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Unsolved and Open Questions Concerning the Recruitment of Herring in the Northwest Atlantic

by

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Introduction

There have been at least three important symposia in the 1970's that have dealt with the issue of the reproductive resilience of fish populations in response to fishing pressure (Blaxter, 1974; Parrish, 1973; Saville, in press), the latest, in 1978, dealing quite specifically with pelagic species. Indeed, the "stock/recruitment" question, which is the approach by which fishery biologists, concerned with the reasonable (if not rational) exploitation of commercially important species, deal with the "density-dependence" question, has aroused perhaps more interest than any other. Despite innumerable papers and reviews, representing in many cases a large amount of imaginative effort, no consensus has emerged or, in my opinion, is even likely to. Instead, we seem to have confirmed George Bernard Shaw's opinion of science in general when he claimed that to answer a single question, science has to ask ten new ones!

Under these circumstances, yet another review of environmental and biological factors controlling the recruitment of herring in the Northwest Atlantic (not to mention the impact of fishing) is unlikely to lead to further clarification. Instead, I am attempting to ask different kinds of questions aimed at removing the obstacles to consensus. I am taking a lead from an interesting and, to me, important paper by Slobodkin (1972) that has been almost ignored since its publication.

Slobodkin is directly concerned with demonstrating that the concept of any generalizable maximum ecological efficiency (such as the one enshrined in the "10% Rule") must be incorrect and for sound theoretical reasons.

This demonstration, in fact, was to repudiate his own much more widely recognized paper of 1962 which proposed that there was such a maximum ecological efficiency towards which, in evolutionary terms, adaptational pressures would tend (Slobodkin 1972).

While this reversal of opinion has obvious implications on, for example, theories which are based on bio-energetics, Slobodkin has a much more general point to make .

Ecological theories, he maintained, should be based on evolutionary theories and, as a result, comments on the validity of evolutionary theories are valid also in ecological theory. The crucial point concerns not "Ecological Efficiency," or indeed, "efficiencies" at all, but the kinds of variables that are permissible as elements of ecological theories.

The reason for this can be quoted directly:

> "..... the pressures being put on ecology at the moment are enormous. We are being asked to make intellectual bricks without empirical straw, and somehow we will hate to respond, not only because of the financial and political power of the people asking us, but because, in fact, there are real questions of environmental health in a broad sense that really do require an answer. It, therefore, becomes of paramount importance to discover ways of avoiding intellectual false leads. that is, it becomes of major practical and intellectual importance to develop a meta-theory of ecology, which permits us to choose between theoretical constructions on some grounds other than long-term programs of data collection." (Slobodkin 1972, p. 298-299).

In an era of apparently continually shrinking resources, any promise of a parsimony of means deserves serious consideration. It is of particular interest that Slobodkin reached this conclusion following his participation as Rapporteur in two Symposia devoted to topics related to fisheries-management. These were the Symposium on Marine Food Chains (Steel 1970) which produced the evidence that convinced Slobodkin of the inconstancy of ecological efficiency and that on Stock & Recruitment (Parrish 1973).

In fact, I will concentrate more on the implications of the term meta-theory but, before doing so, will summarize his argument and list some of his conclusions.

Natural selection acts on individuals of particular times and places - it is coercive as an evolutionary force because of its local or "intensive" nature. Ecological Efficiency, by contrast, involves "extensive" or "global" variables; in this instance, the summation of the food consumption by individuals in one trophic level, and of its total yield to another population at another's. Ecological efficiency is the ratio of these two global variables. It cannot be coercive as an evolutionary agent and cannot therefore be, inevitably, maximized or optimized by adaptation. Any ecological theory that depends on the assumption of maximization or optimization must then be suspect. Population characteristics identified by Slobodkin as global, extensive variables besides Ecological Efficiency include total population size, total efficiency, total complexity, and life expectancy; by implication, production/biomass ratios are also to be included. A simple extension of his theory is applied by Slobodkin to interacting populations, that is to communities or multi-species interactions and the same kind of constraints are deduced. Clearly, if Slobodkin is to be taken seriously, a great deal of re-thinking will be necessary, particularly as "maximizing" is the essence of much of mathematical population theory and, for the most part, without examining the variables involved as to their nature in relation to Slobodkin's thesis.

Slobodkin's intention however was to stimulate a more general critical attitude in both generating new concepts and in giving credence to them once they have been introduced. The building up of a meta-theory, a body of generally accepted ideas and facts in any given field that can be used to decide on the likelihood of a theory being correct.

I will therefore concentrate on two elements of a proposed meta-theory for the study of herring recruitment that should be recognizable as fundamental. The first concerns the biological nature of herring stocks and, the second, the question of factors determining their absolute abundance - the "total population size" of Slobodkin.

