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Fisheries Oceanography and the Nature of Carrying Capacity for Larval Marine Fishes

by

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INTRODUCTION

As a background to facilitate the application of new environmental data to the NAFO fisheries management, this essay reviews recent fisheries management science responses to environmentally induced variabilty in yield. From this, attention is drawn to year-class-strength formation processes as being the connection between the environment and eventual yield fluctuations in well managed fisheries. Deriving the premises largely ad authoritatum, the larval stage is concluded to be the time when the environment expresses its effects. A recent theory, density-dependent interactive growth and mortality, is used as a working hypothesis to explore and review the interaction of larval fishes and their environment. The question then becomes, what is the nature and source of the variations in relevant environmental indices? To answer this, an exploration of the literature on the North Sea is reported. The basic conclusion is that attention to very large scale atmosphere circulation indices is required, and that we have only just begun to examine how these are translated into local effects on larval fish survivorship.

For reasons that I hope will become clear, the most important question in fisheries oceanography is currently:

> "How does ocean climate variability affect the year-class strength of commercial fishes?"

The economic payoff theoretically possible from predictions based on an answer to this question has resulted in investment by the industralized maritime mations into studies of the survivorship of eggs, larvae, and juveniles of marine fishes. A large number of such studies were being conducted during the seventies, at least one in every major fishing region. I have tried to look for a robust paradigm and supporting research examples that will allow a reasonable address to the above question in the Northwest Atlantic. The analysis of researches in other areas should identify oceanographic factors that can be expected to 'drive' the Northwest Atlantic ecosystems.

FISHERIES SCIENCE

The ICES symposia 'Stock and Recruitment' held in 1980 (Parrish 1973), 'Marine Ecosystems and Fisheries Oceanography' held in 1976 (Parsons et al. 1978), 'Early Life History of Fish' held in 1973 (Blaxter 1974) and the 'North Sea Fish Stocks-Recent Changes and Their Causes' held in 1975 (Hempel 1978), have served well to create an international scientific community that is cooperatively searching for anwers to questions in fisheries oceanography. Today's fisheries biologist is less than ever an interpreter (or rather a haruspex) of fisheries catch statistics. The modern researcher, to judge from the papers of these symposia, must be facile in physical and biological oceanography, population and community ecology, meterology, climatology, myriad instrument techniques, must possess calmness in the face of the computerized mathematical statistics of modern stock assessment techniques, and have a knack for engineering. Somewhere along the line a modicum of investigative biological thinking (Pielou 1981) is required, but often overlooked.

An air of desperation induced by the crashes of many of the world's largest fisheries in the sixties and seventies the pressure to produce annual stock assessments, and in NAFO, 5 year predictions of catches and quotas, amplifies this remark in the summary of the 'Stock and Recruitment' symposium 11 years ago...

> "In short, the field of fisheries science, like all other aspects of environmental science and ecology has taken on an urgency and a hectic quality that were absent in the past. This may be beneficial or it may simply result in rapid movement without forward progress" (Slobodkin 1973).

By 1981 we have watched the populations crashes of several stocks that were felt to be under a theoretically sound management regime[1]. Our response from the concept of maintaining the maximum possible exploitation pressure on a fish population, retreating from'MSY' to the safer grounds of $F_{0.1}$ or $F_{2/3MSY}$ (Larkin 1977; Doubleday 1976; Gulland 1978). This can be recognized as an abandonment of simplistic theory and a healthly return to empiricism: surely no one really believed marine populations could be managed on the basis of models with 3 or 6 parameters and no reference to the environment? Secondly, a necessar interest arose in the mechanics behind stock abundance. New theories of marine abundance were required, theories able to cope with shifts in ocean climate, changes in fish distribution, environmental and multi-species interferences with year-classes strength formation, and that formed a connection to the rest of biological science by reference to the central paradigm, evolution. A recent appraisal of ecological modelling by Pielou (1981) provides valuable guidelines for the generation of these theories, with warnings of the poorly appreciated difficulties involved. The responses of fishes to their environment must be shown to be adaptations that maximize the probability of reproductive success of each individual involved. The applications of fishing pressure to evolved systems can only be dealt with predictively if we understand what the fishes are trying to do (Isles 1978), and the problems they have to overcome to survive in an environment that is hostile, noisy and dilute.

YEAR-CLASS STRENGTH PREDICTION AS THE OBJECTIVE OF FISHERIES SCIENCE

Fisheries management might be considered to have, as its objective, leaving the sexually mature biomass of each fish stock at a level, just before each spawning season, that maximizes the number of eventual new recruits to the commercial fishery. The theory has long existed to optimally harvest (for either dollars or protein yield) a recruiting year-class based on growth and mortality rate calculations Beverton and Holt 1957). Without an exception that I am aware of, for every stock we still seek to determine what this optimal sexually mature biomass is. The branch of fisheries science addressed to this problem is called the 'Stock and Recruitment Problem'. It is a conceptually simple problem in a single species context, that defies solution. Scattergrams of stock biomass and the year-classes sizes that re produced from the gametes of that stock are infamous for their lack of correlation; the relationship is considered to be obscured, classically, by variability in other components of the ecosystems. These other components include fluctuating abundances of invertebrate and vertebrate predators upon fish eggs and larvae, competition within and between species of larval fish (neither of which has been demonstrated), varying predation by larger fish upon the juvenile stages, variation in the production and availability of food for larvae and juveniles, varying physical conditions that directly affect the survival of young fish (such as transport,

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[1] See "Symposium on the Biological Basis of Pelagic Fish Stock Management - Aberdeen, Scotland, 3-7 July 1978". In the Northwest Atlantic, this must include the Gulf of St. Lawrence herring and the Newfoundland capelin stocks.

respitation rate), and not unexpectedly, the interactions of all possible combinations from this list. Undoubtedly many stock-recruit investigations would become clearer if the independent variable, "stock biomass", were more carefully represented as "viable eggs" as emphasized by Beverton and Holt (1957) and Ricker (1958).

Fisheries oceanography, as a field within the science of fisheries management should therefore be primarily involved searching for explanations of the variance around stock-recruit relationships. Its role in this search is to provide testable mechanisms that control the survivorship of the early life history of fish. The integral of this survivorship determines the percentage of eggs that will eventually appear as recruits to the fisheries. The mechanisms involved often depend upon the time-frame that the question is posed under. The correlation of year-class strengths to a matrix of all available environmental indices and associated lag vestors (not to mention the linear combinations possible), is an obviously ill-conditioned problem, and fisheries managers are justifiably cautious of relying upon a priori correlations for predictions. Reasons for a low return from naive statistical searches for correlations are discussed in Akenhead et al. (1981), Sharp (1981) and Austin and Ingham (1978). The absence of a mechanistic model in such correlations can be expected to lead to failures in predictions as conditions extended to the correlation change. Famous examples of dead correlations are Carruthers et al. (1951) for North Sea haddock, Chase (1955) for Georges Bank haddock, Lett and Kohler (1976) for Gulf of St. Lawrence cod, and Bannister et al. (1974) for North Sea plaice. Akenhead et al. (1981) list some of the outstanding local correlations of fish and environment, adding to longer lists compiled by Tomczak (1977) and Hela and Levastu (19). Particularly interesting are environment-recruitment correlations that do not have significant stock effects. Southwest Nova Scotia herring recently have been correlated to wind and sea level fluctuations with 86% of recruitment explained. Stock size was not important variable (Sinclair, Iles, and Sutcliffe 1980). Gulf of Maine yellowtail was presented by Sissenwine (1974) as being largely 'driven' by sea surface temperature and not having a significant contribution from stock size. The environment explained 83% of the variance over a long time series. In stark contrast, Deriso (1981) presents a delay-difference model for yellowtail that explains 76% of the catch record without any reference to environmental effects. A similar contrast between successful environmental correlation and equally successful stock effects modelling exists for Gulf of St. Lawrence lobsters. Sutcliffe (1973) presents lobsters as a correlate with the sum of freshwater discharges into the Gulf, but a contrasting auto-correlation model (Boudreault et al. 1977) of lobster landings in the Magdalen Islands explains 46% of variation without reference to the environment. These are mentioned merely as two recent and local contributions to the long-standing fisheries vs. environment disputes, the most famous of which include the Thompson-Burkenroad dispute over Pacific halibut (Skud 1975), the California sardine collapse (Iles 1973; Murphy 1966), and the changes in the North Sea fisheries (Hempel 1978a,b; Cushing 1980). No doubt a similar agreement is about to begin over the recently documented changes in the Northwest Atlantic ecosystem, given the recent population explosion of sand-eels in the Gulf of Maine and Scotian Shelf (Sherman et al. 1981) in a period of great changes in climate and fishing pressure.

