

## Population richness of marine fish species

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### Abstract

Within the distributional range of a species the number of self-sustaining populations can vary, from one population for panmictic species such as American eel to many populations as observed in Atlantic salmon. This "species-level" characteristic is defined here as "population richness." Aspects of geographic patterns in population richness in the northern Atlantic for Atlantic salmon, American shad, rainbow smelt, Atlantic herring, Atlantic cod, haddock, winter flounder, yellowtail flounder, Atlantic mackerel, and European eel are described. It is concluded that events at the early life-history stages, involving "retention" of the eggs and larvae in relation to particular physical oceanographic features, are involved in the definition of population richness.

**Keywords :** Population richness, marine fish species, temporal variability.

*Richesse des populations d'espèces marines.*

### Résumé

Au sein de l'aire de distribution d'une espèce, le nombre de populations quasi-permanentes peut varier, à partir d'une seule population pour une espèce panmictique comme l'anguille d'Amérique jusqu'à de nombreuses populations comme chez le saumon de l'Atlantique. Ce caractère au niveau de l'espèce est appelé ici «richesse en population». Certains aspects des types géographiques de richesse de population pour le saumon atlantique l'alose canadienne, l'éperlan d'Amérique, le hareng de l'atlantique, la morue, l'églefin, la plie rouge, la limande à queue jaune, le maquereau, et l'anguille d'Europe sont présentés. On conclut que des événements durant les premières phases de la vie, impliquant la «rétention» des œufs et des larves par rapport à certains facteurs océanographiques physiques contribuent à la définition de la richesse en population.

**Mots-clés :** Population, poissons marins, variabilité.

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## INTRODUCTION

There are four aspects of populations that may be usefully considered when the question of regulation of numbers is addressed—pattern, richness, absolute abundance, and temporal variability (*fig. 1*). The first two aspects are species-level characteristics; a species

is composed of relatively discrete self-sustaining populations that are distributed in particular spatial and temporal patterns. In the oceans these spatial patterns in the distribution of populations are frequently observed to persist on ecological time scales. To the degree that such patterns are not ephemeral they should be interpretable. Further, there are marked differences between species in the number of com-

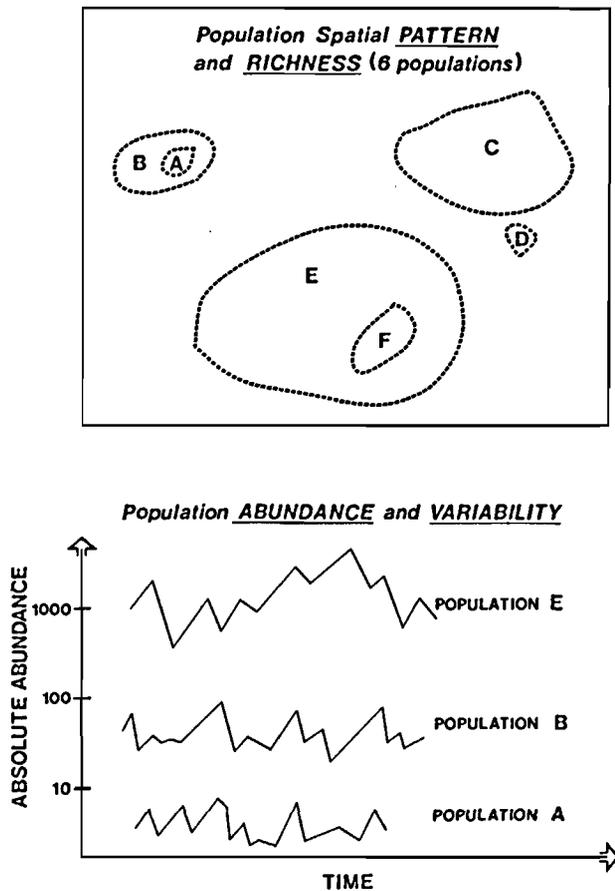


Figure 1. — Schematic representation of the four components of the population regulation question—pattern, richness, abundance, and variability.

ponent populations, from one (for so-called panmictic species) to a large number, reckoned in the dozens. This species-level characteristic is defined here as “population richness.”

Of the four aspects of the population regulation question, the latter two are population-level characteristics. Some populations of a particular species contain many individuals, others a much smaller number. For individual marine fish species the range of absolute abundances between component populations has been observed to cover several orders of magnitude. In the oceans, just as geographic patterns in populations are observed to persist, populations under moderate fishing pressure have been observed to have characteristic absolute abundances that also persist (Blaxter, 1985; Iles and Sinclair, 1982). Finally, the total number of individuals in a population varies from year to year, usually well within an order of magnitude for age-structured populations. It is this latter aspect of the population regulation question, because of the economic impacts on the fishing industry, that has received the bulk of the attention in the fisheries literature. It may have been premature to

have addressed this fourth aspect of population regulation without prior understanding of the processes regulating pattern, richness, and absolute abundance.

In this paper differences between marine fish species in population pattern and richness are reviewed. It was this particular question that was the focus of much of the research of the International Council for the Exploration of the Sea (ICES) prior to about 1930. Key contributions were made by Damas, Heincke, Hjort and Schmidt (see Sinclair and Solemdal, 1987 for a historical review). Hjort (1926, p. 30-31) states,

“...an attempt has been made to determine the spawning areas of the principal fish, plaice, herring, cod, haddock, to define the spawning migrations, the nurseries where the young fish develop, etc. It is hoped it may in this way be possible to find the general laws for the appearance of biological groups...”

By “groups”, Hjort meant “populations”. This research question is picked up again here, in the expectation that the accumulated observations on pattern and richness since the 1930’s may provide further understanding.

Evolutionary biology and ecology overlap in important ways on the population regulation question. Pattern and richness are the very features of the biological species concept that were a critical contribution by the systematists to the evolutionary synthesis (Chetverikov, 1926; Rensch, 1929; Dobzhansky, 1937; Mayr, 1942). However, the between-species differences in population richness have not been accounted for. Because “population thinking” is central to fisheries management in the definition of biologically meaningful management units, the accumulated observations on population pattern and richness of marine fish species are perhaps unique relative to other animal groups. The interpretation of this extensive body of information may be of general interest well beyond its fisheries context (this perspective on population richness is extracted from the larger essay of Sinclair, 1988).

