed of 1 cm/sec and a perceptive distance of 5 mm, a larvae can search 3 litres of water per hour. Blaxter (1962) determined the maximum swimming speed of larvae 8 mm long was 3 cm/sec while those 20 mm long can swim 30 cm/sec. There is a sudden increase in the swimming performance of larvae around 15 mm when the caudal fin is formed. However, intensive activity is costly to larvae. Holliday et al. (1964) report that the metabolic rate increases 10 times from resting to a highly active state.

Larvae will begin to feed while still in the yolk sac stage. At this time they eat primarily copepod nauplii and eggs, mollusc larvae, and green food. Usually their diet shifts to large particles such as pseudocalanus as they become larger. The average size of food taken depends on the size of the larvae, and this is related to the gape of the jaw (Fig. 8). Thus larger larvae hatched from larger eggs have an advantage in that they are able to feed on larger particles. Environmental effects are important in jaw development. When temperatures are high the lower jaw of herring larvae does not develop properly, thus the presumed advantage of large size at hatch is offset not only by decreased survival but also by a suspected interference with normal development of feeding behavior and prey capturing ability (Alderdice and Velsen 1971).

Herring larvae will dart at anything that comes within approximately 5 mm of them. The movement of prey is not essential to initiate the feeding drive. However, herring larvae rarely reach their capacity for ingestion. Arthur (1956) examined the composition of food items in the guts of herring in relation to the distribution of food in the water and found the ingested food was not distributed randomly, implying selection. He came to the conclusion that although larvae will strike at almost any particle, not all are ingested.

The appetite of larvae is probably negatively correlated with the amount of food in the gut as it is with adult fish (Brett 1971). It has been observed that the rate of gut clearance by larvae is positively related to temperature (Fig. 9). Thus, with higher temperatures and more food available larvae will presumably be able to grow faster in addition to satisfying a raised basal metabolic rate.

Hentschel (1950) found 20 times more food in the stomachs of herring larvae during the day than during night. Blaxter (1965) illustrates that there is a threshold light intensity at which larvae will begin to feed (Fig. 10) and confirmation of this hypothesis can be found in the field indicating the larvae are indeed more active daytime feeders (Fig. 11). This would indicate that the use of vision is extremely important to larvae in their feed behavior. However, light also raises the metabolic rate of larvae and therefore their demand for food.

The effect of temperature on larvae is both direct, operating through bioenergetic responses and indirect, controlling the food supply. Hjort (1914) postulated that the mortality of larvae from starvation, due to an insufficient supply of plankton of suitable size, is the most important cause of the decline in abundance of a year-class. However, Grauman (1973) found that variation in food supply explained only 25% of variations in larval abundance. A similar study by Corlett (1965) showed that variations in abundance of plankton explained only 57.4% of the change in year-class size of Barents Sea cod.

It would seem that when temperature is below that required to produce a threshold density (Kerr 1971) of plankton for larvae, small changes would be important in determining survival. However, when plankton reaches densities at which larvae can satiate, a further rise in temperature, and the resulting increase in available food, would be of little importance.

Temperature affects the development rate of larvae and can reduce the time spent drift feeding on slow moving plankton (Sysoeva and Degterva 1965). Since larvae at this stage are extremely susceptible to predation, as well as being reliant on temperature to determine their food abundance. As they grow in length, their ability to swim improves (Blaxter 1962) so they are more able to avoid predators and gather food. When larvae starve for a period of 5-7 days, they essentially lose their ability to eat, and in this weakened state succumb to predation. Thus, the food supply will ultimately determine the degree of larval survival and predation simply crops those which would possibly die anyway.

