Atlantic Herring: Stock Discreteness and Abundance

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Summary. The number of genetically distinct herring stocks is determined by the number of distinct, geographically stable larval retention areas. Spawning sites in these areas may be highly localized or dispersed. Absolute population size mostly depends on the retention area available to the density-dependent larval-postlarval stage. Although the extreme seasonal range of spawning time shown by Atlantic herring is not fully accounted for by a new hypothesis, current theory is not supported by the hypothesis or by empirical data. The management implications are discussed.

A single species of marine fish can occur over a wide area within which its distribution is essentially discontinuous. Subareas can be recognized that have a characteristic population or set of subpopulations, either of which may be recognized as stocks in both the biological sense and as the preferred units of management (*1*). The biological importance of the stock concept as the management unit centers on the question of whether there is restriction of gene flow to a degree that effectively isolates the population units. This determines whether reproductive resistance to exploitation is a common property of the populations as a whole or of individual subpopulations. Although stocks are recognized and labeled for the most important commercial species of fish, there is no generally accepted, formal ecological theory that accounts for their distribution, range of population size, and other life-history parameters such as growth rates, age, and size at maturity. In fact, the taxonomic status and interrelationships of these units at the infraspecific level is in doubt, both for individual species and in general terms (*2–4*).

The Complexity of Herring Stocks

Atlantic herring may have the richest stock structure of all marine fish species (*3–6*). Several dozen stocks have been described or are recognized from the northwest Atlantic, and there may be even more in the east. The latitudinal range of herring distribution alone cannot explain this richness; for example, the range of mackerel is as great as that of herring, but far fewer stocks of mackerel are recognized (*7*). In addition to their multiplicity, Atlantic herring stocks collectively combine other unusual characteristics. Each stock has its own, seasonally fixed spawning period (*8*) of a relatively few weeks' duration, but the mean spawning times of different stocks differ substantially. In the eastern Atlantic, for example, spawning of one stock or another has been recorded throughout the year (*9, 10*). This is the more remarkable because Atlantic herring feed predominantly on zooplankton, and in the temperate latitudes, to which herring is restricted, zooplankton production is markedly seasonal (*11, 12*). All Atlantic herring lay demersal eggs, but stocks vary greatly in the depth of the spawning area and substrate preference (*13*). In many well-documented instances, the spawning area of a particular stock is so precisely and persistently located as to strongly imply homing by the spawning population (*14*).

The seasonally predictable behavior of the herring stock is matched by the seasonal behavior of fishing fleets (*15*), and this predictability may account, to a significant degree, for the vulnerability of herring stocks to overexploitation (*16*). Finally, the range of population size for known and recognizably discrete stocks covers several orders of magnitude from perhaps hundreds or a few thousand metric tons to several million (Table 1). A comprehensive stock theory for herring should take into account all of these characteristics, as well as the fact that mixing among individuals known to have spawned at different places or times, or both, occurs in nursery areas, summer feeding areas, and overwintering areas (*5, 17*).

Life History Patterns and Isolating Mechanisms

The genetic isolation of population units of herring (or those of any animal) must involve the spawning stage and may also involve the prespawning aggregatory stage. What has become more and more obvious from work in the northwest Atlantic is that there is a low degree of stock mixing of herring at the larval stage. Representative larval distributions in October (Fig. 1A) of autumn-spawning stocks in the northwest Atlantic show well-segregated and identifiable spawning areas. These groups do not metamorphose before the winter, and they overwinter as larvae, as do their east Atlantic counterparts (*11, 18–20*). Their distribution in the spring, some 6 months later, is similar to that observed shortly after spawning (*20*). The environment is, tidally, very energetic but, despite the small size of herring larvae and their consequent relative lack of motility, the location and distributions of individual larval populations are maintained by a process of larval retention (*19, 21, 22*) so that their integrity is not compromised.

In the instances shown in Fig. 1B, there are physical features that are well predicted by the Simpson and Hunter stratification parameter (*23*) and that correspond closely to the larval distributions. Changes in the value of this parameter indicate the transition between vertically well mixed and stratified regions in tidally energetic seas during the seasons of surface heating (*23–25*). The resultant temperature "fronts," defined by critical values of the parameter, are observed from the spring to autumn months. Larval distributions in the area that includes Georges Bank, the Gulf of Maine, and the Bay of Fundy (Fig. 1B) of four recognizable spawning areas (southwest Nova Scotia, Grand Manan, Georges Bank, and Nantucket Shoals) lie to a large degree within vertically well-mixed areas bounded by transition zones where the stratification parameter changes rapidly in the horizontal dimension.