It must first be conceded that, in discussing the stock/recruitment question in herring, we should be able to define what is meant by a stock and, secondly, if the recruitment question is to account for the variation of recruitment and without this variation, the problem would be solved by reasonably accurate data and without the need to resort to theory, we must first of all account for the fact of the absolute abundance of stocks. According to Slobodkin, there is no purely biological theory to account for absolute abundance and we are considering the variation of a population characteristic that cannot itself be explained!

A Review of Concepts of Stock Structure in Herring

The original 19th century concept of herring stock structure was formed as the result of observations on fishing and landing patterns. These implied a single stock of herring that moved in east Atlantic waters around the Britis Isles in, broadly, an clockwise direction.

The sub-division of this total herring population took place at an early development in the history of the scientific study of herring (Heinke 1898; Ewart 1883), but the first "modern" analysis of the question, i.e. in the light of neo-Darwinist theory was by Blaxter (1958) whose list of questions posed by the existence of herring "races" remains largely unanswered, even today.

These questions were:

1) What is their (biological) nature?
2) How many are there?
3) How did they originate?
4) How do they remain distinct?
5) How are they related to each other?

Blaxter pointed out that the concept of "race" in ecology had been developed mainly from the study of terrestrial ecology and that in terrestrial ecology, geographical isolation was an important characteristic that was the basis for both analysis and explanation.

The difficulty presented by the herring situation was that the discrete spawning groups that could be recognized - the elements whose status was to be determined - bred at different times of the year as well as, in many instances, different locations.

This added another dimension to the problem, that of time.

In addition, it was clear that individuals of different spawning groups could be found together outside the spawning period as adults and/or as immature fish. These individuals found together outside the spawning period could not usually be identified as to spawning group, and the "mixing" problem resulted, one that has dominated herring biology throughout its modern existence.

It is interesting to follow Blaxter's arguments because they illustrate a constraint that was imposed by the current knowledge in the field of biochronometry. Blaxter quoted Baker and Baker (1936) (a paper published in the same year as the formulation of the Bunning Hypothesis - the first clear statement on internal timing mechanisms) (Bunning 1936) to the effect that it is unlikely that a biological system could incorporate an exact timing mechanism. If this is so then the argument runs so:

1) Differences in spawning time are the main and obvious criteria for distinguishing herring races.
2) Spawning is controlled by hormones.
3) Hormones are controlled by environmental (<u>not</u> internal clocks).
4) Unlike temperature and salinity, day-length is invariant from year to year - "is a rigid stimulus."
5) If herring spawning groups react to day-length to maintain their characteristic spawning times, then spring and autumn spawners are genetically distinct.

Blaxter also pointed out that spawning at different times of the year, especially on the part of herring sharing the same adolescent distribution, meant that two groups were reacting either to two differnt stimuli <u>or</u> to different values of the same stimulus. In either case, genotypic differences were positively indicated.

Blaxter had began by examining primarily four groups of herring:

Atlanto-Scandian	spring spawners
North Sea	autumn spawners
Scottish west coast (Minch)	spring spawners
" " " "	autumn spawners

His conclusion was that the autumn spawners were different species and the geographical variants, the Atlanto-Scandian and the Minch spring spawners were sub-species. In fact there was a hierarchical organization of herring groups based firstly on the criterion of difference in spawning time and secondly on geographical location. It is interesting to speculate what criteria would have been used if intrinsically timed seasonal hormonal cycles could be assumed as a basis for a theory of herring stock structure.

For completeness, it must be pointed out that recognition of genetic isolation betwen specific herring groups on the basis of merisitic (VS) and morphometric (size at age) differences that were significantly greater than the variation within groups has generally been conceded (e.g. Johansen 1924). These seem to be more common (or better documented) in the east Atlantic.

The structure of Northwest Atlantic herring stocks in the Gulf of St. Lawrence has been analyzed recently (Ware and Henricksen, 1978). The study was based largely on the analysis of landings data from inshore fisheries, and again a heirarchical organization of stock structure is proposed, this time of three tiers.

There are important differences in the method of separation of stocks, for Ware and Henricksen use the same criteria - the deduced spawning time - all three heirarchical levels. The difference between the spring and autumn spawning is recognized at the primary level, but for both within the autumn and spring primary spawning groups, secondary sub-groups two or more "runs" are discerned.

The definition of terms used "stocks" and "groups" is not explicity given and there is indeed some ambiquity and even inconsistency in the use of the terms throughout the text, but no suggestion of recogniton of species or sub-species is made and while four groups (in the two top levels) are definitely considered to be likely genetic isolates[1], the third level the "run" is probably not. The difference in time between these "runs" is not large enough to be sustained.

It will be noted that the possibility of segregation on the basis of geographical separation - the second criterion used by Blaxter is not considred by Ware and Hendriksen.