Following metamorphosis very little is known about the ecology of any of our commercially important species until the recruit into the adult stock. However, some important information can be gained into this portion of the life history through the back calculation of otoliths or scales. Density-dependent ℓ_1 growth has been demonstrated for both gadoid (Raitt 1939) (Fig. 12) and clupeid populations (Iles 1967, 1973). From the discussions in this paper so far, many mechanisms seem to be operating which would tend to destabilize the initial attempts of the population to provide some stability through the production of eggs. Since density-dependent growth has never been demonstrated for adult clupieds, but has been for gadoids (Lett and Doubleday 1976), it implies that the biomass of herring stocks must be tuned in to the carrying capacity of their environment during the first year of life in contrast to gadoids which can trim their biomass during their entire life. The possible mechanism by which herring can simultaneously stabilize both their ℓ_1 length and year-class size to fit within this productive constraint is described by Lett and Kohler (1976).

Many scientists have studied the recruitment process by studying the different portions of the early life history of fish. Cushing (1975a) discusses larval drift and the need for synchronization with the production cycle. Others have examined eggs, the influence of egg condition on larvae, the condition of juveniles, larval feeding, and so on. However, few have considered the recruitment process as being part of the general life history of the fish population or the community dynamics as a whole. One wonders whether if in the past efforts have been blinded by the complexity of minutia.

Cushing (1975b) has taken a holistic look at recruitment, which is really quite unique, in relation to natural mortality. He suggests that a female fish may spawn for n years and to replace itself it must generate two spawning adults by the end of its life. Ricker (1945) has defined the critical length in a population as that at which the growth rates and mortality rates are equal. There should be a critical age at which the specific growth rate equals the specific mortality rate. Thus, the cohort adds biomass to the stock to replace losses; within the life of the cohort biomass reaches a maximum at the critical age in the unexploited stock and after that age no increment in stock can be expected. Hence, the cohort should have to replace itself in numbers. The initial number in a cohort is a function of stock and the stock replaces itself each year as the cohort reaches the critical age. The pattern of growth and mortality is determined between hatching and recruitment and so the mode of replacement of stock each year is independent from cohort to cohort. Fish of ages greater than the critical age will of course contribute to the fecundity of the population.

Ware (1975) feels that Cushing's model is only partly true since it assumes natural mortality and growth rates are density-dependent functions of age. He states that this can only be approximately true, for it is well known that growth is determined more by the current size of a fish and the food available to it than it is by time alone. Clearly, it would be far more accurate to eventually describe the death process as a size and density-dependent function of the available food supply and predation rate.

Ricker (1954), Lett el al. (1975), and Lett and Kohler (1976) have shown that predation and cannibalism by older individuals on juveniles and larvae is an important link in the recruitment mechanism, and it is at this stage the year-class is trimmed to fit within the productive constraints of the environment. In summary then, it appears from our current knowledge that recruitment in fish populations is regulated largely through variations in growth rates and predation pressure, with environmental effects being a limiting factor on the general carrying capacity of the population.

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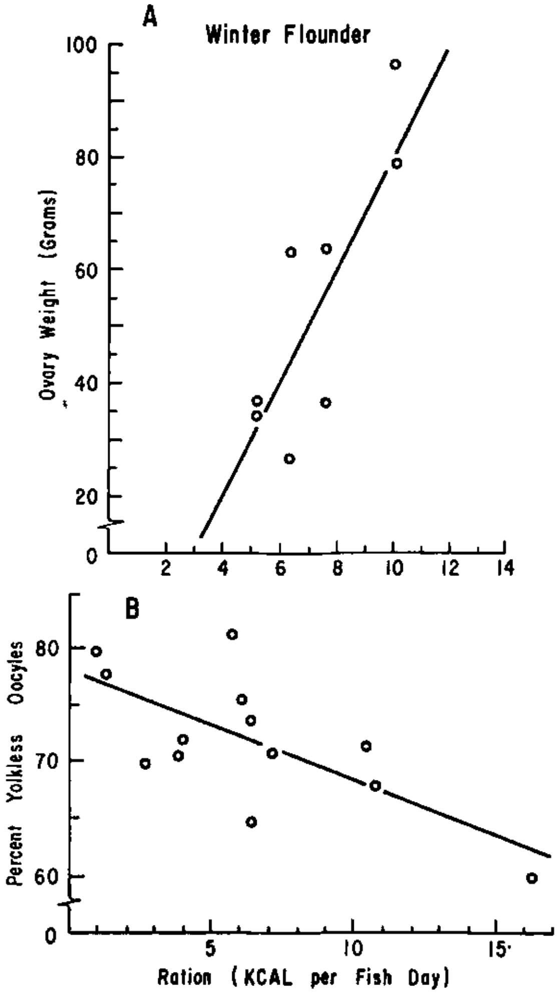

