Foreword

The book chapter authored by Derek Iles and published in 1974 under the title “*The Tactics and Strategy of Growth in Fishes*” was a major conceptual advance in understanding the growth of fishes.

Notably, it demonstrated conclusively that the reproduction of fish does not influence their growth, but rather it showed that “*far from growth depending on maturity; on the contrary, maturity depends on growth*.”

However, Iles’ chapter was part of a book whose 22 contributions, including the ‘Epilog’ by Ray Beverton, assembled in honor of Michael Graham, is hard to access. Moreover, the references to all this book’s chapters are combined in a single alphabetical list, making it difficult to photocopy and share a complete version of Iles’ paper, which may be why it is inaccessible through Google Scholar.

The full reference of this chapter is:

Iles, D. 1974. The Tactics and Strategy of Growth in Fishes, Chapter 16, p. 331-345 *In*: In: E.R. Harden-Jones (ed.) *Sea Fisheries Research*. Elek Science, London.

To facilitate the sharing of this chapter, this PDF not only reproduces it, but also includes its 87 references, as extracted from the book’s bibliography on pages 331 to 345.

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11 November 2023

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THE TACTICS AND STRATEGY OF GROWTH IN FISHES

T. D. ILES

INTRODUCTION

Growth is a simple and rather vague term to describe the integrated results of very complex processes and it is a curious fact, as Gray (1929) remarked, that in metazoans it can often be defined by relatively simple algebraic equations involving only a few basic parameters. Fishes illustrate the complexities of growth as well as any group of animals; in their range of form and size, longevity, and type of life-history, as in the variety of trophic specialisation, they can lay claim to being the most diverse of all vertebrate groups. Nevertheless, it has been possible to derive growth equations which adequetely represent overall growth patterns of many species and which can be put to use, for instance, in the solution of yield equations (von Bertalanffy, 1934; Beverton and Holt, 1957). This is true despite the fact that fishes generally, and freshwater fishes in particular, may exhibit a marked ability to vary their growth in response to changing environmental conditions (Larkin, Terpenning and Parker, 1957; Svärdson, 1950, 1951; Burd, in Burd and Cushing, 1962). This suggests that in fishes characteristic patterns of growth exist whose analysis may provide a better understanding of their adaptations to the environment.

An analysis of this kind must be accompanied by an appreciation of the fact that growth patterns may change throughout the life history (Parker and Larkin, 1959; Gulland, 1964) and of the provision, stressed by Gray (1929), that the data on which generalisations are based are as precise and reliable as possible.

Although no satisfactory comprehensive definition of growth is possible, it can be defined in relation to a particular study. Here we will be dealing with the interrelationships of somatic growth and gonad development, both on a seasonal and on a life-history basis, and soma and gonad are considered separately. As far as the soma is concerned, seasonal changes in 'condition' resulting from the storage and subsequent use of such components as fat and protein are not taken to represent growth, which is defined as increase in length. Gonad growth is considered under the term 'maturation'.

LIFE-HISTORY AND GROWTH PATTERN

For many of the commercially important marine species, exploitation—and hence reliable sampling—becomes important only relatively late in the growth history as the fish approach or achieve sexual maturity. In many of these species the age of individual fish can be determined by the assessment of annual rings on otoliths and other skeletal structures, but the data so obtained refer only to the current size and age and the earlier growth history cannot be studied. In some species, however, the appearance of clearly differentiated annual rings on scales, whose linear growth approximates to the proportionality of that of the fish themselves, allows the use of back calculation (Lea, 1910, 1913) to estimate the length of individuals at the end of each of the preceding years of growth. As Lee (1912) pointed out, this means that the data become multiplied severalfold and their value is enhanced, for not only is the study of the growth of immature fish made possible when only the sexually mature population is available for sampling, but also the earlier growth can be reassessed each time a year-class reappears in a fishery, and the precision of growth estimates can thus be determined.

The East Anglian herring fishery is an annual fishery exploiting prespawning adult fishes, whose growth for the current year is complete (Iles, 1971); their scales are admirably suited for back calculation. Scale data have been analysed to cover growth over a period of nearly thirty years, from 1939 to 1967, and for each separate age of growth from the first to the sixth (Iles, 1967, 1968, 1971). Growth indices were calculated which, in effect, compensate for differences in length at the beginning of the growth season, and it was possible to allow for the various factors which come under the heading of Lee's phenomenon (Lee, 1912) and which have often been considered to detract from the value of back-calculated estimates (Lee, 1912, 1920; Jones, 1958).

The resulting data refer to a period during which major changes in growth occurred at all stages of the life history, both in response to environmental changes (Burd, in Burd and Cushing, 1962) and also, it is concluded (Iles, 1968), as a result of the changes in the abundance of herring caused by the fishery (Cushing and Bridger, 1966). An analysis of this variability is given in Table 1. This is the correlation table matrix for all possible between-age comparisons when the same growth years are compared. The table demonstrates significant patterns in the variability. There is, for example, a marked discontinuity in the reaction of O-group

Table 1 Values of the correlation coefficient (r) and its square (r^2) for between-age comparisons of the growth indices of East Anglian herring for the period 1939–67.