Similarly in the western North Sea (Fig. 2), there is a good correspondence

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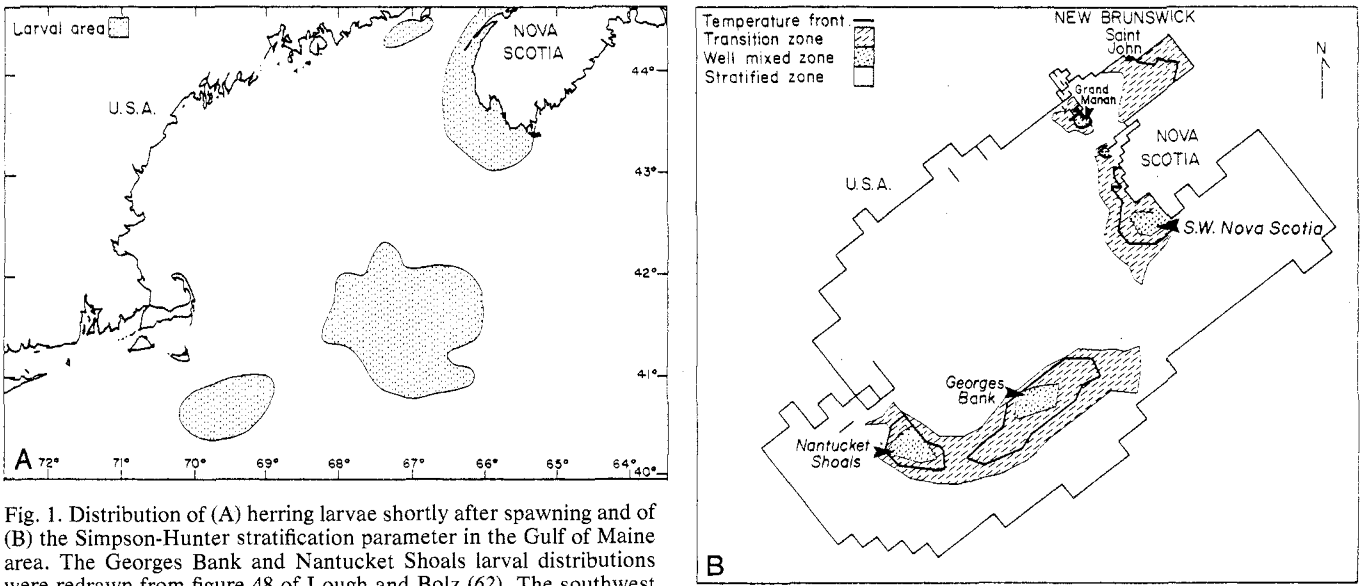


Fig. 1. Distribution of (A) herring larvae shortly after spawning and of (B) the Simpson-Hunter stratification parameter in the Gulf of Maine area. The Georges Bank and Nantucket Shoals larval distributions were redrawn from figure 48 of Lough and Bolz (*62*). The southwest Nova Scotian and Grand Manan larval distributions are from our data (*63*). The stratification parameter distributions were redrawn from Garrett *et al.* (*24*).

between the boundary conditions depicted by the stratification parameter and the limits of larval distributions soon after spawning among North Sea spawning groups. Major stocks are well identified, but so also are minor stocks such as those spawning off Berwick and historically in the Blackwater Estuary. There are discrepancies between the size of the physical features and the larval distributions, and these may indicate the effect to which fishing activity has reduced the capacity of the stocks to colonize the available larval area. The degree to which larval distributions are maintained over winter is not known.