Figure 1. A. Illustrates the relationship between the energy of the daily ration and the weight of the ovary. B. Relationship of ration size to the percentage of yolkless oocytes within the ovary. Both reproduced from Tyler and Dunn (1976).

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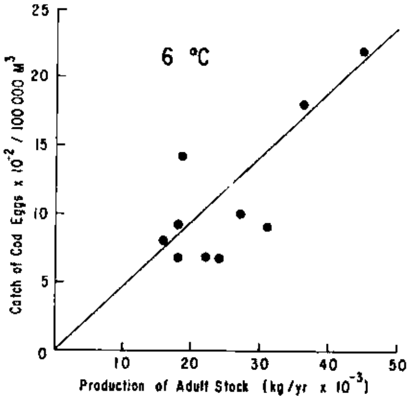

Figure 2. Relationship between production of the adult stock of Gulf of St. Lawrence cod and the average catch per unit effort of eggs. Values have all been corrected to 6°C.

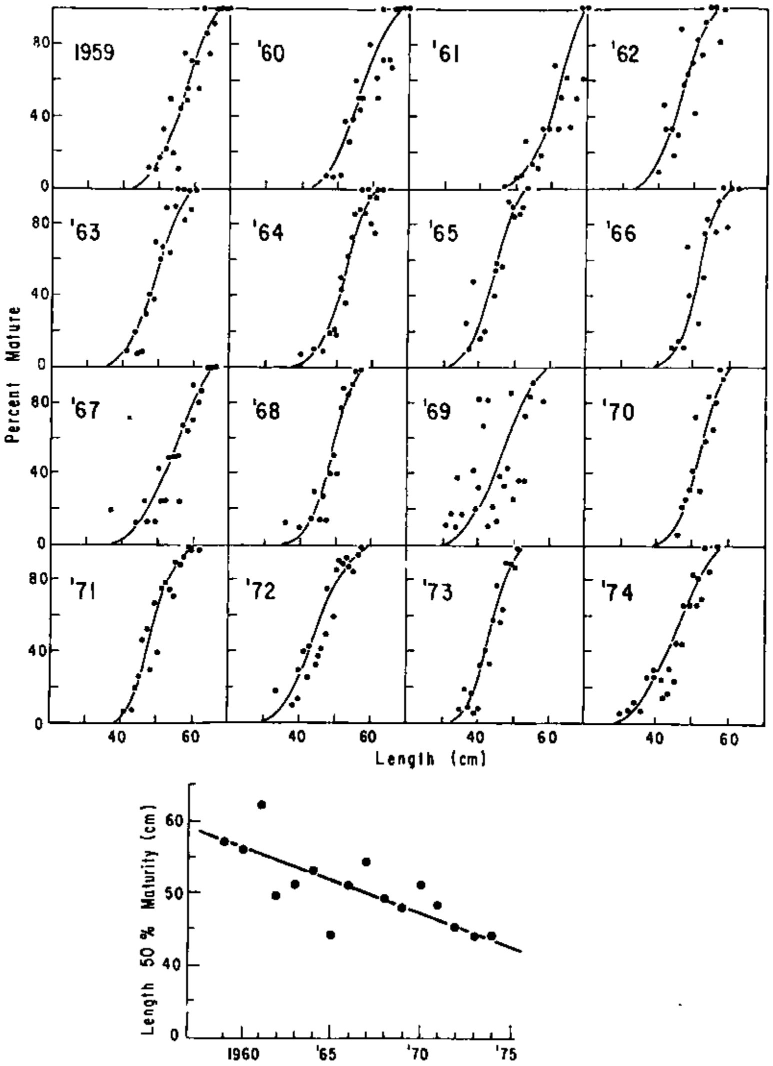

Figure 3. A series of maturity ogives over time to illustrate a 13 cm drop in the length of 50% maturity between 1959 and 1974. Curves for Gulf of St. Lawrence cod.

