Nature and Adequacy of Biological Data Bases: Plankton

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Introduction

A major objective of biological oceanography is to quantify the processes regulating food web structure and dynamics. This would allow the construction of appropriate models. In the context of the Climate and Fisheries Workshop, a desirable model would be one which relates the regulation of fishery dynamics to interacting biotic and physical factors. Such models differ from and would supplement those presently used to reach fishery management or sustainable yield decisions. They would emphasize the time-dependent coupling of the different trophic levels and the influence of the physical field on such coupling. Ideally, for example, this would allow quantitative modeling of the linkage (and prediction) between wind intensity and herbivorous fish yields in upwelling areas. Unfortunately, fishery biologists and plankton biologists have tended to work independently of each other. Fishery biologists have tended to ignore lower trophic levels, which they usually treat only cursorily. Thus, chlorophyll is usually the measure of phytoplankton abundance used, and displacement or settling volume the measurement of zooplankton abundance. These static observations are usually valueless. Plankton biologists emphasize phytoplankton/zooplankton relationships, and have essentially ignored higher trophic level dynamics such as grazing and nutrient excretion impacts on plankton dynamics. Thus, the common view that plankton studies have contributed minimally to our knowledge of fisheries dynamics, and vice versa, is not surprising. There has been virtually little effort in the United States to carry out appropriate studies with the total food web in mind.

In the following synopsis I will outline some aspects of plankton biology which may be helpful toward bridging this artificial gap between plankton and fishery biologists. Hopefully, it will also encourage much needed coherent field and laboratory studies to clarify how primary production passes up the food web to support fisheries. Or, as a fishery biologist might prefer to view it, how a given fishery is regulated by lower trophic levels.

Some Characteristics of Plankton Dynamics

Seasonal Cycles

The intensity of phytoplankton production varies seasonally, in addition to regional differences in total annual production. This seasonal variation is reflected in a series of abundance pulses over an annual cycle. Figure 1 illustrates that one or two major phytoplankton blooms are characteristic of representative regions. When viewed on a global scale, three general patterns are evident (Figure 2). Arctic waters are characterized by a single annual pulse. Temperate waters are generally two-pulsed systems, and in tropical waters a dampened cycle of modest population oscillations occurs. In enriched nearshore waters the annual bloom pattern consists of a series of blooms of irregular duration and magnitude rather than exhibiting the one- or two-pulsed trends depicted in Figures 1 and 2.

The significance of these bloom patterns is that a continuous, even production and flow of
phytoplankton carbon is not available to the food web. During the major blooms a large amount of excess carbon may be produced over that grazed. This surplus is degraded microbially within the water column or on the sea floor. Moreover, the representative trends in Figures 1 and 2 suggest that low phytoplankton standing stock levels occur during much of the annual cycle.

These characteristics suggest the need for synchronization between herbivore occurrence and production and the regionally characteristic phytoplankton bloom dynamics. With regard to the zooplankton, two types of phasing are apparent (Figures 1 and 2). Zooplankton pulses are either asynchronous with the phytoplankton pulses or they occur simultaneously. The cycles are stated to be unbalanced when the phytoplankton pulse precedes the zooplankton pulse and balanced where the pulses are coincident. In an unbalanced cycle, phytoplankton biomass usually exceeds zooplankton biomass. Unbalanced systems are generally characteristic of polar and temperate waters and upwelling regions. Balanced systems usually occur in oligotrophic, warm seas. The primary factors of the unbalanced cycles are the extraordinarily rapid phytoplankton growth coupled with the temperature-regulated delay in zooplankton growth and reproduction during the major bloom. This temperature-regulated delay in zooplankton growth becomes progressively diminished, with increasing temperature resulting in the balance of cycles in tropical waters. The significance of this characteristic to food web dynamics is that temperature modifies and regulates trophic transfer of phytoplankton carbon. In cycles markedly unbalanced, a considerable amount of phytoplankton carbon may not be available to "desirable" species (herbivores) and degraded by microbial processes. In balanced cycles, a closer coupling between trophic levels occurs, with herbivores being able to take quick advantage of increases in primary production.

A phytoplankton pulse consists of two major elements: bloom inception and bloom termination. The inception of the major annual bloom is usually triggered either by a reduction in vertical mixing (increases the residence time of the phytoplankton within the euphotic zone) or by nutrient enrichment. Our knowledge is sufficient to allow the building
of bloom inception models based on time-dependent physical models in well-mixed, i.e., winter, conditions on the continental shelf, as well as simple one-dimensional models of low-frequency systems such as the central gyres. However, we cannot as yet build satisfactory physical models of stratified conditions to handle seasonal thermocline development, wind mixing, and nutrient cycling.

A corollary of this is the present great difficulty in establishing and modeling the causes of the major bloom termination, which usually occurs during stratified summer conditions (Figures 1 and 2). The observed phytoplankton decline accompanies a reduction in ambient nutrient levels and an increased zooplankton biomass. Zooplankton function in two major processes during this period: as they graze down the phytoplankton, they simultaneously excrete essential nutrients required for continued phytoplankton growth. Presently, we lack sufficient data on the grazing terms and rates of nutrient excretion for key zooplankton species. Secondary production estimates based on cohort analysis of field populations are virtually non-existent. A complicating factor is the degree to which pelagic processes are coupled to benthic activities. Water column depth influences zooplankton abundance and the extent to which pelagic processes are influenced by benthic processes. The benthic community likewise influences water column dynamics through nutrient excretion and grazing on phytoplankton. Figure 3 illustrates that shallow waters support a lower average standing stock of zooplankton than do deeper waters; biomass increases with depth to about 200 m. It is not possible to define precisely the depth at which pelagic processes become uncoupled from benthic influences, but it is evident that there is an onshore-offshore gradient in the relative contributions of the zooplankton and benthos. Benthic activities can be expected to predominate in shallow waters, with the contribution by zooplankton progressively increasing with water column depth. At depths > 100 m zooplankton probably become preeminent and pelagic processes more or less uncoupled from benthic influence (grazing and nutrient excretion). Our knowledge of these benthic processes is likewise minimal.

We can summarize our present abilities to quantify bloom termination dynamics as follows: Biological dynamic models require data sets, presently unavailable, for specification of the values of coefficients, parameters, initial and boundary conditions. Another constraint is the lack of data on zooplankton cohort production or invertebrate predator dynamics. We thus cannot build dynamic models of more than two to three weeks' time because there is inadequate zooplankton and invertebrate predator data to extend the calculations past the life cycle of these organisms.

With regard to modeling of overall dynamics up through the food web, our present capabilities are extremely limited. We do not understand the time-dependent coupling of phytoplankton, zooplankton, larval fish, and invertebrate predators. This sets the time and space limits of present models. With our ability to run phytoplankton models for days and adult fish models for years, the interface data on time scales of months to couple these two types of models are missing (Walsh, personal communication).
Variability in Plankton Cycles

Significant interannual variations in plankton cycles occur where observations have been made over a suitable time period. In Narragansett Bay phytoplankton observations have been made on a weekly basis since 1960 (Figure 4). Here, the annual maximum abundance during the winter-spring bloom varied tenfold from 4500 cells ml\(^{-1}\) (1970) to 42000 cells ml\(^{-1}\) (1963). Time of inception of the winter-spring maximum has varied from December to April. In 4 years, 1970, 1973 to 1975, the annual maximum occurred during August! Maximum abundance during the summer has varied about ninefold, from 7000 cells ml\(^{-1}\) (1967) to 59000 cells ml\(^{-1}\) (1975). The causes of these significant seasonal shifts in peak abundance and year-to-year variations in inception and magnitude of the winter-spring bloom in the unpolluted waters of lower Narragansett Bay are unknown.

Similar variability has been reported from the North Sea in time of inception of the spring bloom, zooplankton biomass, and numerical abundance and length of the zooplankton growing season (Figure 5).

