Northwest Atlantic Fisheries Organization

Serial No. N1246

NAFO SCR Doc. 86/119

SCIENTIFIC COUNCIL MEETING - SEPTEMBER 1986

Interaction of External and Internal Factors in Relation to Recruitment

by

T. D. Iles

Marine Fish Division, Department of Fisheries and Oceans
Biological Station, St. Andrews, New Brunswick, Canada E0G 2X0

> A scientist commonly professes to base his beliefs on observations, not theories... I have never come across anyone who carries this profession into practice... Observation is not sufficient... theory has an important share in determining belief.
>
> Arthur S. Eddington, The Expanding Universe 1933

Introduction

The scientific philosopher Karl Popper is best known for his analysis of the logical basis for scientific knowledge. Instead of basing scientific generalizations on accumulated observations of specific instances - the process of induction that had been accepted as the scientific method since the time of Francis Bacon - he introduced the criterion of testability. His argument was that verification and falsification are logically asymmetrical; no matter how many examples are produced to support a theory, in the strict logical context, a single case is sufficient to refute it. A scientific law is thus conclusively falsifiable but it is not conclusively verifiable, and our knowledge of nature therefore is inevitably provisional, and permanently so. Progress in science is the result of the process of the replacement of one theory by another one than can be shown to be preferable. As a codicil, it was pointed out that the way a theory has been arrived at has no bearing on either its scientific or its logical status. This means that there is no such thing as a "logic of creation" in the sciences and, by the same token, no way of arriving at a theory or hypothesis is illegitimate; the "scientific method" is not a recipe for the generation of ideas but acts as a constraint on their acceptance based on subjecting them to critical test. The belief that science proceeds from observation to theory is widely and firmly held, but it is a mistaken one as is maintained in the quotation that begins this communication, by one of the greatest physicists of this century. Observations are always interpretations and knowledge is an extension of our theories.

SPECIAL SESSION ON RECRUITMENT

While most practising scientists are aware, however vaguely, of Popper's views, they are, after all, the basis of the hypothetico-inductive theory of science popularized by Medawar (1969) - few people are familiar with his later extension of them that serves as the conceptual framework for this contribution to this symposium.

Popper's ideas were developed in connection with a theory of human language as a means of communication, but they are applicable to the more general question of "communication" between animals and the environment, both physical and animate. The traditional view has been that "data" or "signals" from the environment impinge on our sense organs and that these sense data are subsequently "digested" or processed to achieve a sort of "concensus." Popper uses the "bucket theory" (Fig. 1) to illustrate this and makes a distinction between "a posteriori" or "observational" knowledge and "a priori" or non-observational. It is the "observational" aspect that is challenged by Popper who maintains instead that, evolutionarily speaking, all "knowledge" is the invention of animals; information did not and does not stream or pour into the bucket from outside; it was, and is, actively acquired by the organism. It represents the end result of an exploration that is an essential part of the process of adaptation to the environment and that has a unique evolutionary history for each "species." The biological function of this process is to anticipate environmental events and, to this end, sense organs "imbibe" or "extract" environment information that can indicate the state of the environment in both the long and short term, reliably enough to ensure biological continuity-survival.

Popper argues that because sense organs are logically prior to the sense data that they use, the "processing" of these data cannot be the result of a process analogous to induction or generalization. The conclusion must be that all of the animate processes of reproduction and heredity, feeding and assimilation and the behavioral activities of exploration and "problem solving" originate in the organism itself. They represent positive actions <u>on</u>, and not reactions <u>to</u> the environment. Thus, the concept of an environmental "stimulus" or "signal" that <u>causes</u> the release of an action is a mistaken one. The organism and the particular state that it is in determines and chooses and selects those environmental changes that will be significant; the conclusion is that the traditional model of physical causation does not apply to organisms. They have access to an independent and internal source of energy that can be allocated by the organism and expended in different ways and in different amounts, depending on "circumstances."

Now this attitude is strikingly described by Brett (1970) in his discussion of the reaction of fish to the environmental "stimulus" or "signal" of temperature. He first points out that fish gills function primarily as gaseous exchanges, and they are also very efficient heat exchangers with the result that everything has to operate at ambient temperature. Because of this, adaptation to changing temperature is a very complex process; an individual fish may live or may die, be hyperactive or benumbed, migrate or not migrate, etc. at precisely the same temperature, depending on its (internal) state of adaptation at the time. And by "time" is meant time of day, time of year, stage of life history, etc., but all within the context of the individual life-history trajectory; this process of selection of information (not stimuli) operates biologically and the reaction is under the immediate control and direction of hormones. Brett stresses that these processes are very different from processes associated with physical and chemical processes and are very much more complex than is indicated by the ease of measurement of temperature.

This approach goes a long way to deal with the fundamental problem that I have had in dealing with stock/recruitment theory. I have dealt with the question on several occasions and within a comprehensive ecological and biological framework. This has linked large-scale meteorological systems with the recruitment histories of specific fish populations and in a way that has allowed the distinction between the "natural" factors and the effect of fishing (Iles 1973, 1978, 1981a, b), and has allowed the diagnosis of temporal series of events in a large number of cases including most of the "important" ones that have been discussed in the literature. My methods and results have been almost completely ignored. For example, a recent review of the question of recruitment variability by the Chairman of this meeting (Sissenwine 1984) cites 96 references, including a large number on the history of particular stocks that I have analyzed, but without citing either my own work or that derived from, or associated with it.

My contribution to the theme of this meeting, in one sense then, has already been made, has had little or no effect and there is no reason to believe that this will change. I am concerned here with trying to analyze the reasons why this should be so, rather than demonstrating or insisting on the validity of my conclusions in any particular case and in competition with those of the many (indeed the majority of) eminent fishery biologists who have devoted time and effort in this field. My conclusion I can state immediately. There is little or no chance of a rapprochement between my own approach and that of the acknowledged experts in this field and precisely because of the difficulty I have in accepting their assumption of a basically "mechanical" or "physical" basis for the evaluation of the organism - environment interaction that is the common object of study.

