PROBLEMS IN FISH POPULATION FLUCTUATIONS

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Our chairman has defined "fisheries oceanography" as meaning "any kind of oceanography required for the appraisal or exploitation of any kind of organism useful to Man". This, as intended, is a very broad definition. My contribution to this symposium will be confined to a discussion of only one particular set of problems that I believe to be most important in the utilization of fishery resources and afford most exciting opportunities for oceanographic research—namely, fishery fluctuations.

By fishery I mean any harvesting of any living ocean resource, and by fluctuations I mean any irregularity in the amount or the quality of the harvest. Since most of our present commercial harvest from the sea consists of fish, my discussion, terminology and examples pertain to fishes, but most of the concepts are also appropriate to the invertebrates and some even to the flora of the sea.

In considering the problem of fishery fluctuations I have come to realize that there are a great many parallelisms in the discipline and the state of knowledge in fishery biology with those in oceanography. By fishery biology I mean the study of fish populations as dynamic systems—and by oceanography I mean the parallel thing: The study of the ocean as a dynamic system. In defining each of these in this way I am ignoring a great deal that could be included, but I believe I am retaining the central core of each.

The first parallelism is that there are only a few things we can measure. In fishery biology we measure only the fisherman's harvest and the effort he puts into making it, when we really want to know the size of the fish population and how fast it is changing. In oceanography we can only measure the temperature and salinity when we want to know which way the water is running, and how fast. To be sure, in each field we can, by a one-time special effort, get a direct measure (estimate). We can lay a tag-and-recapture project—or a multiple-ship drogue expedition. But these are not routine, every-day events. For the most part we have to deduce what we want to know from something else that we can measure.

Second—and this is largely a consequence of the first—for fish populations we have only a theory to tell us how a fish population reacts to fishing. This relates to a fish population living in a steady environment. In some few instances, and for a limited period of time, we find that a population really does react approximately as the theory says it should. For oceanography we have more theories. But practically all relate to an equilibrium ocean. For some parts of the ocean, sometimes, one of these theories, or a combination of them, seems to explain approximately what actually happens.

Of course the trouble with the theory of fishing is that a fish population reacts to other things besides fishing—things in the variable environment. We assume these things average out—and sometimes they do. But often the time dimension for averaging out is intolerably long. And of course the same thing is true of the ocean. Over a long enough period of time the average ocean probably is an equilibrium ocean, but the measurements we take must be mostly those of an ocean in disequilibrium. I believe it can be said for fishery biology, as it has been said for oceanography, that there is a peculiar dreamlike quality characterizing our descriptions and discussions of the things that we are studying.

As a fishery biologist I venture the further thought that it would be easy to relax and enjoy this dream were it not for fluctuations. They have a nightmare-ish quality that jolts one into reality. And I am reminded that this could be true for oceanographers as well. A year ago this month a group of oceanographers (including the one who first voiced the phrase "peculiar dreamlike quality"), meteorologists, marine biologists, and fishery biologists met at Rancho Santa Fe, bringing with them meteorological, oceanographic, biological and fishery data, to describe what happened in the Northeast Pacific Ocean in 1957 and 1958 and why. It was abundantly clear that there had been a sudden and marked warming of at least the eastern margin of the Pacific from Alaska to Peru, with an assortment of consequences to the oceanic biota. The results of pondering over these events will be published and I will not here attempt to put them before you, except to remark that we still do not know, with any precision, what happened, nor with any degree of assurance, why.

Henry Stommel, in his book on the Gulf Stream, has this to say about fluctuations: (Stommel 1958, p. 136)

> "Many catastrophes of an economic kind, such as the failure of the rice crop in Japan, or of a certain fishery, or years of unusual numbers of icebergs in shipping lanes, are attributed to fluctuations in ocean currents. Very little is really known about such fluctuations. It takes years of careful and expensive observation to produce even a very crude description of them. The scientific programs of our oceanographic institutions are not geared to long-term problems of this kind; there is much pressure for novelty, much temptation to follow the latest fad, and a persistent though erroneous notion that all worth-while problems will eventually be solved by some simple, ingenious idea or clever gadget. A well-planned long-term survey designed to reveal

fluctuations in ocean currents would be expensive and time-consuming. It might even fail, because of inadequacies of the tools we have at hand. But until this burdensome and not immediately rewarding task is undertaken, our information about the fluctuations of ocean currents will always be fragmentary."

Henry Stommel seems somewhat overwhelmed by the task of making the observations needed for describing and elucidating fluctuations in the Gulf Stream. The task probably is even more difficult for describing and elucidating the fluctuations in fish populations, because it is likely that the effects on fish populations of physical and chemical changes in the environment are mediated through several trophic levels in the biota. We will come back to this later.