There is also considerable variability in the predominance of different plankton groups. Figure 6 (Glover, 1961) illustrates the variations in various zooplankton components occurring over a 10-year period on the northern North Sea herring fishing grounds. Three major periods in zooplankton re-

organization are recognizable. From 1949 to 1951, North Sea neritic forms were abundant, which then declined, and more oceanic representatives increased in numbers from 1952 to 1954 and in 1956. During 1957 and 1958 an overall decrease in zooplankton abundance occurred; species showing a distributional pattern intermediate between the North Sea types and the oceanic representative then predominated. A striking example of another type of variability is evident in the dynamics of the copepod *Pseudocalanus elongatus* over a 25-year period in the North Sea (Figure 7). A systematic long-term trend, superimposed on the annual cycle in which the overall annual abundance between 1948 and 1968 has progressively decreased, characterizes this species. This decrease has also been accompanied by a progressively shorter "biological season" (Glover et al., 1974). The copepod *Temora longicornis* reveals a different long-term trend. Although the length of its growing season has remained constant, it has shifted with time, becoming progressively later from 1948 to 1966.

These limited long-term observations clearly establish the significant variability characterizing plankton communities. This variability characterizes both phytoplankton and zooplankton. And it is manifested in species composition, abundance, and time of duration and magnitude of abundance for the total population and individual species. Cause-and-effect relationships cannot be estab-

![Figure 4](image-url) Maximum monthly abundance of the diatom and dinoflagellate populations in the surface waters of lower Narragansett Bay from 1960 through 1974 (Smayda, 1976).
Figure 5. Fluctuations in the plankton in a region of the northeast Atlantic and the North Sea. The results in the upper two pairs of graphs are given as standard deviation units. In the lower two pairs the ordinate values are plotted about the mean values; for calculated trend lines, * = significant at $P = 0.05$, ** $P < 0.01$, and *** $P < 0.001$ (Glover et al., 1974).

Figure 6. The relative seasonal abundance of the plankton of the northern North Sea herring fishing grounds based on Plankton Indicator samples (Glover, 1961).

Figure 7. Abundance of the copepod *Pseudocalanus elongatus* (as average numbers per sample) at monthly intervals from 1948 through 1972 in the east-central North Sea (Glover et al., 1974).
munities have often been reduced to a common property, such as chlorophyll, carbon, or displacement volume as a measure of abundance. In the case of phytoplankton, measurement of primary production has often been the sole measure of phytoplankton availability. However, even a modest awareness of the natural behavior and physiology of phytoplankton and zooplankton reveals that significant interspecific differences occur in their physiology, behavior, and suitability as prey. Thus, in a species succession (Figure 8) the changes in taxa are secondary to the dynamic aspects and food web consequences associated with such successions.

Figure 8. The average abundance of the common species of phytoplankton and copepods in the southern North Sea and over the deep Atlantic part of the Continuous Plankton Recorder Survey region (Glover, 1961).

It is essential, therefore, that the species composition and abundance be routinely established in field studies, including those concerned with fisheries problems. With regard to the phytoplankton, species succession has two interrelated aspects. The species composition influences community structure, and the cell sizes characteristic of the species composition affect community function and trophic interrelationships. In turn, the food “quality” of the phytoplankton species differs interspecifically, and the food value of a given phytoplankton species to a grazer differs between grazer.

The classic example of an unacceptable phytoplankton species as a food source is Phaeocystis pouchetii. This large, gelatinous colonial species blooms extensively during the winter-spring in temperate and polar waters. During these blooms, zooplankton and herring avoid Phaeocystis patches. This avoidance is thought to be related to inimical substances released into the water column by Phaeocystis.

The well-publicized anoxia in the New York Bight during the summer of 1976 was accompanied by an unusual and prodigious bloom of the dinoflagellate Ceratium tripos. While the exact conditions triggering this outbreak are unresolved, one view has contended that the oxygen deficiency resulted from degradation of the ungrazed Ceratium population. Because of its large size, Ceratium tripos may have been ungrazed, which, combined with minimal advective losses and steady recruitment, led to its remarkable population explosion. Extensive shellfish and finfish mortality accompanied this anoxic event. If indeed this event resulted from an ungrazed phytoplankter, then this episode might have been circumvented if some other more suitable phytoplankton species developed during the summer of 1976. This uncertainty illustrates our substantial inability to account for single species dynamics, such as Phaeocystis or Ceratium blooms. There is a growing need to understand single species dynamics at all trophic levels.

There is additional evidence for the need to know the species composition and size characteristics of natural communities. Bivalve larvae, copepods, barnacle larvae are now well known to have very specific food requirements not provided by all species of phytoplankton. Thus, certain species of barnacle larvae will reproduce and metamorphose only when diatoms are provided as a food source; other species require microflagellates exclusively. The pioneering experiments of Lasker and co-workers (see Lasker and Zweifel, 1978) have shown the great importance of phytoplankton species composition and cell size to first-feeding northern anchovy larvae. Durbin and Durbin (1975) have likewise shown that the grazing rates of the Atlantic menhaden Brevoortia tyrannus are a function of particle size and concentration.

Grazers show significant selectivity in their food preferences, even members of the same genus. Figure 9 illustrates this, based on a study of 16 species of tropical euphausiids. Moreover, the food preferences of a maturing predator change with increasing size, or during different stages of growth. Figure 10 illustrates this phenomenon based on a study of the chaetognath Parasagitta elegans.
This diverse evidence strongly suggests the importance of establishing the food preferences of predators over their developmental cycle, the species composition, abundance and organism size structure in natural communities, and the *in situ* dynamics of such key species. Our knowledge of such processes is very skimpy. Yet the evidence suggests that our eventual ability to quantify, model, and predict food web dynamics up through the fisheries will require such understanding. Which organisms are present, in what concentrations, and at what time over the annual cycle are aspects of food web dynamics no less important than total production or efficiency of energy transfer. Lasker's work surely illustrates the value of the type of approach needed if fishery biologists and plankton biologists are to achieve their common research objective: to understand marine food webs.

References


Some Remarks on the Nature of the Fisheries Data Base in the Northwest Atlantic

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Introduction

The principal purpose of this talk is to give a brief outline of the nature of available data that might be used to identify causal relationships between fish production and climatic factors. To achieve true predictive capability, it is necessary that controlling mechanisms be identified — statistical correlations by themselves rarely lead to accurate predictive models. The single most important life process that governs changes in fish production is the recruitment process, which involves maturation, fecundity, spawning, and growth and survival through the egg-larval-juvenile stages. There is strong evidence that the major factors controlling success of year classes for most fish populations operate during the larval stages. Understanding the physical and biological events that control the timing and distribution of egg and larval stages of most species, and their food supply, predators, and subsequent survival, will probably require a multifaceted research program that involves coordinated physical and biological studies over a rather wide range of events in time and space. In short, it will require an ecosystem-oriented program that takes account of multispecies interactions as well as atmospheric and oceanic events.

The Northeast Fisheries Center since its formation in 1972 has been developing such an approach for the continental shelf region from Cape Hatteras to Nova Scotia. Needless to say, we have a long way to go before an adequate time series of data on early life stages of most major species becomes available. However, a good beginning has been made, and in the next five to ten years it is anticipated that a number of key hypotheses about the factors controlling reproductive success and other biotic-abiotic interactions may be tested.

The fishery and related ecosystem data base is classified into four categories: (1) harvest statistics, (2) monitoring biomass components of the ecosystem, (3) estimating production of biota, and (4) process-oriented studies. Each of the four categories provides essential information for development of a marine ecosystem model, and they are arranged in order of increasing complexity in the understanding of factors controlling fish production. After a description of the significance and status of each category, a summary chart will be presented that illustrates the state of knowledge in a very general way.