## EMPIRICAL OBSERVATIONS ON POPULATION PATTERN AND RICHNESS

There is considerable evidence that the population structure and richness of many fish species (*i.e.* the relative degree of population richness) is defined during the early life-history stages. This fact is well recognized for certain anadromous species such as Atlantic salmon (for example Harden Jones, 1968 and Hasler *et al.*, 1978) and American shad (Leggett and Whitney, 1972; Carscadden and Leggett 1975; Dadswell *et al.*, 1983; Melvin *et al.*, 1986). In these two species the population structure is defined in relation to the number of rivers flowing respectively into the northern Atlantic as a whole for Atlantic salmon and the eastern coast of North America for American shad. Three observations are considered important. First,

homing to specific river systems has been convincingly demonstrated. Secondly, the egg and larval phases are completed for both species within specific river systems themselves (*i.e.* the early life-history stages are "retained" by an interaction between the behavior characteristic of the species and the particular physical geography of the river system). Thirdly, there is extensive mixing between populations during the juvenile and adult phases of the life histories. These observations are well documented, and the discreteness at the early life-history stages between populations is easy to visualize. The observation that is stressed here in relation to the subsequent between-species comparisons (*i.e.* that the population richness and pattern are defined at the early life-history stages), even though obvious, is perhaps less well recognized.

The anadromous rainbow smelt (*Osmerus mordax*) is somewhat less population rich than Atlantic salmon and American shad. In Québec waters, for example, only three populations of rainbow smelt have been identified (those spawning in rivers flowing into respectively: (1) the Bay of Chaleur; (2) the south shore of the St-Lawrence Estuary; and (3) the Saguenay fjord) (Fréchet *et al.*, 1983). The authors suggest that smelt do not home in this case to specific natal rivers but rather to one of several rivers flowing into an estuary, fjord, or coastal embayment. Ouellet and Dodson (1985) have shown that the larvae from one of the rivers (the Boyer) flowing into the St-Lawrence Estuary are retained downstream of the natal river, in the St-Lawrence Estuary, by vertical displacements in combination with the two-layer circulation system. The distributional evidence for this anadromous species strongly suggests that the population richness and pattern are again defined at the early life-history stages. In this case the geographic area of retention at the early life-history stage, which it is inferred defines the population structure, is in coastal embayments or estuaries, rather than in a river system itself.

The evidence supporting the hypothesis that population richness is defined at the early life-history stages is not as straightforward in ocean-spawning species, due in part to the long-upheld concept of larval drift as initially defined by Fulton (1889). The evidence that the population richness and pattern of Atlantic herring are defined at the early life-history stages has been summarized by Iles and Sinclair (1982) and Sinclair and Iles (1985). Retention of larvae for the first few months of this phase of the life history has been documented for both coastal embayments or estuaries (Graham, 1972; 1982; Grainger, 1980; Fortier and Leggett, 1982; Henri *et al.*, 1985) as well as open-ocean areas (Boyar *et al.*, [1973] and Bolz and Lough [1984] for Georges Bank). The mechanism by which discreteness is maintained (vertical migration in relation to the tidal circulation) has been well described in estuaries (Graham, 1972; Fortier and Leggett, 1982; Henri *et al.*, 1985) but only inferred in the open-ocean spawning areas. As tidally dominated

circulations are characteristic of many larval distributional areas of Atlantic herring populations, it is probable that such features play a role in facilitating retention.

Much of the evidence concerning larval retention areas for Atlantic herring comes from the northwestern Atlantic. At this stage, there is not a consensus in the literature on the applicability of this concept, or interpretation of the empirical observations, in the northeastern Atlantic. Recent studies on the spawning and early life-history stages of herring spawning in the Buchan area of the North Sea (Kiorboe and Johansen, 1986; Munk *et al.*, 1986; Munk *et al.*, 1987; Richardson *et al.*, 1986*a, b*, and *c*) have tended to support the herring hypothesis of Iles and Sinclair (1982), whereas the interpretation of the results of observations on herring spawning and larval distributions in the Minch area to the west of Scotland (Heath *et al.*, 1985; Heath and MacLachlan, 1987) has not been supportive. Cushing (1986) has argued that there may be fundamental differences between Atlantic herring on the two sides of the Atlantic. A restatement of the herring hypothesis of Iles and Sinclair (1982), as well as a discussion of the critique by Cushing (1986), is given in Sinclair, 1988 (chapter 3). From our reading of the literature, there is considerable support for the conclusion that herring spawn contiguously, with physical features that, with appropriate behavior of the larvae, enhance persistence of larval distributions in particular geographic locations during the first couple of months of the early life-history stages. There is evidence for downstream displacement and dispersal of larval distributions from spawning areas, but not of the magnitude predicted from surface-layer residual currents. Further, the number of populations is a function of the number of physical features that are appropriate for such behavior. There are many such locations within the overall distributional area of the species. Atlantic herring, like Atlantic salmon and American shad, is population rich.

Atlantic cod is also population rich. Maintenance of discrete egg and larval distributions from well-identified spawning populations has been described, for example for Browns Bank, Sable Island Bank, Flemish Cap, Magdalen Shallows, Faroe Bank, Faroe Plateau, and the Lofoten area (the literature support is summarized in *table 1*). The egg and larval distributions, however, generally have been interpreted in relation to drift and dispersal rather than persistence within particular geographic locations. The rich literature on Atlantic cod egg and larval distributions cannot be critically evaluated here, but on the basis of the data summarized in *table 1* alone it is suggested that the population richness and pattern of Atlantic cod are defined at the planktonic egg and larval phases of the life-history. Spawning for most offshore populations is located on banks, and eggs and larvae are very often observed to maintain a discrete distribution on the respective banks for several months. The spatial distributions of cod eggs and larvae on the Scotian Shelf off Nova Scotia at different months