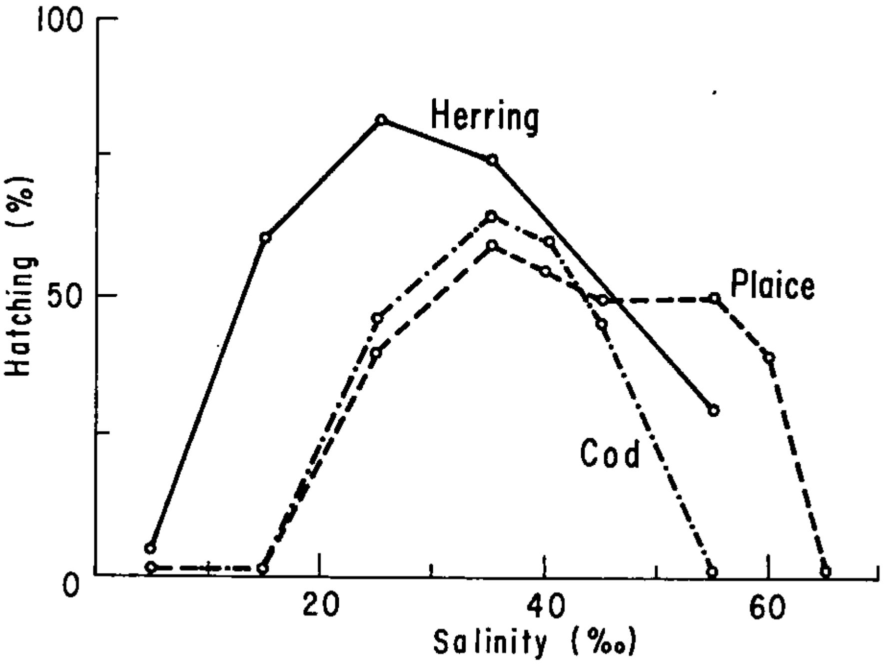

Figure 4. Percentage hatching of herring, cod and plaice eggs in relation to temperature (from Blaxter 1965).

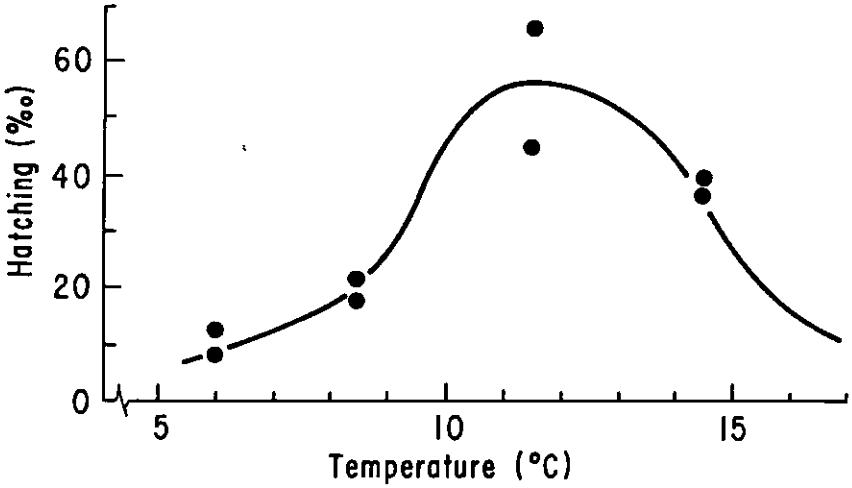

Figure 5. Percentage hatching of herring eggs in relation to temperature (from Blaxter 1956).