Age of growth (years)		*Age of growth (years)*					
		1st	*2nd*	*3rd*	*4th*	*5th*	*6th*
					r		
1st (O group)			0·379	0·629	0·714	0·686	0·721
2nd (I group)		0·144		0·755	0·693	0·684	0·644
3rd (II group)		0·396	0·570		0·911	0·902	0·889
4th (III group)	r^2	0·510	0·480	0·830		0·951	0·933
5th (IV group)		0·471	0·468	0·814	0·904		0·973
6th (V group)		0·520	0·415	0·790	0·870	0·945	

herring to the changes in growth conditions, compared with the similarity that exists for older age pairs, a similarity that becomes more marked with increasing age. This suggests that a discontinuity exists between the earliest stages of the life history and later phases (Iles, 1968). The similarity between the variation in the later ages of growth reflects also the greater extent to which the same spatial distribution is enjoyed by these older fish (Iles, 1971).

For part of the period, however, from 1939 to 1944, the data indicate that environmental fluctuation was limited and that growth conditions were uniform. This period coincided conveniently with the wartime interval when fishing was virtually non-existent (Parish and Saville, 1967). Now, in discussing 'norms' of growth and the possible occurrence of characteristic patterns of growth in fishes, van Oosten (1929) makes the point that these will best be shown up if data are available uninfluenced by variation in annual growth. Because the data for the wartime period fulfil this condition they can be used as an indication of the fundamental growth characteristics of East Anglian herring.

It has been recognised that an important factor determining the growth potential of fishes is the size (or length) at the time of growth (Larkin, Terpenning and Parker, 1957; Parker and Larkin, 1959) and the data can best be demonstrated by plotting the mean annual increment for the period against the mean initial length, for each age group, as in Figure 1. This is the form of plot described by Gulland (1964) from which the parameters of the familiar von Bertalanffy growth equation can be estimated.

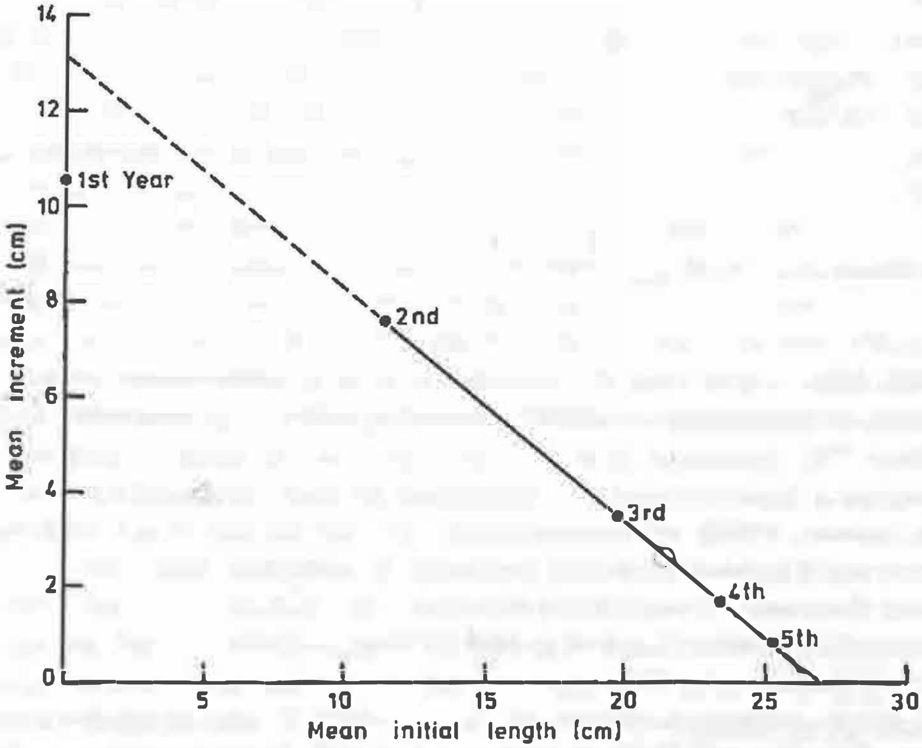

Figure 1 *Annual length increment and initial length for East Anglian herring, demonstrating the regularity of the growth curve.*

The pattern that emerges in Figure 1 can be divided into two phases: a short one including only the increment for the first year of growth, and a longer one which includes all ages from the second to the fifth year, by the end of which over 90% of the expected linear growth has been completed.

We are concerned for the main part with the long period from the second to the fifth year of life. There is a very close approximation to linearity over this period, implying a marked regularity of growth pattern. It indicates, in fact, that there is a constant deceleration of linear increment over this part of the life history, without any appreciable discontinuity. It has long been recognised, of course, that a decline in annual length increments with increasing age and size is one of the most characteristic features of the growth of fishes, one which has recently been reaffirmed by Gerking (1966). What is shown here is that under conditions most likely to reveal characteristic patterns, and with data for which the precision is known to be high (Iles, 1967, 1968, 1971), the regularity is marked and obvious. Its importance lies in the fact that the ages to which this regularity refers include both the preadult stage of the life history and all the ages over which individuals will mature and spawn for the first time (Cushing and Burd, 1957; Burd and Cushing, 1962; Iles, 1968). That is to say, at some age during this phase of the life history all the individual fishes in the population will have produced gonad material, in addition to the extra somatic tissue involved in body growth. The amount of ripe gonad material produced by East Anglian herring is, moreover, relatively great, accounting for 20% or more of the total adult weight on average (Hickling, 1940; Iles, 1971) and, in addition, it has a high protein content (Milroy, 1908; Bruce, 1924), at least as high as that of somatic tissue. The large size of the gonads in East Anglian herring appears to be characteristic for north Atlantic herring (Wynne-Edwards, 1929; Cushing, 1967) and is at the high end of the range of gonad size for teleosts (Peters, 1963).