**Table 1.** — Studies supporting egg and larval retention for haddock and Atlantic cod.

Population	Study
<b>Atlantic cod:</b>	
Browns Bank	O'Boyle <i>et al.</i> , 1984
Sable Island Bank	O'Boyle <i>et al.</i> , 1984
Magdalen Shallows	Lett, 1978
Flemish Cap	Anderson, 1982
Faroe Plateau	Anon., 1979 (inferred from p. 18, 19; Fig. 25,26)
	Anon., 1979 (inferred from p. 18, 19; Fig. 25, 26)
Faroe Bank	Ellertsen <i>et al.</i> , 1986; Wiborg, 1952; 1960a; 1960b
Lofoten area	
<b>Haddock:</b>	
Georges Bank	Smith and Morse, 1985
	O'Boyle <i>et al.</i> , 1984; Koslow <i>et al.</i> , 1985
Browns Bank	O'Boyle <i>et al.</i> , 1984
Sable Island Bank	Saville, 1956; Anon., 1979 (inferred from p. 19, 20; Fig. 28, 29)
Faroe Plateau	Anon., 1979 (inferred from p. 19, 20; Fig. 28, 29)
Faroe Bank	

are illustrated in *figure 2*. The similarity in the patterns of egg and larval distributions at any one time, as well as the persistence of the larval distributions over certain offshore banks between months, led the authors to conclude that cod eggs and larvae for these areas at least are retained in particular physical oceanographic locations. It was inferred that the gyral circulation associated with offshore banks may contribute to egg and larval retention. Gagné and O'Boyle (1984) in a more detailed analysis of the ichthyoplankton data collected on the Scotian Shelf, in conjunction with the groundfish research vessel survey data, strengthened this interpretation of the empirical observations. The observations on the distributions of cod larvae from May to August over the Flemish Cap off Newfoundland suggest the same conclusion (Anderson, 1982). The planktonic early life-history stages are retained over the Flemish Cap itself for several months. Separate populations of cod have been identified on the Faroe Plateau and the Faroe Islands. Spawning locations and 0-group distributions are discrete between the two areas (Anon., 1979). It is concluded that the ichthyoplankton stages are probably retained respectively around the Faroe Islands and over the Faroe Plateau. Even in cases where the juvenile distributional area is not coincident with egg and larval distributional areas, such as the Lofoten and Vestfjord spawning population off northern Norway, there is evidence that eggs and larvae are retained over the offshore banks for a few months (Ellertson *et al.*, 1986). In the presently accepted interpretation the eggs and larvae drift passively from the spawning site to the nursery area to the north and east. An alternate interpretation for this cod population is that the planktonic stages are retained over the banks and within the Vestfjord for a certain period. Subsequently, either at the late larval stage or after metamorphosis they actively migrate to the juvenile

nursery area. It is argued that the very existence of the self-sustaining population in this area is due to the retention characteristics of the Lofoten-Vestfjord physical oceanography. The precise location of spawning is, following this logic, not defined in relation to the residual circulation linking a spawning area to a nursery area, but rather to an area where egg and larval discreteness can be maintained for a few months. In each of the above examples the cod populations have been identified on the basis of adult characteristics. Subsequently, distributional observations on the early life-history stages have suggested that the eggs and larvae are retained in well-defined geographical areas having particular physical oceanographic properties. Mixing between populations of cod does, however, occur at the adult phase during summer feeding (Wisc, 1962) and overwintering (Templeman, 1962). A fuller analysis of the evidence supporting this conclusion for Atlantic cod is under preparation.

Egg and larval retention for haddock spawning on offshore banks has been described for Georges Bank, Browns Bank, Sable Island Bank, and Faroe Plateau and has been inferred for Faroe Bank (literature summarized in *table 1*). Saville (1956) postulated that retention was generated by an anti-cyclonic eddy system around the Faroes. He states (*p.* 11),

"It would seem necessary to postulate such a system in any case to explain the retention of the haddock spawning products within the area and, with the possible exception of 1950, there is no evidence to suggest that there is any appreciable loss of these products by drift out of the area."

It can be inferred from detailed studies of the oceanography of Browns and Georges Banks that larval behavior in addition to the circulation is critical to the persistence of the distributions on the respective Banks. Both Banks are highly dispersive environments. The time scale for dispersion of passive particles off Browns and Georges Banks are respectively 10-15d and 50-60d (P. Smith, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, pers. comm.). Also, residual gyres generated by tidal rectification are characteristic of both Banks (Greenberg, 1983). From drogue studies on Browns Bank at mid-water depths the residence time was, on average, 14d (P. Smith, pers. comm.). In addition, the "event" scale of physical oceanographic phenomena (shelf-water entrainment into warm-core eddies and advection of shelf water seaward due to storms) has been identified as a constraint to egg and larval persistence on shelf banks in this particular area. Yet persistent discrete egg and larval haddock (and cod) are observed on both Banks from March to August (*fig. 3* [from O'Boyle *et al.*, 1984]; *fig. 4a* and *b* [from Smith and Morse, 1985]). In addition, discrete aggregations of 0-group haddock are observed on the respective banks in the autumn. Thus, some behavior has to be attributed to the early life-history, particularly on the smaller Browns Bank, to account for the observed distributions. It is not clear at this stage how depth