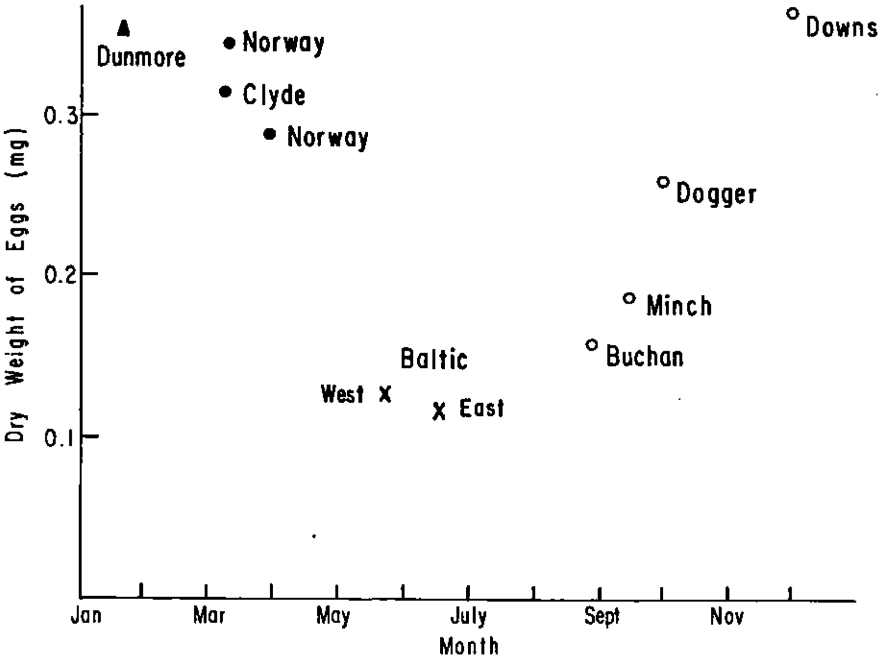

Figure 6. Egg weight in relation to spawning season for different stocks of herring (from Hempel 1965).