Despite the fact that at some time during this stage of the life history large quantities of protein, ultimately derived from the same food sources that sustain body growth, will be newly required for gonad development, there is no indication that the growth pattern is disrupted or disturbed. Indeed, under 'normal' conditions it appears that it is singularly unaffected by the new physiological and metabolic demands which the fish is called upon to meet. The fact that, for most species of fish, unlike those of mammals and birds, growth continues after the attainment of the adult stage is one of the most characteristic features of the growth of fishes. The significance of this has been discussed by Bidder (1932), and fish growth, as a result, is usually characterised as being 'indeterminate' (Hubbs, 1926; Brown, 1957). More recently this characteristic has been considered in relation to the problem of 'ageing' in animals generally (Comfort, 1963).

It has also been claimed that the attainment of sexual maturity in fishes almost always marks a change in growth pattern, it being suggested that a 'reproductive drain' results from the diversion of material to the gonads which is, partly at least, at the expense of material that would otherwise be available for somatic growth. Referring specifically to herring, Lea (1913), in dealing with the phenomenon of apparent change in growth rate raised by Lee (1912), accepted as a basic assumption that the annual increment is, on average, larger in fish which do not develop their sexual products than in fish of the same age which do. This assumption became widely accepted by such prominent pioneers in fisheries biology as Hubbs (1926) and van Oosten (1929). Hubbs, for instance, refers to the attainment of sexual maturity as being accompanied by 'a sharp decline in the growth rate in the case of fishes' (Hubbs, 1926, p. 59). Van Oosten was more specific as to the causal relationships when he suggested that the annual ripening of the sexual products might cause an earlier (seasonal) cessation of growth in mature fish, so that the growth (zone) on the scale for the year might be narrower than it would have been had the fish remained immature. This concept of maturation as representing a reproductive drain which has a direct decelerating affect on growth to an extent that the growth pattern is affected is, indeed, still current. It is mentioned specifically by Brown (1957) as applying to most species of fish. Woodhead (1960), while not implying that growth patterns are necessarily affected, draws attention to the fact that egg production in older and larger fish may lead to predisposition to death, as had already been suggested by Orton (1929) and Beverton and Holt (1957). Magnusson and Smith (1963) associate a reduction in growth rate in both sexes of trout-perch (*Percopsis omiscomaycus*) in their third summer with maturation for the first time, but imply that the effect may be outweighed by other factors. More recently, for north Atlantic herring, Parrish and Saville (1965) maintain that it is a characteristic feature of the growth curves of all known herring stocks that a marked reduction in growth rate occurs at the onset of first maturity, and imply that this is the direct result of the need for the production of gonad material.

This general view has not gone unchallenged and is discussed in detail by Alm (1959). He recognised the widely held opinion that gonad development makes such demands that body growth is directly inhibited, but maintained strongly that the growth curves of a great many fishes in natural populations exhibit a smooth, gradually decreasing curvature and not by any means the sharp decline at maturity that would be expected. He made the pertinent point that whitefish (*Coregonus*) which have already matured in one environment have nevertheless shown an increased growth rate on transfer to another, and this phenomenon of 'growth resumption' has been demonstrated for *Lebistes* by Comfort (1963) and for tropical pond-cultured species *Tilapia nigra* (van Someren and Whitehead, 1959). Alm indeed goes further and maintains that far from growth depending on maturity, on the contrary, maturity depends on growth.

The point to be made is, of course, that if fish growth is generally characterised as decelerating throughout the life history—sometimes after a relatively short period of acceleration (Ricker, 1958)—then one must look for an increase in the rate of deceleration over the period during which the adult stage is reached to establish that growth becomes then subject to an extra inhibition attributable to a 'gonad effect'. There appears to be little evidence that this is at all common.

As far as the herring itself is concerned it is not at all obvious in the data presented by Delsmann (1914) or by Wood (1937) on which the conclusion of Parrish and Saville (1965) is largely based. Nor is it apparent in the extensive data listed by Lea (1910) for the herring of the eastern region of the north Atlantic or in the data presented by the same author (Lea, 1919) for herring stocks in Canadian Atlantic waters. The data presented above for East Anglian herring cannot then be considered as atypical in their lack of indication of a direct 'gonad effect' on somatic growth, and the overall growth pattern and its existence as a common phenomenon in natural populations of fishes is doubtful and certainly not proven. It is indeed possible to apply a more direct test in the case of East Anglian herring, one that follows from the occurrence in this fish of the phenomenon of partial recruitment.

It is a common phenomenon among fishes that members of the same year brood, born during the same relatively short period, do not subsequently mature at the same age. This phenomenon was first described by Sund (1911), and its occurrence in herring stocks is well documented (Lea, 1913). It has been described in detail as characterising the East Anglian herring (Cushing and Burd, 1957) over most of its recorded history and it certainly occurred over the period for which the data under discussion apply. For the East Anglian herring during this period recruitment began, to an appreciable degree, at the end of the third year of life, and the effect of maturation on growth can thus be found by comparing the third year's growth of fish which mature at this age with the growth of the same year class and for the same age (by back calculation) when, one year later, the three-year-old recruits are joined by the remainder of the year class. A gonad effect would be demonstrated by an increase in the estimated third year's increment when sampled at four years of age, compared with the estimate obtained from three-year-old fish. This possibility was tested for the East Anglian herring (Iles, 1971), with the result that no gonad effect could be demonstrated. If one had occurred it would have been large enough to be easily detected in the data. To attempt to resolve the apparent paradox that gonad growth has little or no effect on somatic growth patterns it becomes necessary to consider the way in which growth is controlled and organised.