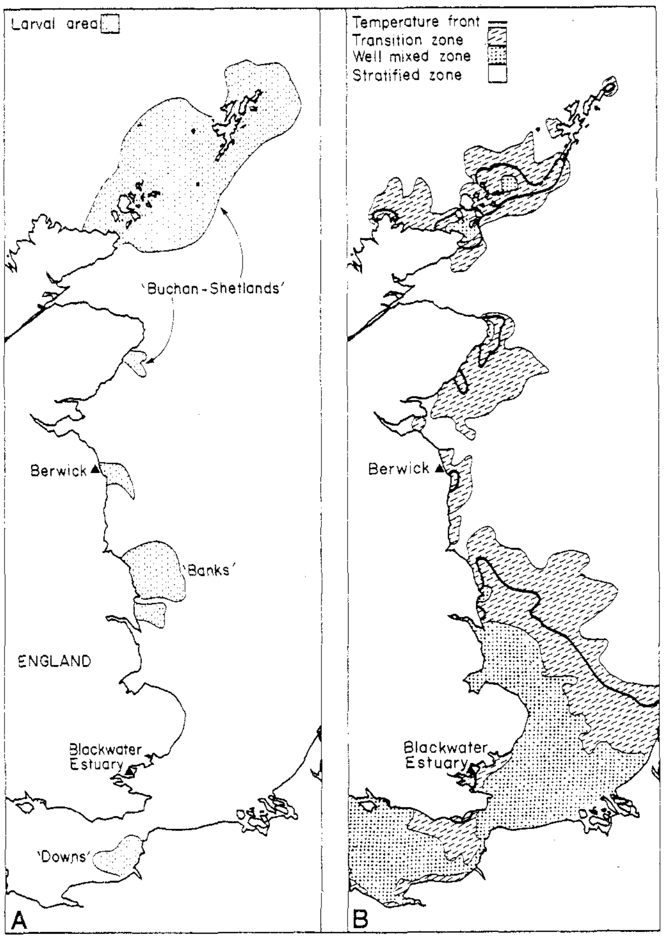


Fig. 2. Distribution of (A) herring larvae shortly after spawning and of (B) the Simpson-Hunter stratification parameter in the western North Sea. Note the correspondence of the larval distributions and fronts for the Banks area. The Downs larval distribution was redrawn from figure 49 of Hempel and Schnack (*64*). The other larval distributions were redrawn from figure 4 of Burd (*65*). The stratification parameter distributions were redrawn from Pingree and Griffiths (*25*).

Detailed information on herring larval distributions at the appropriate spatial scale is not available for the Gulf of St. Lawrence. There is, however, a close association between known spawning locations and areas of more pronounced tidal mixing (Fig. 3), as indicated by the values of the stratification parameter (*26*). Again the detail to which this correspondence applies is convincing; for example, the small spawning population north of Anticosti Island was known to us only by fishermen's reports and has not yet been studied (*3*). Certain Gulf of St. Lawrence spring-spawning populations such as the Escuminac stock (Fig. 3) are not identified with transition values for the parameter. The significance of this is discussed later and leads to a generalization of our hypothesis.

In the Irish Sea (Fig. 4), larval distributions are again not well known. The association to be noted is that of transitional or boundary conditions and spawning localities of individual herring stocks. These are located at inshore ends of the transition zones, except for the spawning area of the Mourne stock, which lies between the ends of two closely spaced zones.

In the Gulf of Maine–Georges Bank–Bay of Fundy area, evidence indicates that tidal residual circulations are associated with the areas of more complete vertical mixing and that these areas are defined and delimited by the zones of transition. The tidal circulations may provide a physical mechanism contributing to larval retention for individual stocks. At Georges Bank and Grand Manan, the circulations take the form of tidally induced anticyclonic gyres (*27*). Off the southwest coast of Nova Scotia the circulation pattern is more complex but equally convincing in its implications; a bottom inshore current has been described that is consistent with the hypothetically predicted, tidally driven centrifugal upwelling (*28, 29*).

Table 1. Range in absolute of size of herring stocks.

Stock name	Spawning stock size (metric tons)*	Reference
Blackwater Estuary	1 to 5 × 10^2	(*59*)
St. Lawrence Estuary	5 to 10 × 10^3	(*60*)
Iceland (summer spawners)	1 × 10^5	(*61*)
Iceland (autumn spawners)	2 × 10^5	(*61*)
Southwest Nova Scotia	4 × 10^5	(*33*)
Georges Bank	1 × 10^6	(*55*)
Norwegian	1 × 10^7	(*58*)

*Approximate stock size during periods of moderate fishing.

In the North Sea area, tidally induced anticyclonic gyres that are not dependent on wind direction are predicted around the Orkneys and Shetlands by a simulation model (*30*). The predicted gyres may represent the residual circulation in the area of the larval distribution of the so-called Shetland component of the Buchan stock (*17*). No retention mechanism has been associated for certain with the "Banks" and "Downs" stocks in the central and southern North Sea, but relatively small-scale cyclonic gyres may be a characteristic feature of tidally induced temperature fronts (*31*). Even without a known, residual current system as an indicator of boundary conditions, temperature gradients across the transition zones could signal a behavioral reaction by larvae to maintain position. During the winter, when the temperature gradients disappear, turbulence and turbidity gradients would still persist.

The common features of the examples given so far are the discreteness of distribution during the early life-history stages of the progeny of individual spawning populations and, in most cases, retention mechanisms with an identifiable physical basis to maintain the discreteness. A key point is that the hydrographic features involved would, by their very nature, tend to be associated with the same geographic locations from year to year. This constancy of tidally induced features parallels the preciseness of location of spawning grounds that characterizes herring (*32*).

The Herring Stock Hypothesis

The hypothesis that emerges is that the number of herring stocks and the geographic location of their respective spawning sites are determined by the number, location, and extent of geographically stable larval retention areas. This hypothesis has consequences that relate to the wide range of mean stock size among herring stocks, the year-to-year variability of recruitment within individual stocks, and the biological basis of fisheries management systems.