> "What we have seen, and probably always will see, from monitoring fisheries, are the stocks' responses to simultaneous exploitation while climate changes. Therefore ascribing the response entirely to either climate change or to fishing activity is impossible" (Pella 1978).

This interrelationship between environmental effects and fishing pressure, leading to dramatic but confounded changes, must exist because destruction of the accumulated spawning stock (speaking in the single-species model) somehow leads to increased sensitivity of fish populations to the environment. The mechanisms of long and short term population persistence in the face of temporal environmental changes (longetivity, migration, stock area, colonization) are sketched in Akenhead (1981b). Intense fishing pressure conceivably removes the population size buffering ability of adult density dependent factors (growth rate, maturity, fecundity, cannibalism, and possibly habitat selection and usage). Somehow this disability and apparently other effects, possibly including reduced interspecies competition (Anderson and Ursin 1977; but see rebuttal in Cushing 1980), leads to a destabilization of population dynamics.

> "One of the curious observations to emerge was the large size, at least on occaision, of the terminal year-class in the history of a fish stock. There seems to be some possiblity that when a stock is about to crash

> completely, its regulatory machinery collapses and the terminal year-class may be very large indeed, although this large size does not have the meaning that it would normally have in a population, i.e. of indicating a relatively healthly stock. No obvious explanation for this was forthcoming at the meeting and even the degree to which the phenomenon occurs was not clear, but it is certainly a curious observation that should be examined more closely" (Slobodkin 1973).

An example of such 'destabilized' year-classes might be the 1963 and 1966 North Sea herring that can now be recognized as that stock's last gasp. The decadal statistics of the North Sea and Georges Bank haddock further illustrates this destabilization. Figure 1 shows that the standard deviation of year-class strength increased greatly in the 1960's when fishing effort rose substantially in both these ecosystems (Grosslein and Hennemuth 1970; Sahrhage and Wagner 1978). The Georges Bank haddock stock suffered the decimation of spawning stock between years of massive recruitment. Stock size, as measured by trawl surveys, declined about 90% between 1963-65 and 1970-72 (Brown et al. 1976). The North Sea haddock, are still a commercial, although hard-pressed stock, with an equally severe reduction of spawning slub in the "inter-recruitment" periods of the 1960's and 1970's.

STOCK AND RECRUITMENT

Fisheries science had a milestone marked by another comment in Slobodkin's summary of the ICES 'Stock and Recruitment' symposium at Arhus in 1970:

> "It was the concensus of the meeting that density dependence does occur in all fish stocks at some point, and this is itself a major transition from earlier dogma" (Slobodkin 1973).

Density dependence in marine fishes is manifested by, among other things, the rather unexpectedly accurate tuning of year-class strength from trillions of eggs to hundreds of millions of recruits, with an accuracy of about an order of magnitude most of the time. Figure 2 illustrates the nature of this variability throughout the early life of California anchoveta (from Smith 1978). Fisheries management techniques normally deal with the dynamics of the last 1 or 2 orders of magnitude of change in numbers and weights of the life of a cohort of fish. Modern fisheries science strives toward a larger perspective, enquiring into the early life history with its rapid changes. The perspective has grown in spatial dimensions as well: fish stocks are recognized as being affected by oceanic changes that occur on very large spatial and time scales (Smith 1978; Garrod and Colebrook 1978). The relevant processes may involve scales of oceanography from decimeters to hundreds of meters (Smith 1978; Owen 1981a). Sheppard and Cushing (1980) make the case that strong density dependence must exist, pointing out that fish would have none of the resilience to, and persistence in spite of, fishing mortality rates several times their natural mortality. Let us take it as a premise, but not too blindly, that year-class strength is a reflection of density dependent processes, albeit these processes are largely obscured at the present. As for when these processes occur...

> "It is now possible to forecast recruitment from year old cod, haddock, plaice and soles in the North Sea, and from cod and haddock of the same age in the Barents Sea. Year-class strength of plaice is probably determined before the little fish arrive on the beaches. Hence the magnitude of recruitment is established in the first year of life" (Cushing 1981a).

This directs the science toward an examination of the first year of the life of fishes, to determine the nature of the population regulation mechanisms that the 'little fish' are subject to (Hempel 1965, Gulland 1965). At present, the planktonic life history of commercial marine fishes is still effectively a black box. Although some laboratories are making remarkable headway (e.g. Theilacker and Dorsey 1981), for nearly every commercial marine species, we still don't know "where the fish come from". Recently, it has become popular to declare that there is no such thing as a stock-recruitment relationship, that the spawning stock obviously does not play a role in the survivorship of the early life history, except for cannibalism. The catastrophic decline of spawning stock is granted status as a trivial consideration: one does not expect recruits when there are no eggs. But such statements do not recognize that, as fisheries ecosystems managers, we really only have one set of state variables to control, the spawning stock size, by means of varying the fishing mortality rates.

From this comes the objective of fisheries management that was stated above. In the context of modern management, however, there are great difficulties in attaining an 'optimal sexually mature biomass'. The most obvious is the trade-off of fish food resources between species or groups of species in a multispecies assemblage, (Anderson and Ursin 1977; Jones 1982). It would not be surprising if some fish biomass, considered harvestable in the single-species mode, may have to be left in the ocean to prevent the usurption of ecosystem resources by 'undesirable species' (Sherman et al. 1981). Whether these are resources for adults or for larval fish is not yet clear.

SURVIVORSHIP OF LARVAL FISH

Multispecies models of fish communities are generally very badly behaved (Levastu and Favourite 1981) unless self-regulating terms for each species are included. Inevitably the stability of marine ecosystems models depends upon a term equivalent to $dN/dt = -bN^2$. possibly heavily disguised. When ever this terms is introduced, it is an admission of ignorance on the part of the ecosystems modelling team, the same admission of ignorance about causes that accompanies the calculation of 'natural mortality' in single-species assessment models. Whenever this term can be recognized in a partial differential equation applied to population dynamics, one must be alert to separate science from dogma. Applying a model like

$$dN/dt = aN-bN^2$$

specifies the eventual population levels, K, since $K = a/b$. The Anderson and Ursin model of the North Sea (1978), for instance makes use of such terms in larval survival, albeit openly. To produce a model that does not contain this pre-determining term requires expanding the detail of species interactions. Food and predators must be invoked with sufficient power to prevent one species from exploding and taking over the resources of the model.

One formulation for larval survival and consequent density-dependent population regulation that has begun to be explored recently is the interactive growth-mortality model (IGM). This idea is at least as old as Ricker and Foerster (1948), that seems to have been rediscovered (Jones 1973), perhaps via Gulland's (1965) extension of Hjort's (1914, 1926) 'critical period' concept. This model was explicity held up for consideration recently by Shepard and Cushing (1980). The 'match-mismatch' model of Cushing (1973) should be considered a special case of the interactive growth-mortality model for the time being.

Using the Shepard-Cushing formulation, the mortality rate is considered a constant 'm', and is applied until the little fish have grown sufficiently to avoid the most intense predation, presumably by invertebrate planktonic predators (especially Ctenophora, Cnidaria, and Euphausiacea). They may escape this mortality regime by growing out of the size range predator interest, by attaining a size sufficient to metamorphisize, or by attaining a size that leads to a behavioural change that takes them out of the predators' habitat. While the question has perhaps never been specifically posed "when can the little fish be considered essentially 'safe'?", this seems obvious in certain situations, such as attaining smolt size in salmon or metamorphosizing and dropping out of the water column for flatfish larvae. This may be a universal feature of marine population dynamics, applicable to the nauplIar stages of copepods, and the 'gravel dwelling' stage of lobsters (which ends about 30-35 mm carapace length, Bernstein and Mann 1981). Information for larval marine fishes is scarce on this topic. The essence of the IGM model is that larval growth rate is considered to be density dependent (e.g. Gulland 1965) and slow growth leads to a longer stag in the relative high predation regime. Alternative mechanisms include suggesting that faster growing larvae, which is to say beetter fed larvae, are able to avoid capture by predators better than poorly fed larvae (Cushing 1975). These alternatives are the equivalent of suggesting that 'm' is also a density dependent term.

The mathematization suggested by Shepard and Cushing (1980) consists of a pair of simple differential equations,

$$\frac{dN}{dt} = mN$$

$$\frac{dW}{dt} = W\frac{g}{1 + N/K}$$

Where g is the maximum attainable expotential growth rate,

m is the instantaneous mortality rate,

W is the weight of an individual fish,

N is the number of fish alive, and

K is the "half-saturation" constant of the Monod or disc equation (Holling 1963).

Integration from a set of starting values for N and W until some weight, W_1, at which the year-class strength is considered to be established, is straight forward numerically. Shepard and Cushing (1980) provide the integrated form.