Although a heirarchical organization at three levels with spawning time as the segregating criterion at each, clearly is dependent on the integrity or constancy of the spawning time of the groups themselves, the precise

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[1] No specific mention is made of "genetic isolation" "gene pool" etc. but Gulf herring eventually spawn with the same segment of the population as their parents" makes this point (ibid., p. V).

mechanism for ensuring this is not absolutely clear. Indeed, they offer no specific explanation and maintain "Also, no one can say what controls the movement of schools so that they appear at roughly the same time each year. It is important simply to note that they do!" (Ware and Hendriksen 1978, p. 7).

Sindermann's (1979) analysis of the stock concept as it applies to herring of the Northwest Atlantic is thorough and well illustrates the nature of the problem. He deals first with definitions that have been derived in relation to the management of herring fisheries and makes the point that there is no need to be concerned whether or not genetic isolation occurs, indeed, if units of management can be realistically recognized. The ultimate utilitarian definition might then be "a practical management unit that allows fishing mortality to be allocated among discrete groups." The problem with this approach is that the issue of practicality cannot be decided except in relation to specific mandates of authority or jurisdiction. It cannot in practice apply to any unit that extends on both sides of any recognized boundary unless the question of allocation not of fishing mortality, but of catch, can be agreed upon by the authorities, or sectional interests concerned.

It is this fundamental point that led, for example, to such a violent reaction to the proposal that the Gulf of Maine-Georges Bank-Nova Scotia "stock" be assessed and managed as a unit. At the other extreme, the impracticality of agreement on the complex political situation in the eastern Atlantic has led to a management defintion that virtually ignores the biological nature of stocks. Sindemann recognizes that there is a biological basis for the stock concept and stresses the genetic criterion of lack of freedom of gene flow and that the individual stocks should be recognizable entities. He rightly emphasizes the segregated spawning unit as a reality that can be recognized, but adds that mixing outside the spawning period prevents identification. He makes the point that there could be no biological stock concept if an individual herring could spawn in more than one recognizable spawning unit during the course of its life history. If fact this may not be quite the point to make. One would group together all those spawning units within which this genetic mixing does occur, but identify larger groupings which do not gain or lose genes from any other analogous groups of spawning units. It is at least possible, for example, that within the general area of southwest Nova Scotia a group of such spawning sites may exist to include, as individual discrete units, Trinity Ledge, Lurcher Shoal, the Tuskets, off Seal Island and even the Scots Bay area within the Bay of Fundy.

Ridgeway (1975) uses a similar criterion as does Sindermann, but on a basis of there being a recognizable and distinct area for each of the "stock complexes" he recognizes. This does not allow for the phenomenon, which is well documented, of small spawning groups, thought to be genetically isolated, that exist within the area of such a stock complex, of which the Grand Manan stock is a good example. Nor of course does it recognize the situation found in the Gulf of St. Lawrence where spawning units, segregated seasonally, occupy much the same spawning locality at different times of the year. Ware and Herrikson (1978) indicate that paired fall and spring spawning localities can be found in all parts of the southern Gulf, except for the Magdalens which had spring spawners only. There is little evidence of spring spawning in the more southern part of the range of the herring of the Northwest Atlantic, the area of concern to Ridgeway, and all of the important stocks are autumn spawners - a point that itself deserves explanation.

If can also be said that there are very few examples in the northwest Atlantic of herring associated with specific spawning localities that differ so much in meristic (e.g. VS) and morphometric (e.g. size at age) characteristics from other herring even in the same area, that it is difficult to deny them full genetic isolation even at the specific level (see above).

It is perhaps not sufficiently appreciated, perhaps because of its obviousness, that to some herring biologists including me, the most convincing proof of "homing", with all that it implies is the very existence of recognizable spawning localities often very precisely delimited within much larger areas of topographical homeogeneity. The USSR data from their spawning bed grap surveys in the 1960's on Georges Bank was used as a basis for the planning of the PSCES submersible survey (Caddy and Iles 1973). All that was needed was for the research vessels to "home" in on the area. Mere inspection of Fig. 1 (taken from Pankratov and Sigajev 1973) shows a degree of structuring within the overall area that is difficult to associate with the random choice of any locality with the necessary substrate characteristics.

On the other hand, Ridgeway (1975), and many others, have found it difficult to accept that "open ocean areas" could be located by homing mechanisms. This may be an instance where the absence of a mechanism to account for a phenomenon should not be allowed to influence a decision as to whether the phenomenon exists or not, a kind of attitude that delayed the acceptance of Continental Drift for fifty years. It is significant is this connection that ornithologists that take up herring biology tend to be convinced quite quickly that herring "home" to their spawning grounds; the evidence is acceptable to them at its face value.