Harvest Statistics

Complete and accurate statistics on removals are of course essential for relating population changes to exploitation rates. Commercial fishery statistics for the northeast United States go back to the late 1800s for a few species, but they usually represent only landings for certain ports, and they do not supply adequate information on location of catches and gear used (Rounsefell, 1948). Statistics improved substantially in 1929, when landings were recorded by gear type and location of catch, days absent from port noted, and trawlers classified by tonnage categories so that estimates of abundance (catch per unit effort) could be derived.
However, the abundance records are adequate only for haddock in the 1930s, and yellowtail flounder in the 1940s. From the 1950s on, statistics are adequate for general abundance analysis for most major commercial species (for which there were directed fisheries by New England fishermen), and a much wider area was encompassed through establishment of the International Commission for the Northwest Atlantic Fisheries (ICNAF), which set up a standardized statistical system for the entire northwest Atlantic. There has been a steady improvement in the completeness (number of species) and refinement of statistics since that time. However, it should be noted that complete ICNAF statistical records (including effort data) for abundance analysis that are on file in the computer at the Northeast Fisheries Center go back only to 1963. With the establishment of extended jurisdiction in 1977, further improvements have been initiated, notably in the Mid-Atlantic area, where statistics were less complete than in New England waters.

Recreational fishery statistics are far less complete than commercial statistics. National postcard surveys were conducted by the U.S. Census Bureau in 1960, 1965, and 1970. In 1974, the National Marine Fisheries Service (NMFS) surveyed the region from Cape Hatteras to Maine. Only a gross measure of catch is available from these surveys. In 1978, the National Marine Fisheries Service began a more intensive recreational harvest survey, and it is expected to provide more accurate results than previous surveys.

Monitoring Biomass Components of the Ecosystem

Fishery statistics by themselves do not provide adequate information on biomass of all important fish species, nor do they provide adequate pre-recruit estimates. Therefore, another source of information is needed which could provide much more complete and unbiased measures of the changes in the size and structure of the finfish biomass as a whole. Similar data are needed on the planktonic and benthic components of the ecosystem if we are to determine how the system changes through time and under different climatic regimes. NMFS established the Marine Resource Monitoring Assessment and Prediction Program (MARMAP) in the early 1970s to provide annual and seasonal monitoring of principal biota on a broad geographic scale. The prototype MARMAP program was begun in 1963, when the Northeast Fisheries Center (NEFC) at Woods Hole, Massachusetts, began a comprehensive bottom trawl survey program designed to provide an annual quantitative inventory of fish populations on the continental shelf off New England.

During the first four years, surveys covered the region from New York to western Nova Scotia (sampling strata 1 to 42; see Figure 1), and were conducted by the NMFS research vessel Albatross IV. In 1967, the survey area was expanded to include the Mid-Atlantic Bight region from New York to Cape Hatteras (sampling strata 61-76), and Albatross IV was joined by a Soviet vessel as part of a cooperative research program under the auspices of the U.S.-U.S.S.R. Bilateral Treaty on Fisheries in the Mid-Atlantic Area. These surveys showed that with standardized and unbiased sampling methods (a critical feature is random selection of stations within strata) and one or two research vessel cruises per year, it was possible to monitor changes in fish populations with sufficient accuracy to add an invaluable new capability for assessment of the status of major stocks and the effects of fishing. In addition, the surveys added a critical new dimension to the assessment data base in the form of a total finfish biomass index, representing virtually all finfish species, which provided for the first time a comprehensive and quantitative measure of the state (abundance, population structure, species composition) of the finfish component of the marine ecosystem.

The value of these indices for fishery assessment studies and ecosystem studies in general was recognized by scientists in many countries, and by 1970 the bottom trawl surveys had become an integral part of the ICNAF survey program, as well as a major component of the developing MARMAP program, and standardized trawl surveys had expanded to include the entire continental shelf, from Cape Hatteras to the Laurentian Channel (Figure 2), involving the United States, the U.S.S.R., and Canada. Examples of how the survey data are used in assessments are given by Sissenwine et al. (1978).

By 1972, the ICNAF survey program had extended east and north to include the Laurentian Channel and the Gulf of St. Lawrence, the Grand Banks off Newfoundland, and the shelf off Labrador and West Greenland, involving Canada, the U.S.S.R., France, West Germany, and the United
Figure 1. Sampling strata used in offshore bottom trawl surveys since 1963. Comparable depth zones and strata sizes used in stratification of the continental shelf east and south of this region. Stations are randomly selected in each stratum.

Figure 2. Part of sampling strata used for bottom trawl surveys off Nova Scotia since 1970 by Canada, the United States, and the U.S.S.R. Note that all countries use the same strata except for strata 82 to 85, 90 to 95, where the United States and Canada strata differ slightly.
Kingdom. The MARMAP program had also expanded by extension of the standard offshore survey south of Cape Hatteras to Cape Canaveral (Cape Kennedy) with surveys on the Delaware II by the Middle Atlantic Coastal Fisheries Center (MACFC) at Sandy Hook, New Jersey. In addition, MACFC established inshore trawl surveys from Rhode Island to Charleston, South Carolina, using smaller vessels and covering the area from the beach out to the inshore limits (15 fathoms) of the offshore surveys. These inshore areas are nursery grounds for many offshore as well as inshore marine species, both sport and commercial, and therefore are of critical importance in understanding the distribution and population processes of many stocks in relation to changes in fishing and environmental factors (including pollutants).

In 1973, a MARMAP contract was let to the South Carolina Marine Resources Institute for monitoring the region from Cape Fear to Cape Canaveral (Cape Kennedy) in close coordination with the surveys conducted by Woods Hole and Sandy Hook. In addition, a new series of spring bottom trawl surveys by Poland and West Germany was begun in the mid-Atlantic and Georges Bank areas for monitoring semipelagic stocks such as mackerel and sea herring. A rough time table of events since 1963 is outlined in Table 1.

Thus, at the present time coordinated and standardized MARMAP trawl surveys are scheduled for fall and spring over virtually the entire continental shelf off the East Coast of the United States (Figure 3), and comparable surveys are being carried out by ICNAF over most of the remaining shelf off the east coast of Canada. In essence, then, we have a MARMAP-type program established over most productive parts of the entire continental shelf of the northwest Atlantic.

The basic minimum routine data recorded for each haul on trawl surveys include the weight and length frequency of each species of finfish, and selected invertebrate species such as squid, lobster, crab, and shrimp. In addition, scales, otoliths, gonads, and stomachs are collected for continuing assessment and ecological studies, including growth, mortality, age structure, reproduction, and feeding interactions of fish populations. Many other special biological samples are taken in support of other programs, such as the NOAA study on contaminants in marine organisms, as well as ecological studies on many marine species conducted by scientists in other government agencies and in universities.

In 1968, Albatross IV began taking a plankton tow at each bottom trawl station for the purpose of monitoring the general distribution of fish eggs and larvae. Since it was possible to make the plankton tow simultaneously with the bottom trawl haul, no additional ship time was required in the survey schedule. Since that time, MARMAP has developed operational procedures and preliminary standards for routine monitoring of the biomass and structure of ichthyoplankton communities, and these standards have been followed as far as possible in the "piggyback" plankton sampling on the trawl surveys.

By coordinating the timing of fall and spring trawl surveys, we thus get a general synoptic picture of both demersal fish and ichthyoplankton communities on the entire East Coast during the warm and cold seasons. The large-scale seasonal picture of plankton communities provided by these surveys is a valuable addition to a number of ongoing and more intensive ichthyoplankton studies (e.g., ICNAF larval herring surveys) by providing information on major variations in water-mass pat-
terns (through the distribution of associated plankters) which may be related to dispersal and survival of the eggs and larvae of the particular species under study. Since 1977, separate ichthyoplankton surveys have been conducted, and the frequency increased to six or more times a year.

Observations on temperature (surface to bottom) have been taken routinely at each trawl station since the beginning of the trawl survey program. Starting this year, an expanded program of hydrographic sampling is being developed as part of the ichthyoplankton surveys. Standard hydrographic transects are being established at various places along the shelf, and profiles of salinity, temperature, oxygen, and several major nutrients (nitrogen, phosphorus, etc.) are to be taken at stations along these transects during the bottom trawl survey, in addition to the routine temperature record at every station. In this way, large-scale patterns of interactions between coastal and slope water masses, and the interrelationships with plankton, will be better defined, as will major fluctuations in water-mass characteristics which may alter the geographic and inshore/offshore distribution of planktonic communities as well as demersal fishes and invertebrates.