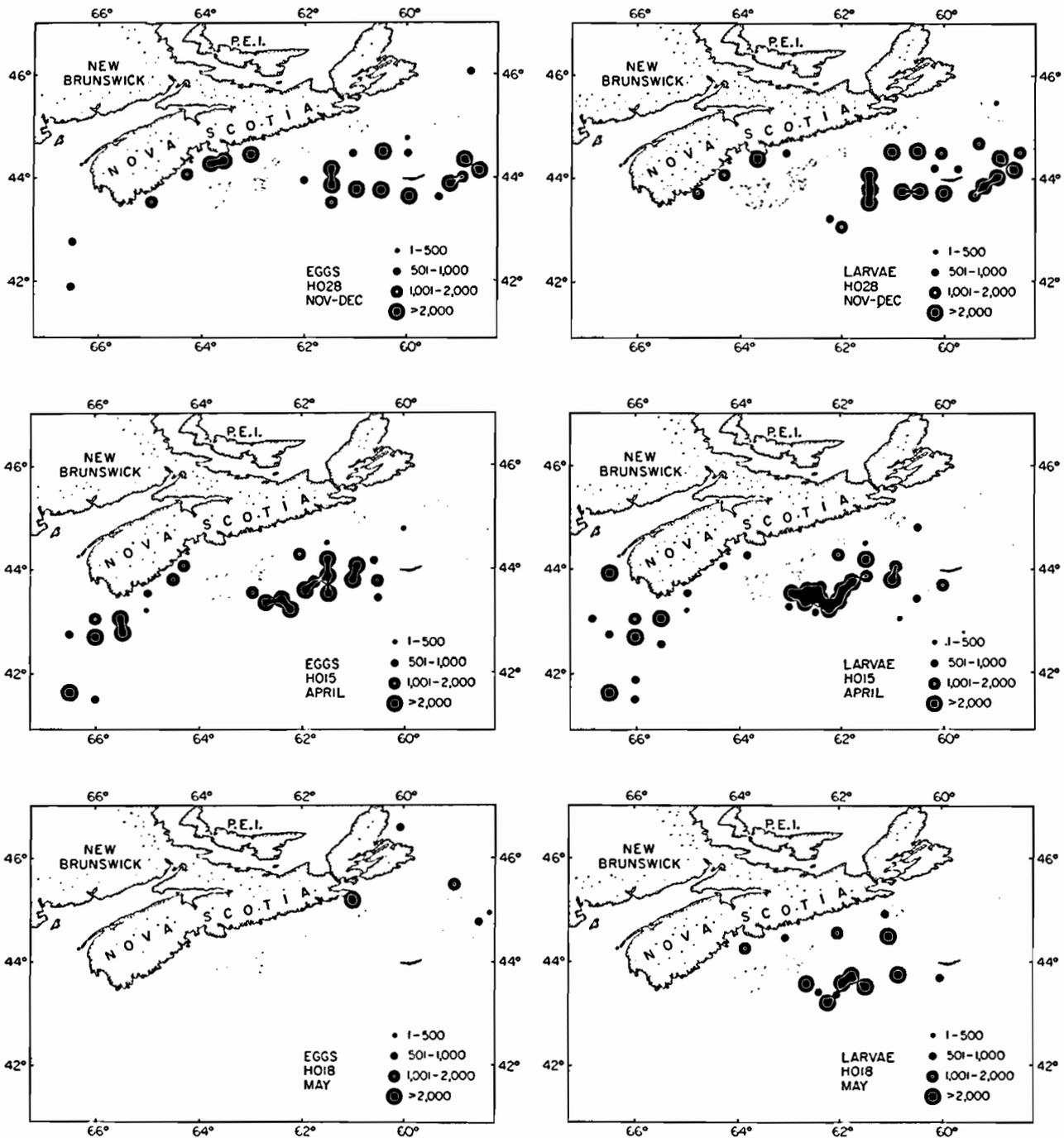


Figure 2. — Distribution of eggs and larvae of Atlantic cod on the Scotian Shelf during winter and spring (reproduced from O'Boyle *et al.*, 1984).

changes by the larvae and post larvae (both diurnal and ontogenetic changes) can account for the observed distributions. There is little shear in the tidal circulation with depth over the top 30 m of the water column within which most of the larvae are distributed. However, wind-generated circulation effects, which are superimposed on the tidal circulation, are

depth specific and may generate sufficient vertical structure to be "used" by vertically migrating larvae to enhance retention over the natal banks.

Tagging results of haddock indicate that: (1) the adult distributional areas are considerably broader than the spawning and egg and larval retention areas; and (2) there is some mixing between haddock of

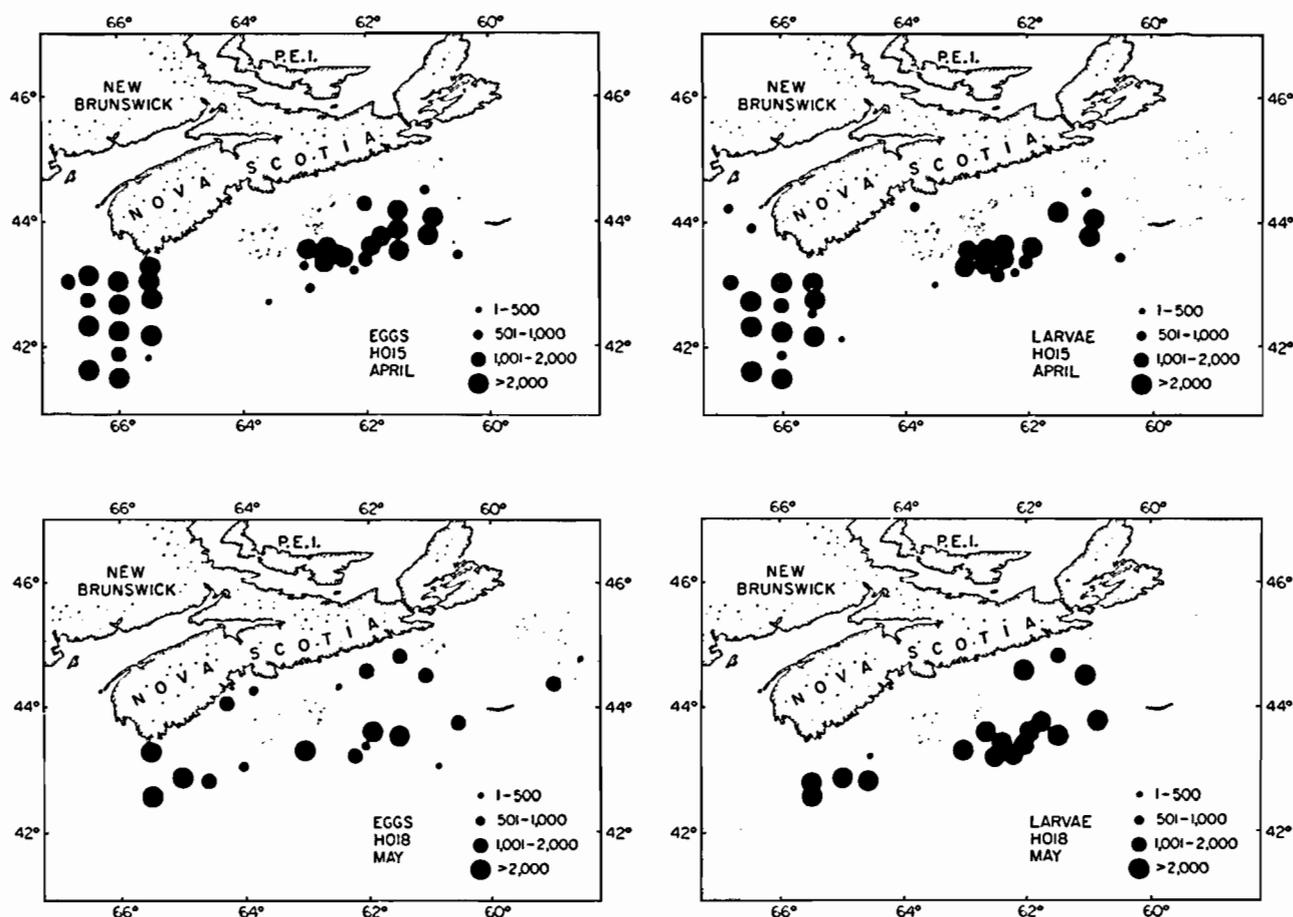


Figure 3. — Distribution of haddock eggs and larvae on the Scotian Shelf during the spring (reproduced from O'Boyle *et al.*, 1982).