The real difficulty that prevents acceptance of homing, particularly for herring that can spawn at different times of year, is that it implies an innate sense both of locality and of time. That living things, and perhaps all living thing, have internal clocks and even calendars that can be referred to is a scientific concept that is only about 40-yr old. That it is a truism in the specific field of biochronometry does not mean that it has penetrated to any significant degree into ecological theory. It is a concept that is quite foreign in its fundamental nature to the so-called exact sciences; it represents "internal" factors that even in biological (evolutionary) theory tend to be looked upon as teleological or vitalistic in their implication. For example, at the recent Woods Hole meeting, when the question was raised it was referred to as "magic." What this really means is that there is no acceptable way that observable facts and data can be used to infer mechanisms of this kind. As discussed above, Ware and Henriksen do not consider it even as a remote possibility.

The conclusion by Sindermann that genetic intermixing is as valid a conclusion from the evidence (and this for specific "stocks" in the Northwest Atlantic) as is isolation is based on the lack of conclusive demonstration of genetic differences. In particular the relatively new methods; such as the electrophoretic analysis of protein for polymorphic variation as a direct measure of gene frequencies, have not had the expected discriminatory power in the one species, herring, that because of the multiplicity of spawning groups, on the face of it should show the clearest results. This fact should perhaps be considered as "neutral" evidence, but tends to be interpreted as negative evidence, because there is not theory to explain the lack of the expected (predicted) result.

In discussing the population genetics aspects of the stock question in herring, Sindermann (1979, p. 146) implies that the integration of the unit stock concept with population genetics dates from Møller (1971), but as shown above, the matter was raised, in a slightly different context, by Blaxter (1958) who himself reviewed briefly the history of the concept amongst herring biologists. Even so the appeal by Sindermann to a different set of biological criteria, rather than to those derived from or used in management aspects of the herring problem is well placed.

For it is my main contention not only that the study of the stock structure of herring is central to the herring management, but also that it deserves study quite independently from the management questions, i.e. that it should be treated as a problem in basic biology. To my mind the attempt to provide an overall explanation or definition of herring stock structure for management purposes, and usually by referenmce to a single sub-area of the whole geographic range of herring, has compromized the search for an understanding of the biological significance of the remarkable phenomenon it represents, and of the adaptions that are the essential elements of the mechanisms involved.

Before indicating the extent of the pehnomenon itself and outlining a personal interpretation of the biological framework within which it operates, it is appropriate that I make an ironic comment concerning Dr. A. G. Huntsman. He was a pioneer in marine ecology in North America and one of the first to point out that there was no science that was designed to explain why animals could be found in a particular place at a particular time. This, incidentally, is an accurate paraphrase of the herring stock structure problem. His vast experience as a naturalist impressed on him the facts of the issue (and not of course only in resepct to herring). However his general attitude as a scientist was "nineteenth-century deterministic," to the degree that he insisted that salmon moved up river and spawned rather than to spawn. Any suggestion of purpose, as a reflection of "internal" factors was unacceptable and the behaviour of animals must therefore be the result of the directing effect of an external environmental factor. This attitude reflects the basic neo-Darwinism dogma that the only internal factors in evolution are random (mutations) and that natural selection is imposed on these as an external, environmental, factor. I maintain that such an attitude, and the constraints it imposes on biological theory, precludes both explanation and understanding of such complex issues as the one on hand.

A Proposed Biological Framework for Herring Stock Structure

The Clupeiodae, the taxonomic group to which herring belongs is very largely marine with some anadromous and a few freshwater forms and is "primitive" in form in terms of the main trends in teleost evolution. Members of this group are also ancient types with a long evolutionary history, and both these characteristics can be associated with their fundamental biological rôle as exploiters of primary and secondary production.

They represent the earliest telost colonizers of the marine environment and a major pathway by which the small-particle-size production in the sea was transferred to higher trophic levels. They represent the original marine forage fish.

Within this group - which is world wide in distribution, Clupea harengus is restricted to the temperate regions of the North Atlantic basin. It is replaced to the north by capelin - (and by Clupea pallasi in some of northern areas) and by other Clupeids to the south. It is an interesting fact that the latitudinal range of herring on the two sides of the Atlantic are displaced relative to each other, the range of the Northwest herring being almost 10° south that of the northeast. On both sides, however, the most significant biological determinant to herring is that it is entirely a zooplankton feeder and that seasonal zooplankton production in its latitudinal range is typically restricted to a few months during the year. More accurately, food of the requisite particle size is reliably available for a relatively short time each year. The relationship between primary and secondary production (and their interaction) as a latitudinal phenomenon has been dealt with by Cushing (1959). To sum up the situation he described, zooplankton production is very substantial, but is more and more concentrated seasonally as latitude increases. An animal adapted to feed exclusively on zooplankton in temperate latitudes must be able to withstand starvation for most of the year.