**Estimating Production of Biota**

The next level of study involves estimation of the actual production of selected components of the ecosystem. In the case of fish production this is done largely on an annual basis, and the techniques and state of the art have been described by Sissenwine et al. (1978). With regard to plankton populations, critical events and production cycles occur over much shorter time scales than for adult fish. A major focus is placed on zooplankton and on larval fish in particular, and here we are considering a time scale of weeks and months to obtain a measure of larval production (as well as survival, etc.) in one season, and usually for only one target species at a time. This is a mesoscale effort and is illustrated by the Georges Bank larval herring surveys.

The approach of the ICNAF survey program was to concentrate sampling in the first 6 months of life on the Georges Bank-Gulf of Maine sea herring stocks. When the surveys were initiated in 1971, the plan was to cover the entire Georges Bank-Gulf of Maine area at least once a month from September to December to monitor larval production and intermixing of larvae from the various spawning sites (see Figure 4 for typical distribution pattern). During the first two years, minimum sampling at each station included oblique hauls with 60-cm Bongos (0.505-mm and 0.333-mm mesh), temperature profiles, and surface salinities. Beginning in March 1973, the Federal Republic of Germany added night sampling of larval herring with Bongos and neuston nets, and in February 1974 the United States began the series of February cruises.

After the formation of the ICNAF Environmental Working Group in June 1974, interest developed in a more comprehensive and intensive investigation of factors controlling success of year classes. In the autumn of 1974, paired 20-cm Bongos with smaller mesh sizes (0.253 mm and 0.053 mm) were added to the standard 60-cm Bongos, and in subsequent years 0.253-mm and 0.165-mm mesh nets were used on the 20-cm Bongos. In May 1975, the Working Group recommended that in addition to monitoring larval herring production more emphasis
should be given to studying circulation in the Georges Bank-Nantucket Shoals area, and that concurrent studies of primary and secondary production should be initiated, as well as fine-scale patch studies. Thereafter, emphasis shifted to the Georges Bank-Nantucket area alone, since vessel support was insufficient for intensive sampling of the whole region (see Figure 5 for revised station pattern). Sampling was expanded to include more complete hydrographic coverage (temperature, O₂, and salinity profiles at each station), and also nutrients, chlorophyll, and primary production when possible.

The program has continued along these lines to date, but only a small fraction of the total data base has been analyzed. Analysis of nutrients, chlorophyll, and primary production is still in progress. Preliminary temperature and salinity plots have been completed for most cruises, and the data has now been
entered into the National Oceanographic Data Center (NODC) computer. Analysis of the full-time series of plankton samples so far has been restricted largely to the 0.505-mm mesh series and to the length frequency and distribution of herring larvae. Sorting of the ichthyoplankton from the 0.333-mm mesh samples was completed by the Polish Sorting Center in December 1977, but the zooplankton components will take at least another year. Only broad-scale changes in structure and abundance of invertebrate zooplankton populations can be derived from these surveys, since significant segments of the population cycles, juvenile stages in particular, are missed with the monthly or bimonthly spacing of cruises.

Very few quantitative phytoplankton studies have been done in the offshore areas. In recent years (1975 to 1976), primary production estimates were made on Georges Bank in conjunction with the ICNAF larval herring surveys. A preliminary report on this work indicated unexpectedly high production values throughout the year, which may

Figure 5. ICNAF larval herring survey sampling stations and cruise track. Coverage within heavy solid line emphasized.
Table 2. Current status of knowledge of biotic components of northwest Atlantic ecosystem and present research efforts. (Two levels of knowledge and activity are indicated: \( \checkmark \) [limited] and \( \times \) [reasonably comprehensive]. Numbers in parentheses refer to time and space scales involved.)*

<table>
<thead>
<tr>
<th>Biota</th>
<th>Species list</th>
<th>Biomass inventory</th>
<th>Annual-seasonal monitoring of biomass and structure</th>
<th>Short-term predictions, abundance fluctuations; mostly individual species</th>
<th>Long-term predictions of multispecies population; understanding dynamics</th>
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*1. Macroscale; annual-seasonal variations, shelf-wide, population scale.
2. Mesoscale; within season variations, selected geographic regions, individual stock scale (e.g., fish stocks).
3. Microscale; hours to 10-day variations (meteorological and oceanographic event scale), restricted areas, small biological units (e.g., plankton patch).

help explain the high productivity for other levels of the food chain (Cohen and Wright, 1978). More detailed studies of primary and secondary production by NEFC are in progress this year in cooperation with the U.S.S.R. and the Brookhaven National Laboratory.

Process-Oriented Studies

The fourth level of study is designed to identify mechanisms which control critical phases of the production cycle of selected components of the ecosystem. An example of such a “microscale” study is the larval herring patch study scheduled for October 1978 on Georges Bank. The purpose of the patch study is to gain a basic understanding of short-term physical and biological mechanisms controlling growth, survival, and dispersal of recently hatched herring larvae and their food organisms from the northeast Georges Bank spawning ground — and the related question of possible mechanisms for their retention on Georges Bank. The proposed study would involve intensive sampling of the horizontal and vertical structure of a patch of larvae by several vessels working simultaneously for a period of 3 to 4 weeks, beginning in October 1978, and include direct measures of water motion using moored current meters, drifting buoys with drogues, and dye experiments. At the present time, up to five vessels are expected to participate in the 1978 patch study. One vessel would do hydrographic and current studies, and another vessel would monitor patch boundaries by continuous high-speed sampling with plankton nets. A third would sample vertical structure and horizontal patchiness with opening-closing samplers, and a fourth would study fine-scale structure of phytoplankton and zooplankton with a plankton pump. A fifth vessel would do quantitative sampling of zooplankton (bottom to surface) in the patch using standard Bongos. At the same time, a sixth vessel is scheduled to provide broad plankton-hydrographic survey coverage for the entire Georges Bank-Gulf of Maine region, similar to that of the IGNAF larval herring survey.

It seems clear that the “microscale” approach will be necessary in order to identify controlling mechanisms in plankton populations. However, the answers are not likely to emerge quickly, because of the complexity of the system and the resources required to conduct such interdisciplinary studies. The implication is that development of predictive fish-production models that incorporate climatic information is going to be a long process.
Summary Status of Knowledge

A very rough outline of the general status of knowledge for the biological components of the marine ecosystem is presented in Table 2. For each of the major biological communities, the current status of information is indexed under five levels increasing in complexity from left to right (from mere knowledge of species composition to the understanding of population dynamics at the multi-species level adequate for long-term predictions). Obviously we have a long way to go. The most likely payoff in terms of developing predictive models for fish production which include climatic factors will be through expansion of knowledge in the plankton and larval fish communities and through an understanding of how they are controlled by physical oceanographic processes.

References


Introduction

Prediction of the distribution and abundance of fish stocks has long been an art, but only recently have significant efforts been expanded to make it a science. Environmental information has been used in artistic and scientific attempts at prediction. However, one of the oldest and most successful examples of prediction of small-scale distribution was made by an itinerant Jewish carpenter about two thousand years ago (New Testament, 33 A.D.), apparently without environmental inputs. It is doubtful that this performance can be matched by present-day fishery managers, for they lack the special insights of this early practitioner.

Other examples of nonscientific predictions of fish distribution can be found in folk legends regarding the timing of fish migrations, some of which involve environmental inputs. For example, Edwards (1965) tells of a belief held by old-time Rhode Island fishermen that the arrival of scup (Stenotomus chrysops) was concurrent with the flowering of dandelions. Long Island and Virginia fishermen on the other hand predict the arrival of shad (Alosa) with the flowering of the shad bush, and weakfish (Cynoscion) with the dogwood or lilac. Further, the interval between flowering of the two trees is an indicator of the success of the weakfish fishery.

Early attempts at scientific prediction of fish abundance using environmental input data included Walford's (1938) efforts to relate the distribution of haddock eggs on Georges Bank to the density structure of the water, Sette's (1943) efforts to relate Atlantic mackerel year-class strength to wind conditions during the pelagic larval stage of development, and Pearson's (1948) study relating fluctuations in blue crab catch to discharge volume in Chesapeake Bay tributaries.