The associated biological concept is that the (distinct) gene pool is made up of all those spawning groups whose larval-postlarval stages come to share the same area of distribution. This concept recognizes the possibility, realized in fact, that more than one spawning location can exist in the same retention area and contribute progeny to the same larval population (*21, 33*). The same concept has also been expressed in the suggestion that the hydrographic features of an area that result in retention act as a focusing device for the homing instinct of herring (*29*).

It follows that it is the physical limits, specifically of the larval and postlarval distributions, that define the biological limits of the stock and of the isolated genetic unit that can be identified with this new stock concept. This hypothesis avoids the difficulties associated with the definition of different stock components in areas where physical mixing occurs at many of the later life-history stages. The aggregated spawning group or groups represent the basis for the individual gene pool, which is coextensive with the segregated part of the life history. The ecological discreteness and discontinuity of the larval-postlarval stages correspond to and reinforce the discreteness and discontinuity of gene pools, which

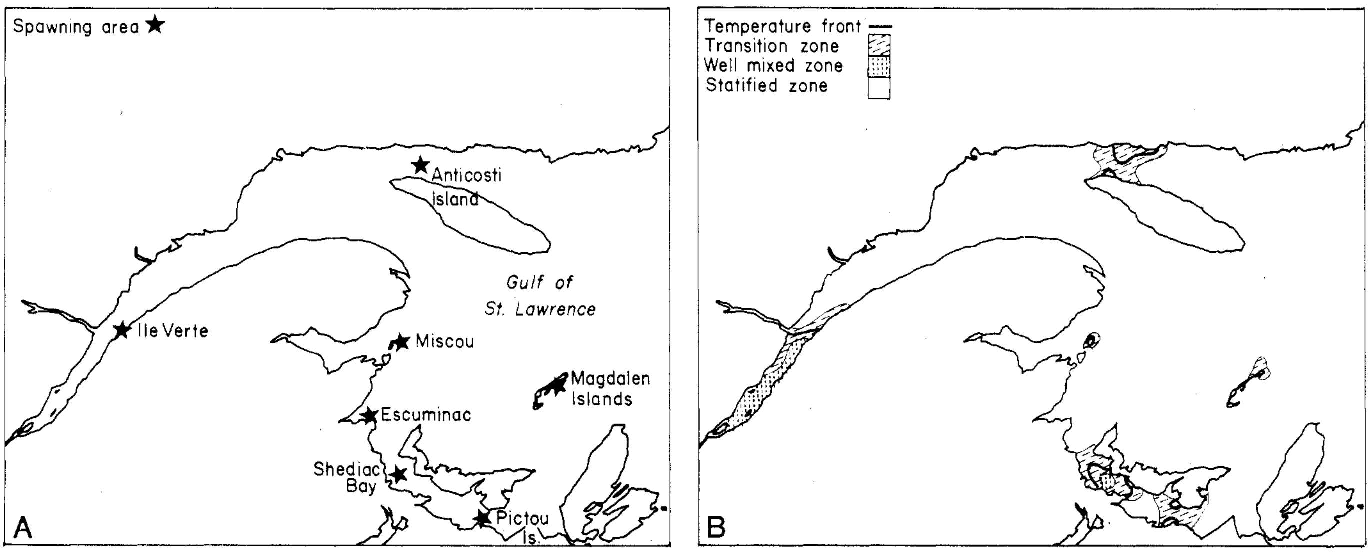


Fig. 3. Distribution of (A) major herring spawning areas and of (B) the Simpson-Hunter stratification parameter in the western Gulf of St. Lawrence. The spawning areas were taken from (*66*). The stratification parameter distributions were redrawn from Pingree and Griffiths (*67*).

are the essence of biological identity and of the structuring of, in this instance, infraspecific units.

The evidence so far presented deals mainly with stocks that inhabit tidally energetic open seas. The early life history of the Norwegian spring-spawning group (Atlanto-Scandian) is spent in the fjords and contiguous waters and may be linked with the two-layer estuarine circulation (*34*). A similar situation has been found for the Gulf of Maine nearshore spawners, for which retention (in estuaries) was described for the first time and a behavioral mechanism was demonstrated to explain it (*21*). The major Gulf of St. Lawrence stock that spawns near Escuminac (Fig. 3) is not associated with a predicted, tidally induced feature, but it does spawn next to a geographically fixed gyre (*35*). The larval populations from the stock spawning in the Bras d'Or Lake on Cape Breton Island, Nova Scotia (*36*), and in the Gulf of Riga in the Baltic Sea (*37*) are retained within enclosed seas; and a similar situation has been described in detail for a stock spawning in a small, long and narrow arm of the sea that is essentially isolated (*38*). The common feature of these examples is, again, a geographically stable retention mechanism associated with each of the stock's spawning areas (*39*).