SEASONAL GROWTH PATTERNS

Growth curves of fishes are usually depicted as being continuous, and in the sense that, each year, increments of length are continually being added this is so. Within each annual period, however, and certainly for temperate species, growth is not a continuous process but takes place only within a limited season which appears to be typical for a species or for a population. It is not easy to define the limits of growth seasons with precision, or to determine the seasonal variation in growth rate, but for species with decipherable annual scale rings, the appearance and increase in size of growth zones outside the last annual ring can be used as a measure of seasonal linear growth. Information of this kind is usually easier to document for freshwater fishes, and recently Gerking (1966) has analysed seasonal growth patterns for various populations of the blue-gill sunfish (*Lepomis macrochirus*). The herring is one marine species for which similar information is available. Lea (1911) described the seasonal growth of young Atlanto-Scandian herring and found that most of the somatic growth was completed during only three months of the year, from May to July. He also concluded that the seasonal growth of herring in Canadian waters followed a similar pattern, although it appeared that the growth season began rather later in the year and was, perhaps, a little shorter (Lea, 1919). He noted that both young and old fish showed similar seasonal growth patterns. Huntsman (1919) followed the seasonal growth of young herring in the Bay of Fundy, his results confirming Lea's conclusions, and he too found similar patterns of seasonal growth among groups of what he considered to be different ages and from different spawning communities. Hodgson (1925) was concerned with the herring of the North Sea and described a relatively short season of about four months from April to July, during which most of the annual increment was completed, and more recently Iles (1964) obtained similar results for herring in the same area.

It appears to be a common feature of these seasonal growth curves that they are sigmoid in shape. There is a period during which growth accelerates, then one of almost regular rapid growth, followed by one during which growth declines, and this pattern conforms to that found to be characteristic of seasonal growth in Gerking's blue-gill sunfish (Gerking, 1966). The difficulty of obtaining accurate information at the beginning of the growth season does leave some doubt as to the exact shape of the curve at this point, but it is thought that the initial period of acceleration is very short (Gerking, 1966). When the herring data are considered there is perhaps surprisingly little difference in the timing and duration of the growth season, either between spawning groups or between age groups. Hardy (1924, p. 17) and Hodgson (1925, p. 25) have remarked on the great overall similarity between the seasonal 'wave' of feeding and the 'wave' of growth in herring, which indicates that feeding and somatic growth are very closely related, but the direct effect of other environmental factors is not as easily discernible, in this instance at least. For, in the North Sea, at any rate, seasonal growth begins at a time when water temperatures are very low, not much above the seasonal minimum, and declines as temperatures are reaching their maximum, a point made by Iles (1964).

The most significant aspect of seasonal somatic growth, however, emerges when the seasonal cycle of gonad growth is also considered. For herring of the North Sea it was found that the period of most rapid somatic growth (April to June) preceded that of gonad growth (July, August and September); the increased gonad growth rate was accompanied by a decline in the somatic growth rate (Iles, 1964). Although this interpretation has been questioned (Parrish and Saville, 1965), in fact such a seasonal separation of gonad and somatic growth is a common phenomenon in fishes.

The suggestion was first made as long ago as 1931 (Heape, 1931, p. 287) and it has since been maintained (Woodhead, 1960) that the majority of fishes show a seasonal decline in growth at the onset of maturation, the extent of which may vary between species and often also between the sexes. For the pilchard Hickling (1945) divided the year into three parts, and found that the ripening of the gonad took priority over growth from April to July; growth occurred from August to

October. According to Milhailovskaya (1957) gonad maturation in the Onega herring takes place from April onwards, but somatic growth does not begin until after spawning, in July and August, and almost identical observations were made by Elwertowski and Maciejczyk (1960) on summer-spawning sprat and by Liamin (1959) for Icelandic summer-spawning herring. Brook (1886, p. 48), referring to the herring of Loch Fyne, says that 'during the period of rapid growth the development of the reproductive elements remains comparatively in abeyance' and examples such as these are not confined to clupeids. Hickling (1930b) found that ripening of the gonad in the hake occurred from January to June; in both of the years of study somatic growth was small from April to August 1931 and there was little or no growth from February to June 1932, but somatic growth was rapid from July or August until the beginning of the next year. Clark (1925), dealing with the atherine fish *Leuresthes tenuis*, records a cessation of growth over the period May to July, when maturation and spawning occurred, and a resumption in the fall. Brown (1946a), for brown trout, refers to a spring maximum and rapid summer growth, followed by an autumn check which coincided with gonad maturation. Van Oosten (1923), concerned with the whitefish (*Coregonus clupeaformis*), records that the sex products began their development at approximately the time when a retardation of somatic growth occurred in late summer. For perch (*Perca fluviatilis*) in Lake Windermere Le Cren (1951) shows that mature fish did not begin to grow in length until after the spawning season in the middle of June and that gonad growth did not get under way until September, after the main growth season.

All this is not taken to imply that separation in time between gonad and somatic growth is complete, but no clear evidence has yet been found to demonstrate that both types of growth can occur at high rates at the same time. It would appear that whereas in birds and mammals, with 'determinate' growth patterns, the reproductive and growth phases are separated as more or less distinct life-history stages, in fishes the separation is on a seasonal basis.