State of the Science and Complications

Recent descriptions of the status of the application of environmental information to fishery predictions have been presented by McHugh (1976) and Johnson and Seckel (1977), principally in the form of case-study examples. Most of the examples chosen demonstrated logical, conceptually linked relationships which reflect true ecological interactions; however, these presentations, plus the much more detailed description of studies in the northeastern Atlantic and adjacent seas by Cushing and Dickson (1976), show that most studies linking fishery variations to short-term and long-term climatic changes are still predominantly empirically derived inferences. Looking further into the literature of fishery biology and oceanography, we can find many accounts of correlations of fishery landings and environmental data which are hardly tenable as reflections of true ecological relationships, in spite of the high statistical correlation coefficients some may involve (Dow, 1964, 1969, 1977; Flowers and Sails, 1972).

In these studies, climatic and fishery yield data were linked in a purely statistical fashion, with no attention paid to the development of a conceptual model or an ecological explanation of the inter-
action between them. They appear to be a search for high correlation coefficients, obtained by multiple regression analysis and trial-and-error adjustment of lag times so that sufficiently high coefficients appear. Dow (1964) and Sutcliffe et al. (1977), for example, lagged temperature cycles until they fit the biotic cycles. This was done with no explanation of cause and effect. The justification appears to have been based upon improved correlation coefficients. The results of studies of climate and fisheries would be far more relevant and useful if they were to begin with a conceptual model of the interaction between the environment and the subject organisms and if statistical techniques were then applied to the data. "Any fairly linear trends could be related to almost any activity of man because most of man's activities are changing in a cumulative manner. It would be no more than flip-pan to relate plankton trends to the illegitimacy rate in teenage girls (because, we hope, nobody would impute a causal relationship) but it might be dangerously misleading to relate them to the quantities of suspended matter in the atmosphere, or the rates of industrial production of mercurial fungicides and organochlorine insecticides (because there are many people who would undoubtedly impute a causal relationship without the essential evidence from all the interacting complex of factors that produce variability in nature)" (Glover et al., 1974).

The environmental variable or variables selected as significant for correlation with biological abundance or distribution data may not be the truly causal factors sought. They may be indices of the causal factors, or, even worse, they may be unrelated to the causal factors. Temperatures of water or air are frequently used in studies of climate and fish abundance, mostly because temperature time series are the most abundant. In many cases, however, temperature is not the causal factor at all, but is once or twice removed from it. For example, as pointed out by L setup and Lynn (1977), the distribution of forage in temperature gradient zones may be a far more important factor in stock distribution than an actual response to the temperature field by the tuna.

Often the most relevant data sets for climate/ fisheries studies are ocean temperatures of currents at the appropriate depths and recruitment or year-class-strength time series. Rarely are two matching sets available, and "proxy" data must be used. Such proxy data may be temperature extrapolated from air temperature records at some distant coastal weather station, currents computed from atmospheric pressure gradients (Nelson et al., 1977), and fishery catch statistics, sometimes converted to catch per unit effort. Drawing conclusions from correlations of sets of such proxy data can be misleading and unwarranted. Unfortunately, the practice of using proxy data is likely to continue to be prevalent, because time series of the primary data required are rare. As for environmental data, time series of subsurface measurements are practically nonexistent, and surface data banks often contain only series of surface temperature and wind data. Time series of biological data are even scantier, with direct assessments of fish abundance very rare. Most estimates are generated from fishery catch statistics, often without effort data.

The use of proxy data can be acceptable or desirable in some circumstances, however, if there is a firm bridge of knowledge from the proxy data to the causal factor to the organism. For example, atmospheric pressure gradients may be acceptable and desirable proxy data for year-class-strength correlations, because the gradients produce the winds that provide the transports of water which carry larvae to estuarine nursery areas of the proper salinity and temperature (Nelson et al., 1977; Chase, 1965).

Many fish stocks, especially the filter-feeding pelagic species, undergo wide variation in population for other than environmental reasons. With those fishes, density-dependent factors such as cannibalism (on eggs and larvae by adults) and competition for food may produce lower survival and recruitment from dense populations of spawners than from smaller populations. These density-dependent factors are manifested in quasi-parabolic spawner-recruit curves for many species. The composition of the population in most stocks under heavy fishing pressure changes from older to younger fish. When the stock size is large, recruitment often exhibits wide ranges of interannual fluctuation. These fluctuations may not, however, be significant to the stock. At lower stock sizes, the range, or variability, in recruitment is less, but of greater significance to the stock, as poor recruitment may be matched with poor environmental conditions. In some fisheries, these and other biological factors are relatively well understood and are accounted for in yield models. Nevertheless, such fisheries occasionally undergo unexpected and unexplained variations in year-class
strength, which are generally attributed to unnamed environmental factors. "Environmental factors are obviously the major controlling forces, but the present state of knowledge concerning the influence of these factors is inadequate for assessment use" (Mackerel Fisheries Management Plan, Mid-Atlantic Fisheries Management Council, March 1978).

All too often, data series collected over several decades are of low quality, totally or in part. In biological series, economic factors which may strongly affect fishing effort could be totally overlooked in catch data: perhaps no distinction is made between abundance and availability to a gear type; significant changes in harvesting technology may be overlooked in catch-effort data (Bell and Pruter, 1958); and in some fisheries the fishermen may deliberately falsify catch or location data to conceal true incomes or violations of area restrictions.

In environmental series, the design of instruments used in measurements might be changed one or more times during the period of record (e.g., from mechanical bathythermographs to expendable bathythermographs), the measurement site might be changed, or technological change might occur in the vicinity of the measurement site (deeper cooling water intakes on larger ships or industrial thermal effects at shore stations). Early data series may not have been quantified at all, such as estimates of sea state or classifications of "good" or "poor" fishery yields.

In addition to problems with poor quality in time series data, the lengths of the series frequently are too short. It is difficult to find government agencies or business enterprises which will remain dedicated to monitoring variations for more than a few decades. It has been said that the interest span of some branches of the United States government is about 4 years. Fortunately, this is an exaggeration, but there is a problem with maintaining continuity of monitoring activities in the face of funding cuts, reorganizations, and staffing freezes.

Most physical oceanographers who have sought to work with marine biologists on ecological studies have encountered at least one who doubts the utility of physical and chemical data. Some population dynamicists begin each study with a set of assumptions, including the assumption that environmental variation has no significant effect on the abundance of the species being studied, to simplify the modeling effort. It is doubtful that there is any species whose variations in abundance are not influenced by environmental changes.

Based on a review of about 50 publications (see "Annotated Bibliography") concerning climate/fisheries interactions, the following complications appear to be common:

1. There is a lack of established causal relationships in many fisheries.
2. Scientists frequently must resort to use of proxy data, environmental and biological.
3. The major variations in a fishery may not be caused by environmental factors.
4. The quality of data time series, especially biological, is often poor and the time series are frequently too short.
5. There is a frequent lack of interest among fishery biologists and managers in using environmental data and relationships for predictive or explanatory purposes.

Biological Considerations in Design of Investigations

The priority criteria for selection of species or stocks for study are generally determined by management needs and not by the potential for success in climate studies. Nevertheless, there are several points to consider which, if addressed, should increase the chances for success in developing climate/fisheries studies. These considerations involve an understanding of those biological processes that are forced by the environment and produce variations in distribution or abundance of a species.

The length of time spent in the water column as a plankter is one of the most critical considerations. A species with a long larval existence is susceptible to predation by filter feeders, changes in food abundance (Lasker, 1978), and currents and winds (Nelson et al., 1977). Species with a fairly short pelagic existence are less likely to show year-to-year fluctuations as they pass quickly from this somewhat precarious existence. Cushing and Dickson (1976), on the other hand, discuss the concept of the match/mismatch between spawning and the spring phytoplankton bloom, and point out that a shorter larval period could lead to an entire year class missing the spring bloom. Cushing (1972) and Bannister et al. (1974) cite an example where the 1963 year class of plaice was excellent following a cold winter, which delayed both larval metamorphosis and the spring bloom. The bloom, which
was intense once it did occur, provided a strong
match with the larvae, resulting in a strong year
class in spite of the prolonged larval period.