To compound the problem, Atlantic herring produces very large quantities of gonad material - over 20% of the total weight - and unlike, for example, the semelparous salmon and capelin, which have extremely high mortalities at first spawning, is iteroparous.

The amount of gonad material produced each year is, relatively speaking, greater than that of most other teleosts so that total metabolic output must be considered relatively large, particularly as the migratory movements of herring in many instances are extensive and even spectacular.

The physiological adaptations that allow these apparent constraints to be overcome involve a high degree of control over seasonal metabolic functions. These, like all metabolic controls, are mediated by the hormonal system and for them to apply in this particular situation they act within quite rigid time constraints. It has been established for Atlantic herring that hormones are produced that control somatic growth, gonad maturation and ovulation, (Blaxter and Holliday 1963). It can be inferred that others exist which control fat metabolism, and migratory movements (Iles 1974).

For example the role of fat assimilation and storage in herring is not only important in determining its dietetic value but conceal to its adaptation as a zooplankton feeder in temperate waters. Enough fat has to be stored and conserved during the brief feeding season to sustain energy requirements for the remainder of the year.

The way in which these different aspects of seasonal physiology interact in the case of southern North Sea herring has been suggested by Iles (1964, 1965, 1974) and two points can be made. Firstly: the necessary control over and the allocation of food resources implies that hormonal direction of physiological activity is governed by an internal timing mechanism that is independent of the major environmental parameters involved in food production. Secondly: differences between "stocks" that spawn at characteristic but different times of year can be explained by differences in the seasonal timing of the various hormonal elements involved in the "seasonality" of Atlantic herring. In terms of adaptational strategy, the solution of the temperate-zooplankton problem on the part of an ancestral herring, spawning at one time of year, created the evolutionary opportunity to spawn at other times of year. The problem in adaptation was "over-solved" and created new opportunities that have been taken advantage of in the evolution of different spawning groups.

For it is a unique feature of Atlantic herring, that, over its range, there is not a single day of the year during which spawning is not occurring somewhere (see for example the ICES Herring Atlas, produced by W. C. Hodgson). This versatility goes far beyond that shown in the "vernal" and "hiemal" races of anadromous fish (Berg 1959) and adds another dimension to that of geographic separation, the single dimension that characterizes the stock structure of many other temperate marine species.

This general hypothesis satisfies two kinds of observations that have already been commented on: that herring in the same locality at the same time segregated by "responding" differently to the same environmental stimulus (Blaxter 1958 makes this specific point) and that the timing of spawning (and of other behavioural traits) in recognizable groups is more constant, year to year, than is the environment, the basic point made by Ware and Henrikson, 1978.

If both of these characteristics can be accepted as representing the effect of "internal," that is, "built in" or "genetic" factors then the central problem of herring stock structure is solved and the available facts that are now the subject of argument can instead be analyzed in a consistent way to provide a solid basis for application to specific management questions.

However the very richness and variety of the stock mosaic that some see as demonstrating the discreteness of stocks, others see as a continuity that cannot be explained on a discrete basis.

The expected resolution of the problem by electrophoretic analysis of protein polymorphism (Sindermann 1979; Odense, Leung and Amand 1973; Ridgeway 1971) would have been the more convincing by its direct link with individual genes and the gene pools which could then be reconstructed. Perhaps it will require a direct demonstration of a characteristic hormonal organization as the expression of a single gene pool to give an answer that can be the basis of a reasonable consensus. Whether this is so or not, I do not see any real hope for the solution of this particular question by methodologies imported from mathematics, statistics or computer science i.e. simulation, multivariate analysis or modelling.

Indeed it has been one purpose of this review of concepts of stock structure to show that there is less certainty now as to the basis for recognizing, identifying and classifying stocks than there was earlier in this century, and as reviewed by Blaxter in 1958.

The question to be answered is whether this uncertainty is such as to preclude the possibility of consensus in any complex management situation. I believe this is so.

To indicate the complexity of the biological situation, I have prepared a list of "stocks" that have been referred to by name in a single sub-area of the northwest Atlantic. This is given in Table 1. This table lists references to groups of herring that might correspond to individual biological entities. As indicated in the "status" column there is a great deal of room for confusion amongst these groups that awaits resolution.

Abundance - the Unexplained Population Characteristic

Besides ecological efficiency, the focus of Slobodkin's thesis, he listed as extensive variables stability, flexibility, total number of organisms including absolute abundance and total area occupied.