different populations during summer feeding and overwintering (for example, McCracken, 1959; Halliday and McCracken, 1970). On the basis of the distributional data at various life-history stages it is inferred that haddock population richness (which is considerably less than that observed for herring and cod) is defined at the planktonic egg and larval phases of the life history. In the northwestern Atlantic, at least, it is of interest that cod populations exist in essentially every location that a haddock population spawns; but there are also many additional geographic locations where only cod populations can persist (*i.e.* the many so-called local cod populations maintained in coastal embayments). This difference between species in their population richness, yet very similar requirements for the early life-history stages, suggests that there may be very subtle differences in the behavior of the larvae that allow cod populations to be more numerous.

Winter flounder population structure has not been well described. There has, however, been an excellent study on the early life history of a selected well-defined population. Pearcy (1962) elegantly demonstrated the interaction between ontogenetic changes in winter flounder behavior at the early life-history stages in relation to the estuarine circulation that

permits maintenance of a discrete early life-history distribution within the Mystic River Estuary. From tagging experiments it has been concluded that winter flounder are relatively stationary and that the species is population rich (Perlmutter, 1947). Saila (1961) showed that winter flounder return to the same area each year to spawn. It is thus not possible to conclude for winter flounder that the population structure itself is defined at the egg and larval phases (as all phases are relatively discrete from contiguous populations); but the behavioral features identified at the early life-history, which are linked to physical oceanographic features, suggest that they are aiding retention of the population in specific geographic areas rather than permitting dispersal through drift.

Similar evidence on egg and larval retention in relation to population patterns can be inferred for yellowtail flounder (*Limanda ferruginea*). Studies on juvenile and adult characteristics and migrations (Lux, 1963) have led to the conclusion that yellowtail flounder are relatively sedentary and that separate populations are sustained in close proximity to each other. For example, separate populations of this species are observed on Georges Bank, Nantucket Shoals to Long Island, and Cape Cod to Cape Ann (*fig. 5*).

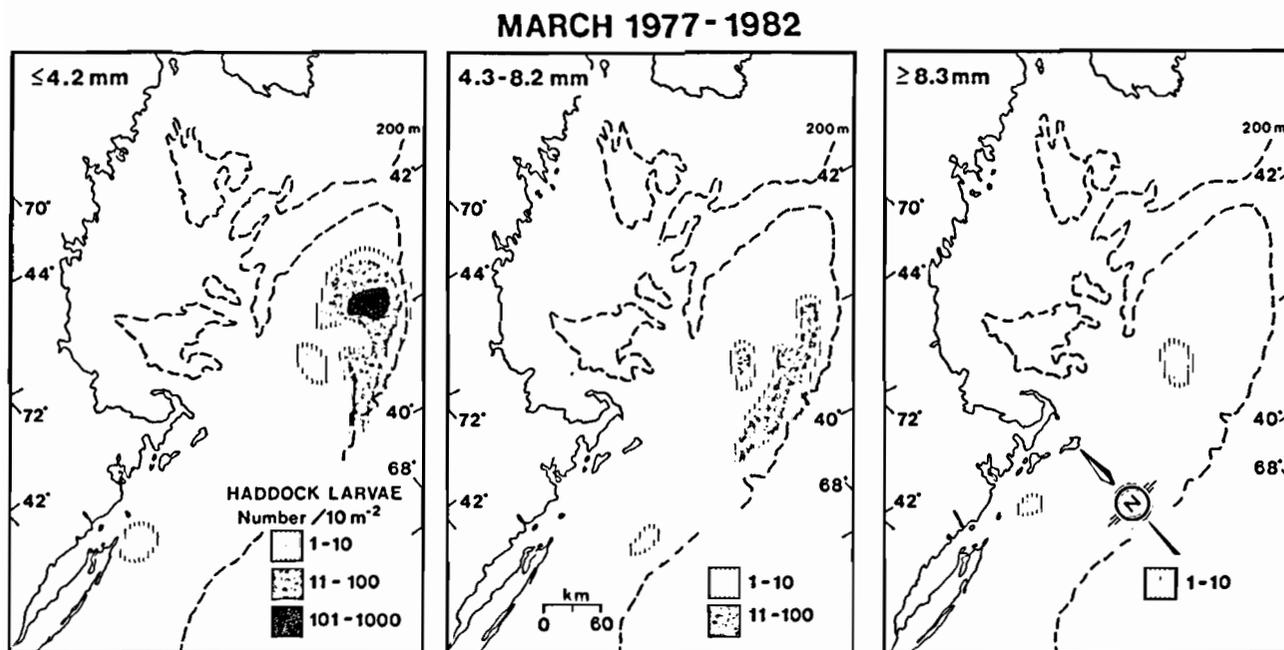


Figure 4a. — Distribution of three size classes of haddock larvae of the Georges Bank population during the month of March (1977 to 1982) (redrawn from Smith and Morse, 1985).