The outcome is an asymptotic attainment of a level for N essentially specified by the choices of 'm' and 'K', provided there are sufficient eggs or early larvae. Too few eggs leads to proportionately smaller numbers of survivors, without reference to dependsatory mortalities. Ignoring variability in 'm' for the moment, this model merely states that larval fishes are able to attain a maximum population level specified by the carrying capacity of the environment for larval fish. This carrying capacity is essentially specified in the constant 'K'. This is a comparatively limited statement, and the term carrying capacity gives one a sense of <u>deja vu</u>. The warnings earlier of incorporating self regulating terms in population models should be recognized as applicable to this term 'K'. This simplistic form does not aid our understanding of the 'planktonic black box'. This model has certain strong implications, particularly that a) the stock-recruitment relationhip is flat-topped, assuming that no other mechanisms such as adult fecundity feedback, are invoked and b) that nearly all the variance of stock-recruit curves is environmental, and not a function of stock size.

The use of the term $(1 + N/K)^{-1}$

essentally trivializes the entire feeding-food interaction with all its complexity. The probabilistic, patchy nature of feeding (Beyer 1980; Vlyman 1977) is completely ignored, even though it is probably of paramount importance (Lasker 1979), and was used in Jones' (1973) original mathematization of larval fish feeding. Nevertheless such a model may be useful. Perhaps the diffusivity of the ocean is sufficient to repeatedly re-configure the patchiness experienced by larval fishes so that an emergent property recognizable as "carrying capacity" can be identified and predicted from the environment. Platt and Denman (1977) present a heuristic index of oceanic diffusivity, indicating the time for a 50% exchange of material within a circle through its circumference is only 10 min for a 10 m diameter and 10 hrs for a 1 km diameters. Moreover, it is only anchoveta (Engraulis) for which patchiness has been shown to be so important, and this genus appears to be exceptionally prone to starvation, with gut clearance times of only a few minutes (Theilacker and Dorsey 1980), early mortality rates of up to 50% per day (Ware, Meniola and Newhouse 1979), and an attack range of only 0.07 body lengths (Hunter 1972).

If survivorship depends upon fast growth, then larvae from comparatively good year-classes should, during their early life, be larger at age than those of poor year-classes. This is the opposite of most investigations, which would like to predict large year-classes by observing that pre-recruits are smaller from increased intra-specific competition. In fact, the size at formation of the first otolith annulua isn't a reliable indicator of year-class size (Hjort 1932, Beacham 1981). Gulland (1965), discussing collections reported by Saville (1956, 1959), suggested that YCS was more related to the number of large larvae alive after some time, than to total numbers of larvae. It may be that strongly length dependent growth rates lead to so-called 'growth compensation' during or immediately after the important IGM phase, covering up the initial growth rate changes. This can be explored using larval aging techniques (Brother, Mathew, and Lasker 1976; for a NAFO region example, Penney and Anderson 1981). Since larval fish growth can be examined in detail now, the IGM model can be tested in the field, although further theoretical work (after Vlymen 1977) is indicated.

The examination of high stock densities is requred if we wish to test that population regulation is accomplished in the ELH and not as an adult stock feedback. It is unrealistic to expect that fisheries science questions will ever be interesting enough to the fishing industry to suspend fishing upon one of the world's fish stock for a decade so that high egg densities can be observed. This leave the probability of getting egg production in the upper hald of the range quite low. Given that the variability of recruitment at low egg production will be partially exhibited at high egg production, it will be a very long time before sufficient data is accumulated to determine if the mean recruitment is lower or not. But if carrying capacity for larval fish can be identified as an environmental correlate and factored out, the problem can be resolved in a much short time series (Gulland 1965).

The decline of recruitment suggested at high stock densities may be a statistical artifact when it is apparently observed. If stock size and recruitments are of independent skewed distributions, then the chance of observing a relatively rare large stock size and an equally occaisional large recruitment from the same year is very small. Large year-classes will show up with more modal stock sizes, just because that is where the bulk of the observations are made. As Larkin (1973) introduced, we force an arbitrary domed curve that begins at the origin, responds to the fully exhibited variance in YCS at near-modal stock sizes, then declines in the "undersampled" righthand side. For example, if stock and recruitment were completely uncorrelated, with each having 4/5 of the observation in the captured time-series at or below modal frequency, then only $(1-4/5)^2$ or 0.04 of the observations would be expected in the region corresponding to the two tails of these independent distributions as in Fig. 5. The resulting descent of a fitted dome-shaped curve is a sampling and statistics problem equivalent to unbalanced cells in a two-way ANOVA.

At the highest stock levels, surplus egg production releases enough larval fish to require a consideration of the potential for the destruction of the larval food resource to an overcompensation of the density feedback mechanism, leading to unanticipated losses of potential recruits. In some cases it may not be a real problem, since adult density-dependent effects would reduce the energy allocated for gamete production in the population. The decline of recruitment at high stock levels could be due to reduced output of viable eggs, not to an 'oversaturation' of the larval habitat. Sahrhage and Wagner (1978) present egg production versus recruits plots for North Sea haddock that include the years 1946, 1964, 1965, 1966, and 1970 when egg production have been extremely large. There is a suggestion (subject to the inadequate sampling warning above) that recruitment could be reduced at highest egg densities, but 1) the spawning distribution could have expanded in area, 2) a fixed maturity and fecundity patterns were used, whereas a re-analysis incorporating bioenergetic considerations might differ in egg estimates, and 3) although Ricker curves were fitted, no note of the significance of the density-dependent terms is made. Gulland (1965) presents the same sort of data for Arcto-Norwegian cod, with no apparent decline in recruitment at high stock sizes.

The question of a declining right-hand side of the stock-recruit curve can be examined by extending the mechanism of Shepard and Cushing at least on more step, and eventually examining the proposed mechanisms and responses in the field. Either the trophic level above or below the larval fish must be modeled to include effects from initial larval fish numbers. In the Shepard and Cushing formulation, the predatory trophic level is modeled as part of a single constant 'm' and the food trophic level is just another constant, 'K'.

The food trophic level has its own dynamics, of course, especially since cohorts of prey increase in particle size and decrease in numerical abundance just like larval fish, but with an order of magnitude change in the size scale. If larval fish can substantially deplete their prey cohorts when abundant, which is a premise of the density-dependent mechanism we are discussing, then later, after the numbers of fish are reduced and they are seeking the survivors of the initially food limited period, it may be that the high mortality levied on their food leads to a continued food limitation. The term $(1 + N/K)^{1}$

provides only the first mode of response of the larval fish growth-mortality interaction. The second mode exists if K at time t is potentially a function of N_0, i.e. if larval fish can, early on, destroy a resource they could use later.

Jones (1973) proposed a yet unexamined aspect of the larval fish-copepod interactions, noting that the food is growing in sizes in a fashion that might correspond to the increasing optimal particle size of the growing fish. Copepods can be expected to be 'playing the same game' of surplus early numbers and density-dependent interactive growth and mortality. Early losses to a cohort of nauplii from superabundant larval fish would lead to enhanced growth and survival of the remaining nauplii, particlarly if they could outgrow the size range of interest to, or capability of the larval fish modal length. Since nauplii and copepodites are pressing the phytoplankton, a third levl of density-dependence exists. One of the outcomes of this hierarchical model, which might be called the 'interactive growth-trophic dynamics' model, is a counter-argument to the match-mismatch hypothesis for YCS variability (Cushing 1973). If the fish eggs hatch late relative to the copepod egg production and hatch, slowed development of the nauplii from competition within their trophic level could compensate for the missed timing of the larval fish. Contraindicating this mechanism is the probability that nauplii and copepods are not food limited during spring bloom conditions in the Northwest Atlantic. Where phytoplankton does not bloom, however, perhaps as a result of an initially deep vernal thermocline, food effects and intra-specific competition are more plausibly induced. Vidal (1980) reported that food was saturating to development times of *Calanus pacificus* and *Pseudocalanus* sp. at 2.5 ppm. Since this is very roughly 2.5 micrograms chlorophyll per liter, compared to 0.5 $\mu g l^{-1}$ as an average for the Northwest Atlantic (Strickland 1960; Sutcliffe, Sheldon, and Prakash 1970) this indicates a potential at least for a buffering of the effects on larval fish of hatching slightly later than the optimum.

As a first reaction, it seems that combining these individually stabilized components would result in a very stable model, and yield larval fish survivors after a sufficient time that depended mainly upon the initial nutrient pool, as opposed to the initial number of diatoms, nauplii, or fish larvae. The scenario of physical structures and processes erected to stage this sort of model within could easily overwhelm the biology. However the point that remains is that these physical scenarios are then the essence of fisheries oceanography.