I believe that I am closer to the position described by Popper and hope to demonstrate this much, at any rate, by the analysis of some specific examples that deal not with recruitment, per se, but with an aspect of recruitment that has not been ignored to the same degree and that was reviewed by Iles and Sinclair in 1982. This concerns, in the narrow sense, the question of "passive-drift" or "retention" and, in the wider sense, the spatial and temporal structure of marine communities and particularly at the level of the planktonic stage. The relevance of this to the theme of this meeting is obvious. The teleost larval stage is planktonic (with very few exceptions); it is generally accepted to be the part of the life history at which both the absolute abundance (Iles and Sinclair 1982) and its year-to-year variability (Cushing 1967) of a fish stock is largely established; it is also characterized in the accepted theory of fish migration (Harden Jones 1968) as entirely passive, as playing no positive part in the linking up of the life history into an organic whole. According to Harden Jones, the spatio-biological continuity of the life history is broken at this stage and has to be re-established by later life-history stages. It is for all of these reasons that I will be dealing with the concepts of "passive drift," the spatial heterogeneity of plankton and fish migration.

The Planktonic Stage of Marine Life Histories

The derivation of the word "plankton" with its implication of the "errant wanderer" implies a concept of biological and ecological "passiveness" which has dominated marine ecology since its inception; it is this concept that is being questioned. The approach I take is to analyze three specific cases from the literature that are sufficiently different in subject matter and type of physical (hydrographic) structure that is involved to cover a reasonably complete range and so to allow broader generalizations to emerge. These cases will be discussed subsequently in relation to two fields of study that have been identified as representing separate disciplines: that of "Spatial Patterns in Plankton Communities" (Steele 1978) and that of "Mechanisms of Migration in Fishes" (McCleave et al. 1984). The systhesis aimed for is one that focusses on the life-history aspects of the population as the fundamental biological unit that should be our major concern.

Hudson River Controversy

The Hudson River Controversy is an excellent example, both of the waste of research effort and money incurred as a result of assuming a purely physical basis for the distribution of early life-history stages of fish and of the reality of what I refer to as "biological modulation" (Iles and Sochasky 1985).

The judgement described above is not mine, but that of the commentators on the history of the controversy (Barnthouse et al. 1984). At issue was the degree to which the (early) life-history stages of the anadromous striped bass (Morone saxatilis) would be entrained in a proposed major hydroelectric scheme on the Hudson River. This led to many years of litigation on the part of the utility company and the United States Environmental Protection Agency in the evaluation of the results of "tens of millions of dollars" spent on research over more than a decade.

Many simulation models were derived without leading to a concensus between the antagonists. All were based on assumptions equivalent to that of "passive drift" downstream on the part of eggs and larval stages. The demonstration that "eggs and larvae" tended to accumulate around the salt front of the estuary led to a subsidiary hypothesis that an upper layer of fresh water moved downstream and a lower layer of salt water moved upstream.

Diurnal vertical migration by larval was supposed (hypothetically) to convert this physical feature into an "endless belt," in a model that involved a purely mechanical interaction of an unexplained behavioral pattern on the part of the larvae, the vertical migration and the hydrography. In discussing this, Barnthouse et al., and presumably all the protogonists, ignored Graham's work on herring larvae in the Sheepscote Estuary (Graham 1972) (not to mention Nelson's work on oyster larvae in the Chesapeake estuary, more than 50 years before) Moreover, the assumption of a regular diurnal movement in the analysis clearly is inconsistent with the lunar periodicity of the tidal regimes which afforded the only possible mechanism for the observed "retention" of the larvae of the striped bass on the basis of the assumptions of the model.

It was not until empirical models, based on the enormous data base accumulated over the years of research, were elaborated, that common ground for agreement was reached. The important conclusions that emerged (Swartzman et al. 1978; Christensen et al. 1981) were that the laws of hydrodynamic transport (which included a diffusion effect in an attempt to achieve a more realistic match between fact and model) could not account for the facts of the larval distribution and population dynamics.

Striped bass larvae were transported downstream far more slowly than the hydrodynamic models predicted. The Harden Jones criterion for passive drift, that larvae and water currents moved at the same rate, was not met and passive drift was refuted as the agency. Even at this, the full implications were not realized by Barnthouse et al. in their critique, for the "biological modulation," the degree to which prediction was not met was accounted for formally and conventionally by an empirically derived "transport avoidance factor." While this, of necessity, defeated the object of the simulation models, which was "the accurate prediction of movement and distribution based on realistic description of the underlying physical processes," no attempt was made to develop biological theories that were consistent with the observed facts and to account for the discrepancy.

All of this is familiar, for there is a parallel failure of hydrological analysis to account, quantitatively, for the persistence of plankton populations, on Georges Bank (Colton and Temple 1961). This is still accepted, by most workers, as a physical "paradox" rather than as a demonstration of the operation of complex biological mechanisms. The conclusions drawn by Barnthouse et al. (1984) included: that more understanding of underlying biological processes are needed and that short-cuts to solutions cannot be found through elaborate modelling exercises. Direct assessment techniques were more useful for addressing the answerable questions than were the hydrodynamic transport models and population simulation models - and at a fraction of the cost.

Clarke's Sagitta Populations on Georges Bank

A second example does involve Georges Bank and an important member of the holoplankton considered to be a significant predator on herring larvae, the chaetognath Sagitta elegans. Clarke et al. (1943) produced an excellent, and deservedly considered as a classic, paper on the Georges Bank population of S. elegans that complemented the work of Redfield and Beale (1940) in the Gulf of Maine of Huntsman and Reid (1921) in the Bay of Fundy and Gulf of St. Lawrence and the classic work in the east Atlantic of Russell (1932, 1933, 1939). Sagitta elegans on Georges Bank reaches a length of 30 mm and a mean maximum length of some 23 mm (Clarke et al.) and is therefore one of the larger species in the plankton, but even so, it was assumed to be very much a "passive" organism in its relation to the hydrography of the system.