The central question that faces the Larval Herring Task Force is to explain the variability of the abundance of individual stocks or of groups of stocks. Slobodkin maintains that the process of adaptation, mediated through natural selection, cannot generate a trend towards any specific, fixed, maximized or optimized absolute population size. How then can we explain its variation? The analogy he uses to illustrate his case is immediately recognizable to fishery biologists. A global quota for a fish stock can be fixed by an external agency such as, for example, NAFO, but it is not enforceable unless it is translated into local, intensive variables, e.g. individual catches at individual locations. In addition, and as an essential requirement, a communication system must be available to integrate the information from the individual boats and, at the proper time, pass instructions back to the individuals to elicit the required response. There can be no such external agency admissible to science (if we exclude the GOD factor) and, thus, no direct relationship between a biological characteristic and absolute abundance. If we accept the Slobodkin-type argument, then we have to explain both the existence of a characteristic mean abundance and account for its variance. One way of transforming the question of stock and recruitment is to ask how an individual herring "perceives" that it is a member of a small or, conversely, a large population, and how distinction can be made between a natural change in total population abundance and one mediated by fishing pressure. At the primary and obvious level of argument, one cannot characterize an apparent change in physiological state as a direct adaptation to a change in abundance. If, indeed, the response is a compensatory one (such as density-dependent growth-linked, for example, to increased specific fecundity), then it must be explained indirectly.

In fact, a comparison of the biological characteristics of different herring stocks confirms that there is no consistent correlations between any biological parameters and absolute population size. The absolute size of individual stocks can be shown to vary over about five orders of magnitude. Maximum levels of catch over reasonably representative periods are an acceptable criterion. The range is from about 10^6 m. tons for the Atlanto-Scandian stock to 2×10^5 for the Georges Bank stock to 1×10^5 for the Nova Scotia stock to 2×10^4 for the Magdalen Island stock to 5×10^3 for the Grand Manan stock to 5×10^2 for the Blackwater Estuary stock.

No biological stock parameter or groups of parameters is correlated with this basic population parameter. The parameters that can be eliminated include growth rate, absolute (individual) size, fecundity, spawning time, latitudinal range, etc. Indeed, and as an example, while the trophic level of a zooplankton feeder offers the opportunity for large population size that, as a whole, herring is noted for, this is not associated with a particularly high level of egg production. Compared to Gadoids, Pleuronectides and, as a significant example Mola mola, the sunfish, herring egg production, in numbers, is relatively low.

In fact, in the last decade or so, there have been developments which offer a reasonable hope of explaining both absolute abundance and its variation. These were initiated by Graham's work in the Penobscot estuary which demonstrated that the integrity of specific areas of distribution of the larval stage was maintained, by an interaction between larval behaviour and hydrographic factors. This was extended by Iles (1970) to include the concept of transport and retention of larvae in the much more open Bay of Fundy area, as the larval territory of the Nova Scotia stock. Later, the suggestion was made that stock abundance was determined at the larval post-larval stage, which is now orthodox, and by the size of area "available" to it. In addition, the localization of spawning sites within a retention area would be determined by the probability that hatched larvae from that locality would be retained (Iles, 1975). Obviously, the food production of the area (and per unit area) would be the other major factor involved. The idea of retention had, by then, been applied also to the Georges Bank area (see Sindermann, 1979), so that a reasonably comprehensive explanation might be forthcoming that would have a significant effect in reducing conceptual complexity.

However, the details of the behavioural mechanisms shown by the larvae are still to be defined, described and demonstrated; the implications are of internal factors with a built-in timing ability that, as indicated above, are not generally recognized as available as basic assumptions for ecological theories. Moreover, the interaction with hydrographic factors is then, by its very nature, not passive. Passive direction and larval drift are not capable of explaining the observed phenomena; the relationship between biology and hydrography cannot be defined by the concepts derived from either discipline in isolation.

And, even if such an explanation of abundance is possible, its development will depend, to a large degree, on the solution of the "stock" question itself. The analysis of adaptive mechanisms must deal with the basic adaptational unit, the genetically isolated stock.

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Table 1. Herring stocks of the western Atlantic.