This brings us to the question of the nature and sources of variations in the environment relevent to the growth of larval fish. To explore this question, I have elected to examine the North Sea ecosystem, and to recount the developments of our understanding of the area. The revie is not complete by any means, I have taken up only one or two threads from the efforts that have woven our present conception of the Northeast Atlantic.

The Northeast Atlantic

The length and detail of time-series data on marine ecosystems dynamics is nowhere exceed by the North Sea and English Channel. The ICES Symposium of 1975 (Hempel 1978) draws together the information necessary to establish biological events from about 1920 to the first years of the seventies.

A rise from 1.2 x 10^6 T.a^{-1} North Sea fisheries yield from 1909-1960, to 2.7 10^6 T.a^{-1} yield 1961-73 (from Holden 1975) was accompanied by a shift in community composition. Herring and mackerel stocks crashed after 1965. Year-classes of gadoids, particularly haddock, that were well beyond the range of historical records, increased gadoid stocks by a factor of 40.5 from 1961 to 1968 (Sahrharge and Wagner 1978; Cushing 1980). In a rebuttal to the Anderson and Ursin (1978) claim that this was a multispecies effect from increased fishing pressures, Cushing discounted food and predation effects, with this conclusion:

> "...the gadoid upsurge is of climatic origin quite independent of the interactions between species in the North Sea. The timing of the event during a period of climatic deterioration, the similar events in the Irish Sea and the wide spread nature of the increase amongst all gadoid species in different regions of the North Sea combine to support this thesis" (Cushing 1980).

Changes in the cod and herring spawning grounds, in the possible northward shift of some boreal-Mediteranean species, increased chlorophyll and decreased zooplankton also can be taken as evidence of a climatic shift of this time (Hempel 1975b).

A parallel series of events occurred in the Gulf of Maine-Georges Bank fisheries at the same time (Sherman 1981). At this point, it can not be decided if the herring - sand eels - cod events is these two systems, are indeed linked by climate, or merely by the coincident increase of fishing mortalities beyond the tolerance of the previous ecosystem configuration.

The tendency to look for climatic effects in fisheries ecosystems changes is a predeliction of the U.K. fisheries biologists, since their data series extend far enough back to have seen a previous sudden reconfiguration, about 1930. This was documented mainly in the English Channel (Southward 1962; Russel et al. 1971; Russel 1973), and is known as the Russel cycle. Cushing (1979) attempted to make the case for a shift in ecosystem configuration that was symmetrical about the mean Northern Hemisphere temperature which rose and fell about 0.25°C on a century scale from about 1890 to about 1945. While there may well be grounds for such a large scale mechanism, the climate signals from the North Sea region are more abrupt changes (Hill and Dickson 1978), and the biological explanations for recruitment changes must be site-specific.

The phosphate level in the English Channel in 1920 was very rich at relatively shallow depths in comparison to the 1950 level. The pre-Russel-cycle English Channel euphotic zone nutrients correspond to the level of nutrients post-Russel cycle found at 700 m, "from which no known mechanism can cause it to upwell" (Cooper 1955). The connection between a water mass abundance and the biological events of the Russel cycle is intriguing, and this singular observation has led to a large investigation. What causes a decline in the level of intermediate water on a scale like this, with a time span as short as was observed? Bottom water in the North Atlantic is formed by evaporative increases in salinity (e.g. Mediteranean water), and by surface cooling sufficient to cause turnover. Mediterranean water is very obvious and can be ruled out in the English Channel. The intermediate water source must be from arctic cooling. Cooper (1955) hypothesized that cold winters near Iceland form such a water mass, and could upwardly displace the nutrient rich intermediate waters into the euphotic zone. He was probably correct in surmising that a yearly production of this water somewhere 'upstream' must have decreased in the 1930-35 period. This is why Cushing's (1979) application of hemispheric warming is reasonable. This model led to the "Overflow" project (Tait 1961) in an attempt to establish the details of this bottom water movement, since it is formed north of the Scotland-Iceland ridge. As an aisde, this project was the first use of long-term deep morred current meters: it is interesting to note they were used in a project directly originating from a fisheries oceanography problem. This import of such a model of a fisheries ecosystem is not merely regional, as Cooper noted in his original paper:

> "If these views are true, even in part, answers to the problems posed by the fisheries biologists cannot be found only by the study of the shallow waters in which the fish live; knowledge of the deep circulation of the ocean is also required" (Cooper 1955, p. 361).

Support for this "remote causes" paradigm comes from a) noting that the correlation of North Sea haddock year-class strength and local winds (Caruthers et al. 1951) failed after 1937 (Saville 1959). For 1938-57 there is no correlation of wind and haddock year-class strength. The mechanism originally proposed for the correlation appears to be incorrect; since advection of haddock eggs and larvae off Scotland is minimal (Rae 1957); probably the correlation existed because of a third variable temporarily correlated with wind prior to 1937. Nevertheless, the system in which the correlation existed seems to have changed. b) about 95% of the water that enters the North Sea each year is from the North Atlantic. The English Channel, Skagerrak and run-off are small contributions (Hill and Dickson 1978). Now water entering the North Sea will be the result of changes to the Northeastern North Atlantic as a whole. c) should the creation of new bottom water be voluminous in any particular winter, then production in the North Sea should be enhanced that summer following. Comparing the North Sea cod YCS at 2 years to the SST anomaly, the largest year-classes all follow the coldest winters, the years in question being 1963, 1966, 1970 (Dickson and Lee 1972; Hill and Dickson 1978).

The biggest yearclass of plaice was also in 1963. d) a study of T-S patterns in Rockall Channel (west of Scotland) for 1905-1980 (Ellett 1980) indicates that significantly different water was present for January-March from 1908-1935, compared to 1949-80 (Fig. 4). While no data for 1937-47 is reported, this does substantiate these changes in the English Channel in 1935-36 as being an 'upstream' effect. This data set demonstrates persistence of salinity anomalies on a nearly decadal scale, especially a recent pronounced decline from a high in 1968 compared to 1924-34, to a profound low in 1976. This appearance of low salinity off Scotland relates to a similar appearance of water loss than 34.95°/₀₀ in the intermediate salinity minimum at O.W.S. Juliet (52°N 20°W). The 'lower salinity minimum' water at O.W.S. Juliet has a dip and recovery of salinity with a minimum in 1972.

Perhaps this is sufficient to allow the creation of a working hypothesis that long term changes in the North Sea are related to 'upsteam' events. Only to a much lesser extent does this hold for short term changes. The extraordinary haddock year-classes of 1962, 1966 and 1971 (Sahrhage and Wagner 1978) do not appear related to the Rockall Channel temperatures and salinities, or to the German Bight salinities and the indices of cyclonicity and vorticity of winds over the British Isles reported by Hill and Dickson (1977).

A search for explanations might be couched within an hypothesis such as: 'long term climatic phenomena yield conditions that are generally suitable for the appearance of large yearclasses of a particular species in the North Sea by mechanisms involving water mass formation and changes of water movement. However each growing season has unique characteristics that enhance or detract from average conditions'. This appears to be a general conclusion, Tont (1976) demonstrates that in the California Coast system, diatom production variability is controlled by wind-induced upwelling, but invasion of different water masses (i.e. what it is that's being upwelled) results in order of magnitude differences in the quantity of diatoms produced in an upwelling event. New concepts of eastern boundary polewood undercurrents will contribute significantly to understanding production changes associated with upwelling; an initial synthesis reported by Mittelotaedt et al. (1980) is promising.

The search for short-term explanations of fluctuations in YCS is thus directed towards physical factors that control the production cycle. Colebrook (1965) showed how the production cycle varied in amplitude, spread and time of onset due to differences in wind strength, direction, and solar radiation. A time-series of characteristics of the growing season exists from the CPR surveys of the N.E. Atlantic and North Sea. Reid 1978 demonstrates consistent patterns of "greenness", of diatoms, and of Ceratium on the rather coarse meshes of the plankton recorder. Most striking is the loss from 1968 to at least 1973 of the fall diatom bloom, and a reduced persistence of diatoms after spring bloom for this period.

In contrast to Reid's (1978) conclusions of variable timing in the phyoplankton vernal bloom, Colebrook (1978) demonstrates an apparently rigid schedule of spring appearance of Calanus, independent of its abundance (Fig. 5). This has consequences for the match-mismatch model, particularly if the other zooplankton follow this sort of fixed timing.

One of the most significant aspects of the plankton recorder data is the difficulty in establishing local oceanographic correlations to it. For instance Bainbridge et al. (1978) couldn't establish a local environmental correlate to two adjacent regions in northern Scotland, each about 200 x 200 km. One was 15% explained by an index of the rate of summer surface heating, the other area was 33% explained by May to August temperature anomaly. The authors concluded there was "little or no correlation with the various parameters of the physical environment considered".