Thus, Clarke et al. maintain (p. 201) that "...Sagitta may be used as a "current indicator" to aid in unravelling the involved current system of the region." Clearly, a statement such as this precludes absolutely any possibility of conceding that "internal" factors are involved in the resultant distribution. Moreover, this attitude is consistently maintained by Clarke et al. despite the fact that evidence was available for them to conclude "that a definite vertical migration was taking place in both the (central) Mixed Area and the (surrounding) Stratified Area..." This must mean that Clarke et al. did not associate vertical movement in the water column as playing any role in the maintenance of the Georges Bank population. That they recognized a "Bank" population that was distinct from the population of S. elegans described by Redfield and Beale (1940) in the (inshore of Georges Bank) Gulf of Maine is unquestionable, and indeed in their own words, "our ecological interest in the current system lies in the question of the degree of permanence of this eddy (Georges Bank) and in the extent to which the "bank water" can be regarded as biologically isolated from the surrounding regions." Again one must indicate the clear preference for the use of the physical to explain the biological implied in this comment. "Biological modulation" in the sense in which I use it is virtually excluded, and it is a major part of my thesis that this physical approach invariably produces inconsistencies in the analysis and explanation of distributional data. It is the particular merit of this particular case that Clarke et al., beginning with an excellent set of field data, maintain a highly competent argument from their particular viewpoint that clearly exposes the difficulties that they themselves see but are unable to resolve.

Some inconsistencies are not appreciated and the most important one concerns their treatment of the events at the western edge of their study area, that almost coincides with the 69° longitude and lies to the east of the Nantucket Shoals.

On page 214, they maintain that, because the density of Sagitta elegans along this largely logistically determined survey boundary was high, then "... at certain seasons of the year, at least, numbers of this species are transported by westerly current across South Channel towards Nantucket Shoals." Now they also demonstrate that there are two breeding seasons, one in April or May involving large adults, and a later one in the fall. This later one involves a smaller adult size, and produced young that they assume, "slowly mature to produce the relatively large group of adults found in March and April, thus completing the cycle" (p. 220). However, on page 215, they maintain that "at the easternmost stations, only large specimens of Sagitta elegans were taken, whereas at the western stations, the smaller sizes predominated. Evidently the remnant of the older animals persisted chiefly in central and eastern eddies, while the production of younger individuals was beginning most actively in the western part of the Bank." There is no question but that they accept that the Georges Bank population is self-sustaining, but here they are led, by the distributional data, to conclude that "recruitment" (of smaller individuals) takes place in the opposite direction to the movement that they had earlier suggested, also on distributional evidence, had transported the population off Georges Bank to the south and west!

As a side issue, the fact that the adult size in September, at which time herring spawn on Georges, was very much smaller than that in the March to May period, hardly argues for a specific adaptation as a predator on herring larvae!!

Clarke et al. comment on the conclusion reached by Redfield and Beale (1940) to explain the relative richness of the Georges Bank population of Sagitta elegans compared with the relative low level of abundance of the inshore Gulf of Maine. Redfield and Beale (1940) suggested that this reflected the relative hydrographic coherence, or continuity, of the bodies of water involved. The "residence time" in the Gulf of Maine was small because of through-circulation, "dislocating currents" in the words of Redfield and Beale. This was in contrast to the relative permanence of the Georges Bank hydrographic system. Clarke et al. maintain that their results "not only tends to confirm the general suggestions of Redfield and Beale, but also provides strong evidence on the degree of permanence of the (Georges) bank water." But the force, even the validity of the argument, is lost almost immediately. For, as Redfield and Beale themselves pointed out, the central area of the Gulf of Maine has a rich and persistent endemic crustacean population, whose particle size is such as to make them at least as vulnerable as Sagitta to "dislocation currents."

In addition, their analysis of the distribution of two other species of Sagitta (S. serratodentata and S. enflada) that occurred on the eastern and northeastern edge, but did not extend into the "Mixed Area" was also purely hydrographic. They assumed it represented the lack of penetration of the "Mixed Area" by water that had moved onto the eastern edge of the Bank from the south and east.* This, again, involved translating a biological distributional phenomenon into a (deduced) hydrographic phenomenon.

The "obvious" hydrographic analysis was complicated still further by the analysis of the distributional data of the two copepod species Pseudocalanus minutus, which was centred on the Mixed Area, and Calanus finmarchicus, which was virtually absent from the Mixed Area but which virtually surrounded it over the rest of the Bank (Clarke et al. 1936, p. 221, Fig. 10). The conclusion was that "a current carrying Calanus from the Gulf of Maine was flowing around the margin of the Mixed Area and forming a wedge between it and the water masses to the south. At the same time, mixed water, barren in respect to Calanus, from the central eddy of the Mixed Area appears to have been draining off to the west down the middle of the Bank."

They maintain that Calanus, like S. serratodentata and S. enflada is sharply excluded from the Mixed Area, whereas Pseudocalanus and S. elegans are chiefly abundant in it. That there is virtually complete distributional overlap between Calanus and the two Sagitta species along the eastern edge of the Bank, whereas they deduce two currents moving in opposite directions through this area of overlap, is not commented on or explained!

Nor is it realized that the whole basis for their argument is vitiated by the coexistence in the inner Gulf of Maine of a resident "crustacean" population, despite "dislocating currents."

The absence of Calanus from the Mixed Area causes further difficulties. The water of the Mixed Area is derived from the same area, the inner Gulf of Maine, as is Calanus so that temperature and salinity are excluded;

---

*This implies an anticlockwise semi-gyre that is in the opposite direction to the clockwise gyre that sustains the Georges Bank hydrographic system.

predation is rather hopefully invoked and sediment turbulence or some "essential element" that is lacking are all suggested. The conclusion is (and must be, surely) that "other ecological influences besides purely mechanical action of the current systems are apparently controlling the occurrence of *Calanus* on Georges Bank." Similarly, "... it seems probable that additional, as yet undetermined, factors may be important in accounting for the special richness of the population of *Sagitta elegans* in the Mixed Area."

However, in trying to account for the "especially favorable local conditions" for *Sagitta elegans*, once again the comparison with another neighboring *Sagitta elegans* population eliminates all "reasonable" explanations, for these populations exist in stratified waters to the south. This excluded the turbulence and homogeneity as a factor and, also, the shallowness - and the possibility of any specific depth preferences.