Spawning Stock Size and Its Variance

Mention has been made of the large range in population size of individual stocks—greater than four or five orders of magnitude. It is a remarkable feature of modern, quantitative ecological theory that there is no satisfactory explanation of the specificity of absolute population size. For example, it has been suggested that population size, or abundance, is a "global, extensive variable" that cannot therefore be subject to coercive factors of natural selection to result in its own maximization or optimization (*40*). This suggestion is strengthened by comparing population characteristics commonly associated with population size (that is, absolute numbers of individuals). Maximum body size, life-span, age at maturity, absolute and relative fecundity, and gonad size, among other characteristics, vary among herring stocks, but population size does not correlate with these characteristics or with any combination of them. It is not possible to account for the range of population sizes (Table 1) in terms of life-history parameters and strategies that are inferred from them. A simple extension of our hypothesis, however, does offer a reasonable and quantitatively demonstrable explanation.

Small stocks are associated with small hydrographic features [for example, the Ile Verte area of the Gulf of St. Lawrence (Fig. 3)], and large ones with large features [for example, the Georges Bank well mixed zone (Fig. 1)]. The relation between the size of hydrographic features, specifically retention areas, and the size of the stocks occupying the retention areas can be quantified approximately (Fig. 5).

The relation between stock size and retention areas (Fig. 5) is quantitatively convincing over virtually the entire known range of stock size of Atlantic herring as a whole. Our hypothesis therefore implies that absolute stock abundance is largely independent of reproduction, growth, or other biological parameters with which it is usually associated (*41*) and is determined by the interaction of behavioral characteristics and the physical structure of the environment. We suggest that behavioral factors involve selection of site by the spawning group and differential vertical movement by the larvae to effect retention (*19*). It is not likely that the productivity of retention areas can, alone, account for the range of stock size. Primary productivity (per unit area) of the ocean as a whole does not vary by more than a factor of about 5 (*42*). The variability of productivity of retention areas in the temperate latitudes, within which herring are restricted, would be expected to be less than that of the entire ocean.

The hypothesis maintains that, since the size of the retention area largely determines year-class size (and thus, by accumulation of year classes, total stock size), there is a limit to the carrying capacity of the environment imposed at the early life-history stages. The obvious question is how this limit is related to the carrying capacity or its ecological equivalent at the late juvenile and adult stages. It is conceivable, for instance, that the net productive capacity of the retention area is low enough at the early life-history stages to preclude subsequent saturation of the adult environment. This concept has been termed the "recruitment gate" (*43*). If it is accurate, then the inability to detect density-dependent growth effects when adjacent year classes differing in size by a factor of 30 are compared for the Norwegian herring

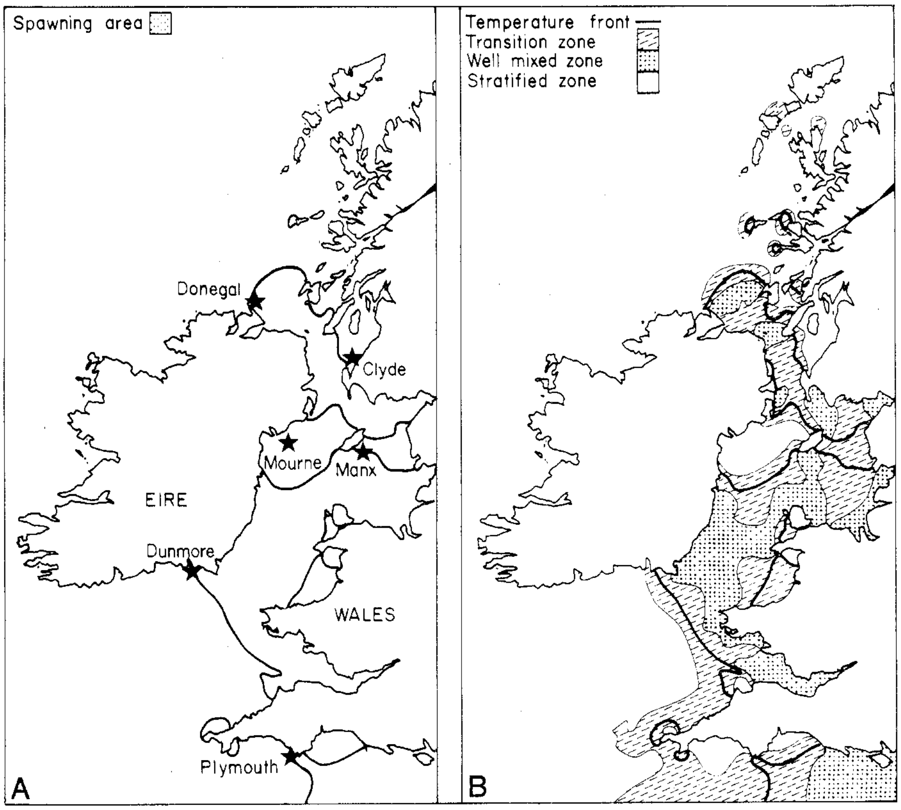


Fig. 4. Distribution of (A) herring spawning areas and of (B) the Simpson-Hunter stratification parameter in the Irish Sea. The spawning areas for the various spawning groups were taken from Cushing (*68*) (Plymouth), Malloy (*69*) (Dunmore), Bowers (*70*) (Mourne and Manx), Parrish *et al.* (*71*) (Clyde), and Hempel and Blaxter (*9*) (Donegal). The spring spawning locations along the west coast of Ireland and autumn spawning locations along the west coast of Scotland are not indicated. The stratification parameter distributions were redrawn from Pingree and Griffiths (*25*).