Glover et al. (1974) gives the time of spring bloom from the CPR data, showing it to be trending later, irregularly, by about 30 days on the series 1948-72. The zooplankton season length declines irregularly, and there is a steady decline in Pseudocalanus, Calanus and "total copepods", as well as "zooplankton biomass". Taken all together, the planktonic changes are indicative of a major reconstruction the pelagic ecosystem. Several impressive statistical analyses of these multivariate data sets have been made. The most fascinating of these is in Garrod and Colebrook (1978). Figure 6 summarizes one of these results. While the frequency of 'westerly weather type' is positively correlated with the first principal component of the CPR zooplankton of the North Sea on a time scale greater than decades. After removing long term trends the correlation is sharply negative, and with a clear 3½ year cycle. A 3 year cycle is pervasive in the North Sea plankton data (Fig. 7), along with another frequency peak at 7½-10 years (Colebrook 1978).

Attempts to explain this are in the domain of global climatic modelling, which exceeds the scales appropriate to fisheries oceanography. These frequency scales are tantalizing clues, however. Three years is about the time for juvenile gadoids to enter into competition with the sexually mature stock, they become sexually mature in twice that, and mackerel, herring and presumably other pelagics become sexually mature in about 3 years. While there is a certain amount of 'grasping at straws' here, if such triannual cyclic wind patterns have always existed, the fish will have evolved responses to exploit them. One cannot help noting that the years of recent large year-classes of the North Sea haddock are 1955, 1958, 1962 1965, 1967, 1970, and 1974, which is a 3 year cycle.

The scales of primary and secondary production important for ichthyoplankton may be smaller than the statistical areas considered by the CPR analysts. Fronts between thermally stratified areas and adjacent regions where bottom friction mixes the water up to the surface using tidal energy (Simpson and Pingaree 1978) form a convergence area which may concentrate the enhanced primary production of the intermittently destablized side (Owen 1981). Presumably these fronts react with the wind fields, to yield varying net productivity from year to year. Presumably it is the existence of such tidally-induced fronts in the shetland area, absent in the Buchans area, that preclude a common environmental correlate to the CPR data of Bainbridge et al. (1978). Fronts such as this do not exist in the NAFO regions 2 and 3 until the Arctic archipelago (Griffiths, Pingaree and Sinclair 1981). Other small scale effects in the physics of the surface could also play a role, and are currently being investigated (Fournier, et al. 1979; Sinclair and Isles 1981). It is still too early to report on the results of this field, except to say that such processes studies are being actively pursued in the Northwest Atlantic, with at least three 'patch' studies in the last three years. Two quotes summarizing the I.O.C. environment-larval fish symposium indicate the direction of modern thought:

> "....a persistant problem area in extracting information about natural limiting processes in fish biology is measurement of ambient physical-biological interactions on appropriate scales. Definitions of the relevantscales is important".

> "....A problem area which appears to have attracted the least attention to date in regard to the available early life history information is the distribution and availability of appropriate larval fish habitat and the means various species of marine fish have evolved to cope with the seasonal, local and open ocean variation in availbility of these "requirements" for reproductive success." G.D. Sharp (1980).

Let us briefly return to the larger and longer scale changes in the North Sea. What accounts for the westerly-type weather and zooplankton correlation on a decadal scale? The entire ocean is involved in wind effects of such a scale, but a first conclusion must be that mid-Atlantic surface waters of low nutrients content are now being introduced into the Northeast Atlantic. This has been previously recognized by Cushing and Dickson (1976), Garrod and Colebrook (1978), Colebrook (1978) among others. A subsurface cyclonic flow of 'subpolar mode water' has been proposed recently (McCartney and Talley 1981). This water mass is formed in the region southeast of the Polar front off of Canada, with a signature of 14.7°C., 36.08°/₀₀. This subpolar mode water is also said to flow into the Norwegian Sea and west of Iceland in great volumes, potentially replacing the waters in the subarctic that chill and sink to form the intermediate and bottom water for Cooper's overflow, as well as being the intermediate water layer available to enter the North Sea.

The Overflow problem has also been recently addressed, since it is far from being resolved: local wind effects are an order of magnitude too weak than the energies required to drive the overflow. The appropriate energy source is the eddies generated by 'baroclinic instability' of the polar front (Willebrand and Meincke 1980). Only major windstorms would be important in overflow. But, by changing spatial scales again, it might be concluded that winds can again be invoked, actually in the generation of these eddies in the polar front:

> "Eddy generation also appears to be mediated by the flow of air from land masses. Worthington (1972), noting great mixed layer depths and high pressure zones associated with outbreaks of cold continental air over the Pacific south of Japan, and over the Atlantic south of New England, believes that the convergent sinking of surface waters occurs as a result, generating anticyclonic eddies. Anderson et al. (1970) consider that the flow instabilities of the Agulhas Current off Durban are induced by offshore wind components indicated by local pressure variations."
> R. W. Owen (1981).

Apparently it will be necessary to invoke the atmosphere and ocean of the entire North Atlantic to account for the changes in the North Sea. The immediate, and extremely unoriginal, conclusion is that both sides of the Atlantic could be demonstrated to be linked in these large scale production processes. If this is so, then the year-class strength of fishes on both sides should be correlated. This was suggested by Templeman (1965) but the data assembled at that time have still not been statistically analyzed. His analysis was renewed by Cushing (1981) to try to show that gadoids were synchronous in recruitment success on a decades scale. The most ambitious foray into this question is Garrod and Colebrook (1978), who generated a correlation matrix of recruitments from stocks on both sides of the Atlantic. They convinced themselves, but in Akenhead et al. (1981) their conclusion is criticized, and the question of year-class synchrony between areas is described as "difficult to demonstrate". The principal components analysis of Garrod and Colebrock's correlation matrix was more successful:

> "The principal components of the recruitments to 18 fish stocks in the North Atlantic were related to periods of predominantly high and low pressure in 20° to 30°W....the first principal component tends to be positive during periods of predominantly high pressure in the central North Atlantic. In other words, the recruitments tend to be positively correlated when northerly winds blow in the northeast Atlantic and when southerly winds blow in the Northwest Atlantic". D. H. Cushing (1981).

CONCLUSIONS

1. year-class strength formation seems to be destablized as a resulted increasing fishing effort.

2. the density-dependent interactive growth and mortality model is still inadequately developed to test in the field, however attention to larval growth rate modelling and observations is warranted. Density dependent growth and mortality of larval fish is respectably concluded but not demonstrated.

3. since there are more correlations of year class strength with environment then with stock size (albeit ephemeral) perhaps we should concentrate on 'saturating larval habitat' with eggs as a stock size objective for a biologically-oriented single-species and management objective.

4. long term climate changes alter the average conditions that lead to species succession on fishing grounds, but annual conditions of the production cycle control short-term year class strength formation. Both of these may be related to winds of the appropriate scales.

5. Not enough attention has been paid to the spatial aspects of year class strength formation, especially in the 50 to 50 kilometer range.