That plankton in general and *Sagitta* in particular can withstand "fairly big" physical changes was already evident (Fraser 1939) so that the conclusion had to rely essentially on:

a) the relative permanence of the water mass - which was really *deduced* from the fact that the *Sagitta* population was self-sustaining on the Bank itself;

b) an unexplained and unidentified "indirect influence" from the bottom itself, absent in deeper water, that favors reproduction and growth.

It must be stressed that all three authors (that included Bumpus!) were highly competent workers - indeed of the highest calibre, and the inconsistencies dealt with above were, for the most part, brought out by their full and frank discussion of the issues.

Two points can be made - that the "paradoxes" were revealed most clearly when the distributions of more than one species in the same area or those of different allopatric populations of the same species were compared. The second is that in one important sense, consistency *was* maintained in that at no time did Clarke et al. resort to explanations that dealt with any of the "internal" factors of the type raised by me in the introduction, and as will be shown below, this inability to concede that the mysterious "element" may be a biological faculty that recognizes space and time in an absolute sense is virtually unanimous, even today.

Savage and Hardy and the Phytoplankton of the North Sea

Another example concerns the North Sea and species of phytoplankton and especially the diatoms Rhizosolenia and Biddulphia. Both are found mainly in mid to deep water, Rhizoselenia being thought to enter the North Sea from the north and Biddulphia from the south and east, the latter being more of a coastal species.

In another classic work of the 1930's, Savage and Hardy (1935) describe the distribution and deduced seasonal movements of these phytoplankton elements in relation to the presumed "avoidance" effect of dense phytoplankton patches on herring schools. Hydrographic data was analyzed, in the way pioneered by Bohnecke (1922), to infer current direction and this was complemented by the use of deep-water drift bottles, under the supervision of another great name in the Marine Biology of the early 20th century, Carruthers.

The analysis by Savage and Hardy (1935) of the phytoplankton distributional data was based entirely on physical factors, mostly "passive drift" and an attempt was made to match the hydrographic data with the distributional data in a dynamic way to demonstrate this. In the same way as already shown for Sagitta and Georges Bank, several severe invonsistencies arise.

In October 1931, a patch of Rhizosolenia was found some 30 miles to the south and west of a Biddulphia patch off the German coast. Later they comment, "Two weeks after, the Rhizosolenia patch had drifted northeast into the Biddulphia zone and the two diatoms were again associated" (Savage and Hardy, p.). They postulate differential passive drift of two species of microplankton in the same current system - a physical impossibility. Indeed, they add "there was a suggestion that the (Biddulphia) mass had drifted slightly in a SE by S direction and had become associated with Rhizosolenia" (Savage and Hardy 1935). Another similar conclusion was reached concerning the flagellate Phaeocystis and on page 17, they say "The configuration and position of the Phaeocystis mass (Fig. 8) is curious in view of the direction of the currents shown in Fig. 7. The main mass appears to have drifted from the west in the wake of Rhizosolenia and partially joined up with a less dense mass near the Dutch coast."

A second type of inconsistency concerns the interpretation of an apparent concentration of diatoms, by "flattening" at the leading edge of the presumed drift. "(This) shape of the patch may well be due to its meeting the current passing up the Dutch coast." Again, if one assumes the "passive contaminant" approach, this cannot be explained.

A third type of inconsistency concerns the nature of the water movements themselves, particularly near the south and west edge of the Dogger Bank. The identification of two patches of Rhizosolenia some 110 nautical miles apart, one on the southwest of the Dogger and the other to the northeast some two weeks later is explained by passive drift at an equivalent constant rate that would, for example, be completely incompatible with either the current system as it is now known (Lee 1980) or with the postulated "drift" of herring larvae across the North Sea (Harden Jones 1968; Cushing 1967, 1975; Kamp and Corton 1982). None of these later authors draw attention to this discrepancy, nor do Savage and Wimpenny explain how, in such a volatile environment, annual surveys in the southwest Dogger area reveal patches of Rhizosolenia at much the same time and place over a period of nine years (Fig. 2). The probability of "freeze-framing" patchiness of the type they assume, in the way that they report on, is very low.

These three examples all show how an ingrained belief in a passive role for planktonic forms influences both the interpretation of the observational data and the way in which research is planned and science carried out. It can be shown that this point of view also characterized the thinking of the European pioneers in fisheries biology during the early years of this century and as evidenced particularly in the early volumes of the ICES publication Journal du Conseil, but it still persists.

This can be demonstrated by reference to two volumes of the proceedings on two NATO Conference Series in Marine Sciences, one published in 1978 on Spatial Pattern in Plankton Communities (Steele 1978), the other in 1984 on Mechanisms of Migration in Fishes (McCleave et al. 1984). Both were intended to be authoritative and the contributors represent a cross-section of acknowledged experts in the fields being considered.

Plankton Behavior and the Structure of Marine Ecosystems

Following the managerial successes of ICNAF in the early 1970's, the mid 1970's saw the publication of a number of "texts" on what had become very much a live issue - the interaction of fisheries and biology. In

1976, one of these, The Ecology of the Seas (Cushing and Walsh 1976), contained an article by Steele that leaves little room for misrepresentation as to what was accepted at that time.

Steele (1976) begins by accepting that plankton are supposed to be at the mercy of the sea, concedes that zooplankton can migrate vertically but concludes that any directed horizontal motion (except on a very small scale) appears to be impossible so that the horizontal variations (in distribution) should depend on physical factors. This influences the kind of study that is applied to these systems, and justifies the relevance of research, for example, on salinity distribution and the occurrence of essential nutrients - and treating such environmental factors as "determinants," the "independent variables" of the system.

But, Steele concludes that "in fact, both the microscopic plants and the small zooplankton seems to display much greater variability than the environment in which they live" (Steele 1976, p. 99) - a factual situation that challenges the very assumptions on which Steele's treatment appeared to be based. This does not seem to concern Steele unduly, however, who looks for "corresponding scales of water movement (which will) indicate the probable forces which can disperse and mix these populations."