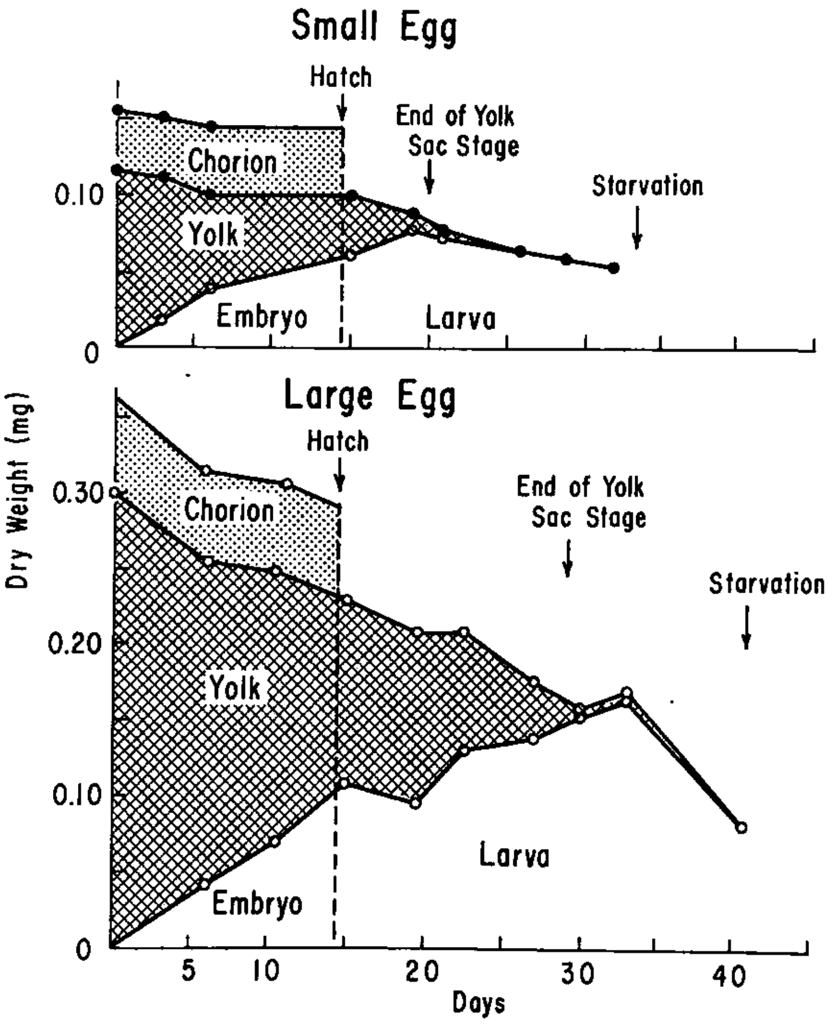

Figure 7. Changes in dry weight of chorion, yolk, embryo, and larvae during the early development of herring. The larvae were not fed and died by starvation (from Blaxter and Hempel 1963).

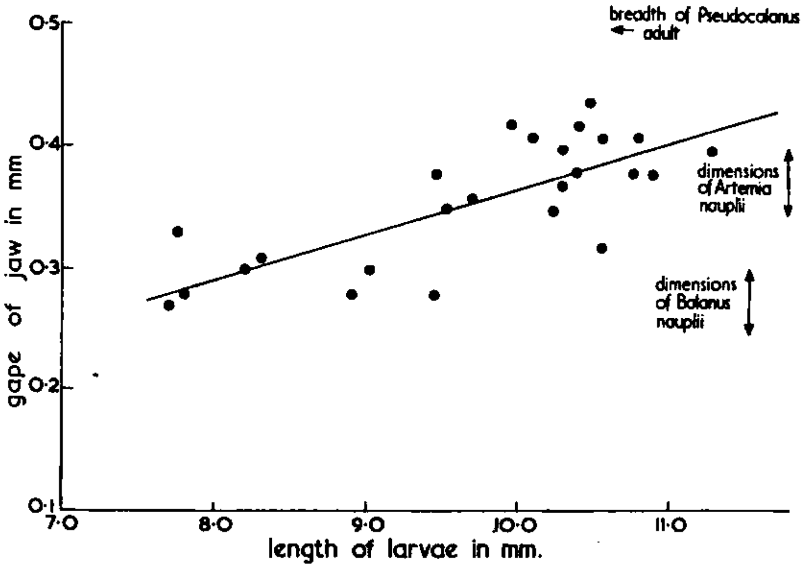

Figure 8. The vertical gape of the jaws of young herring larvae living on their yolk reserves related to length of the larvae (from Blaxter and Hempel 1963).