stock and under lightly fished conditions (*44*) is understandable. That recruitment from the young stages may not overextend the food resources for adults is shown by evidence from the southwest Nova Scotia stock (*45*). Further evidence is provided by the relatively low variation of fecundity to adult weight reported for herring (*46*). Year-class abundance variability apparently does not have a large effect on the gonad-somatic balance. That this has implications as to the competitive status within and between stocks at the adult stage is recognized.

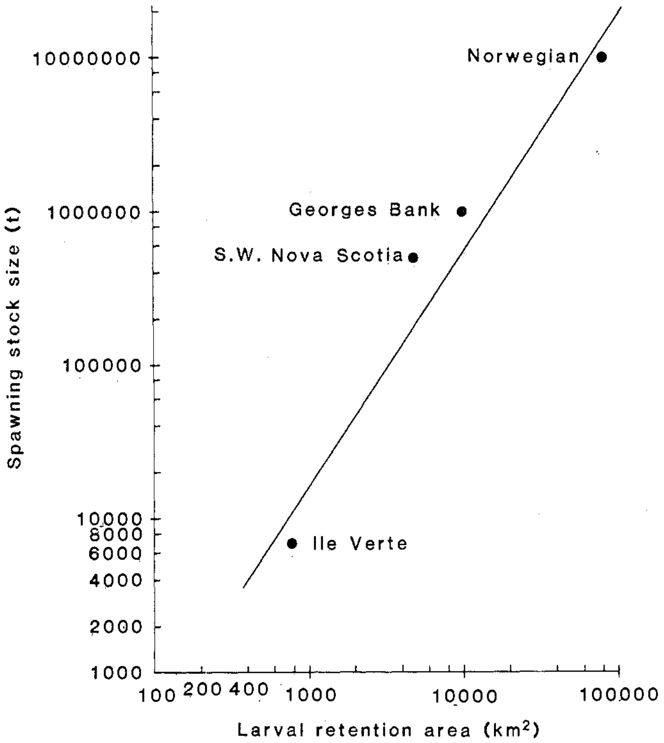
It follows that stock-recruitment mechanisms that include adult stock-dependent feedback (*47*) are generally inappropriate for herring (*48*).

The extension of our hypothesis—that mean year-class size is a function of the size of the larval retention area—is consistent with, and indeed equivalent to, the view that year-class size is determined relatively early in the life history (*49*). The important factors determining year-class size would be operative in the early stages and would generate high (and differential) mortality (*48*). The variability in year-class size, a feature of all fish stocks to some degree, even under low exploitation regimes, need not be associated entirely, or even mainly, with variability in production processes. Indeed, observations on the Nova Scotia stock indicate that year-class size is not correlated with production-linked parameters such as autumn copepod abundance or summer phytoplankton greenness (*50*). On the other hand, it would be expected that the integrity of the retention area, the extent to which the boundary conditions are reliably repeated from year to year, might vary considerably. There is evidence from the Bay of Fundy area that patterns of drift-bottle recovery in individual years vary markedly, which suggests that environmental variability of this kind could be significant (*51*).

Variability in Spawning Times in Herring Stocks

Atlantic herring has a wide and indeed seasonally complete range of stock-specific spawning times (*3, 9, 10*); the range for the species as a whole matches that of any tropical species or complex of species (*52*). Analysis of some common features of the hypothesized retention areas may contribute to an understanding of this variability in spawning time. In the east Atlantic a broad correspondence between the timing of seasonal plankton blooms in different types of production areas and the time of spawning of major herring stocks that inhabit the areas has been shown (*53*), and this correspondence led to a hypothesis concerning the time of spawning (*49*). The time of spawning and larval emergence of individual stocks was considered to be relatively constant so that year-to-year variability in the timing of plankton blooms then resulted in "match or mismatch" and led to varying mortality rates. This match or mismatch was held largely responsible for the degree of year-class variability (*49*). Consideration of the temporal production characteristics of areas near herring spawning grounds does not support the match-mismatch hypothesis.