What neither Steele nor other workers who advocate the matching of water movements and organisms at finer and finer spatial and temporal resultion realize is that the more successful they are in determining the details of the life-history trajectory, the more difficult it becomes to explain the systematic basis for the "choice" by the individual organism of the particular position occupied at the particular time.

Steele (ibid.) does advocate the modelling of <u>interactions</u> between the physical and the biological but this is approached as a mathematical exercise that involves biological "parameters" that are selected for their mathematical convenience. The biological population as an ontogenetic unit and, if we are to believe Mayr (1982), the fundamental unit of modern evolutionary theory, is virtually ignored. Thus, the most meaningful biological aspect of any ecosystem, characterized by Steele (ibid, p. 114) as "population stability" is defined as the ability to absorb fluctuations imposed by "external" factors which are referred to as "the physical environment" and "predators."

This approach does not recognize that the persistence of biological patterns that we see at this particular stage of evolutionary history is a "time-slice" of processes that have a continuous history over the whole of the period of the existence of life on this planet. This has exposed each population unit to a variety of "external" factors that far exceeds in scope the particular set that can be described and measured at this stage of the process. The object of study, the "organism," contains a set of instructions that has met this challenge to survival and it is inconceivable to me that this is the result of a passive response to external signals. To return to the point made by Brett (1970) (see above) on the complexity of the relationship of fish and temperature, the environmental "signal" is interpreted in relation to the current and "unique" environmental situation. Quite apart from the way the "reaction" to the signal is generated there is the logical necessity to compare this current signal with an internal reference standard to "decide" whether any reaction is called for.

Nor do we have to rely on an indefinitely long evolutionary perspective to justify this point. The most recent glaciation was at its height only 15,000 years ago and virtually all the area now occupied by the classical temperate fisheries and in which by far the bulk of fisheries and fisheries ecological theory is based was not available to fish at all.

And, Steele (page 114), to emphasize the gulf between reality and theory, points out that "nearly all theoretical studies of the problem consider the distributions of organisms to be uniform in space and deal with changes in time (May 1973)" which indicated the degree to which biological reality is sacrificed to mathematical "tractibility."

Spatial Patterns in Plankton Communities

The attitude that plankton plays no constructive part in its own spatial (and temporal) organization is maintained virtually unmodified throughout the 1978 synthesis, as the following quotations from Steele's (1978) summary shows:

> "The nature of water movements and dispersion make it impossible to obtain a pure time series of events in the open sea" (Steele 1978, p. 1).

This effectively eliminates the possibility of dissecting out any particular life history and, as the study of recruitment involves just this, the relevance of the study of spatial patterns as outlined here is difficult to accept:

> "Patchiness might be seen as a deviation of the biological spectrum from the physical spectrum of turbulence rather than increases or decreases from a uniform spatial distribution" (Ibid., p. 7).

Neither of these view points accept biological organization; the approach suggests the physical oceanographers treatment of "Stokes Drift" (see below):

> "Phytoplankton are assumed to be carried passively by both horizontal and vertical currents. Zooplankton have little directed movement at horizontal scales above a few meters, but can move vertically over tens of meters in response to diurnal changes in light and also, possibly, in relation to vertical variation in food concentration" (Ibid., p. 9).
>
> "Phytoplankton patches are determined by the interaction of growth and grazing; if (these are) in balance, then phytoplankton variability would depend only on physical factors. This, however, depends on the assumption of spatial uniform herbivore distribution" (Ibid., p. 10).
>
> "...The three-dimensional nature of the physical interactions... make it difficult, if not impossible, to separate horizontal and vertical variability."

There is hardly a statement in this commentary that cannot be analyzed to demonstrate how different the approach is compared to that advocated by the use of the concept of "biological modulation." This exploits environmental heterogeneity to achieve the goal of "closure" of the life history, and it both implies and assumes both spatial and temporal continuity. That this analysis of Steele's summary is not an exaggerated impression of the overall sense of the contributions in this volvume can be easily demonstrated.

Thus, Levin (1978, p. 433) maintains that the "population dynamics depend critically upon the spatio-temporal characteristics of the environment" and even though he does criticize the "classical mathematical approaches," his incorporation of the biological "factors" is in terms of "parameter space," "boundary-layer behavior," etc.

Evans (1978), in dealing with the interaction of the physical horizontal "shear effects" and the biological vertical movements of plankton, treats them essentially as independent, as one is forced to if one is referring to a population average.* The interaction is thus mechanical and not "organic," with the physical factor as the determinant, so that the resultant geographical position does not involve the facultative operation of adaptive factors on the part of plankton.

Fasham (1978) deals with "the application of some stochastic processes to the study of plankton patchiness" which clearly cannot contribute much to the concept of a biological faculty to "create" coherent and consistent "organized" patterns.

---

*The Harden Jones (1968) theory of migration treats the non-tidal residual as an "average" system, over the whole water column and the whole year. This cannot accommodate the life-history aspects or behavioral aspects of planktonic (i.e. fish larval) forms.

And to complete what is only a sample of the approach shared by almost all of the contributors, Pugh (1978, p.) comments that "Steele has pointed out the importance of considering the food chain relationships of marine organisms as these are factors which may affect the spatial structure of the ecosystem." This remarkably banal statement, for it is inconceivable that "food chain relationships" do not affect the structure of the ecosystem, precedes a treatment by Pugh (1978) which ignores the basic taxonomic unit, the population of a particular species, that must also be the functional unit of any ecological system.

Fish Migration and the Recruitment Question

The proceedings of the NATO advanced research conference on fish migration, held in 1982, was published in 1984 (McCleave et al. 1984) and, as is to be expected, expresses a more biologically oriented view.

By this time, the existence of biological mechanisms of a type that must be categorized as "internal" is well attested, and is widely known and accepted in some research fields.