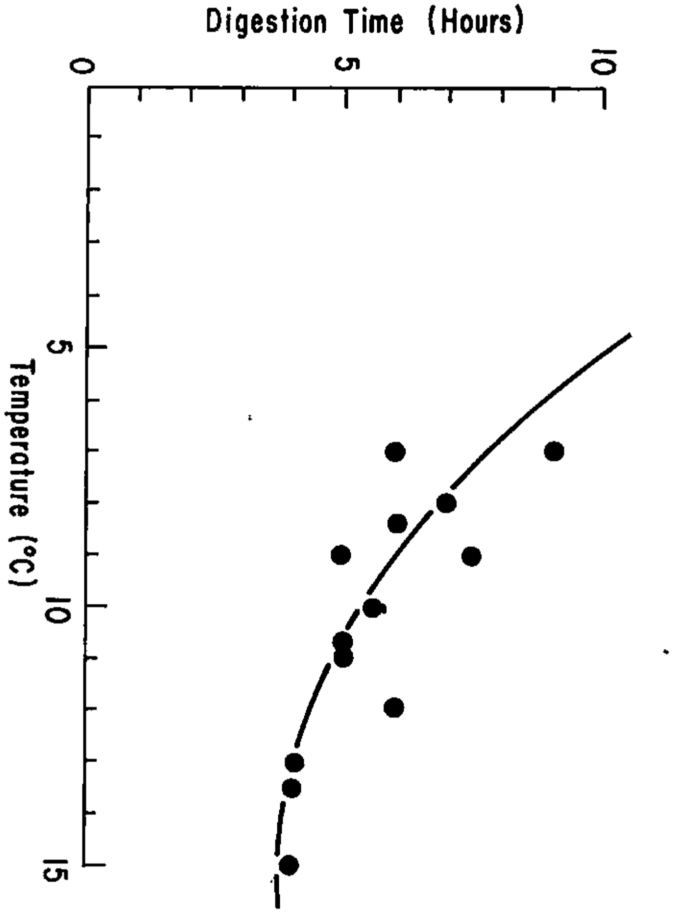

Figure 9. Time to digestion (taken as when gut contents become transparent) at different temperatures (from Blaxter 1965).

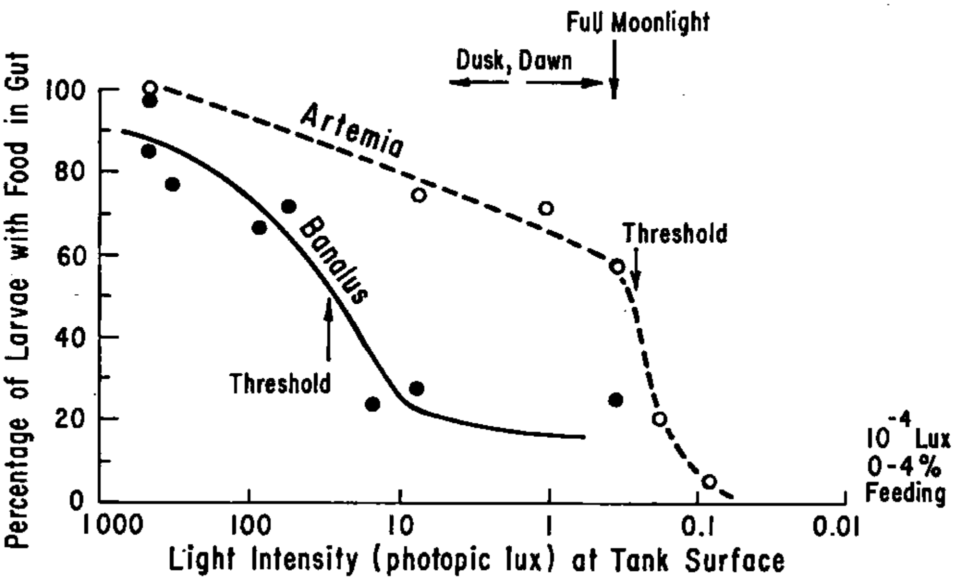

Figure 10. Percentage feeding on Artemia and Balanus nauplii feed at different light intensities (from Blaxter 1965).