What is equally interesting is that, although gonad maturation in fishes may require relatively large quantities of nutritive material, it often occurs during a period of fast (Hoar, 1957; Woodhead, 1960). This has been known for Atlantic salmon for some time; Paton (1898) found that no feeding occurred during passage into the estuary and up river, even in individuals beginning the run with undeveloped gonads, and the same has been shown to apply to Pacific sockeye salmon, *O. nerka* (Idler and Tsuyuki, 1958). Examples are also common in species and families in which maturation and spawning does not lead to the death of a major part, or all, of the adult population. The case for haddock (*Melanogrammus aeglefinus*) is well documented by Homans and Vladykov (1954), who found a progressive decline in feeding with maturation even though food remained available, and data presented by Ritchie (1937) for haddock in Scottish waters imply that a similar situation occurs there. Cod feeding in the north-east and central Barents Sea leave the feeding grounds to begin their migration to the spawning ground in late September as the gonads start to ripen (Woodhead and Woodhead, 1965), and Love and Robertson (1967), maintaining that feeding cessation during maturation is common in fishes, imply that the fact that North Sea cod *can* feed actively throughout the prespawning and spawning period is unusual.

Van Oosten (1923) found that even under conditions of constant food availability, food requirements were less for the whitefish during, at least, the later stages of maturation. For herring Brook and Calderwood (1886) reported that in June and July they failed to find any herring containing food although the gonads were not yet ripe and food was plentiful, and Milroy (1908) made the interesting point that the main growth of the ovaries of herring takes place after the most active feeding period is over. Channon and El Saby (1932) maintain that herring stop feeding in July and that none are found feeding after the beginning of August, which is before full maturation is reached by the population, and Rice (1963) recorded a decline in the feeding rate of Manx herring towards the end of July and before maturation was complete, even though food was available. He suggested that in this instance there was no direct relationship between feeding intensity and maturation stage. In a review of the behaviour and physiology of herring and other clupeids Blaxter and Holliday (1963) stated that winter/spring-spawning herring feed in the late spring and early summer, but, with the development of gonads in late autumn, feeding stops. For the North Sea herring, dealt with by Iles (1964), given that the 'waves' of feeding and of growth are very similar (Hardy, 1924; Hodgson, 1925) and that maturation takes place later than growth season, it follows that, again, gonad maturation coincides with a period of reduced food intake.

All this implies that gonad maturation can be dependent, to a large extent, not on material contemporarily available as a result of the ingestion and digestion of food, but rather on a nutritional 'store' accumulated during the major feeding and growth period. For North Sea herring this question has been dealt with in some detail (Iles, in preparation) by following the seasonal changes of the major somatic components—fat, water and 'protein'—over the growth, maturation and spawning season. It was shown that protein was accumulated in somatic tissue during the feeding and growth phases and that the accumulated material was subsequently lost. Not only did this loss coincide in time with the process of maturation of the gonad, but also the rate of somatic protein loss was very similar to the corresponding rate of increase of protein content of the gonad, so that a mechanism of protein storage in the body and subsequent translocation to the gonad could be accepted.

Le Cren (1951) followed seasonal changes in total condition (i.e. making no distinction between the major components of fat, water and protein) in perch from Lake Windermere, treating the gonads and somatic tissues separately. His results can be interpreted in a very similar way. In mature females, for example, while the total condition (i.e. for gonad and body combined) remained nearly constant during the winter period, there was a decrease in the somatic condition factor as the gonad increased in size. This strongly implied that maturation involved, to some degree at least, the translocation of material previously stored in the body.

That this is so in Atlantic and Pacific salmon is well documented. For Atlantic salmon Paton (1898) drew up a 'balance sheet' of loss from muscle and gain by the ovaries and tested to show that stored material was ample both for maturation and for energy requirements. By 1926 Greene was able to undertake a comprehensive review of the physiology of the spawning migration, and in recent times Idler and Tsuyuki (1958), Idler and Bitners (1960) and Robertson and Wexler (1960) have undertaken detailed biochemical and histological studies of the changes in the tissues and organs of migrating and spawning Pacific salmon. It can be pointed out, however, that a somewhat similar, and perhaps analogous, situation may be quite common in fishes which survive to spawn at annual intervals. In the hake, Hickling (1930b) showed that a seasonal cycle of somatic 'condition' resulted in a surplus which subsequently became available to the developing gonad. He drew a parallel between this situation and that demonstrated for salmon by Paton, and drew attention to results of other workers which indicated that it occurred in several common and abundant marine species. Thus Russell (1914) concluded that there was a transference of material from the somatic tissue to the gonad in the haddock, and D'Arcy Thompson (1917) made the same observation for plaice, as did Graham (1924) for the cod. Hoar (1957) implied that the transfer of protein and fat from body tissues to the gonads when feeding was at a low level is quite common in fishes, and Love and Robertson (1967), while discussing changes in muscle protein fractions in cod, state that the cod draws heavily on its body proteins to supply material for the gonad. They add, significantly, that, unlike the position obtaining in mammals, in fish the extensive depletion of protein reserves occurs quite naturally every year, so that 'loss of condition' is not to be considered, necessarily, as an abnormal state of affairs. What can be added to this is that the seasonal changes in flesh condition, which appear to be intimately related to the way in which the maturation of the gonad is organised, can be observed in fish which neither mature nor spawn.