Thus, a review of fish migration in rivers (Northcote 1984) gives evidence for the existence of "strong visual association with temporary home areas" that implies subsequent "recognition" (p. 328), visual cues, polarized light recognition with a link to solar navigation, the perception and use of magnetic fields (to include magnetic compass orientation), olfactory imprinting of both environmental molecular species and con-specific pheromones and other similar phenomena. These are known to be incorporated into an epigenetic program that determines a varying response pattern that is structured hierarchically and sequentially. This is a much more specific expression of the situation outlined by Brett (1970) (see above) and, significantly, is well established, particularly in anadromous salmonids. This attests both to its existence in the marine environment, as well as fresh water and in an "ancient" and perhaps ancestral group of teleosts (Greenwood et al. 1966). The marked local variation (i.e. applied to "stocks") of a highly adaptive nature and that has a genetic basis is also maintained (Northcote 1984, p. 339), so that it is impossible to deny the existence of such mechanisms and difficult to explain why they are never referred to in any ecosystem model. Even so, there is a curious reluctance to concede the full implication of these facultative characteristics. For example, Johnsen (1984) deals with "chemosensory orientation" in fishes in a "classical" experimental context that talks of "facilitation of directional locomotion between two points," and classifies chemical signals as just another environmental signal and that act as "releasers" for rheotactic movement. That this refers to individuals that Johnsen recognizes had been "imprinted" with specific odors when very young, and thus invested with an internal set of reference standards that were maintained intact and at fixed levels throughout a subsequent section of the life history that experienced quite radically changing environmental conditions, is not seen as somewhat incongruous to the methods actualy advocated. And, we find DeAngelis and Yeh (1984) in the same volume treating the "animal as a mechanism" and applying a model that neither accepts the fact of internal factors nor can be in any way consistent with it.

This lack of discrimination between theoretical approaches which cannot be considered in any way equivalent or consistent is a common feature of modern ecology and one that is not easily accounted for, and that this should be a conspicuous feature of the report of the NATO Advanced Research Institute whose main purpose is to set the course of future studies by scientists (van der Steen 1984, p. 421), emphasizes the problem.

Van der Steen's (1984) call for improved conceptual clarity, to be able to deal with the complexity inherent in the "mechanisms" tht are being studied, is his suggestion for an improvement in the situation. Nevertheless, his characterization of passive drift as a relatively unproblematical notion (van der Steen, p. 434) is puzzling! Van der Steen works in the field of the philosophy of science and makes the point that biologists do not usually consider topics belonging to philosophy.

Walraff's (1984) contribution to the conference proceedings makes the much more pertinent point that biologists in one field are surprisingly ignorant of, or at least unimpressed by, accepted generalities in other fields. His review of bird migration and navigation demonstrates that birds have developed "spontaneous intended directions of migration that are population-specific and permit naive juveniles to fly particular compass directions and distances." Sun, moon and magnetic compasses are indicated - which, incidentally, means that "diel" and "lunar" or "tidal" periodicities are also feasible. The ability to return to a known site from an unknown one is established, and a "map and compass" mechanism is demonstrated. In addition, atmospheric odors are implicated in both navigation and home recognization. All of these are "faculties" in the sense implied by the use of terms such as biological modulation the LTD principle (Iles and Sochasky 1985) and others. In particular, the "map and compass" mechanism is an internal set of permanent reference "materials" tht must have an internal bio-physical basis.

The similarity between birds and fishes, in that they have to complete their life histories in a three-dimensional habitat, is referred to by Walraff as obvious, and the evolutionary success measured as ecological importance and taxonomic diversity of the two classes of vertebrates (with the bony fishes easily the more successful) must surely be associated with their ability, at the population-specific level, to complete their spatial-temporal trajectory.

In the light of all this, the a priori assumption by Harden Jones (1968) that a sense of direction in fishes is unthinkable, and ranked for its acceptability with the anthropocentric "sense of honor" is an unnecessary and unjustified proscription that excludes fish from comparative study across the vertebrate classes within a single phylum.

Thus, the summary contribution to the proceedings (McCleave et al. 1984b) refers to Walraff only in connection with his comment on "redundancy" in the systems that support the faculties of homing, recognition, navigation, etc., and there is little indication that the fact of the existence of these faculties in fishes can be accepted "a priori"; or at least that there are sufficient parallels in incidental evidential support between fish and birds to justify their acceptance as reasonable assumptions in conceptual model making.

Such a reluctance to accept evidence in one taxonomic group as applying to another relatively closely related group that shares some basic and relevant ecological features, if applied in biology generally, would paralyze discussion. Modern evolutionary theory depends on the applicability of results in prokaryotes to the whole of organic life. Key examples in the insects (e.g. Drosophila and Biston bitularia) and in the human (sickle all anaemia) could not possible sustain the weight of argument that they bear currently.

The unwillingness or inability to concede an absolute directional sense in fishes even when it is the most obvious and most parsimonious explanation is well illustrated by Harden Jones (1984, p. 67) discussion of consistent directional swimming at the surface. An inertial system based on the sensitivity of the semicircular canals would have only limited guidance capability and only if reinforced by other "external clues" at regular intervals. These, it has to be concluded, are unlikely in the extreme to exist, for some species at least, and for others only if the bottom was sampled at regular intervals for undefined "topographical clues." How all of this could possibly work unless the fish had an internal directional memory for reference and feedback adjustment is not dealt with. All of this is put forward because, to quote Harden Jones (1968, p. 2), a sense of direction is as unlikely as a sense of honour!!

One senses that there is a basic conflict or confusion between two fundamentally different approaches that could not be resolved, and the summary conclusions of the proceedings are worth careful study and evaluation in this light.

McCleave et al. (1984b, p. 547) maintain that there is already "a sufficient body of knowledge on (their) migrations to obviate the need for data gathering for data gatherings sake" and that what is known should be used to formulate testable hypotheses, that are generated in a conceptually complete framework. But this claim follows a litany of the shortcomings of the current conceptual framework that is so comprehensive as to be virtually complete. Thus, the role of learning is not understood sufficiently; there is little definitive work on the various orienting mechanisms; the effect of directional bias is not quantitatively worked out; the organization of orienting mechanisms is little known, particularly in relation to its hierarchical nature and the degree of redundancy built in; the ontogeny of the sensory systems is poorly understood as is their cyclical variability; the degree to which "true" passive drift accounts for migration is undocumented - a comment that avoids the issue of the purely negative role afforded it in the original Harden Jones (1968) model; the cues that trigger "selective movements" associated with the "new" theory of selective drift are not known, etc.