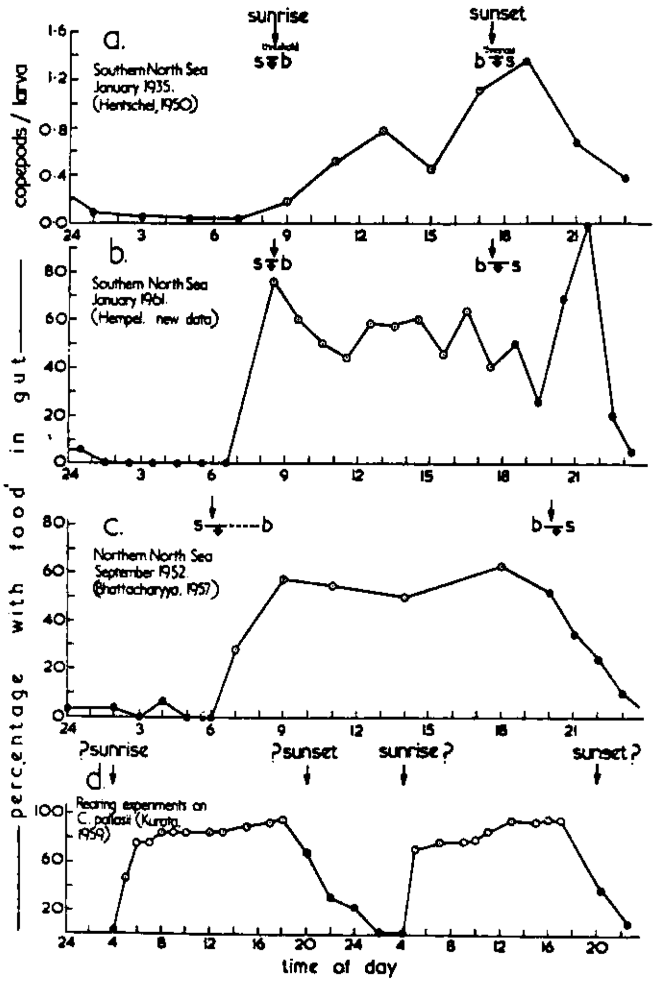

Figure 11. Incidence of feeding at different times of day and night.

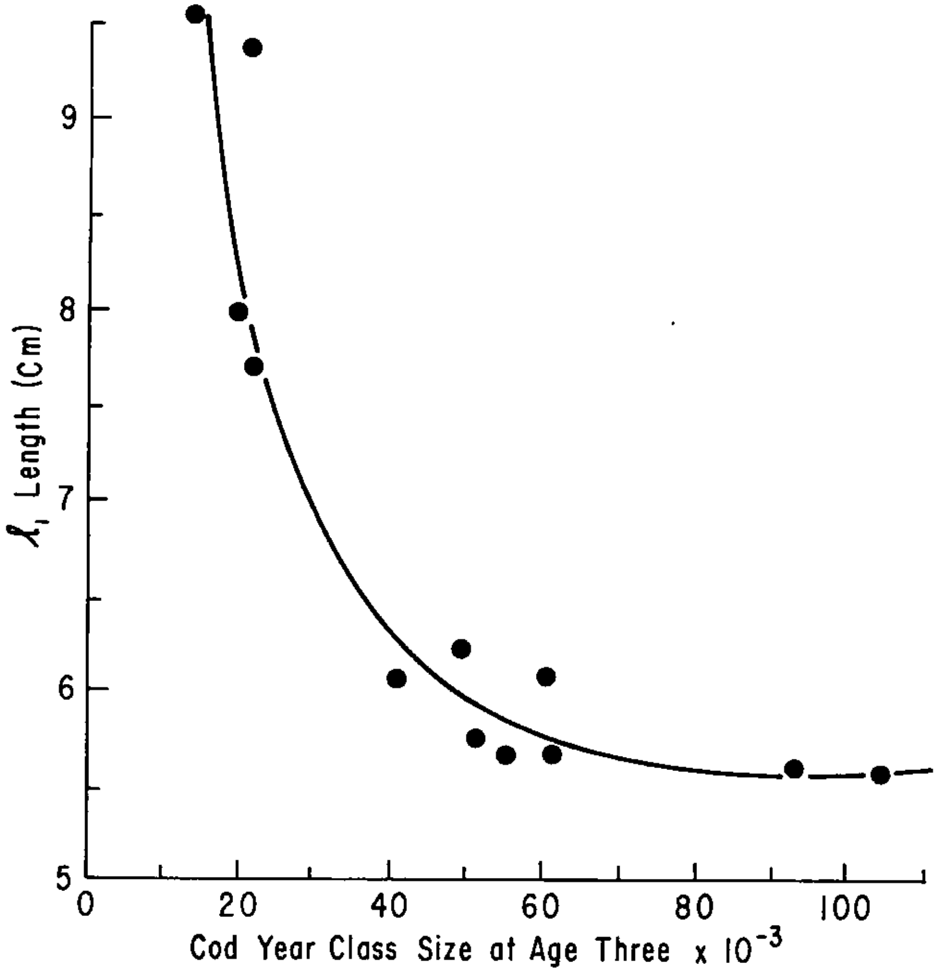

Figure 12. Relationship between yearclass size and ℓ_1 length of southern Gulf of St. Lawrence cod.