SEASONAL CYCLES IN IMMATURE AND MATURE FISH

Hickling (1930) made a detailed comparison of cyclical seasonal changes in mature, adolescent and immature female hake and found in each group, and for both flesh and liver, a close resemblance in the timing and form of the changes in condition or relative heaviness. Differences between the life stages were found in the amplitude of the cycles, which increased from immature to adolescent and from adolescent to mature females. Le Cren (1951), making a comparison between the seasonal cycles of somatic condition of mature female perch and immature three-year-old females, again found that the amplitude was greater for mature fish, but again the timing of the cycles was similar. These more detailed studies confirm more general impressions gained by earlier workers. Thus Johnstone (1914) remarked on a seasonal variation in condition shown by immature plaice in the Irish Sea, and Graham (1924) maintained that the loss of condition in mature cod resulting from spawning is preshadowed by analogous changes in the immatures. In reviewing this earlier evidence, Hickling (1930) interpreted data published by Russell (1914) for haddock in the same light and drew the important conclusion that the seasonal metabolic rhythms, which in mature fish are associated with the spawning cycle, represent no radically new phenomenon but are, rather, the expression of a seasonal rhythm already present in immature fish. Indeed, the basic similarity between the seasonal changes for immature and mature fish has been extended to include even changes in the gonads themselves, which in the adolescent hake can undergo a 'tentative pre-spawning maturation' (Hickling, 1930b, p. 15). More recently, other activities intimately associated with reproduction have been shown to represent an intensification of rhythms already established in juvenile and adolescents, rather than the appearance of new phenomena. Thus the characteristic spawning migration of adult Barents Sea cod is anticipated by the 'dummy' runs of younger fish (Trout, 1957), and by the associated seasonal cycle of thyroid activity (Woodhead and Woodhead, 1965) which, in immature fish, differs again only in amplitude from that shown by the spawning fish.

THE INTERACTION BETWEEN SOMATIC GROWTH AND GONAD MATURATION

The apparent regularity of the growth curves of many fishes over the juvenile, adolescent and at least the initial adult stages of the life history can be presented as something of a paradox. When the seasonal aspects of growth are considered, somatic growth and gonad growth appear to be alternative activities (Woodhead, 1960) and the expectation of a disruption in the growth pattern at puberty, as well as the common use of terms such as 'reproductive drain', could be taken to imply that they are antagonistic, i.e. that they represent a competition for the same resources ultimately derived from the food. In this tactical sense they appear to be opposed, and yet, when the overall growth pattern is considered, a regularity persists over the most relevant part of the life history which appears to be unaffected by the presumed antagonism. Moreover, this has been shown to apply to the one species, the herring, which might be expected to show any effect to a marked degree, not only because of its relatively large gonad size, but also because, as a zooplankton feeder, food is available, reliably and in quantity, for a relatively short time in each seasonal cycle.

What must also be pointed out is that the growth equations—such as the von Bertalanffy equation, and, indeed, more complex mathematical treatments designed to take into account more realistic physiological factors (Paloheimo and Dickie, 1965, 1966a, 1966b)—which have been used commonly in fisheries biology to approximate to the observed overall growth patterns—have been concerned directly neither with the seasonal nature of growth nor the diversion of material to the gonad.

As far as the herring is concerned, it can be demonstrated that gonad growth represents a call on food resources comparable to that represented by somatic growth; so gonad growth is a factor which deserves consideration even if its effect on the overall growth pattern is small or negligible.

Figure 2 is an idealised length for age curve, which is defined by a von Ber-

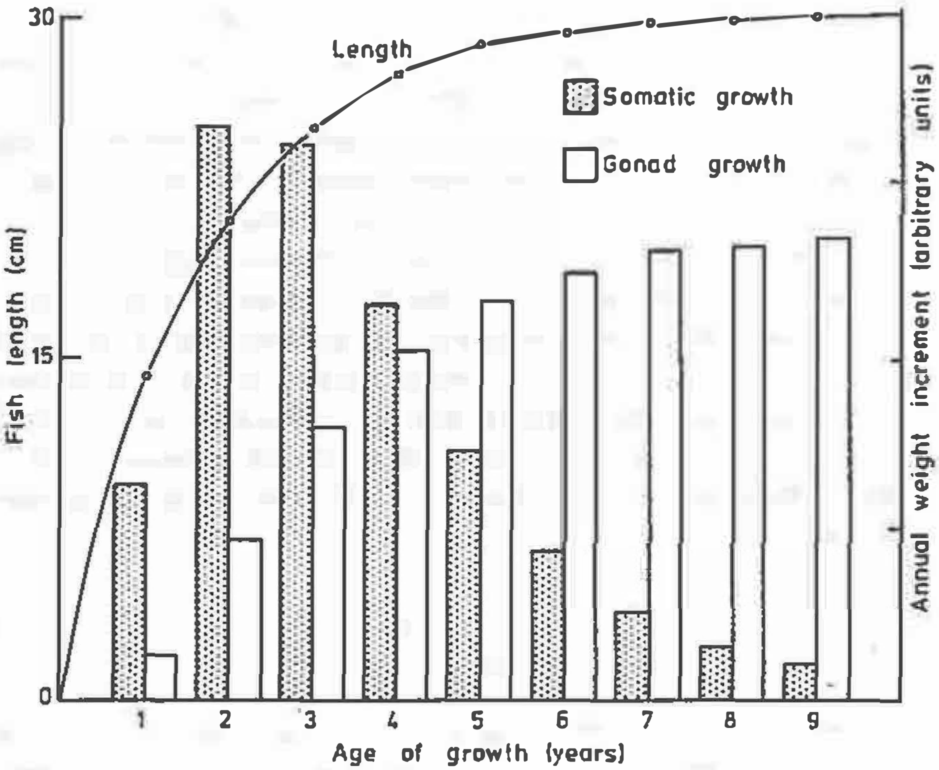

Figure 2 *Annual weight increments of gonad and somatic growth for a 'standard' East Anglian herring (see text).*