It seems clear that the problem of fluctuations lies at the research frontier in both fishery biology and oceanography, and that it is going to be difficult to break through the frontier.

Let us consider again, for a moment, the anatomy of fishery fluctuations. We can discern three principal elements operating to determine the amount of the catch: The abundance of the organism, its availability to the harvester, and the amount of harvesting effort. We shall not here be concerned with the last of these. The amount of harvesting effort is determined by economic conditions. Changes in the amount of effort can be measured, though not easily, and its effects on the amount of catch can be determined and discounted. It is not a problem in biology or oceanography.

Abundance and availability, in contrast, present problems both in biology and oceanography.

We suspect that availability varies widely. For instance, the failure of the albacore fishery from 1928 to 1938 was, we think, an availability phenomenon. The albacore population probably was as large as usual, but did not approach close enough to the coast to enter the range of the fishing fleet.

Availability is a matter of distribution and behavior, both on a coarse-grained pattern as in the albacore failure, and on a fine-grained pattern as in the schooling of fish. It is highly important to the strategy of fishing and to the economy of the fishing industry. Since Professor Uda will, I think, discuss availability in some detail later in this symposium, I shall confine myself to fluctuations in abundance (population size).

Fishing theory says that the annual increase in a population is a function of population size and environmental capacity. If a population "fills" its environment, births and deaths are equal and the population is in equilibrium. When fishing takes place, catch mortality is imposed, the population is reduced below the environment's capacity, births exceed "natural" deaths and the population tends to increase toward the environmental limits. With very intense fishing and a very low population level, the reproductive increase is near its maximum, natural mortality near its minimum, but the annual increase is low because there are few spawners. When fishing is very light and the population near the environmental limits, the spawning population is large but the back-pressure from the environmental limit depresses reproduction or increases natural mortality, or both, so that the annual increase is again small. At some level of population size intermediate between these extremes, where the spawning stock is moderately large and back-pressure from the environment moderately gentle, the annual increase is maximal. Of course, at any level, the population size will be in equilibrium when the annual catch equals the annual increase, but the annual harvest that can be sustained without disturbing the equilibrium will be maximal at the level of population abundance that affords the maximum annual increase.

Fishery biological research has been directed mainly toward determining this level of maximum sustainable yield, using the concepts embodied in this theory. A number of mathematical models have been developed to express these concepts. They assume that the environmental capacity is constant or fluctuates moderately and randomly, and that the observed or computed changes in recruitment and mortality and hence annual yield are functions of population size (or density) alone. These models have proved very useful in studying the population dynamics for some fisheries.

In other populations, including some that support very important fisheries, the effective birthrate, that is, the relative numbers reaching recruitment age, varies widely from year to year, apparently without relation to the size of the spawning stock. This is known by studying the age composition of samples of the catch. From the data on age composition through sufficient number of years, it is possible to estimate the relative number of individuals surviving to fishing size or age from each year's spawning. I shall call this relative number "year-class strength".

I have looked up a few data on relative year-class strength:

	Successive year classes	*The largest was*
Western Atlantic mackerel	among 14	15,000 times the smallest
Eastern North Pacific sardine	21	700
Kodiak (Alaska) herring	28	34
Southeast Alaska herring	20	13

These are all very gross estimates, and should be taken only to indicate that year-class strength often varies through several orders of magnitude.

Year-class strength obviously must be a function of number of eggs spawned, or of survival through the egg stage, through the planktonic larval stages or through the post-planktonic juvenile stages, or a combination of these. No doubt irregularities occur in all stages, but the evidence, still regrettably scanty, points to the survival through planktonic egg and larval stages as being the most likely critical one in determining year-class strength.

Where year-class strength fluctuates widely it is not a function of population size and we must look to environmental causes.

How shall we do this?

Because it is difficult to speak in generalities, I shall employ an hypothetical example. Let us consider a fish population of a species, like the mackerel, the sardine or the anchovy, that spawns in the waters off California.

Through evolutionary time, in the members of such a fish population, there must have evolved an internal biochemical system and a related pattern of behavior that determines the responses to the things sensed in the environment. The behavior pattern must have been so adjusted that it lead to successful reproduction through all of the time involved in its evolution. Otherwise the species would be extinct. If I may speak teleologically, the members of a living fish population, or at least the vast majority of them, must work out problems of navigation and prediction to enable them to find and occupy a specific kind of water mass for spawning.