Studies on the hard clam in Virginia waters
(Castagna, personal communication) have shown
that there is also better recruitment following a cold
winter. In this case, the winter delays spawning,
with the result that the larvae are in the water for
only a short time, and thus provide a mismatch
with predators. Spawning after a warm winter is
more protracted, and larval predators have more
time to feed.

In short, a long larval period generally makes a
species more susceptible to environmental
change, and hence more likely to show interannual
fluctuations.

From the foregoing, it also appears that the
larval period is affected by the severity of the
winter (Cushing, 1972; Bannister et al., 1974; and
Castagna, personal communication), and as such
the winter/larvae relationship is an important
consideration.

The fecundity of a species is an important
consideration, as more fecund species, such as
cod, tend to be stabilized at high population densi-
ties. Higher reproductive capability offsets density-
dependent factors, such as cannibalism, but can
lead to wide fluctuations in abundance if environ-
mental variations increase the egg or larval mor-
tality.

Cannibalism may be a stabilizing factor when
large year classes of juveniles are preyed upon by
the adult stock, thus limiting their number. The
converse follows when large year classes become
adults. This relationship has been demonstrated
for Alaska pollock (Laevastu and Favorite, 1976). It
would follow, then, that noncannibalistic species
may be better candidates for examination, as this
source of biotic variability would be removed.

Variability in abundance and distribution is
greatest near the northern or southern limit of a
species' range, or, as in the case of estuarine
species (oyster), near the limits of its salinity range.
Temperate-zone stocks demonstrate a greater interannual variability than tropical species, as the
annual environmental fluctuations in the temper-
ate zone are greater, and temperate stocks have a
short spawning season when compared to tropical
species that demonstrate a protracted spawn or
one that occurs several times a year. For this
reason, the timing of events in the temperate zone
is critical, as spawning for most species occurs
during the time of greatest environmental change
(e.g., in spring). This lends further credence to
the match/mismatch theory of Cushing and Dickson
(1976), which states that the larval period must
coincide with the appropriate stage of the spring
bloom.

The trophic level occupied by a species or the
level at which it feeds is important. The lower the
position on the trophic chain occupied by a species,
the more rapid its response to environmental
change. This is true both of forage plankton (includ-
ing ichthyoplankton) and of species that feed on
them (e.g., herring, menhaden, anchoveta).

A heavily fished or overfished stock is more
susceptible to environmental fluctuations than is a
more stable or underutilized stock. It has been
pointed out in the Mackerel Fisheries Management
Plan of the Mid-Atlantic Fisheries Management
Council (March 1978) that recruitment is generally
independent of stock size except at low levels of
abundance, and that here “it is clear that environ-
mental factors are significant in controlling recruit-
ment” (p. 91).

Age is an important consideration, as young
fish are often eurythermal and euryhaline. Best
examples of these are the “estuarine-dependent”
species that as juveniles inhabit inshore areas
where temperature and salinity fluctuate widely.
As adults they move offshore into the higher salinity
waters of the shelf or open sea where variations
are slight. The juvenile stages, able to tolerate the
lower salinities and higher summer temperatures,
are safe from many adult predators (Gunter, 1967).

The completeness and availability of the bio-
logical data base is as important as the environ-
mental base. Unfortunately, adequate biological
data bases for climatological studies do not exist
in most cases. The extant data are generally in two
forms, catch or landings, or assessment data from
surveys.

Most catch data exist without supporting effort
data; hence, they are not sufficiently quantitative.
Further, the data bases do not carry accurate data
on recreational catches, which may exceed the
commercial catch by 3 to 10 times.

Catch and landing data are generally reported
by calendar year. For example, the New York bay
scallops fishery runs from October to March. The
October to December 1977 segment is reported
with the catch of “last year” (January to March
1977), and this season's (January to March 1978)
with next year's (October to December 1978). Con-
sequently, interannual variations may be averaged away. Data are available, however, over 20- to 30-year periods, which lends itself to climate-scale analyses.

Assessment data, needed for recruitment estimates, are often of doubtful accuracy due to sampling methods, and are generally over too short a time period for climatological studies. These data, however, can be collected for specific areas such as spawning grounds, during specific seasons, and with concurrent environmental data. Additionally, biologically significant measurements and indices can be made (e.g., condition factors, food habits, annuli measurements, gonad indices).

It is impossible when examining climate-scale bio-environmental interactions to go back and make different measurements. Generally, physical environmental parameters can be inferred from other measurements extant in data bases, even when not actually measured themselves, but this is not so with the biological. If, for example, one has 20 years of length-frequency data for a species and then decides that the winter condition factor (a length/weight relationship) is the critical determinant, it is not possible to go back and make the needed weight measurements. It may be possible, however, from the records at the National Climatic Center, to retrieve minimum winter temperatures and their duration, or ice cover, all of which influence the length/weight relationship (condition factor).

Bio-Environmental Considerations in Design of Investigations

Successful studies of the effects of climatological variations on fish populations require bases of time-series environmental data of high quality. Occasionally, these time series are available for several decades in a study area, but more often the data series are too short in duration, of unacceptable quality, or in the wrong geographic region. In such cases, the inadequate data bases may be used to perform rough tests of hypothesis, or proxy atmospheric data, which are available over wide global areas where no ocean time series exists, and can be used with caution to infer ocean changes if the sea/air linkages are understood. Further attempts to pursue promising theories will require the establishment of environmental monitoring programs for a period of many years. Because such programs are costly and difficult to justify to managers, marine scientists usually are forced to make do with existing data sets or ongoing monitoring programs. Therefore, an inventory of the environmental data available in a potential study area is of critical importance in deciding whether or not to begin a fishery-climatological study.

An understanding of the causal relation between environmental forcing and biological response is a prerequisite to the selection of the species or stock in question. Far too often, for example, we select temperature or temperature anomalies as our independent variable, without understanding the link between environment, in this case temperature, and biota.

One can demonstrate a correlation between anchovy-recruitment success and sea surface temperature off California, which would be merely fortuitous. Lowered sea surface temperatures have no effect on recruitment, but are an indication of upwelling, which, if present during the anchovy postlarval stage, disperses the proper concentration of dinoflagellates and encourages the bloom of diatoms, which are of no nutritional value to the larval anchovy (Lasker, 1978). Reduced temperature is merely a manifestation or index of upwelling.

A fact that is often missed in looking for bio-environmental relationships is that the environmental fluctuation may be affecting the abundance and distribution of the forage and not the stock being examined. The relationship of the Pacific albacore to the coastal upwelling fronts is an example in which there is a response of the albacore to the distribution of their forage and not to the temperature gradient itself (Lauris et al., 1976). The forage too is responding to changes in planktonic abundance associated with the front and not to a physiological response to the thermal field.

Some pelagic or planktonic forms are indicators of climatic-scale events about to happen. The appearance of Indonesian milkfish larvae off the coast of Peru is an indicator of an impending El Niño. Its appearance is explained (Cushing and Dickson, 1976) by the relaxation of the Southern Hemisphere trade winds and subsequent strengthening of the equatorial counter current, which brings tropical western Pacific waters to the eastern Pacific.

River runoff is a popular variable to examine when studying coastal species. But what is the effect of runoff? In the case of the Chesapeake Bay blue crab population, it is a factor in a complex cycle with timing of utmost importance. A dry summer provides a large high-salinity spawning ground at the mouth of the bay. This must be
followed by a wet fall with high runoff to provide a large low-salinity nursery ground. The larvae need high salinity, and the juveniles low salinity. It is the areal extent of the spawning or nursery ground that is of importance; the effects of salinity are secondary (Van Engel, personal communication).

Recent advances in the field of marine resource prediction have not been with parameters such as temperature or salinity but with dynamic processes, the forcing functions such as upwelling indices or indices of Ekman transport. These successes suggest that we are developing better data sets and that we are developing a better understanding of how the physical environment forces changes on the biological side of the system.

Studies relating catch data to physical environmental data are hindered by the fact that the environmental data are often point source (e.g., Ambrose Light Tower), whereas the catch data are from large areas (ICNAF or FAO statistical regions, for example). Biota/environment relationships are masked, due to the geographic disparity.