talanffy curve with parameters $t_0 = 0$, $L_\infty = 30$ cm, $K = 0{\cdot}60$. Also given are annual somatic weight increments for this curve and annual gonad weight increments on the same arbitrary scale. The gonad increments are calculated on the assumption that each year a gonad is produced which weighs 20% of the body weight at the end of the year's growth. In Figure 3 these data are plotted as smooth curves for the somatic weight increment and the total weight increment together, and the ratio of gonad increment/total increment is also given. By about the fourth year of life the gonad requirements already match those of somatic growth, and from then on they exceed them; by the latter stages of the life history, when somatic growth has declined to a low level, the gonad growth is not far short of the level of maximum seasonal somatic growth recorded during the life history. The relationships shown in Figure 2 would be affected if somatic growth in the latter stages of the life history was not asymptotic, as applies to many fish (Parker and Larkin, 1959; Paloheimo and Dickie, 1965) and indeed to many herring stocks (Ricker, 1958), but the general conclusions would stand.

The way in which a regular life-history growth pattern can be achieved without interruption when sexual maturity occurs is suggested, in the first place, by the observation that the onset of seasonal feeding leads to an increase in the level of 'flesh condition'; this is so even when, as for North Sea herring, growth is going on simultaneously (Iles, 1964).

This means that excess material, over and above that being used for growth, is accumulated in the soma. Now perhaps the most general statement that can be made about growth in fishes is that it decelerates throughout the life history

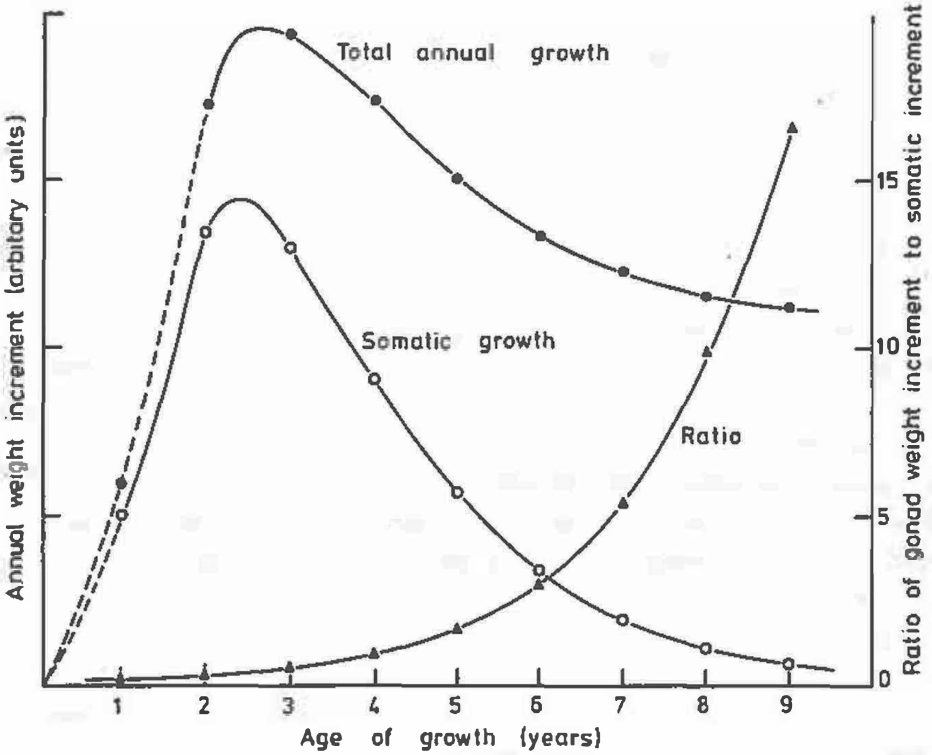

Figure 3 *Annual somatic and gonad growth, and their ratio, for East Anglian herring.*

(Gerking, 1966). Other things being equal, the seasonal level of excess material will depend on the growth rate so that, as growth declines for successive ages, progressively higher seasonal levels will result. A stage will be reached when this excess is enough to provide the bulk, at least, of material needed for maturation, and seasonal cessation of somatic growth would then allow translocation to the gonad. One can therefore say that the rate of deceleration of growth throughout the relevant part of the life history—the overall growth strategy—is an important factor determining at what stage a fish matures and at the same time allows maturation without a major disruption of the growth pattern. A similar conclusion, worded more generally, has been expressed by Alm (1959, p. 119): 'It seems permissible to suppose that this fast deterioration of the growth rate accelerates the differentiation processes, mainly in the gonads, which in their turn produce maturity'. An explanation along these lines would account for both the similarity in seasonal condition cycles between younger and older fish and the differences in amplitude, as well as the fact that in herring the seasonal somatic growth cycle appears to be very similar between juvenile and adult fish (Lea, 1919). It does mean that the factors controlling and organising the physiological processes themselves are intimately involved.