All of this can be summed up in the recognition of "a great need - pervading most of our migration research - for a more fundamental understanding between physical and biological features of the environment and observed behaviour."

I maintain that the recognition of the internal organization of the individual as a member of a population (e.g. "stock") that is the ecological unit is one issue to be considered. Another is that the difference of viewpoint between the "internal" and the "external" is almost complete.

The external viewpoint is dictated by the research interests of the individual and/or group to which he is recognizably affiliated. In this, it is "anthropocentric" in the sense that the questions to be addressed can be expressed only in terms of the technical and intellectual tools that are available, and that are acceptable to the group. This tendency militates against the acceptance of "ideas" or "discoveries" that are generated by other methodologies, and contradicts the axiom (see above), that there is no logic of discovery.

Rickersen (1978) sees the aquatic ecosystem as demonstrating "spatial and temporal heterogeneity" which is the product of many physical processes interacting with many biological processes. For the organism there is no heterogeneity. Unless complete homeogeneity of spatial and temporal events in the life history is maintained, survival is not possible, for itself, or for the population to which it belongs. There is, up to now, no problem; the solution is self-evident, and one that is evolutionarily robust in the Thoday sense (Dawkins 1982).

For those involved with fish migration, the main issue at the moment seems to me to be the difficulty of dealing with the base of the migration triangle of Harden Jones (1968), still acceptable to many (Cushing 1986) and enshrined in the phrase "passive drift." There is no reason not to accept the strong probability of the existence of "navigation," "homing," etc. in fishes and the theory of selective tidal stream transport that is now so popular (Arnold and Cook 1984) can be viewed as one mechanism that is associated with "homing." But given this, there is no reason to restrict the use of such faculties to any one segment of the life history, or conversely, to deny its availability to another. For example, as long ago as 1972, Zijlstra was maintaining that metamorphosing plaice larvae became demersal and actively migrated the 20-40 miles from their drift path to the Waddensea, their nursery. Surely this means that any life-history stage that exhibits depth preference, or vertical movement in the water column, can also "migrate actively" - or more generally control its own position, and in relation to the other members of its population unit. Newly hatched herring larvae show depth selection and vertical migration is established very early on in the larval stage (Blaxter and Hunter 1982). It was precisely this that was advanced as the "ontogenetic principle" (Iles and Sochasky 1985).

The remaining question was phrased by Arnold and Cook (1984b, p.), whether "the underlying mechanism is, as we suspect, based on a succession of temporal cues or, instead, involves a sense of direction on the part of the fish." Accepting this as the question, one might ask which answer is consistent with the following argument.

The same solution has performed adequately over the whole of evolutionary history. The physical changes that have occurred in the north Atlantic over the last ten thousand years or so have been extensive enough to invalidate any theory which depends on the recognition of any particular set of external environmental signals operating to key the life history to any specific contemporary current system. Biological and evolutionary continuity cannot be denied and we are forced to accept an internally controlled and operated system that includes faculties to associate a particular set of "local" conditions with the "global" fact of survival of the life-history unit. The solution must be both internal and general and possess flexibility in the evolutionary scale and fixity in the life-history scale. It may be difficult to recognize this as a prescription for a particular known genetic system, but it is impossible to reconcile it with a contemporaneous set of signals. There are no sign posts in the sea and the concept of external signals should no longer guide the conduct of research.

References

Arnold, G.P., and P.H. Cook. 1984. Fish migration by selective tidal stream transport: first results with a computer simulation model for the European continental shelf. :227-261. In: Mechanisms of migration in fishes. (NATO Conference series. IV, Marine Sciences, Vol. 14). Edited by: J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York.

Barnthouse, L.W., J. Boreman, S.W. Christensen, C.P. Goodyear, W. Van Winkle, and D.S. Vaughan. 1984. Population biology in the courtroom: the Hudson River controversy. Bioscience 34(1) :14-19.

Blaxter, J.H.S., and J.R. Hunter. 1982. The biology of the clupeoid fishes. Adv. Mar. Biol. 20 :1-223.

Brett, J.R. 1970. Fish - the energy cost of living. :37-52. In: Marine Aquiculture. Edited by: W.J. McNeil. Oregon State University Press, Corvallis. :172 p.

Colton, J.B., and R.F. Temple. 1961. The enigma of Georges Bank spawning. Limnol. Oceanogr. 6 :280-291.

Cushing, D.H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge. :278 p.

Cushing, D.H. 1986MS. The migration of larval and juvenile fish from spawning ground to nursery ground. J. Cons. Cons. Int. Explor. Mer :21 p.

Cushing, D.H., and J.J. Walsh. (Editor.) . 1976. The ecology of the seas. W.B. Saunders Co., Philadelphia. :467 p.

Dawkins, R. 1982. The extended phenotype; the gene as the unit of selection. W.H. Freeman and Company, Oxford. :307 p.

DeAngelis, D.L., and G.T. Yeh. 1984. An introduction to modeling migratory behavior of fishes. :445-469. In: Mechanisms of migration in fishes. (NATO Conference series. IV, Marine Sciences, Vol. 14). Edited by: J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York.

Dickson, C.A. 1986MS. [Chedabucto Bay winter herring survey.] Cruise report, E.E. Prince, P330, Jan. 18 to Feb. 2, 1986. Canada Dept. Fish. Oceans, Atl. Fish. Serv. Mar. Fish. Div. :4 p.

Evans, G.T. 1978. Biological effects of vertical - horizontal interactions. :157-179. In: Spatial pattern in plankton communities. NATO Conference Series IV, 3. Edited by: J.H. Steele. Plenum Press, N.Y.

Fasham, M.J.R. 1978. The application of some stochastic processes to the study of plankton patchiness. :131-156. In: Spatial pattern in plankton communities. NATO Conference Series IV, 3. Edited by: J.H. Steele. Plenum Press, N.Y.

Graham, J.J. 1972. Retention of larval herring within the Sheepscot Estuary of Maine. US. Nat. Mar. Fish. Serv. Fish. Bull. 70:299-305.