This water mass must have physical and chemical properties which are tolerable to the biochemistry and biophysics of the eggs to be spawned and the larvae to be hatched from the eggs. Further, by the time larvae have hatched out, and by the time they have fully absorbed the yolk sac, this water mass must contain other organisms suitable for the larvae to feed upon and in such concentrations as will permit the larvae to get enough food for maintenance of metabolic activity and growth. Doubtless the larvae will require larger food particles or more of them as they grow larger. So this water mass must continue to afford an increased and probably different diet through the subsequent months of planktonic larval existence. Finally, when the larvae metamorphose into the juvenile stage and take up an active, rather than a passive, drifting existence, this water mass must have reached a place or a condition which is suitable for juvenile existence. Many marine species spawn in the open sea at a considerable distance from the juvenile nursery grounds. For such a species, the parent must have predicted the trajectory of the water mass over a period of weeks or months.

To be sure, many individuals of the population may fail to navigate properly or to predict accurately and it seems that often the whole population, or most of it, may be in error. Or, alternatively, the conditions in the sea may in some seasons become so anomalous that there are no water masses suitable for the species spawning or the survival of the eggs and larvae after spawning. In any event, there are many year-class failures or near-failures in our widely-fluctuating fisheries. Such failures, of course, must be interspersed with enough successes for the population to be perpetuated. For species with an adult life of several years, several annual failures can happen in succession, and apparently do happen in our widely fluctuating fish populations, without exterminating the species.

I have spoken of the water mass as a thing which maintains its integrity over considerable periods of time. This probably does not happen often for water masses in the surface layer. They undoubtedly undergo changes through insolation and through mixing horizontally and vertically with adjacent waters. In a sense, we could think of a water mass as undergoing an evolution as to its physical and chemical properties and also as to the trophic succession in its biota. Perhaps more frequently than not, the water mass may undergo dissolution instead of evolution and such cases may indeed lead to failure of survival of its larval fish population.

In this connection, it is interesting that there have been reported two instances in which it appears that a water mass was changed so rapidly that the contained fish larvae died almost immediately. One instance, reported by John Colton (1959), was of larvae contained in a mass or parcel of water at the southern edge of Georges Bank in which the temperature, apparently by mixing with Gulf Stream water, had risen rapidly enough to kill the fish larvae it contained. The other instance, reported by Donald Strasburg (1959), was the occurrence of dead larval Frigate mackerel in plankton tows in Hawaiian waters under circumstances suggesting water mixing as the cause. We do not know whether or not such sudden changes can occur in really large enough water masses to determine the failure of a year class, but these reports are suggestive.

However this may be, it appears that one mode of attack on the problem of year-class strength would be the study of the source, the life history, the movements and, perhaps the dissolution of water masses. This infers sea work to observe, with continuity through space and time, many properties of the water and its biota. It suggests, further, that a joining of the physical and biological disciplines might facilitate such a study. The joining of the laboratory experimentalists would probably facilitate the study still more. If we know what properties of the environment the fish is able to sense, and how the fish reacts to the things it senses, we would be led more quickly to observing the things which cause the fish population to maintain or change its distribution, and if we could identify in the laboratory the survival requirement of fish larvae, we would be led more quickly to our observing the critical events in the sea.

In effect, I am proposing the joining of four disciplines: oceanography, fishery biology, marine biology and experimental biology. Possibly additional disciplines may be required. Certainly, instrument systems for recording automatically, with time and space continuity, a number of properties of sea water and its motions would be of tremendous importance. On the biological side, it is quite possible that fish pathology, especially the study of fish larva diseases, may be germane to this study.

To speak in more general terms, it is my belief that in fishery oceanography the challenge and the opportunity lies in studying the changing sea rather than the equilibrium ocean, and in studying the biological consequences of the changes at the various trophic levels. In speaking of "consequences" I mean to include not only the effects on the population numbers, which I have dwelt upon at some length, but also on population distribution and behavior which Professor Uda will soon discuss with us. In the aggregate this implies the necessity of observation of physical and chemical properties of sea water, its motions and mixings, and the numbers, kinds and perhaps stages of the biota inhabiting the waters, all with space and time continuity sufficient to describe the events that take place and to investigate their interrelationships. The biological determinations probably would more readily be made with the aid of laboratory experimental determinations of environmental requirements critical for survival of the various organisms, particularly pelagic fish larvae.

It would seem that this amounts to an undertaking of such vast scale that it may be quite out of line with the importance of fishery resources to our society. However, fluctuations of the ocean and of its plant and animal populations is a problem of significance not only to fisheries. Modern military systems no longer can be based on the average state of the sea, and modern meteorology is no longer uninterested in the possibility that the feed-back to the atmosphere from anomalous sea conditions may have to be considered in extended weather forecasts. We can hope, therefore, that progress in the field does not depend alone on research activities in the interests of developing and utilizing fishery resources, but will benefit also from activities undertaken in the interest of other important activities of mankind.

An indication of trends in this direction is the recent report of the National Academy of Sciences Committee on Oceanography, which, among other things, proposes a great augmentation of effort, much of it along the lines we have considered in this discussion.

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