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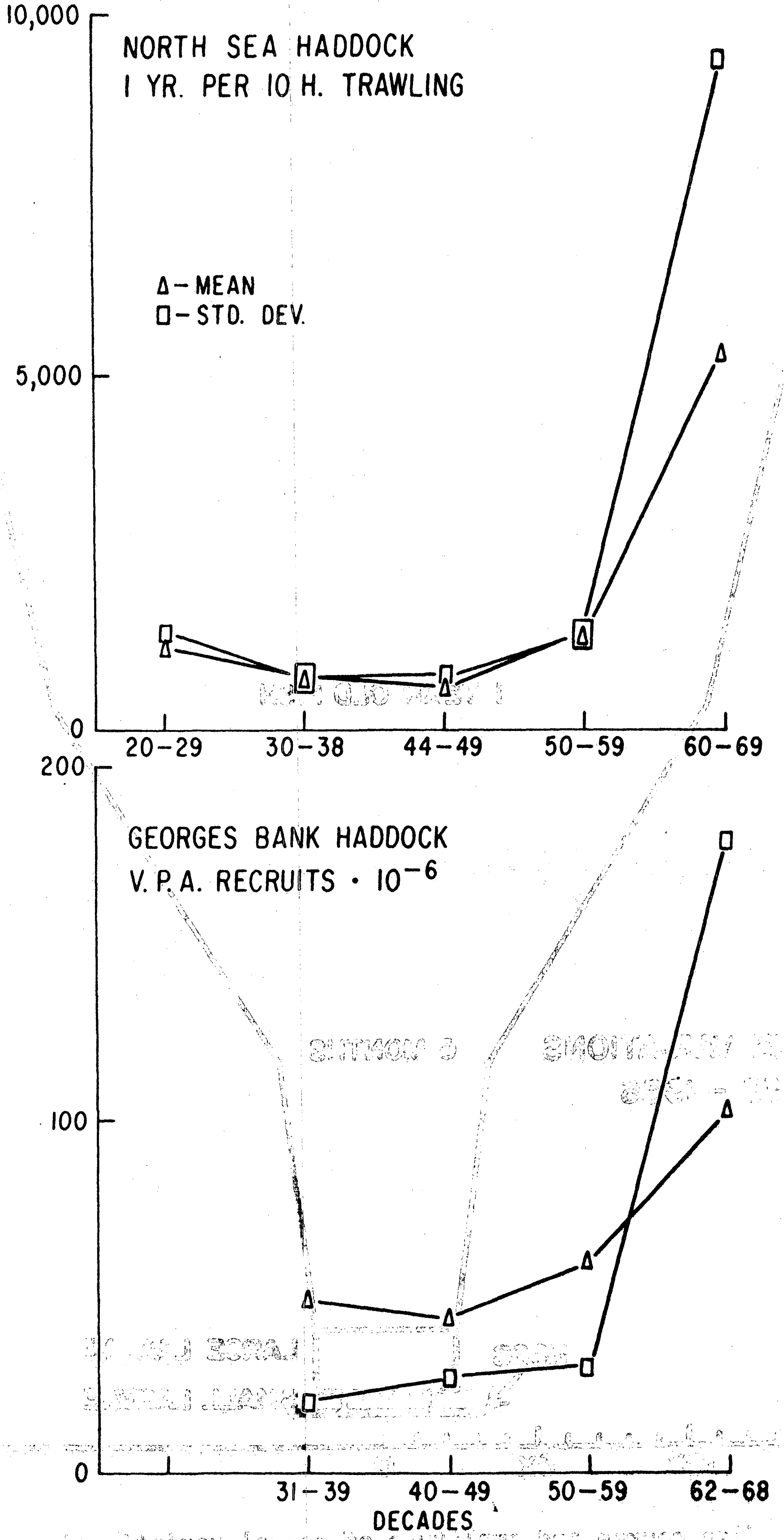

Figure 1. Decadal means and standard deviations of two haddock stocks, showing changes in predictability after 1960.

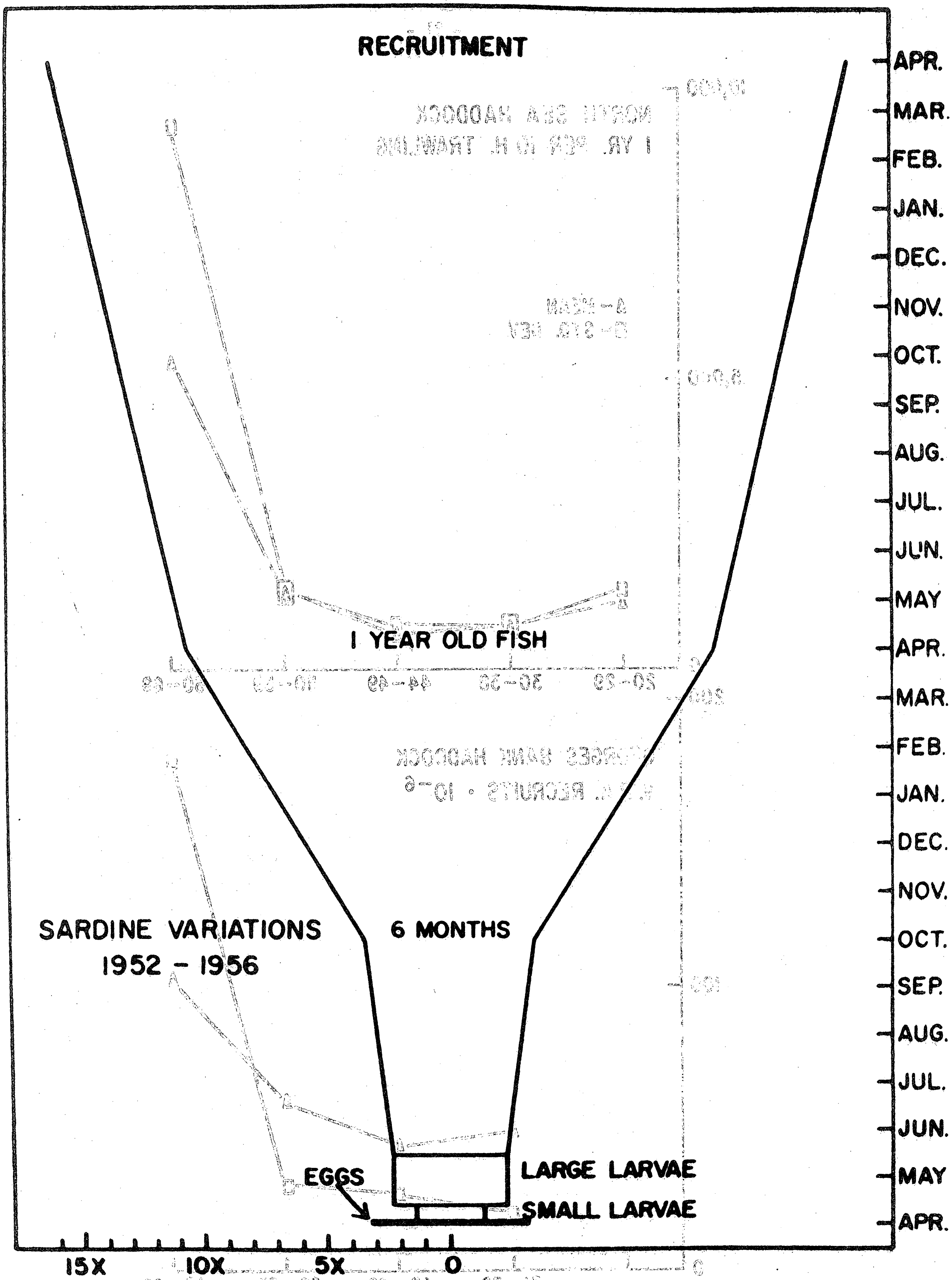

Figure 2. Time course and amplitude of annual variation in numbers of sardine eggs, larvae, juveniles and pre-recruits from 1952 through 1956 (from Smith 1978).