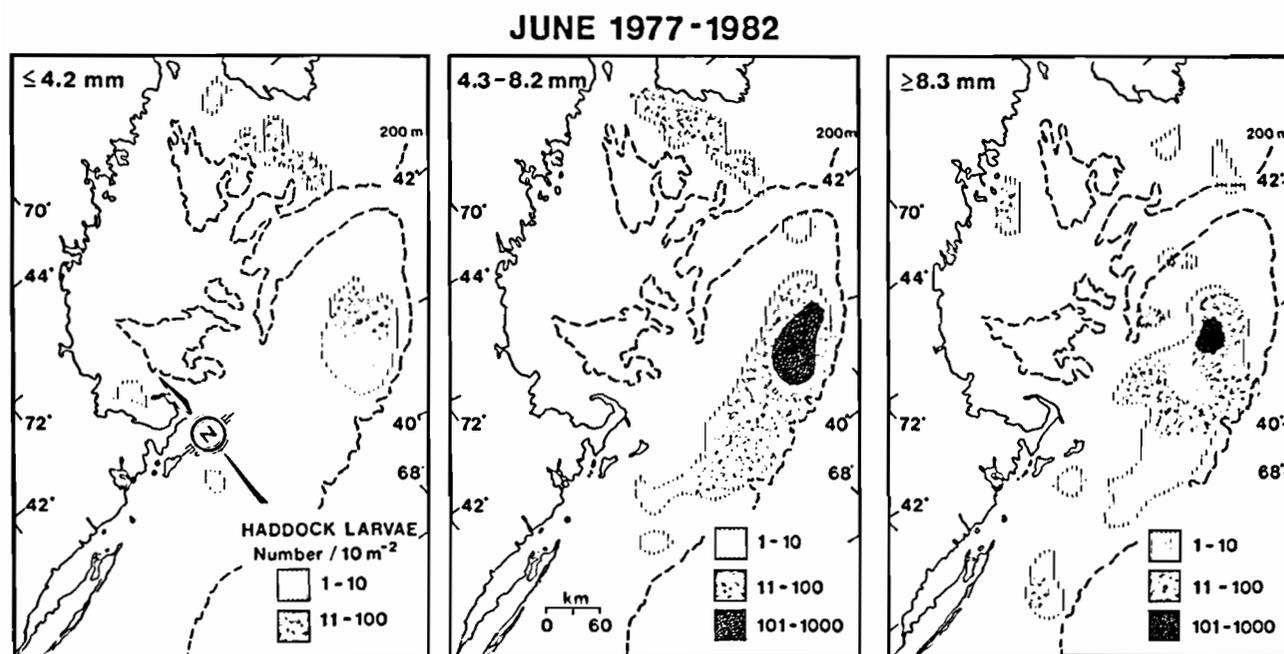


Figure 4b. — Distribution of three size classes of haddock larvae of the Georges Bank population during the month of June (1977-1982) (redrawn from Smith and Morse, 1985).

Smith *et al.* (1978) describe vertical distribution of yellowtail larvae and ontogenetic changes in behavior for the Mid-Atlantic Bight population. They indicate that diel vertical movements and feeding are not directly related. The younger larvae stay below the thermocline. Intermediate-size larvae are observed

throughout the water column with the animals moving through the thermocline. They conclude that larvae greater than 10mm spend some time on the bottom. From the observations on larval behavior and the circulation they also conclude that there is limited dispersal at the larval stage due to the surface-layer and wind-driven currents. Johnson *et al.* (1984)

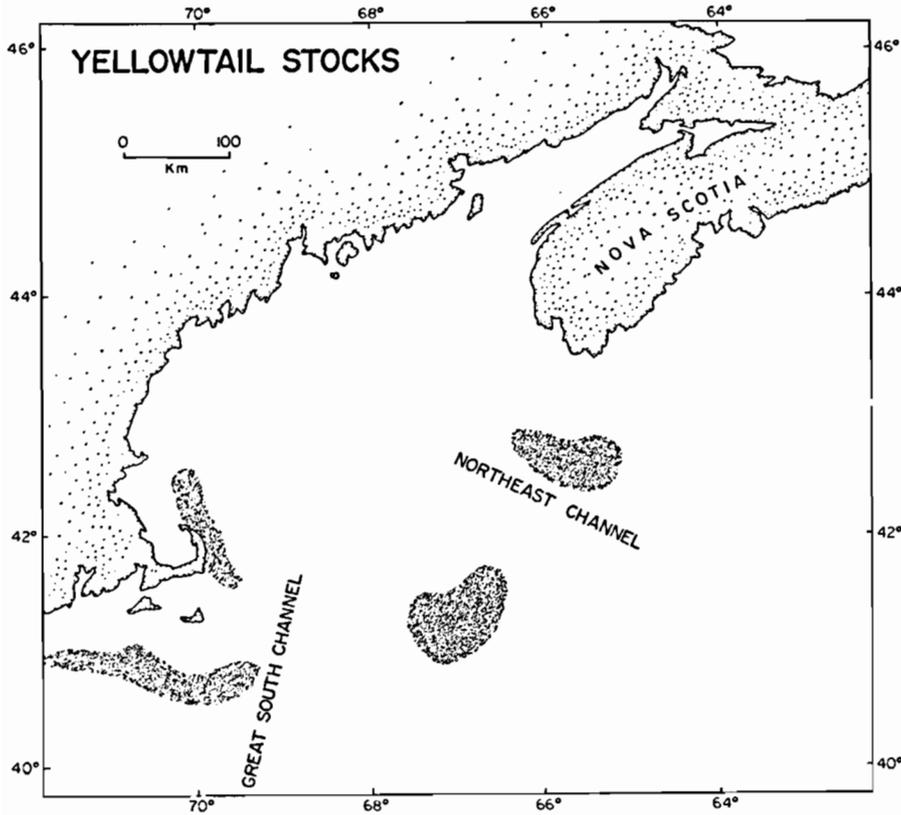


Figure 5. — Distribution of spawning populations of yellowtail flounder in the Gulf of Maine area (redrawn from information in Lux, 1963).