There does seem to be an association between stocks spawning in the summer to autumn period and tidally energetic areas. However, the production regimes in the vicinity of the spawning areas of these stocks are characterized by high and relatively uniform abundances of primary production over the entire non-light-limited period of approximately March to October. This is shown by a comparison of primary production and



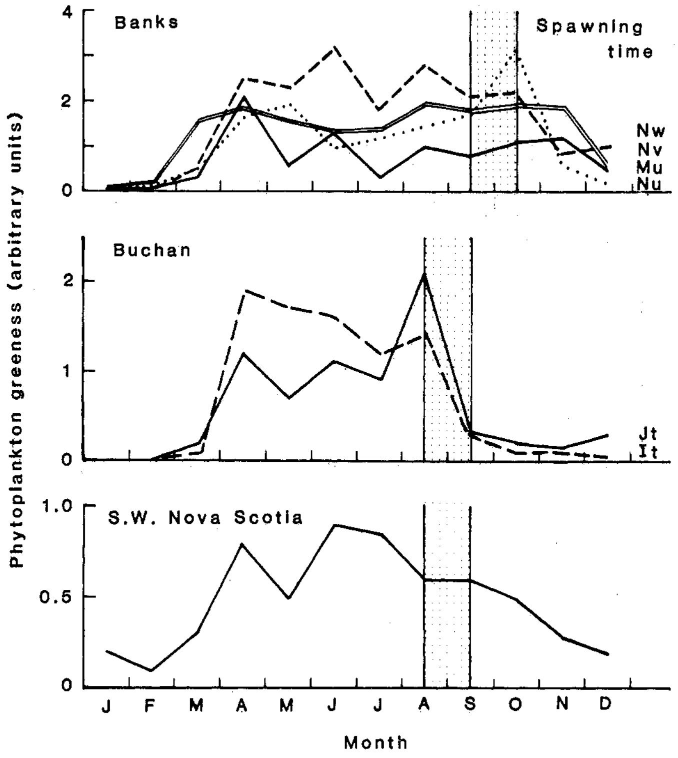


Fig. 5. (left). Relation between spawning stock size in metric tons (*t*) and the respective larval retention areas (*72*). The spawning stock estimates are those observed during periods of moderate fishing when the populations were at relatively natural levels. The data sources are listed in Table 1. Fig. 6. (right). Phytoplankton seasonal distributions in the vicinity of herring spawning areas for three stocks that spawn in tidally energetic seas. The phytoplankton distribution off the southwest coast of Nova Scotia was provided by Sutcliffe (*73*). The other areas (*It, Jt, Nw, Nv, Mu, Nu*) are plankton recorder code squares of 1° latitude by 2° longitude in the North Sea used by Cushing [figure 2 of (*68*)] and in which transition zones for the stratification parameter occur. The vertical lines refer to spawning time, not the 5 percent survival time of Cushing (*68*).

spawning times for three stocks and on both sides of the Atlantic (Fig. 6). Since there does not seem to be a distinct autumn bloom to correspond with spawning, there is no evidence to suggest an adaptational link between spawning time and plankton blooms, at least in these instances. It should be noted that the retention area for the Nova Scotia stock is occupied over the winter when food production and food biomass, as well as water temperature, are low. All overwintering herring larvae of autumn and early winter spawning groups share this environmental feature, which is not consistent with the assumption that food limitation is a constant and continuing factor in generating larval mortality (*54*).

Thus, the plankton production cycles observed within certain larval retention areas defined in our hypothesis do not support the present theory explaining the stock-specific timing of herring spawning. However, further study on the oceanographic conditions within the various larval retention areas may help explain the extensive range in spawning times.

Management Implications

In addition to its purely descriptive aspect, our hypothesis has important management implications. In the northwest Atlantic, the decline in abundance of the Georges Bank stock and the virtual disappearance of signs of spawning on the traditional grounds must be evaluated in conjunction with the continued spawning in the Nantucket Shoals area (*55*). Whether one or two gene pools are involved and, if two, whether the surviving one can invade the territory vacated by the other, is crucial to the prediction of the possible resurgence of the Georges Bank stock. This same question is of equal significance in connection with the fate of small local stocks that may have been depleted by large-scale, mobile fishing efforts, which were intended to exploit large stocks but also exploited the mixed stages of the small local stocks.

In a different context, the management regime in the North Sea is severely constrained in its effectiveness because the progeny of spawning units or groups mix at juvenile, adult feeding, and overwintering stages (*17*). This mixing presents insurmountable difficulties in determining how to allocate catches among different countries in a way that can be related to a recognizable and acceptable biological stock structure. In practice, the biological stock questions have tended to be neglected and viewed as being largely irrelevant to the nature of the practical management unit (that is, all those herring inhabiting the area as a whole) (*56*). Our hypothesis indicates the difficulties in managing stock complexes, such as these in North Sea, Baltic Sea, and Gulf of St. Lawrence herring management units, if a major portion of the fishing mortality is experienced during the "mixed" part of the life history. Even a low fishing mortality for the stock complex as a whole, if differentially applied to individual stocks, can lead to extinction of stock units. Potential rebuilding of a stock complex as a whole will be a function of the number of surviving stock units.