Present Stock	Spawning site (major)	Spawning site (minor)	Spawning time	Substrate	Depth (m)	Temp. (°C)	Meristics	Stock size	Status[a]	Movements (adult)	Movements (juvenile)	References[b]
Georges Bank	Northern Georges, Nantucket Shoals	S.E. Georges, E. of Great South Channel	mid-Sept.-Nov.	Gravel, pebbles, broken shells, few plants	40-50	5-12	low pectoral fin ray count; low VS high keel		S	South to Long Is. Chesapeake Bay in winter	Some believe Bay of Fundy; some believe W. Maine	1,3,6,11,13 14,39,40,43, 57,61,64,66, 75,76,78,79
Gulf of Maine	Jeffreys Ledge, Stellwagen Bank	Cape Eliz., Isle of Shoals, Penobscot Bay, Cape Ann	Sept.-Oct.	Clay, sand, rock, gravel, boulder	49-59	7-9.6			S	South and to mid-Atl. Bight in W.	North to Bay of Fundy? Juvenile diff. N & S	1,2,6,10,14 57,61,63,64 65,75,78.
Grand Manan	SW Grand Manan, G.M. Banks	Maine shore?	Fall-Aug.-Oct.			8-9			S	?	?	6,21,24,27, 28,53.
Bay of Fundy Spring	Head of Bay of Fundy, Minas Channel?		Spring	Mud, sand	Shallow	?		Small	?	?	?	24,27,46,47,
Scots Bay	Scots Bay		Summer-July	Mud, sand	Shallow	?		Small	?	?	?	47.
S.W. Nova Scotia	Trinity-Lurcher	Brier Is., Seal Is., N. of Digby, S.W. of Yarmoutn	July→ October	Sand-gravel	11-13	?		Large 330,000?	S	Winter S. to Cape Cod or to Canso	?	6,21,24,27, 35,36,40,45, 47,61,62,70, 75.
Atlantic Coast of N.S.	Along coast, Canso → Cape Sable	Small bays etc. on coast	Aug.→ Sept.	Clay-gravel		?	Low VS	65,300?	S	?	?	6,16,44,58, 59,72,73,74 75.
Chedabucto Spring Spawners	S. side of Chedabucto Bay, up Guysborough R	Coddles Hbr. Dover, Whitehead	April-June	Clay	Shallow	?		?	S	?	?	32,40,44,58
Bras d'Or Lake-St. Ann's Bay	Bras d'Or Lake-St. Ann's Bay		Spring	?	?	?	VS similar to Atl. coast of N.S.	?	?	May be Gulf of St. Lawrence spring herring	?	74.
Banquereau	Near shore of N.S. (Chedabucto Bay?)	Shallow areas of Scotian Shelf	Fall				High number of keeled scales; high *Anisakis* infestation	?	?	Migrate to Banquereau in winter from where? Spawn on N.S. coast?	No juveniles on Banquereau ?	17,18,20,23 32,40,53,71
Sable Island	Same as Banquereau?		Fall	?	?	?	Different VS count but same *Anisakis* infestation as Banquereau		?			18,20,53.
Sable Island	?	?	Spring	?	?	?			?			18,20.
Grey Sole & Artimon	Cape Breton shore?		Fall	?	?	?		?	?	Same stock as Banquereau	Move to Gabarus & Sydney Bay	17.

a) S indicates reasonable evidence for an individual "stock". ? indicates lack of such evidence.

b) The numbers in the last column refer to the numbers in the bibliography.

Table 2. Provisional listing of "identifiable" herring stocks from historical sources.

Historical Stock	Spawning site (major)	Spawning site (minor)	Spawning time	Substrate	Depth (m)	Temp. (°C)	Stock size	Status[a]	Comments	Ref.[b]
Gulf of Maine	Cape Elizabeth, Cape Ann	Areas south to Block Island	Sept.→Nov.	?	?	?	?	Not sure if 1 stock Cape Eliz. may be stock	Sp. was reported to be continuous from G.M. to Cape Elizabeth and sparse south of this. Little known of offshore. Georges was thought not important.	6,49.
Grand Manan	30 mi^2 SE of Grand Manan		June→late fall July→Sept. peak		Shallow to deep	8-9	Large	S	Grand Manan was once thought to be the chief spawning grounds of the Bay of Fundy.	25,26,27,28,29,49,55.
Oak Bay	Oak Bay		Spring	Gravel-mud	?	?	Small	S	Large fish overwintered from Quoddy Head → Lepreau and spawned in Oak Bay in spring; last seen ~1900.	28,49,55.
Quoddy River herring	?	?	?	?	?	?	?	?	These large, fat fish moved into area to feed in summer. Didn't know where they came from. They didn't contain spawn.	49,55.
Ten Mile Creek→ Rogers Head	Ten Mile Creek→ Rogers Hd.	-	Summer	?	?	?	Small	?	Came suddenly for a few years, then disappeared in 1884. Huntsman (1953) believed they were part of the Grand Manan stock migrating through the Bay of Fundy.	28,49,54,67.
Minas Channel Spring spawners	Minas Channel (south side)	-	Spring	Mud-sand	Shallow	?	Small	S	Common until the 1930's. It is not clear if they still exist today.	27,46.
Annapolis, Kings Co., N.S.	Annapolis Basin, Kings Co. shore	-	Summer ?	?	?	?	Large	S	May be part of today's southwest Nova Scotia stock or Scots Bay stock.	28,49,55.
Head of St. Mary's Bay	Head of St. Mary's Bay		Spring	Mud	Shallow	?	Small	?	Last reported in the 1930's; doesn't appear to exist today. May be part of Brier Is.-Digby historical spring spawners.	27,46.
Brier Is.→Digby Gut	Brier Is.→ Digby Gut		Spring - April-May	?	?	?	?	S	Reported in 1800's; moved to Grand Manan to feed after spawning. Not reported in 1900's except perhaps St. Mary's Bay spring spawners.	49,55.
Halifax spring spawners	St. Margaret's Bay eastward	Small bays, coves, river mouths	May	Soft bottom	Shallow	?	?	S	May be the stock that spawns in Chedabucto in spring today.	44.
Halifax fall spawners	All along coast east and west of Halifax		July-Sept. (earlier in west)	?	?	?	?	S	Probably is the fall stock seen in this area today.	42,44.