HORMONAL CONTROL OF GROWTH PROCESSES

The key role played by hormones in coordinating the activities of animals of all kinds with seasonal changes in the environment is of course fully recognised (Clark, 1965), as is the fact that fishes possess a well developed endocrine system comparable with that of other vertebrates (Hoar, 1957; Holliday, 1965; Barr, 1965). The existence of separate growth hormones and gonadotrophic hormones in herring (as well as a luteinising hormone controlling ovulation and hence spawning itself) has been demonstrated by Holliday (1960a, 1960b), and evidence of the activity of the first two is inferred by Iles (1964) from data on seasonal somatic growth and maturation. Relatively little detailed information is available on the interaction between endocrine systems and environmental stimuli (Holliday, 1965; Woodhead and Woodhead, 1965), and knowledge of the intermediary metabolism involved in endocrine function is almost non-existent in fishes (Barr, 1965). However, that intrinsic or endogenous seasonal rhythms can exist is being increasingly stressed (Woodhead and Woodhead, 1965), partly because the direct correlation of environmental factors with the resultant effect on the physiology of fishes is a common tendency.

Brown (1957) found, in brown trout, that even under constant environmental conditions the physiological cycles of maturation and of growth are maintained at the same time of year, a finding that is implied by van Oosten's observations on whitefish in aquaria (van Oosten, 1923). Holliday (1965) maintains that certain fish endocrine activities have inherent rhythms which, although reinforced by environmental stimuli, are independent of them. Woodhead and Woodhead (1965) are more explicit in believing that seasonal rhythms in physiological activity are innate, the role of environmental factors being to time them precisely.

Of the environmental factors considered, light—acting through photoperiodicity—is becoming accepted as playing a major role in influencing the timing of seasonal physiology, rather than other factors such as temperature. Referring to the breeding cycle, Woodhead and Woodhead (1965) conclude that in many marine fish the photoperiod is critical, provided that temperature does not deviate from the normal seasonal range.

Gerking (1966), when considering seasonal somatic growth, with particular reference to freshwater fishes, maintains that the generally accepted view that temperature affects growth has not been conclusively demonstrated in natural populations, and refers to evidence implicating changing day length as a factor. It has been pointed out (Iles, 1965) that the rate of seasonal growth in herring is not simply related to seasonal temperature changes. In temperate regions day length and its rate of change is a reliable indicator for the time of the year, although light *per se* is not involved directly in the metabolic processes being regulated.

The occurrence of intrinsic seasonal cycles of hormones controlling the fate of ingested and assimilated food material can lead to marked variability in the tactical growth pattern. For instance, there is no need for assimilation of food and growth to be synchronous. Brown (1946a) found in brown trout that increases in weight (condition) and in growth rate (length) were separated by two-week intervals, thus generating alternating cycles of change in condition and in length, and a similar type of short-term fluctuation was described by Swift (1955) for the same species and by Birkett (personal communication) for *Tilapia mossambica*. This implies that the incorporation of food into the metabolic pool on the one hand and the anabolic process of growth on the other are distinct processes.

It is as if the increase in condition represents the preparation of material which, in these instances, is incorporated permanently into the body.

Assimilated food need not necessarily be subsequently diverted towards somatic growth. Le Cren records a relatively small, but nevertheless real, increase in condition in April for mature perch, which precedes the growth season and which is associated with the final stages of maturation, and this type of situation is recorded also for the Onega herring (Mikhailovskaya, 1957) and for a sprat population (Elwertowski and Maciejczyk, 1960), for both of which the initial burst of feeding leads not to somatic growth but to maturation. The double feeding period of the Icelandic summer-spawning herring, which brackets the spawning period, may represent a similar case.

It is significant that much of the information discussed above refers to the herring, because this species is faced with formidable problems in adapting to dependence on a source of food showing markedly seasonal fluctuations in availability and abundance. Yet, in spite of this, more than any other temperate marine species it is differentiated into groups which differ widely in the seasonal timing of physiological processes, most notably of course that of spawning itself. Blaxter (1958) pointed out that this implies that the different groups apparently show different responses to the same stimuli, since they often share a common environment, and Iles (1964) drew attention to the broad relationship between the distribution of different spawning groups and differences in the nature of the productive cycles over the species range. This relationship was examined in more detail by Cushing (1967), who interpreted the grouping of herring into differing spawning groups as an adaptation towards the differing production cycles. The question arises: to what degree are these adaptations the result of the development of intrinsic controlling mechanisms, differing in detail in the timing of the production of the hormones controlling the physiological processes involved, and to what extent they are affected by fluctuations in environmental conditions from one year to the next? Gerking (1966) has emphasised the need to study seasonal aspects of growth in order to determine the nature of interactions between the regulatory factors and food supply, but stresses the difficulties in direct quantitative investigation, particularly of the hormonal factors. Detailed comparison of the seasonal physiology of different herring populations might well throw light on the relative importance of intrinsic and environmental factors, particularly if comparison could be made over a period when the environment, and particularly food supply, varied significantly, so that the sensitivity of the regulatory mechanisms to change could be tested.

In any case the emphasis on the fact that, in temperate fishes at least, growth is a seasonal phenomenon, and that many fundamental aspects of growth are explicable only in terms of this seasonality, is well placed. In this instance an apparently relatively featureless pattern of growth strategy appears to have been achieved by tactical organisation, implying subtle and sophisticated adaptations.

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