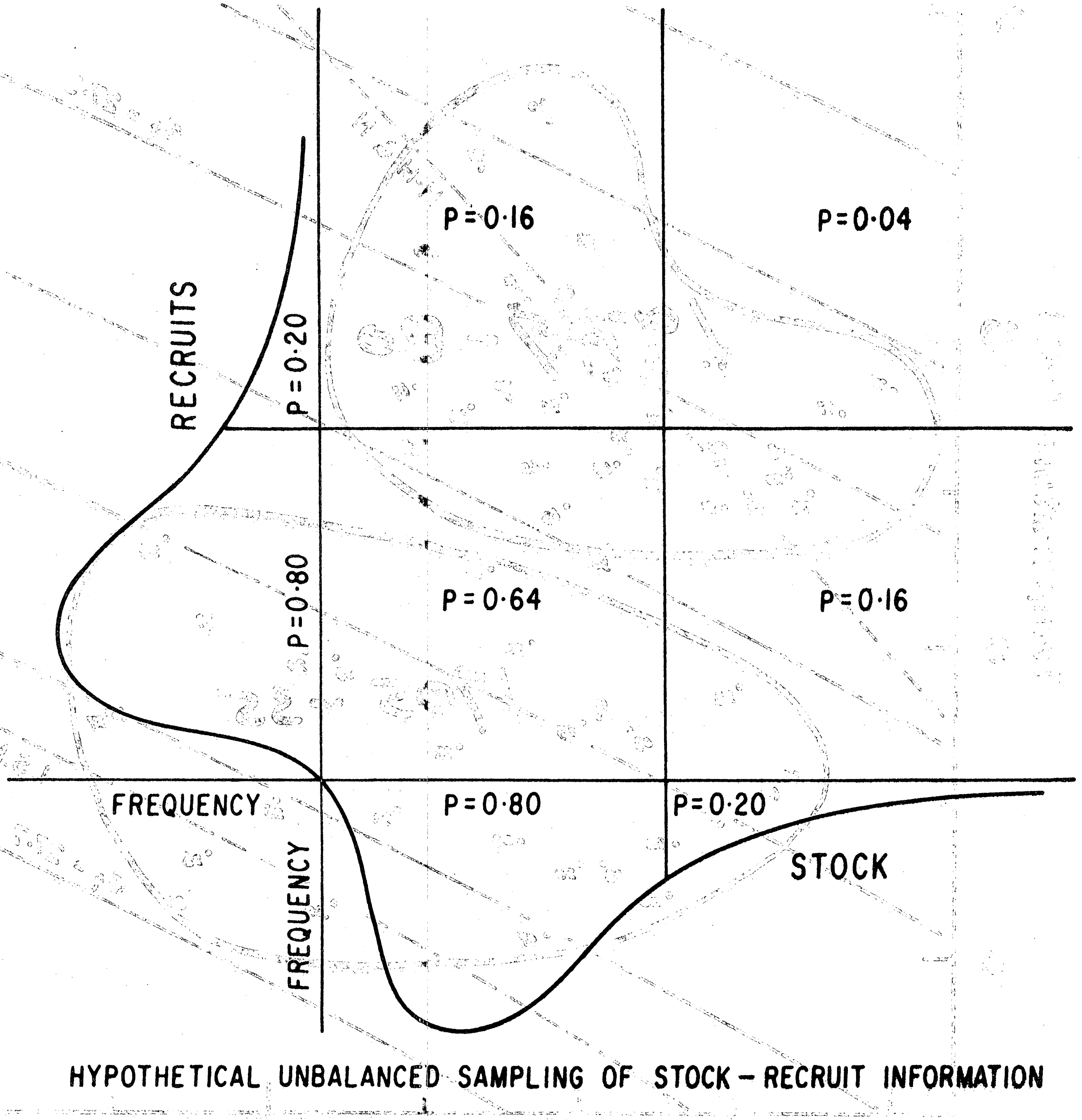

Figure 3. Hypothetical unbalanced sampling of stock-recruit information.

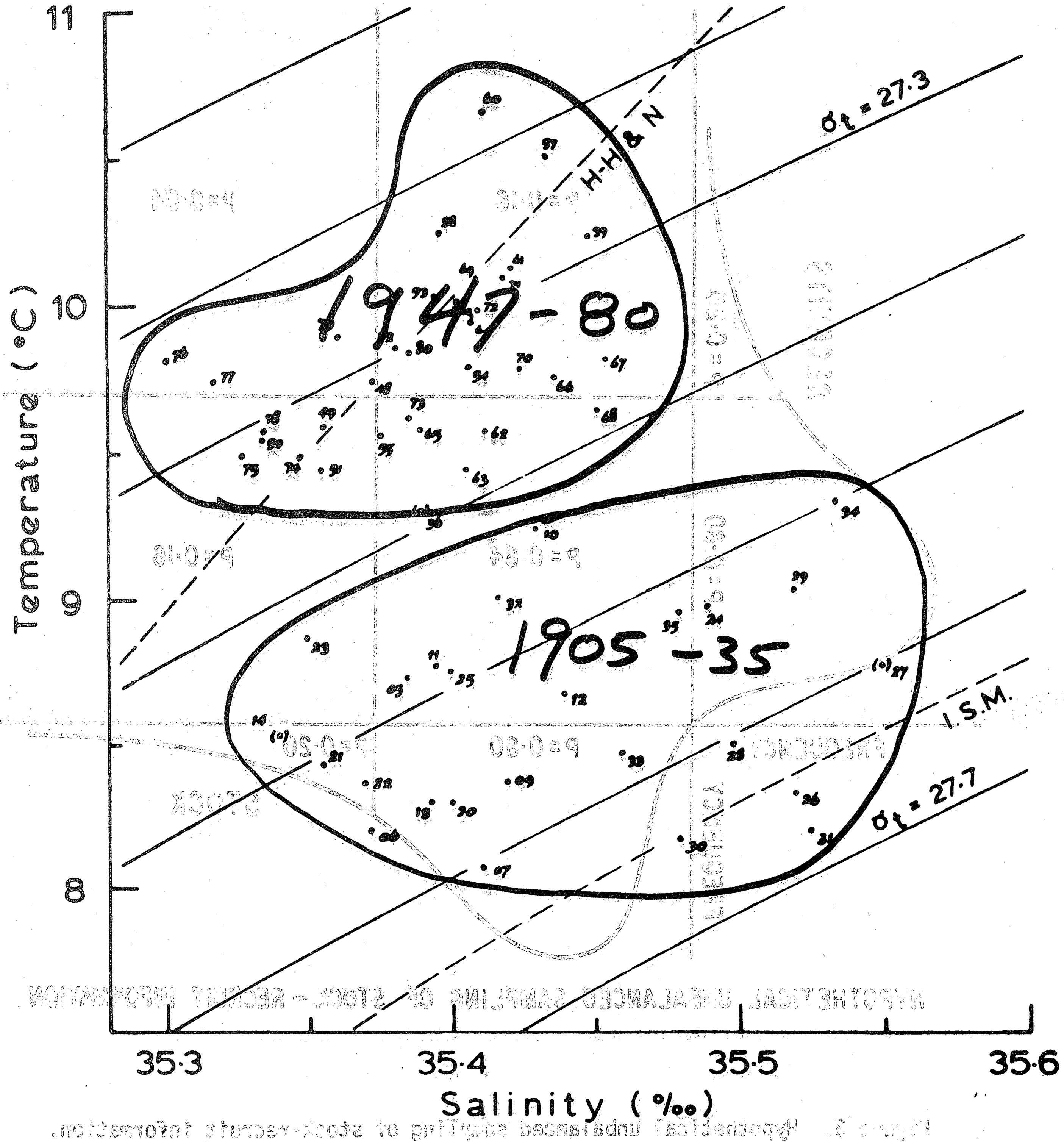

Figure 4. Temperature-salinity diagram for January-March Rockall Channel means 1905-1980. Note the shift after 1935 (from Ellett 1980)

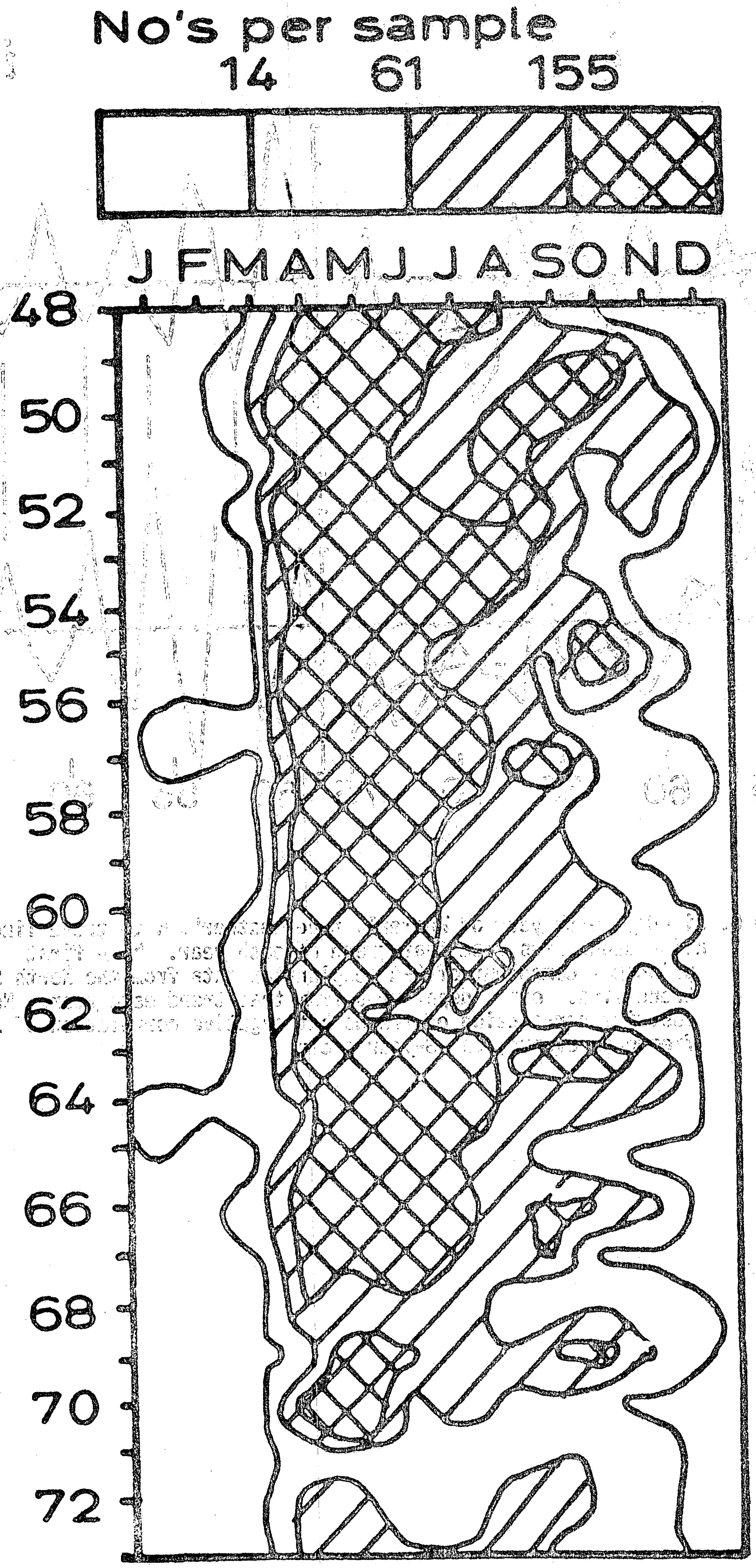

Figure 5. A contoured diagram of the monthly logarithmic means of abundance of Calanus, from the western-central North Sea 1948-1970, demonstrating the apparently fixed schedule spring appearance (from Colebrook 1978).