The yield to a mobile fishery managed on a stock complex basis would be expected to cascade downward. In a mobile gear fishery on a stock complex then, total effort must be restricted to a level much lower than would be appropriate for the individually assessed stocks to avoid individual overfishing without the possibility of replenishment from the remainder. An alternative, viable management strategy would be to severely limit the fishery to the nonmixed spawning areas. Relatively high and stable catches have been taken from both the North Sea and the Gulf of St. Lawrence over a long time period when the stock complexes were subject, largely, to spawning fisheries only (*57*).

References and Notes

1. The *Proceedings of the North American Council on Fisheries Investigations* [1931-33 (No. 2), (Ottawa (1935)] record an early attempt to subdivide the northwest Atlantic into smaller areas. The distinguished group of fishery biologists and hydrographers that were involved agreed on boundaries that later became the basis for the subdivision of the Convention Area of the International Commission for the Northwest Atlantic Fisheries (ICNAF) into management areas. The general correspondence between the biological units of species such as cod, for example, and the ICNAF subareas allowed the development of the sophisticated international management scheme set up in the 1970's. The divisions demonstrated the group's understanding of the dual nature of the factors that underlie the structure of marine ecosystems. It is this dual nature, resulting from an interaction of the biological and physical factors, that we are stressing.
2. A case has been made that certain individual herring stocks should be recognized as distinct species, for example, W. Schnakenbeck [*J. Cons. Cons. Perm. Int. Explor. Mer* **6**, 28 (1931)]; J. H. S. Blaxter [*Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer* **143**, 10 (1958)], and more recent reviews by T. D. Iles and C. H. Hatt (*3*). D. M. Ware and B. L. Henriksen [*Can. Fish. Mar. Serv. Tech. Rep. 800* (1978)] and C. J. Sindermann (*4*) discuss the difficulty in setting up general criteria that can allow the separation and identification of taxonomic groups within the species that are consistent through all life-history stages. The tendency has been to accept a classification that corresponds to management units that are politically acceptable at the lowest level of common interest.
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74. K. Howes and J. B. Sochasky helped in the final preparation of this article. B. Sutcliffe, late of the Bedford Institute of Oceanography, pioneered work in this area and we benefited greatly from his comments and advice.

Philip Handler: An Appreciation (13 August 1917–29 December 1981)

DeWitt Stetten, Jr.

Philip Handler's many achievements in world affairs should not mask the fact that he was fundamentally a scholar. We can detect early evidences of this scholarship in his weekly visits to the community library as a small child. According to his mother, he would withdraw seven volumes, the maximum allowable, returning those which he had consumed during the preceding week. This habit of reading abundantly and omnivorously persisted throughout his life. It certainly contributed to his early intellectual development, leading to a baccalaureate degree at the College of the City of New York before his 19th birthday and a Ph.D. in biochemistry 3 years later from the University of Illinois under the preceptorship of Herbert E. Carter.

Handler then joined the recently established faculty of Duke University School of Medicine where he remained until he was called to assume the presidency of the National Academy of Sciences in 1969. He climbed the academic ladder at Duke achieving the Chairmanship of the Department of Biochemistry in 1950 and was named James B. Duke Professor of Biochemistry in 1961, a title which he still had at the time of his death. He was surely one of the leaders of the Duke faculty which earned for that school its high position as a source of well-trained physicians and of gifted investigators in the biomedical sciences. He sponsored many graduate students and authored many important papers, particularly in relation to the metabolism of nicotinamide, biological oxidations, and the biochemical aspects of Darwinian evolution.

During these years Handler served on many important advisory groups. He was elected president of his major professional society, the American Society of Biological Chemists, in 1962. He was a member of the National Science Board and served as its chairman from 1966 to 1970. He also participated in many advisory functions at the National Institutes of Health during the period of the Institutes' most rapid growth. He was a firm advocate of the concept of training grants and an early proponent of the notion that in addition to the categorical institutes there ought to be at least one institute dedicated not to a disease area or an organ system, but rather to the support of the basic medical sciences. This notion ultimately led to the establishment of the National Institute of General Medical Sciences.

In addition to his more than 200 papers in scientific journals, Philip Handler was a coauthor with the late Abraham White and with Emil Smith and myself of *Principles of Biochemistry*, first published in 1954. He persevered as a contributor through the first six editions and was anticipating continued participation in the seventh edition at the time of his death. His remarkable familiarity with current developments in the field of biochemistry in the face of many demands upon his time and effort was certainly in part due to his continuing association with this work. His great breadth of knowledge, his familiarity with the litera-

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