a) S indicates reasonable evidence for an individual "stock". ? indicates lack of such evidence.

b) The numbers in the last column refer to the numbers in the bibliography.

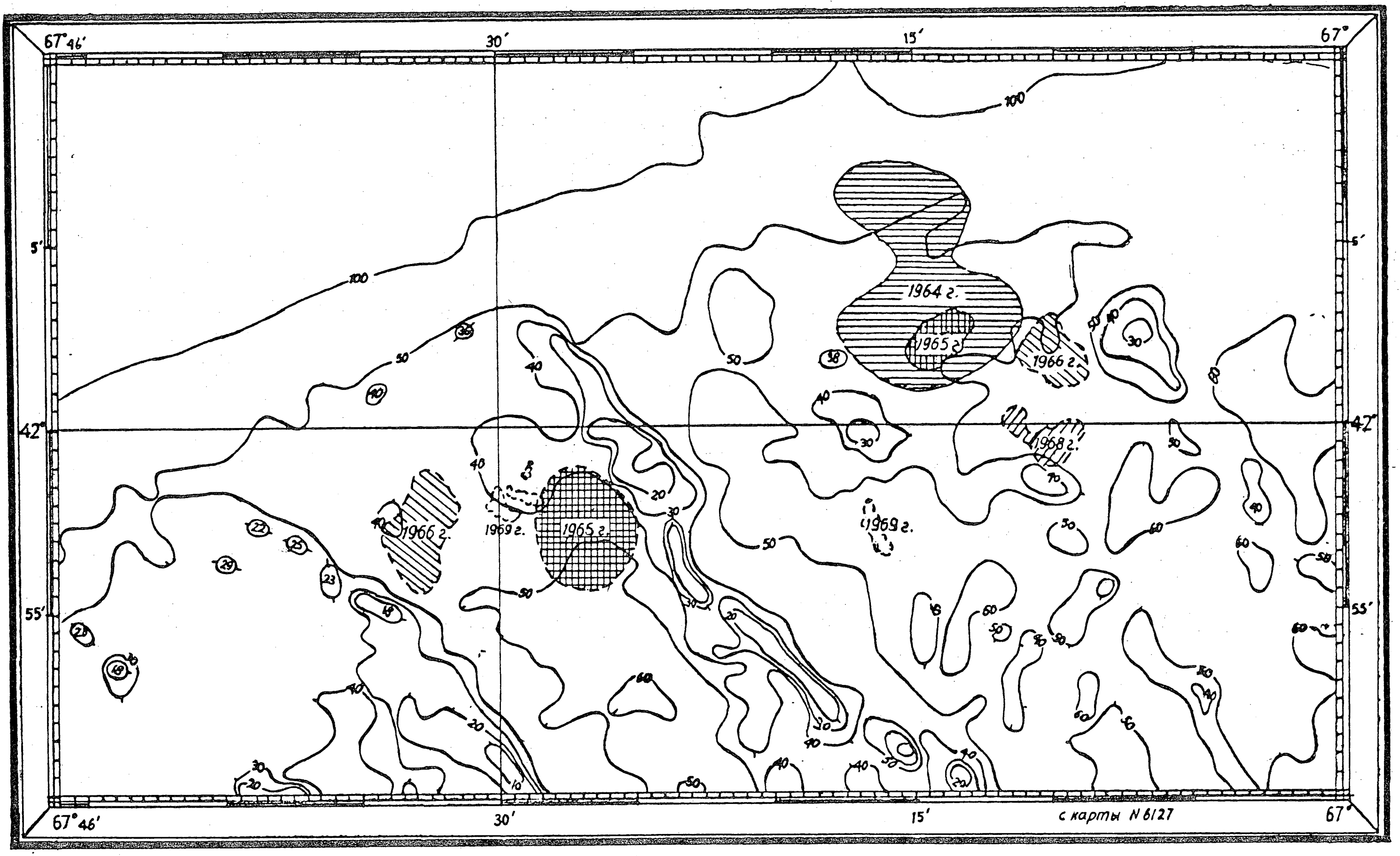

Fig. 1. Distribution of herring eggs on Georges Bank, 1964-1966 and 1968. (Zinkevich,1970)