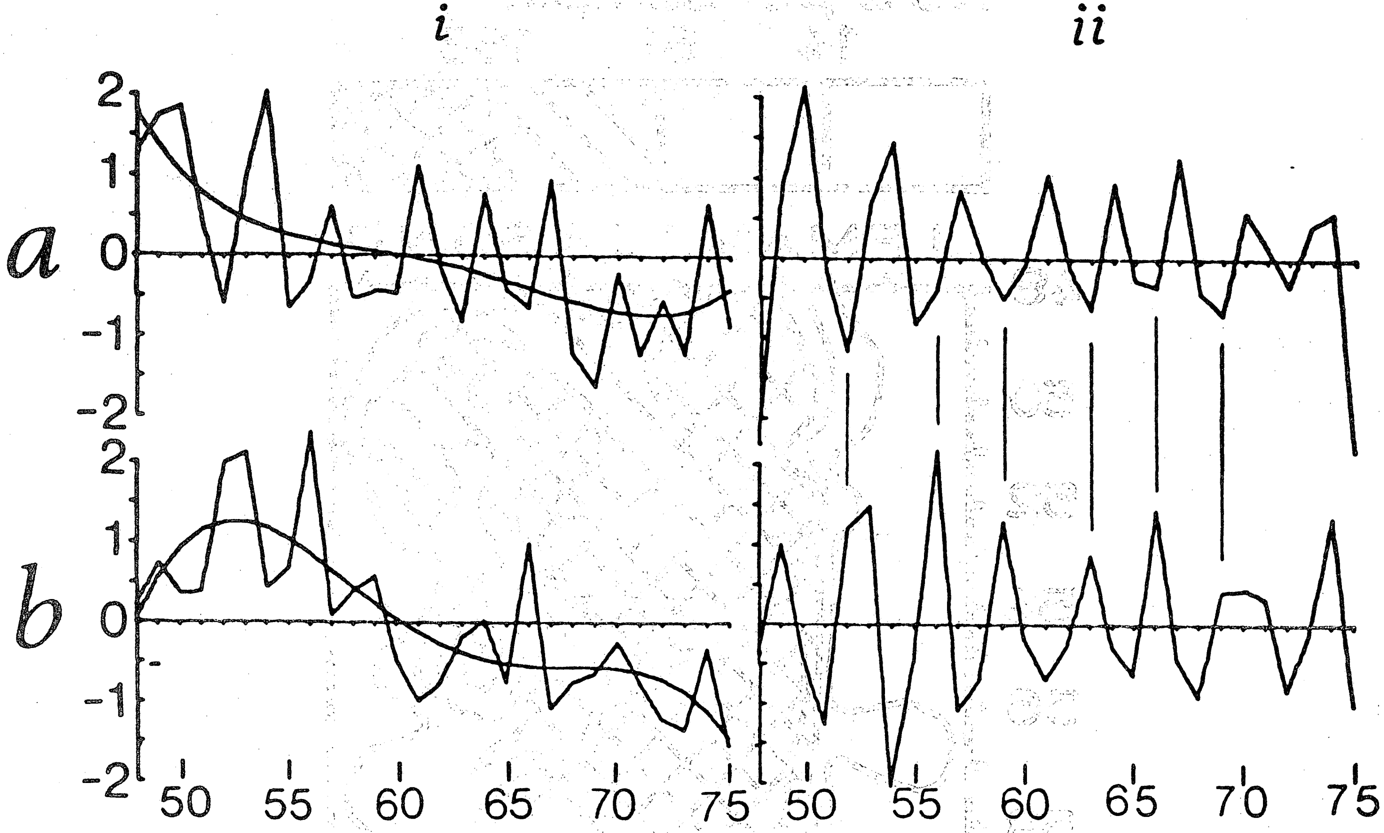

Figure 6. ai - Days each year of Westerly type weather', with trend line. aii - departures from that trend of each year. bi - first principal component of CPR zooplankton data from the North Sea, with trend line. bii - departures from that trend each year. Note positive correlation of trends but negative correlation of higher frequency events, and 3-year cycle.

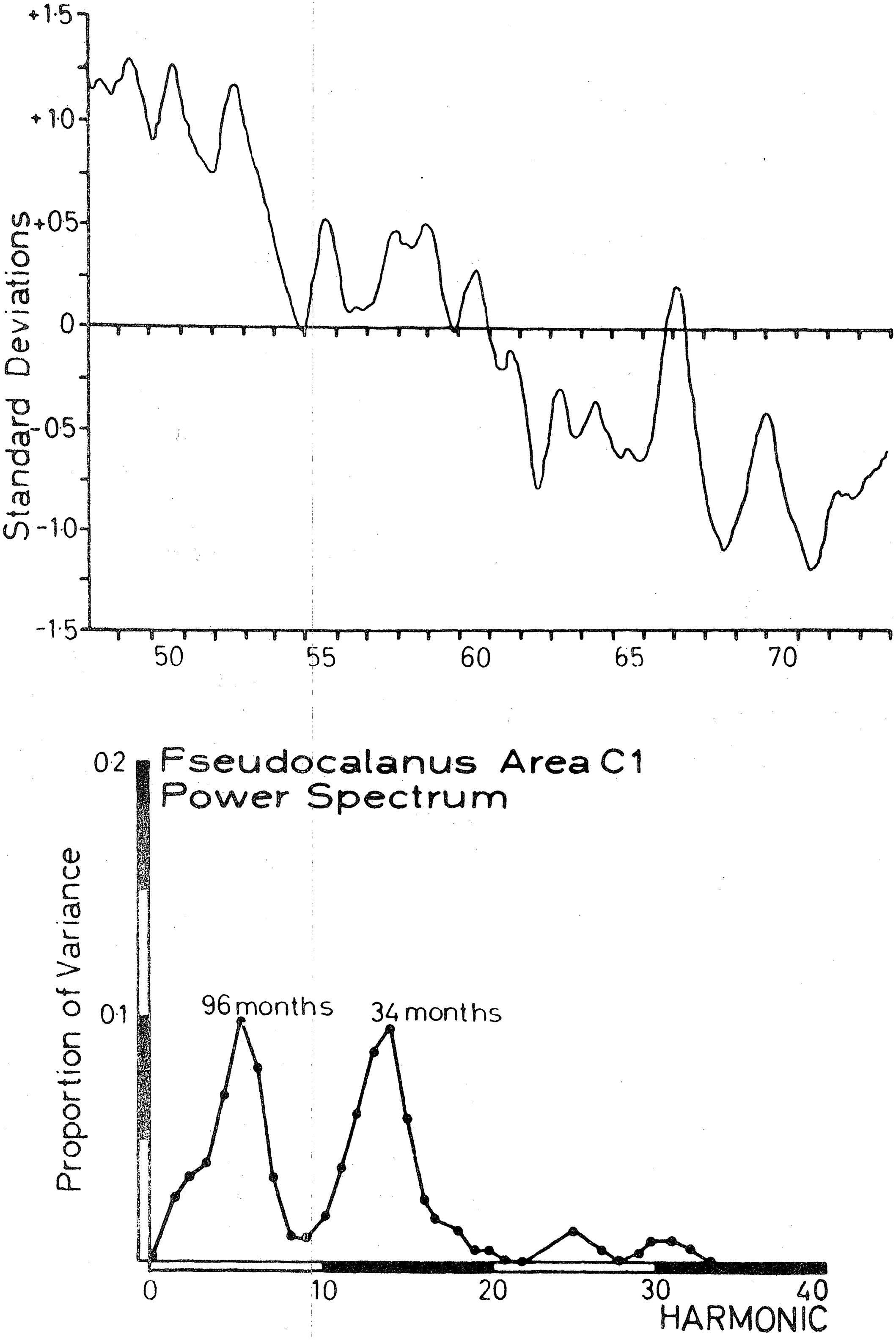

Figure 7. Smoothed anomalies of monthly means of abundance for Calanus and Pseudocalanus in the central North Sea, 1949-1973, and the power spectra of these after removal of linear trends.