Future efforts directed at predicting the abundance and distribution of stocks must give careful consideration to the biotic factors that act as forces, how they occur, and what the forcing function is. Without an understanding of the dynamics of the biota/environment link we will never progress from statistical or empirical models to conceptual and mechanistic models.

References


Annotated Bibliography

1. Bannister, R., D. Harding, and S. Lockwood. 1974. Larval mortality and subsequent year class strength in the plaice. In: The Early Life History of Fish, J. H. Blaxter, ed. Springer-Verlag, N.Y. pp. 21-38. Winter of 1947 very cold, extensive 0° water. Should have altered recruitment, yet (1963?) year class was highest on record. Perhaps cycle was delayed, so more advanced larvae were present.

2. Bell, F., and A. Pruter. 1958. Climatic temperature changes and commercial yields of some marine fisheries. J. Fish. Res. Bd. Canada 15(4):625-683. Most (as of 1958) climate temperature/fish productivity (landings) relationships do not give sufficient provision for changes in fishing effort to explain climate/fish relationships. (Most relationships examined here were air temperature. Editor's note.) "The effects of other variables such as economic conditions, changes in fishing practices and the extent of the removals by man should be accounted for. The possibility of fortuitous relationships must be discounted by exhaustive tests of the representativeness and adequacy of the environmental data, and equal care must be exercised in the selection and evaluation of the fishery data, particularly that of catch per unit effort."

   (1) 1972 SST up 5°C Average SST
   (2) High heat supply in equatorial Pacific Normal circulation
   (3) Intensified Hadley circulation Normal
   (4) Increased flux of angular momentum Normal
   (5) Intensified wind-lat. westerlies

A trough over the eastern U.S. in 1958-59 resulted in the coldest winter to that date since 1917-18. 1939-40 also cold, same 700 mb pattern. 1948-49 warm, with reverse pattern at 700 mb (ridge over eastern U.S.). When (-) off East Coast, then (+) (e.g. '58) warm off California — cold affects Gulf shrimp.

4. Blackburn, M. 1969. Conditions related to upwelling which determine distribution of tropical tunas off western Baja California. Fish. Bull. 68(1):147-176. Tuna were found to aggregate only when pelagic red crabs Pleuroncodes planipes were found. P. planipes are an index of abundant food. Tuna did not aggregate even when temperatures were suitable unless the crab did. Aggregate behavior of the crabs was produced by upwelling in waters of high chlorophyll content.


6. Chase, Joseph. 1955. Winds and temperatures in relation to the brood strength of Georges Bank haddock. J. Cons. Perm. Int. Explor. Mer 217-244. Relates losses in year classes of haddock on Georges Bank to northwest winds, as derived from pressure measurements, during the pelagic season of the larvae. Correlations were improved (to r = .766) by estimating spawning time from air temperature changes. Suggested need for better understanding of relationships before correlations could be improved.


perature and wind on herring of 4 years old and older in the Buchan prespawning fishery. Is shown to be related to spring warming (negative) and north wind (negative).

The 1963 year class of plaice was excellent following a cold winter, which delayed both larval metamorphosis and the spring bloom. The bloom, once it occurred, was intense and matched with the peak of larval abundance. Hence, good survival.

Magnitude of herring recruitment is directly correlated with quantity of winter phosphorus one year after hatching, and number of pilchard eggs is inversely correlated with winter PO₄ 6 months after hatching.
Fish near northern or southern end of range show greater response to climate variation than do those in center. Clupeid and salmonids react quickly, whereas gadoids don’t. Perhaps due to fecundity — more fecund species tend toward stabilization.
Fish with fixed spawning cycles (generally north of 40°N) are more susceptible than those south of 40°, where productivity continues all year.
Spring bloom often occurs at the same time each year, but spring spawning can vary. Match or mismatch is important, as cold water often delays larval abundance — spring bloom is more photoperiod-dependent until productivity is high. Russell cycle during early 30s to 40s general warming, most profound in 1926-35. Reversed from 66 to 72 by general cooling. Named after Russell, its “discoverer.” Ecosystem response is step-like, with sudden changes at beginning and end of cycle.

Compares Maine landings of lobster, scallop, and shrimp with annual average water temperature at Boothbay Harbor. Temperature/biota cycles were lagged until a fit was found. No statistical treatment of data.

Fluctuations in abundance of American lobster and seawater temperature have correlated well during period 1905 to present. Optimum center of catch moving southward as temperatures drop.

Correlated annual average sea surface temperatures at Boothbay Harbor with Maine landing data for 1905-67. Total number of species in Gulf of Maine increased during period of warming. Individual-species-catch correlation coefficients ranged from r = 0.86 for lobster to r = 0.91 for scallop (1939-67). Total catch vs. temperature yields a coefficient of r = 0.63 for the same period.

Sunspot maxima (every 11 years) move mean winter position of Aleutian low from Gulf of Alaska to western Aleutians. Wind-stress transport is reduced by 20 percent in the Gulf of Alaska. Increase in solar constant during rising phase and declining phase. 5-6 year period. SST anomalies also 5-6 year period. These temperature peaks correspond with dominant year classes of:
Pacific herring '53, '58
Dungeness crab '63, '64, '68
Sockeye salmon '52, '56, '61, '65, '70.
11-year cycle also noted by Southward et al., 1975, in Gulf of Maine; 6-year by Lyman for striped bass.

Correlates water temperatures at Boothbay Harbor, St. Andrews, and Lurcher Shoals Lightship with lobster catches (1940-70) pooled for 6, 7, and 8 years (r = .873). Using bottom temperature from lightship improved correlations (r = .943).

Time series w/CPR (Hardy) 1948-72:
(1) Total number of copepods has decreased.
(2) Duration of abundance has decreased from 7.25 to 6.0 months.
(3) Atlantic Ocean waters have extended further north since WW II; however, reversal in recent years.
"...flippant to relate plankton trends to the illegitimacy rate in teenage girls..." Don't use single environmental parameters.

Criticizes methods used by Carruthers in selecting wind data by month (variable) and direction to improve correlations between year-class strength and wind. He demonstrates a good correlation between random numbers using similar techniques.

High correlation between white shrimp landings and rainfall in Texas that year, and the 2 previous years. Brown shrimp show no correlation.

Develops multiple linear regression model relating total population of 4-year-old cod 4 years hence to mean April sea temperatures, meridional Ekman transport, zonal Ekman transport, and total population (spawners) on Flemish Cap. Covered 1955-63 in physical data and 1959-67 in model output (4-year cod population, correlation coefficient of 0.91, conceptual model not clearly described).

Models correlating environmental variables to Dover sole (Microstomus pacificus) and English sole (Parophrys vetulus) year-class strength were developed. Variables considered were temperature, sea level, barometric pressure, indices of offshore and alongshore transport, offshore divergence indices, wind speed, solar radiation, and Columbia River discharge and water quality. In addition to monthly mean values of these factors, the models also considered shorter term measures of environmental variability, such as number of wind direction shift, storm frequency and duration, and factors that measure variability when combined as separate terms in a multiple regression; for example, storm frequency plus wind speed. These short-term variability measurements may reflect production cycles more closely than monthly mean figures. Also considered in the models was spawning power, calculated as egg production summed for each length group.

Worked with abundance and O-group growth data for Pacific sardines for 1933-55. Unaccountably low-survival indices suggested there must be an environmental factor influencing survival. Detected similar simultaneous effects in Canadian herring, salmon, and lake fish, suggesting that a broad-scale environmental feature was responsible. Author used no environmental data; he merely suggested that a climatic change was responsible.

Air/sea interactions in Pacific influence topography of 700 mb circulation patterns, which, in turn, as the steering currents, result in blocking (ridge) cold continental air masses or their passage (trough) far to the south. Hence, SST anomalies along the eastern U.S. seaboard are influenced by them.

Gives examples of relationships between fisheries and climate: Bering Sea salmon and cold weather in 70s, Atlantic menhaden and Ekman transport, Pacific mackerel and upwelling, Dungeness crab and upwelling, skipjack migrations and baroclinic currents, anchoveta and el Niño and atmospheric pressure fields. Points out empirical nature of most climate/fisheries studies.