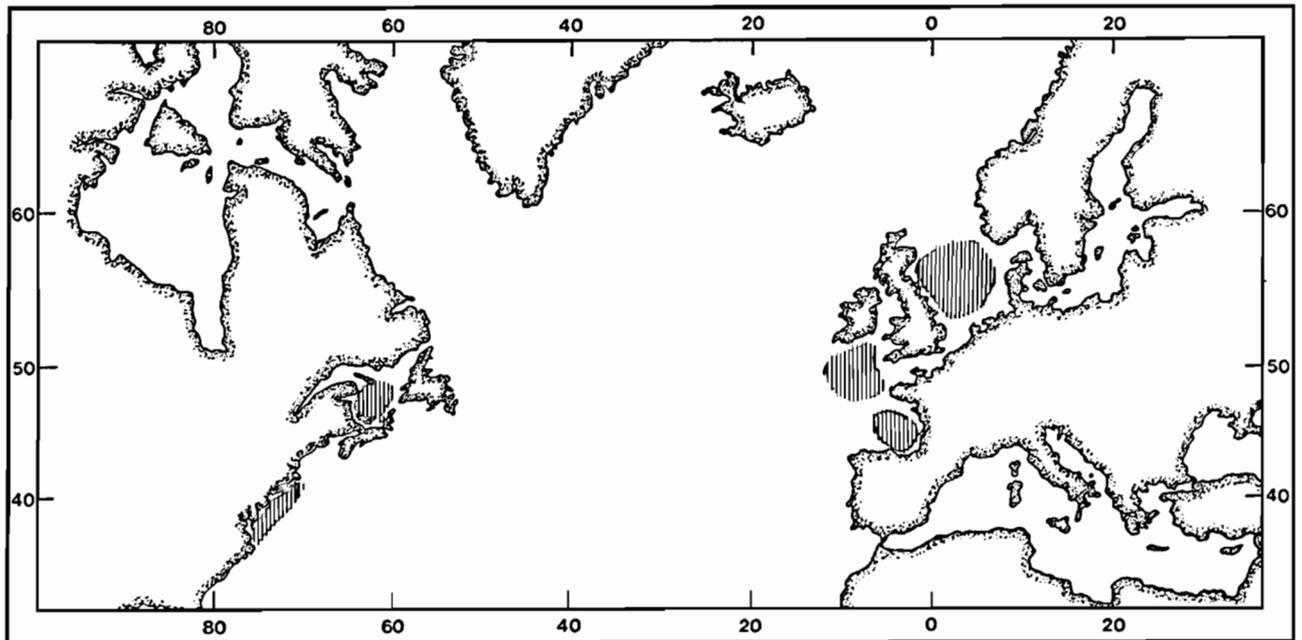
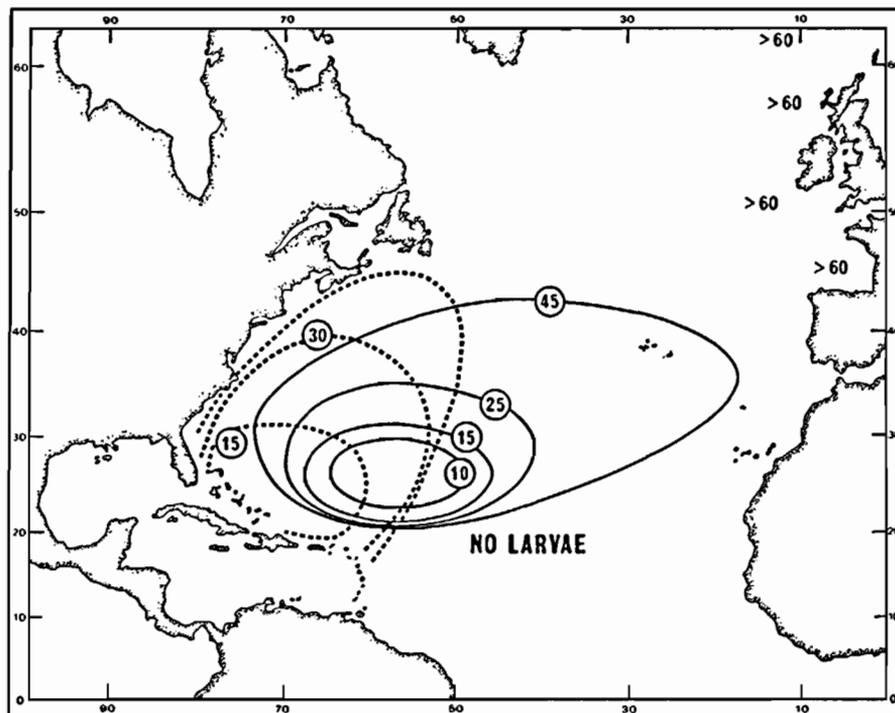


Figure 6. — Larval "retention" areas for Atlantic mackerel, a population-poor species.

Figure 7. — Distribution of larvae of European eel (solid lines) and American eel (dotted lines) (redrawn from Schmidt, 1922).



have discussed the physical basis of larval retention in the Mid-Atlantic Bight (the area of the Smith *et al.* study) in relation to crab population persistence and recruitment variability. On the basis of this limited evidence on yellowtail larval distributions and the more extensive literature on the population patterns of yellowtail flounder it is again argued that the richness and geographic pattern observed are a function of events at the early life-history.

Atlantic mackerel (*Scomber scombrus*) population structure was initially described by Garstang (1899) and Williamson (1900) in the eastern Atlantic and Sette (1943) in the western Atlantic. Subsequent studies have not markedly changed their major conclusions. Atlantic mackerel is not population rich, consisting of only two large populations in the western Atlantic and at least two or three in the eastern Atlantic. Large-scale migrations are characteristic of this species, and during the overwintering adult phase there is mixing between populations. In the western Atlantic there are two definable, albeit extensive, egg and larval distributional areas (the southern Gulf of St-Lawrence and the Mid-Atlantic Bight; see respectively Lett [1978] and Berrien *et al.* [1981]). The egg and larval retention areas for Atlantic mackerel as a whole are illustrated in figure 6. It is argued that the appropriate egg and larval retention areas utilized by this species involve larger-scale circulation features, of which there are not many within the distributional limits of the species. As a result, only two populations can be sustained, for example, in the western Atlantic. Again the population structure of Atlantic mackerel

is inferred to be defined at the early life-history stages (in this case in relation to relatively large physical oceanographic current systems). The discreteness of the egg and larval distributions in the northeastern Atlantic in relation to either population structure or well-defined physical oceanographic features is not well understood (see Hamre, 1980 and Johnson, 1977 for reviews), but it is generally accepted that mackerel is not population rich in comparison with Atlantic herring and Atlantic cod, for example.