Greenwood, P.H., D.E. Rosen, S.H. Weitzman, and G.S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131(4) :339 -456.

Iles, T.D. 1973a. Interaction of environment and parent stock size in determining recruitment in the Pacific sardine, as revealed by analysis of density - dependent 0 - group growth. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164: 228-240.

Iles, T.D. 1978MS. Environmental pressure and intra - and inter - year class competition as determinants of year class size. 22In: Symposium on the biological basis of pelagic fish stock management, Aberdeen, Scotland, July 1978. International Council for the Exploration of the Sea. :28 p.

Iles, T.D. 1981. Cod - herring interaction in the southern Gulf of St. Lawrence. The application of a new stock/ recruitment hypothesis. Int. Counc. Explor. Sea Comm. Meet. 1981(H42) :23 p.

Iles, T.D. 1981. A comparison of two stock / recruitment hypotheses as applied to North Sea herring and Gulf of St. Lawrence cod. Int. Counc. Explor. Sea Comm. Meet. 1981(H48) :24 p.

Iles, T.D., and J.B. Sochasky. 1985. Drift and current selection, transport and retention, dispersal and homing; a review of concepts and principles relevant to the temporal and spatial organization of marine systems. Int. Counc. Explor. Sea Comm. Meet. 1985(L14) :18 p.

Iles, T.D., and M. Sinclair. 1982. Atlantic herring: Stock discreteness and abundance. Science (Wash. D.C.) 215 :627-633.

Johnsen, P.B. 1984. Establishing the physoiological and behavioral determinants of chemosensory orientation. :379-385. In: Mechanisms of migration in fishes. (NATO Conference series. IV, Marine Sciences, Vol. 14). Edited by: J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York.

Jones, F.R.H. 1968. Fish migration. Edward Arnold Publishers Ltd., London. :325 p.

Jones, F.R.H. 1984a. A view from the ocean. :1-26. In: Mechanisms of migration in fishes. (NATO Conference series. IV, Marine Sciences, Vol. 14). Edited by: J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York.

Kamp, G.v.d., and A. Corten. 1982. A hypothesis for the decline of the Dogger Bank herring stock. Int. Counc. Explor. Sea Comm. Meet. 1982 (H30) :15 p.

Lee, A.J. 1980. North Sea: physical oceanography. :467-493. In: Elsevier Oceanography Series 24B. The north - west European shelf seas: the sea bed and the sea in motion. II. Physical and chemical oceanography, and physical resources. Edited by: F.T. Banner, M.B. Collins, and K.S. Massie. Elsevier Scientific Publishing Company, Amsterdam.

Levin, S.A. 1978. Pattern formation in ecological communities. :433 -465. In: Spatial pattern in plankton communities. NATO Conference Series IV, 3. Edited by: J.H. Steele. Plenum Press, N.Y.

May, R.M. 1978. The evolution of ecological systems. Sci. Am. 239(3) :161 -175,242.

Mayr, E. 1982. The growth of biological thought -- diversity, evolution, and inheritance. The Belknap Press of Harvard University Press, Cambridge, Massachusetts. :974 p.

McCleave, J.D., F.R.H. Jones, W.C. Leggett, and T.G. Northcote. 1984. Fish migration studies: future directions. :545-554. In: Mechanisms of migration in fishes. (NATO Conference series. IV, Marine Sciences, Vol. 14). Edited by: J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York.

McCleave, J.D., G.P. Arnold, J.J. Dodson, and W.H. Neill. (Editor.) 1984. Mechanisms of migration in fishes. (NATO Conference series. IV, Marine Sciences, Vol. 14). Plenum Press, New York. :574 p.

Medawar, P.B. 1969. Induction and intuition in scientific thought. Methuen & Co. Ltd., London, England. :62 p.

Nelson, J. 1911. Report of the biologist. Rep. Biol. Dept. N.J. Agric. Coll. Exp. Stn. 31(1910) :183-218.

Nelson, J. 1917. An investigation of oyster propagation in Richmond Bay, P.E.I., during 1915. Contrib. Can. Biol. No. 6(1915-1916) :53-78.

Northcote, T.G. 1984. Mechanisms of fish migration in rivers. :317-355. In: Mechanisms of migration in fishes. (NATO Conference series. IV, Marine Sciences, Vol. 14). Edited by: J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York.

Pugh, P.R. 1978. The application of particle counting to an understanding of the small - scale distribution of plankton. :111 -129. In: Spatial pattern in plankton communities. NATO Conference Series IV, 3. Edited by: J.H. Steele. Plenum Press, N.Y.

Richerson, P.J., T.M. Powell, M.R. Leigh-Abbott, and J.A. Coil. 1978. Spatial heterogeneity in closed basins. :239-276. In: Spatial pattern in plankton communities. NATO Conference Series IV, 3. Edited by: J.H. Steele. Plenum Press, N.Y.

Savage, R.E., and A.C. Hardy. 1935. Phytoplankton and the herring. Part I. 1921 to 1932. Minist. Agric. Fish. Fish. Invest. Ser. II, Vol. 14 (2) :73 p.

Steele, J.H. 1976. Patchiness. :98-115. In: The ecology of the seas. Edited by: D.H. Cushing and J.J. Walsh. W.B. Saunders Co., Philadelphia.

Steele, J.H. 1978. Some comments on plankton patches. :1-20. In: Spatial pattern in plankton communities. NATO Conference Series IV, 3. Edited by: J.H. Steele. Plenum Press, N.Y.

van der Steen, W.J. 1984. Methodological aspects of migration and orientation in fishes. :421-444. In: Mechanisms of migration in fishes. (NATO Conference series. IV, Marine Sciences, Vol. 14). Edited by: J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York.

Wallraff, H.G. 1984. Migration and navigation in birds: a present - state survey with some digressions to related fish behaviour. :509 -544. In: Mechanisms of migration in fishes. (NATO Conference series. IV, Marine Sciences, Vol. 14). Edited by: J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York.

Zijlstra, J.J. 1972. On the importance of the Waddensea as a nursery area in relation to the conservation of the southern North Sea fishery resources. Symp. Zool. Soc. Lond. 29 :233-258.