Develops a conceptual model linking lower water temperatures with stronger year classes, with correlation coefficients ranging from -0.696 to -0.904, depending on period assumed for peak spawning. Lower temperatures favor slower larval development and longer pelagic drift, allowing larvae to reach favorable nursery area before settling to bottom. In warm years, the larvae apparently fall short and perish.

Proposes that monitoring of aggregation of potential larval fish food particles in spawning season along with pertinent environmental variables may be practical way to predict relative recruitment success of pelagic fish. Onset and duration of upwelling events important. Have negative effect on larval survival and recruitment by replacing dinoflagellates with smaller diatoms, which cannot meet dietary needs of larvae. Stratification and stable conditions are required to provide suitable quantity of proper-size phytoplankton.

When East Pacific Transition Zone (subarctic/subtropical) is distinct, albacore migrate along "corridor" and are concentrated, often remaining in Transition Zone for some time. When boundary is diffuse, migration is over broader area, and albacore move rapidly to shore. Reasons are temperature preference, aggregation of food, and thermal gradients — all possibly integrated. Prediction of Transition Zone structure permits operational fishery decisions by industry.

Used surface water temperature at one point in Gulf of St. Lawrence as input for stochastic model for herring along with predation and competition from Atlantic mackerel. Temperature and abundance of O-age-group mackerel affected herring growth rate, but total herring biomass and total pelagic biomass didn't.

Developed negative correlation between sea surface temperatures in New England, Nova Scotia, and Gulf of St. Lawrence with cod landings in ICNAF area 5. Constructed linear equation, in time, for each data set, then conducted statistical analysis of "residuals" from linear plots, in an attempt to refute notion that the two data sets were merely coincident independent linear trends. Correlation coefficients were not particularly high (0.38 to 0.75).

Gives examples of climatic change and impact on yellowtail flounder, oyster, soft clam, and Pacific salmon.

Cold SST caused atmospheric shift in winds.
Northerly winds brought ice farther south. Colder conditions reduced salmon egg and larval survival.

(1) Delays return of adult to spawn.
(2) Cold weather forms “ice dams” in gravel, which erodes surface and exposes eggs.
(3) Reduced water flow, hence O2.
(4) Reduced growth rate in juveniles (when <4°C in 1971-73 slowest growth on record).


Haddock recruitment is dependent upon wind functions. Larvae can be carried over open water, and fail to settle out.


Most year-class size variation, and later fishing stock, was related to fluctuations in upwelling and surface convergence on spawning grounds.


Annual fluctuations in commercial landings of blue crabs “may be” related to strength and timing of river discharge in the Chesapeake Bay tributaries. Excessively cold winters may also have an effect.

Heavy discharge during spawning is bad, and light discharge is good.


Empirical relationship between intensity of upwelling and crab fishery. Strong crab catch lags strong upwelling index by 1.5 years.


Anomalous equatorial Pacific meteorological and oceanographic conditions (e.g., el Niño) are the result of certain large-scale changes in atmospheric and oceanic circulation. These changes appear to be closely associated with variations in amplitude and period of an irregular interannual fluctuation in the atmosphere circulation called the Southern Oscillation. Changes in the Southern Oscillation are monitored and predicted through time series of atmospheric pressure indices.


Haddock recruitment is dependent upon wind functions. Larvae can be carried over open water, and fail to settle out.


Period of 1920 to 1940s shows reduction in herring, cod, and ling coincident with reduction in Calanus and phosphorus (0.8 to 0.4). During period 1940s to 1964, pilchard eggs were abundant. In 1960s to 1971, pilchards' eggs disappeared again, and herring, cod, and ling reappeared.

Suggest “warming of Arctic would affect circulation in North Sea and let Atlantic Ocean waters extend further north.” With winter PO4 as link, winter-hatched herring are (were) inversely related to pilchards hatched the following summer.


Seasonal shifts in Pacific water masses can be used as a predictor for skipjack abundance in the Hawaiian live bait fisheries. Temperature shifts in April is the best predictive index. Early shift, good year; late shift, bad year.


Time-series data are necessary in order to discern climatic-scale events. Oceanographers find work difficult due to lack of marine time series and lack of any ocean data. Atmospheric proxy data exist with good continuous series and with good coverage.

40. Sette, O. E. 1943. Biology of the Atlantic mack-
Pursues hypothesis that "infant mortality" is the key to year-class success. Studied 1932 year class by extensive field sampling of eggs, larvae, and postlarvae; year class failed, so looked for reason. Found that no single stage of development was outstandingly critical, but seemed to be high mortality rate throughout. Probable causes: 1) dearth of food (low zooplankton population), 2) unfavorable winds from northeast drove larvae away from nursery grounds off southern New England instead of toward them as southwestern wind would.


In January 1947, high pressure system over Scandinavia gave high easterly winds over North Sea for 4 weeks. Displaced several species from their spawning grounds (dabs, cod, flounder) and delayed hatching. Dead fish (cod, plaice, and dab) found. Same in 1929.


Develops a complex simulation model of the yellowtail fishery. Used input of average annual air temperature at Block Island along with many biological variables. Model accounted for 83.5 percent of variability in yield, using linear stock-recruitment function, and 83.2 percent using density-independent function.


Nineteenth-century phases for bluefish and weakfish. Bluefish phase associated with seals, capelin, and basking sharks; weakfish phase with herring, mackerel, and menhaden. Bluefish, warm in Europe; weakfish, cool in Europe.


Correlated catches of 17 species in ICNAF Statistical Area 5 with water temperatures in northern Gulf of Maine and Bay of Fundy. Consideration of fishing effort and selecting best lag times improved the correlations. No discussion of cause-and-effect interactions between temperatures and catches.


Discusses warming trend in 1900-40 period to sea water temperature trends at Boothbay Harbor. Related landing statistics for mackerel, lobster, whiting, menhaden, and yellowtail flounder to the air temperature and water temperature records. Relates range extensions of southern species to temperature trends. Points out weakness in the causal inferences which might be drawn from these data.


Points out lack of good long-term set of hydrographic data in ICNAF areas 2 and 3. Uses air temperature record at Jorby Airport, St. Johns, Newfoundland (1872-1952), and water temperature record at St. Andrews, N.B. (1920-52). Visual correlation of temperature data (annual) with rough abundance data (catch, sightings) for mackerel, lobster, squid, billfish, capelin, and cod.


Poorest catches of Hokkaido herring when cold winter 4 years earlier. 1886: 69, 84; 1902: 05, 13, 28, 35, 45.
Herring lay eggs along shore and are susceptible to cold.

   The size of a year class of sardines correlates with average daily summer surface salinities from 1934 to 1941. Salinity is an index of upwelling. Year classes were best for the years where salinities were high.

   Compared water temperature records at Boothbay Harbor with measures of green crab abundance and soft clam harvest. Temperatures declined after 1953 peak. Green crab abundance decreased and soft clam catch increased. Crab response apparently is physiological, both on adult survival and reproductive success, and the reduction of crab population reduced predation on soft clams.

   Predictive relationship between percentage of returning sockeye salmon passing between Vancouver Island and the mainland on their way to the river. Fraser River discharge and wind stress holding fresh water near the coast account for 70 percent of variability. Rain at time of spawn and hours of sunlight can account for 89 percent of variance in stock size off British Columbia from 1930-74 (personal communication to Lasker).

   Good shrimp fishery follows warm winters, and poor follows cold.
   Note: Cold of 1958 and 1976-77 were poor years. Relate to Johnson and McLain.
Matrix of Environmental Factors on Species  
(Numbers refer to references in the Annotated Bibliography)

<table>
<thead>
<tr>
<th>Species</th>
<th>Temperature</th>
<th>Temp trends</th>
<th>Temp extremes (incl. ice)</th>
<th>Salinity</th>
<th>Geostrophic currents</th>
<th>Elman transport</th>
<th>Upwelling</th>
<th>Nutrients</th>
<th>Forage</th>
<th>Indicator org.</th>
<th>Meteorological phenomena</th>
<th>River discharge &amp; precipitation</th>
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