The final example chosen is the European eel because it has been so extensively studied and, perhaps incorrectly, considered to be an anomaly with respect to its population structure. The European eel (similar to shortfin squid and Atlantic menhaden) is population poor. There are disagreements in the literature concerning the systematics of eels in the northern Atlantic (Williams and Koehn, 1984). This uncertainty does not, however, significantly influence the conclusions drawn here. Schmidt (1930) observed no differences in meristics of European eel from his extensive sampling of rivers throughout Europe. These observations were anomalous relative to his observations on herring, cod, and *Zoarces* sp., and there have been ingenious attempts to account for the homogeneity of the observations (for example, Wynne-Edwards, 1962). In the present perspective, however, the European eel results are clearly not anomalous, but rather part of an ordered sequence of population richness. Also the underlying causes of the lack of population richness are plausibly interpretable. For this species the egg and larval retention

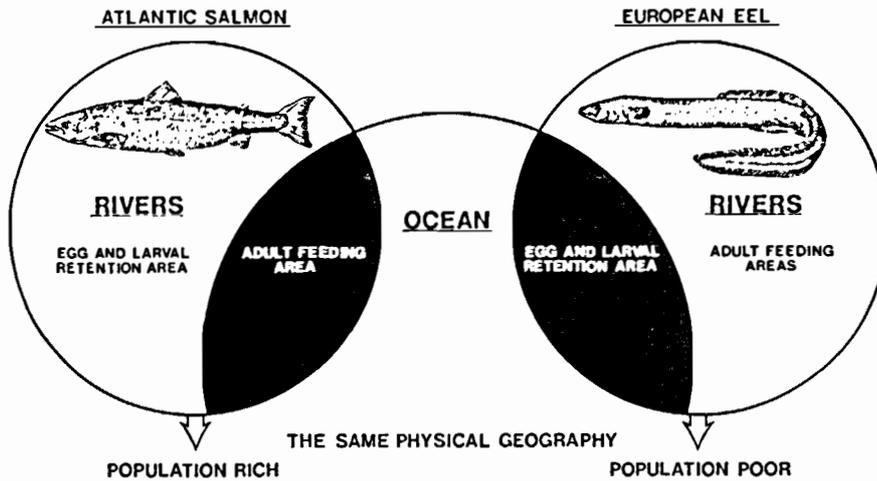


Figure 8. — Schematic representation of the dichotomy in distributions of life-history stages of Atlantic salmon and European eel.

area is the North Atlantic Gyre itself (fig. 7), and there is only one such physical feature within the distributional range of the species (here we consider the European and American eels to be separate species). The distributional details of the early life history and the observations on homogeneity in the meristics of adult eels are described by Schmidt (1922). The conclusions by Schmidt relative to the European eel have recently been questioned by Boëtius and Harding (1985) and Harding (1985). Although the published data by Schmidt indicate remarkable uniformity in meristics between eels sampled from a wide range of rivers throughout Europe, the unpublished data and some subsequent work by the authors demonstrate less homogeneity. In addition, the larval distribution data in the North Atlantic Gyre suggest that the spawning location is more extensive than hypothesized by Schmidt. The subsequent research on the American eel, however, has tended to confirm the conclusion of panmixis for eels (Williams and Koehn, 1984; Kleckner and McCleave, 1985; references therein). At this stage in the debate the general conclusions of Schmidt on panmixis and a single larval distributional area for each of the two eel species in the northern Atlantic has been accepted. This interpretation is supported in a recent review by McCleave *et al.* (1987). It is noted, however, that the strength of the conclusions has been weakened for the European eel (but not the American eel) by the analyses of Boëtius and Harding. Future studies will undoubtedly clarify this question. The relative homogeneity of eels compared to *Zoarces*, Atlantic herring, and Atlantic salmon is not in question.

## DISCUSSION

Representative geographic patterns in populations of fish in the northern Atlantic are summarized above.

What can be inferred from this comparative species description of pattern? There is persistent structure on ecological time scales in the circulation and mixing processes in the northern Atlantic. Each species which we have considered interacts with the physical geography in different ways, even though several of the species share a common overall area of distribution. The differences that have been highlighted here are the locations for sexual reproduction and the subsequent egg and larval distributions (which are particularly sensitive to physical oceanographic processes due to their small size and limited mobility). The behavioral characteristics at different parts of the life history (homing for reproduction and vertical migration of the larvae, for example) vary between species in relation to particular aspects of the physical geography within the overall common distributional area. The matched patterns in populations and particular aspects of the physical geography suggest that behavior in relation to physics provides opportunities

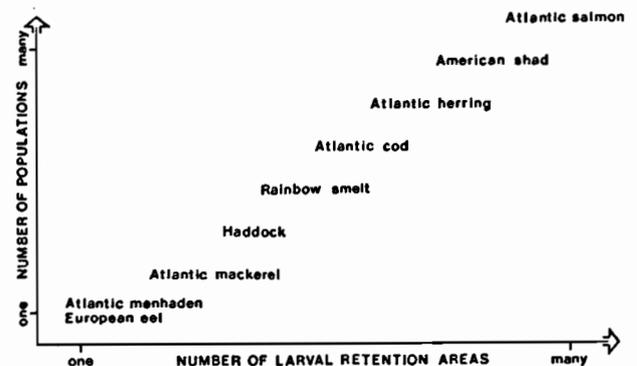


Figure 9. — Continuum in population richness of selected anadromous and marine fish species in the northern Atlantic.

for population persistence. Population patterns appear to be physically defined, and different aspects of the physical geography are used by each species.

In this comparative analysis it is clear that the degree of population richness is defined at the early life-history phases in relation to well-defined physical oceanographic (or geographic) features (rivers, estuaries, coastal embayments, tidal-induced circulation features, banks, coastal current systems, major ocean currents, oceanic-scale gyres). When there are many such physical features (to which the early life history is behaviorally adapted to permit retention) within the distributional range of the species, the species is population rich. With few appropriate physical features, the species is population poor. The extremes in the continuum forcefully and simply demonstrate that it is the early life-history discreteness itself that defines the population richness. The life cycles of Atlantic salmon and European eel are almost mirror images (fig. 8), and for these two species population richness is generated by the early life-history discreteness rather than at the juvenile and adult phases. There is extensive mixing between populations at the adult phase for salmon, and isolation of parts of a panmictic population at the adult phase of eel. It is the

continuity/discontinuity at the early life-history, not at the adult phase that defines the population richness. There is, in addition, sufficient evidence to join these extreme examples, and thus describe the interspecies patterns in population richness as a continuum (fig. 9). This summary of species-specific differences in population richness is in no way exhaustive, but rather a sample of the overall literature. The conclusion, however, that population richness is defined at the early life-history stages in relation to retention-diffusion processes is well supported. Burton and Feldman (1982), from a consideration of a different component of the marine literature (that on the population genetics of estuarine and coastal zone invertebrates), have also concluded that processes during the pelagic early life-history stages influence population structure.

These observations on geographic patterns of populations of marine fish species in the northern Atlantic, and their interpretation, have led us to formulate the "member/vagrant" hypothesis (Sinclair, 1988; Sinclair and Iles, 1987) which addresses the four aspects of populations illustrated in figure 1 (*i. e.*, the regulation of pattern, richness, abundance, and variability).

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